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# Empirical Model With Excellent Statistical Properties for Describing Temperature-Dependent Developmental Rates of Insects and Mites

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## Abstract

Previous empirical models for describing the temperature-dependent development rates for insects include the Brière, Lactin, Beta, and Ratkowsky models. Another nonlinear regression model, not previously considered in population entomology, is the Lobry–Rosso–Flandrois model, the shape of which is very close to that of the Ratkowsky model in the suboptimal temperature range, but which has the added advantage that all four of its parameters have biological meaning. A consequence of this is that initial parameter estimates, needed for solving the nonlinear regression equations, are very easy to obtain. In addition, the model has excellent statistical properties, with the estimators of the parameters being “close-to-linear,” which means that the least squares estimators are close to being unbiased, normally distributed, minimum variance estimators. The model describes the pooled development rates very well throughout the entire biokinetic temperature range and deserves to become the empirical model of general use in this area.

**Key words:** nonlinear regression, square root model, Lobry–Rosso–Flandrois model, close-to-linear

Shi et al. (2016b) presented the most extensive comparative study to date of various models available to describe the effect of temperature on the development rate of insects. Among the six models that they considered, all of which are nonlinear regression models, the one based on the beta function and another based on the square-root model (the latter model also known as the Ratkowsky model and widely used by microbiologists) were previously ignored by zoologists. Shi et al. (2016b) found that the square root model described the pooled developmental rates well throughout the entire biokinetic temperature range, and concluded that it merits wider use in entomology.

In addition to the Ratkowsky model for the effect of temperature on bacterial population growth, there is another model for population growth that has not been generally applied outside of food microbiology, and that is the model developed by Lobry and coworkers (see equation 4) that has the attractive feature that all four of its parameters have biological meaning, and which also enables initial parameter estimates to be readily obtained. In the present study, we examine how this model compares with the behavior of four of the models studied by Shi et al. (2016b).

## Materials and Methods

### Data

We use the same 10 datasets on invertebrates (9 insects and 1 mite) that were employed by Shi et al. (2016b). These are summarized in Table 1.

## Models

The formulae for the five models being compared in this study are as follows, where  $T$  is temperature in degrees absolute and  $r$  is the developmental rate. In the Lactin and Ratkowsky models,  $e$  denotes the base of natural logarithms. All of the other symbols represent model parameters.

Beta model (Yin et al. 1995, 2003; Shi et al. 2016a, b):

$$r = r_m \left( \frac{T_2 - T}{T_2 - T_m} \right) \left( \frac{T - T_1}{T_m - T_1} \right)^{\frac{T_m - T_1}{T_2 - T_m}} \quad (1)$$

Brière-2 model (Brière et al. 1999):

$$r = aT(T - T_1)(T_2 - T)^{1/b} \quad (2)$$

Lactin model (Lactin et al. 1995):

$$r = \lambda + e^{\rho T} - e^{\rho(T_u - (T_u - T)/\delta)} \quad (3)$$

Lobry–Rosso–Flandrois (LRF) model (Lobry et al. 1991; Rosso et al. 1993):

$$r = \mu_{opt} \frac{(T - T_2)(T - T_1)^2}{(T_{opt} - T_1)[(T_{opt} - T_1)(T - T_{opt}) - (T_{opt} - T_2)(T_{opt} + T_1 - 2T)]} \quad (4)$$

Ratkowsky model (Ratkowsky et al. 1983):

**Table 1.** Ten datasets of temperature-dependent developmental rates of invertebrates (9 insects, 1 mite)

Species	Order: Family	Developmental stage	Sample size	Source
<i>Aedes aegypti</i> (L.)	Diptera: Culicidae	Larva	15	Gilpin and McClelland (1979)
<i>Bactrocera dorsalis</i> (Hendel)	Diptera: Tephritidae	Egg	19	Messenger and Flitters (1958)
<i>Bemisia tabaci</i> (Gennadius)	Hemiptera: Aleyrodidae	From egg to adult	7	Xiang et al. (2007)
<i>Drosophila buzzatii</i> Patterson & Wheeler	Diptera: Drosophilidae	From egg to adult	9	de Jong (2010)
<i>Epilachna varivestis</i> Mulsant	Coleoptera: Coccinellidae	Larva	8	Shirai and Yara (2001)
<i>Helicoverpa armigera</i> (Hübner)	Lepidoptera: Noctuidae	Pupa	23	Wu et al. (2009)
<i>Kampinodromus aberrans</i> (Oudemans)	Acari: Phytoseiidae	Egg+larva+1 <sup>st</sup> -2 <sup>nd</sup> nymphs	9	Broufas et al. (2007)
<i>Lipaphis erysimi</i> (Kaltenbach)	Hemiptera: Aphididae	From egg to adult	12	Liu and Meng (2000)
<i>Myzus persicae</i> (Sulzer)	Hemiptera: Aphididae	From egg to adult	11	Liu and Meng (1999)
<i>Toxorhynchites brevipalpis</i> (Theobald)	Diptera: Culicidae	Egg	19	Trpis (1972)

$$\sqrt{r} = b(T - T_1)(1 - e^{c(T-T_2)}) \quad (5)$$

A common feature of the five models is that they all have four parameters, which makes it easier to compare their performance since they all have the same degrees of freedom. Therefore, there is no need to make the kinds of adjustments that are necessary when there are differing degrees of freedom. Irrespective of the criteria used to make decisions such as which model is best from the point of view of goodness-of-fit, and which has better estimation properties, the fact that all have four parameters guarantees that the comparisons will be made on a “level playing field,” which gives each model an equal chance of success and thereby removes the possibility that any one model will be advantaged by the choice of the criteria used for comparing the models.

