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Genetic evaluation of longevity in dairy cattle

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ABSTRACT

Longevity is a highly desirable trait that considerably affects overall profitability. With increased longevity, the mean production of the herd increases because a greater proportion of the culling decisions are based on production. Longevity did not receive adequate attention in breeding programs because genetic evaluation for this trait is generally difficult as some animals are still alive at the time of genetic evaluation. Therefore, three basic strategies were suggested to evaluate longevity for cows: Firstly, cow survival to a specific age, which can be analyzed as a binary trait by either linear or threshold models. Secondly, estimating life expectancy of live cows and including these records in a linear model analysis. Thirdly, survival analysis: a method of combining the information of dead (uncensored) and alive (censored) cows in same analysis. This review represents an attempt to shed a light on different strategies of genetic evaluation of longevity in dairy cattle in most of developed countries.

Keywords: longevity, genetic evaluation, survival analysis.
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INTRODUCTION

It was well known that most national dairy cattle research and breeding programs were mainly oriented toward yield traits (Leitch, 1994). However, functional traits, such as reproduction, longevity, and health traits, are of increased interest to producers to improve herd profitability. Miglior, (2005), in their comparison of international selection indices, reported that selection indices have evolved worldwide, shifting their focus from primarily production to a more balanced breeding approach that includes longevity, udder health, conformation, and reproduction.

Longevity is a highly desirable trait that considerably affects overall profitability (Congleton and King, 1984; Allaire and Gibson, 1992). With increased longevity, the mean production of the herd increases because a greater proportion of the culling decisions are based on production, and the proportion of mature cows, which produce more milk than young cows, is increased. Further, the economic importance of herd life compared with milk production is considered higher than other nonproductive traits (Rogers and McDaniel, 1989; Van Arendonk, 1991; Allaire and Gibson, 1992; Dekkers, 1993).

Longevity is determined by voluntary and involuntary culling decisions of individual farmers. In the process of making decisions on culling, the farmers or producers will take into account production, health, fertility, and other functional traits such as milking speed, milking temperament, and calving ease (Sewalem, 2008). Generally, culling because of poor production is called voluntary culling, and culling for reasons other than poor production is called involuntary culling. Reducing the rate of involuntary culling allows a higher voluntary replacement rate, which can increase profits for a dairy farm.

Numerous suggestions for a definition of the longevity trait have been used such as, total lifetime which is defined as the number of days from birth of cow to culling or death (Gill and Allaire 1976; Hoque and Hodges 1980), functional productive life, which is defined as the number of days from first calving to culling or death adjusted for milk yield (Ducrocq 1987; Caraviello, 2004a), true productive life as previous trait without adjusting to milk yield (Ducrocq, 1988), number of parities (Hargrove, 1969; Jairath, 1994), total lifetime days in milk and total lifetime milk yield (Norman, 1981), average milk yield per day of longevity (Prasad, 1987), average milk yield per day of productive life (Gill and Allaire 1976), average milk yield per day of days in milk (Sadana and Basu 1982) and survival to fixed age (Sundaresan, 1954).

Genetic differences for milk yield will have a major effect on direct measures of survival because low milk yield is a major cause of cow culling. Thus, many studies have proposed analyzing functional productive life (PL), which is generally computed as longevity adjusted for milk yield (Dekkers 1993; Vollema, and Groen 1996; Boettcher, 1998; Emanuelson, 1998; Jairath, 1998; Vollema, and Groen 1998). This trait accounts only for culling that is due to causes other than milk yield. Analyzing productive life before adjusting for yield is complicated because selection goals change over time. Until 1980, milk yield was the primary selection objective of most breeding programs. Now protein yield is the chief goal, and many countries put a negative economic weight on milk yield (Leitch, 1994.).

Due to longevity can be measured in several ways, the genetic evaluation systems are not standardized across countries, making the comparison of sire rankings difficult.

Methods of genetic evaluation of longevity

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).

Several researchers tried to overcome this problem by using one of three basic strategies suggested to evaluate longevity for live cows: cow survival to a specific age can be analyzed as a binary trait by either linear or threshold models (Harris, 1992; Boettcher, 1998; Jairath, 1998; Vollema, and Groen 1998). Unfortunately, this method is associated with a great loss of information. 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, 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).

