

An indirect approach for the estimation of genetic correlations between longevity and other traits

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Abstract

To include functional longevity in selection schemes, the knowledge of the genetic correlations between longevity and other traits in the selection objective is required. In France, as in several other countries, functional longevity is nowadays evaluated using survival analysis models whereas other traits are evaluated using classical linear models. Then, it seems difficult to estimate the genetic relationship between these two types of traits directly from the data. We tried to circumvent this difficulty by computing genetic correlations from the sires' estimated breeding values, using the Multiple Trait Across Country Evaluation (MACE) framework.

Here we present an example of the application of such an approach for the analysis of the relationship between functional longevity and type traits. This study throws light on the danger of this procedure when some assumptions are not checked beforehand. In particular, the existence of non zero residual variances or a choice of bulls with unreliable evaluations may lead to biased or fluctuating results.

1. Introduction

The ability for a cow to delay involuntary culling (i.e., related to her so-called functional longevity) is an economically important trait. Its introduction in selection objectives necessitates the knowledge of its genetic correlation with other traits that are classically evaluated in dairy cattle. In particular, the focus should be placed on the relationship with potential early predictors: Functional longevity is a low heritability trait and, to be reasonably accurate, genetic evaluations of bulls require a incompressible delay until a certain number of daughters are culled. Such a delay is often incompatible with the timing of selection decisions of bulls after progeny test.

In this context, type traits have been repeatedly presented as possible predictors. They are often at the origin of culling decisions, either directly (e.g., when milking becomes difficult because of incorrect teat placement) or indirectly (e.g., a deep udder leads to a higher susceptibility to mastitis). Furthermore, these traits are scored early in life, most often during the first lactation and they have moderate to high heritabilities, which makes selection more efficient.

Some authors (such as Dekkers et al., 1994, or Boldman et al., 1992) tried to predict functional longevity from type scores or type evaluations or to combine this indirect information with direct information on longevity (Weigel, 1996, Jairath et al., 1998). But in all cases, it is necessary to know the genetic correlations between type and functional longevity

In France, functional longevity of dairy bulls is evaluated using a survival model (Ducrocq and Sölkner 1998) whereas breeding values for type traits (as for the other traits) are computed using a classical linear mixed model. Then it is not possible to properly define a joint multivariate distribution of residuals. This prevents the use of REML methodology to estimate genetic parameters directly from the data.

In the literature, there is a well-known situation when genetic correlations are not estimated from performances: in the case of the international (MACE) evaluations run by Interbull, genetic correlations and breeding values are directly estimated from national genetic evaluations (Shaeffer 1994). It is this approach that we have tried to apply to study the relationship between longevity and type traits.

2. Method

The Multiple trait Across Country Evaluation (MACE) procedure was developed in order to evaluate dairy bulls used in several countries. Shaeffer (1994) proposed a multiple trait sire model which considers milk yield estimated breeding values (EBVs) of sires in different countries as different traits. The basic records should be as close as possible to the additive genetic ability of the sire. In particular, they should be made independent from the reliability of the evaluations and from the relationship between sires. This is done using the technique known as deregression (Banos, 1990,

Sigurdsson and Banos, 1995). Genetic correlations between countries are calculated applying REML to these “deregressed” EBVs (Sigurdsson et al., 1996).

The basic model is the following:

$$\mathbf{y}_i = \mu_i \mathbf{1} + \mathbf{Z}_i \mathbf{Q} \mathbf{g}_i + \mathbf{Z}_i \mathbf{s}_i + \mathbf{e}_i \quad (1)$$

where: \mathbf{y}_i is the vector of deregressed breeding values for trait i ; μ_i is the mean of trait i ; \mathbf{Q} is the matrix relating sires to groups of unknown parents; \mathbf{Z}_i is the incidence matrix relating deregressed proofs to sires; \mathbf{g}_i is the vector of effects of unknown parents groups for trait i ; \mathbf{s}_i is the vector of transmitting abilities for trait i as deviations from $\mu_i \mathbf{1} + \mathbf{Q} \mathbf{g}_i$; \mathbf{e}_i is the vector of random residuals. The assumptions about the variance-covariance structure are:

