Effect of Temperature on the Development of *Laodelphax striatellus* (Homoptera: Delphacidae)

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ABSTRACT   Temperature has a significant influence on the development of *Laodelphax striatellus* (Fallén), an important rice pest insect in east Asia. We set eight constant temperatures from 18 to 32°C in 2°C-increments to check the effect of temperature on the developmental rate of this insect species. The developmental durations of eggs and nymphs were observed daily. To ensure the accuracy of developmental durations, 500 initial samples were taken for the nymphal stage at each temperature. Performance-2 model was used to fit these data because this model can provide the lower and upper developmental thresholds simultaneously. The estimate of lower developmental thresholds of eggs (10.0°C) was different from that of nymphs (7.5°C). And the estimate of upper developmental thresholds of eggs (35.5°C) was also different from that of nymphs (30.2°C). However, for male and female nymphs, the difference in the lower developmental threshold is nonsignificant, and the difference in the upper developmental thresholds is very small (95% confidence interval of the difference: [0.007°C, 0.043°C]). The rate isomorphy hypothesis considers that the lower developmental thresholds of different stages for the same insect might be constant. However, the current study provides a counterexample of this hypothesis that the lower developmental threshold of eggs is different from that of nymphs. Thus, we demonstrate that the rate isomorphy hypothesis does not apply all insects. In addition, we used a popular nonlinear model, Lactin model, to fit the developmental rate data of our experiment. And we found that the estimates of lower and upper developmental thresholds by using Performance-2 model were very approximate to those by using Lactin model. The current study provides reliable estimates of thermal parameters for *L. striatellus* by using large experimental samples at different temperatures. It would be useful for exploring the relationship of climate change and the outbreak of this insect on rice.

KEY WORDS   Performance-2 model, lower developmental threshold, upper developmental threshold, sum of effective temperatures, bootstrap percentile

In the investigation of temperature-dependent developmental rates of insects, the thermal limits of development always has been concerned (Uvarov 1931, Wang et al. 1982, Lactin et al. 1995, Brière et al. 1999, Van der Have 2002, Shi et al. 2011). The lower thermal limit of development usually is referred to as the lower developmental threshold, at which the developmental rate equals zero; whereas the upper thermal limit of development can be referred to as the upper developmental threshold, at which the mortality rate is so high that the majority of an insect population cannot normally complete a specific developmental stage. The linear model of $r = a + bT$ is widely used to estimate the lower developmental threshold ($= -\hat{a}/\hat{b}$). Logan et al. (1976) proposed a nonlinear model to estimate the upper developmental threshold. Van der Have (2002) proved that the thermal limits of development could be exactly predicted by the model proposed by Schoolfield et al. (1981). Some investigators built other nonlinear models to estimate the lower and upper developmental thresholds of insects (e.g., Wang et al. 1982, Lactin et al. 1995, Brière et al. 1999, Shi et al. 2011). Among these nonlinear models, Lactin model might be the most popular. It has been cited 200 times so far (1 September 2012, Google Scholar).

The lower developmental thresholds of different developmental stages have been demonstrated to be constant for some insects and mites (Jarošík et al. 2002, 2004; Sandhu et al. 2011). Jarošík et al. (2002) referred to it as the rate isomorphy hypothesis. It still would be necessary and valuable to further demonstrate this hypothesis. In practice, if we hope to know the lower developmental threshold of a species of insect, it would be feasible to do an experiment of temperature-dependent development only on a specific stage of the insect species under this hypothesis. In the previous studies, the rate isomorphy hypothesis has received little attention. Another question is whether the upper

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Table 1. Developmental durations (days) of *L. striatellus* at different temperatures

