DISSERTATION

AN APPLICATION OF SURVIVAL ANALYSIS TO THE GENETIC EVALUATION OF REPRODUCTIVE LIFE OF BEEF FEMALES

Submitted by

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In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2000

COLORADO STATE UNIVERSITY

September 22, 2000

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY LAUREN REIDEL HYDE ENTITLED AN APPLICATION OF SURVIVAL ANALYSIS TO THE GENETIC EVALUATION OF REPRODUCTIVE LIFE OF BEEF FEMALES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

AN APPLICATION OF SURVIVAL ANALYSIS TO THE GENETIC EVALUATION OF REPRODUCTIVE LIFE OF BEEF FEMALES

The primary objective of this study was to develop methodology for animal model survival analysis of reproductive life (**RL**) in beef females. Other objectives were: 1) to determine whether survival analysis of RL results in improved accuracy of prediction over threshold analysis of stayability (**ST**), 2) to investigate the effects of right censoring on parameter estimation and genetic prediction of RL, and 3) to determine whether animal model survival analysis is possible for large-scale genetic evaluation of RL using field data from a beef cattle breed association.

To meet the primary objective, I first developed a computer simulation program that generated RL data for validating and testing the methodology. Reproductive life was defined as the length of time from entering the herd as a replacement female to being culled for reproductive failure. The data were simulated from a Weibull model in a factorial arrangement consisting of two levels of true heritability ($\mathbf{h^2}$) for underlying RL (0.05 and 0.20) and three levels of the Weibull shape parameter (ρ) (0.6, 0.8, and 1.0) with five replicates per cell. Levels of ρ were based on results of three studies reported in the literature. To estimate h^2 for the 30 simulated data sets, I adapted the *maximum a posteriori* Method R (**MAP R**) procedure for threshold analysis of categorical traits by substituting a

Newton-Raphson algorithm appropriate to a Weibull frailty model. Log-frailties were assumed to be multivariate normal with mean **0** and variance $\sigma_a^2\mathbf{A}$, where σ_a^2 was the additive direct genetic variance of RL on the underlying natural logarithmic scale and **A** was Wright's numerator relationship matrix for all animals. In addition, all data were assumed to be uncensored. Twenty h^2 estimates were obtained from each data set, and the results were pooled within each cell. Pooled median h^2 estimates for underlying RL were consistently lower than their true values, which may have resulted from natural selection in the simulated data. Despite the low h^2 estimates, correlations between estimated breeding values (**EBV**) computed using estimated and true h^2 were very high (greater than 0.98), suggesting that the magnitude of h^2 used to evaluate RL does not affect ranking of individual animals.

Analyses of ST were conducted using 10 of the data sets simulated previously with true h^2 of 0.05 and 0.20 and $\rho = 0.8$. Twenty heritability estimates were obtained from each data set using the threshold model MAP R procedure, and the h^2 estimates were pooled within cell. The pooled median h^2 estimates for ST on the underlying liability scale were larger than those for underlying RL (0.0525 vs 0.0378 from data with true h^2 of 0.05, and 0.1608 vs 0.1431 from data with true h^2 of 0.20). Correlations between animal EBV for underlying ST and RL were strongly negative (-0.7796 and -0.7938 for true h^2 of 0.05 and 0.20, respectively), and genetic trends for the two traits were nearly mirror images of one another, suggesting that underlying ST and RL have a high and favorable genetic correlation. However, average accuracies of prediction for RL were approximately 0.10 and 0.15 greater than those for ST among non-foundation animals simulated with true h^2 of 0.05 and 0.20, respectively.

To determine the effects of censoring on heritability estimation and genetic prediction of RL, I modified the simulation program by randomly censoring females based on an input level of censoring (10, 40, and 70%) and then by randomly truncating their phenotypic RL to obtain censored observations. Three data sets were simulated for each level of censoring, both levels of true h^2, and $\rho = 0.8$. The amount of censoring had no apparent effect on estimates of h^2 or breeding value. Heritability estimates and genetic predictions were similar among all levels of censoring, including that of no censoring. Average accuracy decreased more rapidly as the level of censoring increased. Average accuracies obtained from uncensored data were about 0.10 higher for non-foundation animals than those from 70% censored data, even though the number of animals increased with the level of censoring.

A genetic evaluation of RL was conducted for the Red Angus Association of America (**RAAA**) using cow disposal information collected through its Total Herd Reporting (**THR**) program. Reproductive life was defined as the length of time in yr from when a cow produced her first calf as a two-yr-old to when she was culled for infertility or censored, whichever came first. The RAAA provided disposal records on 113,943 dams, which were combined with 670,342 calving records on 176,512 dams from the ST evaluation conducted in January, 2000. The data were edited to retain only those cows who calved annually since age two and who had the opportunity to participate in THR either by calving or by being culled in 1995 and later. The cows were assigned to contemporary groups using the same contemporary group designations from the ST evaluation. Further editing eliminated contemporary groups in which all observations were censored or in which there was no variation among observations. The final data set consisted of records on 8,504 dams in 912

contemporary groups, of which 69.76% were censored. The median h^2 estimate was 0.0532, in contrast to 0.10 used in the ST evaluation. Genetic trends in EBV for underlying RL and ST were nearly mirror images of one another, as for trends obtained from simulated data. Correlations between EBV for RL and ST were moderately high and favorable (-0.5322 for all animals and -0.4605 for sires). When ST was evaluated for only those animals in the RL analysis, average accuracies of prediction were lower for ST than for RL (0.1340 vs 0.1816).

The results of this study show that animal model survival analysis is feasible, even with large data sets and large amounts of censoring, and yields higher accuracy of prediction than threshold analysis of similar traits.

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ACKNOWLEDGMENTS

Graduate school has been, to say the least, an intellectual experience. It has also been one of personal growth. After nearly six years of being pushed past my limits, I have gained more confidence in myself. I once thought I couldn't, but now I know I can.

Although several people have inspired me along the way, two of the more influential persons are my advisers, Bruce Golden and Rick Bourdon. Without them, I don't think I'd be where I am today.

Thank you, Bruce, for giving me another chance. I didn't think I had it in me, but perhaps you knew I did. I'd also like to thank you for helping me realize my creative potential. I used to believe that creativity was synonymous with artistic talent, but you taught me otherwise.

Rick, as you retire from academia, I want you to know that your teaching made a real difference to the life of at least one person. Your conceptual approach to animal breeding stimulated my curiosity, and your kindness and understanding through dark times gave me the courage I needed to persevere.

I'd also like to thank my other two committee members, Jack Whittier and Phil Chapman. Jack, I admire your patience in getting through the mathematics of this project, and I appreciate your practical questions and comments regarding its relevance. Phil, you showed me that no one knows everything. By the way, a *P*-value is the probability of getting

a test statistic as extreme or more extreme than the observed value given that the null hypothesis is true.

A special thanks goes to Patrick, John, Fahad, and especially Sam. It becomes more difficult to make friends as you get older, but all of you have become dear to my heart. I think of you as my brothers, and I'll miss you when I'm gone. Good-bye, my friends.

"Curiosity is one of the permanent and certain characteristics of a vigorous mind."

—Samuel Johnson

DEDICATION

Don, how do I begin to express my gratitude for all that you've done throughout our life together? You've been with me every step of the way, and I consider this accomplishment to be as much yours as it is mine. With all my love, I dedicate this dissertation to you.

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CHAPTER 1

INTRODUCTION

Reproductive efficiency is considered the most important economic factor in beef cattle production (Taylor, 1994). According to Andersen (1999), successful reproductive management involves producing: 1) yearling heifers that cycle and become pregnant early during their first breeding season, 2) two-yr-old cows that breed back early during their first lactation, and 3) mature cows that calve annually after fixed breeding seasons of limited duration.

Recent developments in genetic prediction methodology have resulted in the production of selection tools to genetically improve these aspects of female reproduction in the form of expected progeny differences (**EPD**) for heifer pregnancy, rebreeding, and stayability. Production of these EPD involves defining the traits on a binary scale and analyzing the binary measurements using a threshold model. Threshold models are relatively easy to apply and have been used successfully with large amounts of field data from beef cattle breed associations.

Consider sustained fertility as only one aspect of female reproduction. Genetic improvement in sustained fertility would allow producers to minimize costs associated with developing replacement heifers and to recover development and maintenance costs of mature cows through annual calf production. Stayability, defined for national cattle evaluation as the probability that a cow will remain in the herd until six years of age or beyond given that

she calved prior to age six, is a measure of sustained fertility, but only when reproductive failure is the primary reason for culling cows (Snelling, 1998). Stayability EPD may also represent genetic differences in other factors that contribute to reasons why cows are either retained or disposed of by beef cattle producers. In addition, compared to other traits, considerably more time is required to collect data for accurate evaluations of stayability (Andersen, 1999).

As an alternative to stayability EPD, one approach is to define sustained fertility on a continuous time scale and analyze the measurements using a technique called survival analysis. Survival analysis has been used in the dairy industry for several years in genetic evaluations of length of female productive life. A key feature of survival analysis is that records on animals still in the herd at the time of evaluation may be included. These records, called censored records, are not complete but do provide some information as to the lower bounds of animals' productive lives.

Survival analysis may improve accuracy of genetic predictions for sustained fertility (Snelling, 1998). However, the methodology requires detailed culling information not usually available for beef cattle populations and involves complex models that may not be suitable for large data sets. On the other hand, because of the growing interest among beef breed associations toward whole herd, or inventory-based, reporting systems, data required for survival analysis of sustained fertility may soon be available for many beef breeds. In addition, computer technology has advanced to such a degree that processing vast amounts of data, even with complex models, is possible. Therefore, further investigation of survival

analysis is needed to determine whether it is feasible for genetic evaluation in the beef industry.

Objectives

The primary objective of this study was to develop methodology for animal model survival analysis of sustained fertility in beef females. Other objectives were: 1) to determine whether survival analysis of sustained fertility results in improved accuracy of prediction over threshold analysis of stayability, 2) to investigate the effects of censoring on parameter estimation and genetic prediction of sustained fertility, and 3) to determine whether animal model survival analysis is feasible for large-scale genetic evaluation of sustained fertility based on field data from a beef cattle breed association.

CHAPTER 2

REVIEW OF LITERATURE

Introduction to Survival Analysis

Some traits of economic importance in livestock species are best measured by the length of time between two events. For example, cow-calf producers may want to minimize replacement costs by delaying the number of years it takes for females entering the breeding herd to be culled for infertility or other reasons. Other beef cattle producers may want to reduce feed costs by shortening the number of days it takes for slaughter cattle entering the feedlot to attain a prespecified fat thickness. Dairy producers are typically interested in maximizing the number of months from the beginning of the first lactation to the last test day in their cows. For horse breeders, increasing the number of years a horse participates in racing, jumping, or another performance event may be important to offset the costs of training.

Observations on traits measured in units of time are examples of survival data, and the statistical treatment typically used to analyze survival data is called survival analysis. The techniques of survival analysis are described in several textbooks (e.g., Kalbfleisch and Prentice, 1980; Cox and Oakes, 1984; Klein and Moeschberger, 1997). In addition, Ducrocq (1999a) provides an introduction to survival analysis with an emphasis on applications to animal breeding.

Probability Functions

Let T be a nonnegative random variable, either discrete or continuous, that represents the failure time of an individual from a homogeneous population. The probability distribution of T may be specified by several different, but interrelated, functions. Four functions particularly useful in characterizing survival data are the survival function, $S(t)$, the probability density function, $f(t)$, the hazard function, $h(t)$, and the expected residual life function, $r(t)$ (Klein, 1996).

Survival Function. The survival function is defined for both continuous and discrete T as the probability that an individual survives to or beyond time t. Mathematically, $S(t) = P(T \geq t)$, where $0 \leq t < \infty$. The survival function is nonincreasing with $S(0) = 1$ and $\lim_{t \to \infty} S(t) = 0$. If T is continuous, then $S(t)$ is a continuous monotone decreasing function and is the complement of the cumulative distribution function, $F(t)$, where $F(t) = P(T \leq t) = 1 - S(t)$. If T is discrete, then $S(t)$ is a nonincreasing left-continuous step function.

Probability Density (Mass) Function. The probability density (mass) function for continuous (discrete) T describes the unconditional probability of failure occurring at time t. The probability density function is defined by $f(t) = \lim_{\Delta t \to 0^+} \frac{P(t \leq T < t + \Delta t)}{\Delta t} = F'(t) = -S'(t)$, where $f(t) \geq 0$ and $\int_0^\infty f(t)\,dt = 1$. Note that the relationship $f(t) = -S'(t)$ implies that $S(t) = \int_t^\infty f(u)\,du$. The probability mass function is given by $f(t_j) = P(T = t_j)$, where $t_j \in t_1 < t_2 < \cdots$. Analogous to its relationship with $f(t)$ in the continuous case, $S(t) = \sum_{t_j \geq t} f(t_j)$ in the discrete case.

Hazard Function. The hazard function specifies the instantaneous failure rate, or the probability that an individual experiences failure in the instant immediately following time t. It is the conditional probability of failure at time t given survival to t. If T is a continuous random variable, then $h(t) = \lim_{\Delta t \to 0^+} \frac{P(t \le T < t + \Delta t \mid T \ge t)}{\Delta t} = \frac{f(t)}{S(t)} = -\frac{d}{dt} \ln S(t)$. If T is discrete, then $h(t_j) = P(T = t_j \mid T \ge t_j) = f(t_j)/S(t_j)$, where $t_j \in t_1 < t_2 < \cdots$.

The hazard function is always nonnegative, but its shape may vary. In general, the hazard function may be increasing, decreasing, constant, bathtub-shaped, or hump-shaped (Klein, 1996). Increasing hazard rates occur when there is a natural aging or wearing out in the population. Decreasing hazard rates are less common but may arise when there is an early possibility of failure, for example, after an organ transplant. Bathtub-shaped hazards may be appropriate in populations followed from birth, where early deaths resulting from infant diseases are followed by a period of stabilization and then an increase in deaths from natural aging. Hump-shaped hazards are often used in analyzing survival times after surgery, where there is an initial increase in risk due to complications from the procedure followed by a steady decrease in risk as the patient recovers.

The hazard function is fundamental to survival analysis (Smith and Allaire, 1986; Klein, 1996; Ducrocq, 1999a). It is usually more informative about the underlying mechanism of failure than the survival function or the probability density (mass) function (Klein and Moeschberger, 1997). In addition, hazard functions are often more convenient to apply than the other probability functions when there are censored data or different types of censoring mechanisms (Cox and Oakes, 1984).

Expected Residual Life Function. Another function that may be useful in some applications (Kalbfleisch and Prentice, 1980) is the expected residual life function, $r(t)$, which measures the mean remaining lifetime at time t. For continuous T, $r(t) = E[T - t | T \geq t] = \int_t^{\infty} \frac{S(u)du}{S(t)}$, where $r(0) = E[T] = \int_0^{\infty} S(u)du = \mu$. It can be shown using integration by parts and other algebraic manipulations that $S(t) = \frac{r(0)}{r(t)} \exp[-\int_0^t \frac{du}{r(u)}]$, which implies that $r(t)$ uniquely determines a continuous survival distribution with a finite mean (Kalbfleisch and Prentice, 1980).

These functions are related in such a way that if any one of the functions is known, the other three can be uniquely determined (Klein, 1996). This relationship is important in terms of modeling survival data because one function may be easier or more convenient to apply than another (Ducrocq, 1997). In addition, the appropriate function to use may depend on available data (Kalbfleisch and Prentice, 1980) or on the types of estimates and inferences required by the study (Klein and Moeschberger, 1997).

Continuous Parametric Distributions

Usually the probability distribution of the random variable T is not known, but in many applications of survival analysis, certain parametric distributions are assumed not only because of theoretical considerations regarding biological and physical phenomenon but also because of their mathematical simplicity and popularity within a given field (Klein and Moeschberger, 1997; Ducrocq, 1999a). Some of the more common continuous distributions are discussed below.

Exponential. Because of its mathematical simplicity and other desirable properties, the one-parameter exponential distribution is important to the understanding and

development of survival analysis techniques (Klein and Moeschberger, 1997). The probability density function for the exponential distribution is $f(t) = \lambda \exp(-\lambda t)$, where $\lambda > 0$ and $t \geq 0$. The corresponding survival and hazard functions are $S(t) = \exp(-\lambda t)$ and $h(t) = \lambda$, respectively. These three functions are shown graphically in Figure 2.1 for $\lambda = 0.5$.

One of the properties of the exponential distribution is its lack of memory, defined mathematically as $P(T \geq t+z \mid T \geq t) = P(T \geq z)$. This property is reflected in constant values over time for both the hazard rate and the expected residual life and leads to the interpretation that survival to a given point in time has no effect on the probability of failure in the next instant or over an extended period of time.

Another property of the exponential distribution is that the random variable T may be transformed into a random variable Y having a simple linear model representation. The linear expression for Y is obtained by transforming $T = e^{Y}$ to get the density function $f(y) = \exp(y + \ln\lambda - e^{y+\ln\lambda})$, where $-\infty < y < \infty$, and showing that $Y = \ln T$ is equivalent to $Y = \alpha + W$, where $\alpha = -\ln\lambda$ and W has a minimum extreme value distribution.

The minimum extreme value distribution has probability density function $f(w) = \exp(w - e^{w})$ for $-\infty < w < \infty$. It is unimodal with mean $-\gamma$, where $\gamma \approx 0.5772$ is Euler's constant, and variance $\pi^2/6$ (Figure 2.2). The minimum extreme value distribution is commonly used as the error distribution in the classical linear regression approach to modeling the effects of covariates on survival (Klein and Moeschberger, 1997).

Although the exponential distribution is theoretically important, it has practical limitations. For example, its constant hazard rate may be too restrictive for most health and industrial applications (Klein and Moeschberger, 1997). However, it has been demonstrated

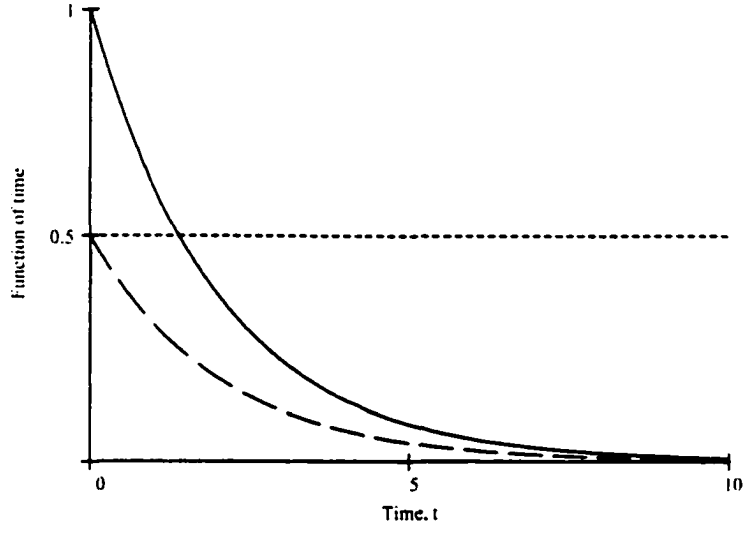

Figure 2.1. The survival (——), probability density (– – –), and hazard (-----) functions of an exponential distribution with parameter $\lambda = 0.5$.

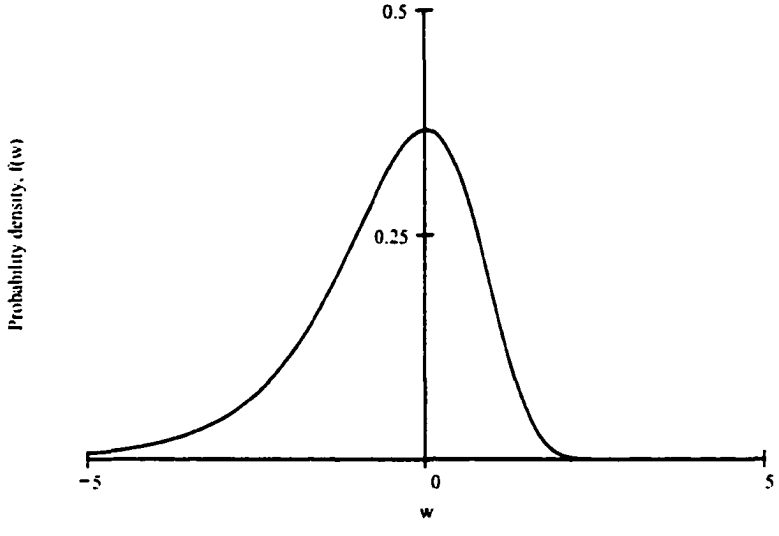

Figure 2.2. The probability density function of the minimum extreme value distribution.

to closely describe the length of time from the first to the second myocardial infarction in humans and the time from diagnosis to death for some cancers (Afifi and Clark, 1990).

Weibull. The Weibull distribution is a two-parameter generalization of the exponential that allows for flexibility in modeling hazard rates that are dependent on time (Klein and Moeschberger, 1997). The Weibull probability density function is $f(t) = \lambda\rho(\lambda t)^{\rho-1}\exp[-(\lambda t)^{\rho}]$, defined for $t \geq 0$, $\lambda > 0$, and $\rho > 0$, where λ is referred to as the scale parameter and ρ as the shape parameter. The corresponding survival function is given by $S(t) = \exp[-(\lambda t)^{\rho}]$. Figures 2.3 and 2.4 show how the value of ρ affects the shape of $f(t)$ and $S(t)$ for $\lambda = 1$.

The hazard function for the Weibull distribution is given by $h(t) = \lambda\rho(\lambda t)^{\rho-1}$. When $\rho = 1$, the Weibull distribution simplifies to the exponential, and thus, the hazard function is constant over time (i.e., $h(t) = \lambda$). For $\rho > 1$, the hazard rate increases over time, and for $\rho < 1$, the rate decreases over time (Figure 2.5).

As for exponentially distributed T, a random variable with a Weibull distribution may be transformed into a random variable with simple linear model form. Using a similar procedure to that described above, the linear expression for Y is obtained by transforming $T = e^{Y}$ to get the density function $f(y) = \rho\exp[\rho(y + \ln\lambda) - e^{\rho(y+\ln\lambda)}]$, where $-\infty < y < \infty$, and showing that $Y = \ln T$ is equivalent to $Y = \alpha + \sigma W$, where $\alpha = -\ln\lambda$, $\sigma = \rho^{-1}$, and W has a minimum extreme value distribution.

The Weibull distribution has been widely used in both industrial and biomedical applications of survival analysis (Klein and Moeschberger, 1997). The popularity of the Weibull distribution for empirical work stems from the simplicity of its probability functions

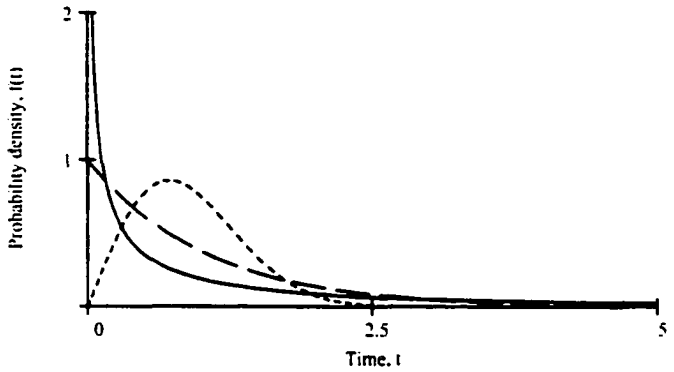

Figure 2.3. Probability density functions of Weibull distributions with parameters $\lambda = 1$ and $\rho = 0.5$ (—·—), $\rho = 1$ (– – –), and $\rho = 2$ (-----).

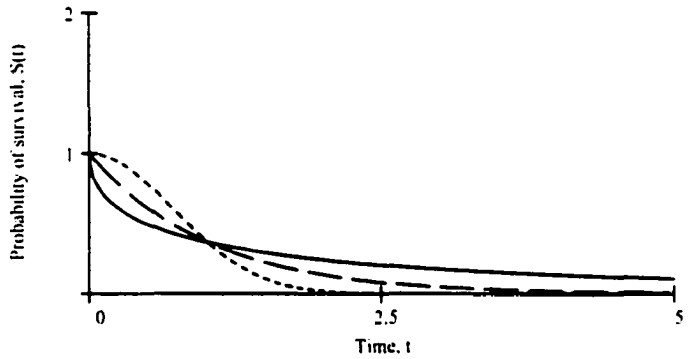

Figure 2.4. Survival functions of Weibull distributions with parameters $\lambda = 1$ and $\rho = 0.5$ (—·—), $\rho = 1$ (– – –), and $\rho = 2$ (-----).

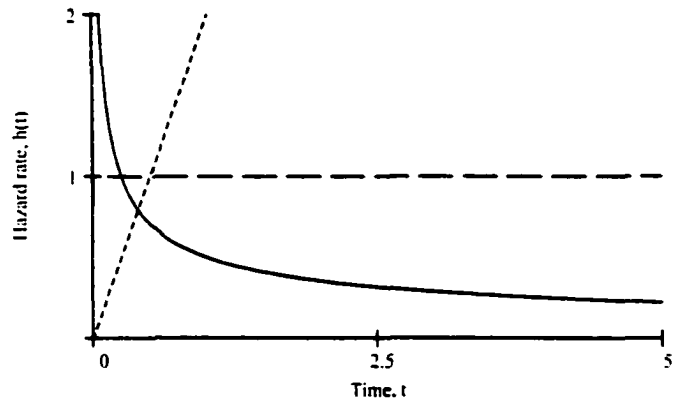

Figure 2.5. Hazard functions of Weibull distributions with parameters $\lambda = 1$ and $\rho = 0.5$ (—·—), $\rho = 1$ (– – –), and $\rho = 2$ (-----).