$\text{var}(\mathbf{e}_i) = \mathbf{R}_i \sigma_{ei}^2$, $\text{cov}(\mathbf{e}_i, \mathbf{e}_j) = \mathbf{0}$, $\text{var}(\mathbf{s}) = \mathbf{A} \otimes \mathbf{G}$ with $\mathbf{G} = \{r_{Gij}\}$, where r_{Gij} is the sire (co)variance between traits i and j , \mathbf{A} is the relationship matrix between all males (sires and maternal grand-sires), σ_{ei}^2 is the residual variance for trait i and \mathbf{R}_i is a diagonal matrix whose diagonal elements are equal to the inverse of the number of daughters included in the calculation of the deregressed proofs.

There is nothing in the method that restrict it to across country evaluation. However, its application to the estimation of the genetic correlation between functional longevity and type traits faces three obstacles, that we would like to tackle:

- The first one is related to the one of the main features of MACE, i.e., the absence of residual correlations between traits. In the international evaluation framework, EBVs of a given sire in different countries are estimated using distinct samples of daughters. Their performances are not influenced by the same unidentified environmental effects. In the case of the within country EBVs, this property is not verified: records on different traits from the same females may have been used to evaluate their sires for these traits. What is the impact on the correlations of the incorrect assumption of residual correlations?
- The second difficulty is the use of type traits EBVs obtained from a multiple trait analysis. In an international evaluation, national EBVs are computed independently in different countries. In the French evaluation, each type trait EBV is enriched by information from correlated traits. If this particularity is ignored during deregression, what is its influence on the estimates of genetic correlations with longevity in the MACE context?
- Finally, we do not know the potential impact of the use of low reliability deregressed proofs on the

estimation of genetic correlations. In other words, what should be the minimum number of daughters that a sire should have for his proof to be included in the estimation of genetic parameters? This question is not so critical for production traits evaluation, for which progeny tests schemes ensure accurate evaluations. It is a more troublesome problem, when one analyses low heritability traits resulting in low reliability EBVs.

To answer these questions, we first performed different test runs on a moderate size data set of the Normande breed. Then, the methodology was applied on complete data files from the Normande and Holstein breed.

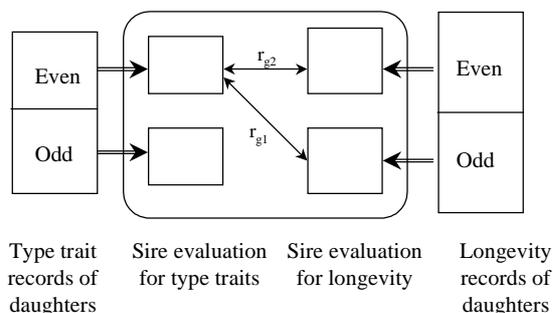
The required programs for the deregression and for estimation of genetic correlations were those used for the Interbull international evaluation on production traits (see acknowledgements)

3. A test for the Normande breed

3.1. Initial scheme

To answer our first query, we needed genetic evaluations of sires for functional longevity and type traits obtained from daughters raised in distinct environments, in order to ensure the independence of residuals for the different traits. Records of cows used for the type traits evaluation were distributed into two groups. The same partition was applied to the records used for the longevity evaluation. The partition rule had to be as independent as possible from the performances and had to clearly define distinct environments. The rule that we chose was based on the herd identification number: a first group included all cows in herds with an even identification number. Cows in herds with an odd number were in the second group. This partition is illustrated in figure 1.

Figure 1: Creation of two independent data sets for each evaluation.



Then, four independent genetic evaluations were performed: two for type traits, two for functional longevity, respectively on the “even” data set and

on the "odd" data set. If there exists a residual correlation between type traits and longevity, and if the method is very sensitive to the postulation of zero residual correlation, the within data set estimates of genetic correlations r_{g2} will be modified, compared to the between data set estimation r_{g1} for which the MACE assumption of independent environment is a priori correct.

3.2. Type traits evaluations

The data: we used records of all cows scored between October 1995 and December 1997 in contemporary groups (herd-round-classifier combinations) of at least 5 animals. This resulted in 68342 recorded animals in 7787 contemporary groups. After partition, the "even" (E) data set included 33650 records in 3902 contemporary groups and the "odd" (O) data set had 34692 records in 3885 contemporary groups.

