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Evaluation of non-linear models to describe development and fertility of codling moth at constant temperatures

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ABSTRACT

Developmental rate of immature stages and age-specific fertility of females of codling moth at constant temperatures was modeled using non-linear models. The equations of Enkegaard, Analytis, and Bieri 1 and 2 were evaluated based on the value of adjusted R^2 (R^2_{adj}) and Akaike information criterion (*AIC*) besides coefficient of determination (R^2) and residual sum of squares (*RSS*). All models have goodness of fit to data especially for development [R^2, R^2_{adj}, *RSS* and *AIC* ranged 0.9673-0.9917, 0.8601-0.9861, 0.08-6.7x10^{-4} and (-75.29) – (-46.26) respectively]. Optimum temperature (T_{opt}) and upper threshold (T_{max}) were calculated accurately (T_{opt} and T_{max} ranged 29.9-31.2°C and 35.9-36.7°C) by all models. Lower temperature threshold (T_{min}) was calculated accurately by Bieri-1 model (9,9-10,8°C) whereas Analytis model (7,0-8,4°C) underestimated it. As far as fertility is concerned the respective values were better fitted near the optimum temperature (in 30°C) [R^2 ,R^2_{adj}, *RSS* and *AIC* ranged 0,6966-0,7744, 0,5756-0,6455, 2,44-3,33 x10^{-4} and (-9,15)-7,15 respectively].

KEYWORDS: codling moth, development, fertility, non-linear models, temperature.

Introduction

Codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae) is a notorious fruit-boring pest that has extended its original distribution from the natural apple forest of Central Asia to all apple growing regions of the world, except eastern China and Japan (Mills 2005). In addition, codling moth has frequently been recorded as a pest of pear, Asian pear, walnut and occasionally apricot, peach, and plum (Barnes 1991). Similarly, this pest was considered as a key pest in apple orchards of Iran (Radjabi 1986). Understanding the factors affected codling moth development and implementing this information in forecasting models enable effective timing of control methods (Kührt et al. 2006, Ranjbar Aghdam et al. 2009).

Temperature is the most important environmental factor influencing the dynamics of mite and insect pests and their natural enemies (Huffaker et al. 1999). The developmental rate of codling moth is governed by environmental temperature (Rock and Shaffer 1983). Temperature-driven models are most often used to predict the activity and seasonal population dynamics of pests and natural enemies in field conditions (Frazer and McGregor 1992, Brière and Pracros 1998). Phenological models have been developed for codling moth to predict emergence of adults from the overwintering generation, eclosion of eggs, larval and pu-

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pal development, and generation time (Falcon and Pickel 1976, Geier and Briese 1978, Setyobudi 1989, Brunner et al. 1982, Rock and Shaffer 1983, Dastqeib and Seyedoleslamy 1988, Pitcairn et al. 1992, Howell and Neven 2000). Commonly applied phenological models, have been developed to predict emergence of codling moth adults from the overwintering generation, eclosion of eggs, larval and pupal development and based on a linear relationship between temperature and developmental rate. However, experiences with phenological models for codling moth have indicated that low and high temperature effects should not be ignored since linear phenological models inaccurately simulate development at high temperatures (Howell and Neven 2000). All of these models were based on a linear relationship between temperature and developmental rate (Rock and Shaffer 1983, Dastqeib and Seyedoleslamy 1988, Howell and Neven 2000).

Developmental rate, expressed as the reciprocal of time taken to change from one stage to another (Cossins and Bowler 1987), is nil at the lower temperature threshold, increases with temperature before leveling off at the optimal temperature and then decreases rapidly as the upper temperature threshold is approached (Roy et al. 2002). This relationship is curvilinear near extremes, but approximately linear at moderate temperatures (Wagner et al. 1984). Therefore, in order to describe the developmental rate more realistically and over a wide range of temperatures, several non–linear models have been applied (e.g. Bieri et al. 1983, Enkegaard 1993, Briere et al. 1999, Roy et al. 2002, Arbab et al. 2006, Zahiri et al. 2010). Similarly, some mathematical models have been used to describe fecundity or fertility at different temperatures (Bieri et al. 1983, Enkegaard 1993, Lanzoni et al. 2002, Kontodimas 2004, Kontodimas et al. 2007). These models provide value estimates for lower and upper temperature thresholds and optimal temperature of a given stage in addition to the description of developmental rate or fecundity at different temperatures.

