



# A simple model for describing the effect of temperature on insect developmental rate

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## ABSTRACT

The linear and Logan models are usually used to describe the effect of temperature on insect developmental rate. The linear model is often used to estimate the lower developmental threshold. However, it cannot be used to calculate the upper developmental threshold. Additionally, it fails to describe developmental rates near, at, and above the optimal developmental temperature. The Logan model can reflect temperature-dependent developmental rates from the lower to upper developmental thresholds. It is often used to compute the optimal developmental temperature and the upper developmental threshold, but it is not used to compute the lower developmental threshold. To avoid the disadvantages of these two models, we develop a new model, the 'performance model' on the basis of the impact of increasing temperature on enzyme activity and denaturation. The performance model was first used by Huey and Stevenson (Amer. Zool. 19, 357–366) to provide a statistical description of the impact of body temperature on performance, but they did not provide underlying physiological mechanisms. Few studies have used the performance model to analyze the temperature-dependent developmental rates of insects, perhaps because of the lack of a theoretical justification. Here, we provide a theoretical justification to use the model and we use the performance model to evaluate the developmental rate data of two insect species. We found that the performance model has advantages over the linear and Logan models, and that the lower and upper developmental thresholds can be simultaneously obtained from this model.

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## Introduction

Temperature plays a crucial role in development time of insects (Taylor, 1981). Developmental rate (i.e., the reciprocal of developmental time) is usually used to quantify the effect of temperature. In general, developmental rate gradually rises to an optimal developmental temperature and then drops rapidly at higher temperatures.

Many relevant models have been built to describe the effect of temperature on developmental rate (e.g., Janisch, 1932; Davidson, 1944; Stinner et al., 1974; Logan et al., 1976; Sharpe and DeMichele, 1977; Whalon and Smilowitz, 1979; Schoolfield et al., 1981; Taylor, 1981; Wang et al., 1982; Ryoo and Cho, 1988; van der Have, 2002; Ikemoto, 2005). However, the linear and Logan models are probably the most widely employed examples. The linear model is effective in describing developmental rate below the optimal developmental temperature and has three advantages: its goodness-of-fit is satisfactory at below-optimal developmental temperatures; it yields a lower thermal threshold below which developmental rate equals zero; and it is simple to estimate. However, the linear model is not applicable to temperatures approaching or exceeding the optimum. Because the linear model assumes that developmental rate is an increasing

function of temperature, the upper developmental threshold does not exist. However, this assumption holds only in the mid-temperature range (Campbell et al., 1974). Using the linear model to predict developmental rates beyond the optimal developmental temperature will lead to larger differences between the observed and theoretical values.

Logan et al. (1976) built an analytic model to quantify the temperature-dependent rate phenomena in arthropods. They developed two different models to quantify rates below and above the optimum temperature. They then combined the two models into a single analytic solution, which we refer to as the *Logan model*. The use of the Logan model has two advantages: it covers temperatures above and below the optimum, and it can be used to estimate the upper developmental threshold. However, the lower developmental threshold cannot be obtained because the curve of the Logan model does not cross the *x*-axis. Thus, the linear model is needed for calculating the lower developmental threshold. The theoretical values of developmental rates near the lower developmental threshold calculated by the Logan model are apparently larger than those estimated by the linear model.

In the current study, we build a new model to eliminate the disadvantages of the linear and Logan models. This model is the same as the product of two exponential equations proposed by Huey and Stevenson (1979), which we refer to as the 'performance model.' Huey and Stevenson (1979) used this model to explore the effect of

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body temperature on specific performance parameters, such as the jumped distance of frogs, but few studies (e.g., Shi and Ge, 2010) have applied this model to describe the effect of temperature on insect developmental rate. In addition, we utilize the developmental rate data of two insect species to test the applicability of the performance model.

