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Abstract

Temperature greatly affects the developmental duration of insects at their different stages, and many mathematical models exist for describing their temperature-dependent developmental rates. It is important to choose a suitable model to predict outbreaks of pest insects under climate change. However, previous comparisons among these models were usually based on a single species. In the present study, we compared the six nonlinear models (the Briére-1, Briére-2, Lactin, Performance-2, beta, and Ratkowsky models) based on the goodness of fit and the trade-off between the model's goodness of fit and structural complexity, using 10 temperature-dependent developmental rate datasets on insects to make the conclusions general. We found that the square root model (i.e., the Ratkowsky model) fitted all datasets well, and the curve shape produced by this model also approximates the curve shape of thermodynamically based mathematical models. The square root model was originally derived to be applicable to the growth rates of bacteria, and until now it has been generally ignored in entomology. We were mainly concerned with the predicted results obtained by using this model on observations of temperature-dependent developmental rates. We found that the square root model described well the pooled developmental rates in the low-, mid-, and high-temperature ranges, and we believe that it merits wider use in entomology.

Key words: goodness of fit, nonlinear, pest outbreak, square root model, structural complexity

Evidence has demonstrated that temperature has a significant influence on the developmental rate of insects (Uvarov 1931, Campbell et al. 1974). Under global climate change, pest outbreaks exhibit more complex dynamics and become more difficult to be predicted. To predict the developmental duration of important agricultural and forest pest insects exposed to different temperatures, many mathematical models have been proposed (e.g., Logan et al. 1976; Sharpe and DeMichele 1977; Schoolfield et al. 1981; Wang et al. 1982; Lactin et al. 1995; Brière et al. 1999; Ikemoto 2008; Shi et al. 2011; Régnière et al. 2012; Wang et al. 2013). These models have also been tried in the study of the effect of temperature on the growth rate of ectotherms (e.g., insects, mites, spiders, crabs, shrimps, fishes). Yin et al. (1995) proposed a beta function to reflect the effect of temperature on the developmental rate of crops. Ratkowsky et al. (1983) proposed a square root model to predict the effect of temperature on the growth rate of bacterial cultures. However, the latter two models have received little attention in entomological investigations. The previous studies in entomological research frequently compared the Logan, Lactin, and Briére models using a single species. From different studies, the conclusion as to which was the best model was usually different. In addition, the majority of previous studies used small sample sizes ranging from five to eight temperatures, which made the estimates of the parameters of the nonlinear models less precise.

In the present study, we chose several nonlinear models and data of temperature-dependent developmental rate with large sample sizes to examine the models' trade-off between goodness of fit and structural complexity. We attempted to find a general model that could well describe the majority of datasets on temperature-dependent developmental rates of insects. This work is also motivated by the studies of ontogenetic growth equation for animals and plants. A beta sigmoid growth equation obtained from the integral of the beta function has showed better fitting flexibility than some traditional growth models such as the exponential, Gompertz,

Logistic, and von Bertalanffy models (Yin et al. 2003, Voorend et al. 2014, Shi et al. 2016). Thus, it is valuable to further compare the existing temperature-dependent developmental or growth models to find a better model than the beta function. Then we can obtain more new candidate ontogenetic growth models by using the integral form for the developmental or growth equation.

Materials and Methods

Data

Ten datasets of temperature-dependent developmental rates of insects were chosen (among which Sample 2 is a predatory mite, not an insect species). Table 1 lists the studied species, developmental stages, sample sizes, and data sources. We also compared the fitted results by using the mean and raw data of developmental rates of female fruit flies (*Drosophila buzzatii* Patterson & Wheeler; i.e., Sample 10).

Models

In the present study, we used a total of six nonlinear models that all have the "conceptual" lower and upper developmental thresholds (T_1 and T_2) at which developmental rates equal zero.

(i) Briére-1 equation (Brière et al. 1999):

$$r = aT(T - T_1)(T_2 - T)^{1/2} \qquad (1)$$

Here, r represents developmental rate at temperature T; a is a constant; T_1 and T_2 represent "conceptual" lower and upper developmental thresholds at which developmental rates equal zero.

