Advances in dairy cattle breeding research

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Abstract

This paper selectively reviews breeding objectives, genetic evaluation systems, use of individual genes and the design of breeding programs. Consideration of costs in the breeding objective shows that feed conversion efficiency (FCE) is the most important trait. A simple model of nutrient requirements suggests that FCE is more highly correlated with milk yield in a low nutrition environment than in a high nutrition environment. An international experiment to test this hypothesis could be worthwhile. Mastitis resistance, fertility and longevity are important traits, but as much for their effect on milk income as costs. Research on genetic evaluation systems is focusing on use of test day yields, international evaluations, non-additive variance, non-linear models and the use of individual genes. Models with a non-linear relationship between traits and possibly censored data (e.g. between milk yield and days open) deserve investigation. Individual genes and mapped QTL can be included in genetic evaluations by use of linear models, combined segregation-linkage analysis or finite locus or gene based models. The use of these genes will lead to the selection of young bulls and heifers to breed bulls, thus reducing generation intervals and increasing genetic gain, but with an increase in variability of response or risk. Methods to make selection more robust to errors in parameter estimates, biased data and bad luck are needed.

Introduction

This paper reviews a wide field of research including breeding objectives, selection criteria, genetic evaluation systems, use of individual genes and design of breeding programs, but it does so very selectively, and I have attempted to introduce some new ideas and suggest priority areas for future research.

2. Breeding objectives

Breeding objectives for dairy cows have been reviewed by Groen *et al.* (1997) and the methodology for setting objectives by Goddard (1998a). The economic value of milk components depends on the milk payment system and has been considered elsewhere. Therefore, I will concentrate on traits other than yield and milk composition.

A very simple objective might be

Profit = Income – Animal costs – Feed costs

Following Smith *et al.* (1986), I have assumed that, in the long term, there are no fixed costs: all costs are proportional to either the amount sold (and reflected in the price received), or the number of animals maintained or the amount of feed required. Visscher *et al.* (1994) argued that in a pasture based system most costs are proportional to the amount of feed used including the cost of land. Consequently, in pasture based systems, the feed costs can account for 80% of the total costs. Brascamp *et al.* (1985) argued that the average profit from dairying, when all costs are included, is close to zero or else investment capital would flow into the industry until profit, after allowing return on investment as a cost, returned to near zero. Therefore, in the profit function above, on average, Income = Animal costs + Feed costs. Then the economic weight of each trait is the increase in profit due to a one unit increase in that trait while all other traits are held constant (note that mean profit is zero before this change but not after it). For simplicity, I will assume that all income comes from sale of milk, although the calculations could be extended to include income from calves and cull cows. Thus, the simplified profit function contains just three traits: milk yield, feed conversion efficiency (FCE) and animal costs. The relative economic weights of these three traits depend only on the average animal costs as a proportion of total income (p). A 1% increase in milk yield or a 1% decrease in animal costs causes an increase in profit which is p% of income, while a 1% increase in FCE causes a (1-p)% of income increase in profit. Economic weights depend on the other traits included in the profit function. Here the economic weight for milk production is reduced because FCE is also included in the model. Consequently, the benefit from increasing yield, while FCE is held constant, is only a reduction in the animal costs. This is true whether or not the output of milk is fixed provided that mean profit equals zero. Thus, provided feed costs are greater than animal costs (per unit of milk), the economic weight for FCE is greater than that for milk yield (when expressed per percentage change in each trait).

If animal costs are a small proportion of total costs, the economic weight of traits that reduce costs per animal are unlikely to be high. Mastitis resistance and fertility are two traits that affect cost per animal, but they also affect income through effects on milk yield. In theory, effects on yield should not be counted as part of the economic weight of mastitis or fertility because yield is already in the profit function. However, in practice yield may be measured in such a way that these effects are not included and therefore need to be included as part of the economic weight of fertility or mastitis.

