55th Annual Meeting of the European Association for Animal Production in Slovenia, Bled
Paper PG6.8

Estimation of Gompertz growth curve parameters by a non-linear mixed effects model

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Abstract

Simulated growth data with parameters appropriate for pigs were generated through a 2 step process. First, a linear mixed model was used to produce Gompertz growth curve coefficients for each pig. Then, 30 weekly weights were produced using the coefficients. Simulated pedigree had 3 generations without selection: 10 unrelated grandsires and 200 sires, each with 24 tested offspring. A method based on Taylor series approximation was applied to estimate breeding values for curve parameters and the corresponding (co)variance components. In every iteration, a working variate (sum of predictions by linearized model and a non-linear model residual) was utilized to solve location and dispersion parameters of the linearized model. Approach required only minor changes to existing software for random regression models. In addition to data from full growing period, a truncated time trajectory data was analyzed to test the approach when animals are slaughtered prematurely. Truncation was at slaughter weight 115kg, which reduced the number of measurements to 11 per pig on average. From 50 replicates with full data the bias of estimates of three genetic variances were 1% of the parameter values, on average. For the truncated data bias increased to 19% and -23% for first and third parameter. Results of this study indicated the capability of linearization approach to estimate original parameters satisfactorily for full data, but not as well for truncated data.

1. Introduction

Growth of animal is often documented by measuring several longitudinal observations in time until adult weight is attained. However, field data in animal production may be incomplete. For example, adult weight is often unavailable due to earlier slaughter age. Statistical analysis of growth data may be most appealing by non-linear functions, because they can describe the entire growth process in terms of a few parameters, and predictions outside the data range can be made more reliably than by linear models. A commonly used model is a Gompertz function, where parameters can have biological meaning. However, non-linear models are more complicated to estimate than linear models, and several algorithms have been proposed to solve the parameters and variance components of non-linear mixed-effects models ([2], [4], [6], [7]).

Frequentist methods apply either numerical integration or approximation methods based on linearization of integral of the likelihood function. We will consider approximation based on second-order Taylor series expansion with respect of random effects as presented by Wolfinger and Lin [7]. They gave two alternative approaches to select points of expansion: zero-expansion method uses expected value, and EBLUP-expansion method uses predicted value of random effects. Here, the latter method is considered. In linearizing methods it has been a common way to alternate between a penalized non-linear least-squares step and a linear mixed effects step ([2], [3]), whereas algorithm introduced here alternates between Henderson's mixed model equations and restricted maximum likelihood (REML) estimation of linear mixed effects model. Therefore, using EBLUP-expansion allows use of common methods for linear mixed effects models and use of existing programs after small changes.

The presented procedure is similar to that commonly used in animal breeding for linear traits. Variance components estimated by REML are used in mixed model equations to solve location parameters. Consequently, even large models and data sets can be analysed when variance components have been estimated. The advantage of the presented method is generality. The method can be used for different special cases because it is developed for general non-linear mixed models.

Aim of this work was to describe and examine performance of the EBLUP-expansion method in animal breeding through simulation using the Gompertz function as growth model in pigs. The simulation also considered estimation using truncated data, where slaughter weight is much below adult weight.

2. Materials and methods

2.1 Simulation

Gompertz growth function is one of the most frequently used curves in growth mathematics. We assumed that the weights of each individual followed the Gompertz law:

$$y_{ij} = \alpha_i \exp(-\beta_i \exp(-\kappa_i t_j)) + e_{ij},$$

where y_{ij} is the observed weight of individual i at time j, t_j is age in days at time j, α_i, β_i and κ_i are the parameters of the Gompertz function for the ith animal and e_{ij} is random residual term. The biological meaning of the parameter α_i is the adult weight, κ_i is the rate of exponential decay of the initial growth rate and β_i is related to weight at birth ($t = 0$).

