

Temperature-Dependent Development of *Exorista larvarum* (Diptera: Tachinidae): An Efficient Candidate for Biological Pest Control

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ABSTRACT

Climatic conditions are the most important factor in the distribution and abundance of living organisms, with temperature serving as a critical factor influencing the development of insect pests and their natural enemies. Thermal models are a key component of modern integrated pest management (IPM) systems. The *Exorista larvarum* (Linnaeus, 1758) (Diptera: Tachinidae), a gregarious larval endoparasitoid, serves as a biocontrol agent against several lepidopteran pests affecting both forest and agricultural ecosystems. To optimize the mass rearing of *E. larvarum* and improve its application in IPM programs, the developmental times of this parasitoid were investigated under seven constant temperatures (15-35 °C) in laboratory conditions. We applied two linear and 26 nonlinear models to describe the temperature-dependent development rate of *E. larvarum*. The lower temperature threshold (T_0) and thermal constant (K) were estimated to be 5.09 °C and 389.41 DD using the ordinary linear model and 9.73 °C and 292.74 DD using the Ikemoto model, respectively. Among the nonlinear models, Performance-2, Beta, Janisch/Kontodimas, Analytis-1, and Analytis-3/Kontodimas were the best models to describe the temperature-dependent development rate of the parasitoid. The estimated T_{fast} values by Performance-2 and Janisch/Kontodimas models were 33.2 and 31.4 °C, respectively, closely were the closest to T_{fast} observed (32.5 °C). Our findings can help to gain new and valuable insights into the biology of *E. larvarum* and provide essential information that can be incorporated into forecasting models of this parasitoid.

Keywords: Biocontrol, degree day, developmental rate, temperature thresholds, tachinid fly.

INTRODUCTION

Understanding insect adaptation to climatic conditions is pivotal for effective pest management (Bale *et al.*, 2002; Kang *et al.*, 2009). Temperature is a critical climatic factor that profound effects on the development of pests and their natural enemies. Consequently, calculating temperature-dependent development and thermal requirements utilizing thermal

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models is important for creating forecast models. This practice not only facilitates the comprehension of thermal adaptations among natural enemies but also their synchrony with hosts. Thermal requirements, often utilized as a predictive basis, become integral components in the strategic implementation of integrated pest management (IPM) systems (Haghani *et al.*, 2007a, b). Moreover, thermal requirements provide some essential information on the biology of natural enemies, enhancing their effectiveness as biological control agents (Haghani *et al.*, 2009; Iranipour *et al.*, 2010; Pakyari *et al.*, 2011; Walker, 2011; Baek *et al.*, 2014; Park *et al.*, 2016; Mirhosseini *et al.*, 2018; Farazmand *et al.*, 2020; Yazdanpanah *et al.*, 2022).

While factors such as nutrition, humidity, temperature and photoperiod significantly influence development rate and should be considered when applying predictive models (Gillbert and Raworth, 1996), thermal traits may vary across species, populations, and developmental stages (Honek, 1999). Nevertheless, laboratory-derived estimations of thermal requirements remain valuable for identifying temperature ranges conducive to stable population growth (Pilkington and Hoddle, 2006). This information is particularly useful for identifying geographical areas where undesirable temperature circumstances may impede the establishment of permanent populations of biological control agents (Hoelmer and Kirk, 2005).

Exorista larvarum (Linnaeus, 1758) (Diptera: Tachinidae), a polyphagous gregarious larval endoparasitoid of Lepidoptera, is well known as an effective candidate for biological control of forest and agricultural lepidopterous defoliators (Grenier, 1988; Cerretti and Tschorsnig, 2010; Benelli *et al.*, 2017; Dindo and Nakamura, 2018). This parasitoid can be mass-produced, and the availability of various mass-rearing techniques for this tachinid makes it a suitable candidate for industrial-scale production and release against its host pests (Benelli *et al.*, 2018).

An important step in the mass production of parasitoids under laboratory conditions and their inundative release in the field, as well as a fundamental requirement for any biological pest control program, involves evaluating the optimum temperature for the development of parasitoids (Meirelles *et al.*, 2015). Temperature, as one of the most important environmental factors (Taylor, 1981; Gilbert and Ragworth, 1996; Gorji *et al.*, 2008; Johnson *et al.*, 2016; Amjad Bashir *et al.*, 2022), significantly affects the abundance, distribution, immature development, adult emergence, fecundity, longevity, and parasitism capability of parasitoids (Liu *et al.*, 2012). Also, temperature can be utilized in specifying optimal circumstances for parasitoids, timing their release, forecasting the incidence of their host pests, knowledge of temperature effects on pests or parasitoids, and their adjustment to climatic circumstances plays a pivotal role in the success or failure of a biocontrol program (Agbodzavu *et al.*, 2020; Moradi

et al., 2023). Because of its importance relative to other environmental factors, temperature is frequently used as input in mathematical models that are vigorous tools for describing the effect of temperature on insect development and predicting their population growth potential (Mirhosseini et al., 2017). The application of thermal models promises for monitoring natural enemies and to be invaluable in the implementation of pest management programs (Paes et al., 2018; Sampaio et al., 2021; Malekera et al., 2022).

