

Selection for longevity in dairy cattle



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1998-09-02

Selection for longevity in dairy cattle

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Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op woensdag 2 september 1998
des namiddags te vier uur in de Aula

0201 2589 7

Vollema, A.R., 1998. Selection for longevity in dairy cattle. Doctoral thesis, Animal Breeding and Genetics Group, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands.

In a dairy cattle breeding program, selection should be on functional longevity rather than on uncorrected longevity. The heritability of functional longevity is below 10%, but data on the length of productive life of cows are easily obtained from milk recording databases. Survival analysis is needed for an unbiased prediction of breeding values for young bulls, because this method makes proper use of information on cows that have not been culled at the moment of data collection. When sufficient data on the realized longevity of the daughters of a bull are not available, conformation traits have to be used as predictors. Especially the udder, feet and legs, and rump angle are important factors in determining longevity. The results from this thesis help breeding organizations to implement selection for longevity in their breeding program.

ISBN 90-5485-878-8

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Stellingen

1. De tijdelijke daling van de gemiddelde levensduur van de Nederlandse zwartbonte koeien in de jaren tachtig was te wijten aan de invoering van de melkquotering en de verdringingskruising van het Fries Hollandse door het Holstein Friesian melkveeras. (*Dit proefschrift*)
2. Het scoren van het exterieurkenmerk "type" is overbodig. (*Dit proefschrift*)
3. Fokken op ongecorrigeerde levensduur in een melkveefokprogramma voegt niets toe. (*Dekkers, J.C.M., 1993. J. Dairy Sci., 76: 1433; Strandberg, E., 1997. Paper G3.2 of 48th EAAP, Vienna; dit proefschrift*)
4. Als de productieve levensduur van koeien bekend is en als men de beschikking heeft over voldoende computercapaciteit, moeten levensduurgegevens geanalyseerd worden met behulp van de *survival analysis*. (*Dit proefschrift*)
5. De correlatie tussen het percentage eiwit en het percentage vet in de melk van een koe wordt overschat als niet de percentages, maar de hoeveelheden eiwit en vet genetisch bepaald zijn. (naar *Yule, G.U., 1910. J. Roy. Stat. Soc., series A, 73: 644*)
6. Het bouwen van geboorde, gesegmenteerde tunnels is ook in de slappe, natte Nederlandse bodem een goed alternatief voor het gebruik van traditionele bouwmethoden.
7. Gezien het grote aantal "snelwegveeartsen" in Nederland is de ziektereregistratie van melkkoeien via dierenartsen geen haalbare kaart.
8. Bij de milieu-inspectie wordt geen afweging gemaakt tussen ammoniak- en CO_x-uitstoot.
9. Holsteinisering en de Elfstedentocht zijn beide voorbeelden van verdringing van het Friese erfgoed.
10. Meepraten is niet hetzelfde als meedenken, maar het één kan niet zonder het ander.
11. Het gaat er niet om wat waar is, maar wat men denkt dat waar is.

Stellingen bij het proefschrift van Ant R. Vollema: "Selection for longevity in dairy cattle." Wageningen, 2 september 1998.

oan heit en mem
aan Johan

Tu ne quaesieris, scire nefas, quem tibi, quem mihi
finem di dederint; ut melius quidquid erit pati....
Spem longam reseces, dum loquimur fugerit invida
aetas; carpe diem, quam minimum credula postero.

Q. Horatius Flaccus

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Chapter 1

Introduction

The longevity of a dairy cow measures the time she produces in a herd, and it is determined by her milk production, health, fertility, and workability. Traits reflecting the production of a cow are usually called primary traits, and traits reflecting health, fertility, and workability secondary traits. The relevance of primary traits is easily seen because an increase in production directly results in a higher output of a farm. Improving secondary traits results in a decrease of costs, to which in the past little attention has been paid in animal breeding. Only the Nordic countries included direct selection on secondary traits in their breeding programs. Nowadays, interest in secondary traits has increased worldwide: many countries are working on or are already predicting breeding values for secondary traits like mastitis resistance, calving ease, and milking speed (Interbull, 1996). The higher valuation also is expressed in their new name: functional traits (Groen *et al.*, 1997).

Culling reasons

Apart from cows that die, the longevity of a dairy cow is completely determined by the culling decision-making of the farmer. Both Renkema and Stelwagen (1979), Sol *et al.* (1984), and Van de Venne (1987) concluded that 70% of the culling of dairy cows in The Netherlands was caused by a disease in the broad sense. Within this category unsatisfactory reproduction was the main reason for culling. Culling for low production mainly took place during the first lactation (Van de Venne, 1987).

It has to be emphasized that the farmer determines the actual longevity of cows. The farmer weights the performance of cows for primary and functional traits and decides whether to cull a cow or not. In practice, this means that it is nearly impossible to make a clear distinction between culling for production and culling for functional traits. For example, a high producing cow will be bred more often before she is culled for low fertility than a low producing cow. Dohoo and Martin (1984) indicated that there are two methods to evaluate reasons for culling. The first method uses the farmer's stated reason for culling, which gives an impression of the most immediate and pressing shortcoming of the cow. However, this method does not give insight in the other reasons for culling. An improvement would be to ask farmers for more than one culling reason (e.g., Sol *et al.*, 1984), but in this case, the relative weighting of the different culling reasons is probably not uniform and thus hard to interpret. The second method

of Dohoo and Martin (1984) evaluates indirect reasons for removal, such as disease history and previous milk production. To use this method, data on these indirect reasons, such as veterinary records, have to be known, which might not always be the case.

Relevance of longevity

Rendel and Robertson (1950) identified four ways by which increased longevity increases profit: 1. by reducing the annual costs of replacements per cow in the herd; 2. by increasing the average herd yield through an increase in the proportion of cows in the higher producing age-groups; 3. by reducing the replacements which have to be reared, and therefore allowing an increase in size of the milking herd for a given acreage; and 4. by an increase in the possibilities for voluntary culling. The actual profit from an increased longevity of cows depends on the production circumstances of a farmer: for instance, if there is a quota system, extra production of the herd is of no extra value. Renkema and Stelwagen (1979) concluded that the yield resulting from a longer longevity is subject to the law of diminishing returns. An increase in the genetic potential for longevity increases the realized longevity, but not as much as the genetic potential allows (Van Arendonk, 1985). Farmers will use the extra space for selection to cull more heavily on production or reproduction or both. Several authors (Dekkers, 1994; Stott, 1994; Van Arendonk, 1985) concluded that the proportion of involuntary culling governs the potential longevity and thus the economic advantage of longevity.

The economic value of longevity has often been estimated. VanRaden and Wiggans (1995) made an overview of the relative economic values of yield and herd life from the literature, and concluded that the ratio between both values was on average 2.5:1 which was in line with their own estimate. All estimates were expressed on a genetic standard deviation basis. The variation between estimates was large (range 0.8:1 to 8.0:1) emphasizing that the economic value of longevity depends on the production circumstances, although some variation is also caused by the difference in methods used to calculate the economic value.

Renkema and Stelwagen (1979) calculated the optimum length of productive life of a cow with an average milk production without diseases as 10 to 14 lactations. However, they did not consider variation in production and

functional traits within a herd. Van Arendonk (1985) showed that cows producing below the herd average had relatively a much lower optimal length of productive life than the cows producing above average. For instance, the optimal length of productive life of a cow producing at 70% of the herd average will be 5 months, while this will be 8 years for a cow producing at 130% of the herd average. In 1979 the average actual length of productive life in The Netherlands was 4.5 lactations (Renkema and Stelwagen, 1979), and Van de Venne (1987) found an average length of productive life of 3.5 years in 1986. The reasons for this decline in realized longevity can be changed prices of replacement heifers, the carcass price of culled cows, the rapid introduction of Holstein Friesian genes in the population, and the fast genetic improvement for milk potential. However, there is a growing concern about this decrease in realized longevity of dairy cows. Nowadays much emphasis is on sustainability of production systems and welfare of animals, and it is felt that in this respect an increased realized longevity would be one of the desired changes in dairy production. However, as stated before, the actual longevity of dairy cows is largely determined by the farmer's decision making. Breeding programs can contribute to an increased longevity of dairy cows by including this trait into breeding programs. In this way at least the potential longevity of dairy cows can be improved, and by providing breeding values for longevity to the farmers they may become more aware of, and pay more attention to, the longevity of their own cows.

Longevity in breeding programs

The production of a cow is recorded routinely in many countries, and breeding values for production traits are easily obtained. Although in some countries health and fertility traits are recorded as well, in other countries they are not. Breeding value prediction for functional traits is then based on correlated traits, such as somatic cell count or conformation traits. An alternative is the use of longevity. The longevity of cows can be easily calculated from milk recording records, if one assumes that the last known test day is the last day of a cow's life. Because longevity is determined by production and functional traits, longevity corrected for milk production is a better measure for functional traits than uncorrected longevity (Dekkers, 1993). This corrected longevity is usually called functional longevity. Because culling

decisions are made within herds, the correction for production has to be on a within-herd basis as well (Van Arendonk, 1985).

Breeding organizations have to make many choices if they want to include longevity in their breeding program. First, they have to decide what their breeding goal is, so what they want to breed for exactly: uncorrected longevity, functional longevity, or residual longevity, which is longevity corrected for other traits which are in the breeding goal. Uncorrected longevity can be seen as containing all traits that are relevant to the farmer, including milk production. Because in most breeding programs milk production is recorded routinely, functional longevity could be used to breed for all functional traits simultaneously. In breeding programs where some functional traits are measured directly, residual longevity might be used to avoid double-counting of traits.

Second, it has to be decided which trait will be used to define longevity. A distinction can be made between traits that measure the whole lifetime of a cow, such as herd life or length of productive life, and stayability traits which measure whether or not a cow survived until a certain moment in time, such as stayability until 36 months of age or survival of the third lactation. Lifetime traits can be measured only after a cow's death, but contain all information possible on a cow's longevity. Stayability traits are binary traits and contain less information (e.g., if a cow did not survive until 36 months of age it is unknown how far before that moment in time she was culled, if she did survive it is unknown how much longer she will live) but can be measured at any moment.

Instead of looking at these different traits, a different method than the well known restricted maximum likelihood based on best linear unbiased prediction may be an alternative to analyse longevity traits. If a cow is still alive at the moment of data collection, her record on longevity is called censored. A censored record can be seen as the minimum longevity the cow will reach, and not using such records means loss of information. Cox (1972) described the method of survival analysis in which not the actual longevity of a machine, human being, or animal is analysed, but the risk of failure or death. In this procedure, censored records can be included in the analysis as well. Another advantage of the method is the possibility to model effects in a time-dependent way, thus it is expected that such models mimic reality better. Famula (1981) introduced this method in animal breeding. Smith and Quaas (1984) were the first to estimate genetic parameters with survival analysis. In 1987, Smith's

survival analysis program became available but its feasibilities were rather restricted (Smith, 1987). In 1994, Ducrocq and Sölkner presented their programs for survival analysis, which are more general applicable (Ducrocq and Sölkner, 1994). The programs have been updated continuously since then and used by various researchers for different purposes (e.g., Gröhn *et al.*, 1997; Ringmar-Cederberg *et al.*, 1997; Vukasinovic *et al.*, 1997). Of course other authors have written other programs as well. For instance, Korsgaard (1996) implemented a Gibb's sampling algorithm in her program. Thus, the third choice is which method a breeding company wants to use.

Fourth, breeding organizations have to decide which traits they want to use in their index for longevity. Longevity itself is easily recorded but, as indicated before, it may take a long time before the information is available. Even when using stayability traits or survival analysis, there is a certain timespan needed to obtain enough information for a reliable breeding value prediction. Compared with a breeding program solely aiming at improved milk production, breeding for longevity only using information on longevity itself will always increase the generation interval. Therefore, it might be useful to include predictive traits in the index as well. Intuitively, conformation traits are good predictors of longevity. They can be measured early in a cow's life and attention is already paid to them in breeding programs because they are expected to have correlations with functional traits. Furthermore, if functional traits are recorded they also can be used to predict longevity, as good as longevity can be used to measure functional traits. However, if breeding for longevity is aimed at improving underlying functional traits it would be more effective to select for these functional traits directly.

Aim and outline of this thesis

The aim of this thesis is to investigate parameters that influence the choices breeding organizations have to make when they want to incorporate longevity into the breeding program. In Chapter 2 an overview of the literature containing estimates of heritabilities of longevity traits, correlations among longevity traits, and correlations between longevity and conformation traits is presented. Various factors influencing the results of these studies are identified and discussed. In Chapter 3 the heritability of longevity traits and genetic correlations among them are estimated using a REML algorithm on Dutch data.

The total data available was split into separate datasets according to the year of birth of the cows. The achieved longevity per cow was severely influenced by the large-scale crossing with Holstein bulls in the mid-eighties, as well as by the implementation of the quota system in 1984. Also the heritability of longevity traits was influenced. In Chapter 4 the correlations between longevity and conformation traits are estimated, again using a REML algorithm on Dutch data. Again data on cows with different years of birth were used and differences were found between results from these separate datasets as well. In Chapter 5 the method of survival analysis was used to predict breeding values of sires and these breeding values were compared with those from the more traditional methods of phenotypic averages of daughters and best linear unbiased prediction. Because differences between methods were substantial and survival analysis was assumed to be the best way to analyze longevity data the relationship between longevity and conformation traits was investigated using survival analysis (Chapter 6). In the General Discussion issues concerning the incorporation of longevity in breeding programs that are addressed in previous chapters are summarized and related to the Dutch situation. Issues that have not been addressed in previous chapters are addressed here.

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Chapter 2

Longevity of dairy cows: a review of genetic variances and covariances with conformation

Ant R. Vollema

Abstract

Heritability of longevity traits, genetic correlations among longevity traits, correlations between longevity and conformation traits, and regression models using conformation traits to explain longevity were reviewed. Estimates based on dairy cows from literature from 1970 onwards were incorporated. Lifetime and stayability traits, and functional and uncorrected longevity traits were considered. Heritability estimates were generally lower than 10%, and traits measured later in life had a higher heritability. Estimates were generally lower for functional than for uncorrected longevity traits. Genetic correlations among longevity traits were generally high. When using conformation traits to predict longevity, traits concerning the udder and feet and legs were most important.

key words: genetic parameters, longevity, conformation, dairy cows, review

Introduction

Longevity is a trait of increasing importance in dairy cow breeding schemes. Much research has been done, and is still being done, on estimation of the genetic parameters which are needed to incorporate longevity into a breeding program. Many different definitions of longevity are used and many different methods of analysis, and results differ greatly. Because conformation traits can be measured early in life, their value as predictors of longevity has often been investigated. Reviews of the literature were made in the past, but they were either not published in a journal, or not very extensive. Moreover, many were published over ten years ago (Burnside *et al.*, 1984; Dekkers and Jairath, 1994; Ducrocq, 1987; Harris, 1992; Strandberg, 1985). This paper aims to give an overview of the estimated heritability of longevity traits, genetic correlations among them, and correlations with conformation traits. It is confined to studies on data on dairy cows, which appeared as full papers in refereed journals, from 1970 onwards. For every reference, the estimate, amount of information, model, method of analysis, and additional remarks (such as breed of the cows, opportunity groups) are given. Factors possibly influencing the estimates (e.g., grade versus registered cows, model of analysis) are discussed. This review may particularly be useful for researchers who need to know "the" genetic parameters of longevity traits, or "the" relationship between conformation and longevity traits, for, for instance, a simulation study or estimation of breeding values.

Traits

Longevity reflects a cow's ability not to be culled. Culling reasons include low production, disease, and low fertility. Culling for low production is usually referred to as voluntary culling, culling for disease and low fertility as involuntary culling.

In the literature, various definitions of longevity are used. First one can make a distinction between "corrected" and "uncorrected" longevity traits. Corrected longevity traits are corrected for milk production, thus aiming to give better measurements of involuntary culling (Dekkers, 1993). Corrected traits are also called "functional" longevity traits, analogous to traits causing involuntary culling such as diseases, which are called "functional" traits. Second, one can make a distinction between "lifetime" and "stayability" traits. Lifetime traits measure the whole lifespan of a cow. These can be measured only after the death of a cow, but contain complete information on longevity. Stayability traits measure whether or not a cow is alive at a certain point in time (e.g., at a fixed number of months from birth or first calving). These traits can be measured at any point in time, but because they are binary traits they do not contain complete information on a cow's longevity. For instance, a cow that did not survive up to 36 months of age can have any lifespan that is shorter than those 36 months, and if she did survive, it is unknown how much longer she will live. A compromise between the higher information content of lifetime traits and the earlier availability of stayability traits is to use opportunity groups. Opportunity groups consist of animals with the same maximum lifespan that can be recorded. Instead of waiting until all have been culled, a maximum lifespan (opportunity) is assigned to cows: if they are culled before this maximum is reached, their actual lifespan is known, otherwise the maximum opportunity is taken as their lifespan.

In this study, longevity traits are divided into four classes: lifetime, stayability, miscellaneous, and functional traits. The following definitions and abbreviations (used in the tables) are given:

lifetime traits:

- herdlife (**HL**): time period between birth and culling;
- length of productive life (**LPL**): time period between first calving and culling;
- total milk production (**TMP**): lifetime milk production summed over lactations;
- number of days in lactation (**NDL**): lifetime milking days summed over

lactations;

- number of lactations (**NLC**);

stayability traits (0/1):

- stayability until a certain number of months of age (e.g., **AGE36**, **AGE72**);
- stayability until a certain number of months after first calving (e.g., **PL12**, **PL36**);
- survival of a certain lactation;

miscellaneous traits:

- total months in milk at 84 months of age (**MIM84**);
- probability of surviving from one lactation to the other;

functional traits:

- longevity traits corrected for production are indicated by a prefix "functional" (abbreviated **F**, e.g., **FHL**, **FNLC**, **FAGE72**).

Most studies are based on data retrieved from milk recording records, which means that only cows that calved at least once are included. In the literature, sometimes a different name for a certain trait is used. For instance, some researchers use the term "true" when they refer to uncorrected longevity traits (Boldman *et al.*, 1992; Ducrocq *et al.*, 1988; Harris *et al.*, 1992). Also, "herdlife" is sometimes used when the length of productive life is meant (Dekkers *et al.*, 1994; Short and Lawlor, 1992). In all cases, the name and definition as described above have been used in this review. Traits describing lifetime profit have been excluded, because they entirely depend on assumptions that have been made for cost components and prices.

Most authors use well-known methods such as Henderson III and REML. An alternative method to evaluate longevity that is increasingly being used in animal breeding is survival analysis (e.g., Ducrocq *et al.*, 1988; Smith and Quaas, 1984). Instead of modelling longevity itself, the hazard of being culled is modelled with this method. Because the hazard is modelled, it is possible to include also the so-called "censored" records, i.e., records of cows that are still alive at the moment of data collection. Also with this method, non-linear models can be used in the analysis. Furthermore, it is possible to include time-dependent variables. Disadvantage of the method is the relatively large amount of computer capacity that is needed to perform the analysis.

Table 1. Heritability estimates of uncorrected lifetime traits.

Author	Estimate						# Records	Model	Method	Remarks
	HL	LPL	TMP	NDL	NLC					
Boldman <i>et al.</i> (1992)	0.03						53,830	sire model	REML	grade cows
Chauhan <i>et al.</i> (1993)	0.028	0.006	0.017		0.005		44,933	sire model	REML	
Dentine <i>et al.</i> (1987)	0.033 0.031 0.035						7,924 15,868 23,792	sire model	Henderson III	grade cows registered cows combined data
Ducrocq <i>et al.</i> (1988)		0.085 ¹					87,338	Weibull sire model	survival analysis	
Fürst and Sölkner (1994)		0.14 0.14 0.15	0.22 0.20 0.26				208,857 198,483 116,432	sire/mgs model	tilde-hat approx. to REML	Simmenthalers (incl. crosses) purebred Simmenthalers Braunvieh*Brown Swiss
Gill and Allaire (1976)	0.26	0.25	0.25		0.23		933	sire model	Henderson III	cows from 8 herds
Harris <i>et al.</i> (1992)	0.06 0.07 0.04	0.02 0.05 0.03					39,910 21,453 ?	sire model	REML	Guernsey, 48 mo opp. ² Guernsey, 72 mo opp. Guernsey, 48 mo opp., registered cows
Hoque and Hodges (1980)	0.10	0.10	0.11		0.09		30,738	sire model	Henderson III	
Jairath <i>et al.</i> (1994)		0.08	0.13	0.09	0.07		82,835	sire model	REML	
Klassen <i>et al.</i> (1992)			0.10	0.07	0.05		34,322	sire model	REML	

Table 1 (continued).

Author	Estimate						?	
	HL	LPL	TMP	NDL	NLC	sire model		
Norman and Van Vleck (1972)			0.09		0.11	1,639		
Rogers <i>et al.</i> (1991a)	0.02					> 119,000	REML	Jersey, grade cows Jersey, registered cows Jersey, combined data
Short and Lawlor (1992)	0.04					45,515	REML	grade cows
	0.10					80,126		registered cows
	0.07					125,887		combined data
Smith and Quaas (1984)	0.13					227,091	survival analysis	datasets dependent on definition of censored records
	0.06					449,325	REML	Swedish Red&White
Strandberg (1992)		0.046				12,027 ³	sire model	
		0.075				8,361 ⁴		
VanRaden and Klaaskate (1993)					0.085	1,984,038	sire model	
Vollema and Groen (1996)	0.136	0.136	0.172	0.140	0.132	94,935	sire model	cows born in 1978
	0.109	0.110	0.134	0.116	0.098	166,324	sire model	cows born in 1982
	0.040	0.036	0.104	0.048	0.032	38,957	sire model	cows born in 1985
	0.037	0.035	0.087	0.042	0.036	38,957	animal model	cows born in 1985
Vukašinović <i>et al.</i> (1995)		0.12				9,224	sire model	Brown Swiss, 48 mo opp.
		0.13						Brown Swiss, 66 mo opp.
		0.14						Brown Swiss, 84 mo opp.
Weigel <i>et al.</i> (1995)		0.06				433,116	sire model	

¹ Pseudo-heritability² Opportunity to 48 mo of age³ Unselected data⁴ Selection on > 120 d in 2nd lactation, and > 15 mo productive life

Results

Heritability of and genetic correlations among longevity traits are given in several tables and will be discussed per table. Phenotypic correlations between longevity and conformation traits are given in a separate table, as are genetic correlations. In each table the author(s), year of publication, estimates of either heritability or correlation, number of records used in the analysis, model and method of analysis, and additional remarks are given. Results of regression models are reported in the text. Unless mentioned otherwise, all data are on Holstein cows.

Heritability

Table 1 contains heritability estimates of uncorrected lifetime traits. For herdlife, most estimates are in the range of 0.03 - 0.13. The weighted average equals 0.081 (including all estimates in the table weighted according to the number of records). For length of productive life, most estimates are in the range of 0.04 - 0.15, with a weighted average of 0.092. The weighted average of all estimates for total milk production is 0.17. For number of days in lactation, heritability estimates are in the range of 0.04 - 0.14, and the weighted average is 0.10. Heritability estimates of number of lactations are mostly in the range of 0.03 - 0.13. The weighted average of the estimates is 0.084.

Apart from herdlife, all heritability estimates of Chauhan *et al.* (1993) are considerably lower than the estimates from other studies. In contrast, Gill and Allaire (1976) found extremely high estimates, which was explained by the limited number of data used in the analysis. However, the number of data used by Chauhan *et al.* (1993) was sufficient to have reasonably low standard errors on the estimates. The authors did not give an explanation.

Two authors made use of survival analysis: Ducrocq *et al.* (1988) and Smith and Quaas (1984). Their heritability estimates are well within the range of the other estimates in this table. From Smith and Quaas (1984) it can be seen how the selection of data influences the estimation. In the first data set (227,091 records) only cows with code "died or sold for beef" were considered to be culled, in the second data set (449,325 records) cows were also considered culled if the herd remained in the milk recording scheme but the cows disappeared from the data files. This phenomenon of data selection influencing

the results is not limited to survival analysis: Strandberg (1992) also found different heritability estimates from selected and unselected data by using a REML algorithm.

Vollema and Groen (1996) estimated heritability by using data on cows with different years of birth. Estimates decreased with increasing year of birth. The authors claim that this is due to the implementation of the quota system, and the crossbreeding with Holstein-Friesian bulls in the mid-eighties. Analysing the same data file with both a sire and an animal model gave similar results, which is not very surprising because with low heritable traits, most information comes from the sire side even when using an animal model.

Harris *et al.* (1992) and Vukašinović *et al.* (1995) used data from different opportunity groups. Heritability estimates differed between opportunity groups in Harris *et al.* (1992), but not very much in Vukašinović *et al.* (1995). Estimates tended to be higher with increasing opportunity.

In general, heritability estimates using data on Simmenthalers, Braunvieh, and Brown Swiss cows are higher than those using data on other breeds. Although the limited number of data in Vukašinović *et al.* (1995) might be an explanation for the high estimates, the number of data in Fürst and Sölkner (1994) was sufficiently large and the estimates did not differ much.

Heritability estimates of total milk production are generally higher than those of other lifetime traits, as can be expected, because total milk production is a product of length of productive life and the highly heritable milk production per day. Heritability estimates of number of lactations tend to be slightly lower; this trait contains less information.

Table 2 contains heritability estimates of stayability until a certain number of months of age and of productive life. Most estimates of stayability until a certain number of months of age are in the range of 0.02 - 0.06, so lower than the heritability of lifetime traits. DeLorenzo and Everett (1986) found higher estimates (0.12 and 0.15 for stayability up to 41 and 54 months of age respectively) using a logistic linear model. Vollema and Groen (1996) also found relatively high estimates, ranging from 0.01 to 0.19. Most estimates of stayability until a certain number of months after first calving are in the range of 0.01 - 0.04. Compared with the heritability estimates of stayability until a certain number of months of age, those until a certain number of months after first calving are lower. Both types of stayability only differ by the age at first

Table 2. Heritability estimates of stayability until a certain number of months of age and of productive life.

Author	Estimates			# Records	Model	Method	Remarks
	# mo.	I	II				
<i>stayability until a certain number of months of age</i>							
DeLorenzo and Everett (1986)	41	0.12	0.28	18,941	logistic linear sire model	Newton-Rhapson iteration	I: uncorrected II: corrected to underlying normal scale ¹
Dentine <i>et al.</i> (1987)	48	0.044	0.018	0.013	13,818 ²	sire model	I: grade cows II: registered cows III: combined data
Hudson and Van Vleck (1981)	54	0.035	0.016	0.024	13,207		
	84	0.024	0.035	0.036	7,924		
	36	0.0223			97,555	sire model	Henderson III
	48	0.0397					
	60	0.0500					
	72	0.0529					
	84	0.0507					
Short and Lawlor (1992)	54	0.02	0.06	0.05	I: 45,515	sire model	I: grade cows II: registered cows III: combined data
	84	0.03	0.05	0.04	II: 80,126 III: 125,887		
Van Doormaal <i>et al.</i> (1985)	42	0.051			243,348 ³	sire model	Henderson's "breeders" new method
	54	0.040					
	66	0.045					
	78	0.059					
VanRaden and Klaaskate (1993)	48	0.050			1,984,038	sire model	REML

Table 2 (continued).

