

Implementation of a Routine Genetic Evaluation for Longevity Based on Survival Analysis Techniques in Dairy Cattle Populations in Switzerland

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ABSTRACT

Genetic evaluation of sires for functional longevity of their daughters based on survival analysis has been implemented in the populations of Braunvieh, Simmental, and Holstein cattle in Switzerland. A Weibull mixed sire-maternal grandsire survival model was used to estimate breeding values of sires with data on cows that calved since April 1, 1980. Data on Braunvieh and Simmental cows included about 1.1 million records, data on Holstein cows comprised about 220,000 records. Data contained approximately 20 to 24% right-censored records and 6 to 9% left-truncated records. Besides the random sire and maternal grandsire effects, the model included effects of herd-year-season, age at first calving, parity, stage of lactation, alpine pasturing (Braunvieh and Simmental), and relative milk yield and relative fat and protein percentage within herd to account for culling for production. Heritability of functional longevity, estimated on a subset of data including approximately 150,000 animals, were 0.181, 0.198, and 0.184 for Braunvieh, Simmental, and Holstein, respectively. Breeding values were estimated for all sires with at least six daughters or three granddaughters in the data. Breeding values of sires are expressed in months of functional productive life and published in sire catalogs along with breeding values for production traits.

(Key words: survival analysis, length of productive life, genetic evaluation, dairy cattle)

Abbreviation key: LPL = length of productive life.

INTRODUCTION

Dairy cattle breeding in Switzerland has a long tradition. With increased economic pressure in the last de-

cares, Swiss farmers have had to adopt selection principles that result in a productive, robust, and efficient cow. Since the milk quota system was introduced in the seventies, more attention has been paid to functional traits such as fertility, disease resistance, and longevity (Böbner, 1994). Increased longevity affects overall profitability of milk production by reducing replacement costs and increasing the proportion of mature, high producing cows in a herd. It also enables a greater selection response, because fewer animals have to be replaced and, thus, higher selection intensity of cows is possible. Moreover, breeding for increased longevity is considered more ethical because the selection is aimed at improvement of health and fitness, i.e., well-being of the cow and not at productivity. A trait of particular interest for the breeder is functional longevity, which is independent of production and reflects the fertility, health, and overall fitness of the cow.

Until recently, longevity in Swiss dairy cattle populations has not been considered in breeding programs. Stayability, expressed as a percentage of daughters of a sire still alive after the first lactation, has been recorded for test sires, but no genetic evaluation has been conducted. Longevity has been left out of breeding programs because genetic evaluation for this trait is generally difficult. Some animals are still alive at the time of genetic evaluation, and only the lower bound of their eventual productive life is known. To exclude such records from the evaluation or to consider them exact would lead to biased results (Ducrocq, 1994). Therefore, such records must be treated as censored. Several researchers tried to overcome this problem by using binary survival traits such as whether or not a cow survives until certain age (Everett et al., 1976) or lactation (Schaeffer and Burnside, 1974). Unfortunately, this method is associated with a great loss of information. Van Raden and Klaaskate (1993) proposed replacing censored records by so-called projected records based on currently available information and estimating breeding values using a BLUP animal model. However, the information from partial records appears insuffi-

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cient to accurately predict the complete length of productive life (Ducrocq, 1997). Another difficulty is that traditional methods for genetic evaluation based on linear models, such as BLUP, cannot be properly used for genetic evaluation for longevity because the overall longevity of an animal results from a product rather than from a sum of effects influencing the trait (Beilharz et al., 1993). In addition, some of the effects that influence productive life, such as milk production, herd size, or management, vary with time. Moreover, the distribution of longevity data is extremely skewed and often unknown. Thus, methods based on assumption of normality have only limited use in the analysis of longevity data (Egger-Danner, 1993).

The attitude of animal geneticists and breeders toward genetic evaluation of longevity has changed considerably since it was found that survival analysis can be used in analyzing longevity data. Survival analysis comprises statistical methods originally developed for research in epidemiology and engineering. Survival analysis combines information on dead (uncensored) and alive (censored) individuals, enables a proper statistical treatment of censored records, and accounts for nonlinear characteristics of longevity data. The survival analysis approach is based on the concept of hazard rate, i.e., probability (risk) of being culled at certain time t , given that the cow has been alive prior to t . The hazard rate is usually modeled as a product of a baseline hazard function, representing the natural aging process, and an exponential function of effects that supposedly influence the culling process, such as herd-year-season, milk production level, or genetic effects (e.g., sire effect). The hazard rate can be modeled for all records, uncensored as well as censored records.