Currently, various linear and nonlinear models are usually utilized to calculate the development of insect pests and natural enemies (Ranjbar aghdam et al., 2009; Mirhosseini et al., 2018) and determine the relationship between temperature and their development rate (Worner, 2008). The thermal constant (K), expressed in degree-days above the developmental zero, represents the amount of physiological time required for an insect to complete its development (Campbell et al., 1974). This parameter can be estimated accurately using linear models, which assume a constant rate of development within a specific temperature range. However, because insect development deviates from linearity at temperature extremes—both high and low—nonlinear models are essential for accurately determining the optimum temperature for development and the upper thermal threshold. Thermal thresholds and optimum temperature significantly impact the entire main life processes of poikilothermic organisms due to the limitations imposed by temperature on their biological performance (Roy et al., 2002).

Given the critical influence of temperature on the development and efficiency of natural enemies, the present research aimed to assess the thermal requirements and developmental responses of *E. larvarum* under constant temperatures. This exploration serves as a prerequisite for the mass rearing and effective deployment of *E. larvarum* in biological control programs. Although the only study that has previously examined the effect of temperature on the biological parameters of *E. larvarum* is that by Simoes (2004), our research offers novel insights by employing two linear models and several nonlinear models to evaluate the influence of temperature on the development of this promising parasitoid. The results of this study could be beneficial for designing an exhaustive program to manage different lepidopterous defoliators in forest and agricultural systems, thereby enhancing the application of this parasitoid in future IPM programs.

MATERIALS AND METHODS**Insect Cultures**

In 2019, a laboratory stock colony of *E. larvarum* was initially established using adults reared from larvae and pupae of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae). The host material collected from forested areas in northern Iran, Guilan province, Rezvanshahr, Paresar, Sandian (37°34'16.94" N, 49°7'27.30" E, 5 m a.s.l.). The emerged parasitoids were identified using the key of Tschorsnig and Herting (1994), which is widely recognized for its reliability in tachinid identification (Karami *et al.*, 2023). To reduce inbreeding risk, we periodically introduced field-collected individuals from wild populations into the colony during 2021. The colony was maintained in the Entomology Laboratory of the Faculty of Agriculture, Tarbiat Modares University, Tehran, using last-instar larvae of the greater wax moth, *Galleria mellonella* Linnaeus (Lepidoptera: Pyralidae), as a factitious host for continuous rearing. This developmental stage was chosen as the most suitable one for parasitism by *E. larvarum* according to Mellini *et al.* (1993), and Dindo *et al.* (2003). The greater wax moth larvae were reared on an artificial diet (Campadelli, 1987) at 30 ± 1 °C, $65 \pm 5\%$ RH and in total darkness. This host is widely used in parasitoid rearing due to its proven suitability for development, compatibility with low-moisture artificial diets that reduce contamination risk, and greater convenience and safety compared to natural hosts (Campadelli, 1988; Mellini and Coulibaly, 1991; Delobel and Laviolette, 1969). The adults of parasitoid were maintained in clear and cubic Plexiglas cages ($30 \times 30 \times 30$ cm, with 80–100 adults per cage) in a growth chamber at 26 ± 1 °C, $65 \pm 5\%$ RH, and a photoperiod of 16: 8 (L: D) h. The adult tachinids were fed on sugar cubes, cotton balls soaked in a honey and water solution (20% honey) and distilled water in drinking cups with soaked cotton (Dindo *et al.*, 1999; Dindo *et al.*, 2007; Depalo *et al.*, 2010; Benelli *et al.*, 2018; Dindo *et al.*, 2019; Martini *et al.*, 2019; Dindo *et al.*, 2021). The sugar cubes and drinking cups were changed weekly, but soaked cotton balls were renewed 4-5 times per week.

Experimental Setup

To start the experiment, last instar larvae of *G. mellonella* were exposed within a cage to 5–7 day-old mated females of *E. larvarum* (2–3 larvae per female), as females of this age exhibit higher oviposition rates (Dindo *et al.*, 1999), and the parasitized larvae were removed from the cage approximately one hour after exposure, once 4–5 eggs were laid on their body surface. These larvae were then transferred individually into ventilated 0.2 ml micro tubes (This

maintenance procedure minimizes dropping out eggs from the body surface of the larvae) and placed at seven constant temperatures of 15, 20, 26, 30, 32.5, 34 and 35 ± 1 °C, relative humidity of $65 \pm 5\%$ and a photoperiod of 16: 8 (L: D) h. in growth chambers. After 24 h., the surplus eggs were removed, and only one egg was kept on the surface body of each larva, and a total of 100 parasitized larvae were randomly selected as a cohort for each temperature. Each parasitized larva was considered as a replicate. The remaining eggs development was checked daily until the eggs hatched, upon egg eclosion and subsequent parasitoid larval penetration into host larvae, the parasitized larvae were transferred individually into the transparent cylindrical plastic containers (10 cm in diameter by 8 cm in height) with lots of small round holes (1 mm diameter) in their lids for ventilation. These larvae were not provided with any food throughout the experimental period. The subsequent stages were spent in these plastic containers in the same conditions as above. To confirm the successful penetration of the newly hatched parasitoid larvae and determine the duration and mortality of the immature stages of *E. larvarum*, monitoring was carried out daily and the wax moth larvae were examined under a stereomicroscope until the parasitoids reached adulthood.