In addition to each model having four parameters, there are some other features that are comparable among the five models. Four of the models, viz. the Beta, Brière-2, LRF, and Ratkowsky models, have, respectively, a “notional” minimum and a “notional” maximum temperature for growth ( $T_1$  and  $T_2$ , respectively). Mathematically, when  $T=T_1$ , or when  $T=T_2$ , the development rate is zero, as these are points on the graphs at which the curves intersect the temperature axis. This is not necessarily the observed minimum or the observed maximum temperature for growth, which is usually several degrees above  $T_1$  or several degrees below  $T_2$ , respectively. Of the five models, only the Lactin model lacks a parameter that is interpretable in this manner. It does have a “temperature” parameter  $T_u$ , described as the “upper lethal temperature,” but its estimated value from data is too high for it to be of any practical use. However, although the Lactin model lacks a  $T_1$  or  $T_2$  parameter, the model has two intersections with the temperature axis, so that the equivalent of these notional temperatures can be evaluated numerically.

### Stochastic Assumption

In fitting a mathematical model using the criterion of least squares, as is the case in the present study, it is necessary to make a stochastic assumption, one which describes how the variability of the response variable, in this case the developmental rate, changes as the temperature changes. This question was dealt with in detail by Ratkowsky (2003), to which the reader is referred. Briefly, in fitting data for bacterial growth, previous experience showed that the variability (or variance, as is the more formal term used in statistics) was homogeneous (i.e., approximately constant) if square root of rate rather than rate was used as the response variable. Some other workers, e.g., Schaffner (1998), have used logarithm of rate rather than square root of rate. Often there is not a great difference between the results obtained using these two approaches, but either transformation often gives different results than when the untransformed rate

is used. Shi et al. (2016b) used the untransformed rate; in this study we will use the square root of rate as the response variable, and we may expect to get results that differ, to some extent at least, from what was obtained in that study. Note that the Ratkowsky model (equation 5) already has the square root of rate on the left-hand side of the “=” sign. Therefore, no further transformation is necessary, and the least squares procedure is applied to the model as it stands. For the other four models (equations 1–4), it is necessary to take the square root of both sides of each of the expressions. For example, the Brière-2 model would be fitted in the following form, after the square root function has been applied to both sides of the equation:

$$\sqrt{r} = [aT(T - T_1)(T_2 - T)^{1/b}]^{0.5}$$

Similar transformations are applied to the Lactin, Beta, and LRF models, so that the left-hand side of each model is the square root of the rate rather than the rate itself.

### Measures of Nonlinear Behavior

Nonlinear regression models differ from linear regression models in a number of important ways. The first difference is in the manner in which the least squares estimates of the model’s parameters are obtained. For a linear model, there is an explicit noniterative solution leading directly to the least squares estimates of the parameters. In contrast, a nonlinear regression model employs iteration with the hope that successive solutions will improve upon the solution obtained in the previous step and that eventually convergence to the least squares estimates will be obtained. Convergence is usually considered to have occurred when the sum of squares of the differences between the observed and predicted values of the response variable (which, in this study is the square root of developmental rate) is a minimum and changes by only a minute amount with each iteration. In theory, if the error term (the difference between the observed and fitted transformed rates) is assumed to be an independent and identically distributed normal random variable, then the least squares estimators of the parameters of a linear regression model are unbiased, jointly normally distributed, and have minimum variance among the class of regular estimators (see Seber and Wild 1989). That is, their variance meets the minimum variance bound given by the Cramér-Rao inequality, which establishes that no set of unbiased estimators can be “better” than the least squares estimators. For a nonlinear regression model, the least squares estimators do not have those desirable properties for small sample sizes. Only when the sample sizes become large can one say that the least squares estimators approach the so-called “asymptotic” property of being unbiased, normally distributed minimum variance estimators. The question is “How large is large?,” which is not easily answered. It all depends upon the model/data set combination. Some model/data set combinations

achieve the desirable properties with very small sample sizes, and these have been labeled “close-to-linear” by [Ratkowsky \(1983\)](#). Other model/dataset combinations are so “far-from-linear” that the “asymptotic” properties are approximated only for unrealistically large samples. Therefore, the focus of attention of the approach of [Ratkowsky \(1983, 1990\)](#) has been to seek out models that, in combination with data of a reasonably small sample size, result in close-to-linear estimators, leading to ready interpretation of the results.

### Curvature Measures of Nonlinearity

[Bates and Watts \(1980\)](#) proposed the curvature measures of nonlinearity, the intrinsic and the parameter-effects curvatures, which are global measures of assessing whether a model/data set combination is close-to-linear or not. The intrinsic nonlinearity is determined by the curvature of the “solution locus” (also known as the expectation surface) at the least squares estimates of the parameters, and is an inherent property of the model that cannot be altered by reparameterization. Fortunately, most nonlinear regression models have low intrinsic nonlinearity, which means that if the original parameterization is not close-to-linear, parameterizations may be found (referred to as model reparameterization) which have close-to-linear behavior, even if the original parameterization exhibits far-from-linear behavior. The [Bates and Watts \(1980\)](#) intrinsic and parameter-effects curvatures are assessed using a readily calculated critical curvature value, which is a function of the sample size, the number of parameters of the model, and a user-chosen significance level, commonly  $\alpha = 0.05$ , which we also use here.

### Bias, Excess Variance, Skewness, Kurtosis

In addition to the global curvature measures of nonlinearity, other measures of nonlinear behavior are available that focus on the model’s individual parameters. These include measures of the bias ([Box 1971](#)), the skewness ([Hougaard 1985](#)), and the kurtosis ([Haines et al. 2004](#)) in the least squares estimators. Except for the measure of bias in the least squares estimator derived by [Box \(1971\)](#), it is only recently that they have become available in standard statistical packages. The Hougaard skewness measure was incorporated into PROC NLIN in SAS/STAT vers. 7.1 (1999) and thus was the earliest available of the useful statistical measures of nonlinearity. [Ratkowsky \(1990\)](#) suggested that the skewness measure was reasonably close-to-linear if its absolute value was less than 0.25, and that if the measure was greater than 1, considerable nonlinear behavior was present. [Haines et al. \(2004\)](#) felt that the lower cutoff was too liberal, and suggested that the slightly more conservative 0.15 was a more appropriate rule-of-thumb for deciding whether the model was reasonably close-to-linear. In the present work, we adopt a compromise cutoff criterion, where the absolute value of the standardized skewness measure  $|g_1| \leq 0.2$  indicates “good” behavior, where  $0.2 < |g_1| \leq 0.5$  indicates “moderate” nonlinearity, and where  $|g_1| > 0.5$  denotes “bad,” i.e., far-from-linear, behavior.