	18°C	20°C	22°C	24°C	26°C	28°C	30°C	32°C
Egg (♂ plus ♀)	13.29 ± 0.97 (522)	11.09 ± 0.87 (1070)	9.91 ± 0.58 (528)	8.2 ± 1.19 (566)	7.06 ± 0.76 (1052)	6.03 ± 0.45 (775)	5.86 ± 0.65 (549)	5.6 ± 0.66 (465)
Nymph (♂ plus ♀)	31.63 ± 3.32 (468)	25.19 ± 2.8 (477)	22.34 ± 2.46 (415)	19.43 ± 2.9 (432)	18.23 ± 2.27 (428)	15.56 ± 1.55 (468)	25.18 ± 4.84 (203)	23.41 ± 5.09 (96)
Nymph (♂)	31.2 ± 3.11 (230)	24.7 ± 2.78 (233)	21.99 ± 2.49 (213)	18.73 ± 2.84 (210)	17.78 ± 2.18 (199)	15.21 ± 1.42 (230)	23.95 ± 4.32 (100)	22.69 ± 5.27 (49)
Nymph (♀)	32.05 ± 3.46 (238)	25.65 ± 2.75 (244)	22.72 ± 2.39 (202)	20.1 ± 2.81 (222)	18.62 ± 2.27 (229)	15.9 ± 1.59 (238)	26.38 ± 5.04 (103)	24.15 ± 4.84 (47)

The number in parentheses represents the effective sample size. Only 500 random samples were used for the nymphal stage at every temperature (<32°C). At 32°C, 465 samples were used.

developmental thresholds of different stages for the same insect are constant. Even at the same stage for the same insect, the development durations of males might be different from those of females at different temperatures (Wu et al. 2009).

Laodelphax striatellus (Fallén) (Homoptera: Delphacidae), is a serious economic pest insect of cereals, including rice (*Oryza sativa* L.) and maize (*Zea mays* L.) with wide latitudinal geographic distribution in China. This insect transmits various virus diseases of cereals (Xia 1962, Lin et al. 1990, Li et al. 2011), in addition to the damage it causes by sap sucking. In the temperate and subtropical regions, the species displays a nymph diapause at the third or the fourth instar in response to short photoperiods and relatively low temperatures (Cai et al. 1964, Kisimoto 1989). In the current study, we carried out an experiment on the effect of temperature on the development of *L. striatellus*. We observed the developmental durations of eggs and nymphs, and tested whether there is a significant difference in the lower (upper) developmental thresholds between two stages. Male and female nymphs were distinguished, and we compared the thermal parameters of two sexes.

Materials and Methods

Experiment. Two hundred couples of adult *L. striatellus* collected in Nanchang County (28° 46′ N, 115° 50′ E) in May of 2011, Jiangxi Province, were used for the current study. The planthoppers were stock-cultured on stems of American sloughgrass, *Beckmannia syzigache* (Steud.) Fernald at 25°C and a photoperiod of 15:9 (L:D) h. They were raised in the laboratory for one generation before use. The eggs produced on the first day and the newly-hatched nymphs were transferred to the temperatures of 18, 20, 22, 24, 26, 28, 30, and 32°C for analyzing the effect of temperature on their developmental durations. Approximately fifty nymphs were put in a glass tube (180 mm in length and 32 mm in diameter) containing the stem of American sloughgrass. There were 10 tubes for each temperature treatment. The hatching of nymphs and emergence of adults were recorded daily.

Performance Model. Shi et al. (2011) have proposed two performance models for describing the temperature-dependent developmental rates of insects:

$$r = c \cdot (1 - e^{-K_1(T - T_{\min})}) \cdot (1 - e^{K_2(T - T_{\max})}) \qquad [1.1]$$

