LETTER TO THE EDITOR

Confidence interval of intrinsic optimum temperature estimated using thermodynamic SSI model

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Abstract The intrinsic optimum temperature for the development of ectotherms is one of the most important factors not only for their physiological processes but also for ecological and evolutional processes. The Sharpe–Schoolfield–Ikemoto (SSI) model succeeded in defining the temperature that can thermodynamically meet the condition that at a particular temperature the probability of an active enzyme reaching its maximum activity is realized. Previously, an algorithm was developed by Ikemoto (Tropical malaria does not mean hot environments. *Journal of Medical Entomology*, 45, 963–969) to estimate model parameters, but that program was computationally very time consuming. Now, investigators can use the SSI model more easily because a full automatic computer program was designed by Shi *et al.* (A modified program for estimating the parameters of the SSI model. *Environmental Entomology*, 40, 462–469). However, the statistical significance of the point estimate of the intrinsic optimum temperature for each ectotherm has not yet been determined. Here, we provided a new method for calculating the confidence interval of the estimated intrinsic optimum temperature by modifying the approximate bootstrap confidence intervals method. For this purpose, it was necessary to develop a new program for a faster estimation of the parameters in the SSI model, which we have also done.

Key words approximate bootstrap confidence intervals, bias-corrected and accelerated, bootstrap percentiles, development rate, temperature

Introduction

To elucidate the effects of temperature on ectotherm development, Ikemoto (2005) proposed a definitive concept; that is, the intrinsic optimum temperature T_Φ for development. The temperature exhibits the minimum effects on enzymes inactivation related to development at low and high temperatures. T_Φ is the most important parameter

in the useful nonlinear thermodynamic model (Sharpe–Schoolfield–Ikemoto [SSI] model; Ikemoto, 2005, 2008; Shi *et al.*, 2011), which was developed on the basis of the SS model developed by Sharpe & DeMichele (1977) and Schoolfield *et al.* (1981). The SSI model equation is expressed as follows:

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

where $r(T)$ represents the development rate (the dependent variable) at an absolute temperature T (the independent variable). All the other parameters are constants: T_L, T_H, and T_Φ represent the absolute

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[Correction added on 2 July 2012, after first online publication: Appendix S1 has been added as a Supporting Information.]

Table 1 Summary of symbols used.

Symbol	Description
r	Mean development rate (1/day)
T	Absolute temperature (K) (273.15 K $= 0°$C)
R	Gas constant (1.987 cal/deg/mol)
ΔH_A	Enthalpy of activation of the reaction that is catalyzed by the enzyme (cal/mol)
ΔH_L	Change in enthalpy associated with low-temperature inactivation of the enzyme (cal/mol)
ΔH_H	Change in enthalpy associated with high-temperature inactivation of the enzyme (cal/mol)
T_L	Temperature at which the enzyme is 1/2 active and 1/2 low-temperature inactive (K)
T_H	Temperature at which the enzyme is 1/2 active and 1/2 high-temperature inactive (K)
T_Φ	Intrinsic optimum temperature at which the probability of enzyme being in the active state is maximal (K)
ρ_Φ	Development rate at the intrinsic optimum temperature T_Φ (1/day) assuming no enzyme inactivation

temperatures; ΔH_A, ΔH_L, and ΔH_H represent the enthalpy changes; R is the universal gas constant; and ρ_Φ is the approximate development rate at T_Φ. The detailed definitions of all the constants are shown in Table 1. In this definition, T_Φ must have the relationships with the other constants as follows (Ikemoto, 2005):

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

Under the conditions given in equations (1) and (2), the reversed denominator of equation (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:

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

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 ectotherms; however, the confidence interval of estimated T_Φ is not yet known. Here, we present a method and a program to calculate the

confidence interval of estimated T_Φ. These method and program enable investigators to use the SSI model in a more satisfactory way.

Further improvement of the program from SSI-P to OptimSSI-P

Ikemoto (2005, 2008) established a program for estimating the constants in the SSI model; however, the procedures in the estimation of each constant were difficult because the model has multiple constants. The program works well but it is very time consuming. Shi *et al.* (2011) succeeded in developing a new program (SSI-P) that runs on R software for a faster estimation of the parameters in the SSI model. One complete run of the SSI-P takes less than 1 min. However, we need a much faster computing for assessing the T_Φ estimate with its confidence interval because the procedure might be extraordinarily time consuming.

Thus, it was obligatory to speed up the running of the SSI-P, which Shi *et al.* (2011) achieved. Consequently, we succeeded in constructing a new program (OptimSSI-P) by incorporating the optimization algorithm of Nelder & Mead (1965). The algorithm is now utilizable as the optim function in R software.

