A matrix approach to the statistics of longevity in the gamma-Gompertz and related mortality models*†

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Abstract

BACKGROUND: The gamma-Gompertz model is a fixed frailty model in which baseline mortality increases exponentially with age, frailty has a proportional effect on mortality, and frailty at birth follows a gamma distribution. Mortality selects against the more frail, so the marginal mortality rate decelerates, eventually reaching an asymptote. The gamma-Gompertz is one of a wider class of frailty models, characterized by the choice of baseline mortality, effects of frailty, distributions of frailty, and assumptions about the dynamics of frailty.

OBJECTIVES: To develop a matrix model to compute all the statistical properties of longevity from the gamma-Gompertz and related models.

METHODS: I develop a matrix version of the gamma-Gompertz model using the vec-permutation matrix formulation for age-stage models.

RESULTS: The model permits calculation of the mean, variance, coefficient of variation, skewness and all moments of longevity, the marginal mortality and survivorship functions, the dynamics of the frailty distribution, and other quantities. The matrix formulation extends naturally to other frailty models. I apply the analysis to the gamma-Gompertz model (for humans and laboratory animals), the gamma-Makeham model, and the gamma-Siler model, and to a hypothetical dynamic frailty model characterized by diffusion of frailty with reflecting boundaries.

The matrix model permits partitioning the variance in longevity into components due to heterogeneity and to individual stochasticity. In several published human data sets, heterogeneity accounts for less than 10% of the variance in longevity. In laboratory populations of five invertebrate animal species, heterogeneity accounts for 46% to 83% of the total variance in longevity.

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Contents

1 Introduction

The gamma-Gompertz (G-G) model is one of a class of models that investigate the effects on survival and longevity of cryptic heterogeneity — heterogeneity that is either unobservable or unobserved — in mortality (e.g. **??????**). The goal of this paper is to present a matrix formulation that permits easy computation of all the properties of the G-G model, and of other related models for heterogeneity in mortality.

The G-G model specifies a baseline age-specific mortality rate and modifies this baseline by a factor, called frailty, that reflects the heterogeneity among individuals. The baseline mortality function is the Gompertz model, in which mortality increases exponentially with age t,

$$\mu(t) = ae^{bt}. \tag{1}$$

Frailty is introduced as a proportional hazard multiplier z; the mortality of an individual with frailty z at age t is

$$\mu(z,t) = z\mu_0(t) \tag{2}$$

where $\mu_0(t)$ is the baseline mortality schedule.

The dynamics at any age of a cohort subject to such a mortality model depend on the distribution of frailty. Let that distribution at age t be $\pi(z,t)$. Because frailty is cryptic, observations on the cohort reveal not the individual mortality schedules, but rather the marginal mortality rate

$$\mu^*(t) = \int \pi(z,t)\mu(z,t)dz \tag{3}$$

The survivorship function of an individual of frailty z is

$$\begin{aligned} S(z,t) &= \exp\left(-\int_0^t \mu(z,x)dx\right) &(4)\\ &= S_0(t)^z &(5)\end{aligned}$$

where $S_0(t)$ is the survivorship resulting from the baseline mortality schedule $\mu_0(t)$. The marginal survivorship function is

$$S^*(t) = \int \pi(z,0)S(z,t)dz. \tag{6}$$

The dynamics of the cohort differ from the dynamics of any frailty class because the distribution of frailty changes as the cohort ages (**?**). The more frail individuals tend to die sooner, and the cohort is progressively dominated by individuals of lower frailty. The distribution of fraility is

$$\pi(z,t) = \frac{\pi(z,0)S(z,t)}{\int \pi(z,0)S(z,t)dz}. \tag{7}$$

In the G-G model, frailty is a fixed property of an individual, and the cohort begins life with frailty distributed according to a gamma distribution

$$z \sim \text{gamma}(k,\lambda) \tag{8}$$

with shape parameter k and scale parameter[1] λ. The mean and variance of z are $E(z) = k/\lambda$ and $V(z) = k/\lambda^2$. Thus, when $E(z) = 1$, the distribution is given by gamma $\left(1/\sigma^2, 1/\sigma^2\right)$.

[1]The probability density function is

$$\text{gamma}(k,\lambda) = \frac{1}{\Gamma(k)\lambda^k}\, z^{k-1}e^{-z/\lambda}. \tag{9}$$

The marginal mortality rate (3) for the G-G model is a sigmoid function of age,

$$\mu^*(t) = \frac{ae^{bt}}{1 + \frac{a\sigma^2}{b}\left(e^{bt} - 1\right)} \tag{10}$$

(**?**), converging to an asymptote at b/σ^2 as t gets large. Thus, the G-G model is an attractive explanation for the widely observed pattern of decelerating increase in mortality with age, in both humans and other species (e.g., **????**).

Although it is simple to state, and widely used, deriving the consequences of the G-G model is mathematically challenging. **?** has recently obtained an expression for life expectancy at birth, by integrating the survivorship function (24). The result, a function of the Gompertz parameters a and b and the gamma distribution parameters k and λ, is written in terms of the Gaussian hypergeometric[2] function ${}_2F_1$:

$$e_0(a, b, k, \lambda) = \frac{1}{bk}\ {}_2F_1\left(k, 1; k+1; 1 - \frac{1}{b\lambda}\right) \tag{11}$$

Life expectancy, however, is only one of many demographic properties implied by a mortality model. My goal here is to present a matrix formulation that provides all the moments of longevity, various measures of life disparity, and the full dynamics of the joint distribution of age and frailty. It will become apparent from the construction of this model that it applies equally to a much broader class of frailty models, and I will present examples.

Section 2 derives the matrix model, using methods developed for cases in which individuals are jointly classified by age and stage. Section 3 derives the fundamental matrix, the moments of longevity, the distribution of age at death, and other indices from the matrix model including (Section 3.4) the dynamics of the frailty distribution over the life of the cohort. Section 4 analyzes an example from **?**. Section 5 discusses some interesting generalizations and explores several other examples.

2 The matrix formulation of the gamma-Gompertz model

Notation. In what follows, matrices are denoted by upper-case boldface letters, and vectors by lower-case boldface letters. Where necessary, the dimensions of matrices and vectors are denoted by subscripts; thus $\mathbf{I}_n$ is an identity matrix of order n and $\mathbf{1}_n$ is a $n \times 1$ vector of ones. The vector $\mathbf{e}_i$ is the ith unit vector. The symbol $\circ$ denotes the Hadamard, or element-by-element product. The symbol $\|\mathbf{x}\|$ denotes the 1-norm of the vector $\mathbf{x}$. The number of age classes is ω and the number of frailty groups is g.

The matrix G-G model is an age-stage classified model in which stages correspond to frailty classes. Age-stage classified matrix models have been analyzed in other contexts by **???** and **?**. The model is created using the vec-permutation formalism (**?**) and analyzed using absorbing Markov chain theory (**???**)

Note that two parameterizations of the gamma distribution are widely used. Equation (9) is common in demography. MATLAB uses the parameterization

$$\text{gamma}(k, \theta)$$

where k is a shape parameter and θ is a rate parameter. In this parameterization, $E(z) = k\theta$ and $V(z) = k\theta^2$. Thus in MATLAB the distribution with mean equal to 1 is gamma $\left(1/\sigma^2, \sigma^2\right)$.

[2]For more on the Gaussian hypergeometric distribution, see **?** Abramowitz and Stegun (1965, 15.1.1), or the online version in the NIST Digital Library of Mathematical Functions, `http://dlmf.nist.gov/15`.

To construct the matrix G-G model, let us introduce some notation. Age is described by a set of discrete age classes $1, \ldots, \omega$. The baseline mortality rates are contained in a vector $\boldsymbol{\mu}_0$ of dimension $\omega \times 1$. For the Gompertz mortality model, the baseline mortality rate vector is

$$\boldsymbol{\mu}_0 = a \begin{pmatrix} e^{0b} \\ e^{1b} \\ e^{2b} \\ \vdots \\ e^{(\omega-1)b} \end{pmatrix} \tag{12}$$

Frailty is described by a set of g discrete frailty classes; the frailty values of these classes are given by a $g \times 1$ vector $\mathbf{z}$. To create the frailty classes, first specify a maximum frailty, where the cumulative gamma distribution reaches some high value; say, 0.9999. Since very high values of frailty are rapidly eliminated, this end of the distribution is, in practice, not very important. Then specify a minimum value of frailty as some very small number; for the applications reported here, a value on the order of 10^{-7} was adequate. Since individuals with very low frailty will persist for a long time in the population, it is important that $z_{\min}$ be small.

Experience suggests that logarithmically spaced values between $z_{\min}$ and $z_{\max}$ work well, because they provide more detail in the frailty distribution at the low end, precisely where individuals will persist the longest. An alternative is to evenly divide the inverse of the cumulative distribution function, so that values are most closely spaced where the concentration of initial probability is greatest. Given the vector $\mathbf{z}$ of frailty classes, the vector of mortality rates by age, for frailty class i, is

$$\boldsymbol{\mu}_i = z_i \boldsymbol{\mu}_0 \tag{13}$$

The distribution of individuals among frailty classes at age t is given by the vector $\boldsymbol{\pi}(t)$; the initial frailty distribution of the cohort is given by $\boldsymbol{\pi}(0)$. In the matrix G-G model, $\boldsymbol{\pi}(0)$ is a discrete gamma distribution with mean of 1 and a specified variance.

2.1 Constructing transition matrices and the vec-permutation model

To construct the age-stage model, define a survival matrix for each frailty class, and a matrix of frailty transitions for each age class, as follows.

1. Create a survival matrix $\mathbf{U}_i$ for each frailty class i. It contains survival probabilities on the first subdiagonal and zeros elsewhere, and is of dimension $\omega \times \omega$.

$$\mathbf{U}_i = \begin{pmatrix} 0 & 0 & \cdots & 0 \\ e^{-\mu(z_i,0)} & 0 & \cdots & 0 \\ \vdots & \ddots & & \vdots \\ 0 & \cdots & e^{-\mu(z_i,\omega-1)} & 0 \end{pmatrix} \tag{14}$$

2. Create a matrix $\mathbf{D}_j$ describing transitions among frailty classes for each age class j. In the gamma-Gompertz model, frailty does not change, so $\mathbf{D}_j = \mathbf{I}_g$ for all j.

3. Create block-diagonal matrices $\mathbb{U}$ and $\mathbb{D}$ by placing the $\mathbf{U}_i$ (respectively, $\mathbf{D}_j$) on the diagonal with zeros elsewhere. Both matrices are of dimension $\omega g \times \omega g$.

$$\mathbb{U} = \begin{pmatrix} \mathbf{U}_1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \mathbf{U}_g \end{pmatrix} \qquad \mathbb{D} = \begin{pmatrix} \mathbf{D}_1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \mathbf{D}_g \end{pmatrix} \tag{15}$$

In the gamma-Gompertz model, $\mathbb{D} = \mathbf{I}_{\omega g}$.

The state of the cohort at age t is given by a vector $\tilde{\mathbf{n}}(t)$, which is derived from the array

$$\mathcal{N}(t) = \begin{pmatrix} n_{11} & \cdots & n_{1g} \\ \vdots & & \vdots \\ n_{\omega 1} & \cdots & n_{\omega g} \end{pmatrix} \tag{16}$$

that describes the abundance of all age-frailty categories. The population vector is

$$\tilde{\mathbf{n}} = \operatorname{vec} \mathcal{N}^{\mathsf{T}}; \tag{17}$$

that is,

$$\tilde{\mathbf{n}} = \left(\begin{array}{c} n_{11} \\ \vdots \\ \hline n_{1g} \\ \vdots \\ \hline n\omega 1 \\ \vdots \\ n_{\omega g} \end{array} \right) \tag{18}$$

The ith block of entries in $\tilde{\mathbf{n}}$ contains a sub-vector giving the abundance of the frailty classes within age class i.

