

Review Article

Development of breeding objectives for beef cattle breeding: Derivation of economic values

J.F. Kluyts¹, F.W.C. Nesor^{1#} and M.J. Bradfield²

¹Department of Animal Science, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa

²Agricultural Business South Africa (Pty) Ltd., P.O. Box 543, Irene 0062, South Africa

Abstract

The purpose of this article is to review the development of breeding objectives in beef cattle breeding and the derivation of economic values. There seems to be general consensus that definition of breeding objectives should be the primary step in the design of structured breeding programs. Development of the breeding objective can be described in terms of the following phases: specification of the breeding, production and marketing system, identification of sources of income and expense in commercial herds, determination of biological traits influencing income and expense, derivation of economic values, choice of selection criteria, and estimation of phenotypic and genetic parameters. The modelling methods to derive economic weights can be divided into simulation, dynamic programming and profit functions.

Keywords: Beef cattle, breeding objectives, economic values

[#]Corresponding author. E-Mail: nesorfw@sci.uovs.ac.za

Introduction

There seems to be general consensus that definition of breeding objectives, and developing selection criteria based on them, should be the primary step in the development of structured breeding programs (Smith, 1985; Ponzoni, 1986; Ponzoni & Newman, 1989; Newman *et al.*, 1992; Fewson, 1993a). The maximisation of profit is probably the simplest (and most important) possible breeding objective (Harris, 1970). Therefore, the main aim of any selection program should be the improvement of traits of economic importance. When these traits are easily measured, progress is largely dependent on the effective utilisation of the additive genetic variance. Obviously, this necessitates accurate identification of traits and accurate estimates of genetic parameters for these traits under selection. Breeding objectives should, however, also account for inputs/costs as well as outputs/income.

Breeding in all classes of livestock has moved from a purebred appearance orientation to a performance (either purebred or crossbred) orientation. Unfortunately, the evolution from a performance orientation to an economic orientation has been incomplete (Harris & Newman, 1994). Placing breeding objectives into a mathematical form on a sound economic basis is the key to integrating modern developments in animal breeding into more purposeful industry programs. Where consensus is reached about an economic breeding objective, this objective can be used in conjunction with genetic predictions to rank animals within a breeding population.

In practice, several or many traits influence an animal's value, although they do so in varying degrees (Hazel, 1943). Information on several traits can be combined in an index by a special use of Fisher's discriminant function, as proposed by Smith (1936) and Hazel (1943). The genetic gain which can be made by selecting for several traits simultaneously within a group of animals is the product of the selection differential, the correlation between the aggregate breeding value and the selection index and genetic variability. The greatest opportunity of increasing the progress from selection is by ensuring that the correlation between the breeding objective and selection index is as large as possible. Hazel (1943) presented a multiple correlation method of constructing optimum selection indices. However, to solve the simultaneous equations the economic parameters (relative economic values), genetic parameters (heritability, genetic correlations) and phenotypic parameters (standard deviation, correlations) of/among traits must be known (Hazel, 1943). In addition, accuracy and cost of measurement of genetic means determine the definition of the breeding objective (Harris, 1970; Groen, 1989).

Although performance recording of beef cattle has been in operation for over 40 years in South Africa, breeding objectives and multitrait selection indices have not yet been implemented in the livestock industry. However, over the last decades several foreign scientists have studied the theory of breeding objectives and applied the principles to beef cattle breeding. The purpose of this article is, therefore, to review the development of breeding objectives and the derivation of economic values.

Breeding objective / Economic selection index

When selection is applied to the improvement of the economic value of the animal, it is generally applied to several traits simultaneously (Hazel, 1943; Falconer & Mackay, 1996). When these traits differ in variability, heritability, economic importance, and in the correlation among their phenotypes and genotypes, index selection has been more effective than independent culling levels or sequential selection (Hazel & Lush, 1943; Hazel *et al.*, 1994). With index selection, selection is applied simultaneously to all the component traits together, with an appropriate weight being given to each trait according to its relative economic importance, its heritability and the genetic and phenotypic correlations among the different traits (St-Onge *et al.*, 2002).

Therefore, with simultaneous selection for several traits (characters), the objective is to achieve maximum genetic progress toward a stated economic goal (Du Plessis & Roux, 1999) or to improve the net merit (Weigel *et al.*, 1995; Wilton *et al.*, 1998), economic efficiency (Dekkers, 1991) or the aggregate breeding value of animals. The aggregate breeding value represents a fundamental concept, the breeding objective, which is seldom fully implemented in livestock breeding industries (Harris & Newman, 1994). The breeding objective or goal towards which breeders are progressing, is a particular combination of weighing factors (economic weights) and genetic information (estimated breeding values, EBV's) of all the characters to be improved (Falconer & Mackay, 1996; Bourdon, 1997). Since change in breeding objectives requires time, these objectives should be defined according to future market values rather than historical data (Harris & Freeman, 1993). When the objective is maximum improvement in economic merit, the index can appropriately be called an economic selection index (Gibson & Kennedy, 1990). If the economic values of traits of economic importance are linear functions of the trait values, the optimum selection index can be derived as a simple function of the genetic and phenotypic (co)variance matrices, and the vector of economic weights (Hazel, 1943; Pasternak & Weller, 1993). Assigning monetary values to the characters is, however, not necessarily the best method of improvement (Falconer & Mackay, 1996).

Henderson (1963), as quoted by Harris & Newman (1994), noted that in Hazel's (1943) approach, optimum selection toward a breeding objective:

$$H = \sum_1^n a_i G_i \quad (1)$$

requires selection on an index or criterion (which correlates best with H):