Author	# mo.	Estimates			# Records	Model	Method	Remarks
		I	II	III				
Vollema and Groen (1996)	36	0.040	0.115		94,935	sire model	REML	cows born in 1978; I: uncorrected II: corrected to underlying normal scale ¹
	48	0.080	0.149					
	60	0.116	0.187					
	72	0.108	0.171					
	36	0.053	0.129		166,324	sire model	REML	cows born in 1982; I: uncorrected II: corrected to underlying normal scale ¹
	48	0.076	0.128					
	60	0.087	0.137					
	72	0.072	0.119					
	36	0.012	0.092		38,957	sire model	REML	cows born in 1985; I: uncorrected II: corrected to underlying normal scale ¹
	48	0.012	0.038					
	60	0.020	0.036					
	72	0.032	0.050					
	36	0.007	0.054		38,957	animal model	REML	cows born in 1985; I: uncorrected II: corrected to underlying normal scale ¹
	48	0.013	0.042					
	60	0.023	0.041					
	72	0.029	0.046					
<i>stayability until a certain number of months after first calving</i>								
Rogers <i>et al.</i> (1991a)	20	0.03	0.04	0.04	> 119,000	sire model	REML	Jersey cows; estimates corrected to underlying normal scale ¹ ; I: grade cows, II: registered cows, III: combined data
Syrstad (1979)	36	0.017			> 70,000	sire model	anal. of var. among and within sires	

Table 2 (continued).

Author	# mo.	Estimates			# Records	Model	Method	Remarks
		I	II	III				
Van Doormaal <i>et al.</i> (1985)	17	0.025	0.010		I: 243,348 ³ II: 118,362	sire model	Henderson's new method	I: breeders II: milkers
	30	0.040	0.017					
	43	0.039	0.023					
	55	0.033	0.033					
Vollema and Groen (1996)	12	0.044	0.106		94,935	sire model	REML	cows born in 1978; I: uncorrected II: corrected to underlying normal scale ¹
	24	0.088	0.157					
	36	0.112	0.177					
	48	0.108	0.173					
	12	0.060	0.129		116,324	sire model	REML	cows born in 1982; I: uncorrected II: corrected to underlying normal scale ¹
	24	0.080	0.131					
	36	0.082	0.128					
	48	0.071	0.120					
	12	0.012	0.069		38,957	sire model	REML	cows born in 1985; I: uncorrected II: corrected to underlying normal scale ¹
	24	0.008	0.021					
	36	0.020	0.034					
	48	0.028	0.045					
	12	0.007	0.040		38,957	animal model	REML	cows born in 1985; I: uncorrected II: corrected to underlying normal scale ¹
	24	0.009	0.023					
	36	0.025	0.043					
	48	0.026	0.041					

¹ by the method of Van Vleck (1972)

² number of grade cows given, approximately twice as much registered cows

³ cows surviving to the maximum opportunity get a probability for the next stayability

calving, which seems to take away some of the genetic variance. Both DeLorenzo and Everett (1986) and Vollema and Groen (1996) corrected their estimates to an underlying normal scale, which in all cases caused a considerable increase. Heritability first tends to increase with increasing number of months at evaluation of stayability, and then decrease with further increasing number of months. Hudson and Van Vleck (1981) explained that the variance of a binomial trait increases with more equal proportions in each category. At an intermediate number of months, the frequency of cows surviving is 50%, so heritability is highest here. Table 3 contains heritability estimates of survival of a certain lactation. Most estimates are in the range of 0.01 - 0.12. Heritability first tends to increase with increasing lactation number, and decrease again with further increasing lactation number, except in Madgwick and Goddard (1989), where the heritability estimate of survival of the first lactation is relatively high compared with that of subsequent lactations. The authors give no explanation for this. They split their total data set with 235,000 records into two subsets: one with cows first calving prior to 1979, and one with cows first calving after 1979. Heritability estimates of cows before 1979 are generally higher than those of cows after 1979. As in Vollema and Groen (1996), estimates based on data from an earlier period are higher than those from a later period. The reason behind this might be the same for both studies: in The Netherlands and in Australia Holstein cows became more popular and superseded the Dutch Friesian and Jersey cows respectively.

Dong and Van Vleck (1989) found relatively high heritability estimates for survival of the first lactation, which might be explained by the small number of data on a limited number of herds. Cue *et al.* (1996) found higher heritability estimates for Jersey than for Holstein cows, and even higher for Ayrshire cows. Visscher and Goddard (1995) also found a higher heritability for Jersey than for Holstein cows, both for survival of a certain lactation and for survival of a certain lactation given survival of the previous lactation. Heritability of the latter trait is generally lower.

Heritability estimates of months in milk at 84 months of age are not presented in a table. VanRaden and Klaaskate (1993) introduced this trait and found a heritability of 0.085. Weigel *et al.* (1995) found a heritability of 0.06, which is consistent with the earlier estimate. The weighted average of the two estimates is 0.081.

Table 3. Heritability estimates of survival of a certain lactation.

Author	Estimate for lactation i						# Records	Model	Method	Remarks
	i = 1	i = 2	i = 3	i = 4	i = 5	i = 6				
Brotherstone and Hill (1991a)		0.053	0.065	0.067			19,294	sire model	REML	classified herds
Brotherstone and Hill (1994)		0.027	0.038	0.044	0.045		275,188	sire model	REML	model included heterosis and recombination loss
Cue <i>et al.</i> (1996)		0.026	0.046				59,623	sire model	REML	Jersey cows
		0.051	0.094				45,396			Ayrshire cows
		0.146	0.132				6,599			two datasets with 15 herds each
Dong and Van Vleck (1989)	0.11						3,063	animal model	REML	
	0.12						3,077			
Madgwick and Goddard (1989) ¹	0.053	0.004	0.012	0.022	0.037	0.018	253,000	sire model	REML	1st calving < 1979
	0.028	0.005	0.005	0.012	0.007					1st calving > 1979
Rogers <i>et al.</i> (1991) ²	0.05						22,179	sire model	REML	Jersey, grade cows
	0.08						97,316			Jersey, registered cows
	0.08						119,817			Jersey, combined data
Schaeffer and Burnside (1974)	0.04	0.08					46,074	sire model	iterative MINQUE	
Short and Lawlor (1992)	0.01						45,515	sire model	REML	grade cows
	0.03						80,126			registered cows
	0.01						125,887			combined data
Visscher and Goddard (1995) ³		0.05	0.07	0.07	0.07	0.03	19,269	sire model	REML	Jersey cows
		0.22	0.21	0.13	0.14	0.06	8,768			
Visscher and Goddard (1995) ⁴	0.03	0.03	0.02	0.02	0.03		37,247 ⁵	sire model	REML	
	0.07	0.08	0.04	0.02	0.03		10,798 ⁵			Jersey cows

¹ probability of survival from i to i + 1 year post first calving

² corrected to an underlying normal scale by method of Van Vleck (1972)

³ stayabilities until lactation i

⁴ probability of survival from lactation i to i + 1

⁵ smallest number of cows is given; numbers are: for i = 1, 190,830 and 41,964; for i = 2, 164,911 and 43,824; for i = 3, 104,702 and 28,704; for i = 4, 63,940 and 18,159; and for i = 5, 37,247 and 10,798; for Holstein and Jersey cows respectively

Table 4 contains heritability estimates of functional lifetime traits. For functional herd life, estimates ranged from 0.02 to 0.10 with a weighted average of 0.065. The heritability estimates of functional length of productive life are in the range of 0.02 - 0.10, and the weighted average is 0.069. The heritability estimates of functional lifetime traits increase with increasing opportunity (Harris *et al.*, 1992; Vukašinović *et al.*, 1995). Vollema and Groen (1996) were the only reference that considered functional total milk production, functional number of days in lactation, and functional number of lactations. The weighted averages of the heritability estimates were 0.10, 0.084, and 0.073 respectively. Of all traits in this study, heritability decreased with increasing year of birth.

Heritability of functional traits are expected to be lower than heritability of uncorrected lifetime traits, because functional traits have been corrected for highly heritable production traits. In Table 1, the weighted average heritability of herd life equals 0.081, but most estimates are around 0.03. Boldman *et al.* (1992) found a heritability estimate of 0.03 for herd life, using the same data and method with which they found an estimate of 0.03 for functional herd life. Also Ducrocq *et al.* (1988) found the same heritability for functional length of productive life as for its uncorrected equivalent using the same data and method, as found Short and Lawlor (1992) and Rogers *et al.* (1991a). However, Harris *et al.* (1992), Vollema and Groen (1996), and Vukašinović *et al.* (1995) found a lower heritability for functional than for uncorrected lifetime traits.

Heritability estimates using data on Guernsey cows (Harris *et al.*, 1992) are not substantially higher than estimates for Holstein cows. However, it should be noted that the maximum opportunity for Guernsey cows equals 72 months (approximately 4 lactations), and that this estimate is higher than the estimates of data with less opportunity. Estimates for Jersey and Brown Swiss cows are a little lower than for Holstein cows. For the Jersey cows (Rogers *et al.*, 1991a), this may be caused by the linear and quadratic correction for yield. The other references corrected only linearly for production; due to the quadratic correction the heritability of functional length of productive life will be lower.

Table 5 contains heritability estimates of functional stayability until a certain number of months of age and of productive life. Heritability of stayability until a certain number of months of age ranged from 0.01 to 0.06, increasing with increasing age at evaluation of stayability. Compared with the heritability

Table 4. Heritability estimates of functional lifetime traits.

Author	Estimate							Remarks		
	FHL	FLPL	FTMP	FNDL	FNLC	# Records	Model			
Boldman <i>et al.</i> (1992)	0.03					53,830	sire model	REML linear within herd last lactation yield	grade cows	
Ducrocq <i>et al.</i> (1988)		0.085 ¹				87,338	Weibull sire model	REML survival analysis	within herd level of yield	
Harris <i>et al.</i> (1992)	0.02 0.05 0.03					39,910 21,453 ?	sire model	REML	linear and quadratic within herd-year last lactation milk, fat, and protein yield	Guernsey, 48 mo opp. ² Guernsey, 72 mo opp. Guernsey, 48 mo opp., only registered cows
Rogers <i>et al.</i> (1991a)						5,622 26,034 31,992	sire model	REML	linear and quadratic first lactation yield	Jersey, grade cows Jersey, registered cows Jersey, combined data
Short and Lawlor (1992)						45,515 80,126 125,887	sire model	REML	within herd first lactation yield	grade cows registered cows combined data
Vollema and Groen (1996)	0.104 0.078 0.036	0.100 0.079 0.035	0.112 0.101 0.075	0.104 0.084 0.039	0.096 0.068 0.036	94,935 166,324 38,957	sire model sire model animal model	REML	"lactation value"	cows born in 1978 cows born in 1982 cows born in 1985
Vukašinić <i>et al.</i> (1995)		0.03 0.04 0.05				9,224	sire model	REML	relative yield within herd	Brown Swiss, 48 mo opp. ³ Brown Swiss, 66 mo opp. Brown Swiss, 84 mo opp.

¹ Pseudo-heritability

² Opportunity to 48 mo of age

³ Opportunity to 48 mo after first calving

Table 5. Heritability estimates of functional stayability until a certain number of months of age and of productive life.

Author	# no.	Estimates			# Records	Model	Method	Correction	Remarks
		I	II	III					
<i>stayability until a certain number of months of age</i>									
Hudson and Van Vleck (1981)	36 48 60 72 84	0.0160 0.0252 0.0312 0.0371 0.0407			97,555	sire model	Henderson III	estimates corrected for variance in yield	
Vollema and Groen (1996)	36 48 60 72	0.016 0.044 0.080 0.076	0.032 0.046 0.056 0.052	0.007 0.010 0.021 0.028	I: 94,935 II: 166,324 III: 38,957	sire model	REML	lactation value	I: cows born in 1978 II: cows born in 1982 III: cows born in 1985
<i>stayability until a certain number of months of productive life</i>									
Rogers et al. (1991a)	20	0.03	0.04	0.04	I: 15,391 II: 70,170 III: 85,945	sire model	REML	linear and quadratic first lactation yield	I: Jersey, grade cows II: Jersey, registered cows III: Jersey, combined data
Vollema and Groen (1996)	12 24 36 48	0.032 0.048 0.076 0.080	0.037 0.049 0.054 0.052	0.003 0.005 0.023 0.025	I: 94,935 II: 166,324 III: 38,957	sire model	REML	lactation value	I: cows born in 1978 II: cows born in 1982 III: cows born in 1985

Table 6. Genetic correlations among uncorrected lifetime traits.

Author	Traits and estimates			# Records	Model	Method	Remarks	
Chauhan <i>et al.</i> (1993)	<i>HL</i>	0.290	<i>LPL</i>	44,933	sire model	REML		
	<i>TMP</i>	0.773	<i>NLC</i>					0.486
	<i>HL</i>	0.306						0.294
	<i>LPL</i>						0.890	
Gill and Allaire (1976)	<i>NLC</i>	0.95	<i>LPL</i>	933	sire model	Henderson III	cows from 8 herds	
	<i>TMP</i>	0.99						
Hoque and Hodges (1980)	<i>TMP</i>	0.98	<i>LPL</i>	30,738	sire model	Henderson III		
	<i>HL</i>	1.0						0.98
	<i>LPL</i>							1.0
Jairath <i>et al.</i> (1994)	<i>NDL</i>	0.99	<i>LPL</i>	82,835	sire model	REML		
	<i>TMP</i>	0.97						0.97
	<i>NDL</i>	1.00						0.98
	<i>LPL</i>						0.98	
Klassen <i>et al.</i> (1992)	<i>NLC</i>	0.95	<i>NDL</i>	34,322	sire model	REML		
	<i>TMP</i>	0.97						0.97
	<i>NLC</i>	0.98					0.98	
Norman and Van Vleck (1972)	<i>TMP</i>	0.98		1,639	sire model	?		
Vollema and Groen (1996)	<i>HL</i>	0.870	<i>LPL</i>	38,957	sire model	REML	cows born in 1985	
	<i>NLC</i>							0.986
	<i>NDL</i>							

estimates of uncorrected stayability until a certain number of months of age by the same authors (see Table 2), these estimates are lower. Heritability estimates of functional stayability until a certain number of months after first calving ranged from 0.003 to 0.08. Heritability by Rogers *et al.* (1991a) was the same as those of the uncorrected equivalents (Table 2), but that by Vollema and Groen (1996) was lower.

For the heritability estimates of functional survival of the first lactation only one reference was found (Rogers *et al.*, 1991a). Estimates were 0.05, 0.08, and 0.08 for grade, registered, and combined data respectively. Data were on Jersey cows.

Genetic correlations among longevity traits

Table 6 contains genetic correlations among uncorrected lifetime traits. Most correlations are very high, around 0.97. One exception is Chauhan *et al.* (1993), who estimated quite low genetic correlations among various lifetime traits (ranging from 0.290 to 0.890), especially between herd life and other traits.

Table 7 contains genetic correlations among stayability. The method of Calo *et al.* (1973) corrects for the different number of cows used for the breeding value estimation of each sire, and generally causes an increase in the estimated genetic correlation. In general, correlations are high (around 0.8), and increasing when the moments of measurement of two traits are closer together, as can be expected with two traits that have a part-in-whole relationship. Van Doormaal *et al.* (1985) found some very low correlations between stayability until 42 and 66 months of age, and between stayability until 42 and 78 months of age (0.288 and 0.219 respectively), but did not give an explanation. In the same study, the genetic correlations among stayability until a certain number of months of productive life were generally higher than those among stayability until a certain number of months of age, using the same "milkers" data.

Table 8 contains genetic correlations between lifetime traits and stayability. Estimates were very high, ranging from 0.86 to 1.00. In Vollema and Groen (1996), no difference was found between correlations between lifetime traits and stayability until a certain number of months of age, and correlations between lifetime traits and stayability until a certain number of months of productive life.

Table 7. Genetic correlations among uncorrected stayability until a certain number (x) of months of age (AGE_x) and of productive life (PL_x).

Author	Traits and estimates		# Records ¹	Model	Method	Remarks
DeLorenzo and Everett (1982)	AGE48	AGE72	333,608	sire model	correlations between sire PTAs ²	
	AGE48	0.88				
Everett <i>et al.</i> (1976)	AGE48	AGE60	124,706	sire model	correlations between sire PTAs ²	
	AGE36	0.94				
	AGE48	0.82				
	AGE60	1.00				
	AGE72	1.00				
	AGE72	1.00				
Hudson and Van Vleck (1981)	AGE48	AGE60	97,555	sire model	Henderson III	
	AGE36	0.80				
	AGE48	0.76				
	AGE60	0.95				
	AGE72	0.95				
	AGE72	1.00				
	AGE72	0.96				
Short and Lawlor (1992)	AGE54	AGE84 ³	45,515 ⁴	sire model	REML	
	AGE54	0.76				
	AGE84 ³	0.93				
	AGE84 ³	0.91				
Van Doormaal <i>et al.</i> (1985)	AGE42	AGE66	118,362	sire model	Henderson's new method	"milkers"
	AGE54	0.288				
	AGE66	0.880				
	AGE66	1.10				
	PL17	PL55	118,362			"milkers"
	PL30	0.886				
	PL43	1.21				
	PL43	0.945				
	PL43	1.14				
	PL17	PL55	233,348			"breeders"
	PL30	0.983				
	PL43	0.952				
	PL43	0.983				
	PL43	1.00				
	PL43	1.04				

Table 7 (continued).

Author	Traits	AGE48	AGE60	AGE72	# Records	Model	Method	Remarks
Vollema and Groen (1996)	AGE36	0.872	0.847	0.995	38,957	sire model	REML	cows born in 1985
	AGE48		1.000	1.000				
	AGE60			0.971				
	PL24	0.733	0.896	0.880				
	PL24		1.000	1.000				
	PL36			0.992				
	PL12		0.996	1.000				
	AGE36	1.000	0.776	0.867				
	AGE48	0.798	0.985	1.000				
	AGE60	0.882	1.000	0.998				
	AGE72	0.996	1.000	0.996				
	PL12		0.996	1.000				
	PL24		0.776	0.867				
	PL36		0.985	1.000				
	PL48		0.976	0.976				

¹ In case of different opportunity groups, lowest group size is given

² Correction by method of Calo *et al.* (1973)

³ Estimates based on grade cows, registered cows, and combined data respectively

⁴ Number of grade cows given, number of registered cows is 80,126

Table 8. Genetic correlations between uncorrected lifetime traits and stayability until a certain number (x) months of age (AGE_x) and of productive life (PL_x).

Author	Traits and estimates				# Records	Model	Method	Remarks
Short and Lawlor (1992)	PL ¹	PL ¹	PL ¹	LPL ¹	45,515 ²	sire model	REML	
	AGE54	AGE54	AGE54	AGE54				
Vollema and Groen (1996)	AGE84	AGE84	AGE84	AGE84	38,957	sire model	REML	cows born in 1985
	NLC	NLC	NLC	NLC				
	HL	HL	HL	HL				
	PL12	PL24	PL36	PL48				
	NLC	NLC	NLC	NLC				
	HL	HL	HL	HL				

¹ Estimates based on grade cows, registered cows, and combined data respectively

² Number of grade cows given, number of registered cows is 80,126

Table 9. Genetic correlations between survivals of different lactations.

Author	Lactations and estimates					# Records	Model	Method	Remarks
Brotherstone and Hill (1991a)	3	4				19,294	sire model	REML	
	2	0.907	0.732						
	3	0.885							
Brotherstone and Hill (1994)	3	4	5			275,188	sire model	REML	
	2	0.98	0.98	0.94					
	3	0.99	0.96						
	4	0.98							
Cue <i>et al.</i> (1996)	3	3	3			59,623	sire model	REML	
	2	0.902	0.894 ²	0.884 ³					
Madgwick and Goddard (1989)	2	3	4	5		253,000			correlations between sire PTAs ¹
	1	1.02	0.99	0.24	-0.21				
	2	0.75	0.97	-0.16					
	3	0.95	-0.09						
	4	-0.28							
	2	3	4	5	6	7	8	9	
	1	0.78	0.44	1.00	0.85	0.79	0.01	0.51	0.25
	2	0.77	0.77	1.00	0.81	1.12	-0.03	0.69	0.36
	3		0.38	0.43	0.90	0.79	-0.52	0.51	0.58
	4			0.90	1.00	1.00	0.01	0.80	0.00
	5			1.11	1.11	0.31	0.71	0.42	0.06
	6			0.23	0.23	0.95	0.35	0.42	0.06
	7			0.09	0.09	0.35	0.09	0.06	0.06
8			0.09	0.09	0.09	0.09	0.09	0.09	
									1st calving > 1979
									1st calving < 1979

Table 9 (continued).

Author	Lactations and estimates					# Records	Model	Method	Remarks
Visscher and Goddard (1995)	3	4	5	6	6	19,269	sire model	REML	
	2 ⁴	0.86	0.86	0.83	0.66				
	3	0.98	0.98	0.91					
	4	0.99	0.99	0.92					
	5			0.92					
	3	4	5	6	6	8,768	sire model	REML	Jersey cows
	2 ⁴	0.72	0.68	0.79	0.80				
	3	0.99	0.86	0.92					
	4		0.88	0.93					
	5			0.97					

¹ correction by method of Calo *et al.* (1973)

² estimate based on 45,396 Jersey cows

³ estimate based on 6,599 Ayrshire cows

⁴ stayability until lactation i

Table 9 contains genetic correlations among survivals of different lactations. In most references, genetic correlations were high (0.72 - 0.99) and generally higher when the lactation numbers were closer together. This indicates that the main reason for culling is different in different lactations, as could be concluded from specific studies on this topic (Sol *et al.*, 1984; Van de Venne, 1987; Westell *et al.*, 1982). Only Madgwick and Goddard (1989) found much lower and more diverse estimates, ranging from -0.52 to 1.12. This is the only reference found where genetic correlations between different longevity traits were negative. The authors explain this by the low heritability of the longevity traits, and, therefore, the low accuracy of the sires' predicted transmitting abilities. The estimated genetic correlations have large standard errors possibly resulting in correlations greater than 1 or less than -1.

Table 10 contains genetic correlations among miscellaneous traits. Months in milk at 84 months of age has very high genetic correlations with number of lactations, stayability at 48 months of age, and length of productive life (0.982 - 0.992) (VanRaden and Klaaskate, 1993; Weigel *et al.*, 1995). Visscher and Goddard (1995) estimated genetic correlations among probabilities of surviving from one lactation to the following. Their estimates were reasonably high, ranging from 0.37 to 0.96, and decreasing when the lactations considered were further apart, as could be expected.

Table 11 contains genetic correlations between uncorrected and functional longevity traits. Genetic correlations were generally high (0.58 - 0.98), which is quite surprising. Longevity has a relatively strong correlation with within-herd production (e.g., Jairath *et al.*, 1994; Norman *et al.*, 1996; Visscher and Goddard, 1995; Vukašinović *et al.*, 1995), so the correlation between uncorrected longevity and longevity corrected for milk production is expected to be low. However, it is not expected to be zero, because genetic correlations are dealt with, and correction for production is usually done at phenotypic level.

Table 12 contains genetic correlations among lifetime traits for different opportunity groups. All correlations among either uncorrected or functional longevity traits were over 0.90. Genetic correlations were higher between opportunity groups that were closer together, as one could expect. Genetic correlations between uncorrected and functional longevity traits for different opportunity groups were lower, ranging from 0.72 to 0.92.

Table 13 contains genetic correlations among longevity traits in grade and

Table 10. Genetic correlations among miscellaneous uncorrected longevity traits.

Author	Traits and estimates		# Records	Model	Method	Remarks
VanRaden and Klaaskate (1993)	MIM84	NLC 0.992	1,984,038	sire model	REML	
Visscher and Goddard (1995)	prob. 1-2 ¹	prob. 2-3 0.95	19,269	prob. 3-4	sire model	REML
	prob. 2-3	prob. 4-5		prob. 5-6		
	prob. 3-4	0.67		0.37		
	prob. 4-5	0.79		0.57		
		0.96	0.80	0.92		
Weigel <i>et al.</i> (1995)	prob. 1-2	prob. 2-3 0.96	8,768	prob. 3-4	sire model	REML
	prob. 2-3	prob. 4-5		prob. 5-6		
	prob. 3-4	0.94		0.96		
	prob. 4-5	0.97		0.98		
		0.98		0.98		
		0.97				Jersey cows
	MIM84	LPL 0.99	433,116	sire model	REML	

¹ Probability of surviving lactation 1 to 2

Table 11. Genetic correlations between uncorrected and functional longevity traits.

Author	Traits and estimates		# Records	Model	Method	Remarks
Boldman <i>et al.</i> (1992)	<i>FHL</i>	<i>HL</i> 0.84	53,830	sire model	REML	
Ducrocq <i>et al.</i> (1988)	<i>FLPL</i>	<i>LPL</i> 0.74	87,338	Weibull sire model		correlation between sire evaluations
Short and Lawlor (1992)	<i>FLPL</i>	<i>AGE54</i> 0.76	45,515	sire model	REML	grade cows
		<i>AGE84</i> 0.91				
	<i>FLPL</i>	<i>AGE54</i> 0.92	80,126	sire model	REML	registered cows
		<i>AGE84</i> 0.96				
	<i>FLPL</i>	<i>AGE54</i> 0.89	125,887	sire model	REML	combined data
		<i>AGE84</i> 0.95				
Vollema and Groen (1996)		<i>HL</i> 0.809	38,957	sire model	REML	cows born in 1985
	<i>FNDL</i>	<i>AGE36</i> 0.829				
	<i>FHL</i>	<i>AGE72</i> 0.952				
	<i>FAGE36</i>	<i>AGE72</i> 0.916				
	<i>FAGE72</i>	<i>AGE72</i> 0.965				
	<i>AGE72</i> 0.878	<i>AGE72</i> 0.642	<i>AGE72</i> 0.947			

Table 12. Genetic correlations among uncorrected and functional lifetime traits for different opportunity groups.

Author	Traits ¹ and estimates		# Records	Model	Method	Remarks
Harris <i>et al.</i> (1992)	HL72	FHL48	21,543	sire model	REML	Guernsey cows
	HL48	FHL72				
	HL72	FHL48				
Vukašinović <i>et al.</i> (1995)			9,224	sire model	REML	Brown Swiss cows
	LPL66	FLPL66				
	LPL48	FLPL48				
	LPL84	FLPL84				
	FLPL48	FLPL66				
	FLPL66	FLPL48				
	FLPL84	FLPL84				

¹ Numbers indicate the number of months of age or productive life of opportunity

Table 13. Genetic correlations between longevity traits in grade and in registered cows.