### Profile $t$ Plots

A profile  $t$  plot for a specific parameter of a nonlinear regression model is a plot of the likelihood ratio pivotal statistic versus the Wald pivotal statistic ([Bates and Watts 1988](#), [Cook and Weisberg 1990](#)). For a linear model, the two statistics are indistinguishable, being a set of points lying on a straight line. For a close-to-linear model, the two statistics differ only slightly, and visually they are close to lying on a straight line that can be included in the graph as a set of “target” values. For a far-from-linear model, the two statistics will differ markedly and deviate greatly from the target straight line.

Although [Haines et al. \(2004\)](#) have done some work using measures based on skewness and kurtosis to predict the closeness or otherwise of the Wald and likelihood-based confidence intervals, there is no agreed objective criterion for judging profile  $t$  plots. However, with a little bit of experience, one soon learns to gauge parameter estimator behavior by visual assessment of the profile  $t$  plots.

### Confidence Curves

A confidence curve contains a scatter plot of constrained parameter values plotted against the  $t$  value. For a close-to-linear model, the graph will appear to be wedge-shaped, with the points on the plot closely matching the pair of straight lines that intersect at a  $t$  value of zero. For a far-from-linear model, the graph will diverge sharply from this wedge-shaped appearance. Visually, therefore, in the absence of an objective criterion, it is straightforward to distinguish the different degrees of model behavior ranging from close-to-linear to far-from-linear, as is also the case with profile  $t$  plots.

### Histograms of Parameter Estimates

Further indicators of nonlinear behavior are histograms of the estimators of the individual parameters. A close-to-linear model will produce histograms that very closely resemble those of normal distributions. Far-from-linear models invariably have long-tailed distributions, in which the bias, the skewness and the kurtosis are readily discerned.

### Pairwise Scatter Plots

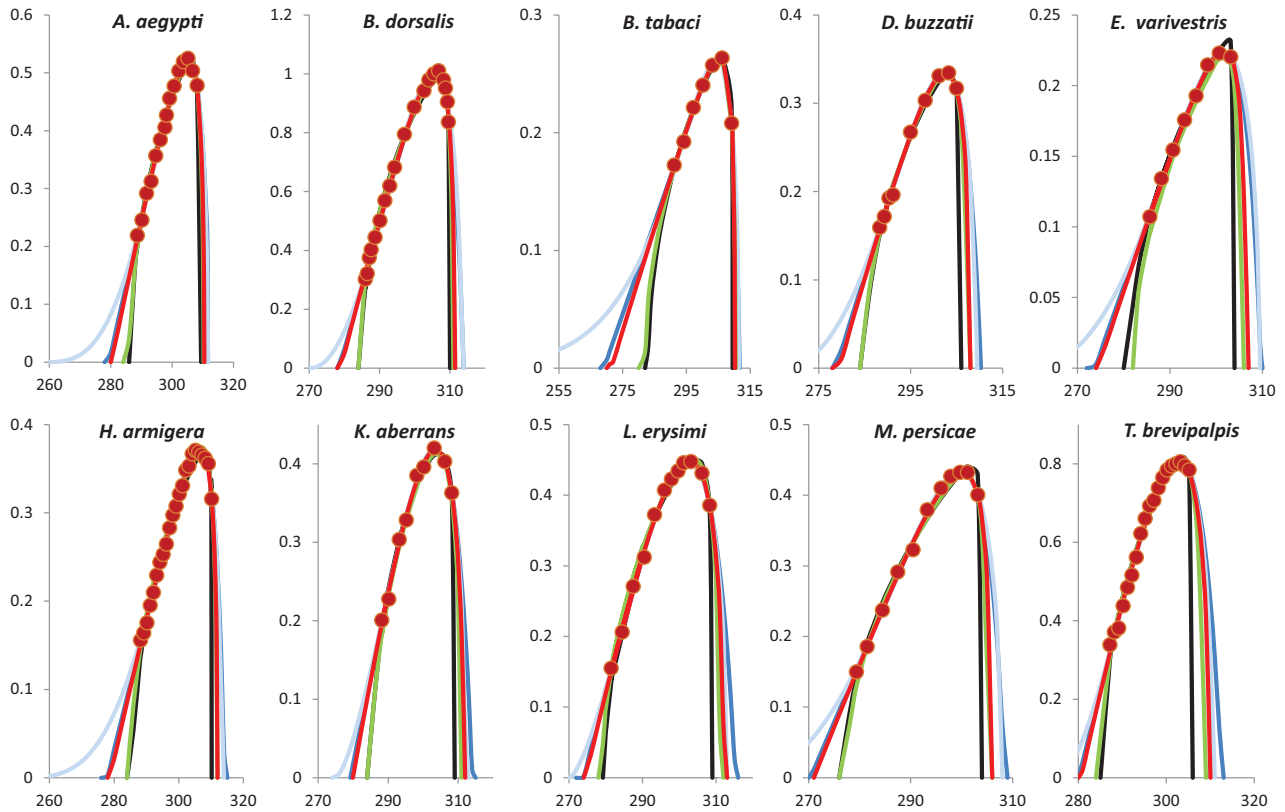
For normally distributed random variables, pairwise scatter plots of the parameter estimates are elliptical in shape. This contrasts clearly with far-from-linear models, which are curved and elongated, rather than elliptical in shape.