## Models

### Logan model

According to the study of Logan et al. (1976), developmental rate ( $r$ ) is a piecewise function of temperature:

$$r(T) = \begin{cases} \psi \exp(\rho T) & \text{for } T \text{ in Phase I} \\ C_0[1 - \exp(-\tau)] & \text{for } T \text{ in Phase II} \end{cases} \quad (1)$$

where  $\psi$  is developmental rate at a base temperature above the lower developmental threshold ( $T_1$ );  $\rho$  is the increase rate to the optimal developmental temperature ( $T_0$ );  $T$  is an ambient temperature variable above the lower developmental threshold;  $C_0$  is a constant;  $\tau = (T_2 - T)/\Delta T$ ;  $T_2$  is the upper developmental threshold;  $\Delta T$  is the width of the high temperature boundary layer, which can be regarded as a constant  $z$  for simplicity in the non-linear fitting;  $T$  in Phase I denotes  $T \in [T_1, T_0]$ ;  $T$  in Phase II denotes  $T \in [T_0, T_2]$ . Logan et al. (1976) proved that Eq. (1) during the entire interval  $[T_1, T_2]$  could be described as

$$r(T) = \psi \left[ \exp(\rho T) - \exp\left(\rho T_2 - \frac{T_2 - T}{z}\right) \right]. \quad (2)$$

When  $dr/dT=0$ , we can estimate the optimal developmental temperature,

$$T_0 = T_2 - \frac{z \log(\rho z)}{\rho z - 1}. \quad (3)$$

It is necessary to point out that  $T_1$  could not be included by the original Logan model although Drost et al. (1998) and Bonato et al. (2007) introduced it into the Logan model

$$r(T) = a \exp(-\rho T_1) \left[ \exp(\rho T) - \exp\left(\rho T_2 - \frac{T_2 - T}{z}\right) \right], \quad (4)$$

where  $a$  is constant. In fact, their expression only increases the possible error of parameter estimations because it requires five rather than four parameters (namely letting one estimation of  $\psi$  become two estimations of  $a$  and  $T_1$ ). Accurate  $T_1$  cannot be obtained, and the modified Logan model may increase the Akaike information criterion (AIC) due to an additional parameter (Angilletta, 2006).  $AIC = -2L + 2K$ , where  $K$  is the number of parameters including the error and  $L$  denotes the maximized log-likelihood value. To add an additional parameter will increase the AIC. A higher AIC usually indicates a worse model fitting. Hence, we use the original Logan model to fit the data in the current study.

### Performance model

We assume the effect of temperature on developmental rate has two parts: positive effect and negative effect. There is

$$r = cf(y_1, y_2). \quad (5)$$

where  $c$  is a constant;  $f(\cdot)$  is enzyme contribution function, which represents the integrated effect of enzyme activity change and enzyme conformation change due to increasing temperature on developmental rate;  $y_1$  is the contribution function of enzyme activity

change;  $y_2$  is the contribution function of enzyme conformation change (i.e., enzyme denaturation). A simple but practical formulation of  $f(\cdot)$  is

$$f(y_1, y_2) = y_1 \times y_2 \quad (6)$$

Let  $y_1(T)$  be an increasing function of temperature, and let  $y_2(T)$  be a decreasing function of temperature. Eq. (6) can reflect the tradeoff between the positive contribution to developmental rate due to enzyme activity increase and the negative contribution to developmental rate because of enzyme conformation change with increasing temperature.

Like most chemical reactions, enzyme activity increases with increasing temperature. Higher temperature increases the chance of a successful collision of reacting molecules resulting in an increased reaction rate (Bennett and Frieden, 1969). An increase of 10 °C will enhance the activity of most enzymes by 50–100%. At low temperatures, enzyme denaturation can happen, though only rarely. At high temperatures, however, enzyme denaturation is common. As a consequence, a simple assumption is that  $y_1(T)$  and  $y_2(T)$  are both linear functions of temperature. Then we have

$$\begin{cases} \frac{dy_1}{dT} = K_1 \\ \frac{dy_2}{dT} = -K_2 \end{cases}, \quad (7)$$

where  $K_1$  is the increase rate and  $K_2$  is the decrease rate. Eq. (7) has a solution

$$\begin{cases} y_1(T) = K_1 T + C_1 \\ y_2(T) = -K_2 T + C_2 \end{cases}, \quad (8)$$

where  $C_1$  and  $C_2$  are both constants. Then we have

$$r(T) = c(K_1 T + C_1)(-K_2 T + C_2), \quad (9)$$

If the negative contribution to developmental rate due to enzyme conformation change with increasing temperature is neglected (i.e.,  $y_2 = 1$ ) developmental rate is actually a linear function of temperature. We refer to Eq. (9) as the *simplified performance model*. When  $dr/dT=0$ , we have the theoretical value of the optimal developmental temperature based on Eq. (9):

