Genetic Improvement of Dairy Cattle

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Introduction

Dairy cattle are one of the most highly studied, genetically, of all domesticated mammalian species. Genetic improvement of dairy cattle involves determining which improvements are desirable, which traits provide information on the goal, how heritable those traits are and how to evaluate them, and how to design a breeding programme to achieve the goals. This chapter describes how to determine which goals should be established in order to emphasize profit or efficiency as the ultimate goal of the dairy enterprise. The traits typically measured are listed, along with how they are related and the genetic parameters utilized in the selection process. Evaluation procedures used to establish genetic rankings are derived from observations on related animals and are reviewed. Scientific innovations, such as artificial insemination (AI), marker assisted selection and cloning, are reviewed, as well as their effect on the design of breeding programmes.

Breeding Objectives

The first task in the design of breeding programmes is to define the breeding objective. The usual purpose of breeding programmes is assumed to be an economic one, i.e. to increase the profitability of dairy farming. Therefore, the objective is defined by a profit function, which shows how a change in each trait influences profit. This profit function is based on a bioeconomic model of the farm and obviously depends on the prices the farmer receives for milk and other products and the prices he/she pays for inputs. The methodology for defining profit functions is reviewed by Gomez *et al.* (1997) and Goddard (1998) and an example of its application to pasture-based dairy farming is given by Visscher *et al.* (1994).

Profit functions

The profit function can be non-linear if the effect of a trait on profit is curvilinear. For instance, the effect on profit of increasing fertility might decrease as the mean fertility of the herd increases. However, the profit function can usually be approximated by a linear function:

$$\text{profit} = \Sigma\, a_i\, \text{bv}_i$$

where bv_i is the breeding value for the ith trait and a_i is the economic weight for the ith trait. Thus a_i is the effect on profit of a 1-unit increase in trait i when all other traits are held constant.

The economic weights for a particular trait depend on the other traits that are included in the profit function. For instance, if feed intake is included in the profit function, the economic weight for cow body weight is positive, because increasing body weight increases income from the sale of cull cows. However, if feed intake is not included in the profit function, the economic weight of body weight may be negative, because larger cows have greater feed requirements for maintenance. Generally, including all traits that directly affect income and costs in the profit function is best, but a common practice has been to leave feed intake out of the profit function and to adjust the economic weights of other traits to reflect the change in intake caused by a change in each of the other traits. Thus, the economic weights can be thought of as partial regression coefficients of profit on the breeding value for each trait.

It is important to distinguish between the traits which form the objective and the traits upon which selection is based (selection criteria). For instance, long herd life and low incidence of mastitis may be goals, but selection for those traits is inconvenient because herd life is only known late in life and mastitis is not necessarily recorded. However, conformation traits, such as udder depth, may be genetically correlated with herd life and mastitis incidence and consequently may be useful selection criteria. In this situation, udder depth would not be part of the breeding objective.

Profit can be viewed from the perspective of the individual farmer, the industry or the community and expressed per litre of milk, per cow or per farm. If, when all costs are included, mean profit is close to zero, and market signals are passed along the chain from consumer to cattle breeder, then the relative economic weights are the same from all perspectives and for all units of expression. Mean profit is expected to be close to zero when returns to capital, management and labour are included as costs; otherwise, investment capital would flow into the industry until profitability declined to that of alternative investments.

However, if market signals are not passed along the marketing chain, economic weights can be severely distorted. Quotas are an example of artificial prices leading to distorted market signals and distorted breeding objectives. Gibson (1989) shows how quotas decrease the economic weight for the product under quota. In consequence, farmers may point genetic improvement in a direction that does not maximize the economic benefit to the community as a whole.

The yields of milk, fat and protein are the major determinants of income to dairy farmers and the most important traits in the objective. Their relative economic weights depend on the pricing formula by which farmers are paid. If feed intake is not included in the profit function, the economic weights for milk, fat and protein need to include the extra feed cost associated with extra yield. If the milk is used for manufacturing, the protein is most valuable and the fat is of some value, but the volume is of negative value because it must be transported from farm to factory and evaporated to make some products. Combining the prices received with the feed costs for products, Visscher *et al.* (1994) derived economic weights for Australian dairying of protein ($\$3.51\ \mathrm{kg}^{-1}$), fat ($\$1.10\ \mathrm{kg}^{-1}$) and volume ($-\$0.04\ \mathrm{l}^{-1}$). When the relative economic weights are expressed per genetic standard deviation, they are 1.0 for protein, 0.4 for fat and −0.4 for volume. Although milk pricing and feed cost vary from country to country and over time, these relative economic weights are not atypical.

Fitness traits

Other traits commonly included in breeding objectives are health, fertility, calving ease, body weight, feed intake, milking speed, temperament and length of herd life. More detailed consideration of their economic weights is given by Gomez *et al.* (1997).

Among health traits, the incidence of mastitis is the most important, because mastitis causes milk loss, treatment costs and reduced milk quality. In Scandinavia, mastitis is recorded and the bulls are progeny-tested for incidence of mastitis among their daughters. However, in most countries only somatic cell count (SCC) is recorded. This trait is genetically correlated with mastitis incidence and hence is a selection criterion, but it also has an economic value of its own if milk price is reduced for milk with high SCC. The economic weight of mastitis per genetic standard deviation is approximately one-quarter to one-half that of milk protein yield.

Cow fertility influences AI and veterinary costs, the interval between calvings and hence the pattern and yield from later lactations. In Europe, the economic weight per genetic standard deviation of cow fertility is estimated to be approximately half that of milk protein yield (Philipsson *et al.*, 1994). However, where dairy calves are of much lower value and where farmers can manage cows with long calving intervals so that those cows have long persistent lactations, the economic weight of cow fertility may be much less.

Calving ease is valuable because dystocia results in veterinary costs, extra labour costs, lost calves and cows, reduced milk yield and infertility. The economic weight depends heavily on the incidence of dystocia, which is usually only high in heifers. Calving ease is affected by the genetic merit of the calf and the cow; therefore, selection needs to consider calving ease as a trait of the cow and of the calf.

