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ORIGINAL RESEARCH PAPER

Mathematical elucidation of the Kaufmann effect based on the thermodynamic SSI model

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Abstract The development rate of insects at hourly fluctuating temperatures is not infrequently different from that at constant temperatures even when the averages of these temperatures are the same. This temperature-dependent development phenomenon has been known as the Kaufmann effect. However, its theoretical analysis has not yet been successfully carried out owing to the insufficiency of mathematical insight especially into quantitative expressions. In insect development, the interrelationships among the three environmental temperatures, namely, the constant and alternating temperatures controlled in the laboratory and the hourly fluctuating temperatures in the natural environment, have not been clarified. Here, we completely succeeded in analyzing this phenomenon and in elucidating the interrelationships by introducing the components of the nonlinear SSI development model, the second derivative, the cosine-wave model of hourly fluctuating temperatures and their variance, and Taylor series. As a result, it has been possible to predict the development rate at fluctuating temperatures in the natural environment using prospective daily maximum, minimum and average temperatures and the development rate at constant temperatures without conducting experiments at alternating temperatures.

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Introduction

Insects sometimes develop at different rates per day at hourly fluctuating temperatures compared with the case at constant temperatures even when the averages of these temperatures are the same. The difference between development rates predicted using nonlinear models at constant and fluctuating temperatures with the same mean temperature has been called the Kaufmann effect when it is specific to temperature-dependent development (Ludwig and Cable 1933; Behrens et al. 1983; Worner 1992; Ruel and Ayres 1999; Ragland and Kingsolver 2008) or the rate summing effect (Worner 1992).

Differences in development time between constant and fluctuating temperatures agree well with predictions based on the non-linear relationship between development rate and temperature. The development rate-temperature curve predicts that when the curve is a concave function or shows deceleration (at high temperatures), the development time will be shorter (higher average rate) at constant temperatures than at fluctuating temperatures with approximately the same mean. The curve predicts that when the curve is a convex function or shows acceleration (at low temperatures), the reverse will be true. This property of the nonlinear development rate function described by the above-mentioned authors has been confirmed not only logically but also experimentally for a given species at alternating temperatures by many authors (e.g., Messenger and Flitters 1958, 1959; Miyashita 1971; Tanigoshi et al. 1976; Foley 1981; Hagstrum and Milliken 1991; Bryant et al. 1999; Liu et al. 2002; Fantinou et al. 2003; Ragland and Kingsolver 2008; Wu et al. 2009).

These achievements, in which basic information on the development rate in relation to temperature was obtained from both the laboratory and natural environment, are valuable. However, it might be necessary to further improve the theoretical frame work of the objectives. The first reason is that some of the characteristics of the nonlinear model curve are insufficiently analyzed. Thus, the borders of the convex and concave parts of the model curves are not known exactly. The second is the need to make fine distinctions concerning the the effects of alternating temperatures between, for example, 2 °C higher and 2 °C lower than the mean for 12 h in the laboratory from the effects of fluctuating temperatures at the same daily mean temperature of 4 °C in nature.

Here, we will attempt to analyze the development rate at constant, alternating and fluctuating temperatures, and suggest the relationships of these temperatures mathematically. On the basis of this analysis, we will be able to not only describe the Kaufmann effect, but also more accurately predict insect development in fields using laboratory data.

Nonlinear development model

The theoretical Sharpe-Schoolfield-Ikemoto (SSI) model based on thermodynamic enzyme activity is a representative model used to express a relationship between temperature and the development rate of poikilotherms. It is actually a direct extension of the Eyring equation (Sharpe and DeMichele 1977; Schoolfield et al. 1981), which is a unique theoretical model among many nonlinear mathematical models for describing temperature-dependent development rates.

Ikemoto (2005, 2008) found a problem with the Sharpe-Schoolfield (SS) model and substantially improved it by not merely replacing the partial parameters in the SS model, but also by introducing the concept of intrinsic optimum temperature T_Φ for the first time. The modified SS model is referred to as the SSI model. Shi et al. (2011) developed a program for estimating the parameters in the SSI model, and Ikemoto et al. (2012) furnished a faster program for estimating the parameters (OptimSSI-P) in this model. The latter program has a corresponding program (mABCSSI-P) for calculating the confidence interval of the estimated T_Φ by modifying the approximate bootstrap confidence (ABC) intervals (DiCiccio and Efron 1992, 1996). These programs can be freely downloaded from the supporting information in the web site of the society.

The SSI model equation is expressed as follows:

$$r(T) = \frac{\rho_\Phi \frac{T}{T_\Phi} \exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{T_\Phi} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T}\right)\right]}, \tag{1}$$

where $r(T)$ is the development rate (dependent variable) at the absolute temperature T (K independent variable). All the other parameters are constants: T_L is the low temperature at which an enzyme is 1/2 active and 1/2 inactive, and T_H is the high temperature at which an enzyme is 1/2 active and 1/2 inactive (K). T_Φ is the intrinsic optimum temperature (K). ΔH_A is the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal mol^{-1}); ΔH_L and ΔH_H represent the enthalpy changes associated with low- and high-temperature inactivations of the enzyme (cal mol^{-1}), respectively. R is the universal gas constant (1.987 cal deg^{-1} mol^{-1}), and ρ_Φ is the approximate development rate at T_Φ. In this definition, T_Φ must have relationships with the other constants as follows (Ikemoto 2005):

$$T_\Phi = \frac{\Delta H_L - \Delta H_H}{R\,\ln\left(-\frac{\Delta H_L}{\Delta H_H}\right) + \left(\frac{\Delta H_L}{T_L}\right) - \left(\frac{\Delta H_H}{T_H}\right)}. \tag{2}$$

Under the conditions given in Eqs. 1 and 2, the reversed denominator of Eq. 1 denotes the probability of an enzyme being in the active state at temperatures optimal for the developmental processes such as cell division and multiplication:

$$P_2(T) = \frac{1}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T}\right)\right]}. \tag{3}$$

Namely, the reversed denominator shows the maximum at T_Φ. Thus, T_Φ is the most valuable thermal parameter for all the development processes in insects and other ectotherms.

