

Estimating development and temperature thresholds of *Ephestia kuehniella*: toward improving a mass production system

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Abstract

The development of the Mediterranean flour moth, *Ephestia kuehniella* (Zeller), was evaluated at 10, 15, 17.5, 20, 22.5, 25, 27.5, 30 and 32.5°C with no lighting. None successfully completed development at 10 and 32.5°C. The total development time from egg to adult emergence was 164, 140, 98, 76, 61, 62 and 50 days, respectively, at the remaining temperatures. The developmental rate of *E. kuehniella* was described by the common linear model and six non-linear models. The lower temperature threshold for the immature stages and the thermal constant for *E. kuehniella* were 9°C and 1111 degree-days (DD) to complete development from egg to newly emerged adult. Non-linear models estimated the lower and upper thermal thresholds (T_{min} and T_{max}) and optimal temperature (T_{opt}). The values of T_{max} calculated by three non-linear models ranged from 34°C to 46°C; T_{opt} for each stage of development varied from 24 and 31°C, consistent with the temperature (30°C) at which the most rapid development occurred. Information on the threshold temperatures for development and thermal requirements can be utilized to predict *E. kuehniella* population dynamics and phenology and to evaluate optimal temperature conditions for mass rearing in stored products.

Keywords: Mediterranean flour moth, development rate, temperature, nonlinear model, no lighting

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Introduction

The Mediterranean flour moth, *Ephestia kuehniella* (Zeller), is a major pest of stored products (Marec, 1991; Hill, 2002; Rees, 2003). The species is often found in flour, grain and where ever starchy products are stored (Sedlacek *et al.*, 1996; Athanassiou *et al.*, 2003, 2005). The species is widely used to rear parasitoids and predators for use in integrated pest management of a number of major pests (e.g., Kim & Riedl,

2005; Hamasaki & Matsui, 2006; Paust *et al.*, 2008), and in fundamental studies in molecular biology, behavior, and biochemistry (e.g., Corbet, 1973; Rahman *et al.*, 2007; Jamoussi *et al.*, 2009).

Many biotic factors affect development and growth of insects but temperature is the single most important abiotic factor affecting the poikilothermic organism development (Rwomushana *et al.*, 2008; Pakyari *et al.*, 2011a). Understanding the relationship between developmental rates and the temperatures a pest species experiences is critical to forecasting the seasonal occurrence of the pest and phenological events in their life cycle, such as egg hatch time, pupation, and adult emergence as well as for planning and implementing mass rearing and integrated pest management strategies (Kim & Lee, 2010; Notter-Hausmann & Dorn, 2010;

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Ahn *et al.*, 2012). Foundational to understanding this relationship is to develop a reliable model of temperature-dependent development for the target species.

An insect's developmental rate is almost linear below the limit of sub-lethal maximum temperatures (Pakyari *et al.*, 2011a; Liu *et al.*, 2014) and a linear model is widely used to describe the relationship between developmental rate and a limited range of temperatures as it enables estimation of the thermal constant and lower temperature threshold (Campbell *et al.*, 1974). The developmental rate is basically zero at and below the lower threshold temperature. At the optimal temperature, development rate is maximal, and drops quickly at temperatures above the optimum (Roy *et al.*, 2002; Pakyari *et al.*, 2011b).

Even though the relationship between developmental rate and temperature is nearly linear at intermediate temperatures, it is curved near the lower and higher threshold temperatures (Wagner *et al.*, 1984). Various nonlinear models have been utilized to describe the relationship between developmental rate and temperature (Roy *et al.*, 2002; Kontodimas *et al.*, 2007; Zahiri *et al.*, 2010; Golizadeh & Zalucki, 2012). Nonlinear models enable estimation of the optimal temperatures and upper threshold temperatures for various stages of an insect's development. Temperature-driven rate models have been utilized to forecast the seasonal population dynamics and activity of pests (Roy *et al.*, 2002; Liu *et al.*, 2014). Wagner *et al.* (1984), Hagstrum & Milliken (1988), and Subramanyam & Hagstrum (1993) highlighted the nonlinear relationship between temperature and development for several beetles of stored product.