$$T_0 = \frac{K_1 C_2 - K_2 C_1}{2K_1 K_2}. \quad (10)$$

Firstly, excessive products may be made by the rapid reaction between enzymes and substrates and may burden organism metabolism. As a result, development will be influenced due to the inordinate metabolism. Secondly, if substrate concentration is fixed before the reaction, the increased reaction due to increasing temperature will gradually reduce substrate concentration, further slowing enzyme activity. That is, development will be also influenced by the decrease of necessary substrate. With temperature increasing, one possible result is the faster reduction of necessary substrates and accumulation of excessive products at higher temperatures than at lower temperatures. These two factors (i.e., the fast reduction of necessary substrates and accumulation of excessive products) may form a negative feedback of enzyme activity increase. At the same time, the positive feedback to enzyme conformation change also exists. For example, although enzyme structure is vulnerable to hyperthermia, it can be protected by heat-shock proteins (HSPs) (Hartl and Hayer-Hartl, 2002). Induced thermo-tolerance is mediated by increased expression of HSPs, which help direct the folding of polypeptides into functional proteins and maintain the functional structure of enzymes by increasing the time to break down and

decreasing the time to recover (Feder and Hoffmann, 1999). Hence, the positive feedback of temperature on HSPs can be indispensable for survival in stressful environments. A more reasonable assumption is to include the two feedbacks caused by the fast reduction of necessary substrates and accumulation of excessive products. Therefore, a new differential equation is as follows

$$\begin{cases} \frac{dy_1}{dT} = K_1(1-y_1) = K_1 - K_1y_1 \\ \frac{dy_2}{dT} = -K_2(1-y_2) = -K_2 + K_2y_2 \\ y_1(T_1) = 0, y_2(T_2) = 0 \end{cases} \quad (11)$$

See Fig. 1 for a heuristic model of the process. It has the solution (see Appendix 1)

$$\begin{cases} y_1(T) = 1 - \exp(-K_1T + K_1T_1) \\ y_2(T) = 1 - \exp(-K_2T_2 + K_2T) \end{cases} \quad (12)$$

Substituting Eq. (12) to Eq. (5), a function of developmental rate can be obtained

$$r(T) = c(1 - \exp[-K_1(T-T_1)])(1 - \exp[K_2(T-T_2)]) \quad (13)$$

which is the same as the performance equation which is made up of the two exponential equations proposed by Huey and Stevenson (1979). The equation proposed by Huey and Stevenson (1979) has been long neglected in the study of the effect of temperature on insect developmental rate because it was not developed from first principles. It was reported as a statistical formula that quantified the effect of temperature on performance parameters of ectotherms, such as the jumped distance of *Rana clamitans* (Huey, 1975; Huey and Stevenson, 1979). We refer to Eq. (13) as the performance model for simplicity.

Optimal developmental temperature cannot be obtained directly from Eq. (13) but can easily be computed via software such as MATLAB 6.5 (MathWorks, 2002, URL: [www.mathworks.com](http://www.mathworks.com)). First, we need to calculate the derivative of Eq. (13).

$$\frac{dr}{dT} = cK_1e^{-K_1(T-T_1)}(1 - e^{K_2(T-T_2)}) - cK_2e^{K_2(T-T_2)}(1 - e^{-K_1(T-T_1)}) \quad (14)$$

Second,  $g(T) = cK_1e^{-K_1(T-T_1)}(1 - e^{K_2(T-T_2)})$  and  $h(T) = cK_2e^{-K_2(T-T_2)}(1 - e^{-K_1(T-T_1)})$  are defined, then  $dr/dT = g(T) - h(T)$ . Third, if the curves of  $g(T)$  and  $h(T)$  are simultaneously drawn in a plane via software, the temperature at which the two curves intersect is the optimal developmental temperature of Eq. (13), i.e., the numerical solution of  $dr/dT = 0$ . In MATLAB 6.5, it is easy to obtain the numerical solution of the optimal developmental temperature (see Appendix 2).

### Application

In this section, we use these models to analyze the effect of temperature on developmental rate from egg to adult of *Bemisia tabaci*, a significant agricultural pest, reared on three species of host plants. The original data are from the studies of Qiu et al. (2003), Xiang et al. (2007) and Bonato et al. (2007). To determine whether the models could be applied to other species, we also used the data of *Axinoscymnus cardilobus* (Huang et al., 2008). We used the temperature and developmental rate data from these papers, and then used the NLINFIT (non-linear least-squares data fitting by the Gauss–Newton method) function of MATLAB 6.5 to fit the non-linear models.

