# Genetic Improvement of Beef Cattle



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# Introduction

The aim of this chapter is to discuss the breeding goals, genetic resources and methods of genetic improvement used in beef cattle breeding. The emphasis is on genetic improvement in temperate production systems. Food and Agriculture Organizatin (FAO) statistics on the world production of beef and veal by continent show that North and Central America have the highest production at

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about 30% of the world total, and Europe follows with about 21% of global production (FAO, 1996; Simm, 1998).

Beef cattle breeding in temperate countries is fairly heterogeneous, so it is worth setting the scene a bit further. In most European countries, over 50% of beef production is from pure dairy or dual-purpose breeds, either from cull cows, from male calves or from surplus female calves not required as dairy herd replacements. Traditionally, beef breeding goals and criteria were usually considered in dairy and dual-purpose breeds. However, there is often little or no emphasis on beef traits today, in dairy breeds. In addition to this direct contribution from dairy herds, there is an indirect contribution to beef production through crossing of dairy cows to beef bulls. This produces beef × dairy calves for slaughter and, in some countries, beef × dairy suckler cows (i.e. cows kept for rearing beef calves).

Many European countries have only a small specialized beef cattle breeding industry - in many cases, this comprises purebred terminal sire breeds to supply beef bulls for crossing in dairy or dual-purpose herds. In contrast, pure beef breeds account for a high proportion of total production in France and, to a lesser extent, in Italy and Spain. In Britain and Ireland, suckler herds of beef x dairy cows, derived as a by-product of the use of beef bulls in dairy herds, make an important contribution to total output. In other major temperate beef-producing countries, such as the USA, Canada, parts of South America, New Zealand and parts of Australia, beef production is based on extensively grazed or ranched cows, mainly of pure British beef breeds, like the Hereford, Aberdeen Angus and Shorthorn, or crosses among them. In some of these countries, such as the USA, Canada and parts of Australia, this extensive preweaning regime is usually followed by a more intensive finishing period in feedlots. The extensive nature of many production systems, and the widespread use of crossbred animals in the commercial sector of most beef industries means that performance recording and genetic improvement are usually concentrated in a relatively small sector of the population.

*Bos indicus* and Sanga beef breeds have been widely used in tropical areas in developing countries. Their use in tropical and subtropical regions of developed countries, such as Australia, has increased markedly in the last few decades, but more emphasis is now being placed on their crosses with *Bos taurus* breeds in an attempt to increase productivity and product quality.

# **Breeding Goals**

From the brief introduction above, it is apparent that there are two broad categories of beef production in many countries: (i) beef production from dairy and dual-purpose herds; and (ii) beef production from specialized beef herds. Within the specialized beef sector, there is further differentiation into terminal sire and maternal breeds, crosses or lines. Terminal sire breeds also get used in dairy and dual-purpose herds. Each of these categories of use requires a distinct set of beef breeding goals, or at least different priorities, and these are discussed below. However, some more general issues of formulation of breeding goals are described first.

# Formulation of breeding objectives

Breeding objectives stipulate the animal characteristics to be improved and the desired direction for genetic change. They should be constructed in a manner that allows them to play an appropriate role, together with parameters such as heritability and correlations, as part of a genetic evaluation system, in order to facilitate ranking of animals on genetic merit and implementation of an effective breeding programme design.

To this end, breeding objectives are generally expressed as economic weightings, which describe the economic impact of a unit change in each trait of commercial importance. These economic weightings can be used directly to help evaluate different breeds and crosses, or, more commonly, they can be used in conjunction with genetic parameters and knowledge of population structure to rank animals on an index of genetic merit in monetary units.

The breeding objective traits are not necessarily the same as the selection criterion traits that are measured and used to make selection decisions. For example, lean percentage may be a breeding objective and ultrasonically measured backfat thickness a selection criterion. Knowing the genetic relationship between these two traits permits selection index methods to target the former, using data on the latter.

There are two approaches to calculating these weightings – the economically rational approach and the 'desired gains' approach.

### The economically rational approach

The classic approach to calculating economic weightings is economically rational – it takes no account of genetic parameters. This makes sense in that the value of making a unit change in a given trait should not be influenced by how difficult it is to generate this change. These difficulties can be handled appropriately at the genetic evaluation phase. In this setting, breeding objectives should reflect the costs and returns involved in a production system, and should not consider costs and gains generated in a breeding programme.

*Help from biological modelling* The economically rational approach assumes that we know the genetic parameters (heritabilities, genetic correlations and phenotypic correlations) for all traits that are measured and/or of economic importance. However, this is often not the case in beef production systems, where it is extremely difficult to measure many of the traits of true importance, such as mature size, the shape of the growth and feeding curves and the patterns of tissue deposition. Such traits are often ignored when developing breeding objectives and yet their direct or indirect effect on profit can be large. In particular, the effect of mature size on production efficiency is such that selecting for

efficiency as measured between fixed ages or fixed weights can be quite misleading (Kinghorn, 1997).

The approach generally assumes that the biological interactions among traits are linear in nature. However, this is often not the case in meat production systems, where relationships can be complex, such as the effect of fatness on maternal ability and juvenile survival in heterogeneous environments. It is possible that relationships are neutral at the current levels of trait expression, but that with genetic change in selected traits, thresholds are passed and/or relationships develop.

Biological modelling of production systems can be used to predict such changes. This modelling usually involves a mixture of mechanistic and empirical features (Ball *et al.*, 1998). Mechanistic features give powers of extrapolation beyond what we get through use of empirically derived parameters, such as heritabilities and linear correlations. However, biological modelling cannot be used to reliably separate predictions of genetic relationships and phenotypic relationships, and this casts doubt on its power to help set breeding objectives. In practice, it seems that biological modelling can play a quality-control role, to predict any deleterious effects of breeding objectives set through use of an economically rational approach.

*Units of expression* All economic weightings in a breeding objective should have the same basis for units of expression, such as 'dollars per head'. Choice of this basis can have an important influence of the consequences of using the breeding objective. A simple basis for unit of expression, such as 'dollars per head', can be used for situations in which all traits are directly related to economic costs or returns, and thus excludes reproductive traits, whose effect is at least partly manifested through progeny. A less simple basis is 'dollars per breeding cow per year', which accommodates both production and reproduction traits. In all cases, each trait should use this same basis. Delays in returns due to expression in progeny can be accommodated by considering the pattern of flow of genes through the population, and discounting future returns to give current values (McClintock and Cunningham, 1974).