Data Analysis and Thermal Modeling

Prior to analysis, the data were tested for normality and found to meet the assumptions of parametric analysis. A one-way ANOVA was conducted to evaluate the effect of temperature on the total developmental time of *E. larvarum*, using SPSS software (version 27.0). Mean comparisons were performed using Tukey's HSD test at a significance level of $P < 0.05$. To describe the development rate of *E. larvarum*, we assessed the efficiency of two linear and 26 nonlinear models, utilizing ArthroThermoModel (ATM) software (Table 1) (Mirhosseini *et al.*, 2017).

Excluding temperature 34°C from data analysis due to being beyond the linear portion of developmental rate and its elimination is essential for the accurate assessment of T_0 (Ikemoto and Takai, 2000), the linear models were used to estimate the lower temperature threshold (T_0) and thermal constant (K) of *E. larvarum*. Three criteria including Sum of Squared Error (*SSE*), adjusted coefficient of determination (R^2_{adj}), and Akaike Information Criterion (*AIC*) (Table 1) were used to assess the nonlinear models. All fitted nonlinear models were ranked using *AIC*, as the best statistical criterion (Akaike, 1974), and the model(s) with the smallest value of this parameter was considered the best model for describing the temperature-dependent development of parasitoid.

RESULTS

The parasitoid completed its development at all tested temperatures, with the exception of 35 °C. At this temperature, egg hatching failed, so starting the development experiments was impossible. Temperature had a significant effect on total developmental time of *E. larvarum* ($F= 4410.778$; $df= 5, 313$; $P<0.001$). The mean total developmental time decreased until reaching 32.5 °C, after which it increased at 34 °C (Table 2). Individuals reared at 15 °C had the longest total developmental time. In contrast, those reared at the temperature range of 20–34 °C showed a significantly shorter total developmental time, ranging from 23.04 to 15.33 days, respectively (Table 2).

The relationship between temperature and the parasitoid developmental rate was described using various linear and nonlinear thermal models. Table 3 shows the estimated thermal constant (K) and lower temperature threshold (T_0) values for the immature stages of *E. larvarum* utilizing two linear models. The ordinary model produced a higher thermal constant estimate and a lower T_0 estimate compared to the Ikemoto model. Additionally, the Ikemoto model exhibited a higher r^2_{adj} than the other linear model, indicating a slightly greater confidence in the parameter estimates provided by this model.

The nonlinear models for the total developmental time of *E. larvarum* were assessed and ranked by AIC criterion (Table 4). According to AIC rankings, the Performance-2, Beta, Janisch/Kontodimas, Analytis-1 and Analytis 3/Kontodimas models provided more accurate descriptions of the temperature-dependent developmental rates of *E. larvarum* total immature stages compared to others (Table 5).

The lower temperature threshold (T_0) for the total immature stages of the parasitoid was estimated using the Beta nonlinear model, yielding a result consistent with that obtained from the Ikemoto linear model. On the other hand, the low temperature thresholds estimated by Analytis-1 and Analytis-3/Kontodimas were approximately equivalent to the estimate provided by the ordinary linear model. The maximum value of this parameter was estimated by the Performance-2 nonlinear model.

The upper temperature threshold (T_{max}) values were overestimated, and none of the above-mentioned nonlinear models did not offer a realistic and precise estimate of this crucial temperature. The T_{max} values estimated by these models for total immature stages were between 43 and 45 °C, which are higher than the observed data because eggs were not able to hatch at 35 °C.

In Table 5, the observed development time was compared to the development time estimated by the five best nonlinear models at six constant temperatures. Notable point in this comparison is the clear proximity between the estimated and observed development time values. Figures 1 and 3 illustrate the relationship between temperature and the developmental rate of total immature stages of *E. larvarum*, as modeled by the ordinary linear model and the five best nonlinear models, respectively. Additionally, Figure 2 presents the effect of temperature on the developmental time of total immature stages of *E. larvarum* based on the Ikemoto linear model.

Fastest developmental temperature (T_{fast}) values calculated by fitted nonlinear models for *E. larvarum* are displayed in Table 6. The estimated T_{fast} values derived from the Performance-2 and Janisch/Kontodimas models were in close accordance with the observed T_{fast} .

DISCUSSION

To the best of our knowledge, no previous studies have estimated the thermal requirements for the immature *E. larvarum* development. Therefore, our findings provide fundamental information on the biology of this parasitoid which will result in its more successful application as an efficient biocontrol agent against different lepidopterous defoliators in both forest and agricultural ecosystems.

