

A comparison of parametric methods of modeling mosquito survival using temperature and age-dependent mosquito survival data

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ARTICLE INFO	ABSTRACT
<p><i>Article History:</i> Submitted: 30 October 2018 Accepted: 13 May 2020 Available online: June 2020</p> <p><i>Keywords:</i> Mathematical modelling Climate change Mosquito population dynamics <i>Anopheles gambiae</i> <i>Anopheles stephensi</i> Malaria Vector-borne diseases</p>	<p>It is estimated that malaria affects over 200 million people every year, and accounts for about 750,000 deaths during the same period. The disease control measures often include interventions aimed at reducing the survival of the adult female <i>Anopheles mosquitoes</i>. Whereas research effort has been paid to evaluate the effects on the vector survival, little research has been done on how temperature and time affect the vector adult life-history parameters. This paper sought to compare the performance of four parametric models, namely; Gompertz, gamma, Weibull, and exponential models to determine the best model for analyzing the survival of the female <i>Anopheles mosquito</i>. Using data from a mosquito survival experiment, the paper compared the performance of the models in fitting mosquito mortality. The results showed that temperature and age are significant predictors of vector mortality. In addition, the Gompertz model fitted the data on the adult <i>A. gambiae</i> and <i>A. stephensi</i> better than the Weibull, Gamma, and the Exponential models. The findings of the current paper are useful in parameterizing reliable mathematical models that examine the potential impact of temperature as well as global warming on the transmission of malaria.</p>
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1. Introduction

The adult female *Anopheles mosquito*, *Anopheles gambiae sensu stricto*, plays a significant role in the transmission of vector diseases in Africa [1]. They are the sole vectors for the transmission of the human malaria pathogen, *Plasmodium*. Malaria is among the most significant infectious diseases globally, which is estimated to affect over 200 million people annually, and causes about 750,000 deaths over the same period [2]. The World Health Organization's 2017 Malaria report [2] shows that in 2016, malaria cases increased to 216 million, while deaths reduced to 445,000. Significant research attention in this area has been focused on how malaria can be reduced or eliminated. In this regard, the research focus has been on the interventions of the *Plasmodium* parasite in humans, as well as those designed to interrupt the transmission of the parasite by mosquitoes. The vector control measures have included interventions aimed at reducing the survival of the adult female *Anopheles mosquitoes*. While these factors are important, the survival of the adult female *Anopheles mosquitoes*, which is one of the most significant components of their ability to transmit vector-borne pathogens such as *plasmodium virus*, has attracted little attention [3]. A high survival rate of the arthropod vectors

allows the vectors to produce more offspring, which in turn increase their chances of becoming infected, spread over greater distances; survive for longer as well as improving their chances of delivering effective bites throughout their lifetime. According to Brady et (2013) [4], small changes in the survival rates of the vectors often results in large pathogen transmission changes. In addition, the survival rate differences often influence the vector's geographical distribution as well as their seasonality.

Research interests in quantifying factors affecting the vector's survival rates and how the vector affects disease transmission have been considerable [5,6]. With the emergence of climate change and global warming as significant human health threats, particularly by increasing vector-borne diseases and water-borne diseases, it is logical that we observe temperature consistently as a key factor influencing the vector survival [7]. The few studies existing on the survival of the vector indicate that mosquito survival depends on temperature, rainfall, and humidity, and other factors such as mosquito density, genetic diversity, as well as its ability to find blood [1,7,8]. It was also noted [4] that other factors such as photoperiod as well as humidity are important, but the effect of temperature is the most rigorously quantified limiting factor for vector survival.