Here, we put

$$f_\rho(T) = \rho_\Phi \frac{T}{T_\Phi}, \tag{4}$$

$$f_A(T) = \exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{T_\Phi} - \frac{1}{T}\right)\right], \tag{5}$$

$$f_L(T) = \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T}\right)\right], \tag{6}$$

$$f_H(T) = \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T}\right)\right]. \tag{7}$$

Then, we obtain the first and second derivatives of $r(T)$ as follow:

$$r'(T) = \frac{\rho}{T_{\Phi}} \cdot \frac{f_A(T)}{RT} \cdot P_2(T) \times [H_A + RT - \{H_L f_L(T) + H_H f_H(T)\}\, P_2(T)] \tag{8}$$

$$r''(T) = \frac{\rho}{T_{\Phi}} \cdot \frac{f_A(T)}{R^2T^3} P_2(T) \cdot [\{H_A - RT - Q(T)P_2(T)\} \times \{H_A + RT - Q(T)P_2(T)\} + R^2T^2 - P_2(T)\{H_L^2 f_L(T) + H_H^2 f_H(T) - Q^2(T)P_2(T)\}], \tag{9}$$

where

$$Q(T) = H_L f_L(T) + H_H f_H(T). \tag{10}$$

A numerical example is shown in Fig. 1a using the empirical data set of the *Drosophila melanogaster* at constant temperatures reported by Ludwig and Cable (1933). The SSI model line fitted so well for all of the data points that it was possible to analyze exactly as follows. The first derivative line shown in Fig. 1c, which is illustrated by Eq. 8, indicates the slope on a given point of the SSI model curve. An intersection point (T_1) of the horizontal axis shows the temperature at which the development rate attains its maximum. The second derivative line shown in Fig. 1d, which is illustrated by Eq. 9, has two intersection points (T_2, T_3) of the horizontal axis, which suggests the presence of inflection points within the temperature range from 0 to 50 °C. Between both points the left one at lower temperature T_2 is more important because it is within the practical temperature range for insect development. Thus, the SSI model curve is convex at temperatures lower than this point, suggesting the accelerated increase in development rate. At temperatures higher than this point, the curve is concave, suggesting the accelerated decrease in development rate. This property must always be realized in the SSI model for insect development.

Hourly alternating temperatures and development

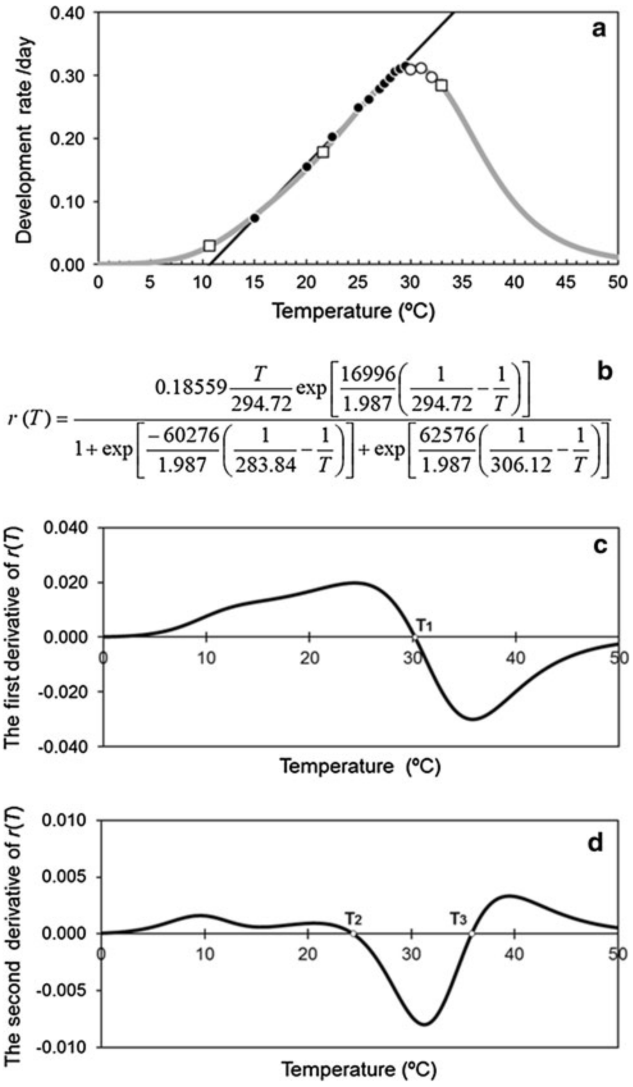
The adjusted development rate per day $r_a(T_{Aa})$ at two temperatures (T_1, T_2) for their respective continuous hours (h_1, h_2) in a day (normally $h_1 + h_2 = 24$ h) can be expressed using the SSI model for constant temperatures. The equation is

$$r_a(T_{Aa}) = \frac{r_c(T_1) \cdot h_1 + r_c(T_2) \cdot h_2}{h_1 + h_2}, \tag{11}$$

where T_{Aa} is the daily average (mean) hourly alternating temperature:

$$T_{Aa} = \frac{T_1 \cdot h_1 + T_2 \cdot h_2}{h_1 + h_2}. \tag{12}$$

Ludwig and Cable (1933) also examined the development rate using two daily alternating temperatures. One of their experimental designs was as follows. For experiments at 20 and 30 °C, the pupae of the common fruit fly (*Drosophila melanogaster* Meigen, Diptera: Drosophilidae) were exposed for the first 24 h to 20 °C and the second 24 h to 30 °C. Three curves estimated using Eqs. 11 and 12 for the three types of alternating temperature are shown in Fig. 2. The figure shows that the development rate at peak temperatures is



$$r(T) = \frac{0.18559 \dfrac{T}{294.72} \exp\left[\dfrac{16996}{1.987}\left(\dfrac{1}{294.72} - \dfrac{1}{T}\right)\right]}{1 + \exp\left[\dfrac{-60276}{1.987}\left(\dfrac{1}{283.84} - \dfrac{1}{T}\right)\right] + \exp\left[\dfrac{62576}{1.987}\left(\dfrac{1}{306.12} - \dfrac{1}{T}\right)\right]}$$

