Temperature-Dependent Development and Temperature Thresholds of Codling Moth (Lepidoptera: Tortricidae) in Iran

Author(s): Hossein Ranjbar Aghdam, Yaghoub Fathipour, Gholamreza Radjabi, and Mohammadreza Rezapanah

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HOSSEIN RANJBAR AGHDAM,[1] YAGHOUB FATHIPOUR,[1,2] GHOLAMREZA RADJABI,[3] AND MOHAMMADREZA REZAPANAH[3]

ABSTRACT Developmental rate models and biological parameters estimated from them, especially lower and upper temperature thresholds and optimal temperature, can help to forecast phenological events of codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), in apple orchards. We studied the developmental time of immature stages of codling moth at eight constant temperatures ranging from 10 to 35°C and modeled their developmental rate as a function of temperature using 13 published nonlinear and 2 linear models. Data were fitted to developmental rate models and temperature thresholds and the optimal temperatures were estimated. The models were evaluated based on adjusted coefficient of determination (R^2_{adj}) and Akaike information criterion (*AIC*), in addition to coefficient of determination (R^2) and residual sum of squares (RSS). The thermal constants were 79.80, 312.60, 232.03, and 615.32 DD for egg, larva, pupa, and overall immature stages of codling moth, respectively, using the Ikemoto and Takai linear model. The Ikemoto and Takai linear model estimated lower temperature thresholds as 9.97, 8.94, 10.04, and 9.63°C for egg, larva, pupa, and overall immature stages, respectively. Among the nonlinear models, the third-order polynomial fit the data well. This model estimates optimal temperature accurately. Brière-1 and Brière-2 accurately estimated the lower and upper temperature thresholds considering model evaluation criteria and accuracy of estimations.

KEY WORDS codling moth, *Cydia pomonella*, development, thermal threshold, linear and nonlinear models

The codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), is one of the most devastating pest insects in apple orchards worldwide (Dorn et al. 1999). This pest occurs in all of the apple orchards of Iran (Radjabi 1986), where one to four generations are present each year, and insecticide applications for control of this pest are needed beginning with the appearance of the first larval generation in approximately mid-May (Behdad 1991). Understanding the factors governing *C. pomonella* development and implementing this knowledge into forecast models enables effective timing of interventions and increases efficacy and success of control measures (Kürt et al. 2006).

Temperature is a critical abiotic factor influencing the dynamics of mite and insect pests and their natural enemies (Huffaker et al. 1999). The rate of development of codling moth is governed by environmental temperature (Rock and Shaffer 1983). Phenological models, using physiological time data, have been developed for codling moth to predict emergence of adults from the overwintering generation, eclosion of eggs, larval and pupal development, and generation time (Falcon and Pickel 1976, Geier and Briese 1978, Brunner et al. 1982, Rock and Shaffer 1983, Dastqeib and Seyedoleslamy 1988, Setyobudi 1989, Pitcarin et al. 1992, Howell and Neven 2000). These models, all based on a linear relationship between temperature and developmental rate, have been used with varying degrees of success to time pesticide application for codling moth control (Rock and Shaffer 1983, Dastqeib and Seyedoleslamy 1988, Howell and Neven 2000). Linear approximation enables the estimation of lower temperature thresholds and thermal constants within a limited temperature range (Campbell et al. 1974, Honěk 1999, Howell and Neven 2000, Jarošik et al. 2002). Because of their complexity, curvilinear models have not been routinely used (Howell and Neven 2000).

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 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 nonlinear models have been applied (Stinner et al. 1974, Logan

[1] Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, PO Box 14115-336, Tehran, 1497713111 Iran.
[2] Corresponding author, e-mail: fathi@modares.ac.ir.
[3] Iranian Research Institute of Plant Protection, Tehran, 1985713133 Iran.

et al. 1976, Lactin et al. 1995, Brière et al. 1999, Roy et al. 2002, Kontodimas et al. 2004, Arbab et al. 2006). These models provide value estimates of lower and upper temperature thresholds and optimal temperature for development of a given stage.

The objectives of this study were to develop knowledge of the thermal characteristics of a codling moth population collected from the Maragheh region in Iran and to estimate accurately optimal temperature and temperature thresholds using nonlinear temperature-driven rate models in addition to linear models.

Materials and Methods

Rearing Methods

Codling moths were originally collected in 2005 from apple orchards of the Maragheh region, East Azerbaijan (Northwestern Iran), using trunk banding. One-faced fluted cardboard bands (one 15- to 20-cm-wide band per tree) were placed around the trunks of the trees to serve as pupation sites for wandering larvae. The bands were placed before the larvae begin to leave the apples to find pupation sites and removed before moth emergence. Codling moths used in this study were the F_2 generation of collected mature larvae. Larvae were reared on an artificial diet developed by Bathon (1981) and modified by Rezapanah (2001). We used cubic plastic media containers (2.5 cm height by 2.5 cm diameter with cap; Behin Plastic, Tehran, Iran) for individual codling moth larvae. Fluted fiberboard pieces were placed into these containers (see rearing conditions below) to provide a suitable pupation site for mature larvae. Fiberboard containing cocoons were removed and placed into similar new containers. Every 24 h, any emerged moths were transferred to transparent plastic jars (15 by 15 cm: height by diameter; Behin Plastic) for mating and oviposition. The bases of the jars were covered with rough cloth to prevent oviposition on this surface. Wax paper sheets were crumpled and flattened and fitted into the inner surface of the jar walls to provide an oviposition surface. Moist cotton pieces provided water requirements of the moths during mating and oviposition. The cotton pieces and oviposition substrates were replaced daily.