For stored-product pest moths comprehensive data are available on the temperature influences on development times of insects reared at various humidity levels and on different diets (Subramanyam & Hagstrum, 1993). Previous studies provide information on the influence of temperature and humidity on *E. kuehniella* at 16L:8D photoperiod but over a limited range of temperatures (20–30°C) (Siddiqui & Barlow, 1973; Subramanyam & Hagstrum, 1993). For mass production of this moth factory managers prefer to rear in the dark (saves on lighting costs) and in some cases maintaining life history stages at low temperatures can be advantageous (to delay development). Estimates of upper lethal temperatures would be useful as it better defines the thermal bounds within which a rearing facility will need to operate.

Our aim was to clarify the survival and developmental rate of each stage of *E. kuehniella* at a range of constant temperatures thereby facilitating the development of factory based mass rearing of this species. We reared immatures in the dark which is not normally done for this species. We calculated the lower threshold temperature and thermal constant for each stage of *E. kuehniella* using a linear model. In addition, nonlinear models were utilized to estimate the optimal temperatures and upper temperature threshold for each stage.

Material and methods

Our primary laboratory culture was built up utilizing 0.02 g of eggs gathered from infested wheat flour acquired from the Biological Control Research Institute of Gorgan, Iran. The eggs were put on a mix of 30 g yeast powder and 970 g wheat flour. The eggs were kept in metal containers (30 × 20 × 5 cm) wrapped with black cloth. The culture was maintained under room conditions set at 28 ± 2°C, 50 ± 5% relative humidity (RH), and a photoperiod of 0:24 (L:D) h.

Fifty pairs of moths (a male and female <12 h old) were obtained from the laboratory culture, placed in a Plexiglas oviposition box (6 × 6 × 17 cm) and provisioned with cotton soaked with 5% sugar–water as a source of nourishment. The mouth of the container was covered with a fine mesh gauze cover. Eggs laid were gathered daily from the gauze and individually moved to Petri dishes (50 mm diameter, 10 mm deep) utilizing a no. 0 brush. Each egg was stuck onto a black cardboard with sugar solution (10%).

Eggs ($n = 100$) were incubated and monitored daily and developmental characteristic of *E. kuehniella* were determined at nine temperatures: 10, 15, 17.5, 20, 22.5, 25, 27.5, 30 and 32.5°C (each ±0.5°C), 50 ± 5% RH, and a photoperiod of 0:24 (L:D) h in incubators (Binder KBWS 240, Germany). After eggs hatched, larvae at each temperature were transferred to Petri dishes provided with 20 mg of artificial diet (97% wheat flour + 3% yeast powder) until pupation (Coelho & Parra, 2013). These Petri dishes were placed in growth chambers with constant temperature at 15, 17.5, 20, 22.5, 25, 27.5, 30 and 32.5°C (each ±0.5°C) for development of larvae and pupae and monitored once daily.

Upon adult emergence the sex of the adults was determined to estimate the male to female ratio. For sex determination of adults, we used the morphology of the abdominal tip; in females remains quiet with the abdomen tip raised well above the level of her body with her ovipositor protruding 2–4 mm (Brindley, 1930). Survival rates of each stage were evaluated.

Temperature and development rate

The relationship between the temperature and rate of development was estimated utilizing the common linear model and six non-linear models (table 1). The common linear model or degree-day (DD) model estimates a lower threshold temperature and thermal constant (K), as follows:

$$D_r = a + bT,$$

where T is the temperature (°C), D_r is the rate of development (days⁻¹), a is the intercept, and b is the slope. The thermal constant (K , DD) and the lower threshold temperature (T_0) were evaluated as follows: $T_0 = -a/b$ and $K = 1/b$ (Campbell *et al.*, 1974).