(Cox and Oakes, 1984). In addition, the Weibull and the exponential are the only distributions whose regression models may be classified as both proportional hazards and accelerated failure time models (Kalbfleisch and Prentice, 1980; Ducrocq, 1997; Ducrocq, 1999a).

Gamma. Like the Weibull distribution, the gamma distribution is a two-parameter generalization of the exponential. However, it is not as mathematically tractable as the Weibull and is rarely used in survival analysis.

The density function of the gamma distribution is given by $f(t) = \frac{\lambda^{\beta} t^{\beta-1} \exp(-\lambda t)}{\Gamma(\beta)}$, where $t \geq 0$, $\lambda > 0$, and $\beta > 0$. Here, $\Gamma(.)$ denotes the gamma function, λ represents the scale parameter, and β is the shape parameter. The survival function is $S(t) = 1 - I(\lambda x, \beta)$, where $I(.)$ denotes the incomplete gamma function. The hazard function, $h(t) = \frac{f(t)}{S(t)}$, is constant for $\beta = 1$, monotone increasing with $h(0) = 0$ and $\lim_{t \to \infty} h(t) = \lambda$ for $\beta > 1$, and monotone decreasing with $h(0) = \infty$ and $\lim_{t \to \infty} h(t) = \lambda$ for $\beta < 1$ (Figure 2.6).

The gamma distribution is equivalent to the exponential distribution for $\beta = 1$ and the Erlangian distribution for $\beta = k$, where k is an integer (Cox and Oakes, 1984). In addition, the gamma approaches the normal distribution as $\beta \to \infty$ and gives a chi-square distribution with $\nu = 2\beta$ degrees of freedom when β is an integer and $\lambda = \frac{1}{2}$.

Log-normal. A random variable T is said to follow a log-normal distribution if its natural logarithm, $Y = \ln T$, follows a normal distribution. The log-normal distribution is used frequently in survival analyses because of its relationship to the normal distribution. Like the normal distribution, the log-normal distribution is completely specified by two parameters, μ and σ^2, the mean and variance of Y.

The log-normal density function is defined for $t \geq 0$ and $\sigma > 0$ as $f(t) = \phi(\frac{\ln t - \mu}{\sigma})/t$, where $\phi(.)$ is the standard normal probability density function. Its survival function is given by $S(t) = 1 - \Phi(\frac{\ln t - \mu}{\sigma})$, where $\Phi(.)$ is the standard normal cumulative distribution function. The hazard function of the log-normal is hump-shaped, such that it has a value of zero when $t = 0$, increases to a maximum, and then decreases, approaching zero as t becomes large (Figure 2.7).

The log-normal is easy to apply if there is no censoring, but with censoring it becomes computationally burdensome (Kalbfleisch and Prentice, 1980). Other drawbacks to the log-normal distribution are its sensitivity to analysis of small t (Ducrocq, 1999a) and its decreasing hazard for large t (Klein and Moeschberger, 1997). However, some researchers have observed that the log-normal distribution is appropriate for estimating both ages at onset and survival times for certain diseases (Klein and Moeschberger, 1997).

Other Distributions. There are many other distributions that can be used to model survival data. Among these are the log-logistic, the Gompertz-Makeham, the inverse Gaussian, and the Pareto distributions, which have received some attention in the literature (Klein and Moeschberger, 1997). However, any distribution defined over nonnegative values is a possible candidate for modeling survival data, and even those distributions with negative real values are possible with appropriate transformations of the random variable T (Cox and Oakes, 1984).

Model Selection

With so many options, selecting a distribution appropriate to the data may not be obvious (Ducrocq, 1999a), but several statistical methods, both formal and informal, are

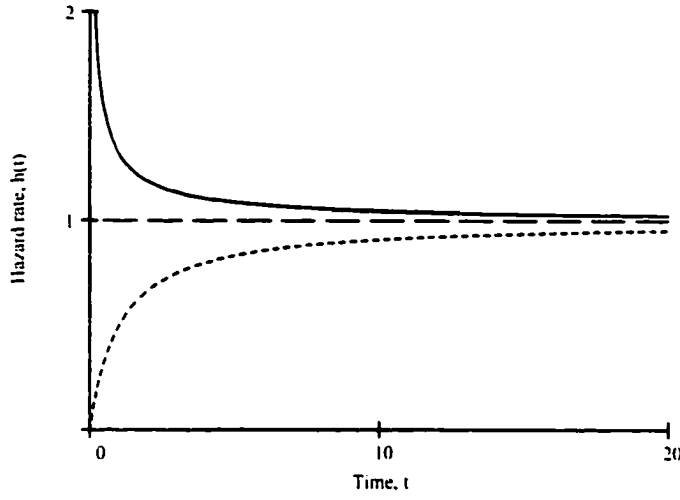

Figure 2.6. Hazard functions of gamma distributions with parameters $\lambda = 1$ and $\beta = 0.5$ (——), $\beta = 1$ (– – –), and $\beta = 2$ (-----).

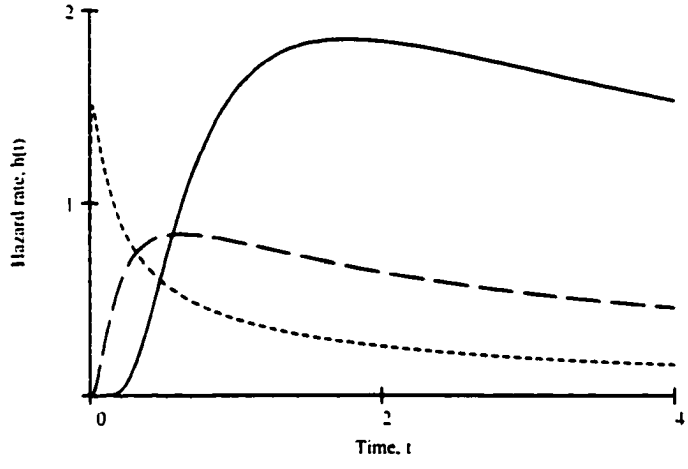

Figure 2.7. Hazard functions of log-normal distributions with parameters $\mu = 0$ and $\sigma = 0.5$ (——), $\sigma = 1$ (– – –), and $\sigma = 2$ (-----).

available for choosing the best model among competitors and for assessing goodness of fit (Kalbfleisch and Prentice, 1980).

One of the more formal methods is to fit a relatively complex model, such as the three-parameter generalized gamma distribution or the four-parameter generalized F distribution, that includes several simpler models as special cases. Discrimination among the simpler models is then facilitated by examining parameter estimates obtained from the more complex model (Ducrocq, 1999a).

Another strategy is to fit different log-linear models and check whether the distribution of residuals from each model resembles the error distribution associated with that model (Kalbfleisch and Prentice, 1980; Ducrocq, 1999a). For example, the distribution of residuals for the log-linear form of the exponential and Weibull models should resemble the minimum extreme value distribution.

Empirical checks of some distributions may be obtained by plotting a function of the hazard vs a function of time. For example, an empirical check of the exponential distribution is obtained by plotting the cumulative hazard function, $H(t) = -\ln S(t)$, vs t. The resulting plot should be a straight line through the origin with slope λ. An empirical check of the Weibull distribution is accomplished by plotting $\ln H(t)$ vs $\ln t$. This plot should result in a straight line with slope ρ and intercept $\rho \ln \lambda$ (Kalbfleisch and Prentice, 1980; Klein and Moeschberger, 1997).

In many applications, however, there are insufficient data to select models through empirical analysis (Cox and Oakes, 1984), and researchers must rely only on their knowledge of the subject (Ducrocq, 1999a). In this case, distributions can be judged qualitatively using

six criteria: 1) their technical convenience for statistical inference, 2) their capability of representing both over- and under-dispersion relative to the exponential distribution, 3) the availability of reasonably simple survival, probability density, and hazard functions, 4) the behavior of their survival functions for small and large values of t, 5) the shapes of their hazard functions, and 6) any connections with special stochastic models of failure (Cox and Oakes, 1984).

Characteristics of Survival Data

Survival data possess several characteristics that require special statistical treatment. The most distinctive feature of survival data is the possibility of censoring and truncation. In addition, survival data are never negative, and their distribution, often unknown, may be extremely skewed.

Censoring. Censoring occurs in survival data when either the first event (the origin) or the second event (the end point) of the time period of interest is not observed for some individuals. For example, consider a cow's reproductive life, for which the origin may be defined as the date on which the cow is selected as a replacement female and the end point as the date on which the cow is culled for reproductive failure. The date the cow entered the breeding herd may not be known because the cow was purchased as a pregnant female. Likewise, her culling date may not be known because the cow's records were discontinued after she was sold to a different herd or simply because the cow has not yet been culled.

There are essentially four kinds of censoring: right, left, double, and interval censoring (Klein and Moeschberger, 1997). The most common kind of censoring is right censoring, which occurs if an individual has yet to experience the event of interest by the end

of the observation period. Right censoring may be further classified as type I censoring if the end of the observation period occurs at a fixed time or type II censoring if it occurs after a fixed number of failures. Left censoring occurs when an individual experiences the event prior to the beginning of the observation period. Double censoring is a combination of right and left censoring, such that an individual experiences the first event prior to observation and has yet to experience the second event at the end of observation. A more general type of censoring is interval censoring, for which it is known that the individual experiences the event only within a certain time interval, not at a specific point in time (Klein and Moeschberger, 1997).

Censoring may also be characterized by the mechanism that acts upon the data (Kalbfleisch and Prentice, 1980). When the censoring mechanism is random, it is assumed that the censoring times of the individuals in the study are independent of their potential failure times so that knowledge of the distribution of censoring times does not provide any information about the actual failure times (Ducrocq, 1999a). Random censoring includes type I censoring as a special case and also occurs in studies where individuals enter at random over the duration of the study and the analysis is carried out at a prespecified time (Kalbfleisch and Prentice, 1980).

Unfortunately, there is no statistically satisfying way of validating the assumption of random censoring (Ducrocq, 1999a). One approach is to analyze the data treating censored records as uncensored and then check whether the conclusions of the analysis change. Researchers may also use their knowledge of the subject matter to determine whether there are any reasons (e.g., selection) to suspect that censored individuals live longer or shorter

than uncensored individuals. However, if the number of censored records is limited, the assumption of random censoring may not be too critical (Ducrocq, 1999a).

Another censoring mechanism is independent censoring, which occurs if there is a conditional independence between censoring and failure times. It is defined as any censoring mechanism that, when applied at time t, depends only on the complete history of the study up to time t and on any random mechanisms external to the failure process (Kalbfleisch and Prentice, 1980). Under independent censoring, individuals may not be selectively censored if they appear to be at high or low risk of failure. Both type I and type II censoring are examples of independent censoring.

Censoring may also be informative or noninformative, depending on whether or not the censoring times are associated with the parameters of interest. Other censoring mechanisms may depend arbitrarily on previous failure or censoring times or on the values of the covariates included in the model (Kalbfleisch and Prentice, 1980).

An understanding of the censoring mechanism is essential when using maximum likelihood procedures for parameter estimation. If there is some association between censoring and failure times, specialized techniques must be invoked (Klein and Moeschberger, 1997). Otherwise, construction of the likelihood is fairly straightforward, such that contributions to the likelihood function for uncensored, right censored, and left censored data are $f(t)$, $S(C)$, and $1 - S(C)$, respectively, where t denotes the failure time and C denotes the censoring time.

Censoring greatly complicates an analysis even when the censoring mechanism is simple and well understood (Kalbfleisch and Prentice, 1980). However, censored

observations should be included in the analysis because, among other considerations, they contain partial information about actual failure times. In mortality studies, for example, individuals that are longer lived tend to be those who are right censored (SAS, 1989). Thus, excluding censored records or treating them as complete records may result in erroneous or biased results (Ducrocq, 1994; Vukasinovic, 1999).

Truncation. Truncation occurs when observations are valid conditionally upon the occurrence of a particular event. If the event is some condition that must occur prior to the event of interest, the observation is said to be left truncated. Left truncation frequently occurs in medical studies in which a subject must have received a particular treatment (e.g., an organ transplant) prior to follow-up. Right truncation occurs when only those individuals who have experienced the event (e.g., failure) are included in the sample, and any individual who has yet to experience the event is not included (Klein and Moeschberger, 1997).

Truncation should not be confused with censoring. Truncated records are complete records, whereas censored records contain only partial information (Vukasinovic, 1999). In some situations, however, truncation may be combined with censoring. For example, left truncated individuals may be followed from the time they receive a particular treatment until either failure or right censoring, whichever occurs first (Klein and Moeschberger, 1997).

Because truncation depends upon the occurrence of a particular event, conditional probabilities must be used in constructing the likelihood function (Klein and Moeschberger, 1997). Assuming that truncation time Y is independent of failure time t, the contribution to the likelihood for left truncated data is $f(t)/S(Y)$. For right truncated data, the contribution is $f(Y)/[1 - S(Y)]$.

Other Characteristics. Another feature of survival data is that the explanatory variables associated with failure time may themselves vary with time. For example, risk of culling for infertility may change at various stages of the cow's reproductive cycle, being higher during pregnancy testing and lower just prior to weaning. In addition, the explanatory variables may have a multiplicative rather than additive effect on failure time, requiring nonlinear estimation procedures (Vukasinovic, 1999).

Modeling Explanatory Variables

In previous sections of this chapter, populations were assumed to be homogeneous. However, in most cases, there are independent, or explanatory, variables upon which failure time depends. Taking this type of information into account requires modifications to the probability functions used in survival analysis.

Suppose that $\mathbf{x} = (x_1 \cdots x_n)'$ is a vector of explanatory variables and $\boldsymbol{\beta} = (\beta_1 \cdots \beta_n)'$ is a vector of regression parameters. The hazard function of an individual with covariates $\mathbf{x}$ may be written as $h(t) = h(t; \mathbf{x})$. Although the relationship between $\mathbf{x}$ and $h(t)$ may be modeled in several ways, the most common approach is through regression. Two general classes of regression models are the proportional hazards models and the accelerated failure time models (Kalbfleisch and Prentice, 1980).

Proportional Hazards Models. Under a proportional hazards model, the hazard function may be written as $h(t; \mathbf{x}) = h_0(t)\exp(\mathbf{x}'\boldsymbol{\beta})$. The term $h_0(t)$ is called the baseline hazard function and represents the average hazard function of the entire population. The term $\exp(\mathbf{x}'\boldsymbol{\beta})$ is specific to individuals with covariates $\mathbf{x}$. This term is always positive and

acts multiplicatively on $h_0(t)$. The survival function for a proportional hazards model is $S(t;\mathbf{x}) = S_0(t)^{\exp(\mathbf{x}'\beta)}$, where $S_0(t) = \exp[-\int_0^t h_0(u)\,du]$.

The proportional hazards model has the property that the ratio of the hazard functions between two individuals with different covariates is a constant that does not vary with time. For example, let the hazard functions for individuals i and j be $h(t;\mathbf{x}_i) = h_0(t)\exp(\mathbf{x}_i'\beta)$ and $h(t;\mathbf{x}_j) = h_0(t)\exp(\mathbf{x}_j'\beta)$, respectively. The quantity $h(t;\mathbf{x}_i)/h(t;\mathbf{x}_j)$ is equal to $\exp[(\mathbf{x}_i' - \mathbf{x}_j')\beta]$, which is a constant that does not depend on t.

The baseline hazard function may be specified by a parametric distribution, such as the exponential or the Weibull, or it may be left completely arbitrary. When $h_0(t)$ is left arbitrary, the proportional hazards model is then called a Cox model. The statistical method most often used to estimate β for a Cox model is a semi-parametric procedure called Cox's partial likelihood (Kalbfleisch and Prentice, 1980).

There are two useful generalizations of the proportional hazards model (Kalbfleisch and Prentice, 1980). The first is stratification, for which the baseline hazard differs for specific subsets of the data. Suppose that the population is divided into k subclasses, or strata, based on some treatment. Then the hazard at time t for an individual with covariates $\mathbf{x}$ that received treatment k may be written as $h(t;\mathbf{x},k) = h_{0,k}(t)\exp(\mathbf{x}'\beta)$. It can be shown that the hazards of two individuals with different covariates are proportional if they belong to the same stratum, but if they belong to different strata, say k and k', the coefficient of proportionality is multiplied by $h_{0,k}(t)/h_{0,k'}(t)$. Stratification is applicable to situations in which the explanatory variable does not have a multiplicative effect on the hazard.

The second generalization allows for explanatory variables to vary with time. For example, the stage of a cow's reproductive cycle may influence her failure time, such that she has a higher risk of being culled during pregnancy testing than she does while nursing a calf. This type of explanatory variable, denoted by $\mathbf{x}(t)$, is called a time-dependent covariate. The hazard function of an individual with time-dependent covariates is given by $h(t;\mathbf{x}) = h_0(t)\exp[\mathbf{x}(t)'\boldsymbol{\beta}]$. Note that the ratio of hazards between two individuals is no longer constant over time unless the difference between the vectors of covariates for these two individuals does not vary with time.

Accelerated Failure Time Models. Under an accelerated failure time model, the hazard function is defined as $h(t;\mathbf{x}) = h_0(te^{\mathbf{x}'\boldsymbol{\beta}})e^{\mathbf{x}'\boldsymbol{\beta}}$, or equivalently $h(t;\mathbf{x}) = h_0(t')e^{\mathbf{x}'\boldsymbol{\beta}}$ for $t' = te^{\mathbf{x}'\boldsymbol{\beta}}$. Here, the covariates not only act multiplicatively on the hazard as for the proportional hazards model but also induce a time scale change. If $\mathbf{x}'\boldsymbol{\beta}>0$, then $\exp(\mathbf{x}'\boldsymbol{\beta})>1$ and time is accelerated. If $\mathbf{x}'\boldsymbol{\beta}<0$, then $\exp(\mathbf{x}'\boldsymbol{\beta})<1$ and time is decelerated.

The accelerated failure time model is a special case of the log-linear model. Suppose that the log-linear model for T is given by $Y = \ln T = \mathbf{x}'\boldsymbol{\beta} + W$, where W is an error variable with density f_W. Exponentiation of Y gives $T = \exp(\mathbf{x}'\boldsymbol{\beta})\exp(W)$. Substituting $T^* = \exp(W) > 0$, where T^* has hazard function $h_0(t^*)$ independent of $\boldsymbol{\beta}$, it follows that $T^* = T\exp(-\mathbf{x}'\boldsymbol{\beta})$ and the hazard function at time t for an individual with covariates $\mathbf{x}$ is

$$\begin{aligned} h(t;\mathbf{x}) &= h_0[t\exp(-\mathbf{x}'\boldsymbol{\beta})]\exp(-\mathbf{x}'\boldsymbol{\beta}) \\ &= h_0[t\exp(\mathbf{x}'\boldsymbol{\beta}^*)]\exp(\mathbf{x}'\boldsymbol{\beta}^*), \end{aligned}$$

where $\boldsymbol{\beta}^* = -\boldsymbol{\beta}$.

A special property of the exponential and Weibull models is that they are the only two models that belong to both the proportional hazards and the accelerated failure time families of regression models. The hazard function of the Weibull proportional hazards model is

$$\begin{aligned} h(t) &= h_0(t)\exp(\mathbf{x}'\boldsymbol{\beta}) \\ &= \lambda\rho(\lambda t)^{\rho-1}\exp(\mathbf{x}'\boldsymbol{\beta}) \\ &= \lambda\rho(\lambda t)^{\rho-1}\exp\left[\frac{(\rho-1)\mathbf{x}'\boldsymbol{\beta}+\mathbf{x}'\boldsymbol{\beta}}{\rho}\right]. \end{aligned}$$

Substituting $\boldsymbol{\beta}^* = \boldsymbol{\beta}/\rho$ and noting that $\exp[(\rho-1)\mathbf{x}'\boldsymbol{\beta}^*] = [\exp(\mathbf{x}'\boldsymbol{\beta}^*)]^{\rho-1}$, the hazard function may be rewritten as

$$\begin{aligned} h(t) &= \lambda\rho[\lambda t\exp(\mathbf{x}'\boldsymbol{\beta}^*)]^{\rho-1}\exp(\mathbf{x}'\boldsymbol{\beta}^*) \\ &= \lambda\rho(\lambda t^*)^{\rho-1}\exp(\mathbf{x}'\boldsymbol{\beta}^*), \end{aligned}$$

where $t^* = t\exp(\mathbf{x}'\boldsymbol{\beta}^*)$. Further simplification gives $h(t) = h_0(t^*)\exp(\mathbf{x}'\boldsymbol{\beta}^*)$, which by definition is the hazard function for an accelerated failure time model.

An alternative expression for the Weibull hazard function that may be useful in some situations is

$$\begin{aligned} h(t) &= \lambda\rho(\lambda t)^{\rho-1}\exp(\mathbf{x}'\boldsymbol{\beta}) \\ &= \rho t^{\rho-1}\lambda^{\rho}\exp(\mathbf{x}'\boldsymbol{\beta}) \\ &= \rho t^{\rho-1}\exp(\rho\ln\lambda + \mathbf{x}'\boldsymbol{\beta}) \\ &= \rho t^{\rho-1}\exp(\mathbf{x}^{*\prime}\boldsymbol{\beta}^*), \end{aligned}$$

where $\boldsymbol{\beta}^{*\prime} = (\rho\ln\lambda, \boldsymbol{\beta}')$ and $\mathbf{x}^{*\prime} = (1, \mathbf{x}')$. In this expression, only one parameter, namely ρ, describes the baseline hazard, and $\rho\ln\lambda$ acts as the intercept on the logarithmic scale (Ducrocq, 1999a).

Frailty Models. The regression models given above are based on the assumption that survival times of distinct individuals are independent of one another. Although this assumption may be valid in many experimental settings, it may be suspect in others (Klein and Moeschberger, 1997). For example, in animal breeding applications, observations may be correlated through the genetic relationships among individuals in the population.

When there is an association among individuals within the population, use of a frailty model is recommended. A frailty is an unobservable random effect that multiplicatively affects the hazard of individuals or groups of individuals. When the frailty term is defined separately for each individual, the frailty component extracts part of the unobserved variation among individuals and allows for a correction of overdispersion, or the discrepancy between the true variance of the observations and the one specified by the model. When the frailty term is defined for a group of individuals, it describes the shared unobservable characteristics that act on the hazard of each member in the group. In either case, the proportional hazards model can be extended to include the frailty term (Ducrocq, 1999a).

The hazard function for an individual with covariates $\mathbf{x}$ and frailty term v is given by $h(t;\mathbf{x}) = h_0(t)\exp(\mathbf{x}'\boldsymbol{\beta})v$. The transformation $v = \exp(u)$ allows the hazard to be written as $h(t;\mathbf{x}) = h_0(t)\exp(\mathbf{x}'\boldsymbol{\beta} + u)$. To expand further, if $\mathbf{u} = (u_1 \cdots u_m)'$ is a vector of log-frailties and $\mathbf{z} = (z_1 \cdots z_m)'$ is an incidence vector relating the log-frailties to the individual, then the hazard function becomes $h(t;\mathbf{x},\mathbf{z}) = h_0(t)\exp(\mathbf{x}'\boldsymbol{\beta} + \mathbf{z}'\mathbf{u})$, which resembles a classical linear mixed model.

The frailty terms associated with individuals or groups of individuals are assumed to be an independent sample from a particular distribution (Klein and Moeschberger, 1997).

Traditionally, a one-parameter gamma distribution has been attached to the frailty terms because of its flexibility and mathematical convenience. Other distributions that have been considered include the positive stable, the inverse Gaussian, and the uniform distributions (Klein and Moeschberger, 1997; Ducrocq, 1999a). In quantitative genetics, however, the assumption of the infinitesimal polygenic model suggests a log-normal distribution for the frailties, or equivalently, a normal distribution for the log-frailties (Ducrocq, 1999a).

Analytical Procedures

The basic approaches to estimation in survival analysis include nonparametric, semi-parametric, and parametric methods. Only parametric methods will be discussed because the parametric approach is better suited to handle the large, complex models encountered in animal breeding (Kachman, 1999).

Likelihood Construction. Parametric estimation is facilitated through construction of a likelihood function. A critical assumption of likelihood construction is that censoring and failure times are independent (Klein and Moeschberger, 1997). If this assumption holds, then the likelihood function is the product of the contributions from the various kinds of censored and truncated observations.

For situations in which only uncensored and right censored data are modeled, the likelihood function to be maximized is given by

$$\begin{aligned} L &= \prod_{i \in UC} f(t_i) \prod_{i \in RC} S(t_i) \\ &= \prod_{i \in UC} h(t_i) S(t_i) \prod_{i \in RC} S(t_i) \\ &= \prod_{i \in UC} h(t_i) \prod_{i} S(t_i), \end{aligned}$$

where t_i denotes the failure or censoring time of the ith individual and UC and RC are the sets of uncensored and right censored observations, respectively.

The logarithm of this function, which has the same maximum because of its monotonicity, is

$$\begin{aligned}\ln L &= \sum_{i \in UC} \ln f(t_i) + \sum_{i \in RC} \ln S(t_i) \\ &= \sum_{i \in UC} [\ln h(t_i) + \ln S(t_i)] + \sum_{i \in RC} \ln S(t_i) \\ &= \sum_{i \in UC} \ln h(t_i) + \sum_{i} \ln S(t_i).\end{aligned}$$

Note that all observations contribute $\ln S(t_i)$ to the log-likelihood, but only uncensored observations contribute $\ln h(t_i)$. The log-likelihood can then be expressed using an indicator variable. If W is the indicator variable such that $w_i = 0$ if $i \in RC$ and $w_i = 1$ if $i \in UC$, then $\ln L = \sum_i [w_i \ln h(t_i) + \ln S(t_i)]$.