Each of the parameters α_i, β_i, κ_i was described by a linear effects model such that full model is

$$\begin{aligned} y_{ij} = {} & (x_{\alpha_i} b_{\alpha_i} + z_{\alpha_i} u_{\alpha_i} + w_{\alpha_i} p_{\alpha_i}) \\ & \exp(-(x_{\beta_i} b_{\beta_i} + z_{\beta_i} u_{\beta_i} + w_{\beta_i} p_{\beta_i}) \\ & \exp(-(x_{\kappa_i} b_{\kappa_i} + z_{\kappa_i} u_{\kappa_i} + w_{\kappa_i} p_{\kappa_i}) t_j)) + e_{ij}, \end{aligned}$$

where $(b_{\alpha_i}, b_{\beta_i}, b_{\kappa_i})$ are fixed effects, $(u_{\alpha_i}, u_{\beta_i}, u_{\kappa_i})$ are random genetic sire effects and $(p_{\alpha_i}, p_{\beta_i}, p_{\kappa_i})$ are random non-genetic animal effects. It is assumed that

$$\begin{pmatrix} \mathbf{u} \\ \mathbf{p} \\ \mathbf{e} \end{pmatrix} = \mathrm{N}\left(\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \begin{pmatrix} \mathbf{G} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \end{pmatrix} \right),$$

where **G** is covariance matrix for genetic sire effect, **P** is covariance matrix for non-genetic animal effect and **R** is residual covariance matrix. Further, it is assumed that $\mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A}$, where $\mathbf{G}_0$ is 3×3 additive genetic covariance matrix by animal and **A** is matrix of additive relationships between animals. Similarly, covariance matrix for non-genetic animal effect **P** was assumed to be identically and independently distributed for animal i, $\mathbf{p}_i \sim \mathrm{N}(\mathbf{0}, \mathbf{P}_0)$. Finally, the residuals were assumed to be independent, $\mathbf{R} = \mathbf{I}\sigma_e^2$.

Measurement of weight was generated in two steps, where the first step generated Gompertz function coefficients and the second step the growth observation with the coefficients. The Gompertz model was used to analyse simulated growth data with parameters appropriate for pig growth. (Co)Variance matrices in the simulations were for genetic sire effect

$$\mathbf{G}_0 = \begin{bmatrix} 10 & & \\ -0.06 & 0.01 & \\ -0.0003 & 0.00001 & 0.0000003 \end{bmatrix}$$

and for non-genetic animal effect

$$\mathbf{P}_0 = \begin{bmatrix} 60 & & \\ -0.36 & 0.06 & \\ -0.003 & 0.00006 & 0.0000028 \end{bmatrix},$$

where the order of the Gompertz parameters is α, β, κ. Residual variance σ_e^2 was equal to one.

Data included 4800 tested animals. The pedigree had 3 generations with 10 founder grandsires. Each of the 10 grandsires had 20 half-sib sons which had each 24 tested progeny. Two data sets were made: complete and truncated time trajectory data. The complete data had 30 equally distanced observations between 50 and 253 days. The truncated time data had slaughter weights up to 115 kg which occurs at about 120 days. This reduced the number of measurements to 11 per pig on average, i.e., almost two thirds of the data were discarded. The truncated time trajectory data was analysed to test the approach when animals are slaughtered before gaining adult weight. Relative bias, standard deviation (SD) and mean squared error (MSE) were calculated from 50 replicates and used as descriptive statistics in the simulation study.

2.2. Method to estimate the values of the growth parameters

General form of the non-linear mixed model is

$$\mathbf{y} = f(\mathbf{X}, \mathbf{b}, \mathbf{Z}, \mathbf{u}) + \mathbf{e},$$

where $\mathbf{y}$ is $n \times 1$ -vector of observations, f is the non-linear model function, $\mathbf{b}$ is $p \times 1$ -vector of fixed effects and $\mathbf{u}$ is $q \times 1$ -vector of random effects, $\mathbf{e}$ is $n \times 1$ -vector of random residual, and $\mathbf{X}$ and $\mathbf{Z}$ are design matrices of fixed and random effects, respectively. Assumptions for random effects are as given previously. For simplicity, denote unknown elements of all random and residual covariance matrices by parameter vector $\boldsymbol{\theta}$.