Economic weights calculated on a 'dollars per head' or 'dollars per breeding cow per year' basis suffer a potentially important drawback. They relate to dollars per livestock unit, rather than dollars per resource unit, such as 'dollars per hectare'. As an example, consider two breeds of beef cattle:

	Value of weight	Value of food	Profit per	Dollar
Breed	at slaughter	consumed	head	efficiency
Small Large	\$1000 \$1800	\$500 \$1000	\$500 \$800	2:1 1.8:1

The large breed would be targeted by a breeding objective based on 'dollars per head'. However, a breeding objective based on 'dollars per hectare' would target the small breed. A breeding objective based on dollars per resource unit will usually be more appropriate, as long as proper account is made of any fixed costs per head. Economic values can be calculated from several different perspectives, e.g. with the aim of maximizing the profitability of an enterprise for an individual producer, or with the aim of improving the efficiency of a national livestock industry. Amer (1994) and Weller (1994) discuss these different approaches and the attempts to unify them. In the former category, increasingly sophisticated models have been proposed for deriving economic values, including enterprise models which reoptimize management following genetic improvement (e.g. Amer *et al.*, 1996, 1997).

#### The 'desired gains' approach

An alternative approach to developing breeding objectives, the 'desired gains' approach, involves declaration of the relative magnitudes of genetic gain desired in the traits of importance. The breeding objective calculations still result in relative economic weights, but these are now influenced by genetic parameters, with generally greater economic weightings for traits that are more difficult to change. A simple subset of this approach is the restricted index, in which the objective is set up to give a predicted zero genetic change in one or more nominated traits. Examples are restrictions for no change in backfat or birth weight.

Brascamp (1984) describes methods that can be used for both restriction and desired gains. He also shows how to use a mixture of the economically rational and the 'desired gains' approaches, with some traits constrained to prechosen levels of response and others influenced just by production economics. In all cases, relative economic weights are calculated, which is useful for demonstrating the 'effective economic weights' that nominated desired gains or restrictions imply.

# Breeding goals for beef production systems

#### Beef breeding goals in dairy and dual-purpose breeds

At first sight, it seems efficient to breed for both milk and meat production from the same type of animal. However, most of the evidence suggests that there is an unfavourable genetic correlation between milk production and growth or carcass characteristics (e.g. Pirchner, 1986).

Some breeds or strains, such as the Simmental strains in several continental European countries, have achieved fairly high productivity in both milk and beef traits, as a result of many generations of selection. Even for these strains, it is difficult to compete nationally and internationally with both specialized milk and specialized beef breeds. As a result, there is a general trend towards milk production from more specialized dairy cattle breeds and strains. In some countries, there is still an attempt to limit the expected deterioration in beef merit by performance-testing dairy bulls for growth and conformation, and preselecting bulls on these traits prior to progeny-testing for milk production. In other countries, the deterioration in beef merit of the specialized dairy strains is compensated for, at least partially, by crossing those females not required to breed replacement dairy heifers to specialized beef breeds. So, in temperate dairying countries with large-scale specialized industries, breeding goals in dairy breeds have little or no emphasis on beef traits. Even in dual-purpose breeds, the emphasis on beef traits is likely to be secondary to that on milk traits (Simm, 1998).

#### Terminal sires for use in dairy herds and specialized beef herds

Terminal sire beef breeds (i.e. those specially selected to sire the slaughter generation of animals) are used in dairy herds, for two main purposes. The first is to mate to dairy heifers to reduce the risk of calving difficulties, compared with that following matings to a dairy sire. The second is to mate to mature dairy cows that are not required to breed replacement dairy heifers.

Difficult calvings are costly, both directly and because they delay rebreeding, depress milk production and compromise both cow and calf survival and welfare. Hence, dairy heifers have often been mated to bulls from one of the easier-calving beef breeds, such as the Hereford, Aberdeen Angus and Limousin. However, mating dairy heifers to a beef bull is becoming less common as more dairy producers recognize that their heifers are often the highest genetic-merit animals in the herd, and hence valuable as dams of replacements. Also, the wider availability of calving-ease evaluations in dairy breeds means that it is easier to select a dairy sire suitable for mating to heifers.

As the incidence of calving difficulties is lower in mature cows than in heifers, there is more scope to select beef bulls for other attributes to maximize returns from calf sales. Many beef-cross calves born on dairy farms are sold at a young age. So increasing calf weight and conformation (muscularity or shape) is an important breeding goal for dairy farmers choosing a beef breed, or an individual beef sire – although increasing weight and conformation tends to conflict with the aim of reducing calving difficulties.

The performance of beef-cross calves in later life is of little direct concern to most dairy farmers, although, in theory, sire breeds or individual sires with high genetic merit for later performance ought to result in higher rewards in the marketplace. These market signals work reasonably well at the level of sire breed. There is less widespread discrimination among sires within a breed, although in some countries artificial insemination (AI) companies, beef breed societies or recording agencies have schemes to identify and promote beef sires for use in dairy herds which combine acceptable calving ease with good growth and carcass characteristics.

In many of the specialized beef production systems in temperate countries, there is widespread use of crossbreeding. Often this is to achieve complementary use of breeds. Usually small or medium-sized breeds or crosses are used as dam lines, and larger breeds are used as terminal sires. Larger breeds are valuable as terminal sires as they usually have a faster growth rate and produce leaner carcasses at a given weight than smaller breeds. Although ease of calving is still important when terminal sire breeds are used in specialized beef breeding herds, their main role is to improve the growth and carcass characteristics of their crossbred offspring. The definition of carcass merit depends to some extent on whether commercial animals are sold at live auctions or directly to abattoirs, but it usually encompasses some measure of weight, fatness and conformation. (Breed and sex may also modify the price.) In theory, good communication between sectors of the industry should mean that breeding goals are similar, whether animals are marketed dead or alive. However, in practice they often differ.

In many North American and East Asian markets, a premium is paid for high marbling – that is, high levels of visible intramuscular fat in the eye muscle. Particularly in North America, this premium for marbling is based on its value as an indicator of good eating quality. Recently, interest in marbling in several exporting countries has been fuelled by its importance in the lucrative Japanese beef market.

Meat eating quality is becoming an increasingly important issue with consumers and the meat industry in richer countries. The post-slaughter treatment of carcasses, especially chilling rate, ageing and method of hanging, are known to have important effects on eating quality (Dikeman, 1990; Cuthbertson, 1994). However, there is less information on preslaughter effects on beef eating quality, such as breed, breeding value within breed or production system. The information that is available suggests that there are breed differences in indirect measures of meat quality, especially marbling, colour and fibre type. There are differences in tenderness between breed types: double-muscled breeds generally have the most tender meat, followed by other B. *taurus* breeds, with *B. indicus* breeds ranking lowest. There are less consistent differences in tenderness between the non-double-muscled *B. taurus* breeds, or between any of the breed types, in juiciness and flavour. Despite this, there are consistent reports of substantial within-breed genetic variation in both indirect and direct measures of eating quality (Kemp, 1994). This indicates that there is scope for improvement through within-breed selection, although, in the absence of good live-animal predictors of eating quality, this is difficult to achieve without progeny-testing. In future, molecular markers of eating quality may allow more efficient selection programmes.