[Gebremariam \(2014\)](#) describes in detail the code (SAS statements) that is necessary to generate output which enables the user to make decisions about whether a model/dataset combination is close-to-linear or not. In this paper, we will give many such instances of such output, for the 10 datasets in combination with the five different models studied.

## Results

The 10 graphs depicted in [Fig. 1](#) show how the five models in this study fit the data for each of the 10 datasets. The red dots represent the raw data, and the solid lines are the fitted curves after the least squares estimates of the parameters are obtained. Broadly, a specific model tends to behave in a similar way for each of the datasets. In the following paragraphs, it is possible to make the following general observations about the results of fitting the five models to the 10 datasets of [Fig. 1](#).

1] The worst-fitting model is unquestionably the Brière-2 model, as its error mean square (EMS) is generally higher, often much higher than for any other model, ranking fifth (i.e. the worst) for 8 of the 10 datasets, and ranking fourth for the remaining two datasets ([Table 2](#)). Although this model fits the data comparably to the other models in the suboptimal temperature region, it does very badly in the vicinity of the optimal temperature for growth. Compared to the other four models, it has the highest  $T_{opt}$  value for each of the 10 datasets ([Table 3](#)). At temperatures not greatly in excess of  $T_{opt}$ , the model plunges downwards to intersect the temperature axis to give a notional maximum temperature for growth,  $T_2$ , such that  $T_2 - T_{opt}$  is smaller than for any other model, ranging from 0.4–4.1 K.



**Fig. 1.** Raw data (red dots) for 10 datasets and fitted values for each of the five models to those data. Light blue (Beta model), black (Brière-2 model), green (Lactin model), red (LRF model), dark blue (Ratkowsky model). The X-axis shows temperature in degrees K and the Y-axis shows the square root of rate.

**Table 2.** Goodness of fit of the five models to the 10 data sets

Species	Model					
	Sample size	Beta	Brière-2	Lactin-2	LRF	Ratkowsky
<i>Aedes aegypti</i>	15	39 <sup>1</sup>	204 <sup>5</sup>	128 <sup>4</sup>	54 <sup>3</sup>	42 <sup>2</sup>
<i>Bactrocera dorsalis</i>	19	427 <sup>4</sup>	541 <sup>5</sup>	187 <sup>1</sup>	195 <sup>2</sup>	326 <sup>3</sup>
<i>Bemisia tabaci</i>	7	20 <sup>5</sup>	12 <sup>4</sup>	8.1 <sup>3</sup>	5.9 <sup>1</sup>	7.0 <sup>2</sup>
<i>Drosophila buzzatii</i>	9	19 <sup>1</sup>	53 <sup>5</sup>	41 <sup>4</sup>	22 <sup>3</sup>	21 <sup>2</sup>
<i>Epilachna varivestris</i>	8	7.5 <sup>5</sup>	7.0 <sup>4</sup>	6.3 <sup>3</sup>	5.2 <sup>1</sup>	5.6 <sup>2</sup>
<i>Helicoverpa armigera</i>	23	18 <sup>3</sup>	75 <sup>5</sup>	41 <sup>4</sup>	14 <sup>1</sup>	15 <sup>2</sup>
<i>Kampinodromus aberrans</i>	9	51 <sup>1</sup>	132 <sup>5</sup>	87 <sup>4</sup>	55 <sup>3</sup>	53 <sup>2</sup>
<i>Lipaphis erysimi</i>	12	25 <sup>1</sup>	192 <sup>5</sup>	108 <sup>4</sup>	29 <sup>3</sup>	28 <sup>2</sup>
<i>Myzus persicae</i>	11	35 <sup>3</sup>	134 <sup>5</sup>	105 <sup>4</sup>	26 <sup>2</sup>	25 <sup>1</sup>
<i>Toxorynchites brevipalpis</i>	19	132 <sup>1</sup>	466 <sup>5</sup>	352 <sup>4</sup>	165 <sup>3</sup>	150 <sup>2</sup>
	Average rank	2.5 <sup>3</sup>	4.8 <sup>5</sup>	3.5 <sup>4</sup>	2.2 <sup>2</sup>	2.0 <sup>1</sup>

Note: All entries in the table are error mean squares (EMS) and have been multiplied by  $10^6$ . The superscript after the entries indicates the rank position in each row (1 = best; ...; 5 = worst).

2] The Lactin model also tends to be a poor-fitting model in comparison to the other models. From Table 2, that model ranks fourth in goodness-of-fit for 7 of the 10 datasets and was the third-worst fitting for two datasets. Its fitted values closely mirror those of the Brière-2 model in the suboptimal region, with the two models giving very similar predictions for all 10 datasets. For some of the datasets, this close agreement between the two models occurs near the optimum temperature for growth and in the superoptimal region as well. The Lactin model was a good-fitting model only for the *Bactrocera dorsalis* dataset (Table 2).

3] The Beta model varies greatly in terms of goodness-of-fit, ranging from being the best-fitting model for five of the datasets to being the worst-fitting model for two datasets (Table 2). For all 10 datasets, this model gives unrealistic estimates of  $T_1$ , the notional minimum temperature for growth (Fig. 1, Table 3), the fitted value often being up to 20–30 K below that for any other model. For the *Bemisia tabaci* dataset, the estimate of  $T_1$  was 0 K, i.e. absolute zero. Similar unrealistic estimates were also obtained by Shi et al. (2016b) for these same datasets using the Beta model, under a different stochastic assumption than in the present study.