In our previous studies (Ranjbar Aghdam et al. 2009a,b) temperature dependent development of codling moth was determined using linear and some non-linear models and age specific life table parameters were calculated. In the current study the objective is the evaluation of non-linear models to describe both the development of immature stages as well the age-specific fertility of the females of the collected population of codling moth from the Maragheh region in Iran.

Materials and Methods

Laboratory rearing

The specimens of codling moth were originally collected from the apple orchards of the Maragheh region (37°20'N, 46°21'E), Eastern Azerbaijan (Northwestern Iran) using trunk banding in 2005. Corrugated cardboard bands (15-20 cm wide) were placed around the trunk of the trees served as pupation sites for wondering larvae. Bands were placed before the larvae begin to leave the apples in search of pupation sites and removed before moth emergence. F2 generation of the collected codling moth was used in this study. Rearing was conducted at eight constant temperatures (10, 14, 20, 25, 27, 30, 33, and 35±0.5°C), 50±10% RH, and under a photoperiod of 16:8 (L:D) h in growth chambers. Codling moth larvae were reared on an artificial diet developed by Bathon (1981) and modified by Rezapanah (2001). Capped, plastic media containers (2.5cm cubes) were used to rear codling moth larvae individually. In order to provide a suitable pupation site corrugated fiberboard pieces were placed into these containers. Then the fiberboard pieces, with the cocooned larva inside them, were removed into similar new container and held under the same conditions as larvae. Male and female moths were separated by isolating pupae just before adult emergence. Emerged moths (at least 12 pairs) were transferred to transparent plastic jars (15cm in diameter, 15cm in height) daily for mating and oviposition. The bases of the jars were covered by rough cloth to prevent oviposition. Wax paper sheets first were crumpled, then flattened and fitted into the inner surface of the jar walls to provide a suitable oviposition surface. Moistured cotton piece provided water requirements for moths during mating and oviposition. The cotton pieces and oviposition substrates were replaced daily.

Temperature-dependent development

In order to determine developmental rate of codling moth at the above-mentioned conditions, 200-600 eggs aged < 24 h old, that were laid on the wax paper sheets, were incubated at 10, 14, 20, 25, 27, 30, 33, and 35°C. All eggs were checked daily for eclosion. This study was continued with 100-300 neonate larvae, each less than 24 h old, in larval stage, considering the rate of mortality at each temperature. Experimental individuals were monitored daily to determine the developmental stage and mortality.

Age-specific fertility

In order to study the adult codling moth fertility, newly emerged moths from each temperature were kept under the same conditions as described for the oviposition jars. Laid eggs were kept at the same conditions until hatching. All of the eggs were checked for hatching daily. Finally, the number of the fertile eggs that were laid per female per day was recorded. Age-specific fertility (m_x) (=number of the female fertile eggs / female / day) was calculated. Age-specific fertility was used for goodness-of-fit test in selected (described below) non-linear models.

Non-linear mathematical models

Several non-linear models are used to describe the relationship between temperature and developmental rate or fecundity of insects or mites (Bieri et al. 1983, Enkegaard 1993, Lanzoni et al. 2002, Kontodimas et al. 2004, Arbab et al. 2006, Kontodimas et al. 2007, Ranjbar Aghdam et al. 2009). In this study the following non-linear descriptive models were used to describe relationship between temperature and codling moth developmental rate or fertility.

Enkegaard model

This non-linear model was suggested by Enkegaard (1993) and used to fit the data on developmental rate and age-specific fertility by some of authors (Enkegaard 1993, Kontodimas 2004, Kontodimas et al. 2007). The equation of the Enkegaard model is as as follows:

$$r(T) = (a + b \times T) \times [e(-(c + d \times T))],$$

where *r(T)* is developmental rate or age-specific fertility, T is temperature or female adult age, depending on fitted data, a, b, c and d are empirical constants. This model was used to fit the data of codling moth developmental rate and age-specific fertility.