Fig. 1 Development rate at constant temperatures expressed by Eq. (1) of the SSI model and some characteristics of the model *curve* and *line*. **a** The *filled* and *open circles* are the observed values that were used to estimate the model parameters. The *filled circles* were also used for the linear fitting to the reduced major axis, whereas the open circles were excluded from the linear fitting. The *curve* indicates the development rates estimated using OptimSSI-P (with the optional selection 'optTL = 0'), whereas the *line* denotes the development rates obtained by the linear fitting. The three *open squares* denote the estimated rates at T_L, T_{Φ} and T_H. The presented data are from female pupae of *Drosophila melanogaster* reported by Ludwig and Cable (1933). **b** SSI model Eq. (1). **c** The first derivative expressed by Eq. (7). **d** The second derivative expressed by Eq. (8)

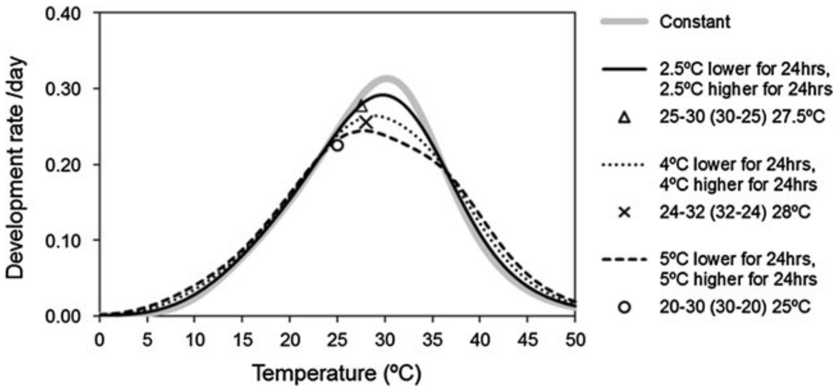


Fig. 2 Development rate at three types of alternating temperatures. The three estimated *curves* are drawn by applying Eq. (11) and intersecting with the SSI model *line* estimated at constant temperatures (Fig. 1a) at two intersection points for the horizontal axis shown in Fig. 1d. Each observed data point (Δ, X, O) almost fitted well on each estimated *line*. The presented data are from female pupae of *Drosophila melanogaster* reported by Ludwig and Cable (1933)

lower than the SSI model curves estimated at constant temperatures (Fig. 1a). It should be noted that three curves intersect with the SSI model curve estimated at constant temperatures at the two intersection points for the horizontal axis shown in Fig. 1d. Each observed data point fits well to each estimated curve.

In Fig. 3, results of two other examples of estimation at alternating temperatures are shown. One example is the case of the egg, larval and pupal stages of the diamondback moth (*Plutella xylostella* Linnaeus, Lepidoptera: Plutellidae; Liu et al. 2002). The other example is that of the female pupal stage of the cotton bollworm (*Helicoverpa armigera* Hübner, Lepidoptera: Noctuidae; Wu et al. 2009). These results also indicate the clear relationship between the $r_c(T)$ (constant) curve and the $r_a(T_{Aa})$ (alternating) curve, and the exact conformity between the cross points of the two curves and the $r_c''(T) = 0$ points. Moreover, the data points obtained for alternating temperatures in the laboratories indeed fit to the $r_a(T_{Aa})$ lines.

Natural fluctuating temperatures and development

In the examination of the relationship between alternating temperatures and development, two temperatures are usually selected to simplify results. However, it is possible to select many temperatures for each hour. Equations 11 and 12 are generalized as follows:

$$r_f(T_{Af}) = \frac{\sum_{i=1}^{h} r_c(T_i)}{h}, \tag{13}$$

where T_{Af} is the daily average hourly fluctuating temperature; T_i is the temperature at each ith hour. Accordingly, T_{Af} is

$$T_{Af} = \frac{\sum_{i=1}^{h} T_i}{h}. \tag{14}$$

Using the environmental temperature at each hour and these equations, the daily development rates of field insects could be traced exactly by accumulating them. In such a case, the h values in those equations are 24 units.

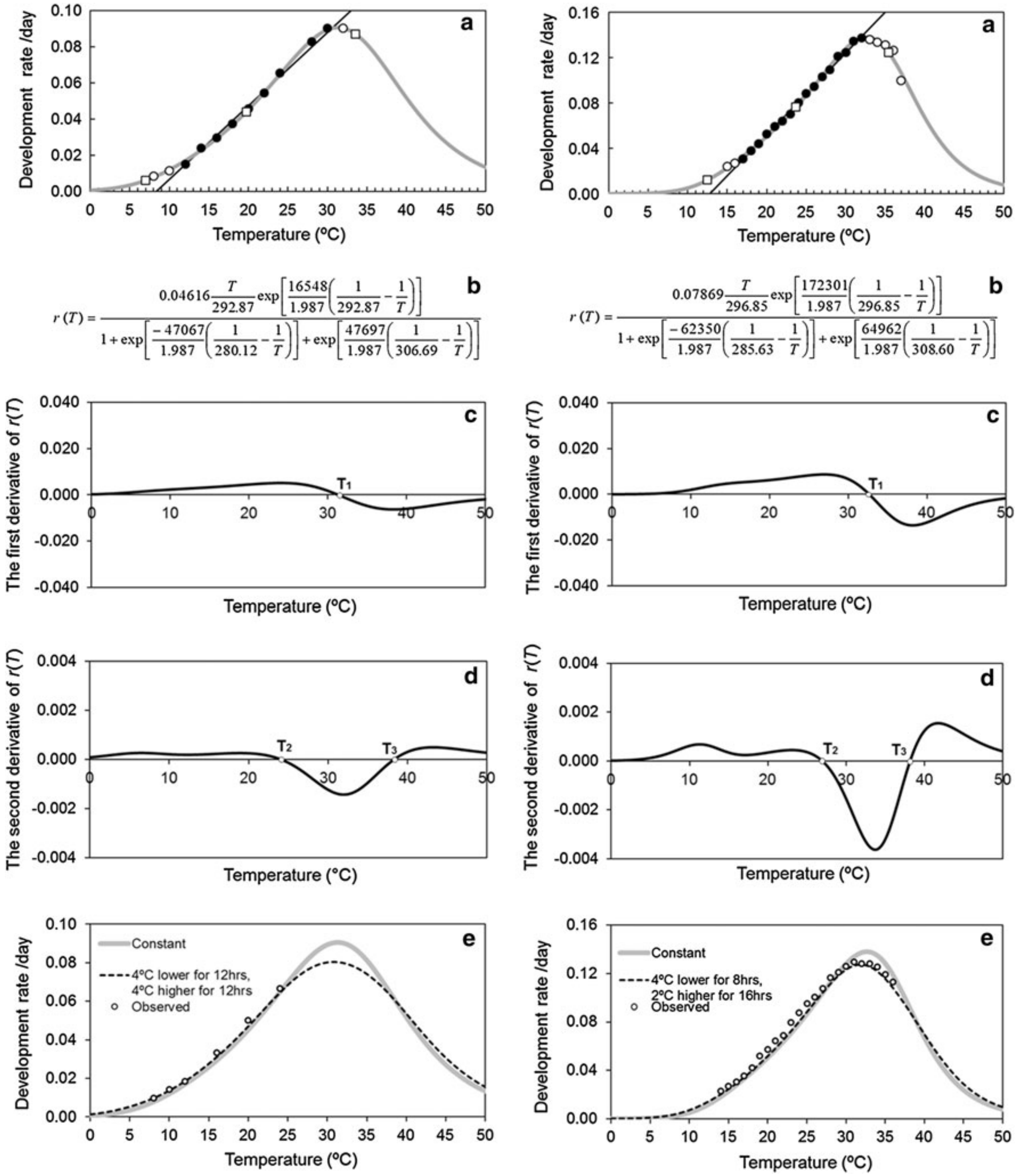
Prediction of development rate at natural fluctuating temperatures