Prior research on the interventions and control of malaria has often focused on interrupting the transmission of the parasite by mosquitoes. Scientists have sought to disrupt the survival of mosquitoes using such factors as temperature, and age. To better understand the impacts of the individual factors on the survival of the vectors, many parametric models have been built for measuring their effect. These include the exponential, gamma, Weibull, Gompertz models among others. However, significant variations are usually observed across vector populations by applying a specific model. As such, models have been cross-validated with different cohorts. Therefore, the aim of this paper was to compare, using temperature and age-dependent data, the performance of four parametric models, namely, Gompertz, gamma, Weibull, and exponential models to determine the best model for analyzing the survival of the female *Anopheles* mosquito. The current investigation attempts to validate a predictive model based on mosquito mortality data by survival analysis.

2. Materials and methods

This section focuses on the description of data, the parametric methods for regression model used to analyse the data, and the criterion used to select the best-fit model for the vector survivorship.

2.1 Data sources

Data from the Malaria transmission experiment, which was collected from the Dryad Digital Repository, was considered. The data consists of 2279 mosquitoes with 8 variables [10]. The data was collected from a lab experiment where *Anopheles gambiae* and *Anopheles stephensi* were reared under standard insectary conditions at $27 \pm 0.5^\circ\text{C}$, 80 percent humidity, 12 hours light:12 hours dark photoperiod, and on a 10 percent glucose diet. After emerging, three-day-old female adult mosquitoes were randomly distributed into the 18 x 18 x 18 cm cages. There were a total of 150 cages representing one of the 18 treatment groups consisting of three mean temperatures (27°C , 30°C , and 33°C), two infection treatments (P. falciparum-infected, and blood-fed controls), and three Diurnal Temperature Ranges (DTR $0^\circ\text{C} \pm 0^\circ\text{C}$; DTR $6^\circ\text{C} \pm 3^\circ\text{C}$, and DTR $9^\circ\text{C} \pm 4.5^\circ\text{C}$ [10].

There were two replicates of *Anopheles gambiae*, and 3 replicates of *Anopheles stephensi* experiments and the mosquitoes in each experiment were deprived of sugar solution for 12 hours prior to being introduced to either the uninfected blood meal or *Plasmodium falciparum* culture to minimize inter-culture variations and ensure similar dosages [10]. Directly after the blood feeds, the

mosquitoes were introduced into the appropriate temperature treatments and maintained on a 10 percent sugar solution daily. The average temperatures and the diurnal temperature ranges were selected based on the microclimate data collected from the various housing types throughout the transmission season in Tanzania, India, and Chennai [10].

The midguts and salivary glands were dissected on the 7th day, and the 15th day post-infection for each *P. falciparum* exposed to the treatment group to quantify the effects of variation in mean temperature, diurnal temperature ranges, and treatment measures of the vector competence. The number of dead mosquitoes was counted in each cage throughout the experiment to quantify the effects of temperature fluctuation on the daily mortality [10].

2.2 Parametric Methods of Regression

The parametric methods for regression modeling considered in this paper are the exponential, Weibull, gamma, and the Gompertz models.

2.2.1 Exponential Distribution

The exponential distribution is an important distribution in survival studies, which researchers often choose to describe life patterns. It is often referred to as a purely random failure pattern, and famous for its lack of memory, which requires that the age of a person, animal, or organism does not affect failure survival [11]. Whereas the distribution does not adequately describe many survival data, its understanding facilitates the treatment of more general situations. The distribution is characterized by a constant hazard rate, whereby a high hazard rate value is an indication of high risk and short survival, and a low hazard rate value is an indication of low risk and long survival.

The exponential distribution can be parameterized by its mean α with the probability density function

$$f(t) = \frac{1}{\alpha} e^{-t/\alpha} \text{ for } t > 0 ; \alpha > 0 \quad (1)$$

