A comparison of different thermal performance functions describing temperature-dependent development rates

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ABSTRACT

The impact of temperature on developmental duration of insects has been long kept a high profile in the studies of insect pests. The relationship between developmental rate, which is the reciprocal of developmental duration, is generally represented by a straight line over a range of moderate temperature; over two ranges of extreme temperature (i.e., low temperatures and high temperatures), the relationship cannot be accurately reflected by a straight line (Campbell et al., 1974). For describing the effect of constant temperature on developmental rate over the full range of temperature, some non-linear models were proposed. To analyze the effect of temperature on ectothermic performance, twelve non-linear functions, including Gaussian, Logan1, Logan2, Performance, Wang–Lan–Ding, Sharpe–Schoolfield, Ratkowsky, Brière1, Brière2, Weibull, modified Gaussian and exponentially modified Gaussian functions, are compared using the coefficient of determination, adjusted coefficient of determination, Akaike information criterion (AIC), Bayesian information criterion (BIC), corrected Akaike information criterion (AICC) and a new method best on a weighted average of the five listed indicators. These models were compared using the development rate data of two species of insects at the egg stage. We found that the Performance, Brière1 and Brière2 functions are all very suitable for explaining temperature-dependent development rates. The three functions both belong to the asymmetrical skew thermal performance curves, and show better goodness-of-fit than the symmetrical Gaussian function. The Performance function might be the best function, because it can reflect the linearity between temperatures and developmental rates below the optimal developmental temperature.

1. Introduction

Many experiments have proved that temperature plays a crucial role in developmental rates, and some functions have been proposed to describe the effects of temperature on insect developmental rates (e.g., Logan et al., 1976; Logan, 1988; Sharpe and DeMichele, 1977; Schoolfield et al., 1981; Taylor, 1981; Wang et al., 1982; Ratkowsky et al., 1983; Brière et al., 1999). These functions are often used in different investigations. Comparing these functions is valuable for predicting the effect of temperature on developmental rates, because we cannot judge which function is most suitable for describing temperature-dependent developmental rates without a comparison.

Smits et al. (2003) used the adjusted coefficient of determination to compare five functions: the Logan1, Logan2, Brière1, Brière2 and Ratkowsky functions (see Table 1), describing temperature-dependent development rates, and they concluded

that the second model proposed by Brière et al. (1999) was the best and that the Ratkowsky model et al. (1983) also exhibited good features. Angilletta Jr. (2006) compared another five thermal performance functions: the Gaussian, Quadratic, Weibull, modified Gaussian and exponentially modified Gaussian functions, by calculating their Akaike weights, and he concluded that the Gaussian function (Taylor, 1981) was the best because it had the highest Akaike weight. In fact, temperature-dependent developmental rates can be regarded as a kind of thermal performance (Huey and Stevenson, 1979; Huey and Kingsolver, 1989; Angilletta Jr. et al., 2002). With thermal performance, the curve of the development rate should be skewed (Huey and Kingsolver, 1989). Thus, the conclusion that the symmetrical Gaussian function is the best should be examined further.

In this paper, we employed temperature and development rate data extracted from some published papers to compare twelve functions by calculating the coefficient of determination, adjusted coefficient of determination, AIC, BIC and AICC. We combined these indicators into a single indicator using a weighted mean method in order to find which function is the best for describing the temperature-dependent development rate. Another aim of our

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Table 1
List of functions describing temperature-dependent development rates.