Among six nonlinear models commonly found in the literature, five of them can be used to estimate the lower and upper threshold temperature and optimal temperature for development: the Analytis-3/Kontodimas16 (Kontodimas *et al.*, 2004), Logan6/Lactin2 (Lactin *et al.*, 1995), Janish/Kontodimas (Kontodimas *et al.*, 2004), Janish/Rosha (Rochat & Gutierrez, 2001), and Logan6/Lactin1 (Lactin *et al.*, 1995) (table 1).

Model fit was assessed on the following criteria: (1) the coefficient of determination (R^2); a higher value of R^2 demonstrates better fit, and (2) the residual sum of square (RSS); a lower RSS demonstrated better fit.

The R^2 value is not suitable for separating models with a different number of parameters since models with more parameters will generally give a superior fit. We utilized (3) the adjusted coefficient of determination R^2_{adj} , and (4) the Akaike information criterion (AIC), which are independent of the parameter number. A 'good' model should have a lower AIC value (Akaike, 1974; Vucetich *et al.*, 2002), where AIC is:

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

where n is the number of observations, p is the number of

Table 1. Mathematical models utilized to describe the influence of temperature on the development of *Ephestia kuehniella*.

Reference	Model	Equation
Kontodimas <i>et al.</i> (2004)	Analytis-3/Kontodimas 16	$r(T) = a(T - T_{\min})^2(T_{\max} - T)$
Davidson (1942, 1944)	Davidson logistic	$r(T) = \frac{k}{1 + e^{a-bT}}$
Lactin <i>et al.</i> (1995)	Logan 6/Lactin 2	$r(T) = e^{\rho T} - e^{\rho T_{\max} - ((T_{\max} - T)/\Delta)} + \lambda$
Lactin <i>et al.</i> (1995)	Logan 6/Lactin 1	$(T) = e^{\rho T} - e^{\rho T_{\max} - ((T_{\max} - T)/\Delta)}$
Kontodimas <i>et al.</i> (2004)	Janish/Kontodimas	$r(T) = \frac{2}{D_{\min}(e^{k(T-T_{\text{opt}})} + e^{-\lambda(T-T_{\text{opt}})})}$
Rochat & Gutierrez (2001)	Janish/Rosha	$r(T) = \frac{2C}{a^{(T-T_m)} + b^{(T_m-T)}}$

In Analytis-3/Kontodimas 16 model, *a* is an empirical constant, *T* is the rearing temperature (°C), and *T*_{max} is the higher threshold temperature. In the Davidson logistic model, *a*, *b*, and *K* are empirical constants and *T* is the rearing temperature (°C). In both Logan 6/Lactin 2 and Logan 6/Lactin 1 models, *T* is the rearing temperature (°C), ρ is a constant defining the rate of optimum temperature, *T*_{max} is the higher threshold temperature, Δ is the temperature range over physiological breakdown becomes the overriding influence and λ forces the curve to intercept the *y*-axis at a value below zero and thus allows the estimation of a low threshold temperature. In the Janish/Kontodimas model, *T* is the rearing temperature (°C), *D*_{min} is the lower threshold temperature, *T*_{opt} is the optimum temperature, and *K* and λ are empirical constants. In the Janish/Rosha model, *T* is the rearing temperature (°C), *a*, *b*, and *C* are empirical constants, and *T*_{min} is the lower threshold temperature.

model parameters involving the intercept, and SSE is the residual sum of squared error. A higher value of *R*²_{adj} demonstrates a better fit (Pakyari *et al.*, 2011a). *R*²_{adj} was evaluated from the below equation:

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

where *n* is the observations number, *p* is the model parameter numbers, and *R*² is the nonlinear regression coefficient.

