Chapter 7

Deriving Economic Weights

7.1 Definition of the Breeding Objective

As noted in Chapter 3, the *breeding objective* can be thought of as the overall goal of our breeding program. The purpose of the breeding objective is to aid the following decision-making processes:

1) within-line or -breed selection, i.e. which animals to chose as parents
2) across line or breed selection, i.e. which lines or breeds to use in the production system
3) evaluation of investments in breeding programs and design of breeding programs, i.e. the breeding objective provides the criterion to quantify and maximize returns on investments in the breeding program.

Ideally, we would want to use the same breeding objective for all three purposes but that may not always be possible. In addition, it is important to consider who is the decision maker in animal breeding and selection decisions. Harris (1970) argued that breeding objectives should be concerned with the individual producer’s interest, because the producer’s primary reason for buying certain breeding stock at a certain price will be based on an assessment of how the animals will contribute to the efficiency of the farm. In practice, however, other factors may also play a role. Commercial breeding companies, in turn, will make breeding decisions that will allow them to increase their profitability or economic efficiency, which will be driven primarily by market share. The latter is again driven by the buying decisions of their customers, i.e. the producers.

A breeding objective need not be economic. For example, in many pet species it is tempting to believe that the breeding objective must be maintenance of ridiculous appearance and congenital abnormalities. But in the context of this course we will assume that the breeding objective is essentially an economic objective.

An obvious and attractive economic breeding objective would be to maximize profit, and, for many years, it was essentially taken as read that this was the breeding objective. This acceptance was, however, more because little attention was given to defining breeding objectives rather than because of any great conviction on the part of animal breeders.

As will be discussed, maximizing profit still appears to be a logical goal for most, perhaps all, animal breeding programs. But there are a few tricky issues still to be resolved, such as whose profit is being maximized? Is this profit to the producer (farmer), to the breeding organization, to the processor, to the retailer, to the consumer, or to the whole industry? A breeding company, for instance, might see clearly that it is their own profit they wish to maximize. But do they do that by maximizing the producer's profit, the processors' profit, or someone else's profit, or some combination of other people's profit? Or indeed, is it related at all to other people's profit?
In general, an important question is who obtains extra profit from genetic improvement? Consider the farmer who uses animals genetically improved for growth to slaughter, be they beef cattle, pigs, poultry, fish, or whatever. These animals will grow faster and more efficiently, therefore costing less and, if quality is improved, perhaps bringing in more income. His profit increases. Perhaps if he were the only farm with genetically improved animals he could maintain that increased profit. But simple market economics tells us that if many farmers increase their profits, this translates to more efficient production which, with competition, leads to a reduction in prices. Thus some, perhaps all of the farmer’s increase in profit is eventually lost to the processor, the retailer and eventually the consumer.

Dickerson (1970, 1978) recognized some of these problems and concluded that in a competitive world, the only reasonable breeding objective was economic efficiency, defined as the ratio of production income divided by production costs. Taking an industry-wide perspective, particularly from the consumer’s point of view, economic efficiency has a certain appeal. It is a measure that maximizes the difference between value and cost and it is independent of the size of the production system. But it still faces the problem that a breeding organization and their clients, the producers, will both prefer to maximize their net income and will be little concerned with efficiency unless maximum efficiency equates with maximum profit.

In this Chapter, the basic concepts of quantifying the effects of genetic change on profit will be described, along with the consequences for deriving economic weights for use in selection indexes, both linear and non-linear. Some of the differences between perspectives will be highlighted, along with attempts to unify the various approaches in a single framework of “scaling” as proposed by Smith, James and Brascamp (1986) and its extension to deal with the special case of production quotas. Some alternative methods of deriving economic weights are reviewed in a later Chapter.

### 7.2 Definition of the Aggregate Genotype

When considering the first purpose of a breeding objective listed in section 7.1, that of developing a criterion for selection, the question becomes on what basis parents should be selected in order to maximize the average value profit in the progeny generation. One approach, which has been advocated by some (e.g. Meuwissen and Goddard, 1997), would be to consider profit as a trait, record profit on individual animals, estimate breeding values for the trait ‘profit’, and select animals with the highest EBV for profit. There are, however, a couple of problems with this approach

1) it requires individual records for profit, which may be difficult to obtain or only late in an animal’s lifetime
2) all traits that affect profit will not be recorded on all animals
3) the definition of the trait ‘profit’ changes as economic parameters change, requiring consideration of the trait ‘profit’ as a separate trait under different economic circumstances
4) EBV for profit may not combine the traits that contribute to profit in an optimal manner.

Phenotypic data for profit is a function of phenotypes for individual traits (e.g. milk yield and feed intake). The contribution of each trait to profit is, however, determined based on phenotypic relationships, which may not be optimal from a genetic perspective, considering
Some of these concerns may be alleviated to some degree by including profit as a trait in a multiple-trait BLUP evaluation, along with all the traits that affects profit. Meuwissen and Goddard (1997) showed that the resulting EBV for profit was a rather robust and accurate selection criterion. The main limitation of this approach, however, is that all traits that affect profit will not be recorded on all animals. The use of EBV for profit as a selection criterion will be further discussed in sections 7.3.7.

An alternative approach to select for profit, which was advocated by Smith (1939) and Hazel (1943) and has now been generally accepted as the preferred method for economic selection, is to derive a linear aggregate genotype and to use this to derive a linear selection index using the procedures described in Chapter 6. Following Chapter 6, the aggregate genotype can be described as:

\[ H = v_1g_1 + v_2g_2 + \ldots + v_ng_n \]

where \( g_i \) is the genetic value for trait \( i \), and \( v_i \) the corresponding economic value. The purpose of the aggregate genotype is to describe genetic variation in the breeding objective as completely as possible in terms of a linear function of genetic values for biological traits, along with economic values for those traits. In contrast to considering profit as a trait, this allows description of the genetic aspects of the breeding objective in terms of biological rather than economic traits; biological traits tend to be more consistent over time and are not affected by changes in economic parameters. The aggregate genotype, thereby, separates the genetic from the economic aspects of the breeding objective, which is an advantage from the perspective of estimation of genetic parameters and breeding values, as well as from the perspective of economics. For example, with EBV available for biological traits, alternative economic circumstances can be easily accommodated by changing the economic values in the aggregate genotype.