Bieri-1 model

This equation was used to fit the data on developmental rate and age-specific fertility by some authors, e. g. Bieri et al. (1983) and Kontodimas (2004). The Bieri–1 model is as follow equation:

$$r(T) = [a \times (T - x_{\max})] - [b^{(T - x_{\min})}]$$

where *r(T)* is developmental rate or age-specific fertility, T is temperature or adult female age depending on the fitted data, x_{max}, x_{min}, a, and b are empirical constants (x_{max}, x_{min} represent the lower and upper temperature threshold or the days of starting and stopping of oviposition). As previous, we used this model to fit the data of codling moth temperature-dependent developmental rate and age-specific fertility.

Bieri-2 model

This equation was used to fit the data on developmental rate and fecundity by some authors, e. g. Bieri et al. (1983) and Kontodimas (2004). We used this model for the same purpose. The Bieri–2 model is as follow equation:

$$r(T) = a \times \frac{(T - x_{\min})}{b^{(T - x_{\min})}}$$

where *r(T)* is considered as developmental rate or age specific fertility (m_x), *T* is temperature for developmental rate or female adult age for age-specific fertility, depending on the fitted data, x_{min}, *a,* and *b* are empirical constants .

Analytis Model

The Analytis model was first developed to determine the relationship between temperature and developmental time of phytopathogenic fungi and plant pests (Analytis 1980, 1981). However, some authors used this model not only to describe development but also to determine fertility of insect pests and their natural enemies at different temperatures (Kontodimas 2004, Kontodimas et al. 2007). The expression of this model is:

$$r(T) = a \cdot (T - x_{min})^n \cdot (x_{max} - T)^m$$

where *r(T)* is developmental rate or age-specific fertility, *T* is temperature or adult female age depending on the fitted data and x_{max}, x_{min}, *a, m* and *n* are empirical constants (x_{max}, x_{min}, represent the lower and the upper thresholds for development or the first and the final age of oviposition).

Model evaluation

All of the non-linear models were assessed for goodness-of-fit to data based on the following four statistical criteria:

i- The coefficient of determination (R^2): Higher value of R^2 indicates better fit.

ii- The residual sum of square (*RSS*): Lower value of *RSS* indicates better fit.

Since the value of R^2 is not an appropriate criterion to discriminate between models with different numbers of parameters (models with more parameters usually provide better fit), we used two other statistics:

iii- The Akaike information criterion (*AIC*): The *AIC* is calculated using the following equation:

$$AIC = n \cdot \ln(RSS / n) + 2p,$$

where *n* is the number of observations and *p* the number of model parameters. With this criterion, we sought the model with the lowest *AIC* (Akaike 1974, Burnham and Anderson 2002, Angilletta 2006, Ranjbar Aghdam et al. 2009).

iv- The adjusted coefficient of determination (R^2_{adj}):

$$R^2_{adj} = 1 - \frac{(n-1)}{(n-p)} \cdot (1 - R^2),$$

where *n* is the number of observations, *p* is the number of model parameters, and R^2 is the coefficient of determination. As *AIC,* this criterion is parameter independent. Higher value of R^2_{adj} indicates better fit (Rezaei and Soltani 1998, Ranjbar Aghdam et al. 2009).

Statistical analysis

The effect of temperature on the developmental rate of codling moth immature stages was analyzed using one-way ANOVA. If significant differences were detected, the means of developmental rate were compared using Duncan's multiple range test (a=0.05) among the studied constant temperatures (SPSS 2004). The non-linear regressions for the development and fertility of codling moth were analyzed with the Marquardt algorithm (Marquardt 1963) using the JMP (v. 4.02; SAS Institute 1989) and SPSS (SPSS 2004) statistical programs.