(ii) Briére-2 equation (Brière et al. 1999):

$$r = aT(T - T_1)(T_2 - T)^{1/b} \qquad (2)$$

Here, the parameters are the same as those in the Briére-1 equation except an additional parameter b, which makes the curve fitting more flexible. Then the Briére-1 equation is substantially a special case of the Briére-2 equation when $b = 2$.

(iii) Lactin equation (Lactin et al. 1995):

$$r = \lambda + e^{\rho T} - e^{\rho T_u - (T_u - T)/\delta} \qquad (3)$$

Here, λ, ρ, T_u, and δ are constants. And T_u is defined as the upper "lethal" temperature, which is higher than the "conceptual" upper developmental threshold (Lactin et al. 1995). In the Lactin equation, there are no T_1 and T_2 parameters. However, the curve produced by

the Lactin equation has two intersections with the X-axis (i.e., Temperature-axis). We can obtain T_1 and T_2 by a numerical method.

(iv) Performance-2 equation (Shi et al. 2011, Wang et al. 2013):

$$r = c(T - T_1)\left(1 - e^{K(T - T_2)}\right) \qquad (4)$$

Here, c and K are constants. This equation supersedes the Performance-1 equation (Wang et al. 2013), which has more parameters and produces a very similar curve shape to the Performance-2 equation.

(v) Beta equation (Yin et al. 1995, 2003; Shi et al. 2016):

$$r = r_m \left(\frac{T_2 - T}{T_2 - T_m}\right)\left(\frac{T - T_1}{T_m - T_1}\right)^{\frac{T_m - T_1}{T_2 - T_m}} \qquad (5)$$

Here, r_m represents the maximal developmental rate at temperature T_m. Note: all parameters in the beta equation have clear meanings.

(vi) Ratkowsky equation (Ratkowsky et al. 1983):

$$\sqrt{r} = c(T - T_1)\left(1 - e^{K(T - T_2)}\right) \qquad (6)$$

This equation looks like the Performance-2 equation except there is a square root of r in the leaf-hand side of equation. Thus, this equation is often called the square root equation.

Model Evaluation

In order to compare the goodness of fit and the trade-off between model's goodness of fit and structural complexity among these six nonlinear models, we used the residual sum of squares (RSS), coefficient of determination (R^2), adjusted coefficient of determination (R^2_{adj}), root mean square error (RMSE), and corrected Akaike information criterion (AIC_c).

$$RSS = \sum_{i=1}^{n} (r_i - \hat{r}_i)^2 \qquad (7)$$

Here, n represents the sample size; r_i represents the i-th observation of developmental rate, and r_i with a hat represents the predicted developmental rate.

$$R^2 = 1 - \frac{\sum_{i=1}^{n} (r_i - \hat{r}_i)^2}{\sum_{i=1}^{n} (r_i - \bar{r}_i)^2} \qquad (8)$$

Table 1. Ten datasets of temperature-dependent developmental rates of insects

Sample	Species	Order: Family	Developmental stage	Sample size	Source
1	*Helicoverpa armigera* Hübner	Lepidoptera: Noctuidae	Pupa	23	Wu et al. (2009)
2	*Kampimodromus aberrans* Oudemans	Acari: Phytoseiidae	Egg + larva + 1st–2nd nymphs	9	Broufas et al. (2007)
3	*Toxorhyynchites brecipalpis* Theobald	Diptera: Culicidae	Egg	19	Trpis (1972)
4	*Bactrocera dorsalis* Hendel	Diptera: Tephritidae	Egg	19	Messenger and Flitters (1958)
5	*Aedes aegypti* L.	Diptera: Culicidae	Larva	15	Gilpin and McClelland (1979)
6	*Bemisia tabaci* (B-biotype) Gennadius	Hemiptera: Aleyrodidae	From egg to adult	7	Xiang et al. (2007)
7	*Lipaphis erysimi* Kaltenbach	Hemiptera: Aphididae	From egg to adult	12	Liu and Meng (2000)
8	*Myzus persicae* Sulzer	Hemiptera: Aphididae	From egg to adult	11	Liu and Meng (1999)
9	*Epilachna varivestis* Mulsant	Coleoptera: Coccinellidae	Larva	8	Shirai and Yara (2001)
10	*Drosophila buzzatii* Patterson & Wheeler	Diptera: Drosophilidae	From egg to adult	9–1,204[a]	de Jong (2010)

[a] 9 is the number of mean data of developmental rates, and 1,204 is the number of raw data of developmental rates.