Mathematical bases

The past events related to the natural development rate could be described using the SSI model, the development rate data obtained at constant temperatures and the climate records for the area. The past records in the same season could also help realize the same purpose. However, the temperature records worldwide are usually limited to only monthly mean, maximum and minimum temperatures. Here, we will present a mathematical solution to this limitation.

At a constant temperature, the value of a dependent variable (development rate) is fixed at a value of an independent variable (temperature). In contrast, the independent variable can be expressed by the Taylor series until the second order at which temperature normally fluctuates around an average:

$$\begin{aligned} r_f(T_{Af}) &\approx r_c(T_{Af}) \\ &\quad + \frac{r_c'(T_{Af}) \cdot E[T_f - T_{Af}]}{1!} + \frac{r_c''(T_{Af}) \cdot E[(T_f - T_{Af})^2]}{2!} \\ &= r_c(T_{Af}) + \frac{1}{2} r_c''(T_{Af})\, V[T_f] \end{aligned} \tag{15}$$



$$r(T)=\frac{0.04616\frac{T}{292.87}\exp\left[\frac{16548}{1.987}\left(\frac{1}{292.87}-\frac{1}{T}\right)\right]}{1+\exp\left[\frac{-47067}{1.987}\left(\frac{1}{280.12}-\frac{1}{T}\right)\right]+\exp\left[\frac{47697}{1.987}\left(\frac{1}{306.69}-\frac{1}{T}\right)\right]}$$

$$r(T)=\frac{0.07869\frac{T}{296.85}\exp\left[\frac{172301}{1.987}\left(\frac{1}{296.85}-\frac{1}{T}\right)\right]}{1+\exp\left[\frac{-62350}{1.987}\left(\frac{1}{285.63}-\frac{1}{T}\right)\right]+\exp\left[\frac{64962}{1.987}\left(\frac{1}{308.60}-\frac{1}{T}\right)\right]}$$

Fig. 3 Two examples of the development rate at alternating temperatures. The *left panels* show data at the egg, larval and pupal stages of the diamondback moth (*Plutella xylostella* Linnaeus, Lepidoptera: Plutellidae) (Liu et al. 2002). The *right panels* show the data at the female pupal stage of the cotton bollworm (*Helicoverpa armigera* Hübner, Lepidoptera: Noctuidae) (Wu et al. 2009). These results also indicate the clear relationship between the $r_c(T)$ (constant) and $r_a(T_{Aa})$ *curves* and the exact conformity between the cross points of the two lines and $r_c''(T) = 0$ points. Moreover, the data points obtained at the alternating temperatures in the laboratories indeed fit to the $r_a(T_{Aa})$ *lines*

where $V[T_f]$ is the variance of hourly fluctuating temperatures T_f around the average temperature T_{Af}. Although the discrepancy between the curve of the constant temperature model $r_c(T_c)$ and that of the fluctuating temperature model $r_f(T_{Af})$ was known as a theorem of "Jensen's inequality," the applications of Eq. 15 may cover many fields such as engineering and economics, focusing on the fact that the smaller the variance, the higher the accuracy. In entomology a similar approximate expression of the relationship between spatial distributions and population growth has been suggested by Yamamura (1989). The detailed proof of the equation is given in the "Appendix."

Thus, the SSI model predicts that when the curve shows a downward concave trend, the development rate will be higher at constant temperatures than at fluctuating temperatures at the same average temperature. When the curve shows a downward convex trend, the reverse will be true. The borders on the SSI model line between the downward convex curve and the downward concave curve are clearly shown as the intersection points between the $r_c''(T)$ curve line and the horizontal axis (Figs. 1, 2, 3). Accordingly, a quantitative proof for the Kaufman effect is mathematically completed. However, how is the variance in Eq. 15 estimated from simple climate records? Practically, this is an important remaining problem.

Variance determination

Variances in the cosine-wave simple model

To approximate the hourly temperature fluctuations, we suggest a simple cosine-wave model as follows:

$$g(h) = \begin{cases} \mu - \lambda\cos\left(\pi\frac{h}{h_d}\right), & \text{for } h \le h_d \\ \mu + \lambda\cos\left(\pi\frac{h-h_d}{24-h_d}\right), & \text{for } h > h_d \end{cases} \tag{16}$$

where h is the hour in a certain day, $h_d = h_M - h_m$ (h_M the hour at which the temperature is maximum (T_M) in a day, h_m the hour at which the temperature is minimum (T_m) in a day; mod 24), $\lambda = (T_M - T_m)/2$ and $\mu = (T_M + T_m)/2$. Following this equation, it is possible to estimate the temperature at each hour using only the maximum and minimum daily temperature records and their corresponding hours (when they are not known exactly, the rounded values are sufficient for estimating the variance because the variance is not affected by the hours). Then, the variance is expressed by the variable T_d ($=T_M - T_m$),

$$V_{f(CSW)}(T_d) = \frac{1}{2}\left(\frac{T_M - T_m}{2}\right)^2 = 0.125 \cdot T_d^2 \tag{17}$$