Famula (1981) was the first author who proposed survival analysis as a method to analyze longevity data in dairy cattle. Smith (1983) and Smith and Quaas (1984) used survival analysis techniques to estimate breeding values of sires based on the length of productive life of their daughters. These techniques were then elaborated (Ducrocq, 1987) and further developed and adjusted for large-scale applications (Ducrocq and Sölkner, 1994, 1998).

Routine genetic evaluation of sires based on survival analysis was implemented 1997 in France (Ducrocq, 1999), in 1998 in Germany (Pasman and Reinhardt, 1999), and in 1999 in the Netherlands (De Jong et al., 1999). Research projects are under way in many other European countries (e.g., Schneider and Miglior, 1999) and Canada (Boettcher, 1999; Dürr, 1999).

Preliminary research on using survival analysis in genetic evaluation for longevity in Switzerland has recently been conducted (Vukasinovic et al., 1997; 1999). The pilot genetic evaluation of sires for the length of

productive life based on survival analysis was conducted in May 1999 for three main dairy breeds: Braunvieh, Simmental, and Holstein. Breeding values for sires were first published in December 1999 for Holstein and in May 2000 for Braunvieh; breeding values for Simmental bulls are to be released by January 2001.

The objectives of this paper are to describe the method for genetic evaluation for functional longevity and to discuss the results of the first genetic evaluation.

MATERIALS AND METHODS

Data

The data for genetic evaluation of longevity were extracted from the production and pedigree databases of Braunvieh, Simmental, and Holstein breed. The data included all lactation records on cows that calved since April 1, 1980. Length of productive life (**LPL**) was defined as the number of days between the first calving and the last test day entered in the database. As suggested by the Breeders' Associations, records were considered uncensored if no entry was available at least 150 d after the last recorded test day, because the number of cows that "disappeared" from the data due to export to other countries or herds abandoning the milk recording system was negligible. Records on cows still alive at the time of data extraction were considered right censored. For cows calving before April 1, 1980, only the part of lactation started after that date was considered ("left-truncated" records). Cows changing herds during their productive life were considered right censored, left truncated, or both, depending on when and how many times the change of herd occurred. For those cows, only the time period spent in the herd in which a cow had the largest number of lactations recorded was considered. This restriction was necessary to meet certain computational requirements.

Breeding values were estimated for all sires with at least six daughters in the data. Maternal grandsires were also considered. If a maternal grandsire had fewer than three granddaughters, he was assumed unknown. The pedigree file comprised all sires and two generations of their male ancestors.

Characteristics of the data used in the first genetic evaluation are given in Table 1.

Model

The model used for genetic evaluation is a Weibull mixed survival model with time-dependent covariates defined on three different time scales. The function $\lambda(t)$, which represents the hazard of the cow after t days of her productive life, at calendar date t' , t_1 days after her

Table 1. Characteristics of the data used in the first genetic evaluations.

Item	Braunvieh	Simmental	Holstein
Total records (no.)	1,123,937	1,129,610	222,870
Censored (%)	24.2	24.3	20.8
Left truncated (%)	9.5	8.6	5.8
Sires with daughters/granddaughters (no.)	26,420	26,153	2284
Total sires in pedigree (no.)	27,940	27,307	2398

first calving, and t_2 days after her current calving, is modeled as

$$\lambda(t) = \rho t^{\rho-1} * \exp \{ \text{hys}(t') + \text{fc} + \text{pa}(t_1) + \text{ls}(t_1, t_2) \\ + \text{alp}(t_1) + \text{m}(t_1) + \text{p}(t_1) + \text{s} + \frac{1}{2} \text{mgs} \}$$

where:

- ρ is one of the parameters describing the baseline hazard function (the second parameter is implicitly included in the exponential part of the model and represents the 'overall mean').
- $\text{hys}(t')$ is the time-dependent combined random effect of herd, year, and season at calendar time t' , with changes on April 1 and October 1 each year. These dates are chosen because the most intensive changes in culling policy within herd are expected to occur shortly before the end of the quota period (the quota period in Switzerland is defined from May 1 to April 30) and before the beginning of the winter period. The herd-year-season effect is assumed to follow a loggamma distribution with the parameters (γ, γ) . The parameter γ , which is a measure of the variance of the hys effect, was estimated previously using a subset of the data. The hys effect was algebraically integrated out in the analysis and therefore not explicitly computed.
- fc is the fixed time-independent effect of age at first calving with seven levels, from <26 to >37 mo, with steps of approximately 2 mo. The definition of age classes differs slightly among the breeds to ensure an approximately equal size of each class.
- $\text{pa}(t_1)$ is the fixed time-dependent effect of parity. The effect of parity is considered to account for increased risk of culling in younger cows. Parities 1 through 6 in Braunvieh and Simmental and 1 through 5 in Holstein are considered. Effect of parity was considered unchanged from parity 6 onwards in Braunvieh and Simmental and from parity five onwards in Holstein.
- $\text{ls}(t_1, t_2)$ is the fixed time-dependent effect of stage of lactation within parity, t_1 days after first calving, with changes at $t_2 = 0, 30, 60, 180, 240,$ and 300 d after the current calving. This effect is included to account for changing intensity of culling during each lactation.
- $\text{alp}(t_1)$ is the fixed time-dependent effect of calving year, calving season, geographic zone, and alpine pasturing, with changes at each new calving. Two calving seasons were defined: April to September and October to March. Four geographic zones were distinguished according to the altitude of the area where the farm is located. The information on whether the cow spent the summer on alpine pastures is included to account for the influence of alpine pasturing on longevity. This effect is included in the model because alpine pasturing is considered a part of tradition and is very specific for Swiss dairy herds, especially Braunvieh and Simmental. The alp effect is omitted for Holsteins because only a very small proportion of cows are sent to the alpine pastures.
- $\text{m}(t_1)$ and $\text{p}(t_1)$ are the time-dependent effects of within-herd deviations for milk yield and the sum of fat and protein content. Effects are within parity with five classes for milk yield: $<80\%$, 80 to 94% , 95 to 104% , 105 to 120% , and $>120\%$ of the herd average and five classes for the sum of fat and protein content: $<94\%$, 94 to 97% , 98 to 101% , 102 to 106% , and $>106\%$ of the herd average. Classes are based on the age-adjusted 305-d lactation records, with changes at each new calving. Cows without standard lactation records in the current lactation are assigned to the same production class as in the previous lactation. Uncensored records on first-lactating cows without standard lactation records were arbitrarily assigned to class 2 (second-worst) for milk yield and class 3 (average) for fat and protein content. The effects of within-herd production are included to account for voluntary culling based on poor production. The number of production level classes defined in the model is small compared with other studies (e.g., Ducrocq, 1999). Defining more than five production level classes is currently not possible in this data due to the small average herd size in Switzerland.
- s and mgs are random effects of the sire and the maternal grandsire of the cow. When the maternal grandsire is not known, the term $\frac{1}{2} \text{mgs}$ is ignored. The s and mgs effects are grouped in a vector s as

sumed to follow a multivariate normal distribution with a variance-covariance matrix $\mathbf{A}\sigma_s^2$.

The heritabilities of functional longevity were assumed 0.181, 0.198, and 0.184 for Braunvieh, Simmental, and Holstein, respectively (Table 2). These heritability values were previously estimated on a subset of data containing about 150,000 records and using the same model as described above. The estimated heritability values for all three breeds are greater than obtained in other studies using methods other than survival analysis (e.g., Boettcher et al., 1998). This is due to the transformation of estimated heritabilities from the unobservable log scale to more 'realistic' original scale using Taylor series expansion (Ducrocq and Casella, 1996). The heritabilities on the original scale are based only on uncensored observations.

Computations

All computations have been conducted using the software The Survival Kit V.3.0 (Ducrocq and Sölkner, 1998). Values of the sire and hys variance and the ρ parameter of the baseline hazard function obtained on a subset of the data (shown in Table 2) were used in the subsequent estimation of breeding values.