The variable T can also be parameterized using its rate λ with the following probability density function

$$f(t) = \lambda e^{-\lambda t} \text{ for } t > 0 ; \lambda > 0 \quad (2)$$

Using the mean parameterization, the cumulative distribution function of the variable T would be given as follows:

$$F(t) = P(T \leq t) = 1 - e^{-t/\alpha} \text{ for } t > 0 \quad (3)$$

The survivor function of T would be given by:

$$S(t) = P(T \geq t) = e^{-t/\alpha} \text{ for } t > 0 \quad (4)$$

The hazard function of T would be given by:

$$h(t) = \frac{f(t)}{S(t)} = \frac{1}{\alpha} f \text{ort } > 0 \quad (5)$$

The cumulative hazard function of T would be given by:

$$H(t) = -\ln S(t) = \frac{t}{\alpha} f \text{ort } > 0 \quad (6)$$

The exponential distribution has been successfully used by researchers to model the mosquito vector mortality rates accounting for the effects of seasonal variations in the vector recruitment [12]. A recent study by Brand, Rock, and Keeling [13] successfully used the model for the survival in vector-borne disease transmission and control.

2.2.2 Weibull Distribution

The Weibull distribution, which was developed by Weibull in 1951, is a generalized exponential distribution with a shape distribution equal to one. It has found wide application in studies examining the reliability as well as the human disease mortality since it allows the survival distribution for populations whose risk is either decreasing, increasing, or constant [14]. The main contrast between the Weibull and the Exponential distribution is that the Weibull distribution is not based on the assumption of a constant hazard rate, hence has a wider application as compared to the exponential distribution.

The shorthand $T \sim \text{Weibull}(\alpha, \beta)$ indicates that the random variable T is Weibull with scale parameter $\alpha > 0$ and shape parameter $\beta > 0$. The variable T has probability density function:

$$f(t) = \frac{\beta}{\alpha} t^{\beta-1} e^{-\left(\frac{1}{\alpha}\right)t^\beta} f \text{ort } > 0 \quad (7)$$

The cumulative distribution function of T is given by:

$$F(t) = P(T \leq t) = 1 - e^{-\left(\frac{1}{\alpha}\right)t^\beta} f \text{ort } > 0 \quad (8)$$

The survivor function of T is given by:

$$S(t) = P(T \geq t) = e^{-\left(\frac{1}{\alpha}\right)t^\beta} f \text{ort } > 0 \quad (9)$$

The hazard function of T is given by:

$$h(t) = \frac{f(t)}{S(t)} = \frac{\beta}{\alpha} t^{\beta-1} f \text{ort } > 0 \quad (10)$$

The cumulative hazard function of T is given by:

$$H(t) = -\ln S(t) = \frac{1}{\alpha} t^\beta f \text{ort } > 0 \quad (11)$$

The Weibull distribution has been successfully used to model for survival time in various vector development and survival studies. For instance, Degallier et al. [15] successfully applied the model in examining how the local environment affected the aging and mortality of mosquitoes in Fortaleza, Brazil [15]. In comparison with other parametric models, the Weibull model provided a better fit for mosquito survival data as compared to other models. Stone et al. [16] also applied the Weibull model to assess how plant community composition influenced the vectorial capacity and fitness of the *Anopheles gambiae* mosquito.

2.2.3 Gamma Distribution

The gamma distribution encompasses two distributions: the exponential distribution and the chi-square distribution. The distribution was used by Phelan and Roitberg [17] to assess how food, temperature, and water depth influenced the diving activity of mosquitoes. The shorthand $T \sim \text{gamma}(\alpha, \beta)$ indicates that the random variable T has a gamma distribution. A gamma random variable T with positive scale parameter α and a positive shape parameter β has probability density function:

$$f(t) = \frac{t^{\beta-1} e^{-t/\alpha}}{\alpha^\beta \Gamma(\beta)} \text{ for } t > 0 \quad (12)$$

The cumulative distribution function of T is given by:

$$F(t) = P(T \leq t) = \frac{\Gamma(\beta, t/\alpha)}{\Gamma(\beta)} \text{ for } t > 0 \quad (13)$$

Where $\Gamma(s, t) = \int_0^\infty t^{s-1} e^{-t} dt$ is an incomplete gamma function, and $\Gamma(s) = \int_0^\infty t^{s-1} e^{-t} dt$ is the gamma function.