$$I = \sum_{i=1}^n (b_i X_i) \quad (2)$$

where H = aggregate breeding value, a_i = economic weight for trait i , G_i = breeding value for trait i , I = selection index, b_i = a selection index weighing factor, X_i = a phenotypic measure and n = number of traits. In matrix notation the unrestricted index would be $I = \mathbf{b}'\mathbf{X}$, where \mathbf{X} is a $n \times 1$ vector of sources of information, \mathbf{b} is a $n \times 1$ vector of weighing factors. The elements of \mathbf{b} are chosen as to maximise genetic gain in a total (aggregate) breeding value or breeding objective defined as $A_T = \mathbf{v}'\mathbf{a}$, where \mathbf{v} is a $m \times 1$ vector of economic values (weights) and \mathbf{a} is a $m \times 1$ vector of breeding values for the traits in the breeding objective. The optimum set of selection index coefficients is those which maximise the correlation (r_{HI}) or minimise the squared deviation between the selection index and the aggregate genotype (breeding objective) (Weller, 1994). Hazel (1943) showed that maximum r_{HI} is achieved when $\mathbf{Pb} = \mathbf{Gv}$. Selection index weights are then calculated as $\mathbf{b} = \mathbf{P}^{-1} \mathbf{Gv}$, where \mathbf{G} is a $n \times m$ genetic variance – covariance matrix for m traits affecting profitability and n correlated indicator traits and incorporates the additive genetic relationships between sources of information; \mathbf{P} is a $n \times n$ phenotypic (co)variance matrix of correlated indicator traits; and \mathbf{v} is a $n \times 1$ vector of relative economic values (Cunningham *et al.*, 1970; James, 1982; Gibson & Kennedy, 1990; Fewson, 1993b; MacNiel *et al.*, 1994).

A useful modification developed by C. R. Henderson was the separated application of the selection index in two steps (Hazel *et al.*, 1994). The first step is the estimation of individual breeding values, through

multitrait analysis, for each trait included in the definition of the aggregate breeding value. The second step is application of the relative economic weights. This separation has two important advantages. It permits use of the most complex and accurate Best Linear Unbiased Prediction (BLUP) techniques to estimate individual breeding values for each index trait, including adjustment for differing amounts of information and then allows the economic weights applied to vary with differing selection objectives, depending upon how different breeds are used in a breeding system or the particular production and marketing system, without recalculating breeding values.

A clear distinction should be made between the traits in the breeding objective and the characters used as selection criteria (Ponzoni & Newman, 1989). Traits that appear in the breeding objective should be those that are economically important and therefore directly linked to the costs and returns of the production situation. By contrast, the selection criteria are the characters used in the estimation of the breeding values of animals. For example, lean percentage may be a breeding objective, and ultrasonically measured backfat thickness a selection criterion. Scrotal circumference, which has as such no economic value, may be the criterion for male and female fertility which are economically very important. It is obvious that some traits might affect profitability in one market but not in another. The greatest economic value to commercial cow-calf producers (weaner market) is increased weaning rate (maternal and reproductive characteristics) and weaning weight (pre-weaning growth). Feeders, on the other hand, are more interested in post-weaning growth and consumption characteristics. Furthermore, consumer judgments of product quality such as tenderness, flavour and juiciness have no value to the commercial cow-calf producer who is not compensated for them (Melton, 1995). Troublesome traits (difficult or expensive to measure) in the breeding objective are often replaced with indicator traits. Food intake is an example of a trait that has often been left out of the breeding objectives for grazing beef cattle because it is extremely difficult to measure. The breeding objective should describe how well animals suit a particular production purpose, a given market and environment. It is, therefore, obvious that breeding objectives will differ in different situations but the basic principle will remain the same and that is to maximise profit.

Using a breeding objective has several advantages (Barwick *et al.*, 1991):

- It will enable breeders to use the combination of EBV's that gives them most (total) genetic progress for their particular situation. These EBV's are the potential selection criteria. The importance of individual EBV's (traits) does depend on the breeding objective.
- It will enable breeding to be targeted for specific markets. The ability and capacity to target specific markets successfully is, however, not an easy process (McDaniel & Darden, 1987; Thompson & Strickland, 1999).
- It will enable EBV's to be used more efficiently and enhances the value of existing EBV's by relating their interpretation to farm profit (Charteris *et al.*, 1998).
- It will have financial rewards throughout the whole industry.

The beef cattle industry has a history of chasing and promoting maximum values (e.g. maximum weight). Yet, according to Beilharz *et al.* (1993), when environmental resources are limited, all major components of fitness are naturally selected towards intermediate optimal values. As all morphological features of a phenotype, its development, growth and actions of movement require environmental resources, this situation applies to most characters, not only to components of fitness. Therefore, almost every quantitative trait in any species has an intermediate optimum (Crow, 1986). Saying that breeding should be for an optimum rather than a maximum is just another way of saying that selection should be in a balanced way (Barwick *et al.*, 1991). This brings up the question, what is the balance that is needed between traits for maximum profitability (i.e. the breeding objective)?

Ponzoni & Newman (1989) developed a sequential procedure to derive breeding objectives for domestic livestock. Development of the breeding objective can be described in terms of the following phases. The first four phases concern economic aspects while the last two are genetic in nature:

- Specification of the breeding, production and marketing system.
- Identification of sources of income and expense in commercial herds.
- Determination of biological traits influencing income and expense.
- Derivation of the economic values of each trait.
- Choice of selection criteria.
- Estimation of phenotypic and genetic parameters.

Breeding, production and marketing system

Specifying the breeding system involves defining the role of the breed (for which the breeding objective is being defined) in the production system (Ponzoni & Newman, 1989). In broad terms the roles could be general purpose, maternal line or terminal sire line. The role of the breed influences the amount of genes present in the various segments of the production system.

Specification of the production and marketing system involves the description of how animals are fed and managed, the age composition of the herd, the replacement policy and ages of animals at marketing and slaughter (Newman *et al.*, 1992). Defining herd composition aids in identifying age and numerical distribution of the herd, the number of replacements required each year, the number of animals of all classes available for marketing each year, and is required in the calculation of the economic values as not all traits are expressed with the same frequency or at the same time. A particular problem that arises is that a bull never expresses his genotype for all traits (e.g. days to calving, milk production) and that in his descendants the traits may be expressed quite unequally. Therefore, a standard unit of expression for a trait under consideration was defined by McClintock & Cunningham (1974) as one expression of a trait in the progeny in the year in which the mating (insemination) took place. The unit used was a single mating or insemination, which may lead to either a male or female offspring. If the former, it will result in a single expression of his genotype (e.g. weaning weight). If the later, it may result in several expressions of his genotype in the daughter (e.g. milk production) and the possibility of further expressions of all his traits in grand progeny and more remote descendants. Therefore, the value of a unit of genetic superiority for a trait, as realized through one mating, depends on the economic value per unit of superiority and the number of times that superiority is expressed. Factors which determine the numbers of standard units of expression of an animal's genotype for different traits following one successful mating (insemination) are:

- The probability that the mating results in a female offspring and she is kept for breeding purposes. This factor is a function of the population structure (e.g. cow replacement rate).
- The degree of relationship of the animal to the descendants in which his/her genotype is expressed. If we limit consideration to additive genetic merit, the contribution of a parent to a descendant's genotype, is halved for each generation separating the parent from the particular descendant.
- The number of years separating each such expression from the year in which the mating took place.
- The number of years after the mating/insemination that is taken into account.