Function	
Gaussian	$a \exp\left[-\frac{1}{2}\left(\frac{T-b}{c}\right)^2\right]$
Logan1	$a\left[\exp(bT) - \exp\left(bc - \frac{c-T}{d}\right)\right]$
Logan2	$a\left[\frac{1}{1+k\exp(-bT)} - \exp\left(-\frac{c-T}{d}\right)\right]$
Performance	$k(1-\exp[-a(T-m)])(1-\exp[b(T-n)])$
Wang–Lan–Ding (W–L–D)	$k\frac{(1-\exp[-a(T-m)])(1-\exp[b(T-n)])}{1+\exp[-r(T-c)]}$
Sharpe–Schoolfield (S–S)	$\dfrac{k\frac{T}{298.16}\exp\left[\frac{c}{R}\left(\frac{1}{298.16}-\frac{1}{T}\right)\right]}{1+\exp\left[\frac{a}{R}\left(\frac{1}{m}-\frac{1}{T}\right)\right]+\exp\left[\frac{b}{R}\left(\frac{1}{n}-\frac{1}{T}\right)\right]}$
Ratkowsky	$(a(T-m)(1-\exp[b(T-n)]))^2$
Brière1	$aT(T-m)\sqrt{n-T}$
Brière2	$aT(T-m)(n-T)^{1/b}$
Weibull	$a\left(\frac{d-1}{d}\right)^{1-d/d}\left[\frac{T-b}{c}+\left(\frac{d-1}{d}\right)^{1/d}\right]^{d-1}\exp\left(-\left[\frac{T-b}{c}+\left(\frac{d-1}{d}\right)^{1/d}\right]^d+\frac{d-1}{d}\right)$
Modified Gaussian (MG)	$a\exp\left[-\frac{1}{2}\left(\frac{|T-b|}{c}\right)^d\right]$
Exponentially modified Gaussian (EMG)	$\exp\left[\frac{1}{2}\left(\frac{b}{a}\right)^2-\frac{T-c}{a}\right]\left[\text{erf}\left(\frac{1}{\sqrt{2}}\left[\frac{c}{b}+\frac{b}{a}\right]\right)+\text{erf}\left(\frac{1}{\sqrt{2}}\left[\frac{T-c}{b}-\frac{b}{a}\right]\right)\right]$

study is to further examine whether or not the thermal performance curve is skewed. This determination is very important because thermal performance is closely related to ectothermic evolution (Huey and Kingsolver, 1989).

2. Thermal performance function

Table 1 lists twelve thermal performance functions, the Gaussian (Taylor, 1981), Logan1 (Logan et al., 1976), Logan2 (Logan, 1988), Performance (Huey and Stevenson, 1979), Wang–Lan–Ding (Wang et al., 1982), Sharpe–Schoolfield (Sharpe and DeMichele, 1977; Schoolfield et al., 1981), Ratkowsky (Ratkowsky et al., 1983), Brière1 (Brière et al., 1999), Brière2 (Brière et al., 1999), Weibull (Angilletta Jr., 2006), modified Gaussian (Angilletta Jr., 2006) and exponentially modified Gaussian (Naish and Hartwell, 1988). Most of the functions are considered good models to describe the effect of temperature on the development rate (Taylor, 1981; Wang et al., 1982; Logan, 1988; van der Have, 2002; Smits et al., 2003). Here, the exponentially modified Gaussian function was taken from Naish and Hartwell (1988).

3. Statistical methods

There exist many indicators for comparing fitted non-linear models, such as the residual sum of squares (RSS), coefficient of determination (R^2), adjusted coefficient of determination (R^2_{adj}), Akaike information criterion (AIC), Bayesian information criterion (BIC), corrected Akaike information criterion (AICC) and Akaike weight (Smits et al., 2003; Burnham and Anderson, 2004; Angilletta Jr., 2006):

$$\text{RSS} = \sum_{i=1}^{N}(V_i - \hat{V}_i)^2, \tag{1}$$

where N denotes the sample size, V_i denotes the observed development rate at the ith temperature and $\hat{V}_i$ denotes the expected development rate at the ith temperature.

$$R^2 = 1 - \frac{\sum_{i=1}^{N}(V_i - \hat{V}_i)^2}{\sum_{i=1}^{N}(V_i - \overline{V})^2}, \tag{2}$$

where $\overline{V}_i$ denotes the mean of the observed development rates at all temperatures.

$$\text{AIC} = -2L + 2K, \tag{3}$$

where K is the number of parameters including the error and L denotes the maximized log-likelihood value. L can be obtained from RSS and N:

$$L = -\frac{N}{2}\ln\left(\frac{\text{RSS}}{N}\right). \tag{4}$$

$$\text{AIC} = -2L + 2K. \tag{5}$$

$$\text{BIC} = -2L + K\ln(N). \tag{6}$$

$$\text{AICC} = -2L + 2KN/(N-K-1). \tag{7}$$

If the candidate models are given, we can select the best one by comparing their Akaike weights. In general, the model with the highest Akaike weight is the best one. When there are S candidate models, the Akaike weight of the jth model is

$$w_j = \frac{\exp(-(1/2)\Delta_j)}{\sum_{k=1}^{S}\exp(-(1/2)\Delta_k)}, \tag{8}$$

where $\Delta_j = \text{AICC}_j - \min(\text{AICC})$, $j = 1, 2, 3, \ldots, S$ and $\min(\text{AICC})$ denotes the minimum AICC value in all S candidate models.