The log-likelihood for the Weibull model may be written as

$$\begin{aligned}\ln L &= \sum_i w_i \ln[\lambda \rho (\lambda t_i)^{\rho - 1}] + \ln[\exp(-(\lambda t_i)^{\rho})] \\ &= \sum_i w_i \ln(\rho \lambda^{\rho} t_i^{\rho - 1}) - \exp[\ln(\lambda t_i)^{\rho}] \\ &= \sum_i w_i \ln[(\rho / t_i)(\lambda t_i)^{\rho}] - \exp[\ln(\lambda t_i)^{\rho}] \\ &= \sum_i w_i [\ln(\rho / t_i) + \rho \ln \lambda + \rho \ln t_i] - \exp(\rho \ln \lambda + \rho \ln t_i).\end{aligned}$$

Ignoring an additive constant associated with $\rho \ln \lambda$, the expression simplifies to $\ln L = \sum_i w_i [\ln(\rho / t_i) + \rho \ln t_i] - \exp(\rho \ln t_i)$, which does not involve the parameter λ.

The log-likelihood function may also be generalized to include fixed and random effects. Continuing with the Weibull example under the assumption that the log-frailties are

multivariate normal, i.e., $\mathbf{u} \sim MVN(\mathbf{0}, \mathbf{G})$, where $\mathbf{G} = \sigma_a^2 \mathbf{A}$, σ_a^2 is the additive direct genetic variance, and $\mathbf{A}$ is Wright's numerator relationship matrix, it can be shown (Kachman, 1999) that

$$\ln L = \sum_i [w_i(\ln \frac{\rho}{t_i} + \rho \ln t_i + \mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}) - \exp(\rho \ln t_i + \mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u})] - \frac{1}{2}\ln|\mathbf{G}| - \frac{1}{2}\mathbf{u}'\mathbf{G}^{-1}\mathbf{u}$$
$$= \sum_i [w_i(\ln \frac{\rho}{t_i} + \rho \ln t_i + \eta_i) - \exp(\rho \ln t_i + \eta_i)] - \frac{1}{2}\ln|\mathbf{G}| - \frac{1}{2}\mathbf{u}'\mathbf{G}^{-1}\mathbf{u}.$$

In this expression, η_i (also called the risk factor) was substituted for $\mathbf{x}_i'\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{u}$ and an additive constant associated with the log-frailties was removed.

Numerical Maximization. For parametric frailty models, the log-likelihood function is often nonlinear, requiring numerical iteration rather than analytical techniques for maximization (Klein and Moeschberger, 1997). In general, iterative methods that are based on derivatives of the function to be maximized tend to perform best (Reverter, 1994). Klein and Moeschberger (1997) suggest three derivative-based, or gradient, methods for estimation in multivariate survival models.

The first of these, the method of steepest ascent, requires only first derivatives of the log-likelihood function. This method is robust to the starting values used in the iteration, but may require a large number of rounds to converge to a maximum. The second is the multivariate extension of the Newton-Raphson procedure. This method, which requires both first and second derivatives of the function, converges quite rapidly when the starting values are close to the root, but may not converge when the starting values are poorly chosen. The third strategy is Marquardt's method, which is a compromise between the other two methods.

It uses a blending constant that controls how closely the algorithm resembles the method of steepest ascent or the Newton-Raphson procedure. A fourth gradient method is Fisher scoring, which is a quasi-Newton procedure characterized by replacing the second derivative with its expected value (Harville, 1977; Reverter, 1994). Although similar to Newton-Raphson, Fisher scoring usually requires more iterations to converge.

In general, implementation of the Newton-Raphson and Fisher scoring algorithms for maximizing ln $L(\theta)$ involves solving the system of equations $\theta^{[k+1]} = \theta^{[k]} + \mathbf{I}^{-1[k]}\mathbf{g}^{[k]}$, where $\theta = (\beta\ \mathbf{u})'$, $\mathbf{I}$ is the information matrix, $\mathbf{g} = \frac{\partial \ln L(\theta)}{\partial \theta}$ is the gradient vector, and k is the round of iteration. For the Newton-Raphson algorithm, $\mathbf{I} = -\frac{\partial^2 \ln L(\theta)}{\partial \theta \partial \theta'}$, or the negative of the Hessian matrix, and for Fisher scoring, $\mathbf{I} = E[-\frac{\partial^2 \ln L(\theta)}{\partial \theta \partial \theta'}]$ (Kalbfleisch and Prentice, 1980; Ducrocq, 1990; Klein and Moeschberger, 1997).

Manipulation of $\theta^{[k+1]} = \theta^{[k]} + \mathbf{I}^{-1[k]}\mathbf{g}^{[k]}$ leads to

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}\mathbf{X} & \mathbf{X}'\mathbf{R}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}\mathbf{X} & \mathbf{Z}'\mathbf{R}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix}^{[k]} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{u}} \end{bmatrix}^{[k+1]} = \begin{bmatrix} \mathbf{X}'\mathbf{R}\mathbf{y}^{*} \\ \mathbf{Z}'\mathbf{R}\mathbf{y}^{*} \end{bmatrix}^{[k]},$$

which resembles Henderson's mixed model equations. For a Weibull model with normally distributed log-frailties and known σ_a^2 and ρ, the system of equations for the Newton-Raphson algorithm can be obtained by defining $\mathbf{R} = -\frac{\partial^2 \ln L(\theta)}{\partial \eta \partial \eta'}$ and $\mathbf{y}^{*} = \eta + \mathbf{R}^{-1}\mathbf{v} = \eta + \mathbf{R}^{-1}\frac{\partial \ln L(\theta)}{\partial \eta}$, where $\mathbf{R}$ is a diagonal matrix and $\mathbf{y}^{*}$ is called the vector of working variates (Kachman, 1999). Individual elements of $\mathbf{R}$ and $\mathbf{y}^{*}$ are $R_{ii} = \exp(\rho \ln t_i + \eta_i)$ and $y_i^{*} = w_i - R_{ii} + R_{ii}\eta_i$, respectively, where $w_i = 0$ if $i \in RC$ and $w_i = 1$ if $i \in UC$.

Although there is no general rule for declaring convergence of iterative algorithms, some suggestions include stopping when changes in the log-likelihood are small, when changes in the current parameter estimates are small, or when values of the gradient are small (Reverter, 1994). Klein and Moeschberger (1997) also suggest stopping when the squared sum of differences in solutions is small.

The modal estimates of θ obtained from Newton-Raphson and Fisher scoring are identical and are usually termed maximum *a posteriori* estimates (Tempelman, 1998). Prediction error variances are computed from the diagonal terms of $\mathbf{I}^{-1}$ evaluated at $\hat{\theta}$ (Tempelman, 1998; Ducrocq, 1999a).

Although the computations involved in these methods are very similar to those in linear mixed model implementations and should not be considered difficult (Tempelman, 1998), censoring can lead to some problems in estimation (Kachman, 1999). For example, if all records in a fixed effect group are right censored, then the estimate of the risk factor for that group will go to negative infinity. In addition, the algorithms may not converge when ρ and η are estimated simultaneously, and it may be necessary to fix ρ to obtain reasonable estimates of η.

Variance Component Estimation. Several approaches have been developed to estimate the variance components, or dispersion parameters, of frailty terms in mixed survival models. For example, Klein and Moeschberger (1997) suggest an expectation-maximization algorithm to estimate the dispersion of gamma-distributed frailties in a Cox model. Korsgaard et al. (1999b) outline a Bayesian procedure using Gibbs sampling and data augmentation for right censored Gaussian data. Also from a Bayesian perspective, Ducrocq

and Casella (1996) propose using Laplacian integration to obtain a saddle point approximation of the marginal posterior density of the dispersion parameter of the random effects. Many of these procedures, however, are not suitable for complex models or large applications (Ducrocq, 1999a). In addition, when frailties are correlated through a relationship matrix, estimation may be computationally intractable, being limited by slow convergence and prohibitive computer processing requirements (Ducrocq, 1999b).

In animal breeding applications, it is often desirable to have heritability estimates, rather than estimates of the dispersion parameters. For log-linear survival models with known error distributions, heritabilities are easily expressed, but their interpretation may be quite difficult. Although these heritabilities may be transformed from the logarithmic scale to the original time scale using Taylor series expansions (Ducrocq, 1999a), the transformation is not necessary for purposes of genetic evaluation (B. L. Golden, personal communication).

To express heritability on the logarithmic scale, consider a single-trait Weibull mixed animal model. It can be shown that the log-linear form of this model is

$$\mathbf{y} = \ln \mathbf{t} = -\ln \lambda \mathbf{1} - \frac{1}{\rho}\mathbf{X}'\boldsymbol{\beta} - \frac{1}{\rho}\mathbf{Z}'\mathbf{u} + \frac{1}{\rho}\mathbf{w},$$

where $\boldsymbol{\beta}$ is a vector of fixed effects, $\mathbf{X}$ is an incidence matrix relating fixed effects in $\boldsymbol{\beta}$ to the observations in $\mathbf{y}$, $\mathbf{u}$ is a vector of random direct genetic effects, $\mathbf{Z}$ is an incidence matrix relating random effects in $\mathbf{u}$ to observations in $\mathbf{y}$, and $\mathbf{w}$ is a vector of random errors. Furthermore, $\mathbf{u} \sim MVN(\mathbf{0}, \sigma_a^2 \mathbf{A})$, where $\mathbf{A}$ is Wright's numerator relationship matrix for all animals, and the w_i's are from a minimum extreme value distribution with mean -.5772 and

variance $\pi^2/6$. Defining heritability as $h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_e^2)$ and recognizing that $\sigma_e^2 = \pi^2/6$, heritability on the logarithmic scale may be estimated as $\hat{h}^2 = \hat{\sigma}_a^2/(\hat{\sigma}_a^2 + \pi^2/6)$ (Ducrocq, 1999b).

Applications of Survival Analysis in Animal Breeding

Dairy Cattle

Historical Developments. Adaptation of survival analysis to animal breeding began in the dairy industry with the pioneering work of Famula (1981), who proposed an exponential survival model for censored data as an alternative to stayability models for binary observations. A few years later, Smith and Quaas (1984) applied a Cox proportional hazards model that included a fixed genetic group effect and random herd and sire effects to obtain heritability estimates of herd life from records on 587,013 Holstein cows. Their methods were generalized by Smith and Allaire (1986), who described a maximum *a posteriori* procedure for estimation and prediction in Cox regression models with large numbers of fixed and random effects.

Ducrocq et al. (1988a, 1988b) justified using a Weibull distribution with time-dependent covariates to model length of productive life in dairy cows and demonstrated the feasibility of incorporating survival analysis into large-scale sire evaluation. Realizing the need for software designed to accommodate mixed model survival analyses of large data sets, Ducrocq and Sölkner (1994, 1998, 1999) created *The Survival Kit*, a package written in Fortran 77 that can be applied to both Cox and Weibull frailty models. Other advances in the application of survival analysis to dairy cattle breeding were the derivation of a Bayesian procedure for estimating genetic parameters using a known relationship matrix among

animals (Ducrocq and Casella, 1996) and the first within-breed sire evaluation for length of productive life (Ducrocq, 1994).

Since 1997, sire evaluations for length of productive life have been conducted routinely for all of the dairy breeds in France, and several other European countries have implemented mixed model survival analyses in their dairy evaluations (Ducrocq, 1997; Vukasinovic, 1999). However, one of the concerns has been that young sires have low reliabilities for length of productive life, and their evaluations are not useful for selection purposes.

Indicator Traits. To circumvent this problem, several researchers (e.g., Vollema and Groen, 1997; Vukasinovic et al., 1997; Bünger and Swalve, 1999) have investigated the possibility of using type traits as indicators of longevity. Type traits are measured early in a cow's life, are more heritable than direct measures of herd life, and have moderate genetic correlations with herd life (Del Pilar Schneider et al., 1999). The information provided by type traits may be used to predict herd life directly (Essl, 1998), or it may be combined with measurements of herd life to improve accuracy of evaluation (Weigel et al., 1998; Pasman and Reinhardt, 1999).

Using type trait information in analyses of productive life requires precise estimates of the genetic correlations between type traits and herd life (Larroque and Ducrocq, 1999a), but methodology for multiple-trait survival analysis has yet to be developed (Ducrocq, 1999b). Approximate methods have been employed for estimating the genetic correlations between type and longevity, but the estimates that have been reported are generally low to moderate and may be biased because of different culling practices among herds (Essl, 1998)

and nonlinear relationships between traits (e.g., Larroque and Ducrocq, 1999b; Sölkner and Petschina, 1999). Essl (1998) suggests that improvements in accuracy associated with using type traits as indicators of productive life are questionable and concludes that type scores are not a sufficient selection substitute for herd life measurements.

Health Disorders. In the dairy industry, an increasing amount of emphasis has been placed on health management in order to minimize disease-related losses (Beaudeau et al., 1999). Because culling for disease may be influenced by the timing and severity of the disease, past milk production and reproductive performance of the cow, and herd characteristics over time, survival models with time-dependent covariates have been developed to determine the impact of health disorders on productive life (e.g., Beaudeau et al., 1995; Gröhn et al., 1997, 1998; Emanuelson et al., 1998).

However, the relative importance that health disorders have on productive life depends on the quality of culling information provided by dairy producers (Beaudeau et al., 1999). Culling reasons are subjective measures that are influenced not only by characteristics of the cow but also by economic factors not related to disease (Beaudeau et al., 1995; Bascom and Young, 1998). For example, it may be more cost-effective for producers to delay culling because of high replacement costs. In other situations, producers may cull cows in order to adjust herd size so as not to exceed milk quotas. Beaudeau et al. (1999) recommend further investigation to interpret the meaning and assess the reliability of reported culling information before culling reasons are used as relevant selection criteria in the genetic improvement of longevity.

Beef Cattle

Using data recorded over a 24-yr period on a commercial herd of Angus females, Schons et al. (1985) computed age-specific survivorship, survival and mortality rates, and expected herd life for seven full and 15 partial cohorts. Birth was considered to occur at age zero, and death was defined as leaving the herd for any reason. Average productive life for complete and nearly complete cohorts was 4.49 ± 0.09 yr, and estimates of the age-specific survival and mortality rates showed high survivability to age 11. The results were used to characterize the herd as having good management, high pregnancy rates, consistent replacement rates, and physically sound cows.

Tanida et al. (1988) used data from Schons et al. (1985) and data recorded over a 30-yr period on a Hereford herd in Arizona to examine the genetic aspects of longevity, defined as reproductive lifespan. In the Hereford herd, heritabilities for longevity estimated from daughter-dam regression and paternal half-sib analysis were 0.16 ± 0.08 and 0.26 ± 0.08, respectively. In the Angus herd, the heritability estimate from daughter-dam regression was 0.05 ± 0.15. Curves for age-specific survivorship and age-specific survival rate were markedly different among daughters of the Angus sires. Results from this study provided evidence of moderate genetic variation for reproductive lifespan in beef cattle.

Azzam et al. (1991) considered the Weibull, log-normal, and linear hazard rate distributions to model time to first postpartum estrus in beef females. The linear hazard rate distribution with parameters changing at three points in time was the only distribution that provided a good fit to the data. However, the authors cautioned that this distribution may not

be useful for estimating postpartum interval using survival analysis techniques because of its mathematical intractability.

Arthur et al. (1993) fit Weibull models to evaluate herd life for 993 cows of three breeds (purebred Hereford, a beef composite, and a dairy–beef composite). Herd life was defined as the length of time from entering the breeding herd as yearling heifer to culling. Cows were culled primarily for failure to wean a calf every year, but also were culled for severe calving problems, bad udders, and leg and feet problems. Estimates of the shape parameter (ρ) for the three breeds ranged from 1.100 to 1.238, indicating an increasing hazard over time. Average ages at disposal were 3.7, 4.5, and 5.2 yr for the Herefords, beef composites, and dairy–beef composites, respectively. The Hereford cows had a faster rate of removal at all ages compared to cows of the other two breeds.

In a similar study, Vega-Murillo et al. (1999) used survival analysis to investigate herd life of 537 females in a four-breed diallel design consisting of Red Poll, Brown Swiss, Hereford, and Angus. A Weibull model was applied to explain the effect of breed composition on herd life, defined as the number of days from the first breeding season of the cow to her termination from the herd. The model included breed composition and year of birth as fixed effects and sire within breed of sire as a random effect. The shape parameter was estimated to be 0.81 ± 0.04, indicating a decreasing baseline hazard rate. Breed group differences were significant ($P < 0.01$) and suggested that purebred cows had a higher risk of leaving the herd at any given time than crossbred cows.

Cunningham et al. (1999) conducted a genetic analysis of length of productive life using data on 25,512 Simmental cows from 22 herds representing 1,647 sires. Length of

productive life was defined as the number of days from first calving to the day the cow disappeared from the herd. The baseline hazard function was assumed to follow a Weibull distribution. Four models, in which sire and management group were random effects with normal and log-gamma distributions, respectively, were evaluated. Estimates of sire variance for the four models ranged from 0.016 to 0.036, and estimates of the gamma parameter were between 2.74 and 3.10, inclusive.

Swine

Using the life table approach, Lopez-Serrano et al. (1998) estimated hazard functions for 21,870 Large White and 14,944 Landrace sows to determine the instantaneous risk of disposal due to lameness and disease after correction for litter performance. A higher proportion of Large White (20.1%) than of Landrace (17.5%) sows were culled from first to second parity, but after the second parity, the hazard rates of the Landrace exceeded those of the Large White.

Brandt et al. (1998) used a Cox model with time-dependent covariates to investigate factors affecting the survival rate of crossbred sows in weaner production. Litter performance and insemination success had the greatest effect on sow productive life, whereas factors associated with gilt selection were least important. Of the variables related to gilt selection, leg quality score was the most influential.

Sheep

In an application of survival analysis not related to animal breeding, Scrivner et al. (1987) used life tables to estimate survival, probability density, and hazard functions for the evaluation of data on single and twin lambs lost to coyote predation. Although survivorship

was not statistically different for singles vs twins, 87% of the missing animals were twin lambs. One conclusion from the study was that survival analysis provides more information as to how predation varies across time than traditional statistical methods.

Poultry

Contrary to popular belief, genetic evaluations based on survival analysis are not restricted to sire and sire–maternal grandsire models. Researchers have focused on these models because of computational, not theoretical, limitations. Although animal models have not been used in large-scale applications, they have been employed in other studies. For example, Ducrocq (1999b) cites an unpublished study in which an animal model was incorporated into a genetic evaluation for length of productive life of laying hens. However, the correlation between the animals' estimated breeding values and the average estimated breeding values of their parents were .98, indicating that the information contributed by each animal was limited, especially if the animal was censored (V. P. Ducrocq, personal communication).

Horses and Donkeys

Cox models have been used to investigate risk factors associated with the occurrence of lameness in horses (Ross et al., 1998) and of hyperlipemia, a condition affecting lipid metabolism, in donkeys (Reid et al., 1996). Increased risk of lameness was associated with stallions and geldings vs mares, active vs breeding horses, and horses from small vs large operations (Ross et al., 1998). In Reid et al. (1996), female donkeys and donkeys of obese body condition were more at risk of developing hyperlipemia than males or those of

moderate and poor body condition. Increased age was also associated with higher risk of hyperlipemia.

Ricard and Fournet-Hanocq (1997) used a variation of the Cox model for grouped data to study the length of competitive life of French jumping horses. Only performance records of stallions and geldings (n = 42,393) were analyzed because the competitive lives of mares are often interrupted for reproductive reasons. The horses were the offspring of 4,851 sires, and 43.3% of the horses' records were right censored. The model included several fixed effects as well as a random sire effect assumed to have log-gamma distribution. Heritability of length of competitive life was estimated to be 0.18.

Survival Analysis of Reproductive Life in Beef Females

The application and implementation of survival analysis to large-scale genetic evaluation of reproductive life in beef females will depend to a large extent on three factors. First, female reproductive data must be collected and made available by beef breed associations. Second, computer resources must be capable of handling the computational demands and complexities of animal model survival analysis. Third, genetic evaluations based on survival analysis must be economically feasible.

Data Availability

A major obstacle to survival analysis of female reproductive life is the lack of reproductive data on cows. Although female reproductive data—whether or not a cow was exposed to breeding, conceived, calved, and then raised that calf to weaning—are among the most easily collected and economically important data that can be recorded, beef cattle

performance programs have traditionally focused on recording and evaluating measurements taken on calves (Snelling, 1998).

In the past decade, however, breed associations in the United States and Canada have become interested in recording programs that emphasize collection of data on all animals in a herd rather than on only those animals a breeder intends to register (Golden, 1997; Cunningham, 1998). The idea behind such programs, called inventory-based or whole-herd reporting systems, is to encourage complete reporting of data (Golden, 1997). Two major benefits of such systems are the elimination of reporting bias from incomplete or selective reporting and the opportunity to gain additional information for the genetic evaluation of female reproductive traits (Golden, 1996).

Whole-herd reporting can simply involve recording performance data for all calves, reasons for reproductive failure of cows, and reasons for disposal of animals that go out of production. Taken to an extreme, whole-herd reporting can require lifetime records from conception to slaughter for every animal in all seedstock and commercial herds (Snelling, 1998). To be effective, however, a whole-herd reporting program should require a minimum of calf weaning weight records and cow and calf disposal information (Golden, 1997).

In general, there are three types of whole-herd performance programs (Gibb, 1995). The first type has an inventory-based fee structure in which nearly all fees are collected on a per cow basis with all other services provided at little or no cost. The second type is based on a herd assessment fee with additional fees for registrations, transfers, and other association services. The third type of program is voluntary. This type has no herd assessment fee, but members are given the opportunity to report reasons for cow disposal.

Although some information may be gained under a voluntary program, the major benefits of a whole-herd reporting system are not realized unless all members of the breed association participate and all cows are enrolled in the program (Golden, 1997).

When whole-herd reporting is based on all females exposed to breeding, the information that is collected may be used to enhance stayability evaluations (Snelling, 1998). Stayability is defined as the probability that a cow will remain in the herd to at least age six given that she was selected as a replacement heifer (Snelling, 1994). Stayability was developed as a concession to lack of complete reporting and uses information on reported calves to determine whether a cow had a calf at or after age six. However, with this information, there is no way to distinguish between calves that were never reported and calves that were never born (Snelling, 1998). Whole-herd reporting can directly improve the accuracy of stayability evaluations because information is available on all calves, not just those that are registered (Gilbert, 1997).

Stayability is a composite measure of culling in that it is impossible to differentiate between cows that did not conceive and cows that did not produce a registered calf (Gilbert, 1997). It is a reasonable measure of sustained fertility only when reproductive failure is the primary reason for culling young cows (Snelling, 1998). Recording annual reproductive status and disposal information should enable more reliable predictions of sustained fertility by allowing reproductive failure to be separated from other reasons for culling (Snelling, 1998).

Whole-herd reporting can enhance the reliability of evaluations that are currently computed for female reproductive traits. It also provides an opportunity to expand national

cattle evaluation to other traits, including reproductive life (Snelling, 1998). However, the information gained from whole-herd reporting systems may not be useful for a number of years. Compared to other traits, considerably more time is required to obtain data for accurate evaluations of sustained fertility. Nevertheless, adoption of whole-herd reporting by beef breed associations will ensure the quality of female reproductive data in years to come (Andersen, 1999).

Analytical Considerations

Although reproduction is a primary factor affecting the profitability of cow-calf operations (Snelling, 1995; Golden, 1996; Andersen, 1999), efforts to address reproduction in national cattle evaluation have been limited. One reason for this limitation, which has already been addressed, is the lack of data on female reproductive traits. Another reason is that some reproductive traits are not well-suited to analysis by conventional linear mixed model techniques.

Snelling (1995) describes a nonlinear procedure for analyzing stayability and heifer pregnancy data. Both of these traits are considered to be binary traits, for which observations fall into one of two possible categories. The category expressed by an individual is assumed to be dependent on an underlying phenotypic value relative to a fixed threshold. The analytical procedure involves using the threshold concept to develop a nonlinear analog to Henderson's mixed model equations and applying a Newton-Raphson iteration strategy to obtain predictions of breeding values on the underlying continuous scale.

To estimate variance components associated with binary traits, Snelling (1995) suggests using the Method R procedure (Reverter et al., 1994). Method R is based on the

expectation that the regression of more accurate predictions on less accurate predictions equals one. Binary iteration is used to obtain estimates of the variance components that result in a computed regression equal to its expectation. According to Snelling (1995), the Method R procedure may be more appropriate for large data sets than other estimation techniques because convergence of Method R for a single subsample is attained in relatively few iterations and the procedure does not require inversion of the coefficient matrix.

Nonlinear threshold models are a feasible alternative to conventional linear models for analyzing categorical measures of reproduction (Snelling, 1995). They have been combined with animal models to estimate heritabilities and predict genetic merit for stayability, heifer pregnancy, and calving ease in several beef breeds (Snelling, 1995; Andersen, 1999).

Survival models are also nonlinear, but are potentially more complex than threshold models. In addition, large-scale genetic evaluations of length of productive life in dairy cattle have been restricted to sire and sire-maternal grandsire models because of computational demands, and adaptation of survival analysis to animal models may not occur for several years (Ducrocq, 1999b). However, current computer resources are capable of processing large amounts of data associated with nonlinear animal models, and computer technology continues to advance.

Economic Feasibility

Under whole-herd reporting systems, genetic evaluations of reproductive life should result in improved reliability over current stayability analyses (Golden, 1997; Snelling, 1998). Although the improvement in reliability may be negligible, especially with few years

of recorded data, any potential increase in accuracy of genetic evaluations for sustained fertility should be weighed against the costs of development and implementation. Selection tools for reproductive traits are limited, and because of the importance of reproduction to the cow-calf sector of the beef cattle industry, development of expected progeny differences for reproductive traits should be a priority (Andersen, 1999).