Registered	Grade				
	<i>F surv. lact. 1</i> ²	<i>FPL20</i>	<i>FLPL</i>	<i>AGE54</i>	<i>FLPL</i>
Rogers <i>et al.</i> (1991a) ¹					
<i>Func. surv. lact. 1</i>	0.94	1.19	0.79		
<i>FPL20</i>	0.78	1.04	0.48		
<i>FLPL</i>	0.85	0.99	0.54		
Short and Lawlor (1992)					
<i>Surv. lact. 1</i>	0.46	0.35	0.34	0.39	0.35
<i>AGE54</i>	0.36	0.36	0.31	0.38	0.30
<i>AGE84</i>	0.35	0.35	0.36	0.41	0.39
<i>LPL</i>	0.33	0.33	0.31	0.37	0.30
<i>FLPL</i>	0.29	0.24	0.30	0.32	0.35

¹ Jersey cows

² Functional survival of the first lactation

Table 14. Phenotypic correlations¹ between longevity and conformation traits.

Author	Traits	Correlation #	Records	Remarks
Boldman <i>et al.</i> (1992)	HL - dairyness	0.07	53,830	grade cows
	FHL - fore udder att./udder depth	0.06		
Brotherstone and Hill (1991a)	surv. lact.2 ² - rear udder width/ teat placement	0.083	23,071	
	surv. lact.3 - total score	0.170		
	surv. lact.4 - total score	0.152		
Cue <i>et al.</i> (1996)	surv. lact.2 - dairy conformation	0.103	59,623	
	surv. lact.3 - dairy conformation	0.103		
	surv. lact.2 - dairy conformation	0.099	45,396	Jersey cows
	surv. lact.3 - dairy conformation	0.112		
De Haan <i>et al.</i> (1992)	surv. lact.2 - dairy conformation	0.141	6,599	Ayrshire cows
	surv. lact.3 - dairy conformation	0.128		
	LPL - final score	0.15	7,479	grade cows
	LPL - final score	0.22		
DeLorenzo and Everett (1982)	AGE48 - type ³	-0.04	461,233	registered cows
	AGE72 - type	-0.06		
Everett <i>et al.</i> (1976)	AGE36 - type ³	-0.09	352,368	
	AGE48 - type	-0.10		
	AGE60 - type	-0.11		
	AGE72 - type	-0.08		
	AGE84 - type	-0.06	124,706	
Harris <i>et al.</i> (1992)	HL45 ⁴ - rear udder height	0.06	4,571	registered Guernsey cows
	FHL48 - stature	-0.06		

Table 14 (continued).

Author	Traits	Correlation	# Records	Remarks
Klassen <i>et al.</i> (1992)	TMP - dairy character	0.22	34,322	
	NLC - angularity	0.18		
	NLC - angularity/style	0.15		
Norman and Van Vleck (1972)	TMP - sharpness	0.16	1,639	
	NLC - sharpness	0.13		
Norman <i>et al.</i> (1996)	NLC - final score	0.12	3,895	Ayrshire cows
	NLC - final score	0.18	7,997	Brown Swiss cows
	NLC - final score	0.16	20,179	Guernsey cows
	NLC - final score	0.22	71,731	Jersey cows
	NLC - dairy character	0.24	628	Milking Shorthorn
Rogers <i>et al.</i> (1991b)	func. surv. lact. ¹⁵ - final score	0.09	47,019	Jersey cows, registered
	FPL20 - final score	0.09	32,249	
	FLPL - final score	0.12	9,819	
Short and Lawlor (1992)	AGE54 - final score	0.10	45,515	grade cows
	AGE84 - final score	0.05		
	LPL - final score	0.11		
	FLPL - final score	0.09		
	AGE54 - final score	0.20		
	AGE84 - final score	0.13	80,126	registered cows
	LPL - final score	0.23		
	FLPL - final score	0.21		
	AGE54 - final score	0.16		
	AGE84 - final score	0.10		
	LPL - final score	0.19	125,887	combined data
	FLPL - final score	0.16		

Table 14 (continued).

Author	Traits	Correlation	# Records	Remarks
Vukašinović <i>et al.</i> (1995)	LPL48 ⁴ - rear udder/udder quality	0.19	9,224	Brown Swiss cows
	LPL66 - rear udder/udder quality	0.19		
	LPL84 - udder quality	0.19		
	FLPL48 - teat length	0.08		
	FLPL66 - teat length	0.09		
	FLPL84 - teat length	0.09		
Weigel <i>et al.</i> (1995)	MIM84 - final score	0.18	433,116	

¹ Only strongest correlation per longevity trait is given

² Survival of lactation 2

³ No other conformation traits analysed

⁴ Numbers indicate the number of mo of opportunity

⁵ Functional survival of lactation 1

registered cows. Results of Rogers *et al.* (1991a) indicate that especially functional length of productive life is a different trait in grade and registered cows (genetic correlation of 0.54). Both stayability traits (functional survival of the first lactation and functional stayability until 20 months of productive life) have genetic correlations close to unity. In Short and Lawlor (1992) all traits analysed had a genetic correlation less than 0.5 between grade and registered cows. Short and Lawlor (1992) also performed the same analysis using only transmitting abilities of sires with a minimum reliability of 50%. Results are not shown here, but the genetic correlations between grade and registered cows increased by a maximum estimate of 0.67.

Phenotypic correlations between longevity and conformation traits

Table 14 contains phenotypic correlations between longevity and conformation traits. For each reference, only the strongest correlation per longevity trait is given if more than one conformation trait was analysed. Correlations were generally low; the strongest one was 0.24 between number of lactations and dairy character for Milking Shorthorns (Norman *et al.*, 1996). DeLorenzo and Everett (1986) and Everett *et al.* (1976) analysed only the phenotypic correlations between stayability and type, which appeared to be negative.

Genetic correlations between longevity and conformation traits

Table 15 contains genetic correlations between longevity and conformation traits. As for the phenotypic correlations, only the strongest correlation is given if more than one conformation trait was analysed. Genetic correlations are generally stronger than phenotypic correlations. The strongest correlation within its theoretical bounds is 1.00 between functional length of productive life and fore udder attachment for Jersey cows (Rogers *et al.*, 1991b). Again the majority of the estimates was positive, although compared with the phenotypic correlations more negative values were found. Negative correlations were mostly found between longevity traits and type, and between longevity and conformation traits which relate to body measurements. There seems to be a difference between genetic correlations in grade and registered cows; not only in magnitude but also in which conformation trait is strongest correlated.

Table 15. Genetic correlations¹ between longevity and conformation traits.

Author	Traits	Correlation #	Records	Method	Remarks
Boldman <i>et al.</i> (1992)	HL - fore udder attachment	0.47	53,830	REML	grade cows
	FHL - udder depth	0.47			
Brotherstone and Hill (1991a)	surv. lact.2 ² - total score	0.65	19,294	REML	
	surv. lact.3 - total score	0.62			
	surv. lact.4 - rear udder width	0.52			
Cue <i>et al.</i> (1996)	surv. lact.2 - rump angle	0.151	59,623	REML	
	surv. lact.3 - stature	-0.111			
	surv. lact.2 - stature	0.307	45,396		Jersey cows
	surv. lact.3 - stature	0.267			
	surv. lact.2 - dairy conformation	0.398	6,599		Ayrshire cows
	surv. lact.3 - dairy conformation	0.301			
Dekkers <i>et al.</i> (1994)	FLPL - bone quality	0.28	13,441	regression of FLPL on conformation ETA	grade herds registered herd mixed herds
	FLPL - final class/general appearance	0.39	13,131		
	FLPL - final class/general appearance/ mammary system	0.34	37,030		
DeLorenzo and Everett (1982)	AGE48 - type ³	-0.05	461,233	method of Calo <i>et al.</i> (1973)	
	AGE72 - type	-0.08	333,608		

Table 15 (continued).

Author	Traits	Correlation #	Records	Method	Remarks
Dentine <i>et al.</i> (1987)	AGE48 - type ³	0.00	7,924	correlations of sire grade cows	
	AGE54 - type	-0.12		evaluations with	
	AGE84 - type	-0.01		PD type	
	HL - type	-0.08			
	AGE48 - type	0.27	15,868		registered cows
	AGE54 - type	0.24			
	AGE84 - type	0.25			
	HL - type	0.22			
	AGE48 - type	0.28	23,792		combined data
	AGE54 - type	0.21			
	AGE84 - type	0.21			
	HL - type	0.19			
Everett <i>et al.</i> (1976)	AGE36 - type ³	-0.11	352,368	method of Calo <i>et al.</i>	
	AGE48 - type	-0.14	283,665	(1973)	
	AGE60 - type	-0.15	223,704		
	AGE72 - type	-0.11	170,608		
	AGE84 - type	-0.09	124,706		
Harris <i>et al.</i> (1992)	HL48 ⁴ - strength	-0.74	4,571	REML	Guernsey cows, registered
	FHL48 - strength	-0.73			
Klassen <i>et al.</i> (1992)	TMP - dairy character/angularity	0.53	34,322	REML	
	NDL - angularity	0.49			
	NLC - angularity	0.44			
Norman and Van Vleck (1972)	TMP - typical head	3.74	1,639	?	very variable results
	NLC - typical head	3.69			

Table 15 (continued).

Author	Traits	Correlation #	Records	Method	Remarks
Rogers <i>et al.</i> (1989)	AGE48 - strength/body depth	-0.25	173 ⁵	method of Calo <i>et al.</i> (1973)	
	AGE54 - body depth	-0.36			
	AGE84 - teats rear view	0.18			
	HL - body depth	-0.24			
Rogers <i>et al.</i> (1991b)	FAGE48 - teats rear view	0.29	143 ⁵	REML	both longevity and conformation traits corrected for PD milk
	FAGE54 - body depth	-0.23			
	FAGE84 - udder depth	0.27			
	FHL - udder depth	0.22			
	func. surv. lact.1 ⁶ - final score	0.78	9,969	REML	Jersey cows, grade herds not participating in type appraisal
	FPL20 - dairy form	0.83	6,465		
	func. surv. lact.1 - final score, fore udder attachment, rear udder height, front teat placement	0.34	18,525	REML	Jersey cows, registered herds not participating in type appraisal
	FPL20 - udder depth	0.82	12,798		
	FLPL - fore udder attachment	1.00	4,556		
	func. surv. lact.1 - udder depth	0.82	47,019	REML	Jersey cows, registered herds participating in type appraisal
FPL20 - rear udder height	0.54	32,249			
FLPL - fore udder attachment	0.68	9,819			

Table 15 (continued).

Author	Traits	Correlation #	Records	Method	Remarks
Short and Lawlor (1992)	AGE54 - dairy form	0.37	45,515	REML	grade cows
	AGE84 - udder depth	0.23			
	LPL - strength	-0.27			
	FLPL - udder depth	0.39			
	AGE54 - final score	0.49	80,126	REML	registered cows
	AGE84 - final score/udder depth	0.38			
	LPL - final score	0.47			
	FLPL - final score	0.54			
	AGE54 - dairy form	0.46	125,887	REML	combined data
	AGE84 - final score	0.30			
	LPL - final score	0.40			
	FLPL - udder depth	0.44			
Van Doormaal <i>et al.</i> (1986)	AGE17 - dairy character	0.32	236 ⁵	phenotypic correlations	"breeders"
	AGE30 - dairy character	0.35		between sire proofs for	
	AGE43 - final class/general appearance	0.41		stability and	
	AGE55 - final class/general appearance	0.42		conformation	
			143 ⁵	traits	
	AGE17 - dairy character	0.29			"milkers"
	AGE30 - dairy character	0.23			
	AGE43 - mammary system	0.20			
	AGE55 - mammary system	0.15			
	AGE17 - size	-0.19	77 ⁵		
	AGE30 - rump	-0.14			
	AGE43 - fore udder	0.09			
	AGE43 - rump/feet&legs	-0.09			
	AGE55 - rump	-0.12			

Table 15 (continued).

Author	Traits	Correlation #	Records	Method	Remarks
Visser and Goddard (1995)	surv. lact.2 ⁷ - dairy character	0.35	19,269	REML	
	surv. lact.3 - dairy character	0.28			
	surv. lact.4 - dairy character	0.24			
Vukašinović <i>et al.</i> (1995)	surv. lact.2 - angularity	0.73	8,768	REML	Jersey cows
	surv. lact.3 - angularity	0.82			
	surv. lact.4 - angularity	0.86			
	LPL48 ⁴ - udder quality	0.58			
	LPL66 - udder quality	0.65			
	LPL84 - udder quality	0.66			
Weigel <i>et al.</i> (1995)	FLPL48 - teat placement	0.66	9,224	REML	Brown Swiss cows
	FLPL66 - teat form/teat placement	0.71			
	FLPL84 - teat form	0.72			
	MIM84 - final score	0.32			
		433,116	REML		

¹ Only strongest correlation per longevity trait is given

² Survival of lactation 2

³ No other conformation traits analysed

⁴ Numbers indicate the number of mo of opportunity

⁵ Number of sires

⁶ Functional survival of lactation 1

⁷ Survival until lactation 2

Regression models of longevity traits on conformation

phenotypic regressions

Berger *et al.* (1973) used data on 6 herds and found that yield and type score accounted for 6 to 21% of the variability in productive life.

Brotherstone and Hill (1991a) calculated phenotypic linear and quadratic regression coefficients of survival of lactations 2, 3, and 4 on conformation and production traits. Nearly all regression coefficients were significant. When fitting a model to explain survival of the third lactation, the coefficient of multiple determination (R^2 , which measures how much variation in the dependent variable can be accounted for by the model) was 0.0256 when only milk production traits were fitted, 0.0507 when production and total score were fitted, and 0.053 when production, total score, and all linear conformation traits were fitted. Similar values were obtained for survival of the second lactation (0.0252, 0.0483, and 0.0497 respectively).

Burke and Funk (1993) concluded that linear conformation traits accounted for approximately 14% of the variation in longevity after herd and production effects were considered. Udder traits were the most important conformation traits, of which fore udder attachment had the highest marginal R^2 (0.0136). Both the linear and the quadratic regression coefficients of all conformation traits were significant.

Foster *et al.* (1989) found three linearly scored conformation traits with a linear and quadratic relationship with herd life, namely stature, udder depth, and rump width. These traits had an optimum score. Dairyiness and rear legs side view only had significant linear coefficients. For rump side view and foot angle significant cubic regression coefficients were found as well. A model containing herd and linear and quadratic effects of conformation traits to explain herd life had an R^2 of 0.559.

Honnette *et al.* (1980) found that final score had a significant quadratic regression coefficient when explaining length of productive life or total milk production. The R^2 for length of productive life was 0.112 and for total milk production 0.152.

Norman *et al.* (1981) calculated a maximum R^2 of 0.242 when all conformation traits were used linearly to explain number of lactations, 0.246 when both linear and quadratic effects were taken into account, and 0.254 when the model contained linear and quadratic effects and interactions between

the linear components. For a model including milk and fat production besides conformation traits, these values were 0.323, 0.326, and 0.333 respectively.

genetic regressions

Regression coefficients of longevity on sires' estimated breeding values for conformation traits are often used to estimate genetic regressions. Brotherstone and Hill (1991a) calculated both linear and quadratic regression coefficients of survival of lactations 2, 3, and 4 on conformation traits for registered cows. Only a few of the quadratic coefficients were significant. Stature, body depth, rump angle, rump width, foot angle, fore udder attachment, rear udder width, udder depth, teat placement, teat length, and total score had significant linear regression coefficients.

In a subsequent study, Brotherstone and Hill (1991b) used data on both registered and grade cows. Only linear regressions were performed. There was no evidence that regression coefficients were substantially different for grade than for registered cows.

Burke and Funk (1993) found the highest marginal R^2 for udder traits. The linear regression coefficients were always significant, and for most conformation traits the quadratic coefficient was significant as well.

Dekkers *et al.* (1994) calculated linear, quadratic, and cubic regression coefficients of functional length of productive life of daughters on estimated transmitting abilities of sires, using data on grade and registered herds. Only a few cubic coefficients were significant, namely for rump, bone quality, and fore udder attachment in grade herds, and for feet and legs, rear udder, and rump width in registered herds. In grade herds, some traits had significant quadratic coefficients, which was not the case in registered herds. In registered herds, more linear coefficients were significant than in grade herds. The maximum percentage of variance in functional length of productive life of daughters explained by estimated transmitting abilities of sires for conformation traits was 69% in grade and 81% in registered herds, including all traits with linear and quadratic coefficients.

Rogers *et al.* (1988) regressed sire proofs for functional stayability until 54 and 84 months of age on predicted difference for conformation traits, based on either grade or registered daughters. In grade cattle, functional stayability until 54 months of age was significantly associated with stature, body depth, udder

depth, and teats rear view. Functional stayability until 84 months of age was only significantly associated with udder depth and teats rear view. In registered cattle, most conformation traits were associated with survival to both ages. Udder depth and teats rear view had the highest correlations with survival in both grade and registered cows. The maximum R^2 of models containing yield and all conformation traits were 0.33 and 0.23 for functional stayability until 54 and 84 months of age for grade cows, and 0.34 for both functional stayability until 54 and 84 months of age for registered cows.

Van Doormaal *et al.* (1986) used three different data files to investigate the relationship between sire proofs for stayability and conformation traits. For the "milkers" data, none of the conformation traits had significant regression coefficients. For the "milkers paying attention to conformation" data, dairy character, feet and legs, and mammary system explained the highest percentage of the variation in stayability traits (R^2 ranging from 0.04 to 0.12). For the "breeders" data, dairy character, general appearance, final class, mammary system, and rump explained the highest percentage of variation variation (R^2 ranging from 0.17 to 0.24).

Indirect prediction

Boldman *et al.* (1992) found that indirect prediction of herd life from conformation traits had a maximum reliability of 0.56, but it was more reliable than direct breeding value estimation with 75 or fewer progeny. Results were of grade cows. Brotherstone and Hill (1991b) gave an example in which it was more accurate to base selection on the sire's progeny test for longevity (40 daughters) than on his own progeny test for type. Weigel *et al.* (1995) had a maximum reliability of indirect prediction of months in milk at 84 months of age of 0.52 if yield and conformation traits were included. If the predicted months in milk at 36 months of age was included as well, the reliability increased to 0.72.

Visscher (1995) showed that the genetic correlation coefficient estimated with a REML algorithm from a half sib design can be grossly overestimated, especially with few sires, few progeny per sire, and a large number of conformation traits. He used the estimates of Short and Lawlor (1992) to create a selection index combining milk and conformation traits to breed for functional length of productive life. The accuracy achieved was 0.795, while the optimum

accuracy was 0.813, so a loss in response of 2.2% occurred. This does not seem much, but an index containing milk and conformation traits only had a 3.6% higher accuracy compared with an index containing only milk.

In none of the studies in this review the reliability of an index combining predictor traits and direct information on longevity has been investigated. In practice, breeding values of young bulls might be estimated using conformation data on daughters, and putting more weight on longevity when these data on their daughters become available. Also breeding values from earlier generations should be included in such an index. The method used to evaluate the bulls could be either BLUE, as is commonly used nowadays, or survival analysis. Survival analysis has great advantages, but requires a relatively large computer capacity. However, Ducrocq and Sölkner (1997) are working on a new version of their computer programs to perform survival analysis, which should make it possible to use survival analysis for national evaluation of bulls.

Discussion

Choice of longevity trait

If longevity is to be incorporated into a breeding program, we should evaluate a trait with a high heritability that can be measured early in life. But before even considering heritability and generation intervals, it is important to define the breeding goal. If the interest is primarily in lifetime production of cows, total milk production as only selection criterium would be a good choice. However, often a distinction between longevity and production is desired. It should be noted that longevity is largely dependent on within-herd production. Therefore it is argued that functional longevity instead of uncorrected longevity should be incorporated into the breeding goal to avoid double counting and to have a measure for "potential longevity", or the ability of a cow to delay involuntary culling. Argument against this is that if proper adjustment is made for (genetic) correlations between longevity and production, it does not matter whether uncorrected or functional longevity is used. However, it is then assumed that unbiased genetic parameters are known (Kennedy *et al.*, 1993). Dekkers (1993) outlined that estimates of genetic parameters for longevity from half sib correlations are biased as a result of culling on production. Adjustment of longevity for production does not remove all bias but it becomes smaller. So if a breeding goal with both longevity and production is desired, functional

longevity should be used.

Considering only the heritability of a trait, total milk production would be the trait of choice. This trait has major drawbacks. Like all lifetime traits, its inclusion would increase the generation interval considerably compared with a situation where selection would only be for milk production. Moreover, total milk production is the product of longevity and production, so there is a danger of double counting production when selection is for both longevity and production. Functional total milk production is a trait that is hard to interpret. Also, in some countries only records of 305-d milk production are stored, so total milk production cannot be calculated. In general, the data available might limit the choice of the longevity trait.

If a large increase in the generation interval is not desired, an alternative could be the use of stayability traits, which can be measured at any moment in time but contain less information and thus have a lower heritability than longevity traits that measure the whole lifespan of a cow. Genetic correlations between stayabilities and lifetime traits were high but part of these high correlations are due to part-in-whole relationships (Table 8). Comparing the heritability estimates of stayability until a certain number of months of age with those of stayability until a certain number of months after first calving (Table 2), the latter tend to have lower values. The two classes of traits only differ by age at first calving, which thus seems to contain some genetic variation as well. However, when comparing the heritability estimates of herd life with those of length of productive life (Table 1), no clear difference is found.

Correcting heritability estimates of binary traits to an underlying normal scale always increased the estimates obtained (DeLorenzo and Everett, 1986; Vollema and Groen, 1996). Van Vleck (1972) indicated that heritability on the normal scale as obtained by his method would be slightly overestimated, in particular with low or high values of the fraction of animals still alive and with high normal heritability. With stayability traits that are not measured very early or very late (so with a reasonable fraction of cows culled or still alive) the overestimation will not be great. If stayability traits are used in a breeding program, the uncorrected heritability estimates should be used. An alternative would be the use of threshold models, which already take into account the fact that binary traits contain less information than continuous traits. In none of the studies in this review it has been investigated whether the advantages of the

use of lifetime traits over the use of stayability traits outweigh the disadvantages.

Another alternative for using lifetime traits might be the use of lifetime traits which are analysed at one moment that all cows have the opportunity to reach a certain age (e.g., 48 mo). Heritability of herdlife, length of productive life, functional herdlife, and functional length of productive life are generally higher at a higher number of months of opportunity (Harris *et al.*, 1992; Vukašinović *et al.*, 1995; Tables 1 and 4). This effect is stronger for the functional than for the uncorrected longevity traits. The genetic correlations among herdlife and length of productive life for different opportunity groups were high (≥ 0.95 ; Table 12), as was the case for functional herdlife and functional length of productive life (≥ 0.92 ; Table 12). It seems that little information is lost when using data on cows with a smaller period of opportunity of being culled, although, of course, a minimum period of opportunity is necessary to obtain reliable estimates.

A third alternative is the use of a different method instead of a different trait: survival analysis. This method uses information on cows that have not been culled yet at the moment of data collection, because the instantaneous hazard of being culled is analysed instead of the longevity achieved. For comparison, with the use of opportunity groups, cows that are still alive at that moment are treated as if their longevity achieved equals the period of maximum opportunity. Danner *et al.* (1993) concluded that survival analysis had clear advantages over BLUP for stayability traits, especially for early prediction of longevity.

Reliability of estimates

It does not seem wise to rely on a single estimate of the heritability of a longevity trait, given the large range observed in estimates. For instance, Gill and Allaire (1976) have high estimates of heritability, which is explained by the limited number of data they used, resulting in large standard errors of the estimates. However, even using large data sets might give extreme results (e.g., Chauhan *et al.*, 1993; for heritability estimates of length of productive life, total milk production, and number of lactations in Table 1). Vollema and Groen (1996) showed that estimates by using data on an upgrading population are different from estimates using data on a more stable population. Something similar is seen in Madgwick and Goddard (1989). Thus it is recommended to

base estimates on data that resemble the current population as much as possible, and to re-estimate these parameters over time (Vollema and Groen, 1996). Also the way in which culled cows are defined has an impact on the heritability estimates (Smith and Quaas, 1984; Strandberg, 1992). All references clearly indicate from which period their data are, and most references also indicate how culled cows were defined. However, it is hard to interpret this information if one is not familiar with the history and current situation of dairy cow breeding in the country in question.

Grade versus registered herds

Results of Rogers *et al.* (1991a, Table 13) indicate that not all functional longevity traits are the same for grade and registered Jersey cows. For Holsteins, Short and Lawlor (1992, Table 13) found that all longevity traits analysed had low genetic correlations between grade and registered cows.

It is not clear whether or not heritability estimates differ between grade and registered cows. From Dentine *et al.* (1987) and Harris *et al.* (1992) it can be concluded that such a difference does not exist, but results of Short and Lawlor (1992) contradict this. Results of Rogers *et al.* (1991a) are not conclusive in this respect. Van Doormaal *et al.* (1985) found different heritability estimates from data of "breeders" and "milkers" herds, which might be compared with registered and grade herds respectively.

Short and Lawlor (1992) did not find different genetic correlations among longevity traits for grade and registered cows (Tables 7, 8, and 11). Also Van Doormaal *et al.* (1985) did not find clear differences between breeders and milkers (Table 7).

De Haan *et al.* (1992) and Short and Lawlor (1992) found different phenotypic correlations between longevity and final score for grade and registered cows. Other studies included conformation traits other than final score as well, and found different correlations for grade and registered cows. Not only were the correlations generally stronger in registered herds, but also the conformation trait with the strongest correlation with longevity differed. In grade herds, traits reflecting the mammary system seem most important, while in registered herds, traits such as type, final class, and general appearance are important as well. Only Rogers *et al.* (1991b) did not find considerable differences in genetic correlations between longevity and conformation traits

between grade and registered cows.

From Brotherstone and Hill (1991b) no evidence could be found that genetic regression models differed between grade and registered cows. However, Dekkers *et al.* (1994), Rogers *et al.* (1988), and Van Doormaal *et al.* (1986) found different models for grade and registered cows. The maximum variance in longevity explained by conformation traits was higher for registered than for grade cows, as could be expected.

In this review, only a distinction between grade and registered cows was made. However in general it seems likely that longevity is correlated with different traits if a different breeding goal is defined. The distinction in breeding goals between grade and registered herds is most obvious in the U.S.; in other countries different criteria may be used to distinguish herds with different breeding goals.

Methods of analysis

The heritability estimates through REML and Henderson III do not show significant differences, taking into account that the high estimates of Gill and Allaire (1976) using Henderson III are due to the limited number of data. Survival analysis gives better corrections for fixed effects in the model, so the heritability estimates are expected to be higher. However, results of Ducrocq *et al.* (1988) and Smith and Quaas (1984) using survival analysis do not differ from results of studies using REML or Henderson's III method.

Correction to functional traits

Correcting longevity traits for production aims to correct for farmer's opinion about the production capacity of a cow. The resulting functional longevity trait is a better measurement for all other reasons a farmer might have for culling cows. The production trait that is used to correct should reflect the criteria used by the farmer to make culling decisions on production. So, because culling occurs within herds, correction for production should be on a within-herd basis as well. Rogers *et al.* (1991a) is the only reference found that does not correct within herds. In every country the culling criteria for production will be different, so having different correction factors is justified. Some references correct only for milk production, others include milk, fat, and protein production. Because milk, fat, and protein production have high correlations, the results may not

differ much.