Results and Discussion

There was no development at 10 and 35°C. Developmental rate of the immature stages of codling moth at 14, 20, 25, 27, 30, and 33°C is given in Table 1. Developmental rate was increased with increasing temperature except at 33°C. One-way ANOVA revealed a significant difference between developmental rates of all immature stages at the temperatures examined ($P < 0.001$ and $df = 5$ in all cases, $F_{egg} = 146.76$, $F_{larva} = 36.12$, $F_{pupa} = 5.83$, and $F_{immatur\ stages} = 48.53$). Based on Duncan's multiple range test at 95% confidence level developmental rate of the larval, pupal and overall immature stages were located in the first group at 27, 30 and 33°C (with the shortest developmental time) and developmental rate of codling moth eggs were located in this group only at 30 and 33°C. The lowest developmental rate (the longest developmental time) for all of the immature stages was observed at 14°C.

All fitted and some measurable parameters were estimated by regression analysis, whereas some other measurable parameters were calculated by solving the equations or their first derivatives. The values of estimated criteria for model evaluation are presented in Table 2.

Values of fitted coefficients and measurable parameters of evaluated models for describing immature development of codling moth are presented in Table 3. The curves of the influence of temperature on developmental rate of overall immature stages fitted by each model are shown in Fig. 1.

All reared adults were able to reproduce at 20, 25, 27 and 30°C, but not at 14 and 33°C, where no fertile eggs were produced or mating failed. The highest values of age-specific fertility (m_x) were 4.00, 7.08, 15.37, and 3.12 females / female / day at 20, 25, 27 and 30°C, respectively. In addition, the highest fertility was observed at 27°C among examined temperatures.

On average, the greatest number of eggs laid per female was 89.25 at 25°C and the lowest was 20.18 at 30°C. The age-specific fertility (number of female eggs per female per day) increased from 20 to 27°C but declined at 30°C. The values of estimated criteria for model evaluation are presented in Table 4. Values of fitted coefficients and measurable parameters of evaluated models for describing codling moth age-specific fertility are presented in Table 5. The curves of the age-specific fertility, which fitted to four non-linear models at four constant temperatures, are shown in Figure 2.

This work is the first attempt to find the best non-linear models to describe both codling moth development and fertility at different temperatures. All models have high goodness of fit to data especially in describing development [R^2, R^2_{adj}, RSS and AIC ranged 0.9673-0.9917, 0.8601-0.9861, 0.08-6.7x10^{-4} and (-75.29) – (-46.26) respectively]. Optimum temperature (T_{opt}) and upper threshold (T_{max}) were calculated accurately (T_{opt} and T_{max} ranged 29.9-31.2°C and 35.9-36.7 °C) by all models. Lower temperature threshold (T_{min}) was calculated accurately by Bieri-1 model (9.9-10.8°C) whereas the Analytis model (7.0-8.4°C) underestimated it (Kontodimas et al. 2004).

As far as fertility is concerned the respective values were less fitted [R^2, R^2_{adj}, RSS and AIC ranged 0.2969-0.7744, 0.1211-0.6455, 2.44-224.96x10^{-4} and (-9.15)-57.7 respectively]. However, near the optimum temperature (30°C) goodness of fit to data was high also for fertility [R^2, R^2_{adj}, RSS and AIC ranged 0.6966-0.7744, 0.5756-0.6455, 2.44-3.33 x10^{-4} and (-9.15)-7.15 respectively].

Conclusively, this work described accurately the temperature-dependent development and age-specific fertility of a codling moth population from the Maragheh, Northwest Iran, using non-linear models at least at the range of the tested temperatures. The results of the current study can be used to predict development and population increase of codling moth in different temperatures and enable us to make accurate decision for controlling this pest.

TABLE 1. Developmental rate (days^{-1}, mean ± SE) of codling moth immature stages at six constant temperatures (n = number of individuals).