For instance, in Canada, the survival of cows in each of the first three lactations is recorded as a binary trait and evaluated with a multiple-trait linear animal model (Jairath, 1996) in which survival in each lactation is considered as a separate trait. Relative simplicity is an attractive feature of this approach. However, linear models are not as appropriate for analysis of binary response traits, as they are only appropriates for continuously distributed traits, such as milk production. Therefore, some precision in the analysis of herd life could be gained by threshold model which was less simple but more statistically appropriate (Gianola 1982). Threshold analyses account for the categorical nature of the phenotype by modeling an underlying normal distribution with truncation points. Both theoretical and empirical results indicate greater estimates of heritabilities from threshold models than from linear models (Gianola, 1979; Weller and Ron 1992), suggesting increased accuracy of EBV when threshold models are used for genetic evaluation.

In the second strategy, Van Raden and Klaaskate (1993) proposed estimating life expectancy of live cows and including these records in a linear model analysis. One of the most drawbacks of this method represented by estimates based on incomplete data are regressed toward the mean, and therefore have lower heritability and variance than do complete records (Meijering and Gianola 1985; Weller, 1988; Van Raden, 1991). By use of this method first proposed by Weller, (1988), incomplete records were multiplied by a factor to bring all records to an equal genetic variance. Because the incomplete records have lower heritability, this strategy results in greater residual variance for the incomplete records. To solve this problem the records are weighted in the mixed model equations according to their residual variances. The third method is survival analysis or consideration of cows still alive as censored records (Vukasinovic, 1997; Boettcher, 1998; Emanuelson, 1998; Vollema, and Groen 1998). Although, the previous methods could be applied to either animal or sire models, survival analysis can only be applied to sire models, and evaluations will be biased if the number of daughters per sire with complete records is low (Vukasinovic, 1997).

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 Solkner, 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, 1999), Italy (Schneider et al., 2000), and Switzerland (Vukasinovic, 2001). Further, at the time of genetic evaluation of a cow, we know only the lower bound of each animal's productive life, and excluding such records or considering them as complete would lead to a bias. Survival analysis using a proportional hazard model as suggested by Smith and Quaas (1984) and represent an alternative method for evaluation of sires based on the length of productive life of their daughters. Ducrocq, (1988) showed that proportional hazard models could be used for the analysis of length of productive life. Ducrocq and Solkner (1998) developed the survival kit typically used by animal breeders for large populations. Survival analysis combines information on uncensored and censored records, which enables a proper statistical treatment of censored records and accounts for the nonlinear characteristic of longevity data. It also offers several advantages over the linear model that is currently used in Canada, including 1) precision can be increased by accounting for differences in days of productive life between cows that survive for the same number of lactations, 2) censored records eliminate the need to wait for 2 yr before using a lactation record, and 3) higher estimates of heritability are yielded in comparison with the linear model, suggesting increased reliability of sire EBV. Generally, a better model used to estimate genetic parameters, should produce greater heritability estimates. Heritability estimates for milk production, for example, were around 0.25 when sire linear models were still used for official genetic evaluations in North America. The estimates then jumped to 0.30to 0.35 with the implementation of animal models and now are expected to increase again because of the imminent adoption of test-day models in most developed countries (Jamrozik, 1997). These changes in heritability occurred because the models have improved their abilities to account for environmental effects and, consequently, to isolate the additive variance associated with the trait of interest. Therefore, if survival analysis really provided a better description of the failure times of dairy cows than did the popular linear models, one should expect to get higher heritability estimates for the herd life traits by using survival models.

Survival analysis has also been used to evaluate measures of longevity in horses (Ricard and Fournet-Hanocq, 1997) and swine (Ringmar-Cederberg, 1997). Theoretically, both the threshold and survival models clearly have advantages over the linear model.

International Genetic Evaluation of longevity

Longevity in dairy cattle is internationally recognized as an important trait for the dairy industry; and it can affect overall profitability considerably (van Arendonk, 1991). Today, nationally predicted sire breeding values for longevity are available in many countries around the

world (Miglior, 2005). The internationalization of dairy cattle breeding requires that dairy bulls must be compared across countries, since a lack of information on foreign bulls compared with domestic bulls could lead to wrong selection decisions (Mark, 2002).