Some references correct for production in the first lactation, others use the production in the last lactation. In principle, using the last lactation production would be the most correct one because this is the actual production at culling. However, references that use production in the first lactation argue that production in the last lactation may be reduced due to illness. Using the production in the last lactation would then overestimate the functional longevity. Assuming that the repeatability of production over lactations equals one, it would be best to use production in the first lactation. However, this repeatability is approximately 0.5 (Maijala and Hanna, 1974), so both methods are suboptimal. Using survival analysis, production can be modelled in a time-dependent way, so production records of all lactations can be taken into account. Ducrocq *et al.* (1988) applied such a model, and their heritability estimates of functional length of productive life were not different from other references.

From the regression analyses, some references found a significant quadratic relationship between milk production (per lactation or per day) and longevity (results not shown). Reasoning behind this phenomenon is that if a cow produces too much milk, she will get problems with her health and/or fertility, which will decrease longevity. However, it is doubtful if a quadratic production trait reflects the farmer's appreciation of a high-producing cow. Harris *et al.* (1992) and Rogers *et al.* (1991a) corrected both linearly and quadratically for milk production. Their heritability estimates were slightly lower than those of other references.

Non-additive effects

Few references have included non-additive effects in their model of analysis. Fürst and Sölkner (1994) found that non-additive effects in models slightly decreased the heritability of longevity traits. Brotherstone and Hill (1994) estimated quite considerable effects of heterosis and recombination loss.

Differences between breeds

Holstein cows always had the lowest heritability. The references on Guernsey, Simmenthalers, crosses between Braunvieh and Brown Swiss, Brown Swiss, and Jersey cows consistently found a higher heritability of longevity

traits. Correlations among longevity traits were all strong, independent of breed of the cows. There was no indication that certain conformation traits would be more important for explaining longevity in one breed than in another.

Opportunity groups

From Harris *et al.* (1992) and Vukašinović *et al.* (1995) it can be concluded that heritability of lifetime traits increase with increasing opportunity of longevity. From Table 14 it can be concluded that if data on longevity are collected when not all cows have been culled yet, these data highly resemble data that are collected later. However, a minimum fraction of cows has to be culled at the moment of data collection to obtain reliable estimates. When using lifetime traits in a breeding program, it is not necessary to wait until all cows have really been culled.

Conclusions

In general, heritability of longevity traits are below 10%. Heritability of stayability traits are lower than that of lifetime traits. Heritability of functional longevity traits are lower than that of uncorrected longevity traits.

Genetic correlations among longevity traits are generally high. Stayability might be a good alternative to lifetime traits in breeding programs, even though its information content and heritability are lower. In none of the studies in this review it has been investigated whether the disadvantage of a lower heritability of stayability traits outweighs the advantage of a shorter generation interval, if compared with lifetime traits. Genetic correlations between lifetime traits collected at different possible ages of cows are high, indicating that when using lifetime traits in breeding programs, it is not necessary to wait until all cows have been culled.

Longevity traits differ between grade and registered cows. Heritability of longevity traits in grade and registered cows are of the same magnitude. Relationships between longevity and conformation traits are different: in grade cows, udder traits have the strongest relationships, whereas in registered cows, traits describing the general appearance of a cow have the strongest relationships.

Especially conformation traits describing the mammary system of a cow, and to a lesser extent the feet and legs, appear to be useful to predict longevity.

In registered cows, also traits describing the overall appearance of a cow are important. Genetic correlations between longevity and conformation traits are stronger in registered than in grade cows, and thus prediction is more accurate for registered than for grade cows. Reliability of breeding value estimation of longevity using conformation traits of daughters is approximately 55% at maximum. It would be best to have an index combining information on conformation and longevity, including information on relatives.

Acknowledgments

The Royal Dutch Cattle Syndicate is acknowledged for providing funding for this study. Many useful comments of Ab Groen on earlier versions of this paper were much appreciated.

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Chapter 3

Genetic Parameters of Longevity Traits of an Upgrading Dairy Cattle Population

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Journal of Dairy Science, 79 (1996): 2261-2267
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Abstract

Longevity reflects the ability of a cow to avoid culling for low production, low fertility, or illness. Longevity could be used in breeding programs if genetic parameters were known. Various measures are used for longevity. In this study, lifetime measures including number of lactations, total milk production, number of days in milk, herd life, and length of productive life were analyzed. Also analyzed were stayability measures (dead or alive) to 36, 48, 60, or 72 mo of age and 12, 24, 36, or 48 mo of productive life. Measures of longevity were also analyzed after correction for milk production during first lactation (functional longevity traits). Data on 1,727,988 cows were used to calculate average longevity traits per year of birth. All cows were known to have been culled. Longevity decreased from 1978 through 1984 and increased in 1985. Possible causes for the decrease of longevity were implementation of the quota system and introduction of Holstein Friesian genes. Heritabilities of longevity traits were estimated for cows born in 1985 (38,957 records), 1982 (166,324 records), and 1978 (94,935 records) after data were edited to require at least 25 daughters per sire and 10 cows per herd. Phenotypic and genetic correlations were estimated for the 1985 data file. Heritability estimates differed between years of birth, and estimates of functional traits were lower than those of uncorrected longevity traits. Genetic correlations between uncorrected longevity traits were high (0.733 to 1.000); phenotypic correlations were lower (0.131 to 0.980). Genetic correlations between uncorrected and functional longevity traits were high (0.577 to 0.975).

Key words: longevity, dairy cattle, genetic parameters

Abbreviation key: AGE36, AGE48, AGE60, AGE72 = stayability, mo of age (36, 48, 60, or 72); F = functional (used as prefix); HL = herd life; LPL = length of productive life; NDL = number of days in lactation; NLC = number of lactations; PL12, PL24, PL36, PL48 = stayability, mo of productive life (12, 24, 36, or 48); TMP = total milk production.

Introduction

The value of longevity traits in selection programs for dairy cattle is still a major point of discussion. In principle, there are two approaches to include longevity in a breeding program. The first is to select for longevity directly, the second is to select for the underlying functional traits as the breeding goal, using longevity in the information index. This latter approach indirectly selects for traits that are difficult to measure or that are not recorded routinely.

Longevity is a measure of the success of the cow to survive both voluntary and involuntary culling. Decreasing the level of involuntary culling improves the economic returns of a dairy enterprise by allowing a herd manager more flexibility for voluntary culling mainly for low milk production, and by reducing the replacement rate (18). A wide variety of measurements of longevity have been studied (Chauhan *et al.*, 1993; DeLorenzo and Everett, 1986; Dentine *et al.*, 1987;

Ducrocq *et al.*, 1988; Hoque and Hodges, 1980; Hudson and Van Vleck, 1981; Jairath *et al.*, 1994; Klassen *et al.*, 1992; Short and Lawlor, 1992; Van Doormaal *et al.*, 1985; Weigel *et al.*, 1995). To improve longevity traits as a better measurement of involuntary culling, they can be corrected for milk production (Dekkers, 1993). Longevity traits can be categorized as lifetime or stayability traits. Stayability traits contain information about whether a cow is alive at a certain time point (e.g., at a fixed number of months from birth or first calving). These traits can be measured at any time point, but because the traits are binary traits, they do not contain all the information about cow longevity. If a cow has a stayability of 0, it is not known how far before the time point at which the stayability was assigned she was culled; if her stayability equals 1, it is unknown how much longer she will live. Lifetime traits do contain all information available, but can be measured only after the death of the cow.

Before longevity traits are included in a breeding program, it is important to know the heritabilities and correlations of these traits. Many researchers (Chauhan *et al.*, 1993; DeLorenzo and Everett, 1986, Dentine *et al.*, 1987; Ducrocq *et al.*, 1988; Hoque and Hodges, 1980; Hudson and Van Vleck, 1981; Jairath *et al.*, 1994; Klassen *et al.*, 1992; Short and Lawlor, 1992; Van Doormaal *et al.*, 1985; Weigel *et al.*, 1995) have estimated these heritabilities and correlations, but only a limited number of traits have been considered. Also, all these studies used data on cows that were present during a certain time period. For instance, Chauhan *et al.* (1993) used data on cows having milk records in the period September 1979 to December 1987. This assumes that longevity traits were the same genetic traits across time. Because it was expected that changing population dynamics would influence the genetic parameters of longevity traits, this study uses data on cows born during different time periods and known to be culled.

Objectives of this paper are to give an overview of the phenotypic trend in longevity of dairy cows in The Netherlands, to estimate the heritabilities of a wide variety of longevity traits (both lifetime and stayability traits), and the genetic and phenotypic correlations of those traits, and to determine whether the heritability estimates of longevity traits differ between time periods.

Materials and methods

Materials

Complete lactation records of Dutch black and white cows (Holstein Friesian and

Dutch Friesian) born from 1978 through 1985 were obtained from the Royal Dutch Cattle Herdbook (Nederlands Rundvee Syndicaat, Arnhem, The Netherlands). From 1978 on, detailed data on production and pedigree were available for Dutch dairy cows. To allow cows to die before the moment of data collection (December 1994), 1985 was taken as the most recent year of birth. Using later years of birth was expected to give a substantial downward bias of the longevity traits. Only cows that had at least one test-day milk yield were in the data file. Cows had a complete longevity record (i.e., had been culled at the moment of data collection). Cows with unknown sire were excluded. Production and longevity information on cows that produced in more than one herd were accumulated across herds. In total, data on 1,727,988 cows were available. Numbers of cows per year of birth are in Table 1.

Table 1. Number of cows per year of birth.

	Year of birth							
	1978	1979	1980	1981	1982	1983	1984	1985
Cows, no.	186,499	204,705	215,035	239,458	264,034	270,506	223,967	123,784

To estimate variances of longevity traits, three data files were used: cows born in 1978, 1982, or 1985. The most recent data file (1985) was used to estimate genetic correlations among longevity traits. To reduce computational efforts, data of each year of birth were further edited separately so that each sire had at least 25 daughters and each herd had at least 10 cows. Herds were defined as herd of first calving. Records on 94,935 cows (733 sires), 166,324 cows (908 sires), and 38,957 cows (628 sires) were utilized in the 1978, 1982, and 1985 data file, respectively.

Traits

The following definitions and abbreviations of longevity traits were used. Lifetime traits were the number of lactations initiated (**NLC**), production over all lactations (total milk production regardless of lactation length, **TMP**, kilogrammes), days in milk summed over lactations (number of days in lactation, **NDL**), time between birth and last test day (herdlife, **HL**), and time between first calving and last test day (length of productive life, **LPL**). Stayability traits were stayability until 36 (**AGE36**), 48 (**AGE48**), 60 (**AGE60**), or 72 (**AGE72**) mo of age; stayability until 12 (**PL12**), 24 (**PL24**), 36 (**PL36**), or 48 (**PL48**) mo after first calving.

A second set of functional longevity traits was considered in which each trait was pre-corrected for milk production in first lactation. This correction was performed by a linear regression of lactation value for first lactation on each longevity trait. Lactation value is a net merit index used to compare phenotypic performances of cows within herd for milk, fat, and protein production (standardized for lactation length, season of calving, and age at calving)(Handboek NRS, 1993). Traits corrected for milk production are indicated by the prefix F: e.g. FNLC, FHL, FLPL, FAGE60, FPL36. All lifetime traits were tested for normality using the UNIVARIATE procedure (SAS, 1990) and were found to be normally distributed.

Means by years of birth of HL, LPL, and TMP were computed to show phenotypic trends in longevity. Heritabilities and correlations were estimated for all longevity traits. Heritability of first lactation 305-d milk production was estimated as a reference.

Methods

Means were calculated using the MEANS procedure (SAS, 1990). Phenotypic correlations were calculated using the CORR procedure (SAS, 1990). Heritabilities and genetic correlations were estimated using the VCE program by Groeneveld (1993). Heritabilities for the 1985 data file were estimated using an animal model. For comparison, uncorrected longevity traits were analyzed with a sire model as well. Heritabilities for the 1978 and 1982 data files and genetic correlations were estimated using a sire model. The following model was used:

$$Y_{ijklmn} = \text{herd}_i + \text{birthmo}_j + \text{HF}_k + \text{calvmo}_l + \text{animal}_m/\text{sire}_m + e_{ijklmn}$$

where

Y_{ijklmn} = observation on the longevity trait,

herd_i = fixed effect of herd i ,

birthmo_j = fixed effect of the month of birth j ,

HF_k = fixed effect of the Holstein Friesian group k ,

calvmo_l = fixed effect of the month of last calving l ,

animal_m = random effect of the animal m (animal model),

sire_m = random effect of the sire m (sire model), and

e_{ijklmn} = random residual term.

Nine genetic groups were defined according to the percentage of Holstein Friesian

genes: 0%, 12.5%, 25%, ... , 100%. If rounding was necessary, it occurred towards the race of the sire. To account for seasonal effects, month of last calving was included in the model. Reasons for seasonal effects could be a desired calving pattern or culling of cows mainly because the milk production quota of a given farmer was nearly attained. Because the quota year ends on April 1, cows that have been culled in February or March might not have been culled if the quota was not close to having been met (Ducrocq, 1994).

The pedigree file for the animal model contained all known pedigree information. The pedigree file for the sire model contained sire, maternal grandsire, paternal grandsire, and paternal great grandsire, if known. Of the cows born during 1978, 26.7% had unknown maternal grandsires. All cows were daughters of 733 bulls; of these, 0.14% had unknown sires and 58.3% had unknown maternal grandsires (paternal great grandsires for the cows). Of the cows born during 1982, 26.7% had unknown maternal grandsires. Cows were daughters of 907 bulls; of these, 0.11% had unknown sires and 38.9% had unknown maternal grandsires. Of the cows born during 1985, 16.9% had unknown maternal grandsires. Cows were daughters of 605 bulls, of which all sires were known and 32.7% had unknown maternal grandsires themselves.

Univariate analyses were performed to estimate heritabilities. Bivariate analyses were performed to estimate genetic correlations. Estimates of genetic correlations were only reported when the heritability estimates from the bivariate analyses corresponded to estimates from the univariate analyses. This was done because VCE does not clearly indicate the reliability of its output, so a separate check was needed to avoid, for instance, reporting results from local maxima. Heritability estimates of binary traits (stayability traits) were corrected to an underlying normal scale by the method of Van Vleck (1972).

Approximate standard errors of the estimates of heritability and genetic correlation were calculated using formula 10.15 and 19.4 from Falconer (1989), respectively.

Results and discussion

Trend

Figure 1 shows average HL, LPL, and TMP per year of birth. Both HL and LPL show similar trends: a steady decrease until 1984 and a sudden increase in 1985. The difference between HL and LPL is age at first calving, which remains relatively

constant. In April 1984, the European Union quota system was implemented, and the total number of dairy cows in The Netherlands was reduced by 20%, which was the main reason for the decreased longevity of the cows born in the years directly before 1984. Another reason might be the introduction of Holstein Friesian genes. The percentage of Holstein Friesian genes of cows born during 1978 is 6.1% versus 53.3% of cows born during 1985. This fast increase has been facilitated by short generation intervals. Less cows born during 1985 were in the data file (see Table 1). This small number can not only be due to the 20% extra culling of cows. The quota system also caused a large tendency to breed the lower producing cows with beef bulls: inseminations with beef bulls increased by 13%. Calves from matings with beef bulls were not in the data. Also, with later year of birth, the chance of cows being still alive at the moment of data collection (and thus not in the data) increases. Mean HL and LPL of birth year 1985 were at the original level of 1978 (approximately 2100 and 1300 d, respectively).

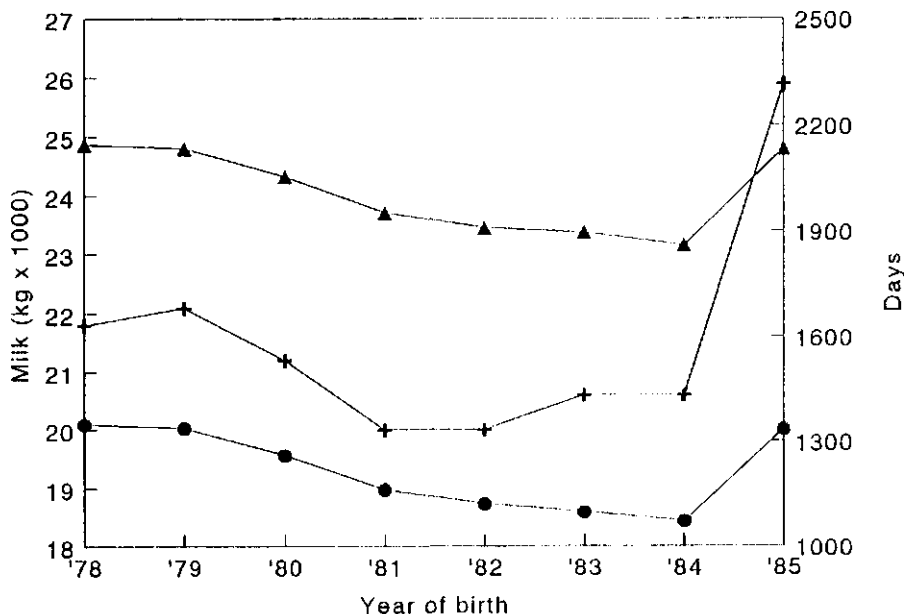


Figure 1. Means of TMP (+)(left X axis, 1000 kg), and HL (▲) and LPL (●)(right X axis, d), per year of birth.

Total milk production is a direct product of longevity and production per day. Both production per day of productive life and per day in milk largely increased over time (1978: 16.14 and 19.12 kg, respectively; 1985: 19.40 and 22.96 kg, respectively). The large increase in TMP for 1985 is a result of the increase in longevity and increased daily milk production.

Heritabilities

Heritability estimates of 305-d milk production during first lactation (Table 2) were within the range reported in the literature (Maijala and Hanna, 1974; Van der Werf and De Boer, 1989), but were different for the animal and sire models. Surprisingly, the estimate using an animal model was lower than that using sire models. Animal models account for the effect of prior selection, which might have been more heavily on milk production. When analyzing low heritable traits (such as longevity) with an animal model, most information comes from the sire component, and the difference between sire and animal models is expected to be small. Heritability estimates of longevity traits with both models were indeed found generally low and comparable. In general, heritability estimates for the 1978 data file were much higher than for the 1985 data file; estimates for the 1982 data file were intermediate.

In the literature, heritability estimates of NLC were around 0.07 (Hoque and Hodges, 1980; Jairath *et al.*, 1994; Klassen *et al.*, 1992; Van Vleck, 1972), except for the 0.005 of Chauhan *et al.* (1993). Heritability estimates of TMP are around 0.11 (Hoque and Hodges, 1980; Jairath *et al.*, 1994; Klassen *et al.*, 1992), again except for Chauhan *et al.* (1993), who found an estimate of 0.017. Heritability estimates of NDL were around 0.08 (Jairath *et al.*, 1994; Klassen *et al.*, 1992). Heritability estimates of HL were either around 0.03 (Chauhan *et al.*, 1993; Dentine *et al.*, 1987) or around 0.10 (Hoque and Hodges, 1980; Short and Lawlor, 1992; Smith and Quaas, 1984). Heritability estimates of LPL are around 0.08 (Ducrocq *et al.*, 1988; Hoque and Hodges, 1980; Jairath *et al.*, 1994; Short and Lawlor, 1992; Weigel *et al.*, 1995), again except for Chauhan *et al.* (1993), who found an estimate of 0.006.

Heritability estimates of stayabilities until a certain month of age were around 0.03 (Dentine *et al.*, 1987; Hudson and Van Vleck, 1981; Short and Lawlor, 1992; Van Doormaal *et al.*, 1985) and generally increased as month of age increased. This increase was consistent in the 1985 data file as well, but not in the

Table 2. Heritability estimates of 305-d first lactation milk production and uncorrected longevity traits in the 1978, 1982, and 1985 data files, analyzed with an animal or a sire model (SE of estimates ranged from 0.01 to 0.02 for MILK, and from 0.003 to 0.01 for longevity traits).

Trait ¹	1985 Animal model	1985 Sire model	1982 Sire model	1978 Sire model
MILK	0.238	0.328	0.400	0.388
NLC	0.036	0.032	0.098	0.132
TMP	0.087	0.104	0.134	0.172
NDL	0.042	0.048	0.116	0.140
HL	0.037	0.040	0.109	0.136
LPL	0.035	0.036	0.110	0.136
AGE36	0.007 (0.054) ²	0.012 (0.092)	0.053 (0.129)	0.040 (0.115)
AGE48	0.013 (0.042)	0.012 (0.038)	0.076 (0.128)	0.080 (0.149)
AGE60	0.023 (0.041)	0.020 (0.036)	0.087 (0.137)	0.116 (0.187)
AGE72	0.029 (0.046)	0.032 (0.050)	0.072 (0.119)	0.108 (0.171)
PL12	0.007 (0.040)	0.012 (0.069)	0.060 (0.129)	0.044 (0.106)
PL24	0.009 (0.023)	0.008 (0.021)	0.080 (0.131)	0.088 (0.157)
PL36	0.025 (0.043)	0.020 (0.034)	0.082 (0.128)	0.112 (0.177)
PL48	0.026 (0.041)	0.028 (0.045)	0.071 (0.120)	0.108 (0.173)

¹ MILK = milk production in first lactation; NLC = number of lactations initiated; TMP = total milk production; NDL = number of days in lactation; HL = herd life; LPL = length of productive life; AGE36, AGE48, AGE60, AGE72 = stayabilities until 36, 48, 60, or 72 mo of age; PL12, PL24, PL36, PL48 = stayabilities until 12, 24, 36, or 48 mo of productive life

² Heritabilities corrected to an underlying normal scale between parentheses

1978 and 1982 data files (see Table 2). DeLorenzo and Everett (1986) estimated heritabilities of 0.12 and 0.15 for stayabilities until 41 and 54 mo of age, respectively, which increased to 0.28 and 0.26 after correction to an underlying normal scale. In this present study, correction to a normal scale increased heritability estimates towards the level of the heritabilities of lifetime traits (see Table 2). If stayability traits are used in a breeding program without using a threshold model, the uncorrected heritabilities should be used. In the literature, heritability estimates of stayabilities until a certain number of months from first calving were around 0.03 (20), without correction to a normal scale. In Table 2, similarity is apparent for both types of stayability traits (AGE and PL). Heritability estimates of AGE36 and PL12 are comparable, as are those of AGE48 and PL24, AGE60 and PL36, and AGE72 and PL48.

Heritability estimates of lifetime traits were generally higher than those of

stayability traits (see Table 2). However, because lifetime traits can be measured only after a longer time period, their superiority in breeding programs might be limited due to the prolonged generation interval they cause. Another alternative might be the use of survival analysis, because this method allows for incomplete lifetime records. To make use of survival analysis at least a part of the cows needs to have a complete lifetime record. Furthermore, the method does not allow estimation of covariances. However, survival analysis would give a better, time dependent, correction for fixed effects. In the data files used in this study, not all competitive herdmates were included, as data files were made according to year of birth. Thus, the effect of herd in the model was based on only a limited number of cows from a herd, and was assumed to be constant over time.

Table 3 contains heritability estimates of functional longevity traits in data files from 1985, 1982, and 1978. Estimates for the 1978 data file are much higher than for the 1985 data file, and estimates for the 1982 data file are intermediate, as for uncorrected longevity traits (see Table 2). In the literature, heritability estimates of FLPL were about 0.06 (Ducrocq *et al.*, 1988; Short and Lawlor, 1992). Heritability estimates of functional stayabilities were around 0.030, increasing as number of months increased (Hudson and Van Vleck, 1981). This increase is shown by Table 3 as well.

Heritabilities of functional traits are usually lower than those of uncorrected traits, as might be expected because correction is for milk production, which is a highly heritable trait. However, the choice of which traits (functional or uncorrected) should be used in a breeding program depends solely on the breeding goal.

In general, the difference between heritability estimates from the animal and sire model are minor, as might be expected from the structure of the data. Heritability estimates in this study are comparable with literature values. However, differences among the years of birth are quite large. There are at least three possible explanations. First, the dairy population has been under strong selection during the period considered. Selection was mainly on milk production, but because longevity is a correlated trait, its genetic variance might have been decreased as well. Second, the percentage of Holstein Friesian genes increased tremendously (from 6.1% in the 1978 data file to 53.3% in 1985). Third, under the quota system, farmers base culling decisions on a shorter planning horizon, thus increasing environmental variation of longevity traits. The range in literature values

Table 3. Heritability estimates of functional longevity traits in the 1978, 1982, and 1985 data sets (SE of estimates ranged from 0.002 to 0.008).

Trait ¹	1985	1982	1978
	Animal model	Sire model	Sire model
FNLC	0.036	0.068	0.096
FTMP	0.075	0.101	0.112
FNDL	0.039	0.084	0.104
FHL	0.036	0.078	0.104
FLPL	0.035	0.079	0.100
FAGE36	0.007	0.032	0.016
FAGE48	0.010	0.046	0.044
FAGE60	0.021	0.056	0.080
FAGE72	0.028	0.052	0.076
FPL12	0.003	0.037	0.032
FPL24	0.005	0.049	0.048
FPL36	0.023	0.054	0.076
FPL48	0.025	0.052	0.080

¹ FNLC = functional number of lactations; FTMP = functional total milk production; FNDL = functional number of days in lactation; FHL = functional herd life; FLPL = functional length of productive life; FAGE36, FAGE48, FAGE60, FAGE72 = functional stayabilities until 36, 48, 60, or 72 mo of age; FPL12, FPL24, FPL36, FPL48 = functional stayabilities until 12, 24, 36, or 48 mo of productive life

is partly due to the mixture of birth years in the data used. Also studies differed in economic and population aspects. When longevity traits are used in a breeding program, heritability estimates should be from a population that resembles the population in the breeding program. Recommendations are to use the most recent data possible, and to reestimate heritabilities over time. If population dynamics change, estimation of heritabilities that will hold for future generations is impossible, especially for longevity traits which are measured later than, e.g., milk production or conformation traits.

Genetic and phenotypic correlations

Table 4 contains genetic and phenotypic correlations among longevity traits. Because heritabilities were different for different years of birth, it was expected that genetic correlations were different as well. Genetic correlations were only

estimated for the 1985 data file, because this is the most recent data file and thus most useful for practical implementation nowadays. Most bivariate analyses involving NLC, TMP, and LPL did not converge. Number of iterations was not restricted. Different starting values were tried without success. In general, genetic correlations among longevity traits were high (> 0.73). Genetic correlations were usually higher than phenotypic correlations, which is similar to literature results (Chauhan *et al.*, 1993; Hudson and Van Vleck, 1981; Short and Lawlor, 1992; Van Doormaal *et al.*, 1985). Both genetic and phenotypic correlations among lifetime traits were high (> 0.87). In the literature, genetic correlations among lifetime traits were always higher than 0.90, usually with slightly lower phenotypic correlations (Chauhan *et al.*, 1993; Jairath *et al.*, 1994; Klassen *et al.*, 1992; Short and Lawlor, 1992). Because of the high genetic correlations among lifetime traits, it does not matter much which trait is used in the breeding program.

Table 4. Genetic (above diagonal) and phenotypic correlations (below diagonal) of uncorrected longevity traits in the 1985 data set (SE of estimates ranged from 0.0 to 0.1).