CHAPTER 3

MATERIALS AND METHODS

Development of Statistical Methodology

Simulation Program

In order to meet the objectives of this dissertation, I first developed a computer simulation program (Appendix A) that generated female reproductive life (**RL**) data. These data were used to validate and test the statistical methodology as well as to compare genetic evaluations of RL and stayability and to investigate the effects of censoring on parameter estimation and genetic prediction of RL.

The program was designed to simulate a beef cattle breeding herd over a 20-yr period from an input seed value. It started by generating 125 foundation sires and 2,500 foundation dams in a 1:20 male:female ratio. Initial ages between one and 10 yr (integers) were randomly assigned to both sires and dams. Sires were assumed to have no progeny at the beginning of the simulation, but dams were assumed to have one progeny less than their initial age.

Reproductive life was defined as the length of time from entering the breeding herd at one yr of age to being culled for reproductive failure. Although RL is a sex-limited trait of females, both foundation sires and dams were assigned phenotypes for RL. The phenotypes were based on the Weibull distribution and determined using the formula $P_i = \exp[-\ln\lambda - 1/\rho(BV_i - E_i)]$, where P_i is the ith animal's phenotype for RL, BV_i is the ith

animal's underlying breeding value for RL, and E_i is the error component associated with animal i. Breeding value, having an inverse relationship with phenotypic value, was defined as $BV_i = a_i \sigma_a$, where σ_a denotes the standard deviation of the additive direct genetic variance of RL on the underlying natural logarithmic scale. Values of a_i and E_i were randomly generated from the standard normal and minimum extreme value distributions, respectively. The scale parameter λ was calculated for given shape parameter ρ assuming a median RL of five yr (equivalent to a median age of six yr) with no random effects present.

Each foundation animal was required to have a phenotype for RL consistent with its initial age to allow at least one breeding season for sires and at least one calf for dams. If this condition was not met, another foundation animal was simulated.

The foundation group was randomly mated to produce the first calf crop. Each dam produced a calf, and sex of calf was randomly assigned using a 50:50 male:female ratio. Reproductive lives for the calves were determined as for the foundation animals; however, breeding values were computed to take into account the Mendelian sampling effect (Φ) adjusted for the calves' level of inbreeding. Breeding values for the ith calf were calculated as $BV_i = \frac{1}{2}(BV_i^s + BV_i^d) + \Phi_i$, where BV_i^s and BV_i^d are the breeding values of the sire and dam, respectively, and $\Phi_i = a_i \sigma_a [\frac{1}{2}(1 - \bar{F}_p)]^{0.5}$, with a_i and σ_a defined as before and $\bar{F}_p$ defined as the average inbreeding coefficient of the calf's parents (Van Tassell et al., 1995). A total of 50,000 calves were produced over 20 yr, but only those entering the breeding herd were used in the analyses.

Both sires and dams were replaced with calves from the current calf crop if their phenotype for RL would not permit another breeding season for sires or another calf for

dams. Replacement calves were selected only on the basis of their order of production, such that calves that were produced first were more likely to be selected as replacements than those produced last. Replacement females with a phenotypic RL less than one yr were assumed to enter the breeding herd for purposes of genetic evaluation but were not eligible to produce a calf.

Experimental Design

A total of 30 breeding herds were simulated in a 2 × 3 factorial arrangement consisting of two levels of heritability (0.05 and 0.20) and three levels of the Weibull shape parameter (0.6, 0.8, and 1.0) with five replicates per cell. The two levels of heritability (h^2) represent relatively low and high values of heritability for reproductive traits, respectively. The levels of the shape parameter (ρ) were based on results from three studies that reported culling information on beef females.

The Weibull Shape Parameter

As part of larger investigations, Etienne and Martin (1979), Núñez-Dominguez et al. (1991a, 1991b, 1992), and Meek (1997) and Meek et al. (1998) compiled culling data at various ages for beef cows in different herds. Although several reasons for disposal were reported by each study, all three provided information on culling for infertility. I used this information to compute age-specific probabilities of culling for reproductive failure within each herd and then applied survival analysis techniques to obtain estimates of ρ.

In a study on lifetime cow productivity, Etienne and Martin (1979) analyzed culling data on 144 Angus females born from 1958 to 1963 and observed until 1977, when only eight of the cows were still in production. Cows were removed from the herd for several

reasons, but the most common (60.4%) was reproductive failure, or being diagnosed as not pregnant approximately 60 d after the end of the breeding season.

Núñez-Dominguez et al. (1991a, 1991b, 1992) collected data on 156 purebred Angus, Shorthorn, and Hereford cows and 172 first-cross cows born from 1960 to 1963 and followed them until 1975 to determine 1) the effects of heterosis on survival and dentition, 2) the effects of age at first calving on lifetime production, and 3) the effects of heterosis on the economic efficiency of lifetime productivity, respectively. In these studies, two different culling policies were examined. Under the actual culling policy, heifers diagnosed as not pregnant from their first breeding season were culled. After the first breeding season until 10 yr of age, only cows failing to conceive in two successive years or those seriously sick or injured were culled. Cows over 10 yr of age were culled when they were diagnosed as not pregnant. Under the imposed culling policy, all cows regardless of age were removed from the data set when diagnosed as not pregnant from any given breeding season. Reasons for disposal included infertility, mortality, and physical impairments. Probabilities of culling at various ages were compared between straightbred vs crossbred cows (Núñez-Dominguez et al., 1991a, 1992) and between cows managed to calve first as two-yr-olds vs three-yr-olds (Núñez-Dominguez et al., 1991b) for each culling policy.

Meek (1997) and Meek et al. (1998) evaluated the economic value of lifetime production of beef cows using cost and production data compiled during 1996 from a ranch in the sandhills of Nebraska. The breeding herd of the ranch consisted of 702 composite, 81 Angus × Hereford, and 52 Hereford cows managed to calve first at two yr of age (Meek, 1997). Records on the cows were used to determine the percentage of cows culled between

the ages of one and 12 yr because of poor performance, failure to conceive, calf loss, and death. Cows that failed to conceive each year were sold as open cows in the fall.

The age-specific probabilities of culling, or hazard rates, for reproductive failure for each data set are shown in Table 3.1. Using these data, I computed the cumulative hazards over time, denoted by $H(t) = -\ln S(t)$ where t is time, and regressed $H(t)$ on t and ln $H(t)$ on ln t as empirical checks of the exponential and Weibull models, respectively.

The regressions of $H(t)$ on t did not provide as good of a fit to the data as the regressions of ln $H(t)$ on ln t. Recall that the exponential model is appropriate if the regression of $H(t)$ on t results in a straight line going through the origin. In all but two cases, the intercept was different from zero. The regressions of ln $H(t)$ on ln t provided an extremely good fit to the data (R^2 = 0.9768 to 0.9939), with the exception of the regression associated with the Etienne and Martin (1979) data set (R^2 = 0.8497). For this data set, the fit to the Weibull model was improved (R^2 = 0.9856) by eliminating the single culling observation at age two. Although the residuals for all regressions appeared to have a nonlinear relationship with the natural logarithm of time, the distributions of residuals for the log-linear forms of the exponential and Weibull models should resemble the minimum extreme value distribution. Parameter estimates of the intercept and slope from the regressions of ln $H(t)$ on ln t are given in Table 3.2, along with corresponding estimates of the Weibull scale parameter (λ) and the median age at culling.

The values of ρ shown in Table 3.2 are less than one and range from 0.60 to 0.91, indicating a decreasing hazard over time. These values are similar to those reported by Vega-Murillo et al. (1999) and Strandberg and Roth (1999), which were 0.81 ± 0.04 for herd

Table 3.1. Age-specific probabilities of culling for reproductive failure of beef cows based on data obtained from the literature.

Age at breeding (yr)	Probability of culling for reproductive failure					
	Etienne and Martin (1979)	Meek et al. (1998)	Núñez-Dominguez et al. (1991b)[a,b]	Núñez-Dominguez et al. (1991b)[a,c]	Núñez-Dominguez et al. (1992)[a,d]	Núñez-Dominguez et al. (1992)[a,e]
1	0.007	0.147	0.179	--	0.174	0.153
2	0.163	0.128	0.134	0.186	0.164	0.145
3	0.103	0.086	0.069	0.140	0.069	0.058
4	0.067	0.042	0.120	0.120	0.155	0.096
5	0.031	0.042	0.082	0.124	0.075	0.044
6	0.087	0.042	0.077	0.126	0.172	0.050
7	0.123	0.042	0.152	0.091	0.173	0.171
8	0.071	0.042	0.081	0.213	0.139	0.147
9	0.032	0.042	0.091	0.248	0.078	0.096
10	0.035	0.042	0.118	0.200	0.104	0.116
11	0.061	0.040	--	--	--	--
12	0.098	0.040	--	--	--	--
13	0.143	--	--	--	--	--
14	0.273	--	--	--	--	--

[a]Under the imposed culling policy.
[b]Cows managed to calve first as two-yr-olds.
[c]Cows managed to calve first as three-yr-olds.
[d]Straightbred cows.
[e]First-cross cows.

life in beef cattle and 0.79 and 0.32 for functional productive life and fertility-determined length of productive life, respectively, in dairy cattle.

Most studies of length of productive life in dairy cattle have reported estimates of ρ that are greater than one (Strandberg and Roth, 1999). In addition, Arthur et al. (1993) estimated ρ to be between 1.100 and 1.238 for herd life in three breeds of beef cattle, and

Table 3.2. Parameter estimates of the intercept and slope for regressions of ln $H(t)$ on ln t [a] and corresponding estimates of the Weibull scale parameter (λ) and median age at culling based on data obtained from the literature.

Data set	Intercept ($\rho \ln \hat{\lambda}$)	Slope[b] ($\hat{\rho}$)	Scale parameter ($\hat{\lambda}$)	Median age at culling[c] (yr)
Etienne and Martin, 1979	-1.86 ± 0.05	0.71 ± 0.03	0.07	10.21
Meek et al., 1998	-1.79 ± 0.05	0.60 ± 0.03	0.05	11.65
Núñez-Dominguez et al. (1991b)[d,e]	-1.75 ± 0.04	0.78 ± 0.02	0.11	6.89
Núñez-Dominguez et al. (1991b)[d,f]	-1.76 ± 0.07	0.91 ± 0.04	0.14	6.62
Núñez-Dominguez et al. (1992)[d,g]	-1.77 ± 0.05	0.88 ± 0.03	0.13	5.94
Núñez-Dominguez et al. (1992)[d,h]	-1.89 ± 0.07	0.81 ± 0.04	0.10	7.56

[a] $H(t) = -\ln S(t)$, where t is time.
[b] Equivalent to the Weibull shape parameter.
[c] Based on age at first breeding.
[d] Under the imposed culling policy.
[e] Cows managed to calve first as two-yr-olds.
[f] Cows managed to calve first as three-yr-olds.
[g] Straightbred cows.
[h] First-cross cows.

S. D. Kachman (personal communication) determined ρ to be 1.587 ± 0.015 in an analysis of length of productive life in Simmental. Although it may seem that the risk of culling should increase over an animal's life due to the natural aging process, the risk of culling for reproductive failure in beef cows may in fact be bathtub-shaped over time, being highest at two and three yr of age, leveling off at intermediate ages, and then increasing at older ages. Table 3.1 provides some evidence to support this hypothesis.

Data

Descriptive statistics of the simulated breeding herds and observations on female RL are given in Tables 3.3 through 3.6. Values in these tables are averages compiled from the five data sets representing each cell in the 2 × 3 factorial arrangement defined by true h^2 and ρ. Tables 3.3 and 3.4 describe all simulated breeding animals, but Tables 3.5 and 3.6 summarize only those observations on breeding females born in yr one and later. I excluded observations on 1) foundation dams because of the constraints imposed by the simulator on the calculation of their RL and 2) breeding males because RL is a sex-limited trait. All remaining observations were assumed to be uncensored.

Tables 3.3 through 3.6 show how h^2 and ρ changed the population structure and the distribution of observations among the simulated data sets. In general, as ρ increased, the tails of the Weibull survival function became shorter, decreasing median RL. Animals remained in the herd for a shorter period of time, causing an increase in the replacement rate and, correspondingly, in the number of breeding animals over a 20-yr period. On the other hand, higher h^2 increased median RL, and fewer animals were given the opportunity to enter the breeding herd.

As the number of breeding animals increased with larger ρ and smaller h^2 (Table 3.3), the number of parents of these animals also increased (Table 3.4). As expected, the average number of breeding progeny decreased for the dams. The reason for the slight increase among sires was that the ratio of sires to dams decreased. Each sire had a greater opportunity to breed more dams and thus produce more breeding progeny.

The median RL in Table 3.5 are similar to those reported for research herds in Table 3.2. Although the maximum RL were not realistic measures for beef cattle, I did not truncate these observations. I wanted to maintain precision of the observations for validating and testing the statistical methodology. In addition, I did not believe that the observations would have a large impact on the results: 1) Relatively few observations exceeded realistic values for RL, and dams with these observations were only allowed to produce a maximum of 20 calves. 2) At the levels of heritability used to simulate the data, the calves' records were more valuable for predicting the dams' breeding values for RL than the dams' own records. 3) When transformed to their natural logarithms, observations on RL were in a much narrower range (Table 3.6).

Figures 3.1 and 3.2 not only show the effects of h^2 and ρ on RL but also indicate the presence of a selection mechanism on RL. Although I did not model selection in the simulation program, true breeding values for RL on the underlying scale decreased over time and phenotypic values increased. (Recall from pp 44-45 that breeding value has an inverse relationship with phenotypic value.) The trends were more pronounced for data simulated with $h^2 = 0.20$ vs $h^2 = 0.05$. In a preliminary investigation in which I imposed annual culling of all females at different levels of h^2, these trends were not apparent, suggesting natural selection for increased RL. According to Essl (1998), natural selection among artificially selected individuals still exists to some extent and continually forces longevity to increase.

Analytical Procedures

Heritability Estimates. Twenty heritability estimates were obtained from each of the 30 data sets. To estimate heritabilities, I used an animal model maximum *a posteriori*

Table 3.3. Descriptive statistics of breeding animals simulated at two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Weibull shape parameter (ρ)	Breeding animals (n)	Breeding males (n)	Breeding females (n)	Breeding females (%)
0.05	0.6	6,923.4	326.2	6,597.2	95.29
	0.8	8,380.6	378.0	8,002.6	95.49
	1.0	9,552.4	416.2	9,136.2	95.64
0.20	0.6	5,876.2	281.0	5,595.2	95.22
	0.8	6,904.8	323.4	6,581.4	95.32
	1.0	7,891.6	360.2	7,531.4	95.44

Table 3.4. Descriptive statistics of the parents of breeding animals simulated at two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Weibull shape parameter (ρ)	Sires (n)	Breeding progeny per sire (n)	Dams (n)	Breeding progeny per dam (n)
0.05	0.6	304.6	22.79	963.6	7.19
	0.8	359.2	23.35	1,467.2	5.71
	1.0	399.2	23.95	1,976.0	4.84
0.20	0.6	263.4	22.33	718.8	8.19
	0.8	308.0	22.43	1,026.4	6.73
	1.0	343.6	22.97	1,392.6	5.67

Table 3.5. Descriptive statistics of actual observations[a] of female reproductive life (RL) simulated at two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Weibull shape parameter (ρ)	Actual observations (n)	Average CG[b] size (n)	Median RL (yr)	Maximum RL (yr)
0.05	0.6	4,097.0	204.85	5.82	677.36
	0.8	5,502.6	275.13	5.64	258.41
	1.0	6,636.2	331.81	5.56	107.04
0.20	0.6	3,095.2	154.76	9.26	5,337.42
	0.8	4,081.4	204.07	8.36	757.17
	1.0	5,031.4	251.57	7.62	345.54

[a]Phenotypic values.
[b]Contemporary group.

Table 3.6. Descriptive statistics of underlying observations[a] of female reproductive life (RL) simulated at two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Weibull shape parameter (ρ)	Underlying observations (n)	Mean (ln yr)	SD (ln yr)	Min. (ln yr)	Max. (ln yr)
0.05	0.6	4,097.0	1.44	2.18	-11.95	6.46
	0.8	5,502.6	1.50	1.63	-8.16	5.50
	1.0	6,636.2	1.52	1.33	-7.15	4.66
0.20	0.6	3,095.2	1.98	2.35	-11.21	8.47
	0.8	4,081.4	1.92	1.79	-8.47	6.61
	1.0	5,031.4	1.86	1.43	-7.10	5.82

[a]Natural logarithms of the phenotypic values.

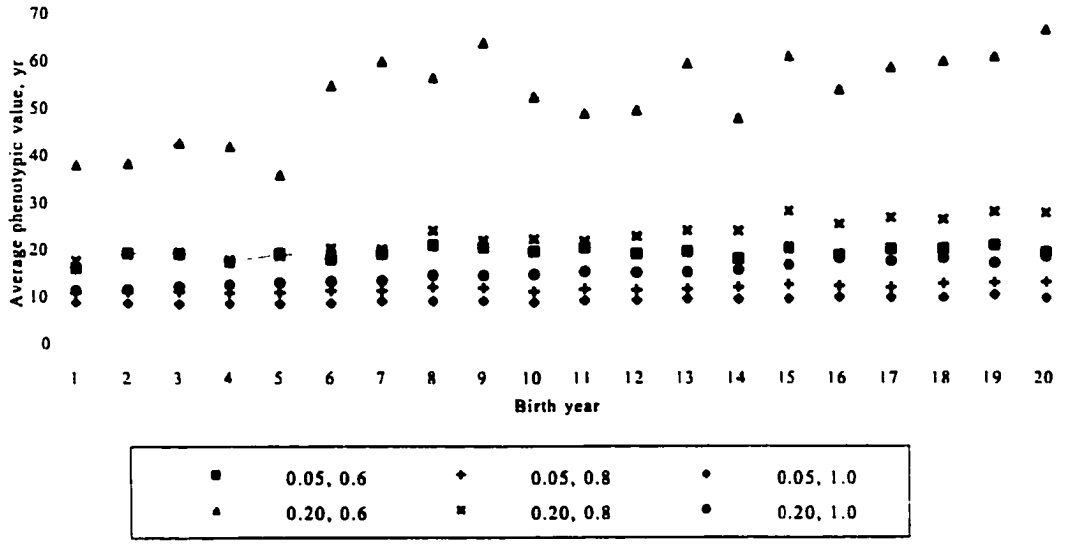

Figure 3.1. Average phenotypic values by birth year for female reproductive life (RL) simulated using two levels of true heritability (0.05 and 0.20) and three levels of the Weibull shape parameter (0.6, 0.8, and 1.0).

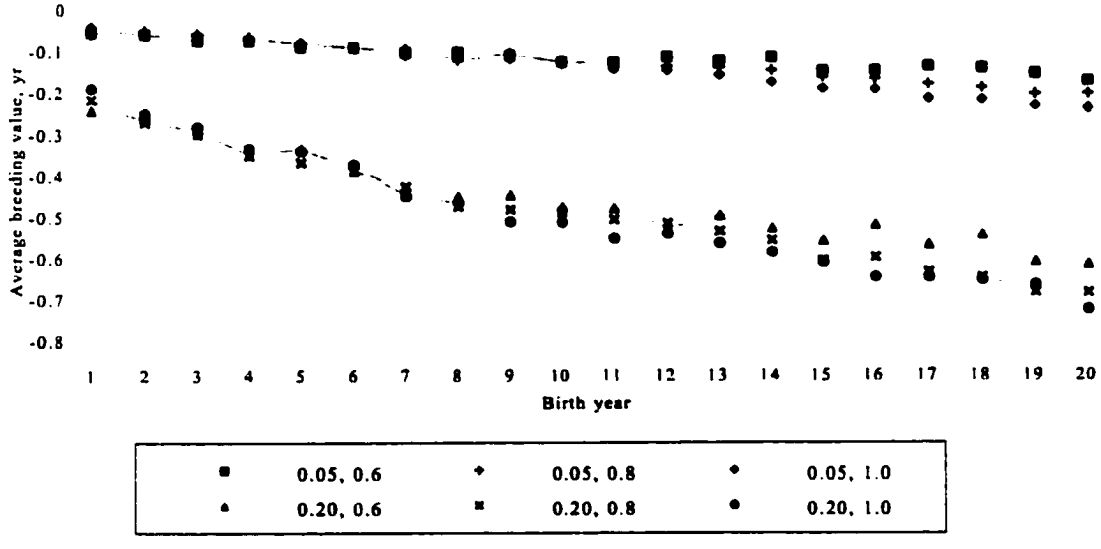

Figure 3.2. Average breeding values by birth year for female reproductive life (RL) simulated using two levels of true heritability (0.05 and 0.20) and three levels of the Weibull shape parameter (0.6, 0.8, and 1.0).

Method R (**MAP R**) procedure similar to that developed by Snelling (1994) for use with binary threshold models and later used by Snelling et al. (1995) and Hyde et al. (1995, 1996) to analyze stayability of beef females. The major difference between the two procedures was in the system of Newton-Raphson equations used to compute maximum *a posteriori* (**MAP**) solutions. The software I developed for the MAP R procedure specific to survival models is given in Appendix B.

As for the threshold model MAP R procedure (Snelling, 1994), in the survival model MAP R procedure, the regression of low accuracy MAP solutions on higher accuracy MAP solutions was used to estimate heritability. High accuracy solutions were based on all observations, whereas low accuracy solutions were based on randomly selected 50% subsamples of the data.

For each subsample, binary iteration (i.e., bisection) was used until the regression of low on high MAP solutions was between 0.9999 and 1.0001 or a maximum of 15 rounds was reached. If the regression was greater (less) than 1.0001 (0.9999), h^2 was too low (high) and h^2 was adjusted accordingly. Within each round of binary iteration, Newton-Raphson iteration was applied to obtain the required MAP solutions.

The MAP solutions of $\boldsymbol{\beta}$ and $\mathbf{u}$ on the underlying logarithmic scale were obtained from the system of equations (Kachman, 1999)

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}\mathbf{X} & \mathbf{X}'\mathbf{R}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}\mathbf{X} & \mathbf{Z}'\mathbf{R}\mathbf{Z}+\mathbf{G}^{-1} \end{bmatrix}^{[k]} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{u}} \end{bmatrix}^{[k-1]} = \begin{bmatrix} \mathbf{X}'\mathbf{R}\mathbf{y}^{*} \\ \mathbf{Z}'\mathbf{R}\mathbf{y}^{*} \end{bmatrix}^{[k]},$$

where $\hat{\boldsymbol{\beta}}$ and $\hat{\mathbf{u}}$ denote vectors of estimated fixed effects and frailties (i.e., random effects) on the logarithmic scale, **X** and **Z** denote incidence matrices of zeros and ones relating the effects in $\hat{\boldsymbol{\beta}}$ and $\hat{\mathbf{u}}$ to observations in $\mathbf{y}^*$, $\mathbf{G} = \sigma_a^2\mathbf{A} = \text{var}(\mathbf{u})$ such that σ_a^2 is the additive direct genetic variance of the log-frailties and **A** is Wright's numerator relationship matrix, and k is the round of iteration. In addition, **R** is a diagonal matrix defined as $\mathbf{R} = -\frac{\partial^2 \ln L(\theta)}{\partial \eta \partial \eta'}$ and $\mathbf{y}^*$ is a vector of working variates defined as $\mathbf{y}^* = \eta + \mathbf{R}^{-1}\mathbf{v} = \eta + \mathbf{R}^{-1}\frac{\partial \ln L(\theta)}{\partial \eta}$, where $\theta = (\beta\ \mathbf{u})'$ and $\eta = \mathbf{x}'\beta + \mathbf{z}'\mathbf{u}$. For the ith observation, $R_{ii} = \exp(\rho \ln t_i + \eta_i)$ and $y_i^* = w_i - R_{ii} + R_{ii}\eta_i$, where $w_i = 0$ if $i \in RC$ and $w_i = 1$ if $i \in UC$. For unknown observations, as for sires, foundation dams, and females not included in the subsamples, $R_{ii} = 0$ and $y_i^* = 0$.

Observations on female RL were assumed to be uncensored and were transformed to their natural logarithms prior to analysis. In addition, all breeding animals were included in the numerator relationship matrix, and because of the effect of year on RL due to natural selection, year born (equivalent to contemporary group) was included as the only fixed effect. Fixed effect classes in the complete and partial data sets were required to have variation among observations to ensure convergence of the Newton-Raphson iteration algorithm (Snelling, 1994). Convergence of the MAP solutions was declared when the mean squared difference between the two most recent solution vectors was less than 0.00001 or when the number of rounds reached 20.

Genetic Predictions. Predictions of genetic merit, or estimated breeding values, for underlying RL were obtained for all animals using Newton-Raphson iteration with both true and estimated heritabilities. Estimated h^2 was the overall median estimate for each cell in the factorial arrangement defined by the two levels of true heritability (0.05 and 0.20) and

the three levels of the Weibull shape parameter (0.6, 0.8, and 1.0). Product moment and Spearman rank correlations were calculated between the simulated true breeding values and the estimated breeding values and also between both sets of estimated breeding values.

Accuracies. Accuracies associated with the genetic predictions for RL were computed as $r_i = [1 - \frac{PEV_i}{\sigma_a^2(1 + F_i)}]^{0.5}$, where r_i is the ith animal's accuracy, PEV_i is the error variance of the ith animal's prediction, and F_i is the ith animal's inbreeding coefficient. Prediction error variances were obtained from the diagonal elements of the inverse of the coefficient matrix assembled in the last round of Newton-Raphson iteration (Snelling, 1994; Tempelman, 1998). Average accuracies of the genetic predictions were computed as estimates of the expected correlations between true and estimated breeding values and were compared to the actual correlations described above.