Feed for cows costs money, so the economic weight for feed intake (when milk yield and other traits are held constant) is negative. The size of this economic weight depends on the proportion of all costs that are proportional to the feed requirement of the herd. In grazing systems, most costs are related to farm size and this in turn determines total feed available. However, in environments where cows must be housed, the housing cost is large and therefore the proportion of all costs due to feed is reduced, as is the economic weight for feed intake.

It has been suggested that the economic weight of feed intake should be positive because cows with high intakes would have better health and fertility and could be fed a less energy-dense, less expensive ration. Including health and fertility in the profit function directly would be logical, so they do not contribute to the economic weight of feed intake. However, when considering selection criteria, the genetic correlations between intake, disease and fertility would need to be considered. The ability of cows to sustain milk yield when fed a less expensive diet is a trait separate from feed intake, which should be investigated further.

Milking speed is of economic value because slow milkers increase the labour cost of milking. In some milking systems, the variability of milking speed is important, because one slow cow can delay the whole shed. In fact, the objective might be to reduce the total labour needed for milking, but to do this we would need to identify the traits of the cow which determine total labour needed and which show genetic variability. Good temperament, while it may be difficult to assign a monetary value to it, is valued highly by dairy farmers in Australia and New Zealand who milk large numbers of cows and want to avoid the disruption and danger caused by wild cows.

A long mean herd life increases profitability, because it decreases replacement costs and increases the proportion of the herd in the most productive, mature age-groups. However, culling of cows is a management decision of the farmer and is done to minimize the economic loss caused by cows of low production, fertility or health. Thus, when these traits are included in the profit function, culling for these reasons should not be included in the definition of herd life. The correct procedure is to include the trait 'reduced herd-life due to traits not in the profit function' (Goddard, 1998). If all traits causing culling were included directly, it would not be necessary to include herd life in the breeding objective.

Economic weights differ between countries and individual farms and are likely to change in future. Possible changes might be caused by environmental effects of dairy farming or automated milking machines that demand cows with a consistent udder anatomy.

Genetic Variation

Genetic parameters indicate the rate of genetic change that is possible and are required for estimation of genetic merit. Of these parameters, heritability describes what portion of the variation (variance) in a trait is of genetic origin and correlations among these traits indicate how genetic change in one trait can affect others. When multiple traits are evaluated, covariances indicate to what degree the information from one trait affects others. If an animal has more than one observation for a trait, repeatability describes the expected similarity among those observations. Other genetic parameters include the effects of dominance, individual genes, breed, inbreeding, heterosis (crossbreeding) and the interaction of genetics with the environment.

Breed differences

The world dairy cattle population is classified into breeds, most of which originally arose in Europe. Registry organizations maintain pedigree records, which enable animals to be traced to the origin of the breed, or importation. With globalization, selection goals have become more similar, and the technology to support high yields is available around the world, particularly in temperate regions. In this environment, the Holstein breed has become dominant, because of its high yield. The Jersey has emerged as the primary alternative breed, because of high component yields and smaller size, along with the collection of Red breeds. Other breeds have regional importance. Crossbreeding programmes have been proposed as a way of upgrading indigenous cattle to a high-producing breed or as a way of obtaining the benefits of hybrid vigour. Table 18.1 displays the differences in yields for the five most common dairy breeds in the USA.

Within-breed variation

Yield traits

Milk yield is usually defined as production during the 305 days following calving, with milk produced after this period not included in genetic evaluations. Individual lactations (parities) of a cow are generally regarded as repeated measurements of the same genetic trait, although some countries have implemented multitrait systems that allow for correlations of < 1.00 among parities. Estimates of heritabilities for milk, fat and protein yields are quite similar across countries (Table 18.2), with heritability estimates for percentage fat and protein content usually much higher than for total yield. Dominance variation has been found to be of minor importance for yield traits, as Misztal *et al.*

Table 18.1. Standardized lactation averages by breed for 1,861,284 cows with records used in genetic evaluations and calving in 1996 in the USA.

Breed	% of cows	Milk	Fat %	Protein %
Ayrshire	0.5	7102	3.9	3.3
Brown Swiss	0.9	8088	4.0	3.5
Guernsey	0.7	6431	4.5	3.5
Holstein	92.4	9962	3.6	3.1
Jersey	5.5	6848	4.6	3.8

Table 18.2. Genetic parameters used for national evaluation of Holstein yield traits by ten countries that provide bull evaluations for the International Bull Evaluation Service (Interbull).

	Heritability					
Country	Milk yield*	Fat yield*	Fat content†	Protein yield*	Protein content†	Repeatability†
Australia	0.25	0.25	0.45	0.25	0.60	0.50
Canada	0.33	0.33	–	0.33	–	–
Denmark	0.29	0.27	–	0.30	–	–
France	0.30	0.30	0.50	0.30	0.50	–
Germany	0.30–0.36	0.25–0.35	0.40	0.26–0.34	0.25	–
Italy	0.30	0.30	–	0.30	–	0.50
New Zealand	0.35	0.28	–	0.31	–	0.60
The Netherlands	0.35	0.35	–	0.35	–	–
United Kingdom	0.35	0.35	–	0.35	–	0.55
USA	0.30	0.30	–	0.30	–	0.55

*Source: Interbull (1997).
†Source: Interbull (1992).

Table 18.3. Estimated sire standard deviations (diagonal) and genetic correlations (above diagonal) considered in the Interbull evaluation for dairy production traits of February 1998; sire standard deviation estimates reflect the scale for record preadjusting in various countries and are expressed in kg (lbs in the USA).

	CAN	DEU	DNK	FRA	ITA	NLD	SWE	USA	GBR	NZL	AUS
CAN	11.75	0.91	0.91	0.95	0.93	0.93	0.91	0.96	0.93	0.80	0.84
DEU		7.50	0.91	0.92	0.90	0.93	0.90	0.89	0.90	0.77	0.80
DNK			7.29	0.91	0.90	0.94	0.94	0.91	0.93	0.76	0.81
FRA				9.73	0.95	0.93	0.91	0.95	0.93	0.78	0.82
ITA					8.65	0.91	0.90	0.95	0.91	0.77	0.81
NLD						7.70	0.94	0.93	0.93	0.80	0.83
SWE							8.58	0.90	0.91	0.76	0.80
USA								21.66	0.92	0.77	0.81
GBR									6.50	0.81	0.84
NZL										4.72	0.90
AUS											4.08

CAN, Canada; DEU, Germany; DNK, Denmark; FRA, France; ITA, Italy; NLD, Netherlands; SWE, Sweden; USA, United States of America; GBR, United Kingdom; NZL, New Zealand; AUS, Australia.