Most studies have not included FCE as a trait in the profit function. That is they have not calculated the economic weight of milk yield while holding FCE constant. Typically they have assumed that feed intake increases with milk yield but not so much that FCE remains constant. Consequently they have found the economic weight of milk yield to be higher than that calculated above. To aid comparison with other studies, I will now assume a profit function which does not include FCE as a trait but which increases feed intake to meet the requirement of increased milk yield. Economic weights per genetic standard deviation for mastitis and fertility (Philipsson *et al.*, 1994) have been claimed to be as high as half the economic weight of milk yield (when FCE is not included in the profit function). However, these results depend on the specific production system assumed and I am concerned that some double counting of effects on milk yield may still be occurring (see also discussion by Groen *et al.*, 1997). Fertility is important in seasonal calving systems or if the value of calves is very high, but in north America and parts of Australia where neither of these apply, the optimum inter-calving interval may be 14 months and there is little benefit in reducing it below the existing mean. Even in these circumstances, other fertility traits still have a value because, for instance, they affect semen and insemination costs, but this supports an economic weight much less than half that of milk yield. Other health traits will also affect animal costs but are not as important as mastitis and fertility. Selection for milk yield is expected to reduce fertility and resistance to mastitis. If this occurs, and if the economic value of these traits increases as the mean declines, then they should be given a greater economic weight than would be calculated based on the current means. However non-genetic improvements in fertility and mastitis resistance may compensate for the expected genetic decline.

Two other traits considered important by Australian dairy farmers are temperament and milking speed. Temperament is valued highly for quality of life reasons and milking speed somewhat less highly, because it affects milking time and hence labour costs. Length of herdlife is also economically important with an economic weight up to half that of milk yield (Visscher *et al.*, 1994). Much of the culling in dairy herds is voluntary culling for reasons such as infertility, mastitis, low production, poor temperament. Therefore, the trait in the profit function should be ‘culling for reasons not already included in the profit function’. Consequently, as the profit function is made more complete, the economic weight of length of herdlife declines. Alternatively, the effect of mastitis on herdlife can be excluded from the economic weight of mastitis, but the herdlife trait in the breeding objective defined to include culling for mastitis.

3. Selection Criteria

Although breeding objectives should be as complete as possible, this does not mean that all traits should be recorded and included in the selection criteria. Whether or not to record a trait depends on whether it increases the accuracy of selection enough to cover the cost of recording, analysing and explaining the new traits.

Consider the case of a profit function with two uncorrelated traits and assume we already record the more important. Should we record the second trait? Assume that selection is on EBVs based on large progeny tests so we can treat the EBVs as if they were 100% accurate, and that the second trait has an economic weight per genetic standard deviation s times the first trait. The accuracy of selection using the first trait only is a fraction $\sqrt{1/(1+s*s)}$ of the accuracy obtained by recording both traits. Table 1 lists this accuracy for some values of s showing that recording a trait that is ¼ as important as the main trait improves the accuracy of selection by only 3%.

Table 1. Accuracy of selection (r_{TI}) and prediction error variance (PEV) when a second trait is deleted from the selection criterion

Economic weight of the second trait relati to the first	Genetic correlation between traits = 0.00		Genetic correlation between traits = -0.50	
	r_{TI}	PEV	r_{TI}	PEV
1.00	0.70	0.50	0.50	0.75
0.50	0.89	0.20	0.87	0.25
0.25	0.97	0.06	0.97	0.06

Calculations of r_{TI}, such as these, imply that the gains from recording traits other than the most important are small. However perhaps that is not the correct conclusion. The variability of selection response depends on $1\text{-}r_{TI}^2$ and Table 1 shows that recording additional traits reduces variability of response substantially. Table 1 also shows that r_{TI} benefits more from including a second trait when the genetic correlation between the traits is unfavourable, but the gain in accuracy are still not great. However, if the profit function is non-linear so that a decline in the second trait is more costly than an increase is valuable, or when the traits combine non-linearly, the benefit from recording a second trait may be larger than indicated in the table. My conclusion is that we do not seem to have a clear method by which we decide which traits to record and use for selection.

Genetic evaluation for somatic cell count is now common. Recording mastitis would improve the accuracy of EBVs for this trait, but is limited by the cost of recording. Similarly, EBVs for fertility and other health traits are restricted by failure to record the necessary data.

4. Feed Conversion Efficiency

FCE is favourably correlated with milk yield so, even though it is more important than yield, the benefit from recording it is limited by this genetic correlation. The correlation is reported to be >0.8 in most studies (Veerkamp, 1998), but this may be misleading because some studies have fed according to production and almost no studies have measured feed intake over a full year.