Statistical analysis

The temperature treatment influence on the development, sex ratio, and mortality during each stage was tested utilizing one-way analysis of variance (ANOVA). Normality tests were used to determine whether a data set is well-modeled by a normal distribution. If data were not normal, we utilized the arcsin-square root transformation for proportional data. If significant treatment effects were found, multiple mean comparisons were made utilizing the least significant difference (LSD) test (*P* < 0.05). The ANOVA was accomplished utilizing MINITAB software (MINITAB INC., 2000). The SPSS statically program (V. 13.0; SPSS, 2004) was utilized to estimate temperature-dependent models.

Results

Temperature development time studies

E. kuehniella completed development from egg to adult at seven temperatures between 15 and 30°C; none successfully completed development at 10 and 32.5°C (table 2).

Temperature had a significant effect on the egg development of *E. kuehniella* (table 2). No *E. kuehniella* egg could survive at 10°C. Mean egg development time ranged from 4.2 days at 30°C to 13.5 days at 15°C. Larval mean development time ranged from 37.6 days at 30°C to 110.6 days at 15°C. Pupal development ranged from a mean of 9.2 days at 27.5°C to 36.6 days at 15°C. Mean total development ranged from 50 days at 30°C to 164 days at 15°C (table 2).

Survivorship for immature stages was highest at 22.5°C (table 2). Egg mortality was high at 30 and 32.5°C (table 2).

Sex ratio (male to female) of *E. kuehniella* was in favor of females in the range of 20–30°C. This suggests males are less heat tolerant and females less cold tolerant, with a 50% sex ratio at intermediate temperatures.

Model assessment

The linear model demonstrated a good fit to the data for the entire immature stages with high *R*² (>0.95) and *R*²_{adj} (>0.94) values (table 3). From the linear regression model *E. kuehniella* needed 1111 DD to finish development from egg to adult with a lower threshold temperature of 9°C.

All six models fitted the data well within the temperature range 15–30°C (table 4, fig. 1). The values of AIC, RSS, *R*², and *R*²_{adj} utilized to estimate the goodness-of-fit for each model demonstrated that Analytis-3/Kontodimas 16, with the highest values for *R*² and *R*²_{adj} and the lowest values for AIC and RSS, provided the best fit to the data (table 4). The *R*²_{adj} for six non-linear models for all developmental stages were in the range of 0.595–0.990 (table 4). The Analytis-3/Kontodimas 16 model had the highest *R*²_{adj} for all immature stages (table 4). The *T*_{opt} for the development of egg, larvae, pupa, and the egg–adult stage estimated by the Janish/Kontodimas model ranged between 24 and 28°C. The *T*_{min} and *T*_{max} for the development of egg, larvae, pupa, and the egg–adult stage estimated by the Janish/Kontodimas and Logan6/Lactin1 ranged between 4 and 13°C and 34 and 38°C, respectively (table 5), whereas *T*_{max} from the Analytis-3/Kontodimas 16 model were much higher (table 5).

Discussion

Our studies demonstrated that *E. kuehniella* is strongly affected by temperature, as expected (Siddiqui & Barlow, 1973; Subramanyam & Hagstrum, 1993; Coelho & Parra, 2013; Pakyari *et al.*, 2016). All development times were longer at low temperatures than at the higher temperatures within the range of 15–30°C. Over the range of 20–30°C, survival from egg to adult exceeded 50% except at 25°C; at 15°C, it was 33%. Jacob & Cox (1977) found survival from egg to adult exceeded 50%, over the range of 15–28°C but was lower (36%) at

Table 2. Development time (day \pm SE) and stage survival (%) of immature stages of *Ephestia kuehniella* at eight constant temperatures.