**Table 3.** Comparison of parameter estimates of the five models for invertebrate growth

Data set	$T_1$	$T_2$	$T_{opt}$	$r_{opt}$	Model
<i>Aedes aegypti</i>	256.4	311.7	305.0	0.2727	Beta
	286.1	308.2	306.6	0.2746	Brière-2
	285.9	310.3	305.7	0.2727	Lactin
	280.2	310.5	305.3	0.2733	LRF
	279.3	312.7	305.1	0.2758	Ratkowsky
<i>Bactrocera dorsalis</i>	270.1	313.3	305.3	1.0006	Beta
	284.5	309.6	307.3	0.9750	Brière-2
	284.0	310.9	306.7	1.0371	Lactin
	278.9	311.4	306.0	1.0246	LRF
	278.5	313.9	305.5	1.0117	Ratkowsky
<i>Bemisia tabaci</i>	0	311.5	304.5	0.0687	Beta
	282.9	309.2	306.8	0.0702	Brière-2
	281.9	310.4	305.6	0.0696	Lactin
	271.4	310.2	305.6	0.0697	LRF
	269.1	311.7	305.3	0.0700	Ratkowsky
<i>Drosophila buzzati</i>	264.9	309.2	302.4	0.1121	Beta
	285.0	305.1	303.7	0.1167	Brière-2
	284.7	307.3	302.9	0.1136	Lactin
	279.4	307.9	302.6	0.1127	LRF
	278.7	310.3	302.5	0.1118	Ratkowsky
<i>Epilachna varivestis</i>	256.0	309.4	301.7	0.0499	Beta
	281.2	303.2	302.8	0.0547	Brière-2
	282.2	305.4	301.9	0.0491	Lactin
	274.4	306.4	301.7	0.0506	LRF
	273.7	309.7	301.6	0.0506	Ratkowsky
<i>Helicoverpa armigera</i>	247.2	313.3	306.1	0.1375	Beta
	285.6	310.2	308.0	0.1352	Brière-2
	285.0	311.9	307.1	0.1403	Lactin
	278.7	312.0	306.6	0.1383	LRF
	277.8	314.2	306.4	0.1392	Ratkowsky
<i>Kampinodromus aberrans</i>	274.7	312.1	303.4	0.1754	Beta
	285.2	308.7	304.6	0.1712	Brière-2
	285.1	310.9	304.0	0.1711	Lactin
	279.9	311.6	303.6	0.1754	LRF
	279.2	314.1	303.4	0.1762	Ratkowsky
<i>Lipaphis erysimi</i>	270.0	312.9	302.5	0.2015	Beta
	279.6	308.5	304.5	0.2023	Brière-2
	279.0	311.1	303.6	0.2068	Lactin
	274.5	312.1	302.8	0.2022	LRF
	273.9	315.3	302.5	0.2015	Ratkowsky
<i>Myzus persicae</i>	253.4	307.8	299.7	0.1873	Beta
	277.0	303.2	302.4	0.1981	Brière-2
	277.3	305.2	300.8	0.1876	Lactin
	271.0	305.8	300.2	0.1895	LRF
	270.3	308.5	299.9	0.1901	Ratkowsky
<i>Toxorynchites brevipalpis</i>	275.4	310.5	302.7	0.6529	Beta
	285.0	305.5	303.8	0.6673	Brière-2
	284.7	308.4	303.2	0.6640	Lactin
	280.6	309.7	302.8	0.6540	LRF
	280.1	312.6	302.7	0.6562	Ratkowsky

4] The overall best-fitting models, if performance is judged by consistency over the whole of the datasets, are the Ratkowsky model, which ranked best once, second-best eight times, and third-best once, to give an average rank of 2.0, and the LRF model, which ranked best three times, second-best twice, and third-best five times, for an average rank of 2.2. There was very little difference between the goodness-of-fit for these two models for six of the datasets, if judged by their error mean squares (Table 2). One consistent difference over all datasets is that  $T_1$ , the notional minimum temperature for growth, is lower for the Ratkowsky model than for the LRF

model, ranging from 0.4–2.3 K; also,  $T_2$ , the notional maximum temperature for growth, is higher for the Ratkowsky model than for the LRF model, ranging from 1.5–3.3 K (see Table 3 and Fig. 1). The consequence of this is that the biokinetic temperature range is broader for the Ratkowsky model than it is for the LRF model (2.9–4.0 K), but the whole of this difference occurs at temperatures that are well away from where there are actual growth observations.

### Nonlinear Behavior of Parameter Estimators Overall Measures

An overall measure of the nonlinear behavior of the least squares estimators of the parameters is provided by the root-mean-square intrinsic (IN) and root-mean-square parameter-effects (PE) nonlinearity measures of Bates and Watts (1980). These values are summarized for the five models and the 10 datasets in Table 4. Consistent clear conclusions can be made from the entries in this table. All models, in combination with all datasets, had nonsignificant IN values, meaning that the curvature of the solution locus in the vicinity of the minimum sum of squares is adequately low for each of the models. The models differ greatly in terms of their PE values, however. The worst-behaving model is the Brière-2 model, as it has some conspicuously extreme values for some of the datasets, and was significantly higher than the critical curvature value based on  $\alpha=0.05$  for all 10 datasets. The other model which was significantly higher than the critical curvature value for all 10 datasets was the Ratkowsky model, which ranked fourth overall. The Beta model exceeded the critical value for nine of the datasets, with one conspicuously large PE value, and ranked third overall. The model which ranked second-best was the Lactin model, whose PE value exceeded the critical value for eight of the datasets, but which never had a conspicuously large PE value. Unquestionably, the best model was the LRF model, which only had a significantly high PE value for three of the datasets, and in no case was its value conspicuously high.

