Sustainable dairy cattle breeding: illusion or reality?

V. Ducrocq[*]

Introduction

The increase of milk production per lactation over the last 50 years has been tremendous. Genetic progress on production has increased at a steady pace of 50 to 100 kg a year in most breeds in developed countries. Given the nearly universal negative genetic correlation between production and functional traits - fertility, resistance to mastitis and other diseases, functional longevity - it is not surprising that the general robustness of dairy cows is decreasing concurrently (Jorjani et al, 2007). In many other cases, it is the consequence of short term profit objectives, without consideration of long term biological constraints. Functional traits are difficult to select by classical means because of their low heritability but they exhibit a large genetic variability and are therefore easy to deteriorate…

During the initial phases – say, until the eighties – farmers coped with this decrease in fitness by adapting the environment to these better cows. This is getting more and more difficult. Hence, breeding programs worldwide have been devoting much more attention to functional traits, following the path paved by Nordic countries.

Despite these efforts, the situation got somewhat worse over the last decade: the continuous increase in genetic potential for production is no longer followed by an equivalent increase in real production. Cost reduction is now a primary objective in herds of increasing size and with less manpower, in particular costs related to low fitness or low fertility, leading to involuntary culling and extra costs (vet and AI). In the US (Rogers, 2005) as well as in European countries, some farmers are turning to crossbreeding or even to other breeds to cope with decreased fitness.

In this paper, I list the reasons why there is hope, even in the Holstein breed, not only to stop the decline of functional traits, but even to reverse the direction of their genetic trend. Animal breeders resort to classical tools to generate sustainable genetic trends: they can broaden the panel of functional traits considered, improve genetic evaluations or make better use of these genetic evaluations in breeding programmes. In the following paragraphs, I will briefly review the recent trends and shifts regarding these alternatives. Due to lack of space, many relevant references will be missing but they do exist…

Improving sustainability via classical approaches

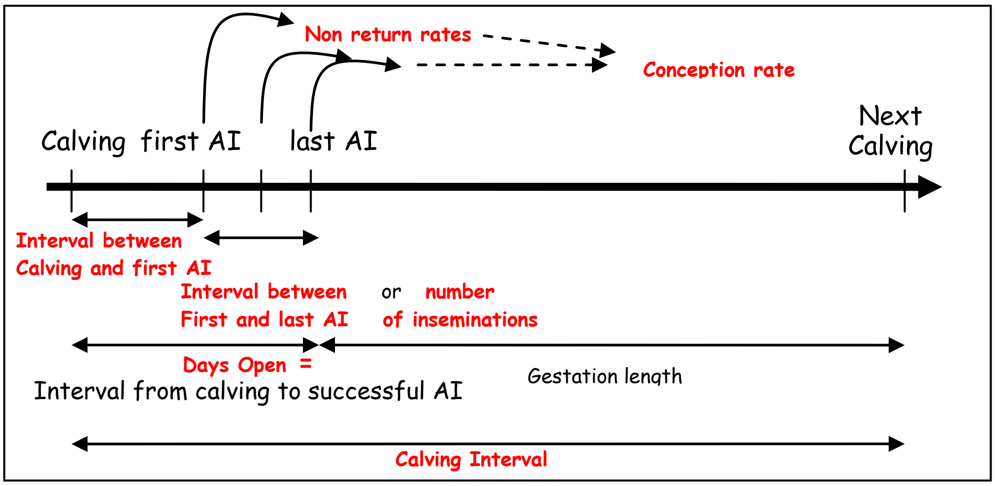
Traits considered: inventory and recent evolutions

Fertility: A decade ago, female fertility traits were rarely considered in breeding programmes or were most often limited to simplistic ones directly extractable from milk recording data, such as calving intervals or days open. Fertility is a composite trait which can be decomposed in various basic traits (figure 1). Furthermore, most of these traits cannot be considered as genetically identical for heifers and adult cows, the latter being influenced by concurrent production, in contrast with the former. The heterogeneity of traits for which a national genetic evaluation was implemented led to headaches for international evaluations. To bypass the difficulty to jointly evaluate very different traits, Interbull defined 4 main groups of traits (Jorjani, 2009): ability to conceive separately for heifers (T1) and adult cows (T3), ability to recycle after calving (T2), interval measures of ability to conceive (T5). A

[*] INRA, UMR1313 - Génétique Animale et Biologie Intégrative, 78352 Jouy-en-Josas, France

fifth group (T4) includes a combination of T3 and T5 for those countries that had only T5 traits. Perhaps even more than the recognition that selection on only one component of fertility was suboptimal, the determination to be represented in international lists for most - if not all- of these groups led many countries to diversify their female fertility traits (e.g., Wall et al (2003), Liu et al (2008)) over time.