Temperature	Stage				Sex ratio (%)
	Egg	Larvae	Pupa	Total immature	
10	–	–	–	–	–
15	13.5 \pm 0.09a (100%)	110.6 \pm 1.69a (57%)	36.6 \pm 1a (89%)	163.8 \pm 2.8a (51%)	37
17.5	9.7 \pm 0.11b (93%)	102.1 \pm 2.23b (41%)	23.9 \pm 0.21b (87%)	140.3 \pm 4.24b (35%)	45
20	7.3 \pm 0.18c (100%)	73.7 \pm 2.37c (60%)	17.8 \pm 0.22c (94%)	98.4 \pm 3.77c (52%)	52
22.5	5.9 \pm 0.06d (89%)	55.7 \pm 1.18d (72%)	12.7 \pm 0.53d (54%)	75.9 \pm 1.67d (61%)	52
25	4.3 \pm 0.08ef (90%)	48.6 \pm 1.85e (100%)	11.0 \pm 0.12e (54%)	61.0 \pm 1.81e (54%)	49
27.5	4.3 \pm 0.05ef (87%)	47.5 \pm 1.34e (57%)	9.2 \pm 0.21f (84%)	62.0 \pm 2.22e (48%)	69
30	4.2 \pm 0.14f (77%)	37.6 \pm 0.93f (71%)	9.2 \pm 0.29f (72%)	50.2 \pm 1.29f (53%)	68
32.5	4.5 \pm 0.1e (67%)	–	–	–	–

Sex ratio is the percentage female.

Table 3. The parameters calculated by the common linear regression model between development rate (D_r) and temperature (T) for different immature stages of *Ephestia kuehniella*.

Stage	Regression	R^2	R^2_{adj}	P	Lower temperature threshold ($^{\circ}\text{C}$)	Thermal constant (K) (DD)
Egg	$D_r = -0.11 + 0.012T$	0.95	0.94	0.0002	9.17 \pm 0.0002	83.3 \pm 0.01
Larva	$D_r = -0.0095 + 0.0012T$	0.97	0.97	0.0001	8.06 \pm 0.003	833.3 \pm 0.08
Pupa	$D_r = -0.0596 + 0.0059T$	0.97	0.96	0.0001	10.09 \pm 0.003	169.2 \pm 0.089
Total immature	$D_r = -0.0085 + 0.0009T$	0.97	0.99	0.0001	9 \pm 0.00007	1111.1 \pm 0.001

Table 4. Performance of non-linear models describing the relationship between temperature ($^{\circ}\text{C}$) and development rates for all immature stages of *Ephestia kuehniella*.

	Model	R^2	RSS	R^2_{adj}	AIC
Eggs	Analytis-3/Kontodimas 16	0.946	0.00161	0.937	-64.089
	Davidson logistic	0.932	0.00202	0.920	-62.285
	Logan 6/Lactin 2	0.890	0.00326	0.872	-58.432
	Janish/Kontodimas	0.859	0.00420	0.835	-58.409
	Janish/Rosha	0.859	0.00420	0.835	-58.409
Larvae	Logan6/Lactin1	0.874	0.00373	0.854	-57.36
	Analytis-3/Kontodimas 16	0.969	0.0000078	0.954	-89.95
	Davidson logistic	0.964	0.0000091	0.957	-90.902
	Logan 6/Lactin 2	0.968	0.0000079	0.936	-87.861
	Janish/Kontodimas	0.970	0.0000074	0.940	-88.319
Pupae	Janish/Rosha	0.969	0.0000077	0.942	-88.041
	Logan6/Lactin1	0.958	0.000011	0.950	-89.904
	Analytis-3/Kontodimas 16	0.991	0.000054	0.990	-78.406
	Davidson logistic	0.990	0.000081	0.988	-77.603
	Logan 6/Lactin 2	0.997	0.00002	0.994	-81.359
Egg-adult	Janish/Kontodimas	0.932	0.00043	0.918	-63.899
	Janish/Rosha	0.932	0.000429	0.918	-63.899
	Logan6/Lactin1	0.951	0.000307	0.941	-66.236
	Analytis-3/Kontodimas 16	0.972	0.0000044	0.955	-93.959
	Davidson logistic	0.973	0.0000042	0.955	-94.284
	Logan 6/Lactin 2	0.971	0.0000046	0.942	-91.648
	Janish/Kontodimas	0.974	0.0000041	0.948	-92.453
	Janish/Rosha	0.971	0.0000046	0.942	-91.648
	Logan6/Lactin1	0.733	0.0001	0.595	-72.094

The best fit model for each stage is highlighted (see text for criteria).