The joint age-frailty composition of the cohort is projected as

$$\tilde{\mathbf{n}}(t+1) = \tilde{\mathbf{U}}\tilde{\mathbf{n}}(t) \tag{19}$$

where the projection matrix is

$$\tilde{\mathbf{U}} = \mathbb{D}\mathbf{K}\mathbb{U}\mathbf{K}^{\mathsf{T}} \tag{20}$$

In equation (20), $\mathbf{K}$ (to be more precise, $\mathbf{K}_{\omega,g}$) is the vec-permutation matrix, or commutation matrix (**??**); see **?** for a demographic description.

Because frailty is fixed in the gamma-Gompertz model, $\tilde{\mathbf{U}}$ reduces to $\tilde{\mathbf{U}} = \mathbf{K}\mathbb{U}\mathbf{K}^{\mathsf{T}}$. However, it is good practice to retain the matrix $\mathbb{D}$ as a reminder of its potential use when frailty is dynamic rather than static.

2.2 The absorbing Markov chain

The matrix $\tilde{\mathbf{U}}$ is the transient matrix of an absorbing Markov chain **????**. The transition matrix of this chain is

$$\mathbf{P} = \left(\begin{array}{c|c} \tilde{\mathbf{U}} & 0 \\ \hline \tilde{\mathbf{M}} & \mathbf{I} \end{array} \right) \tag{21}$$

where $\mathbf{M}$ is a mortality matrix describing the transitions from transient (i.e., living) states to absorbing (i.e., dead) states. The fundamental matrix of the chain defined by $\tilde{\mathbf{U}}$ is

$$\tilde{\mathbf{N}} = \left(\mathbf{I}_{\omega q} - \tilde{\mathbf{U}}\right)^{-1} \tag{22}$$

with dimension $\omega g \times \omega g$. The (i, j) entry of $\tilde{\mathbf{N}}$ is the expected number of visits to state i, conditional on starting in a state j, where states describe the full joint age $\times$ frailty distribution. From the fundamental matrix we can compute all the statistics of the cohort survival properties. We turn now to these analyses.

3 Analysis of the model

The fundamental matrix $\tilde{\mathbf{N}}$ of the joint chain contains all the information necessary to derive the marginal survival function $\mathbf{s}^*$ (a vector of dimension $\omega \times 1$) and the corresponding marginal fundamental matrix $\mathbf{N}^*$ (of dimension $\omega \times \omega$).

3.1 The marginal survival function

To obtain the marginal dynamics of the cohort age distribution, first average the columns of $\tilde{\mathbf{N}}$ over the initial frailty distribution. If, as in the gamma-Gompertz case, the initial frailty distribution has positive support only in the first age class, the result is

$$\tilde{\mathbf{s}} = \tilde{\mathbf{N}} \left[\mathbf{e}_1 \otimes \boldsymbol{\pi}(0) \right].$$

This column vector gives the average, over $\boldsymbol{\pi}(0)$, of the number of visits to each age-frailty state by an individual in the first age class.

Next, sum the rows of the vector $\tilde{\mathbf{s}}$ within each frailty class to obtain the marginal mean number of visits to each age class for an individual in the initial cohort. Because the underlying demographic model is age-classified, a transient state (i.e., an age class) *can be visited at most once; hence the mean number of visits is the probability of visiting.* Thus the vector of mean number of visits is in fact the marginal survivorship function $\mathbf{s}^*$:

$$\begin{aligned} \mathbf{s}^* &= \left(\mathbf{I}_\omega \otimes \mathbf{1}_g^\mathsf{T} \right) \tilde{\mathbf{s}} && (23) \\ &= \left(\mathbf{I}_\omega \otimes \mathbf{1}_g^\mathsf{T} \right) \tilde{\mathbf{N}} \left[\mathbf{e}_1 \otimes \boldsymbol{\pi}(0) \right] && (24) \end{aligned}$$

3.2 The marginal fundamental matrix

The fundamental matrix $\tilde{\mathbf{N}}$ gives the number of visits to each age-frailty class. We need the marginal fundamental matrix $\mathbf{N}^*$, which gives the expected number of visits to each age class. All the statistics of longevity can be obtained from this matrix (e.g., **?????**). To obtain $\mathbf{N}^*$, note that the vector $\mathbf{s}^*$ is the first column of $\mathbf{N}^*$, and that the full matrix is

$$\mathbf{N}^* = \begin{pmatrix} s_1^* & 0 & 0 & \cdots & 0 \\ s_2^* & \frac{s_2^*}{s_2^*} & 0 & \cdots & 0 \\ s_3^* & \frac{s_3^*}{s_2^*} & \frac{s_3^*}{s_3^*} & \cdots & 0 \\ s_4^* & \frac{s_4^*}{s_2^*} & \frac{s_4^*}{s_3^*} & \cdots & 0 \\ \vdots & \vdots & \vdots & \cdots & 1 \end{pmatrix} \tag{25}$$

(**?**, Eq. 10.5.4)[3] This can be written

$$\mathbf{N}^* = \left[\mathbf{s}^* \mathbf{1}_s^\mathsf{T} \operatorname{diag} \left(\mathbf{s}^* \right)^{-1} \right] \circ \mathbf{Y} \tag{26}$$

where $\mathbf{Y}$ is a lower triangular matrix with ones on and below the diagonal and zeros elsewhere.

[3] It seems appropriate to note that Keyfitz presented this result in the first edition of the book in 1977.

3.3 Longevity, variation, and disparity

When longevity statistics are calculated from $\mathbf{N}^*$, they give the marginal results for the cohort starting with the initial frailty distribution $\boldsymbol{\pi}(0)$. These include the following.

1. The moments of the number of visits to each of the transient states. Because transient states (age classes) in an age-classified model can be visited no more than once, these moments may be less interesting in the G-G model than in models with more complicated stage structure. Letting $\mathbf{N}_i^*$ be the matrix of the ith moments of the number of visits, $\mathbf{N}_1^*$ is given by (25), and the higher moments include

$$\begin{aligned}
\mathbf{N}_2^* &= \left(2\mathbf{N}_{\mathrm{dg}}^* - \mathbf{I}\right)\mathbf{N}_1^* && (27)\\
\mathbf{N}_3^* &= \left[6\left(\mathbf{N}_{\mathrm{dg}}^*\right)^2 - 6\mathbf{N}_{\mathrm{dg}}^* + \mathbf{I}\right]\mathbf{N}_1^* && (28)\\
\mathbf{N}_4^* &= \left[24\left(\mathbf{N}_{\mathrm{dg}}^*\right)^3 - 36\left(\mathbf{N}_{\mathrm{dg}}^*\right)^2 + 14\mathbf{N}_{\mathrm{dg}}^* - \mathbf{I}\right]\mathbf{N}_1^*. && (29)
\end{aligned}$$

   where $\mathbf{N}_{\mathrm{dg}}^*$ is a diagonal matrix with the diagonal elements of $\mathbf{N}_1^*$ on the diagonal and zeros elsewhere (e.g., **???**); for a mathematical source see **?**.

2. The moments and statistics of longevity. Longevity is equivalent to the time until absorbtion in one of the absorbing states. The vector $\boldsymbol{\eta}_1$ of mean longevities (i.e., life expectancies) of each age class is obtained from the column sums of $\mathbf{N}^*$, and subsequent moments as follows, where $\boldsymbol{\eta}_i$ is the vector of ith moments of longevity:

$$\begin{aligned}
\boldsymbol{\eta}_1^{\mathsf{T}} &= \mathbf{1}_\omega^{\mathsf{T}}\mathbf{N}^* && (30)\\
\boldsymbol{\eta}_2^{\mathsf{T}} &= \boldsymbol{\eta}_1^{\mathsf{T}}\left(2\mathbf{N}^* - \mathbf{I}\right) && (31)\\
\boldsymbol{\eta}_3^{\mathsf{T}} &= \boldsymbol{\eta}_1^{\mathsf{T}}\left[6\left(\mathbf{N}^*\right)^2 - 6\mathbf{N}^* + \mathbf{I}\right] && (32)\\
\boldsymbol{\eta}_4^{\mathsf{T}} &= \boldsymbol{\eta}_1^{\mathsf{T}}\left[24\left(\mathbf{N}^*\right)^3 - 36\left(\mathbf{N}^*\right)^2 + 14\mathbf{N}^* - \mathbf{I}\right]. && (33)
\end{aligned}$$

   (**???**). These moments provide a complete set of longevity statistics, including the variance, standard deviation, coefficient of variation, and skewness of longevity:

$$\begin{aligned}
V\left(\boldsymbol{\eta}\right)^{\mathsf{T}} &= \boldsymbol{\eta}_2 - \boldsymbol{\eta}_1 \circ \boldsymbol{\eta}_1 && (34)\\
SD(\boldsymbol{\eta}) &= \sqrt{V(\boldsymbol{\eta})} && (35)\\
CV\left(\boldsymbol{\eta}\right) &= \mathrm{diag}\left(\boldsymbol{\eta}_1\right) SD\left(\boldsymbol{\eta}\right) && (36)\\
Sk\left(\boldsymbol{\eta}\right) &= \mathrm{diag}\left(V(\boldsymbol{\eta})\right)^{-3/2}\left[\boldsymbol{\eta}_3 - 3\boldsymbol{\eta}_1 \circ \boldsymbol{\eta}_2 + 2\boldsymbol{\eta}_1 \circ \boldsymbol{\eta}_1 \circ \boldsymbol{\eta}_1\right] && (37)
\end{aligned}$$

3. The joint and marginal distributions of age and stage at death. Becasue the matrix G-G model is an age-stage structured model, the joint and marginal distributions of age and frailty class at death are obtained using the mortality matrix $\tilde{\mathbf{M}}$ in (21).

   If $\tilde{\mathbf{M}}$ is created by defining absorbing states corresponding to the age and frailty class at death, then $\tilde{\mathbf{M}} = \mathrm{diag}\left(\mathbf{1}_{\omega g}^{\mathsf{T}} - \mathbf{1}_{\omega g}^{\mathsf{T}}\tilde{\mathbf{U}}\right)$. Then column j of the matrix

$$\tilde{\mathbf{B}} = \tilde{\mathbf{M}}\tilde{\mathbf{N}} \qquad (38)$$

   gives the joint distribution of age and frailty at death, conditional on reaching the age-frailty combination in column j (**?**).

Averaging the first g columns of $\tilde{\mathbf{B}}$ over the initial frailty distribution gives a vector $\tilde{\boldsymbol{\phi}}$ containing the distribution of age and frailty at death of a cohort with initial frailty distribution $\boldsymbol{\pi}(0)$:

$$\tilde{\boldsymbol{\phi}} = \tilde{\mathbf{B}} \left[\mathbf{e}_1 \otimes \boldsymbol{\pi}(0) \right] \tag{39}$$

The marginal distributions of age and of frailty at death can be shown to be

$$\boldsymbol{\phi}^*_{\text{age}} = \left(\mathbf{I}_\omega \otimes \mathbf{1}_g^\mathsf{T} \right) \tilde{\boldsymbol{\phi}} \tag{40}$$

$$\boldsymbol{\phi}^*_{\text{frailty}} = \left(\mathbf{1}_\omega^\mathsf{T} \otimes \mathbf{I}_g \right) \tilde{\boldsymbol{\phi}} \tag{41}$$

3.4 Projecting the distributions of frailty and age

The population vector giving the abundance by age and frailty class is projected by the matrix $\tilde{\mathbf{U}}$ in (20):

$$\tilde{\mathbf{n}}(t+1) = \tilde{\mathbf{U}} \tilde{\mathbf{n}}(t) \tag{42}$$

If, as in the G-G model, the initial cohort has support only in the first age class, with distribution $\boldsymbol{\pi}(0)$, then $\tilde{\mathbf{n}}(0) = \left(\mathbf{e}_1^\mathsf{T} \otimes \mathbf{I}_g \right) \boldsymbol{\pi}(0)$.

Let $\tilde{\mathbf{p}}(t)$ be the vector giving the *proportional* age-frailty distribution at time t. It is projected by

$$\tilde{\mathbf{p}}(t+1) = \frac{\tilde{\mathbf{U}} \tilde{\mathbf{p}}(t)}{\| \tilde{\mathbf{U}} \tilde{\mathbf{p}}(t) \|}, \tag{43}$$

with $\tilde{\mathbf{p}}(0) = \tilde{\mathbf{n}}(0) / \| \tilde{\mathbf{n}}(0) \|$.

