

Gauss's Mortality Formula: A Demometric Analysis with Application to the Feral Camel Population in Central Australia

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Abstract

A life table for the feral camel population in central Australia is constructed, using an extension of the Gompertz distribution, which was first proposed in a note by the famous mathematician Gauss. It is shown that under certain conditions some important life table parameters can be represented by simple formulae. The derived life table is then used to formulate both a continuous and a discrete model of the camel population. The models yield an annual growth rate of about 7%, a net reproduction rate of about 2.3, and a mean age of population of only 7 years.

Key Words: Life table, stable model, life expectancy, Leslie matrix, Gompertz distribution

1. Introduction

The number of feral camels in central Australia has increased significantly since their release. In this paper, different quantitative methods are proposed to analyze the demographic characteristics of the camel population. From limited data, a life table is constructed using an extension of the Gompertz distribution (Gauss life table distribution). The life table model provides a good approximation of the mortality in these populations. It can be used to estimate and forecast many parameters of the life table and of the corresponding stationary population, e.g., the average and median remaining life expectancies can be calculated. For a given life table, the concept of the stable population model can be applied to the camel population, whereas a stable population is a population with an unvarying age distribution where fertility and mortality are constant. By using the stable model, it is possible to estimate the mean age and other important parameters of the camel population. Finally, a discrete, age-structured model of the population growth is proposed that uses the Leslie-matrix, which is well known in demography.

2. Gauss's Mortality Formula

2.1 Formulation of the Model

In the bequest of the famous mathematician C.F. Gauss (1777-1855) is a note¹ about an analytical mortality formula:

$$\log l(x) = \alpha + \beta \cdot b^x + \gamma \cdot c^x,$$

¹ Königliche Gesellschaft der Wissenschaften zu Göttingen (1900), Hrsg.: Carl Friedrich Gauss, Werke, Band 8, 161-162: Eine Ausgleichformel für Mortalitätsdaten, (<http://gdz.sub.uni-goettingen.de>).

which he fitted to life data for ages $x \geq 3$. From a current demographic view, his formula is called a cumulative force of mortality function, or a cumulative hazard rate function. An early discussion of the Gauss mortality formula is found in Loewy (1906).

Gauss published the following estimates of the parameters:

$$\begin{aligned}\alpha &= 0.48213 \\ \log \beta &= -3.33769 \\ \log \gamma &= -0.32075 \\ \log b &= 0.039097 \\ \log c &= -0.0042225\end{aligned}$$

The antilogs are easily obtained:

$$\begin{aligned}\beta &= 0.00045953 \\ \gamma &= 0.47780424 \\ b &= 1.0942 \\ c &= 0.9903\end{aligned}$$

Consequently, the survivor function of the life table distribution of Gauss is given by:

$$l(x) = 10^{-(\alpha + \beta \cdot b^x + \gamma \cdot c^x)}$$

An alternative formulation of the cumulative force of mortality function (cumulative hazard rate) is given by:

$$H(x) = c + \frac{A}{k} \cdot e^{kx} - \frac{B}{g} \cdot e^{-gx}, \text{ where}$$

$$\begin{aligned}c &= \alpha^{\ln 10} \\ A &= \beta \cdot \ln b \cdot \ln 10 \\ B &= \gamma \cdot \ln c \cdot \ln 10 \\ g &= -\ln c \\ k &= \ln b\end{aligned}$$

$$\text{If } c = \frac{B}{g} - \frac{A}{k}, \text{ then } l(0) = 1.$$

The survivor function is:

$$l(x) = e^{-H(x)},$$

and the force of mortality is calculated by:

$$\frac{dH(x)}{dx} = \mu(x) = -\frac{dl(x)}{l(x)} = A \cdot e^{kx} + B \cdot e^{-gx}, \text{ where}$$

$-\frac{dl(x)}{dx}$ is the death density function.

Special cases of the Gauss mortality law are the well-known laws of:

1. Gompertz : $B = 0$, (B. Gompertz, 1779-1865): $\mu(x) = A \cdot e^{kx}$

and

2. Makeham: $g = 0$ (W. Makeham, +1892): $\mu(x) = A \cdot e^{kx} + B$

On the other hand, the Gauss formula is a special case of the mortality law of Lazarus (1867, p 33):

$$\mu(x) = A \cdot e^{kx} + h + B \cdot e^{-gx}, \text{ if } h = 0.$$

This model has been proposed and applied to primates by Siler (1979). An extension can be found in Thiele (1871), where h is replaced by $h(x)$.

