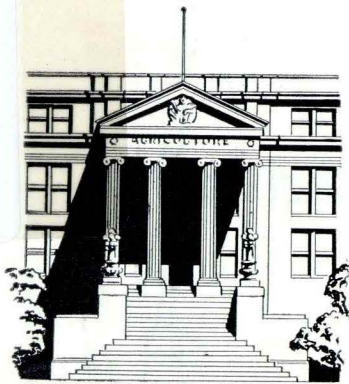


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Description and Measurement Of Rates of Early Mortality In the Pig

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SUMMARY

This bulletin demonstrates the use of life tables in studying the early mortality experienced in pigs. The plot of the surviving fraction is useful in describing the general course of mortality in the postnatal period. Comparison of survival curves are accomplished most effectively by studies of age-specific mortality rates.

The logarithm of the mortality rates in pigs declines linearly with the logarithm of time before maturity in a manner analogous to the linear increase in mortality rate found in man after age 30. This relationship

allows quantitative comparisons between different groups on the basis of the slope and intercept of the line fitted to the age-specific mortality rates.

The quantitative measurement of mortality is hindered by many unique characteristics of the length of life in the early postnatal period. The transformation of length of life to a quantitative variable based on the normal distribution allows the variation in mortality to be analyzed between and within small groups, such as litters and paternal half-sib classes.

Description and Measurement of Rates of Early Mortality in the Pig¹

by D. F. Cox²

Approximately one-fourth of all pigs born die before they are 5 months old. These deaths are studied in many areas of research where pigs serve as experimental animals. The species is employed not only to study the problems connected with its use in agriculture but also to investigate biological phenomena in such subjects as gerontology, physiology and radiation biology. Methods for describing and measuring the expression of early mortality are useful in many of these situations. The immediate objective of this bulletin is to describe the pattern of early mortality in pigs and to outline quantitative methods for measuring the forces that control it. The ultimate objective is to use such methods to gain a greater understanding of the forces that lead to death.

REVIEW OF LITERATURE

The records on births and deaths in humans have been collected, tabulated and studied for several centuries. The empirical relationship between the rate of mortality and age during the period of senescence in humans was derived in 1825 by Gompertz (4) and is still used in the study of mortality. The statistical problems concerning measurements of the length of life have been investigated for reasons varying from the increasing importance of aging in human medicine to the need for quality control in modern industry. An extensive review of the statistics connected with life testing has been presented by Mendenhall (6).

Many biological investigations have employed the life table, and several works have described the structure, use and limitations of these tables (3). Pearl (8) made use of life tables to study mortality in organisms other than man. The biology of aging has received increasing attention in recent years. The underlying processes that control mortality have been studied with the objective of understanding the quantitative relationships between mortality rates and age. Comfort (1) has presented a general discussion of the biological aspects of senescence. A collection of

works that demonstrates the wide scope of this field has been compiled by Strehler (11).

Ionizing radiation has been a special stimulus to the research in this field. The effects of time and radiation on living systems are similar in many aspects, and these results have encouraged further consideration of general theories of mortality and aging (10).

The pattern of mortality in early life before sexual maturity has received less theoretical and detailed attention. Mammals characteristically have a high mortality rate at and immediately following birth. The rate of mortality declines rapidly as the individuals mature and reaches a low point just before sexual maturity. Agricultural researchers have recognized for a long time the importance of the 25 to 30 percent death loss occurring before market age in pigs. Improved management, nutrition and sanitation, as well as different breeding programs, have reduced these losses. The effects of different breeding programs on the numbers weaned have been summarized by Craft (2). The influence of such factors as inbreeding, age of the dam, season of birth and litter size on survival have been studied in many sets of data. The methods generally used have not discriminated between varying ages of death but rather have used some single measure such as the percentage of pigs born that are weaned.

The mortality of organisms has often been used as a measure of treatment response in toxicology and biological assay investigations. The percentage mortality, or some transformation of the percentage such as probit or angular transformations, are well known measures. These methods do not assign scores to individual animals, which is often essential in analysis of the quantitative genetics involved. A more detailed study of mortality was given by Kincaid (5). He transformed the length of life into a normally distributed variable that would be amenable to more refined quantitative analysis. The actual mechanics of this transformation will be discussed later.

NATURE AND CONSTRUCTION OF A LIFE TABLE

The life table is a device commonly used to describe the course of mortality in a concise form. The period of life that is under study is divided into

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convenient age intervals. The probability of death is calculated for each interval from the mortality experienced in a population specified with respect to time, sex, genetic basis, environmental circumstances or other criteria. These probabilities are used to construct a description of the number of individuals surviving to various ages in a hypothetical cohort that start together and are followed over the period. A complete life table would cover the entire life span. In pigs, however, where just a few selected individuals are permitted to live much, if any, past the age when reproduction might begin, only partial or incomplete life tables can be obtained. A life table covering the first 154 days of life in 3,218 pigs is given as table 1. This table was constructed from the records obtained at the Iowa Agricultural and Home Economics Experiment Station on purebred Duroc and Hampshire pigs from 1954 to 1960.