A simple model of production and intake is as follows. The total feed consumed (Y) is divided into that used for maintenance (N) and that used for milk production (M). This assumes that eventually a cow must reach a sustainable state in which she returns to the same body weight at calving as the last time she calved. Assume there is no variation in the efficiency with which feed not required for maintenance (M) is converted to milk so that milk yield is just a constant times M and we can treat M as milk yield for these calculations. With this simple model and assuming reasonable parameters such as those in Table 2, it is impossible to generate a correlation between yield and FCE that is as high as that between yield and intake. However, Veerkamp(1998), in a review of the literature, found the genetic correlation between intake and yield was only 0.45 - 0.65 (i.e., lower than between yield and FCE). This discrepancy between the prediction of the model and actual estimates is because intake and yield were typically measured during a period in which the highest yielding cows are losing weight. Thus cows, which lost weight during the period of measurement, appear highly efficient, but this high efficiency is not sustainable because the cow cannot indefinitely lose weight. If a sustainable yearly cycle is considered, the genetic correlation between FCE and milk yield is almost certainly lower than usually reported and perhaps about 0.7. Consequently, the benefit in r_{TI} from recording FCE is larger than previously thought. Considering an objective which contains only yield and FCE, the benefit is a gain of 20% if feed costs are 80% of total costs and 8% if feed costs are 50% of all costs.

Table 2. Correlations between milk yield, intake and FCE (means are of feed partitioned to production and maintenance relative to that for maintenance; CV is coefficient of variation)

	Yield	Maintenance	Intake	FCE
Mean	2	1	3	
CV	0.10	0.08	0.08	0.033
Milk yield		0.40	0.95	0.68
Maintenance			0.66	-0.40
Intake				0.43

This approach to formulating breeding objectives and selection criteria including FCE has been challenged by others. They point out that selection for high FCE is selection for reduced intake at the same level of milk yield, and they argue that this will accentuate the energy deficit in early lactation and perhaps increase the incidence of infertility and health disorders. These concerns can be overcome by recognising that the objective is FCE over a complete and sustainable lactation cycle and by recording fertility and health traits and selecting on them directly. The simple model of intake described makes it clear that the aim is to improve FCE by increasing yield and reducing maintenance requirements, not by reducing intake while leaving requirements unchanged. Nevertheless, low maintenance requirements might be correlated with poor fertility or health and, if that were so, the genetic parameters would need to reflect that fact.

This analysis does not solve the problem of which traits to record. It may be that recording intake is not profitable. If any recording of intake is to be done it should be considered in relation to a complete objective including fertility and health traits. It is tempting to consider recording residual feed intake because this would account for differences in weight loss during the recorded period. However, this is just one linear combination of the traits recorded and it is more logical to use normal selection index calculations to maximise the correlation between selection criterion and objective. Although the breeding objective should include feed intake over a complete production cycle, this does not mean that we must measure feed intake over a complete cycle. The selection criteria might be based on intake measured over a short period, provided we use the correct genetic covariances among the traits measured and those in the breeding objective.

The simplest traits to record, which are correlated with maintenance requirement and hence with FCE, are body weight and other measures of size such as hip height or the type trait stature. Depending on the correlations between these traits and maintenance requirements, recording them may generate much of the benefits from recording intake. One might expect that smaller cows with the same milk yield would suffer increased stress and more culling, but this does not appear to be the case (Rogers *et al*., 1991; Boldman *et al.*, 1992; Harris *et al*., 1992).

Another argument advanced for selecting for high feed intake (ie low FCE) is that cows with a high intake could be fed a less expensive diet. There is no direct evidence for this. If this is the breeding objective, it would be much simpler to feed a less expensive diet and record milk yield.

5. Genotype by environment interactions (G x E)

The yields of milk in different environments are different traits that are not perfectly correlated. Genetic correlations among yields in North America and European countries are high (e.g., > 0.9), but lower between these countries and Australia (0.82) and New Zealand (0.77). This pattern suggests that the critical factor in the environment is level of feeding. The Northern Hemisphere countries use a high feeding level whereas New Zealand relies on pasture and Australia is in-between. This interpretation is supported by studies within countries that have found the genetic correlation between yield in high producing and low producing herds to be about 0.8-0.9 (Veerkamp and Goddard, 1998). All these genetic correlations (r_g) are likely to be slightly underestimated due to differences in the definition of yield and because any imperfections in the statistical model tend to cause an underestimate of r_g. However this cannot account for the pattern of correlations observed.