Figure 1 shows the survivor-, the death density-, and the force of mortality functions of the Gauss mortality formula, using his parameter estimates. Some important demographic parameters have been calculated for ages $x \geq 0$ with numerical methods:

Expectation of life:	51.4 years
Normal or modal age:	74.6 years
Median age:	58.5 years
Average age of the stationary population:	32.7 years
Keyfitz entropy:	0.417
Gumbel measure:	0.786

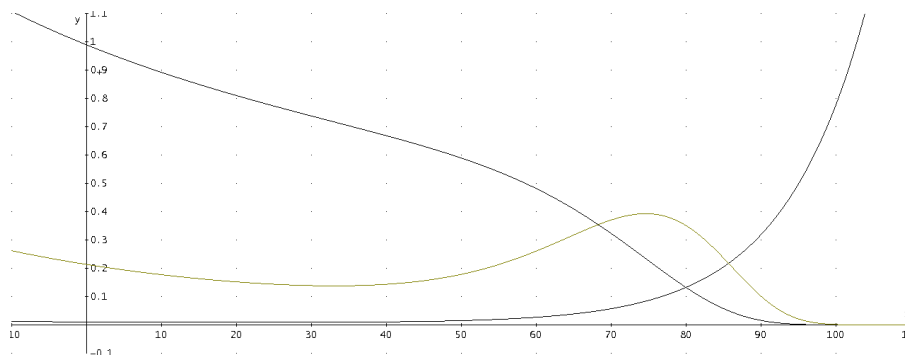


Fig. 1: Survivor-, death density- (has been multiplied by a factor of 20), and force of mortality- functions of the Gauss mortality distribution.

2.2 A Simplified Model and its Parameters

Important demographic parameters of the Gauss mortality distribution

$$F(x) = 1 - l(x) = 1 - \exp\left(\frac{A}{k} - \frac{B}{g} - \frac{A}{k} \cdot e^{kx} + \frac{B}{g} \cdot e^{-gx}\right)$$

cannot be determined analytically; some parameters may be calculated approximately for a special case. For this reason, we regard the force of mortality function, which comprises two parts. The first part is a decreasing function of x , whereas the second part is an increasing function of x . If we assume that the growth rate g is high, such that $e^{-gx} \approx 0$, then $l(x)$ is mainly determined by the increasing part of the force of mortality function, and we can approximate the survivor function after a certain age x by:

$$l_s(x) = \exp\left(\frac{A}{k} - \frac{B}{g} - \frac{A}{k} \cdot e^{kx}\right) = e^{-\frac{B}{g}} \cdot \exp\left(\frac{A}{k} - \frac{A}{k} \cdot e^{kx}\right) = e^{-\frac{B}{g}} \cdot l_{Go}(x),$$

where $l_{Go}(x)$ is the survivor function of the Gompertz distribution.

Now it is easy to calculate the modal value for adult ages by differentiating $l_s(x)$ twice. We get the same formula as in the Gompertz distribution, viz.

$$m = -\frac{\ln\left(\frac{A}{k}\right)}{k} \quad (\text{see, e.g., Pflaumer, 2011}).$$

The median survival time at age x is the time at which half of the survivors $l(x)$ will have died. Formally, the median survival time can be computed by:

$$\frac{l(x + \tilde{e}(x))}{l(x)} = 0.5.$$

Substituting for $l(x)$, the survivor function of $l_s(x)$ leads to

$$\frac{\exp\left(\frac{A}{k} - \frac{B}{g} - \frac{A}{k} \cdot e^{k(x+\tilde{e}(x))}\right)}{\exp\left(\frac{A}{k} - \frac{B}{g} - \frac{A}{k} \cdot e^{kx}\right)} = 0.5.$$

Solving this equation for the median survival time at age x yields

$$\tilde{e}(x) = \frac{\ln\left(\frac{A \cdot e^{k \cdot x} + k \cdot \ln 2}{A}\right)}{k} - x \quad \text{for } x > a, \text{ where } a \text{ is an age with } e^{-ga} \approx 0. \text{ The same}$$

formula applies to the median survival time of the Gompertz distribution (see, e.g., Pflaumer, 2011).

$$\text{Solving } \left(\frac{A}{k} - \frac{B}{g} - \frac{A}{k} \cdot e^{kx}\right) = 0.5 \text{ yields the median survival time at age } 0,$$

$$\tilde{e}(0) = \frac{\ln\left(1 + \frac{k \cdot \ln 2}{A} - \frac{B \cdot k}{A \cdot g}\right)}{k},$$

provided $e^{-\frac{B}{g}} > 0.5$.