The individuals included were all pigs that were apparently alive at the initiation of birth and seemingly capable of extra-uterine existence. Any pigs recorded as showing signs of decomposition, indicating death prior to birth, were excluded from the results. Those pigs in which pulmonary respiration did not occur were termed as dead at birth. These individuals die either before, during or after birth but before breathing. For the purposes of this discussion, these individuals are considered to die at birth. To determine accurately whether pulmonary respiration occurred, the lungs of the individual pig must be examined. This is not routinely done, thus some individuals are probably misclassified. However, the presence of fetal membranes, the condition and the position of the pig when found are factors which can be used in most cases to determine whether the pig lived and breathed after birth.

In describing the components of a life table, reference will be made to table 1.

Age Intervals. The first 154 days are divided into convenient intervals of time which, in the present instance, are not of equal length. The first interval consists of time from the initiation of birth through the 24 hours following birth and includes those individuals classed as dead at birth.

Rate of Mortality Per Unit Time, q_x . The number dying during each interval expressed as a fraction of the number alive at the beginning of the interval constitutes the rate of mortality. These rates are derived from the actual experience in a specified

population and are put on a per-day basis. To avoid extended decimals, the rates are converted into the average number dying per day over the interval per 1,000 alive at the start of the interval.

Number living, l_x . The individuals from the cohort that live to the beginning of each interval of age are called the surviving fraction. Some convenient round number, such as 10,000, is chosen to represent the initial hypothetical population.

Number Dying, d_x . The number of individuals dying during each interval is obtained by multiplying the total rate of mortality by the number of individuals surviving to the start of the interval.

These four columns represent the minimum structure of a life table. Often other components are added, such as expectation of further life at given ages. All the other functions that are used, however, are derived from the basic mortality rates such as those given in the second column of table 1.

USE OF LIFE TABLES IN STUDYING MORTALITY

Two functions of the values in the life table are generally used to describe and compare the mortality in various groups. The survival curve, which consists of a plot of the surviving fraction with time, is used when a description of the nature and course of mortality is desired. The rates of mortality at specific ages are used when the object is to compare the mortalities experienced in two or more distinct groups.

Surviving Fraction

Examples of survival curves of each breed taken from data represented in table 1 are given in figs. 1 and 2. These curves are based on the data for all pigs born and apparently capable of extra-uterine existence. This includes stillborn pigs, but not late fetal deaths.

The curves indicate the general nature of the early mortality experience in pigs. The high death losses that are incurred at birth and during the first few days of life are evidenced by the steep slope of the survival curves at those times. In general, about 50 percent of the total mortality to 154 days occurs at birth or in the first 48 hours of life. The mortality occurring after the first week of life represents only 20 percent of the total that takes place in the first 154 days.

The pattern of mortality in the two breeds is given in fig. 1. The curves show the same general trends for both breeds. The Durocs maintain a higher percent surviving than the Hampshires at all ages. Comparisons between survival curves must be undertaken cautiously, however. An early difference in the rate of mortality can separate the curves over their entire course, even though the mortality rates are alike at later ages. Since the survival curve must have a zero or negative slope, the level at any point is highly dependent on its previous position. Com-

Table 1. Life table based on 3,218 births in Duroc and Hampshire pigs from 1954 to 1960 at the Iowa Agricultural and Home Economics Experiment Station.

Age interval (days)	Daily rate of mortality per 1,000 alive q_x	Number living at beginning of the interval l_x	Number dying during the interval d_x
Dead at birth or in the first day	139.5	10,000	1,395
1 to 2	28.9	8,605	248
2 to 3	30.9	8,357	258
3 to 4	22.3	8,099	180
4 to 5	19.2	7,919	152
5 to 7	14.2	7,767	221
7 to 14	5.2	7,546	273
14 to 28	2.3	7,273	236
28 to 154	0.2	7,037	221
Survivors		6,816	

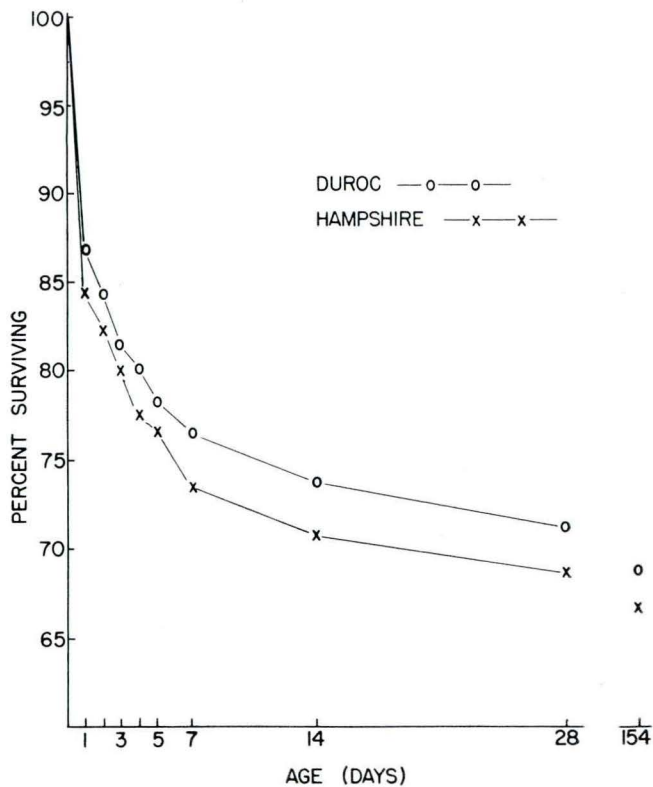


Fig. 1. Survival from birth to 154 days in the Duroc and Hampshire breeds.