The existence of these G x E mean that each country should select on the basis of EBVs for production under its own conditions, but these EBVs should use all available data, including international data, as the INTERBULL EBVs do. Can the recording of yield under a range of environments be used to increase the accuracy of selection for the breeding objective in each country? Consider the simple model of feed intake used earlier. What will happen if we vary the quality and quantity of feed on offer to the cows? I will assume that the ranking of genotypes for intake stays the same but, as nutrition declines, the variation in intake declines. Table 3 shows the correlations predicted by this model. To generate a genetic correlation of 0.8 between milk yield in a high nutrition environment and a low nutrition environment requires that the standard deviation of intake be only 0.4 times as great in the restricted environment. Under these conditions yield in either environment is still correlated with FCE in the same environment, but yield in the poor environment is especially correlated with FCE in the good environment. This is because yield in the poor environment and FCE in either environment are correlated with low maintenance requirements. Yield in the good environment has a correlation of only 0.23 with FCE in the poor environment. This is a very important parameter for countries with low nutrition environments and which import most of their genetic improvement from northern America and western Europe.

Table 3. Correlations between traits milk yield and feed conversion efficiency (FCE) measured in a high (h) and low (l) nutrition environment.

	Milk-h	FCE-h	Milk-l	FCE-l
Milk-h	-	0.68	0.81	0.24
FCE-h		-	0.98	0.87
Milk-l			-	0.76
FCE-l				-

The model of intake and yield used here is almost certainly too simple. For instance, there may be traits, other than low maintenance requirement, that increase adaptation to a pasture diet. However, a more realistic model might well not change the main conclusions very much. These conclusions are important and relatively easily tested. Specifically, is yield in a high nutrition environment poorly correlated with FCE under poor nutrition, whereas yield under poor nutrition is highly correlated with FCE in all environments? If this were true it would encourage progeny testing of bulls simultaneously in countries with both high and low nutrition environments.

6. Genetic Evaluation Systems

Genetic evaluation systems have been continuously researched and upgraded in an effort to increase the correlation between EBVs and the breeding objective. Calculation of EBVs is usually based on an animal model BLUP. Recent trends in research have been the use of international data, test-day data, multi-trait models, non-linear models, non-additive genetic variation and inclusion of individual genes.

The use of test-day yields instead of lactation yields as data for the BLUP should increase the accuracy of EBVs for two reasons:

- better modelling of environmental effects through herd-test-day terms,
- better modelling of random effects by treating yields at different times as different traits.

It appears that the genetic correlation between early and late lactation yields is only about 0.5 (Kaiser and Goddard, unpublished). If yields at different stages of lactation are to be recognised as different traits, then it is reasonable to treat different lactations as different traits also. This implies the use of a multi-trait model with many traits. Estimation of the (co)variances among all these traits can be improved by using covariance functions which utilise the ordering of yields within a lactation (Veerkamp and Goddard, 1998). An equivalent model can be constructed using random regression, although estimates of variance components using these models have so far proved unreliable (Van der Werf *et al.*, 1998). Both methods reduce the dimensionality of the multi-trait model which can improve the accuracy of the EBVs because less parameters must be estimated, and reduce the computer resources needed (Wiggans and Goddard, 1997).

Multi-trait models would also seem appropriate for groups of correlated traits where some records are typically missing or censored such as yield, fertility and survival.

Non-linear models have usually been used for discrete traits such as calving ease. A topic that has had little consideration is non-linear relationships between traits. For instance, yields are sometimes corrected for days open using a non-linear function. However days open is a trait with some genetic variance, so it should be included as a y-variable. One method is to analyse yield corrected (non-linearly) for days open and days open as two traits in a multi-trait model. However, days open may be missing on many records in a non-random manner. An EM algorithm similar to Ducroq and Besbes (1993) may be possible, but alternatively MCMC methods offer a very flexible way to fit complex models and deserve further consideration.

Non-additive inheritance such as dominance, epistasis, mitochondrial, maternal effects, and gene imprinting could affect milk yields. Analyses done to date suggest the variance components associated with these effects are small (e.g., Kaiser *et al.*, 1998). Even if these non-additive effects exist, the use that can be made of them is limited. For instance, including dominance in the model improves the accuracy of predicting breeding value and phenotype only marginally even if the loci in the simulated data all show dominance (Goddard, 1998b).

There is no guarantee that more complex models yield more accurate EBVs. We should test this empirically rather than rely on the argument that because they represent the biology more closely they must be better. Complex models rely on modelling the inter-relationships among many parts such as traits; this modelling may be incorrect and relies on estimates of the parameters in the model. An alternative is to analyse profit or a trait closely related to it directly. This would in theory be less accurate but may be more robust (Meuwissen and Goddard, 1997a). Visscher and Goddard (1995) found the heritability of 'lifetime profit' to be 0.13 to 0.19.