The survivor function of T is given by:

$$S(t) = 1 - \frac{\Gamma(\beta, t/\alpha)}{\Gamma(\beta)} \text{ for } t > 0 \quad (14)$$

The hazard function of T is given by:

$$h(t) = \frac{f(t)}{S(t)} = \frac{t^{\beta-1} e^{-t/\alpha}}{(\Gamma(\beta) - \Gamma(\beta, t/\alpha)) \alpha^\beta \Gamma(\beta)} \quad (15)$$

The cumulative hazard function is given by:

$$H(t) = -\ln S(t) = -\ln \left(1 - \frac{\Gamma(\beta, t/\alpha)}{\Gamma(\beta)} \right) \text{ for } t > 0 \quad (16)$$

The hazard function of the distribution gives rise to a variety of forms depending on the value of the gamma parameter.

2.2.4 Gompertz Distribution

The Gompertz distribution is derived from the Gompertz-Makeham family of distributions. The model is very closely related to the Weibull distribution in the sense that it represents the log of a Weibull distribution. The model provides a very close fit to adult mortality in contemporary developed nations [18]. The Gompertz distribution is based on the assumption that there is a law of mortality that explains the existence of common age patterns of death [19]. The shorthand $T \sim \text{Gompertz}(\delta, \kappa)$ indicates that the random variable T has the Gompertz distribution with parameters δ and κ . A Gompertz random variable T with shape parameters δ and κ has probability density function

$$f(t) = \delta\kappa^t e^{-\delta(\kappa^t-1)/\ln(\kappa)} \text{ for } t > 0; \kappa > 0; \delta > 0 \quad (17)$$

The cumulative distribution function of T is given by:

$$F(t) = P(T \leq t) = 1 - e^{-\frac{\delta(\kappa^t-1)}{\ln(\kappa)}} \text{ for } t > 0 \quad (18)$$

The survivor function of T is given by:

$$S(t) = P(T \geq t) = e^{-\frac{\delta(\kappa^t-1)}{\ln(\kappa)}} \text{ for } t > 0 \quad (19)$$

The hazard function of t is given by:

$$h(t) = \delta\kappa^t \text{ for } t > 0 \quad (20)$$

The cumulative hazard function of T is given by:

$$H(t) = \frac{\delta(\kappa^t - 1)}{\ln(\kappa)} \text{ for } t > 0 \quad (21)$$

The model has been widely used in actuarial and biological applications as well as in demography. Clements and Peterson [20] used the model to analyze the mortality and survival rates in wild mosquito populations. The model has also been applied in the analysis of the effects of larval food quantities on the capacity of adult mosquitoes to transmit human malaria. Therefore, it would be interesting to see how the model performs in analyzing the effect of temperature and age-dependent survival in mosquitoes.

2.3 Model Selection Criteria

The objective of the current paper was to compare the efficacy of the exponential model, the gamma model, the Weibull model, and the Gompertz model in fitting the temperature and age-dependent mosquito survival data. It involves comparing the goodness of fit of the four parametric models in regard to fitting of the observed data. In the context of model selection, the assumptions are that the statistical inference is model-based and that there is only one correct model or best fit model that suffices as the best model for making inferences [21]. The objective of model selection can be achieved by use of Akaike’s Information Criterion (AIC), Log-likelihood (-2LL) or the Bayesian Information Criterion (BIC) [21].

2.3.1 Akaike’s Information Criterion (AIC)

The AIC is a powerful, multimodal inference that can be used to determine the model that the model that best describes the factors that influence the variable of interest [22]. The method was first described by Akaike (1973) as a strategy for comparing various models on a given outcome. For instance, the researcher in the present paper is interested in what variables influence the survival of mosquitoes, and how the variables may influence the survival of mosquitoes. Akaike (1973) demonstrated that the best model is determined by calculating an AIC score as follows:

$$AIC = 2K - 2 \ln(L) \quad (22)$$

Where k represents the number of parameters and L represents the likelihood function's maximized value. The constant 2 is used for historical reasons [22]. The AIC value is interpreted such that the lower value of AIC indicates a better model.