In this paper, we propose a new weight as a reference indicator (we call it z weight for simplicity), which integrates the above-mentioned indicators to select the best model:

$$z_i = \frac{D_i}{\sum_{j=1}^{S}D_j}, \tag{9}$$

where D_i is the weighed mean of standardized indicators, $i = 1, 2, 3, \ldots, S$ and D_i can be calculated using the following formula:

$$D_i = \frac{1}{5}\left(\frac{|R_i^2 - \min(R^2)|}{\max(R^2) - \min(R^2)} + \frac{|R^2_{adj,i} - \min(R^2_{adj})|}{\max(R^2_{adj}) - \min(R^2_{adj})}\right.$$
$$+ \frac{|\text{AIC}_i - \max(\text{AIC})|}{\max(\text{AIC}) - \min(\text{AIC})} + \frac{|\text{BIC}_i - \max(\text{BIC})|}{\max(\text{BIC}) - \min(\text{BIC})}$$
$$+ \left.\frac{|\text{AICC}_i - \max(\text{AICC})|}{\max(\text{AICC}) - \min(\text{AICC})}\right), \tag{10}$$

where $\max(x)$ denotes the maximum x value in all S candidate models, x_i denotes the x value of the ith candidate model and $i = 1, 2, 3, \ldots, S$. In this paper, we choose R^2, R^2_{adj}, AIC, BIC and AICC to calculate D_i because these indicators may often be used. We assume that combining these indicators is enough to compare candidate models. Of course, we can combine other indicators, such as the deviance information criterion (DIC) (Ellison, 1996, 2004) and the residual information criterion (RIC) (Shi and Tsai, 2002; Leng et al., 2008), in a way similar to that specified by Eq. (10).

The coefficient of determination R^2 is usually used to estimate the goodness-of-fit of fitting observed data. It is rather effective on estimating the fitting of the linear regression. As to the fitting of non-linear regressions, there exist more than 2 parameters. Using more parameters can generally have better effect on fitting

the observed data, which can obtain a high R^2. However, more parameters will lead to the complexity of models. It is difficult for us to try to explain the real meanings of these parameters. Thus, a model with few parameters and relative high R^2 can be popular if we do not care its reaction mechanism which is regarded as the basis of building such a model. The adjusted R^2, AIC, BIC and AICC all consider the complexity of a model when adding the parameters to it. However, a credible mathematical model must consider other factors. A crucial factor is the parameters' real meanings. With respect to a non-linear model of temperature-dependent developmental rate, the activity and denaturation of enzyme at a particular temperature should be considered. Another factor is the presence of the linear relationship between mid-temperatures and corresponding developmental rates. Albeit the linear relationship is often violated probably due to the high morality, the models built for developmental rate must involve such linear relationship. It should be considered as an important criterion for estimating models.

4. Results

We employed twelve functions to fit the data of two species of insects, the diamondback moth (*Plutella xylostell*) and the silverleaf whitefly (*Bemisia tabaci*, B-biotype).