As it only takes 1/1000–1/100 seconds to complete a run for a dataset of temperature-dependent development rates. Moreover, it is unnecessary to set an increment of a specified parameter in the SSI model during the parameter fitting that was proposed by Shi *et al.* (2011). For example, the following increments in Shi *et al.* (2011) are unnecessary now: setting an increment of T_Φ as 0.5 K and setting the increment of ΔH_L or ΔH_H as 500 cal/mol. In addition to such advantages, an important revision for the estimation T_L has been made. In the SSI-P, T_L was replaced by the development zero temperature (*t*) in K, which is designated as an estimated development zero temperature calculated from the reduced major axis by the Ikemoto & Takai (2000) method for the linear model. Although this replacement is practically acceptable, theoretically, T_L should be assumed as an unknown parameter. OptimSSI-P has allowed this change in the calculation process without being time consuming. However, such a replacement is sometimes required when the data points that are used to carry out the curve fitting are absent in the low-temperatures range, namely, in the S-shape tail of the model curve. Thus, OptimSSI-P is optional for the selection of for the replacement (optTL $= 0$), although the default setting is optimization in the calculation process (optTL $= 1$). In the following context, we will provide

the algorithms of these two programs, and compare the estimated confidence intervals by them.

OptimSSI-P algorithm

Step 1: Carry out a linear fitting by the reduced major axis (Ikemoto & Takai, 2000) on the data of development rate versus temperature in degrees Celsius over the intermediate temperatures. The thermal range performing the linear fit should be chosen by users. Then the development zero temperature (t in degrees Celsius) and the accumulative effective temperature (k in degree days) can be obtained. Set two options of T_L. If optTL $= 0$, we fix the final value of T_L to be t in K; if optTL $= 1$, we set the initial value of T_L to be t in K. The default option is optTL $= 1$.

Step 2: Carry out a linear fitting by the reduced major axis (Ikemoto & Takai, 2000) on the data of log development rate versus reciprocal absolute temperature over the intermediate temperatures. Let the estimated slope be β. Then, we fix the final value of ΔH_A to be $-R\beta$, where R is the universal gas constant.

Step 3: Set the initial value of T_Φ to be 298.15K; set the initial values of ΔH_L and ΔH_H (i.e., IniHL and IniHH) to be $-50\,000$ and $50\,000$, respectively.

Step 4: Build an optimization function of χ^2 related to development rate. If optTL $= 1$, T_Φ, ΔH_L, ΔH_H, and T_L are considered as unknown parameters in the development rate function, that is, equation 1; if optTL $= 0$, T_Φ, ΔH_L, and ΔH_H are considered as unknown parameters (but T_L as a known parameter) in the development rate function. T_H is also calculated by equation 2; and $\rho_\Phi = (T_\Phi - t)/k$.

Step 5: Use the development rate function and observations of development rate function to minimize χ^2. Then we could obtain those unknown parameters: T_Φ, ΔH_L, ΔH_H, and T_L for the option of optTL $= 1$; T_Φ, ΔH_L, and ΔH_H for the option of optTL $= 0$. In practice, for reducing the deviation on the parameter estimate owing to the local optimization, we set nine combinations of (IniHL-40 000, IniHL, IniHL+40 000) and (IniHH-40 000, IniHH, IniHH+40 000) during performing the optimization procedure. We finally choose the combination of ΔH_L and ΔH_H that can lead to the least χ^2.

Table 2 shows the comparison of fitted parameters between the SSI-P and OptimSSI-P. Both programs can provide satisfactory goodness-of-fit based on χ^2. By comparison, the OptimSSI-P can provide a smaller χ^2 than that of the SSI-P. Therefore, the OptimSSI-P is better in the exceptional running speed and accuracy.

Confidence interval of T_Φ estimated by the modified ABC method (mABCSSI-P)

In statistics, bootstrap is a computer-based method for assigning measures of accuracy to sample estimates (Efron & Tibshirani, 1994). Generally, it falls in a broader class of resampling methods similar to the Monte-Carlo Simulation. The bootstrap is, in practice, used to estimate the properties of an estimator (such as the variance) by measuring those properties when resampling replications approximate an unknown distribution. This can be implemented by constructing a number of resampling replications of the observed dataset. The suitable number of times of randomized resampling is usually 2 000–10 000. Therefore, it was necessary to speed up the running of the SSI-P for obtaining the standard error or a confidence interval of T_Φ. There are some types of bootstrap methods to calculate the confidence interval, such as bootstrap percentile, bootstrap-t, and BC$_a$ methods. Here, the approximate bootstrap confidence intervals (ABC) method (Efron & Tibshirani, 1994) was selected as the most appropriate method to evaluate T_Φ.