#### Breeding replacement females for specialized beef herds

The main breeding goals for cows in specialized beef herds, in addition to adequate growth and carcass merit, are good fertility, ease of calving, good maternal ability (which includes adequate milk production and good mothering ability) and low or intermediate mature size, to reduce cow maintenance requirements. These individual goals are sometimes aggregated into measures like weight of calf weaned per cow per annum, or weight of calf weaned per kg cow mature weight per annum.

The ability of animals to withstand extreme climates and to tolerate low-quality feed and periods of feed shortage is also important in some areas, and there is often concern about possible genotype × environment interactions for these 'adaptation' traits. These traits are often difficult to define, and the most practical route for within-breed improvement is often simply to record and select on performance in the harsh environment concerned (Simm *et al.*, 1996). The emphasis on each of these traits will vary depending on the production system and breed or crossbreed type of cow used. In some cases, the traits of importance will be best improved by selection; in others, they will be best improved by crossbreeding. For instance, the fertility of crossbred cows is usually high, as a result of heterosis, and so is of somewhat less concern in selection within the component breeds (Simm, 1998).

# **Breed Resources and Crossbreeding**

# **Evaluating breed resources**

Genetic evaluation of breed resources is relatively simple wherever good estimates of mean performance are available for the environment and production systems of interest. This is because the effects involved can be measured with high accuracy from much data, and can be treated as fixed effects. These effects constitute an inventory of genetic resources, and the economic value of each breed genotype can be estimated by simply multiplying predicted performance for each trait by its corresponding economic weight, and summing across traits. In contrast, when we come to evaluating the genetic merit of individual animals, there are many fewer data available per estimate, and the random nature of breeding values makes the process more much more difficult, especially for traits that are difficult to measure, such as feed conversion efficiency and disease resistance.

Breed evaluations can be extended to evaluation of different crossbreeding systems, with breeding objectives being calculated according to the specific role of each component breed or cross. For example, the breeding objective for a terminal sire breed would involve little or no pressure on female fertility traits, as these will only be important within that breed, which will constitute only a small part of the total system.

# An overview of crossbreeding theory

#### The value of crossbreeding

The key reasons for crossbreeding are listed here.

- The averaging of breed effects. For example, to get an animal of intermediate size to fit a particular pasture cycle or market demand. This may involve either regular systems of crossing or the creation of composite breeds (e.g. Cundiff *et al.*, 1986).
- Direct heterosis. Crossbred individuals often exhibit heterosis. Heterosis is measured as the extra performance of the crossbreds over the weighted average of their parent breeds. The percentage increase in performance ranges from about 0 to 10% for growth traits and 5 to 25% for fertility traits (e.g. Gregory *et al.*, 1991). The effect of heterosis on the total production

system can be even more than this, as effects accumulate over traits (e.g. Cundiff *et al.*, 1986).

- Maternal heterosis. Crossbred cows can exhibit considerable heterosis in their ability to raise fast-growing, viable offspring.
- Sire-dam complementation. A good crossbreeding system aims to use breeding cows that are of small or intermediate mature size (but not so small that dystocia is a problem), as well as fertile. When a large terminal-sire breed is used, the proportion of feed directed to growing animals is increased and the production system benefits accordingly.
- Possibly cheap source of breeding animals. This is evident in some crossing systems – for example, in the British and Irish beef industries, where many suckler cows have come from matings between beef bulls and dairy cows.

# The genetic basis of heterosis

We need to know the genetic basis of heterosis in order to predict the value of untested genotypes. There are two genetic mechanisms postulated as causing heterosis effects.

- Dominance: where the individual's parents come from two different breeds, the individual will carry a wider range of alleles, sampled from two breeds rather than just one. It is thought that this equips the individual better to perform well, especially under a varying or stressful environment. We would thus expect dominance to be a positive effect, and there is much evidence to support this.
- Epistasis: when we cross breeds, alleles have to interact or 'cooperate' with alleles at other loci which they are 'not used to'. The crossbred animal may thus be out of harmony with itself, and we predict that epistasis, if important, is a negative effect.

The dominance model of heterosis is widely assumed and used, and so this model will be taken here. It should be borne in mind that epistatic loss could cause errors in prediction based on the dominance model alone.

Breed dominance is greatest when all loci consist of two alleles derived from different breeds, as in a first cross ( $F_1$ ). Other crosses show a proportion of this heterosis, equal to the proportion of loci that are heterozygous with respect to breed of origin. This can be seen in the column  $D_d$  (dominance for the direct subtrait) in Table 20.1.

Table 20.1 shows how to predict the merit of untested crossbred genotypes given estimates of crossbreeding effects. These are additive (A) or 'purebreed' effects for each of the three example breeds, and dominance (D) or heterotic effects, here assumed equal for each pair of breeds. Subscripts denote the direct subtrait (d) and the maternal subtrait (m) – both of these being of some importance for weaning weight in cattle. A least-squares analysis of the form  $\hat{\beta} = (X'X)^{-1} X'Y$  can be used to estimate the crossbreeding effects (in vector  $\hat{\beta}$ ) from merit (*Y*), where *X* is the matrix formed by the body of Table 20.1. The section 'Evaluating breed resources' outlines the simple

**Table 20.1.** Example of the prediction of merit of weaning weight from estimated crossbreeding parameters. Multiply the coefficients shown in the body of the table by the values of the corresponding effects (see text). Adding the products gives the prediction of weaning weight, merit, in the last column.

Effects:	Mean	A <sub>d1</sub>	$A_{d2}$	A <sub>d3</sub>	A <sub>m1</sub>	A <sub>m2</sub>	A <sub>m3</sub>	D <sub>d</sub>	D <sub>m</sub>	
Values (kg):	280	+20	0	-20	-6	-1	+7	20	10	Merit
Breed 1	1	1	0	0	1	0	0	0	0	294.0
Breed 2	1	0	1	0	0	1	0	0	0	279.0
Breed 3	1	0	0	1	0	0	1	0	0	267.0
Best $F_1$ (1 $\times$ 2)	1	0.5	0.5	0	0	1	0	1	0	309.0
Best 3 Breed-X $(1 \times 23)$	1	0.5	0.25	0.25	0	0.5	0.5	1	1	318.0
Best Backcross $(1 \times 12)$	1	0.75	0.25	0	0.5	0.5	0	0.5	1	311.5
Balanced (1, 2)	1	0.5	0.5	0	0.5	0.5	0	0.5	0.5	301.5
Synthetics (1, 2, 3)	1	0.33	0.33	0.33	0.33	0.33	0.33	0.67	0.67	300.0
Optimum (1, 2)	1	0.63	0.37	0	0.63	0.37	0	0.47	0.47	302.4
Synthetics (1, 2, 3)	1	0.57	0.31	0.12	0.57	0.31	0.12	0.56	0.56	303.0
Rotations (1, 2)	1	0.5	0.5	0	0.5	0.5	0	0.67	0.67	306.5
(1,2,3)	1	0.33	0.33	0.33	0.33	0.33	0.33	0.86	0.86	305.7

Synthetics at equilibrium; rotations at equilibrium and averaged over years.