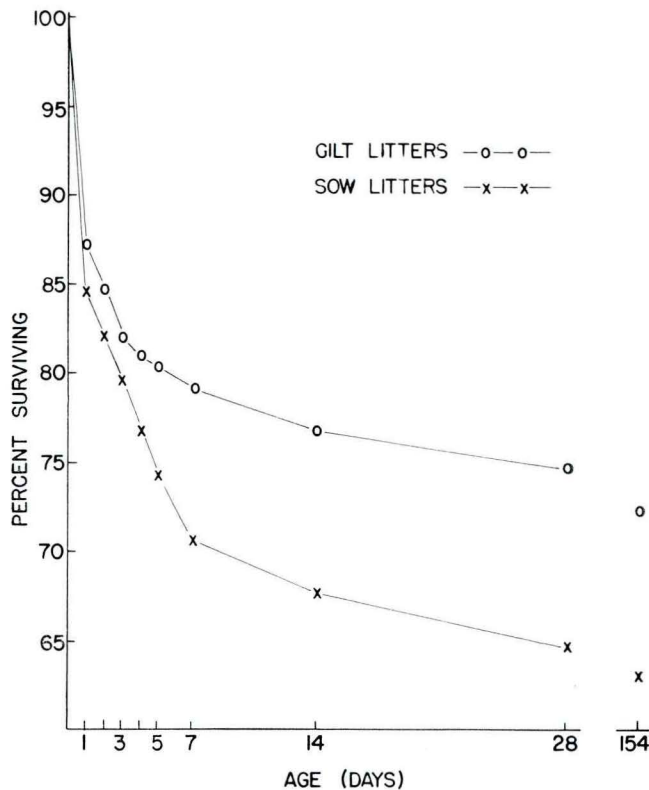


Fig. 2. Survival from birth to 154 days in gilt and sow litters.

parison between survival curves should be made on the basis of the relative slopes at different times. The slope of the curve, or the mortality rate, will be discussed more fully later.

The curves in fig. 2 represent the pattern of survival among individuals born in litters from two classes of females. The litters were grouped into those that represent the first litter produced by a female and into those that are from second or later litters produced by a female. For convenience these can be termed as gilt and sow litters, respectively. The relative frequency of these age classes was approximately the same in each breed so that breed differences were not considered.

These curves are more divergent than those of the two breeds (see fig. 1). The rate of survival in sow litters is considerably below that occurring in litters from the younger females. The slopes of these two curves are noticeably different in the period from 3 to 7 days, and this period produces the great disparity in the curves. In reference to this comparison it should be mentioned that while the older females lose a higher percentage of pigs they still wean slightly larger numbers than do the younger females. This occurs because the litter size at birth is larger among the older sows.

Rate of Mortality

The difficulties that arise in using survival curves for comparisons can be partly avoided by the use of mortality rates for this purpose. The rate of mortality is the slope of the survival curve as a fraction of the number living. These rates at specific ages do not necessarily depend on the rates at other ages. The instantaneous rate of change in the number living as a fraction of the total number alive is often called the force of mortality and is designated as u_x . Algebraically, the force of mortality at age x can be written in the following manner:

$$u_x = - \frac{d \ln l_x}{dx} = - \frac{1}{l_x} \cdot \frac{dl_x}{dx}$$

Since the slope of the survival curve is always negative, the minus sign is included so that the value of u_x is always a positive number.

The logarithm of age-specific death rate has been found to be approximately linear with time in human and other populations after sexual maturity. The relationship is expressed in the Gompertz equation as follows: $R_x = R_0 e^{ax}$ where R_x is the rate at time x and R_0 the hypothetical rate at $x=0$. The Gompertz coefficient, a , expresses the rate of exponential increase.

Just as the force of mortality can be shown to increase exponentially with time after maturity in humans, so the force of mortality can be shown to decrease approximately exponentially with the logarithm of time before maturity in pigs. To gain more precision in the estimates of mortality rates, the age intervals in table 1 were extended so that time between birth and 5 months was divided into three intervals. An approximation to the daily mortality rate

at the midpoint of the interval was obtained from the following expression:

$$q_{(x+t/2)} = \frac{2(1 - \frac{1}{x+t})}{a(\frac{1}{x+t} + \frac{1}{x})}$$

where t is the length of the interval. This total rate is merely the number dying during the interval divided by the average number living during the interval. The total rate is put on a daily basis by dividing by the number of days in the interval, symbolized by a . The three intervals were: (a) from birth through the first day, (b) from the first day through the sixth day and (c) from the seventh day through the 154th day. The mortality rate plotted against the logarithm of the time at the midpoint of these intervals is given in fig. 3 for each breed separately. An approximate linear relationship is evident.