(1998) estimated additive and dominance effects to be 41–44% and 5–7%, respectively, of phenotypical variance for Holstein milk, fat and protein yields in the USA. Dominance variation is due to interactions among genes at a specific locus. When all gene action is additive, each gene adds its influence to the expressed merit of the animal. When there is dominance, one member of the allele pair masks the expression of the other. Dominance variation measures the size of this influence. Genetic correlations were reported to be 0.69 between milk and fat yields, 0.90 between milk and protein yields, and 0.78 between fat and protein yields for registered US Holsteins (Misztal *et al.*, 1992).

Genetic standard deviations and correlations among countries for protein yield are in Table 18.3. The correlation is highest between the USA and Canada (0.96) and lowest between New Zealand and all other countries (0.76 to 0.81) except Australia (0.90). These differences are related to the management systems predominant within the country (grazing in Australia and New Zealand vs. confinement feeding in North America and Europe). The lower correlations for Australia and New Zealand indicate an interaction between genotype and environment; that is, somewhat different genes are required for high performance in North America and Europe from those required in Australia and New Zealand.

The genetic correlations among the individual parities provide an indication of the appropriateness of the assumption that later lactations are repeated observations of the lactation trait. Table 18.4 reports results from Spain (Garcia-Cortez *et al.*, 1995) showing declining correlations as lactations are more distant. One reason for lactations not having a correlation of 1 is because cows reach their mature production level at different rates. Genetic differences between merit for individual lactations can be due to this factor.

Lactation production is measured by sampling approximately 1 day of production per month. The correlations among the individual daily productions

Table 18.4. Heritabilities, additive and residual correlations between the first four lactations for protein yield obtained in a four-trait analysis.*

Lactation	First	Second	Third	Fourth
First	**0.24**	0.89	0.78	0.69
Second	0.39	**0.25**	0.86	0.66
Third	0.32	0.42	**0.26**	0.65
Fourth	0.23	0.35	0.46	**0.19**

*Heritabilities on diagonals, additive genetic correlations above diagonals and residual correlations below diagonals.

Table 18.5. Heritabilities (on diagonal and bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for protein yields.

Lactation stage*	First	Second	Third	Fourth
First	**0.15**	0.92	0.83	0.75
Second	0.47	**0.15**	0.97	0.92
Third	0.40	0.56	**0.18**	0.97
Fourth	0.32	0.45	0.58	**0.18**

*Lactation stage: first, test day nearest to 43 between 6 and 80 days; second, test day nearest to 118 between 81 and 155 days; third, test day nearest to 193 between 156 and 230 days; fourth, test day nearest to 268 between 231 and 305 days.

indicate how the stages of lactation are related. These correlations for first-lactation Holsteins were estimated by Gengler *et al.* (1997). Table 18.5 provides these correlations. As with lactation yields, correlations decline as test days become more distant.

Conformation traits

Visual appraisals of cows for conformation (type) traits have been collected for many years. In many countries, conformation traits are scored on a linear scale and include udder, locomotion and other body traits. Heritability estimates for conformation traits are given in Table 18.6 for ten major dairy countries that participate in Interbull. Additive and dominance effects were estimated to be 45 and 7%, respectively, of phenotypical variance for stature, 28 and 8% for strength, 34 and 10% for body depth, 23 and 5% for dairy form, and 24 and 5% for fore udder attachment in US Holsteins (Misztal *et al.*, 1998).

Reproduction traits

To reduce losses from difficult calvings, calving ease (performance) is often considered when breeding heifers. Heritability estimates for calving ease range from 0.05 (Australian Holsteins) to 0.15 (US Holsteins) (Interbull, 1996). A genetic correlation of −0.27 between daughter and dam calving performance is assumed for Canadian dairy cattle (Interbull, 1996).

Workability traits

Workability traits include milking speed, temperament and likeability. Heritability estimates for milking speed range from 0.21 (Canadian dairy

Table 18.6. Heritability estimates used for national evaluation of conformation traits by ten countries that provide bull evaluations for Interbull (from Interbull, 1996).

Country	Udder*	Locomotion†	Other body traits‡
Australia	0.17–0.33	0.10–0.20	0.17–0.45
Canada	0.08–0.24	0.07–0.20	0.18–0.40
Denmark	0.17–0.43	0.09–0.30	0.16–0.63
France	0.30	0.30	0.50
Germany	0.30–0.36	0.25–0.35	0.40
Italy	0.30	0.30	–
New Zealand	0.35	0.28	–
The Netherlands	0.35	0.35	–
United Kingdom	0.35	0.35	–
United States	0.30	0.30	–

*Includes texture; depth; fore attachment; rear attachment height and width; support; suspensory ligament; cleft; and teat length, placement and diameter (thickness).

†Includes rear leg set and view (side and rear), hock and bone quality, and foot angle.

‡Includes size, stature, strength, capacity, body length and depth, top line; rump length, width, and angle; chest width and floor, thurl (pin) width and set, loin, bone quality, angularity, dairy character (form), muzzle width.

breeds) to 0.25 (Australian Holsteins). Australia also reports heritability estimates of 0.16 for temperament and 0.20 for likeability.

Health traits

The health trait of most concern to dairy producers is resistance to mastitis. Milk samples collected to determine fat and protein content are also evaluated for SCC, an indicator of udder health. High cell counts are associated with mastitis and depressed milk yield. Because SCC data are positively skewed and have markedly heterogeneous variances among groups, they are usually transformed to log, base 2, equivalents (somatic cell scores (SCS)). Somatic cell scores have a more normal distribution and a higher heritability than SCC (Ali and Shook, 1980), though a lower genetic correlation with clinical mastitis (Shook, 1988).