The model: wires' EBVs were obtained from the multiple trait animal model currently used for the national evaluation of 23 type traits:

$$\mathbf{y}_i = \mathbf{X}\mathbf{b}_i + \mathbf{Z}\mathbf{a}_i + \mathbf{e}_i$$

where \mathbf{y}_i is the vector of observations for trait i (scores from 1 to 9, from 1 to 5 for milking speed, true measure in cm for size traits); \mathbf{b}_i is the vector of fixed herd-round-classifier, age at calving and stage of lactation effects; \mathbf{a}_i is the vector of additive genetic effects for trait i ; \mathbf{X} and \mathbf{Z} are incidence matrices; and $E(\mathbf{a})=\mathbf{0}$, $E(\mathbf{e})=\mathbf{0}$.

$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} \otimes \mathbf{R} \end{bmatrix}$, where \mathbf{A} is the relationship matrix. $\mathbf{G} = \{\sigma_{aij}^2\}$ and $\mathbf{R} = \{\sigma_{eij}^2\}$ are the genetic and residual (co)variance matrices between traits. In order to measure the impact of EBVs obtained from a multiple trait evaluation on the correlations when this is not accounted for in the deregression step of the MACE approach, two evaluations were performed, for each ("even" and "odd") data set: a multivariate one and a univariate one. In total, 1789 bulls were evaluated from the "even" data set and 1788 from the "odd" one.

3.3. Functional longevity evaluations

The data: we used the observations from daughters of AI sires milk recorded between December 1st 1984 and May 1st 1997. This represented 990100 cows, or 496719 in the "even" data set and 493381 in the "odd" data set.

The model: again, the same Weibull mixed model as for the national evaluation was used (Ducrocq and Sölkner,1998). It states that the hazard rate $h(t)$ of a cow, t days after her first

calving, i.e., her limiting probability of being culled at t given she was alive just prior to t , is:

$$h(t) = h_0(t) \exp\{\mathbf{x}'(t)\boldsymbol{\beta} + \mathbf{z}'(t)\boldsymbol{\delta} + s_u + 0.5s_v\}$$

where $h_0(t) = \lambda\rho(\lambda t)^{\rho-1}$ is a baseline Weibull hazard function (with $\rho=2$) which describes the ageing of the population. The exponential term includes all fixed and random effects that are supposed to increase or decrease the baseline hazard. These consist of:

- environmental effects $\mathbf{x}'(t)$, some of them being time-dependent;
- time-dependent effects $\mathbf{z}'(t)$ of production traits (milk yield, fat and protein content, expressed as deviation from the herd-year mean) in order to approximate functional longevity, by adjusting the evaluation for the main source of voluntary culling, which is low production;
- the additive genetic contributions s_u and $0.5s_v$ of the sire and of the maternal grand-sire of the cow

The assumed sire variance is 0.039, which corresponds to an approximate heritability of 0.161 on the observed scale. In total, 4153 sires were evaluated both from the "even" and from the "odd" data sets.

3.4. Estimation of genetic correlations

From the complete file of genetic evaluations of all bulls, three subsets were created:

- File A includes all sires evaluated for type traits with at least 10 daughters in the "even" data set and in the "odd" data set, as well as, for the longevity evaluation, at least 10 uncensored daughters in the "even" and in the "odd" data sets. Only univariate type proofs are considered here. In total, file A is made of 158 evaluated sires, with 66 extra ancestors and 5 groups of unknown parents.
- File B is as file A, replacing univariate by multivariate type evaluations.
- For file C, the minimum requirement is decreased to 5 daughters in each data set ("even" and "odd", "longevity" and "type"). Again, only uncensored daughters are considered for the longevity evaluation. As for file A, only univariate type proof are take into account. The number of bulls is increased to 302 with 76 ancestors and 5 groups of unknown parents.

4. Results of the test

Systematic bivariate analyses were performed to compute correlations between all combinations of traits. All estimates of genetic correlations between "trait 1 in the 'even' data set" and "trait 2 in the

‘odd’ data set” (E-O) as well as between “trait 1 in the ‘odd’ data set” and “trait 2 in the ‘even’ data set” (O-E) should not be influenced by any nonzero residual correlations, and their variation should only reflect sampling variance. In contrast, within data set estimates (denoted as “E-E” and “O-O”) obtained from evaluations originating from the same environment and partly based on the same animals may be biased.