Purebreed	When no cross is better
F <sub>1</sub> cross	When direct heterosis is important
3-breed cross	When both direct and maternal heterosis are important
4-breed cross	When paternal heterosis is important as well
Backcross	When only two good parental breeds are available and/or when direct heterosis is not important
Rotational cross	When females are too expensive either to buy in or to produce in the same enterprise
Open or closed synthetic	When both males and females are too expensive. A few initial well-judged importations establish the synthetic, and it can then either be closed (which helps to establish a breed 'type') or left open to occasional well-judged importations

**Table 20.2.** General recommendations on use of crossbreeding.

approach that can be used to consider all breeding objective traits to help predict the economic merit of different crosses.

#### Choice of crossing system

Gregory and Cundiff (1980) reported maternal and direct dominance effects between *B. taurus* breeds at 14.8% and 8.5%, respectively, for weight of calf weaned per cow exposed. This indicates the importance of crossbred cows in the production system, even though maternal dominance is generally reduced at older ages, for example at slaughter age. Gregory and Cundiff used these figures to estimate the genetic merit of a wide range of crossing systems in beef cattle.

The best crossing system to use depends to a large extent on the value of the breeds available, as well as the amount of heterosis expressed in crossbred animals. This is illustrated in Table 20.2 by describing the conditions under which each crossbred genotype is worthy of choice.

Of course, care should be taken to consider factors other than the predicted genetic merit of candidate crosses for the traits of importance. The key factor here is the cost of maintaining structured crossing systems, where separate breeding units are required to give an ongoing supply of purebred and/or crossbred parents. These costs often outweigh the genetic benefits of more structured crosses, especially in low-fecundity species such as cattle, where the parental breeding units must be relatively large to supply the final cross.

# Breeds and crosses used in beef production

Clearly the predominance of black and white strains in the dairy industry means that they are major contributors to beef output, both directly through surplus calves and cull cows and, in some countries, indirectly through their contribution to the genetic make-up of suckler cows. However, the increasing specialization for milk production in black and white strains means that their predominance is often seen as a disadvantage in beef production. Because of the economic incentive towards specialization for milk production in most temperate countries, the biggest opportunity to improve beef output from dairy breeds is through crossing surplus females to specialized beef breeds.

Of the specialized beef breeds in Europe, the French breeds, particularly the Charolais and Limousin, and to a lesser extent the British breeds, particularly the Hereford and Angus, are most common (Simm, 1998). The popularity of the French breeds is probably due to their high growth rates or high lean meat yield, while the popularity of the British breeds is probably due to their relatively low incidence of calving difficulties (Liboriussen, 1982; Thiessen *et al.*, 1984; Cundiff *et al.*, 1986; Gregory *et al.*, 1991; Amer *et al.*, 1992). Also, the traditional British breeds, especially the Aberdeen Angus, have had something of a renaissance recently, because of perceived benefits in eating quality.

The increased use of the specialized French breeds as terminal sires in Europe, often at the expense of the traditional British breeds, is mirrored in many other temperate beef-producing countries. However, the British breeds remain important in breeding herds, either as purebreds or as components of crossbred maternal lines, in many of these countries (e.g. the USA, Canada, Australia, New Zealand).

Although statistics on numbers of animals are useful, several less numerous breeds have a disproportionate influence through the use of AI, especially in dairy herds. For example, in the UK there are relatively small numbers of purebred Belgian Blue cattle, but this breed was responsible for the second largest number of beef inseminations made by the main AI organizations in 1993/94. The growth in importance of this breed is due to its ability to sire high-conformation crossbred calves, with acceptable levels of calving ease, when mated to dairy cows. In several major beef producing countries (e.g. the USA, Australia), there is growing interest in the use of composite breeds, especially as maternal lines. The use of these animals is efficient when rotational crossing is impractical or when several breeds have important contributions to overall merit. The growth in interest in composite breeds is in part based on the results of very extensive research progress at the US Meat Animal Research Center in Nebraska over the last few decades (e.g. Gregory *et al.*, 1991).

*Bos indicus* and Sanga breeds have been increasingly used in crossing systems in tropical beef production regions. There is a general trend to keep the proportion of genes from these breeds low in order to avoid deleterious effect on meat quality. However, research suggests that more variation in meat quality is caused by management and processing factors than by proportion of *B. indicus* genes (Hearnshaw *et al.*, 1998).

# **Selection Within Breeds**

#### Evaluating individuals

What causes an exceptional animal to be so much better than its contemporaries? There are two basic reasons.

**1.** The gene variants (alleles) it has inherited are more favourable and/or they are present in more favourable combinations, making the animal genetically superior.

**2.** It has probably experienced a better 'environment', through good management or good luck.

In seeking genetic change, we are not really interested in how much 'environmental advantage' an animal has had – because that source of superiority cannot be transmitted to the next generation. Moreover, in selection programmes, we are generally not interested in the combination of alleles, as, in general, these combinations cannot be transmitted to the next generation (in the case of intralocus dominance) or are only weakly transmitted (in the case of interlocus epistasis).

We want to be able to choose the animals with alleles that will have the most beneficial effect on progeny, and we do this by selecting animals on the basis of their estimated breeding values. Breeding value (denoted by *A*, signifying additivity of effect) is a description of the value of an animal's alleles to its progeny. In general, we do not know which alleles an animal carries, so we can never fully know what an animal's breeding value is. However, we can estimate it from a wide range of information sources.

The simplest estimate of an animal's breeding value is that based on just its phenotypic superiority (*P*, phenotype as a deviation from the contemporary mean):

$$\hat{A} = \frac{V_A}{V_P} P = b^2 P$$

where  $\hat{A}$  is estimated breeding value (EBV) and  $\wedge$  denotes 'estimate', and  $b^2 = \frac{V_A}{V_P}$  is heritability of the trait concerned. In conceptual terms, the phenotypic superiority of the animal, *P*, is regressed or shrunk according to the proportion of phenotypic variation in the trait concerned which is due to effects that cannot be transmitted between generations.