Longevity

Longevity is an overall measure of a cow's fertility and disease resistance and is often referred to as survival, stayability or productive life. In countries including Canada, France, Germany and the Netherlands, longevity is adjusted to reflect the effect of culling for low milk yield, whereas countries such as New Zealand, Australia and the USA report overall longevity. Because of culling for low yield, milk yield has a moderate correlation with overall longevity and contributes to a higher heritability for overall longevity than is found for the adjusted measure. Regardless of whether culling for low yield is considered, heritability estimates for longevity are < 0.10 for all major dairy countries (Interbull, 1996).

Inbreeding and heterosis

An animal is inbred if its parents are related. More technically, the inbreeding coefficient is the probability that an animal receives the same gene from both parents. A simple way to detect inbreeding is to determine if the same ancestor appears in the pedigree of both the sire and dam, creating the possibility of passing on the exact same gene to offspring through both parents. A consequence of industry-wide intense selection of bulls is the increase in inbreeding within the population. The use of an animal model for evaluation tends to further increase inbreeding, because families of animals tend to be selected. The consideration of all relationships tends to make the evaluations of family members similar.

Calculation of inbreeding is computationally intensive and without special techniques would require a matrix of the order of the size of the population. VanRaden (1992) proposed a method that constructs the relationship matrix of one animal at a time, thus greatly reducing memory requirements. He expressed inbreeding relative to a base population that is assumed unrelated and non-inbred. With this base, inbreeding is a measure of increase in homozygosity since that base. Inbreeding levels for the Holstein population in the USA are given in Fig. 18.1. The base population was animals born before 1960. For the 20 years until 1980, inbreeding increased slowly at about 0.044% year^{-1}. More recently, during the period from 1988, the rate of increase has been 0.275% year^{-1}.

A consequence of receiving the same genes from both ancestors is that the likelihood of undesirable recessives increases. This leads to decreased productivity called inbreeding depression. For Holstein cows in the USA Wiggans *et al.* (1995) found the values given in Table 18.7.

Heterosis can be viewed as the opposite of inbreeding and describes an increase in heterozygosity, reducing the likelihood of deleterious homozygous recessives. Heterosis measures the degree that offspring exceed the average of

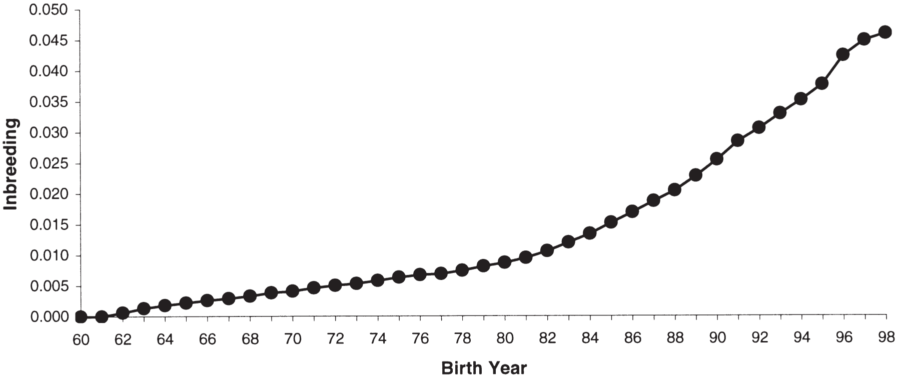

Fig. 18.1. Average inbreeding by birth year for US Holsteins.

Table 18.7. Estimates of inbreeding depression for a 1% increase in inbreeding for US Holsteins.

Trait	Inbreeding depression
Milk (kg)*	–29.6
Fat (kg)*	–1.08
Protein (kg)*	–0.97
Days of productive life (days)†	–13.07
First calving interval (days)†	+0.26
Somatic cell score (scores)†	–0.004

*Wiggans *et al.* (1994).
†Smith *et al.* (unpublished observations).

Table 18.8. Effect of heterosis on lactation yield for Holstein–Jersey crosses in New Zealand (from Harris *et al.*, 1996).

Trait	Effect of heterosis
Fat (kg)	+6.8
Protein (kg)	+5.0
Live weight (kg)	+7.2
Survival (%)*	+4.7

*First to second lactation.

the performance of their parents, the magnitude of which depends on the genetic distance between the parents. Heterosis is usually a result of breed crosses. If the parental breeds are quite different in the trait, the benefit of heterosis is unlikely to make the progeny competitive with the higher producing parental breed. Heterosis may contribute a significant advantage in fitness. In New Zealand, where most milk is used in manufacturing, the Jersey breed (less milk, but high in fat) is perceived as competitive with Holstein (more milk, but less fat) and the progeny of crossing these breeds are highly regarded (Table 18.8).

Heterosis has also been a concern in Europe, with the introduction of semen and embryos from North America. In this situation, the crossbred progeny were backcrossed to the North American bulls, so the performance of generations past the F_1 is important. If epistatic gene combinations in the parent breeds have a positive effect on yield, often breaking these combinations up in subsequent generations will reduce yield. The loss of these epistatic effects is called recombination loss. Table 18.9 shows estimates of recombinant loss, which are negative, meaning that the segregating generations perform worse than expected from the performance of the parent breeds and the F_1. Although epistasis is a possible cause of these results, there are also other possible explanations, i.e. preferential treatment of the F_1.

Table 18.9. Estimates of heterosis and recombination for several European populations (from Harbers, 1997).

Country	Breed	Trait	Heterosis (kg)	Recombination (kg)
NL	HF × DF	Milk	120.0	–100.0
		Fat	6.0	–1.3
		Protein	4.4	–3.5
D	HF × RD	Milk	210	–2382
		Fat	10	–77
		Protein	7	83
UK	HF × F	Milk	100	–156
		Fat	4.5	–2.1
		Protein	3.6	–3.8
NL	HF × MRY	Milk	140	–295
		Fat	6.0	–11.1
		Protein	5.3	–8.2

NL, Netherlands; D, Denmark; UK, United Kingdom; HF, Holstein Friesian; DF, Dutch Friesian; RD, Red Danish; F, Friesian; MRY, Dutch MRY.

Genotype × environment interaction

An interaction between genetics and environment exists when the effect of genes is different in different environments. This can lead to a reranking of animals. Even if the ranking does not change, a smaller response in one environment is still indicative of an interaction. Procedures to account for heterogeneous variance and scale effects may eliminate this interaction.