Plots of mortality rate against the logarithm of time for each breed in fig. 3 show a small difference in the breeds at each point. The curve in fig. 1 showed a greater survival percentage among the Durocs at

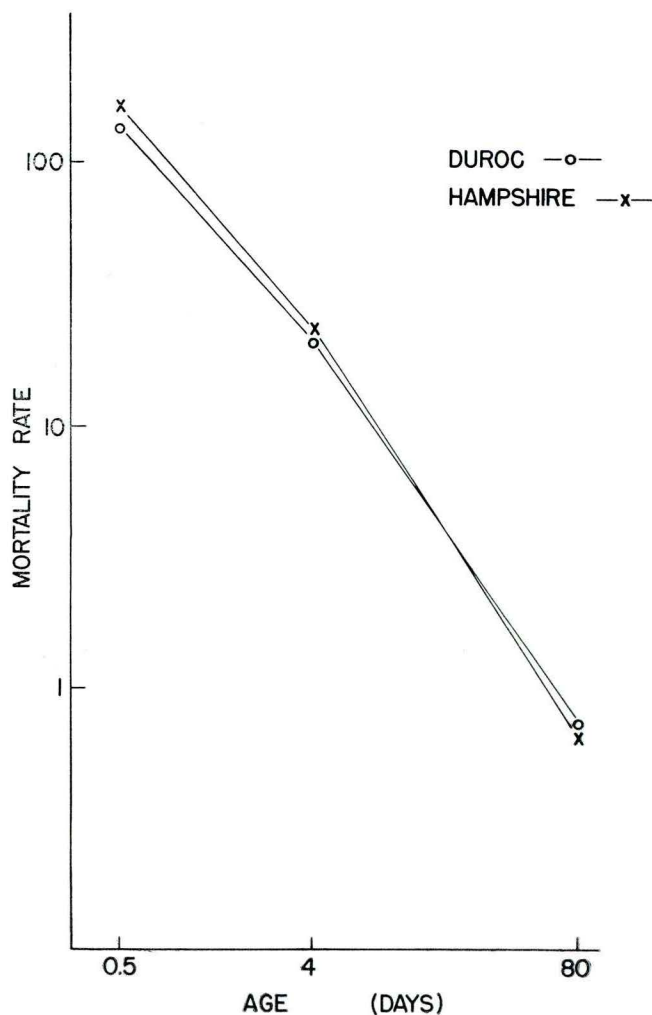


Fig. 3. Mortality rates per 1,000 population at specified ages for the Duroc and Hampshire breeds.

all ages. The plot in fig. 3, however, shows that the death rate was actually higher among the Durocs than it was among the Hampshires in the period after 1 week up to 154 days of age. This demonstrates the difficulty of using the survival curve in comparisons between groups and points out the advantages of the age-specific mortality rate.

The difference between the mortality in individuals from gilt and sow litters is shown in fig. 4. The sow-litter mortality is higher than that of gilt litters at all ages but most especially during the period from 1 to 7 days. This was also evident in the graph of survivorship in fig. 2. Another set of mortality rates is plotted in fig. 5 because of its general interest. The difference in mortality between the sexes is shown separately for each breed at the three age intervals. While the differences are not statistically significant, the Duroc males show a higher mortality than the Duroc females at each interval. The situation in the Hampshire breed is opposite

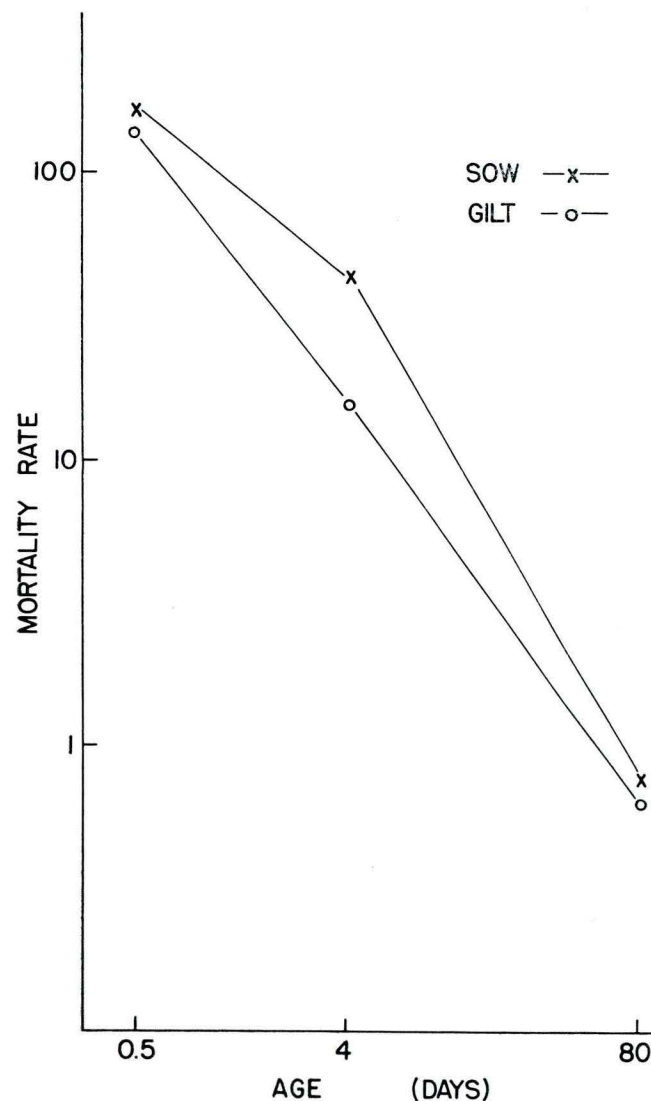


Fig. 4. Mortality rates per 1,000 population at specified ages for gilt and sow litters.