Estimated Breeding Values

Breeding values of sires are published in months of productive life. Breeding values in days are calculated by multiplying the obtained sire solution by two and computing the expected survivor curves for the reference daughters of each sire. The expected productive life of daughters is then calculated by adding up fractions of daughters still alive at each day of productive life from 1 to 5457 (15 yr), which is assumed to be the maximal possible length of productive life. The breeding value of each sire is expressed as a difference between the expected productive life of daughters and the expected productive life of daughters of a 'base sire', which is obtained by computing the expected survivor curve using the average solution of all sires born between 1981

and 1985. The base reference is equal for all three breeds. The base reference for all three breeds was chosen because the group of sires born 1981 to 1985 is large, with a large average number of uncensored daughters. Sires' breeding values in days are then divided by 30 to obtain breeding values in months.

Reliability of Breeding Values

Usually, the reliability of sire's breeding value is calculated as

$$R^2 = 1 - \frac{\text{asymptotic prediction error variance}}{\sigma_s^2},$$

where the asymptotic prediction error variance is obtained from the diagonal term of the inverse of the information matrix (= negative Hessian of the log-likelihood function). With large datasets, however, it is virtually impossible to obtain the inverse of the information matrix. Therefore, the reliability of breeding values must be approximated by the common equation derived from the selection index theory:

$$R_{prog}^2 = \frac{n}{n + \frac{4 - h^2}{h^2}}$$

where R_{prog}^2 is the reliability of the breeding value of a sire with progeny (pedigree information ignored), n is the number of uncensored daughters, and h^2 is the heritability of LPL. The reliability depends on the number of uncensored daughters only and is not affected by the number of censored daughters. Therefore, the reliability of the breeding value for a young sire with only few daughters with complete productive life is relatively low. For two sires with a same total number of daughters, the one transmitting shorter productive life will have higher reliability of the EBV because a larger proportion of his daughters will be culled.

If pedigree information for a sire is available, the 'full' reliability can be approximated as follows:

$$R_{full}^2 = \frac{\frac{1}{4}R_{gsire} + R_{prog} + 2 \times \frac{1}{4}R_{gsire} \times R_{prog}}{1 - \frac{1}{4}R_{gsire} \times R_{prog}},$$

where R_{gsire} is the reliability of the breeding value of bull's sire.

Table 2. Estimated parameters of the baseline hazard function (ρ), hys effect (γ), sire variances (σ_s^2), and heritabilities on log (h_{log}^2) and original (h_{orig}^2) scale used in genetic evaluation for longevity and previously obtained on a subset of data.

Estimated parameter	Braunvieh	Simmental	Holstein
ρ	1.41	1.22	1.53
γ	3.04	4.11	3.75
σ_s^2	0.033	0.030	0.036
h_{log}^2	0.064	0.062	0.072
h_{orig}^2	0.181	0.198	0.184

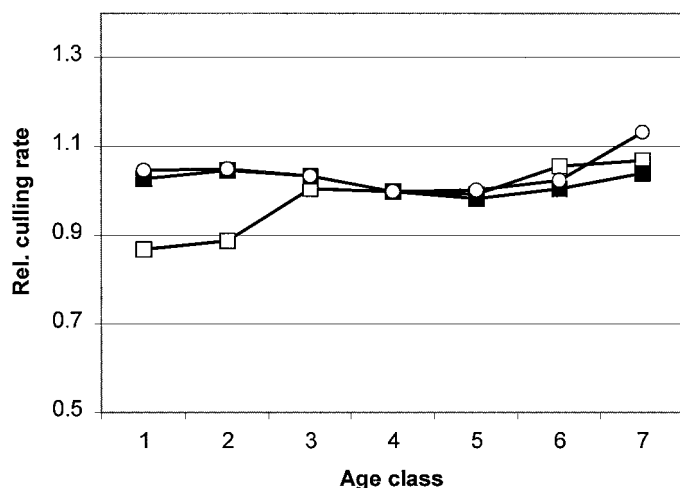


Figure 1. Relative culling rate for age at first calving in Braunvieh (□), Simmental (■), and Holstein (○) breed. Age classes were defined from <26 to >37 mo at approximately 2-mo intervals.

RESULTS AND DISCUSSION

Fixed Effects

The results for fixed effects are expressed as relative culling rates, defined as the ratio between the estimated risk of being culled under the influence of a certain environmental factor and the average risk, which is usually set to one. Values larger than one indicate higher culling risk associated with the environmental factor. Relative culling rates smaller than one indicate lower culling risk, i.e., increasing effect of the environmental factor on longevity.