Experimental Conditions

Rearing was conducted at eight constant temperatures (10, 14, 20, 25, 27, 30, 33, and 35 ± 0.5°C), 50 ± 10% RH, and a photoperiod of 16:8 (L:D) h in growth chambers (Binder, Tuttlingen, Germany). The environmental conditions of each chamber were monitored with a temperature and relative humidity data logger (175-H2; Testo, Lenzkirch, Germany).

Egg Development

Two hundred to 600 eggs, each <24 h old, on wax paper were incubated at 10, 14, 20, 25, 27, 30, 33, or 35°C. All eggs were checked daily for eclosion.

Larval Development

Larvae (100–300) <24 h old, based on the rate of larval mortality at examined temperatures, were reared at one of the above temperatures in growth chambers. The larvae were placed singly in larval rearing containers using an artist's brush (size 000) under a laminar hood. During the first 48 h of larval development, the light intensity in growth chambers was kept very subdued (one 30-W fluorescent light per growth chamber) to prevent neonate larvae leaving the medium. Then the light intensity was increased (four 30-W fluorescent lights per growth chamber). Development was considered complete when larvae began spinning cocoons. At this time, fluted fiberboard pieces were placed in each container to serve as cocooning-pupation sites. Larvae-rearing containers were inspected for cocoons daily. The fiberboard pieces with cocoons were moved to another similar container.

Pupal Development

Cocoons <24 h old were held at 10, 14, 20, 25, 27, 30, 33, or 35°C. Containers were checked and all emerged moths collected daily.

Developmental Rate and Mathematical Models

Developmental rate is the reciprocal of developmental time in days. These rates are used in linear and nonlinear models where data are added daily (Arbab et al. 2006). Development is completed when the sum of daily developmental rate values equals 1 (Curry et al. 1978). Therefore, the integral of the developmental rate function along time can be used to simulate the development of an organism exposed to different temperatures (Arbab et al. 2006). Therefore, the common and Ikemoto and Takai linear and 13 nonlinear descriptive models were used to determine relationship between temperature and codling moth developmental rate (Table 1). The parameters of interest are the lower and upper temperature thresholds (T_{min} and T_{max}, respectively), the optimal temperature (T_{opt}), and the thermal constant (K). Most models are able to estimate two or more parameters. The models that estimate all of the temperature thresholds and optimal temperature are the Analytis, Hilbert and Logan, equation-16, Lactin, Briere-1, and Briere-2 (Table 1).

In addition to the common linear model, the Ikemoto and Takai linear model was used to obtain more reliable estimates of the lower temperature threshold and thermal constant (Ikemoto and Takai 2000). The Ikemoto and Takai linear formula is shown in the following equation:

$$(DT) = K + T_{min}D \qquad [1]$$

where D is the duration of development (days), T is temperature (°C), T_{min} is the lower temperature threshold, and K is the thermal constant. This equation is derived from the common linear model. The Ike-

Table 1. Mathematical models used to describe the effect of temperature on the developmental rate of codling moth and their capacity to estimate four important biological parameters

Model	T_{min}	T_{opt}	T_{max}	Thermal constant	Reference
Linear (common; Ikemoto and Takai)	●	○	○	●	Campbell et al. 1974, Frazer and McGregor 1992, Roy et al. 2002, Kheradmand et al. 2006, Golizadeh et al. 2007, and others
Sigmoid (logistic)	○	○	○	○	Davidson 1942, 1944; Kontodimas et al. 2004; Arbab et al. 2006
Brière-1	●	●	●	○	Brière et al. 1999; Roy et al. 2002; Kontodimas et al. 2004; Haghani et al. 2006, 2007
Brière-2	●	●	●	○	Roy et al. 2002; Zamani et al. 2006; Haghani et al. 2006, 2007; Golizadeh et al. 2007; and others
Logan-6	○	●	●	○	Logan et al. 1976, Roy et al. 2002, Kontodimas et al. 2004, Haghani et al. 2007, and others
Logan-10	○	●	●	○	Logan et al. 1976, Roy et al. 2002, Kontodimas et al. 2004, Golizadeh et al. 2007, and others
Lactin	●	●	●	○	Lactin et al. 1995, Tasi and Liu 1998; Kontodimas et al. 2004, Zamani et al. 2006, Golizadeh et al. 2007, Haghani et al. 2007, and others
Third-order polynomial (Harcourt equation)	○	●	●	○	Harcourt and Yee 1982, Lamb et al. 1984, Brière et al 1998, Kontodimas et al.2004
Equation-16	●	●	●	○	Kontodimas et al. 2004
Analytis	●	●	●	○	Analytis 1977, 1979, 1980, 1981; Kontodimas et al. 2004; Arbab et al. 2006
Hilbert and Logan	●	●	●	○	Hilbert and Logan 1983, Roy et al. 2002
Lamb ($T \le T_{opt}$) ↑	○	●	○	○	Lamb 1992, Roy et al. 2002, Kontodimas et al. 2004, Arbab et al. 2006
Taylor	○	●	○	○	Taylor 1981, Taylor 1982, Roy et al. 2002
Stinner ($T \le T_{opt}$) ↑	○	○	○	○	Stinner et al. 1974, Logan 1988, Kontodimas et al. 2004, Arbab et al. 2006

In this study, we fitted the Lamb and Stinner equations at temperatures $\le T_{opt}$, because in the upper temperatures, the no. of observations was less than the no. of estimated parameters.