2.3.2 Bayesian Information Criterion (BIC)

The BIC is a popular tool used by researchers for the selection of statistical models. It is preferred by many researchers due to its computational simplicity as well as its good performance in various modelling frameworks where other distributions have proved to be elusive [23]. Under the assumption that the model errors are independently and identically distributed in accordance to a normal distribution, and that the boundary condition that the derivative of the log likelihood with respect to the true variance is zero, the formula for BIC is given as follows:

$$BIC = -n \ln(\hat{\sigma}_e^2) + k \ln(n) \quad (23)$$

Where $\hat{\sigma}_e^2$ is the error variance given by:

$$\hat{\sigma}_e^2 = \frac{1}{n} \sum_{i=0}^n (x_i - \bar{x})^2$$

Under the assumption of normality, a more tractable version is given by:

$$BIC = X^2 + k \cdot \ln(n) \quad (24)$$

Just like the AIC, the BIC value is interpreted such that the lower value of BIC indicates a better model.

The statistical analyses were conducted using the R software. The AIC and BIC values for each model were conducted, and the model with the smallest AIC and BIC selected as the best fit model.

3 Results

3.1 Data Exploration

The dataset under consideration consists of 2279 observations. The variable of age is considered in terms of days post-infection, and is measured on an interval scale while the temperature is considered in as the average temperature and diurnal temperature range. There are no cases of missing values in the present dataset. Figure 1 below illustrates a Kaplan Meier plot of the data. Out

of the 2279 mosquitoes considered, 931 mortalities were recorded in a period of 15 days.

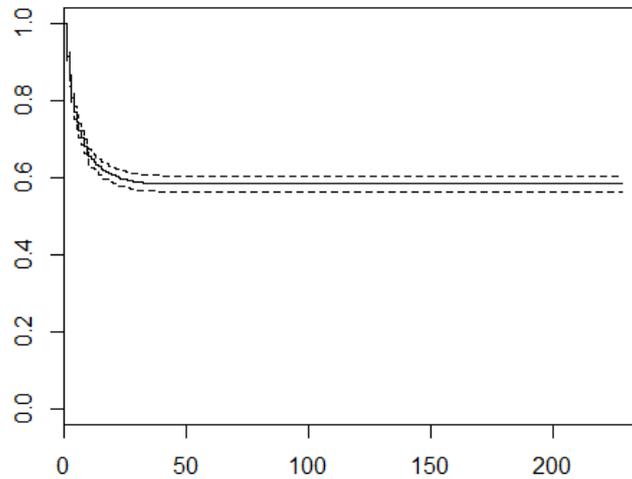


Figure 1. The Kaplan Meier Curve showing survival probability on the Y-axis and time (hours) on the X-axis.

3.2 Model Selection

Since the goal of the paper is to determine whether age and temperature are significant factors affecting the survival of mosquitoes and determine the model that best fits mosquito survival data, model selection forms the center of focus of this data analysis. Using the flexsurfreg() function in R, the mosquito survival data was fitted using four different models: the exponential, gamma, Weibull, and Gompertz model. In the next section, a comparison of the covariates is offered.

3.2.1 Comparison of Covariates

Table 1 below shows that the variables of age and average temperature are significantly associated with the survival time for all the four parametric models considered. Under the exponential model, the coefficients of age and temperature were found to be statistically significant predictors of mosquito survival ($p < 0.05$) at 0.05 level of significance. Similarly, the variables were found to be statistically significant under the Weibull (Temperature: $p = 0.013$, Age: $p = 0.0004$), gamma (Temperature: $p < 0.05$, Age: $p = 0.05$), and Gompertz (Temperature: $p < 0.05$, Age: $p = 0.05$).