The effects of age at first calving did not have a large influence on the length of productive life, although a certain trend could be observed. In Braunvieh, the relative culling risk increases almost linearly with increasing age. In Simmental and in Holstein this effect is more curvilinear, with slightly increased risk for those cows that calve very early and, especially, very late (Figure 1). The higher culling risk in late calvers may be due to fertility problems.

The results of time-dependent fixed effects were very similar in all three breeds. To avoid redundancy, Figures 2 to 5 illustrating these effects are shown for one breed only. The discussion of the results can be considered general for all three breeds.

The effects of parity and stage of lactation must be interpreted with caution because they are strongly associated with the time scale. Instead of interpreting these effects individually, it is more appropriate to look at the estimated hazard function:

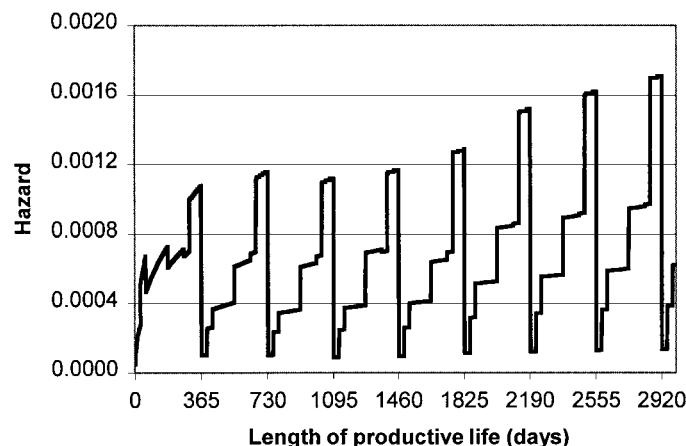


Figure 2. Estimated hazard function of a reference Braunvieh cow with standard 305-d lactations and 365-d calving intervals.

$$\hat{\lambda}(t) = \rho\lambda^{\rho-1} * \exp(pa(t_1) + ls(t_1, t_2)),$$

which leads to the definition of a 'reference cow'. Figure 2 shows the estimated hazard function for a reference Braunvieh cow with standard 305-d lactations and 365-d calving intervals. In general, the estimated hazard stays approximately constant in the first four lactations and increases gradually after that point, because older cows are at higher risk of dying or culling for involuntary reasons. From the second lactation onwards a characteristic pattern of the hazard function within each lactation can be observed: the hazard is low in the beginning of lactation immediately after calving, then in-

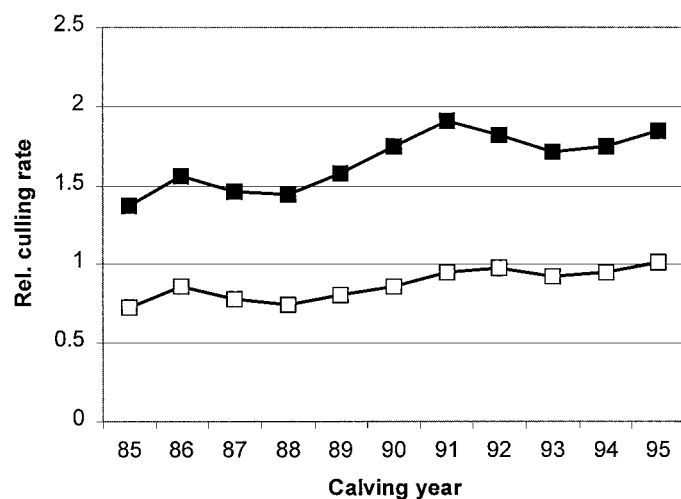


Figure 3. Relative culling rate for cows on summer alpine pasturing (□) and those not on alpine pasturing (■) in Simmental breed in different calving years, averaged over all geographical zones and calving seasons.