●, index for model ability to estimate parameter; ○, index for model disability to estimate parameter.

moto and Takai linear model represents a straight line with $X = D$ and $Y = DT$ (Ikemoto and Takai 2000).

Temperature Thresholds and Parameter Estimation

Standard temperature indices were calculated either directly from the models or by using a graphic method as described below.

Lower Temperature Threshold. This temperature is often referred as the lower temperature threshold (Kontodimas et al. 2004) or the zero development temperature (Howell and Neven 2000). However, at the lower temperature threshold (T_{min}), no measurable development is detected or the rate of development is zero. It can be estimated from the linear model as the intercept of the development curve with the temperature axis. It can also be estimated directly from some nonlinear models. The SE of T_{min} was calculated from the following equation when a linear model was used:

$$SE_{T_{min}} = \frac{\bar{r}}{b} \sqrt{\frac{s^2}{N \times \bar{r}^2} + \left(\frac{SE_b}{b}\right)^2} \qquad [2]$$

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, Kontodimas et al. 2004).

Optimal Temperature. At the optimal temperature (T_{opt}), the rate of development is maximum. It may be estimated directly from the equations of some nonlinear models or as the parameter value for which their first derivatives equals zero. The SE of T_{opt} was esti-

mated from the nonlinear models (Kontodimas et al. 2004).

Upper Temperature Threshold. At the upper temperature threshold, the rate of development is zero or life cannot be maintained for a long time. Most nonlinear models can estimate this temperature. The SE of T_{max} was estimated from nonlinear models (Kontodimas et al. 2004).

Thermal Constant. The thermal constant (K) determines the amount of thermal units (degree-days) that are needed to complete development. This parameter can be estimated from the linear model as the reciprocal of the slop (b). The thermal constant cannot be estimated from nonlinear models. The SE of K was estimated with the following equation (Campbell et al. 1974, Kontodimas et al. 2004:

$$SE_K = SE_b / b^2 \qquad [3]$$

Statistical Analysis

For statistical analysis, data were checked for normality using the Kolmogorov-Smirnov test. The effect of temperature on the developmental time of codling moth immature stages was analyzed using one-way analysis of variance (ANOVA). If significant differences were detected, the means of developmental time were compared using pooled SDs at the studied constant temperatures. The ANOVA was carried out using Minitab software (MINITAB 2000).

Because we detected no development at 10 and 35°C, data from both temperatures were omitted from

Table 2. Developmental time of the codling moth immature stages at six constant temperatures

Stage	Temperature (°C)	Number of individuals	Minimum developmental time (d)	Maximum developmental time (d)	Mean developmental time ± SE (d)
Egg	14	410	17	21	18.67 ± 0.04
	20	537	8	11	9.34 ± 0.04
	25	289	4	6	4.80 ± 0.02
	27	405	4	6	4.52 ± 0.03
	30	477	4	5	4.04 ± 0.01
	33	135	4	5	4.19 ± 0.03
Larva	14	38	53	71	58.34 ± 0.67
	20	81	23	43	32.38 ± 0.47
	25	120	14	28	18.77 ± 0.25
	27	150	13	22	15.44 ± 0.14
	30	79	13	20	15.62 ± 0.20
	33	37	13	19	17.22 ± 0.23
Pupa	14	24	50	64	56.29 ± 0.76
	20	58	20	35	26.36 ± 0.40
	25	79	12	17	14.73 ± 0.15
	27	91	9	16	12.69 ± 0.11
	30	52	9	14	11.96 ± 0.15
	33	22	9	15	± 0.26
Egg-pupa	14	24	125	144	± 1.12
	20	58	59	81	68.46 ± 0.55
	25	79	33	48	37.86 ± 0.28
	27	91	28	39	32.24 ± 0.22
	30	52	28	37	31.48 ± 0.28
	33	22	30	36	34.19 ± 0.28

the goodness-of-fit test. Also, in the linear models, the last data value of developmental rate or developmental time at 33°C was omitted because it deviated from a straight line. The omission was necessary for the correct calculation of the T_{min} and K (DeClerq and Degheele 1992). For the common linear model, the developmental rate of egg, larva, pupa, and overall immature stages was regressed against temperature using linear regression (SPSS 2004). In addition, the Ikemoto and Takai linear model was used for estimating the parameters.

Four criteria were used to assess the performance of mathematical models:

1. The coefficient of determination (R^2). Higher values of R^2 indicate a better fit.
2. The residual sum of square (RSS). Lower values of RSS indicate a better fit.

The coefficient of determination and residual sum of square were commonly used for model evaluation. However, the R^2 value is not appropriate for discriminating between models with different numbers of parameters because models with more parameters always provide a better fit. Therefore, we used two other statistics that are parameter independent.

3. The Akaike information criterion (AIC). With this criterion, we sought the model with the lowest AIC, which is the function that minimizes the loss of information (Akaike 1974, Burnham and Anderson 2002, Vucetich et al. 2002, Angilletta 2006). The AIC is calculated using the following equation:

$$AIC = n \ln\left(\frac{SSE}{n}\right) + 2p \qquad [4]$$

where n is the number of observations, p is the number of model parameters including the intercept, and SSE is the sum of the squared error.