The maximum life span can be estimated as the age of the last and single survivor of a population of size N , according to a suggestion of Gumbel (1937) and Finch & Pike (1996). Assuming the simplification $l_s(x)$, one gets from

$$l(\omega) = \frac{1}{N},$$

the maximum life span as

$$\omega = \frac{\ln\left(1 + \frac{k \cdot \ln N}{A} - \frac{B \cdot k}{A \cdot g}\right)}{k}.$$

3. Estimation of a Life Table for the Feral Camel Population of Central Australia

3.1. General Remarks

The camels in central Australia are mostly dromedaries and are descendants of animals imported during the second part of the 19th century. Most of the more than 10,000 animals imported originally came from the northwest region of the former British India (see, e.g., Heucke, 1995). Dromedaries were necessary for the exploration and development of the central arid regions of Australia. They were used for transport, supply, and construction. They became useless with the appearance of motorized transportation in the early 20th century, and many were released into the wild. The size of their population increased quickly. The camel population was estimated at just under one million in 2008. This number of camels was found to cause significant environmental damage and in 2010, the government approved a control plan. The Australian Feral Camel Management Project aims to reduce the overabundance of feral camels through culling and mustering for sale. Because of recent culling and drought, the number of camels has dropped. The current population is estimated to be around 750,000 (see Australian Feral Camel Management Project, 2012).

3.2. Construction of the Life Table

We use the data given by Heucke (1995) for the construction of the life table, which according to Pople & McLeod (2010), is the most complete dataset on camel demographics. Heucke (1995), who studied together with Dörge (1995) a captive feral camel population in a large enclosure in central Australia, estimated that 29% of newborn camels died soon after birth. He observed a yearly mortality rate of about 4% from external influences. In order to consider the age influence of the mortality, he made a rather heuristic approach and finally concluded that the total mortality rate is about 7% per year (see Heucke (1995), p. 97 f.). With these assumptions, he calculated a life table. Apart from his heuristic approach, this procedure is open to criticism because he obtained a life table with constant hazard rates after the age $x = 1$. However, hazard rates should increase at a certain age. His life table function follows an exponential distribution

$l(x) = \exp(-0.07 \cdot x)$ for $x \geq 1$. Pople & McLeod (2010) estimated that camels can live for 40 years, and that about 2% of camels are older than 30 years of age.

With this additional information, we make the following basic assumptions for the life table:

1. $l(1) = 0.71$
2. A survivor rate of 96% between the ages from 1 to 20
3. $l(30) = 0.02$
4. $l(40) = 0$
5. Linear interpolation between the ages 20 and 30, and 30 and 40.

After fitting the Gauss life table distribution²

$$l(x) = \exp\left(\left(\frac{A}{k} - \frac{B}{g}\right) - \frac{A}{k} e^{k \cdot x} + \frac{B}{g} e^{-g \cdot x}\right)$$

to the data ($x = 0, 1, 2, \dots, 40$), we finally obtain:

$$\begin{aligned} A &= 0.0197 \\ k &= 0.0836 \\ B &= 0.6637 \\ g &= 1.661 \end{aligned}$$

Because the growth rate g is high, we can use the following approximation for older ages:

$$l_s(x) = e^{-\frac{B}{g}} \cdot \exp\left(\frac{A}{k} - \frac{A}{k} \cdot e^{kx}\right)$$

In Figures 2 and 3 important life table functions are illustrated. Demographic key parameters, life expectancies and median survival times at age x are shown in Table 1. A complete abbreviated life table is given in Table 2. The life expectancies at age x have been calculated by numerical integration.

² Fitting the Lazarus-Siler model to the data did not yield satisfactory results.