Fig. 2 displays the fitted results using the performance model. The fitted lower and upper developmental thresholds and the shortest developmental durations at the optimal developmental temperatures are shown in Table 1. The estimated lower developmental temperatures using the linear and performance models are approximate, and the estimated upper developmental temperatures and optimal developmental temperatures using the Logan and performance models are approximate.

There are several other non-linear models to describe the temperature-dependent developmental rates. The performance model still shows advantages relative to these non-linear models (Shi and Ge, 2010). Please see the work of Shi and Ge (2010) for a complete discussion of these advantages.

### Discussion

Why can the Logan model reflect the effect of temperature on insect developmental rate? If we relax the restriction of  $f(y_1, y_2) = y_1 \times y_2$ , the question is easy to answer. Assume  $f(y_1, y_2) = (1 - y_2) - 1/(1 - y_1)$  with  $y_1$  and  $y_2$  substituted by Eq. (12), then an expression similar to the Logan model can be obtained:

$$r(T) = c \exp(-K_2T_2)[\exp(K_2T) - \exp(K_1T - K_1T_1 + K_2T_2)] \quad (15)$$

which can be described as

$$r(T) = p_1[\exp(p_2T) - \exp(p_3T + p_4)] \quad (16)$$

Here  $p_1, p_2, p_3$  and  $p_4$  are the model parameters. In fact, the Logan model can be also written as this simplified formula.  $y_1(T)$  is an increasing function of  $T$  and  $y_2(T)$  is a decreasing function of  $T$ , the difference of  $(1 - y_2) - 1/(1 - y_1)$  is capable of exhibiting the tradeoff between the influence due to enzyme activity increase and the influence due to enzyme formation change with increasing temperature. Another competitive assumption of the enzyme

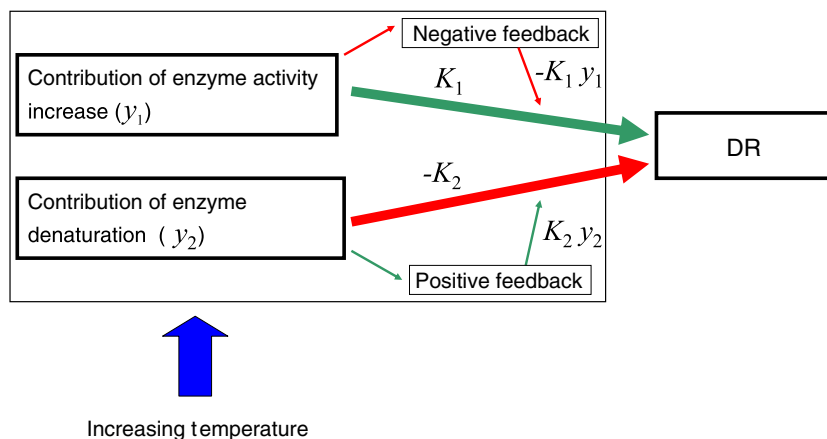
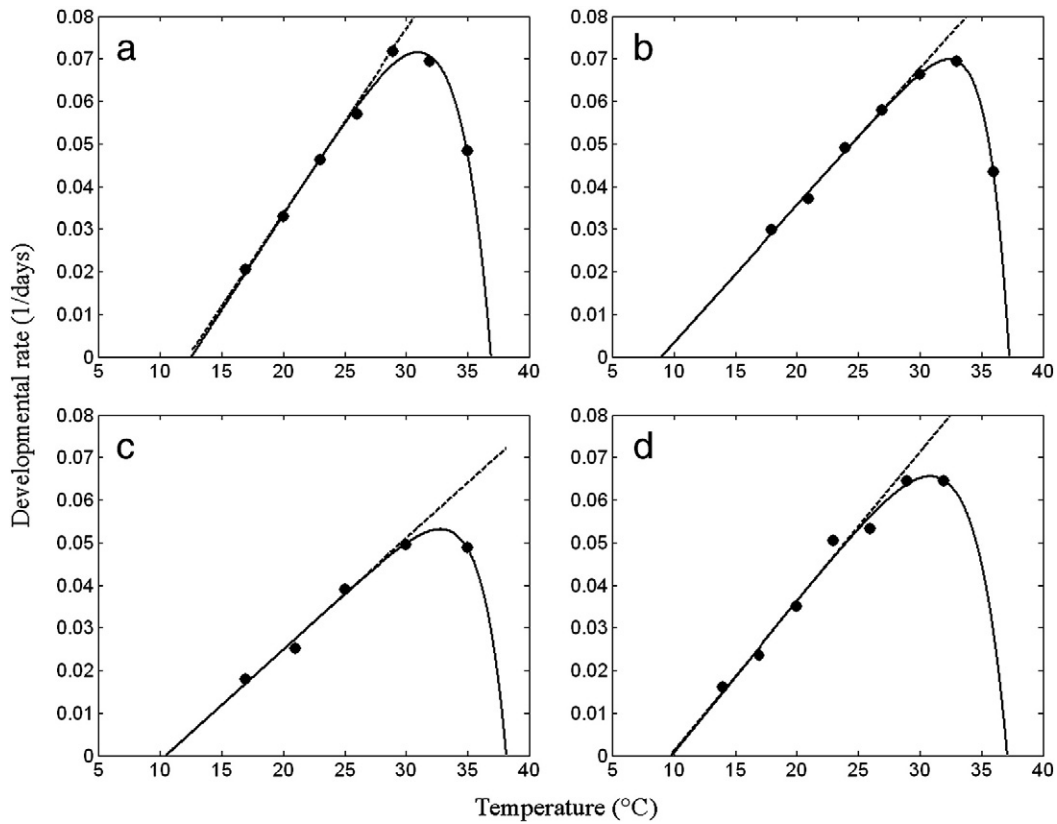