Frequentist parameter estimation maximizes the likelihood function, which in this case is

$$\begin{aligned} L(\mathbf{b}, \boldsymbol{\theta} \mid \mathbf{y}) = {} & (2\pi)^{-\frac{n}{2}} \mid \mathbf{R} \mid^{-\frac{1}{2}} (2\pi)^{-\frac{q}{2}} \mid \mathbf{G} \mid^{-\frac{1}{2}} \\ & \int \exp\left(-\frac{1}{2} (\mathbf{y} - f(\mathbf{X}, \mathbf{b}, \mathbf{Z}, \mathbf{u}))^T \mathbf{R}^{-1} (\mathbf{y} - f(\mathbf{X}, \mathbf{b}, \mathbf{Z}, \mathbf{u})) - \frac{1}{2} \mathbf{u}^T \mathbf{G}^{-1} \mathbf{u} \right) d\mathbf{u}. \end{aligned} \tag{1}$$

Only in some cases a closed form is found when differentiating the likelihood with respect to the parameters. Thus, the integral is often solved numerically. However, numerical methods for non-linear functions may be slow in convergence and numerically unstable. Instead, we used approximation where the integral function is linearized with Taylor series expansion. The following paragraphs explain the linearization method, which uses second-order Taylor expansion around points of expected values for the random effects ([3], [4], [7]).

Second-order expansion for the exponent part of the integral, is made about the predicted BLUP value before integration of the likelihood function. Thus, approximation of the logarithmic likelihood function for function (1) will be

$$\begin{aligned} l^*(\mathbf{b},\boldsymbol{\theta}\,|\,\mathbf{y}) = & -\frac{1}{2}n\ln(2\pi)-\frac{1}{2}\ln(|\,\tilde{\mathbf{Z}}^{*T}\mathbf{R}^{-1}\tilde{\mathbf{Z}}^{*}\mathbf{G}+\mathbf{I}\,||\,\mathbf{R}\,|) \\ & -\frac{1}{2}(\mathbf{y}-f(\mathbf{X},\mathbf{b},\mathbf{Z},\tilde{\mathbf{u}}))^{T}\mathbf{R}^{-1}(\mathbf{y}-f(\mathbf{X},\mathbf{b},\mathbf{Z},\tilde{\mathbf{u}}))-\frac{1}{2}\tilde{\mathbf{u}}^{T}\mathbf{G}^{-1}\tilde{\mathbf{u}}, \end{aligned} \tag{2}$$

where $\tilde{\mathbf{Z}}^* = \partial f/\partial\mathbf{u}^T\,|_{\mathbf{u}=\tilde{\mathbf{u}}}$ and $\tilde{\mathbf{u}}$ is the empirical BLUP-estimate of random effects.

Pinheiro and Bates ([3], [4]) used approximation of logarithmic likelihood function (2) in estimation of parameters. Thus, estimation was penalized non-linear least-squares problem. However, Wolfinger and Lin [7] continued evaluation of function (2). Denote $\mathbf{V}=\mathbf{Z}^*\mathbf{G}\mathbf{Z}^{*T}+\mathbf{R}$. Then $|\,\tilde{\mathbf{V}}\,| = |\,\mathbf{R}\,||\,\mathbf{I}+\tilde{\mathbf{Z}}^{*T}\mathbf{R}^{-1}\tilde{\mathbf{Z}}^{*}\mathbf{G}\,|$, $\tilde{\mathbf{V}}^{-1}=\mathbf{R}^{-1}-\mathbf{R}^{-1}\tilde{\mathbf{Z}}^{*}\mathbf{G}(\mathbf{I}+\tilde{\mathbf{Z}}^{*T}\mathbf{R}^{-1}\tilde{\mathbf{Z}}^{*}\mathbf{G})^{-1}\tilde{\mathbf{Z}}^{*T}\mathbf{R}^{-1}$ and the logarithmic likelihood function in equation (2) can be written

$$\begin{aligned} l^*(\mathbf{b},\boldsymbol{\theta}\,|\,\mathbf{y}) = & -\frac{1}{2}n\ln(2\pi)-\frac{1}{2}\ln|\,\tilde{\mathbf{V}}\,| \\ & -\frac{1}{2}(\mathbf{y}-f(\mathbf{X},\mathbf{b},\mathbf{Z},\tilde{\mathbf{u}})+\tilde{\mathbf{Z}}^{*}\tilde{\mathbf{u}})^{T}\tilde{\mathbf{V}}^{-1}(\mathbf{y}-f(\mathbf{X},\mathbf{b},\mathbf{Z},\tilde{\mathbf{u}})+\tilde{\mathbf{Z}}^{*}\tilde{\mathbf{u}}). \end{aligned} \tag{3}$$

This is the base for estimation of location parameters and variance components introduced below.