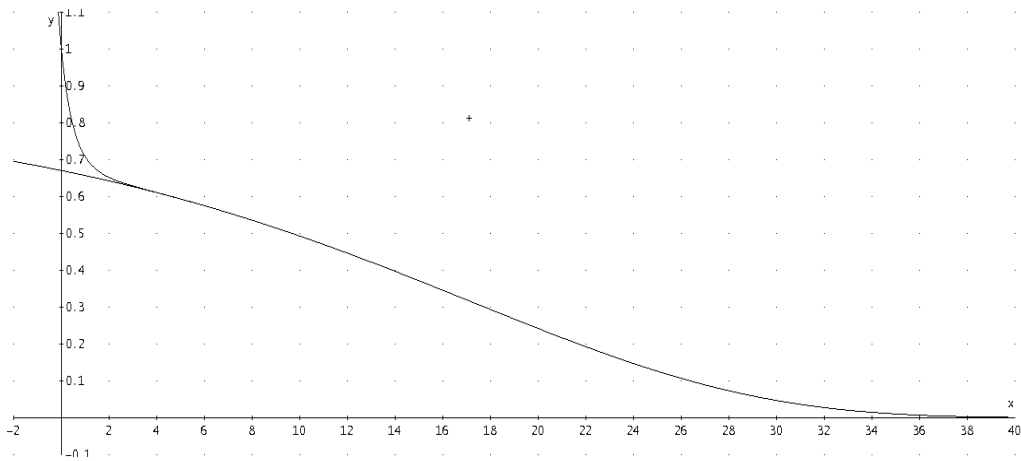


Fig. 2: Survivor functions $l(x)$ and $l_S(x)$.

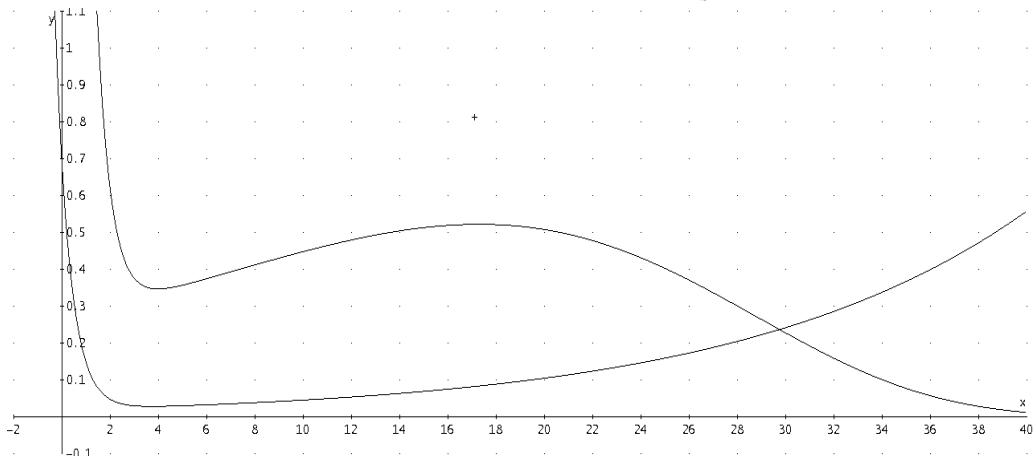


Fig. 3: Death density function $-\frac{dl(x)}{dx} \cdot 20$ and the force of mortality function $\mu(x)$.

Table 1: Demographic key parameters.

Parameter	Exact values (numerical integration)	Formula values
Life expectancy e_0	11.25	-
Median survival time \tilde{e}_0	9.68	9.68
Normal or modal age m	17.29	17.29
Keyfitz entropy H	0.86	-
Mean age of the stationary pop. μ_S	10.48	-
Maximum age ω ($N = 10^6$)	48.56	48.56
Maximum age ω ($N = 10^5$)	46.35	46.35

Table 2: Abbreviated life table of the feral camel population.

Age x	Proportion surviving to age x	Probability of dying Between ages x to x+1	Force of mortality at age x	Life expectancy at age x	Median Survival time at age x exact	Median survival time at age x formula
x	$l(x)$	$q(x)$	$\mu(x)$	$e(x)$	$\tilde{e}(x)$	$\tilde{e}(x)$
0	1.0000	0.2912	0.683	11.25	9.68	16.41
5	0.5935	0.0308	0.030	13.32	12.89	12.89
10	0.4928	0.0463	0.045	10.51	9.83	9.83
15	0.3717	0.0695	0.069	8.10	7.29	7.29
20	0.2421	0.1036	0.105	6.10	5.26	5.26
25	0.1263	0.1531	0.159	4.49	3.71	3.71
30	0.0470	0.2230	0.242	3.23	2.57	2.57
35	0.0105	0.3184	0.367	2.28	1.75	1.75
40	0.0011	0.4413	0.558	1.58	1.18	1.18