4. The adjusted coefficient of determination (R^2_{adj}). As AIC, this criterion is parameter independent. A higher value of R^2_{adj} indicates better fit (Rezaei and Soltani 1998). R^2_{adj} was calculated from the following equation:

$$R^2_{adj} = 1 - \left(\frac{n-1}{n-p}\right)(1 - R^2) \qquad [5]$$

Table 3. Linear regression equations, lower temperature threshold (T_{min}), and thermal constant (degree-days) of codling moth immature stages using two linear models

| Linear model	Stage	Linear equation	T_{min} ± SE (°C)	Thermal constant (DD) ± SE	R^2	Adjusted R^2	P
Common	Egg	DR = −0.1339 + 0.01299 T	10.31 ± 1.39	76.96 ± 7.58	0.9717	0.9623	0.002
	Larva	DR = −0.0301 + 0.00328 T	9.18 ± 1.92	304.91 ± 38.79	0.9536	0.9382	0.004
	Pupa	DR = −0.0459 + 0.00444T	10.34 ± 1.25	225.22 ± 19.65	0.9776	0.9703	0.001
	Egg-pupa	DR = −0.0165 + 0.00167 T	9.89 ± 1.60	597.69 ± 65.98	0.9647	0.9529	0.003
Ikemoto and Takai	Egg	DT = 79.80 + 9.97D	9.97 ± 0.78	79.80 ± 7.79	0.9819	0.9758	0.001
	Larva	DT = 312.60 + 8.94D	8.94 ± 1.92	312.60 ± 32.10	0.9647	0.9529	0.002
	Pupa	DT = 232.03 + 10.04D	10.04 ± 0.59	232.03 ± 17.53	0.9897	0.9862	0.000
	Egg-pupa	DT = 615.32 + 9.63 D	9.63 ± 0.81	615.32 ± 58.28	0.9793	0.9724	0.001
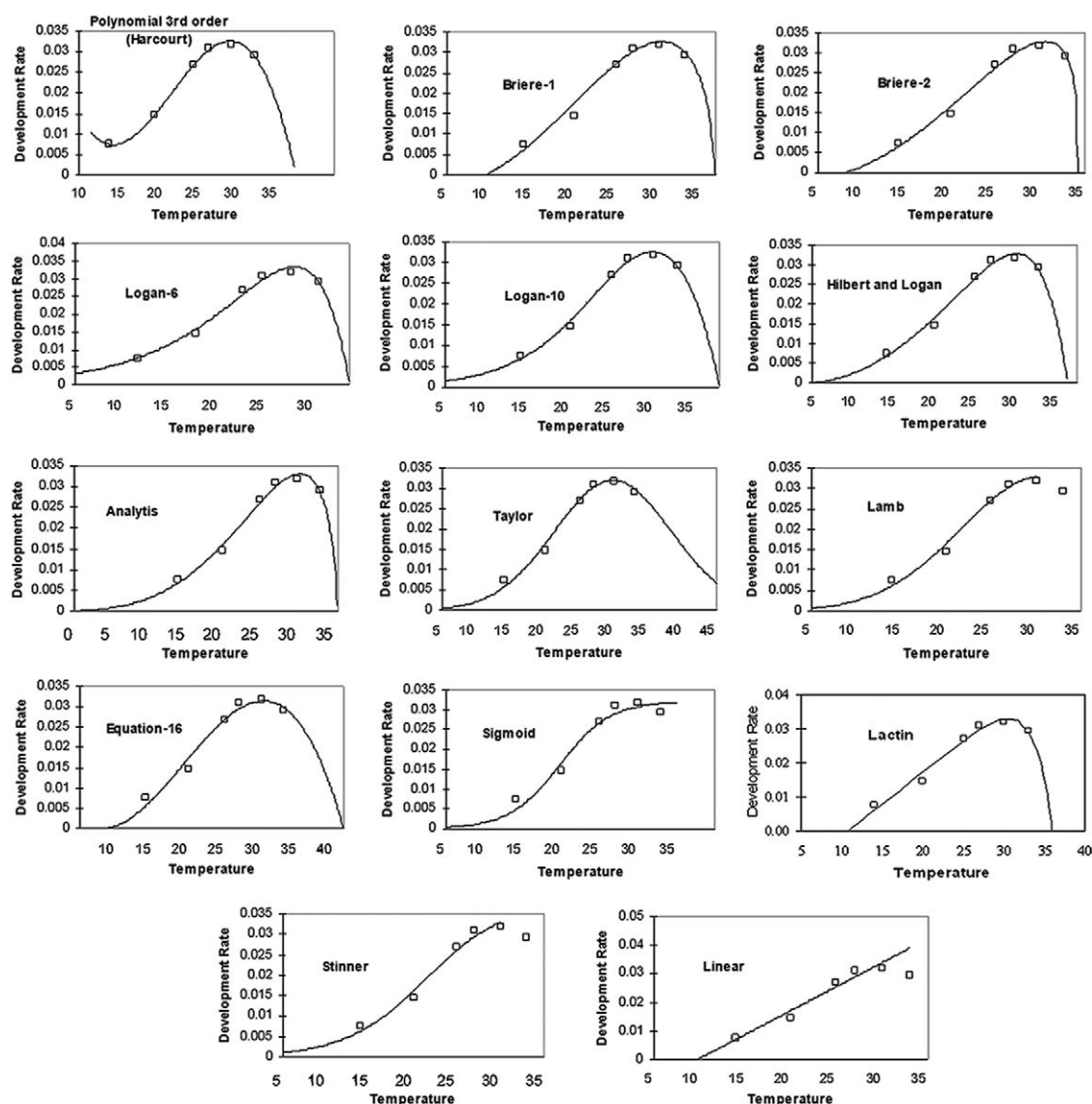
Fig. 1.   Fitting 1 linear and 13 nonlinear models to observed values of developmental rates (1/d) of overall immature stages at studied constant temperatures (°C). □, observed data.