Selection on phenotype gives a percentage response that depends on:

- selection intensity the smaller the proportion retained for breeding, the higher the response;
- generation interval the younger the average age of parents, the faster the rate of response;
- heritability the higher the heritability the higher the response;
- coefficient of variation (CV) the higher the CV, the higher the response.

The last two factors generally differ between traits. Table 20.3 gives estimates of these for a number of traits in beef cattle.

#### Use of information from relatives - best linear unbiased prediction

In selecting animals to act as parents, we are interested in choosing those with the most favourable alleles. An animal's own performance gives an indication of the value of its alleles to its progeny. However, some of this animal's alleles are also carried by each of its relatives, and so the performance of an animal's relatives can be used to give a more accurate assessment of the alleles it carries.

Thus progressive breeding programmes make use of information from all known relatives. This is of most value when heritability is low – when an

Trait	CV (%)	Heritability (%)
Age at first calving	5.7	6
Conception rate – cows*	61.8	17
Perinatal mortality – direct*	674.1	10
Scrotal circumference	8.0	48
Birth weight – direct	12.3	31
Birth weight – maternal	12.6	14
Weaning weight – direct	12.3	24
Weaning weight – maternal	13.6	13
Postweaning gain	13.7	31
Mature cow weight	12.1	50
Gross food conversion ratio	11.0	32
Backfat depth at constant age	24.5	44
Dressing percentage	3.2	39
Marbling score, constant age	34.1	38
Eye muscle area, constant age	10.1	42
Tenderness	18.2	29

**Table 20.3.** Coefficient of variation (CV, phenotypic standard deviation divided by mean) heritability estimates for a range of traits in beef cattle (condensed from Simm, 1998, after Koots, 1994a, b).

\*These traits are binomially distributed with a high mean, making CV figures less meaningful.

animal's own performance is a poor indicator of breeding value. As heritability increases, there is a diminishing proportional value of information from relatives, until, at a heritability of unity, an animal's own performance is a perfect indicator of its breeding value, with no room for improvement due to relatives' information.

Traditionally, information from different classes of relatives is combined, after correction for environmental effects, using selection indices. However, today, the method of choice for predicting breeding values, which is an extension of selection index methods, is best linear unbiased prediction (BLUP). Kennedy (1981) and Van Vleck *et al.* (1989) give digestible descriptions of BLUP techniques and Kinghorn (1997) gives a small example analysis. This section will not review these, but the following list describes the key properties of BLUP EBVs.

- Estimated breeding values are generally additive. For example, if a bull has an EBV of  $\hat{A} = +20.0$  kg and a cow has  $\hat{A} = +10.0$  kg for 400-day weight, then the prediction is that progeny will have a 400-day weight superiority of (20.0 + 10.0) / 2 = 15.0 kg. This is actually a prediction of progeny genetic value, but, as progeny dominance deviation and environmental deviation are unknown and thus have 'expectations' of zero, it is also a prediction of progeny breeding value and phenotype. Note also that the proportion of parental superiority in EBV that is transmitted to progeny is unity, after accounting for halving due to meiosis. Thus the heritability of EBVs is unity, as they have been pre-regressed.
- Best linear unbiased prediction makes full use of information from all relatives. It does this by use of the numerator relationship matrix, which describes the predicted number of alleles per locus shared by descent between each pair of animals. It is not necessary for BLUP to give separate attention to sib testing, progeny testing, own performance, etc. Use of information from all relatives (even those long dead) is simultaneously handled. This gives greater flexibility, more accurate EBVs and more selection response.
- Best linear unbiased prediction predicts breeding values and accounts for fixed environmental effects simultaneously (management group, herd, season, year, etc.). This means that animals can be compared across groups, giving wider scope for selection. For example, comparing across age-groups means that older animals have to prove their competitiveness at every round of selection. This property of BLUP usually accounts for most of its advantage over less powerful methods.
- Best linear unbiased prediction gives genetic trends. The ability to compare the EBVs of animals born and measured in different years means that year mean EBVs can be calculated and genetic trends reported.
- Best linear unbiased prediction can cater for non-random mating such that bulls can be compared via their progeny even if some were allocated better cows. This can only be done where the cows were allocated on the

basis of their recorded performance, such that BLUP can account for their EBVs when evaluating the bulls concerned.

• Best linear unbiased prediction can account for selection bias. For example, consider ranking bulls on the weaning weights of their daughters at their first two calvings. The worse bulls, who had worse daughters, will have benefited more from culling of daughters on first weaning performance. However, BLUP accounts for this, given that the information used to make selection decisions (first weaning results in this case) is included in the data set.

BLUP analyses are generally provided as a bureau service in association with organized recording schemes.

Outputs from a BLUP analysis includes EBVs (or  $\hat{A}$  values) for each of the traits fitted - which can include both measured criterion traits and breeding objective traits, even if there is missing information on the latter. The breeder only needs to weight EBVs for the objective traits by their economic weights to provide а selection index which s/he can select on: Index =  $a_1\hat{A}_1 + a_2\hat{A}_2 + a_3\hat{A}_3 + \dots$  The selection index is itself an EBV for economic merit.

Some traits are mediated through the maternal environment. For example, weaning weight is influenced genetically not only by the genes in the calf, but also by the genes in its mother, mediated through the maternal environment (e.g. milk supply). Thus the numerator relationship matrix for maternal effects on weaning weight is determined by relationships among the dams of the calves measured. This means that a single set of observations on weaning weight can give rise to both direct EBVs and maternal EBVs. If a breeder is selecting a terminal sire, s/he should ignore the maternal EBV, as this source of genetic merit will never be expressed. However, in order to maximize the weaning weight of the selected bull's grandprogeny via daughters, selection should be based on  $\frac{1}{2}$ EBV<sub>maternal</sub> +  $\frac{1}{4}$ EBV<sub>growth</sub>. This is actually a prediction of the performance of these grandprogeny, and the coefficients result from the fact that the grandprogeny benefit on average from one-quarter of the bull's genes for direct effects, and one-half of the bull's genes, in their mothers, for maternal effects.

#### Estimated breeding values across breeds

There is an increasing interest in genetic evaluations using information from crossbred animals and genetic evaluations on crossbred animals. Pollak and Quaas (1998) give the technical basis of this and a description of example cases. As a simple concept, analysis can be done to estimate all breed and heterosis effects and to simultaneously fit breeding values in a BLUP analysis. This leads to the prediction of progeny merit from any mating pair, based on the breed constitution of the progeny and the EBVs (free of breed and heterosis effects) of the parents.