$$r = m \cdot (T - T_{\min}) \cdot (1 - e^{K_2(T - T_{\max})}) \qquad [1.2]$$

Here, r represents the developmental rate (days^{-1}) at temperature T (°C); $T_{\min}$ represents the lower developmental threshold; $T_{\max}$ represents the upper developmental threshold; and c, m, K_1, and K_2 are parameters to be fitted. These two performance models have very similar shapes during fitting the data of developmental rate. Performance-2 model (i.e., equation 1.2) is actually a simplification of the Peformance-1 model (see Shi et al. 2011 for details). However, Performance-1 model has more parameters than Performance-2 model. That means the former is more complex in model structure, which will produce a larger Akaike Information Criterion (AIC) or corrected AIC than the latter (Angilletta 2006, Shi and Ge 2010). In the current study, we used Performance-2 model to fit the temperature-dependent developmental rates of *L. striatellus*. It is necessary to point out that Performance-1 model was used by Huey and Stevenson (1979) to describe the temperature-dependent jumping distances of a species of frog and Performance-2 model's square root was used by Ratkowsky et al. (1983) to describe the temperature-dependent growth rates of bacteria. Moreover, a temperature at which the developmental rate is predicted to be maximal in Performance-2 model, is also concerned in the current study. For simplicity, we referred to it as the fastest development temperature (T_f). Finally, we tested whether the estimate of lower developmental threshold by Performance-2 model is approximate to that by the linear model of $r = a + bT$.

Table 2. Lower developmental threshold (*t*) and sum of effective temperatures (*k*) of *L. striatellus* estimated by using the traditional linear model

	t (°C)	SE(t)	k (degree-days)	SE(k)	R^2
Egg (♂ plus ♀)	10.17	0.08	109.52	0.62	0.873
Nymph (♂ plus ♀)	7.51	0.16	319.63	3.32	0.776
Nymph (♂)	7.73	0.22	307.94	4.37	0.791
Nymph (♀)	7.31	0.23	331.04	4.82	0.775

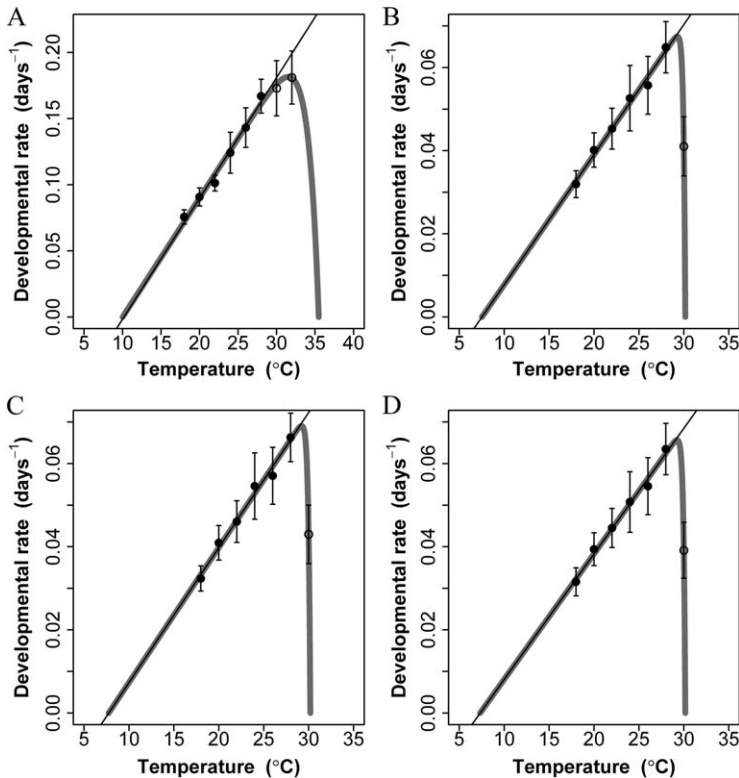Table 3. Parameter estimates of Performance-2 model for describing the developmental rates of *L. striatellus*

	m	K_2	T_{min} (°C)	SE(T_{min})	T_{max} (°C)	SE(T_{max})	T_f (°C)	SE(T_f)	R^2
Egg (♂ plus ♀)	0.009007	0.695442	10.00	0.06	35.49	0.31	31.50	0.11	0.8679
Nymph (♂ plus ♀)	0.003129	5.288950	7.51	0.13	30.17	0.00	29.27	0.01	0.7623
Nymph (♂)	0.003248	4.702234	7.73	0.17	30.19	0.01	29.21	0.03	0.7764
Nymph (♀)	0.003021	5.081778	7.31	0.20	30.17	0.00	29.24	0.01	0.7647

Comparing Two Estimates of One Thermal Parameter. For comparing two estimates of one thermal parameter in Performance-2 model (e.g., T_{min}), we used the bootstrap method (Efron and Tibshirani 1994) to obtain two groups of bootstrap replications. Then the 95% confidence interval (CI) of the difference between these two groups of bootstrap replications was calculated. If the CI includes zero, it implicates that there is no significant difference between these two estimates of the thermal parameter; otherwise, the difference is significant (see Sandhu et al. 2011 for details).