For the first species of insect, the results are illustrated in Fig. 1 and Table 2. The Brière2 function had the highest Akaike weight and z weight; the z weight of the Performance function was higher than the z weight of any other function except for the Brière2 function. The Logan1, Logan2, Wang–Lan–Ding, Sharpe–Schoolfield, Ratkowsky and Brière1 functions also reflected the effect of temperature on the development rate. However, the Ratkowsky function exhibited an unrealistic expectation because it is impossible for development rates above the upper developmental threshold to increase rapidly. Thus, this function is unsuitable for predicting temperature-dependent development rates. The remaining functions displayed a bad fit. We also excluded the Wang–Lan–Ding function as a candidate function
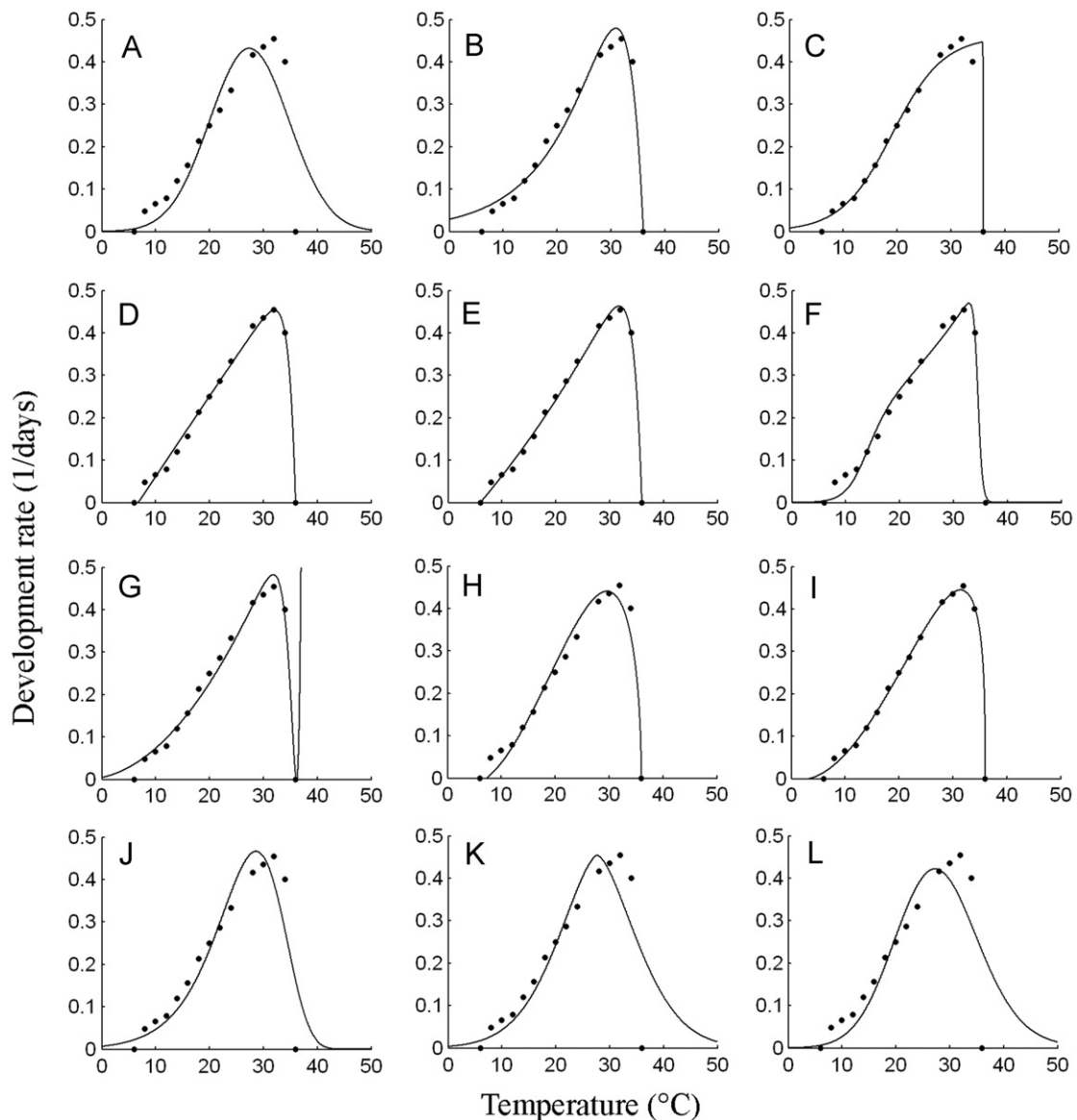
Fig. 1. The relationship between temperatures and development rates of the diamondback moth (*Plutella xylostella*) at its egg stage predicted by twelve functions. Each datum is the mean of development rates at a constant temperature; data were taken from Chen and Liu (2003). (A) Gaussian function; (B) Logan1 function; (C) Logan2 function; (D) Performance function; (E) Wang–Lan–Ding function; (F) Sharpe–Schoolfield function; (G) Ratkowsky function; (H) Brière1 function; (I) Brière2 function; (J) Weibull function; (K) Modified Gaussian function; (L) Exponentially Modified Gaussian function.

Table 2
Goodness-of-fit evaluation of *Plutella xylostell* at its egg stage ($N=15$).