National sire breeding values (BV) for longevity can be computed using, for example, linear, random regression, or survival models (Solkner and Ducrocq, 1999; Veerkamp, 2001; Caraviello, 2004b). Prediction of international sire breeding values for longevity using multiple-trait across country evaluation (MACE) was found to be feasible in several studies (Van der Linde and de Jong, 2002, 2003; Jakobsen, 2004).

Since 1994, the International Bull Evaluation Service (Interbull) has provided international genetic evaluations using MACE following the methodology introduced by Schaeffer (1994) and subsequently refined by, among others, Sigurdsson, (1996), Sullivan (1999), and Fikse and Banos (2001).

National genetic evaluations for direct longevity from 19 countries [Australia (AUS), Austria (AUT), Belgium (BEL), Canada (CAN), Denmark (DNK), Finland (FIN), France (FRA), Germany (DEU), Hungary (HUN), Ireland (IRL), Israel (ISR), Italy (ITA), New Zealand (NZL), Spain (ESP), Sweden (SWE), Switzerland (CHE), the Netherlands (NLD), the United Kingdom (GBR), and the United States

(USA)] and from one or more of the following breeds: Brown Swiss, Guernsey, Holstein, Jersey, Red Dairy Cattle, and Simmental, were used for the February 2007 routine international genetic evaluation.

The data set used to calculate the international BV for direct longevity consisted of 123,833 national sires'BV after editing (Forabosco, (2009).

International EBV for direct longevity are calculated by Interbull and are made available to the member countries. The member countries can publish direct longevity or they can combine it with predictors (combined longevity). Most of the member countries include longevity in their total merit index. Through Web sites and magazines, sires' BV is circulated among the dairy breeders and the dairy breeding industries can benefit from this information. Longevity has become a very important trait internationally and the extra visibility provided through the launch of Interbull evaluations has led to many national improvements and helped breeders focus more attention on longevity.

Trait	Model	Example reference		
Stayability until x months of life (0/1)	Linear (sire or animal)	Everett et al.,(1976)		
Survival (0/1) per lactation	Linear ('repeatability' sire)	Madgwick and Goddard (1989)		
Survival (0/1) per lactation	Linear (multivariate animal or sire)	Jairath et al., (1998)		
Months of productive life	Linear (animal)	Van Raden and Klaaskate (1993)		
Number of lactations	Linear (animal)	Brotherstone et al., (1997)		
Time (of culling)	Proportional hazard (sire or animal)	Ducrocq and Casella (1996)		
Survival $(0/1)$ as a function of time	Linear (random regression, animal or sire)	Veerkamp et al., (1999)		
Source: Visscher, (1999)				

Table 1. Traits and models for genetic analysis of longevity in dairy cattle

Table 2. Estimation of total herd life (months) in some breeds of cattle	e
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Source of data	Country	Breed	No. observations	Longevity (months)
Parker et al., (1960)	USA	HF	-	67
Gaalaas and Plowman (1963)	USA	HF	3879	61.6
Hoque and Hodges (1980)	Canada	HF	51599	72
Silva et al., (1986)	USA	HF	1552	67.9
McAllister et al., (1987)	Canada	HF	313	53.19
Ponce de Leon and Gomez (1988)	Cuba	HF	1254	75.6
Short and Lawlor (1992)	USA	HF	80126	65.2
Vollema and Groen (1996)	Netherlands	HF	38957	70
Puski et al., (2002)	Hungarian	HF	2789	55.9-63.9
Al-Samarai (2006)	Iraq	HF	4468	85.86
Garcia-Peniche et al., (2006)	USA	HF	1844358	50.3
Fisteag et al., (1983)	Romania	F	430	83.66
Muresan et al., (1986)	Romania	F	556	102.8
Wilcox et al., (1966)	USA	JER	1000	71.2
Silva et al., (1986)	USA	JER	1681	72.8
Silva et al., (1986)	USA	GUE	1418	68.1
Cruickshanket al., (2002)	USA	GUE	18725	58.9
McAllister et al., (1994)	Canada	AYR	250	50.76
		TH	837	87.36
Sharma and Singh (1974)	India	SAH	371	91.80
		RS	164	91.92
Basu et al., (1983)	India	TH	958	94.55
Patel et al., (1983)	India	KAN	815	109.2