### Individual Parameters

The PE value, as used in the previous paragraph, is an overall nonlinearity measure of the full set of four parameters in each model, and does not provide information about any specific parameter. To assess the estimation performance of a specific parameter, it suffices to use the Hougaard (1985) measure of skewness, and results are presented in Table 5, where G indicates good behavior (absolute value of Hougaard skewness  $|g_1| \leq 0.2$ ), M indicates moderate behavior ( $0.2 < |g_1| \leq 0.5$ ), and B indicates bad behavior ( $|g_1| > 0.5$ ). The best-behaving model is the LRF model, which has a preponderance of good (G) scores for three of its parameters, viz.  $T_1$ ,  $T_{opt}$  and  $\mu_{opt}$ . For  $T_2$ , there are no G values and a preponderance of bad (B) scores, which indicates that estimates of this parameter are likely to be biased and conspicuously nonnormally distributed. All other models have at least two parameters that have a preponderance of B scores. For example, for the Brière-2 model the parameters  $T_2$  and  $b$  had high skewness values for each data set, in addition to  $T_1$  having no G scores. The remaining parameter,  $a$ , which had five G scores, also had four B scores. Thus, at least two parameters and sometimes all four parameters of the Brière-2 model can be expected to have biased, nonnormal estimators. For the Beta model, parameter  $T_1$  is consistently bad and  $T_2$  is often bad and never good. For the Lactin model, its bad behavior is spread out among all parameters, there being three datasets for which all four parameters are badly behaved. For the Ratkowsky model, only the parameter  $T_1$  has

**Table 4.** Assessment of nonlinear behavior, intrinsic and parameter-effects curvatures of the models

	Nonlinearity measure	Beta model	Brière-2 model	Lactin model	LRF model	Ratkowsky model
<i>A. aegypti</i>	RMS IN <sup>a</sup>	0.0387 <sup>ns</sup>	0.0597 <sup>ns</sup>	0.1632 <sup>ns</sup>	0.0688 <sup>ns</sup>	0.0609 <sup>ns</sup>
	RMS PE <sup>b</sup>	1.7413 <sup>*d</sup>	4.2649 <sup>*</sup>	0.6556 <sup>*</sup>	0.3139 <sup>ns</sup>	2.0152 <sup>*</sup>
	Crit. curvature	0.5458	0.5458	0.5458	0.5458	0.5458
<i>B. dorsalis</i>	RMS IN	0.0476 <sup>ns</sup>	0.0719 <sup>ns</sup>	0.0796 <sup>ns</sup>	0.0603 <sup>ns</sup>	0.0727 <sup>ns</sup>
	RMS PE	1.1504 <sup>*</sup>	1.0191 <sup>*</sup>	0.2555 <sup>ns</sup>	0.2126 <sup>ns</sup>	2.1468 <sup>*</sup>
	Crit. curvature	0.5721	0.5721	0.5721	0.5721	0.5721
<i>B. tabaci</i>	RMS IN	0.0670 <sup>ns</sup>	0.0180 <sup>ns</sup>	0.0663 <sup>ns</sup>	0.0289 <sup>ns</sup>	0.0524 <sup>ns</sup>
	RMS PE	25.7475 <sup>*</sup>	10.9552 <sup>*</sup>	0.9351 <sup>*</sup>	0.4206 <sup>*</sup>	1.8711 <sup>*</sup>
	Crit. curvature	0.3312	0.3312	0.3312	0.3312	0.3312
<i>D. buzzatii</i>	RMS IN	0.0696 <sup>ns</sup>	0.0718 <sup>ns</sup>	0.2043 <sup>ns</sup>	0.1006 <sup>ns</sup>	0.1000 <sup>ns</sup>
	RMS PE	3.9085 <sup>*</sup>	6.1820 <sup>*</sup>	1.5026 <sup>*</sup>	0.5198 <sup>*</sup>	6.19993 <sup>*</sup>
	Crit. curvature	0.4389	0.4389	0.4389	0.4389	0.4389
<i>E. varivestis</i>	RMS IN	0.0759 <sup>ns</sup>	0.0126 <sup>ns</sup>	0.2209 <sup>ns</sup>	0.0919 <sup>ns</sup>	0.1111 <sup>ns</sup>
	RMS PE	5.5583 <sup>*</sup>	130.6542 <sup>*</sup>	0.9084 <sup>*</sup>	0.6889 <sup>*</sup>	6.8404 <sup>*</sup>
	Crit. curvature	0.3956	0.3956	0.3956	0.3956	0.3956
<i>H. armigera</i>	RMS IN	0.0291 <sup>ns</sup>	0.0376 <sup>ns</sup>	0.0930 <sup>ns</sup>	0.0392 <sup>ns</sup>	0.0405 <sup>ns</sup>
	RMS PE	1.3217 <sup>*</sup>	1.7136 <sup>*</sup>	0.3516 <sup>ns</sup>	0.1463 <sup>ns</sup>	1.0188 <sup>*</sup>
	Crit. curvature	0.5877	0.5877	0.5877	0.5877	0.5877
<i>K. aberrans</i>	RMS IN	0.0651 <sup>ns</sup>	0.0942 <sup>ns</sup>	0.1225 <sup>ns</sup>	0.0928 <sup>ns</sup>	0.0778 <sup>ns</sup>
	RMS PE	1.3876 <sup>*</sup>	2.8603 <sup>*</sup>	2.3511 <sup>*</sup>	0.3399 <sup>ns</sup>	7.4045 <sup>*</sup>
	Crit. curvature	0.4389	0.4389	0.4389	0.4389	0.4389
<i>L. erysimi</i>	RMS IN	0.0334 <sup>ns</sup>	0.0818 <sup>ns</sup>	0.1316 <sup>ns</sup>	0.0520 <sup>ns</sup>	0.0431 <sup>ns</sup>
	RMS PE	0.4685 <sup>ns</sup>	2.3620 <sup>*</sup>	0.7098 <sup>*</sup>	0.1709 <sup>ns</sup>	3.1486 <sup>*</sup>
	Crit. curvature	0.5105	0.5105	0.5105	0.5105	0.5105
<i>M. persicae</i>	RMS IN	0.0464 <sup>ns</sup>	0.0265 <sup>ns</sup>	0.2253 <sup>ns</sup>	0.0598 <sup>ns</sup>	0.0654 <sup>ns</sup>
	RMS PE	1.4749 <sup>*</sup>	36.9597 <sup>*</sup>	0.6078 <sup>*</sup>	0.2878 <sup>ns</sup>	2.0574 <sup>*</sup>
	Crit. curvature	0.4926	0.4926	0.4926	0.4926	0.4926
<i>T. brevipalpis</i>	RMS IN	0.0506 <sup>ns</sup>	0.1633 <sup>ns</sup>	0.1936 <sup>ns</sup>	0.0930 <sup>ns</sup>	0.0731 <sup>ns</sup>
	RMS PE	1.3651 <sup>*</sup>	3.2567 <sup>*</sup>	1.0016 <sup>*</sup>	0.3840 <sup>ns</sup>	8.5795 <sup>*</sup>
	Crit. curvature	0.5721	0.5721	0.5721	0.5721	0.5721

<sup>a</sup>RMS IN—Root mean square intrinsic curvature.