Function	K	R^2	R^2_{adj}	AIC	BIC	AICC	w_i	z_i
Gaussian	4	0.7812	0.7216	−70	−67	−66	0.0000	0.0073
Logan1	5	0.9723	0.9612	−99	−96	−92	0.0000	0.0960
Logan2	6	0.9894	0.9836	−112	−107	−101	0.0000	0.1120
Performance	6	0.9937	0.9902	−119	−115	−109	0.0000	0.1209
Wang–Lan–Ding	8	0.9963	0.9925	−123	−117	−99	0.0000	0.1205
Sharpe–Schoolfield	7	0.9862	0.9758	−106	−101	−90	0.0000	0.1029
Ratkowsky	5	0.9861	0.9806	−110	−106	−103	0.0000	0.1106
Briere1	4	0.9715	0.9637	−101	−98	−97	0.0000	0.0987
Briere2	5	0.9999	0.9999	−190	−187	−184	1.0000	0.1916
Weibull	5	0.7868	0.7014	−69	−65	−62	0.0000	0.0030
Modified Gaussian	5	0.8601	0.8041	−75	−71	−68	0.0000	0.0343
EMG	4	0.7686	0.7055	−69	−66	−65	0.0000	0.0023
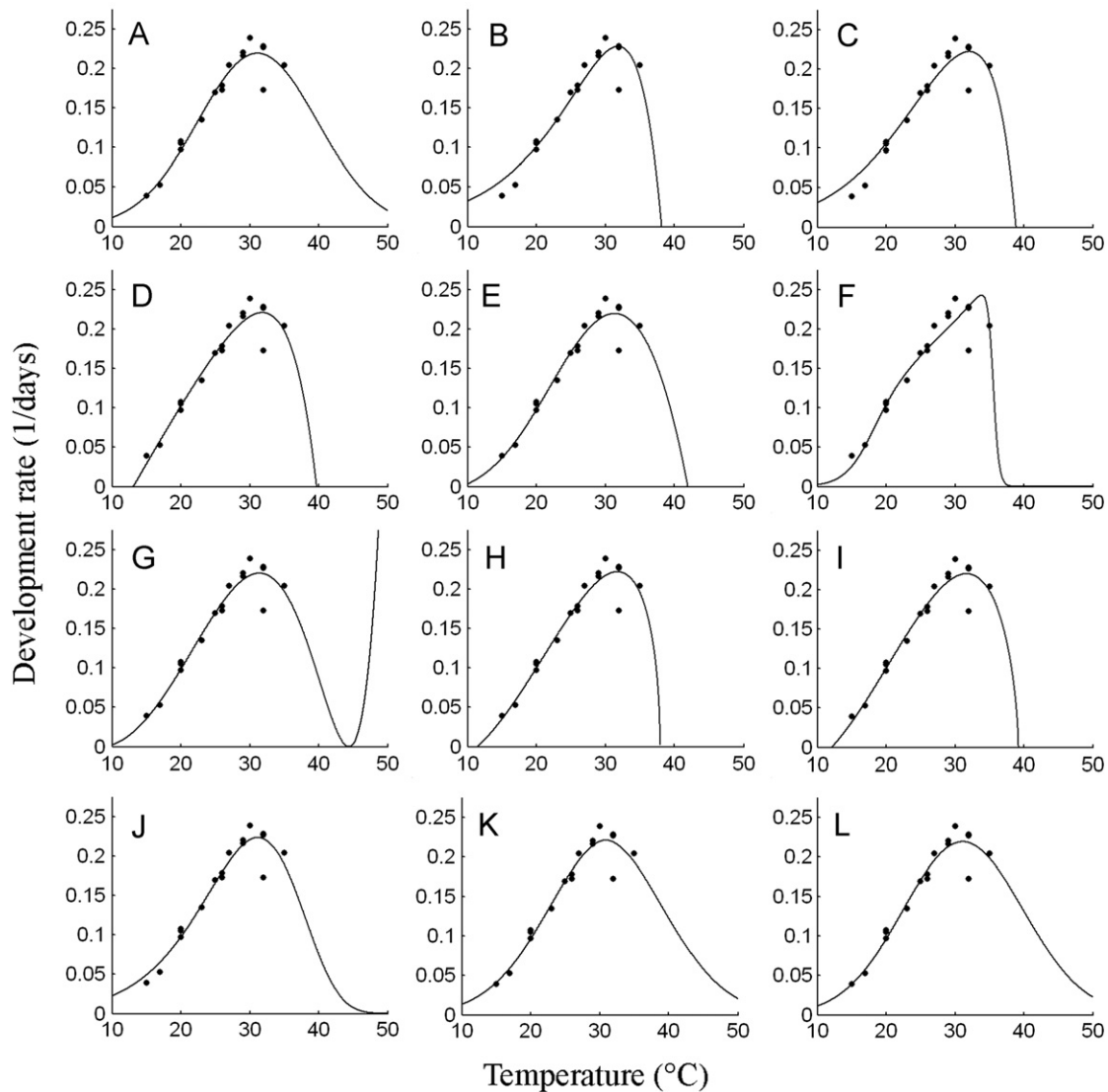
Fig. 2. The relationship between temperatures and development rates of the sliverleaf whitefly (*Bemisia tabaci*) (B-biotype) reared on eggplants at its egg stage predicted by twelve functions. Each datum is the mean of development rate at a constant temperature; data were taken from Wang and Tsai (1996), Qiu et al. (2003) and Qu et al. (2005). (A) Gaussian function; (B) Logan1 function; (C) Logan2 function; (D) Performance function; (E) Wang–Lan–Ding function; (F) Sharpe–Schoolfield function; (G) Ratkowsky function; (H) Brière1 function; (I) Brière2 function; (J) Weibull function; (K) Modified Gaussian function; (L) Exponentially Modified Gaussian function.