An interaction reduces the value of information from other environments. Interbull evaluations incorporate correlations between countries of less than 1, effectively assuming some genotype × environment (G × E) interaction. In the extreme, G × E interaction is a concern in introducing high-producing cattle into marginal environments to upgrade indigenous cattle. It may be that the native cattle are well adapted to the harsh conditions and will survive in environments where the improved cattle do not. Thus the native cattle are superior in that environment.

Individual genes affecting milk production

Yields of milk and its components are classical quantitative traits affected by many genes, as well as environmental factors. However, this does not exclude the possibility that there are some individual genes which have a moderate effect. If these genes could be identified, it would increase our understanding of the genetics of milk production and be of practical use when selecting for increased production.

Originally, attention focused on those few genes whose inheritance could be easily followed, for instance blood groups, blood protein and milk protein polymorphisms (Ng-Kwai-Hang *et al.*, 1984, 1986, 1987; Kroeker *et al.*, 1985;

Gonyon *et al.*, 1987; Aleandri *et al.*, 1990; Van Eenennaam and Medrano, 1991a, b; Bovenhuis *et al.*, 1992; Bovenhuis and Weller, 1994; Famula and Medrano, 1994; Ehrmann *et al.*, 1997). Only in the last case (milk proteins) was there an obvious reason to expect that these genes would affect milk production. Many experiments found significant effects of single genes on milk production traits, but generally they have not been large enough or consistent enough to have been used in commercial breeding programmes. To understand the inconsistency of the results, it is necessary to understand the reasons that could cause an association between an animal's genotype at a specific locus and its milk production.

1. The gene could have a direct effect on milk production.
2. The gene could be in linkage disequilibrium with a gene affecting milk production.
3. The gene could be linked to a gene for milk production in linkage equilibrium in the population but in linkage disequilibrium in the sample of families studied.
4. The effect could be totally spurious and due to the statistical analysis ignoring the family structure of the animal samples. (For instance, a particular allele may occur largely in the descendants of one exceptional ancestor, causing the appearance that this allele increases milk production.)
5. False-positive results are expected in one in 20 tests and many significant tests are carried out because there are several markers multiplied by several traits.

Some, but not all, experiments have attempted to distinguish between these five causes of association. Hines (1990) reviewed work in his own laboratory and elsewhere on blood groups, transferrin and milk proteins in Holstein and Guernsey cattle. Among the most consistent effects of blood groups and proteins were an effect of the B blood group on fat % and transferrin type on milk yield, both in Holsteins. Although these appear to be direct effects, rather than linked markers, they could be due to linkage disequilibrium between the marker and a quantitative trait locus (QTL) for milk production.

The milk protein genes are more logical candidates for a direct effect on milk production and do show somewhat more consistent results, although there are still clear differences between experiments. These have been reviewed by Bovenhuis and Weller (1994), as well as Hines (1990).

At the β-lactoglobulin gene, the AA genotype tends to have the highest protein %, with an advantage of about 0.03% over the BB genotype. This occurs because the AA genotype increases the concentration of β-lactoglobulin itself (Ng-Kwai-Hang *et al.*, 1987; Ehrmann *et al.*, 1997), and hence whey. There may be some compensatory decrease in casein % (Ng-Kwai-Hang *et al.*, 1986) but not enough to eliminate the increase in total protein %. There is a tendency, usually non-significant, for the AA genotype to increase milk yield by up to 100 l. This may explain part of the decrease in casein %. The AA genotype also decreases fat % by about 0.05% compared with the BB genotype. The consistency of this effect suggests it is due to the β-lactoglobulin gene itself, but Bovenhuis and Weller (1994) also found evidence for a gene linked to β-lactoglobulin affecting fat %.

The κ-casein gene also affects the concentration of its own protein, with the BB genotype causing the highest concentration. In AB heterozygotes, the concentration of B protein in the milk is almost twice that of A protein (Van Eenennaam and Medrano, 1991b). This effect is most easily explained by a polymorphism in a regulatory region of the gene which is in linkage disequilibrium with the polymorphism in the coding region. This explanation is supported by the absence of an effect of κ-casein genotype in breeds other than Holstein. Due to this increase in κ-casein, the total protein % is about 0.05% higher in BB than AA genotypes. The yield of protein (kg) in most studies is also highest in BB genotypes, but there is no consistent effect on milk volume. There is no consistent effect on fat % or yield, although Hines (1990) suggested a QTL for fat % linked to κ-casein.

The effect of the β-casein genotype is less clear-cut than that of β-lactoglobulin and κ-casein, but it appears that, in Holsteins, the B allele increases the production of β-casein (Kroeker *et al.*, 1985; Ng-Kwai-Hang *et al.*, 1987; Ehrmann *et al.*, 1997) and hence increases casein % (Ng-Kwai-Hang *et al.*, 1986) and protein %. The advantage of the B allele does not lead to an increase in protein yield (kg), due to a possible depressing effect on milk volume. There have been some studies with significant effects of β-casein genotype on fat %, with the A_1 and B alleles associated with highest fat % (Ng-Kwai-Hang *et al.*, 1984, 1986; Bovenhuis *et al.*, 1992; Bovenhuis and Weller, 1994).

At the α_{s1}-casein locus, the C allele increases protein %, possibly because it increases the proportion of α-casein itself (Ng-Kwai-Hang *et al.*, 1987; Ehrmann *et al.*, 1997). However, the C allele does not cause a consistent increase in protein yield and in fact the B allele appears to be more often associated with the highest milk yield.

At the β-lactoglobulin and κ-casein genes, the BB genotypes have the highest ratio of casein to whey proteins and they also have greater cheese yield and shorter renneting times than the AA genotypes (Graham *et al.*, 1984; Marziali and Ng-Kwai-Hang, 1986; Aleandri *et al.*, 1990).

In summary, evidence is building that the genotype at milk protein loci has its primary effect on the synthesis of its own protein. Poorly understood regulatory mechanisms may then lead to changes in the synthesis of other proteins and perhaps even milk volume and fat. In addition, there is evidence for genes affecting fat % which are linked to the casein complex and β-lactoglobulin (Ron *et al.*, 1994).

With the advent of deoxyribonucleic acid (DNA) technology other candidate genes have been investigated, and prolactin (Cowan *et al.*, 1990) and growth hormone (Hoj *et al.*, 1993; Falaki *et al.*, 1996) are reported to affect milk production.