The third and fourth factors both concern the displacement in time of the expression of an animal's genotype. The basis of the procedure is that deferred returns are worth less than the same returns now. It was viewed by McClintock & Cunningham (1974) as compound interest in reverse and they called the procedure the discounted gene flow technique. Therefore, traits such as birth weight, weaning weight, etc. are expressed only once if the progeny is male. However, if the resultant progeny is female and is kept for breeding purposes, the traits will be expressed repeatedly in all her descendants.

One can assume that a hierarchical structure exists in the South African beef cattle industry (Van Zyl, 1983; Kluyts, 1993). Stud (elite) or bull breeding herds, multiplier herds and commercial herds can be distinguished. Most genetic improvement arises from the breeding herds (seedstock sector). This genetic improvement is replicated in the multiplier herds that serve the commercial sector. The commercial herds produce virtually all of the product (meat), but they are dependent on the breeding herds for permanent genetic improvement. This multilevel structure suggests that genetic improvement made in the seedstock sector should be directed toward its use in the commercial sector to satisfy consumer demands. However, in a conventional industry, improvement in the breeder's economic benefit is a major incentive for selection strategies to change (Howarth & Goddard, 1998). Likewise, economic signals indicating consumer desires should migrate from consumers to seedstock producers (MacNiel, *et al.*, 1994).

Identification of sources of income and expense

The identification of sources of income and expense in commercial herds enables the development of a profit equation ($P = I - E$), where profit (P) is a function of income (I) and expense (E) (Ponzoni & Newman, 1989). Amer & Fox (1992) formulate a profit equation of the general form as:

$$\pi = f(\mathbf{X} \mathbf{P} \mathbf{C}_v \mathbf{C}_f) \quad (3)$$

where \mathbf{X} is a vector of traits or animal characteristics, \mathbf{P} is a vector of output prices, \mathbf{C}_v a vector of variable input prices and \mathbf{C}_f a vector of fixed input prices. \mathbf{C}_v and \mathbf{C}_f are typically considered to be constant for all levels of farm output. Equation (3) for a meat production enterprise can be in the form (Brascamp *et al.*, 1985; Smith *et al.*, 1986):

$$\pi = N(nwV - nC_1d - C_2) \quad (4)$$

where N is the number of breeding females producing n offspring per year, w is weight of the product per offspring with value V per unit grown over d days. C_1 is the cost per day of growth per individual and C_2 is the cost per female per year.

Agricultural economists have frequently used a Cobb Douglas production function to represent the technical relationships between levels of input bundles B and C , and output (y) (Amer *et al.*, 1994a):

$$y = \alpha w B^\beta C^\gamma \quad (5)$$

For a meat enterprise, w is the carcass weight of individual animals sold and α is a constant. The exponents β and γ are partial elasticities of production. These show the proportional change in output obtained when the corresponding input bundle is changed by one percent. Profit from an animal enterprise constrained by the Cobb Douglas production function is calculated from the profit equation (Amer *et al.*, 1994a):

$$\pi = yv - Bp_B - Cp_C \quad (6)$$

where v is the price per unit of output, p_B and p_C are prices per unit for inputs B and C , respectively.

Harris (1970) suggested that, in the development of a mathematical function describing the livestock enterprise, income (I) and expense (E) can be combined in different ways as either Profit ($P = I - E$), Return on investment ($\Phi = I/E$) or Cost per unit production ($Q = E/I$). However, Ponzoni (1988) indicated that when P was equal to zero, as suggested by Brascamp *et al.* (1985) and $\Phi = Q = 1.0$, the relative economic values from P , Φ and Q were the same.

The cost of animal products depends primarily upon the efficiency of three basic functions, namely reproduction, female production (milk) and growth of the young (Dickerson, 1970). To assess the economic importance of improvement in each major biological component of performance, it is helpful to separate total costs into those for the producing and reproducing female population as well as progeny growing to market size. Similarly, animal products are obtained directly from the female (milk) and from growth of her progeny (meat). Therefore, income depends on the sale of weaners, surplus heifers and cull cows as well as the value per animal sold. Expenses depend on food intake, the value of the food per kg, husbandry cost, marketing cost as well as fixed costs. Fixed costs are those costs incurred by the producer independent of the level of herd production. All other costs are variable costs and vary with the level of production (Ponzoni, 1986).

Determination of biological traits influencing income and expense

During this phase the profit equation is expressed as a function of biological traits that impact on income, expense or both (Ponzoni & Newman, 1989). Choosing selection criteria and organising logically based performance recording is difficult unless the traits that have to be improved have been identified and their relative economic importance has been established (Ponzoni, 1986). All criteria with a major impact on the efficiency of commercial production should be reflected in the traits chosen for the breeding objective (Fewson, 1993b). This statement is, however, open to different interpretations as the term "major impact" is ambiguous. It should be noted that in addition to the primary performance traits such as growth rate, feed conversion, feed intake and lean meat percentage, there are also secondary (indirect) traits such as fertility, longevity and calving ease which should be considered as traits having a major impact on efficiency. Furthermore, criteria of product (meat) and quality (marbling, tenderness) are also related to economic efficiency. The major impact of a trait on the efficiency of commercial production should be able to be validated. The term major also implies that a limitation should be set to the number of traits involved in the breeding objective. The economic weights for certain traits may turn out to be negligible. These traits could therefore be excluded from the breeding objective (Weller, 1994). This is, however, difficult to predict *a*

priori. Since some less important traits may have non-zero economic values, Melton (1995) used t-values to reflect the statistical confidence in the coefficient estimate (economic value). It is important to note that only economic aspects are valid for the choice of traits in the breeding objective, as genetic parameters are considered later when the breeding values are estimated. The paucity of information on economic, phenotypic and genetic parameters for certain traits may, however, discourage the formal derivation of economic values and the inclusion of the trait in the breeding objective.