The marginal age vector and the marginal proportional age distribution vector are obtained by summing over frailty classes within age classes, as in (40) for the death distribution. They are given by

$$\mathbf{n}^*(t) = \left(\mathbf{I}_\omega \otimes \mathbf{1}_g^\mathsf{T} \right) \tilde{\mathbf{n}(t)} \tag{44}$$

$$\mathbf{p}^*(t) = \left(\mathbf{I}_\omega \otimes \mathbf{1}_g^\mathsf{T} \right) \tilde{\mathbf{p}(t)} \tag{45}$$

The marginal fraility vector and the marginal proportional frailty distribution are obtained by summing $\tilde{\mathbf{n}}$ and $\tilde{\mathbf{p}}$ over age within each frailty class, as in (41) for the death distribution:

$$\mathbf{m}^*(t) = \left(\mathbf{1}_\omega^\mathsf{T} \otimes \mathbf{I}_g \right) \tilde{\mathbf{n}}(t) \tag{46}$$

$$\boldsymbol{\pi}(t) = \left(\mathbf{1}_\omega^\mathsf{T} \otimes \mathbf{I}_g \right) \tilde{\mathbf{p}}(t) \tag{47}$$

From the marginal distribution $\boldsymbol{\pi}(t)$ of frailty, all the statistics, particularly the mean and variance, of frailty can be calculated, to quantify the effects of selection as a function of age.

4 An example: Swedish females

An example of the calculations is provided by using the G-G parameters a, b, and k estimated by **?** from period mortality data on Swedish females from 1891 to 2010. I used these parameters, for the arbitrarily selected year 1950, to create the matrices $\approxeq$ and $\mathbb{D}$ ($\hat{a} = 0.0340$, $\hat{b} = 0.1200$, $\hat{k} = 8.2300$). Calculations were carried out with $\omega = 150$ age classes and $g = 100$ logarithmically spaced frailty classes. The results are shown in a series of figures. The marginal mortality rate $\mu*(t)$ is shown in Figure 1. That rate increases nearly exponentially until about age 75, at which point the effects of selection become apparent and the increase decelerates; mortality converges to an asymptote at about age 100.

4.1 Statistics of longevity

The mean, standard deviation, coefficient of variation, and skewness of longevity, computed from $\mathbf{N}^*$ using (34)–(37), are shown in Figure 2. The remaining life expectancy and its standard deviation both decrease with age, but the relative variation, as measured by the coefficient of variation, increases up to about age 90 and then decreases slightly. The distribution of longevity goes from negative to positive skewness with increasing age.

4.2 Dynamics of frailty

The selection against more frail individuals is seen in the dynamics of the distribution of frailty $\boldsymbol{\pi}(t)$ (Figure 3). Both the mean and the standard deviation of frailty decrease with age, with the decline becoming visually evident after about age 50. The CV of frailty is known to remain constant with age in the G-G model. In the matrix calculation, it is very nearly constant, increasing slightly at about age 75.

4.3 Effects of the G-G parameters

The matrix formulation makes it easy to explore the effects of the G-G parameters on the statistics of longevity. Figures 5–7 show the effects of varying a, b, and the variance, $1/k$, of the frailty distribution over several orders of magnitude around the values for Swedish females in 1950.

Life expectancy declines with increases in a; roughly speaking, a 10-fold increase in a reduces life expectancy at birth by about 10 years (Figure 5). The standard deviation of longevity also declines with increasing a, more dramatically at older ages. Together, these changes i lead to a coefficient of variation that increases with a. The skewness of the distribution of longevity also increases with a. When measured at birth, it is negative, but by age 60 skewness changes from negative to positive as a increases.

Increases in b also reduce life expectancy (Figure 6). The standard deviation of longevity peaks at an intermediate value of b, and declines sharply at higher or lower values. The coefficient of variation of longevity increases with b until at older ages it eventually declines. At very high values of b the expectation and standard deviation of longevity at older ages become zero and the coefficient of variation is undefined.

The effects of changes in the variance $\sigma^2 = 1/k$ of the initial frailty distribution $\boldsymbol{\pi}(0)$ are shown in Figure 7. Expected longevity is relatively insensitive to the σ^2 until it becomes much higher than that observed for Swedish females, at which point the mean, variance, and coefficient of variation of longevity all begin to increase with σ^2. The skewness of longevity increases to a peak (at values much higher than those observed), and then declines again at extremely high values of σ^2.

4.4 Numerical reliability

Based on his results using the Gaussian hypergeometric function (11), **?** reports a life expectancy of 77.29 years for Swedish females in 1950. Evaluating his formula with the Gaussian hypergeometric function as implemented in MATLAB or in Wolfram Alpha gives a result of 76.22 years. The matrix calculation yields 77.23 years or, when adjusted by 0.5 years to correspond to a trapezoidal integration of the survival function, 76.73 years. The differences among the various implementations of the calculation are small (Table 1).

Because the matrix calculation is a discrete model, the results are influenced by the number of frailty classes g and the number of age classes ω included in the model. The number of frailty classes determines how closely $\boldsymbol{\pi}(0)$ can approximate a gamma distribution, and the ability of $\boldsymbol{\pi}(t)$

to capture the distribution of frailty at late ages when selection has been operating for a long time. The number of age classes determines the extent to which the longevity statistics are influenced by the death of all remaining individuals at age ω, which is not part of the G-G model, but must appear in any finite state approximation.

Figure 4 shows the effect of choices of ω and of g on the expectation and the standard deviation of longevity. For these parameters, choosing $\omega > 100$ and $g > 40$ provides reliable estimates of both the mean and the variation of longevity for this data set. Too small a value of ω reduces both the mean and the standard deviation, because the survival curve is truncated at age ω.

5 Generalizations and extensions of the model

The calculations of $\mathbf{N}^*$, $\mathbf{s}^*$, and all the quantities derived from them depend only on the vec-permutation model structure (20). As a result, the analysis can be extended from the G-G model to other models for baseline mortality, other models for the effects of frailty, other frailty distributions, and other models for the dynamics of frailty. I describe some of these extensions here.

5.1 Models for baseline mortality

The baseline mortality schedule $\boldsymbol{\mu}_0$ is used to create the frailty-specific mortality schedules $\boldsymbol{\mu}_i$ in equation (13). These schedules are used to create the matrices $\mathbf{U}_i$ that appear in (15). The Gompertz model is only one possible choice of a baseline schedule. Here, I examine some alternatives; results, in the same format as Figures 2, 3, and 5–7 are collected in Appendix A.

For example, the Gompertz-Makeham model

$$\mu(x) = ae^{bx} + c, \tag{48}$$

is obtained by adding an age-independent morality hazard c to the Gompertz model. The gamma-Makeham model results from incorporating a porportional frailty effect

$$\boldsymbol{\mu}_i = z_i \left(ae^{bi} + c \right) \tag{49}$$

where the z_i have a gamma distribution at age 0.

Simply modifying $\boldsymbol{\mu}_0$ in equation (13) transforms the G-G model to the gamma-Makeham model, with

$$\boldsymbol{\mu}_0 = \begin{pmatrix} e^{0b} \\ \vdots \\ e^{(\omega-1)b} \end{pmatrix} + c \begin{pmatrix} 1 \\ \vdots \\ 1 \end{pmatrix} \tag{50}$$

All analyses of the gamma-Makeham model then follow from $\tilde{\mathbf{N}}$, computed from $\boldsymbol{\mu}(z)$, just as with the G-G model.

? estimated the parameters in the gamma-Makeham model as part of an analysis of the effects of education on the mortality of male and female cohorts in Turin, Italy, from 1971 to 2007. I analyzed the data for the baseline cohort of women, for which AIC calculations indicated that the gamma-Makeham model was much more well-supported by the data than the G-G model (**?**). Figure A.1 shows the expectation, standard deviation, CV, and skewness of remaining longevity as a function of age. The patterns are qualitatively similar to the gamma-Gompertz results for Swedish females (Figure 2). Selection reduces the mean and the standard deviation of frailty as age approaches 100, and the log of the marginal mortality rate increases with age in a sigmoid fashion (Figure A.2).

There is no reason to stop at the gamma-Makeham model. **?** and **?** have added gamma-distributed frailty to the Siler model for mortality

$$\mu_0(x) = e^{a_1 - b_1 x} + e^{a_2 + b_2 x} + e^{a_3} \tag{51}$$

where $\exp(a_1 - b_1 x)$ is a declining force of infant mortality, $\exp(a_2 + b_2 x)$ is an increasing force of old age mortality, and $\exp(a_3)$ is a constant force of background mortality. An analysis of the gamma-Siler model requires only substituting this expression for $\boldsymbol{\mu}_0$ for the gamma-Gompertz mortality function in (12).

? estimated parameters for a gamma-Siler model for cohorts of Swedish females born from 1875–1916. Here I show results for the year 1900. The expectation, standard deviation, CV, and skewness of remaining longevity are shown as functions of age in Figure A.3. The patterns differ from those of the G-G and gamma-Makeham models mainly in that they show the effects of the infant mortality term. This effect is also apparent in the marginal mortality function (Figure A.4c) which declines sharply after birth, remains low, and then increases, eventually reaching a plateau at older ages.

These examples use parametric functions for the baseline mortality schedule, but they can easily be extended to semiparametric or nonparametric estimates. The estimated mortality function simply needs to be incorporated into the matrices $\mathbf{U}_i$.

5.2 Models for the effects of frailty

In the G-G model, frailty affects mortality as a proportional hazard. Other models for the effects of frailty can be incorporated into the construction of the matrices $\mathbf{U}_i$, by replacing the proportional hazard formulation in (13) with an expression appropriate to the frailty effects.

For example, **?** briefly considered a model with accelerated aging, in which

$$\mu(z, x) = \mu_0(zx) \tag{52}$$

and point out that, if the baseline mortality schedule is Gompertz, then small changes in z can have large effects on the mortality, especially at later ages. Figure 3 of **?** shows an example with two frailty classes.

Accelerated failure time (AFT) models typically specify frailty in terms of its effect on the survival function, so that

$$s(z, x) = s(zx) \tag{53}$$

which implies that

$$\mu(z, x) = z\mu(zx). \tag{54}$$

To incorporate such a model in the matrix calculations require only an appropriate change in the the expression (13) for the mortality rate of each frailty class.

5.3 Models for the distribution of frailty

The gamma distribution is attractive as a distribution of frailty for its mathematical properties, and theoretical results suggest that it is likely to underlie mortality trajectories that reach a plateau at old ages (**?**). However, any initial distribution $\boldsymbol{\pi}(0)$ can be incorporated in the calculation of the marginal survival $\mathbf{s}^*$ in (24), and the dynamics of the frailty distribution generated by (47). This includes other parametric distributions as well as specification of discrete frailty classes (e.g., **?**).

5.4 Models for the dynamics of frailty

In the G-G model, frailty is a fixed property of an individual. However, individual heterogeneity may be dynamic, increasing (debilitation) or decreasing (recuperation) over time due to stress, disease, etc. The matrix model readily incorporates any finite-state Markov chain as a model for dynamic heterogeneity, by properly specifying the matrices $\mathbf{D}_i$, for $i = 1, \ldots, \omega$.

For example, **?** considered a model with two frailty states, z_1 and z_2. Individuals begin life with frailty z_1 with mortality schedule $\mu_1(x)$, and change from state one to state two at a rate $\lambda(x)$. The second frailty state might represent a morbid event such as a heart attack. This model generalizes to a model considered by **?** and **?** with a countably infinite number of frailty classes. The mortality rate is $\mu_i = \mu_0 + z_i\mu$, and frailty increases at the rate $\lambda_0 + z_i\lambda$. The debilitation process leads to a stochastic increase in individual frailty over time. The resulting sigmoid trajectory of marginal mortality cannot be distinguished for that produced by the G-G model with an additive Makeham term (**??**).