A more systematic approach to finding genes for milk production is to map QTL, using a linkage study and a collection of genetic markers that cover all 30 chromosomes. Using a granddaughter design (Weller *et al.*, 1990), Georges *et al.* (1995) found five chromosome regions that affected milk, fat or protein yield. One QTL mapped to chromosome 6, which includes the casein loci, but the QTL mapped to a different part of the chromosome.

When performing significance tests with 159 genetic markers, as Georges *et al.* (1995) did, there is a high probability of false positives. To guard against this, Georges *et al.* used a very stringent significance level. This reduces the likelihood of false positives but means that some QTL that were segregating in their families are likely to have missed detection. Ashwell *et al.* (1997) performed a similar but smaller experiment, with only 16 markers and a less stringent significance test. They found many markers that were significant for some trait in some family, but a number of these are expected to be false positives.

Other studies vary in the stringency of their significance tests and hence their trade-off between too many false positives and failing to detect QTL that are segregating. However, cases of agreement between studies confirm the presence of QTLs.

Boichard and Bishop (1997) confirmed the existence of a QTL affecting protein yield and milk yield near the beginning of chromosome 1, found by Georges *et al.* (1995). Both Mosig (1998) and Ron (1998) reported a QTL for protein % on chromosome 3 at about 50 centimorgans (cM). On chromosome 6, there appear to be at least two QTL (Kuhn, 1996), one around 30–50 cM (Georges *et al.*, 1995; Boichard and Bishop, 1997; Gonaz-Raya, 1998; Mosig *et al.*, 1998) and one around 80 cM (Mosig *et al.*, 1998), close to the casein genes. The first QTL increases milk volume without changing fat and protein yield and so decreases fat % and protein % (Georges *et al.*, 1995) or at least protein % (Spelman *et al.*, 1996). On chromosome 9, Georges *et al.* (1995) found a QTL affecting fat and protein yield at about 60 cM; in a similar location Mosig (1988) detected a QTL affecting protein % (they did not measure the effect on other traits); and Vilkki *et al.* (1997), in a different breed, found evidence, although not significant, for a QTL affecting milk and protein yield.

In contrast, on chromosome 10, Georges *et al.* (1995) found a QTL at about 20 cM affecting fat %, Mosig (1998) a QTL at about 40 cM affecting protein % and Ron (1998) a QTL at about 80 cM affecting protein %. On chromosome 23, Boichard and Bishop (1997) and Ashwell *et al.* (1997) found suggestive evidence for a QTL affecting fat yield. The prolactin gene also maps to chromosome 23.

It seems likely that, with further research, many QTLs affecting milk production will be mapped and hopefully these genes will eventually be identified. Some will probably turn out to be known genes, such as the caseins, and some previously unknown genes.

Genetic Evaluation

The goal of a genetic evaluation system is to produce rankings of animals that will enable progress in attaining a breeding objective when selection decisions are made based on the rankings. Both national and international genetic evaluation systems have been developed over the last 60 years. As statistical techniques and computing power have advanced, evaluation systems have become more accurate in estimating genetic differences.

Evaluation models

One of the earliest methods for genetic evaluation of dairy bulls was a daughter–dam comparison. This method assumed that the difference in yield between a bull's daughter and its dam resulted from the genetics of the bull; that is, the effect of environment was assumed to be constant. The daughter–dam comparison was followed by the herdmate comparison, which accounted for the effect of environment by comparing animals that produced in the same herd and calved during the same season. However, the daughter–dam comparison did not account for genetic differences between herds or consider the genetic contribution from parents. Relationships among cows through their sires (and later maternal grandsires) were able to be accounted for by using best linear unbiased prediction procedures with a sire model, thereby joining the genetic considerations of the daughter–dam comparison and the environmental considerations of the herdmate comparison.

Currently, an animal model is used by nearly all major dairy countries. An animal model allows consideration of all relationships among animals and results in simultaneous evaluation of cows and bulls. A particular animal's evaluation is a function of the evaluations of its parents and its progeny, as well as its own records. However, because the system is simultaneous, information from one animal can affect the evaluations of others.

In Australia, New Zealand and the north-eastern USA, the lactation measure is calculated from yield deviations on individual test days. This test-day model allows more accurate accounting for environment, because effects of specific test days are estimated. The test-day model is an animal model that uses the test-day yields instead of the lactation yields as input. One advance in this model is to allow for genetic differences by test day. Jamrozik *et al*. (1997) of Canada have proposed fitting a lactation curve for each cow and lactation as a random genetic effect. An alternative proposed by Wiggans and Goddard (1997) is to define test-day yields as separate effects which are correlated and to analyse them in a multitrait analysis. Both of these approaches support analysis of persistency and should reduce the fluctuation in evaluations of bulls when many second-crop daughters' partial lactation records are added. This fluctuation may be caused by daughters whose lactation curves differ from the norm.

National evaluations

Each country has adapted its evaluation system to model the structure of its data. Some of the ways in which systems differ include calculation of lactation records, parameter estimates, accounting for age, definition of environmental groups, definition of unknown-parent groups, accounting for inbreeding and heterosis, and reporting scale for evaluations.

International evaluation

The extensive marketing of bull semen and embryos internationally has generated an interest in international comparison of bulls. The Interbull Centre in Uppsala, Sweden, combines bull evaluations from participating countries to generate rankings that include the bulls from all countries, but reported on each country's evaluation scale. This multitrait, across-country evaluation (MACE) (Schaeffer, 1985) recognizes correlations of less than one between performance in different countries, so the rankings may differ. The MACE procedure was first used in 1994. Previously, conversion equations were used. The Interbull Centre also conducts research to improve international ranking and ways to extend the procedure to other traits.

Traits evaluated

Milk yield is the fundamental trait analysed, although milk fat percentage determination has been part of most milk recording systems since the beginning. With the growing importance of manufacturing and the improvements in laboratory equipment, determination of protein content has become almost universal in major dairy producing countries. Somatic cell count collection is also widespread and is used as an indicator of udder health and the presence of subclinical mastitis. Most countries also have a programme to collect conformation trait data. Recent research effort has focused on using these traits to select for increased profitability through prolonged herd life or greater disease resistance or as an indicator of maintenance cost.