Comparisons Between Stayability and Survival Analyses of Simulated Data

Stayability (ST) was analyzed using 10 of the data sets simulated previously at both levels of true h^2 and $\rho = 0.8$. I defined ST as the probability of a female having a calf at or after age six given selection as a replacement heifer. Stayability observations were obtained from the simulated data by denoting all RL observations less than five yr a failure ("0") and all those greater than or equal to five yr a success ("1"). Note that a RL of 5 yr is equivalent to an age of six yr. The average incidence rates of successes and failures for five data sets at each level of h^2 are given in Table 3.7. Differences in incidence rates for ST between levels of heritability reflect differences in median RL.

I tried to develop a method for converting true heritability of RL on the underlying logarithmic scale to true heritability of ST on the underling liability scale using a three step

Table 3.7. Incidence rates of stayability (ST) observations based on reproductive life (RL) data simulated using two levels of true heritability (h_{RL}^2) and one level of the Weibull shape parameter ($\rho = 0.8$).

True heritability of RL (h_{RL}^2)	Observations (n)	Failures (%)	Successes (%)
0.05	5,502.6	46.93	53.07
0.20	4,081.4	38.37	61.63

approach that involved converting heritability of underlying RL to heritability of observed RL, then heritability of observed RL to heritability of observed ST, and finally heritability of observed ST to heritability of underlying ST.

For both traits, conversion formulas for expressing heritability on the underlying scale in terms of heritability on the observed scale are available in the literature. Ducrocq (1999a) provides a formula for converting heritability of underlying RL to heritability of observed RL, and Snelling (1994) describes Dempster and Lerner's approach for expressing heritability on the underlying liability scale to that on the observed threshold scale.

To develop a formula for converting heritability of observed RL to that of observed ST, I first modeled observed RL as a binary response by defining the probability of surviving beyond time T as a success to obtain the multi-hit model discussed by Kalbfleisch and Prentice (1980). I then assumed that the multi-hit model for observed RL and the probit threshold model for observed ST were equivalent and applied the delta method (Ducrocq, 1999a; Korsgaard et al., 1999a), which is based on the variance of a first-order Taylor series expansion of a function, to develop an expression for the additive genetic variance associated with the probit threshold model in terms of the additive genetic variance of the multi-hit model.

Although this approach seemed reasonable to me, I decided against using it for several reasons. First, Korsgaard et al. (1999a) reported that the conversion formula of Ducrocq (1999a) "appears dubious". Second, Dempster and Lerner's conversion formula is an approximation and requires knowing the true probability of success on the observed scale (Snelling, 1994). Third, I was uncertain whether ignoring fixed effects in the application of the delta method was technically correct.

Therefore, I estimated heritability of underlying ST using the **dscat** procedure developed by Kaiser (1996) for the Animal Breeder's Tool Kit (Golden et al., 1992). This procedure is a performance-programmed application of Method R for estimating h^2 from a multivariate model consisting of one categorical and any number of continuous traits. In addition, **dscat** uses Fisher scoring rather than Newton-Raphson iteration to obtain animal MAP solutions.

To obtain genetic predictions and estimates of the fixed effect solutions for ST on the underlying liability scale, the threshold model MAP R procedure described by Snelling (1994) and Snelling et al. (1995) was applied. Contemporary group, defined by year born, was the only fixed effect present in the model, and animal was the only random effect. Contemporary groups were checked for variation in observations because the Newton-Raphson algorithm used in the MAP R procedure will not converge if all observations within a fixed effect group are the same (Snelling, 1994). Convergence of the MAP solutions was declared when the mean squared difference between the two most recent solution vectors was less than 0.00001 or when the number of rounds reached 20.

Accuracy associated with each animal's prediction for ST was computed as $r_i = [1 - \frac{PEV_i}{\hat{\sigma}_a^2(1+F_i)}]^{0.5}$, where r_i is the ith animal's accuracy, PEV_i is the error variance of the ith animal's prediction, and F_i is the ith animal's inbreeding coefficient. Prediction error variances were obtained from the diagonal elements of the inverse of the coefficient matrix assembled in the last round of Newton-Raphson iteration (Snelling, 1994; Tempelman, 1998).

Correlations were obtained between solutions computed on the underlying scale for RL and ST using true and estimated h^2, respectively. Differences in accuracies between the genetic predictions for the two traits were also obtained.

The Effects of Right Censoring on Parameter Estimation and Genetic Prediction

I modified the simulation program to accommodate right censoring of observations on RL. The level of censoring was based on an input percentage, and an integer between one and 100 was randomly assigned to each replacement female with phenotype for RL greater than one. If the assigned integer was less than or equal to the input level of censoring, then the replacement female was considered to be censored, and her censoring time was randomly assigned as an integer between one and the largest integer less than her phenotypic value for RL. For example, if the heifer's phenotype for RL was 7.45 yr, then her censoring time was a randomly generated integer between one and seven. Females with a phenotype less than one were not censored to avoid transformed observations of zero.

A total of 18 simulated data sets were created for true heritabilities of 0.05 and 0.20, a shape parameter of 0.8, and censoring levels of 10, 40, and 70% using three of the same seed values from previous simulations. Table 3.8 summarizes the observations for each level

of h^2 and percentage of censoring averaged over three replicates per cell. The actual percentage of censoring was lower than the simulated percentage because of the constraint I imposed in the simulator of not censoring females with an observed RL less than one. Consequently, median RL for censored females were fairly consistent within level of heritability, but median RL for uncensored females decreased as the level of censoring increased. As the level of censoring increased, a greater proportion of uncensored females had an observed RL less than one.

I estimated heritabilities using the survival model MAP R procedure described above and obtained MAP predictions on the underlying logarithmic scale using both true and median estimates of h^2. The only fixed effect was contemporary group, defined by year born, and the only random effect was animal. Each contemporary group was first checked for variation in censoring status, such that contemporary groups with only censored observations were excluded from the analysis, and then for variation in the transformed observations. According to Kachman (1999), if all records in a fixed effect group are right censored, then the estimate of the risk factor for that group will go to negative infinity.

Accuracies associated with the genetic predictions were computed as $r_i = [1 - \frac{PEV_i}{\hat{\sigma}_a^2(1+F_i)}]^{0.5}$, where r_i is the ith animal's accuracy, PEV_i is the error variance of the ith animal's prediction, and F_i is the ith animal's inbreeding coefficient. Prediction error variances were obtained from the diagonal elements of the inverse of the coefficient matrix assembled in the last round of Newton-Raphson iteration (Snelling, 1994; Tempelman, 1998).

Table 3.8. Descriptive statistics of censored and uncensored observations of female reproductive life (RL) simulated at two levels of true heritability (h^2), one level of the Weibull shape parameter ($\rho = 0.8$), and four levels of censoring.

True heritability (h^2)	Level of censoring (%)	Observations (n)	Censored observations (%)	Median RL (yr)	
				Censored	Uncensored
0.05	0	5,502.60[a]	--	--	5.64
	10	5,605.67[b]	8.41	3.00	5.55
	40	6,259.33[b]	33.78	3.00	4.76
	70	6,973.33[b]	58.96	3.00	2.70
0.20	0	4,081.40[a]	--	--	8.36
	10	4,213.67[b]	8.84	4.00	8.01
	40	4,706.00[b]	34.88	4.33	6.96
	70	5,153.33[b]	60.59	4.33	4.53

[a]Averaged over five data sets.
[b]Averaged over three data sets.

I compared the mean accuracies of all animals and sires only at each level of censoring (0, 10, 40, and 70%) to determine the effects of censoring on accuracy of genetic prediction for RL. Because of the changes in population structure imposed by censoring, such that censored females were replaced sooner and by different females than if they were uncensored, I did not compare accuracies on an individual basis.

Genetic Evaluation of Female Reproductive Life in Red Angus Cattle

A major obstacle to survival analyses of female RL in beef cattle is the lack of reproductive data on cows. Although female reproductive data are among the most easily collected and economically important data that can be recorded, beef cattle performance programs have traditionally focused on recording and evaluating measurements taken on calves (Snelling, 1998).

In the past decade, however, breed associations in the United States and Canada have become interested in recording programs that emphasize collection of data on all animals in a herd rather than on only those animals a breeder intends to register (Golden, 1997; Cunningham, 1998). The idea behind such programs, called inventory-based or whole-herd reporting systems, is to encourage complete reporting of data (Golden, 1997). Two major benefits of such systems are the elimination of reporting bias from incomplete or selective reporting and the opportunity to gain additional information for the genetic evaluation of female reproductive traits (Golden, 1996).

The Red Angus Association of America (**RAAA**) was the first beef breed association to adopt an inventory-based reporting system when it implemented Total Herd Reporting (**THR**) in 1995 (Gilbert, 1997). Under THR, breeders must account for the production of all females in their herd each year. The annual data required by THR for each cow on inventory are either 1) a calf record, whether dead or alive, 2) a reason code as to why the cow did not calve, or 3) a cow disposal code. Unless one of the three items is reported, the cow is inactivated (Hough and Ponder, 1998).

Data

The RAAA provided disposal information collected by the THR program through April, 2000. The information included records on 138,957 animals and consisted of each animal's identification number, its disposal code, and the date the RAAA received the disposal information from the breeder. I selected only those dams with a valid dam disposal code (Table 3.9) and combined these data with 670,342 calving records on 176,512 dams

Table 3.9. Distribution of Red Angus cows by reason for disposal.

Disposal code	Reason for disposal[a]	Cows culled (n)	Cows culled (%)
9	Died — age	1,253	1.10
10	Culled — physical defect	1,961	1.72
11	Culled — fertility	8,153	7.16
12	Culled — performance/productivity	12,663	11.11
13	Culled — temperament	627	0.55
14	Culled — age	4,538	3.98
15	Culled — other, including sold but not transferred	84,748	74.38
		113,943	100.00

[a]Ponder, 2000.

used in the ST evaluation conducted by Colorado State University for the January, 2000, Red Angus sire summary.

I defined RL as the length of time in years from when a cow produced her first calf as a two-yr-old to when she was culled for infertility (disposal code = 11) or censored, whichever came first. Because RL is a measure of sustained fertility, each cow was required to produce at least one calf annually until culling or censoring. In addition, I considered only those cows who had the opportunity to participate in the THR program, either by calving or by being culled in 1995 or later.

From the data set used in the ST evaluation, 129,995 cows calved as two-yr-olds, or between 639 and 1,003 d of age. Of these cows, 93,918 produced at least one calf each year, which was determined by computing their calving intervals and verifying that all calving intervals of each cow were between 8 and 16 mo (245 to 485 d). Of the cows that produced

at least one calf each year, only 19,063 calved or were culled for infertility in 1995 and beyond.

The RL of the dams were computed in yr from the number of days between the birth date of their first calf and their culling or censoring date divided by 365. All RL were required to be greater than zero and were transformed to their natural logarithms prior to analysis.

A cow's culling date was considered to occur on January 1 or July 1 of the year the RAAA received the cow inventory report from the breeder. It was assigned as January 1 if the report was received between January 1 and June 30 and as July 1 if it was received between July 1 and December 31. The censoring date was December 1, 1999, which was the date the RAAA submitted calving records to Colorado State University for the ST evaluation.

After the initial editing process, the dams were assigned to contemporary groups using the same contemporary group designations from the ST evaluation. I checked the contemporary groups for variation in censoring status (0 = censored, 1 = uncensored) and for variation among observations. Contemporary groups in which all observations were censored or in which there was no variation among observations were eliminated.

The final data set consisted of observations on 8,504 dams in 912 contemporary groups, of which 69.76% were censored. Table 3.10 provides descriptive statistics of the observations in the final data set. Median RL was higher for censored females than uncensored females, but the uncensored observations on the underlying scale had a greater range.

Table 3.10. Descriptive statistics of actual and underlying observations of reproductive life (RL) for censored and uncensored Red Angus cows (n = 8,504).

Statistic	Actual RL (yr)		Underlying RL (ln yr)	
	Censored[a]	Uncensored[b]	Censored[a]	Uncensored[b]
Median	2.8000	1.9069	1.0296	0.6455
Mean	3.3564	2.7863	0.9741	0.7351
SD	2.1878	1.6692	0.5330	0.6084
Minimum	0.2356	0.0822	-1.4456	-2.4987
Maximum	13.7480	11.8548	2.6209	2.4727

[a]n = 5,932.
[b]n = 2,572.

Analytical Procedures

In order to use the survival model MAP R procedure, I first had to estimate the Weibull shape parameter. I compiled data on dams born in 1992 who calved as two-yr-olds in 1994 and computed their probabilities of being culled for infertility in 1995 through 1999 as a percentage of the cows that calved in the previous year (Table 3.11). Using the same technique for determining levels of the shape parameter when developing the survival model MAP R procedure, I computed *H(t)*, the cumulative hazard, from these probabilities and then regressed ln *H(t)* on ln *t*. Estimates of the intercept ($\rho \ln \lambda$) and slope (ρ) were 0.8887 ± 0.0358 and 0.9405 ± 0.0286, respectively, with an R^2 for the regression of 0.9963.

I estimated heritability of RL using the survival model MAP R procedure described previously and obtained MAP predictions of RL on the underlying logarithmic scale using the median estimate of h^2. The only fixed effect in the model was contemporary group, and the only random effect was animal.

Table 3.11. Probabilities of culling for infertility for 1992-born Red Angus cows from 1995 through 2000.

Year	Cows that calved in previous year (n)	Cows culled for infertility in current year (n)	Cows culled for infertility in current year (%)	Cumulative percentage of cows culled for infertility (%)
1995	5,765	142	2.4631	2.4631
1996	4,400	96	2.1818	4.6449
1997	3,571	81	2.2683	6.9132
1998	2,908	47	1.6162	8.5294
1999	2,280	50	2.1930	10.7224
2000	1,062	34	3.2015	13.9239

The numerator relationship matrix was developed from pedigrees of the dams, their parents, and their grandparents. There were 20,917 animals in the pedigree file, and these animals were represented by 3,401 sires and 14,979 dams. The 8,504 dams with observations on RL were represented by 1,572 sires and 6,659 dams.

Accuracy associated with each animal's MAP prediction for RL was computed as $r_i = [1 - \frac{PEV_i}{\hat{\sigma}_a^2(1+F_i)}]^{0.5}$, where r_i is the ith animal's accuracy, PEV_i is the error variance of the ith animal's prediction, and F_i is the ith animal's inbreeding coefficient. Prediction error variances were obtained from the diagonal elements of the inverse of the coefficient matrix assembled in the last round of Newton-Raphson iteration (Snelling, 1994; Tempelman, 1998). All results were compared to those from the ST evaluation.

CHAPTER 4

RESULTS AND DISCUSSION

Development of Statistical Methodology

Heritability Estimates

Heritability estimates obtained from each of the 30 simulated data sets are given in Table 4.1. Pooled estimates for each cell of the two by three factorial arrangement of h^2 and ρ are shown in Table 4.2. Both median and mean h^2 estimates are presented, but only median estimates will be discussed because of recent research indicating that the means of h^2 estimates obtained from the Method R procedure are biased (S. Mahabir, personal communication).

The pooled median estimates were consistently less than their true values, particularly when true h^2 was 0.20. Although I do not know the reason for the underestimation, one explanation may be due to the natural selection for RL evident in the simulated data. Theoretically, selection in one direction over many generations will reduce the genetic variation in a trait (Bourdon, 1997), and thus decrease heritability.

In another study involving simulated data, Ducrocq and Casella (1996) reported consistent overestimates of the genetic variance for length of productive life. Their estimates were obtained from a Laplacian integration technique applied to an animal model. They attributed the overestimates to a larger number of parameters being integrated out of the joint posterior density with an animal model than with a sire model.

Table 4.1. Median and mean heritability (h^2) estimates for reproductive life (RL) obtained from data sets simulated using two levels of true h^2 and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Data set	Heritability estimates (n)	Median $\hat{h}^2$	Mean $\hat{h}^2$	SEM
0.05	0.6	1	20	0.0408	0.0428	0.0020
		2	14[a]	0.0144	0.0206	0.0024
		3	20	0.0430	0.0445	0.0021
		4	20	0.0356	0.0404	0.0018
		5	20	0.0403	0.0367	0.0034
	0.8	1	20	0.0366	0.0404	0.0023
		2	20	0.0376	0.0750	0.0117
		3	20	0.0346	0.0333	0.0023
		4	20	0.0251	0.0394	0.0029
		5	20	0.0557	0.0541	0.0022
	1.0	1	20	0.0354	0.0318	0.0032
		2	20	0.0464	0.0481	0.0051
		3	20	0.0537	0.0491	0.0025
		4	20	0.0322	0.0347	0.0028
		5	20	0.0300	0.0302	0.0008
0.20	0.6	1	20	0.1484	0.1740	0.0095
		2	20	0.1465	0.1560	0.0038
		3	20	0.2588	0.2177	0.0178
		4	20	0.1250	0.1404	0.0114
		5	20	0.1465	0.1591	0.0165
	0.8	1	20	0.1982	0.2049	0.0162
		2	20	0.1030	0.1118	0.0044
		3	20	0.1382	0.1361	0.0032
		4	20	0.1416	0.1331	0.0094
		5	20	0.1641	0.1226	0.0107
	1.0	1	20	0.1370	0.1355	0.0018
		2	20	0.1924	0.1632	0.0100
		3	20	0.1523	0.1263	0.0081
		4	20	0.1494	0.1784	0.0107
		5	20	0.1162	0.1221	0.0048

[a]Six estimates did not converge and approached zero.

Table 4.2. Pooled median and mean heritability (h^2) estimates for reproductive life (RL) obtained from data sets (n = 5) simulated using two levels of true h^2 and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Heritability estimates (n)	Median $\hat{h}^2$	Mean $\hat{h}^2$	SEM
0.05	0.6	94[a]	0.0381	0.0381	0.0013
	0.8	100	0.0378	0.0464	0.0030
	1.0	100	0.0352	0.0388	0.0016
0.20	0.6	100	0.1465	0.1694	0.0062
	0.8	100	0.1431	0.1417	0.0055
	1.0	100	0.1370	0.1451	0.0041

[a]Six estimates did not converge and approached zero.

Table 4.3. Descriptive statistics of contemporary group (CG) solutions computed using true[a] and estimated[b] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	CG (n)	Mean (ln yr)	SD (ln yr)	Min. (ln yr)	Max. (ln yr)
0.05	0.6	20	-1.3883	0.0786	-1.5331	-1.2263
			-1.4060	0.0790	-1.5509	-1.2444
	0.8	20	-1.7152	0.0626	-1.8451	-1.6081
			-1.7347	0.0648	-1.8703	-1.6231
	1.0	20	-2.0574	0.0676	-2.1932	-1.9322
			-2.0811	0.0707	-2.2233	-1.9500
0.20	0.6	20	-1.5933	0.1092	-1.7976	-1.4212
			-1.6575	0.1144	-1.8746	-1.4740
	0.8	20	-1.9287	0.1036	-2.1224	-1.7310
			-2.0001	0.1112	-2.2066	-1.7833
	1.0	20	-2.2533	0.0935	-2.4360	-2.0862
			-2.3366	0.1084	-2.5437	-2.1412

[a]First line of cell.
[b]Second line of cell.

I recorded the computer execution times for estimating heritabilities, but detailed results are not presented because I used several different computers and other users were running jobs concurrently. In general, it took approximately one to two d to get 20 h^2 estimates from each data set, taking longer for larger data sets. For each h^2 estimate, it took approximately 10 rounds of binary iteration until convergence, and for each round of binary iteration, it took two to three rounds of Newton-Raphson iteration until convergence. Five to seven rounds of Newton-Raphson iteration were usually required during the first round of binary iteration. Based on personal experience, these statistics were very similar to those usually obtained during MAP R threshold analyses.

Genetic Predictions

Contemporary group solutions for underlying RL computed using true and the pooled median estimates of heritability are summarized in Table 4.3. The solutions are similar, but those computed using estimated heritability were lower on average and had a slightly higher standard deviations than those computed using true heritability. Trends over time for the contemporary group solutions (not shown) were essentially flat with a slight downward slope, which was more apparent for data sets simulated with a true heritability of 0.20.

Descriptions for true and estimated breeding values (**EBV**) for underlying RL are given for all animals and sires only in Tables 4.4 and 4.5. In contrast to the contemporary group solutions, EBV computed using estimated heritabilities were higher and had a slightly lower standard deviation than EBV computed using true heritabilities. Most likely, this results from the slight difference in the augmentation of the random effects block of the Newton-Raphson mixed model equations.

Table 4.4. Descriptive statistics for all animals of true breeding values[a] and estimated breeding values computed using true[b] and estimated[c] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Animals (n)	Mean (ln yr)	SD (ln yr)	Min. (ln yr)	Max. (ln yr)
0.05	0.6	6,923.4	-0.0920	0.2898	-1.1142	1.0563
			-0.0119	0.1062	-0.6262	0.4571
			-0.0096	0.0886	-0.5340	0.3812
	0.8	8,380.6	-0.1046	0.2925	-1.2609	1.0408
			-0.0186	0.1130	-0.6701	0.4347
			-0.0150	0.0944	-0.5745	0.3698
	1.0	9,552.4	-0.1170	0.2960	-1.2726	1.0864
			-0.0173	0.1207	-0.6429	0.5155
			-0.0128	0.0977	-0.5270	0.4253
0.20	0.6	5,876.2	-0.3459	0.6068	-2.8283	1.8485
			-0.0441	0.3067	-1.7918	1.0821
			-0.0377	0.2574	-1.5684	0.8854
	0.8	6,904.8	-0.3743	0.6134	-2.6056	1.9020
			-0.0586	0.3298	-1.7747	1.2276
			-0.0485	0.2769	-1.5257	1.0089
	1.0	7,891.6	-0.3894	0.6245	-2.7839	1.9941
			-0.0652	0.3422	-1.8294	1.1981
			-0.0508	0.2806	-1.5649	0.9733

[a]First line of cell.
[b]Second line of cell.
[c]Third line of cell.

Table 4.5. Descriptive statistics for all sires of true breeding values[a] and estimated breeding values computed using true[b] and estimated[c] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Sires (n)	Mean (ln yr)	SD (ln yr)	Min. (ln yr)	Max. (ln yr)
0.05	0.6	326.2	-0.0852	0.2875	-0.8796	0.7700
			-0.0073	0.1491	-0.5322	0.4571
			-0.0061	0.1268	-0.4632	0.3812
	0.8	378.0	-0.0984	0.2968	-1.0828	0.8341
			-0.0183	0.1532	-0.5649	0.4347
			-0.0151	0.1307	-0.4962	0.3698
	1.0	416.2	-0.1100	0.2999	-0.9804	0.7359
			-0.0100	0.1672	-0.5456	0.5152
			-0.0075	0.1388	-0.4579	0.4253
0.20	0.6	281.0	-0.3192	0.6101	-2.1229	1.4612
			-0.0414	0.3936	-1.2802	1.0414
			-0.0408	0.3434	-1.1510	0.8589
	0.8	323.4	-0.3579	0.6181	-2.2790	1.5319
			-0.0394	0.4189	-1.5358	1.1525
			-0.0356	0.3685	-1.3952	0.9764
	1.0	360.2	-0.3469	0.6371	-2.1380	1.6288
			-0.0322	0.4290	-1.3116	1.1981
			-0.0263	0.3703	-1.1671	0.9729

[a]First line of cell.
[b]Second line of cell.
[c]Third line of cell.

The magnitude of the true breeding values is very different from the magnitude of the EBV. However, true breeding values, denoted by $\mathbf{u}_{true}$, were simulated using the formula $\mathbf{y} = -\ln\lambda\,\mathbf{1} - \frac{1}{\rho}(\mathbf{u}_{true} - \mathbf{e})$, and estimated breeding values, denoted by $\mathbf{u}_{est}$, were obtained from the model $\mathbf{y} = \mathbf{Xb} + \mathbf{Zu}_{est}$. In the first model, **y** was the vector of transformed observations on RL and **e** was the vector of error terms from an extreme value distribution associated with the observations in **y**. In the second model, **y** was also the vector of transformed observations, **b** was the vector of contemporary group effects, and **X** and **Z** were incidence matrices of zeros and ones relating fixed contemporary group and random animal effects to observations in **y**.

Trends in the true breeding values and EBV over time (not shown) depicted a decrease in breeding value, but true BV decreased at a much faster rate than EBV and the decrease was more pronounced for data simulated using a true heritability of 0.20. The value of ρ seemed to have no effect on the breeding values, as it was incorporated into the contemporary group solutions.

Table 4.6 shows product moment and Spearman rank correlations between EBV computed using true and estimated heritabilities for all animals and sires only. The correlations were all very high (greater than 0.98). As expected, they were greater for sires and for data simulated with a heritability of 0.20. The correlations decreased with increasing values of ρ, but heritability estimates also decreased with increased values of ρ. The correlations presented in Table 4.6 lend support to the hypothesis of Snelling (1994) that the heritabilities used to predict genetic merit have more influence on the scale of predictions and accuracies than on the relative merit of an individual animal compared to other animals in the evaluation.

Table 4.6. Correlations for all animals and sires between estimated breeding values computed using true and estimated heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Product moment correlations		Spearman rank correlations	
		Animals	Sires	Animals	Sires
0.05	0.6	0.9986	0.9991	0.9934	0.9990
	0.8	0.9983	0.9988	0.9940	0.9986
	1.0	0.9970	0.9979	0.9927	0.9978
0.20	0.6	0.9960	0.9974	0.9827	0.9971
	0.8	0.9947	0.9965	0.9835	0.9966
	1.0	0.9931	0.9957	0.9832	0.9954

Accuracies

Tabes 4.7 and 4.8 provide summaries of the accuracies associated with EBV computed using true and estimated heritabilities for all animals and sire only. In general, accuracies of the predictions increased with h^2, but also with ρ because of the increase in population size. Accuracies were smaller for EBV computed using estimated heritabilities, but these heritabilities were lower than the true heritabilities. As expected, average accuracies of sires were higher than those for all animals.