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

Results

Developmental Time

No development occurred at 10 or 35°C. The developmental time of all immature stages of codling moth at six constant temperatures are presented in Table 2. One-way ANOVA showed a significant effect of temperature on developmental time for all codling moth life stages ($P < 0.0001$). Mean egg developmental time incubation period of codling moth varied from 4.04 d at 30°C to 18.67 d at 14°C. Egg developmental

time decreased with increasing temperature up to 30°C and then increased at 33°C. Larval developmental time ranged from 58.34 d at 14°C to 15.62 d at 30°C. The larval developmental time increased up to 17.22 d at 33°C. Pupal developmental time was from 56.29 d at 14°C to 11.96 d at 30°C and then increased to 12.50 d at 33°C.

Model Evaluation

Linear Models. Both of the linear models showed an acceptable fit to data for all immature stages. The linear regression equation, the lower temperature threshold (T_{min}), and the thermal constant (K) of codling moth immature stages are presented in Table

3. The Ikemoto and Takai linear model had a higher value of R^2 and R^2_{adj} values than the common linear model (Table 3), indicating a slightly higher degree of confidence in parameter estimates provided by the Ikemoto and Takai model. The common model tended to give higher estimates of T_{min} and lower estimates of the thermal constant than the Ikemoto and Takai model.

Nonlinear Models. Most nonlinear models fit the data well. The curves of the influence of temperature on developmental rate of overall immature stages fitted by each model are shown in Fig. 1. The values of R^2, RSS, AIC, and R^2_{adj} used to determine the goodness-of-fit the models (Table 4) showed that the third-order polynomial (Harcourt model) with the highest value for R^2 and R^2_{adj} and the lowest values for RSS and AIC had the best fit to data for development of each immature stage and for overall immature development. Furthermore, the sigmoid or logistic model had the poorest fit to data among nonlinear models. Other models including Brière-1, Brière-2, Logan-6, Logan-10, Hilbert and Logan, equation-16, Taylor, and Lactin also fit the data acceptably. The values of measurable parameters of the linear and nonlinear developmental rate models are presented in Table 5. Among the nonlinear models, Brière-1, third-order polynomial, and Brière-2 were used to estimate the lower temperature threshold, the optimal temperature, and the upper temperature threshold, respectively (Tables 6 and 7).

Discussion

Phenological models, using developmental time data, have been developed for codling moth to predict emergence of adults from the overwintering generation, eclosion of eggs, larval and pupal development, and generation time (Falcon and Pickel 1976, Falcon et al. 1976, Geier and Briese 1978, Riedl and Croft 1978, Brunner et al. 1982, Rock and Shaffer 1983, Setyobudi 1989, Howell and Neven 2000). These models, all based on a linear relationship between temperature and development rate, have been used with varying degrees of success (Rock and Shaffer 1983) to time pesticide sprays for control of codling moth. The assumption of linear relationship is not true for low- and high-end temperatures (Howell and Neven 2000). Some experiences with phenological models for codling moth have indicated that low and high temperature effects cannot be ignored, and linear phenological models inaccurately simulate development at high temperatures (Howell and Neven 2000). Ours is the only study to examine the effect of temperature on codling moth development using nonlinear developmental models at constant temperatures.

The findings of Howell and Neven (2000) concerning mean developmental time of the overall immature stages were consistent with the results of our study at similar temperatures. However, based on our results, 30°C can be considered as the optimal temperature for development (Table 2). The time required for egg development was short compared with that required

Table 4. Comparison of 14 developmental rate models based on the no. of parameters (NPAR), coefficient of determination (R^2), residual sum of squares (RSS), Akaike information criterion (AIC), and adjusted R^2 (R^2_{adj}) for predicting egg, larva, pupa, and overall immature development of codling moth