Genetic trend for yield

Average breeding value of cows by birth year is a common measure of genetic trend and an indication of the success of a national breeding programme. However, the evaluation model and the adjustments for age effects can affect trend estimates. Table 18.10 shows the trend in breeding values for yield traits

Table 18.10. Genetic trend in yield traits of US Holstein cows born in 1994.

Trait	Trend (kg)	% of mean production
Milk	131	1.3
Fat	3.9	1.1
Protein	4.1	1.3

of US Holstein cows. Because trend has been increasing in recent years, the values are specific for cows born in 1994.

Economic indices

With the large number of traits analysed, it is necessary to define a breeding goal and develop an index that weights individual traits according to their contribution to that goal. In many countries, there is a negative weight on milk volume, because of the cost of production, hauling and removal. Protein yield receives heavy weight in most indices. Scandinavian countries have an extensive system for collection of health data and include health traits in their index.

Future enhancements

With the rising cost of labour, most milk recording systems are attempting to find less expensive ways to collect data. This has led to the popularity of a.m.–p.m. plans where only one milking per month is recorded, at alternating times (a.m. or p.m.). Large herds with electronic meters able to collect daily weights find that collection of samples is a considerable inconvenience and so collect samples only quarterly. A test day model is well suited to accommodate a wide range of testing plans.

With the advances in DNA technology, genes that influence yield of milk and components are likely to be discovered. Evaluation systems can be adapted to estimate the effect of various alleles and improve accuracy of evaluations by using that information.

Design of Breeding Programmes

Estimated breeding values (EBVs) provide cattle breeders with a tool for identifying the best bulls and cows for breeding. Genetic progress is also affected by which specific matings are made. The design of breeding programmes specifies how these cattle are mated. In dairy cattle, research into the design of breeding programmes has focused on obtaining maximum benefit from new technology, especially reproductive technology, such as AI and multiple ovulation and embryo transfer (MOET).

Artificial insemination

The availability of AI led to breeding programmes based on progeny testing. A group of young bulls are progeny-tested by producing a number of daughters each. After the progeny test, bulls selected for widespread use are mated to produce replacement heifers and a new generation of young bulls. These young bulls are bred from the best cows available. Selection of cows to produce replacement heifers is also practised, but is of limited value because the low reproductive rate of cows means that nearly all cows are needed to maintain the herd size. Thus there are four types of selection decisions: bulls to breed bulls, bulls to breed cows, cows to breed bulls and cows to breed cows, but the selection intensity on the fourth pathway is low.

The design parameters which have attracted most attention are the proportion of cows to be mated to young bulls, the number of young bulls' progeny tested per year and the number of daughters per young bull. The optimum values of these parameters vary widely between studies, from 15% to almost 100% of cows mated to young bulls and 20 to 400 daughters per young bull. For a given-size population of cows, these two parameters determine the number of young bulls to be progeny-tested (Skjervold and Langholz, 1964; Van Vleck, 1964; Lindhe, 1968; Hinks, 1970; Hunt *et al.*, 1972; Brascamp, 1973; Oltenacu and Young, 1974; Petersen *et al.*, 1974; Stitchbury and Goddard, 1985; Dekkers *et al.*, 1996).

Several factors explain the different optima found. If the rate of genetic progress is the objective, the optimum number of daughters per bull is low and the optimum proportion of cows mated to young bulls is high (Skjervold and Langholz, 1964). However, if the economic benefit from the programme is the objective, the optimum number of daughters per bull is higher and the proportion of mating to young bulls is reduced (Van Vleck, 1964; Lindhe, 1968; Hinks, 1970; Brascamp, 1973; Petersen *et al.*, 1974; Dekkers *et al.*, 1996). Because it is expensive to purchase and raise new bulls, it costs less to produce an extra daughter from a bull already being tested than the first daughter from a new bull (Meuwissen and Goddard, 1997). Also, discounting future benefits favours using proved bulls instead of young bulls, so that the benefits of selection are achieved more quickly.

The breeding objective also affects the optimum design. If the objective is for dual-purpose cattle, bulls can be selected for progeny-testing based on their own performance (i.e. growth rate). This increases the optimum proportion of matings to young bulls and increases the number of daughters per young bull. However, if the objective includes traits of low heritability (e.g. mastitis resistance and fertility), the optimum number of daughters per young bull increases (Skjervold and Langholz, 1964; Meuwissen and Woolliams, 1993).

As the population size increases, the optimum proportion of matings to young bulls decreases, the number of daughters per bull increases, the number of bulls' progeny tested increases and the rate of genetic gain increases (Skjervold and Langholz, 1964; Stitchbury and Goddard, 1985). In practice, the advantages of large population size are being exploited by the use of a 'global' breeding programme in which bulls to breed bulls are selected from a worldwide pool of bulls. These optima are comparatively flat, so there is little cost in departing slightly from the optimum value of a parameter. When economic benefit in specialized dairy cattle is the objective, 100–200 daughters per young bull is close to the optimum and in fact major dairy breeding programmes are using such designs (Van Vleck, 1964; Lindhe, 1968; Hinks, 1970; Brascamp, 1973; Petersen *et al.*, 1974; Stitchbury and Goddard, 1985; Dekkers *et al.*, 1996).

Multiple ovulation and embryo transfer

At first, the availability of MOET did not appear to be of much value to dairy breeding programmes, because it was too expensive to use on the 'cows to breed cows' pathway and the cows to breed bulls were already highly selected. New designs were needed to gain benefit from MOET. Nicholas and Smith (1989) proposed nucleus breeding herds, with selection of bulls based on the performance of their sibs and older relatives. In the so-called 'adult' scheme, bulls and cows were selected at 3½ years of age, when the cows have a partial lactation record. In the 'juvenile' scheme, bulls and cows were selected at 15 months of age, based on their parents' EBVs. With MOET, both nucleus schemes had faster predicted genetic gain than a traditional progeny-testing programme. More recent calculation of the predicted rates of genetic gain have reduced the superiority of the nucleus MOET schemes, but not eliminated it (Lohuis *et al.*, 1993; Lohuis, 1995). These designs have a reduced generation interval but less accurate selection than progeny testing. In practice, the very short generation interval is hard to achieve.