Every individual need not begin with the same frailty. **?** considered a model in which the cohort starts with some intial frailty distribution, and then frailty of each individual proceeds in accordance with the LeBras model. **?** modelled the dynamics of frailty as a diffusion process, in which individuals may, with equal probability, become more frail or recuperate to a lower frailty level.

To incorporate dynamic heterogeneity into the matrix model, consider a hypothetical model where individual frailty changes as a diffusion process with reflecting boundaries. Frailty is as likely to increase as to decrease, but it cannot decline below 0 or increase above some maximum limit. If the changes in frailty follow a diffusion process, then the discrete time transition matrix $\mathbf{D}$ can be written

$$\mathbf{D} = e^{k\mathbf{Q}} \tag{55}$$

where $\mathbf{Q}$ is the intensity matrix of a continuous-time, nearest-neighbor random walk with

$$q_{ij} = \begin{cases} 1 & j = i - 1 \\ -2 & j = i \\ 1 & j = i + 1 \\ 0 & \text{otherwise} \end{cases} \tag{56}$$

except that $q_{1,1} = q_{g,g} = -1$. The coefficient k adjusts the speed of diffusion (e.g., **?**). Unlike the LeBras model, this diffusion model does not change the rate of indisposition or recuperation as the frailty changes, but such dynamics can be easily incorporated.

Adding diffusion to the G-G model for Swedish females gives the results shown in Figure 10. Both life expectancy and the standard deviation of longevity are maximized at intermediate values of diffusion. There is a balance between creation of diversity by diffusion, and removal of diversity by selection (a balance familiar from mutation-selection calculations in population genetics). At sufficiently high rates of diffusion, individual move among frailty levels so rapidly that they cannot avoid exposure to high levels of frailty (this reduces life expectancy), and because all individuals experience this random movement the variance in frailty is also reduced.

The interaction between the creation of heterogeneity by diffusion and its elimination by selection is shown in Figure 11. The standard deviation of frailty increases from its value at birth, under the impact of diffusion. Eventually, mortality increases enough to reduce the variation by selection. At very high levels of diffusion, the heterogeneity is almost totally determined by the diffusion. At low levels of diffusion, the increase in heterogeneity is smaller, and its reduction due to selection more prominent.

5.5 Some animal mortality patterns

In an exploration of the effects of heterogeneity on the distribution of age at death, **?** estimated G-G parameters from data on laboratory populations of five species of invertebrate animals: a bean beetle (*Callosobruchus maculatus*), the medfly (*Ceratitis capitata*), the fruit fly *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, and a parasitoid wasp (*Diachasimimorpha longicaudata*.) Because the estimated G-G parameters for these species do not appear in the original paper, they are listed here in Table B.1.

These species exhibit considerably greater variance in frailty than do the human examples considered so far, ranging from 0.90 to 2.18. In contrast, estimates of the initial variance for Swedish females from 1891 to 2010 range from 0.10 to 0.14 (**?**). Figure 9 shows the marginal mortality rate for each species as a function of age, with age and mortality rate both standardized relative to life expectancy at birth. The marginal mortality rates reaches a plateau at an age of about 1 life expectancy, at a standardized mortality rate of 0.1 to 0.5. Further interspecific analyses would be interesting.

6 Heterogeneous frailty vs. individual stochasticity

Inter-individual variance in longevity is often interpreted as evidence of heterogeneity among individuals in their mortality risks. This interpretation is incorrect, because variance in longevity also arises from *individual stochasticity*; the random variation in the fates of indivduals subject to the same risks as they move through the life cycle (**???**). The only way to partition variance into components due to heterogeneity and to individual stochasticity is with a model that contains both sources; the matrix formulation here does so.

Thus, the variance in longevity shown in Figure 8 contains both components. As the variance in the initial frailty distribution $\boldsymbol{\pi}(0)$ approaches zero, the remaining variance in longevity is due to individual stochasticity. It is apparent from Figure 8 that the observed variance in longevity is only slightly greater than that accounted for by individual stochasticity.

This is not always the case: Table 2 compares the decomposition of the variance for Swedish females (the G-G, gamma-Makeham, and gamma-Siler mdoels) with that for the animal species from **?**. In the human populations, heterogeneity accounts for only 2–7% of the variance in longevity. The greater variance in frailty in the experimental animal data makes a much higher contribution to the variance in longevity, from 46% to 83%.

It is important to remember that the relative contributions of individual stochasticity and individual heterogeneity depend not only on the variance in frailty, but also on the mortality schedule, and deserve further empirical investigation.

7 Conclusions

The gamma-Gompertz and related frailty models provide a powerful way to analyze the mortality of heterogeneous cohorts (**?**). They do so by capturing the interacting effects of changing mortality with age and selection among individuals with different frailty states. Frailty models can be characterized by their components:

1. a baseline mortality rate,
2. a mode of action by which frailty affects the baseline mortality rate,
3. the dynamics of individual frailty over time, and

4. an initial distribution of frailty.

In the matrix G-G model, the baseline mortality rate follows the Gompertz model (1) and frailty affects the baseline as a proportional hazard, as in (13). The frailty dynamics are fixed, so that $\mathbb{D}$ in (15) is an identity matrix, and the initial distribution $\boldsymbol{\pi}(0)$ is a gamma distribution with a mean of 1. Many other models can be created by changing one or more of these components. The result, however, is always a model classifying individuals by two criteria: age and frailty. The vec-permutation matrix model (20) methodologically keeps track of both criteria, and makes it easy to calculate the properties of the joint age×frailty distribution, the marginal age-specific mortality and survival functions, and a complete set of statistics of longevity.

Table 3 gives a step-by-step protocol for the analysis of the G-G model. Other choices of baseline mortality rate (e.g., the Makeham model or the Siler model considered in Section 5.1), the action of frailty (e.g., accelerated failure time models), the dynamics of fraility (e.g., the frailty diffusion models discussed in Section 5.4), or the initial distribution of frailty require only simple modifications of the appropriate steps in Table 3.

The effects of model parameters on the statistics of longevity, shown in Figures 5, 6, 7, and 8, reveal interesting patterns. In the G-G model, life expectancy declines with increasing values of a and b, which is not unexpected. It increases with increasing variance in initial frailty, which is less intuitively easy to explain. The effects on variance, CV, and skewness of longevity are more diverse. The standard deviation of longevity declines with increases in a, is maximized at intermediate values of b, and increases with initial variance in frailty. The skewness of longevity increases with increases in a and b, and increases and eventually declines again with increases in initial variance in frailty.

Variance in longevity is sometimes interpreted as evidence of inequality among individuals within the population, but this is not necessarily true. The variance calculated from a specified mortality schedule assumes that all individuals experience the rates defined by that schedule; hence differences among individuals reflects the stochastic outcome of those rates. Frailty models, however, include heterogeneity among individuals, so manipulation of the variance of the initial frailty distribution $\boldsymbol{\pi}(0)$ makes it possible to decompose variation in longevity into contributions from individual stochasticity and heterogeneous frailty (Figure 8. In several human mortality studies based on the gamma-Gompertz, gamma-Makeham, and gamma-Siler models, the contribution of heterogeneous frailty to the variance in longevity is small (2% – 7%). In a set of laboratory studies of invertebrate animals, it is much higher (50%–80%; see Table 2). More analyses of such patterns will be presented elsewhere.

Finally, I note that the results here provide connections to several other problems related to frailty. First, there is no need to limit the analysis to age-classified models. The effects of frailty on stage-classified (e.g., educational status, health status) or multi-stage models can be analyzed simply by using the appropriate formulation in $\mathbb{U}$. The formulation as an absorbing Markov chain can be used to compute likelihood functions from data on individuals. This is used by animal ecologists working with mark-recapture data (e.g., **??**) and implemented in some software packages (**??**). Because frailty is inherently unobserved, issues of identifiability arise, which can also be addressed using the Markov chain formulation (**?**).

Finally, it is a significant advantage that the matrix model is directly amenable to sensitivity analysis using matrix calculus methods (e.g., **???????**) These methods provide the sensitivity of the moments of longevity, the joint distribution of age and stage at death, and the survivorship and mortality functions to changes in any of the parameters of the model.

8 Acknowledgments

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9 Tables

Table 1: Comparison of life expectancy results from **?**, from this paper, and from Missov's theorem implemented in MATLAB and calculated using Wolfram Alpha. The adjusted value from this paper has had 0.5 years subtracted to make the result directly comparable to a trapezoidal computation of the integral of $S^*(t)$. For the matrix calculations, $\omega = 150$ and $g = 100$.

Source	Expected longevity
Missov (2013)	77.29
Missov via Matlab	76.22
Missov via Wolfram	76.22
Matrix method	77.23
Matrix method (adjusted)	76.73

Table 2: Decomposition of the variance in longevity for human populations and laboratory populations of invertebrate species. The variance σ^2 in initial frailty, the variance $V(\eta)$ in longevity and the components of $V(\eta)$ due to individual stochasticity and to heterogeneous frailty, and the proportion of the variance due to heterogeneity. Species are listed in order of increasing initial variance in frailty. Data from **?**.

Species	σ^2	$V(\eta)$	Stochasticity	Heterogeneity	Proportion
Sweden 1950 G-G	0.122	122.9	114.1	8.72	0.071
Turin G-M	0.096	351.6	347.3	104.3	0.012
Sweden 1900 G-S	0.120	1091.7	1074.1	17.60	0.016
nematode	0.90	18.0	9.7	8.3	0.46
fruit fly	0.94	88.1	46.1	42.0	0.48
beetle	1.31	12.7	5.2	7.5	0.59
medfly	1.34	81.8	29.5	52.3	0.64
wasp	2.18	30.3	5.1	25.2	0.83

Table 3: A protocol for analysis of the gamma-Gompertz model.

1. Specify the Gompertz parameters a and b, and the gamma distribution paramater k. Choose values for the numbers of age classes ω and the number of frailty classes g.
2. Generate the baseline mortality vector $\boldsymbol{\mu}_0$ from (12)
3. Specify the frailty classes z_i, $i = 1, \ldots, g$, and the discrete approximation to the gamma distribution $\boldsymbol{\pi}$. Logarithmically-spaced frailty classes are recommended.
4. Create the matrices $\mathbf{U}_i$, for $i = 1, \ldots, g$, as in equation (14).
5. Create the block diagonal matrices $\mathbb{U}$ and $\mathbb{D}$ according to (15).
6. Create the joint transition matrix $\tilde{\mathbf{U}}$ according to (20).
7. Analyze the model
   (a) Compute the fundamental matrix $\tilde{\mathbf{N}}$ from (22).
   (b) Compute the marginal survival function $\mathbf{s}^*$ from (24).
   (c) Generate the marginal fundamental matrix $\mathbf{N}^*$ from (25).
   (d) Generate life expectancy and other indices of longevity from $\mathbf{N}^*$ using (26)–(37).
8. Project the dynamics of the age-railty distribution $\tilde{\mathbf{n}}(t)$ with (42). Obtain the marginal age abundance vector $\mathbf{n}^*$ using (44) and the marginal age distribution vector $\mathbf{p}^*$ using (45).
9. Obtain the marginal frailty abundance vector $\mathbf{m}^*$ using (46) and the frailty distribution $\boldsymbol{\pi}(t)$ from equation (47).
10. If desired, create the mortality matrix $\tilde{\mathbf{M}}$ and generate the distributions of age and of frailty at death from equations (39)–(41).