Model	NPAR[a]	Egg				Larva				Pupa				Overall immature stage			
		R^2	RSS (×10⁻⁴)	AIC	R^2_{adj}	R^2	RSS (×10⁻⁴)	AIC	R^2_{adj}	R^2	RSS (×10⁻⁴)	AIC	R^2_{adj}	R^2	RSS (×10⁻⁴)	AIC	R^2_{adj}
Linear (common)	2	0.9717	7.8	−47.69	0.9623	0.9536	0.83	−61.13	0.9382	0.9776	0.71	−62.07	0.9703	0.9647	0.16	−71.01	0.9529
Logistic or sigmoid	3	0.9787	6.77	−48.54	0.9645	0.9344	1.25	−58.67	0.8907	0.9797	0.74	−61.82	0.9662	0.9569	0.21	−69.38	0.9280
Brière-1	3	0.9812	5.96	−49.30	0.9687	0.9668	0.63	−62.78	0.9447	0.9868	0.48	−64.41	0.9780	0.9770	0.11	−73.26	0.9617
Brière-2	4	0.9851	4.74	−48.68	0.9627	0.9743	0.49	−62.29	0.9357	0.9909	0.33	−64.66	0.9772	0.9828	0.08	−73.17	0.9570
Logan-6	4	0.9848	4.84	−48.55	0.9620	0.9818	0.34	−64.48	0.9546	0.9906	0.34	−64.48	0.9766	0.9866	0.07	−73.97	0.9665
Logan-10	5	0.9916	2.68	−50.10	0.9580	0.9857	0.27	−63.87	0.9285	0.9971	0.10	−69.83	0.9855	0.9926	0.03	−77.05	0.9630
Lactin	4	0.9809	6.03	−47.23	0.9522	0.9644	0.60	−61.04	0.9211	0.9862	0.50	−62.12	0.9655	0.9754	0.12	−70.73	0.9383
Third-order polynomial	4	0.9949	1.61	−55.15	0.9872	0.9926	0.14	−69.81	0.9815	0.9990	0.03	−79.05	0.9975	0.9974	0.01	−85.64	0.9935
Equation-16	3	0.9784	6.90	−48.42	0.9640	0.9568	0.82	−61.20	0.9280	0.9832	0.61	−62.98	0.9720	0.9705	0.15	−71.39	0.9508
Analytis	5	0.9870	4.14	−47.49	0.9350	0.9791	0.39	−61.66	0.8955	0.9929	0.26	−64.09	0.9645	0.9876	0.06	−72.89	0.9380
Hilbert and Logan	5	0.9904	0.05	−73.66	0.9520	0.9782	0.42	−61.19	0.9910	0.9934	0.24	−64.53	0.9670	0.9904	0.05	−73.66	0.9520
Lamb ($T \le T_{opt}$)	4	0.9876	3.41	−41.96	0.9752	0.9753	0.44	−52.20	0.9506	0.9936	0.20	−56.15	0.9872	0.9859	0.06	−62.16	0.9718
Taylor	3	0.9887	3.60	−52.33	0.9812	0.9720	0.53	−63.82	0.9583	0.9935	0.23	−69.83	0.9892	0.9846	0.08	−75.17	0.9743
Stinner ($T \le T_{opt}$)	3	0.9869	3.61	−41.68	0.9738	0.9712	0.51	−51.46	0.9424	0.9920	0.26	−54.83	0.9840	0.9926	0.08	−60.73	0.9652

[a] Number of parameters.

Table 5. Values of fitted coefficients and measurable parameters of 14 developmental rate models to describe immature stages development of the codling moth

Model	Parameters	Egg	Larva	Pupa	Overall immature stages
Linear (common)	A	−0.1339	−0.0301	−0.0459	−0.0165
	b	0.0130	0.0033	0.0044	0.0017
	T_{min}	10.31	9.18	10.34	9.89
	K	76.96	304.91	225.22	597.69
Brière-1	a	14.53×10^{-5}	4.022×10^{-5}	5.10×10^{-5}	2.00×10^{-5}
	T_{min}	9.6450	8.8676	9.8042	9.6188
	T_{max}	37.6185	36.3525	37.2604	36.5508
	T_{opt}	31.25	30.70	31.22	30.40
Brière-2	a	26.34×10^{-5}	6.60×10^{-5}	9.00×10^{-5}	3.40×10^{-5}
	T_{min}	7.9722	6.5188	8.1904	7.7659
	T_{max}	34.4440	33.9961	34.3895	34.1260
	m	4.0547	3.9298	3.9046	3.8342
	T_{opt}	31.20	30.70	31.02	30.70
Logan-6	ψ	0.0613	0.0266	0.0359	0.0118
	ρ	0.1689	0.1657	0.1711	0.1704
	T_{max}	36.6712	36.1734	36.5002	36.1906
	Δ	5.7836	5.9324	5.7683	5.7743
	T_{opt}	30.8879	30.2410	30.7319	30.4162
Logan-10	α	0.4792	0.2292	0.1827	0.0845
	ρ	0.1866	0.1574	0.1818	0.1734
	T_{max}	40.0964	38.8673	39.5984	38.7735
	Δ	6.2452	6.6197	6.4093	6.4024
	K	105.4232	91.5731	105.4656	102.2182
	T_{opt}	33.8512	32.2476	33.1891	32.3711
Lactin	ρ	0.0111	0.0034	0.0043	0.0018
	T_m	39.6357	41.0808	40.9746	43.0451
	Δ	2.2536	2.1360	2.1090	2.2827
	y	−1.1216	−1.0336	−1.0474	−1.0198
	T_{min}	10.37	9.83	10.65	10.78
	T_{max}	36.44	35.74	36.18	31.02
	T_{opt}	31.40	30.56	31.01	35.93
Third-order polynomial (Harcourt equation)	a	-9.0×10^{-5}	-3.0×10^{-5}	-3.0×10^{-5}	-1.4×10^{-5}
	b	59.0×10^{-4}	19.6×10^{-4}	20.1×10^{-4}	9.2×10^{-4}
	c	−0.1138	−0.0385	−0.0385	−0.0179
	d	0.7308	0.2531	0.2453	0.1161
	T_{opt}	30.00	29.76	30.60	29.84
	T_{max}	38.93	38.28	39.61	38.43
Equation-16	a	3.7×10^{-5}	1.1×10^{-5}	1.3×10^{-5}	0.57×10^{-5}
	T_{min}	7.9376	7.5159	8.1076	8.1093
	T_{max}	43.3850	41.3481	42.7492	41.5254
	T_{opt}	30.60	30.10	31.20	30.40
Analytis	a	9.2×10^{-6}	9.2×10^{-9}	2.6×10^{-6}	7.3×10^{-9}
	T_{min}	0.0048	−10.1100	0.0099	−6.9336
	T_{max}	34.8674	34.5111	34.8576	35.0121
	n	2.8419	4.1114	2.8903	4.0276
	m	0.3555	0.4190	0.3762	0.4941
	T_{opt}	31.00	30.40	30.87	30.35
Lamb ($T \leq T_{opt}$)	R_m	0.2524	0.0665	0.0858	0.3256
	T_m $(= T_{opt})$	31.6119	31.2695	31.4477	31.0727
	$T_{ơl}$	9.4788	9.8052	9.3858	9.3293
Sigmoid (logistic)	a	5.3482	5.0324	5.3938	5.4117
	b	0.2616	0.2608	0.2660	0.2736
	c	0.2591	0.0657	0.0873	0.0326
Taylor	R_m	0.2468	0.0637	0.0836	0.0316
	T_m $(= T_{opt})$	30.9122	29.6918	30.6414	29.9478
	$T_{ơ}$	9.0574	8.7660	8.8934	8.5990
Hilbert and Logan	Ψ	0.2125	0.6340	1.7924	0.2125
	T_0	5.5579	3.2715	4.4538	5.5579
	d	48.8589	69.3089	99.1662	48.8589
	T_L	35.9055	38.1625	41.3152	35.9055
	Δ	3.6909	3.0796	3.7130	3.6909
	T_{min}	5.88	3.40	4.10	5.88
	T_{opt}	30.62	30.02	30.62	30.62
	T_{max}	36.91	36.23	37.14	36.91
Stinner ($T \leq T_{opt}$)	a	4.7974	4.3220	4.7934	4.6808
	b	−0.2218	−0.2039	−0.2221	−0.2193
	c	0.2901	0.0781	0.0988	0.0379