In this study, development was observed across all temperatures except at 35 °C, showing that this temperature lies beyond the conductive range for the development of *E. larvarum*. Combining calculates from both linear and nonlinear models offered an accurate prediction of the first appearance of *E. larvarum* adults in forest and agricultural ecosystems. This analysis revealed that this parasitoid could develop within a temperature range of 15–34°C, a favorable feature for its potential role as a biological control agent in management programs. The extensive geographic distribution of *E. larvarum* across various provinces of Iran, each with diverse climatic conditions, is a clear witness of this claim (Modarres Awal, 1994; Karimpour *et al.*, 2005; Saeidi, 2011; Ghahari, 2017; Karami *et al.*, 2023).

The results obtained demonstrated a significant impact of temperature on the developmental time of this parasitoid. The duration of total immature stages exhibited a negative correlation with temperature up to 32.5 °C, and then increased. Conversely, the development rate increases as the temperature rises, reaching its peak and subsequently declining to zero at the upper temperature threshold (T_U) (Mirhosseini *et al.*, 2017).

The assessment of temperature thresholds and thermal constants for the development of natural enemies can considerably contribute to the choice of the most appropriate natural enemy to be utilized in various environmental circumstances (Perdikis and Lykouressis, 2002).

The observed linear relationship between temperature and the development rate of *E. larvarum* across the 15–32.5 °C range indicates strong thermal dependence in the biology of this parasitoid. Estimation of the lower temperature threshold (T_0) and the thermal constant (K) using both the ordinary and Ikemoto linear models confirmed this trend. However, the Ikemoto model demonstrated greater accuracy as evidenced by a higher R^2_{adj} coefficient, for modeling temperature-dependent development in this species. These findings align with previous studies on other natural enemies, where the Ikemoto model often provides a better predictive performance (Aghdam *et al.*, 2009; Jafari *et al.*, 2022). The reliable estimation of T_0 and K are essential for predicting field development rates and optimizing mass-rearing or biological control strategies under varying thermal conditions.

The value of the lower temperature threshold (T_0) for the *E. larvarum* immature stages was found to be 9.7 °C using the Ikemoto model which was in agreement with Foerster and Doetzer (2002) who reported 9.3 °C as a lower threshold temperature from eggs to adulthood for another tachinid, *Peleteria robusta* (Wiedman). Lower values for the low temperature threshold were estimated by Walker (2011) and Park *et al.* (2016) for *Chaetophthalmus dorsalis* (Malloch) (7.3 and 7.4 °C for females and males, respectively) and *Exorista japonica* (Townsend, 1909) (7.8 °C), respectively. The thermal constant calculated with the Ikemoto linear model for total development of *E. larvarum* (292.7 DD) was lower than previously reported values for other tachinid flies: *E. japonica* (370.4 DD) (Park *et al.*, 2016), *P. robusta* (457.5 DD) (Foerster and Doetzer, 2002), and *C. dorsalis* (366.7 and 333.3 DD for females and males, respectively) (Walker, 2011). The differences among their results and our reports may be due to the difference in the host and parasitoid species, the difference in rearing techniques and experimental conditions, along with differences in data analysis procedure.

The temperature maximizing developmental rate, commonly termed the fastest developmental temperature (T_{fast}), may not necessarily align with the temperature that maximizes overall population fitness, as the benefits of accelerated development may be counterbalanced by increased mortality rates. In the present study, the maximum developmental rate was recorded at 32.5 °C among all examined temperatures, and can be intended as the observed fastest developmental temperature. Some of the nonlinear models can be applied directly to calculate T_{fast} (Kontodimas *et al.*, 2004; Mojib-Haghghadam *et al.*, 2019).

The T_{fast} values calculated by Performance-2 and Janisch/Kontodimas for the parasitoid immature stages were 33.2 °C and 31.4 °C, respectively. These two models appear to offer realistic values of T_{fast} compared with other models. In other words, T_{fast} denotes the temperature at which the developmental rate reaches its maximum and the developmental time is minimized (Moallem *et al.*, 2017; Shamakhi *et al.*, 2018). From a biological control perspective, a shorter pre-adult period is considered advantageous for agents such as parasitoids, as it reduces generation time and can enhance population growth potential. This trait is particularly valuable for improving the efficiency and rapid establishment of parasitoid populations in the field (Milenovic *et al.*, 2023; Wyckhuys *et al.*, 2024).