The ABC method is an analytical approximation to the BC$_a$ method (Efron & Tibshirani, 1994) to cut down the 2 000 or so bootstrap simulations for estimating a confidence interval. Indeed, the ABC method involves no simulation at all, which was surprising, especially because the method gives excellent results for smoothly differentiable statistics such as the correlation coefficient (Efron, 2003). Therefore, the ABC method is appropriate in terms of providing accurate results with the smallest loads of calculation. This method was developed by DiCiccio & Efron (1992, 1996). And it has been included by a standard package of "boot" in R software. We used the abc.ci function in the "boot" package to estimate the confidence intervals of parameters in the SSI model. The abc.ci function is, in fact, a nonparametric ABC method (see Efron & Tibshirani, 1994 for details).

The number of data point is usually small in such kind of dataset of temperature-dependent development rates. However, the structure of SSI model used to fit the dataset is complex. Therefore, the original method to correct bias (equation [4.11] published in DiCiccio & Efron, 1992) was not powerful. Thus, we added the modifications to the original procedure. Namely, we select CI which is not a narrower CI but a smaller bias between the estimation by OptimSSI and median by ABC. The smaller value of epsilon (ε) of ABC method is much more appropriate (equation [4.8] published in DiCiccio & Efron, 1992). However, when we use the small value of epsilon (ε), the original ABC could be scarcely able to give a reasonable

Table 2 Comparison of fitted results between SSI-P and OptimSSI-P programs.

Parameter (Unit)	Sample 1		Sample 2		Sample 3		Sample 4		Sample 5		Sample 6	
	SSI-P	OptimSSI-P	SSI-P	OptimSSI-P	SSI-P	OptimSSI-P	SSI-P	OptimSSI-P	SSI-P	OptimSSI-P	SSI-P	OptimSSI-P*
T_Φ (K)	295.15	294.94	293.15	293.17	289.15	289.36	295.65	294.90	296.01	296.03	293.15	292.93
ρ_Φ	0.1069	0.1047	0.3274	0.3281	0.0928	0.0947	0.54215	0.5039	0.14974	0.1499	0.03116	0.03056
ΔH_A	16 651	16 651	21 855	21 855	16 442	16 442	18 005	18 005	19 442	19 442	15 902	15 903
ΔH_L	−72 500	−87 697	−85 000	−80 925	−58 000	−51 037	−61 000	−81 715	−72 000	−68 034	−58 500	−60 119
ΔH_H	67 500	68 024	59 500	59 585	42 500	42 727	56 500	55 452	66 500	66 489	67 000	65 328
T_L (K)	285.18	286.10	285.394	285.12	278.57	277.90	285.00	286.00	286.40	286.01	281.62	281.62
T_H (K)	306.47	306.48	303.90	303.90	303.61	303.61	307.82	307.75	306.95	306.97	304.39	304.40
χ^2	0.002544	0.002345	0.014521	0.014374	0.000319	0.000184	0.016540	0.010199	0.001440	0.001382	0.000100	0.000096

Sample 1: *Kampimodromus aberrans* (Acari: Phytoseiidae), egg + larva + first–second nymphal period in Broufas *et al.* (2007).

Sample 2: *Toxorhynchites brevipalpis* (Diptera: Culicidae), egg period in Trpis (1972).

Sample 3: *Rhopalosiphum maidis* (Homoptera: Aphididae), larva and nymphal period in Kuo *et al.* (2006).

Sample 4: *Bactrocera dorsalis* (Diptera: Tephritidae), egg period in Messenger & Flitters (1958).

Sample 5: *Aedes aegypti* (Diptera: Culidae), larval period in Gilpin & McClelland (1979).

Sample 6: *Epilachna varivestis* (Coleoptera: Coccinellidae), larval period in Shirai & Yara (2001).