for larval and pupal development. Its consistently narrow range of developmental time makes the egg an excellent stage to use for phenological models (Brunner et al. 1982, Howell and Neven 2000).

The lower temperature threshold for codling moth has been reported to be as low as 8.0°C or as high as 11.1°C (Falcon and Pickel 1976, Falcon et al. 1976). Based on our study, lower temperature threshold for

Table 6. Estimating temperature thresholds and optimal temperature of codling moth using common linear and some nonlinear developmental rate models

Model	Immature life stages	T_{min} (°C)	T_{opt} (°C)	T_{max} (°C)	Acc		
					T_{min}	T_{opt}	T_{max}
Linear (Ikemoto and Takai)	Egg	9.97	[a]	[a]	+	[a]	[a]
	Larva	8.94	[a]	[a]	+	[a]	[a]
	Pupa	10.04	[a]	[a]	+	[a]	[a]
	Overall immature stages	9.63	[a]	[a]	+	[a]	[a]
Linear (common)	Egg	10.31	[a]	[a]	+	[a]	[a]
	Larva	9.18	[a]	[a]	+	[a]	[a]
	Pupa	10.34	[a]	[a]	+	[a]	[a]
	Overall immature stages	9.89	[a]	[a]	+	[a]	[a]
Brière-1	Egg	9.64	31.25	37.62	+	−	−
	Larva	8.87	30.70	36.35	+	+	−
	Pupa	9.80	31.22	37.26	+	−	−
	Overall immature stages	9.62	30.40	36.55	+	+	−
Brière-2	Egg	7.97	31.20	34.44	−	−	+
	Larva	6.52	30.70	34.00	−	+	+
	Pupa	8.19	31.02	34.39	+	−	+
	Overall immature stages	7.76	30.70	34.13	−	+	+
Logan-6	Egg	[a]	30.89	36.67	[a]	+	−
	Larva	[a]	30.24	36.17	[a]	+	−
	Pupa	[a]	30.73	36.50	[a]	+	−
	Overall immature stages	[a]	30.42	36.19	[a]	+	−
Logan-10	Egg	[a]	33.85	40.10	[a]	−	−
	Larva	[a]	32.25	38.87	[a]	−	−
	Pupa	[a]	33.19	39.60	[a]	−	−
	Overall immature stages	[a]	32.37	38.77	[a]	−	−
Third-order polynomial (Harcourt equation)	Egg	[a]	30.00	38.93	[a]	+	−
	Larva	[a]	29.76	38.28	[a]	+	−
	Pupa	[a]	30.60	39.61	[a]	+	−
	Overall immature stages	[a]	29.84	38.43	[a]	+	−
Equation-16	Egg	7.94	31.60	43.38	−	−	−
	Larva	7.52	30.10	41.35	−	+	−
	Pupa	8.11	31.20	42.75	+	−	−
	Overall immature stages	8.11	30.40	41.52	+	+	−
Analytis	Egg	0.00	31.00	34.87	−	+	+
	Larva	−10.11	30.40	34.51	−	+	+
	Pupa	0.01	30.87	34.86	−	+	+
	Overall immature stages	−6.94	30.35	35.01	−	+	+
Hilbert and Logan	Egg	5.88	30.62	36.91	−	+	−
	Larva	3.40	30.02	36.23	−	+	−
	Pupa	4.10	30.62	37.14	−	+	−
	Overall immature stages	5.88	30.62	36.91	−	+	−
Lamb ($T \leq T_{opt}$) ↑	Egg	[a]	31.61	[a]	[a]	−	[a]
	Larva	[a]	31.27	[a]	[a]	−	[a]
	Pupa	[a]	31.45	[a]	[a]	−	[a]
	Overall immature stages	[a]	31.07	[a]	[a]	−	[a]
Taylor	Egg	[a]	30.91	[a]	[a]	+	[a]
	Larva	[a]	29.69	[a]	[a]	+	[a]
	Pupa	[a]	30.64	[a]	[a]	+	[a]
	Overall immature stages	[a]	29.95	[a]	[a]	+	[a]