To choose the best nonlinear model(s) for describing temperature-dependent developmental rates of *E. larvarum* total immature stages, the adjusted R^2 (R^2_{adj}), Akaike Information Criterion (AIC), and estimated temperature-related biological parameters (Akaike, 1974; Kvalseth, 1985; Kontodimas *et al.*, 2004) were used. As the best statistical criterion to validate models, the lowest value of AIC was used to rank the fitted nonlinear models (Akaike, 1974; Larranaga and Bielza, 2014). Moreover, the nonlinear models are frequently verified by observed developmental data and biological criteria (Zahiri *et al.*, 2010; Soltani Orang *et al.*, 2014; Aghdam and Nemati, 2020; Yazdanpanah *et al.*, 2022). In the present research, the observed development time was compared to the estimated development time because a usual manner for evaluating the precision of calculated crucial temperatures is according to their comparison with experimental data (Kontodimas *et al.*, 2004). Notable point in this comparison is a clear-cut close between the estimated development time values and the observed development time values, from which, it can be concluded that the values estimated by these models are accurate and reliable to a large extent. According to our findings, the nonlinear Performance-2, Beta, Janisch/Kontodimas, Analytis-1, and Analytis 3/Kontodimas models best described the developmental rate of *E. larvarum*. The calculated T_{fast} by Performance-2 model was similar to the observed T_{fast} (32.5 °C).

In conclusion, the results demonstrated that *E. larvarum* could be an effective biocontrol agent in forest and agricultural ecosystems over a vast range of temperatures. Evidently, parameters calculated in the present research were derived in the laboratory under totally determined climatic circumstances, despite the reality that parasitoids are subjected to more complicated and oscillating circumstances in their natural environment. However, results from this study can offer a starting point for extending a model that could be employed to the Iranian population

of *E. larvarum* and if they to be applied in association with other ecological data can be invaluable in the development and implementation of pest management programs.

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Table 1. Linear and nonlinear models for fitting to the development rate of *Exorista larvarum* as a function of temperature.

Model	Equation	Reference
Ordinary linear model	$R(T) = a + bT$	(Campbell et al. 1974)
Ikemoto linear model	$DT = K + T_0 D$	(Ikemoto and Takai 2000)
Pradhan-Taylor	$R(T) = R_m \times \exp\left[\frac{-1}{2} \left(\frac{T - T_m}{T_\sigma}\right)^2\right]$	(Pradhan 1945, Taylor 1981)
Davidsons logistic	$R(T) = \frac{K}{1 + e^{(a-bT)}}$	(Davidson 1942, 1944)
Logan-6	$R(T) = \psi [e^{\rho T} - e^{(\rho T_U - \tau)}], \quad \tau = \frac{T_U - T}{\Delta_T}$	(Logan et al. 1976)
Hilbert and Logan	$R(T) = \psi \left[\frac{(T - T_0)^2}{((T - T_0) + D^2)} \right] - e^{-\left(\frac{T_U - (T - T_0)}{\Delta_T}\right)}$	(Hilbert and Logan 1983)
Lactin-1	$R(T) = e^{\rho T} - e^{\left(\rho T_U - \frac{T_U - T}{\Delta_T}\right)}$	(Lactin et al. 1995)
Lactin-2	$R(T) = e^{\rho T} - e^{\left(\rho T_U - \frac{T_U - T}{\Delta_T}\right)} + \lambda$	(Lactin et al. 1995)
Logan-10	$R(T) = a \left[\frac{1}{1 + K e^{-\rho T}} - e^{-\tau} \right], \quad \tau = \frac{T_U - T}{\Delta_T}$	(Logan et al. 1976)
Analytis-1	$R(T) = P \delta^n (1 - \delta)^m, \quad \delta = \frac{T - T_0}{T_U - T_0}$	(Analytis 1977, 1980)
Analytis-2	$R(T) = [P \delta^n (1 - \delta)]^m, \quad \delta = \frac{T - T_0}{T_U - T_0}$	(Analytis 1977, 1980)
Analytis-1/Allahyari	$R(T) = P \delta^n (1 - \delta^m), \quad \delta = \frac{T - T_0}{T_U - T_0}$	(Allahyari 2005, Zahiri et al.2010)
Analytis-3	$R(T) = a(T - T_0)^n (T_U - T)^m$	(Analytis 1977, 1980)
Briere-1	$R(T) = aT(T - T_0)(T_U - T)^{\frac{1}{2}}$	(Briere et al. 1999)
Briere-2	$R(T) = aT(T - T_0)(T_U - T)^{\frac{1}{n}}$	(Briere et al. 1999)
Analytis-3/Kontodimas	$R(T) = a(T - T_0)^2 (T_U - T)$	(Kontodimas et al. 2004)

Janisch/Kontodimas

$$R(T) = \frac{2}{DK(T - T_{opt})^{-\lambda(T - T_{opt})_{\min}}}$$

(Janisch 1932, Kontodimas et al. 2004)

Janisch/Rochat

$$R(T) = \frac{2c}{a^{(T - T_u)} + b^{(T_u - T)}}$$

(Rochat and Gutierrez 2001)

Sharpe and DeMichele

$$R(T) = \frac{T e^{(\phi - \Delta H_A^\ddagger / T) / R}}{1 + e^{(\Delta S_L - \Delta H_L / T) / R} + e^{(\Delta S_H - \Delta H_H / T) / R}}$$

(Sharpe and DeMichele 1977)