4.1. Influence of nonzero residual correlations

This was studied in two situations:

- Correlations between type traits: the objective here was to compare the results derived from the MACE methodology with the estimates obtained by REML and used as input parameter in the multiple trait evaluation. Table 1 presents some of the within- and across- data sets estimates of genetic correlations that were computed from file A. The “MACE” genetic correlations from the across data set analysis are consistent, and reasonably close to the REML results, although some (sampling?) variation exists.

The within data set estimates are systematically larger than the REML estimates. As expected, these estimates are biased upwards (in absolute value) when residual correlations are moderately high (0.2 to .5 here).

- Correlations between longevity and type traits: these are reported in table 2, when estimated from file A. The across data sets estimates on one hand (E-O and O-E), and the within data set estimates on the other hand (E-E and O-E) are relatively close. If nonzero residual correlations between longevity and type traits exist, they seem to be not strong enough to bias substantially the estimation of genetic correlations, as in the between type traits situation.

From the across data set estimation, udder traits as well as milking speed are the traits most strongly related to functional longevity ($\rho = -0.17$ to -0.54), especially udder depth (UD, defined as udder-hocks distance) and overall udder score (OUS, a global score given by the classifier). The negative sign corresponds to a favourable relationship: the more shallow the udder, the lower the culling risk. It should also be remembered that longevity is adjusted for milk production. Udder depth being negatively correlated with milk yield, the effect of udder depth on longevity (i.e., including voluntary culling for low milk production) would be underestimated without such a correction.

Correlations with feet and legs traits are also favourable (around -0.2). Sickled hocks and a bad feet and legs score given by the classifier mean higher culling risk. For capacity traits, the results are more variable with a favourable correlation of

production-adjusted longevity with height at sacrum (HS) and a slightly unfavourable relationship with chest depth (CD) and chest width (CW). Muscularity traits are unfavourably correlated with longevity. There is no way to know whether this is due to a real antagonism between functional longevity and muscularity or to a tendency to first cull more profitable cows in terms of carcass revenue.

4.2. Influence of the type of analysis

This was done by comparing across data sets (E-O and O-E) estimates of genetic correlations computed from files A and B, i.e. from deregressed univariate and multivariate type proofs. The results are presented in table 3. For all traits, the impact of the number of traits considered together in the type traits evaluation appears limited. This conclusion may not be valid in all cases and needs to be verified in other situations but at least here, the type of analysis may be ignored, when genetic correlations are computed from deregressed proofs.

4.3. Influence of restrictions on the number of daughters

File A included a rather limited number of males evaluated with a reasonably large number of daughters. To study the impact of the proofs reliabilities on the estimation of genetic correlations in the MACE context, file C was created with a less restrictive minimum number of daughters. Table 3 presents the across data sets estimates of genetic correlations obtained from these two files of EBVs.

While estimates “E-O” and “O-E” from file A are relatively close, the same estimates for file C are farther apart. The inclusion of EBVs with very low reliabilities clearly altered the accuracy of the estimation of the genetic correlations. It seems necessary to restrict the procedure to the more reliable EBVs. At least here, given the limited number of bulls in the analysis, it appears difficult to increase this lower limit to more than 10 daughters per sire.

5. Application to the complete Normande and Holstein data sets

After these tests on the Normande breed, it seemed fairly safe to directly estimate the genetic correlations between longevity and type from the national multitrait type evaluations, using EBVs from sires with at least 10 (uncensored) daughters and assuming the absence of residual correlations.