Temperature (°C)	Codling moth immature stages			
	Egg	Larva	Pupa	Overall immature stages
14	0.05356 ± 0.00012 (n=410)	0.01722 ± 0.00018 (n=38)	0.01784 ± 0.00024 (n=24)	0.00750 ± 0.00062 (n=24)
20	0.10798 ± 0.00044 (n=537)	0.03146 ± 0.00050 (n=81)	0.03788 ± 0.00057 (n=58)	0.01466 ± 0.00012 (n=58)
25	0.21015 ± 0.00125 (n=289)	0.05430 ± 0.00064 (n=120)	0.06837 ± 0.00065 (n=79)	0.02703 ± 0.00019 (n=79)
27	0.22477 ± 0.00133 (n=405)	0.06551 ± 0.00056 (n=150)	0.07933 ± 0.00071 (n=91)	0.03114 ± 0.00020 (n=91)
30	0.24811 ± 0.00044 (n=477)	0.06477 ± 0.00076 (n=79)	0.08432 ± 0.00113 (n=52)	0.03189 ± 0.00028 (n=52)
33	0.24037 ± 0.00017 (n=135)	0.05850 ± 0.00089 (n=37)	0.08082 ± 0.00191 (n=22)	0.02929 ± 0.00025 (n=22)

TABLE 2. Evaluation of four nonlinear models for predicting egg, larva, pupa and overall immature development of codling moth.

Model	NPAR	Stage	R^2	RSS (10^{-4})	R^2_{adj}	AIC
Bieri-1	4	Egg	0.9789	6.70	0.9472	-46.60
		Larva	0.9673	0.63	0.9182	-60.78
		Pupa	0.9851	0.54	0.9628	-61.71
		Overall immature stages	0.9750	0.13	0.9374	**-70.25**
Bieri-2	3	Egg	0.9858	4.60	0.9763	-50.85
		Larva	0.9814	0.36	0.9690	-66.16
		Pupa	0.9917	0.32	0.9861	-66.94
		Overall immature stages	0.9850	0.08	0.9745	**-75.29**
Analytis	5	Egg	0.9849	5.08	0.9247	-46.26
		Larva	0.9720	0.58	0.8601	-59.24
		Pupa	0.9901	0.40	0.9503	-61.57
		Overall immature stages	0.9793	0.12	0.8966	**-68.50**
Enkegaard	4	Egg	0.9858	4.60	0.9644	-48.86
		Larva	0.9814	0.36	0.9784	-64.16
		Pupa	0.9917	0.31	0.9792	-64.95
		Overall immature stages	0.9847	0.08	0.9617	**-73.32**

NPAR: Number of parameters, R^2: Coefficient of determination, *RSS*: Residual sum of squares, *AIC*: Akaike information criterion, R^2_{adj}: Adjusted R^2.

TABLE 3. Values of fitted coefficients and measurable parameters of four nonlinear models to describe immature stages development of codling moth.

Model	Parameters	Egg	Larva	Pupa	Egg-Pupa
Bieri-1	a	0.0137	0.0036	0.0047	0.0019
	b	1.6976	1.6137	1.6685	1.5603
	x_{min}	38.0970	40.6967	40.1807	42.7674
	x_{max} ($\approx t_{min}$)	10.6727	9.9539	10.7457	10.8212
	t_{opt}	31.19	30.48	31.03	30.48
	t_{max}	36.10	35.72	36.04	35.91
Bieri-2	α	-0.1203	-0.0307	-0.0414	-0.0159
	b	0.8428	0.8458	0.8416	0.8409
	x_{min} ($\approx t_{max}$)	36.6526	36.1540	36.4807	36.0522
	t_{opt}	31.00	30.20	30.68	30.31
Analytis	a	29.1336 x10^{-5}	5.9305x10^{-5}	9.3844 x10^{-5}	5.4981 x10^{-5}
	T_{min}	7.3434	6.9623	7.3962	8.4057
	T_{max}	36.3208	36.2075	36.1840	36.1208
	n	1.9107	1.9310	1.9290	1.7864
	m	0.4300	0.5173	0.4368	0.4794
	t_{opt}	31.0	30.0	30.8	30.1
Enkegaard	a	6.0947	0.0094	0.0006	0.0044
	b	-0.1663	-0.00026	-0.00002	-0.00012
	c	6.5921	1.2859	-1.4528	1.3774
	d	-0.1710	-0.1675	-0.1724	-0.1733
	t_{opt}	30.81	29.99	30.48	30.25
	t_{max}	36.65	36.15	36.48	36.10

TABLE 4. Evaluation of four nonlinear models for predicting codling moth fertility at four constant temperatures.