Fig. 1. Illustration of the model's underlying hypothesis for the effect of temperature on developmental rate (DR).



**Fig. 2.** Influence of temperature on developmental rate: (a) *Bemisia tabaci* biotype B reared on eggplant; (b) *Bemisia tabaci* biotype B reared on cucumber; (c) *Bemisia tabaci* biotype B reared on tomato; (d) *Axinoscyrnus cardilobus* reared on *Bemisia tabaci*. The solid lines denote the performance model; the dashed lines denote the first-order Taylor series expansion of the performance model at  $T_1 + 10$ ; the closed circles denote the observed data.

contribution function  $f(\cdot)$  can follow:  $f(y_1, y_2) = y_1 - 1/y_2$ , which can be further described as

$$\frac{r(T)}{c} = 1 - \exp(-K_1T + K_1T_1) - \frac{1}{1 - \exp(K_2T - K_2T_2)} \quad (17)$$

because  $f(y_1, y_2) = y_1 - 1/y_2$  can reflect the tradeoff between two effects with increasing temperature as well. However, we did not try to use Eq. (17) to fit the data of developmental rate. An important reason is that the Logan model has an obvious disadvantage relative to

the performance model. Hence, it is unnecessary to use Eq. (17) again, which is similar to the Logan model.

Wang et al. (1982) built a model analogous to the performance model:

$$r(T) = \frac{K(1 - \exp[-K_1(T - T_1)])(1 - \exp[K_2(T - T_2)])}{1 + \exp[-\kappa(T - T_o)]} \quad (18)$$

where  $K$  and  $\kappa$  are both constants. They used a different method to build this model. We must admit that this model shows better flexibility while fitting the observed data relative to Eq. (13) due to an additional denominator  $1 + \exp[-\kappa(T - T_o)]$ . If we set  $\kappa = 0$ , Eq. (18) is the same as Eq. (13), namely the performance equation. According to the definition of the optimal developmental temperature, the derivative of  $r(T)$  at the optimal developmental temperature should equal zero, namely  $r'(T_o) = 0$ . However, Eq. (18) does not meet the condition. Despite the disadvantage, Wang et al.'s model can fit the observed data very well because of the similarity to the performance model.