The mean accuracy was used as an estimate of the expected correlation between true breeding values and EBV. Both product moment and Spearman rank correlations were close to but consistently higher than expected for all animals (Table 4.9), but these comparisons varied among sires (Table 4.10). Although mean accuracy is intended to reflect the expected value of the correlation between true and predicted breeding values, its computation does not

account for selection within the population or bias that may result from nonlinear procedures (Snelling, 1994). In this study, the simulated data did show evidence of natural selection for decreased RL on the underlying scale.

Table 4.7. Descriptive statistics for all animals of accuracies of estimated breeding values computed using true[a] and estimated[b] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Animals (n)	Mean	SD	Min.	Max.
0.05	0.6	6,923.4	0.3048	0.2122	0	0.7499
			0.2786	0.1952	0	0.7112
	0.8	8,380.6	0.3435	0.2069	0	0.7740
			0.3146	0.1910	0	0.7342
	1.0	9,552.4	0.3671	0.2024	0	0.7961
			0.3302	0.1841	0	0.7487
0.20	0.6	5,876.2	0.3994	0.3086	0.0016	0.8679
			0.3667	0.2856	0.0019	0.8402
	0.8	6,904.8	0.4464	0.2994	0.0016	0.8933
			0.4088	0.2781	0	0.8654
	1.0	7,891.6	0.4798	0.2887	0.0016	0.9057
			0.4362	0.2669	0	0.8770

[a]First line of cell.
[b]Second line of cell.

Table 4.8. Descriptive statistics for all sires of accuracies of estimated breeding values computed using true[a] and estimated[b] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Sires (n)	Mean	SD	Min.	Max.
0.05	0.6	326.2	0.5075	0.1312	0	0.7497
			0.4685	0.1251	0	0.7112
	0.8	378.0	0.5401	0.1320	0.0255	0.7740
			0.5001	0.1270	0.0218	0.7342
	1.0	416.2	0.5640	0.1279	0.0436	0.7961
			0.5141	0.1232	0.0355	0.7487
0.20	0.6	281.0	0.6686	0.1448	0.0378	0.8618
			0.6264	0.1444	0.0307	0.8327
	0.8	323.4	0.6919	0.1428	0.0848	0.8933
			0.6489	0.1443	0.0678	0.8654
	1.0	360.2	0.7126	0.1341	0.1295	0.9057
			0.6658	0.1372	0.1001	0.8770

[a]First line of cell.
[b]Second line of cell.

Table 4.9. Descriptive statistics for all animals of correlations between true breeding values and estimated breeding values computed using true[a] and estimated[b] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Animals (n)	Expected correlation[c]	Product moment correlation	Spearman rank correlation
0.05	0.6	6,912.8	0.3048	0.3539	0.3224
			0.2786	0.3531	0.3224
	0.8	8,325.0	0.3435	0.3999	0.3725
			0.3146	0.3989	0.3707
	1.0	9,458.6	0.3671	0.4099	0.3843
			0.3302	0.4057	0.3800
0.20	0.6	5,834.0	0.3994	0.4813	0.4441
			0.3667	0.4788	0.4412
	0.8	6,934.0	0.4464	0.5157	0.4834
			0.4088	0.5107	0.4789
	1.0	7,941.4	0.4798	0.5470	0.5124
			0.4362	0.5409	0.5058

[a]First line of cell.
[b]Second line of cell.
[c]Equivalent to mean accuracy.

Table 4.10. Descriptive statistics for all sires of correlations between true breeding values and estimated breeding values computed using true[a] and estimated[b] heritabilities for underlying reproductive life (RL) simulated using two levels of true heritability (h^2) and three levels of the Weibull shape parameter (ρ).

True heritability (h^2)	Shape parameter (ρ)	Sires (n)	Expected correlation	Product moment correlation	Spearman rank correlation
0.05	0.6	320.8	0.5075	0.4941	0.4681
			0.4685	0.4935	0.4679
	0.8	369.8	0.5401	0.5609	0.5516
			0.5001	0.5583	0.5507
	1.0	415.2	0.5640	0.5578	0.5472
			0.5141	0.5532	0.5438
0.20	0.6	276.4	0.6686	0.6286	0.6228
			0.6264	0.6235	0.6169
	0.8	320.8	0.6919	0.6472	0.6428
			0.6489	0.6396	0.6379
	1.0	361.6	0.7126	0.6967	0.6857
			0.6658	0.6869	0.6780

[a]First line of cell.
[b]Second line of cell.
[c]Equivalent to mean accuracy.

Comparisons Between Stayability and Survival Analyses of Simulated Data

Heritability Estimates

Table 4.11 provides median h^2 estimates for underlying ST and RL obtained from the same data. Although there is no apparent relationship between estimates obtained from individual data sets, the pooled estimates for ST are higher than those for RL. I expected the reverse to occur. Generally, greater heritabilities are obtained from threshold models than from linear models because nonlinear methods may be able to detect more genetic variation

Table 4.11. Median heritability (h^2) estimates for stayability (ST) and reproductive life (RL) obtained from RL data simulated using two levels of true h^2 and one level of the Weibull shape parameter ($\rho = 0.8$).

True h^2_{RL}	Data set	h^2_{ST} estimates[a] (n)	Median $\hat{h}^2_{ST}$	h^2_{RL} estimates (n)	Median $\hat{h}^2_{RL}$
0.05	1	37 (1)	0.0762	20	0.0366
	2	26 (1)	0.0905	20	0.0376
	3	23 (56)	0.0273	20	0.0346
	4	24 (22)	0.0343	20	0.0251
	5	51 (4)	0.0476	20	0.0557
	Pooled	161 (84)	0.0525	100	0.0378
0.20	1	42 (0)	0.1693	20	0.1982
	2	52 (0)	0.1050	20	0.1030
	3	66 (1)	0.2156	20	0.1382
	4	51 (0)	0.1811	20	0.1416
	5	54 (0)	0.1195	20	0.1641
	Pooled	265 (1)	0.1608	100	0.1431

[a]Number in parentheses is the number of h^2 estimates that converged to a value less than zero.

than linear methods (Snelling, 1994). For similar reasons, I thought survival model estimates would be higher than threshold model estimates. In fact, Boettcher et al. (1999) obtained heritability estimates for functional herd life in Canadian Holstein of 0.04, 0.07, and 0.10 from linear, threshold, and survival models, respectively. However, Vollema and Groen (1998) reported lower heritabilities of longevity from survival than from linear analyses, which was atrributed to the inclusion of herd-year-season as a random effect in the Weibull survival model.

When comparing heritability estimates for ST and RL, one must consider that the traits were not the same and were analyzed under different assumptions. Although the same data were used in both analyses, the threshold model accounted for variability on a continuous standard normal underlying scale and the survival model accounted for variability on a continuous logarithmic underlying scale. The relationship between traits on the underlying scale is unknown, and it is possible that h^2 for underlying ST is indeed higher than h^2 for underlying RL.

Genetic Predictions

Descriptions of the underlying contemporary group solutions and EBV for ST and RL are given in Tables 4.12 through 4.14. More interesting are the genetic trends for underlying ST and RL depicted in Figures 4.1 and 4.2. The genetic trends are nearly mirror images on one another, but the trend for RL decreases more rapidly than the trend for ST increases. (Recall that a decreasing trend in underlying RL is associated with an increasing trend in phenotypic RL.) Similar trends in the contemporary group solutions were also obtained (not shown), but these trends were essentially flat for both traits.

Table 4.12. Descriptive statistics of contemporary group (CG) solutions on the underlying scale for stayability (ST)[a] and reproductive life (RL)[b] based on RL data simulated using two levels of true heritability (h^2) and one level of the Weibull shape parameter ($\rho = 0.8$).

True h^2	CG (n)	Trait	Mean	SD	Min.	Max.
0.05	20	ST	0.0626	0.0756	-0.0676	0.2227
		RL	-1.7152	0.0626	-1.8451	-1.6081
0.20	20	ST	0.2925	0.1245	0.0872	0.5403
		RL	-1.9287	0.1036	-2.1224	-1.7310

[a]Computed using estimated heritability.
[b]Computed using true heritability.

Table 4.13. Descriptive statistics for all animals of estimated breeding values on the underlying scale for stayability (ST)[a] and reproductive life (RL)[b] based on RL data simulated using two levels of true heritability (h^2) and one level of the Weibull shape parameter (ρ = 0.8).

True heritability (h^2)	Animals (n)	Trait	Mean	SD	Min.	Max.
0.05	8,380.6	ST	0.0135	0.0687	-0.2658	0.3273
		RL	-0.0186	0.1130	-0.6701	0.4347
0.20	6,904.8	ST	0.0243	0.1702	-0.6828	0.7720
		RL	-0.0586	0.3298	-1.7747	1.2276

[a]Computed using estimated heritability.
[b]Computed using true heritability.

Table 4.14. Descriptive statistics for all sires of estimated breeding values on the underlying scale for stayability (ST)[a] and reproductive life (RL)[b] based on RL data simulated using two levels of true heritability (h^2) and one level of the Weibull shape parameter (ρ = 0.8).

True heritability (h^2)	Sires (n)	Trait	Mean	SD	Min.	Max.
0.05	378.0	ST	0.0150	0.0968	-0.2658	0.3198
		RL	-0.0183	0.1532	-0.5649	0.4347
0.20	323.4	ST	0.0207	0.2385	-0.6816	0.7173
		RL	-0.0394	0.4189	-1.5358	1.1525

[a]Computed using estimated heritability.
[b]Computed using true heritability.

The strong relationship between ST and RL is also indicated by correlations between predictions (Table 4.15). All correlations are strongly negative, ranging from -0.7326 to -0.8425. Stronger correlations are associated with predictions from data sets simulated with h^2_{RL} = 0.20 vs 0.05 and with predictions for sires only vs all animals.

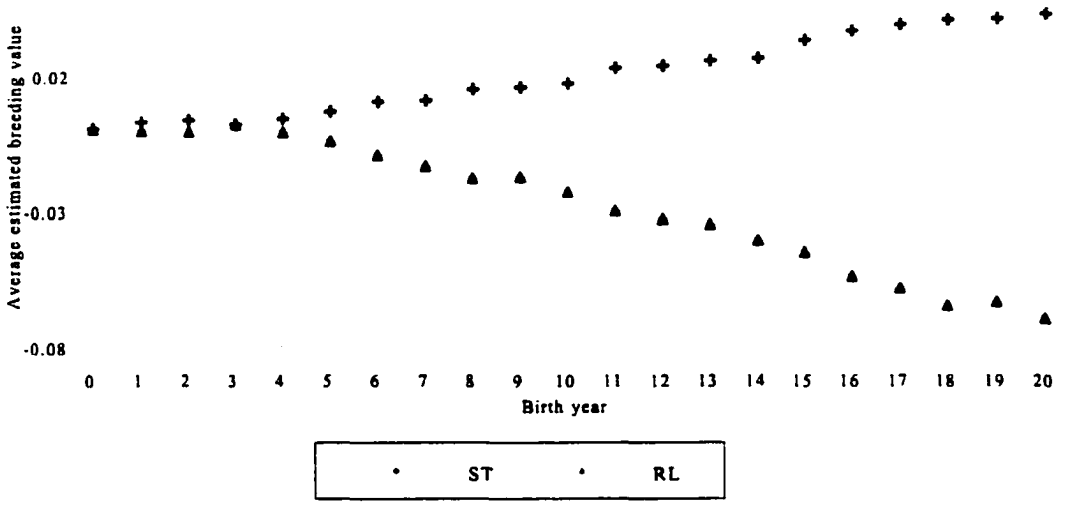

Figure 4.1. Average estimated breeding values for underlying reproductive life (RL) and stayability (ST) by birth year based on RL data simulated using a true heritability of 0.05 and a Weibull shape parameter of 0.8.

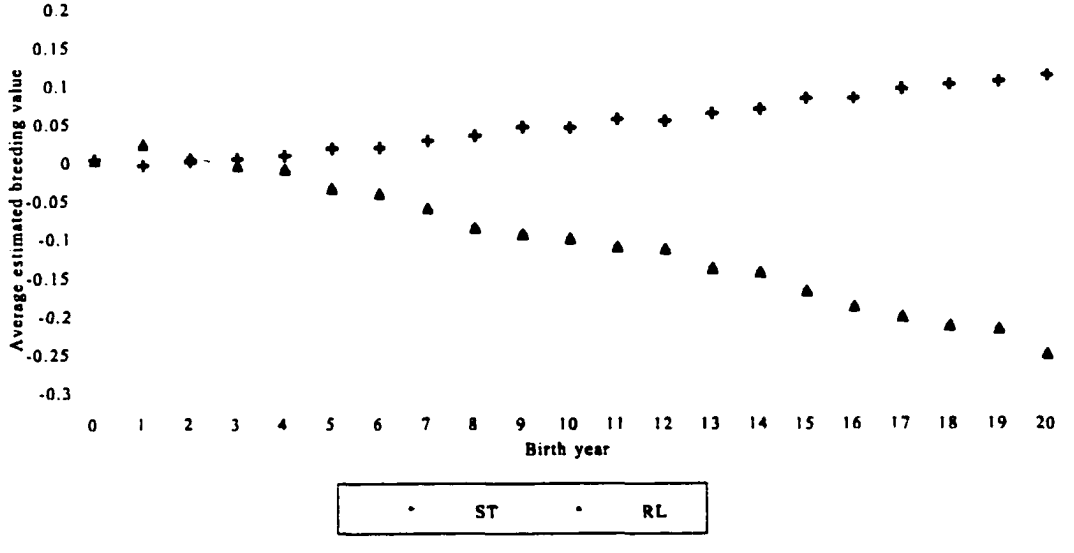

Figure 4.2. Average estimated breeding values for underlying reproductive life (RL) and stayability (ST) by birth year based on RL data simulated using a true heritability of 0.20 and a Weibull shape parameter of 0.8.

Table 4.15. Correlations for all animals and sires between estimated breeding values (EBV) for underlying stayability (ST)[a] and reproductive life (RL)[b] based on RL data simulated using two levels of true heritability (h^2) and one level of the Weibull shape parameter ($\rho = 0.8$).

True heritability (h^2)	Product moment correlations		Spearman rank correlations	
	Animals	Sires	Animals	Sires
0.05	-0.7796	-0.7931	-0.7326	-0.7854
0.20	-0.7938	-0.8425	-0.7334	-0.8330

[a]Computed using estimated heritability.
[b]Computed using true heritability.

Accuracies

Although the relationship between EBV suggests that animals rank the same between traits, accuracies associated with the traits are very different (Tables 4.16 and 4.17). Accuracies for RL are higher on average than accuracies for ST. The differences between accuracies are more pronounced for sires than for all animals and for data simulated using a true heritability of 0.20 vs 0.05 (Figure 4.3).

However, the differences in accuracy are only estimates. The true differences are not known because predictions for ST were computed using estimated rather than true heritabilities. Nevertheless, the results suggest that although there is a strong relationship between predictions for ST and RL, predictions for RL may be associated with higher accuracy, and in some instances, may be more appropriate selection tools to genetically improve sustained fertility of beef females.

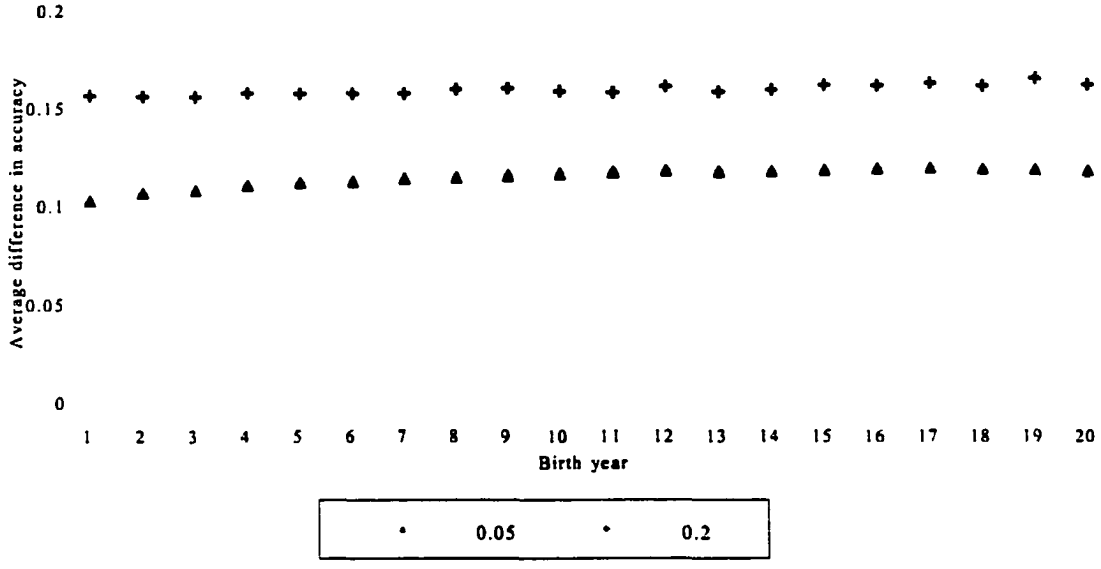

Figure 4.3. Average differences in accuracy by birth year of estimated breeding values of underlying reproductive life (RL) and stayability (ST) based on RL data simulated using two levels of true heritability (0.05 and 0.20) and a Weibull shape parameter of 0.8.

Table 4.16. Descriptive statistics for all animals of accuracies of estimated breeding values on the underlying scale for stayability (ST)[a] and reproductive life (RL)[b] based on RL data simulated using two levels of true heritability (h^2) and one level of the Weibull shape parameter ($\rho = 0.8$).

True heritability (h^2)	Animals (n)	Trait	Mean	SD	Min.	Max.
0.05	8,380.6	ST	0.2583	0.1537	0	0.6321
		RL	0.3435	0.2069	0	0.7740
0.20	6,904.8	ST	0.3351	0.2243	0	0.7679
		RL	0.4464	0.2994	0.0016	0.8933

[a]Computed using estimated heritability.
[b]Computed using true heritability.

Table 4.17. Descriptive statistics for all sires of accuracies of estimated breeding values on the underlying scale for stayability (ST)[a] and reproductive life (RL)[b] based on RL data simulated using two levels of true heritability (h^2) and one level of the Weibull shape parameter ($\rho = 0.8$).

True heritability (h^2)	Sires (n)	Trait	Mean	SD	Min.	Max.
0.05	378.0	ST	0.4178	0.1072	0.0364	0.6321
		RL	0.5401	0.1320	0.0255	0.7740
0.20	323.4	ST	0.5520	0.1290	0.0619	0.7679
		RL	0.6919	0.1428	0.0848	0.8933

[a]Computed using estimated heritability.
[b]Computed using true heritability.

The Effects of Right Censoring on Parameter Estimation and Genetic Prediction

Heritability Estimates

As for uncensored data, pooled median h^2 estimates for censored data were consistently lower than their true values (Table 4.18). However, the amount of censoring did

not seem to have an effect on the h^2 estimates. Ducrocq and Casella (1996) reported similar results when they applied a Laplacian integration technique to obtain heritabilities from simulated data with 50% to more than 80% censoring.

Genetic Predictions

Contemporary group solutions and EBV for all animals are summarized in Tables 4.19 and 4.20. Average contemporary group solutions decreased as the level of censoring increased. According to Kachman (1999), the log-likelihood and gradient of censored individuals are always negative, leading to the implication that if all records in a fixed effect group are censored, then the estimate of the risk factor for that group will approach negative infinity. Thus, it stands to reason that as the level of censoring increases, the average contemporary group solution should become more negative.

Table 4.18. Pooled median and mean heritability (h^2) estimates for reproductive life (RL) obtained from data sets[a] simulated using two levels of true h^2, one level of the Weibull shape parameter ($\rho = 0.8$), and four levels of censoring.

True heritability (h^2)	Level of censoring (%)	Median $\hat{h}^2$	Mean $\hat{h}^2$	SEM
0.05	0	0.0378	0.0464	0.0030
	10	0.0476	0.0579	0.0028
	40	0.0457	0.0499	0.0034
	70	0.0317	0.0385	0.0027
0.20	0	0.1431	0.1417	0.0055
	10	0.1729	0.1474	0.0074
	40	0.1187	0.1274	0.0044
	70	0.1680	0.1681	0.0052

[a]n = 5 for uncensored data and n = 3 for censored data.

Table 4.19. Descriptive statistics of contemporary group (CG) solutions for underlying reproductive life (RL) simulated using two levels of true heritability (h^2), one level of the Weibull shape parameter ($\rho = 0.8$), and four levels of censoring.

True heritability (h^2)	Level of censoring (%)	CG (n)	Mean (ln yr)	SD (ln yr)	Min. (ln yr)	Max. (ln yr)
0.05	0	20	-1.7152	0.0626	-1.8451	-1.6081
	10	20	-1.7796	0.0759	-1.9118	-1.6338
	40	20	-1.9877	0.0805	-2.1362	-1.8310
	70	20	-2.3206	0.0845	-2.4743	-2.1563
0.20	0	20	-1.9287	0.1036	-2.1224	-1.7310
	10	20	-2.0058	0.1008	-2.1865	-1.8387
	40	20	-2.2498	0.1508	-2.5586	-1.9896
	70	20	-2.6190	0.1453	-2.9199	-2.3685

Table 4.20. Descriptive statistics for all animals of estimated breeding values for underlying reproductive life (RL) simulated using two levels of true heritability (h^2), one level of the Weibull shape parameter ($\rho = 0.8$), and four levels of censoring.

True heritability (h^2)	Level of censoring (%)	Animals (n)	Mean (ln yr)	SD (ln yr)	Min. (ln yr)	Max. (ln yr)
0.05	0	8,380.60	-0.0186	0.1130	-0.6701	0.4347
	10	8,476.67	-0.0205	0.1177	-0.6171	0.4937
	40	9,129.33	-0.0123	0.1110	-0.5780	0.4584
	70	9,853.67	-0.0187	0.1013	-0.5181	0.4066
0.20	0	6,904.80	-0.0586	0.3298	-1.7747	1.2271
	10	7,042.67	-0.0487	0.3174	-1.6435	1.2062
	40	7,525.67	-0.0527	0.3169	-1.5766	1.1399
	70	7,979.67	-0.0700	0.3032	-1.3592	1.1219

Censoring did not seem to have an important effect on the EBV of underlying RL. The standard deviation and range of EBV tends to decrease with more censoring, particularly for data simulated with a true heritability of 0.20. Most likely, the narrower range results from obtaining records on censored females by truncating their actual observations for RL. The distribution of average EBV by birth year (Figures 4.4 and 4.5) shows little, if any, effect due to censoring. The trends are very similar, and any deviations are probably the result of random sampling within the simulation.

Accuracies

As expected, the reduced amount of information from censored records decreased accuracy of prediction for RL (Table 4.21). Figures 4.6 and 4.7 shows that the decrease was more pronounced as the level of censoring increased, even as the number of animals increased. The difference in accuracy between no censoring and 70% censoring was approximately 10 points on average for non-foundation animals. If accuracies were obtained from data sets of similar size and population structure, the difference likely would be larger.

Using both simulated and real dairy cattle data, Vukasinovic et al. (1999) also noted that accuracy decreased with an increased proportion of censored records. In addition, accuracy improved when relationships among sires were considered and when fewer daughters of the sires were censored. However, from the results of the analysis involving real data, a reasonably high rank correlation (0.70 to 0.80) between estimated transmitting abilities of the sires and estimated transmitting abilities from the reference data could be obtained when up to 65% of the records were censored.

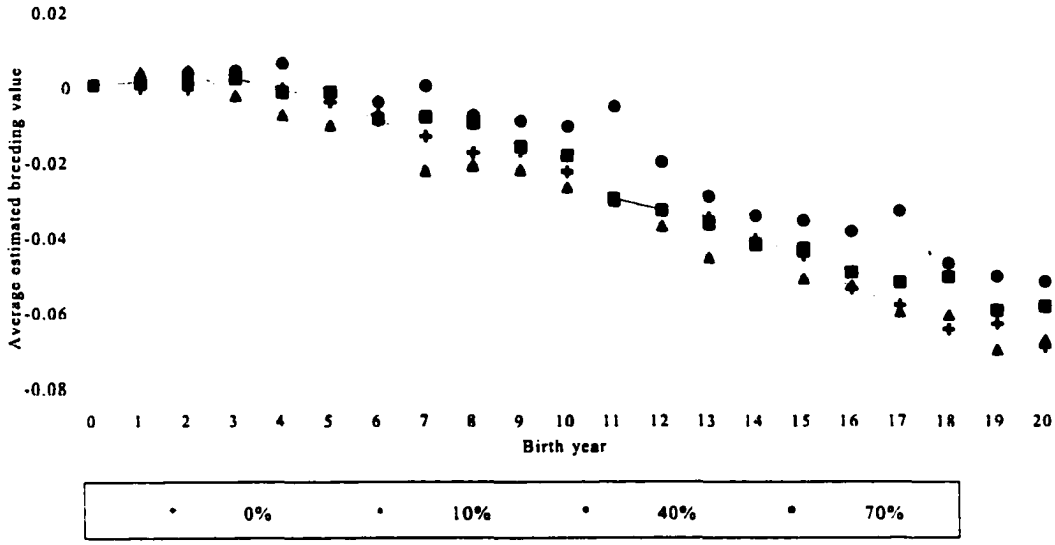

Figure 4.4. Average estimated breeding values by birth year of underlying reproductive life (RL) simulated using a true heritability of 0.05, a Weibull shape parameter of 0.8, and four levels of censoring.