because we found that the derivative of the function at the optimal temperature did not equal zero, and because it had a lower z weight than the Performance function. For any thermal performance function, the derivative of the function at the optimal temperature should be zero because it is a basic definition of the optimal temperature for development.

For the second species of insect, the results are shown in Fig. 2 and Table 3. The Gaussian, modified Gaussian and exponentially

Table 3
Goodness-of-fit evaluation of *Bemisia tabaci* at its egg stage ($N=18$).

Function	K	R^2	R^2_{adj}	AIC	BIC	AICC	w_i	z_i
Gaussian	4	0.9476	0.9363	−147	−143	−144	0.3464	0.1240
Logan1	5	0.9210	0.8967	−137	−133	−132	0.0012	0.0469
Logan2	6	0.9243	0.8927	−136	−131	−128	0.0002	0.0385
Performance	6	0.9415	0.9172	−141	−135	−133	0.0018	0.0799
Wang–Lan–Ding	8	0.9464	0.9089	−138	−131	−122	0.0000	0.0588
Sharpe–Schoolfield	7	0.9147	0.8682	−132	−126	−121	0.0000	0.0000
Ratkowsky	5	0.9463	0.9298	−144	−140	−139	0.0393	0.1071
Briere1	4	0.9432	0.9310	−145	−142	−142	0.1680	0.1127
Briere2	5	0.9440	0.9268	−143	−139	−138	0.0270	0.1011
Weibull	5	0.9479	0.9319	−145	−140	−140	0.0519	0.1114
Modified Gaussian	5	0.9419	0.9240	−143	−138	−138	0.0193	0.0957
EMG	4	0.9475	0.9363	−147	−143	−144	0.3449	0.1239

modified Gaussian functions showed an unexpectedly good fit. However, this finding may result from the lack of development rate data at and near the upper developmental threshold. According to a report from Nava-Camberos et al. (2001), *B. tabaci* (B-biotype) at the first instar and third instar stages, reared on two cultivars of cotton, cannot complete development at 35 °C (i.e., the development rate is zero at this temperature). We estimate that *B. tabaci* (B-biotype) at the egg stage, reared on eggplants, cannot complete development above 40 °C. If data were available at the higher temperature, the Gaussian, modified Gaussian and exponentially modified Gaussian functions should have shown a bad fit, as illustrated in Table 2. When we excluded the Ratkowsky and Wang–Lan–Ding functions as candidate models, the Brière1 function showed the highest z weight. The Brière2 and the Performance functions exhibited good fit as well, although their z weights were slightly lower than those of the Brière1 function. The Logan1, Logan2 and Sharpe–Schoolfield functions do not have any advantages in comparison with the Performance function and the two models proposed by Brière et al. (1999) for any indicator listed in Table 3.

In conclusion, we found that the Performance, Brière1 and Brière2 functions are all extremely suitable for describing the effect of temperature on insect development rates according to our study. There is no evidence to prove that the Sharpe–Schoolfield and the two Logan functions are unsuitable for achieving the same outcome, and yet we obtained lower goodness-of-fit scores from these models in comparison to the Performance, Brière1 and Brière2 functions. The last three models were the best for calculating thermal limits (see Table 4). We further infer that the three functions represent the best expressions of thermal performance to date.