Table 1 : Genetic correlations between some type traits in the Normande breed (File A)

Traits	Across data set (E-O and O-E) “MACE” framework	Within data set (E-E and O-O) “MACE” framework	True REML results genetic correlation (residual correlation)
FUA-UD	0.54 / 0.51	0.63 / 0.58	0.47 (0.21)
UB-TDR	0.51 / 0.44	0.60 / 0.59	0.53 (0.20)
RLS-FLS	0.83 / 0.86	0.89 / 0.90	0.84 (0.36)
HS-CW	0.37 / 0.50	0.52 / 0.55	0.33 (0.32)
WP-RL	0.42 / 0.44	0.55 / 0.56	0.44 (0.41)
MB-MT	0.58 / 0.56	0.66 / 0.70	0.66 (0.50)

FUA : Fore udder attachment ; UD : udder depth; UB : Udder balance ; TDR : Teat direction rear ; RLS : Rear leg set ; FLS : Feet and legs score ; HS* : height at sacrum ; CW* : Chest width ; WP* : width at pins ; RL* : Rump length ; MB: Muscularity on back; MT : Muscularity at thighs.

* in cm (scored from 1 to 9 otherwise).

Table 2 : Estimated genetic correlations between functional longevity and various type traits in the Normande breed: (File A) using the “MACE” framework

	Type trait	Across data sets		Within data sets	
		E-O	O-E	E-E	O-O
Udder	FUA	-0.22	-0.17	-0.28	-0.29
	RUA	-0.48	-0.44	-0.50	-0.30
	UB	-0.34	-0.34	-0.46	-0.38
	TDR	-0.39	-0.36	-0.38	-0.40
	TPF	-0.29	-0.28	-0.31	-0.29
	SL	-0.35	-0.34	-0.37	-0.31
	UD	-0.50	-0.50	-0.51	-0.45
	OUS	-0.52	-0.54	-0.55	-0.55
Feet and Legs	MS	-0.30	-0.35	-0.28	-0.31
	RLS	-0.26	-0.15	-0.25	-0.23
Capacity	FLS	-0.22	-0.22	-0.33	-0.29
	HS	-0.24	-0.22	-0.21	-0.17
	CW	0.08	0.24	0.21	0.16
	CD	0.11	0.09	0.03	0.19
	RL	-0.17	-0.03	-0.01	-0.13
	WP	-0.05	0.08	-0.03	0.04
	RA	-0.25	-0.21	-0.21	-0.29
	OFS	-0.15	-0.11	-0.11	-0.04
Muscularity	MB	0.19	0.24	0.18	0.17
	ML	0.10	0.10	0.11	0.07
	MR	0.09	0.19	0.17	0.09
	MT	0.04	0.05	0.04	-0.05
	OMS	0.17	0.18	0.20	0.07

FUA : Fore udder attachment ; RUA: Rear udder attachment; UB : Udder balance ; TDR : Teat direction rear ; TPF: Teat placement front; SL: suspensory ligament; UD : udder depth = udder-hocks distance; OUS: overall udder score; MS: Milking speed; RLS : Rear leg set ; FLS : Feet and legs score ; HS* : height at sacrum ; CW* : Chest width ; CD*: Chest depth; RL*: Rump length; WP* : width at pins ; RA: Rump angle; OFS: Overall frame score; MB: Muscularity on back; ML: Muscularity at loin; MR: Muscularity at rump; MT: Muscularity at thighs; OMS: Overall muscularity score

* in cm (scored from 1 to 9 otherwise, 1 to 5 for milking speed).

Table 3 : Estimated genetic correlations between functional longevity and various type traits in the Normande breed: using the across data sets (E-O and O-E) “MACE” framework for file A (univariate type evaluation ; at least 10 daughters per evaluation), file B (multivariate; at least 10 daughters) and file C (univariate; at least 5 daughters)