10 Figures

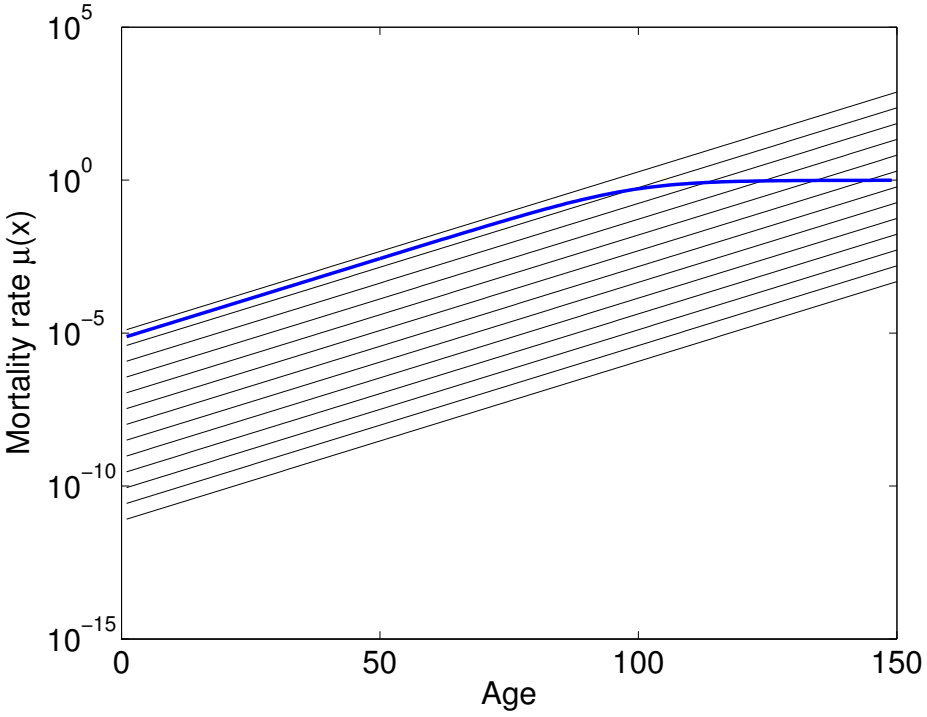
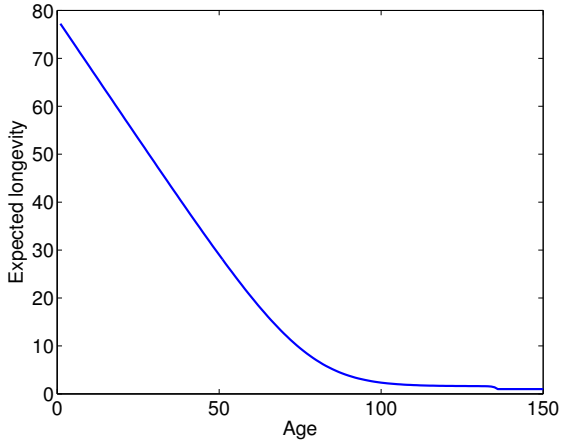
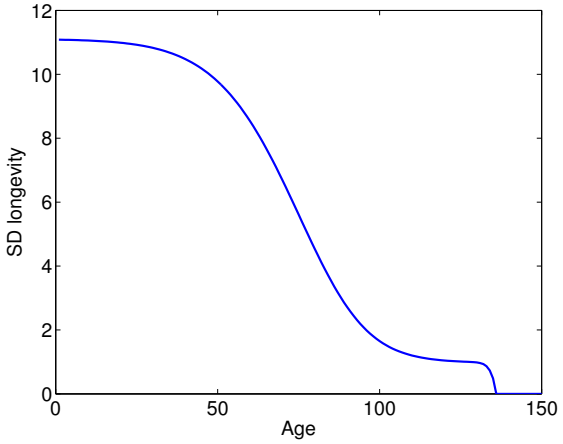


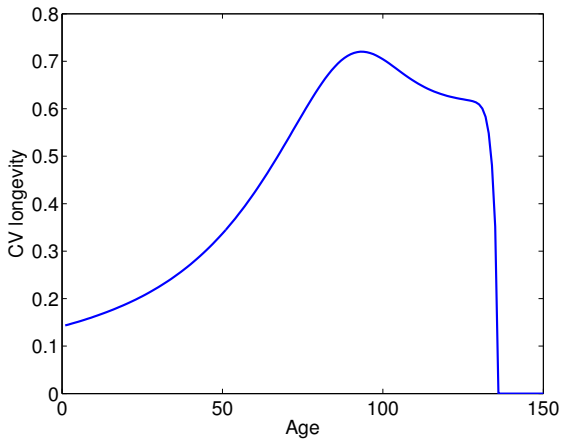
Figure 1: Gamma-Gompertz mortality rate $\mu(t)$ as a function of age, t. Black lines show the age-specific mortality rates for a few of the frailty classes in the model. The blue line shows the marginal hazard $\mu^*(t)$. Parameters for Swedish females as reported in **?** for the year 1950.



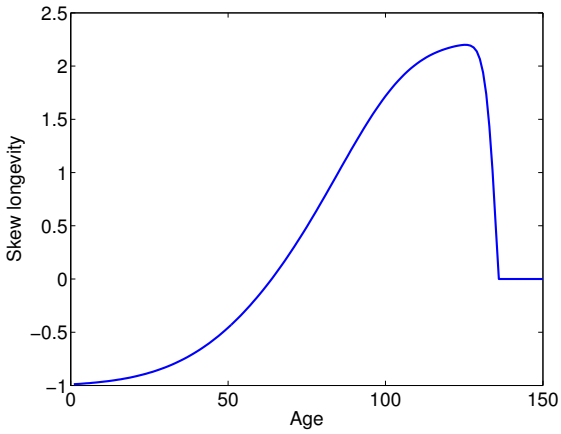
(a) Life expectancy



(b) Standard deviation of longevity

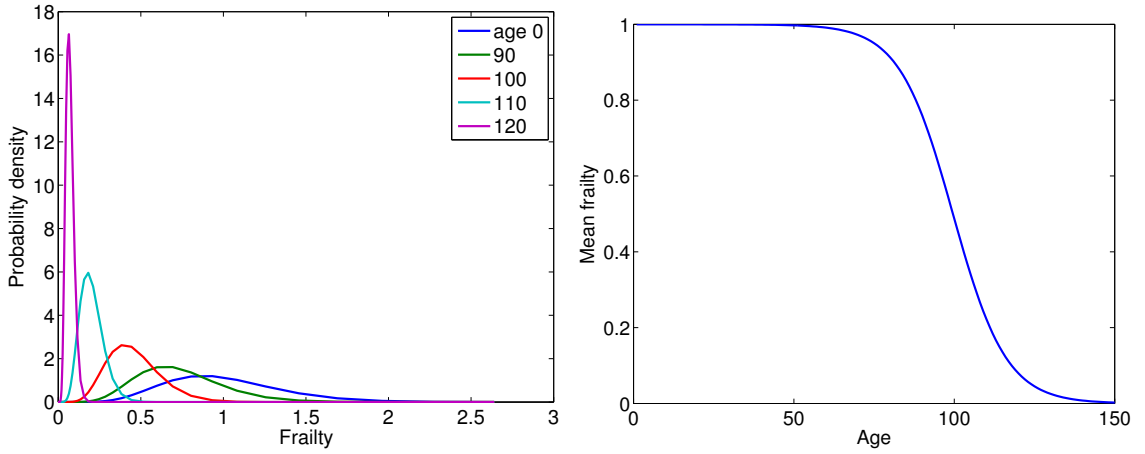


(c) CV of longevity



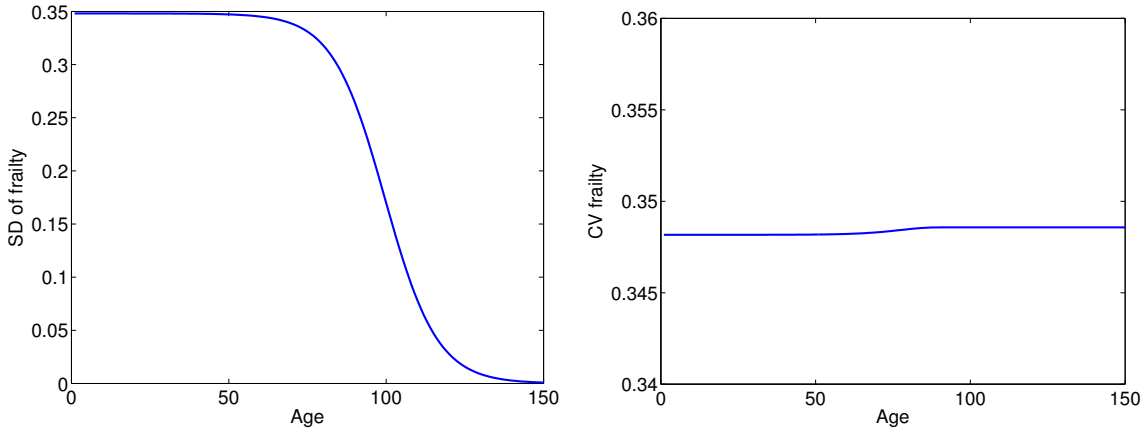
(d) Skewness of longevity

Figure 2: Statistics of longevity for the gamma-Gompertz model, as a function of age, using parameters reported in **?** for the year 1950. (a) Life expectancy. (b) Standard deviation of longevity. (c) Coefficient of variation of longevity. (d) Skewness of longevity. [add vertical line at age 110]



(a) Frailty distribution

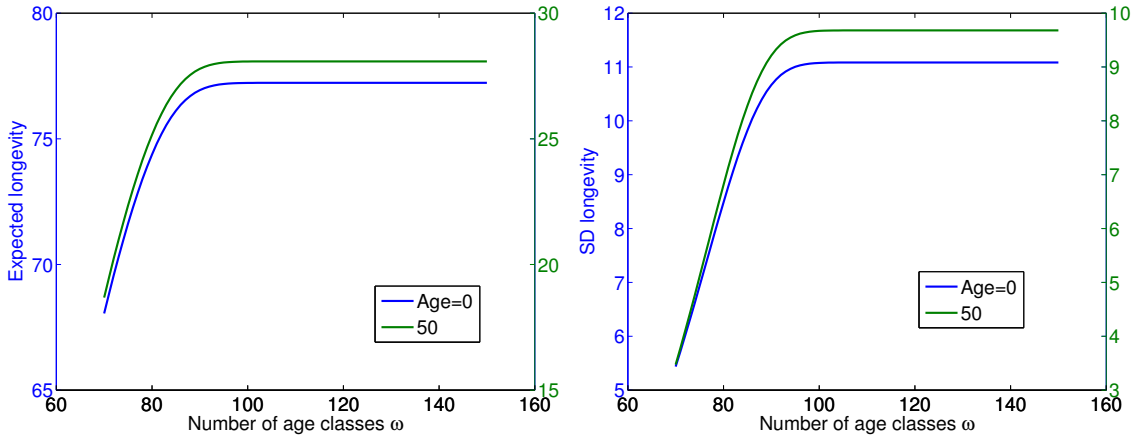
(b) Mean frailty



(c) Standard deviation of frailty

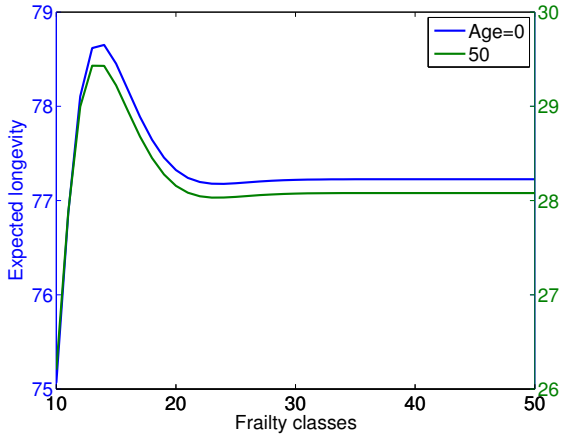
(d) CV of frailty

Figure 3: Changes due to selection in the distribution of frailty, and in the mean, CV, and skewness of that distribution, over the life of a cohort. Parameters for Swedish females, as reported in **?** for the year 1950.