3.3 Discussion

The most frequently used life table parameter is the life expectancy at age x , which is the average number of years of life remaining for persons who have attained a given age x . The median survival time at age x is the time at which half of the survivors $l(x)$ will have died. The key parameters of the life table: life expectancy and median survival at birth are very low because of the high mortality at young ages. The Keyfitz entropy H , is very high at $H = 0.86$. A proportional increase of the force of mortality function at all ages of 1% leads to a decrease of the life expectancy at birth of 0.86%. The modal or normal age is about 17 year, i.e., most camels die at the age of about 17. With the proposed model, it is possible to estimate the maximum age, which, when a population of 1 million camels is assumed, is nearly 50. A life table can also be interpreted as a stationary population where the number of births equals the number of deaths per year. The function $l(x)$ in this case is not a survival function, but must be regarded as the age structure of a population. The density of the age structure is obtained by:

$$\frac{l(x)}{\int_0^{\omega} l(x) dx} = \frac{l(x)}{e_0}$$

The mean age of the stationary population is 10.5 years, which is also very low because of the high mortality at young ages.

The approximation formulae for the median, the normal age, and the maximum age are very good in this case, because the absolute value of the growth rate g of the force of mortality function is high.

4. Stable Camel Population Model

4.1 Theory

Now it is possible to formulate a population model for the camels. We use the continuous stable model, which is well known in demography. Only a brief overview of the stable theory in demography is given here. Detailed explanations and interpretations of the parameters are found elsewhere, e.g., Keyfitz (1968, 1977).

A population with an invariable age structure and a fixed rate of increase is called a stable population. The stable age structure is given by:

$$c(x)dx = e^{-rx} \cdot l(x)dx .$$

The stable intrinsic growth rate r , can be determined by solving the characteristic equation:

$$1 = \varphi(r) = \int_{\alpha}^{\beta} e^{-rx} l(x) m(x) dx ,$$

where $m(x)$ is the maternity function, and $l(x)m(x)$ is the net maternity function. The limits of the integral are the youngest fertile age α and the highest β . The function $\varphi(r)$ crosses the vertical axis at

$$\varphi(0) = \int_{\alpha}^{\beta} l(x) m(x) dx = R_0$$

the net reproduction rate. The extent to which women of given age x , on average contribute to the births of future generations is expressed by Fisher's reproductive value:

$$v(x) = \frac{1}{e^{-rx} l(x)} \int_x^{\beta} e^{-ra} l(a) m(a) da .$$

Keyfitz (1977) showed that the population momentum can be estimated by:

$$M = \frac{b \cdot e_0 \cdot (R_0 - 1)}{r \cdot \mu \cdot R_0}$$

where b is the birth rate and μ is the mean age of child bearing in the stationary population.

4.2 Results

Following Heucke (1995), we will first estimate the maternity function $m(x)$. The birth interval of most females was 1.85 years, but for females who lost their newborns, the birth interval was only 1.2 years. The weighted average birth interval was 1.662 years. With the lowest fertile age $\alpha = 5$ and the highest fertile age $\beta = 30$, we obtain a total

fertility rate of $\frac{25}{1.662} = 15.04$. If the sex ratio is 1, then the reproduction rate is 7.52.

Assuming a rectangular distribution between the limits, we get the continuous maternity function:

$$m(x) = \frac{7.52}{25} = 0.3008 \quad \text{for} \quad 5 \leq x \leq 30$$

With the estimated survivor function the relevant parameters can be determined by numerical integration (see Table 3). The population momentum is calculated by using the formula, whereby the birth rate of the stable population is given by:

$$b(r) = \frac{1}{\int_0^{\infty} e^{-rx} l(x) dx}$$

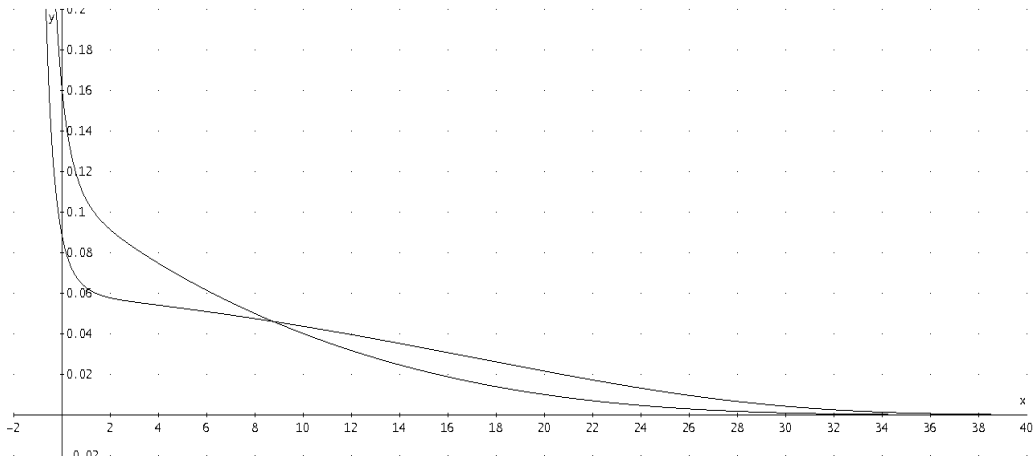


Fig. 4: Stationary and stable age structure ($r = 0.0684$).

Table 3: Relevant parameters of the stable population.

Parameter	Value
Intrinsic rate of growth r	0.0684
Net reproduction rate R_0	2.34
Mean age of child bearing μ	11.36
Stable birth rate b	0.1606
Mean age of the stable population $\mu(r)$	7.22
Population momentum M	1.117

Important demographic parameters of the camel population are summarized in Table 3. The net reproduction rate is 2.34, which is not very high. It means that one female camel is replaced by a little more than two female calves. This or even a higher size of the net reproduction rate can also be observed in human populations. However, because the mean age of child bearing of 13.6 years is low, the net reproduction rate of 2.34 leads to an annual growth rate of nearly 7%. This growth rate was also obtained by Pople & McLeod (2010), who applied a discrete model of only three classes (0-1, 2-5, 6-40), and who also used the vital data from Heucke (1995). The population momentum of $M = 1.117$ means that the population would continue to grow around another 12%, even if fertility dropped suddenly to replacement levels ($R_0 = 1$).

Figure 4 illustrates the age structures of the stable growing ($r = 0.0684$) and the stationary ($r = 0$) camel population. The high growth rates produce a young age structure, which is reflected by the young mean age of around 7 years. Table 4 shows the population proportions in different age classes. Less than 5% of the camels are over 20 years old.

Table 4: Stable age structure.

Age class	Proportion
0-5	0.460
5-10	0.266
10-15	0.151
15-20	0.077
20-25	0.033
25-30	0.011
30-35	0.002
35-40	0.000

The reproductive value in Table 5 is the total number of female offspring, discounted with the intrinsic population growth rate, who can expect an x-year old female camel. The reproductive value is especially high at ages between 5 and 15 because of the high mortality at young ages. Harvesting or culling young adult camels is more than twice as effective as harvesting or culling the newborn offspring.

Table 5: Reproductive values at age x.

x	0	1	2	3	4	5	15	20	25	30
v(x)	1	1.51	1.76	1.95	2.15	2.37	2.03	1.67	1.3	0

The impact of relative changes of fertility and mortality on the intrinsic growth rate is illustrated in Table 6. A doubling of mortality (proportional change of the force of mortality function in all age classes) finally leads to a stationary population, if fertility is kept constant. Fertility has to be reduced in all age classes by 60% in order to achieve a stationary population, if mortality is unchanged. Other combinations of percentage increases in mortality and percentage reductions in fertility, and their impact on the growth rate, can be seen in Table 6. The effect on the life table of doubling the force of mortality function and the death probability function is presented in Figures 5 and 6, respectively, where the death probability is $q(x) = 1 - \frac{l(x+1)}{l(x)}$.

Table 6: Intrinsic growth rate dependent on relative chances of fertility (f) and mortality (h).

h \ f	0%	-10%	-20%	-30%	-40%	-50%	-60%
0%	0.068	0.059	0.049	0.038	0.026	0.012	-0.005
10%	0.061	0.052	0.042	0.031	0.019	0.004	
20%	0.054	0.045	0.035	0.024	0.011	-0.003	
30%	0.046	0.037	0.027	0.016	0.004		
40%	0.039	0.030	0.020	0.009	-0.004		
50%	0.032	0.022	0.013	0.002			
60%	0.024	0.015	0.005	-0.006			
70%	0.017	0.008	-0.002				
80%	0.010	0.001					
90%	0.002	-0.007					
100%	-0.005						