	Type trait	File <u>A</u>	File <u>B</u>	File <u>C</u>
Udder	FUA	-0.22 / -0.17	-0.24 / -0.20	-0.26 / -0.18
	RUA	-0.48 / -0.44	-0.52 / -0.47	-0.51 / -0.40
	UB	-0.34 / -0.34	-0.38 / -0.39	-0.42 / -0.35
	TDR	-0.39 / -0.36	-0.40 / -0.37	-0.34 / -0.29
	TPF	-0.29 / -0.28	-0.30 / -0.29	-0.26 / -0.18
	SL	-0.35 / -0.34	-0.36 / -0.35	-0.33 / -0.28
	UD	-0.50 / -0.50	-0.51 / -0.50	-0.51 / -0.47
	OUS	-0.52 / -0.54	-0.52 / -0.54	-0.49 / -0.47
	MS	-0.30 / -0.35	-0.31 / -0.37	-0.30 / -0.32
Feet and legs	RLS	-0.26 / -0.15	-0.23 / -0.17	-0.16 / -0.12
	FLS	-0.22 / -0.22	-0.25 / -0.20	-0.21 / -0.25
Capacity	HS	-0.24 / -0.22	-0.24 / -0.23	-0.32 / -0.21
	CW	0.08 / 0.24	0.10 / 0.24	0.08 / 0.25
	CD	0.11 / 0.09	0.10 / 0.06	0.05 / 0.07
	RL	-0.17 / -0.03	-0.18 / -0.07	-0.25 / -0.06
	WP	-0.05 / 0.08	-0.04 / 0.06	-0.08 / -0.05
	RA	-0.25 / -0.21	-0.27 / -0.24	-0.22 / -0.14
	OFS	-0.15 / -0.11	-0.15 / -0.11	-0.23 / -0.15
Muscularity	MB	0.19 / 0.24	0.19 / 0.23	0.18 / 0.20
	ML	0.10 / 0.10	0.12 / 0.11	0.06 / 0.13
	MT	0.09 / 0.19	0.11 / 0.18	0.08 / 0.17
	MS	0.04 / 0.05	0.04 / 0.08	0.07 / 0.05
	OMS	0.17 / 0.18	0.17 / 0.18	0.19 / 0.17

Trait definition: as in table 2

Three files of official proofs were created, for the Normande and the Holstein breeds:

- File NO comprised 359 evaluated males, 106 ancestors and 5 groups of unknown parents;
- File NO88 contained 283 evaluated males born after January 1, 1988 as well as 124 ancestors and 5 groups of unknown parents. This restriction was included to avoid the inclusion in the analysis of old sires with a lot of uncensored daughters (so with a very reliable evaluation on longevity) but very few daughters scored according to the most recent recording scheme for type;
- File HF88 included for most traits 2648 evaluated sires also born after January 1, 1988, 377 ancestors and 13 groups of unknown parents. Since the type recording system had changed twice during the studied period, scoring of some type traits were more recently introduced. For rear udder attachment and heel depth, 2586 sires with EBVs, 375 ancestors and 13 groups of unknown parents were kept. For fore udder attachment and temperament, only 889 sires had reliable EBVs and

246 male ancestors and 10 groups of unknown parents were also included.

5.1. Comparison of results obtained with the different data sets in the Normande breed

Estimates of genetic correlations obtained from file A (table 3) and file NO (table 4) are fairly similar for capacity and muscularity traits. The relationship with longevity is more favourable in the complete data set for the two feet and legs traits and for some udder traits, in particular for fore udder attachment and udder balance. When a restriction on year of birth of sires is added (file NO88, table 4), the correlation estimates with udder traits are varying much more: the estimates are large in absolute value for fore udder attachment and suspensory ligament and even very large (much larger than with files A or NO) for udder balance, udder depth and overall udder score. For other traits, the correlations are either stable or closer to 0

Table 4 : Estimated genetic correlations between functional longevity and various type traits in the Normande and the Holstein breeds using the complete data sets

	Type traits	File <u>NO</u>	File <u>NO88</u>	File <u>HF88</u>
Udder	FUA	-0.39	-0.48	-0.06
	RUA	-0.32	-0.26	-0.24
	UB	-0.53	-0.72	-0.27
	TDR	-0.31	-0.29	-0.12
	TPF	-0.21	-0.15	-0.14
	SL/UC	-0.41	-0.47	-0.20
	UD	-0.53	-0.61	-0.43
	OUS	-0.55	-0.63	
	TL			-0.13
	DTS			-0.17
	MS	-0.34	-0.33	-0.17
Feet and Legs	RL	-0.17	-0.05	-0.01
	FLS	-0.31	-0.25	
	HD			-0.01
Format	HS	-0.17	-0.13	-0.05
	CW	0.17	0.17	
	CD	0.07	0.05	0.03
	RL	-0.05	-0.03	-0.03
	DP	-0.02	0.00	
	RW			0.01
	RA	-0.20	-0.15	-0.07
	OFS	-0.11	-0.11	
Muscularity	MB	0.16	0.06	
	ML	0.08	0.00	
	MR	0.18	0.14	
	MT	0.11	0.10	
	OMS	0.14	0.06	
Temperament	TE			-0.12