Sh and
DeMichele/Schoolfield

$$R(T) = \frac{\rho_{(25^\circ C)} \frac{T}{298} \exp[\frac{\Delta H_A^\ddagger}{R} (\frac{1}{298} - \frac{1}{T})]}{1 + \exp[\frac{\Delta H_L}{R} (\frac{1}{T_{1/2L}} - \frac{1}{T})] + \exp[\frac{\Delta H_H}{R} (\frac{1}{T_{1/2H}} - \frac{1}{T})]}$$

(Schoolfield et al. 1981)

Sh and
DeMichele/Kontodimas

$$R(T) = \frac{T \exp(a - b/T)}{1 + \exp(c - d/T) + \exp(f - g/T)}$$

(Kontodimas et al. 2004)

Polynomial (cubic)

$$R(T) = a_0 T^3 + a_1 T^2 + a_2 T + a_3$$

(Harcourt and Yee 1982)

SSI model

$$R(T) = \frac{\rho_\phi \frac{T}{T_\phi} \exp[\frac{\Delta H_A}{R} (\frac{1}{T_\phi} - \frac{1}{T})]}{1 + \exp[\frac{\Delta H_L}{R} (\frac{1}{T_L} - \frac{1}{T})] + \exp[\frac{\Delta H_H}{R} (\frac{1}{T_H} - \frac{1}{T})]}$$

(Ikemoto 2005, 2008)

Performance-1

$$R(T) = c(1 - e^{-K_1(T - T_0)})(1 - e^{K_2(T - T_u)})$$

(Shi et al. 2011)

Performance-2

$$R(T) = m(T - T_0)(1 - e^{K_2(T - T_u)})$$

(Shi et al. 2011)

Wang

$$R(T) = \frac{m[1 - \exp(K_1(T - T_0))][1 - \exp(K_2(T - T_u))]}{1 + \exp(-c(T - T_0))}$$

(Wang et al. 1982)

Ratkowsky

$$\sqrt{R(T)} = c(T - T_0)(1 - e^{K(T - T_u)})$$

(Ratkowsky et al. 1983)

Beta

$$R(T) = r_m \left(\frac{T_u - T}{T_u - T_{opt}} \right) \left(\frac{T - T_0}{T_{opt} - T_0} \right)^{\frac{T_{opt} - T_0}{T_u - T_{opt}}}$$

(Yin et al. 1995)

T = Temperature, R = Development rate, D = Development time, T_0 = Lower temperature threshold, T_u = Upper temperature threshold, T_{opt} = Optimum temperature (equals T_{fast} in the text). Other notations are model constants. For more details on the concepts of the parameters see Mirhosseini *et al.* (2017).

Table 2. Developmental time in days (mean \pm SE) of *Exorista larvarum* reared on *Galleria mellonella* at seven constant temperatures.

Temperature (°C)	Total developmental time (day)	N
15	55.06 \pm 0.37 ^a	52
20	23.04 \pm 0.24 ^b	76
26	17.43 \pm 0.15 ^c	61
30	15.92 \pm 0.11 ^{cd}	75
32.5	15.13 \pm 0.13 ^d	52
34	15.33 \pm 0.33 ^d	3
35	No eggs hatched	ND

N, sample size; Means followed by different letters in the column of total developmental time are significantly different (Tukey's test; $P < 0.05$).

Table 3. Parameters of two linear regression models and r^2 values for temperature-dependent developmental rates *Exorista larvarum* reared on *Galleria mellonella*.

Method	Equation	r^2_{adj}	P	T_0 (°C)	K (DD)
Ordinary	$R = -0.013075 + 0.002568T$	0.88	<0.01	5.09	389.41
Ikemoto and Takai	$DT = 292.744 + 9.7275D$	0.90	<0.01	9.73	292.74

T_0 , lower temperature threshold (no measurable development is detected); K, thermal constant (total effective temperature).

Table 4. All fitted nonlinear models for temperature-dependent total developmental time of *Exorista larvarum* reared on *Galleria mellonella*.

Model	SSE	R^2_{adj}	AIC	Rank
Pradhan-Taylor	0.007	0.92	-3416.36	6
Davidsons logistic	—	—	—	—
Logan-6	—	—	—	—
Hilbert and Logan	—	—	—	—
Lactin-1	0.011	0.88	-3273.94	10
Lactin-2	0.008	0.91	-3382.98	8
Logan-10	—	—	—	—
Analytis-1	0.006	0.93	-3452.49	4
Analytis-2	—	—	—	—
Analytis-1/Allahyari	—	—	—	—
Analytis-3	—	—	—	—
Briere-1	0.007	0.92	-3409.34	7
Briere-2	—	—	—	—
Analytis-3/Kontodimas	0.006	0.93	-3450.59	5
Janisch/Kontodimas	0.006	0.94	-3476.04	3
Janisch/Rochat	0.008	0.90	-3350.90	9
Sharpe and DeMichele	—	—	—	—
Sh and DeMichele/Schoolfield	—	—	—	—
Sh and DeMichele/Kontodimas	—	—	—	—
Polynomial (cubic)	—	—	—	—
SSI model	—	—	—	—
Performance-1	—	—	—	—
Performance-2	0.005	0.94	-3505.10	1
Wang	—	—	—	—
Ratkowsky model	—	—	—	—
Beta model	0.006	0.94	-3481.40	2