Derivation of economic weights

The net genetic improvement which can be brought about by selection among a group of animals is the sum of the genetic gains made for the several traits which have economic importance (Hazel, 1943). It is, therefore, logical to weigh the gain made for each trait by the relative economic importance of that trait. Economic theory suggests that optimisation objectives at farm level would cause adjustments in levels of variable inputs and output in response to a genetic trait change (Amer *et al.*, 1994a). The estimated effects on farm profits are commonly termed economic weights and are used in selection indices to determine the weight to be placed on each genetic trait when selecting animals so as to maximise profit. Therefore, the relative economic value for each trait depends upon the amount by which profit may be expected to increase for each one unit of improvement in that trait, independent of effects from changes in other traits included in the definition of aggregate breeding value (breeding objective) (Hazel, 1943). Dickerson (1970) defined relative economic importance in terms of expected reduction in cost per unit of equivalent output rather than an increase in profit.

Not all traits in the objective are expressed at the same time, or with the same frequency (Newman *et al.*, 1992). These may be accounted for in deriving economic values by either calculating all income and expenses in one year (which accounts for frequency but not time lag) or by discounting (which accounts for both frequency and time lag) (Ponzoni & Newman, 1989). Economic values calculated by different methods and different discount rates (Newman *et al.*, 1992) are presented in Table 1.

Table 1 Economic values (NZ\$) calculated by different methods and different discount rates

Trait	Income and expense per year	Discounted gene flow		
		0%	5%	10%
Calves weaned /cows joined	251.63	198.45	127.40	86.83
Carcass weight – Steers	0.668	0.486	0.362	0.285
Heifers	0.361	0.160	0.120	0.094
Cows	0.188	0.013	0.008	0.005
Food intake – Steers	-0.016	-0.012	-0.010	-0.008
Heifers	-0.016	-0.012	-0.010	-0.008
Cows	-0.014	-0.033	-0.012	-0.015

Discounted expressions can be calculated with different programs which are based on the discounted gene flow techniques of McClintock & Cunningham (1974) or the method of diffusion coefficients (McArthur & Del Bosque Gonzalez, 1990). The method of diffusion coefficients differs from the gene flow method in that it accounts only for the delay between the birth of the animal and the first time of expression of the improvement. The gene flow method accounts for the same delay and additionally for the delay between the joining and birth of the animal (Barwick & Graser, 1997). The number of discounted expressions of a trait is a function of the number of progeny or later descendants of the animal in question and the annual discount factor. The discount factor accounts for the fact that economic benefit at time t is more valuable than at time $t + 1$. Therefore, traits expressed sooner after selection should receive more emphasis.

The use of profit equations to integrate the cost and returns of a production system was proposed by Moav & Moav (1966) to compare the profitability of lines and crosses. Moav & Hill (1966) used the partial derivatives of the profit equation as economic weights for within-line selection. It should be emphasised that the partial derivatives are taken at mean performance for the traits concerned because the aim is to estimate the effect on profit of changes in these means (Brascamp *et al.*, 1985). The profit equation and the economic weights derived from it depend on the perspective taken, whether in the national interest, in the producers

interest or per unit of investment made (Brascamp *et al.*, 1985). However, the improved stocks have to serve all interests simultaneously since all are involved in the same production system.

The profit equation (4) can also be expressed with different bases, per female, per individual or per unit of product. The relative economic weights (Table 2) are different for the three forms (bases) of the profit equation (Brascamp *et al.*, 1985).

Table 2 Profit equations and economic weights for number of offspring (n), days of growth (d) and weight of product (w) for three bases of evaluation

Basis of evaluation	Profit equation	Economic weight		
		$\delta\pi/\delta n$	$\delta\pi/\delta d$	$\delta\pi/\delta w$
Per female	$P_F = nwV - nC_1d - C_2$	$wV - C_1d$	$-nC_1$	nV
Per individual	$P_I = wV - C_1d - C_2/n$	C_2 / n^2	$-C_1$	V
Per unit product	$P_P = V - C_1d/w - C_2/nw$	C_2 / n^2w	$-C_1 / w$	$1/w^2 (C_1d + C_2/n)$

If profit is zero, by considering profit as a cost of production (so called “normal profit” in economics), the relative economic weights are the same for all perspectives. However, this viewpoint of Brascamp *et al.* (1985) uses two assumptions. One is that averages for the traits are independent of the basis of evaluation. The second is that the economic parameters are also independent of the basis of evaluation. This may not be the case.

The use of profit equations for deriving economic weights has led to anomalies both in theory and in practice. According to Smith *et al.* (1986) these anomalies can be removed by imposing two conditions. One is that any extra profit from genetic change that can be matched by rescaling the size of the production enterprise should not be counted since it can be achieved without any genetic change. Only savings in cost per unit of product value should be included. The second condition is that changes that correct previous inefficiency should not be counted. Thus, it is assumed that resources are efficiently used, and changes in output will require proportional changes in input. This means that fixed cost, such as variable cost, should be expressed per unit of output, rather than fixed total enterprise cost (Dickerson, 1970). Application of these two conditions is shown by Smith *et al.* (1986) to give economic weights that are identical on different bases. With rescaling it becomes apparent that the only way real genetic improvements can be obtained is by improving the efficiency of the production system (Smith *et al.*, 1986).

McArthur (1987) criticised the rescaling theory of Smith *et al.* (1986), arguing that a farm faces decreasing marginal returns with an increase in the scale of the enterprise and thus, if operating at an optimum, the farm could not scale up its output without a loss of profits per unit of input. Since neither the argument of Brascamp *et al.* (1985) nor that of Smith *et al.* (1986) uses formal production economics theory when addressing the problem of different bases for economic weights, Amer & Fox (1992) proposed a general approach which is based on the neoclassical theory of the firm. This theory has evolved as economists have attempted to explain the behaviour of competitive firms in transforming materials into goods and services desired by consumers. The goals of farm managers are assumed to be profit maximisation or cost minimisation. Amer & Fox (1992) considered input prices to be unaffected by genetic improvement due to the relative small shares of individual animal industries in input markets. The model is set in the long run in line with conventional economic theory dealing with technological change. In the long run, costs such as capital investment, which are considered to be fixed in the short run, are treated as variable. Genetic improvement programs involve considerable development and adoption time periods. In the process of developing this approach, Amer & Fox (1992) showed that the conventional approach and the rescaling arguments are based on a very restrictive set of assumptions about the behaviour of farming enterprises.