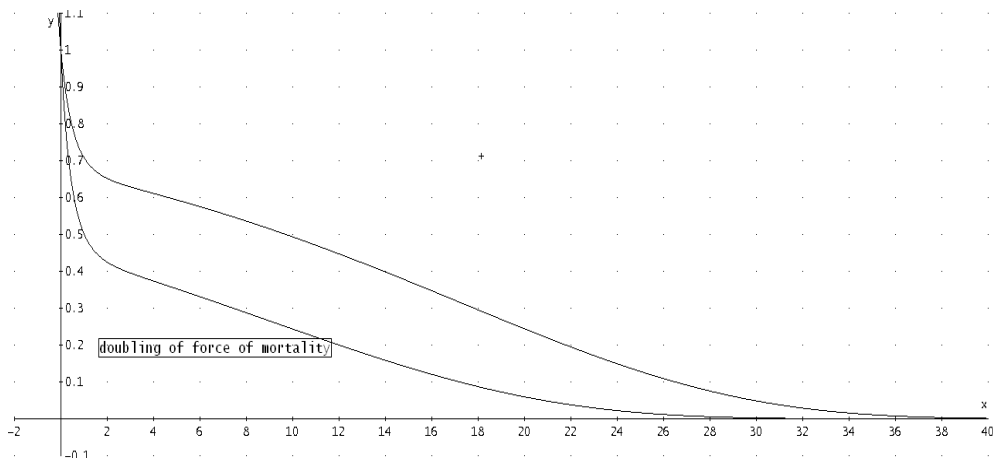


Fig. 5: Effect of doubling of $\mu(x)$ on the survivor function.

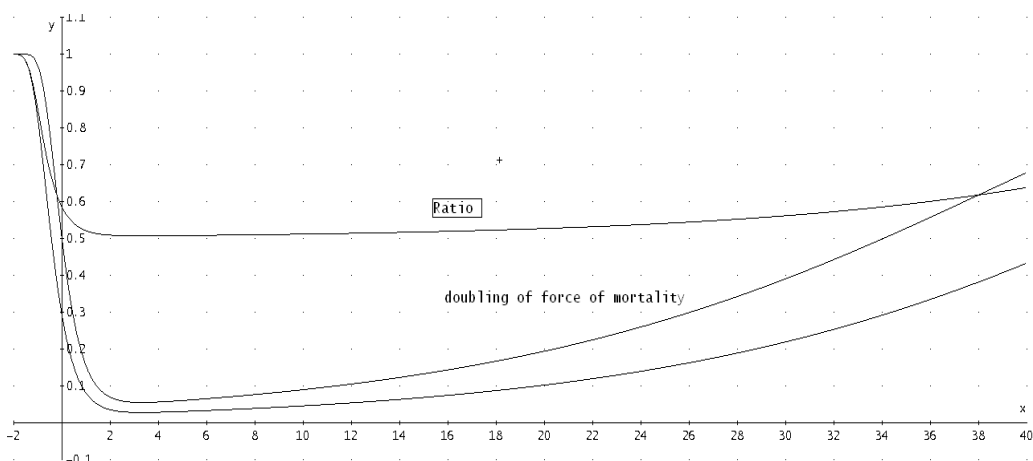


Fig 6 : Effect of doubling of $\mu(x)$ on the death probability function.

5. A discrete camel population model

A discrete model is required in order to make projections and any type of sensitivity analyzes. A population projection model (for females and without migration) that is generally used, is based on the well-known cohort-component method, and leads to a population projection that is broken down into categories of age and sex (c.f., e.g., Land, 1986). This model is based on a projection of the population through its components, fertility, and mortality. The initial population that is broken down into categories of age and sex is taken as the basis for the model. It is reduced by the number of deaths for each interval in the projection time frame by means of age- and sex-specific death rates. The number of births will be determined with help from age-specific birth rates for surviving women. The entire birth figure will then become the new birth-cohort in the projection model. The following representation of the cohort-component method refers back to Leslie (1945). The projection model for the female population is represented by the following recurrence equation:

$$n_{t+1} = L_t \cdot n_t \text{ for } t=0,1,2,\dots$$

The vector n_t represents the number of women in the different age classes at time t . After one projection interval, the population n_{t+1} , broken down into age, can be obtained by multiplying n_t with the projection matrix L_t . The projection or the Leslie matrix contains in the first row, age-specific maternity rates and in the subdiagonal, the age-specific survivor rates. Otherwise, it contains only zeros (c.f., Keyfitz, 1977)

$$L = \begin{pmatrix} 0 & 0 & m_1 & \dots & 0 \\ s_1 & 0 & 0 & \dots & 0 \\ 0 & s_2 & 0 & \dots & 0 \\ 0 & 0 & s_3 & \dots & 0 \\ \vdots & \vdots & & & \vdots \\ 0 & 0 & \dots & s_{n-1} & 0 \end{pmatrix}.$$