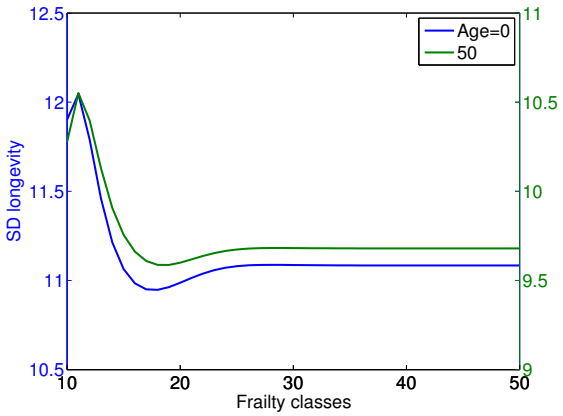


(a) Life expectancy

(b) SD of longevity

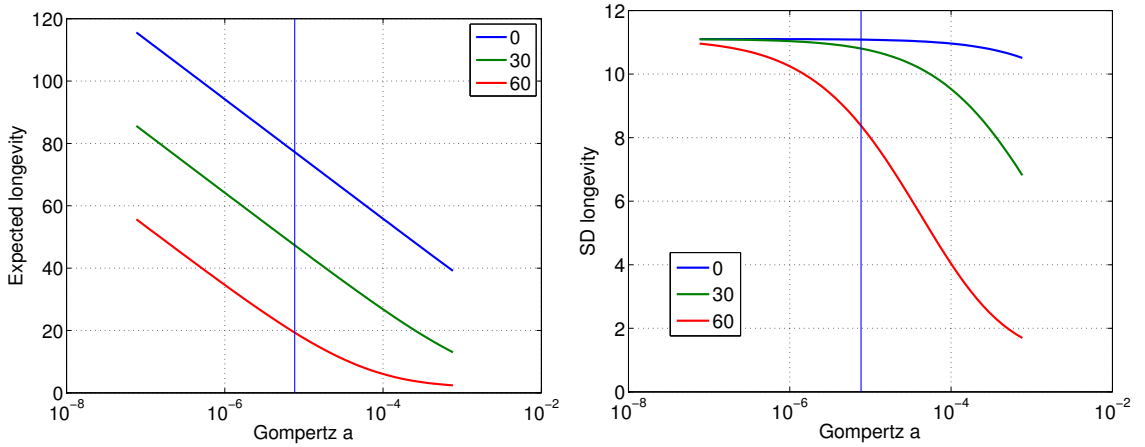


(c) Life expectancy



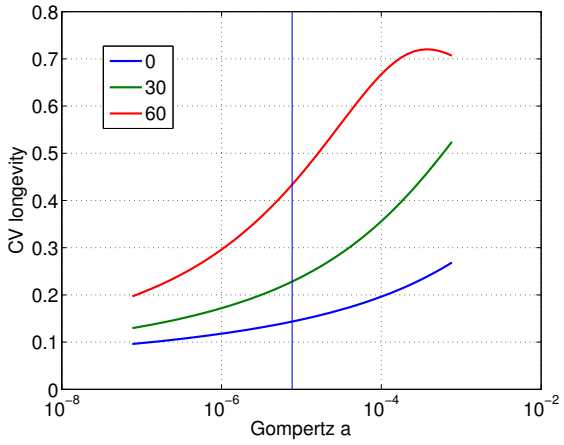
(d) SD of longevity

Figure 4: Effect of the number of age classes (ω) and the number of frailty classes (g) on the estimates of life expectancy and the standard deviation of longevity, at ages 0 and 50. (a) and (b) show the effects of age classes, with $g = 100$. (c) and (d) show the effect of the number of frailty classes, with $\omega = 150$.

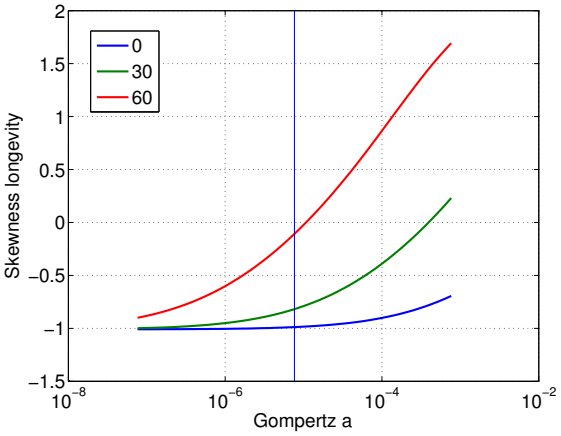


(a) Life expectancy

(b) Standard deviation of longevity

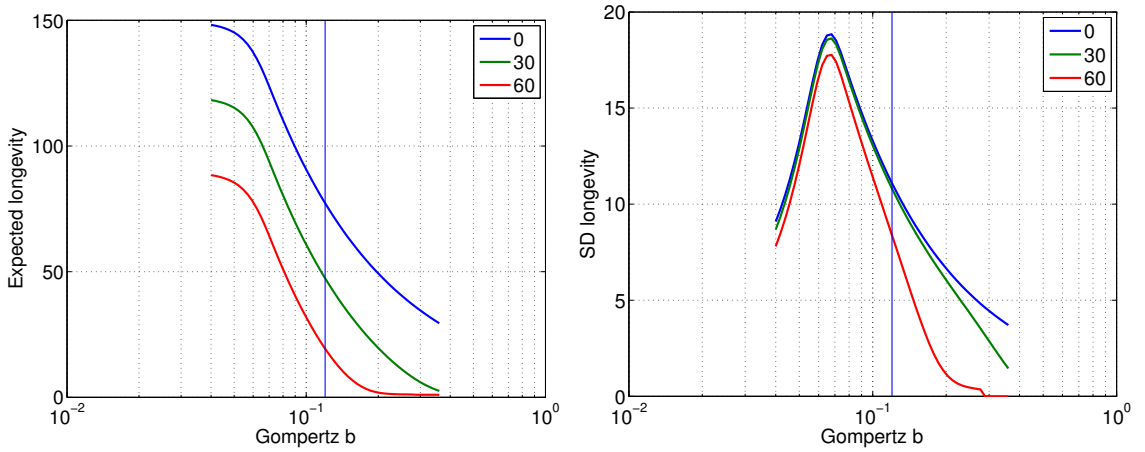


(c) CV of longevity



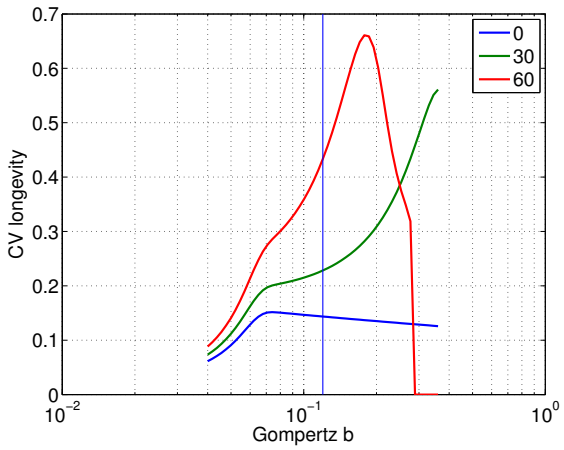
(d) Skewness of longevity

Figure 5: Statistics of longevity for the gamma-Gompertz model, using parameters reported in **?** for Swedish females in 1950, as a function of the Gompertz parameter a.

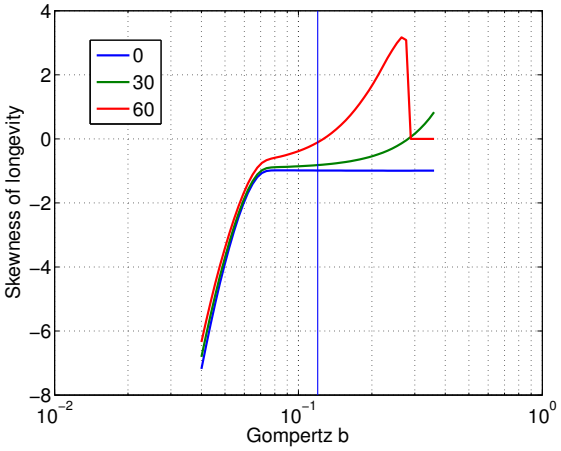


(a) Life expectancy

(b) Standard deviation of longevity

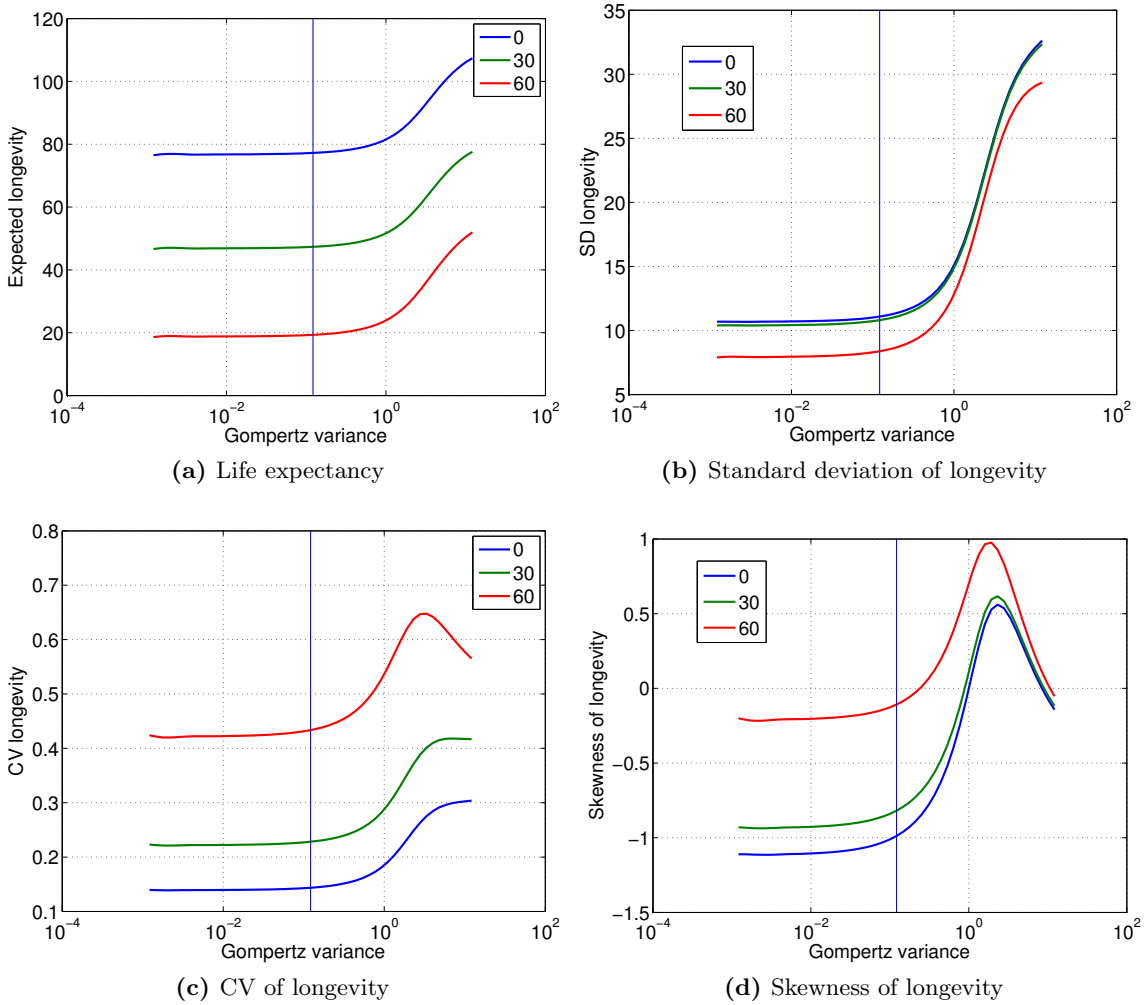


(c) CV of longevity



(d) Skewness of longevity

Figure 6: Statistics of longevity for the gamma-Gompertz model, using parameters reported in **?** for Swedish females in 1950, as a function of the Gompertz parameter b, for ages 0, 30, and 60 years.