Temperature	Model	NPAR[a]	R^2	RSS	R^2_{adj}	AIC
20°C	Enkegaard	4	0.3679	22.87	0.2564	9.79
	Bieri-1	4	0.4202	224.96	0.3171	57.70
	Bieri-2	3	0.3701	23.09	0.3001	7.99
	Analytis	5	0.2969	28.38	0.1211	16.32
25°C	Enkegaard	4	0.6477	66.50	0.5772	31.80
	Bieri-1	4	0.6704	58.46	0.6045	29.33
	Bieri-2	3	0.6477	66.50	0.6037	29.80
	Analytis	5	0.4692	106.80	0.3175	42.80

TABLE 4 (continued). Evaluation of four nonlinear models for predicting codling moth fertility at four constant temperatures.

Temperature	Model	NPAR[a]	R^2	*RSS*	R^2_{adj}	*AIC*
27°C	Enkegaard	4	0.4242	141.40	0.2083	37.60
	Bieri-1	4	0.4353	137.51	0.2235	37.27
	Bieri-2	3	0.4242	141.40	0.2962	35.60
	Analytis	5	0.6251	91.99	0.4110	34.44
30°C	Enkegaard	4	0.6966	3.39	0.5828	-7.15
	Bieri-1	4	0.6913	3.33	0.5756	-7.38
	Bieri-2	3	0.6966	3.39	0.6292	-9.15
	Analytis	5	0.7744	2.44	0.6455	-9.09

NPAR: Number of parameters, R^2: Coefficient of determination, *RSS*: Residual sum of squares, *AIC*: Akaike information criterion, R^2_{adj}: Adjusted R^2.

TABLE 5. Values of fitted coefficients and measurable parameters of four nonlinear models to describe age-specific fertility of codling moth at four constant temperatures.

Model	Parameters	Temperature			
		20°C	25°C	27°C	30°C
Analytis	a	0.0425	0.0302	7×10^{-9}	2.2×10^{-9}
	D_{min}	4.0251	2.00	0.1321	0.6647
	D_{max}	17.5453	14.9998	15.0113	17.3506
	n	0.9808	0.5589	2.0239	1.0071
	m	1.1478	2.1235	7.5592	7.4821
Bieri-1	a	-0.2038	-0.7297	-1.1395	-0.3200
	b	0.7545	0.6888	0.5564	0.4371
	x_{max}	21.3063	15.5050	10.5789	9.7237
	x_{min}	5.6604	6.8774	4.4553	1.4208
Bieri-2	a	0.9534	4.2357	7.1904	2.5463
	b	1.1749	1.3088	1.4928	1.5869
	x_{min}	0.5736	0.4773	0.2658	0.0903
Enkegaard	a	-0.5508	-4.1051	-2.0869	-0.0377
	b	0.9300	8.6015	7.8510	0.4178
	c	-0.2038	0.5802	-0.0189	-1.8490
	d	0.1736	0.2691	0.4007	0.4618