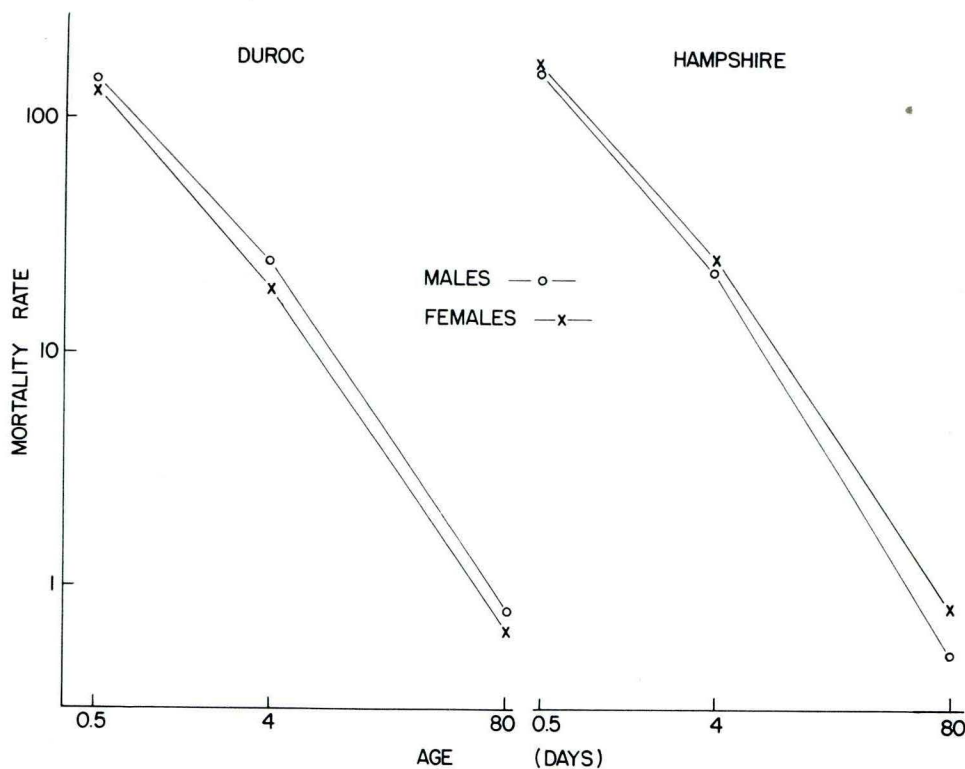


Fig. 5. Mortality rates per 1,000 population at specified ages for males and females in the Duroc and Hampshire breeds.

that of the Durocs, with females showing higher mortality than males in each interval.

Studies on mortality in other species, especially in humans, often employ estimates of the parameters in the Gompertz equation for comparisons between groups of individuals. For example, in mice a prolonged exposure to radiation increases the slope of the Gompertz plot. However, a single exposure does not change the slope but increases the intercept of the line at time zero by an amount proportional to dose (9).

One example will be presented to show how a similar use can be made of the linear relation between mortality rates and the logarithm of time in the early ages of pigs. The mortality rate occurring in each of three age intervals was calculated from all individuals born in gilt litters during the spring of 1957, 1958 and 1959. These seasons and age-of-dam classes were chosen since the total number of pigs were roughly comparable in each—207, 263 and 275 pigs, respectively. A plot of the logarithm of these values versus the logarithm of time at the midpoints of the intervals is given in fig. 6. The graph shows the three lines to be roughly parallel but differing in level. The characteristics of the lines in fig. 6 can be described quantitatively in terms of the regression coefficients (b) and the intercept (a). The values of these functions are given in table 2 with the standard errors derived from a pooled estimate of residual variation. From these limited data it appears that seasonal influences have little effect on the slope of these lines but considerable influence on the general level of mortality. The logarithms of days were coded by adding the logarithm of the first class, one-half day, to all values. This sets the first class at zero

and measures the others from this point. The intercept, a , therefore, is the logarithm of mortality rate at the midpoint of the first class.

The method clearly can be extended to cover other situations where the mortality rates in various groups of individuals are under study.

THE QUANTITATIVE MEASUREMENT OF MORTALITY

Need and Difficulties of Quantifying the Data

Descriptions and comparisons based on life-table functions are most useful in situations where a large number of individuals are contained in the groups under consideration. Individuals delineated by major environmental influences, breed classifications or sex differences are examples of such groups. The analysis of quantitative genetic variability, however, entails comparisons between much smaller groups. For example, differences between paternal half-sib and full-sib classes are commonly used in genetic investigations. Daily mortality rates within groups of such small size are determined only with high sampling errors since a relatively few individuals are exposed to the risks. The variability among individual animals within a litter is also useful in many analyses. Infor-

Table 2. Slopes and intercepts of lines relating the logarithm of the mortality rate and logarithm of time in three seasons.

Year	Slope (b)	Intercept (a)
1957	-1.094	4.13
1958	-1.063	4.76
1959	-1.128	5.18
Standard error	0.053	0.14

mation of this nature can only be obtained if a score or measurement is made on each individual.