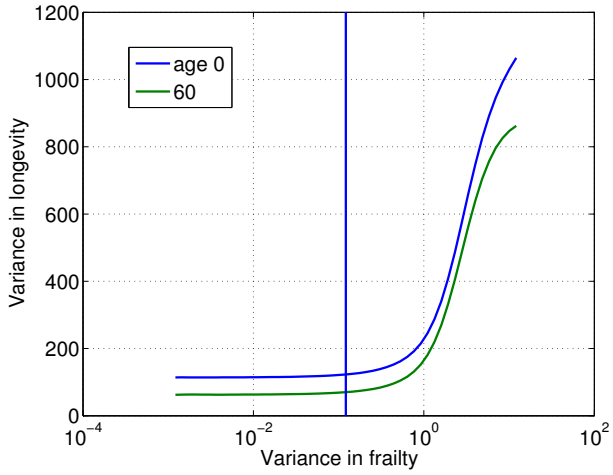
(a) Life expectancy

(b) Standard deviation of longevity

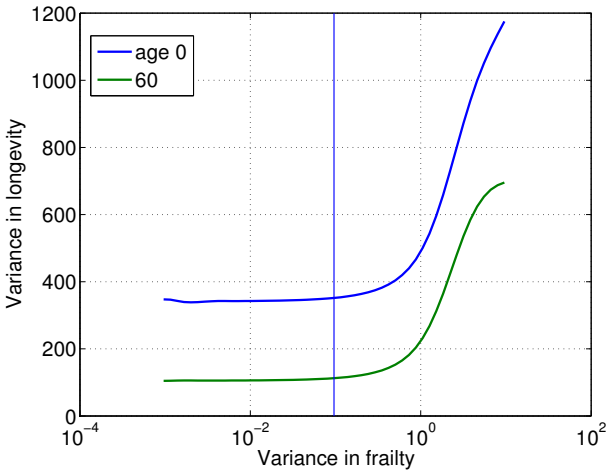
(c) CV of longevity

(d) Skewness of longevity

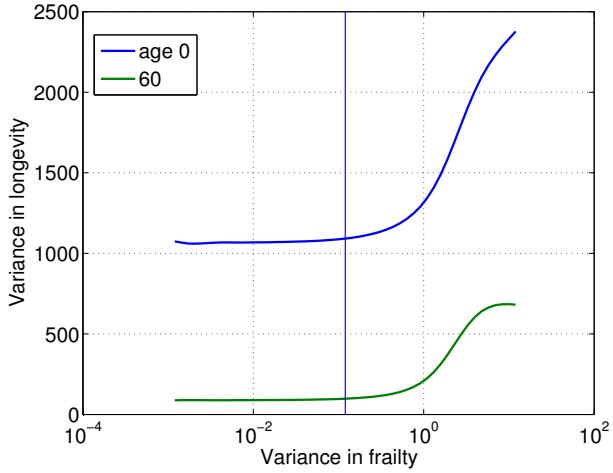
Figure 7: Statistics of longevity at ages 0, 30, and 60 years for the gamma-Gompertz model as a function of the variance in the gamma distribution of frailty (equal to $1/k$). Parameters as reported in **?** for Swedish females in 1950. The vertical lines indicate the observed value of variance.



(a) Gamma-Gompertz model



(b) Gamma-Makeham model



(c) Gamma-Siler model

Figure 8: The variance of longevity, at ages 0 and 60, as a function of the variance of the initial frailty distribution. (a) The gamma-Gompertz model, calculated from parameters reported by **?** for Swedish females in 1950. (b) The gamma-Makeham model, calculated from parameters reported by **?** for a cohort model of the female population of Turin. (b) The gamma-Siler model, calculated from parameters reported by **?** for Swedish females born in 1900. The vertical lines indicates the observed values of initial variance in frailty.

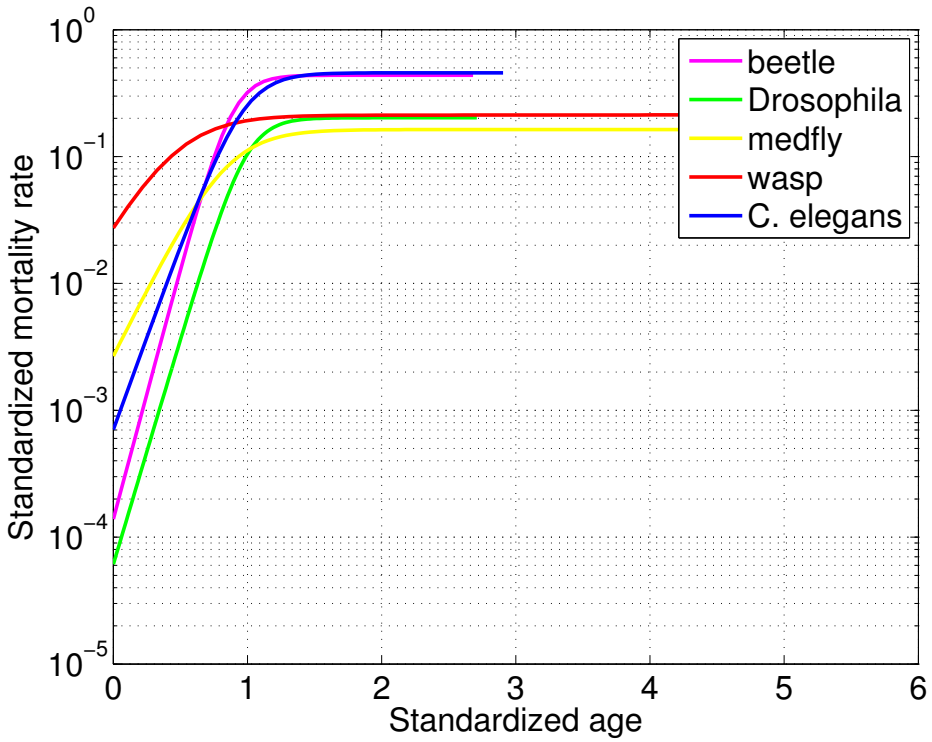
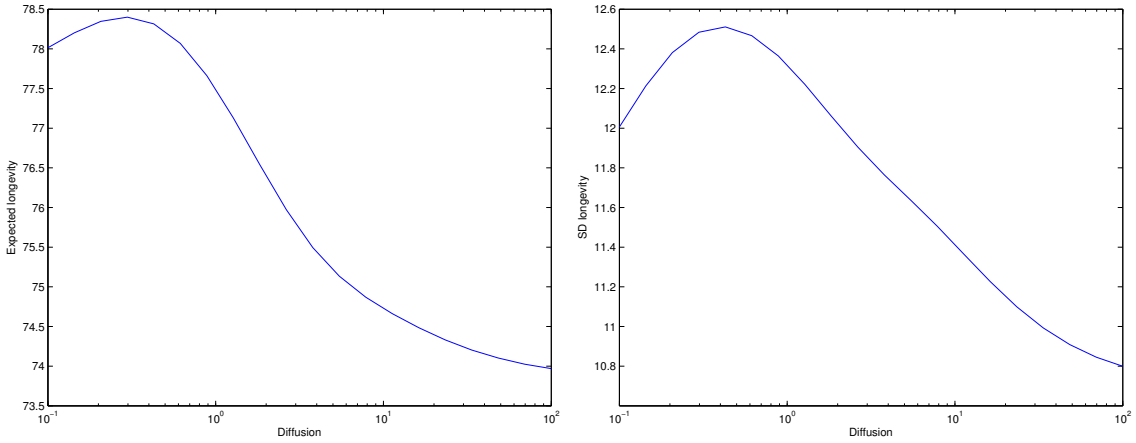


Figure 9: The marginal mortality rate $\mu^*(t)$ as a function of standardized age t, for five species of invertebrate animals, based on G-G parameters estimated by **?**. The age abcissa is scaled by dividing age by the life expectancy at birth. The mortality rate is standardized by multiplying by the same life expectancy.



(a) Life expectancy **(b)** Standard deviation of longevity

Figure 10: The expectation and the standard deviation of longevity at birth for the gamma-Gompertz model with added diffusion of frailty. Parameters as reported in **?** for Swedish females in 1950.

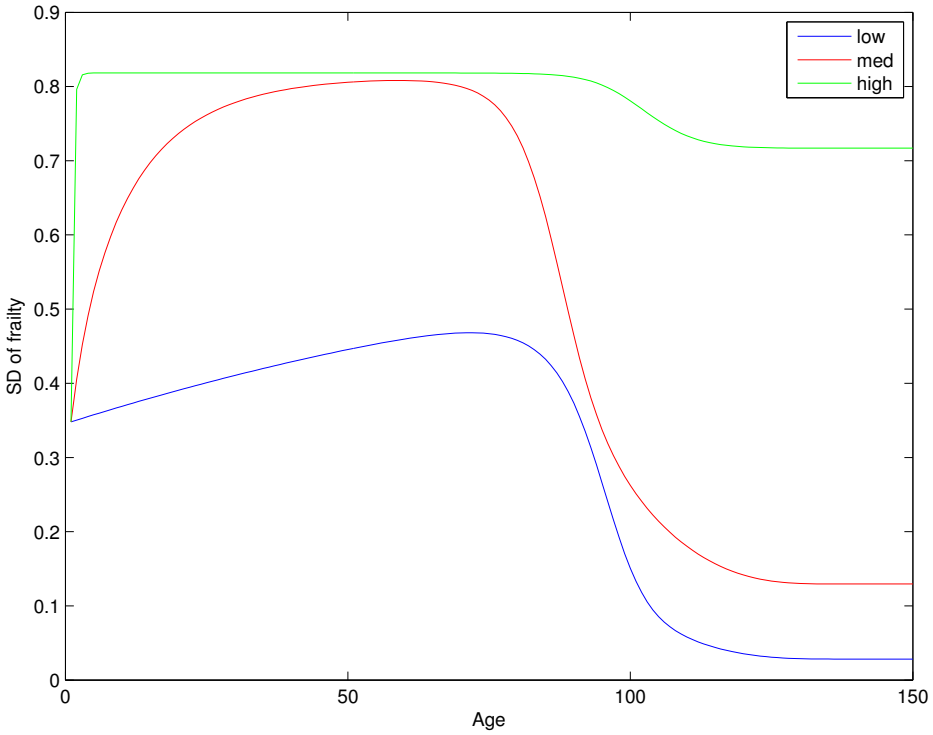
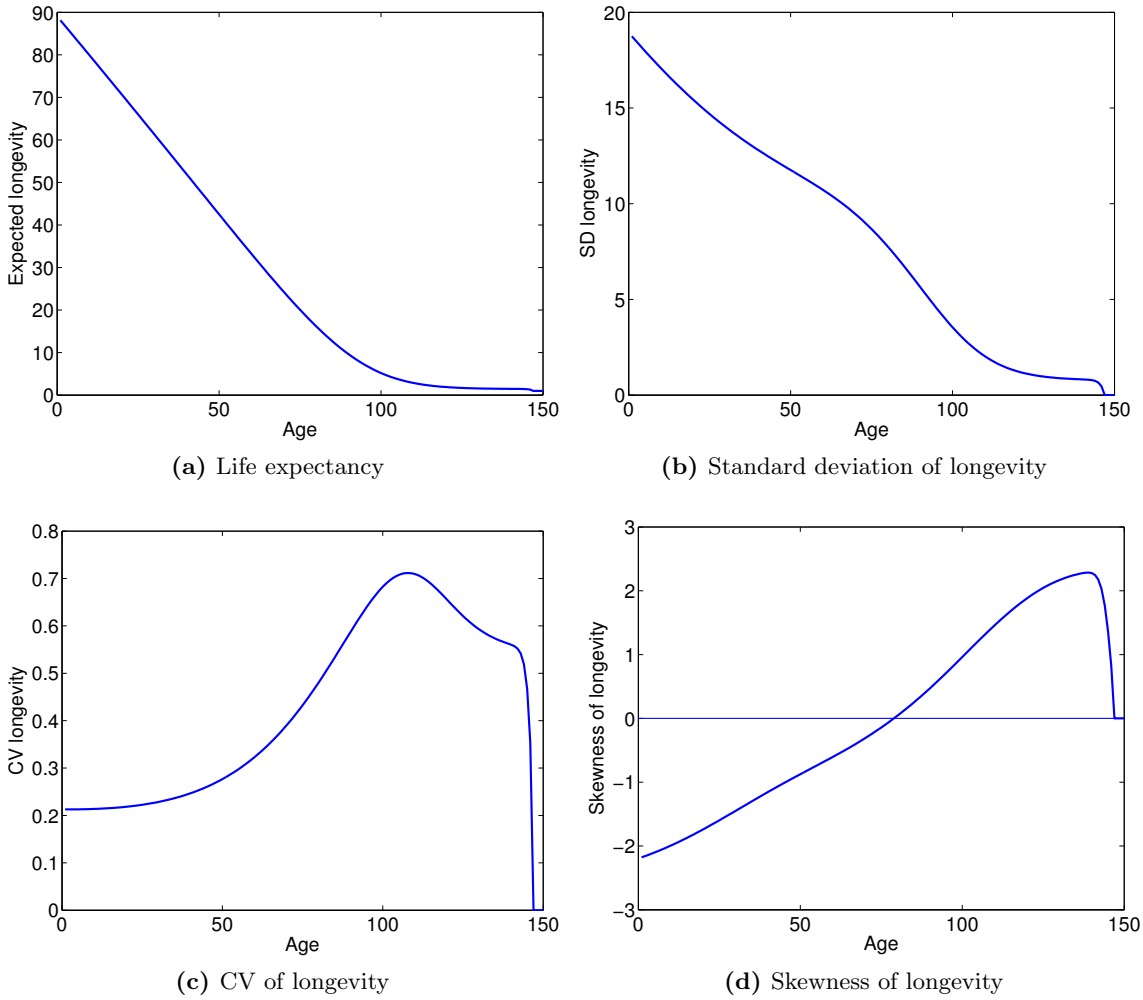


Figure 11: The standard deviation of frailty in a gamma-Gompertz model with diffusion of frailty, at low, medium, and high values of diffusion. Parameters as reported in **?** for Swedish females in 1950.