The performance and Logan models are superior to the linear model in the curve fitting when all the data are included. We can obtain a satisfactory goodness-of-fit via the performance model relative to the linear model. Even so, the linear model is still attractive for its simplicity. In addition, the linear model can be fitted without specifying the preliminary values of parameters which are required for the non-linear models. If we can accept the Logan model for exploring the effect of temperature on developmental rate in spite of the difficulty in choosing the preliminary values of parameters for the non-linear fitting, accepting the performance model for the same purpose seems to be reasonable. As shown in Fig. 2, the performance model has a shape similar to the line before the optimal developmental

**Table 1**  
Comparison among three models.

Object	Model	R <sup>2</sup>	T <sub>1</sub> (°C)	T <sub>o</sub> (°C)	T <sub>2</sub> (°C)	*D (T <sub>o</sub> ) (days)
<i>B. tabaci</i> reared on eggplant	Linear	0.9982	12.2	–	–	–
	Logan	0.9886	–	31.0	37.0	13.7
	Performance	0.9923	12.6	31.0	36.9	14.0
<i>B. tabaci</i> reared on cucumber	Linear	0.9952	8.6	–	–	–
	Logan	0.9961	–	32.0	37.7	14.3
	Performance	0.9972	9.0	32.4	37.3	14.3
<i>B. tabaci</i> reared on tomato	Linear	0.9870	10.2	–	–	–
	Logan	0.9928	–	32.5	39.4	18.8
	Performance	0.9909	10.5	32.9	38.2	18.8
<i>A. cardilobus</i> reared on <i>B. tabaci</i>	Linear	0.9795	9.3	–	–	–
	Logan	0.9783	–	30.4	36.7	15.0
	Performance	0.9854	9.8	30.9	37.1	15.3

\* D (T<sub>o</sub>) denotes the developmental time from egg to adult at the optimal temperature.

temperature. This indicates a close relationship between the linear and performance models. For displaying the relationship more clearly, we derived the first-order Taylor series expansion of the performance at  $T=x$ ,

$$r_x(T) = c(1 - e^{-K_1(x-T_1)})(1 - e^{K_2(x-T_2)}) - c[K_1 e^{-K_1(x-T_1)}(1 - e^{K_2(x-T_2)}) - K_2 e^{K_2(x-T_2)}(1 - e^{-K_1(x-T_1)})](x-T). \tag{19}$$

Charnov and Gillooly (2003) found that the lower developmental threshold (i.e.,  $T_1$ ) is about 10 °C below the mean developmental temperature for ectotherms in nature ('10 °C' rule). Thus, the first-order Taylor series expansion of the performance model agrees with the linear model when  $x = T_1 + 10$ . Fig. 2 also shows the comparison between the first-order Taylor series expansion of the performance model and the observed data. Let  $f(y_1, y_2) = (y_1 \times y_2)^2$  and replace  $y_1$  with the first-order Taylor series expansion of  $y_1$  at  $T_1$ . Substituting the result to Eq. (5), we have

$$\sqrt{r(T)} = \sqrt{c}K_1(T-T_1)(1 - \exp[K_2(T-T_2)]). \tag{20}$$

which becomes the Ratkowsky model (Ratkowsky et al., 1983). This equation is used mainly to describe the temperature-dependent developmental rates of microorganisms. The Ratkowsky model can be modified slightly to describe the temperature-dependent developmental rates of insects:

$$r(T) = \sqrt{c}K_1(T-T_1)(1 - \exp[K_2(T-T_2)]). \tag{21}$$

That is, the square root effect is neglected. This equation can be regarded as a related model of the performance model because they have the similar shapes.

Although we prefer the performance model because of the underlying physiological considerations, the evidence from the experimental data at low temperatures near the true developmental threshold is lacking. Hence it is difficult to accurately estimate the lower developmental threshold. In a sense, the precise lower developmental threshold merely exists in theory. The difference between the estimated values of the lower developmental threshold from the linear model and the performance model does not exceed 0.5 °C. Distinguishing such small differences will not be easy in environmental chambers, where the variation in temperature is often great. In conclusion, results from the linear fitting may be adequate, even though we prefer the performance model.