Considering the importance of the rate isomorphy hypothesis, we also used the method of rotating regression line (Shi et al. 2010) to test whether there is a significant difference in the lower developmental thresholds (calculated by the linear model coefficients) between eggs and nymphs or between male and female nymphs.

Results

Table 1 exhibits the developmental durations of eggs and nymphs. From the mean of developmental duration, the developmental duration of nymphs (male plus female) is largely longer than that of eggs at every temperature, whereas the development duration of female nymphs is slightly longer than that of male nymphs at every temperature. Because the probability distribution function of developmental durations at the nymphal stage was unknown, the two-sample Kolmogorov–Smirnov test was used. There is a significant difference ($P < 0.05$) in the developmental durations between male and female nymphs at every temperature (from 18 to 30°C). The mortality at the nymphal stage at 30 and 32°C reached 59.4 and 79.4%, respectively. As a rule of thumb, the data of developmental rate at the extreme low or high temperatures with survival rate ≤30% should be excluded

Fig. 1. Peformance-2 fit to the data of developmental rate of *L. striatellus*: (A) for the eggs, (B) for the nymphs (male plus female), (C) for the male nymphs, and (D) for the female nymphs. The gray curve is the predicted values by Performance-2 model, the dark solid line shows predictions from the traditional linear model, the open and closed circles are the observed values used in the nonlinear Performance-2 fit, the closed circles are observed values used in the linear fit.

**Table 4. Parameter estimates of Lactin model for describing the developmental rates of *L. striatellus***

	λ	ρ	T_u (°C)	δ	T_{min} (°C)	T_{max} (°C)	T_f (°C)	R^2
Egg (♂ plus ♀)	−1.073908	0.007587	38.19	1.480880	9.40	35.63	31.47	0.8685
Nymph (♂ plus ♀)	−1.021180	0.002925	30.24	0.065538	7.17	30.06	29.68	0.7622
Nymph (♂)	−1.022607	0.003028	30.51	0.141130	7.38	30.13	29.41	0.7762
Nymph (♀)	−1.019929	0.002830	30.44	0.121915	6.97	30.10	29.47	0.7647

during carrying out a nonlinear fit. Therefore, the data of developmental rate at 32°C were not used during carrying out Performance-2 fit to the data of nymphs.

Table 2 displays the estimates of lower developmental threshold (t) and sum of effective temperatures (k) for eggs and nymphs by the linear model. The corresponding standard errors were calculated according to the formulae proposed by Campbell et al. (1974). The estimate of lower developmental threshold for eggs is higher than that for nymphs. By using the method of rotating regression line (Shi et al. 2010), there is a significant difference in the lower developmental thresholds between these two stage ($P < 0.05$). However, there is no significant difference in the lower developmental thresholds between male and female nymphs ($P = 0.596 > 0.05$).