Variances in the cosine-wave adjusted model

Although the cosine-wave simple model can provide some appropriate fittings to real circadian rhythms of temperature, the daily average temperature is simply determined, namely, $(T_M + T_m)/2$. Therefore, an improved model is needed:

$$g(\alpha;h) = \begin{cases} \mu - \lambda\cos\left(\pi\left(\frac{h}{h_d}\right)^{\alpha}\right), & \text{for } h \le h_d \\ \mu + \lambda\cos\left(\pi\left(\frac{h-h_d}{24-h_d}\right)^{\frac{1}{\alpha}}\right), & \text{for } h > h_d \end{cases} \tag{18}$$

$$S(\alpha) = \left|\frac{1}{24}\sum_{h=0}^{23} g(\alpha;h) - \mu\right| \cong 0, \tag{19}$$

where $S(\alpha)$ is the performance function for determining the value of α that minimizes $S(\alpha)$. In practice, it is suitable to use Goal-Seeking software in the Excel tool menu (Excel 2010; Microsoft, Redmond, WA, USA) for the solution. Because the cosine-wave adjusted model can give an almost correct daily average temperature for recorded data from the natural environment, it is expected to obtain a more accurate variance from the general meteorological records summarized as the maximum, minimum and average temperatures only (Fig. 4).

The recorded hourly temperatures and the hourly temperatures estimated using the cosine-wave model, and their variances are shown in Table 1. The sampled date for each meteorological station was selected for the largest range of (T_d) temperatures in a day of the previous year. Because Chichibu and Asahikawa Cities are basin-inland areas, the diurnal variations of temperatures are larger than those in other areas in Japan. The T_d ($=T_M - T_m$) range of 14.9–22.2 °C results in a large variance from 27.6 to 61.9; in contrast; T_d of 7.4 °C in oceanic Naha gives a small variance of 6.9. There is a negligible difference of 1.2 at the maximum between the variance estimated using the cosine-wave adjusted model and that calculated using actual recorded values (Table 1).

For predictive purposes, it might be more appropriate to use the normal values of hourly temperatures calculated using long-term records than the real-time daily records. In Table 2, the variances of hourly temperatures were examined using the monthly mean of normal values in 30 years. The differences of estimated values among the five areas and their monthly fluctuations were well reflected in the regional and seasonal characteristics. Therefore, the cosine-wave models might be superior for estimating the variance of hourly temperatures in a day. These differences might be sufficiently applicable for Eq. 15; the detailed discussion about these differences will be continued below.

Variances in pulse-wave model

Let us assume that the daily alternating temperatures can be recorded with two values, T_M and T_m. The graph of

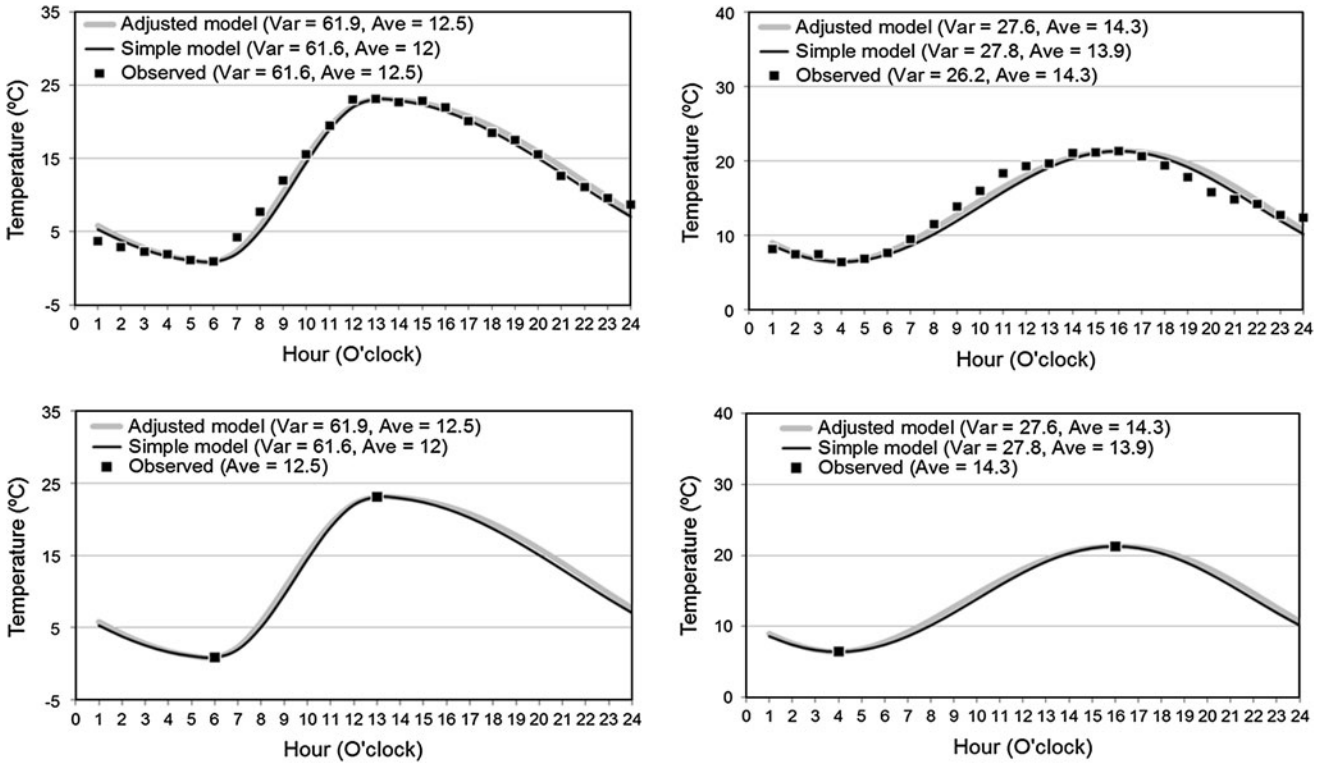


Fig. 4 Cosine-wave models fitted using for hourly fluctuating temperatures. The *left panels* are data from Chichibu City on 9 April 2012, and the *right panels* are those from Asahikawa City on 20 May 2012. The *upper panels* are fitted using the hourly temperature data set. The *lower panels* are fitted using only the maximum, minimum and average temperatures. The detailed information is shown in Table 1

temperature is demonstrated by using a pulse-wave, and then we denote by S_M and S_m (hrs) the durations of T_M and T_m, respectively. We note that $T_d = T_M - T_m$ and $S_M + S_m = 24$. Similarly to Eq. 12, the average of alternating temperatures is given by

$$T_{a(S_M:S_m)} = T_M \cdot \frac{S_M}{24} + T_m \cdot \frac{S_m}{24}. \tag{20}$$