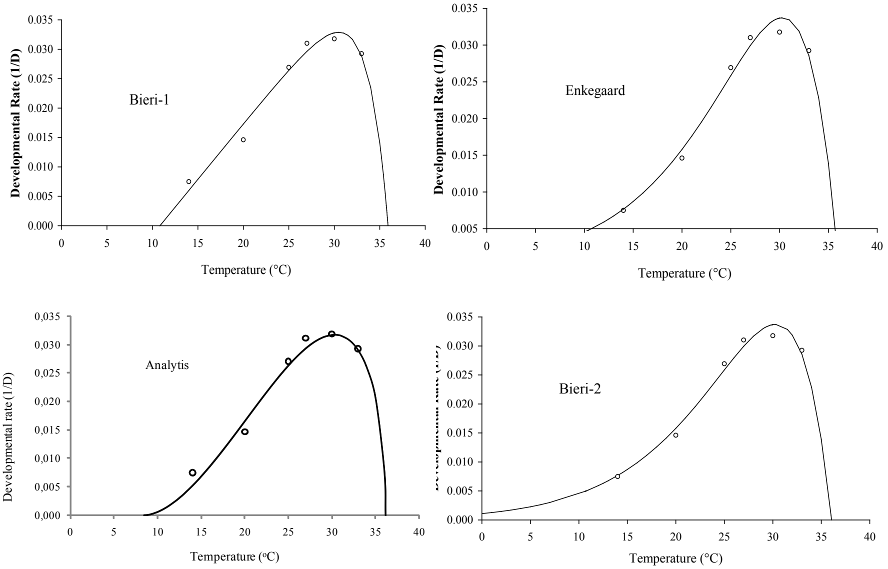

FIG. 1. Fitting non-linear models to observed values of developmental rates (1/Day) of overall immature stages at studied constant temperatures (°C). Open circles represent observed data.

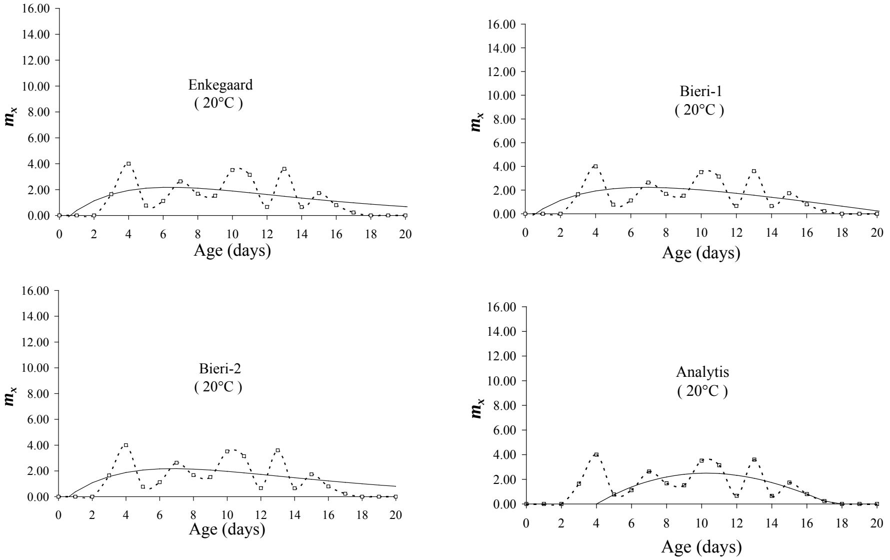

FIG. 2. Fitting non-linear models to observed values of age-specific fertility (m_x) of codling moth at four constant temperatures. Dotted lines and open squares represent observed data.