Tess *et al.* (1983) constructed a deterministic computer model to simulate biological and economic inputs and outputs for life cycle performance. This bioeconomic model simulates the effects of genetic changes in components of performance (weaning rate, growth rate, milk production) on several measures of production efficiency (e.g. feed or monetary inputs/kg of live weight). The approach used in constructing the model was to account as accurately as possible for the biological and economic inputs needed to sustain a

predetermined genetic level of performance. Under this approach, inputs (feed and non feed costs) are treated as dependent variables determined by genetic levels for the various performance traits (Tess *et al.*, 1983). Groen (1988) also indicated the sensitivity of economic values towards changes in prices and elements that influence quantitative relationships between levels of genetic merit and levels of inputs and outputs. A bioeconomic model was elaborated by Phocas *et al.* (1998) to derive economic values for 25 traits in purebred French beef cattle selection schemes.

Harris & Freeman (1993) used a linear programming model to derive economic weights for yield traits and herd life under various economic conditions and production quotas. The model allowed optimisation of the system over time, simultaneously optimising management, resource and capital allocation as well as optimising future genetics of the animal. A linear programming problem may be written as (Harris & Freeman, 1993):

$$\begin{aligned} \max z &= \mathbf{c}'\mathbf{x} \quad \text{subject to meeting the following linear constraints:} \\ \mathbf{Ax} &\{\leq \geq\} \mathbf{b} \end{aligned}$$

where z is the value of the objective function (e.g. net income), \mathbf{c} is a $1 \times n$ vector of objective function coefficients per unit of activity (e.g. price per unit product), \mathbf{x} is a $n \times 1$ vector of activity levels (e.g. amount of a certain input), \mathbf{A} is a $m \times n$ matrix of resource or technical coefficients and \mathbf{b} is a $m \times 1$ vector of resource limits. Two properties characterise a linear programming problem. The first is additivity, in which levels of activities are additive in their combined effect. The second is proportionality, in which a multiplicative relationship exists between units of a resource required and the number of units produced (Harris & Freeman, 1993). Solving a linear programming model involves choosing activities in such a way as to obtain an optimal plan. An optimal plan maximises the objective function and is feasible for satisfying the constraints (Sivarajasingam *et al.* 1984). Linear programs are usually solved iteratively by using a simplex method or variant of this method (Harris & Freeman, 1993).

Conventional selection index theory assumes that the total merit or profitability of animals is a linear function of measurable traits (Hazel, 1943). However, in some cases merit (profit) may be a non-linear function of these traits (Moav & Hill, 1966; Amer *et al.*, 1994). Non-linear profit equations cause difficulty because the economic value of a trait is not constant but changes as the population mean changes (Goddard, 1983) and no uniformly "best" solution exists (Pasternak & Weller, 1993). A similar problem may arise when the economic value of a trait depends on management decisions (e.g. herd size, cost of buildings, age at breeding or marketing) taken by the farmer (Groen, 1989). In order to maximise a non-linear profit function it seems reasonable to consider non-linear selection indices (Goddard, 1983). Kempthorne & Nordskog (1959) suggested restricted selection indices while Wilton *et al.* (1968) derived a quadratic index, which minimise the sum of squared differences between the index and genetic merit for a quadratic profit function. Gibson & Kennedy (1990), however, concluded that constrained indices should be avoided for economic genetic selection since the linear index is by definition optimal. This is in agreement with Goddard's (1983) findings, that for any profit equation (even non-linear) the linear index derived by the graphical method of Moav & Hill (1966) either achieves the maximum increase in profit possible for a given intensity of selection, or reaches the maximum of the profit surface with the minimum intensity of selection. This conclusion is in line with the basic assumption of quantitative genetics that it is the additive value of genes which determines response to selection. Estimating of economic weights by $\mathbf{a} = \partial y / \partial \mathbf{x}$ ($a = \delta \pi / \delta x$) should therefore be satisfactory. However, maxima or intermediate optima for some traits may be quite common especially in situations where natural fitness is an important part of profitability (Beilharz *et al.*, 1993). In these cases continued use of the index based on $\mathbf{a} = \partial y / \partial \mathbf{x}$ will also be unsatisfactory (Goddard, 1983). The economic weights for traits that are already at an optimum, are non-linear (Gibson & Kennedy, 1990). However, unless the non-linearity is extreme, non-linearity will cause second order effects that are of minor importance in relation to the rate of genetic gain expected. In such cases a linear selection index will be very close to optimum. Therefore, the appropriate economic weight for a trait at an optimum is zero, and if the population moves away from the optimum following selection, the economic weight should be continuously adjusted to equal the tangent to the profit curve at the population mean for that trait. This is in agreement with the suggestion of Ponzoni *et al.* (1998) that non-linearity can be accommodated by periodically revising the economic value assigned to the trait in question. Hovenier *et al.* (1993) developed a method to calculate marginal income functions and to derive economic values for traits with an intermediate

optimum. Wilton *et al.* (1998; 2002) described a bioeconomic modelling method to overcome the problems associated with the non-linear relationship between economic value and level of performance in traits.

Bright (1991) concluded that the simplified linear profit equations are likely to be sufficiently accurate in most circumstances. Significant error is only likely to occur when the variable input exhibits a large coefficient or when the trait change is proportionally large. In practice, most individual coefficients tend to be small and trait changes are not likely to be large. However, the economic weight refers to only one production period, whereas in fact the gain from a trait change may well continue into the future (Bright, 1991). Pasternak & Weller (1993) presented an iterative method, based on the method of Moav & Hill (1966) to derive the optimum linear selection index for any number of traits with linear or non-linear profit functions. For non-linear profit functions the index weights will be functions of the trait means prior to selection and to selection intensity. When all traits in the profit function are included in the selection index, Pasternak & Weller (1993) phrased the problem in terms of non-linear programming, as follows:

$$\begin{aligned} &\text{maximize: } f(\mathbf{X} + \mathbf{\Phi}) \\ &\text{subject to: } \mathbf{\Phi}' \mathbf{G}^{-1} \mathbf{P} \mathbf{G}^{-1} \mathbf{\Phi} \leq i^2 \end{aligned}$$

where $f(\mathbf{X} + \mathbf{\Phi})$ is the profit function of the vector of economic traits after selection, \mathbf{X} is the vector of trait means prior to selection, $\mathbf{\Phi}$ is the vector of genetic changes in the traits in \mathbf{X} due to selection, \mathbf{G} and \mathbf{P} are the genetic and phenotypic variance-covariance matrices of the traits in \mathbf{X} , and i is the selection intensity.