These age-specific survivor rates are calculated for five-year age groups as follows:

$$s_i = \frac{{}_5L_{x+5}}{{}_5L_x} \text{ for } x = 0, 5, 10, \dots \text{ and } i = 1, 2, 3, \dots$$

$$m_i = \frac{{}_5L_0}{2l_0} \left(F_x + \frac{{}_5L_{x+5}}{{}_5L_x} F_{x+5} \right) \text{ for } x = 0, 5, 10, \dots \text{ and } i = 1, 2, 3, \dots$$

$$\text{with } {}_5L_x = \int_x^{x+5} l(x)dx \text{ and } F_x = \int_x^{x+5} m(x)dx.$$

Further details about the calculation of the elements of the vector and matrices of the projection model are found elsewhere, e.g., in Keyfitz (1977) or Pflaumer (1988).

The growth factor is represented by λ , which is the dominant eigenvalue of the matrix. If $\lambda > 1$, then the population grows; if $\lambda < 1$ it shrinks; in the case of a stationary population, the growth factor is $\lambda = 1$.

The elements of the Leslie matrix are given in Table 7.

Table 7: Elements of the Leslie matrix for the camel population.

	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40
0-5	0.41	0.904	0.86	0.802	0.733	0.503	0	0
5-10	0.814	0	0	0	0	0	0	0
10-15	0	0.796	0	0	0	0	0	0
15-20	0	0	0.708	0	0	0	0	0
20-25	0	0	0	0.593	0	0	0	0
25-30	0	0	0	0	0.456	0	0	0
30-35	0	0	0	0	0	0.308	0	0
35-40	0	0	0	0	0	0	0.173	0

The results of the discrete model are similar to those of the continuous model. The stable eigenvalue is $\lambda = 1.408$, which means a yearly growth rate of 7.1%, because:

$$r = \sqrt[5]{1.408} - 1 = 0.071.$$

The net reproduction rate is calculated as $R_0 = 2.332$. The population momentum of $M = 1.13$ is determined by projecting the population 100 projection steps, which equals 500 years.

The age structure and the reproductive values of the discrete model are shown in Table 8. The original stable eigenvector has been multiplied by a scalar so that the sum of the elements yields one. There is no real difference between the continuous and the discrete age structures.

Table 8: Stable age structure (Leslie model) and reproductive values.

Age class	Proportion	Reproductive Value*	Reproductive Value**
0-5	0.460	1.821	1.821
5-10	0.266	2.200	2.232
10-15	0.151	1.849	1.880
15-20	0.077	1.487	1.526
20-25	0.033	1.094	1.159
25-30	0.011	0.508	0.650
30-35	0.002	0	0
35-40	0.000	0	0

*) Calculated by numerical integration of the continuous reproductive value function;
 **) left eigenvector of the Leslie matrix with an arbitrarily chosen $v(0-5)=1.821$.

6. Conclusion

Gauss's mortality formula has the potential to describe the behavior of mortality rather accurately in all ages unlike Gompertz's law, which is only valid for more advanced ages. The basis of an effective camel population control is a reliable life table and the resulting stable population model. The premises of a stable model are constant growth rates in the past. In this case, the actual age structure is more or less identical with the model age structure. Therefore, the influence of the changes of vital rates on important demographic parameters can be analyzed with the model. The model is also suitable for the estimation of parameters that could otherwise not be observed empirically, e.g., the mean age of the population. However, the models are only as good as their assumptions. Further research is necessary, and two approaches should be pursued. Biologists need to provide data on the vital rates that are more specific. Demographers and statisticians need to perform sensitivity analyzes with their models, in order to examine the impact of different assumptions on the results. For example, one has to answer the question; How important is the chosen mortality law? Additionally, the uncertainty in modeling the vital rates as stochastic variables needs to be considered.

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