Assume variance component vector $\boldsymbol{\theta}$ as known. Maximum likelihood (ML) estimation for the parameters **b** and **u** leads to solving equations:

$$\begin{aligned} \mathbf{X}^{*T}\mathbf{R}^{-1}(\mathbf{y}-f(\mathbf{X},\tilde{\mathbf{b}},\mathbf{Z},\tilde{\mathbf{u}})) &= \mathbf{0} \\ \mathbf{Z}^{*T}\mathbf{R}^{-1}(\mathbf{y}-f(\mathbf{X},\tilde{\mathbf{b}},\mathbf{Z},\tilde{\mathbf{u}})) &= \mathbf{G}^{-1}\tilde{\mathbf{u}}, \end{aligned} \tag{4}$$

where $\mathbf{X}^* = \partial f/\partial\mathbf{b}^T$ and $\tilde{\mathbf{b}}$ is estimate of fixed effects **b**. When denoted $\mathbf{Y}=\mathbf{y}-f(\mathbf{X},\mathbf{b},\mathbf{Z},\mathbf{u})+\mathbf{X}^*\mathbf{b}+\mathbf{Z}^*\mathbf{u}$, equations (4) can be written as

$$\begin{bmatrix} \mathbf{X}^{*T}\mathbf{R}^{-1}\mathbf{X}^{*} & \mathbf{X}^{*T}\mathbf{R}^{-1}\mathbf{Z}^{*} \\ \mathbf{Z}^{*T}\mathbf{R}^{-1}\mathbf{X}^{*} & \mathbf{Z}^{*T}\mathbf{R}^{-1}\mathbf{Z}^{*}+\mathbf{G}^{-1} \end{bmatrix}\begin{pmatrix} \tilde{\mathbf{b}} \\ \tilde{\mathbf{u}} \end{pmatrix}=\begin{bmatrix} \mathbf{X}^{*T}\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{Z}^{*T}\mathbf{R}^{-1}\mathbf{Y} \end{bmatrix}. \tag{5}$$

This is similar to mixed model equations for linear models, and already established methods for solving linear models can thus be used to analyse pseudo-data **Y** created from the original data **y** with $\tilde{\mathbf{b}}$ and $\tilde{\mathbf{u}}$ equal to their most recent estimates.

After solving estimates of the location effects, profile likelihood is used to estimate variance components by setting $\mathbf{b}=\tilde{\mathbf{b}}(\boldsymbol{\theta})$. Logarithmic likelihood function of parameter vector $\boldsymbol{\theta}$ can be written with pseudo-data as

$$l^*_{ML}(\boldsymbol{\theta}) = -\frac{1}{2}n\ln(2\pi)-\frac{1}{2}\ln|\,\mathbf{V}\,|-\frac{1}{2}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})^{T}\mathbf{V}^{-1}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})\Big|_{\mathbf{b}=\tilde{\mathbf{b}}(\boldsymbol{\theta})}\,. \tag{6}$$

Derivative of equation (6) with respect to $\boldsymbol{\theta}$ gives

$$-\frac{1}{2}\operatorname{tr}\left(\mathbf{V}^{-1}\frac{\partial\mathbf{V}}{\partial\boldsymbol{\theta}_j}\right)+\frac{1}{2}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})^{T}\mathbf{V}^{-1}\frac{\partial\mathbf{V}}{\partial\boldsymbol{\theta}_j}\mathbf{V}^{-1}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})\Big|_{\mathbf{b}=\tilde{\mathbf{b}}(\boldsymbol{\theta})}\,. \tag{7}$$

Maximum likelihood estimates of the variance components are found by equating (7) to zero and solving for $\boldsymbol{\theta}$.