Table 1: Comparison of Covariates

Parameters	Exponential		Weibull		Gamma		Gompertz	
		Sig.		Sig.		Sig.		Sig.
Age	0.1701*	<0.005	0.0775*	<0.005	0.0960*	<0.005	0.0046*	<0.005
Temperature	0.0650*	<0.005	-0.2805*	<0.005	0.3004*	<0.005	0.0567*	<0.005

The values are expressed as a maximum likelihood estimate (Standard error), *-significant coefficients

3.2.2 Model Selection

Table 2 below shows the values of the log-likelihood (-2LL), Akaike’s Information Criterion (AIC) and the Bayesian Information Criterion (BIC) criteria for the fitted models. The log-likelihood results

provide strong evidence that the Gompertz model (-2LL=-4138.59) is the best fit model for the mosquito survival data, followed by the Weibull (-2LL=-4764.97), gamma model (-2LL=-4822.81), and the exponential model (-2LL=-5707.03) in that order. The -2LL results were confirmed by the AIC and BIC criteria, which showed the lowest values for the Gompertz model (AIC= 8285.18, BIC= 8308.11), followed by the Weibull (AIC= 9537.95, BIC= 9560.87), Gamma (AIC= 9653.62, BIC= 9676.55), and the Exponential model emerged as the worst model of the four (AIC= 11420.06, BIC= 11437.25).

Table 2: Model Selection Criteria

Parametric distributions	Model selection criteria		
	-2LL (Log-Likelihood)	AIC	BIC
Exponential	-5707.03	11420.06	11437.25
Weibull	-4764.97	9537.95	9560.87
Gamma	-4822.81	9653.62	9676.55
Gompertz	-4138.59	8285.18	8308.11

3.2.3 Graphical Goodness of fit test

The goodness-of-fit of a model describes how well a model fits a set of observations. Whereas measures of goodness-of-fit above gives a summary of the discrepancy between the observed values and the expected values of the dataset under the four models, fitted line plots of the models given in figures 2, 3, 4, and 5 display the relationship between the variables of age and temperature and the survival of the mosquitoes. In addition, the models display the efficacy of each model in fitting the survival data.

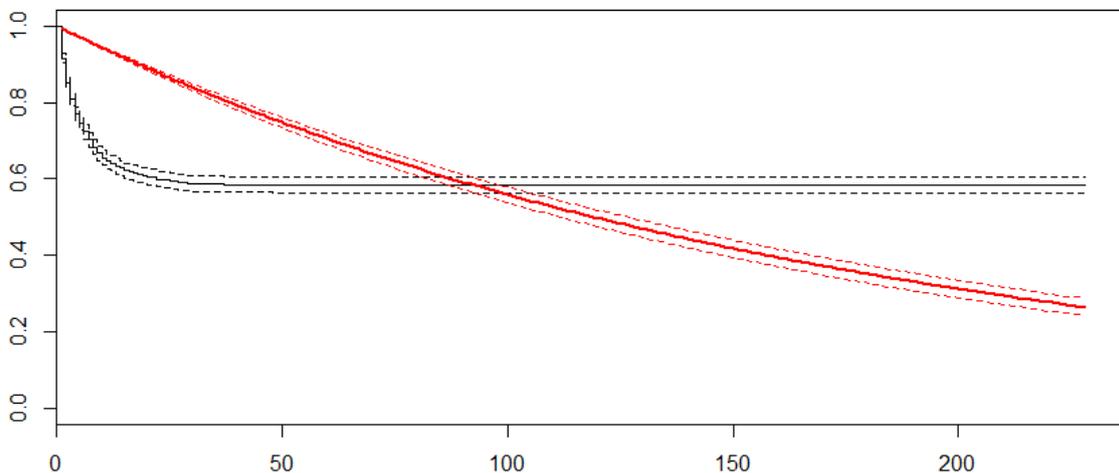


Figure 1. Exponential Model data plot showing survival probability on the Y-axis and time (hours) on the X-axis.

The data plot under the exponential model shows that the model is a poor fit. The black curve represents the survival curve as estimated by the Kaplan-Meier process, and the black dotted lines represent the 95% confidence interval. On the other hand, the red line and the red dotted lines represent the abstract function fitted by the exponential model and the confidence interval respectively. The objective of the model selection process is to achieve a model where the red and black curves to get close to each other. In the exponential model, the red and black curves are far from each other, indicating a poor fit.