<sup>b</sup>RMS PE—Root mean square parameter-effects curvature.

<sup>c</sup>ns—Not significant,  $P > 0.05$ .

<sup>d</sup>\*—Significant,  $P < 0.05$ .

consistently good (or more rarely moderate) estimation behavior, with the estimators of  $T_{\max}$  and  $b$  being bad for half of the datasets.

Corroboration of the efficacy of individual parameter estimators is obtained from the profile  $t$  plots (Supp. Fig. 1, see Supp. Material 1 [online only] for details), the confidence curves (Supp. Fig. 2, see Supp. Material 1 [online only] for details), and the parameter distribution histograms (Supp. Fig. 3, see Supp. Material 1 [online only] for details). These figures contain results only for the *Aedes aegypti* dataset, but that is sufficient to establish that there is close agreement between conclusions drawn from use of the Hougaard skewness measure and other measures of nonlinear behavior, as patterns that develop among the parameter estimators for one dataset tend to be consistent over all of the datasets.

## Discussion

Decisions about whether or not a nonlinear regression model is a good one have usually been based in the past upon goodness-of-fit considerations only. We argue here that this is inadequate. Of course, a model that does not fit the data well is unlikely to be of further interest to the modeler who wants to determine the relationship between the response variable and the explanatory variable. But goodness-of-fit is only one aspect of a model's efficacy, and there are usually several models, as there are in the present study, which succeed in fitting the data well, at least for some of the data

sets. Aside from fitting the data well, a good mechanistic model should have readily interpretable parameters. We believe that the parameters of the model should all be close-to-linear, so that their least squares estimators are almost unbiased, normally distributed, minimum variance estimators. Finally, since nonlinear regression models are generally solved by iteration, it is desirable to have a model for which good initial parameter estimates can be obtained. In the following paragraphs, we discuss how the five models fare according to these various criteria by which good model behavior may be judged.

The five models studied here can be broken down into three groups based upon goodness of fit. Two models stand out as providing very good fits to the data, viz. the Ratkowsky model and the LRF model (Table 2). The LRF model has three parameters,  $T_1$ ,  $T_{opt}$  and  $\mu_{opt}$ , which are close-to-linear, as adjudged by all of the measures employed to assess nonlinear behavior. The estimates of these parameters have low bias, low skewness and their histograms are close to being normally distributed. They have almost linear profile  $t$  plots and confidence curves which are indicative of close-to-linear behavior. The fourth parameter,  $T_2$ , does not have a close-to-linear least squares estimator, but the extent of nonlinear behavior is not very large. We will examine this in more detail below. Although the Ratkowsky model fits observed data very well, the estimator of only one of its parameters, viz.  $T_1$ , is consistently close-to-linear. In contrast, the estimators of parameters  $T_2$  and  $b$  never scored good

**Table 5.** Assessment of nonlinear behavior, individual parameters

	Beta model				Brière model				Lactin model				LRF model				Ratkowsky model			
	$r_m$	$T_1$	$T_2$	$T_m$	$a$	$T_1$	$T_2$	$b$	$\lambda$	$\rho$	$T_u$	$\delta$	$T_1$	$T_2$	$T_{opt}$	$\mu_{opt}$	$T_1$	$T_2$	$b$	$c$
<i>A. aegypti</i>	G	B	M	G	M	M	B	B	M	M	B	B	G	B	G	G	G	B	M	M
<i>B. dorsalis</i>	G	B	M	G	G	M	B	B	G	G	M	M	G	M	G	G	G	M	M	M
<i>B. tabaci</i>	G	B	M	G	G	B	B	B	G	G	G	M	M	M	G	G	G	M	M	M
<i>D. buzzati</i>	G	B	B	M	B	M	B	B	B	B	B	B	G	B	G	G	M	B	B	M
<i>E. varivestis</i>	G	B	B	B	G	M	B	B	M	M	M	M	G	B	B	M	M	B	B	B
<i>H. armigera</i>	G	B	M	G	G	M	B	B	G	G	M	M	G	M	G	G	G	M	M	G
<i>K. aberrans</i>	G	B	B	G	B	B	B	B	B	B	B	B	G	B	G	G	G	B	B	M
<i>L. erysimi</i>	G	B	M	G	B	B	B	B	B	M	B	B	G	M	G	G	G	M	B	G
<i>M. persicae</i>	G	B	B	M	G	M	B	B	M	M	B	B	G	B	G	G	G	M	M	M
<i>T. brevipalpis</i>	G	B	B	B	B	M	B	B	B	B	B	B	G	B	B	G	G	B	B	M

Key:

G (good):  $|g_1| \leq 0.2$ .

M (moderate):  $0.2 < |g_1| \leq 0.5$ .

B (bad):  $|g_1| > 0.5$ .

(“G”) behavior in any dataset. Together with the estimator of  $c$ , which scored good behavior for only two datasets, they generally have sufficient bias, skewness, and nonnormal histograms to exclude them as being close-to-linear.