Instead of ML-estimates, REML-estimates are commonly used in practise. These estimates account for loses in degrees of freedom caused by estimation of fixed effects $\mathbf{b}$. The logarithmic likelihood function is now

$$l^*_{REML}(\boldsymbol{\theta}) = -\frac{1}{2}n\ln(2\pi) - \frac{1}{2}\ln|\mathbf{V}| - \frac{1}{2}\ln|\mathbf{X}^{*T}\mathbf{V}^{-1}\mathbf{X}^*| - \frac{1}{2}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})^T\mathbf{V}^{-1}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})\Big|_{\mathbf{b}=\tilde{\mathbf{b}}(\boldsymbol{\theta})}. \quad (8)$$

Thus, equating derivative of equation (8) to zero gives

$$-\frac{1}{2}\mathrm{tr}\left(\mathbf{P}\frac{\partial\mathbf{V}}{\partial\boldsymbol{\theta}_j}\right) + \frac{1}{2}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})^T\mathbf{V}^{-1}\frac{\partial\mathbf{V}}{\partial\boldsymbol{\theta}_j}\mathbf{V}^{-1}(\mathbf{Y}-\mathbf{X}^*\mathbf{b})\Big|_{\mathbf{b}=\tilde{\mathbf{b}}(\boldsymbol{\theta})} = \mathbf{0}, \quad (9)$$

where $\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1}\mathbf{X}^*(\mathbf{X}^{*T}\mathbf{V}^{-1}\mathbf{X}^*)^{-1}\mathbf{X}^{*T}\mathbf{V}^{-1}$. Solutions in $\boldsymbol{\theta}$ are the REML-estimates of the variance components.

Approximate ML-solutions of location parameter effects and variance components are obtained by iteratively solving equations (5) and (7) until convergence. Correspondingly, REML-solutions for EBLUP-expansion are obtained by iteratively solving equations (5) and (9). Here the linear mixed effects model $\mathbf{Y} = \mathbf{X}^*\mathbf{b} + \mathbf{Z}^*\mathbf{u} + \mathbf{e}$ is fitted for pseudo-data $\mathbf{Y}$ and working vectors $\mathbf{X}^*$ and $\mathbf{Z}^*$, where $\mathbf{u} \sim \mathrm{N}(\mathbf{0}, \mathbf{G}(\boldsymbol{\theta}))$ and $\mathbf{e} \sim \mathrm{N}(\mathbf{0}, \mathbf{R}(\boldsymbol{\theta}))$.

2.3. Implementation

The presented method required implementation of the linearization procedure to linear mixed model program. We implemented the Gompertz growth model using cyclically MiX99 for solving mixed model equations and DMU for REML estimates of covariance components. Crucial for implementation is capability of fitting random regression models, which option is build in MiX99 [5] and was added in DMU by Kettunen et. al. [1].

In addition to including the necessary Gompertz function formulas to MiX99, variance components needed some reparametrization. Because variance component of κ is close to zero, convergence was accelerated by introducing time scaling during the estimation. In every iteration round scaling factor s, equal to most recent estimated value for parameter κ, was used. Thus, time t_j associated with observation j in the data was multiplied by the scaling factor before starting an estimation step. Consequently, variance component estimate for the scaled parameter κ^* was larger than for the original parameter κ.

3. Results and discussion

Average number of cycles with mixed model equations solve and REML procedure were 7 for the full data simulation. For the truncated time trajectory data the average number of cycles increased to 11, indicating a decrease in stability. Residual error variance converged well and was estimated to be almost exactly the original value used in the simulations.

Simulation statistics for variance components of genetic sire effects $\mathbf{G}_0$ are in Table I. The estimated variance components were in good agreement with the initial parameter values when the full data was analysed. Analysis for truncated time trajectory data showed larger bias, but order of magnitude for estimated values were still reasonable with SD larger than bias. Estimated variance component for parameter β agreed with original value, but for parameters α and κ bias was 19% and -23%, respectively. This more unreliable estimation of truncated time trajectory data appeared also in standard deviations. Relative SD increased from 0.14 to 0.36 on average for parameters α and κ, but only to 0.18 for parameter β. For all covariance components relative SDs are large. Especially estimation of covariance between α and κ was unstable.