The nucleus and progeny-testing designs could be combined by opening the nucleus to élite cows from the general population and by using progeny-tested bulls as sires within the nucleus ('hybrid' schemes). Meuwissen (1991) showed that MOET increased genetic gain by 13% in these hybrid schemes. Estimated breeding values, which can compare animals across age-groups, provide a logical way to select between bulls and cows of different ages, and inside and outside the nucleus. In this way, some young bulls and some proved bulls can be used as sires within the nucleus.

Selection on EBV maximizes the genetic merit of the next generation, but it is not necessarily the policy which maximizes the merit of future generations. There may be an advantage in selecting animals with a lower EBV but of lower reliability, because this improves the opportunity for selection in later generations (Goddard and Howarth, 1994). For instance, Meuwissen (1991) found that selecting cows outside the nucleus on EBV could actually decrease the rate of genetic gain. Similarly, it might be worthwhile to use young bulls to breed bulls even if they have a lower EBV than the best proved bulls. However, the improvement in genetic gain by doing this is usually small.

With aspiration of oocytes from the ovaries, followed by *in vitro* maturation and fertilization (*in vitro* embryo production (IVEP)), it is possible to increase the reproductive rate of cows above that possible with MOET and to achieve a further small increase in genetic gain (Kinghorn *et al.*, 1991; de Boer and Van Arendonk, 1994; Leitch *et al.*, 1995; Lohuis, 1995).

Minimizing inbreeding

Intense selection implies a small number of parents for the next generation and in time this causes inbreeding. Small effective population size and inbreeding cause inbreeding depression, increased incidence of recessive abnormalities, reduced genetic variation and random fluctuations in the mean of the population. Consequently, it is desirable to minimize inbreeding and maximize genetic gain, which, because they are conflicting objectives, implies some trade-off between them (Leitch *et al.*, 1994). In traditional progeny-testing schemes, the number of bulls used in the nucleus or used to breed bulls largely determines the rate of inbreeding. Most studies have found the optimum balance between genetic gain and inbreeding was to use two new bulls each year (Skjervold and Langholz, 1964; Hunt *et al.*, 1974; Petersen *et al.*, 1974; Stitchbury and Goddard, 1985). This high intensity of selection may not be appropriate for large populations, such as the global black and white cow population (Goddard, 1990). Fortunately, slight differences in breeding objectives between countries can lead to different bulls being selected in different countries, and consequently the total number of bulls used is increased (Goddard, 1990).

Nucleus schemes using MOET, with their short generation intervals, have higher rates of inbreeding than traditional designs. When minimizing inbreeding or variance of the mean is part of the objective, this causes the optimum design to move toward use of proved bulls and an open nucleus. There is also an advantage to factorial mating schemes in which each cow is mated to several bulls (Leitch *et al.*, 1994; Meuwissen and Woolliams, 1994; Luo *et al.*, 1995).

As the reproductive rate of cows increases (e.g. by using IVEP), the number of cows needed as parents decreases and this further increases inbreeding. Optimum designs may then use as many bulls as cows in a square factorial mating system or even more bulls than cows, because the accuracy of selection of bulls is less than that of cows at 4 years of age (de Boer and Van Arendonk, 1994).

Cloning

The technology to produce many genetically identical cows may soon be available (Seidel, 1996). Cloning would not greatly increase the rate of genetic gain in the nucleus (de Boer and Van Arendonk, 1994). However, it could dramatically reduce the amount by which the average commercial cow lags behind the nucleus. In this scenario many clones would be produced and distributed as embryos to commercial dairy farmers. This would provide a once-only lift in the genetic merit of the commercial cow population, but it would be necessary to maintain existing breeding programmes to generate ongoing genetic improvement.

Marker-assisted selection

Some genes that cause variation in milk yield or other important traits have been identified or mapped by linkage to genetic markers, and the number of these genes will undoubtedly increase (Ng-Kwai-Hang *et al.*, 1984, 1986, 1987; Kroeker *et al.*, 1985; Gonyon *et al.*, 1987; Aleandri *et al.*, 1990; Van Eenennaam and Medrano, 1991; Bovenhuis *et al.*, 1992; Bovenhuis and Weller, 1994; Famula and Medrano, 1994; Ehrmann *et al.*, 1997). Deoxyribonucleic acid tests for genotype at these loci provide additional information on the genetic value of bulls and cows and so could lead to more accurate selection. The genotype information is most useful for traits which are otherwise difficult to select for or for genes which show non-additive gene action (Larzul *et al.*, 1997).

Computer simulations of MOET nucleus herds show that tests for markers linked to QTL could increase the rate of genetic gain by up to 20% (Ruane and Colleau, 1996; Meuwissen and Goddard, 1997). However, in traditional progeny testing programmes the benefit is less (Spelman and Garrick, 1997). It takes some years before the maximum benefit from the markers is achieved because the initial data are used to establish linkage phase. In the long term, the benefit from markers declines, because the QTL to which they are linked becomes fixed and so the markers are no longer useful. In the very long term, selection using the markers may even achieve less progress than selection ignoring the markers (Gibson, 1994). If a test existed for the QTL itself, instead of the markers linked to it, this would allow faster genetic progress and be easier to implement, because data to establish linkage phase would not be needed.

A DNA test is available for one mutation at the melanocyte-stimulating hormone (MSH) locus, which causes red coat colour (Klungland *et al.*, 1995), and for some disease genes, such as citrullinaemia (Dennis *et al.*, 1989). These tests help to identify carriers of undesirable genes but the economic benefit from this is usually small compared with an increase in traits such as milk protein yield.

Conclusions

Rapid progress in genetic improvement of dairy cattle has been achieved in recent years. This progress has resulted from a focus on yields of milk and components, the traits of primary economic importance. The investment of producers in milk recording and AI organizations in testing a large number of young bulls each year has been an important contribution to this success. Data collection is somewhat easier with dairy cattle than with some other farm species, because of the intensive nature of production and the relatively high value of the individual animals. This situation has led to a highly developed system of data collection, genetic evaluation and young sire development. Future developments in marker-assisted selection, evaluation methods and breeding plans hold promise for further increases in the rate of genetic improvement.

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