5. Discussion

In the investigation of the effect of temperature on insect development rates, the linear function is often used to calculate the lower developmental threshold. For example, Wang and Tsai (1996) used the Sharpe–Schoolfield function to calculate temperature-dependent development rates of *B. tabaci* (B-biotype); however, they still employed the linear function to calculate the lower developmental threshold. Chen and Liu (2003) used the Wang–Lan–Ding function to predict the impact of temperature on the development rate of the diamondback moth; however, they also compared the lower developmental threshold computed by the linear function with the thermal limit from the Wang–Lan–Ding function. Bonato et al. (2007) used the Logan1 function to describe the temperature-dependent development rate of *B. tabaci* (Q-biotype) and calculated the lower developmental

Table 4
Comparison of four models in estimating thermal limits.

Function	*Plutella xylostell*		*Bemisia tabaci*	
	m (°C)	n (°C)	m (°C)	n (°C)
Linear	6.68	–	12.54	–
Performance	6.76	36.00	13.06	39.71
Briere1	7.27	36.00	11.44	37.97
Briere2	3.29	36.00	12.07	39.22

The linear function was used to fit data only for temperatures under 30 °C; the remaining three functions were employed to fit all observed data. m denotes the lower developmental threshold; n denotes the upper developmental threshold.
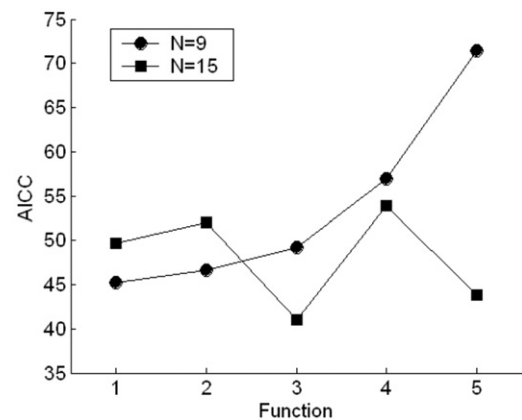
Fig. 3. Influence of the sample size on AICC. In the *x*-axis, "1" represents the Gaussian function; "2" represents the Quadratic function; "3" represents the modified Gaussian function; "4" represents the Weibull function; "5" represents the exponentially modified Gaussian function. Fix the values of RSS in the four functions, and change the sample size. Data of AICC ($N=9$) were taken from Angilletta Jr. (2006); data of AICC ($N=15$) were simulated assuming that the values of RSS in five functions were constants. In the case of $N=15$, the MG and EMG functions are both better than the Gaussian because their values of AICC are both lower than the Gaussian's.

threshold with the linear function. Qiu et al. (2003) and Qu et al. (2005) both used the liner function to calculate the lower developmental threshold of *B. tabaci* (B-biotype). Since the linear function is considered as the best model to reflect temperature-dependent development rates over a certain temperature range (Chen and Liu, 2003; Angilletta Jr., 2006; Bonato et al., 2007), the best non-linear function using all observed data should produce a good prediction for thermal limits, including the lower developmental threshold and the upper developmental threshold. Regarding data for *P. xylostell*, although the z weight obtained
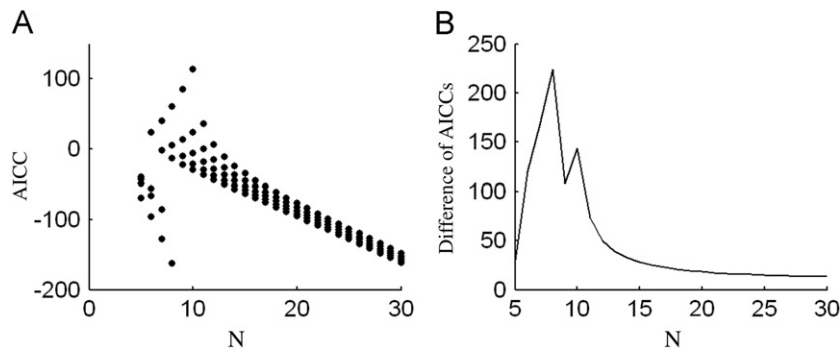
Fig. 4. Combined impacts of the sample size and the number of model parameters on the AICC. (A) AICC; (B) Difference between the maximum AICC and the minimum AICC. Here the RSS is assumed to be a constant 0.1; K ranges from 4 to 8; N ranges from 5 to 30. Albeit the AICC is affected by the RSS, the difference between the maximum AICC and the minimum AICC within a same sample size can keep stable, that is to say, the difference is a constant regardless of the change of the RSS. The difference is just related to the range of K, namely the number of parameters.