Figure 1: decomposition of female fertility traits



Resistance for mastitis: With the exception of Nordic countries which have benefited for many years from an outstanding health data collection system, selection for resistance to mastitis bas been traditionally envisioned through selection on a correlated trait: somatic cells score (SCS). SCS only party explain clinical mastitis occurrence (CM). For a more complete selection for udder health, three non exclusive alternative strategies are being implemented: 1) the use of other traits as predictors of udder health, such as udder morphology traits or milking speed; 2) the utilization of test-day SCS data to derive a proxy for mastitis occurrence (de Haas et al, 2008) or 3) the implementation of systems to centralize health information collected by farmers. The latter is the option chosen in France leading to a new genetic evaluation on mastitis occurrence in June 2010. Data centralisation is done through milk recording technicians and must go through customized editing steps before being considered as reliable.

Type traits: For decades, type traits have been advocated by many farmers and semen salesmen as traits on which strong selection should be applied in order to increase cow longevity. This image has been severely altered in the recent past. Size (or height) is receiving considerable attention worldwide in most breeds, while its relationship with fitness is at best doubtful, and in some production systems, clearly unfavourable (Pryce et al, 2009). In contrast with usual belief, too large body depth was also found to be associated with lower fertility and longevity (e.g., Larroque et al, 1999). Dairy character – or its aliases: dairy form, dairyness or angularity- have been shown over and over to be extremely detrimental, and now receive a negative weight in the US TPI (Lawlor et al, 2005). Dairy character is strongly opposed to body condition score, to fertility and to mastitis resistance (Lassen et al, 2003). Hence, a serious clarification of the value of type traits should be undertaken, but certainly not left only to elite breeders, as their objectives diverge from those of most commercial dairymen. Traits such as angularity, body condition score (Pryce et al, 2001), body depth or rump angle are useful but mainly as predictors of (bad) fertility!

The choice of relevant type traits should be based on an objective assessment of their influence on other functional traits such as fertility, mastitis resistance, workability or longevity. The relationship between type traits and longevity is often obscured by the fact that the apparent effect may be simply an artefact: constant ill-advised promotion for “ideal cows” that are tall, deep and skinny has led to voluntary culling on “beauty standard“ in particular in registered herds, counterbalancing their real effect. For example, Larroque et al; (1999) found no impact of size on longevity in French commercial herds, in contrast with a positive effect in herds practicing systematic type recording.

In fact, the vast majority of studies show a beneficial impact of udder traits, and above all of udder depth, on functional longevity, on resistance to mastitis and milking speed. The general consensus is that type composites should give a predominant weight to udder traits.

For feet and leg traits, the situation is less clear: a few traits are routinely collected and evaluated nationally and internationally. But they generally have a low heritability and are more heterogeneous between countries. Indeed, their importance depends a lot on the major local production systems. Because of their disappointingly low correlation with, e.g., actual longevity, some countries have tried to exploit more relevant data sources, such as claw disorders information collected by hoof trimmers (e.g., van der Linde et al (2010)).

Calving traits: Dystocia and stillbirth are very important functional traits with potentially severe consequences on production, fertility and general health, especially at first calving. Direct and maternal effects are routinely evaluated together. In contrast with other functional traits, general trends over time are unclear. In France, no decline has been observed, so an active improvement of these traits is not really looked for. Instead, calving ease proofs are used to avoid risky matings by using sires with favourable ease of birth EBV on heifers and on daughters of unfavourable bulls for calving ease.

Longevity: Among the list of functional traits, longevity has a particular status: it can be seen as a global indicator of fitness on which selection can be applied to get more robust animals. For this purpose, the interest should focus on functional longevity (FL), that is to say, the ability to elude involuntary culling related to sterility, diseases, lameness, etc. In most breeds, the proportion of involuntary culling is increasing and in Holstein, possibilities for voluntary selection on production traits are reduced, leading to convergence of true and functional longevity. FL is a complex multi-factorial trait and requires a special statistical treatment: cows still alive have a censored measure of length of productive life (LPL) and the environmental factors influencing risk of being culled (season, parity, herd size, etc) are changing at the same time as LPL is measured. Because of its low heritability and its relatively late availability, LPL is often considered as a trait which is not sufficient by itself, despite its high economic weight (often the highest over all functional traits). It has to be complemented with early predictors. In practice, many countries do not publish direct longevity evaluation but a combination of direct and indirect predictions.