BS = Brown Swiss; GUE = Guernsey; HF = Holstein; JER = Jersey; F = Friesian, AYR= Ayrshire, RS=Red sindhi, SAH=Sahiwal, TH=Tharparkar, KAN= Kankrej

Table 3. Estimation of productive life (months) in some breeds of cattle

Table 3. Estimation of productive life (months) in some breeds of cattle				
Source of data	Country	Breed	No. observations	Productive life (months)
Gill and Allaire (1976)	USA	HF	923	35.5
Hoque and Hodges (1980)	Canada	HF	51599	43
Tigges et al., (1986)	USA	HF	1552	43.8
Ponce de Leon and Gomez (1988)	Cuba	HF	1254	45
Short and Lawlor (1992)	USA	HF	80126	37.7
Dekkers et al., 1994	Canada	HF	13131	33
Jairath et al., 1994	Canada	HF	82835	27.7
Vollema and Groen (1996)	Netherlands	HF	38957	43.3
Smith et al., (1998)	USA	HF	2610123	33
Settar and Weller (1999)	Israel	HF	82196	33.6
Vukasinovic et al., (1999)	Switzerland	HF	224847	33.9
Beaudeau et al., (2000)	France	HF	3589	38.5
Chirinos et al., (2002)	Spain	HF	78842	30.5
Ojango et al., (2002)	Kenya	HF	1355	40.5
Caraviello et al., (2004a)	USA	HF	8915	23.1 - 25.2
Al-Samarai (2006)	Iraq	HF	4468	53.16
Garcia-Peniche et al., (2006)	USA	HF	1844358	21.76
Hare et al., (2006)	USA	HF	2292550	32.7
Terawaki and Ducrocq (2009)	Japan	HF	787598	38.6
Fisteag et al., (1983)	Romania	F	430	53.59
Sadana and Basu (1982)	India	JER	232	37.2
Rogers et al., (1991)	USA	JER	26034	36.2
Norman et al., (1996)	USA	JER	71731	37.1
Ducrocq (1994)	France	NOR	103214	28
Vukasinovic et al., (1997)	Switzerland	BS	52862	32.4
		TH	837	41.6
Sharma and Singh (1974)	India	SAH	371	41.7
		RS	164	42.6

BS =Brown Swiss; HF = Holstein; JER = Jersey; F = Friesian; RS=Red sindhi, SAH=Sahiwal, TH=Tharparkar; NOR= Normande

Country Model		Heritability	Trait definition	Number	Date of
		h²		of sires	data
Italy	SM, SA	0.08	Productive life span	5749	> 1980
Switzerland	SM, SA	0.18	Productive life span	2912	> 1980
France	SM, SA	0.10	Productive life	13009	> 1985
Netherlands	SM, SA	0.10	Productive life span	8954	> 1988
Germany & Austria	SM, SA	0.12	Functional herd life	14752	> 1979
Denmark	SM, SA	0.117	Productive life span	13284	> 1984
Sweden	SM, MT	0.08	Survival rate at 2 nd calving	4439	> 1984
Canada	AM, MT	0.0975	Survival in the first three lactations	7648	> 1980
New Zealand	AM, ST	0.055	Herd life	7801	> 1988
USA	AM, ST	0.085	Till 84 months	25399	> 1960
Israel	AM, ST	0.11	Days from first calving to 2922 d	727	> 1985
UK	AM, MT	0.06	lifespain	5016	> 1986
Australia	AM, RP	0.025	Probability of surviving from one year to the next	5761	> 197.
Ireland	AM, MT	0.016	Survival to next lactation	1238	> 1980
Belgium	AM, RR	0.106	Survival over successive lactations	524	> 1973
Finland	SM, SA	0.12	Stayability from first calving	3456	> 1988
Hungary	SM, SA	0.05	Productive life span	1834	> 1988
Spain	SM, SA	0.115	Productive life span	1339	> 1986

Table 4. Information for 19 countries providing national genetic evaluation data for the International Bull Service routine evaluation for direct longevity.

SA = Survival Analysis, SM = Sire Model, AM = Animal Model, MT = Multitrait Analysis, ST = Single Trait Analysis, RP= repeatability model, RR= random regression model.

Source: Forabosco, (2009)

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