from the Brière2 function is slightly higher than that obtained from the Performance function, the lower developmental threshold predicted by the Brière2 function does not approximate that predicted by the linear function, in comparison with the lower developmental threshold predicted by the Performance function. Concerning data for *B. tabaci* (B-biotype), although the z weight obtained from the Brière1 function is the highest among the Performance and two Brière functions, the predicted lower developmental threshold by this function exceeds the predicted value using the linear function by 1.10 °C; the difference between the lower developmental threshold predicted by the Performance function and the lower developmental threshold predicted by the linear function is less than 0.55 °C. The predicted upper developmental threshold by the Brière1 function is the lowest among the predicted upper developmental thresholds by the Performance and two Brière functions. In comparison with the two Brière1 functions, the Performance function can reflect the best linear relationship between temperatures and developmental rates below the optimal developmental temperature. We doubt that using the two models proposed by Brière et al. (1999) causes over-fitting, although the models can fit the data well.

Angilletta Jr. (2006) concluded that the Gaussian function was the best function to describe thermal performance. It is apparent that his conclusion is based on a small sample size with 9 data points. With a small sample size, the number of parameters of the candidate functions can markedly affect the conclusion (see Fig. 3). If we want to use the AICC as an indicator for comparing candidate models with a parameter range [3, 7] (i.e., K belongs to [4, 8]), we suggest that the sample size should not be less than 15, as a rough estimate, in order to reduce the influence of the sample size in calculating the AICC (see Fig. 4).

This study also shows that thermal performance curve should be skew. The Performance and two Brière functions are all better than the symmetrical Gaussian function when fitting the observed data. The optimal developmental temperature is more close to the upper developmental threshold than to the lower developmental threshold. The shape of thermal performance can be divided into two segments: an approximately straight line over a range between the lower developmental threshold and the optimal developmental temperature, and a rapidly descent curve over a range between the optimal developmental temperature and the upper developmental threshold. Campbell et al. (1974) proposed a viewpoint that there were two segments below the optimal developmental temperature: a non-linear curve below a particular low temperature, and an approximately straight line over the range between the particular low temperature and the optimal developmental temperature. In other words, they considered the linear relationship between temperatures

and developmental rates could hold merely over a range of moderate temperature. However, the morality is rather high at any low temperature near to the lower developmental threshold. The non-linear relationship might be a deviation from the linear relationship due to a high morality. And the non-linearity might be amplified by differential morality (Honĕk et al., 2003). Although this study is mainly concerned of the effect of temperature on developmental rates of insects, it can be valuable for investigating other thermal performances, such as the net reproductive rate and intrinsic rate (Huye and Berrigan, 2001). As a matter of fact, many functions that were originally built for describing temperature-dependent developmental rate have been employed to analyze the impacts of temperature on intrinsic rate (e.g., van Rijn et al., 1995; Bonato et al., 2007; Sandhu et al., in press). The key question is what leads to the skewness of the developmental rate curve. Sharpe and DeMichele (1977) proposed an important assumption that development was regulated by a single control enzyme whose reaction rate determined the developmental rate of the organism. The assumption has been long neglected in the investigation into temperature-dependent developmental rate. Jarošík et al. (2002, 2004) found that all the lower developmental thresholds at different developmental stages for a particular species of insect or mite are nearly identical. It further confirmed the hypothesis of rate isomorphy (van Rijn et al., 1995). They also attributed rate isomorphy to this kind of mysterious rate-controlling enzyme. If we admit the existence of the enzyme, the skewness of developmental rate curve might be attributable to the reactions of this kind of enzyme to high temperatures. Too high temperatures can result in the denaturation of the enzyme. Unveiling the Mystery of the rate-controlling enzyme (or a group of enzymes) will doubtlessly help us understand the detailed mechanism of development of insects. And whether all thermal performances are affected by this kind of enzyme (or this group of enzymes) deserves further studies.

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