However, without very good width of data, it is very difficult to get a reliable splitting of breed direct and maternal effects. Moreover, the genetic correlation between breeding values over different breeds of mate may be significantly less than unity – such that, for example, the EBV ranking of a group of Angus bulls might depend on what breed of cow they are to be mated to.

One problem with implementation is the general need to rank breeds and crosses on the breeding objective traits. There is much room for argument over the publishing and use of such values. This is one reason why genetic evaluations across breeds may take place more readily behind the closed doors of large breeding corporations.

# Systems of testing

Most beef cattle genetic improvement programmes are based on performance testing or progeny testing. Both of these depend on performance recording. Essentially, this involves recording the identity, pedigree, birth date, sex and performance (e.g. live weights) of individual animals, plus any major management groupings or treatments likely to influence performance.

#### Performance testing

Since many of the traits of interest in beef cattle can be recorded in both sexes and prior to sexual maturity, there is a fairly long history of performance recording and performance testing in beef breeding. This dates from the 1940s and 1950s in the USA and slightly later in many other countries. Today performance testing is usually the responsibility of breed associations (e.g. in the USA), government departments or agencies receiving some government support (e.g. in many European countries) or private agencies, either alone or in partnership with each other.

Compared with the situation in dairy cattle breeding, a relatively low proportion of beef cattle are performance-recorded. This is partly because of the greater distinction between commercial and breeding herds than in the dairy industry – especially in countries where crossbreeding is widespread. For example, performance-recorded animals comprise less than 2% of the total beef cattle population in the USA (Middleton and Gibb, 1991), Australia and the UK. However, even within the purebred beef sector, there is usually a much lower proportion of recording than in the dairy industry.

Most performance testing schemes involve recording the preweaning performance of all animals on-farm. In some countries, postweaning performance continues to be measured on farm. In others, central performance testing is used. Central testing of beef cattle has been quite widely used worldwide since the 1950s, especially in the USA, Canada and Europe. It involves submitting some animals, especially higher-performing bulls, from the breeders' own farms to a central station, where they are compared with bulls from other herds in a uniform environment. Despite the potential benefits of this, the correlations between the performance of bulls in central stations and the subsequent performance of their progeny is often lower than expected. This is often attributed to large pretest environmental effects.

#### Progeny testing

In many countries there is a deliberate strategy of first performance-testing and then progeny-testing bulls, with selection at each stage. As with performance testing, progeny-testing schemes either operate on-farm or at central testing stations.

Sequential testing is particularly common in the specialized beef breeds in France. Large numbers of purebred animals are performance-recorded on farm for weights at birth, 120 and 210 days, and for muscular and skeletal development at weaning (Ménissier, 1988; Bonnett *et al.*, 1994). The best males from on-farm recording are brought to central testing stations after weaning, and tested further from 8 to 14 months of age. About 35 of the best of these bulls go on to be progeny-tested to assess their daughters' maternal ability, in central progeny test stations.

Progeny testing causes an increase in generation interval, with potentially negative effects on overall selection response. An appropriate breeding programme design is thus needed to balance the effects on increased selection accuracy and increased generation interval. In some cases, the high accuracies generated by progeny testing are themselves of commercial value in the seedstock marketplace, and this should also be taken into account.

# Cooperative breeding schemes

Although most breeding schemes revolve around performance testing or progeny testing, as outlined above, there are some variations that deserve special mention. The first of these are cooperative breeding schemes, such as group breeding schemes and sire referencing schemes. Group breeding schemes usually involve formation of a central nucleus herd, formed from élite cows from cooperating members' herds. When the nucleus is larger than the members' herds, or when recording and selection are more effective, genetic progress can be accelerated. Perhaps because of the relatively high legal and financial commitment required, and the growth in uptake of national across-herd genetic evaluation procedures, there seems to have been a decline in interest in cattle group breeding schemes over the last decade or so. However, formal or informal sire referencing schemes have been established in several breeds in France, Denmark, Britain, the USA and elsewhere, either before or during this period. These schemes involve the use of an agreed panel of sires on a proportion of the cows in each member's herd, usually by AI. In some cases, these schemes have been formed specifically to create or strengthen genetic links between herds to allow more accurate across-herd or across-test genetic evaluations.

#### Traits recorded

Generally, on-farm performance recording schemes around the world have concentrated on measuring live weights at regular intervals (or growth rates between these), together with visual scores of muscularity and measurements or scores of height or skeletal development. The development of mobile, reasonably accurate ultrasonic scanners in the 1970s and 1980s allowed measurements of fat and muscle depths or areas to be included in some on-farm recording schemes. Typically these measurements are taken on or over the eye muscle at one of the last ribs, or in the loin region of animals at about a year or 400 days of age. At least in theory, one of the benefits of central testing is that it permits more frequent and more comprehensive measurements to be made. For example, it is rarely practical to measure feed intake of individual animals on farms, but it is fairly common in central performance test stations. Similarly, progeny testing allows actual carcass measurements to be obtained.

Terminal-sire characteristics have generally dominated beef breeding schemes in Europe. With the exception of some breeding schemes in France, few maternal characteristics, such as fertility, have been recorded. As a result, what little objective selection there has been for maternal characteristics has been on traits like calving ease, birth weight and 200-day weight, which are of importance in both terminal sire and maternal lines. However, until recently, methods of separating direct and maternal genetic influences on these traits have not been in widespread use. Maternal traits have received more attention in North America, Australia and New Zealand, where specialized beef herds account for a far higher proportion of beef output. Genetic evaluations for scrotal size (which is an indicator of both male and female fertility and age at puberty) and female fertility (measured as days from the start of the mating period to calving) have been introduced recently for some breeds in Australia and New Zealand. Evaluations for scrotal size and mature cow weight have been introduced for some breeds in the USA.

Many of the traits concerned with reproduction have fairly low heritabilities. However, many are economically important, and there is substantial variation in them, so there is both the incentive and scope for genetic improvement.

Direct heritabilities of growth traits tend to be moderately high, while maternal heritabilities tend to be slightly lower (Table 20.3). The heritabilities of carcass traits tend to be even higher than those for growth traits. However, carcass traits have to be assessed either indirectly on live candidates for selection (e.g. by ultrasonic measurements), or directly on progeny or other relatives of the candidates for selection, so they are not as easy to improve as it seems at first sight. For more details of genetic parameters, see Koots *et al.* (1994a, b).