Other traits: Nordic countries are including other functional traits in genetic evaluations, in particular health traits based on a systematic disease recording system (Aamand, 2006). These include reproductive, digestive and feet and legs diseases. They are characterized by a low incidence, a low heritability but a large genetic variance.

Recent advances in genetic evaluations

Many functional traits exhibit characteristics which are in conflict with the usual hypotheses of regular linear model analyses. Examples are 0/1 traits, censored traits, zero-inflated traits (e.g., interval from first to successful AI (I1SAI)), traits with heterogeneous genetic or residual variances, etc. Considerable work has been accomplished in the recent past to adapt evaluation models and methods to these characteristics. Genetic evaluations have been implemented using threshold traits (Gianola and Foulley, 1983) for calving ease scores, censored threshold models for number of AI (Gonzalez-Recio et al, 2005), survival analysis for length of productive life (e.g., Ducrocq, 2005) or fertility data (Schneider et al, 2005), zero-inflated Poisson models for I1SAI (Rodrigues-Motta et al, 2007), mixture models for somatic cell scores (Gianola et al, 2004), or structural models to account for heterogeneous residual variances (e.g., for type traits in France). Despite generally encouraging results, these more complex approaches are not always routinely implemented in national evaluations. Several reasons can be put forward: the lack of general software available (censored threshold models), the difficulty to perform multivariate analyses or evaluations accounting for all genetic relationships (e.g., an animal model for survival analysis), convergence or estimability problems (mixture models). This is somewhat disappointing because the scope for gains is substantial: it has been shown that a threshold model accounting for heterogeneous residual variances considerably improves the predictive power of genetic evaluations on calving ease (Ducrocq, 2000; Kizilkaya and Tempelman, 2005), with a gain larger than when a linear model is replaced by a threshold model. Similarly, Caraviello et al (2004) and others showed that in presence of censoring and time-dependent environmental effects, a sire survival model leads to more accurate predictions of daughters' LPL than a classical animal model.

Total merit index

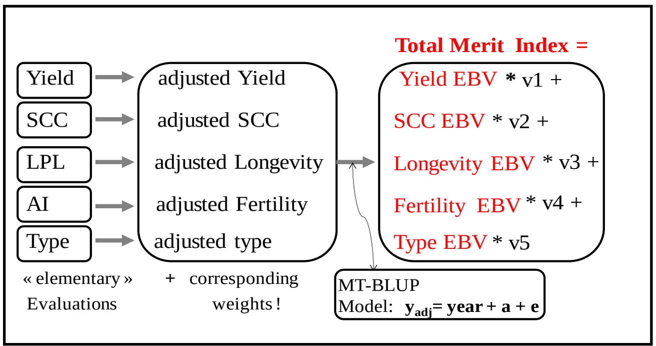
Until the late nineties, breeding goals for dairy cattle included few traits worldwide. With the noticeable exception of Nordic countries, these were mainly production and type traits, with ½ to ¾ of the total weight on production. With the urgency to stop the decline of functional traits, breeding goals were made broader and more balanced in many countries (e.g., van Raden, 2001). Nowadays, the relative weight given to production is generally between 30 and 50%. In Germany, a Total Merit Index for fitness, called RZfit, was introduced with great success in 2009 with a 90% weight on functional traits (S. Rensing, *pers. comm.*). This appears as a real achievement in the direction of more sustainable breeding goals.

Nevertheless –and with the obvious exception of RZFit - the interpretation of these relative weights requires some caution: a) as it will be shown below, the results of selection on a TMI with such weights may vary a lot depending on the approximations made to actually compute it; b), the relative weights may be attached to traits expressed in different units: phenotypic, genetic or even average EBV standard deviations, as in the US; c) functional traits are not independent: for example, productive life and fertility are genetically correlated, and the weight ascribed to productive life is quite different whether culling for sterility is affected to longevity or to fertility; d) when some traits receive a negative weight, the meaning of a relative weight assuming a sum of 100% is questionable; e) the average reliabilities of the EBV included in TMI vary a lot with the heritability of the trait. As a consequence, the corresponding EBV are more or less variable and whatever their expression mode, they may contribute less to the overall ranking of animals than their economic weight indicates. Indeed, the predominant influence of production EBV in TMI ranking is undeniable, even when there are supposed to represent less than 50% of the total. Alternative ways to express the relative emphasis given to each trait have been proposed (Cunningham and Tauebert, 2009) but there is no consensus so far. An easy criterion to assess this emphasis is to measure the effect of a given selection intensity on expected economic gains or losses for each trait. The situation where the trait is ignored could be used as reference.