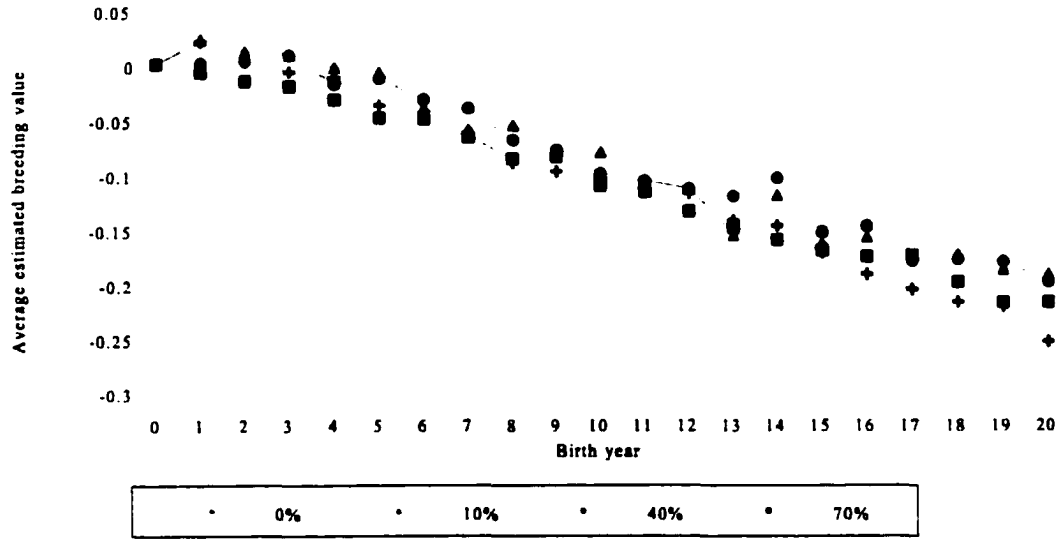

Figure 4.5. Average estimated breeding values by birth year of underlying reproductive life (RL) simulated using a true heritability of 0.20, a Weibull shape parameter of 0.8, and four levels of censoring.

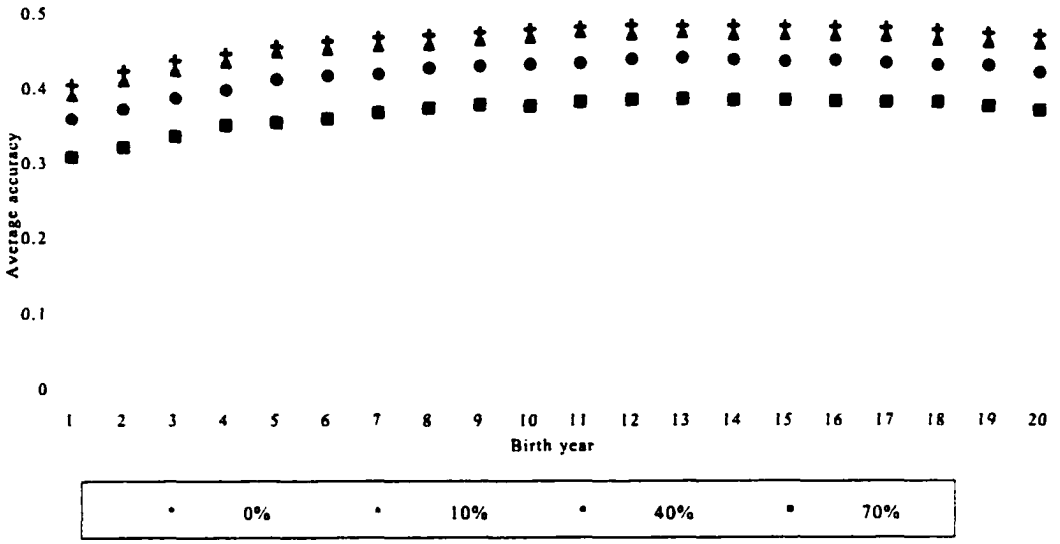

Figure 4.6. Average accuracies by birth year of estimated breeding values of underlying reproductive life (RL) simulated using a true heritability of 0.05, a Weibull shape parameter of 0.8, and four levels of censoring.

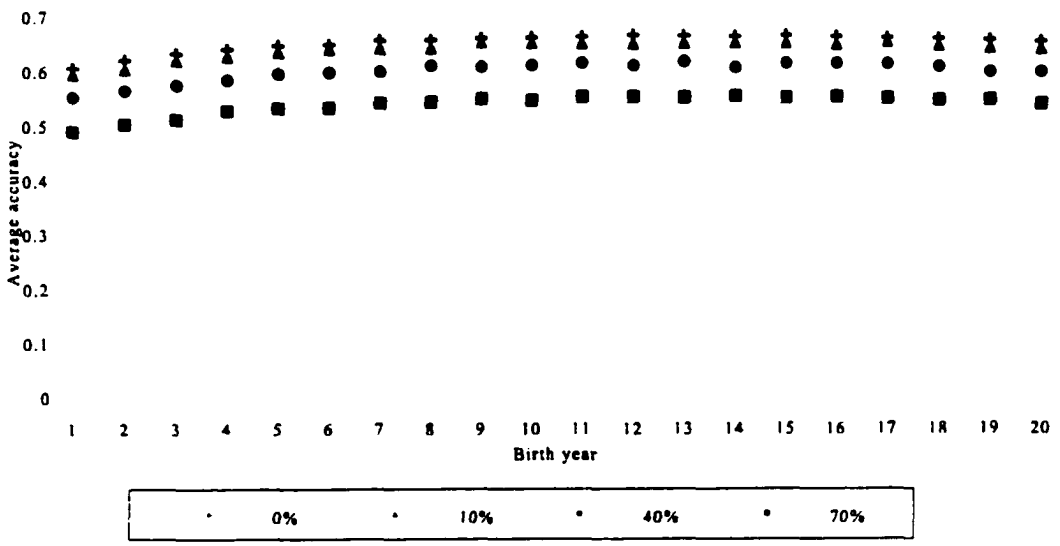

Figure 4.7. Average accuracies by birth year of estimated breeding values of underlying reproductive life (RL) simulated using a true heritability of 0.20, a Weibull shape parameter of 0.8, and four levels of censoring.

Table 4.21. Descriptive statistics for all animals of accuracies of estimated breeding values for underlying reproductive life (RL) simulated using two levels of true heritability (h^2), one level of the Weibull shape parameter ($\rho = 0.8$), and four levels of censoring.

True heritability (h^2)	Level of censoring (%)	Animals (n)	Mean	SD	Min.	Max.
0.05	0	8,380.60	0.3435	0.2069	0	0.7740
	10	8,476.67	0.3364	0.2018	0	0.7656
	40	9,129.33	0.3187	0.1827	0	0.7420
	70	9,853.67	0.2853	0.1565	0	0.6767
0.20	0	6,904.80	0.4464	0.2994	0.0016	0.8933
	10	7,042.67	0.4421	0.2934	0.0016	0.8779
	40	7,525.67	0.4274	0.2709	0.0016	0.8672
	70	7,979.67	0.3919	0.2416	0.0016	0.8354

The predictive power of survival analysis strongly depends on the proportion of censored records in the data (Vukasinovic et al., 1999). An increased proportion of censored records results in lower accuracy of prediction, which is particularly relevant in the evaluation of field data, which may have large amounts of censoring, and in the evaluation of young sires, who typically have a high proportion of censored daughters. Whether survival analysis of RL from large amounts of censored data always results in greater accuracy of prediction than threshold analysis of ST is unknown. An investigation into factors that affect the relative predictive ability of the two methods may be of interest.

Genetic Evaluation of Female Reproductive Life in Red Angus Cattle

Data

Although the RAAA made an unprecedented move when it adopted THR, the quality of the data that have been collected through the program thus far is questionable. From Table

3.9, nearly 75% of all cows have been culled for reasons other than those provided by the RAAA. Perhaps the RAAA needs to expand its list of disposal codes to include reasons frequently encountered by producers such as health disorders, udder characteristics, and conformation of the legs and feet. In addition, breeders may not be recording the disposal information correctly. Either they are not making the additional effort to record specific culling reasons for each cow but designating all cows in their herd as being culled for other reasons, or they may be uncertain as to which code should be reported. For example, more cows have been culled for performance and productivity than for fertility. Some breeders may designate culling for being open as being culled for poor productivity, whereas others may consider being open indicative of infertility.

Beaudeau et al. (1999) recommended investigation to interpret the meaning and assess the reliability of reported culling information before culling reasons are used as relevant selection criteria in the genetic improvement of longevity of dairy cattle. Incorrect disposal information may bias the results of genetic evaluation. To avoid any bias in expected progeny differences (**EPD**) computed from data collected through THR, the RAAA may want to consider an educational program for its members on the correct reporting of disposal information.

Heritability Estimate

From 20 h^2 estimates of underlying RL, the median value was 0.0532 and the mean was 0.0775 ± 0.0080. Estimated h^2 used in the most recent ST evaluation was 0.10 (B. L. Golden, personal communication). As for simulated data, h_{RL}^2 was lower than h_{ST}^2. This result contradicts that of Boettcher et al. (1999), who reported heritability estimates of 0.04,

0.07, and 0.10 from linear, threshold, and survival model analyses, respectively, of functional herd life in Canadian Holsteins. Although the relationship between h^2 for ST and RL is unknown, the difference between h^2 estimates for Red Angus may be partly attributed to the difference in data sets used to obtain the estimates.

Genetic Predictions

Estimated breeding values of ST and RL on the underlying scale are summarized in Table 4.22 for 20,917 animals and 2,602 sires. For both traits, the minimum and maximum EBV are associated with sires, indicating a wide range of EPD in these traits for sire selection. Although it is difficult to interpret the difference in magnitude of mean EBV between ST and RL, there does appear to be a relationship between them (Figure 4.8). The genetic trends for ST and RL show the same linear relationship as for trends obtained from simulated data. Average EBV for ST on the underlying liability scale increase over time, and average EBV on the underlying RL scale decrease over time. Upon closer examination, peaks in the trend of one trait correspond to dips in the other. The genetic trends and correlations (Table 4.23) between underlying EBV for ST and RL provide evidence that ST may indeed be reflective of sustained fertility in populations in which the primary reason for culling is reproductive failure. Although out of the scope of this dissertation, an investigation of the genetic relationship between ST and RL may be of interest.

Accuracies

Accuracies associated with the genetic predictions for RL and ST are presented in Table 4.24. Mean accuracies for RL were much lower than for ST. However, accuracies for RL were obtained from observations on 8,504 dams and genetic relationships among 20,917

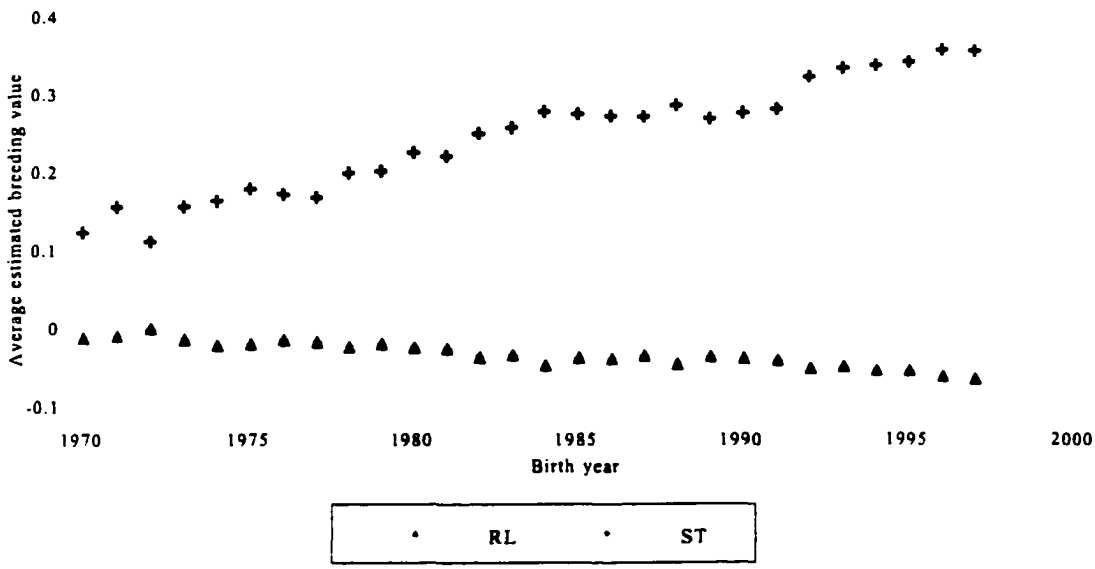

Figure 4.8. Average estimated breeding values on the underlying scale for reproductive life (RL) and stayability (ST) by birth year of 20,736 Red Angus cattle.

Table 4.22. Descriptive statistics of estimated breeding values on the underlying scale for reproductive life (RL) and stayability (ST) in different groups of Red Angus cattle.

Group	Trait	Mean	SD	Minimum	Maximum
Animals[a]	RL	-0.0477	0.0766	-0.4120	0.3516
	ST	0.2885	0.1668	-0.8765	1.0263
Sires[b]	RL	-0.0435	0.0820	-0.4120	0.3516
	ST	0.2763	0.1895	-0.8765	1.0263

[a]n = 20,917.
[b]n = 2,602.

Table 4.23. Correlations between estimated breeding values (EBV) on the underlying scale for reproductive life (RL) and stayability (ST) in different groups of Red Angus cattle.

Group	Observations (n)	Product moment correlation	Spearman rank correlation
Animals	20,917	-0.5322	-0.5013
Sires	2,602	-0.4605	-0.4252
High accuracy sires[a]	584	-0.4309	-0.4111
High accuracy sires[b]	16	-0.6767	-0.7735

[a]Accuracy of EBV for ST ≥ 0.70.
[b]Accuracy of EBV for RL ≥ 0.50.

Table 4.24. Descriptive statistics of accuracies of estimated breeding values for reproductive life (RL) and stayability (ST) in different groups of Red Angus cattle.

Group	Trait	Mean	SD	Minimum	Maximum
Animals[a]	RL	0.1816	0.0907	0	0.7204
	ST[c]	0.3370	0.1289	0	0.9436
	ST[d]	0.1338	0.0889	0	0.6682
Sires[b]	RL	0.1923	0.1030	0	0.7204
	ST[c]	0.5612	0.1654	0.0187	0.9436
	ST[d]	0.1491	0.0964	0	0.6682

[a]n = 20,917.
[b]n = 2,602.
[c]Based on 93,416 ST observations.
[d]Based on 8,504 RL observations.

animals, whereas accuracies for ST were computed from observations on 93,416 dams related to 672,733 animals. When an ST evaluation was conducted for only those animals in the RL evaluation, mean accuracies for ST dropped below those of RL. As for simulated data, despite lower h^2 for RL, accuracies of prediction for RL were higher on average than those for ST.

CHAPTER 5

SUMMARY AND CONCLUSIONS

Summary

The primary objective of this study was to develop methodology for animal model survival analysis of RL in beef females. Other objectives were: 1) to determine whether survival analysis of RL results in improved accuracy of prediction over threshold analysis of ST, 2) to investigate the effects of right censoring on parameter estimation and genetic prediction of RL, and 3) to determine whether animal model survival analysis is possible for large-scale genetic evaluation of RL using field data from a beef cattle breed association.

To meet the primary objective, I first developed a computer simulation program that generated RL data for validating and testing the methodology. Reproductive life was defined as the length of time from entering the herd as a replacement female to being culled for reproductive failure. The data were simulated from a Weibull model in a factorial arrangement consisting of two levels of true h^2 for underlying RL (0.05 and 0.20) and three levels of the Weibull shape parameter (0.6, 0.8, and 1.0) with five replicates per cell. Levels of ρ were based on results of three studies reported in the literature. To estimate h^2 for the 30 simulated data sets, I adapted the MAP R procedure for threshold analysis of categorical traits by substituting a Newton-Raphson algorithm appropriate to a Weibull frailty model. Log-frailties were assumed to be multivariate normal with mean **0** and variance $\sigma_a^2\mathbf{A}$, where σ_a^2 was the additive direct genetic variance of RL on the underlying natural logarithmic scale and

A was Wright's numerator relationship matrix for all animals. In addition, all data were assumed to be uncensored. Twenty h^2 estimates were obtained from each data set, and the results were pooled within each cell. Pooled median h^2 estimates for underlying RL were consistently lower than their true values, which may have resulted from natural selection in the simulated data. Despite the low h^2 estimates, correlations between EBV computed using estimated and true h^2 were very high (greater than 0.98), suggesting that the magnitude of h^2 used to evaluate RL does not affect ranking of individual animals.

Analyses of ST were conducted using 10 of the data sets simulated previously with true h^2 of 0.05 and 0.20 and $\rho = 0.8$. Twenty heritability estimates were obtained from each data set using the threshold model MAP R procedure, and the h^2 estimates were pooled within cell. The pooled median h^2 estimates for ST on the underlying liability scale were larger than those for underlying RL (0.0525 vs 0.0378 from data with true h^2 of 0.05, and 0.1608 vs 0.1431 from data with true h^2 of 0.20). Correlations between animal EBV for underlying ST and RL were strongly negative (-0.7796 and -0.7938 for true h^2 of 0.05 and 0.20, respectively), and genetic trends for the two traits were nearly mirror images of one another, suggesting that underlying ST and RL have a high and favorable genetic correlation. However, average accuracies of prediction for RL were approximately 0.10 and 0.15 greater than those for ST among non-foundation animals simulated with true h^2 of 0.05 and 0.20, respectively.

To determine the effects of censoring on heritability estimation and genetic prediction of RL, I modified the simulation program by randomly censoring females based on an input level of censoring (10, 40, and 70%) and then by randomly truncating their phenotypic RL

to obtain censored observations. Three data sets were simulated for each level of censoring, both levels of true h^2, and $\rho = 0.8$. The amount of censoring had no apparent effect on estimates of h^2 or breeding value. Heritability estimates and genetic predictions were similar among all levels of censoring, including that of no censoring. Average accuracy decreased more rapidly as the level of censoring increased. Average accuracies obtained from uncensored data were about 0.06 higher for all animals and 0.10 higher for non-foundation animals than those from 70% censored data, even though the number of animals increased with the level of censoring.

A genetic evaluation of RL was conducted for the RAAA using cow disposal information collected through its THR program. Reproductive life was defined as the length of time in yr from when a cow produced her first calf as a two-yr-old to when she was culled for infertility or censored, whichever came first. The RAAA provided disposal records on 113,943 dams, which were combined with 670,342 calving records on 176,512 dams from the ST evaluation conducted in January, 2000. The data were edited to retain only those cows who calved annually since age two and who had the opportunity to participate in THR either by calving or by being culled in 1995 and later. The cows were assigned to contemporary groups using the same contemporary group designations from the ST evaluation. Further editing eliminated contemporary groups in which all observations were censored or in which there was no variation among observations. The final data set consisted of records on 8,504 dams in 912 contemporary groups, of which 69.76% were censored. The median h^2 estimate was 0.0532, in contrast to 0.10 used in the ST evaluation. Genetic trends in EBV for underlying RL and ST were nearly mirror images of one another, as for trends

obtained from simulated data. Product moment correlations between EBV for RL and ST were moderately high and favorable (-0.5322 for all animals and -0.4605 for sires only). When ST was evaluated for only those animals in the RL analysis, average accuracies of prediction were lower for ST than for RL (0.1338 vs 0.1816).

Conclusions

The results of this research show that survival analysis applied to animal model parameter estimation and genetic prediction is possible, even with large data sets and large amounts of censoring. In addition, it yields higher accuracy of prediction than threshold analyses of similar traits, which is particularly important in the selection of young bulls.

Although the methodology I developed is feasible for national cattle evaluation (NCE) of RL, some concerns arose during the course of this study. First, in some instances, it took up to three days to obtain heritability estimates using these methods. However, programming of the methodology was not optimized for performance, and other users were running jobs concurrently. Furthermore, heritabilities are typically estimated only once every few years for breed associations. The time involved will most likely not be problematic in terms of turnaround times for NCE and will most likely be shortened because of the continued developments in computer technology.

Second, all results were presented on the underlying natural logarithmic scale for RL and are not easy to interpret. Transforming the results to the observed scale would give RL EBV in terms of the relative risks of sires for having daughters that are culled for reproductive failure, such that EBV greater than one are associated with greater risk, and those less than one are associated with less risk. This transformation is frequently applied

to report EBV of length of productive life in the dairy industry, but it may not be useful in the beef industry.

In the beef industry, reproductive efficiency is undoubtedly economically important. One way to improve reproductive efficiency is to maximize the pregnancy rate of the cows in the herd until the cows are no longer profitable for one reason or another (e.g., old age). Perhaps RL EBV should be expressed in terms of a sire's potential to produce daughters who are likely to become pregnant each year until some optimal disposal age. In this way, RL EBV would be very similar to stayability EBV, with which beef producers are already familiar.

Third, even with ST evaluations, it has taken several years for beef breed associations to collect enough data for analysis. Because the culling information required for survival analyses of RL is more detailed than the information required for ST evaluations and is not completely recorded by most breed associations, it may take even longer to obtain high-quality RL evaluations. For example, the RAAA had culling information on 138,957 animals since the inception of THR in 1995, but only 8,504 dams had valid RL observations. Although it may seem that continued effort into adoption of whole-herd reporting schemes by other breed associations would not be economically feasible, other information can be gained from these programs that has yet to be used in development of selection tools. For example, cow disposal records also provide information regarding health disorders and structural flaws, which may be important traits in the future.

Theoretical questions that arose during this study include: 1) Why are heritabilities underestimated from the procedures presented in this dissertation?, 2) How can the Weibull

shape parameter be estimated more accurately?, and 3) What is the genetic relationship between RL and ST? In answer to the first question, preliminary tests should be run using simulated data to determine whether the downward bias is in fact due to natural selection. If not, then the subsampling procedure used in Method R should be investigated to determine whether it is appropriate for highly skewed, nonlinear data. The second question may be answered by developing a multivariate survival model or an extension of the random regression procedure, in which values of ρ are obtained for individual animals. To investigate the third question, a mathematical derivation of the relationship between traits would be useful, as well as a procedure for estimating genetic correlations between two nonlinear traits. In addition, it may be of interest to determine the circumstances, if any, under which ST has higher accuracy of prediction than RL.

Given appropriate data, it appears that survival analysis would be feasible for large-scale genetic evaluation of female reproductive life and would provide better selection tools than other methods to genetically improve sustained fertility in beef females. I recommend that breed associations require mandatory reporting of disposal information on all animals, not just cows, and that researchers assess other aspects of animal model survival analysis.