Multi-trait models use estimates of the (co)variance matricies in place of the true parameters. Consequently the resulting EBVs are less accurate than expected and this error increases sharply with the number of traits. One example of this problem occurs when many type traits are used to calculate EBVs for longevity. The estimation errors in the genetic covariance matrix make the EBVs for longevity appear much more accurate than they actually are (Visscher, 1994; Goddard and Thompson, 1998). This problem cannot be overcome by examining the estimated covariance matrix and selecting the most informative traits to include in the EBV calculations. Methods of minimising these problems through bending and shrinking have been suggested, but more research to find the best solution is needed. One useful approach is to re-estimate selected parameters or the accuracy of a proposed index in a completely independent data set.

An obvious source of inaccuracy in EBVs is bias in the data, such as that caused by preferential treatment of some cows in a herd. The decrease in mean EBV of bulls from parent average to first crop daughters to second crop daughters is evidence of bias in the EBVs at least. Genetic evaluation systems already include features designed to minimise the effects of this bias. For instance, the inclusion of herd x sire interactions is mainly to limit the damage done by a group of half-sisters in one herd. The main advantage of including additional genetic effects in the model, such as cytoplasmic inheritance or dominance deviations, may be to reduce bias in EBVs due to preferential treatment of groups of related cows. If this is our aim should not we address it directly rather than as a by-product of other models? How much bias is in the data, can we detect it and how do we minimise its effect? At least one AI stud believes the bias is so great that they do not use the yield of a cow or her female ancestors when selecting bull dams. Conversely, the small variance components estimated for non-additive effects argue that preferential treatment of related cows is not common.

7. Individual Genes

Typing individual genes, using DNA technology, provides a new source of data to increase the accuracy of selection and to increase our understanding of dairy traits. Three classes of genes can be recognised:

- genes mapped using linkage to random markers,
- identified genes,
- genes which are neither mapped nor identified.

Several genes affecting milk yield and composition have been mapped (Georges *et al.*, 1995). Their gene substitution effects are in the range half to one standard deviation. These effects are likely to be overestimates because they are the largest of many estimated. Nevertheless it is surprising that such large genes are segregating for traits which have long been subject to selection.

None of the genes that have been mapped in the genome screens have so far been identified but that is an obvious target for current research. The main genes known to affect milk production are the milk protein genes. The discrepancies among published estimates of the effects of these genes on yield of milk, fat and protein should warn us about the difficulties of estimating the effects of new genes or mapped chromosome segments. The clearest result is that polymorphism at κ-casein and β-lactoglobulin affect the synthesis of their own protein and hence its concentration as a proportion of all protein (Van Eenennaam and Medrano, 1991; Ehrmann *et al.*, 1997). These effects are probably due to polymorphisms in the control regions of the genes rather than those in the coding region which are the basis for typing the alleles. This implies that there is linkage disequilibrium between the alleles in the coding and control regions, which is not unexpected given the tight linkage between them. These genes affect the manufacturing properties of the milk. It has recently been claimed that some alleles of β-casein trigger diabetes in children that are predisposed to it, but the evidence for this is not yet convincing.

The milk protein genes have not been used for selection, in part because their effects are not large enough or reliable enough. AI studs with the relevant information are now considering the use of the genes mapped by markers. This information is difficult to use because the linkage phase between the QTL and the markers can be different in every family. Fernando and Grossman (1989) and Goddard (1991) showed how to incorporate marker data into BLUP calculation of EBVs. These models assume an infinite number of QTL alleles and cannot cope with dominance. An alternative approach uses a combination of segregation analysis and mixed models and can utilise dominance at the QTL (Meuwissen and Goddard, 1997b). Henshall and Goddard (1998) found that this new approach could generate faster genetic gain from marker assisted selection when dominance existed at the QTL, but in some simulations performed worse than the BLUP based method.

In the absence of marker data, segregation analysis can only demonstrate the existence of major genes with very large effects. I am not aware of any for milk production. However models based on a finite number of genes can be used to analyse quantitative traits in place of the usual infinitesimal model. The first finite loci or gene based models assumed that all genes had the same effect to make them computationally tractable (Stricker and Fernando, 1998), but MCMC techniques allow much more flexible models to be used (Goddard, 1998b). The advantage of these models is that they can fit non-additive effects such as dominance (Pong-Wong *et al.*, 1998) and a combination of individual genes and polygenes more easily than infinitesimal models (Goddard, 1998b).

8. Design of breeding programs

Since Nicholas and Smith (1983) there have been many studies claiming that a MOET nucleus herd would make faster genetic gain that progeny testing programs, yet we are still using progeny testing!? There are several reasons for this:

- the gains from MOET were initially overestimated,
- they did not assume the large number of bulls now progeny tested world wide,

- the market for semen expects reliable EBVs,
- some traits are less heritable than milk yield,
- the migration path from progeny testing to nucleus herd is not easy.