EBV on functional traits are often available only on males and with a sufficient reliability obtained too late to be used efficiently when actual selection decisions are taken. Early predictors can be added to increase this reliability. This is frequently done using selection index (SI) theory. A proper application of SI to combine EBV from early predictors and functional traits supposes the computation of weights that depend on the reliability of each EBV, on the genetic and residual correlations between traits and on the fraction of progeny that are recorded on each pair of traits. In practice, this step is often approximated and the same coefficients or the same fractions of progeny are used in all situations (Weigel et al, 1998, van Raden, 2001). Given the complexity of a strict SI approach for TMI calculations, EBV of elementary traits are often combined using economic weights, without any consideration for correlations and differences in reliability. Such approximations are often ignored and may have a significant impact on selection efficiency.

In France, a general strategy was developed to circumvent these difficulties (Ducrocq et al, 2001, paper available upon request). The basic idea is to approximate a Multiple Trait BLUP animal model evaluation (MTAM). MTAM has a number of desirable features. In particular, it effectively merges all information sources with their proper weight, and therefore properly accounts for residual correlations and differences in reliabilities, in contrast with usual SI implementations. MTAM also prevents biases in genetic trends due to selection on correlated traits. A full implementation of a MTAM evaluation for all traits of interest together is clearly unfeasible: traits are described with different models, some traits may be recorded several times on the same animal; they may have heterogeneous variances or they may not be adequately analysed with linear models.

Figure 2: illustration of the two-step approach to compute a total merit index from an approximate multiple-trait BLUP animal model (Ducrocq et al, 2001)



v_i is the economic weight of the i^{th} trait.

SCC, LPL, AI= somatic cell count, length of productive life, success or failure at each AI

The proposed approximation (figure 2) is conceptually simple : for each trait, a univariate (or multivariate in the case of type traits) animal model evaluation is performed and used to compute for each cow an average record corrected for all environmental effects (including permanent environmental effects if necessary). Simultaneously, an associated weight is derived to quantify the amount of information summarized. For nonlinear traits such as longevity, approximations have been proposed (Ducrocq, 2001). These pre-corrected data are then analysed together with a BLUP MTAM approach, weighing each observation accordingly. Because of the pre-correction, a simple model with just a mean and an additive genetic effect can be used for all traits, or even better (Ducrocq et al, 2003), the overall mean can be replaced by a year of birth effect. This year effect leads to a robust estimation of genetic trends, as it corrects for potential discrepancies in genetic trends in the univariate evaluations which do not account for selection on correlated traits. Then, all ingredients for a correct calculation of TMI are available for all males as well as – and this is crucial - for all females. The optimal weights are simply the economic weights of the traits. Other essential by-products of such an evaluation are EBV optimally combining direct and indirect information from early predictors for each functional trait – e.g., longevity or fertility. The gains in reliability are substantial for young bulls and females (table 1).

Table 1: Gain in reliability (%) in longevity when other functional traits and selected typed traits are added as early predictors (Montbéliarde breed, Ducrocq et al, 2008)

Year of birth of the bull	Direct longevity	adding other functional traits	adding functional and type traits
1994	77	+1	+4
1998	66	+3	+9
2000	47	+6	+18
2001	37	+7	+20

This approach was validated by simulation (Lassen et al, 2007a,b). For a relatively broad breeding goal, the true genetic gain with this approach was about 12% larger than with the univariate approach and only 3% smaller than a true MTAM, which is unfeasible in practice.

Role of International Evaluations

Interbull is nowadays running international evaluations on most functional traits: udder health, longevity, calving, female fertility, workability and conformation (Jorjani et al, 2007). This favours international exchange of semen of top bulls for functional traits. However, emphasis is still extremely strong on type traits, despite the limitations mentioned above. Across country genetic correlations are lower for most functional traits than for production or type, because of differences in data collection system, trait definition and in genetic evaluation models. Low correlations lead to difficulties for foreign bulls to appear in top lists. Of course, all efforts for homogenizing practices and traits definition are beneficial.