*In this case, T_L was directly replaced by t in K (development zero temperature) according to the linear fitting as in the OptimSSI-program with the option of optTL = 0 instead of that estimated using the optimization procedure as in the OptimSSI-Program with the option of optTL = 1 because of the lack of data points in the low-temperature range.
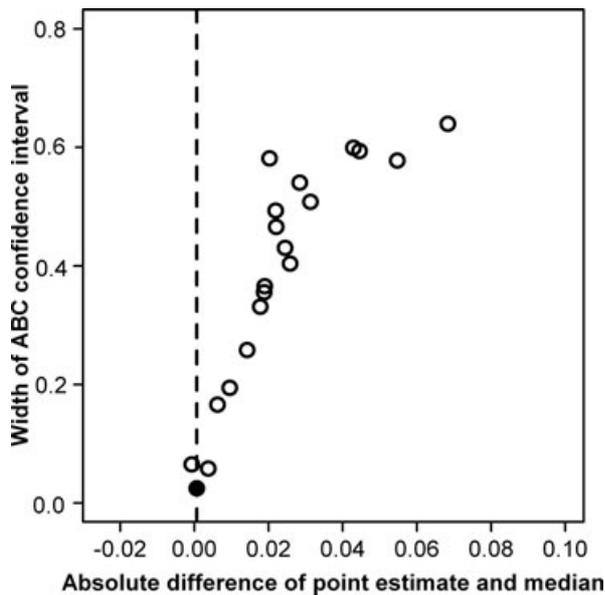
Fig. 1 Example of shrinking tendency of confidence intervals according to reduction of differences between point estimate by OptimSSI and median by ABC (IniTphi = 300 K). The presented data are from Trpis (1972) (Sample 2 in Table 2).

result. Thus, we added the modification for the procedure of ABC instead of modification for the body of ABC because of the difficulties.

On the operation of the ABC method a modification was done in the followings. The function ε, which limits the range of the fluctuations of data, usually needs to be determined before a shadow bootstrapping of the program. Here, trial calculations were conducted with the value of ε

from 0.001 to 5.0. Then, the values of the confidence limits were selected when the point estimation of T_Φ, which was calculated by the OptimSSI-P and the median of T_Φ, which was derived from the modified ABCSSI method were very approximate (Fig. 1).

The confidence intervals estimated by the mABCSSI method were shown in Table 3 in comparison with those estimated by the bootstrap percentile method and/or the BC_a method. The mABCSSI method gave the narrowest confidence intervals relative to the bootstrap percentile method and/or BC_a method. Owing to some limitations in the basic procedure, the times required by using mABC-SSI to estimate a confidence interval was smaller than the usual number of $\geq 2\,000$ required by using the bootstrap percentile method and/or the BC_a method (Efron & Tibshirani, 1994), but less than 200 times are enough for the cases with very small sample size, for example, the sample size from 6 to 19.

We provided the corresponding programs based on R statistical software (http://www.r-project.org/) for performing the OptimSSI-P and for estimating the confidence interval of intrinsic optimum temperature in Appendix S1 (R version 2.13.1; Platform: i386-pc-mingw32/i386 [32-bit]).

Discussion

Sample size and mABCSSI method

Regarding a small sample, it would be unrealistic to accurately estimate the confidence intervals by only using

Table 3 Confidence intervals (CIs) of T_Φ (K) assessed by mABC-P program.

	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6*
T_Φ by OptimSSI-P[1]	294.943 8	293.166 0	289.363 8	294.898 0	296.026 0	292.930 6
Median of T_Φ in mABC[2]	294.939 4	293.159 0	289.348 9	294.892 4	296.038	292.929 1
At ε function	1.9	0.7	0.07	0.1	1.7	0.9
Difference between (1) and (2)	0.004 4	0.007 0	0.014 8	0.005 6	−0.012 0	0.001 5
mABC 95% Lower CI	294.46	292.94	288.74	294.72	295.69	292.90
95% Upper CI	295.11	293.46	293.01	295.16	296.28	293.84
Bootstrap 95% Lower CI	292.11	291.93	284.41	292.27	293.30	289.20
95% Upper CI	299.59	294.90	294.02	297.45	298.16	295.90
Number of times of resampling	2 000	2 000	2 000	2 000	2 000	2 000
BC_a 95% lower CI	290.72	291.64	283.98	291.82	293.34	289.36
95% Upper CI	298.34	294.49	293.42	297.07	298.20	295.99
Number of times of resampling	2 000	2 000	2 000	2 000	2 000	2 000

The modified ABCSSI method gave narrower confidence intervals than the bootstrap percentile method and/or BC_a method. The data are the same as those shown in Table 2.
*See the explanation in Table 2.

less than 10 data points for curve fitting and 4 for linear fitting, even though we succeed in estimating the intervals. In general, some statistical software only provide the standard error by the bootstrap or Jackknife by a default of 20, such as SPSS. For the estimation of standard error, the number 25 of bootstrap samples might be sufficient (Efron & Tibshirani, 1994). Indeed, the program can run to estimate T_Φ by using the replications of development rates (i.e., the crude data of development rates) at every temperature instead of by the mean or median of development rates at a temperature. For example, for five different temperatures on an experiment, there are many replications at each temperature. Suppose 30 insect replications at each temperature, the total number of data reaches 150. Our program should be enough for the crude data like this example.