Defining the economic value of genetic improvement of different traits requires an adequate description of the production system. Simple profit equations describing the relationship between genetic change and enterprise profit may be adequate for very simple production systems. More complex systems are better described by computer modelling (Bourdon & Brinks, 1987; Lamb *et al.*, 1992; Wilton *et al.*, 2002). Amer *et al.* (1994b) used bioeconomic models to derive economic values for a limited number of traits in particular segments of the production system. These ignore the reality that animals must perform in all segments and levels of a production system. Koots & Gibson (1998a) developed a bioeconomic model of an integrated beef production system to derive economic values for genetic improvement of multiple traits. In this study (Koots & Gibson, 1998a) economic values were derived by estimating the change in profit resulting from a small (0.05 phenotypic standard deviation) change in a given trait while holding all other traits constant. The breeding objective was assumed to be profit maximisation.

Selection of beef sires to improve a population of animals (either purebred or composite) and choice of sires to use in commercial production programs involving crossbreeding are two distinctly different aspects of cattle breeding (Wilton *et al.*, 2002). Rankings of sires evaluated for use on a range of populations were found to be sensitive to the means of those populations. Evaluations of purebred sires based on progeny results in that population would, therefore, be inappropriate for use in commercial populations or for breed improvement of a population to use in crossbreeding. Customisation of evaluations is possible through bioeconomic models for variables such as price grids and population means as influenced by choices of breeds and crossbreeding programs (Wilton *et al.*, 1998).

Studies by Bourdon & Brinks (1987) and MacNiel *et al.* (1994) have treated traits as being independent of each other. However, in constructing bioeconomic models for estimation of economic values, careful attention must be paid to the exact definition of traits and the inter-relationships among them (Koots & Gibson, 1998a). Since the conversion of economic values to selection index weights assumes linear genetic relationships among traits, no allowance is made for non-linear relationships among traits. Apart from being an over-simplification of reality, this approach can lead to unrealistic impressions about the potential value of genetic change by attributing substantial economic values to each trait of a highly interdependent set. Since selection indices are linear, the non-linear interdependencies among traits cannot be accounted for in subsequent derivations of selection indices and should be accounted for by directly incorporating them into the model (Koots & Gibson, 1998a).

According to Wolfvò *et al.* (1995) two different procedures for calculating economic weights for ordered categorical traits in cattle can be found in the literature. The first approach is that an increase in the frequency in one class is connected with exactly the same decrease in frequency of one of the adjacent classes. In calculating the economic weight only changes in the frequencies of these two classes were considered. The second approach assumed an underlying normal distribution and the economic weight for the transformed (liability) trait were calculated.

Economic values/weights may vary from breed to breed, between sexes or from region to region within the same breed. This is illustrated in Table 3 (Amer *et al.*, 1994b).

Table 3 Economic values (\$/animal) for changes of 1% of the mean in average daily gain (ADG) (+12 g/day), feed intake (FI) (- 80 g/day⁻¹), dressing percentage (DP) (+6%) and fat depth (FD) (- 0.1mm) for breeds by sex

Sex ^a Breed	ADG		FI		DP		FD	
	S	H	S	H	S	H	S	H
Charolais	3.8	4.0	1.9	1.9	8.5	8.1	-0.8	-0.9
Simmental	4.0	4.1	1.9	1.8	8.2	8.0	-0.6	-0.9
Limousine	4.2	4.2	1.9	1.8	8.0	7.6	-0.5	-1.1
Hereford	3.4	2.8	1.4	1.3	7.9	6.6	0.8	0.3
Angus	3.4	2.5	1.4	1.1	7.7	5.9	0.6	-0.1

^a S – steers; H - heifers

Differences in economic weight for ADG between breeds and sexes can be attributed to differences in the number of days on feed and the dressing percentage for each breed. Daily feed intake economic weights were also affected by number of days on feed for each breed. Differences in dressing percentage can be attributed to the higher slaughter weights of exotic breeds compared to British breeds and of steers relative to heifers. However, these differences in economic weights are relatively small and are unlikely to affect the efficiency of selection (Amer *et al.*, 1994b).

Economic values may change, even while the breeding program is in progress if permanent shifts in market demand occur (Hazel, 1943). Amer *et al.* (1994a) extended a neoclassical economic model, based on the Cobb Douglas type production function, to the long run and found that the absolute size of economic weights can depend to a large extent on the profit equation method used. This is in agreement with the findings of Melton *et al.* (1979; 1993). Groen (1989), Koots & Gibson (1998b), Lazenby *et al.* (1998) and St-Onge *et al.* (2002) found that absolute and relative economic values vary with fluctuations in prices and costs. For instance, the economic value of mature size decreases with an increase in feed costs. In addition, different management (production) systems, different marketing systems and different genotypes (breed role, relative performance of traits) gave markedly different economic values (Wilton *et al.*, 1968; Bourdon & Brinks, 1987; Lamb *et al.*, 1992; Hazel *et al.*, 1994; Koots & Gibson, 1998b). This is illustrated in Table 4 (Koots & Gibson, 1998a)

Table 4 Estimated economic values for traits under a pure-breeding or rotational crossing system (PB), a dam line (DL) and a sire line (SL)

Trait	PB	DL	SL
Mature size (kg)	3.62	-1.33	3.24
Calving ease – d (% U)	3.81	6.49	4.56
Calving ease – m (% U)	3.81	10.98	0.00
Cow fertility	14.72	18.56	0.00
Calf survival	17.53	18.11	9.43
Cow survival	3.72	4.24	0.00
Peak milk yield	0.45	0.46	0.00

An example of the influence of the relative performance of traits on economic values is the level of performance in reproductive traits (Table 5) and the relationship between market weight and carcass grade. The economic values for improvement in cow fertility traits depend on the phenotypic values of the traits. Definition of breeding objectives is, therefore, complicated because the phenotypic values for reproductive traits are expected to vary across farms and years and might also change with genetic progress (Amer *et al.*,

1996). Moav & Hill (1966) also demonstrated that, the higher the present level of reproductive performance, the greater the improvement necessary to produce the same increase in profit.