Trait ¹	NLC	TMP	NDL	HL	LPL	AGE36	AGE48	AGE60	AGE72	PL12	PL24	PL36	PL48
NLC		... ²	...	0.870	...	0.971	0.936	0.859	0.902	0.882	0.939	0.893	0.934
TMP	0.880	
NDL	0.924	0.939		...	0.986
HL	0.907	0.901	0.951		...	0.910	1.000	0.999	1.000	0.884	1.000	1.000	1.000
LPL	0.928	0.916	0.970	0.980	
AGE36	0.312	0.305	0.345	0.367	0.351		0.872	0.847	0.995	1.000	0.776	0.867	0.954
AGE48	0.500	0.477	0.522	0.555	0.538	0.506		1.000	1.000	0.798	0.985	1.000	1.000
AGE60	0.686	0.668	0.713	0.747	0.733	0.254	0.502		0.971	0.882	1.000	0.998	0.976
AGE72	0.735	0.733	0.767	0.807	0.791	0.145	0.286	0.570		0.996	1.000	0.996	...
PL12	0.379	0.358	0.405	0.400	0.414	0.811	0.580	0.297	0.171		0.733	0.896	0.880
PL24	0.581	0.546	0.596	0.596	0.616	0.413	0.799	0.596	0.343	0.501		1.000	1.000
PL36	0.728	0.700	0.749	0.755	0.772	0.226	0.447	0.879	0.628	0.274	0.546		0.992
PL48	0.747	0.742	0.778	0.790	0.803	0.131	0.259	0.515	0.894	0.159	0.316	0.579	

¹ NLC = number of lactations initiated; TMP = total milk production; NDL = number of days in lactation; HL = herd life; LPL = length of productive life; AGE36, AGE48, AGE60, AGE72 = stayabilities until 36, 48, 60, or 72 mo of age; PL12, PL24, PL36, PL48 = stayabilities until 12, 24, 36, or 48 mo of productive life

² No convergence

Lifetime traits had the highest phenotypic correlations with stayabilities that were measured at the longest time period (AGE72 and PL48). The same result would be expected, but was not always found, for the genetic correlations. Genetic correlations of 0.971 between AGE36 and NLC, and of 0.910 between AGE36 and HL suggest that AGE36 has a high predictive value for lifetime traits.

Phenotypic correlations among stayability traits were highest for the stayabilities differing least in time of measurement (e.g., phenotypic correlation between AGE36 and AGE48 equals 0.506; phenotypic correlation between AGE36 and AGE72 equals 0.145). Again, the same relationships would be expected for the genetic correlations but were not always found. This inconsistency has been reported in the literature as well (Hudson and Van Vleck, 1981; Van Doormaal *et al.*, 1985).

Five traits were selected to estimate genetic correlations between uncorrected and functional longevity traits: three lifetime (NLC, NDL, and HL) and two stayability (AGE36 and AGE72) traits. Selection was based on correlations between traits, heritabilities, and convergence in the bivariate analyses (Table 4, except for NDL). Table 5 contains genetic correlations between these uncorrected and functional longevity traits for data from 1985. Bivariate analyses involving NDL and FNLC did not converge. Genetic correlations between uncorrected longevity traits and functional longevity traits were generally lower (0.577 to 0.975) than those among uncorrected longevity traits (0.733 to 1.000, see Table 4). Genetic correlations of FAGE36 with uncorrected longevity traits were lower than of the

Table 5. Genetic correlations between uncorrected and functional longevity traits in the 1985 data set (SE of estimates ranged from 0.01 to 0.10).

Trait ¹	NLC	NDL	HL	AGE36	AGE72
FNLC	... ²
FNDL	0.809	...	0.945	0.829	0.952
FHL	0.690	...	0.902	0.916	0.965
FAGE36	0.641	...	0.577	...	0.642
FAGE72	0.878	...	0.964	0.975	0.947

¹ FNLC = functional number of lactations; FNDL = functional number of days in lactation; FHL = functional herd life; FAGE36, FAGE72 = functional stayabilities until 36 or 72 mo of age; NLC = number of lactations initiated; NDL = number of days in lactation; HL = herd life; AGE36, AGE72 = stayabilities until 36 or 72 mo of age

² No convergence

other functional longevity traits with uncorrected traits. No explanation was found. In the literature, Short and Lawlor (1992) estimated an average genetic correlation between LPL and FLPL of 0.93. In this study, the correlation between HL and FHL was 0.902. The genetic correlation between AGE72 and FAGE72 was 0.947.

Conclusions

Longevity of Dutch dairy cattle has been strongly influenced by the implementation of the EU quota system and the introgression of Holstein Friesian genes. Heritability estimates of longevity traits systematically differed between years of birth, indicating that changes in the population structure affected genetic parameters. Heritability estimates of longevity traits corrected for within-herd differences in milk yield were lower than those of uncorrected longevity traits. Genetic correlations between uncorrected longevity traits were high (around 0.94, range 0.733 to 1.000); phenotypic correlations were generally lower (around 0.59, range 0.131 to 0.980). Genetic correlations between uncorrected and functional longevity traits were high (around 0.84, range 0.577 to 0.975).

Acknowledgments

The authors thank the Nederlands Rundvee Syndicaat for providing the data and financial support. Arnoud van der Lugt and Wim van der Venne are thanked for their technical assistance. The authors express appreciation to Dr Joe Hillers for his valuable comments on an earlier version of this paper.

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Chapter 4

Genetic Correlations Between Longevity and Conformation Traits in an Upgrading Dairy Cattle Population

Ant R. Vollema and Ab F. Groen

Abstract

Genetic correlations between longevity and conformation traits were estimated using data on Dutch black and white cows born in 1978 (11,558 records), 1982 (39,252 records), and 1989 plus 1990 (58,864 records). Longevity traits considered were number of lactations, herdlife, and stayabilities until 36 and 48 mo of age, and their functional equivalents (i.e. the longevity traits corrected for production). For the 1989 plus 1990 data file, only stayabilities until 36 and 48 mo of age were considered. Conformation traits were rear legs set, front teat placement, udder depth, suspensory ligament, and subjective scores for udder, feet and legs, and type. Also investigated was a possible nonlinear relationship between conformation and longevity traits.

Genetic correlations between conformation and longevity traits differed between years of birth, mainly because farmers practiced large-scale upgrading with Holstein Friesian bulls during the period considered, which caused a change in desired type. Therefore, the predictive value of conformation traits for longevity based on data from an upgrading population might be limited. Estimates of genetic parameters should be based on the most recent data possible, and these parameters should be re-estimated over time. From the 1989 plus 1990 data file, subjective scores for udder and feet and legs had the highest predictive values for functional longevity. Quadratic relationships between conformation and longevity traits did exist, but generally the linear relationships prevailed.

Key words: longevity, conformation, genetic parameters, nonlinearity

Abbreviation key: AGE36, AGE48 = stayability, mo of age (36 or 48); F = functional (used as a prefix); HL = herdlife; LSS = subjective score for feet and legs; MP = 305-d milk production during first lactation; NLC = number of lactations initiated; RL = rear legs set (side view); SL = suspensory ligament; TP = front teat placement; TSS = subjective score for type; UD = udder depth; USS = subjective score for udder.

Introduction

Longevity is a trait of increasing importance in breeding programs. When lifetime performances of cows are used to measure longevity, the generation interval increases compared to a breeding program solely aimed at increased milk production. This prolonged generation interval causes a decrease in genetic progress per year (Rendel and Robertson, 1950). Using stayability traits as measures of longevity, the generation interval is likely to increase as well because, in practice, stayabilities are measured after the first lactation, at a minimum of 36 mo of age (DeLorenzo and Everett, 1982; Hudson and Van Vleck, 1981; VanRaden and Klaaskate, 1993). An alternative would be the use of traits that are correlated to longevity and can be measured earlier. Burnside and Wilton (1970) concluded that selection for longevity would be possible only

with predictors of longevity that could be measured early in life and show genetic variation.

Conformation traits can be measured during the first lactation and have reasonable strong genetic correlations with longevity, especially conformation traits describing udder, feet and legs, and overall type (Dekkers *et al.*, 1994; Klassen *et al.*, 1992; Visscher and Goddard, 1995). Functional longevity traits are a measurement of involuntary culling, as are conformation traits (Burnside and Wilton, 1970; Lund *et al.*, 1994).

The Dutch dairy cattle population has been strongly influenced by the implementation of the quota system and large-scale crossbreeding with Holstein Friesian bulls during the 1980s (Vollema and Groen, 1996). These changes might affect the genetic correlations between longevity and conformation traits. The main objective of this study was to investigate the genetic relationship between longevity and conformation traits reflecting udder, feet and legs, and overall type, comparing these correlations for different years of birth to quantify the effect of intensive crossbreeding with Holstein Friesian bulls.

Some conformation traits might have an optimum value with regard to longevity. Several researchers (Burke and Funk, 1993; Dekkers *et al.*, 1994; Foster *et al.*, 1989) found significant quadratic regression coefficients when using conformation traits to explain longevity. In standard programs used for estimation of covariance components, only the linear part of a relation between two traits is considered. A second objective of this paper was to investigate a possible nonlinear relationship between longevity and conformation traits.

Material and methods

Materials

The Royal Dutch Cattle Syndicate (Nederlands Rundvee Syndicaat, Arnhem, The Netherlands) provided lactation and conformation records of Black and White cows (Dutch Friesian and Holstein Friesian cows) born in 1978, 1982, and 1989 plus 1990. Three data files were created according to the year of birth. Cows in the data files had at least one testday milk yield, and their sire was known. Cows born in 1978 and 1982 were known to be culled before the moment of data collection. All cows used in the analyses were classified for conformation during first lactation. Table 1 contains information on the data. Classification started in 1980, and the percentage of farmers participating

Table 1. Data characteristics.

Year of birth	Classified ¹ (%)	Cows (no.)	HF ² (%)	Sires (no.)
1978	29	11,558	6.1%	517
1982	36	39,252	38.3%	762
1989 plus 1990	40	58,864	80.0%	2469

¹ Approximate percentage of participating farmers in the conformation classification program in the year that the cows in the data files were classified.

² Mean percentage of Holstein Friesian genes in data file.

increased rapidly to 42% in 1995 (Nederlands Rundvee Syndicaat, 1995). The mean percentage of Holstein Friesian genes increased substantially over the years of birth (6.1% in 1978 to 80.0% in 1989 plus 1990), showing the upgrading process during these years. The pedigree files of all three data files contained sire, maternal grandsire, paternal grandsire, and paternal great grandsire, if known.

Traits

The chosen longevity traits included two lifetime traits: number of lactations initiated (**NLC**) and days between birth and last test day or herdlife (**HL**). In a previous study (Vollema and Groen, 1996) these two lifetime traits converged best in bivariate analyses. Stayability until 36 mo of age (**AGE36**) was chosen as well. For the 1989 plus 1990 data file, stayability until 48 mo of age (**AGE48**) was included instead of lifetime traits **NLC** and **HL**, because most cows in this data file did not have sufficient time to complete a lifetime record, but all cows had the opportunity to survive to at least 48 mo of age.

A second set of functional traits was analyzed in which each trait was precorrected for milk production in first lactation. For the 1978 and 1982 data files, this correction was performed by a linear regression of lactation value for the first lactation on each longevity trait. Lactation value is the net merit index used to compare phenotypic performances of cows within a herd for milk, fat, and protein production (standardized for lactation length, season of calving, and age at calving) (Nederlands Rundvee Syndicaat, 1993). Farmers use lactation value as a management tool. For the 1989 plus 1990 data file, lactation values were not readily available. Instead of lactation value, 305-d milk production (unadjusted) in the first lactation was used to precorrect longevity traits

phenotypically to functional longevity traits, which are indicated by the prefix F.

The following definitions and abbreviations of conformation traits were used. Objectively scored conformation traits were set of rear legs (side view, **RL**), front teat placement (**TP**), udder depth (**UD**), and suspensory ligament (**SL**). Abbreviations have two characters. Scoring was on a nine-point scale. A score of 1 for **RL** means steep legs, a 1 for **TP** means that the teat placement is wide, a 1 for **UD** means a deep udder, and a 1 for **SL** means a weak suspensory ligament. Conformation traits for udder (**USS**), feet and legs (**LSS**), and type (**TSS**) were scored subjectively from a 65 to 89 scale (Nederlands Rundvee Syndicaat, 1993). Type in The Netherlands is scored as the milk potential of a cow, and may therefore more resemble the American "dairy character" than the American "type" score. Abbreviations have three characters. Also, 305-d milk production during first lactation (**MILK**) was analyzed. Table 2 contains the abbreviations and definitions of all traits analyzed. Per data file, genetic correlations between longevity traits (both uncorrected and functional) and conformation traits and **MILK** were estimated.

Methods

Genetic correlations between longevity traits and conformation traits and milk production were estimated in bivariate runs using the **VCE** program of Groeneveld (1995). The following model was used to analyze the 1978 and 1982 data files:

$$Y_{ijklm} = \text{herd}_i + \text{birthmo}_j + \text{HF}_k + \text{calvmo}_l + \text{sire}_m + e_{ijklm} \quad [1]$$

where

Y_{ijklm} = observation on the longevity trait, conformation trait, or **MILK**,

herd_i = fixed effect of herd i ,

birthmo_j = fixed effect of month of birth j ,

HF_k = fixed effect of the Holstein Friesian group k ,

calvmo_l = fixed effect of month of last calving l ,

sire_m = random effect of sire m , and

e_{ijklm} = random residual term.

The nine genetic groups were defined according to the percentage of Holstein Friesian genes: 0, 12.5, 25, ..., 100. If rounding was necessary, it occurred toward the breed of the sire. To account for seasonal effects, month of last

calving was included in the model. Reasons for seasonal effects could be a desired calving pattern or differences in culling of cows on milk production during the year as a consequence of the quota system. Because the quota year ends on April 1st, cows that are culled in February or March might not have been culled if the quota had not been nearly met (Ducrocq, 1994).

For the 1989 plus 1990 data file, the following model was used:

$$y_{ijkl} = \text{herd} \times \text{birthmo}_i + HF_j + \text{herd} \times \text{calvmo}_k + \text{sire}_l + e_{ijkl} \quad (2)$$

where

herd x birthmo_i = fixed effect of the interaction between herd and month of birth, and

herd x calvmo_k = fixed effect of the interaction between herd and month of last calving.

The interaction terms were included in the model to enable considering the possibility that a certain farmer had problems not producing more than the quota allowed in one particular year but did not have these problems in the next year. For the 1978 and 1982 data files, an interaction term could not be included because not enough data were available. The original 1989 plus 1990 data file (105,170 records) was edited so that each herd x birthmo class contained at least two records.

Approximate standard errors of the estimates of genetic correlations were calculated using formulas 10.15 and 19.4 of Falconer (1989).

The PEST program (Groeneveld, 1990) was used to estimate breeding values in univariate runs for the sires in the 1982 data file, using Model [1] and the mean heritability estimates from the bivariate analyses of longevity and conformation traits (Table 2). The estimated breeding values were used to check the genetic relationships between these traits for nonlinearity. Both the linear and the quadratic regression coefficients of each breeding value for a conformation trait on each breeding value for a longevity trait were calculated separately, using the GLM procedure (SAS, 1990).

Results and discussion

Mean heritabilities

Table 2 contains, in addition to the abbreviations and definitions of the traits, the mean heritabilities and sire variances (only for the 1989 plus 1990

Table 2. Mean estimated heritabilities¹ and mean sire variances¹ (σ_s^2) of the traits analyzed.

Trait ²	1978	1982	1989 plus 1990	
	h^2	h^2	h^2	σ_s^2
<i>Uncorrected longevity traits</i>				
NLC	0.11	0.09
HL	0.13	0.10
AGE36	0.03	0.03	0.03	0.0007
AGE48	... ³	...	0.03	0.0014
<i>Functional longevity traits</i>				
FNLC	0.08	0.06
FHL	0.09	0.07
FAGE36	0.02	0.01	0.03	0.0005
FAGE48	0.02	0.0010
<i>Objectively scored conformation traits</i>				
RL	0.17	0.32	0.17	0.089
TP	0.32	0.43	0.35	0.224
UD	0.31	0.34	0.26	0.120
SL	0.27	0.20	0.25	0.148
<i>Subjectively scored conformation traits</i>				
USS	0.32	0.34	0.34	0.818
LSS	0.41	0.29	0.30	0.656
TSS	0.43	0.29	0.39	0.785
<i>Production trait</i>				
MP	0.41	0.43	0.46	0.090

¹ Averaged over bivariate analyses.

² NLC = Number of lactations initiated; HL = herd life, days between birth and last test day; AGE36 = stayability until 36 mo of age; AGE48 = stayability until 48 mo of age; F = functional, used as a prefix; RL = rear legs set (side view); TP = front teat placement; UD = udder depth; SL = suspensory ligament; USS = udder; LSS = feet and legs; TSS = type; MP = 305-d milk production during first lactation (*1000 kg).

³ Not analyzed in this data file.

data file) from the bivariate analyses of conformation and longevity traits. Compared with results of a previous study (Vollema and Groen, 1996), the heritabilities were very similar. Data were selected to include only classified cows, but this edit hardly affected the heritability estimates for longevity traits.

Genetic correlations between longevity and conformation traits

Table 3 contains estimated genetic correlations between longevity traits, on the one hand, and conformation traits and MILK, on the other hand, based on the 1978 data file. The trait RL showed negative correlations with all longevity traits, although these correlations are stronger with functional (-0.14 to -0.24) than with uncorrected longevity traits (-0.06 to -0.13). Both TP and SL have slightly negative genetic correlations with uncorrected longevity traits, but slightly positive correlations with functional longevity traits, except for the correlation between SL and FAGE36, which equals -0.13. The genetic correlations of TP and SL with AGE36 are stronger than with the other longevity traits (-0.16 and -0.34, respectively). The trait UD shows inconsistent and not very strong genetic correlations with uncorrected longevity traits, but quite strong, positive, correlations with functional longevity traits (0.35 to 0.44).

The subjective traits (USS, LSS, and TSS) showed little or no genetic correlation with uncorrected longevity traits, although correlations with LSS were a bit higher. Genetic correlations between the subjective traits and functional longevity were generally stronger, and all were positive (0.07 to 0.24).

Genetic correlations between MILK and uncorrected longevity traits were

Table 3. Estimated genetic correlations between longevity traits, and conformation traits and milk production in the data file 1978¹.

Trait ²	NLC	HL	AGE36	FNLC	FHL	FAGE36
RL	-0.13	-0.10	-0.06	-0.24	-0.21	-0.14
TP	-0.05	-0.04	-0.16	0.08	0.08	0.07
UD	0.06	0.02	-0.16	0.44	0.39	0.35
SL	-0.03	-0.06	-0.34	0.12	0.08	-0.13
USS	0.10	0.00	0.01	0.23	0.24	0.22
LSS	0.13	0.15	0.11	0.20	0.24	0.15
TSS	-0.03	0.04	-0.07	0.07	0.16	0.18
MP	0.45	0.48	0.74	0.09	0.13	0.20

¹ Standard error of estimates ranged from 0.051 to 0.12.

² NLC = Number of lactations initiated; HL = herd life; AGE36 = stayability until 36 mo of age; F = functional (used as a prefix); RL = rear legs set (side view); TP = front teat placement; UD = udder depth; SL = suspensory ligament; USS = subjective score for udder; LSS = subjective score for feet and legs; TSS = subjective score for type; MP = 305-d milk production in first lactation.

high (0.45 to 0.74). Functional longevity traits would be expected to have much lower correlations with MILK, because these traits were corrected for lactation value of which milk production is an important component. The genetic correlations were 0.09 to 0.20; correlations were not equal to 0 because lactation value comprises other traits as well and because correction was performed on the phenotypic level and within herds.

Table 4 contains estimated genetic correlations between longevity traits, on the one hand, and conformation traits and MILK on the other hand, based on the 1982 data file. Genetic correlations from this data file differed from those from the 1978 data file. The trait UD was not strongly correlated genetically with functional longevity traits, except for the correlation with FAGE36, which was negative (-0.34) but was positive for the 1978 data file (0.35, Table 3). Also, the correlation between UD and AGE36 is relatively strong: -0.30, although this correlation might be partly caused by the negative genetic correlation between UD and MILK (-0.38, not shown). The subjective scores USS, LSS, and TSS show relatively strong (> 0.3) genetic correlations with both uncorrected and functional longevity traits, except the correlations between USS and LSS and between AGE36 and FAGE36 (0.10 to 0.23).

The correlation (0.80) between MILK and AGE36 was very strong in the

Table 4. Estimated genetic correlations between longevity traits, and conformation traits and milk production in the data file 1982¹.

Trait ²	NLC	HL	AGE36	FNLC	FHL	FAGE36
RL	-0.05	-0.01	-0.01	-0.04	-0.01	-0.03
TP	0.07	0.07	-0.14	0.10	0.09	-0.15
UD	0.03	0.02	-0.30	0.09	0.07	-0.34
SL	0.09	0.13	0.14	0.07	0.12	0.17
USS	0.31	0.33	0.10	0.35	0.37	0.15
LSS	0.32	0.32	0.23	0.31	0.32	0.18
TSS	0.47	0.47	0.48	0.46	0.46	0.47
MP	0.39	0.44	0.80	0.33	0.39	0.84

¹ Standard error of estimates ranged from 0.015 to 0.067.

² NLC = Number of lactations initiated; HL = herd life; AGE36 = stayability until 36 mo of age; F = functional (used as a prefix); RL = rear legs set (side view); TP = front teat placement; UD = udder depth; SL = suspensory ligament; USS = subjective score for udder; LSS = subjective score for feet and legs; TSS = subjective score for type; MP = 305-d milk production in first lactation.

1978 data file as well (0.74, Table 3), which is an indication that milk production is an important reason for culling during first lactation. This result was found in earlier, more specific references as well (Hocking *et al.*, 1988; Milian-Suazo *et al.*, 1988; Sol *et al.*, 1984). Correlations between MILK and uncorrected longevity traits were as high as in the 1978 data file (Table 3), but correlations between MILK and functional traits stay on the same high level in contrast to the results from the 1978 data file.

These results indicate that correcting longevity traits for lactation value in the 1982 data file does not affect their relationships with conformation traits and milk production. In other words, lactation value was not the primary culling reason for these cows, and thus functional longevity traits are no longer measures of involuntary culling. The cows born in 1982 were in the middle of the upgrading process, as can be seen in Table 1. The original population of Dutch Friesian cows had deep udders. Crossing these cows with Holstein Friesians decreased UD, so that in the 1982 data file only weak correlations could be found between UD and functional longevity traits (because UD was no longer a trait of major concern), even though these correlations were strong in the 1978 data file. Crossbreeding with Holstein Friesians meant in practice that farmers selected mainly on Holstein Friesian genes instead of production, which explains why little difference exists between correlations with uncorrected and functional longevity traits in the 1982 data file. It also explains why genetic correlations between TSS and longevity traits are strong in this data file: during the period with intensive crossing with Holstein Friesians, TSS was scored as Holstein Friesian type, and farmers selected on Holstein Friesian genes (A. Hamoen, 1996, Chief Inspector of the Royal Dutch Cattle Syndicate, personal communication).

The inclusion of the fixed effect of Holstein Friesian group in the model might not have taken away the effect of selection on Holstein Friesian genes, because the inclusion of Holstein Friesian group in the model does not correct for the differences in competition that cows experience to stay in the herd depending on their percentage of Holstein Friesian genes. In general, cows with low percentages of Holstein Friesian genes had a higher risk of being culled, but this risk depended completely on the competitive herdmates. Including an effect for the interaction of herd and percentage of Holstein Friesian genes might have partly accounted for this, but the only way to correct properly for this

competition effect would be the use of survival analysis. This method not only makes use of censored records, but corrects for fixed effects (e.g., herd) in a time-dependent way as well (Ducrocq, 1994; Smith and Quaas, 1984). However, to make use of survival analysis, the data file analyzed must contain information on all cows that are present at a certain time. This does not hold for the data used in this study because only cows from one year of birth are in each data file without herdmates of other ages. Furthermore, the method does not allow estimation of covariances between traits.

To check whether the genetic correlations between longevity and conformation traits in the 1982 data file would equal those of the 1978 data file if only Dutch Friesian cows were analyzed, a subfile was made. Animals in this subfile were required to be in a herd of only cows with 25% or less Holstein Friesian genes. In total, 3099 cows from the 1982 data file met this requirement. Genetic correlations between longevity and conformation traits were estimated using this subfile. Results were disappointing, because many of the bivariate runs did not converge, and the remaining estimates were diverse and could not be interpreted. Reasons might be the very small amount of data and the failure to consider cows with a higher percentage of Holstein Friesian genes that entered the herd later and were competitors of the original Dutch Friesian cows.

Therefore, the 1989 plus 1990 data file was established and analyzed. The Black and White population was much more stable during this period. Genetic correlations between longevity and conformation traits from the 1989 plus 1990 data file are detailed in Table 5. In general, genetic correlations are positive and strong (0.05 to 0.93); correlations between conformation and functional longevity traits were stronger than between conformation and uncorrected longevity traits. However, the difference was not very large, which may partially be due to the correction of functional longevity traits for the absolute level of 305-d milk production in the first lactation instead of a within-herd measurement of production. Furthermore, it is unclear what effect a different model has on the genetic correlations. The correlations between AGE48 and RL, between FAGE48 and RL, between FAGE36 and MILK, and between FAGE48 and MILK are the only negative ones (-0.17, -0.14, -0.04, and -0.19, respectively). The correlation between FAGE36 and LSS (0.20) was lower than that between AGE36 and LSS (0.22), which was the only case in

Table 5. Estimated genetic correlations between longevity traits, and conformation traits and milk production in the data file 1989/1990¹.

Trait ²	AGE36	AGE48	FAGE36	FAGE48
RL	0.10	-0.17	0.15	-0.14
TP	0.66	0.78	0.70	0.84
UD	0.32	0.56	0.50	0.74
SL	0.20	0.34	0.25	0.43
USS	0.70	0.82	0.78	0.93
LSS	0.22	0.39	0.20	0.43
TSS	0.37	0.62	0.05	0.21
MP	0.61	0.66	-0.04	-0.19

¹ Standard error of estimates ranged from 0.0072 to 0.050.

² AGE36, AGE48 = Stayabilities until 36 and 48 mo of age; F = functional (used as a prefix); RL = rear legs set (side view); TP = front teat placement; UD = udder depth; SL = suspensory ligament; USS = subjective score for udder; LSS = subjective score for feet and legs; TSS = subjective score for type; MP = 305-d milk production in first lactation.

which the genetic correlation between a functional longevity trait and a conformation trait was weaker than between an uncorrected longevity trait and a conformation trait. The relatively weak genetic correlations between longevity traits and RL and SL were found in the 1978 data file as well (Table 3). No strong correlations were found between longevity traits and TP in the 1978 or the 1982 data file (Tables 3 and 4, respectively). Especially USS has very strong correlations with FAGE36 and FAGE48 in the 1989 plus 1990 data file (0.78 and 0.93, respectively). The trait TSS has relatively weak correlations with functional longevity traits, as in the 1978 data file. In the literature, this is found as well especially for grade herds (DeLorenzo and Everett, 1982; Dentine *et al.*, 1987).