A Gamma-Makeham and gamma-Siler models

This appendix collects results on the statistics of longevity and the dynamics of frailty for the gamma-Makeham model and the gamma-Siler model, in the same format used for results from the G-G model in Figures 2 and 3.

A.1 Gamma-Makeham



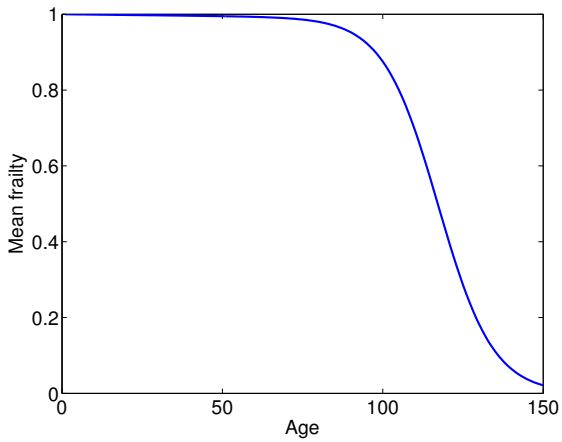
(a) Life expectancy

(b) Standard deviation of longevity

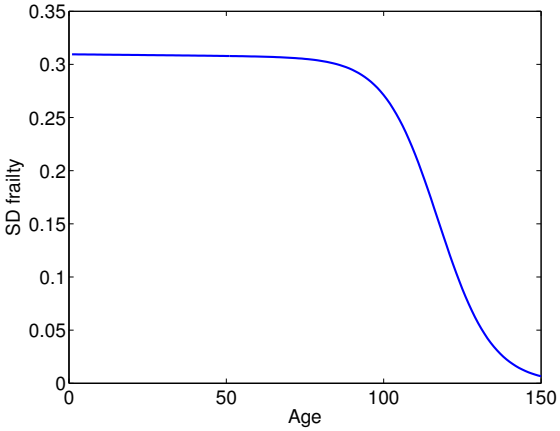
(c) CV of longevity

(d) Skewness of longevity

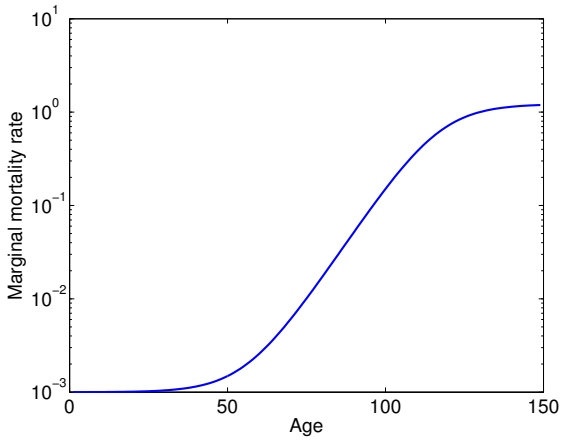
Figure A.1: Statistics of longevity for the gamma-Makeham model, as a function of age. Calculated from parameters reported by **?** for a cohort model for the female population of Turin.



(a) Mean frailty



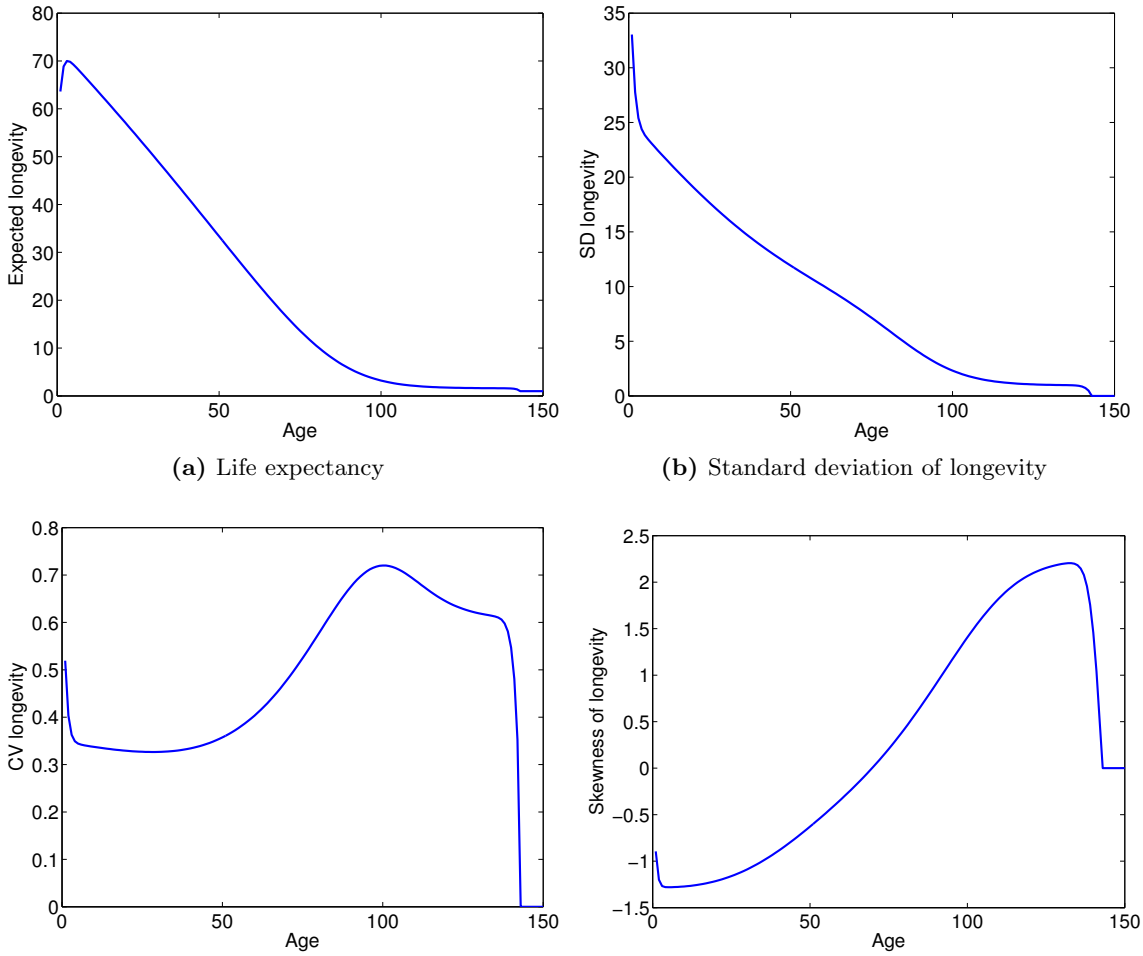
(b) Standard deviation of frailty



(c) Marginal mortality

Figure A.2: Statistics of frailty, and marginal mortality rate $\boldsymbol{\mu}^*$, for the gamma-Makeham model, as a function of age. Calculated from parameters reported by **?** for a cohort model for the female population of Turin.

A.2 Gamma-Siler



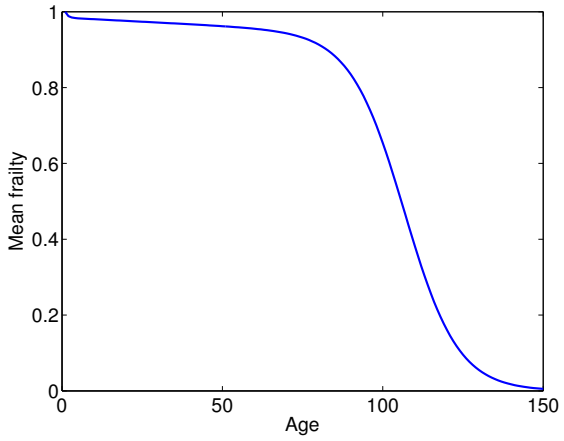
(a) Life expectancy

(b) Standard deviation of longevity

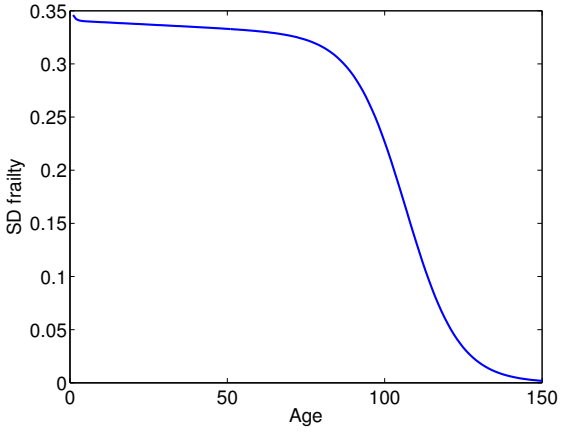
(c) CV of longevity

(d) Skewness of longevity

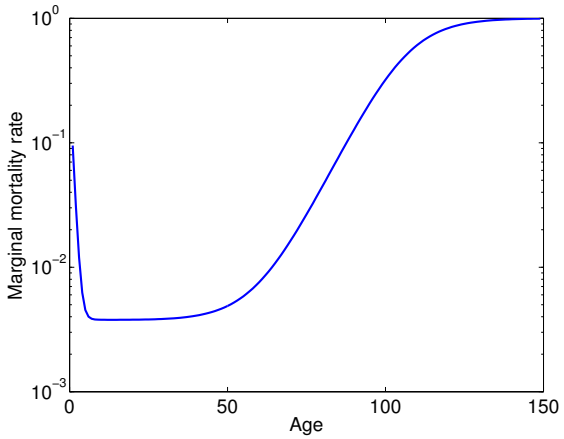
Figure A.3: Statistics of longevity for the gamma-Siler model, as a function of age. Calculated from parameters reported by **?** for Swedish females born in 1900.



(a) Mean frailty



(b) Standard deviation of frailty



(c) Marginal mortality

Figure A.4: Statistics of frailty, and marginal mortality rate $\boldsymbol{\mu}^*$, for the gamma-Siler model, as a function of age. Calculated from parameters reported by **?** for Swedish females born in 1900.

B Parameters for animal species

Table B.1: Gamma-Gompertz parameters for the invertebrate animal species analyzed by **?**; data provided by Horiuchi (personal communication).

Species	a	b	k
Medfly	0.0027	0.2168	0.7530
Nematode	6.9970×10^{-4}	0.4059	1.1264
Wasp	0.0278	0.4575	0.4640
Drosophila	6.0558×10^{-5}	0.1878	1.0796
Beetle	1.3760×10^{-4}	0.5671	0.7721