Table 5 Economic values (£ / 1% change) for conception rate (CR), interval to first post partum estrus (PPI) and calving day (CD) in four herds at either high or low levels of performance in these traits (Amer *et al.*, 1996)

Trait Level of performance Herd	CR		PPI		CD	
	High	Low	Long	Short	5% ^a	10%
A	0.13	0.13	-0.37	-0.20	0.50	0.84
B	0.10	0.13	-0.37	-0.20	0.44	0.85
C	0.34	0.70	-2.77	-0.92	0.63	1.13
D	0.21	0.49	-2.22	-0.56	0.60	1.02

^a Barren rates

Notter *et al.* (1979) showed that important economic traits (high economic values) for maternal breeds (breed role) include components of reproductive rate and weaning weight (milk), but that only growth rate, mature size, calving ease and carcass quality are primary for terminal sire breeds. Economic values are also likely to vary across years (Amer *et al.*, 1996). This suggests a customised approach to estimation of economic values may be warranted. In practice, however, the effects of changes in economic values depend on which traits appear in the index (Koots & Gibson, 1998b). Although many traits were insensitive to changes in production systems, economic values for fertility, calf survival and mature weight did fluctuate considerably (Table 4).

Australian researchers developed a PC program to derive economic weights for beef cattle (Barwick, 1993). This program is a beef breeding objectives and selection indexing package designed for use with genetic evaluation systems (Schneeberger *et al.*, 1992). It is a decision aid which combines EBV's and targets them at the needs of the commercial beef producer. A similar program was developed to compare animals across breeds and crosses (mate or breed of cow is also important) and considers different markets Wilton *et al.* (1998; 2002). Wilton *et al.* (1998; 2002) compared the ranking of Charolais bulls for traits such as post-weaning gain (carcass weight), back fat thickness and marbling, when mated to Charolais x Angus cows and purebred Charolais cows, for different markets (replacement heifers, specialised market for smaller carcass with high degree of marbling). Bulls ranked differently with different mates and for different markets. This is due to the non-linearity of pricing grids for different markets.

Koots & Gibson (1998b) concluded that a small number of selection indices might be sufficient to cover a wide range of production and economic circumstances. Simm *et al.* (1986) also concluded that the selection indices derived by them were fairly insensitive to changes in economic and genetic parameters, and should be sufficiently robust for use in a practical improvement program. If one trait or a few traits dominates the index [as measured by the product of the economic weight (a) and the heritability (h²) for the trait] the efficiency of index selection will be sensitive mainly to changes in that trait (Smith, 1983). If there is a balance among traits in the index (similar ah² values) then only moderate losses in efficiency may be incurred through changes in the economic weights.

According to Howarth & Goddard (1998) diversity between breeding objectives exists at three different levels. It can exist within a single production and marketing system where different objectives may be defined for different lines (e.g. terminal sire and dam lines). Within a single livestock industry several different breeding objectives may be required to define the overall economic objective. This situation would arise when differences between production and marketing systems existed. Between countries, different breeding objectives may be required to maximise the benefits of selection to the country involved. Howarth & Goddard (1998) suggested either a specialised or an averaged objective where selection was for the average of the different objectives. The choice depends on the time horizon, the size of the breeding herd (when taking the effects of inbreeding and genetic drift into account) and the correlations between objectives. This is in agreement with the findings of Wilton (1986) that breeding objectives is difficult to establish because of interactions with a range of factors which may broadly be classified as environmental. One of these factors is the structure of the industry, by which is meant the segmentation of the industry into

purebred and commercial herds. Another set of factors relates to the programs of producing beef. These include market standards as well as level and intensity of production. A third factor is the set of resource constraints or limitations which typically include capital, feed, labour and land (Wilton, 1986).

To summarise, the modelling methods to derive economic weights can be divided into simulation, dynamic programming and profit functions (Weigel *et al.*, 1995). Harris & Freeman (1993) subdivided simulation modelling into positive (data analysis) and normative (bio-economic modelling) methods. However, whatever method is used to estimate economic values, it is necessary to derive accurate profit functions (Von Rohr *et al.*, 1999). This means that returns and costs associated with a change in population mean due to selection must be accounted for. By expressing profit as a function of traits in the breeding objective, the economic values can be obtained by differentiating with respect to each trait, and evaluating the partial derivative at the mean value of all other traits (Ponzoni & Newman, 1989). When estimating the economic value of a trait only terms involving that trait need to be considered, as other terms vanish on differentiation.

Note that in Figure 1 (Amer & Fox, 1992) the slope of the profit curve, calculated as the partial derivative of Equation (3) with respect to the animal characteristic (trait) of interest, is taken to be the appropriate economic weight. When (3) is non-linear, partial derivatives are calculated at the level of the population mean for the specific trait.

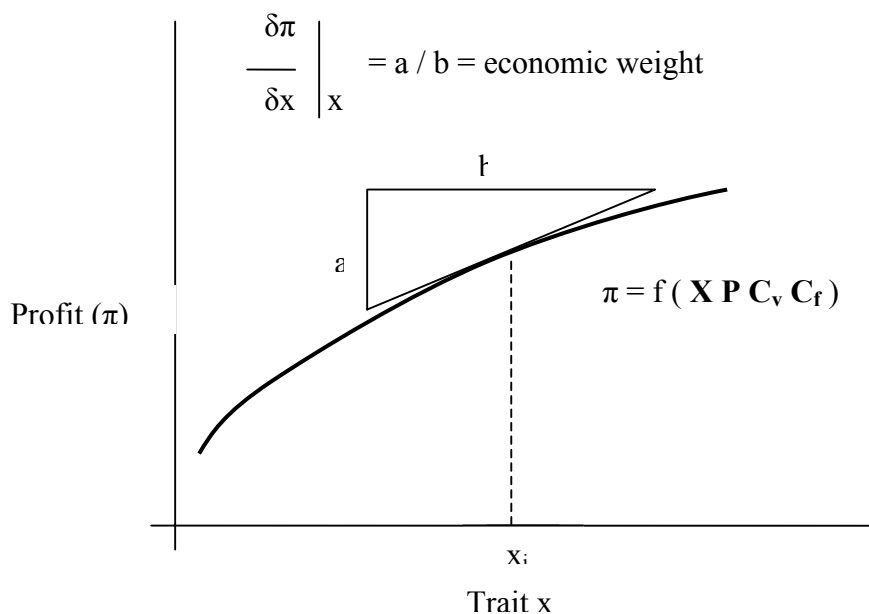


Figure 1 Profit (π) as a function of trait x where x_i represents the population mean