Table 6 contains the estimated genetic correlations among conformation traits and MILK for the 1989 plus 1990 data file. The trait USS had relatively strong genetic correlations with the objectively scored udder traits (0.50 to 0.85), and LSS was correlated strongly with RL (-0.52). Correlations between TSS and the objectively scored udder traits and between USS and LSS ranged from 0.26 to 0.63. As expected, MILK had a relatively strong genetic correlation with TSS (0.64), because classifiers score the milk potential of a cow with this trait.

Table 6. Estimated genetic correlations among conformation traits in the data file 1989 plus 1990¹.

Trait ²	TP	UD	SL	USS	LSS	TSS	MP
RL	-0.16	0.10	0.08	-0.04	-0.52	-0.04	0.10
TP		0.45	0.43	0.85	0.33	0.36	0.08
UD			0.23	0.50	0.20	0.26	-0.16
SL				0.64	0.30	0.38	0.18
USS					0.56	0.63	0.25
LSS						0.47	0.19
TSS							0.64

¹ Standard errors of estimates ranged from 0.0076 to 0.033.

² RL = Rear legs set (side view), TP = front teat placement, UD = udder depth, SL = suspensory ligament, USS = subjective score for udder, LSS = subjective score for feet and legs, TSS = subjective score for type, MP = 305-d milk production in first lactation.

In this study, conformation traits generally had stronger genetic correlations with functional than with uncorrected longevity traits. If, in The Netherlands, FAGE48 would be incorporated in the breeding goal, an index based on 60 daughters per sire and containing information on USS and LSS would give a reliability of 0.74, based on the results from the 1989 plus 1990 data file (Tables 5 and 6). Classifiers are capable of recognizing cows with a long potential herd life. Genetic correlations between conformation and longevity traits might indeed be influenced by the circumstances. When an index containing conformation traits is used to breed for functional longevity, estimates of genetic correlations and heritabilities should be based on the most recent data file possible, and should be re-estimated routinely. It is expected that the most recent data closest resemble the steady state that will be reached. Re-estimation of parameters is necessary either to adjust parameters if the population is still changing, or to check if the steady state has been reached already.

Compared with literature estimates, the level of estimates of genetic correlations between conformation and longevity traits in this study is high, especially for the 1989 plus 1990 data file. The strongest genetic correlation in this study was 0.93; in the literature, the strongest genetic correlations that were based on data from Holstein Friesian cows were usually not higher than 0.5 (Boldman *et al.*, 1992; Dekkers *et al.*, 1994; Klassen *et al.*, 1992; Rogers *et*

al., 1989; Short and Lawlor, 1992; Van Doormaal *et al.*, 1986).

Visscher and Goddard (1995) found considerably stronger genetic correlations between stayability and conformation traits for Jerseys (around 0.8) than for Holsteins (around 0.3). Vukašivonić *et al.* (1995) found genetic correlations up to 0.7 between conformation and longevity traits for Brown Swiss cows. In the literature, conformation and longevity traits were less correlated for Holstein cows than for cows of other breeds.

Rogers *et al.* (1989) found that genetic correlations between conformation and stayability traits were weaker than the genetic correlations that are usually found between conformation and lifetime traits, the strongest being 0.36. However, Short and Lawlor (1992) found no difference in correlations between conformation and lifetime traits or between conformation and stayability traits. In this study, only one stayability trait (AGE36) was considered in all three data files. In the 1978 data file (Table 3), AGE36 had some other genetic correlations than NLC or HL. For instance, the correlation with UD is negative; for NLC and HL, the correlation with UD was small but positive. Also, the correlation between AGE36 and MILK was much higher than that between the other longevity traits and MILK. In the correlations with TSS, however, HL is the only longevity trait with a positive sign. In the 1982 data file (Table 4), AGE36 behaved differently from NLC and HL at some points. Correlations between AGE36 and TP and between AGE36 and UD are negative, for instance, but correlations between NLC and HL and between TP and UD are positive. Also in this data file, the genetic correlation between AGE36 and MILK is higher than between NLC or TP and MILK. Genetic correlations between stayabilities and conformation traits and between lifetime and conformation traits differ partly due to the analysis of stayability traits using continuous models.

Dekkers *et al.* (1994) found 0.39 as the strongest of the genetic correlations between uncorrected longevity traits and conformation traits in registered herds; genetic correlations were lower between conformation traits and FHL in grade herds. Short and Lawlor (1992) also found stronger genetic correlations between conformation and longevity traits for registered than for grade herds. Van Doormaal *et al.* (1986) also found stronger genetic correlations between conformation and longevity traits for "breeders" than for "milkers". Even though they are not the same, it might be assumed that "breeders" are comparable with registered herds, and "milkers" with grade

herds. In all three of these studies, for different breeding goals, different conformation traits were most important in determining longevity. In registered herds, traits such as dairy character, dairy form, final class, and general appearance were most important. In grade herds, traits such as udder depth, feet and legs, and mammary system were important, too. Because, in the present study, genetic correlations between the subjective score for type and longevity traits was mostly relatively low, Dutch data could be compared with data from grade herds even though all cows were registered.

Nonlinear relationships

Because the REML estimates of the genetic correlations between longevity and conformation traits in the 1982 data file were different from expected, the estimated breeding values of the sires ($n = 762$) from this data file were used to check for nonlinearity in the relationship between longevity and conformation traits. Table 7 indicates which conformation traits had significant ($P < 0.05$) linear (L) or quadratic (Q) (or both) regression coefficients when explaining longevity traits in a regression model containing only a mean, linear conformation trait effect, and quadratic conformation trait effect. Especially subjective conformation traits (USS, LSS, and TSS) and MILK had significant nonlinear relationships with longevity traits, but the quadratic component was never significant when the linear was not. Only UD had significant quadratic relationships with HL and FHL while the linear relationships were not significant. Generally, conformation traits that have stronger genetic correlations with longevity (Table 4) also have significant regression coefficients.

Many other researchers (Burke and Funk, 1993; Foster *et al.*, 1989; Honnette *et al.*, 1980; Norman and Van Vleck, 1972) have found significant quadratic regression coefficients when using conformation traits to explain longevity, but Rogers *et al.* (1989) found only significant linear coefficients. Dekkers *et al.* (1994) found both significant quadratic and cubic regression coefficients. The present study investigated only linear and quadratic regression coefficients. Brotherstone and Hill (1991) found significant quadratic regression coefficients when survival was regressed on conformation scores phenotypically, but not when survival was regressed on sires' estimated breeding values for conformation traits. Those results conflict with results from this study, in which regression was on estimated breeding values and quadratic

Table 7. Significance ($P < 0.05$) of linear (L) and quadratic (Q) regression coefficients of sire breeding values of conformation traits on breeding values of longevity using the data file 1982.

Trait ¹	NLC	HL	AGE36	FNLC	FHL	FAGE36
RL	L			L	L	
TP						
UD		Q	L		Q	L
SL					L	
USS	L	L		L	L	
LSS	L + Q	L + Q	L	L + Q	L + Q	L
TSS	L + Q	L + Q	L	L + Q	L + Q	L
MP	L + Q	L	L + Q	L + Q	L + Q	L + Q

¹ NLC = Number of lactations initiated; HL = herdlife; AGE36 = stayability until 36 mo of age; F = functional (used as prefix); RL = rear legs set (side view); TP = front teat placement; UD = udder depth; SL = suspensory ligament; USS = subjective score for udder; LSS = subjective score for feet and legs; TSS = subjective score for type; MP = 305-d milk production in first lactation.

terms were significant.

Keller and Allaire (1987) found intermediate scores for conformation traits were associated with highest scores for survival traits. In the example in the present study of the relationship between FHL and UD, both deep and shallow udders are related to a high FHL, which might cause a problem if FHL is incorporated in a breeding program. Deep udders are not desired, but, when breeding for FHL, UD will go to one of the two extremes. A solution would be the use of assortative mating.

Conclusions

Conformation traits reflecting udder and feet and legs have stronger correlations with functional longevity traits than with uncorrected longevity traits. Care should be used with estimated correlations between conformation traits and longevity when those estimates are based on data from an upgrading population. The large-scale crossbreeding with Holstein Friesians appears to have strongly influenced the desirability of a certain type of cow and decision-making policies for culling. For practical use in a breeding program, estimates of genetic correlation and heritabilities should be based on the most recent data

possible and should be repeated over time. From the most recent data file analyzed in this study, it seems to be sufficient to put USS and LSS in a selection index when breeding for functional longevity in The Netherlands.

Nonlinear relationships between conformation and longevity traits exist, although hardly ever without simultaneous linear relationships. Only UD had a quadratic relation with HL and FHL without a significant linear relationship.

Acknowledgments

The authors thank the Royal Dutch Cattle Syndicate for providing the data and financial support and Arie Hamoen for valuable discussion on changes in conformation traits during the 1980s.

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Chapter 5

A Comparison of Breeding Value Predictors for Longevity using a Linear Model and Survival Analysis

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Submitted to *Journal of Dairy Science*

Abstract

A comparison was made between breeding values of sires for longevity obtained by different methods: phenotypic averages of daughters using only uncensored records, BLUP using only uncensored records, survival analysis using only uncensored records, and survival analysis using both censored and uncensored records. Two datasets were used: one with data from small, and one with data from large herds. Results from both datasets were similar. Different methods of breeding value prediction resulted in different rankings of sires. The phenotypic averages had weak correlations with the other methods of breeding value prediction (≤ 0.46). The REML/BLUP predictor had strong correlations (≤ -0.91) with the survival analysis predictor if they used the same data, and these correlations decreased (≤ -0.60) when censored records were included as well in the survival analysis. REML/BLUP and survival analysis differ mainly due to the different data that can be used (uncensored only versus both censored and uncensored).

Key words: longevity, breeding value, survival analysis

Abbreviation key: LPL = length of productive life; PBV = PEST breeding value; PHEN = phenotypic average of daughters; RR = risk ratio; RRall = risk ratio estimated using all data available; RRun = risk ratio using only uncensored records.

Introduction

Longevity traits reflecting the performance over the entire lifespan of a cow, e.g., total herd life or length of productive life, can only be measured after a cow's death. Effective selection based on these traits is seriously hindered by the time at which this information is available on a sufficient large proportion of the animals. Breeding values based on information of parents or grandparents or both will have a low reliability, because the heritability of longevity is generally low (e.g., Burnside *et al.*, 1984; Short and Lawlor, 1992; Voillema and Groen, 1996). Information on the longevity of daughters of sires becomes available with increasing age of the sires: a higher reliability of breeding value prediction for longevity implies a longer generation interval.

One alternative is the use of so called "stayability" traits: binomial traits that measure whether a cow has survived upto a certain point in time (e.g., at 48 mo of age, or 300 d in lactation, or the beginning of the third lactation). Although stayability traits can be measured at any point in time, they contain less information than traits that measure the whole lifespan of a cow. A second alternative is the use of predictor traits, for example conformation traits which can be measured early in life. However, the maximum reliability of breeding

values predicted from conformation traits is limited (Boldman *et al.*, 1992; Burnside *et al.*, 1984).

A third alternative is the use of survival analysis to obtain breeding values (Ducrocq *et al.*, 1988a and 1988b; Smith and Quaas, 1984). These breeding values differ at two basic aspects from breeding values using "traditional" mixed model analysis: so called "censored" records can be analyzed simultaneously with completed (uncensored) records, and effects can be modeled in a time-dependent way. Censored records are records of cows that have not been culled at the moment of data collection, i.e., their actual lifespan is not known but the time they are alive can be regarded as a minimum of the lifespan they will achieve. In a mixed model analysis, a fixed effect in the model will be estimated once and is assumed to be constant over the whole period of analysis. For a herd-year-season effect, for example, it implies that cows born in the same period but with different herd-lives are affected in the same manner. With survival analysis, whenever a cow enters or leaves the herd, a new herd effect will be estimated. In this way, the reality of cows having to compete with their herdmates for survival is better mimiced. It also provides the opportunity to correct for production in a time dependent way. Dekkers (1993) indicated that longevity corrected for production is a better measure of involuntary culling. This corrected longevity is called functional longevity. Van Arendonk (1985) showed that culling decisions are always taken on a within-herd basis, which implies that correction for production should also be on a within-herd basis. In many studies (e.g., Rogers *et al.*, 1991; Short and Lawlor, 1992; Vollema and Groen, 1996), correction for production has been done for first lactation within-herd production, while in other studies (e.g., Boldman *et al.*, 1992; Harris *et al.*, 1992) the production in the last lactation was used. With survival analysis, it is possible to implement production as a time-dependent effect in the model, which is expected to result in a better model than one which uses either first or last lactation.

In this study, the likelihood of a model containing only the production in the first lactation will be compared with a model containing production as a time dependent variable. Significance of effects in the model will be assessed by survival analysis. Breeding values predicted by a linear model and survival analysis will be compared in two data sets: one with data from small, and one with data from large herds. Using these two data sets enables the calculation of

correlations between longevity in different groups of farms, to investigate a possibly different ranking of sires on different types of farms. For comparison with methods that can only use uncensored data (i.e., the actual longevity has to be known) survival analysis was performed on uncensored data and on data including censored records as well.

Material and methods

Data

Data was provided by NRS (Royal Dutch Cattle Herdbook) and was limited to herds from the province of Friesland. Herds were required to have only Black and White cows (Dutch Friesian/Holstein Friesian). Data was collected in September 1996, and only cows having their first calving after January 1st 1985 were included. Longevity is measured as length of productive life (LPL): the number of days between first calving and last test day. Data was split up in two different data files: one with cows from herds with 25 to 199 cows and one with cows from herds with 200 or more cows in the data file. Data characteristics are in Table 1. A farm with 200 cows in the data file would have 17 heifers calving each year. The number of daughters per sire ranged from 1 to 5611; average was 29.6 in the data from small and 32.0 in the data from large farms. The percentage of censored records was 33.5% and 35.0% for small and large farms, respectively. Also the average LPL and censoring time were almost equal for both data files.

Table 1. Data characteristics.

	Small farms	Large farms
Number of records	139,006	116,579
Number of herds	1,294	431
Number of sires	4,689	3,642
% Censored records	33.5	35.0
Average LPL (uncensored records)	990	1,017
Average censoring time (censored records)	1,007	984

Survival analysis

Survival analysis was performed using the Survival Kit (10). The hazard function was modelled as (Ducrocq *et al.*, 1988a):

$$\lambda(t, z(t)) = \lambda_0(t) \exp\{z(t)'b\}$$

where $\lambda(t, z(t))$ is the hazard function of an individual depending on time t , $\lambda_0(t)$ is the baseline hazard function assumed to follow a Weibull distribution, and $z(t)$ is a vector of (possibly time dependent) fixed and random effects with corresponding parameter vector b . The following effects were included in the model:

- year and month of birth: class effect, independent of time;
- proportion of Holstein Friesian genes: class effect, independent of time;
- age at first calving: continuous effect, independent of time;
- herd*year*season: random class effect, time dependent;
- parity: class effect, time dependent;
- stage of lactation: class effect, time dependent;
- lactation value: continuous effect, time dependent;
- sire: random class effect, independent of time.

The proportion of Holstein Friesian genes had nine classes: 0%, 12.5%, 25%, ..., 100%. The age at first calving was expressed in days. Changes in herd were identified in the data: in both data files 7% of the cows were moved to a different herd at least once during lifetime. If a cow moved from one herd to another after her last known test day, the record was treated as censored from her last known test day on. Four seasons were distinguished, changing on the first of January, April, July, and November each year. The effects of herd and year*season were combined into an interaction term, which was absorbed during analysis and was assumed to follow a gamma distribution and of which the parameter gamma was estimated during analysis. Parity changed at the beginning of each lactation; parities 6 and higher were treated as one class. Stage of lactation changed at calving and at 60, 180, and 300 d after calving. Van de Venne (1987) showed that the risk of culling was high (but slowly decreasing) in the beginning of the lactation, increasing from 60 d until 180 d after calving, then high and stable from day 180 until day 300, and after that

decreasing again. Lactation value is a management index comparing phenotypic performances of cows within a herd for production of milk, fat, and protein (realized or extended 305-d production adjusted for season of calving and age at calving). The herd average per test day is 100 (Handboek NRS, 1993), and the value of the last test day per lactation was used. Lactation value was modeled with changes at each calving. If a cow did not have a lactation value in her last lactation (e.g., because she was culled shortly after calving), the previous lactation value was kept. The sire effect was assumed to follow a multinormal distribution and the variance parameter was estimated during analysis. Relationships between sires were identified through their sires and maternal grandsires.

For continuous effects, the results of the survival analysis are expressed as estimates of the parameter vector **b**; for fixed effects, they are expressed as risk ratios (RR). The estimate of the class with the highest number of uncensored records is arbitrarily set to zero, which corresponds to a hazard of one. The RR is the ratio between the hazard of each class of an effect and the class with the hazard of one.

For survival analysis, the heritability on the log scale was calculated as (Ducrocq and Casella, 1996):

$$h^2_{\log} = [4 * \text{var}(\text{sire})] / [\text{var}(\text{sire}) + \text{var}(\text{hys}) + \text{var}(\text{e})]$$

$$= [4 * \text{var}(\text{sire})] / [\text{var}(\text{sire}) + \text{trigamma}(\gamma) + (\pi^2/6)]$$

where

γ = estimated gamma parameter for the herd * year * season effect;

$\pi^2/6$ = variance of an extreme value distribution.

The heritability on the log scale was transformed to one on the original scale using (V.P. Ducrocq, 1997, personal communication):

$$h^2_{\text{orig}} = h^2_{\log} / [\exp\{\text{nu}/\rho\}]^2$$

where

nu = digamma(γ) - ln(γ) - Euler's constant (= 0.5772);

ρ = Weibull parameter.

Table 2. Risk ratios (RR) of the classes of the fixed effect of percentage of Holstein Friesian genes (HF) on small and large dairy farms.

HF	Small farms			Large farms		
	RR	Sign. ¹	# records (uncensored)	RR	Sign.	# records (uncensored)
0%	1.28	***	8613	1.37	***	2713
12.5%	1.02	NS	421	1.03	NS	149
25%	1.22	***	4668	1.21	***	2062
37.5%	1.08	***	5544	1.14	***	2828
50%	1.00	***	32133	1.07	***	23596
62.5%	1.03	*	5757	1.06	***	4410
75%	0.97	***	23963	1.00	***	24984
87.5%	0.89	***	9556	0.92	***	12554
100%	0.83	***	1745	0.81	***	2454

¹ Significance: NS = not significant, * = $P < 0.05$, *** = $P < 0.001$

rates of cows with over 34 mo of age at first calving, while in this study the maximum age at first calving is 36 mo. The effect of lactation value was negative: -0.033 and -0.037 for small and large farms, respectively ($P < 0.01$ for both data files). The higher the production relative to herdmates, the lower the risk of being culled. The effect of herd*year*season was absorbed so no solution was obtained. Estimates of the time-dependent effects are difficult to interpret because the risk ratio then depends on the baseline hazard ($\lambda_0(t)$) which is different at different times. For example, the estimate of parity 5 cannot be compared with that of parity 1, because they are not evaluated at the same time, and thus the baseline hazard differs.

Genetic parameters

The linear model resulted in estimated heritabilities of functional LPL of 0.076 and 0.066 for the small and large farms, respectively. The heritability estimates on the log scale from the survival analysis using all data available were 0.023 and 0.022, respectively. These estimates on the log scale are substantially lower than those from the VCE analysis, but after transformation to the original scale the results are comparable with results from the VCE analysis: 0.060 and 0.064, respectively. It was expected that the better model

used in the survival analysis compared to the model in the linear analysis would result in higher heritability estimates. One of the reasons why this is not the case might be the inclusion of herd-year-season as random effect. Theoretically it would have been possible to include the lactation value with changes at every test day instead of including one lactation value per lactation. However, this would have resulted in extremely long computing times. Literature estimates of the heritability of functional LPL are around 0.06 (Ducrocq *et al.*, 1988b; Short and Lawlor, 1992; Vollema and Groen, 1996).

Comparison of methods

Table 3 contains the Spearman rank correlations (above diagonal) and Pearson correlations among phenotypic means of daughters of sires, sires' PBV, RRun, and RRall. The rank correlations between these four breeding value predictions on small and on large farms were 0.97, 0.75, 0.81, and 0.93, respectively. The corresponding Pearson correlations were 0.98, 0.82, 0.82, and 0.92. Both correlations are in the same range, thus indicating that there are

Table 3. Spearman rank correlations (above diagonal) and Pearson correlations (below diagonal) on phenotypic means of daughters per sire (PHEN), predicted breeding values from PEST for sires (PBV), and predicted breeding values (Risk Ratios) for sires from Survival Analysis, either using only uncensored records (RRun) or all records available (RRall), using data on cows from small and large farms (total 72 sires with at least 150 uncensored records of daughters in each data set).

	Small farms				Large farms			
	PHEN	PBV	RRun	RRall	PHEN	PBV	RRun	RRall
Small farms								
PHEN		0.46	-0.32	-0.16	0.97	0.24	-0.16	-0.14
PBV	0.38		-0.91	-0.71	0.44	0.75	-0.75	-0.65
RRun	-0.23	-0.93		0.76	-0.30	-0.76	0.81	0.72
RRall	-0.03	-0.60	0.65		-0.17	-0.66	0.73	0.93
Large farms								
PHEN	0.98	0.35	-0.20	-0.03		0.33	-0.23	-0.20
PBV	0.26	0.82 ¹	-0.79	0.09	0.32		-0.94	-0.71
RRun	-0.11	-0.77	0.82	0.61	-0.17	-0.92		0.79
RRall	-0.04	-0.56	0.62	0.92	-0.08	-0.60	0.69	

¹ If corrected for the number of daughters per sire (method of Blanchard *et al.* (1983), the correlation is 0.92

little or no sires with extreme breeding values. Correction of the Pearson correlation between PBV on small and large farms for the number of daughters per sire by the method of Blanchard *et al.* (1983) increased its value to 0.92. The reliability of a selection index of a sire for a trait with a heritability of 0.07 and based on information of 150 daughters is 0.85. It is therefore concluded that all four methods of breeding value prediction are highly comparable between small and large farms.

Differences among methods of breeding value prediction are considerable. The weakest correlation (-0.16) was found between the phenotypic average and RRall on small farms. Strong correlations were found between PBV and RRun (ranging from -0.91 to -0.94). Correlations between these two predictions and RRall were substantially lower, indicating that differences between the linear breeding value prediction and survival analysis are more due to the data that can be analyzed than to the model that can be fitted. Correlations between the phenotypic average and the other methods are always weak (≤ 0.46).

The prediction standard errors of the estimates of sires from the survival analysis decreased when all available records were analyzed instead of only uncensored records. The average prediction standard errors of RRun for the 72 sires with more than 150 uncensored records in both data files were 0.044 and 0.045 for small and large farms, respectively, and of RRall 0.036 and 0.039.

Conclusions

The risk of being culled increased with year-month of birth and age at first calving, and decreased with percentage of Holstein Friesian genes and with a relatively low within-herd production level. Heritability estimates of functional length of productive life are different using a linear model or survival analysis: 0.07 and 0.02, respectively. If the heritability from the survival analysis is transformed to the original scale, the difference disappeared (estimates around 0.06). Different methods of breeding value prediction give different rankings of sires, both in the data from small and from large farms. Phenotypic averages of daughters of sires have low correlations with all three other methods of breeding value prediction. The difference between traditional (linear) mixed model analysis and survival analysis is mainly due to the difference in data that can be analyzed; i.e., survival analysis includes censored records as well.

Acknowledgments

We thank the NRS for providing funding and data, Vincent Ducrocq for providing the Survival Kit and answering numerous questions, and Arnoud van der Lugt for support in running the programs.

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Chapter 6

Conformation Traits in Survival Analysis of Longevity of Dutch Dairy Cattle

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Submitted to Animal Science

Abstract

Survival analysis was used to investigate the importance of conformation traits for longevity in Dutch dairy cows. Data was collected in September 1996 on cows which first calved from 1985 onwards. Herds were required to have at least 25 cows in the data file. The longevity trait analyzed was functional length of productive life, because production within herd was included in the model. When analyzing the effect of a cow's phenotype on her own functional longevity the following conformation traits were significant: capacity, rump angle, angularity, teat length, udder depth, size, type, overall score for udder, and overall score for feet and legs. When analyzing the effect of the breeding value of the cow's sire on her own functional longevity the following conformation traits were significant: capacity, rump angle, udder depth, suspensory ligament, overall score for udder, and overall score for feet and legs. The correlations between breeding values of sires based on longevity of their daughters and national proofs for conformation of that sires were generally strong, except for height, rear legs set, and size. Genetic relationships between length of productive life and conformation traits were stronger than phenotypic relationships.

Key words: longevity, conformation traits, survival analysis

Introduction

Implementing longevity in a breeding program will generally increase the generation interval compared to a scheme only considering production, because the information on longevity of cows only becomes available after they have been culled. Various authors suggest the use of conformation traits as early predictors of longevity, and reasonable genetic correlations between conformation and longevity traits have been found (Van Doormaal *et al.*, 1986; Rogers *et al.*, 1989; Boldman *et al.*, 1992; Short and Lawlor, 1992; Dekkers *et al.*, 1994; Vollema and Groen, 1997b). Especially traits describing the feet and legs, and udder seem to be useful. These studies involve estimation of covariances between longevity and conformation traits using multi-trait (RE)ML procedures. Applying a traditional BLUP for longevity gives predicted breeding values that are not fully correlated with breeding values from survival analysis, differences being mainly due to the inclusion of censored data with survival analysis (Vollema and Groen, 1997a). It is interesting to know whether or not covariances between conformation and longevity will change when including censored data. Current computer programs available for performing survival analysis can not be used to calculate covariances between traits, but allow derivation of the significancies of effects in a model and calculation of regression coefficients.

In this study, survival analysis is used to investigate the amount of variation in functional longevity that is explained by conformation traits. Both phenotypes of cows and breeding values of their sires for conformation traits are used as independent variables, to gain insight in both the relationship between phenotypes for longevity and conformation, and the relationship between the phenotype for longevity and the genotype for conformation. Furthermore, correlations between breeding values of sires for longevity obtained by survival analysis and official national breeding values for conformation traits are obtained to gain insight in the relationship between genotypes for longevity and conformation. These latter correlations can be seen as an approximation of genetic relationships.

Materials and methods

Data was provided by NRS (Royal Dutch Cattle Syndicate) and contained Black and White cows from the province of Friesland, which first calved from January 1, 1985 onwards. Cows from herds that had other breeds of cows as well were excluded. Herds had to participate in the conformation recording scheme and were required to have at least 25 cows in the data file. Data was collected in September 1996. The number of cows in the analysis was 66374 from 1340 herds, daughters of 3259 sires. Survival analysis was performed using the Survival Kit by Ducrocq and Sölkner (1996). The hazard function was modeled as (Ducrocq *et al.*, 1988):

$$\lambda(t,z(t)) = \lambda_0(t) \exp\{z(t)'b\}$$

where $\lambda(t,z(t))$ is the hazard function of an individual, $\lambda_0(t)$ is the baseline hazard function which is only dependent on time and is assumed to follow a Weibull distribution, and $z(t)$ is a vector of (possibly time dependent) fixed and random effects with corresponding parameter vector b . The parameter ρ of the weibull distribution was fixed at 1.375 which was found in an earlier study using data of which the present data set was a subset (Vollema and Groen, 1997a). Different models were used but in all models the following effects were included:

- year and month of birth: class effect, independent of time;
- proportion of Holstein Friesian genes: class effect, independent of time;
- age at first calving: continuous effect, independent of time;
- herd*year*season: random class effect, time dependent;

- parity: class effect, time dependent;
- stage of lactation: class effect, time dependent;
- lactation value: continuous effect, time dependent.