Let me explain the last point. To move to a full nucleus design, you have to use young bulls as sires of sons. Yearling bulls are about 4 years of progress ahead of the proven bulls but lack the selection differential due to progeny testing. This selection differential is about 1.7 genetic standard deviations, whereas four years gain is about 0.8. For a yearling bull to have as high an EBV as the best proven bulls you must be able to select among young bulls based on pedigree with an accuracy of about 0.4. If yearling bulls and heifers are always used for mating then this accuracy is possible and the nucleus scheme is at least competitive with progeny testing. But when the sires and dams of bulls have been selected in a progeny test design, little further selection accuracy is possible among the young bulls. Consequently the best bull is a proven bull and the design does not change to a full nucleus design. A gradual change may occur if even a small number of young bulls are selected as sires of sons, but evaluating young bulls on a 'sire pathway index', instead of an animal model EBV, makes this less likely to occur.

However, current breeding programs do use MOET. They are, in fact, hybrid designs in which a dispersed nucleus breeds bulls which are progeny tested in the wider population (Meuwissen, 1991). The nucleus is defined by the use of bulls that are bull sires. MOET is used in these matings and the heifer offspring are the replacements for the nucleus. In this way MOET is used on the cows to breed cows pathway but only within the nucleus herd.

Selection based on DNA tests could provide the accuracy of selection among young bulls that would result in the best surpassing the best proven bulls. This would tip the program over into a full nucleus design and potentially raise the rate of genetic gain. However, before this can happen we need to map more QTL with significant effects on important traits and we need a structure for collecting data that produces marker assisted EBVs on the young bulls. At the moment, by the time linkage phase is established in a family, that family is no longer supplying young bulls. Alternatively, we must identify the QTL and test for them directly or at least find markers in strong linkage disequilibrium with the QTL.

Even if marker assisted selection is successful, I would advocate that progeny testing be maintained, despite the fact that some young bulls would have the highest EBVs, because:

- without progeny testing dairy farmers will have no way to compare bulls from different companies,
- we will not have markers for all important traits,
- progeny testing may be needed to correct errors in estimates of individual gene effects and to find new genes,
- the variabilty of outcome (i.e., risk) is high with a nucleus design relying on marker assisted selection (Meuwissen and Sonesson, 1998).

If progeny testing is to continue in this new design, it must not be too expensive. We must keep bulls less expensively, and not pay dairy farmers to use young bulls. Performance recording would have to be paid for by the dairy farmers to aid their own management, although AI studs might pay for some selective recording.

9. Conclusions

1. The economic weight of FCE is higher than that of milk yield if feed costs are greater than animal costs.

2. Among other traits, mastitis and fertility are most important with economic weights up to half that of milk yield. However, these estimates may be inflated by double counting the effects on milk production.
3. The choice of traits to record is often not supported by economic analysis.
4. A simple model of FCE suggest that it is less well correlated with milk yield than previously reported, but that it may be more highly correlated with milk yield in an environment with a lower level of nutrition. Conversely, milk yield in a high nutrition environment may be poorly correlated with FCE in a low nutrition environment. These predictions, if confirmed, have important implications for international dairy breeding programs.
5. Non-additive variance in milk yield is small.
6. Genetic evaluation systems are already using test-day data and international data in multi-trait analyses. The number of traits included will probably grow but strategies are needed to control the loss of accuracy from using estimated covariance matrices in place of the true ones.
7. Non-linear models could be developed to account for non-linear relationships between traits, possibly implemented by EM algorithms or MCMC methods.
8. The detection of bias in performance records and minimization of its effect on EBVs should be attacked directly.
9. Individual genes affecting milk production are being mapped and hopefully identified. Methods will be necessary to include information on these genes in genetic evaluation systems. Current options include linear models, segregation analyses and gene-based models.
10. Dairy breeding programs are a hybrid with a dispersed nucleus producing bulls which are progeny tested in the wider population. They will change to a full nucleus design when selection on marker loci gives an accuracy of selection among young bulls of higher than 0.4.
11. A large progeny test in which traits in the breeding objective are directly recorded is a very robust selection method. Complex genetic evaluation systems with many traits and which rely on indirect selection and DNA markers to select young bulls are not so robust. Strategies to increase robustness or decrease risk in future dairy improvement programs are needed.

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