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APPENDIX A

SIMULATION PROGRAM

```
/* surv.c

        Purpose:
                Generate reproductive lives from a Weibull distribution

        Usage:
                surv <seed number>

        Revision Record:
                06/28/99 lrh    Got rid of heterosis and maternal stuff in BLG's datagen
                06/30/99 lrh    Added Weibull parameters (rho and lambda)
                07/01/99 lrh    Added genetic effects
                07/06/99 lrh    Added error and a year counter
                07/08/99 lrh    Added cg effects and corrected survival time calculations
                07/16/99 lrh    Added progeny counter
                07/19/99 lrh    Changed replacement logic to correspond with phenotypic
                                survival times
                07/20/99 lrh    Changed replacement logic to develop heifers for a year
                08/02/99 lrh    Initialized sires and dams to be within certain age ranges
                08/03/99 lrh    Added death and culling indicators
                08/05/99 lrh    Added heifer initialization code
                08/13/99 lrh    Recoded the cg assignments
                08/16/99 lrh    Changed the death and culling indicators
                08/17/99 lrh    Added random culling logic
                08/24/99 lrh    Changed year stuff for computing age at death or culling
                11/24/99 lrh    Added inbreeding stuff for Mendelian sampling
                01/11/00 lrh    Fixed timing of reproductive life to start at age 1
                01/13/00 lrh    Got rid of stuff I didn't need
                01/26/00 lrh    Added code to handle heifers that die before they calve the
                                first time
                02/01/00 lrh    Added code for random censoring of cows
                03/03/00 lrh    Fixed way of dealing with heifers whose p is less than 1

*/
```

```
#include    <stdio.h>
#include    <math.h>

#define     N_ANIMALS 52625
#define     N_SIRES 125         /* Change bull:cow ratio here */
#define     N_DAMS 2500

#define     MALE 1
#define     FEMALE 2

#define     NO 0
#define     YES 1

#define     MAX_S_AGE 10
#define     MAX_D_AGE 10

#define     H2 .05              /* Heritability of reproductive life */
#define     PC_CENS 0           /* Percent censoring */
#define     RHO .6              /* Weibull shape parameter */
#define     T_MED 5.0           /* Stayability age = 6 */

#define     min(a,b) ((a)>(b)?(b):(a))
#define     max(a,b) ((a)<(b)?(b):(a))

struct a {
        int id;
        struct a *sire, *dam;
        short sex;
        short cull_bull, open_cow, not_need;
        int age, nprog, cg;
        double d;
        double g, e, p;
        short uncens;
        double ptrue;
};

struct a animal[N_ANIMALS+N_DAMS+1];
struct a *sires[N_SIRES];
struct a *dams[N_DAMS];
struct a *current_calves[N_DAMS];

struct a unknown =
{
        0,
```

```
        &unknown,
        &unknown,
        0,
        0, 0, 0,
        0, 0, 0,
        0.,
        0., 0., 0.,
        0, 0.
};

double f[N_ANIMALS+1], d[N_ANIMALS+1], l[N_ANIMALS+1];
int svec[N_ANIMALS+1], dvec[N_ANIMALS+1], point[N_ANIMALS+1];

int year = 1;                   /* Year at beginning of simulation */

double lambda = 0.;
double sigma_g = 0.;
double sigma_g2 = 0.;
double sigma_e2 = 0.;

/*************************************************************************/

main(argc, argv)
int argc;
char *argv[];
{
        FILE *fopen(), *fpp, *fpd;

        unsigned i, n = N_SIRES + N_DAMS;
        double get_lamb(), get_sigmag();

        fpp = fopen( "param","w" );
        fpd = fopen( "dat","w" );

        srand48( (long) atoi( argv[1] ) );
        srand( (unsigned) atoi( argv[1] ) );

        lambda = get_lamb();                    /* Calculate lambda */

        sigma_e2 = pow( M_PI, 2. ) / 6.;        /* Calculate variance components */
        sigma_g = get_sigmag();
        sigma_g2 = pow( sigma_g, 2. );

        init_herd();                            /* Initialize herd */
```

```
while ( n < N_ANIMALS ){                    /* Create rest of herd */

        for( i=0; i<N_DAMS; i++ ){          /* Generate one year's calf crop */
                animal[n].dam = dams[i];
                model( &animal[n], n, i);
                n++;
        }

        repl_sires();                       /* Replace parents */
        repl_dams();

        year++;                             /* Increment year */
}

/* Print parameters of model */

fprintf( fpp, "Heritability = %lf\nSigma g2 = %lf\nSigma e2 = %lf\n\n", H2,
        sigma_g2, sigma_e2 );

fprintf( fpp, "Rho = %lf\nMedian Lifetime = %lf\nLambda = %lf\n\n", RHO,
        T_MED, lambda );

fprintf( fpp, "Percent Censoring = %d\n\n", PC_CENS);

/* Print info for each animal */

for(i=0; i<N_ANIMALS; i++){
        fprintf( fpd,
                "%d %d %d %d %d %d %d %d %d %d %lf %lf %lf %lf %d
                %lf\n",
                animal[i].id,
                (animal[i].sire)->id,
                (animal[i].dam)->id,
                animal[i].sex,
                animal[i].cull_bull,
                animal[i].open_cow,
                animal[i].not_need,
                animal[i].age,
                animal[i].nprog,
                animal[i].cg,
                animal[i].d,
                animal[i].g,
                animal[i].e,
                animal[i].p,
```

```
                        animal[i].uncens,
                        animal[i].ptrue
                );
        }

        exit(0);
}

/*************************************************************************/

init_herd()             /* Initialize herd */
{
        init_sires();
        init_dams();
        return;
}

init_sires()            /* Initialize foundation sires */
{
        unsigned i, j;
        double get_norm(), get_extval();
        double get_d();

        for(i=0; i<N_SIRES; i++){

                animal[i].id = i+1;
                animal[i].sire = &unknown;
                animal[i].dam = &unknown;

                animal[i].sex = MALE;

                animal[i].cull_bull = NO;
                animal[i].open_cow = NO;
                animal[i].not_need = NO;

                animal[i].age = nrand( 1, MAX_S_AGE );  /* Must be at least 1 at breeding */

                animal[i].nprog = 0;                    /* No prior info about progeny */

                animal[i].cg = 0;                       /* Foundation animals are in cg 0*/

                animal[i].d = get_d( &animal[i] );      /* Get d value for M sampling */

                animal[i].g = get_norm() * sigma_g;
```

```
                animal[i].e = get_extval();
                animal[i].p = exp( -log ( lambda ) - 1./RHO * (animal[i].g - animal[i].e) );

                animal[i].uncens = YES;
                animal[i].ptrue = animal[i].p;

                if( animal[i].p > animal[i].age - 1 )          /* Can't be dead */
                        sires[i] = &animal[i];
                else                                           /* If so, get another sire */
                        --i;

        }

        return;
}

init_dams()             /* Initialize foundation dams */
{
        unsigned i, j;
        double get_norm(), get_extval();
        double get_d();

        for(i=N_SIRES; i<N_SIRES+N_DAMS; i++){

                animal[i].id = i+1;
                animal[i].sire = &unknown;
                animal[i].dam = &unknown;

                animal[i].sex = FEMALE;

                animal[i].cull_bull = NO;
                animal[i].open_cow = NO;
                animal[i].not_need = NO;

                animal[i].age = nrand( 1, MAX_D_AGE );  /* Must be at least 1 at breeding */

                animal[i].nprog = animal[i].age - 1;            /* Initial number of progeny */

                animal[i].cg = 0;                               /* Foundation animals are in cg 0*/

                animal[i].d = get_d( &animal[i] );              /* Get d value for M sampling */

                animal[i].g = get_norm() * sigma_g;
                animal[i].e = get_extval();
```

```
                animal[i].p = exp( -log ( lambda ) - 1./RHO * (animal[i].g - animal[i].e) );

                animal[i].uncens = YES;
                animal[i].ptrue = animal[i].p;

                if( animal[i].p > animal[i].age )          /* Must calve in yr 1 */
                        dams[i-N_SIRES] = &animal[i];
                else                                       /* If not, get another dam */
                        --i;

        }

    return;
}

/*************************************************************************/

model( an, idn, id )            /* Generate calves */
struct a *an;
unsigned idn, id;
{

        struct a *mate();
        double get_norm(), get_extval();
        double get_d();
        unsigned i, j;
        double k;

        an->id = idn+1;
        current_calves[id] = an;

        an->sire = mate();
        an->sex = nrand( 1, 2 );

        an->cull_bull = NO;
        an->open_cow = NO;
        an->not_need = YES;             /* Change to NO if it becomes a breeding animal */

        an->age = 0;                    /* Set to 0--only used for foundation animals */
        an->nprog = 0;
        an->cg = year;

        an->d = get_d( an );            /* Get d value for Mendelian sampling */
```

```
        an->g = .5 * ( (an->sire)->g + (an->dam)->g ) + get_norm() * sigma_g * sqrt(
                an->d );
        an->e = get_extval();
        an->p = exp( -log ( lambda ) - 1./RHO * (an->g - an->e) );

        an->uncens = YES;
        an->ptrue = an->p;

        if( an->sex == FEMALE && an->p > 1.){
                j = nrand( 1, 100 );
                if( j <= PC_CENS ){
                        an->uncens = NO;
                        an->p = nrand( 1, (int)(floor(an->p)) );
                }
        }

        if( idn+1 <= N_ANIMALS ){          /* Increment number of progeny for parents */
                (an->sire)->nprog++;
                (an->dam)->nprog++;
        }

        return;
}

struct a *mate()                /* Assign sires to dams */
{
        return( sires[ nrand( 0, N_SIRES-1 ) ] );
}

/*************************************************************************/

repl_sires()                    /* Replace sires */
{
        unsigned ppr=0, i;

        for( i=0; i<N_SIRES; i++ ){

                if( dead( sires[i] ) ){          /* Check if it dies */

                        while( current_calves[ppr]->sex == FEMALE ){
                                if( ++ppr >= N_SIRES ){
                                        fprintf( stderr, "Cannot generate enough
                                                replacement sires\n");
                                        exit(-1);
```

```
                        }
                    }

                    current_calves[ppr]->not_need = NO;        /* Change culling code */
                    sires[i] = current_calves[ppr];
                    ppr++;

                }

        }

        return;
}

repl_dams()                 /* Replace dams */
{
        unsigned ppr=0, i;

        for(i=0; i<N_DAMS; i++){

                if( dead( dams[i] ) ){          /* Check if it dies */

                        while( current_calves[ppr]->sex == MALE ||
                (current_calves[ppr]->sex == FEMALE &&
                current_calves[ppr]->p < 1. ) ){

                                if( current_calves[ppr]->sex == FEMALE ) {
                                        current_calves[ppr]->open_cow = YES;
                                        current_calves[ppr]->not_need = NO;
                                }

                                if( ++ppr >= N_DAMS ){
                                        fprintf( stderr, "Cannot generate enough
                                                replacement dams\n");
                                        exit(-1);
                                }
                        }

                        current_calves[ppr]->not_need = NO;        /* Change culling code */
                        dams[i] = current_calves[ppr];
                        ppr++;

                }
```

```
        }

        return;
}

dead( par )                     /* Kill parents */
struct a *par;
{

        par->cull_bull = NO;
        par->open_cow = NO;

        switch( par->sex )

        {
                /* Males */

                case 1:

                        /* Kill foundation sires */

                        if( par->cg == 0 && par->p < par->age + year - 1 ){
                                par->cull_bull = YES;
                                return( 1 );
                                }

                        /* Kill other sires */

                        else if( par->cg != 0 && par->p < year - par->cg ){
                                par->cull_bull = YES;
                                return( 1 );
                                }

                        else
                                return( 0 );

                /* Females */

                case 2:

                        /* Kill dams */

                        if( par->p < (par->nprog + 1) ){
                                par->open_cow = YES;
```

```
                        return( 1 );
                        }

                else
                        return( 0 );

        }
}

/*************************************************************************/

double get_lamb()               /* Calculate lambda */
{
        double lamb;
        lamb = pow( -log(.5), 1./RHO ) / T_MED;
        return( lamb );
}

double get_sigmag()             /* Calculate sigma g from input heritability */
{
        double sig;
        sig = sqrt( H2 * sigma_e2 / (1. - H2) );
        return( sig );
}

double get_extval()             /* Generate extreme value random numbers */
{
        double v1, v2, drand48();
        v1 = drand48();
        v2 = log( (-log( 1. - v1 ) ) );
        return( v2 );
}

double get_norm()               /* Generate standard normal deviates */
{
        double v, gasdev();
        v = gasdev();
        return( v );
}

double gasdev()                 /* Borrowed from Numerical Recipes */
{
        static int iset = 0;
        static double gset;
```

```
        double fac, r, v1, v2;
        double drand48();

        if(iset == 0) {
                do{
                        v1 = 2.0 * drand48() - 1.0;
                        v2 = 2.0 * drand48() - 1.0;
                        r = v1 * v1 + v2 * v2;
                } while( r >= 1.0 );
                fac = sqrt( -2. * log(r) / r );
                gset = v1 * fac;
                iset = 1;
                return (v2 * fac);
        } else {
                iset = 0;
                return( gset );
        }
}

nrand( s, e )                   /* Generate random integers */
int s, e;
{
    return( (rand() % (e - s + 1)) + s );
}

/*************************************************************************/

double get_d( anim )            /* Calculate d values for Mendelian sampling */
struct a *anim;                 /* Got from W. M. Snelling */
                                /* See Meuwissen and Luo, 1992, GSE 24:305 */
{
        int i, j, k, m, is, id, ks, kd, ms, md;
        double fi = 0.e0, r = 0.e0;

        /* Initialize variables for unknown parents */

        svec[0] = 0;
        dvec[0] = 0;
        point[0] = 0;

        f[0] = -1.e0;
        l[0] = 0.e0;
        d[0] = 1.e0;
```

```
/* Initialize variables for current animal */

m = anim->id;
ms = (anim->sire)->id;
md = (anim->dam)->id;

if( ms==0 && md==0 ) {
        svec[m] = 0;
        dvec[m] = 0;
} else {
        svec[m] = max( ms, md );
        dvec[m] = min( ms, md );
}

f[m] = -1.e0;

/* Start loop */

for( i=m; i<=m; i++ ){

        is = svec[i];
        id = dvec[i];
        d[i] = .5e0 - .25e0 * ( f[is] + f[id] );

        if( is == 0 && id == 0 ) {
                f[i] = 0.e0;

        } else {

                fi = -1.e0;
                l[i] = 1.e0;
                j = i;

                while ( j != 0 ){

                        k = j;
                        r = .5e0 * l[k];
                        ks = svec[k];
                        kd = dvec[k];

                        if( ks > 0 ){

                                while( point[k] > ks )
                                        k = point[k];
```

```
                    l[ks] += r;

                    if( ks != point[k] ){
                        point[ks] = point[k];
                        point[k] = ks;
                    }

                    if( kd > 0 ){

                        while( point[k] > kd )
                            k = point[k];

                        l[kd] += r;

                        if( kd != point[k] ){
                            point[kd] = point[k];
                            point[k] = kd;
                        }

                    }

                }

                fi += l[j] * l[j] * d[j];
                l[j] = 0.e0;
                k = j;
                j = point[j];
                point[k] = 0;

            }

            f[i] = fi;

        }

    }

    return( d[m] );

}
```

APPENDIX B

ANALYTICAL SOFTWARE

runit

```
#!/bin/bash

echo Start Time:
date

#SIM_SEED=`date | awk '{print $3, substr($4,7,2) substr($4,4,2) substr($4,1,2)}' | awk
        '{print $1*$2}'`
SIM_SEED=`expr 7324257`
echo runit: SIM_SEED = $SIM_SEED

cd ../sim
surv $SIM_SEED

cd ../survr
surv_R 15 20 5000

mkdir $SIM_SEED
cp ../sim/dat $SIM_SEED
cp ../sim/param $SIM_SEED
cp pseed $SIM_SEED
cp rstats $SIM_SEED
cp summ $SIM_SEED
cp rstats.awk $SIM_SEED

rm pseed rstats ginv num den tl

echo Finish Time:
date
```

```
#       surv_R <# of MR rounds> <# of NR rounds> <# of GS rounds>

#!/bin/bash

#       Set things up

MR=`echo $1 | awk '{print $1}'`
NR=`echo $2 | awk '{print $1}'`
GS=`echo $3 | awk '{print $1}'`

echo Part Seeds > pseed
echo I J High Low Reg Ginv H2 > rstats

setup_w

#       Start outer loop

echo surv_R: Starting outer loop

i=1

while [ $i -le 20 ]

do

        setup_p

        HIGH=1.0
        LOW=0.0

        H2=`echo $HIGH $LOW | awk '{print .5*($1+$2)}'`
        GIVAL=`echo $H2 | awk '{print (6./atan2(0,-1)^2)*(1.-$1)/$1}'`

        echo $GIVAL > ginv

        #       Start inner loop

        echo surv_R: Starting inner loop

        j=1

        while [ $j -le $MR ]
        do
```

```
            cd whole
            ../it_nr $NR $GS
            cd ..

            cd part
            ../it_nr $NR $GS
            cd ..

            mult -tpart/sol -zdata/v t1
            mult t1 whole/sol num
            mult t1 part/sol den

            N=`mprint num | awk '{print $1}'`
            D=`mprint den | awk '{print $1}'`

            REG=`echo $N $D | awk '{print $1/$2}'`
            T_REG=`echo $REG | awk '$1<.9999 {print -1} $1>1.0001 {print 1}
                  $1>=.9999 && $1<=1.0001 {print 0}'`

            echo $i $j $HIGH $LOW $REG $GIVAL $H2 >> rstats

            if [ $T_REG -eq -1 ]
            then HIGH=$H2
            fi

            if [ $T_REG -eq 1 ]
            then LOW=$H2
            fi

            if [ $T_REG -eq 0 ]
            then j=$MR
            fi

            H2=`echo $HIGH $LOW | awk '{print .5*($1+$2)}'`
            GIVAL=`echo $H2 | awk '{print (6./atan2(0,-1)^2)*(1.-$1)/$1}'`
            echo $GIVAL > ginv

            j=`expr $j + 1`

      done

      i=`expr $i + 1`

done
```

```
#       setup_w

#!/bin/bash

rm -r data
mkdir data

cd data

ln -f ../../sim/dat .
ln -f ../../sim/param .

awk 'NR==5 {print $3}' param > rho

awk '$4==2 && $7!=1 && $10!=0 && $14>0. {print $1, $10, $15, log($14)}' dat > t1
awk '{print $2, $3}' t1 | sort | grpvar > t2
awk '($2==1. && $3==0. && $4>1) || $3!=0. {print $1}' t2 | sort -u > t3
sort +1 -2 t1 | join -a1 -e "." -j1 2 -j2 1 -o 1.1 2.1 1.3 1.4 - t3 | awk '$2!="." {print $0}' |
        sort > t4
awk '{print $2, $4}' t4 | sort | grpvar > t5
awk '$3!=0. {print $1}' t5 | sort -u > t6
sort +1 -2 t4 | join -a1 -e "." -j1 2 -j2 1 -o 1.1 2.1 1.3 1.4 - t6 | awk '$2!="." {print $0}' |
        sort -n > dat.w
rm t1 t2 t3 t4 t5 t6

../mk_v

cd ..

rm -r whole
mkdir whole

cd whole

ln -f ../data/dat.w .
ln -f ../data/v.Z .
ln -f ../data/animal .
ln -f ../data/rho .

awk '{print $1}' dat.w > id
awk '{print $2}' dat.w > cg
awk '{print $3}' dat.w > ccode
awk '{print $4}' dat.w > lntime
```

```
awk '$1!="." {print $1}' cg | sort -u -n > cg.list
gen_z -d cg -e cg.list -r lntime -o X
gen_z -d id -e animal -r lntime -o Z

cat cg.list animal | awk '{print .001}' > beta.o

cd ..
```

```
#       mk_v

#!/bin/bash

awk '$7!=1 {print $1, $2, $3}' dat | awk '$2==0 {$2="."} $3==0 {$3="."} {print $1, $2,
        $3}' > ped.w
ainv -v v -i ped.w -o inbred.lst
compress v
awk '{print $1}' ped.w > animal
```

```
#       setup_p

#!/bin/bash

rm -r part
mkdir part

cd part

ln -f ../data/dat.w .
ln -f ../data/v.Z .
ln -f ../data/animal .
ln -f ../data/rho .

PART_SEED=`date | awk '{print substr($4,7,2) substr($4,4,2) substr($4,1,2)}'`
echo $PART_SEED >> ../pseed
echo setup_p: PART_SEED = $PART_SEED

N_OBS=`wc dat.w | awk '{print $1}'`
ranlist -s $PART_SEED -l 1 -u 2 -n $N_OBS > t1

paste dat.w t1 | awk '$5==1 {print $1, $2, $3, $4} $5==2 {print $1, $2, $3, "."}' > t2
awk '$4!="." {print $2, $3}' t2 | sort | grpvar > t3
awk '($2==1. && $3==0. && $4>1) || $3!=0. {print $1}' t3 | sort -u > t4
sort +1 -2 t2 | join -a1 -e "." -j1 2 -j2 1 -o 1.1 2.1 1.3 1.4 - t4 | awk '$2!="." {print $0}
        $2=="." {print $1, ".", $3, "."}' | sort > t5
awk '$4!="." {print $2, $4}' t5 | sort | grpvar > t6
awk '$3!=0. {print $1}' t6 | sort -u > t7
sort +1 -2 t5 | join -a1 -e "." -j1 2 -j2 1 -o 1.1 2.1 1.3 1.4 - t7 | awk '$2!="." {print $0}
        $2=="." {print $1, ".", $3, "."}' | sort -n > dat.p
rm t1 t2 t3 t4 t5 t6 t7

awk '{print $1}' dat.p > id
awk '{print $2}' dat.p > cg
awk '{print $3}' dat.p > ccode
awk '{print $4}' dat.p > lntime

awk '$1!="." {print $1}' cg | sort -u -n > cg.list
gen_z -d cg -e cg.list -r lntime -o X
gen_z -d id -e animal -r lntime -o Z

cat cg.list animal | awk '{print .001}' > beta.o

cd ..
```

```
#       it_nr <# of rounds of NR> <# of rounds of GS>

#!/bin/bash

#       Initialize variables

NR_RNDS=`echo $1 | awk '{print $1}'`
GS_RNDS=`echo $2 | awk '{print $1}'`

CONV_CRIT=.00001

R_SHP=`tail -1 rho`
W_DIR=`pwd`
echo it_nr: Working in $W_DIR

#       Find dimension (total number of columns in X and Z)

X_COL=`head -1 X | awk '{print $3}'`
Z_COL=`head -1 Z | awk '{print $3}'`
N_COL=`echo $X_COL $Z_COL | awk '{print $1+$2}'`

#       Start Newton-Raphson

k=1

while [ $k -le $NR_RNDS ]

do
        echo it_nr: Starting round $k

        #       Build and solve mme's

        ../mk_vecs
        ../mk_Ry -d dat.it -y eta -r $R_SHP -Y ystar -R Rmat
        ../mk_mme
        itgen -m $GS_RNDS -n -zcoef -r rhs -b beta.$k -R beta.o > itgen.out

        #       Calculate convergence factor

        subtract beta.o beta.$k delta
        mult -tdelta delta dtd
        DTDBAR=`mprint dtd | awk '{print $1/nc}' nc=$N_COL`
        cp beta.$k beta.o
```

```
        #       Test for convergence

        CONV_TEST=`echo $DTDBAR $CONV_CRIT | awk '$1<$2 {print 0} $1>=$2
                {print 1}'`

        if [ $CONV_TEST -eq 0 ]
        then
                echo it_nr: Converged on round $k of Newton-Raphson
                awk 'NR>xc {print $1}' xc=$X_COL beta.o > sol
                exit
        fi

        k=`echo $k | awk '{print $1+1}'`
done

echo it_nr: Did not converge after $NR_RNDS rounds of Newton-Raphson
awk 'NR>xc {print $1}' xc=$X_COL beta.o > sol
```

```
#       mk_vecs

#!/bin/bash

XDIM=`head -1 X | awk '{print $3}'`
ZDIM_S=`expr $XDIM + 1`

subm beta.o b 1 1 $XDIM 1
subm beta.o u $ZDIM_S 1

mult X b Xb
mult Z u Zu
sadd Xb Zu eta.sol
mprint eta.sol > eta

paste ccode lntime > dat.it
```

```
/* mk_Ry.c

        Purpose:
                Write R matrix and y star vector for a Weibull survival model
                Use with Newton-Raphson iteration (it_nr)
                Note that 0 = censored record and 1 = uncensored record

        Usage:
                mk_Ry -d (input matrix of log survival times and 0-1 censoring codes)
                        -y (input vector of etas)
                        -r (input value of rho)
                        -Y (output vector of y stars)
                        -R (output R matrix)

        Revision Record:
                10/18/99 lrh    Used notation from Kachman (1999) to revise Warren's
                                st_vw.c

*/

#include        <stdio.h>
#include        <math.h>
#include        <matrix.h>

FILE *fopen(), *fpd, *fpr, *fpy;

double atof(), rhoval;

struct matrix etavec;

main( argc, argv )
int argc;
char *argv[];
{
        unsigned n=0, nz=0;
        int code;
        char obs[15];
        double lnt, w, etaval, rval, yval;

        parse_args( argc, argv );

        fprintf( fpr, "                         " );
        fprintf( fpy, "                         " );
```

```
        while( fscanf( fpd, "%d %s", &code, obs ) != EOF ){

                n++;

                if( strcmp( obs, UNKNOWN ) == 0 ){
                        rval=0.;
                        yval=0.;
                }

                else {
                        nz++;

                        etaval = get_value( &etavec, n, 1 );
                        lnt = atof( obs );
                        w = (double)code;

                        rval = exp( rhoval * lnt + etaval );
                        yval = w - rval * ( 1. - etaval );
                }

                fprintf( fpr, "%.15lg\n", rval );

                if( yval != 0. )
                        fprintf( fpy, "%d 1 %.15lg\n", n, yval );

        }

        rewind( fpr );
        rewind( fpy );

        fprintf( fpr, "DIAGONAL %d %d %d\n", n, n, n );
        fprintf( fpy, "SPARSE %d 1 %d\n", n, nz );

        exit( 0 );
}


parse_args( argc, argv )
int argc;
char *argv[];
{
        extern int optind;
        extern char *optarg;
        int c;
```

```
int dflg=FALSE, yflg=FALSE, rflg=FALSE, Yflg=FALSE, Rflg=FALSE;

while( (c = getopt( argc, argv, "d:y:r:Y:R:" )) != -1 ){

        switch( c ){

                case 'd':
                        dflg = TRUE;
                        if( (fpd = fopen( optarg, "r" )) == NULL ){
                                fprintf( stderr, "mk_Ry: Cannot open %s for
                                        input\n", optarg );
                                exit( -1 );
                        }
                        break;

                case 'y':
                        yflg = TRUE;
                        set_name( &etavec, optarg );
                        get_matrix( &etavec );
                        break;

                case 'r':
                        rflg = TRUE;
                        rhoval = atof( optarg );
                        break;

                case 'Y':
                        Yflg = TRUE;
                        if( (fpy = fopen( optarg, "w" )) == NULL ){
                                fprintf( stderr, "mk_Ry: Cannot open %s for
                                        output\n", optarg );
                                exit( -1 );
                        }
                        break;

                case 'R':
                        Rflg = TRUE;
                        if( (fpr = fopen( optarg, "w" )) == NULL ){
                                fprintf( stderr, "mk_Ry: Cannot open %s for
                                        output\n", optarg );
                                exit( -1 );
                        }
                        break;
```

```
                        case '?':
                                usage();
                }
        }

        if( !( dflg && yflg && rflg && Yflg && Rflg ) )
                usage();

        return;
}

usage()
{
        fprintf( stderr, "mk_Ry: Usage: mk_Ry -d (input matrix of log survival times and
                0-1 censoring codes) \n\t\t\t-y (input vector of etas) -r (input value of rho)
                \n\t\t\t-Y (output vector of y stars) -R (output R matrix) \n" );

        exit(-1);
}
```

```
#       mk_mme

#!/bin/bash

#       Get g inverse

GI=`tail -1 ../ginv`

#       Make coef

mult -tX*Rmat X XtRmatX
mult -tX*Rmat Z XtRmatZ
shcat XtRmatX XtRmatZ - | compress > X.eq.Z

mult -tZ*Rmat X ZtRmatX
mult -tZ*Rmat Z ZtRmatZ
sadd ZtRmatZ -zv*$GI Z.aug
compress Z.aug
shcat ZtRmatX -zZ.aug - | compress > Z.eq.Z

svcat -zX.eq -zZ.eq - | compress > coef.Z
rm X.eq.Z Z.aug.Z Z.eq.Z

#       Make rhs

mult -tX ystar X.rhs
mult -tZ ystar Z.rhs
svcat X.rhs Z.rhs rhs
```