Table 3 shows the fitted parameters in Performance-2 model for eggs and nymphs. Figure 1 displays the comparison between the observed and predicted values of developmental rate. We used the bootstrap percentile method (Sandhu et al. 2011) to analyze three thermal parameters: T_{min}, T_{max}, and T_f. For T_{min}. There is a significant difference between eggs and nymphs (male plus female), because 95% CI of the difference is [2.20, 2.79], not including zero. There is no significant difference in T_{min} between male and female nymphs, because 95% CI of the difference is [−0.08, 0.94] including zero. For T_{max}, there is a significant difference between eggs and nymphs (male + female) because 95% CI of the difference is [4.74, 5.95], not including zero. There is also a significant difference in T_{max} between male and female nymphs, because 95% CI of the difference is [0.007, 0.043], not including zero. However, the upper limit of 95% CI of the difference is still very small (<0.05°C). In this case, we can consider that the upper developmental thresh-
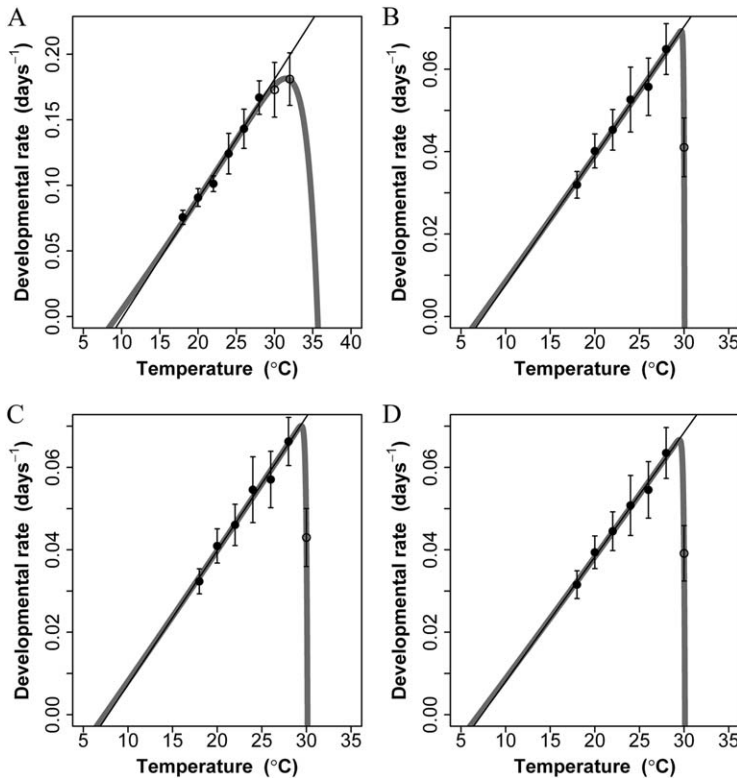
Fig. 2. Lactin fit to the data of developmental rate of *L. striatellus*: (A) for the eggs, (B) for the nymphs (male plus female), (C) for the male nymphs, and (D) for the female nymphs. The gray curve is the predicted values by Lactin model, the dark solid line shows predictions from the traditional linear model, the open and closed circles are the observed values used in the nonlinear Lactin fit, the closed circles are observed values used in the linear fit.
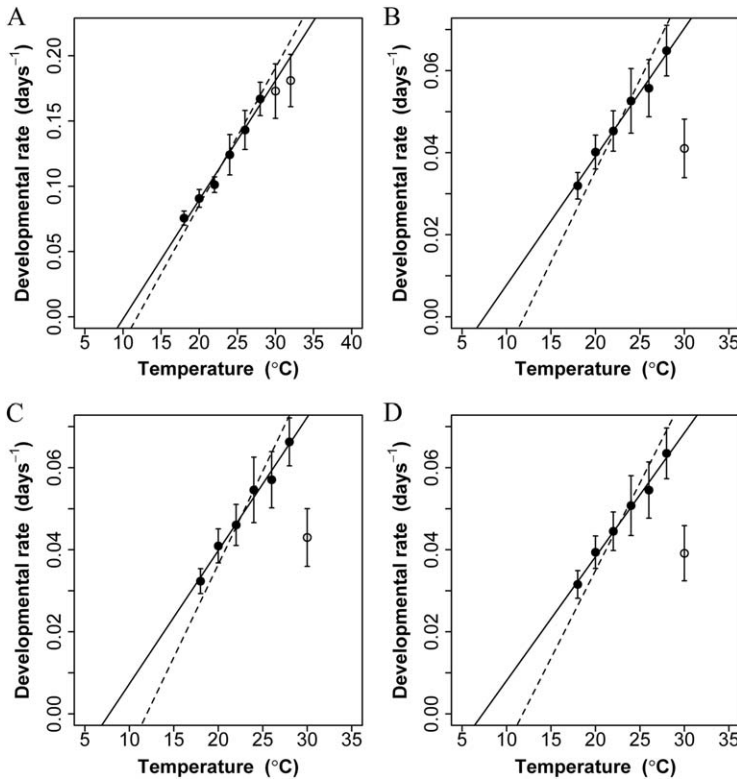
Fig. 3. Comparison of fitting the raw data of developmental rate between the traditional linear model (solid line) and the Ikemoto–Takai linear model (dashed): (A) for the eggs, (B) for the nymphs (male plus female), (C) for the male nymphs, and (D) for the female nymphs.