However, almost all experiments related to thermal development rates of insects were generally arranged at some temperatures; usually, the number of data points (mean values of development rate) was approximately 10. Thus, it is important to investigate the accuracy of the confidence interval of one parameter in the SSI model calculated by the mABC method.

The malaria parasite, *Plasmodium falciparum*, in the body of vector mosquito, *Anopheles gambiae*, shows a thermodynamic development (Ikemoto, 2008). The original data points were 34, as reported in many papers. Figure 2 shows the results the rearrangement to reduce the data points from 34 of the original to 12 or 8 at 1°C or 2°C intervals. The confidence intervals calculated by the mABCSSI method were comparatively stable and small regardless of the sample size (number of data points). In contrast, the intervals calculated by the bootstrap percentile method or bootstrap BC_a method increased with the decrease of the sample size. Thus, the mABCSSI method could provide the narrowest confidence interval of T_Φ.

Evaluation of differences in T$_\phi$ *among three major fruit flies with confidence intervals*

Fruit flies (Diptera: Tephritidae), particularly the melon fly (*Dacus cucurbitae* Coquillett), Oriental fruit fly (*Bactrocera dorsalis* Hendel) and Mediterranean fruit fly, (*Ceratitis capitata* Wiedemann) are among the most destructive agricultural pests in the world through acres and acres of citrus and other kind of fruits at an alarming rate (Aluja & Norrbom, 1999). The melon fly is native to India, and is widely distributed in the most areas of this country. It can be found throughout most of Southern Asia, several countries in Africa, and some island groups in the Pacific. The Oriental fruit fly is widespread through
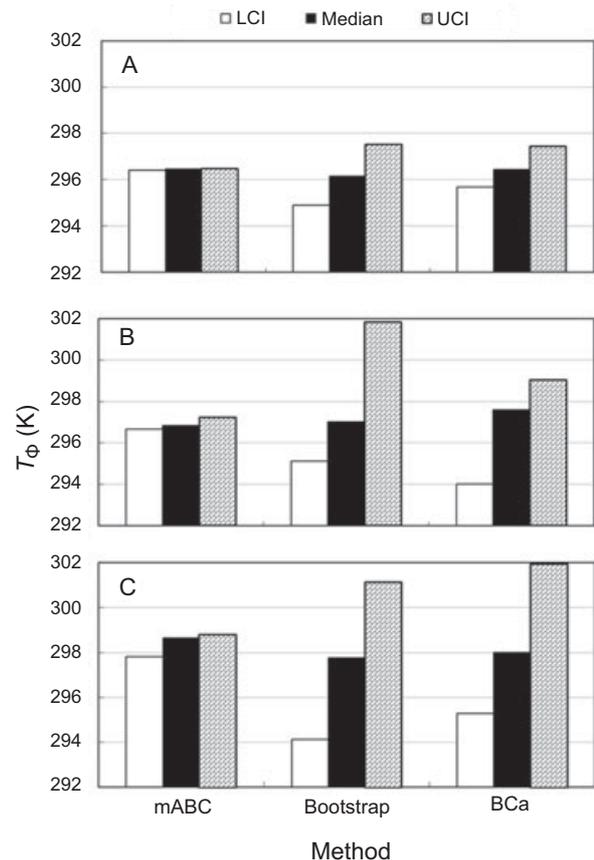
Fig. 2 Comparison among median, lower and upper confidence intervals calculated by the three methods, mABC, bootstrap percentile and BC$_a$. The sample sizes were 34 in A, 12 in B and 8 in C. The sample size was decreases by grouping at 1°C intervals (B) or 2°C intervals (C) from the original sample in A. The confidence intervals calculated by the mABC method were more stable and smaller than those calculated by the other methods. The overall shifts toward a higher temperature from A to C were caused by the smaller number of the original sample in the higher-temperature range. Data were from the malaria parasite, *Plasmodium falciparum* in the mosquito, *Anopheles gambiae* (Ikemoto, 2008).

much of the mainland of Southern Asia and neighboring islands, including Sri Lanka, Taiwan, and the Hawaiian Islands. The Mediterranean fruit fly (i.e., Medfly) is one of the most serious agricultural pests, particularly in the tropics and subtropics. Medfly is common in the Mediterranean, Southern Europe, Western Australia, South and Central America, and Hawaii. Medfly is not yet found in Southern and Southeast Asia.