Trait definition: as in table 2 + UC: Udder cleft; TL: Teat length; DTS: Distance between teats, side; HD: Heel depth; RW: Rump width; TE: Temperament

5.2. Comparison of the Normande and Holstein breeds

Table 4 also presents the estimates of genetic correlations obtained using exactly the same restrictions for the Normande and the Holstein breeds. Only udder traits seem to be genetically related to functional longevity in the Holstein breed. By far the highest correlation estimate is with udder depth. Other udder traits describing udder support (udder balance, rear udder attachment, udder cleft) have smaller but non negligible favourable correlations. This is in contrast with the Normande breed, where most of these other traits were as important as udder depth. Feet and legs and capacity (format) traits were not related at all with longevity (at least after adjustment for production) in the Holstein breed. This absence of other type traits related to longevity is less clear in the Normande breed, where feet and legs score for example has a moderate favourable correlation. These relatively different results for the two breeds reflect distinct selection policies and emphases on type traits, but

in both breeds, the main focus is undoubtedly on udder traits

6. Discussion and conclusion

6.1. Methodology

The estimation of genetic correlations in the “MACE” framework is an interesting approach when it is not possible to directly compute these correlations from the raw data. However, it should be used in practice with great care. We have illustrated 2 points that one should be aware of when analysing MACE results:

- The assumption of zero residual correlations is a strong one. When these residual correlations are moderately high, as between type traits, estimates may be substantially biased. If only genetic correlations are desired, the approach can be used by forcing the absence of residual correlations through an appropriate partition of the data set. In the particular case of the relationship between type traits and functional longevity, we did not find important differences between situations where the evaluations were obtained from the same dataset or

in distinct environments. This suggests that, if nonzero residual correlations exist, they are probably rather small. However, it is advisable to check this assumption each time this “MACE” approach is used.

- The correlation estimates obtained are rather imprecise: the choice of the deregressed sire proofs included in the approximate REML estimation is critical. Clearly, inaccurate proofs should be excluded. This is important for a low heritability trait such as longevity. A restriction on the minimum number of daughters seems unavoidable. But new problems arise, if improper restrictions are imposed. Some of them are specific to longevity traits: if some type traits have been recently introduced, the informative bulls on both type and longevity traits may be limited. Also, if all bulls are included with a relatively high minimum number of uncensored observations, old (proven) bulls may have a strong (biased?) impact on the correlation estimates. More work is needed in this area.

6.2. Genetic correlations

Our estimates of genetic correlation between type traits and functional longevity clearly show the key importance of udder traits, both in the Normande and the Holstein breeds, with a supremacy of udder depth. Its impact on udder health and on workability influences functional longevity. This conclusion is consistent with the phenotypic analysis of the relationship between type and functional longevity in the Holstein breed (Larroque and Ducrocq, 1999, this workshop), where again it was found that udder depth score markedly conditions culling risk. Other studies (e.g., Vollema 1998) found similar results.

The huge difference between the correlation estimates for udder traits in the two breeds was not really expected and needs to be confirmed. The high correlations obtained in the Normande breed with most udder traits may be partly explained by the emphasis that these traits received in selection in the breed: some years ago, it was common to consider that one characteristic of the Normande breed was the large number of cows with bad udders and that a major effort in selection programs had to be made on these type traits. The lower correlations obtained in the Holstein breed may be the consequence of the opposite statement: after production, one of the major factors that greatly contributed to the popularity of the North American Holstein in Europe is udder quality.

After udder traits, feet and legs score appears to be another early predictor of functional longevity in the Normande breed (as found by others, e.g., Vollema, 1998), but not in the French Holstein population. This may be due to a less acute problem in the breed, an inadequate choice of feet

and leg traits and/or a not very efficient scoring system as the very low heritability found (0.07) would suggest.

Acknowledgements

We would like to gratefully acknowledge the help of G. Banos, who kindly supplied us with the deregression and estimation programs developed for the Interbull international evaluations.

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