Methods that use the percentage surviving to a particular age are common. In such cases the deaths are grouped together, regardless of whether they occur a few hours or a few months before the given age. Not all the information on the time of death is fully utilized. Also, the use of this information presents some serious problems.

The age at death has been shown to be distributed in an extremely skewed manner, departing radically from the normal distribution of many quantitative traits. The life span remains unknown for all individuals that are slaughtered as market animals. The biology of maturation suggests that the importance of differences in age at death varies with time; i. e. physiological and chronological age are not equivalent. The use of a logarithmic time scale, as in the analysis of the mortality rate, is one method of compensating for this influence. However, a transforma-

tion that would correct simultaneously for all these difficulties is needed. One possible solution was suggested by Kincaid (5) and will form the basis of the following method.

A Method of Transforming the Length of Life to a Normally Distributed Quantitative Variable

A technique for obtaining an approximate normal distribution in discrete data is to transform the observations to normally distributed scores. The results are first ranked and divided into several groups. The individuals in a given group receive a score corresponding to the mean of that percentage in a normal distribution. The probit transformation, used extensively to study the relationship between dose and mortality in toxicology investigations is based on similar principles. The probit for a given percentage is equivalent to the normal deviate exceeding this percentage in the population. The form of the distribution is not critical when the main interest is estimation of parameters. The usual tests of significance, however, depend on a knowledge of the distribution.

The same approach can be made to the results of early mortality in pigs. The individuals dying within a given period would receive a score corresponding to the normal deviate representing the mean of that group in a normal distribution. For example, if the survivors at slaughter age represent 70 percent of the population, then they would receive a score equivalent to the mean of the upper 70 percent of a standard normal distribution. Likewise, the same treatment would be made for the other age groups down to those dead at birth, which would be represented by the mean of the lower portion of the normal curve they represented. Figure 7 illustrates the distribution of deaths that was presented in table 1. The mean of the areas representing the various lengths of life would be the basis of scores assigned to individuals in these groups.

The basis for such a transformation is an assumption that the processes leading to death are normally distributed along some scale. The scale evidently is not days nor any simple transformation of days. If, however, the variation in a measured quantity is due to a large number of small, additive and independent effects, then its distribution is near normal. The factors causing death can reasonably be considered to conform to this requirement.

The work of Kincaid (5) attempted to include all the mortality that occurred after conception. Some assumptions about the extent of prenatal mortality were made since direct observation was not possible, especially in the early periods. The value assigned to the prenatal mortality influences the relationship among the scores at other ages. Furthermore, since this mortality is not observed, it becomes essentially constant for all groups. Rather than attempt to deal with the problems raised by such an assumption, it was felt that the mortality occurring at or after birth was sufficiently distinct from that occurring prenatally to warrant entirely separate treatment. The present study, therefore, makes no attempt to include the

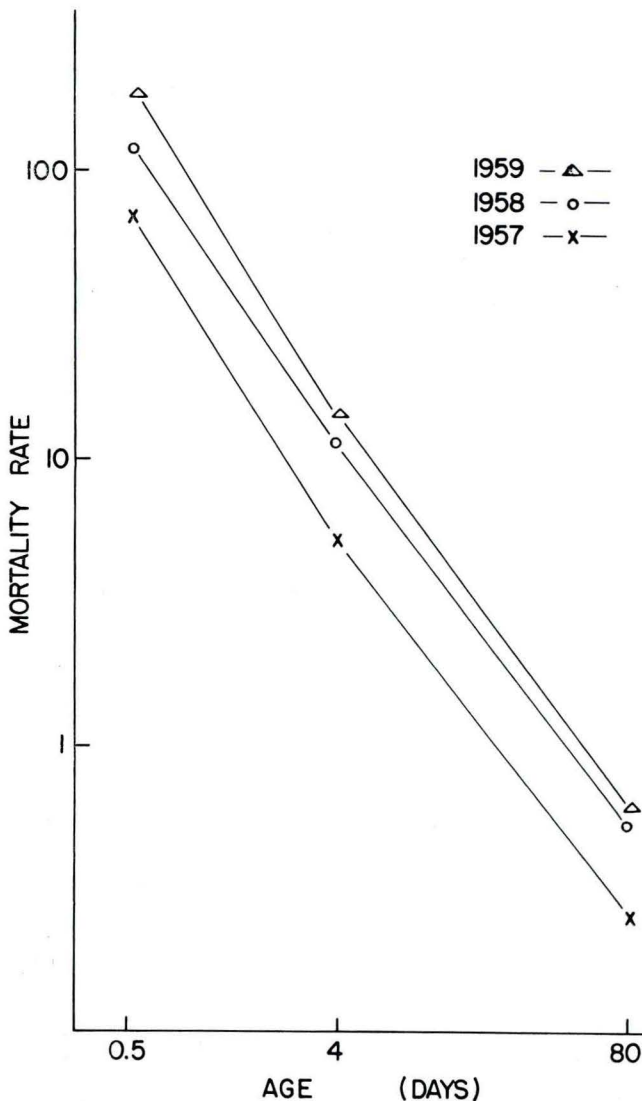


Fig. 6. Mortality rates per 1,000 population at specified ages for individuals in gilt litters during the spring seasons of 1957, 1958 and 1959.