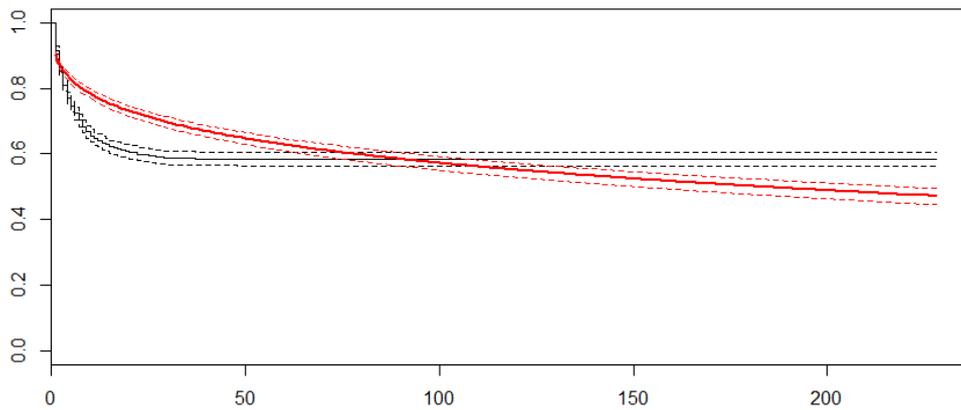


Figure 2. Gamma model data plot showing survival probability on the Y-axis and time (hours) on the X-axis.

Figure 3 displays how the gamma model fits the mosquito survival data. As compared to the exponential model, the gamma model curve is closer to the Kaplan Meier curve, but not as close as the Weibull and the Gompertz model curves.

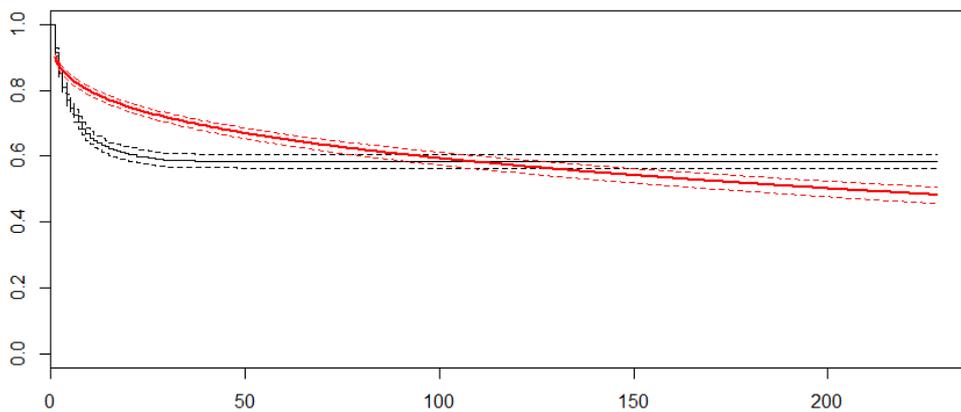


Figure 3. Weibull model data plot showing survival probability on the Y-axis and time (hours) on the X-axis.

Figure 4 is a Weibull model curve of the data compared to the Kaplan Meier curve. Evidently, the Weibull curve is closer to the Gamma model curve, but does not provide the best fit for the data.