Interbull EBV users in importing countries are not always familiar with the use of functional traits EBV that they do not necessarily regard as essential. Proper education of potential users on the importance of international EBV on functional traits should be a major task of Interbull. This is particularly striking in some less developed countries where semen salesmen are able to put on the market completely unsuitable genetic material. It is absurd – or even indecent – to promote in those countries semen from top Holstein bulls on a single country scale. With limiting constraints at various levels (investments, skills, climate, feedings, etc.), how can one believe that farmers will cope with pure or crossbred exotic animals with a genetic potential increasing at a rate of 80 to 100kg per year in the western world? This is the exact definition of the opposite of a sustainable business! For these countries – if imports are needed - Interbull should strongly encourage buyers to focus on

bulls with average or even lower than average EBV for production but with outstanding international EBV for functional traits. There are many of them to choose from and as they are not competitive in their own countries, their semen would be much cheaper!
The next question is on which national scale these bulls should be chosen. If there is no obvious choice – e.g., New-Zealand for countries mainly relying on pasture - a phantom scale could be preferred, as it does not give an advantage to any country by assuming that the importing country has the same correlation with all the others (Tauebert et al, 2008).

Genomic selection

Traditional selection schemes are being turned upside down with the new opportunity to obtain relatively precise genomic evaluations (GEBV) of animals at birth. There are several reasons to believe that this revolution will have a tremendous impact on functional traits:
a) GEBV for functional traits are available on young animals with reliabilities at least comparable to traditional progeny testing, without its usual inconveniences (large progeny groups required, long generation interval); b) global genetic trend will increase. Farmers have difficulties to cope with a too fast increase in genetic merit for production. As a result, there will be room for a stronger emphasis on functional traits; c) more fundamentally, females and males have at birth GEBV with the same reliability. Hence, it becomes possible to select bull dams or even dams of cows on functional traits, with an accuracy unattainable even for old cows with many daughters; d) recent work showed that some health traits have some genetic background that can be revealed using genomic information despite their low incidence (e.g., left-sided displaced abomasum, Mömke et al, 2008 or paratuberculosis, Gonda et al, 2007, among many others); e) because genomic evaluations do not necessarily require exhaustive data collection, new opportunities exist to include into breeding programs new functional traits based on finer phenotypes collected on, e.g., a reduced number of herds.

Conclusion

There is a general consensus that, whatever the angle chosen - economy, welfare, ethics or genetics - decreasing fitness of dairy cows below a point not far from the current one is no longer acceptable. Tremendous progress in classical approaches have been achieved in this direction: TMI give more and more emphasis to functional traits in breeding programs. A broader panel of functional traits is now considered. The direction of selection of some of the most popular type traits has been pertinently reversed (at least on paper, not always in minds). Genetic evaluation methods were adapted to the particular features of the main functional traits. For maximum efficiency, new ways of combining traits into TMI have been set up. International genetic evaluations on functional traits have been implemented and should be strongly advertised, especially in importing countries. Finally, genomic selection may lead to a decisive shift in genetic trend of fitness traits, in particular in opening selection to new, refined traits, with the same effectiveness on male and female pathways.

Efficient breeding for more robust cows is definitely becoming a reality!

References

Aamand, G.P. (2006) *EAAP Scientific Series* 121:275:282.
Banos, G., Brotherstone, S., Coffey, M. P. (2004) *J Dairy Sci* 87: 2669-2676.
Caraviello, D.Z., Weigel, K.A., Gianola, D., (2004). *J. Dairy Sci.* 87:3518-3525.
Cunningham, E.P., Tauebert H. (2009).*J. Dairy Sci.* 92:6192-6196.