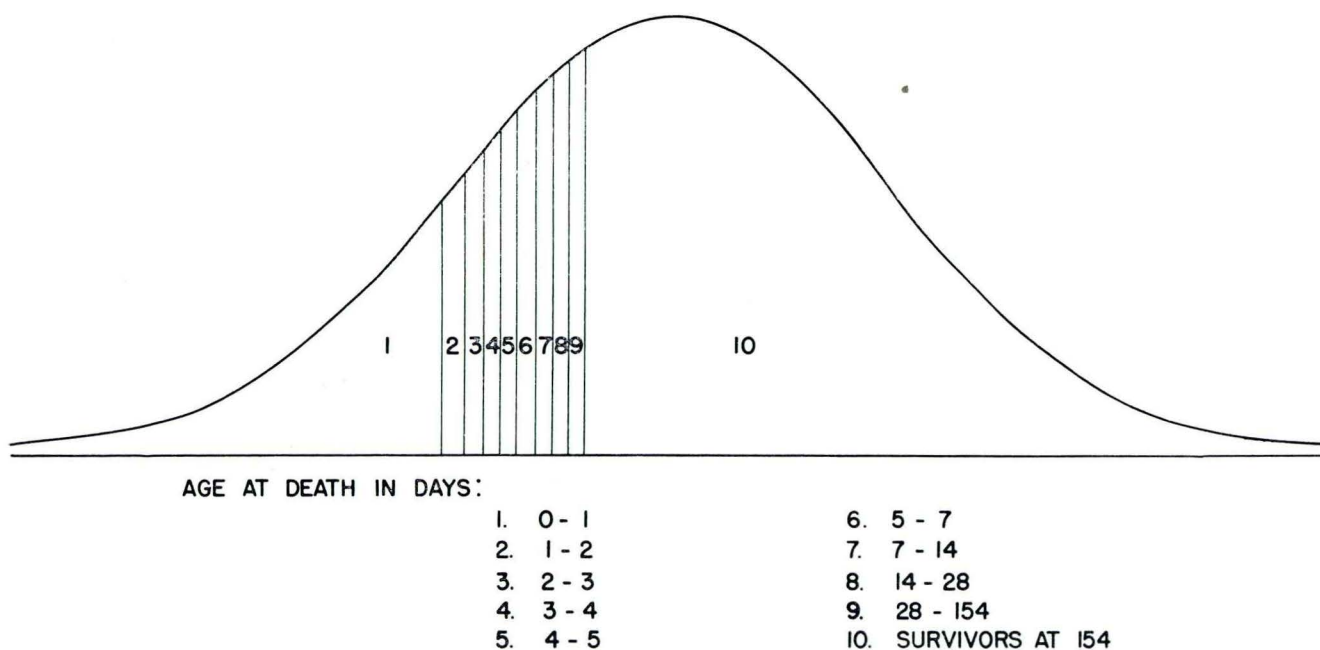


Fig. 7. Portions of the normal curve represented by the age-at-death classes.

prenatal mortality in developing scores based on the normal distribution of deaths after birth.

The mean of the areas of the normal curve represented in fig. 7 in terms of standard normal deviates can be obtained from tabulated values of the normal distribution. For example, the mean, \bar{x}_{12} , of the area bounded by ordinates z_1 and z_2 that represents a fraction, b , of the total population is given by:

$$\bar{x}_{12} = \frac{z_1 - z_2}{b}$$

The mean values for the classes shown in fig. 7 are given in table 3. The last column in this table gives the scores assigned to each age interval. These values were obtained by setting the value of the surviving class at zero and using the positive difference between the mean of this class and the other classes in the table. Each individual in a class is assigned the score for that class. The scores obtained are based on the normal distribution but the groupings, especially in the end classes, are so coarse that the values remain discretely distributed. The transformation improves the classification from one allowing only two classes, alive or dead by a given age, to one that segregates the data into 10 classes. The

Table 3. Scores based on normal deviates representing the means for the classes of age at death.

Age interval (days)	Percentage surviving at beginning of interval	Mean of the class in terms of normal deviates	Normal score
Dead at birth or in the first day	100.00	-1.5936	2.118
1 to 2	86.05	-1.0252	1.549
2 to 3	83.57	-0.9267	1.451
3 to 4	80.99	-0.8445	1.369
4 to 5	79.19	-0.7869	1.311
5 to 7	77.67	-0.7250	1.249
7 to 14	75.46	-0.6462	1.170
14 to 28	72.73	-0.5697	1.094
28 to 154	70.73	-0.5206	1.045
Survivors	68.16	+0.5241	0.000

resulting scores, however, cannot be considered as normally distributed variables, and such rules as having class intervals less than one-fourth of the standard deviation have not been satisfied. Nevertheless, the transformation does quantify the data based on the assumption of an underlying normal distribution of deaths and can be used for more refined analyses of mortality.

Analysis of Mortality Scores

The individual scores derived from the transformation to normal deviates can be used in the same manner as any other quantitative variable in the analysis of variance. The results of an analysis of the data used to derive the scores are given in table 4. The analysis was carried out within breed, season and age-of-dam classes. The value of the correlation among the mortality scores of individuals within paternal half-sib groups was 0.05. The heritability of individual length of life based on this correlation is 0.20 if the average relationship within the sire groups is assumed to be 0.25. The correlation among the mortality scores of litter mates was over twice that among the paternal half-sibs, indicating the important in-

Table 4. Analysis of length of life after transforming days in a normally distributed score.