The proportion of Holstein Friesian genes had nine classes: 0%, 12.5%, 25%, ..., 100%. Changes in herd were identified in the data. It appeared that 7% of the cows was moved at least once during their lifetime. If a cow was moved from one herd to another herd outside the dataset after her last known test day, the record was treated as censored from her last known test day on. Four seasons were distinguished, changing on the first of January, April, July, and November each year. The effects of herd and year*season were combined into an interaction term, which was absorbed during analysis. Parity changed at the beginning of each lactation; parities 6 and up were in the same class. Stage of lactation changed at calving, 60 d after calving, 180 d after calving and 300 d after calving. Lactation value is a management index comparing phenotypic performances of cows within a herd for production of milk, fat, and protein (standardized for lactation length, season of calving, and age at calving). The herd average per test day is 100 (Handboek NRS, 1993). It was modeled with changes at each calving. If a cow did not have a lactation value in her last lactation (e.g., because she was culled shortly after calving), the previous lactation value was kept. Longevity was measured as length of productive life: the number of days between first calving and last known test day. Because a production trait is included in the model, it would be more appropriate to call it functional length of productive life.

Both phenotypes of cows and breeding values of sires for conformation traits were tested for their significance in explaining variation in functional length of productive life with four different alternatives:

1. a model including all conformation traits simultaneously and a sire effect,
2. a model including all conformation traits simultaneously,
3. a model including only objectively scored conformation traits and a separate model with only subjectively scored conformation traits, and
4. a model including only one conformation trait at the time.

Breeding values of sires for longevity were obtained with a model without conformation traits. Comparing a model including the sire effect with a model excluding the sire effect gives insight in the extra genetic variation in longevity that is not explained by conformation traits. In the third alternative, separate

models for objectively and subjectively scored conformation traits were analyzed to analyze the effect of dependencies between the two types of conformation traits. When analyzing all conformation traits in one model, they were corrected for each other. The fourth alternative was restricted to the conformation traits that describe the udder because it was expected that these traits would have the strongest dependencies among them. Due to large computational problems no results were obtained when analyzing the breeding values of the sires for udder traits separately in the survival analysis, so the fourth alternative was only analyzed using phenotypes of cows.

Conformation traits were scored during the first lactation of a cow. The following conformation traits were included: objectively (linearly) scored on scale 1 through 9: height (**HT**, in cm), capacity (**CA**), rump angle (**RA**), rump width (**RW**), angularity (**AN**), rear leg set (**RL**), claw diagonal (**CD**), fore udder attachment (**FU**), teat placement (**TP**), teat length (**TL**), udder depth (**UD**), rear udder height (**UH**), suspensory ligament (**SL**); subjectively (descriptively) scored on scale 65 through 89: size (**SSS**), type (**TYSS**), udder (**USS**), and feet and legs (**LSS**). For the objectively scored conformation traits, a high score indicated a large CA, steep RA, wide RW, strong AN, sickled RL, short CD, strong FU, narrow TP, long TL, shallow UD, high UH, and strong SL. CD was not included in the analysis of phenotypes because only half of the cows in the data were scored for this trait. For the subjectively scored conformation traits, a high score indicated a big SSS, desired TYSS, strong USS, functional LSS, and high TOSS. When analyzing the phenotypes of the conformation traits, the traits scored on a 1 through 9 scale were treated as class variables, and the other conformation traits as continuous variables. The breeding values were national evaluations with an average of 100, and were included as continuous effects. The sire effect was included as a random fixed effect.

Significance was tested by a likelihood ratio test comparing the full model with models excluding one effect at a time. Estimates of the regression coefficients of the conformation traits were obtained. For continuous effects, the solutions from the survival analysis are expressed as estimates of the parameter vector (**b**); for fixed effects, they are expressed as risk ratios (**RR**). The estimate of the fifth class of each trait is arbitrarily set to zero, so the hazard of this effect equals one. The RR is the ratio between the hazard of each class of an effect and the class with the hazard of one. Because $\lambda_0(t)$ is only

dependent on time, it is the same for each class within an effect if evaluated at the same moment. Thus, the RR is calculated as $\exp\{z(t)'b\}$.

As sires were treated as a class effect in the survival analysis their RR is regarded as their breeding value. The correlations between sires' breeding values for longevity obtained by survival analysis without conformation traits in the model and their national breeding values for conformation traits were calculated. Only 55 sires having at least 150 daughters with an uncensored record were used to calculate the correlations between breeding values. The lower limit of 150 uncensored records per sire was imposed to ensure that only breeding values of proven bulls were included.

Results and discussion

Phenotypic scores in survival analysis

Significances of the phenotype of conformation traits are shown in Table 1. The traits CA, RA, AN, TL, UD, SSS, TYSS, USS, LSS, and TOSS are significant ($P < 0.05$) if all conformation traits are analyzed simultaneously in one model, regardless whether a sire effect is included or not. The sire effect does not explain much variation after the phenotypes for conformation traits of the cows are fitted. When analyzing objectively and subjectively scored conformation traits separately, all traits are highly significant ($P < 0.01$) except RW ($P = 0.27$). HT is only significant if SSS is not in the model. De Jong (1996) calculated very strong phenotypic and genetic correlations between HT and SSS of 0.99 and 0.93, respectively. Similarly, RL is only significant if LSS is not in the model; and FU, TP, UH, and SL are only significant if USS is not in the model. In a model with only subjectively scored conformation traits, all these traits remain significant. Thus the effects of RL, FU, TP, UH, and SL are absorbed in the subjectively scored traits. When fitting each udder trait separately in the model all traits are highly significant ($P < 0.01$) which is not surprising because they were already highly significant when fitting objectively and subjectively scored traits separately. When culling decisions are made, farmers take into account the phenotypes of CA, RA, TL, UD and all subjectively scored conformation traits. From this analysis, it is not clear whether culling is on conformation traits directly or on functional traits that are at least partly described by conformation traits.

Table 1. Significancies (P-values) of conformation traits¹ for functional length of productive life in different models.

Model	HT	CA	RA	RW	AN	RL	CD	FU	TP	TL	UD	UH	SL	SSS	TSS	USS	LSS
<i>Phenotypes of cows</i>																	
Conformation + site	.63	.00	.00	.75	.04	.32	-	.65	.91	.00	.00	.38	.05	.00	.00	.00	.00
Conformation	.89	.00	.00	.28	.03	.38	-	.67	.62	.00	.00	.33	.08	.00	.00	.00	.00
Objective traits	.00	.00	.00	.27	.00	.00	-	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
Subjective traits														.00	.00	.00	.00
Single udder traits								.00	.00	.00	.00	.00	.00				.00
<i>Breeding values of sires</i>																	
Conformation + site	.32	.14	.00	.64	.50	.59	.65	.76	.78	.23	.13	.29	.03	.61	.41	.20	.21
Conformation	.36	.00	.00	.06	.36	.72	.31	.68	.17	.20	.63	.03	.00	.14	.07	.00	.00
Objective traits	.56	.59	.00	.00	.56	.15	.00	.07	.00	.11	.14	.14	.00	.00	.54	.03	.01
Subjective traits																	

¹ HT = height, CA = capacity, RA = rump angle, RW = rump width, AN = angularity, RL = rear legs set, CD = claw diagonal, FU = fore udder attachment, TP = teat placement, TL = teat length, UD = udder depth, UH = rear udder height, SL = suspensory ligament, SSS = subjective score for size, TSS = subjective score for type, USS = subjective score for udder, LSS = subjective score for feet and legs.

Table 2 contains the estimates (transformed to RR) for the significant phenotypes of objectively scored conformation traits analyzed simultaneously in one model without a sire effect. The fifth class of every trait is arbitrarily set to 1, and all other classes are expressed as ratios of these. It appears that a large CA results in a higher risk of being culled: cows with the highest score for CA have a 17% higher risk of being culled than cows with the lowest score. In practice, there is an indication that cows with a high score for CA are more often affected by displaced abomasum (A. Hamoen, Chief Classifier of the Royal Dutch Cattle Syndicate, 1997, personal communication). For RA, the RR decreases rather linearly with increasing score. A steep angle is believed to give less problems at calving. Only the highest score, 9, for AN gives a substantial increase of the RR. Thus, if two cows are exactly the same (so the same parity, hys, CA, etc.) except their AN, the cow with score 9 has 15% more chance of being culled than the cow with score 5 for AN. The highest score for TL, so the cows with the longest teats, has the highest RR. The RR for UD is especially high for scores 1 through 3 and then reaches a plateau. Except for RA it appears that the objectively scored traits have a threshold value. For none of the traits an optimum was identified.

Table 2. Estimates and number of uncensored observations (between brackets) per class of significant ($P < .05$) phenotypes of objectively scored conformation traits¹.

Class	CA	RA	AN	TL	UD
1	.97 (166)	1.13 (710)	1.02 (651)	1.00 (1078)	1.45 (103)
2	.91 (849)	1.12 (3534)	1.02 (2568)	.94 (3091)	1.26 (1228)
3	1.01 (2904)	1.06 (6878)	1.02 (5284)	.96 (5445)	1.13 (4407)
4	.97 (4954)	1.03 (7951)	1.00 (7275)	1.00 (7897)	1.05 (7609)
5	1.00 (10780)	1.00 (9478)	1.00 (12719)	1.00 (10687)	1.00 (12981)
6	1.02 (8790)	1.00 (7083)	.98 (7207)	1.01 (7467)	.97 (8012)
7	1.05 (6915)	.98 (3535)	1.03 (3347)	1.06 (3375)	.98 (4560)
8	1.08 (4907)	.95 (2006)	1.03 (2126)	1.05 (2029)	.99 (2362)
9	1.14 (1381)	.89 (471)	1.15 (469)	1.17 (577)	1.00 (384)

¹ CA = capacity, RA = rump angle, AN = angularity, TL = teat length, UD = udder depth.

The phenotypes of subjectively scored conformation traits were analyzed as continuous traits, so the solutions for these effects assume that the risk of being culled increases or decreases linearly with the score for each trait. The estimate for SSS was positive: 0.015 which means that a 5-point higher score results in a 1.08 times higher risk of being culled. In general, high scores for conformation traits relating to body measurements of a cow are associated with a higher chance of being culled. Apparently bigger cows are culled earlier on the farms used in this study. The estimates for the other subjectively scored traits were negative, so higher scores are associated with lower chance of being culled. Estimates were -0.012, -0.018, -0.010, and -0.018 for TYSS, USS, LSS, and TOSS, respectively; which correspond to a decrease in risk of being culled by a factor 0.94, 0.91, 0.95, and 0.91 if the score for a trait is 5 points higher. Weigel (1996) reported a negative correlation between strength and length of productive life, which is an indication as well that the largest cows have the shortest longevity.

Breeding values in survival analysis

When analyzing the national proofs for conformation traits simultaneously in one model and including a sire effect, only RA and SL were significant ($P < 0.05$, see Table 1). When excluding the sire effect from the model CA, UH, USS, and LSS were significant as well. So the sire effect does explain variation for these latter conformation traits if the breeding values of the sires of the cows are fitted, in contrary to when the phenotypes of the cows themselves are fitted. If a culling decision has to be made, the farmer takes the breeding value for CA, RA, UH, SL, USS, and LSS of the cows' sires into account. Of course this influence can be indirect: the phenotypes of the cows are partly dependent on the breeding values of their sires. As can be seen in Table 1, the phenotypes for CA, RA, USS, and LSS were significant as well. If the breeding values for objectively and subjectively scored conformation traits are analyzed separately, RA and UH are not significant anymore ($P = 0.59$ and 0.14 , respectively). One would expect that traits that are significant in a model containing all conformation traits would be also significant if some of the (possibly correlated) traits are taken out of the model, but for these two traits the opposite is true. The breeding values for the traits RW, CD, TP, and SSS become significant ($P < 0.05$) while they were not significant with all traits simultaneously in one

model.

The regression coefficients of the significant conformation traits from the model with breeding values for all conformation traits simultaneously are 0.0082, -0.0099, 0.0044, 0.011, -0.033, and -0.018 for CA, RA, UH, SL, USS, and LSS, respectively. These estimates indicate that a smaller capacity, steeper angle, higher udder, stronger suspensory ligament, high score for udder, and high score for feet and legs are associated with a lower risk of being culled and thus a longer length of productive life.

When analyzing the phenotypes of the cows more conformation traits had a significant effect on longevity than the breeding values of their sires. In making culling decisions, the farmer judges a cow more on her own appearance than on the breeding value of her sire. Maybe the breeding value of the cow herself would explain more variation, although that breeding value also partly depends on the breeding value of her sire.

Correlations between breeding values

The correlations between breeding values of the 55 sires for longevity and conformation traits are in Table 3. Of the objectively scored traits, the breeding value for TP had the strongest correlation with the breeding value for longevity: -0.55. A higher breeding value for TP is associated with a lower chance of being culled. In a previous study (Vollema and Groen, 1997b) TP also was the objectively scored conformation trait with the strongest genetic correlation with functional longevity in the most recent dataset. RL had a weak genetic correlation with functional longevity in that study, as it has in the present study as well. Vollema and Groen (1997b) concluded that the genetic correlation between TYSS and functional longevity was only strong during the process of Holsteinisation. In the present study, TYSS is strongly correlated with risk of culling, and thus longevity, as well. The process of Holsteinisation took place during the eighties and early nineties, so the cows in the data used for this study (1985 through 1996) are likely to be influenced by it.

One might expect that conformation traits of which the phenotype was not significant for the risk of being culled (see Table 1) generally have weak correlations between the breeding values, and vice versa. This did not hold for RW, FU, TP, and UH: these traits were not significant in the phenotypic analysis

Table 3. Correlations between breeding values for longevity (expressed as risk ratios, RR) and breeding values for conformation¹ of 55 sires.

	HT	CA	RA	RW	AN	RL	CD	FU	TP	TL	UD	UH	SL	SSS	TYSS	USS	LSS
RR	-.096	.42	-.27	.36	.35	-.017	-.26	-.41	-.55	.45	-.48	-.39	-.40	-.080	-.38	-.57	-.46

¹ HT = height, CA = capacity, RA = rump angle, RW = rump width, AN = angularity, RL = rear legs set, CD = claw diagonal, FU = fore udder attachment, TP = teat placement, TL = teat length, UD = udder depth, UH = rear udder height, SL = suspensory ligament, SSS = subjective score for size, TSS = subjective score for type, USS = subjective score for udder, LSS = subjective score for feet and legs.

(Table 1) but all breeding values had correlations with the RR that were stronger than 0.36 (Table 3). For SSS the opposite was found: although this conformation trait was highly significant in the phenotypic analysis, its correlation between breeding values was only -0.080. The genetic relationships between length of productive life and conformation traits appears to be stronger than the phenotypic relationship. In the prediction of breeding values for conformation traits the correlations among conformation traits have not been taken into account. In the survival analysis the effects of all conformation traits were estimated simultaneously; in other words, they were corrected for each other and thus their correlations with functional longevity might be different and their significancies will be lower.

Breeding for longevity

In many countries, a breeding value for longevity (or lifetime profit) of sires either contains direct information on longevity of relatives or indirect information on conformation traits (Interbull, 1996). Combining both sources of information into one breeding value prediction is straightforward when (co)variances are known. The relative weighting of both sources has to change during the lifetime of a bull depending on the amount of information becoming available. Both Jairath *et al.* (1996) and Weigel (1996) used the multiple across country evaluation procedure to combine direct and indirect information into one index. However, with this method it is assumed that the residual covariances between traits are zero. Incorporating conformation traits in a survival analysis model does not give a combined index of direct information on longevity and indirect information via conformation. Instead, breeding values from such a model would have to be interpreted as "hazard of being culled corrected for conformation traits". A selection index for longevity would have to combine a RR as breeding value for longevity and a "traditional" breeding value for conformation traits. The model used for the survival analysis should then not contain conformation traits. Problems might arise from non-linear relationships between the phenotypes of longevity and conformation traits (Table 2). Only the linear part of the relationships between phenotypes of longevity and genotypes of conformation, and between genotypes of longevity and conformation has been investigated in this study. This linear part was quite significant for a number of traits (Tables 1 and 3).

Conclusions

Conformation traits can play a role in the prediction of breeding values for longevity. Especially traits describing the size, rump angle, udder, and feet and legs of a cow are significant. Combining both direct and indirect information would require separate breeding value predictions for both sources, that are weighted into one selection index.

Acknowledgments

The Royal Dutch Cattle Syndicate is thanked for providing funding and data. The authors are indebted to Vincent Ducrocq for providing the Survival Kit and valuable assistance in getting the programs running.

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Chapter 7

General discussion

Choices by a breeding organization

As outlined in the Introduction (Chapter 1) of this thesis, breeding organizations have to make four major decisions when incorporating longevity into their breeding program. The distinction between these decisions is not as sharp as suggested there: in practice, one choice will influence the other. The first decision is the breeding goal: uncorrected longevity, functional longevity (correction for milk production only), or residual longevity (correction for all other traits in the breeding goal). This decision depends solely on the purpose for which longevity is included. If the breeding program is aimed at producing cows that will live longer, uncorrected longevity will be the choice. However, it has to be realized that farmers determine the actual longevity of a cow, and that part of the improved genetic potential for longevity is not utilized because farmers will increase voluntary culling (Van Arendonk, 1985). More generally, the economic optimal longevity of a cow is always less than the "technical", or biologically possible longevity, and, as outlined in Chapter 1, the longevity realized is generally even less. On page 4 of this thesis it has been concluded that the economic importance of improving longevity lies in decreasing the proportion of involuntary culling. Another fact that has to be emphasized is that selection for uncorrected longevity will, in practice, mean that selection is mainly for milk production, because the production of a cow compared with her herdmates is by far the most important factor determining longevity (Dohoo and Martin, 1984; Hocking *et al.*, 1988; Vollema and Groen, 1997). Because most breeding organizations for dairy cows will have milk production in their breeding goal and a direct evaluation of milk production traits already, additional information will be provided only by functional longevity. Similarly, if traits other than milk production that influence longevity (i.e., health, fertility, and workability traits) are already in the breeding goal, it can be argued that residual longevity should be incorporated. Correction should take place on the phenotypic scale, because farmers' culling decisions are based on phenotypic observations as well. A measure for production, expressed as a deviation from the herd average, is relatively easy to calculate. It is hardly possible to calculate a phenotypic measure for farmers' culling for functional traits. Also, an index for residual longevity (corrected for all functional traits a farmer takes into account) would be hard to interpret for farmers. Functional longevity can be interpreted as "potential" longevity. Thus, the potential of a cow to survive regardless of

her production is the best alternative to use in practice. Therefore, breeding organizations that are already predicting breeding values for health, fertility, or workability traits might still choose breeding for functional instead of for residual longevity.

The second decision is which trait breeding organizations prefer to define longevity with. The outcome of this decision is closely linked to the outcome of the first decision: when breeding for functional longevity, one will implicitly have a functional longevity trait in the breeding goal. The genetic gain per year depends on the reliability of the index and the genetic variance of the trait (Rendel and Robertson, 1950). The reliability of the index depends partly on the heritability of the trait. From Chapters 2 and 3 the lifetime milk production of a cow appears to have the highest heritability: around 0.17. The other traits describing the lifetime of a cow, such as herdlife, length of productive life, and total number of days in lactation, have a heritability that is around 0.09. Functional lifetime traits have lower heritabilities: around 0.07. Stayability traits are binary traits and thus their information content is less than lifetime traits and their heritability is lower: around 0.05.

Apart from the heritability and variance it is also important to realize how long it will take before data on certain traits become available. In the literature not much attention has been paid to the balance between the low heritability of stayability traits that are known relatively early, and the higher heritability of lifetime traits that take a longer time to be known (Chapter 2). Also in this thesis no attention has been paid to this issue.

Compromises between lifetime and stayability traits are possible. Harris *et al.* (1992) introduced the so-called "opportunity groups": cows are given a maximum lifetime (opportunity), and cows with the same opportunity are in the same group. If cows are culled before their maximum lifetime is achieved, their actual lifespan is known; if not, their maximum lifetime is assumed to be their actual lifespan. VanRaden and Klaaskate (1993) introduced a trait called "months in milk at 84 months of age": the total number of months a cow was in milk until 84 months of age, with a maximum of ten months of milking per lactation. If a cow did not have the opportunity to reach 84 months of age at the moment of data collection, her lifetime was predicted using average herd parameters for survival. Brotherstone *et al.* (1997) used the same approach: if a cow was still alive at the moment of data collection, the number of lactations

she would survive from that moment was predicted using the population expectation. Although both VanRaden and Klaaskate (1993) and Brotherstone *et al.* (1997) showed that their predicted longevity trait had reasonably strong correlations with longevity traits measured, it is doubtful whether analysing predictions as if they were true observations is theoretically justified. The error terms are distributed differently, and predictions should be weighted differently from observations.

Another reason to choose for a certain trait is the data that are available. As stated before, information on longevity can be easily obtained from milk recording data, but using only these data implies that no information on cows that were culled before their first calving is available. In such a case it would not be justified to use herd life as a measure for longevity. Using Canadian data, Hocking *et al.* (1988) found that nearly 25% of the potential heifers were culled or had died before first calving. Martinez *et al.* (1983) found that calf mortality was not only influenced by the sex of the calf, parity of the dam, and gestation length, but also by the sire of the calf. However, their estimate of the heritability of calf mortality was low: 0.01. If only milk recording data are available, a trait describing the productive life of a cow instead of the herd life should be used, and it has to be realized what exactly is measured and thus what is being bred for. Again, the choice of a longevity trait mutually influences the choice of the breeding goal. If data on cows are available from birth onwards, herd life could be used, but a separate trait describing survival until the first calving next to the length of productive life would be more informative. Another example of how the available data influence the trait of choice is given in Brotherstone *et al.* (1997). In general, the trait with the most detailed unit of measurement can identify the most variation between animals and is thus the most informative, which is also reflected in the higher heritabilities of these traits (see Chapters 2 and 3: the heritability of number of lactations is generally lower than that of length of productive life measured in days). But in Great Britain, only 305-d lactation records were stored in the past, and thus Brotherstone *et al.* (1997) had to use number of lactations to measure longevity.

The second choice is also closely related to the question which method to use, i.e., the third choice. For traits other than longevity, breeding values are usually predicted with a best linear unbiased prediction, while for longevity survival analysis can be used. If one chooses to use a stayability trait, one

cannot use survival analysis because this method requires continuous longevity traits (Cox, 1972). Because survival analysis allows the use of censored records, it combines early availability of an index with the use of a lifetime trait. If one chooses to use length of productive life, a Weibull model can be assumed for the baseline hazard, which simplifies the calculations with this method (Ducrocq *et al.*, 1988). Still, this method requires substantially more computer capacity than a best linear unbiased prediction analysis, and for analysing large datasets only a sire model can be used. This might be the reason for not choosing survival analysis in particular situations. However, with current computer capacities in most developed countries it is possible to analyse large datasets with survival analysis (Ducrocq, 1994). When using a sire model, the breeding value for longevity of a cow will be calculated from the breeding value of her sire and her maternal grandsire, assuming that the bulls are unrelated. The loss of information due to the use of a sire model instead of an animal model is expected to be low. Combining these arguments with the fact that survival analysis allows modelling of effects in a time-dependent way, resulting in a more accurate model, yields the conclusion that survival analysis should be used whenever possible. The resulting estimates of hazards can be transformed to traits that are easier to interpret for farmers, such as average expected longevity of daughters of a certain bull.

The fourth choice is traits to be used in the index. The highest correlation between the breeding goal and the selection index is achieved if the same trait is both in the breeding goal and in the index. Depending on the heritabilities of the traits, the correlations among traits, and the number of daughters available for the breeding value prediction, indirect prediction of breeding values (so using different traits in the index than in the breeding goal) might be advantageous over direct prediction. From the literature, the maximum reliability of indirect prediction using conformation traits in the index is less than 60% (Boldman *et al.*, 1992; Weigel *et al.*, 1995). Apart from the question which traits in the index give the highest reliability, problems might arise with the availability of direct information on longevity of daughters in the early life of a bull, especially when using lifetime traits to measure longevity. But even if using stayability traits or survival analysis, it will take longer before an index for longevity can be calculated with the same reliability as the one for milk production. This matter will be discussed in more detail in the following paragraphs. It has to be realized

that, in general, farmers require a breeding value prediction with a certain minimum reliability, while breeding organizations think it more important to have an early prediction.

Factors influencing longevity

To predict unbiased breeding values for longevity, it is important to know the factors that influence longevity. Milk production compared with herdmates is the most important factor, but in making culling decisions, a farmer also considers parity and stage of lactation a cow is in (Ducrocq, 1994; Van de Venne, 1987; Vollema and Groen, 1998). Van Arendonk (1985) showed that the optimum moment of culling within a lactation depends on the relative production level and parity of a cow.

An effect with a large influence on longevity is the herd by year-season interaction. In general, this effect accounts for differences in culling strategies in different seasons, for instance, because a certain calving pattern is desired. When analysing longevity data from a country of the European Union, it is especially important to include a herd by year-season effect in the model. Ducrocq (1994) noticed an increase in culling in the three months preceding the end of the quota year, and also in this thesis the effect of herd by year-season was always found highly significant. In Figure 1 of Chapter 3 of this thesis, the effect of implementation of the quota system on longevity of dairy cows is shown. Not only did the farmers cull an extra 20% of their cows, also their farming strategy changed. Some started a complete new business besides their milking cows, for instance, by growing fish. Others bred their lower-producing cows with beef bulls. When editing the data for the analyses of Chapters 5 and 6, it appeared that many farmers had been milking some of the resulting crossbred cows, presumably because prices of beef calves dropped due to the large supply of such calves and because they had a surplus of feed and housing available. Only very few of these crossbred beef cows were milked for more than one lactation. The culling strategy was apparently different for the crossbred beef cows than for the purebred milking cows. For that reason, herds with crossbred beef cows were excluded from the analysis. However, when predicting national breeding values for longevity, all herds have to be included. A solution could be to regard different breeds of cows within a herd as different subherds, assuming that cows only have to compete with cows of the same

breed or with the same breeding goal within a herd. Another solution could be to include a herd by breed interaction in the model.