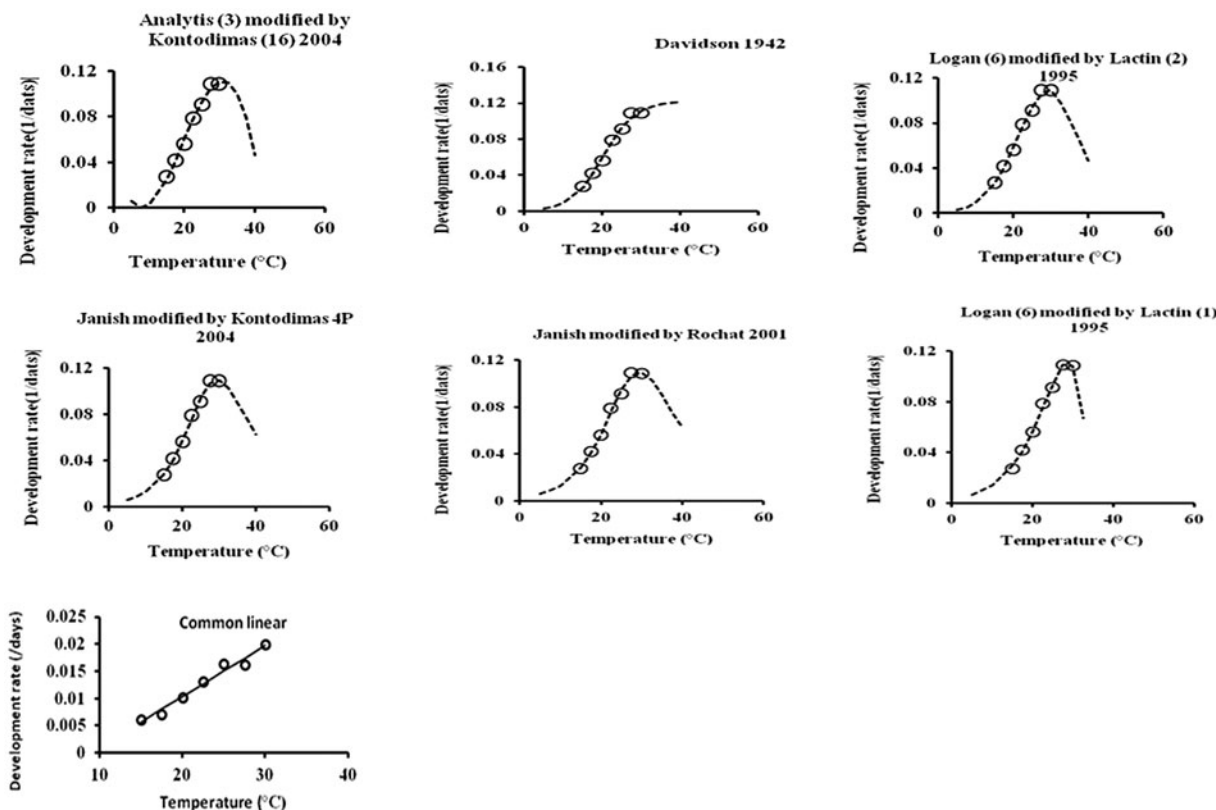


Fig. 1. Fitting the one linear and six nonlinear models to observed values of development rate for overall immature stages of *Ephestia kuehniella*.

Table 5. Parameter values calculated for various non-linear models for the development rate of life history stages of *Ephestia kuehniella* (eggs, larvae, pupae, and egg to adult) as a function of temperature.