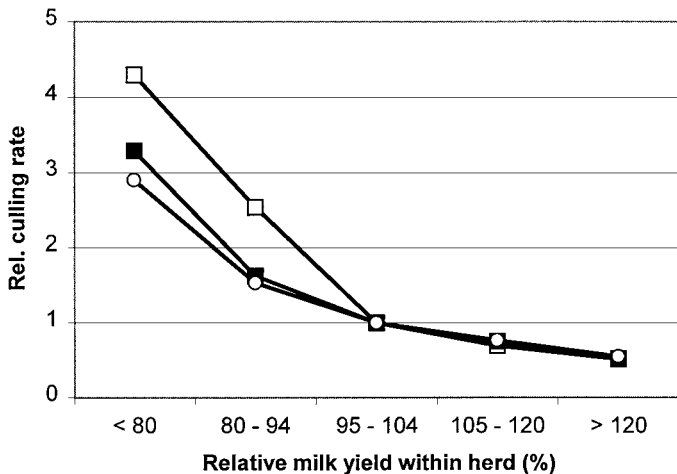


Figure 4. Relative culling rate for within-herd deviations in milk yield in Holstein cows in the first (□), second (■), and third (○) lactations.

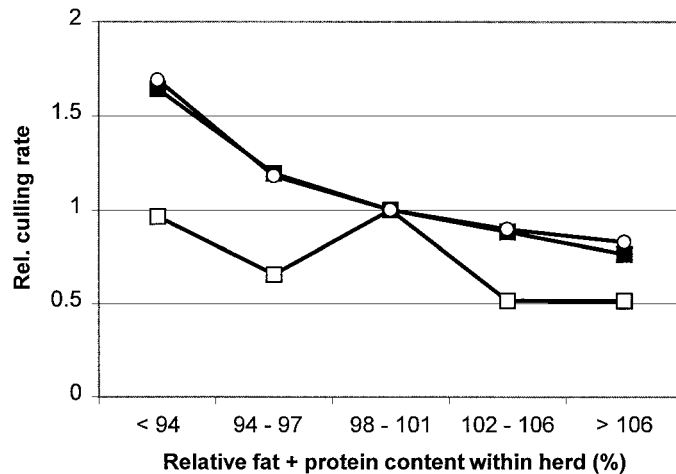


Figure 5. Relative culling rates for within-herd deviations in fat and protein content in Braunvieh cows in the first (□), second (■), and third (○) lactations.

increases with advancing lactation, and eventually reaches its maximum at the end of lactation, when most (nonpregnant) cows are culled. The first lactation deviates from the typical pattern because of the increased hazard at about 60 d after first calving that indicated different selection criteria in first lactating cows.

Alpine pasturing seems to have an extraordinary positive effect on longevity, as can be seen from Figure 3 for the Simmental breed. When averaged over all geographic zones and calving seasons, the culling rate for those cows who spent the summer in the Alps is up to 150% lower than for cows left in the valley. Similar results were found in a previous study in Braunvieh cows (Vukasinovic, 1995). Apparently, longevity of cows that spent the summer in the Alps is positively influenced by environmental and management effects different than those in the valley. These results may confirm the traditional belief that alpine pastures, fresh air, and exercise improve cow's overall fitness and, thus, longevity. However, the results may just indicate that only healthy cows are sent to the Alps, whereas those with poor health, leg problems, or sterility are usually left at home (and culled for reasons other than not being on alpine pasturing).

Within-herd deviation of milk yield has the greatest influence on culling rate in all three breeds. Figure 4 illustrates the relative culling rates for Holstein cows in the first, second, and third lactation. Within each lactation, cows producing less than 80% of the herd average are at 3 to 4 times higher risk than their herd-mates with average production. High producing cows are less likely to be culled. These results illustrate the importance of voluntary culling for milk production.

The voluntary culling for low production is more intensive in the first lactation than in later lactations. Higher risk for culling of low producing cows in later lactations might reflect circumstances that cause low production such as disease or injury. The correction for level of production might be somewhat rough because of the small number of classes, but it seems appropriate for Swiss dairy breeds (the rank correlations between EBV of sires for functional productive life and milk yield were 0.16, 0.00, and 0.01 in Braunvieh, Simmental, and Holstein, respectively).