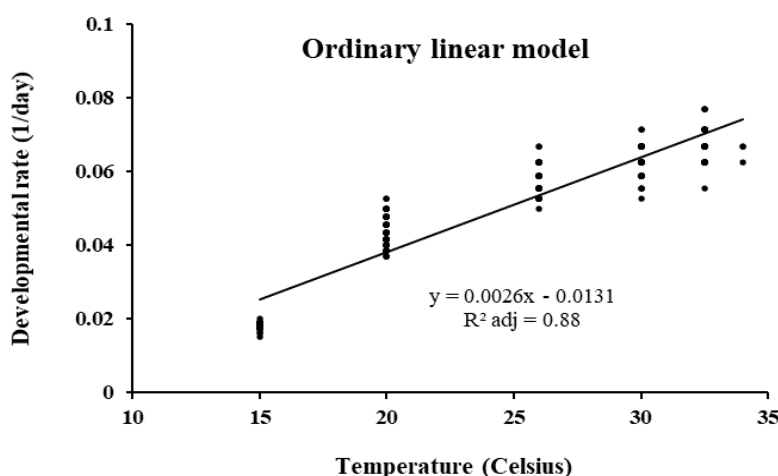
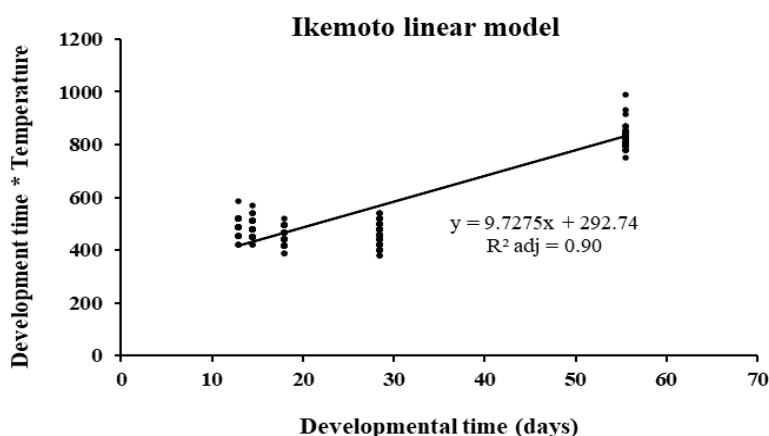
Table 5. Parameters of the five best nonlinear models for temperature-dependent developmental rates of *Exorista larvarum* reared on *Galleria mellonella*.

Rank	Model	Parameter	Values	Temperature	Observed development time	Estimated development time
1	Performance-2	K_2	0.0444 (0.001582, 0.08722)	15	55.06	51.31
		T_0 (°C)	11.26 (10.65, 11.86)	20	23.04	24.10
		T_U (°C)	45 (40.86, 49.14)	26	17.43	16.82
		m	0.00708 (0.003448, 0.01071)	30	15.92	15.50
				32.5	15.13	15.61
				34	15.33	16.07
2	Beta	T_0 (°C)	9.662 (8.661, 10.66)	15	55.06	51.18
		T_U (°C)	45	20	23.04	24.15
		T_{opt} (°C)	30.35 (30.03, 30.67)	26	17.43	16.65
		r_m	0.06463 (0.06398, 0.06529)	30	15.92	15.48
				32.5	15.13	15.77
				34	15.33	16.38
3	Janisch/Kontodimas	D_{min}	24.52 (24.08, 24.95)	15	55.06	48.41
		K	0.01503 (0.0127, 0.01736)	20	23.04	24.52
		λ	0.2211 (0.2089, 0.2333)	26	17.43	16.67
		T_{opt} (°C)	20 (fixed at bound)	30	15.92	15.59
				32.5	15.13	15.57
				34	15.33	15.69
4	Analytis-1	P	0.5086 (0.1284, 0.8888)	15	55.06	47.29
		T_0 (°C)	5.626 (4.04, 7.212)	20	23.04	24.76
		T_U (°C)	45 (35.87, 54.13)	26	17.43	16.85
		m	1.14 (0.3958, 1.883)	30	15.92	15.42
		n	2 (fixed at bound)	32.5	15.13	15.61
				34	15.33	16.20
5	Analytis-3/Kontodimas	T_0 (°C)	5.013 (4.335, 5.69)	15	55.06	46.40
		T_U (°C)	43.92 (42.83, 45.01)	20	23.04	24.91
		a	7.472e-06 (6.492e-06, 8.451e-06)	26	17.43	16.96
				30	15.92	15.40
				32.5	15.13	15.51
				34	15.33	16.06

The values in the parentheses represent 95% confidence intervals. For more details on concepts of the parameters see Mirhosseini *et al.* (2017).