The variance of alternating temperatures can be written as a function of T_d through thefollowing calculation:

$$\begin{aligned} V_{a(S_M:S_m)}(T_d) &= \left(T_{M^2} \cdot \frac{S_M}{24} + T_{m^2} \cdot \frac{S_m}{24}\right) - \left(T_{M^2} \cdot \left(\frac{S_M}{24}\right)^2 \right. \\ &\quad \left. + 2T_M T_m \cdot \frac{S_M}{24} \cdot \frac{S_m}{24} + T_{m^2} \cdot \left(\frac{S_m}{24}\right)^2\right) \\ &= (T_{M^2} - 2T_M T_m + T_{m^2}) \cdot \frac{S_M}{24} \cdot \frac{S_m}{24} \\ &= T_{d^2} \cdot \frac{S_M}{24} \cdot \frac{S_m}{24} \end{aligned} \tag{21}$$

Eq. 21 says that $V_{a(S_M:S_m)}(T_d) = V_{a(S_m:S_M)}(T_d)$. Thus we obtain the following results:

$$V_{a(12:12)}(T_d) = 0.2500 \cdot T_d^2 \tag{22a}$$

$$V_{a(8:16)}(T_d) = V_{a(16:8)}(T_d) = 0.2222 \cdot T_d^2 \tag{22b}$$

$$V_{a(6:18)}(T_d) = V_{a(18:6)}(T_d) = 0.1875 \cdot T_d^2 \tag{22c}$$

Figure 5 shows some of the development rate curves obtained using the SSI model and Eq. 15, assuming the presence of variances of hourly temperatures. The higher values of variance make the deviations larger, especially at the higher temperatures of insect development. However, at temperatures near the intrinsic optimum temperature T_Φ, the deviations are comparatively small. It might be difficult to detect the deviations, especially when the variance is less than 25. The variance of 25 corresponds to the ranges of maximum and minimum temperatures, which are $T_d = 14.1$ °C in the cosine-wave simple model and $T_d = 10.0$ °C in the pulse-wave model of 12 h of alternating temperatures. Generally, at least in Japan, it might be difficult to find any places and any seasons with high variances as far as analyzing the limited data on normal values accumulated over 30 years (1981–2010), as shown in Table 2. Thus, the deviation, namely, the Kaufmann effect, is markedly effective for the seasons or

Table 1 Recorded and estimated hourly temperatures and their variances. Hourly temperatures were estimated using the cosine-wave adjusted model

Hour	Chichibu		Asahikawa		Tokyo		Nagoya		Naha	
	St. no. 47641		St. no. 47407		St. no. 47662		St. no. 47636		St. no. 47936	
	9 Apr 2012		20 May 2012		24 Apr 2012		24 Apr 2012		27 Mar 2012	
	Recorded	Estimated	Recorded	Estimated	Recorded	Estimated	Recorded	Estimated	Recorded	Estimated
1	3.7	5.8	8.1	8.9	14.9	15.5	13.3	14.2	14.7	15.2
2	2.9	4.2	7.4	7.6	15.2	14.9	13.3	13.1	15.0	14.5
3	2.3	2.8	7.4	6.7	15.2	14.5	12.4	12.2	14.4	14.0
4	1.9	1.8	6.4	6.4	14.8	14.3	12.7	11.7	13.6	13.6
5	1.1	1.1	6.8	6.8	14.2	14.2	11.5	11.5	13.3	13.3
6	0.9	0.9	7.6	7.8	14.3	14.3	11.7	12.1	13.2	13.2
7	4.2	2.3	9.4	9.2	15.4	14.7	13.6	13.6	14.0	13.7
8	7.7	5.8	11.5	10.9	16.2	15.4	15.9	15.6	16.0	14.7
9	12.0	10.4	13.8	12.7	17.8	16.5	19.1	18.0	17.2	16.0
10	15.6	15.2	15.9	14.6	18.6	17.9	21.3	20.3	18.3	17.4
11	19.5	19.4	18.3	16.4	20.5	19.4	24.0	22.4	19.7	18.7
12	23.0	22.1	19.3	18.1	21.7	20.9	24.4	24.1	20.0	19.7
13	23.1	23.1	19.6	19.4	22.9	22.2	24.8	25.1	19.8	20.4
14	22.7	23.0	21.0	20.5	23.3	23.1	25.5	25.5	20.6	20.6
15	22.9	22.6	21.1	21.1	23.4	23.4	25.1	25.4	20.5	20.6
16	22.0	21.8	21.3	21.3	23.3	23.1	24.1	25.1	20.2	20.4
17	20.1	20.7	20.6	21.1	21.5	22.5	23.6	24.5	19.3	20.2
18	18.5	19.4	19.4	20.6	20.7	21.8	22.3	23.7	18.6	19.9
19	17.5	17.7	17.8	19.6	19.4	20.9	20.9	22.6	18.1	19.4
20	15.6	15.9	15.8	18.3	17.4	19.9	20.4	21.3	17.5	18.8
21	12.6	13.9	14.8	16.6	17.2	18.9	19.6	19.9	17.5	18.2
22	11.1	11.8	14.2	14.6	17.1	17.9	18.3	18.4	17.4	17.4
23	9.6	9.7	12.7	12.6	17.2	17.0	17.6	16.9	17.1	16.7
24	8.7	7.7	12.3	10.7	17.2	16.2	17.4	15.5	16.4	15.9
T_A	12.5	12.5	14.3	14.3	18.3	18.3	18.9	18.9	17.2	17.2
T_M	23.1	23.1	21.3	21.3	23.4	23.4	25.5	25.5	20.6	20.6
T_m	0.9	0.9	6.4	6.4	14.2	14.2	11.5	11.5	13.2	13.2
$T_M - T_m$	22.2	22.2	14.9	14.9	9.2	9.2	14.0	14.0	7.4	7.4
Var	61.6	61.9	26.2	27.6	9.4	10.4	22.4	24.5	5.7	6.9

Recorded data are cited from the web site of the Japan Meteorological Agency (http://www.jma.go.jp/)

T_A average (mean) temperature (°C), T_M maximum temperature (°C), T_m minimum temperature (°C), *Var* variance

places where the fluctuation of temperatures in a day is quite extreme in global environments.