#### Evaluations across berds, breeds and countries

To be able to compare BLUP EBVs fairly across contemporary groups and years, genetic links are needed between groups and years. In dairy herds, strong links occur automatically because of the very widespread use of AI. In some countries, there is little use of AI in specialized beef breeds, and this has limited the introduction of national across-herd genetic evaluations. However, AI use is higher in other countries. For example, between 20 and 50% of births

in pedigree herds of the major beef breeds in Britain are the result of AI. Also, the recent introduction of foreign breeds to a country or the popularity of imported strains within a breed tends to increase the use of AI. In such cases, there will often be strong enough genetic links between herds and years to make reliable comparisons of EBVs across herds and years.

A major technical limitation to performing evaluations across breeds is that animals of different breeds are rarely kept as contemporaries under similar management and feeding systems. However, as indicated above, across-breed evaluations are becoming feasible using information from crossbred animals or from designed breed comparisons, together with estimates of genetic trends in each of the purebred populations since the breed comparison was made (Amer *et al.*, 1992; Benyshek *et al.*, 1994).

Compared with the situation in dairy cattle, there has been less effort to date in developing international conversions of EBVs or expected progeny differences (EPDs) for beef cattle or performing international genetic evaluations. However, there is growing interest in this area. For example, international conversions have been produced for some beef breeds in use in Canada and the USA. Also, across-country evaluations are being investigated or performed routinely for several breeds in the USA and Canada, France and Luxemburg, and Australia and New Zealand (Benyshek *et al.*, 1994; Graser *et al.*, 1995; Journaux *et al.*, 1996).

These across-flock, breed and country genetic evaluations are starting to have an important impact. They give credible objective comparison between seedstock sources, which in other industries has led to altered buying patterns and a shake-out in the seedstock sector.

#### Indices of overall economic merit

As noted previously, the selection index provides a means of maximizing response in the breeding objective. Briefly, the selection index apportions selection emphasis in the most appropriate way, based on the relative economic importance of traits in the breeding goal, and on the strength of genetic associations between measured traits and breeding goal traits. Until recently, the emphasis in beef cattle breeding in North America has been on using sophisticated methods to produce individual-trait EBVs. In contrast, in Europe, while less sophisticated methods of evaluation were used until recently, selection indices have been quite widely used in both specialized beef breeds and in dairy and dual purpose breeds.

Much of the emphasis in Europe has been on producing indices for terminal-sire characteristics. For example, a terminal-sire index was introduced in Britain in the mid-1980s and used in most breeds until 1997. The selection objective of this index was to maximize the margin between saleable meat yield and feed costs, taking into account the costs of difficult calvings (Allen and Steane, 1985). Index scores were calculated from the animal's own records of calving difficulty score, 200- and 400-day weight and a visual muscling

score. If they were recorded, additional measurements of birth weight, feed intake and ultrasonically measured fat thickness were included, to increase the accuracy of the index.

In the late 1990s, new indices are being introduced for Signet performance-recorded beef herds in Britain. These are more closely linked to market returns (i.e. using associations with carcass weight, fat class and conformation class rather than with saleable meat yield). Also separate indices are being introduced for calving performance and for growth and carcass performance of terminal sires. The calving value ranks animals on genetic merit for calving ease, based mainly on records of birth weight, calving ease and gestation length, while the new beef value ranks them on genetic merit for growth and carcass traits, based mainly on records for weights, fat depth, muscle depth and muscle score. These two indices can be added together to rank animals on overall merit for calving ease and production together. The contributions which the calving value and beef value make to overall merit vary, depending on the importance of calving ease and on variation in the component traits in the breed concerned. However, typically, calving value accounts for about 16% of the variation in overall merit (Amer *et al.*, 1998).

Indices combining BLUP EBVs for reproduction, growth and carcass traits have been developed in Australia. An important feature of these indices is that the economic values applied can be tailored or customized to individual breeders' requirements. This is achieved via a computer software package, which uses data on returns and costs of beef production for individual producers or production systems (Barwick *et al.*, 1994).

#### Evidence of genetic improvement and its value

#### Estimates of genetic change achievable

In theory, changes of at least 1% of the mean per annum are possible following selection for weight or growth traits in beef cattle. However, in practice, rates of change are often lower than this. For example, a review of several beef cattle selection experiments showed that average changes of 0.6% and 0.8% per annum were achieved with selection for weaning and yearling weight, respectively (Mrode, 1988).

The increased uptake of across-herd BLUP genetic evaluations over the last decade has permitted more widespread estimation of genetic trends in industry breeding schemes. For example, Crump *et al.* (1997) show estimated genetic trends in birth weight, 200- and 400-day growth since 1980, for the most numerous performance-recorded beef breeds in Britain. The changes in 200- and 400-day weights ranged from 0.15 to 0.5% of the breed mean per annum for the different breeds.

Trends similar to or lower than these have been reported in several breeds in Canada and Australia (Graser *et al.*, 1984; de Rose and Wilton, 1988). Slightly higher trends in weaning weight have been reported in the US Angus and Hereford breeds (Benyshek *et al.*, 1994). This may be explained partly by the earlier availability of BLUP methods in the US beef industry. It is probably also partly due to the higher herd and population sizes for these breeds in the USA. Similar trends in weaning weight (from about 0.2 to 1.1 kg per annum) and positive trends in muscularity have been reported for the major French breeds between 1991 and 1995 (Journaux *et al.*, 1996).

In most of these studies of industry trends, the rates of change achieved are well below those theoretically possible and below those actually achieved in selection experiments. The apparently low rate of change is partly explained by the fact that selection has not been solely for weight traits. However, it is also partly due to the relatively low use of objective methods of selection and the fact that, in at least some of the countries mentioned, only within-herd comparisons could be made for most of the period concerned.

#### The economic value of genetic improvement

There have been relatively few studies of the value of genetic improvement in beef cattle, although these do show favourable estimates of cost : benefit (Barlow and Cunningham, 1984). A recent study of the costs and benefits of implementation of across-herd BLUP and index selection in the terminal-sire sector of the British beef industry showed that estimated discounted returns exceeded the costs of implementation, including research, within a few years of introduction. Estimated annual discounted returns are expected to reach about \$18 million per annum and to exceed annual costs of implementation by a factor of 30: 1, about 20 years after introduction of these technologies (Simm *et al.*, 1998).

# Molecular and Reproductive Methods

#### Detection and use of quantitative trait loci

Some single loci of major effect, known as major genes or quantitative trait loci (QTL), have been identified and exploited directly. In cattle, these include the double-muscling gene (Georges *et al.*, 1998) and various coat-colour genes. Most such QTL have been detected by inspection of data. However, systematic methods for computer screening have been developed. More importantly, with the recent development of genetic maps for cattle (Barendse *et al.*, 1997; see Chapter 11), genetic marker plus trait performance data can be analysed to detect and locate other QTL of commercial value (reviewed by Kinghorn *et al.*, 1994).