The distribution limits of Medfly in the Hawaiian Islands had shifted from the lowland areas to the cooler
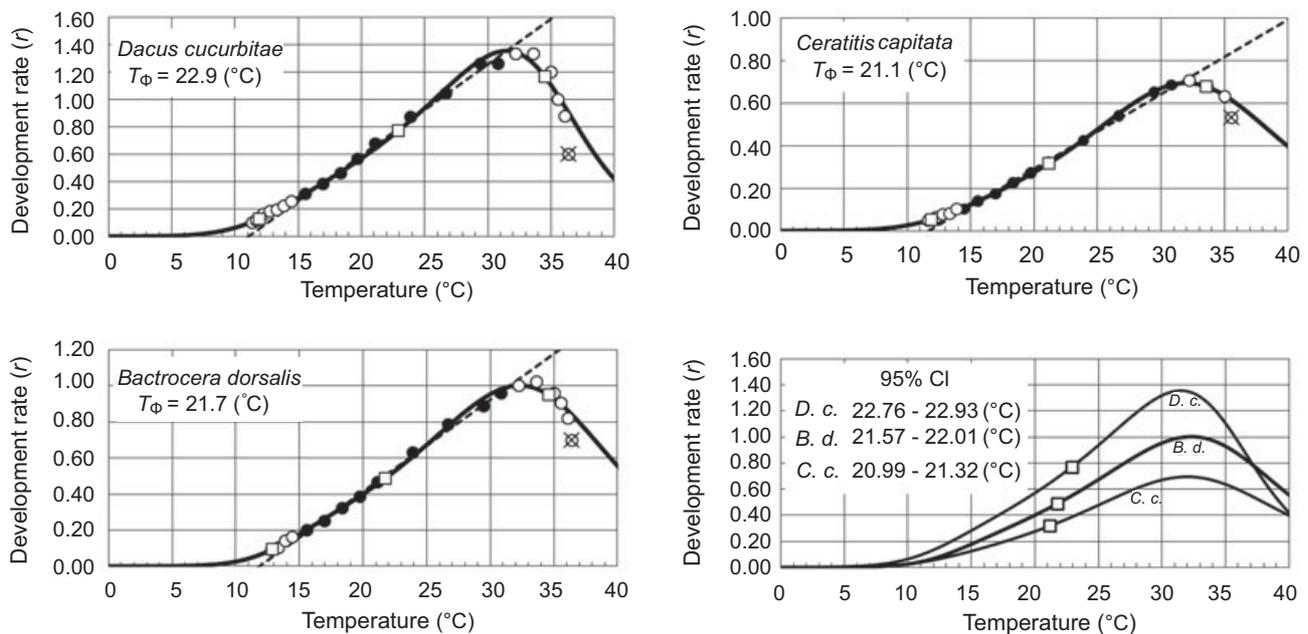
Fig. 3 Comparison of T_Φ and their confidence intervals at 95% among the three species of fruit flies (egg stage). The filled and open circles are the observed values that were used to estimate the model parameters. The open circles marked by X indicate the observed values that were not used during the parameter estimates because their survival rates are below normal (<1%). The filled circles were also used for the linear fitting by the reduced major axis, whereas the open circles were excluded from the linear fitting. The solid curved-line indicates the values of development rate predicted by the OptimSSI-P, whereas the dashed line denotes the values of development rate obtained by the linear fitting. The three open squares denote the predicted mean development rates at T_L, T_Φ, and T_H. The presented data are from Messenger & Flitters (1958).

highland areas following the late invasion of the Oriental fruit fly (Christenson & Foote, 1960). This event indicates that the Oriental fruit fly might favor a warmer environment than the Medfly. Among the three fruit flies, the Melon fly alone is distributed in tropical African areas (Christenson & Foote, 1960). This phenomenon might indicate that the place of origin the melon fly is warmer than that of the Oriental fruit fly. Taking these hypotheses together, we can form a conjecture that the order of the T_Φ values of these fruit flies is melon fly > Oriental fruit fly > Medfly.

The estimated values of T_Φ, which are calculated using the data sets related to egg developmental stages and temperatures of the Hawaiian fruit flies (Messenger & Flitters 1958), are completely in agreement with our assumption as shown in Figure 3. Notably, the confidence intervals of T_Φ values clearly indicate that the values of these fruit flies are statistically significantly different.

On the other hand, the order of development rates in the normal range of temperatures is melon fly > Oriental fruit fly > Medfly as shown in Figure 3. This result indicates a possibility that the world distribution of melon fly would be the widest among the three fruit flies because

the species that can quickly develop could complete its life cycle even at a lower temperature. The melon fly might probably expand its distribution from tropical areas to the subarctic zone in the world, although this species was originally from a subtropical area with $T_\Phi = 22.9°C$. In contrast, Medfly could not further expand its thermal territories owing to its $T_\Phi =$ being $21.1°C$ and its slowest rate of development among the three species.