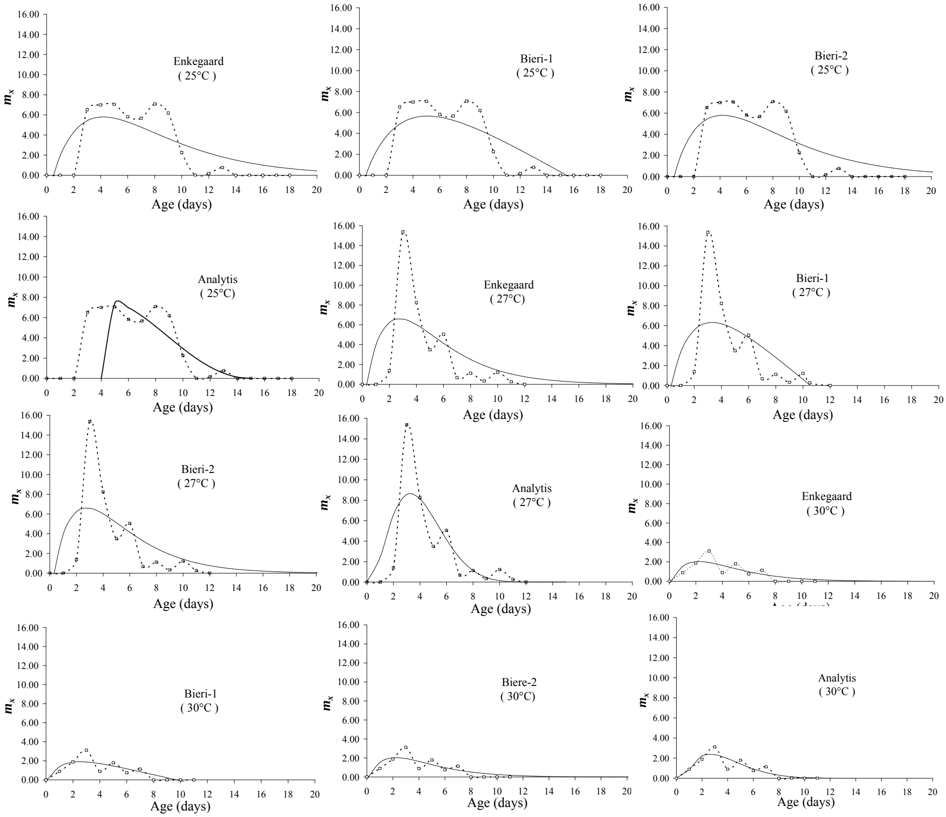

FIG. 2 (continued). Fitting non-linear models to observed values of age-specific fertility (m_X) of codling moth at four constant temperatures. Dotted lines and open squares represent observed data.

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Αξιολόγηση μη γραμμικών μαθηματικών προτύπων για την περιγραφή της ανάπτυξης και της γονιμότητας της καρπόκαψας της μηλιάς σε σταθερές θερμοκρασίες

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ΠΕΡΙΛΗΨΗ

Μελετήθηκε η ανάπτυξη των ατελών σταδίων και η γονιμότητα των θηλέων της καρπόκαψας της μηλιάς *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae) σε σταθερές θερμοκρασίες. Για την καλύτερη περιγραφή των δύο αυτών βιολογικών παραμέτρων ακολούθησε αξιολόγηση μη γραμμικών μαθηματικών υποδειγμάτων η οποία, εκτός από τον συντελεστή προσδιορισμού (R^2) και το άθροισμα τετραγώνων του υπολοίπου (*RSS*), βασίστηκε επιπλέον και στον προσαρμοσμένο συντελεστή προσδιορισμού (R^2_{adj}) και στο πληροφοριακό κριτήριο του Akaike (Akaike information criterion - *AIC*). Δοκιμάστηκαν οι εξισώσεις των Enkegaard, Αναλυτή, Bieri 1 και Bieri 2, οι οποίες έδειξαν καλή προσαρμογή στα δεδομένα, ιδιαίτερα της ανάπτυξης των ατελών σταδίων [R^2, R^2_{adj}, *RSS* και *AIC* κυμάνθηκαν από 0,9673-0,9917, 0,8601-0,9861, 0,08-6,7x10^{-4} και (-75,29) – (-46,26) αντίστοιχα]. Η ιδανική θερμοκρασία ανάπτυξης (T_{opt}) και το ανώτερο θερμοκρασιακό όριο (T_{max}) υπολογίστηκαν ικανοποιητικά από όλα τα πρότυπα (T_{opt}: 29,9-31,2°C και T_{max}: 35,9-36,7°C). Το κατώτερο θερμοκρασιακό όριο (T_{min}) υπολογίστηκε ικανοποιητικά από την εξίσωση Bieri-1 (9,9-10,8°C) ενώ υποεκτιμήθηκε από την εξίσωση Αναλυτή (7,0-8,4°C). Στα δεδομένα της γονιμότητας υπήρξε καλύτερη προσαρμογή στους 30°C, (δηλαδή κοντά στην ιδανική θερμοκρασία) [R^2 ,R^2_{adj}, *RSS* και *AIC* κυμάνθηκαν από 0,6966-0,7744, 0,5756-0,6455, 2,44-3,33 x10^{-4} και (-9,15)-7,15 αντίστοιχα].