At the other end of the goodness-of-fit scale, the Brière-2 and Lactin models fit the data poorly, often producing strings of like-signed residuals and deviating widely from the observed data (Fig. 1). These two models could be excluded from consideration based upon goodness-of-fit alone, but it is also found that they are inadequate with respect to other considerations as well. For example, the Brière-2 model often produces very high parameter-effects nonlinearity (Table 4) and has two parameters ( $T_2$  and  $b$ ) that exhibit bad (“B”) nonlinear behavior for all 10 datasets (Table 5). The Lactin model is more erratic, and has significant parameter-effects curvature for all but two of the datasets (Table 4).

The third “group” of models based upon goodness-of-fit considerations is the Beta model. It was the best-fitting model amongst all models for half of the datasets (Table 2), but a serious flaw is that the model produces an unrealistically low notional minimum temperature for growth ( $T_1$ ), as it also did when a different stochastic assumption was made (Shi et al. 2016b). It is interesting that all four of its parameters have biological meaning, a feature it shares in common with the LRF model. In fact, the four parameters of these two models are the same parameters, viz. a notional minimum temperature for growth, a notional maximum temperature for growth, and an optimal temperature for growth and the growth rate corresponding to that temperature. It is perhaps surprising, or at least instructive, that these models can have such contrasting estimation properties when their parameters have the same meaning.

Based upon the various ways of assessing nonlinear regression models, we can exclude the Beta, the Brière-2 and the Lactin models from further consideration. The choice between models falls to a choice between the good-fitting Ratkowsky and LRF models. However, we have seen that the Ratkowsky model has some failings with respect to the behavior of three of its parameters, with two of them, viz.  $b$  and  $c$ , being nothing more than “curve-fitting” parameters, devoid of biological meaning. Therefore the LRF model emerges as the clear choice as the most suitable model of the five models studied to be used for modeling the development of insects and mites.

We now briefly have a look at the parameter  $T_2$  of the LRF model, which was the only parameter of that model whose least

squares estimator did not have close-to-linear behavior. The output from PROC NLIN in SAS/STAT, version 9.3, provides an estimate of the bias in each of the parameter estimates using the formula of Box (1971). For the 10 datasets considered in this study, the bias in  $T_2$  ranged from 0.0078 to 0.2224 K, a trivial amount when compared to the parameter estimate itself, which ranged from 305.8 to 312.1 K. Since the maximum bias is only ca. 0.2 K, this makes no difference in any practical sense. Therefore, one can be confident, using the LRF model, that estimates of all four of its parameters will not be substantially biased. If a modeler insists upon having a better parameterization, one can seek a new parameter whose least-squares estimator has less bias than that of the parameter in the original parameterization. Indeed, replacing  $T_2$  by the exponential of itself, i.e.,  $\exp(T_2)$ , results in the “new”  $T_2$  having a smaller bias than that of the “old”  $T_2$ . However, adopting the new parameterization in place of the old one may be seen as counterproductive, since one of the desirable features of the LRF model is the fact that all four of its parameters have biological meaning. As the exponential of a temperature is less intuitive than that of the temperature itself, this parameterization is not likely to appeal to potential users of this model.

The output from PROC NLIN in SAS/STAT, version 9.3, provides some additional information not dealt with in this paper. Amongst this output are scatter plots of pairs of parameter estimates for each model. In the case of the LRF model, the six scatter plots ( $T_1$  vs.  $T_2$ ,  $T_1$  vs.  $T_{opt}$ ,  $T_2$  vs.  $T_{opt}$ ,  $T_1$  vs.  $\mu_{opt}$ ,  $T_2$  vs.  $\mu_{opt}$  and  $T_{opt}$  vs.  $\mu_{opt}$ ) are all broad ellipses in shape, with the semimajor and semiminor axes not coinciding with the “X”-axis or the “Y”-axis. This is the shape that one would expect for estimates that conform to a bivariate normal distribution whose parameters are correlated, which is precisely what one expects from close-to-linear least squares estimators for a nonlinear regression model. Rosso et al. (1993) mistakenly believed that the correlations that they found between pairs of parameter estimates for the LRF model were unexpected, but asymptotic theory dictates only that the distribution is bivariate normal, with the absolute value of the correlation coefficient able to take on any value between 0 and 1. The other models give rise to some very different scatter plot shapes. For example, the scatter plots of  $T_u$  vs.  $\delta$  and  $\rho$  vs.  $\lambda$  for the Lactin model are narrow and pencil-shaped, indicating extremely high correlation between these pairs of estimates. This is a result that modelers would prefer not to have. Another extreme type of scatter plot is that of  $T_2$  vs.  $b$  for the



Brière-2 model, where the scatter plot is boomerang-shaped, indicating very nonnormal and therefore far-from-linear least squares estimators. These scatter plots provide confirmatory information about the behavior of the estimators and reinforce conclusions drawn from such measures as the profile  $t$  plots, the confidence curves, and the skewness measure of Hougaard (1985). Other output provided by PROC NLIN in SAS/STAT, version 9.3, includes bootstrap bias-corrected confidence intervals for each of the parameter estimates. When the least squares estimators of the parameters are close-to-linear, these bootstrap confidence intervals are very close to the approximate confidence intervals obtained from asymptotic theory. This is the case for all the parameters of the LRF model, including  $T_2$ . For parameter estimates that have far-from-linear parameter estimators, such as for  $\delta$  in the Lactin model or  $b$  in the Brière-2 model, the bias-corrected bootstrap confidence intervals deviate markedly from those based on large-sample theory. Although the bootstrap estimates are more accurate and therefore preferable to the large-sample values, users are unlikely to want to use nonlinear regression models such as the Beta, Lactin, and Brière-2 models, which tend to exhibit such far-from-linear estimation behavior, when a good-fitting, good-behaving model such as the LRF model is available for general use.

We can conclude that the LRF model is the best of the five models studied, providing close-to-linear least squares estimates to data on the development of insects and mites.

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