T_ϕ and optimize strategy on biological process

Ikemoto (2008) showed that the estimated intrinsic optimum temperatures (T_Φ) for the development of the malaria parasites, *Plasmodium falciparum* and *Plasmodium vivax*, in an adult mosquito and that of the vector mosquito, *Anopheles gambiae* s.s. are all ≈23–24°C. Therefore, these findings indicate that the development of both ectotherms is inhibited at temperatures higher than T_Φ. Indeed, this idea is supported by the characteristics of *P. falciparum* gametocytes referred to as exflagellation occurs in the midgut of *An. gambiae* optimally at 23°C compared with that at 37°C (Ogwan'g *et al.*, 1993), and also the percentage of adult eclosion from the egg
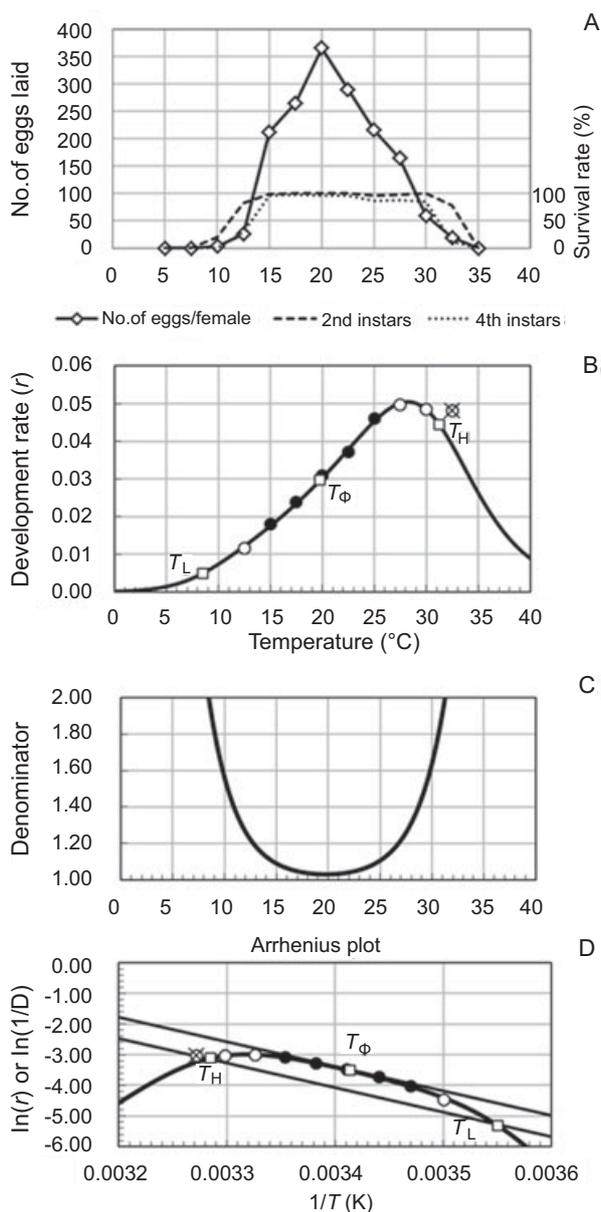
Fig. 4 Estimated T_Φ (19.78°C; confidence interval: 19.75–20.69°C at 95% significance) of Mexican bean beetle *Epilachna varivestis* (Coleoptera: Coccinellidae) in Japan. T_Φ and the temperature at which the maximum number of eggs laid per female is achieved maximum almost correspond to each other, at least in this case (A, B). (C) Relationship between the temperatures (°C) and the values of denominator in SSI model equation (1). The value at T_Φ°C is the smallest as indicating the negative effect for development rate. (D)The representation of (B) is shown with Arrhenius-plot manner showing with reversed temperature (K) and natural logarithm of development rate. Thus, the vertical difference between the upper and lower lines is $\ln(1/2) = -0.693$. The circular symbols in (B) and (D) are same as shown in Fig. 3. The presented data are from Shirai & Yara (2001).

of *An. gambiae* reaches the maximum (≈80%) at ≈24°C (Bayoh & Lindsay, 2003). These findings indicate the close relationship between T_Φ and the life-history strategies of the host and the parasite.

A typical example is found in the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae), in Japan. The survival rates of the larvae are stable approximating to 100% in the temperature range of 15°C–30°C, indicating that the beetle has a wide thermal capacity (Fig. 4). In contrast, the beetle lays the maximum number eggs at ≈20°C with 2°C interval observations (Shirai & Yara, 2001). The T_Φ estimated from the data of Shirai and Yara (2001) on development was 19.78°C with the confidence intervals of 19.75°C–20.69°C at 95% significance (Sample 6 in Table 3). The ≈20°C and the 19.78°C are approximately equal, indicating the optimality criterion of this species (Fig. 4).