Complete picture

The laboratory experiments on insect development rate conducted at constant and alternating temperatures are not a final goal on their own but as a means to predict a future event in an actual environment. Thus, the many methods described above should be related to each other.

At constant temperatures, the temperature and development rate function $r_c(T)$ in the SSI model is well known:

Method 1 When the hourly temperatures for the duration of insect development are known, the real development rate at an average temperature in a day can be directly estimated using Eq. 13.

Method 2 When the maximum and minimum temperatures in a day are only known, the real development rate at an average temperature in a day can be estimated using Eq. 15 after estimating the variance of temperatures in a day using Eqs. 9, 18 and 19.

Table 2 Variances of hourly temperatures estimated from the monthly mean of normal values over 30 years (1981–2010) using the cosine-wave simple model and the cosine-wave adjusted model

Month	Chichibu station		Asahikawa station		Tokyo station		Nagoya station		Naha station	
	Simple	Adjusted	Simple	Adjusted	Simple	Adjusted	Simple	Adjusted	Simple	Adjusted
Jan	21.1	20.6	9.7	9.7	6.8	6.8	8.4	8.2	3.0	3.0
Feb	20.5	20.1	14.0	13.8	7.0	7.0	10.1	9.9	3.1	3.1
Mar	19.5	19.4	9.9	9.9	7.4	7.4	11.8	11.6	3.4	3.3
Apr	21.1	21.0	17.1	17.0	8.2	8.2	13.3	13.1	3.3	3.2
May	17.7	17.5	18.9	18.9	6.8	6.8	11.5	11.3	3.0	2.9
Jun	11.0	10.9	16.0	15.4	5.1	5.1	8.4	8.2	2.6	2.6
Jly	10.1	9.8	12.3	11.8	5.1	5.0	7.6	7.4	3.1	3.0
Aug	11.3	10.9	11.3	11.1	5.4	5.3	9.0	8.5	3.0	2.9
Sep	8.8	8.5	13.5	13.2	4.7	4.5	7.8	7.5	3.0	2.9
Oct	12.5	12.1	14.9	14.8	5.1	5.1	9.5	9.3	2.9	2.8
Nov	18.6	18.0	7.6	7.6	6.1	6.1	9.9	9.8	2.8	2.7
Dec	22.1	21.4	6.3	6.3	6.7	6.7	9.0	8.9	3.0	3.0

The original data were cited from the web site of Japan meteorological agency (http://www.jma.go.jp/). As the temperatures were recorded at 3, 6, 9, 12, 15, 18, 21 and 24 o'clock, each variance was calculated for the temperatures at these times and for the maximum and minimum temperatures

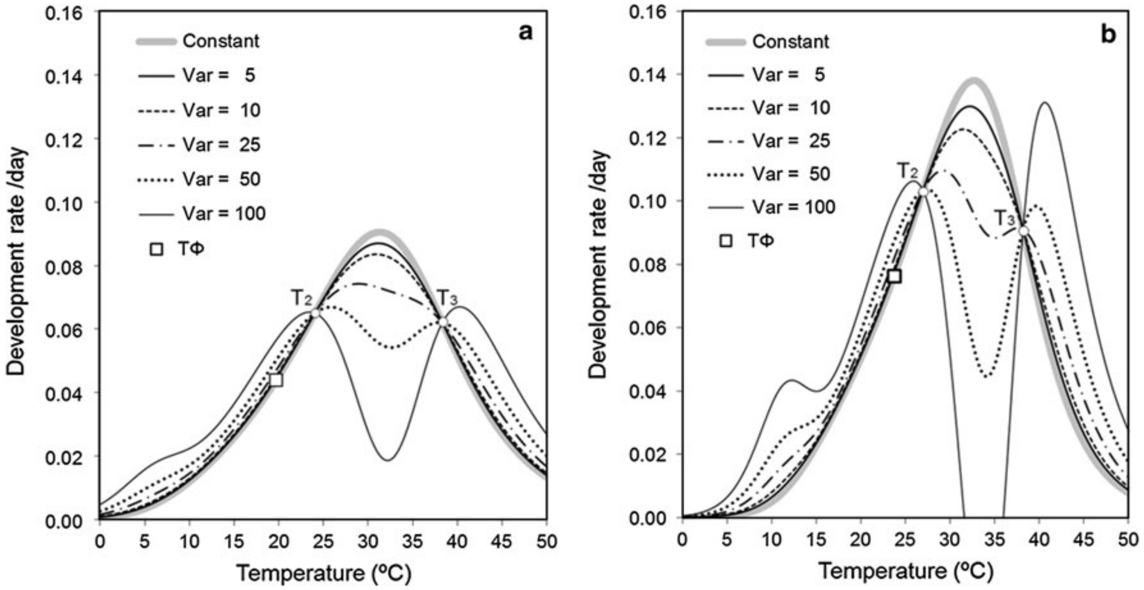


Fig. 5 Development rate *curves* illustrated using the SSI model Eq. (15) with the assumption that the variances of hourly temperatures are known. The *left panel* shows data of the diamondback moth. The *right panel* shows those of the cotton bollworm (see the explanation in Fig. 3)

Method 3 When the maximum and minimum temperatures are known after conducting experiments at alternating temperatures, the real development rate at the mean temperature in a day can be estimated using Eq. 15 after directly calculating or estimating the variance of temperatures in a day using Eqs. 21 or 22a–c. In alternating temperatures, the variance should be adjusted from artificial fluctuation to that under natural fluctuations of temperatures as much as possible. Then, the relationship between $V_{12:12}$ and $V_{\mathrm{f(CSW)}}\,(T_{\mathrm{d}})$ as an example is expressed by

$$V_{\mathrm{f(CSW)}}(T_{\mathrm{d}}) = \frac{1}{2} V_{\mathrm{a(12:12)}}(T_{\mathrm{d}}) \tag{23}$$

which is derived from Eqs. 17 and 22a.