The influence of within-herd deviation of fat and protein content is similar in all three breeds. Figure 5 illustrates the relative culling rate for Braunvieh cows

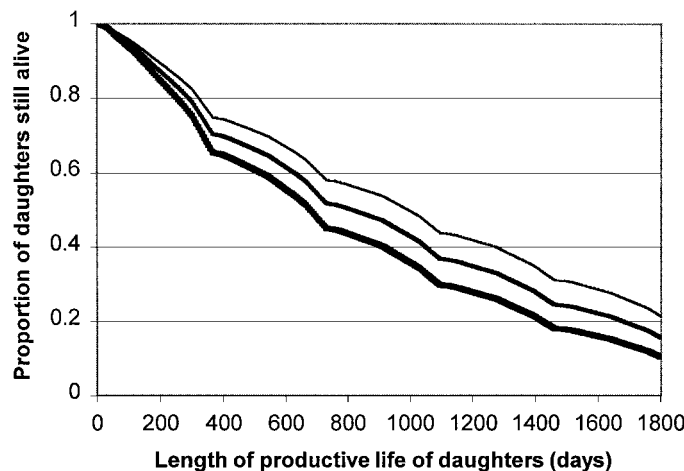


Figure 6. Expected survivor curves for three hypothetical Holstein sires with estimated breeding values of -1 (thick line), 0 (medium line), and +1 (thinnest line) genetic standard deviations.

Table 3. Total number of sires (N) and percentage of sires with reliability of estimated breeding values of min. 50% (%) by year of birth.

Year of birth	Braunvieh		Simmental		Holstein	
	N	%	N	%	N	%
Before 1981	16,750	12	16,612	11	1096	31
1981–1985	4303	16	4953	25	563	26
1986–1990	3421	10	4214	34	529	30
After 1990	943	6	1528	43	210	44

in the first three lactations. Except for the first lactation, cows with a high fat and protein content relative to herd average are at a slightly lower risk than those with fat and protein content below the herd average. However, the differences among the classes are smaller than for milk yield. The unexpectedly high culling rate in the third class of the first lactation is mostly influenced by grouping animals without a lactation record, indicating that grouping might be improved. Future refinements of the model may well consider exclusion of first lactating cows without lactation record or defining a separate class for such cows. Similar to correction for milk yield within herd, the number of production level classes seems to be rather small, but it proved optimal for Swiss dairy breeds (the rank correlations between EBV of sires for functional productive life and fat and protein percentage were ~ 0 in all three breeds).

Estimated Breeding Values

Figure 6 illustrates expected survivor curves for three hypothetical Holstein sires with EBV of -1 , 0 , and $+1$ genetic standard deviations, assuming average levels of the herd-year-season effect, age at first calving, and within-herd deviations for milk yield and fat and protein content. The variation in culling rates during each lactation are clearly indicated. When expressed as expected length of productive life of daughters, a difference of one genetic standard deviation corresponds to approximately 170 d difference in expected length of productive life of the daughters.

The reliability of EBV depends on the number of uncensored records and is low for young sires with few uncensored daughters. Currently, only breeding values with reliability of at least 50% are published. Table 3 shows the total number of sires and the percentage of sires with a reliability of at least 50% by year of birth.

The proportion of sires with reliability over 50% is particularly small in Braunvieh bulls, because of the relatively large proportion of bulls used in natural mating, as opposed to Simmental and Holstein bulls. The obvious problem is that a majority of young bulls (born 1992 and later) have low reliability, which means that their proof is not very useful, because the selection deci-

sion has to be made long before the reliability of breeding values becomes satisfactory.

Increasing the reliability of breeding values for young sires remains one of the most important tasks for the future. Currently, if a young sire has no censored daughters, the reliability of his EBV is based on pedigree information only. The reliability of EBV of young sires could be increased by taking into account weighted information on censored daughters. Moreover, the reliability might be increased by the inclusion of information from early predictors (type traits, SCC, fertility). Inclusion of type traits using MACE techniques (Schaeffer, 1994) seems to be promising and requires further research.

CONCLUSIONS

Genetic evaluation for functional longevity requires specific methods that can use information on both uncensored and censored records and account for nonlinearity of longevity data. Genetic evaluation based on survival analysis has been successfully implemented in the populations of three main dairy breeds in Switzerland.

The genetic evaluation for longevity in Switzerland for Braunvieh and Holstein sires is conducted twice a year, and the EBV are published in sire summaries for all sires with a reliability of the EBV $\geq 50\%$. Currently, the published breeding values help farmers to avoid sires with extremely low breeding values for longevity, thereby preventing a decrease of productive life in the population.

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