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**Appendix 1**

$$\begin{cases} \frac{dy_1}{dT} = K_1(1-y_1) \\ \frac{dy_2}{dT} = -K_2(1-y_2) \\ y_1(T_1) = 0, y_2(T_2) = 0 \end{cases} \Leftrightarrow \begin{cases} \frac{d(1-y_1)}{1-y_1} = -K_1 dT \\ \frac{d(1-y_2)}{1-y_2} = K_2 dT \\ y_1(T_1) = 0, y_2(T_2) = 0 \end{cases} \tag{A1}$$

$$\Leftrightarrow \begin{cases} \ln(1-y_1) = -K_1 T + s_1 \\ \ln(1-y_2) = K_2 T + s_2 \\ y_1(T_1) = 0, y_2(T_2) = 0 \end{cases}$$

$$\Leftrightarrow \begin{cases} y_1(T) = 1 - \exp(-K_1 T + s_1) \\ y_2(T) = 1 - \exp(K_2 T + s_2) \\ y_1(T_1) = 0, y_2(T_2) = 0 \end{cases}$$

where  $s_1$  and  $s_2$  are constants. Then we have

$$\begin{cases} y_1(T_1) = 1 - \exp(-K_1 T_1 + s_1) = 0 \\ y_2(T_2) = 1 - \exp(K_2 T_2 + s_2) = 0 \end{cases}, \tag{A2}$$

which means that the developmental rates at the lower and upper developmental thresholds both equal zero.  $s_1$  and  $s_2$  are known from Eq. (A2),

$$\begin{cases} s_1 = K_1 T_1 \\ s_2 = -K_2 T_2 \end{cases}. \tag{A3}$$

Now substitute Eq. (A3) to the last item of Eq. (A1), we can obtain Eq. (12).

**Appendix 2**

Two functions, 'performance.m' and 'deri.m,' are needed. The latter is the derivative of the former.

**(1) Performance.m:**

```
function r = performance(par, T)
c = par(1);
K1 = par(2);
T1 = par(3);
K2 = par(4);
T2 = par(5);
r = c*(1 - exp(-K1*(T-T1)))*(1 - exp(K2*(T - T2)));
```

**(2) Deri.m:**

```
function rx = deri(par,T)
c = par(1);
K1 = par(2);
T1 = par(3);
K2 = par(4);
T2 = par(5);
x = par(6);
rx = c.*(1-exp(-K1.*(x-T1)))*(1-exp(K2.*(x-T2)))-c.*(K1.*exp(-K1.*(x-T1)))*(1-exp(K2.*(x-T2)))-K2.*exp(K2.*(x-T2)).*(1-exp(-K1.*(x-T1))))*(x-T);
```

Then, we enter the following codes in Command Window of MALAB 6.5:

```
T = [17 20 23 26 29 32 35];
D = [48.71 30.33 21.67 17.57 13.93 14.44 20.67];
```



```

r = 1./D;
parhat = nlinfit(T, r, 'performance', [30 0.005 10 0.5 40])
Tvalue = parhat(3); 0.001: parhat(5);
Theor = performance(parhat, Tvalue);
optimum = find(Theor == max(Theor));
To = Tvalue(optimum)
ro = Theor(optimum)
Do = 1/ro
Rsquare = 1-sum((performance(parhat, T)-r).^2)/sum((r-mean(r)).^2)
plot(Tvalue, Theor, 'k', T, r, 'k', 'MarkerSize', 28, 'LineWidth', 2.0)
hold on
plot(Tvalue, deri([parhat; parhat(3) + 10], Tvalue), 'k-', 'LineWidth', 2.0)
xlabel('Temperature (°C)', 'fontsize', 14)
ylabel('Developmental rate (1/days)', 'fontsize', 14)
set(gca, 'fontsize', 14);

```

Here, we take the data set from *B. tabaci* reared on eggplant from egg to adult (Qiu et al., 2003). 'T' and 'D' represent the experimental temperature and developmental time, respectively. 'parhat' is an array used to save the model parameters, namely [ $c$ ,  $K_1$ ,  $T_1$ ,  $K_2$ ,  $T_2$ ] of the performance model; 'To' is the optimal developmental temperature; 'ro' is the developmental rate at the optimal developmental temperature; 'Do' is the developmental duration at the optimal developmental temperature; 'Rsquare' is the coefficient of determination, namely  $R^2$ ; 'Tvalue' is an array made up of a series of temperatures between the lower and upper developmental thresholds with an increment of 0.001; 'Theor' is an array used to save the theoretical values of developmental rates estimated by the performance model.