However, method 3 can be excluded because it is theoretically possible to predict the development rate in the environment by applying method 2. Hence, the laboratory experiments on alternating temperatures might help detect some important factors that may not conform to the temperature dependency.

Figure 6 shows simulations of method 2 using the data of the diamondback moth (Liu et al. 2002) and the record of hourly temperatures at Nara district, Japan, in the hottest summer season ever recorded, August 2010. The development of the preadult stages was completed at the time

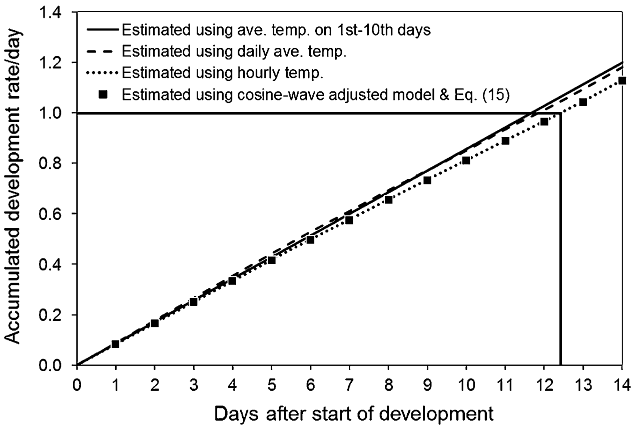


Fig. 6 Simulations for accumulated development rates of the diamondback moth estimated by the four methods. The predictive simulation using the cosine-wave adjusted model, daily maximum–minimum temperature and Eq. (15) enables the detection of negative effects of high temperatures in the midsummer season on the development. Hourly records of temperatures are from the Nara district of Japan obtained in August 2010. (Nara Station no. 47401; Lat., 45°24.9′N; Lon., 141°40.7′E. (http://tenki.jp/past/detail/pref-32.html?year=2010&month=8&day=1) The development was completed (*Y*-axis = 1.0) at noontime on the 13th day. (On the *X*-axis, the interval 0–1 corresponds to the 1st day, 1–2 to the 2nd day 12–13 to the 13th day in August.) The presented data are from the diamondback moth reported by Liu et al. 2002 (see the explanation in Fig. 3)

when the accumulated development rate was just 1.0. The emergence date of the moth was accurately determined by calculating using the temperature at 11 o'clock of 13 August. Almost the same date was estimated using method 2. In contrast, the dates estimated using the mean temperature over the duration of development showed shorter days to emergence, namely, 0.5–1.0 days. These results indicate the decrease in development rate at fluctuating temperatures in the higher temperature regions in comparison with the case of constant temperatures, as shown in Fig. 5. Thus, the efficacy of method 2 is proved.

However, the approach needs to be further tested under different conditions. Additionally, it is important to investigate how well hourly temperature modeling can be conducted for those situations where the actual microclimate is somewhat different to standard meteorologically measured temperature.

The mathematical models for the development rates of insects and mites at fluctuating temperatures suggested here must be of importance for predictive applications, ranging from pest management to conservation in changing climates.

Acknowledgments We sincerely thank Dr. Kohji Yamamura for his invaluable suggestions at the start of this study.

Appendix: derivation of the SSI model for fluctuating temperatures

In the text, the SSI model for fluctuating temperatures is derived employing that for constant temperatures. The model equation provides the expected value of a function, the variable of which is random.

Let f be a smooth function. The Taylor series of $f(x)$ at point x_0 is given by the form

$$f(x) = f(x_0) + f'(x_0)(x-x_0) + \frac{f''(x_0)}{2!}(x-x_0)^2 + \frac{f'''(x_0)}{3\,!}(x-x_0)^3 + \cdots. \tag{24}$$

By ignoring the third and higher order terms, it follows that in the neighborhood of x_0,

$$f(x) \approx f(x_0) + f'(x_0)(x-x_0) + \frac{f''(x_0)}{2!}(x-x_0)^2. \tag{25}$$

Let X be a random variable and let us denote $E[X]$ with the expected value of X, as the variance $V[X]$. Using the above argument, in the neighborhood of $E[X]$, $f(X)$ can be approximately written by

$$f(X) = f(E[X]) + f'(E[X])(X - E[X]) + \frac{f''(E[X])}{2!}(X - E[X])^2. \tag{26}$$

Note that $f(X)$ is a random variable. Taking the expected values of both sides of Eq. 26, we find

$$\begin{aligned} E[f(X)] &= E[f(E[X])] + E[f'(E[X])(X - E[X])] \\ &\quad + E[\frac{f''(E[X])}{2!}(X - E[X])^2] \\ &= f(E[X]) + f'(E[X])E[X - E[X]] \\ &\quad + \frac{f''(E[X]\,)}{2!}E[(X - E[X])^2] \\ &= f(E[X]) + f'(E[X])(E[X] - E[X]) \\ &\quad + \frac{f''(E[X])}{2!}E[(X - E[X])^2] \\ &= f(E[X]) + \frac{1}{2}f''(E[X])\,V[X]. \end{aligned} \tag{27}$$

If $V[X]$ is invariant for any X, $E[f(X)]$ is expressed as a function of $E[X]$ by Eq. 27.

Let us denote T_f as fluctuating temperatures; T_f is a random variable. Write $T_{Af} = E[T_f]$. In the SSI model for fluctuating temperatures, $r_f(T_{Af})$ is obtained by replacing f and X of Eq. (27) with r_c and T_f, respectively, that is,

$$r_f(T_{Af}) = r_c(T_{Af}) + \frac{1}{2}\,r_c''(T_{Af})\;V[T_f]. \tag{28}$$

Jensen's inequality

In order to explain the relationship between the graphs of the constant temperatures model $r_c(T_c)$ and the fluctuating temperatures model $r_f(T_{Af})$, we introduce the following theorem known as "Jensen's inequality." For details, refer to Feller (1966).

Theorem *Let X be a random variable. If f is a convex function, then*

$$E[f(X)] \geq f(E[X]).$$

If f is a concave function, then

$$E[f(X)] \leq f(E[X]).$$

When the two graphs are plotted using the common horizontal axis T, "Jensen's inequality" implies that $r_f(T) \geq r_c(T)$ for T to satisfy $r''_c(T) > 0$; $r_f(T) \leq r_c(T)$ for $r''_c(T) < 0$.

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