Another strong reason to include a herd by year-season interaction in the model is the effect of the crossing with Holstein-Friesian bulls. In the Netherlands, this occurred in the eighties and the original Dutch-Friesian genes in the population of Black-and-White cows were replaced by Holstein-Friesian genes. This "Holsteinization" process is nicely shown in Table 1 of Chapter 4. The effects of the implementation of the quota system and the Holsteinization cannot be separated in the Netherlands. The quota system speeded up the Holsteinization, and together both effects caused a temporary decrease in the longevity of dairy cows realized (Figure 1 of Chapter 3). The growing concern about the decrease in longevity of dairy cows realized seems not to be justified, although this is hard to prove for the dairy cow population nowadays, because these cows have not been culled yet. No estimation of the genetic trend for longevity has been made using Dutch data, but Blanchard *et al.* (1983) found a positive genetic trend for both production and stayability in Jersey cows. Thus, a positive genetic trend for production is not necessarily associated with a negative trend for longevity.

Also in other countries the process of Holsteinization took place and seems to have influenced longevity. For instance, in Australia, Jersey cows were replaced by (crossings of) Holstein cows, and heritabilities of longevity differ between cows which first calved before and after 1979 (Madgwick and Goddard, 1989). The strong correlation between longevity and total score in Great Britain (Brotherstone and Hill, 1991) might be caused by Holsteinization as well. Vollema and Groen (1997) concluded that the correlation between longevity and type was only substantial during the process of Holsteinization.

Ducrocq (1994) found no influence of age at first calving on longevity. However, other researchers (Rogers *et al.*, 1991; Vollema and Groen, 1998; Vukasinovic *et al.*, 1997) did find such an influence. Cows that were younger at first calving had less chance of being culled, and thus had a longer productive life. A high age at first calving can be an indication of problems with fertility, which might be a reason for involuntary culling. The average age at first calving stayed rather constant in the Netherlands (Figure 1, Chapter 3).

Of course, other factors influence longevity as well. For instance, the prices of calves, feed, and carcasses highly influence a farmer's culling decision

and thus the longevity of his cows (Van Arendonk, 1985; VanRaden and Klaaskate, 1993). In theory, these prices can be included in a survival analysis model as time-dependent covariables and their significance can be investigated. In practice, when analysing longevity data, these factors are usually unknown and cannot be included in the model.

Longevity and functional traits

One of the reasons that the research described in this thesis was conducted was the growing demand of Dutch farmers for a breeding value for functional traits. In the Netherlands, disease incidences are not widely recorded but functional longevity might be used as an index for functional traits. Results from the literature on culling reasons of dairy cows show that after milk production, unsatisfactory reproduction was the main stated reason for culling. Another way to approach the relationship between longevity and functional traits is by analysing longevity and data measuring functional traits, e.g., incidence of mastitis, dystocia, number of inseminations per conception, and milking speed. It was intended to use survival analysis on Danish data to obtain the significance and effect of mastitis on culling of dairy cows. In Denmark, it is known which cows have been treated for mastitis. Different data files were created which varied in the length of the period after the mastitis incidence during which mastitis influenced the farmer's culling decision. By comparing the likelihoods of the different models, the model which best described the influence of mastitis on the risk of being culled would be identified. Results of this study are not available yet. Thus, only results from the literature could be included in this thesis.

The genetic relationship between longevity and functional traits was studied by Beaudeau *et al.* (1994a and b). He concluded that udder health and reproductive disorders from both previous and current lactations were the main reasons for culling related to health problems. However, in general a disease had a rather short-term effect; farmers did not consider the whole disease history of a cow in making culling decisions. Udder disorders, teat injuries, milk fever, ketosis, and assistance at calving increased the risk of being culled early in lactation while abortion, metritis, poor reproductive performance, and mastitis resulted in a higher risk of being culled later in lactation. Erb *et al.* (1985) concluded that for heifers mastitis and a failure to conceive at first service were

the most important risk factors. For multiparous cows mastitis, dystocia, and poor breeding performance were the most important. The authors also looked at underlying reasons for culling: milk fever increased the risk of reproductive disorders, and thus contributed to increased culling due to poor breeding performance. Gröhn *et al.* (1997) found something similar: having ovarian cysts was highly significant for culling a cow, but if conception status was included in the model as well, ovarian cysts had no effect.

In this thesis, workability traits are regarded as functional traits, while in other studies they are regarded as primary traits. Madgwick and Goddard (1989) and Visscher and Goddard (1995) estimated the genetic correlation between survival of the first lactation and milking speed and between survival of the first lactation and temperament. Both were found to be around 0.30. Genetic correlations between survival of later lactations and milking speed and between survival of later lactations and temperament were somewhat weaker (around 0.20).

Apparently there is a substantial relationship between risk of being culled, or survival, or longevity, and functional traits. Thus, when breeding for functional longevity, the genetic potential for functional traits will be improved as well. However, from the results of this thesis it cannot be predicted to what degree each functional trait will be improved.

Breeding value prediction

From Chapter 5 it can be concluded that survival analysis is the best method to predict breeding values for longevity, because it allows the inclusion of censored records and thus an unbiased prediction for younger bulls. Vukasinovic *et al.* (1997) concluded that such a breeding value could be based on 30 to 40% censored records, but they did not take into account the relationship between sires. Moreover, their results were influenced by the data selection. From Danner *et al.* (1993) it can be concluded that over 60% of censored records still give a reliable breeding value prediction. In both studies no attention has been paid to the influence of the number of daughters per bull. In Figure 1 the availability of data during the early life of an average breeding bull in the Netherlands is shown. When the bull is 15 months old, his sperm is distributed across the country for a couple of weeks only. His test daughters will be born when he is two years old. On average, each bull has 110 test

daughters. Assuming that all daughters have their first calving at 24 months of age and that their lactation length is 12 months, the available information is sufficient for a reliable breeding value prediction for production when the bull is five years old. At that moment it is decided whether a bull is culled or will be further used as a proven bull. The average culling percentage in the first lactation in the Netherlands is around 30%, so at that time the longevity realized of only 33 test daughters is known. This is not enough for a reliable breeding value prediction to present to farmers, even if using survival analysis.

Therefore, a breeding organization might prefer to use additional traits for early prediction of a breeding value for longevity. Conformation traits are a logic choice, because they can be measured early in a cow's life and have reasonably strong relationships with longevity traits (Chapters 2, 4, and 6). In the Netherlands, around 55% of the farmers participate in the classification program, so around 60 daughters per bull would have information on conformation traits at the end of the first lactation (Figure 1). In practice, a breeding value predictor for longevity will rely on parental information and conformation traits early in a bull's life. With an increasing number of daughters

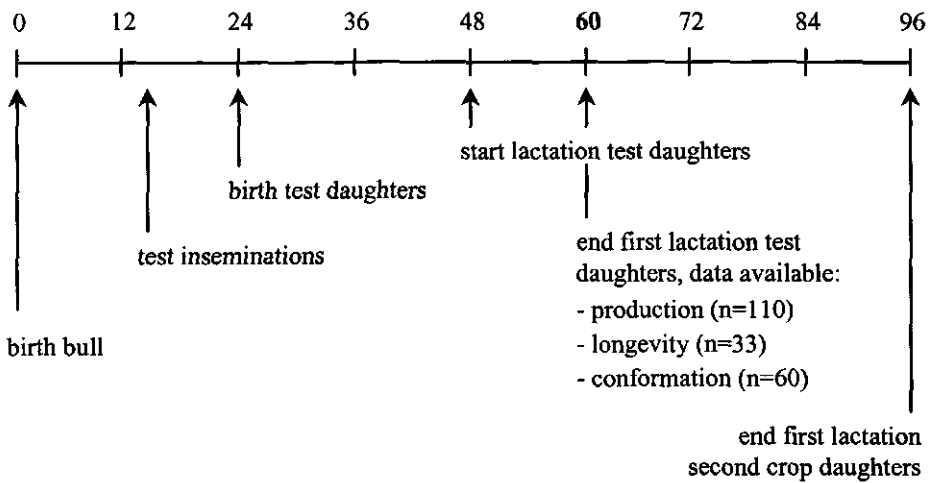


Figure 1. Schematic outline of the availability of data during the early life of a breeding bull in the Netherlands (in months).

being culled, the information on longevity of the daughters will gain importance. Breeding values for longevity and conformation traits will have to be predicted separately and combined into one index. Relationships between longevity and conformation traits have been studied extensively in the literature, but for this breeding value predictor, the relationship between the risk of being culled and conformation traits needs to be known. In Chapter 6 this has been analysed using a limited number of data, but as shown in Chapter 4 the period over which data are available can have a substantial impact on the results found. Thus, it is recommended to estimate the relationships using as recent data as possible, and re-estimate them over time. A possible drawback of the use of conformation traits is that, although the correlations with longevity traits are reasonably strong, it remains unclear whether conformation traits are really correlated with functional traits or whether some farmers practise voluntary culling for conformation as well.

The estimates of sire effects in the survival analysis are on the log scale, and transformed to a risk of being culled on the observed scale. For presentation to farmers it might be more informative to transform the risk ratio of a sire and the baseline hazard function into the average length of productive life of its daughters, or the fraction of daughters surviving a certain number of years of productive life, or to transform it into a standardized breeding value with an average of 100 and a certain standard deviation. Standard errors of estimates of sire effects are expressed on the log scale, and standard errors of the breeding goal are known on the observed scale. Thus, assigning a reliability to a breeding value prediction is not straightforward. An approximation based on the number of informative daughters is a good alternative. Also the genetic gain of longevity expressed as risk of being culled will need a transformation.

Main conclusions

Survival analysis should be used whenever possible to estimate breeding values for longevity. When calculating longevity from milk recording data, functional length of productive life should be analysed. The best way to predict breeding values for longevity in the Netherlands is to combine the risk ratio for sires obtained from a survival analysis which is purely based on the longevity of daughters, with breeding values for conformation traits. Conformation traits describing the udder have the strongest relationship with longevity, followed by

the subjective score for feet and legs and the objective score for rump angle. If milk recording data are joined with birth registration data, this additional information could be used for a separate breeding value for survival until first calving.

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Summary

This thesis deals with several aspects of longevity of dairy cattle. When breeding organizations want to implement longevity in their breeding programs they have to make several decisions. This thesis aims to give tools to make those decisions.

Chapter 2 gives an overview of the literature containing estimates of heritabilities of longevity traits and correlations between longevity and conformation traits. The results of Chapters 3 and 4 of this thesis are included as well. There are many different definitions of longevity. In this thesis, two distinctions are made: 1. between *lifetime* and *stayability* traits, and 2. between *uncorrected* and *functional* longevity traits. Lifetime traits measure the period a cow is alive or producing, and are usually expressed in days. Stayability traits measure whether or not a cow is alive at a certain point in time. Functional longevity traits are corrected for milk production, thus aiming to be a better measure for involuntary culling. In Chapters 1 and 7 of this thesis, *residual longevity* is introduced, which is longevity corrected not only for milk production but also for all other traits that are already in the breeding goal. So far, this trait has not been used in practice. From the literature it is concluded that, in general, heritability of longevity traits is below 0.10. The heritability of stayability traits is lower (around 0.04) than that of lifetime traits (around 0.09), and the heritability of functional longevity traits is lower (around 0.07 for lifetime traits and around 0.03 for stayability traits) than that of uncorrected longevity traits. Genetic correlations among different longevity traits are generally strong. Genetic correlations between longevity and conformation traits are strongest for conformation traits describing the mammary system and, to a lesser extent, feet and legs. The reliability of a breeding value prediction of a sire based solely on the conformation information of his daughters is approximately 55% at maximum.

In Chapter 3, the longevity realized of cows born in different years (1978 through 1985) has been calculated. Longevity of cows born in 1978 through 1984 decreases, and longevity of cows born in 1985 is at the same level as the longevity of cows born in 1978. In 1984, the quota system was implemented in the Netherlands and farmers culled 20% more cows than their normal annual culling percentage. These cows, of course, were born before 1984. Besides this process, during the eighties large-scale crossing with Holstein-Friesian bulls took place. The original Dutch-Friesian cow population was replaced by Holstein-

Friesians, and this process was accelerated by implementation of the quota system. Both processes not only affected longevity of dairy cows realized in the Netherlands, but also the estimates of heritabilities. Data on cows born in 1978, 1982, or 1985 were used to estimate heritabilities, and the estimates were highest for the 1978 dataset, lower for the 1982 dataset, and lowest for the 1985 dataset. Possible explanations are that the population was under strong selection during the period considered, that the genetic background of the population changed, and that under the quota system, farmers base their culling decisions on a shorter planning horizon, thus increasing the environmental variation of longevity traits.

In Chapter 4, data on cows born in different years (1978, 1982, and 1989/1990) were used to estimate genetic correlations between longevity and conformation traits. These parameters were also affected by the changing population structure during the eighties. In the 1978 data file, the correlation between functional herd life and type was rather weak (0.16) while in the 1982 data file, this correlation was very strong (0.46). For the 1989/1990 data file, only stayability traits could be analysed because cows had not had enough time to be culled. The correlation between functional stayability until 48 months of age and type was 0.21. The strongest correlation was between functional stayability and the subjective score for udder (0.93), followed by the subjective score for feet and legs (0.43). The estimate of 0.93 is probably too high but also from other studies it was concluded that, apart from production, the udder is the most important factor determining longevity of a dairy cow. From Chapters 3 and 4 it was concluded that especially in an upgrading population estimates of genetic parameters should be based on the most recent data possible, and that estimation of these parameters should be repeated regularly.

In Chapter 5 the value of a relatively new method in animal breeding was investigated: survival analysis. Survival analysis differs in two aspects from traditional methods of analysis: 1. it correctly utilizes information from censored records, i.e., records of cows that are still alive at the moment of data collection; and 2. effects can be modelled in a time-dependent way, yielding a more realistic model. Breeding values of sires for longevity were estimated in three different ways: as the average realized longevity of the sire's daughters, with a best linear unbiased prediction, and with survival analysis. This was done using data from small and from large farms to identify a possible genotype by

environment interaction. The phenotypic average of the sire's daughters had weak rank correlations with the other two methods of breeding value prediction (ranging from -0.32 to 0.46). The correlation between the best linear unbiased prediction and the survival analysis prediction was strong (-0.91 and -0.94 on small and large farms, respectively) if only uncensored records were used in the survival analysis, and weaker (-0.71 on both small and large farms) if censored records were included as well. Correlations were negative due to the definition of the traits: in the best linear unbiased prediction the length of productive life was analysed, and in the survival analysis the risk of being culled. A long length of productive life is associated with a small risk of being culled. Thus it was concluded that best linear unbiased prediction and survival analysis mainly differ by the data that can be included in the analysis. No different rankings of sires on small or large farms were found with any of the three methods. From the survival analysis, it appeared that cows with a high percentage of Holstein-Friesian genes had a lower chance of being culled than cows with a low percentage, confirming the hypothesis in Chapters 3 and 4.

Even though censored records can be analysed as well in survival analysis, a certain number of uncensored data is needed for a reliable breeding value prediction. Young bulls will probably not have a sufficient large number of daughters that have already been culled. Thus, conformation traits might be used for an early breeding value prediction, because they have reasonably strong correlations with longevity and can be measured early in a cow's life. In practice, a breeding value prediction will contain parental information on longevity, direct information on longevity of a sire's daughters, and indirect information on conformation of a sire's daughters. In Chapter 6 survival analysis was used to investigate the importance of conformation traits for the risk of a cow to be culled. This risk was corrected for milk production. Both the phenotypes of the cows themselves and their sires' breeding values for conformation were included in a model. The cows' phenotypes explained more variation in the risk of being culled than their sires' breeding values. In general, smaller cows with a steep rump angle, shallow udder, high score for udder and for feet and legs had the lowest chance of being culled. Survival analysis was also used to predict breeding values of sires for longevity based solely on the longevity of their daughters. These breeding values were correlated with the sires' national proofs for conformation traits, to obtain approximations of genetic

correlations. The correlations were strong for nearly all conformation traits except height, rear legs set, and size. In the national proofs the conformation traits were not corrected for each other, while in the survival analysis they were.

In Chapter 7 it was argued that survival analysis should be used whenever possible to predict breeding values for longevity, even though with current computer capacities only a sire model can be used. Choosing this method implies that a lifetime trait has to be analysed. If length of productive life is analysed, a Weibull model can be assumed, which simplifies the calculations. In practice, this breeding value prediction will have to be combined with information on conformation to obtain a reliable breeding value for longevity early in a bull's life. Because most breeding programs of dairy cows pay already much attention to milk production, functional longevity will be more informative for breeding decisions than uncorrected longevity.

Samenvatting

In dit proefschrift worden verschillende aspecten van de levensduur van melkkoeien in een fokprogramma belicht. Aan de orde komen de schattingen van erfelijkheidsgraden voor verschillende levensduurkenmerken, de relaties tussen levensduur- en exterieurkenmerken, en de verschillende methoden van fokwaardeschatting voor levensduur. Met behulp van de resultaten die in dit proefschrift beschreven staan, kunnen fokkerij-organisaties gericht kiezen hoe ze een fokwaardeschatting voor levensduur zullen implementeren.

Hoofdstuk 2 geeft een overzicht van de literatuur met schattingen van genetische parameters voor levensduurkenmerken en van de relatie tussen levensduur en exterieur. Ook de resultaten van Hoofdstuk 3 en 4 zijn in dit overzicht verwerkt. Opvallend is het grote aantal verschillende kenmerken dat in de loop der jaren gebruikt is om levensduur te meten. In dit hoofdstuk wordt onderscheid gemaakt tussen kenmerken die de *werkelijke lengte* van de levensduur meten (bijvoorbeeld het aantal dagen tussen geboorte en afvoer, of tussen de eerste afkalving en afvoer) en de kenmerken die de *overleving* tot een bepaald moment meten (bijvoorbeeld het wel of niet afgevoerd zijn op 36 maanden na eerste keer afkalven, of het wel of niet beginnen aan de tweede laktatie). De eerste groep levensduurkenmerken wordt "duurkenmerken" genoemd, de tweede groep "overlevingskenmerken". Daarnaast is onderscheid gemaakt tussen levensduurkenmerken die gecorrigeerd zijn voor melkproductie en kenmerken die dat niet zijn. Gecorrigeerde kenmerken zijn een maat voor de onvrijwillige afvoer van melkkoeien en worden hier functionele levensduurkenmerken genoemd.

De erfelijkheidsgraden van levensduurkenmerken zijn over het algemeen laag (maximaal 0,10). De duurkenmerken hebben een wat hogere erfelijkheidsgraad dan de overlevingskenmerken, en de ongecorrigeerde levensduurkenmerken een wat hogere erfelijkheidsgraad dan de functionele kenmerken.

Uit Hoofdstuk 3 blijkt tevens dat de invoering van de superheffing en het op grote schaal inkruisen met Holstein Friesian stieren ("holsteinisatie") grote invloed hebben gehad op de levensduur van de Nederlandse melkkoeien. Niet alleen is hierdoor de gerealiseerde levensduur in de jaren tachtig tijdelijk gedaald, ook de erfelijkheidsgraad blijkt in deze periode verlaagd te zijn. Uit Hoofdstuk 4 blijkt dat de holsteinisatie ook invloed heeft op de relatie tussen levensduur en exterieur. Was het bij gegevens van vóór of na de holsteinisatie zo dat de

correlaties sterker waren tussen functionele levensduurkenmerken en exterieurkenmerken dan tussen ongecorrigeerde levensduurkenmerken en exterieurkenmerken, tijdens de Holsteinisatie waren beide correlaties ongeveer gelijk. Hieruit blijkt dat correctie voor melkproductie weinig zinvol is voor gegevens uit die periode; kennelijk was de vrijwillige afvoer op een ander kenmerk gebaseerd: type. De correlatie tussen levensduur en type is zwak in gegevens vóór en na de Holsteinisatie, maar bijzonder sterk in de periode tijdens de Holsteinisatie. Ook uit de literatuur (Hoofdstuk 2) wordt duidelijk dat de genetische parameters van levensduurkenmerken afhangen van het fokdoel van de melkveehouders. Zeker in een populatie die aan veranderingen onderhevig is, is het raadzaam genetische parameters te schatten op basis van zo recent mogelijke gegevens en deze schattingen regelmatig te herhalen, om er zeker van te zijn dat de parameters zo goed mogelijk aansluiten bij de huidige populatie.

In Hoofdstuk 5 wordt een nieuwe methode om levensduurkenmerken te analyseren geïntroduceerd: de survival analyse. Deze methode verschilt op twee punten wezenlijk van de methoden die tot nu toe gebruikt werden: 1. gegevens van koeien die nog niet afgevoerd zijn (dus waarvan de gerealiseerde levensduur nog niet bekend is) kunnen in de analyse worden gebruikt, en 2. het is mogelijk om effecten tijdsafhankelijk in het model op te nemen. Zo wordt bijvoorbeeld niet de melkproductie in de eerste of laatste laktatie opgenomen, maar verandert de productie in elke laktatie. Drie verschillende methoden om fokwaarden voor levensduur voor stieren te schatten werden met elkaar vergeleken op basis van de onderlinge (rang)correlaties: de gemiddelde gerealiseerde levensduur (fenotypisch) van de dochters van een stier, de BLUP fokwaarde van een stier en de fokwaarde uit de survival analyse. Het bleek dat het dochtergemiddelde weinig tot niets te maken had met de genetische waarde van een stier voor levensduur. Het verschil tussen fokwaarden verkregen met BLUP en survival analyse kwam voornamelijk voort uit de extra gegevens (namelijk die van de koeien die nog niet afgevoerd zijn) die konden worden geanalyseerd. Tevens werd gekeken of de rangschikking van stieren op grote en kleine bedrijven verschillend was, bijvoorbeeld door een interactie tussen genotype en milieu. Dit bleek niet zo te zijn.

Met survival analyse is het mogelijk gegevens van koeien die nog niet zijn afgevoerd mee te nemen in de analyse. Daardoor krijgen de jongere stieren een zuiverder fokwaarde dan met de tot nu toe gebruikelijke methoden. Echter, er

moet een zeker percentage (uit de literatuur: 30 tot 40%) van de dochters van een stier afgevoerd zijn alvorens een betrouwbare fokwaardeschatting verkregen wordt. Een oplossing zou kunnen zijn om gebruik te maken van een gecombineerde index met informatie over exterieur en levensduur. Exterieur wordt dan gebruikt om vroeg in het leven van een stier een voorspelling van de fokwaarde voor levensduur te doen. Naarmate meer bekend wordt over de werkelijk gerealiseerde levensduur van de dochters van een stier wordt deze directe informatie belangrijker in de fokwaarde voor levensduur. Vandaar dat in Hoofdstuk 6 de relatie tussen levensduur en exterieur met behulp van survival analyse onderzocht is.

Het blijkt dat de fenotypes van koeien voor bepaalde exterieurkenmerken significant verband vertonen met de kans op afvoer (en dus de levensduur) van melkkoeien: inhoud, kruisligging, bespiering, speenlengte, uierdiepte, en de bovenbalkkenmerken ontwikkeling, type, uier en benen. Voor sommige van deze kenmerken (namelijk inhoud, bespiering, speenlengte en uierdiepte) is het verband tussen de score voor het kenmerk en de kans op afvoer niet rechtlijnig. De fokwaarde van stieren voor exterieurkenmerken was minder van invloed op de kans op afvoer van hun dochters. Inhoud, kruisligging, achteruierhoogte, ophangband en de bovenbalkkenmerken uier en benen waren significant. Uit deze analyse is niet te achterhalen of een veehouder de fokwaarde van de vader van een koe meeneemt in zijn afvoerbeslissing, of dat het hier gaat om een indirect effect middels het fenotype van de koe. De correlaties tussen fokwaarden van stieren voor levensduur, geschat met behulp van survival analyse zonder exterieurkenmerken in het model, en officiële fokwaarden voor exterieur varieerden van -0,57 tot 0,45. Deze correlaties zijn een goede benadering van de genetische correlaties. De correlaties waren het sterkst (kleiner dan -0,40 of groter dan 0,40) voor inhoud, vooruieraanhechting, speenplaatsing, speenlengte, uierdiepte, ophangband en de bovenbalkkenmerken uier en benen.

De belangrijkste conclusies van dit proefschrift zijn dat de levensduur van Nederlandse melkkoeien sterk is beïnvloed door het invoeren van de superheffing en het inkruisen met Holstein Friesian stieren. De erfelijkheidsgraad van levensduurkenmerken is laag. Exterieurkenmerken, met name de uier- en beenkenmerken, hebben een redelijk sterke correlatie met levensduur en kunnen dus gebruikt worden als voorspeller van levensduur. Een fokwaarde voor

levensduur in de praktijk moet gebaseerd zijn op directe informatie van de levensduur van dochters van een stier, geanalyseerd met behulp van de survival analyse en gecorrigeerd voor productie, en indirecte informatie van het exterieur van dochters van een stier.

Curriculum Vitae

Ant Regnera Vollema werd op 9 september 1970 geboren te Weidum (Friesland). Na het met succes doorlopen van het Stedelijk Gymnasium te Leeuwarden, begon zij in 1988 met de studie Zoötechniek aan de Landbouwniversiteit te Wageningen. In januari 1994 sloot zij die af met afstudeervakken in de Veefokkerij en Agrarische Bedrijfseconomie. Vanaf 1 februari 1994 werkte zij als Assistent In Opleiding bij de vakgroep Veefokkerij (thans leerstoelgroep Fokkerij en Genetica) aan de mogelijkheden en betekenis van selectie op levensduur in fokprogramma's voor rundvee. Het thans voor u liggende proefschrift is hiervan het resultaat. Vanaf april 1998 werkt zij bij het Nederlands Rundvee Syndicaat aan de praktische invulling van een fokwaarde voor levensduur.

Tige tank!

Ab, voor de dagelijkse begeleiding en het klaarstaan wanneer dat nodig was. Pim en Johan, als vaste leden van de begelcie. Julius, Hans en Gerben, als parttime leden van de begelcie. Het NRS, voor de mede-financiering en het leveren van gegevens, maar zeker ook voor het bieden van een toevluchtsoord in mindere tijden. Arnoud, Wim en anderen: bedankt hiervoor. Marco, sinds jaar en dag kamergenoot: voor eerste hulp indien noodzakelijk. Gerard, voor de niet aflatende pogingen om van de HP een soepel draaiend geheel te maken. Alex, voor het oplossen van alle PC-strubbelingen. Egbert, Erwin, Jaco, Jiang, Joost, Liesbeth, and Piter for the nice discussions on thursday morning. Ada en Maria, niet alleen voor de reizen maar ook voor al het andere wat jullie geregeld hebben. Tette, voor opbouwend kommentaar op de Introduction en General Discussion. Alle andere (ex)collega's. Joe Hillers, for valuable comments on my first paper which gave me the courage to submit it. Vincent Ducrocq, for teaching me how to use survival analysis and more specifically, the Survival Kit. For immediate answering of numerous questions and for close support over a long distance. Arjan, voor je nimmer aflatende inzet en immer belangstellende commentaren. Just Jensen, Per Madsen and Inge Korsgaard, for enabling us to use Danish data on diseases and for supporting Arjan in Foulum. Birgitte en Carolien, voor kletsen, klagen en nog veel meer. Heit en mem, foar jim' belangstelling en stipe, en fansels ek foar alle geweldige wykeinen. Rixt, Nynke, Bram, Marcel en fjirdere famylje. Op it stuit is it bêst mei de kompjoeter! Johan, als laatste genoemd maar nummer één voor nu en altijd.