Here, r_i with a dash represents the mean of the observed developmental rates. And the adjusted coefficient of determination is as follows:

$$R^2_{\text{adj}} = 1 - \frac{n-1}{n-p}\left(1 - R^2\right) \qquad (9)$$

Here, p represents the number of parameters in a nonlinear model including one for the error term. We also used the RMSE because the magnitude of the RMSE can be considered to be the "average deviation" between the observed data and the predicted values.

$$\text{RMSE} = \sqrt{\text{RSS}/(n - p + 1)} \qquad (10)$$

$$\text{AIC}_c = -2L + 2pn/(n - p - 1) \qquad (11)$$

where

$$L = -\frac{n}{2}\ln\left(\frac{\text{RSS}}{n}\right) \qquad (12)$$

We used RSS and R^2 as the indicators to evaluate the model's goodness of fit, and used R^2_{adj}, RMSE, and AIC_c as the indicators to evaluate the trade-off between a model's goodness of fit and structural complexity.

The "nlinfit" function in Matlab 6.5 was used to carry out the nonlinear fitting. For robust estimation, "nlinfit" uses an iterative reweighted least squares algorithm. At every iteration, the robust weights are recalculated based on each observation's residual from the previous iteration. These weights downweight outliers, so that their influence on the fit is decreased. Iterations continue until the weights converge. We provided the Matlab procedures for carrying out the nonlinear fitting for a given dataset of temperature-dependent developmental rates (see Supp Material 1 [online only] for details).

Results

Supp Table 1 (see Supp Material 2 [online only] for details) shows the comparative results. From the viewpoint of a trade-off between the model's goodness of fit and structural complexity (based on the calculated R^2_{adj} or RMSE or AIC_c), the Briére-2 equation was better than the Briére-1 equation in five cases with larger sample size ($n > 10$), but the latter performed better for the datasets with smaller sample size ($n < 10$). However, the Briére-2 equation had a better goodness of fit than the Briére-1 equation for all datasets investigated. Because of an additional parameter, b, the Briére-2 equation is more flexible in producing a curve shape. From Sample 10 with a small sample size of mean data, we found that the Briére-1 equation obtained a better trade-off between the model's goodness of fit and structural complexity than the Briére-2 equation; however, it is worse than the Briére-2 equation when using the raw data. Except for Samples 4 and 7, the Ratkowsky equation had a better goodness of fit than the Briére-2 equation for all other samples. It was also better than the Briére-2 equation based on the calculated R^2_{adj}, RMSE, and AIC_c. Although the beta equation fitted the data of the observed developmental rates well, it was demonstrated to be no better than the Ratkowsky equation from the point of view of goodness of fit or from the trade-off between model's goodness of fit and structural complexity. We also found that the curve shape produced by the beta equation was more similar to that produced by the Ratkowsky equation, relative to the others. For the remaining two equations (i.e., the Lactin and Performance-2 equations), the goodness of fit or the trade-off between model's goodness of fit and

structural complexity was worse than the Briére-2 equation or the Ratkowsky equation. The data showed that in the mid-temperature range, a perfect linear relationship between temperature and developmental rate did not exist. However, the Lactin and Performance-2 equations had assumed a very approximate linear relationship between them. Thus, they could not perform better than the others for most datasets.