old of male nymphs is very approximate to that of female nymphs. For T_f, there is a significant difference between eggs and nymphs (male plus female) because 95% CI of the difference is [2.02, 2.44], not including zero. There is no significant difference in T_f between male and female nymphs, because 95% CI of the difference is [−0.079, 0.008] including zero.

We found that the estimates of lower developmental thresholds for eggs and nymphs by the linear model are rather approximate to those by Performance-2 model (Tables 2 and 3). For testing the difference significance in the lower developmental thresholds between eggs and nymphs or between male and female nymphs, the conclusions from the method of rotating regression line (Shi et al. 2010) for the linear model are the same as those from the bootstrap percentile method (Sandhu et al. 2011) for Performance-2 model.

Discussion

Lactin Model. Lactin et al. (1995) proposed a nonlinear model to describe the effect of temperature on the developmental rates of insects:

$$r = e^{\rho T} - e^{\rho T_u - (T_u - T)/\delta} + \lambda \qquad [2]$$

Here, r represents the developmental rate (days^{-1}) at temperature T (°C); λ, ρ, δ, and T_u are parameters

to be fitted. It was referred to as Lactin model. It is necessary to point out that T_u in this model does not represent the upper developmental threshold (T_{max}), but a constant that is slightly higher than the latter. According to the definition of upper developmental threshold, it is actually the intersection between the developmental rate curve and the abscissa (i.e., the temperature-axis) in the region of high temperatures. Lactin et al. (1995) stated that equation 2 had been derived from Logan model (Logan et al. 1976). However, in Logan model, T_u exactly represents the upper developmental threshold. The lower and upper developmental thresholds are not the direct parameters in Lactin model, and the numerical computations are needed for obtaining their approximations. We used Lactin model to fit the developmental rate data of our experiment, and found that the results are similar to those by using Performance-2 model (Table 4 and Fig. 2). The estimates of lower developmental thresholds by using Lactin model are slightly lower than those by using Performance-2 model. However, the estimates by using Performance-2 model are more approximate to those by using the traditional linear model (Table 2). To our experience, the curve shapes of two performance models in the region of low temperatures (approximating a straight line) are more stable than that of Lactin model. In the region of extreme low temperatures, the developmental rates might deviate
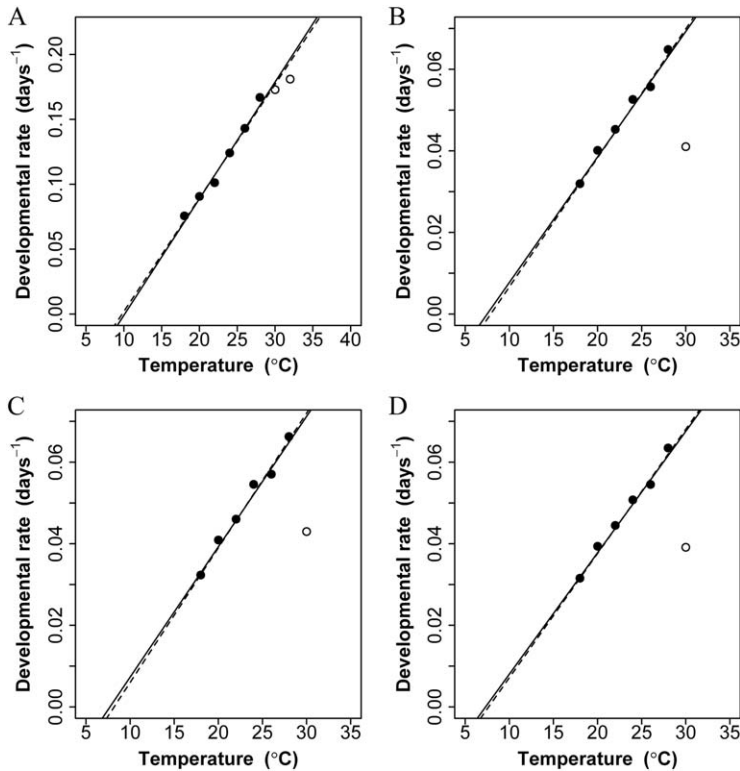
Fig. 4. Comparison of fitting the mean data of developmental rate between the traditional linear model (solid line) and the Ikemoto–Takai linear model (dashed): (**A**) for the eggs, (**B**) for the nymphs (male plus female), (**C**) for the male nymphs, and (**D**) for the female nymphs.