Estimation of (co)variance components for non-genetic animal effects $\mathbf{P}_0$ showed similar results as the genetic sire effects (Table II). The estimated variance components were in good agreement with the true parameter values used to simulate the data, when the full data was used. When truncated time trajectory data was analyzed, uncertainty is seen as larger bias and SD especially for parameters related to α. The bias were 25%, 3% and -2% from original values used in simulations for parameters α, β and κ, respectively. Furthermore, relative standard deviation increased only from 0.02 to 0.04 for parameters β and κ, but to 0.15 for parameter α. However, the magnitude of increase in relative SD for parameter α was small in comparison to increase in bias, so that a huge increase in relative MSE for truncated time trajectory data was due to large bias.

4. Conclusions

The approximation method that used second-order Taylor series expansion for integrant of non-linear likelihood function was found to be useful in estimation of non-linear mixed effects models when growth is modelled by Gompertz function. Usually non-linear estimation is found to be problematic. Although the presented two-step iterative procedure with each step itself being iterative can be regarded as computer intensive, the advantage is easy implementation to the existing programs of linear mixed effects model. Only minor changes are needed relating to linearization procedure. Furthermore, an advantage is the generality of models accepted for the method.

Results from the simulation showed good agreement with the initial values for data, which included observations from the whole growing period. Adult weight was not reached and the latter part of the function curve had no data, when animals were slaughtered prematurely. Especially this had influence for estimation of parameters related to adult weight. Otherwise the results from the simulation were fairly good also for truncated time trajectory data.

References

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Table I. Relative bias (Rel. Bias), standard deviation (Rel. SD) and mean squared error (Rel. MSE) for (co)variance components of genetic sire effects from the simulations for full and truncated data. Subscripts α, β and κ denote the three parameters in the Gompertz function.

		Full data			Truncated data		
Parameter	True	Rel. Bias	Rel. SD	Rel. MSE	Rel. Bias	Rel. SD	Rel. MSE
σ_{α}^{2}	10.0	-0.002	0.144	0.204	0.186	0.358	1.601
$\sigma_{\alpha\beta}$	-0.06	0.013	0.485	0.014	-0.612	0.887	0.068
σ_{β}^{2}	0.01	0.020	0.130	0.0002	0.001	0.180	0.0003
$\sigma_{\alpha\kappa}$	-3.0e-04	-0.054	0.650	0.0001	0.820	1.643	0.0010
$\sigma_{\beta\kappa}$	1.0e-05	0.078	0.496	2.48e-06	-0.009	0.740	5.37e-06
σ_{κ}^{2}	3.0e-07	0.007	0.139	5.67e-09	-0.226	0.370	5.53e-08

Table II. Relative bias (Rel. Bias), standard deviation (Rel. SD) and mean squared error (Rel. MSE) for (co)variance components of the non-genetic animal effect from the simulations for full and truncated data. Subscripts α, β and κ denote the three parameters in the Gompertz function.

		Full data			Truncated data		
Parameter	True	Rel. Bias	Rel. SD	Rel. MSE	Rel. Bias	Rel. SD	Rel. MSE
σ_{α}^{2}	60.0	0.004	0.021	0.026	0.247	0.153	5.036
$\sigma_{\alpha\beta}$	-0.36	0.006	0.064	0.001	-0.519	0.281	0.125
σ_{β}^{2}	0.06	-0.002	0.018	1.88e-05	0.032	0.035	1.35e-04
$\sigma_{\alpha\kappa}$	-0.003	-0.001	0.049	7.10e-06	-0.089	0.318	3.21e-04
$\sigma_{\beta\kappa}$	6.0e-05	-0.009	0.092	5.07e-07	0.025	0.200	2.40e-06
σ_{κ}^{2}	2.8e-06	0.003	0.021	1.24e-09	-0.022	0.045	6.82e-09