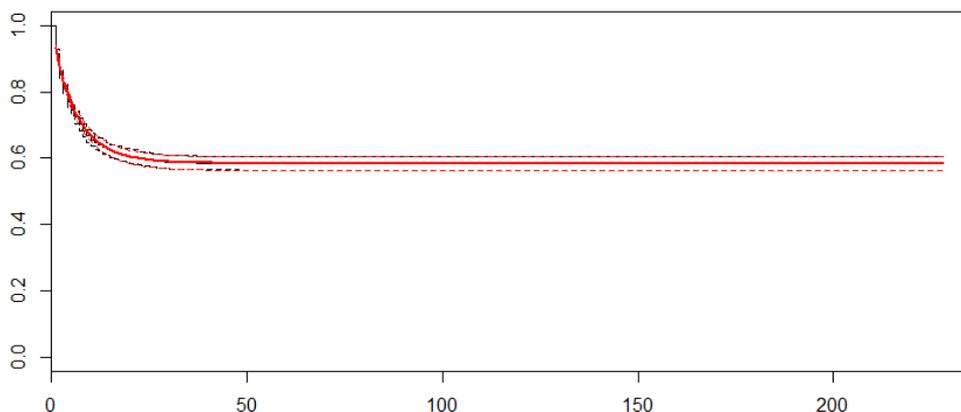


Figure 4. Gompertz model data plot showing survival probability on the Y-axis and time (hours) on the X-axis.

The Gompertz model data plot shown in figure 5 above shows a perfect fit of the observed values and the expected values. The Gompertz model curve lies very close to the Kaplan Meier Curve. Based on the visual assessment of the four curves, the Gompertz model provides the perfect fit for the mosquito survival data.

4 Discussion

The paper used experimental data considering 2279 *Anopheles gambiae* and *Anopheles stephensi* adult female mosquitoes to construct a temperature and age-dependent survival. It reaffirms that environmental temperature affects the survival of *Anopheles gambiae* and *Anopheles stephensi* during their lifetime as adults. The results from the study indicate that changes in the adult temperatures may have a significant impact on the survival of the mosquitoes. There was a statistically significant increase in environmental temperature with every 3°C increase in temperature. These results were consistent with results reported by [7] who used the temperature intervals of 4°C.

In general, the Gompertz survivorship function fitted the mosquito survival data reasonably well, confirming the results by [7], and confirming the age-dependent mortality in adult female *A. gambiae* and *A. stephensi* species of mosquitoes. Early studies [7,24] had reported age-dependent mortality in the laboratory adult *A. stephensi* mosquito populations. Some authors have pointed out that vector-borne disease models tend to dismiss evidence supporting the age-dependent mortality for the sake of tractability, and because of the contradictory evidence between the laboratory and field studies [7], but the findings of this paper further solidify the evidence on the age-dependent vector mortality. This is because the age-independent exponential model is a poor fit.

The findings herein indicate that environmental temperature to which *A. gambiae* and *A. stephensi* are exposed to during their adult stages significantly affect their survival. This has important implications for the *A. gambiae* and *A. stephensi* population dynamics, ecology as well as the transmission of the *Plasmodium* pathogen. The Gompertz model emerges as the best-fit model for fitting data on adult *A. gambiae* and *A. stephensi* survival in the laboratory as compared to the other parametric models such as the exponential, gamma and the Weibull models. The results will help in parameterising reliable mathematical models that examine the potential impact of temperature as well as global warming on the transmission of malaria.

5 Conclusion

This paper offers a comparison of the performance of four parametric models to determine the best model for analyzing the survival of the female *Anopheles* mosquito. The Gompertz, gamma, Weibull, and exponential models were utilized to model the survival of *A. gambiae* and *A. stephensi* species of mosquitoes. The four models differed significantly. The exponential model provided a poor fit of the vector survival data, while the Gompertz model provided a better fit compared to the Weibull, Gamma and the Exponential models. On the other hand, temperature and age were reaffirmed as important predictors of mosquito survival. Overall, the Gompertz model provides powerful statistical tool for the survival analysis of mosquito vector mortality data.

The present study is based on laboratory experiment. Other researchers exploring the problem have suggested a potential contradiction between laboratory data and field studies data [7]. In addition, the experimental design conducted in the present study did not consider differences in humidity, which would affect mosquito development as well as survival. Therefore, the model needs further

confirmation from vector mortality data from the field given its importance in modeling vector population dynamics as well as malaria transmission.

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