from the straight line because of high mortality of reared population. That means these data at extreme low temperatures might be unreliable because these data only reflect the developmental durations of partial samples (i.e., a small part of reared population). However, Lactin model's shape in the region of low temperatures is easily changeable to over-fit the data at low temperatures. Because the concept of lower developmental threshold by using the linear model is widely accepted, we would expect that the estimate of lower developmental threshold by using a nonlinear model should be equal or very approximate to that by using the linear model. In this case, Performance-2 model shows its advantage. Of course, for the data of our experiment, there are small differences in the lower developmental thresholds between using Lactin model and using Performance-2 model because of the lack of the developmental rate data at extreme low temperatures.

Ikemoto–Takai Linear Model. As mentioned above, the linear regression based on the least square method is widely used to describe the temperature-dependent developmental rates in the mid-temperature region. The initial definitions of lower developmental threshold (t) and sum of effective temperatures (k) were made based on the traditional linear model. Ikemoto and Takai (2000) proposed a new method for estimating the lower developmental threshold and sum of effective temperatures:

$$DT = k + tD \qquad [3]$$

Here, D (days) represents the developmental duration at temperature T (°C). The product of D and T was defined as the dependent variable, and D was defined as the independent variable. We refer to equation 3 as the Ikemoto-Takai linear model for simplicity. Because the approximate measure of D in general has certain experimental error (it is impossible for an investigator in practice to observe the development of a species of insect hourly or in a shorter interval), they suggested using the reduced major axis method to estimate the model coefficients of k and t. It seems that to use equation 3 to fit the mean data of developmental rate is feasible. However, to use the mean data of developmental rate will lose many sample information. It would be better to use the raw data of developmental rate (i.e., all replicates of developmental rate at each temperature). In the current study, we compared the estimates of t and k by using the traditional linear model with those by using the Ikemoto–Takai linear model based on the raw data (Fig. 3). The fitted slope of Ikemoto–Takai line was too steep, which resulted in a too high estimate on the lower developmental threshold and a too small estimate on the sum of effective temperatures relative to those by using the traditional linear model. In theory, the estimate of t or k by using the Ikemoto–Takai linear model should not deviate from that by using the traditional linear model

Table 5.   Estimates of *t* and *k* of *L. striatellus* in other studies and test on the rate isomorphy (*P* value)