De Haas, Y., Ouweltjes, W., Ten Napel, J., Windig, J.J., De Jong, G. (2008) *J. Dairy Sci*., 91, 2501-2511.
Ducrocq, V. (2000) *Interbull Bulletin* n° 26: 123-130.
Ducrocq, V. (2001) *Interbull Bulletin* n°27: 147-152.
Ducrocq, V. (2005) *Anim. Sci,* 80, 249-256.
Ducrocq, V. (2006) In *WCGALP8*, August 13-18, Belo Horizonte, Brasil, Comm. n° 26-07.
Ducrocq, V., Boichard, D., Barbat, A., Larroque, H. (2001). In *52nd Meeting European Association Animal Production*, Budapest, Hungary, August 26-29, Book of Abstracts, 7: 2.
Ducrocq, V., Delaunay, I., Boichard, D., Mattalia, S. (2003) *Interbull Bull*. n°30 101–111.
Ducrocq, V., Gion, A., Leclerc, H., Druet, T. (2008). In *59th Meeting of European Association Animal Production*, Vilnius, Lithuania, August 24-27, Book of Abstracts, 14: 269.
Gianola, D., Foulley, J.L. (1983). *Genet. Sel. Evol.* 15:201-224.
Gianola, D., Ødegård, J., Heringstad, B., Klemetsdal, G., Sorensen, D., Madsen, P., Jensen, P., Detilleux, J. (2004) *Genet. Sel. Evol.* 36: 3-27.
Gonda, M. G. Kirkpatrick, B. W, Collins, M. T. (2007) *Animal Genetics*, 38:389-396.
Gonzalez-Recio, O., Chang, Y., Gianola, D., Weigel , K. (2005). *J. Dairy Sci.*,88:3655-3662.
Jorjani, H. (2007) *Interbull Bulletin* n° 37, 144:151.
Jorjani, H., Jakobsen, J.H., Forabosco F., Hjerpe, E., Fikse, W.F. (2007) In *58th Meeting of EAAP*, Dublin, Ireland, August 26-29, Book of Abstracts, 13: 24.
Kizilkaya, K., Tempelman, R.J. (2005) *Genet. Sel. Evol* , 37: 31-56.
Larroque, H., Ducrocq, V. (2001) *Genet. Sel. Evol* , 33, 39-59.
Lassen, J., Hansen, N., Sørensen, M. K., Aamand, G. P., Christensen, L. G., Madsen, P. (2003) *J. Dairy Sci.* 86:3730-3735.
Lassen, J., Sorensen, M.K., Madsen, P., Ducrocq, V. (2007a) *Animal*, 1: 631–636.
Lassen, J., Sorensen, M.K., Madsen, P., Ducrocq, V. (2007b) *Genet. Sel. Evol.*, 39: 353-357.
Lawlor, T.J., Connor, S., Tsuruta, S., Misztal I., (2005) *Interbull Bulletin n*°33: 119-123.
Liu, Z., Jainter, J., Reinhardt, F., Rensing, S., Reents, R. (2008) *J. Dairy Sci.*. 91:4333-4343.
Mömke, S., Scholz, H., Doll, K., Rehage, J., Distl, O. (2008) *J. Dairy Sci.* 91:4383–4392.
Pryce, J.E., Coffey, M.P., Simm, G. (2001) J. Dairy Sci. 84:1508–1515.
Pryce, J.E., Harris, B.L., Bryant, J.R., Montgomerie, W.A. (2009) *EAAP Scientific Series* 126: 99-112.
Rodrigues-Motta M., Gianola, D., Heringstad, B., Rosa, G.J.M., Chang, Y. M. (2007) *J. Dairy Sci.*. 90:5306-5315.
Rogers, W. G. (2005) In *56th Meeting European Association Animal Production*, Uppsala, Sweden, June 5-9, Book of Abstracts, 11: 43.
Schneider, M.d P., Strandberg, E., Ducrocq, V., Roth, A. (2005) *J Dairy Sci.* 88: 2253-2259.
Strandberg, E. (2007). In *58th Meeting European Association Animal Production*, Dublin, Ireland, August 26-29, Book of Abstracts, 13: 2.
Taeubert, H., Liu, Z, Reinhardt, F. (2008) *Interbull Bulletin* n°38: 152-157.
van der Linde C., De Jong, G., Koenen, E.P.C., Eding H. (2010) *J. Dairy Sci. (submitted).*
van Raden, P.M. (2001) *J. Dairy Sci.*, 84 (E. Suppl): E47-E55.
van Raden, P.M. (2002). In *WCGALP7*, August 19-23, Montpellier, France. 29: Comm.01-21.
Wall, E., Brotherstone, S., Woolliams, J.A., Banos, G. ,Coffey, M.P. (2003) *J. Dairy Sci*., 86:4093-4102.
Weigel, K.A., Lawlor, T.J., van Raden, P.M., Wiggans, G.R., 1998. *J. Dairy Sci.*, 81:2040,2044.