Model	Parameter	Eggs	Larvae	Pupae	Egg–adult
Analytis-3/Kontodimas 16	<i>a</i>	0.000046 ± 0.000009	0.0000005 ± 0.000	0.000018 ± 4.586	0.0000011 ± 0.0001
	<i>T</i> _{min}	7.50 ± 0.99	5.04 ± 6.49	7.91 ± 0.913	7.99 ± 3.353
	<i>T</i> _{max}	40.38 ± 1.3	39.96 ± 77.59	42.49 ± 2.419	44.68 ± 17.07
Davidson logistic	<i>K</i>	0.244 ± 0.017	0.037 ± 0.013	0.122 ± 0.007	0.023 ± 0.004
	<i>a</i>	5.216 ± 1.261	3.259 ± 0.479	4.972 ± 0.491	3.846 ± 0.688
	<i>b</i>	0.281 ± 0.074	0.137 ± 0.049	0.245 ± 0.0295	0.180 ± 0.049
Logan 6/Lactin 2	<i>p</i>	0.0126 ± 0.002	0.001 ± 0.000	0.006 ± 0.000	0.001 ± 0.001
	<i>T</i> _{max}	41.78 ± 4.662	42.94 ± 0.000	46.18 ± 197.33	41.21 ± 113.39
	<i>λ</i>	-1.138 ± 0.048	-1.009 ± 0.003	-1.07 ± 0.006	-1.009 ± 0.014
	<i>ΔT</i>	3.812 ± 2.373	0.001 ± 0.000	0.579 ± 2.19	6.494 ± 127.92
Janish/Kontodimas	<i>D</i> _{min}	4.176 ± 0.354	13.33 ± 419.10	9.478 ± 1.396	11.350 ± 243.305
	<i>K</i>	-0.149 ± 0.034	-0.214 ± 0.49	-0.162 ± 0.038	-0.213 ± 0.276
	<i>T</i> _{opt}	27.39 ± 3.132	24.34 ± 24.53	27.11 ± 3.724	28.36 ± 18.69
	<i>λ</i>	-0.104 ± 0.055	0.037 ± 0.11	-0.092 ± 0.079	0.018 ± 0.11
Janish/Rosha	<i>C</i>	0.239 ± 0.02	0.106 ± 0.016	0.106 ± 0.016	0.486 ± 0.054
	<i>a</i>	1.11 ± 0.06	0.85 ± 0.032	0.85 ± 0.032	1.005 ± 4.369
	<i>b</i>	1.16 ± 0.038	0.913 ± 0.073	0.913 ± 0.073	1.004 ± 4.34
Logan6/Lactin1	<i>T</i> _m	27.39 ± 3.13	27.10 ± 3.728	27.10 ± 3.728	30.66 ± 23.63
	<i>ρ</i>	0.159 ± 0.011	41.226 ± 7.726	0.189 ± 0.008	0.287 ± 0.068
	<i>T</i> _{max}	35.96 ± 0.622	37.87 ± 1.834	34.07 ± 0.488	35 ± 0.00
	<i>Δ</i>	6.285 ± 0.412	0.128 ± 0.03	5.279 ± 0.233	5.00 ± 0.000

25°C. Our development time at 25°C (61 days) was lower than that reported by Jacob & Cox (1977) (104 days) but longer than that reported by Siddiqui & Barlow (1973) (46 days). These differences may reflect rearing differences in humidity and

photoperiod utilized in the previous research (Moghadamfar *et al.*, 2018). There was no survival or development at 10°C of any stages. At 32.5°C, eggs survived and larvae hatched but no larvae completed development. A suitable compromise

between short developmental time and high survival rates would be to keep the egg and larvae at 25°C.