Reference	Stage	Temperature range (°C)	*t* (°C)	SE(*t*)	*P*	*k* (degree-days)	SE(*k*)
Noda 1989 (Kamikawa strain)	Egg	17.5–28	12.29	0.44	0.68	101.80	4.29
	Nymph	16–28	11.35	1.04		200.59	17.94
Noda 1989 (Izumo strain)	Egg	17.5–28	11.73	0.22	0.53	113.96	2.24
	Nymph	16–28	10.91	0.73		205.36	12.41
Noda 1989 (Ishigaki strain)	Egg	17.5–28	11.65	0.38	0.90	111.82	3.91
	Nymph	16–28	11.22	0.89		190.72	14.53
Hachiya 1990	Egg	15–25	10.49	0.85	0.76	112.10	9.19
	Nymph	15–25	11.13	0.18		203.22	3.75
Sun et al. 2000	Egg	16–28	10.85	0.79	–	121.05	8.05
	Nymph	–	–	–		–	–
Zhang et al. 2008	Egg	18–27	11.58	–	–	110.05	–
	Nymph	18–27	13.35	–		189.89	–
Hu et al. 2010	Egg	20–28	12.46	1.80	0.94	88.26	12.93
	Nymph	20–28	11.38	2.44		263.89	48.08

too much. Equation 3 should be applicable for the mean data of developmental rate. In fact, Ikemoto and Takai (2000) only suggested using this model to fit the mean data of developmental rate. Then we used two linear models to fit the mean data of developmental rate of *L. striatellus,* and found that the estimates in *t* or *k* are very approximate (Fig. 4). For the raw data of developmental rate, the current study suggests using the traditional linear model rather than the Ikemoto-Takai linear model to estimate these two thermal parameters.

Thermal Parameters and Rate Isomorphy Hypothesis. Food was demonstrated to be an important factor that could significantly affect the developmental rates of insects (e.g., Sharpe and Hu 1980, Johnson et al. 1992, Honěk et al. 2002, Golizadeh et al. 2007). Some investigators have reported the temperature-dependent development of *L. striatellus* reared on rice (Noda 1989, Hachiya 1990, Sun et al. 2000, Zhang et al. 2008, Hu et al. 2010). We extracted their data of developmental rate in the midtemperature range and recalculated the lower developmental threshold (*t*) and sum of effective temperatures (*k*) (Table 5). In addition, we used the method of rotating regression line (Shi et al. 2010) to test whether there was a significant difference in the lower developmental thresholds between eggs and nymphs. The calculated *P* values by using the method of rotating regression line were all >0.05, which supported the rate isomorphy hypothesis that eggs and nymphs should have a common lower developmental threshold. Because there are only a few mean data of developmental rate in these publications, the estimated standard errors of *t* and *k* are large. However, we could draw several basic conclusions: the estimate of *t* of eggs was around 11°C, and the estimate of *k* of eggs was around 110 degree-days (DD); the estimate of *t* of nymphs was also around 11°C, and the estimate of *k* of nymphs was 200 DD. The estimates of *t* and *k* of eggs in these references are approximate to our estimates (Table 2). However, the estimates of these two thermal parameters of nymphs are significantly different from our estimates. The thermal requirement for completing the nymphal stage of *L. striatellus* reared on rice appears to be rather lower than that of *L. striatellus* reared on Amer-

ican sloughgrass. Diet difference (rice versus American sloughgrass) might the main reason. Honěk et al. (2002) reported that the lower developmental threshold observed on 11 diets where *Autographa gamma* larvae complete development in at least two temperatures varied between 9.3 and 11.0°C, whereas the sum of effective temperatures varied between 167 and 353 DD. They further concluded that the larvae fed by different diets had a common *t* and their development was thus isomorphic. In the current study, food also has an important influence on the lower developmental threshold of nymphs of *L. striatellus.* For eggs, food appears to have little influence on *t* or *k*. Effects of different diets on *t* and *k* of other insects deserves further investigation. Jarošík et al. (2011) showed that closely related species shared similar thermal requirements. It might be explained easily by diets because closely related species usually feed on the same or similar food. If diets could not change thermal requirements of a specific developmental stage (e.g., egg), we would expect that closely related species at such a stage would share similar thermal requirements. However, they might not share similar thermal requirements if they feed on different food at another developmental stage (e.g., nymphs). It would also deserve further investigation whether thermal requirements at different developmental stages of the same insect could be affected by different food or not.

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