It is often easier to work with economic weights if they are all scaled relative to each other. The easiest way of doing this is to standardise weights by dividing through the standard deviation of each trait, so that the value now refers to a change of one (usually phenotypic) standard deviation in each trait (Table 6). Urioste *et al.* (1998) expressed economic values in actual monetary units and also in units of additive genetic standard deviations (σ_A). The absolute value of the latter expression ($|EV| \times \sigma_A$) enables the comparison of traits in terms of ‘economic–genetic’ variation available. Alternatively, economic weights can be expressed as a proportion of the value of one trait (usually the smallest value). The expression of economic weights per unit of genotypic and phenotypic standard deviation is important because not all traits are measured in the same unit (Munoz-Luna *et al.*, 1988). The economic weight per σ_P is important for economists while the economic weight per σ_A and per δG is of use to geneticists and breeders.

Table 6 Expressions of economic weights for different traits as either per unit used, per σ_P , per σ_A and per δG (Munoz-Luna *et al.*, 1988)

Trait Method of expression	Weaning weight (kg)	ADG g/day	Age at slaughter (days)	Milk Yield (kg)	Mature weight (kg)	Dystocia (%)
Per unit used	158.12	15269.51	62.11	79.34	-83.49	-169.14
Per σ_P	3130.78	2443.12	2670.59	31737.83	-4174.63	-4888.33
Per σ_A	1434.70	1424.57	1710.01	15868.91	-1913.06	-1466.50
Per δG^a	657.46	830.66	1094.94	7934.46	-876.67	-439.90

^a $\delta G = i \cdot h \cdot \sigma_A$, $i = 1$; ADG – average daily gain

Trait economic values, and thus relative economic values, can only be estimated. They depend on estimates of future production system characteristics, including future prices. This highlights the need for revision of economic values at reasonable intervals of time. Economic values should, however, not be changed continuously in an attempt to chase short term fluctuations of the market, but they should be re-examined if market values appear to have changed in a way likely to last for some time.

Concluding remarks

Breeding and management involve decisions followed by actions. Decisions are based on information of the environment, markets, and traits and on differences between animals and groups of animals. The better the information is, the better the decisions, the more effective the actions and the better the chance of maintaining or increasing profitability in the short and long term.

Performance recording is the systematic measurement of performance traits or of indicators of performance. These records become a data bank and, upon proper manipulation and analysis, are used in breeding and management programs to improve decision making. Performance recording will increasingly be involved in maximising the value of the information per unit of investment in terms of either money and/or time. This means effectively addressing the problem of what traits should be measured, how and when they should be measured and what other data should be recorded. Furthermore, performance recording will increasingly become central to all genetic improvement initiatives, especially as pressures to describe the product (animal) and to increase productivity and product quality, intensify. However, performance recording schemes have been put in place before viable breeding objectives and relative economic values have been evaluated. This defect needs to be addressed.

Unless more effective animal genetic improvement activity for meaningful breeding goals is introduced and sustained, many developing countries will, in future, experience even greater difficulty to meet their food and agricultural imperatives (Djemali & Wrigley, 2002). The effectiveness of breeding strategies depends heavily on the degree of compatibility between production systems, the animal component and physical environment, the social, political and economic environments and the livestock general and specific producer targets. When this context is clearly defined and adequate to support genetic improvement activities, the definition of meaningful breeding goals and the design and implementation of breeding strategies which are increasingly and sustainably used by farmers is feasible.

Animal genetic improvement as an element of livestock development can offer valuable tools to help meet the overall livestock development objective (LDO), if a structured process based on specific frames is dealt with properly prior to deciding what the breeding goals should be and before the detailed operational design of the program is finalised (Djemali & Wrigley, 2002). This sequential analysis should be based on the principles of strategic planning (including a SWOT-analysis) and end with the formulation of a sustainable LDO. This sustainability should make verifiable contributions to improve livestock productivity, reduce the level of risk and uncertainty, increase the protection and effective management of natural resources, be economically viable and meet consumers' needs in a cost effective manner as well as being socially acceptable to both breeders and consumers. The risk of breeding schemes comprises the variance of the selection response and the inbreeding (drift variance) (Meuwissen, 1998), the uncertainty in long term market trends (Lazenby *et al.*, 1998) as well as possible socio-political change (Land, 1981). Grundy *et al.* (1998) and Meuwissen (1998) presented methods to deal with the risk associated with inbreeding. For the genetic improvement element the LDO analysis will have delivered the required institutional, economic and production information. This formal approach is especially important for genetic interventions because of the

relative permanence of genetic change, the time required to make or reverse widespread genetic changes and the depth of the impact of genetic change on production and market systems.

The basic approach to genetic improvement in the beef industry is summarised by the so-called Modern Breeding Approach (Hammond, 1991). According to this approach only three primary components cover all formal and practical aspects of breeding:

- The breeding objective which establishes the direction to breed in economic terms. Although this has been done intuitively in the industry to date, it can also be done using formal calculation. In future it will be necessary to use a formal approach, as outlined above, if the beef industry is to maximise the exploitation of genetics.
- Genetic evaluation which provides the estimates of genetic merit for each animal. Genetic evaluation enables animals to be ranked on their overall economic merit, for a particular breeding objective. These two components are linked by the selection index which is a formally or mentally derived combination of EBV's which has the maximum association with the breeding objective.
- Breeding program design establishes the optimum selection and mating structure.

Meuwissen (1998) also emphasised the fact that definition of breeding objectives, design of breeding strategies and genetic evaluation are interacting components of a genetic improvement program that often cannot satisfactorily be dealt with in isolation. The approach outlined by Hammond (1991) not only requires the identification of different markets and the establishment of market requirements but also that cost-effective and accurate measurements exist which relate to all traits in the breeding objective. This is not currently the case for the range of major production-marketing combinations in the beef industry. Better low cost, direct and indirect measurements of reproduction, production and product, which can be taken early in life, needs to be established. Finally, estimation of the necessary parameters such as economic values, heritabilities and correlations provides the formal backbone to the total breeding operation.

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