Table 6. T_{fast} estimated by fitted nonlinear models for *Exorista larvarum* reared on *Galleria mellonella*.

Model	T_{fast}	Developmental time (day)
Pradhan-Taylor	30.7	15.37
Lactin-1	30.4	21.56
Lactin-2	31.1	14.96
Analytis-1	30.7	15.38
Briere-1	30.9	15.19
Analytis-3/Kontodimas	31	15.34
Janisch/Kontodimas	31.4	15.54
Janisch/Rochat	31	15.28
Performance-2	33.2	15.79
Beta	30.3	15.47

**Fig. 1.** Observed total immature stages development rate of *Exorista larvarum* reared on *Galleria mellonella* (dots) and the ordinary linear model (line).**Fig. 2.** Observed total immature stages development time of *Exorista larvarum* reared on *Galleria mellonella* (dots) and the Ikemoto linear model (line).

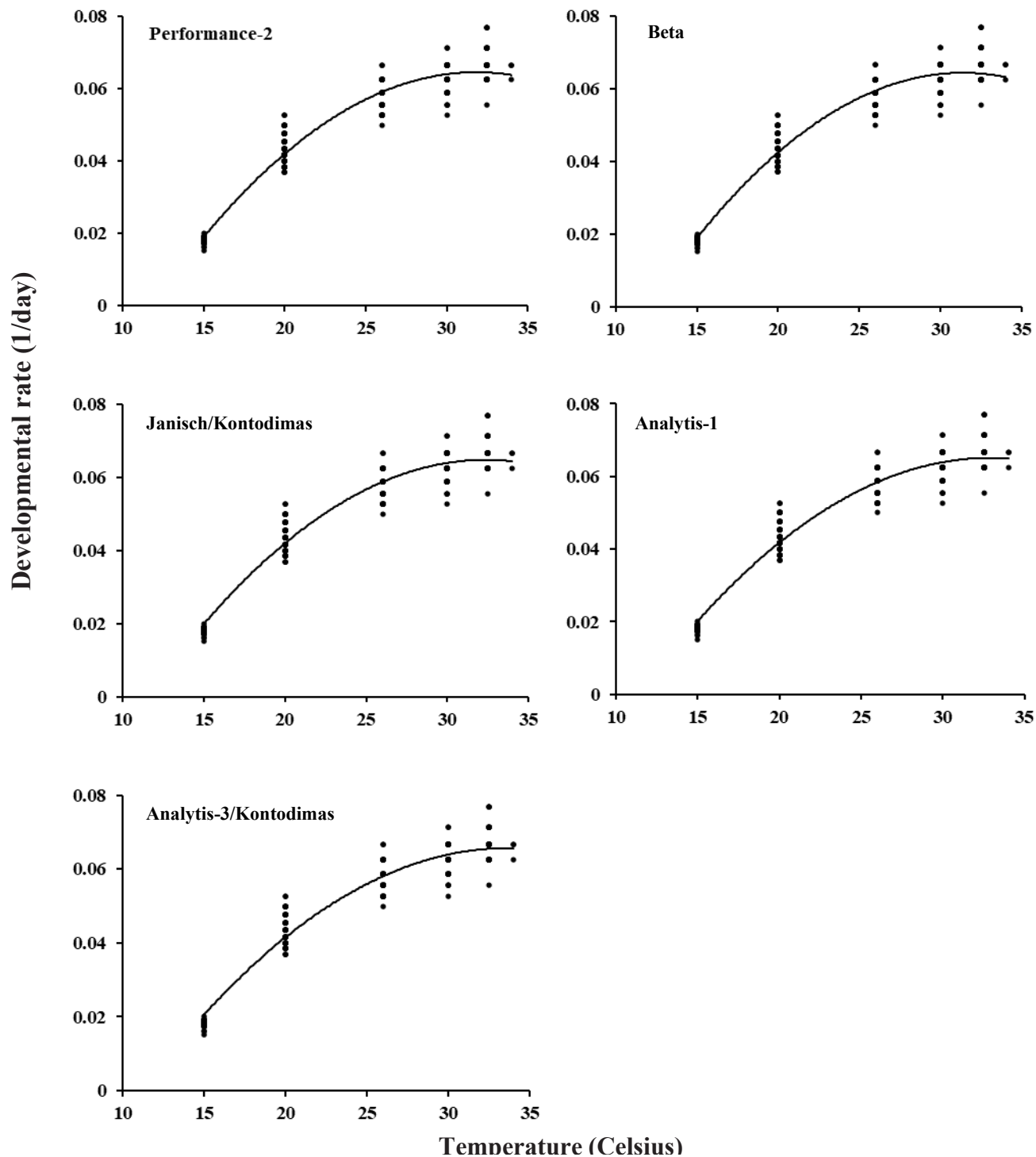


Fig. 3. Observed total immature stages development rate of *Exorista larvarum* reared on *Galleria mellonella* (dots) and the five best nonlinear models (lines).