[a] Not estimated.
Acc, accuracy of the estimated values of the thresholds; +, yes; −, no.

different immature stages of codling moth was between 8.94 and 10.34°C using the common and Ikemoto and Takai linear models, respectively (Table 3) and between 8.87 and 9.80°C using the selected nonlinear models tested (Table 7). In most cited references, the lower temperature threshold of codling moth is considered as 10°C using the common linear developmental rate model (Glenn 1922, Riedl et al.

Table 7. Estimated optimal temperature, temperature thresholds, and applied models to estimate these parameters for different immature stages of codling moth

Life stage	$T_{min} \pm SE$ (°C) model		T_{opt} (°C) model[a]		$T_{max} \pm SE$ (°C) model	
Egg	9.6450 ± 1.8192	Brière-1	30.00	Polynomial third order	34.4440 ± 2.9980	Brière-2
Larva	8.8676 ± 2.2887	Brière-1	29.76	Polynomial third order	33.9961 ± 2.2439	Brière-2
Pupa	9.8042 ± 1.4538	Brière-1	30.60	Polynomial third order	34.3895 ± 2.1139	Brière-2
Overall immature stages	9.6188 ± 1.8277	Brière-1	29.84	Polynomial third order	34.1260 ± 2.1198	Brière-2

[a] SE could not be estimated because T_{opt} in this model was calculated using the graphical method.

1976, Rock and Shaffer 1983, Setyobudi 1989, Pitcarin et al. 1992, Howell and Neven 2000). Howell and Neven (2000) showed the possibility of deriving three T_{min}, 6.9, 9.3, and 10.3°C, for codling moth larvae, depending on the number of points deviating from linearity that are used in calculation. Rock and Shafer (1983) used five temperatures to calculate the lower temperature threshold (9.9°C) even though the data were significantly nonlinear. These results support our findings on the lower temperature threshold using linear and nonlinear models.

Howell and Neven (2000) reported the time required to complete physiological development of codling moth eggs (=thermal constant) to be 87.5 DD with 10°C as T_{min}, a value 12.5 DD lower than that found by Cranham (1980). We estimated the thermal constant of codling moth eggs to be 10.54 and 7.70 DD lower than Howell and Neven (2000) using the common and Ikemoto and Takai linear models, respectively. Based on these findings, consistency of codling moth developmental time in different locations is rejected. In addition, thermal constant values for larval and pupal development from our study are consistent with those of Pickel et al. (1986) and Setyobudi (1989), who reported the thermal constant of codling moth pupae to be 222.2 DD.

The commonly used forecasting models are based on linear regression between developmental rate and temperature, but the x-intercept does not confidently identify the lower temperature threshold (VanKirk and Aliniazee 1981, Hawthorne et al. 1988). If the lower temperature threshold is inaccurate, it can introduce significant error into the growth rate equation (Howell and Neven 2000). Therefore, the lower temperature threshold is a critical factor in determining the physiological developmental time of the codling moth in orchards. In our study, the sigmoid model provided the poorest fit to the developmental data and is only marginally suitable, compared with the other nonlinear models tested, for use in a codling moth developmental model. The third-order model provided the best fit to data. However, between these two are several models with the capacity to accurately estimate important developmental parameters. Furthermore, although the third-order polynomial had the best fit to data between 14 and 33°C, this model cannot provide a real thermal performance curve for development at lower temperatures (<14°C) and also fails to estimate the lower temperature threshold: it was necessary to use another suitable model, the Brière-1, for this purpose. Similarly, we used the Brière-2 to provide a thermal performance curve at higher temperatures (>33°C) and to estimate the upper temperature threshold.

Estimates of T_{max} using the Brière-1, Logan-6, Logan-10, Hilbert and Logan, Lactin, third-order polynomial equations, and equation-16 were higher than the observed values (overestimation). Only Brière-2 and Analytis accurately estimated T_{max}. We therefore selected the Brière-2 as the best model, not only to estimate the upper temperature threshold but also to provide a thermal performance curve at temperatures

>33°C. No other study has examined this parameter using nonlinear models. Pitcarin et al. (1992) reported the upper temperature threshold for the larval stage of codling moth to be 31.1°C. Our findings reject this finding.

This work described the temperature-dependent development of codling moth, *C. pomonella*, populations in Maragheh, northwest of Iran, under the broad range of temperatures generally prevailing in this region and estimated their key bioclimatic parameters. These results can be used to forecast accurately the occurrence of different stages of codling moth in apple orchards and enable us to choose the best time for controlling this pest with greater precision.

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Temperature-Dependent Development and Temperature Thresholds of Codling Moth (Lepidoptera: Tortricidae) in Iran

Aghdam, Hossein Ranjbar; Fathipour, Yaghoub; Radjabi, Gholamreza; Rezapanah, Mohammadreza