Where QTL have been cloned and deoxyribonucleic acid (DNA) tests developed to determine genotype for individual animals, genetic evaluation at QTL is relatively simple. The QTL genotypes can be treated as fixed effects, and these effects can be estimated very accurately, just as fixed effects of breed and cross means can be estimated accurately. The QTL effects may differ between genetic backgrounds (e.g. breeds) and between environments or production systems – and the power to estimate the range of effects involved

constitutes a major advantage over evaluation of polygenes using, for example, BLUP. This advantage extends to the ability to market specific QTL-genotyped seedstock with a performance and product image which is much more tangible than for competing 'high polygenic merit' seedstock.

However, such direct DNA tests may not be as reliable as implied above. Georges *et al.* (1998) located the double-muscled cattle *mb* gene at the myostatin locus. Of the 11 DNA sequence polymorphisms identified at this locus, five would be predicted to disrupt the function of the protein. This means that a DNA test to identify just one of the defective alleles would not be reliable in industry – and so caution is required for any gene locus.

Where QTL alleles can be inferred with imperfect accuracy through use of linked markers, marker assisted selection (MAS) can be used (see Chapter 17 for more detail). As with direct DNA tests for QTL, the value of MAS depends on a number of factors.

- Where heritability is low, the value of information on individual QTL tends to be higher.
- Where the trait(s) of interest cannot be measured on one sex, marker information gives a basis to rank animals of that sex.
- If the trait is not measurable before sexual maturity, marker information can be used to select at a juvenile stage.
- If a trait is difficult to measure, is sex-linked or is measured post-slaughter, marker information can be used instead.

Marker-assisted selection is handicapped by the fact that, unless there is considerable linkage disequilibrium, no one marker allele is consistently associated with a favourable QTL allele, due to recombination events. This means that linkage phase in parents needs to be inferred – something which can be done readily with very large half-sib families, as in dairy cattle. However, beef cattle population structures lead to the need for MAS analysis methods which can operate on general pedigrees, and several appropriate methods have been put forward (for example, van Arendonk *et al.*, 1994).

#### Multiple ovulation and embryo transfer nucleus schemes

The potential value of multiple ovulation and embryo transfer (MOET) in accelerating response to selection was first reported for beef cattle by Land and Hill in 1975. They estimated that responses to selection for growth rate could be doubled by the use of MOET, albeit with higher rates of inbreeding. As in dairy cattle, these original estimates of the benefits of MOET are now believed to be on the high side. Recent estimates suggest that 30% extra progress is possible, compared with a conventional scheme of similar size and with the same rate of inbreeding (Villanueva *et al.*, 1995).

While MOET has been used widely in beef cattle as a means of importing and exporting genetic material, and to multiply newly imported breeds or valuable individuals more rapidly than possible with natural reproduction, it has not been used widely in structured breed improvement programmes to date.

## Sexing and cloning

One of the earliest intended uses of in *in vitro*-produced embryos was to improve the beef merit of calves from dairy or suckler cows, by creating a supply of beef embryos. Initially, the main source of eggs was the ovaries of slaughtered beef heifers. Eggs were collected from beef heifers with a high proportion of continental beef breeds in their genetic make-up, and embryos produced from these by maturing them and then fertilizing them with semen from high-merit proved bulls. These embryos were then marketed for transfer into beef suckler cows or dairy cows. Transfers were made either singly or to create twins, either by transferring an *in vitro*-produced embryo into cows already carrying a natural embryo or by transferring two *in vitro*-produced embryos. Despite a ready supply of ovaries from slaughtered heifers, early techniques produced few transferable embryos per ovary. Also, some *in vitro* culture techniques are implicated in the birth of very large calves, generally with associated calving difficulties (Kruip and den Daas, 1997).

More recently, techniques have been developed to allow the recovery of unfertilized eggs directly from the ovaries of live cows (see Chapter 14 for a review of these and related techniques). These techniques involve collection of eggs through an ultrasonically guided needle inserted into the ovary, usually via the vagina (Kruip, 1994). This type of recovery is called *in vivo* aspiration of oocytes or ovum pick-up (OPU). It has several potential advantages compared with recovery of eggs from slaughtered cows or with conventional embryo recovery techniques. In particular purebred animals of high genetic merit can be used as donors, so the technique is of potential benefit in genetic improvement and not just in dissemination. Moreover, eggs can be collected from donors on a weekly basis, allowing tens or potentially hundreds of embryos to be produced from the same donor. The resulting in vitro fertilization allows for cross-classified mating of males and females, which gives a useful boost in selection accuracy under juvenile breeding schemes, in which young animals are selected before measurement, on the basis of their parents' EBVs (Kinghorn et al., 1991).

In most circumstances, sexing of either semen or embryos is probably of little value in accelerating genetic improvement. However, the development of a cheap, reliable technique for sexing semen in large enough quantities for conventional AI could lead to major improvements in the dissemination of genetic improvement and in the efficiency of beef production. Semen or embryo sexing on a smaller scale could still allow more effective dissemination if it is coupled with *in vitro* production of embryos (Cran *et al.*, 1993).

In genetic improvement programmes, cloning could be used to produce many animals of the same genotype in order to improve the accuracy of evaluation, or to allow evaluation of traits normally measured post-slaughter on some members of the cloned group. This would involve implanting some embryos from each cloned line to produce animals for testing, and freezing others to allow subsequent use (or further cloning) of the best-tested cloned lines in breeding or dissemination programmes. One factor to consider here is that clone testing can give accurate estimates of an individual's genetic value (value of alleles to self), but accuracy of EBV (value of alleles to progeny) from clone testing is limited to  $\sqrt{V_A / V_G}$ , where  $V_A$  is variance due to breeding values and  $V_G$  is variance due to genetic values. Moreover, if cloning is considered only in the context of closed breeding schemes, with fixed numbers of animals tested, then the expected benefits generally diminish or disappear, as keeping more identical animals means that fewer different families can be kept and so selection intensities will be reduced (Villanueva and Simm, 1994).

While the benefits of cloning in genetic improvement may be limited, the potential of the technique to accelerate dissemination of genetic improvement to commercial herds or flocks is great, especially for cloning from adult material. For this potential to be realized, reliable and cost-effective methods for cloning will be required. Also, improved and cost-effective techniques for delivery will be needed, including reliable methods for freezing cloned embryos and subsequent non-surgical transfer.

In many countries, there is public concern over the application of new technologies in animal production. Most people accept the use of animals for a range of purposes, including food production, providing that the animals are treated humanely. However, it is often difficult to decide whether or not a particular treatment is humane. For discussion of these issues with respect to new reproductive technologies, see report of the Ministry of Agriculture (MAFF, 1995).

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