The intrinsic optimum temperature especially with its confidence interval could be used as a good indicator for the geographical distribution and place of origin of related species because they sometimes have the common temperature concerned with their biological processes (Ikemoto, 2003). In addition, the intrinsic optimum temperature could be applied to the construction of a phylogenetic tree within a taxon as a potential useful tool. Additional information on the intrinsic optimum temperature of many ectothermic species is necessary to address questions on biological processes such as the factor of fitness.

Acknowledgments

Disclosure

References

Aluja, M. and Norrbom, A. (1999) *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*. CRC Press, Boca Raton, FL. 984 pp.

Bayoh, M.N. and Lindsay, S.W. (2003) Effect of temperature on the development of the aquatic stages of *Anopheles gambiae*

sensu stricto (Diptera: Culicidae). *Bulletin of Entmological Research*, 93, 375–381.

Broufas, G.D., Pappas, M.L. and Koveos, D.S. (2007) Development, survival, and reproduction of the predatory mite *Kampimodromus aberrans* (Acari: Phytoseiidae) at different constant temperatures. *Environmental Entomology*, 36, 657–665.

Christenson, L.D. and Foote, R.H. (1960) Biology of fruit flies. *Annual Review of Entomology*, 5, 171–192.

DiCiccio, T.J. and Efron, B. (1992) More accurate confidence intervals in exponential families. *Biometrika*, 79, 231–245.

DiCiccio, T.J. and Efron, B. (1996) Bootstrap confidence intervals (with Discussion). *Statistical Science*, 11, 189–228.

Efron, B. (2003) Second thoughts on the Bootstrap. *Statistical Science*, 18, 135–140.

Efron, B. and Tibshirani, R.J. (1994) *An Introduction to the Bootstrap*. p. 436. Chapman and Hall/CRC, New York, NY. 436 pp.

Gilpin, M.E. and McClelland, G.A.H. (1979) Systems analysis of the yellow fever mosquito *Aedes aegypti*. *Fortschritte der Zoologie*, 25, 355–388.

Ikemoto, T. (2003) Possible existence of a common temperature and a common duration of development among members of a taxonomic group of arthropods that underwent speciational adaptation to temperature. *Appllied Entomology and Zoology*, 38, 487–492.

Ikemoto, T. (2005) Intrinsic optimum temperature for development of insects and mites. *Environmental Entomology*, 34, 1377–1387.

Ikemoto, T. (2008) Tropical malaria does not mean hot environments. *Journal of Medical Entomology*, 45, 963–969.

Ikemoto, T. and Takai, K. (2000) A new linearized formula for the law of total effective temperature and the evaluation of line-fitting methods with both variables subject to error. *Environmental Entomology*, 29, 671–682.

Kuo, M.H., Chiu, M.C. and Perng, J.J. (2006) Temperature effects on life history traits of the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: Aphididae) on corn in Taiwan. *Applied Entomology and Zoology*, 41, 171–177.

Messenger, P.S. and Flitters, N.E. (1958) Effect of constant temperature environments on the egg stage of three species of Hawaiian fruit flies. *Annals of the Entomological Society of America*, 51, 109–119.

Nelder, J.A. and Mead, R. (1965) A simplex algorithm for function minimization. *Computer Journal*, 7, 308–313.

Ogwan'g, R.A., Mwangi, J.K., Were, J.B.O., Roberts, C.R. and Martin, K. (1993) Factors affecting exflagelation of invitro-cultivated *Plasmodium falciparum* gametocytes. *American Journal of Tropical Medicine and Hygiene*, 49, 25–29.

Schoolfield, R.M., Sharpe, P.J.H. and Magnuson, C.E. (1981) Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology*, 88, 719–731.

Sharpe, P.J.H. and DeMichele, D.W. (1977) Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology*, 64, 649–670.

Shi, P., Ikemoto, T., Egami, C., Sun, Y. and Ge, F. (2011) A modified program for estimating the parameters of the SSI model. *Environmental Entomology*, 40, 462–469.

Shirai, Y. and Yara, K. (2001) Potential distribution area of the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae) in Japan, estimated from its high-temperature tolerance. *Applied Entomology and Zoology*, 36, 409–417.

Trpis, M. (1972) Development and predatory behavior of *Toxorhyynchites brecipalpis* (Diptera: Culicidae) in relation to temperature. *Environmental Entomology*, 1, 537–546.

Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1. R functions for fast estimating the parameters in the SSI model and the confidence interval of intrinsic optimum temperature.