Source	Degrees of freedom	Mean squares	Expectations of mean squares
Within Breed, Season			
Age-of-Dam Classes	3,172		
Sires	80	1.9456	E+9.395 D+22.115 S
Dams within Sires	219	1.1886	E+9.212 D
Progeny with Dams	2,873	0.5512	E
Correlation among paternal half-sibs			
S/T = 0.05			
Correlation among full-sibs			
D/T = 0.11			
E = 0.5512			
D = 0.0692			
S = 0.0336			
T = E + D + S = 0.6540			

fluence of the common litter environment on mortality. The relative magnitude of such quantities as the genic variance and the variance arising from common litter environments are useful in many areas of animal breeding research. The transformation of the length of life allows the study of these values. The extension of the analysis to include the relationship between length of life and other variables, such as birth weight or litter size, is clearly possible.

DISCUSSION

The relationship between the rate of mortality and age in humans has stimulated research on a general quantitative theory of aging. The object has been to relate the observed facts about the mortality rates with the knowledge of the characteristic biological changes that occur with time. Some of the theories rest on arguments which describe the decline with time of the homeostatic mechanisms (7). Assuming certain distributions of internal fluctuations and external challenges, the exponential increase in mortality is predicted as well as other characteristics of the Gompertz plot. The arguments are based almost exclusively on the period from 35 to 80 years in humans where the Gompertz law is well fitted.

The situation before sexual maturity in most species including man, however, presents a different pattern, with mortality rates declining as the individuals mature. Possibly the decline in mortality before maturity might be considered as a converse of the pattern after maturity. Thus, this decline in mortality would be ascribed to the increased control of the homeostatic mechanisms. The nature of this early mortality might help to explain the mortality in later life. However, the two distinctly different patterns of mortality, before and after puberty, have probably evolved through two entirely different sets of selective forces and, therefore, may not be closely related phenomena.

The plot of the logarithm of mortality rates at the midpoints of three time intervals in the early post-natal period was shown to be approximately linear with the logarithm of days. The use of only three intervals does not allow deviations from linearity to be detected easily. However, the linear trend is still evident if the rates are calculated and plotted at the midpoints of each interval listed in table 1. Figure 8 shows this plot and indicates that some of the deviations from linearity warrant further investigation to determine whether they arise from mere chance fluctuations or other causes. For example, the rate during the second 24 hours of life is actually lower

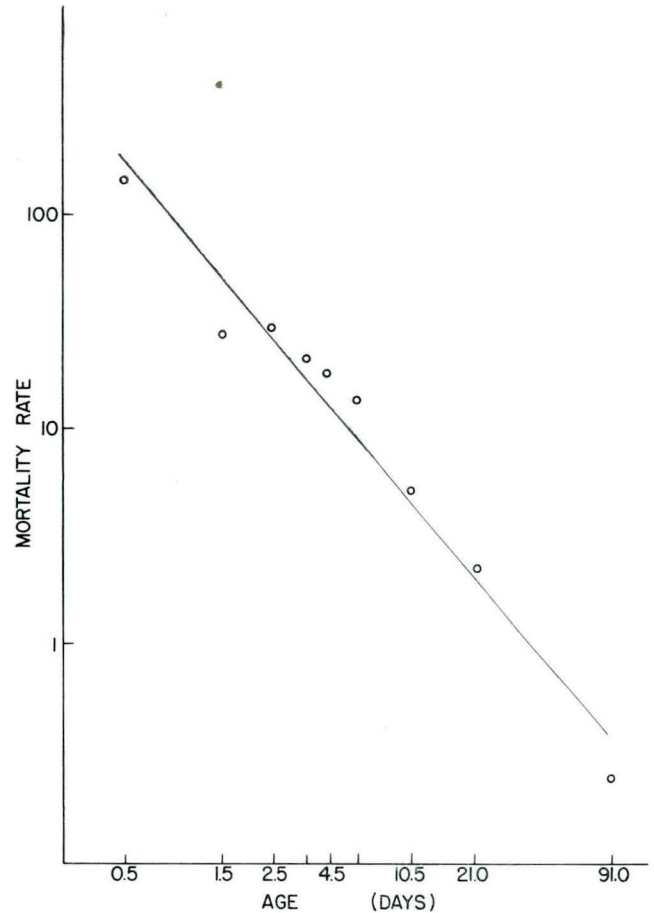


Fig. 8. Mortality rates per 1,000 populations at specified ages with the line fitted to the points to indicate the linear trend.

than that in the third 24-hour period. Possibly this indicates that pigs with sufficient strength to survive birth and the period immediately following can live at least 48 hours even in adverse environmental circumstances.

The Gompertz plot of human adult mortality is known to deviate from linearity, especially at ages less than 30 and more than 80 years. The deviations, while important, do not detract greatly from the usefulness of the Gompertz equation in human studies. The deviations from linearity noted in the plot of early mortality in pigs likewise may be caused by other important factors, but the linear trend appears to be sufficiently marked to be useful in analyses.

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