The lower and upper developmental thresholds are a matter of interest to some investigators, because they want to know the predicted critical temperatures where insects stop developing. Traditionally, the linear fitting was used to calculate the lower developmental threshold by using the developmental rate data in the mid-temperature range. The intersection between the straight line and the X-axis is reckoned as the lower developmental threshold. For estimating the upper developmental threshold, the Logan, Briére, Lactin, and Performance equations are usually used. From the model's goodness of fit or the trade-off between model's goodness of fit and structural complexity, the Lactin equation was better than the Performance-2 equation for each species investigated. The Briére-1 and Briére-2 equations provided an approximate estimate on the "conceptual" upper developmental threshold, but their estimates on the "conceptual" lower developmental threshold were lower than the estimates by using the Lactin and Performance-2 equations. The beta and Ratkowsky equations described the effect of temperature on the developmental rates of insects in the mid-temperature range better than the Lactin and Performance-2 equations.

Supp Figs. 1–11 (see Supp Material 3 [online only] for details) visually exhibit the fitted results using these six nonlinear equations to 10 datasets. There are nine insect species and one mite species (i.e., Sample 2). Supp Figs. 10 and 11 (online only) described the same insect species (*D. buzzatii*), but with different sample sizes. Supp Fig. 10 (online only) used the mean data, whereas Supp Fig. 11 (online only) used the raw data. The open circles represent the observations of developmental rates, and the curves represent the predicted developmental rates based on different nonlinear models. For every species, the aforementioned six nonlinear models were used to fit the data of temperature-dependent developmental rates, respectively.

Discussion

As an empirical method, the predicted lower developmental threshold by using the linear equation in the mid-temperature range usually approximates its actual lower terminating temperature for development. However, the Briére-1, Briére-2, beta, and Ratkowsky equations only provide "conceptual" lower and upper developmental thresholds, and the estimates of these two extreme temperatures by these nonlinear equations do not accord with the actual observed threshold temperatures. Although the Lactin and Performance-2 equations can provide the approximate estimates to the actual developmental thresholds, these two equations cannot reflect an approximate exponential growth relationship between temperature and developmental rate in the low-temperature range (Uvarov 1931, Campbell et al. 1974). If the data of developmental rates at low temperatures are lacking, the Lactin and Performance-2 can fit the data well (see Sample 6 in Supp Fig. 6 [online only]). However, these two equations cannot overall reflect the nonlinear relationship between temperature and pooled developmental rates in the low- and mid-temperature ranges. We believe that these two nonlinear equations can do well on the condition that the data in the low-temperature range are lacking. Thus, we do not approve using the Lactin and Performance-2 equations to fit the data including the developmental rates in the low-temperature range. The Briére-1 and Briére-2
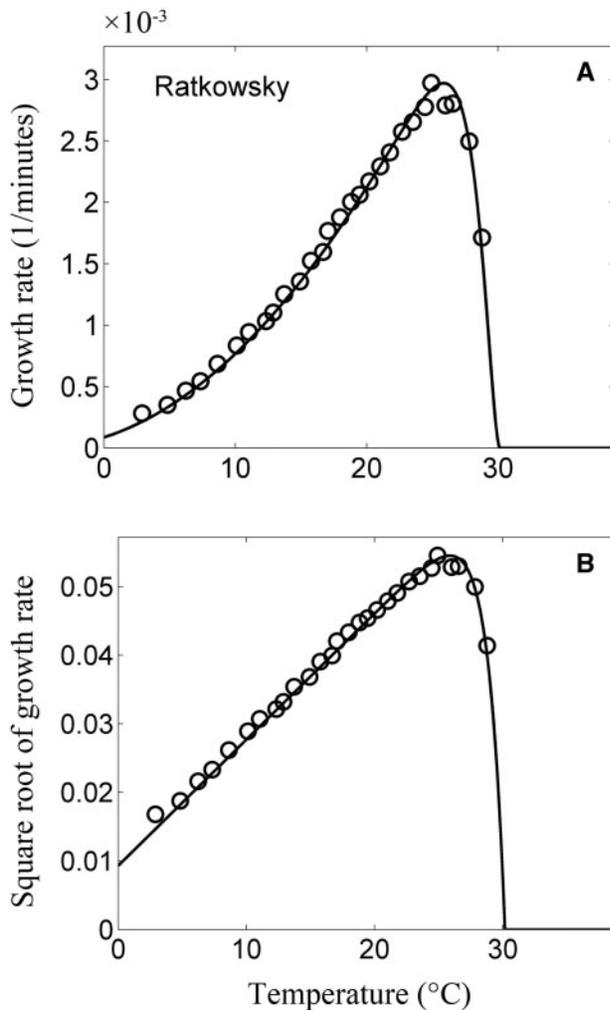
Fig. 1. Effect of temperature on the growth rate of *F. hibernum*. (**A**) Temperature-dependent growth rate. The small open circles represent the observed growth rates (1/min), and the curve represents the predicted growth rates at different temperatures. (**B**) Square root of growth rate.