Our results and various published studies demonstrated that *E. kuehniella* is a factitious host that provides desirable nutritional quality for mass rearing of egg parasitoids. Eggs can be kept at 15°C; they will remain viable but development can be greatly delayed. To increase egg production Coelho & Parra (2013) found adults reared at low temperatures were heavier, laid more eggs, and had longer lifespans than those reared from higher temperatures (28, 30, and 32°C). In addition, high temperatures (above 27.5°C) and low temperatures (10°C) during the larvae stage can lead to adult male sterility of *E. kuehniella* (Siddiqui & Barlow, 1973; Daumal & Boinel, 1994). The highest sex ratio of *E. kuehniella* occurred in the range of 27.5–30°C. A near equal sex ratio of males and females occurred in the range of 22.5–25°C. However, a bias in sex ratio might occur because of many factors (Hardy, 1994); such as host quality (Price, 1997), birth, death (Sapir *et al.*, 2008), and environmental conditions (Wrensch & Ebbert, 1993). Consistently female-biased *E. kuehniella* sex ratios may profit biological control because of increased host for parasitoid mass rearing.

The common linear model (Campbell *et al.*, 1974) is widely utilized for evaluating the thermal constant and lower threshold temperature (Roy *et al.*, 2002; Zahiri, *et al.*, 2010; Pakyari *et al.*, 2011a) as it is easy to calculate (Walgama & Zalucki, 2006; Pakyari *et al.*, 2011a). The lower temperature threshold average value for the different immature stages of *E. kuehniella* was observed to be around 10°C and was near to that found by Subramanyam & Hagstrum (1993) and Howe (1965) (9–10°C). The thermal constant for immatures to complete development (1111 DD) is higher than that found by Subramanyam & Hagstrum (1993) (724 DD). There can be many reasons for such a difference, including diet, different population being used but rearing in the dark is expected to increase development time (Cymborowski & Giebułtowicz, 1976). Moghadamfar *et al.* (2018) investigated development and reproduction of *E. kuehniella* at two photoperiods (continuous darkness and 16L:8D photoperiod) under laboratory condition (30 ± 0.5°C and 50 ± 5% RH). They found that egg and larval development time were significant longer under continuous dark conditions than the 16L:8D photoperiod similar to our findings.

The developmental rate of *E. kuehniella* was well described by six non-linear models but the values of T_{max} calculated by three nonlinear models ranged from 34 to 46°C, much higher than the temperature at which the insects could complete development in our study, 30°C and none developed at 32.5°C. The T_{max} estimated here (34–46°C) is higher than that reported by Subramanyam & Hagstrum (1993) (29.11°C) using the Stinner model and fewer temperatures (20–30°C). The Stinner equation (Stinner *et al.*, 1974) is symmetrical around the optimum and so prone to overestimate the high temperature parameter (Zahiri *et al.*, 2010). The cautionary tale here is that just because a model ‘fits’ it does not necessarily give biologically realistic values.

The most essential parameter evaluated by the non-linear models is T_{opt} , which is the temperature at which physiological processes are at a maximum. The model-averaged calculated T_{opt} for each stage of development varied from 24 to 31°C, which were consistent with the temperature at which the most rapid development rate occurred (30°C). Howe (1965) found 24–27°C as the T_{opt} range, slightly lower than those we estimated. Coelho & Parra (2013) reported a T_{opt}

range for the development of *E. kuehniella* was between 20 and 30°C. Above 30°C there was a sharp decrease of egg development, and the larvae did not survive temperature above 34°C. Maintaining the mass rearing facility for this species within this temperature range will ensure suitable conditions for its basic biology and to produce large number of high quality insects for subsequent use in biological control programs or for research.

Our research demonstrated the temperature dependent development of *E. kuehniella* under a wide range of constant temperatures without light. Our developmental rate model can be utilized to calculate the development time of this species under various conditions of temperatures differing inside an appropriate range with the aim of developing an improved integrate pest management tactics in stored product situations. Information on the thresholds of development and thermal requirements can be utilized to predict *E. kuehniella* population dynamics and phenology and to evaluate optimal temperature conditions for mass rearing for other purposes.

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