## References

- Angilletta Jr., M.J., 2006. Estimating and comparing thermal performance curves. *J. Therm. Biol.* 31, 541–545.
- Bennett, T.P., Frieden, E., 1969. Modern topics in biochemistry. Macmillan, London, UK.
- Bonato, O., Lurette, A., Vidal, C., Fargues, J., 2007. Modelling temperature-dependent bionomics of *Bemisia tabaci* (Q-biotype). *Physiol. Entomol.* 32, 50–55.
- Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P., Mackauer, M., 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* 11, 431–438.
- Charnov, E.L., Gillooly, J.F., 2003. Thermal time: body size, food quality and the 10 °C rule. *Evol. Ecol. Res.* 5, 43–51.
- Davidson, J., 1944. On the relationship between temperature and rate of development of insects at constant temperature. *J. Anim. Ecol.* 13, 26–38.
- Drost, Y.C., van Lenteren, J.C., van Roermund, H.J.W., 1998. Life-history parameters of different biotypes of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in relation to temperature and host plant: a selective review. *B. Entomol. Res.* 88, 219–229.
- Feder, M.E., Hoffmann, G.E., 1999. Heat shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annu. Rev. Physiol.* 61, 243–282.
- Hartl, F.U., Hayer-Hartl, M., 2002. Molecular chaperones in the cytosol: from nascent chain to folded protein. *Science* 295, 1852–1858.
- Huang, Z., Ren, S., Musa, P.D., 2008. Effects of temperature on development, survival, longevity, and fecundity of *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) predator, *Axinoscymnus cardilobus* (Coleoptera: Coccinellidae). *Biol. Control* 46, 209–215.
- Huey, R.B., 1975. Ecology of lizard thermoregulation. Ph. D. Diss., Harvard University.
- Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Amer. Zool.* 19, 357–366.
- Ikemoto, T., 2005. Intrinsic optimum temperature for development of insects and mites. *Environ. Entomol.* 34, 1377–1387.
- Janisch, E., 1932. The influence of temperature on the life-history of insects. *Trans. Roy. Entomol. Soc. Lond.* 80, 137–168.
- Logan, J.A., Wollkind, D.J., Hoyt, S.C., Tanigoshi, L.K., 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environ. Entomol.* 5, 1133–1140.
- Qiu, B., Ren, S., Mandour, N.S., Lin, L., 2003. Effect of temperature on the development and reproduction of *Bemisia tabaci* B biotype (Homoptera: Aleyrodidae). *Entomol. Sin.* 10 (1), 43–49.
- Ratkowsky, D.A., Lowry, R.K., McMeekin, T.A., Stokes, A.N., Chandler, R.E., 1983. Model for bacterial culture growth rate throughout the entire biokinetic temperature range. *J. Bacteriol.* 154, 1222–1226.
- Ryoo, M.L., Cho, K.-J., 1988. A model for the temperature-dependent developmental rate of *Sitophilus oryzae* L. (Coleoptera: Curculionidae) on rice. *J. Stored Prod. Res.* 24, 79–82.
- Schoolfield, R.M., Sharpe, P.J.H., Magnuson, C.E., 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor. Biol.* 88, 719–731.
- Sharpe, P.J.H., DeMichele, D.W., 1977. Reaction kinetics of poikilotherm development. *J. Theor. Biol.* 64, 649–670.
- Shi, P., Ge, F., 2010. A comparison of different thermal performance functions describing temperature-dependent developmental rates. *J. Therm. Biol.* 35, 225–231.
- Stinner, R.E., Gutierrez, A.P., Butler, G.D., 1974. An algorithm for temperature-dependent growth rate simulation. *Can. Entomol.* 106, 519–524.
- Taylor, F., 1981. Ecology and evolution of physiological time in insects. *Am. Nat.* 117, 1–23.
- Xiang, Y., Guo, X., Zhang, F., Li, Z., Luo, C., 2007. Effects of temperature and humidity on the development and reproduction of *Bemisia tabaci* (Homoptera: Aleyrodidae) Biotype B. *Acta Agricul. Bor. Sin.* 22 (5), 152–156 (in Chinese with English abstract).
- van der Have, T.M., 2002. A proximate model for thermal tolerance in ectotherm. *Oikos* 98, 141–155.
- Wang, R., Lan, Z., Ding, Y., 1982. Studies on mathematical models of the relationship between insect development and temperature. *Acta Ecol. Sin.* 2 (1), 47–57.
- Whalon, M.E., Smilowitz, Z., 1979. Temperature-dependent model for predicting field populations of green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *Can. Entomol.* 111, 1025–1032.