developmental rates near the actual upper developmental threshold. However, we found that the degree of curvature of the Ratkowsky equation near the upper developmental threshold was very small when developmental rates in the high-temperature range exhibited a sharp drop with increased high temperatures (see Supp Figs. 1 and 4 [online only]). We also showed an example of growth rate of *Flavobacterium hibernum* McCammon, a lactose-utilizing bacterium from a freshwater Antarctic lake (Fig. 1; McCammon et al. 1988). In fact, the Ratkowsky equation has been demonstrated to apply to many other datasets of growth rates of bacteria (Ratkowsky et al. 2005), as that model was originally developed to describe the temperature dependence of bacterial growth. Schoolfield et al. (1981) consider that the temperature-dependent rate models are applicable to both developmental rate and growth rate of poikilotherms. The Logan model (Logan et al. 1976) is always used to describe the effect of temperature on the developmental rate of insects, and is also used for the growth rate of insects calculated from life table methods. Thus, it is feasible to introduce the Ratkowsky equation to the investigation of temperature-dependent developmental rate of insects, considering its good performance in fitting data.

In all the models, temperatures such as T_1 and T_2 should just be looked upon as mathematical symbols and not predictors of minimum or maximum temperatures of a range at which development can occur. For the square root model (i.e., the Ratkowsky model), Ratkowsky et al. have never maintained that these temperatures are anything more than notional (or notational) temperatures, and there is no organism on Planet Earth (bacterial, archaeal, eucaryotic) that we are aware of which can grow at temperatures approaching T_1 from above. That is, usually the true minimum observable temperature for growth is several degrees (°C or K) above the notional minimum temperature. At the upper end of the temperature scale, the difference between the notional maximum temperature T_2 and the observable maximum temperature T_{max} may be much smaller than at the lower end (perhaps as small as 1°C), so it is very difficult to get reliable data at this upper threshold temperature because of high mortality rates. Thus, we advocate that when using any of the six models, there should be no thoughts that these equations are doing anything more than possibly providing a good fit to existing data on temperature dependence of growth rate. The models simply do not incorporate a prediction of the range of temperature dependence.

Supplementary Data

Acknowledgments

equations also applied to many samples, but the latter was shown to be better than the former actually as a special case of the latter. We consider that the additional parameter (i.e., in the Briére-2 equation) is justified, making data fitting more flexible. The Briére-2 equation was almost applicable to all samples investigated. For Sample 9, the last datum was intentionally excluded to check the predicting abilities of different models. We found that the Briére-2, Lactin, and Performance-2 equations provided an impractical prediction for the developmental rate at the excluded temperature, whereas the beta and Ratkowsky equations provided acceptable predictions at this excluded temperature. In this case, we should approve the use of the Ratkowsky equation rather than the Briére-2 equation. In fact, the curve shape produced by the Ratkowsky equation approximates that produced by the SSI or ROR models based on thermodynamic theories (Ikemoto 2008, Ikemoto et al. 2013, Ratkowsky et al. 2005, Corkrey et al. 2012). These two thermodynamic equations also predicted a slightly concave curve in the high-temperature range. In practice, it is impossible to observe reliable developmental rates at temperatures near the upper developmental threshold because of high mortality at these temperatures. Thus, it is difficult to determine which model is most reasonable in predicting

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