### 7.2.1 Choice of traits to include in the aggregate genotype and selection index

The purpose of the aggregate genotype, i.e. describing genetic variation of the breeding objective in terms of biological traits, drives the criteria for deciding which traits to include in the aggregate genotype:

- In principle, all traits that directly contribute to the breeding objective must be included.
- Traits that have an indirect impact on the objective (e.g. indicator traits) do not belong in the aggregate genotype (they belong in the index).
- Traits that have little or no genetic variation do not need to be included (note that low heritability does not necessarily imply low genetic variation).

In contrast, criteria for inclusion of traits in the selection index are:

- The trait must be recorded such that EBV can be obtained on selection candidates.
- The trait must have reasonable heritability, although as illustrated in Chapter 3, low heritable traits can provide accurate EBV if sufficient data is available (e.g. progeny test).
• The trait must be one of the traits in the aggregate genotype or be genetically correlated to one or more traits in the aggregate genotype.

In development of breeding goals and selection indexes, a clear distinction must be made between economic traits that are included in the breeding goal and indicator traits that are included in the selection index. With regard to interpretation of the selection index, this involves clarification of the role of indicator traits in relation to the economic traits in the breeding goal. For example, a frequent assertion of breeders is the need to include conformation traits in the breeding goal. Although conformation traits can have a direct economic value for breeders who sell breeding stock, conformation only has an indirect economic value in a commercial milk production environment through its relationship with herd life and functionality. In this case, conformation traits should not be in the breeding goal but belong in the selection index as indicator traits for components of the breeding goal. Note that trait recording is not a criterion for including a trait in the aggregate genotype but it is for traits to include in the index.

In development of the breeding goal or aggregate genotype, many alternative traits and trait definitions can be considered for inclusion. For dairy cattle, traits can be generally classified as milk production traits (milk, fat, and protein), reproductive performance traits, health traits, and feed efficiency traits. Workability traits (e.g., temperament and milking speed) are included in some instances also. In a review, Groen et al. (1997) included milk production, days open, clinical mastitis, milking labour, ketosis, milk fever, displaced abomasum, and laminitis as traits in the breeding goal. A breeding goal that consists of production traits and herd life is frequently used as a simplified breeding goal (Dekkers and Jairath, 1994). In such a breeding goal, traits associated with health, reproduction, and workability are compounded into the trait herd life. The advantages of such a breeding goal are that fewer economic and genetic parameters need to be estimated and that it is easier to explain to producers. Using herd life instead of individual traits does, however, reduce the completeness of the breeding goal; Allaire and Keller (1993) estimated that a breeding goal of production and herd life would leave 15% of genetic variation in economic merit unaccounted for. The impact on efficiency of the resulting selection index, however, will be less if phenotypic data on health and fertility traits are unavailable. A logical extension of a breeding goal based on production and herd life is to include udder health (e.g. Colleau and Le Bihan-Duval 1995, Dekkers 1995).

In some cases, proper choice of traits to include in the breeding goal can lead to significant simplifications, for example in relation to genotype by environment interaction (GxE) or non-additive genetic effects. Bourdon (1998) suggested the use of physiological traits for inclusion in the breeding goal to avoid such complications. For example (Goddard, 1998), slaughter weight of beef cattle in the tropics is an economically important trait and could, therefore, be included in the breeding goal. However, this trait has the potential for high levels of GxE. Traits such as growth potential and adaptation to tropical environments are physiological traits that are expected to be less affected by the environment and would be good predictors of slaughter weight under a range of environments. Thus, their inclusion would make the breeding goal more generally applicable to a wider range of environments.

With regard to excluding non-additive genetic effects, Ribeiro et al. (1997) developed a non-linear model for littersize in pigs based on ovulation rate and uterine capacity. In this model, littersize is
primarily determined by ovulation rate if ovulation rate is low and uterine capacity high but primarily driven by uterine capacity if ovulation rate is high. Thus, an aggregate genotype with ovulation rate and uterine capacity would allow a more complete description of the breeding goal in terms of a linear function than inclusion of littersize. An important complication for such an aggregate genotype is of course the need to estimate genetic parameters and population means for the traits ovulation rate and uterine capacity. Another example is the linear plateau model for protein deposition in growing pigs, in which protein deposition increases with energy intake until a plateau is reached, at which point additional energy intake is converted to fat rather than protein. See de Vries and Kanis (1992), Kanis and de Vries (1992), von Rohr et al. (1999), and Hermesch et al. (2003) for derivation of economic values and associated selection strategies.

Care must be taken not to leave traits out of the breeding goal that could lead to suboptimal decisions. For example, ignoring fertility and health could lead to overestimating the benefits associated with increasing yield.

7.2 Methods to Derive Economic Values

Based on the definition of the aggregate genotype, the economic value of trait \( i \) is defined as the effect of a marginal (one unit) change in the genetic level of trait \( i (g_i) \) on the objective function (i.e. profit), keeping all other traits that are included in the aggregate genotype constant. On the basis of this definition, three general methods for derivation of economic values have been used:

1) **Accounting method**: in this method, the economic value is derived as returns minus costs:

\[ v_i = r_i - c_i \]

Where \( r_i \) is the extra return received from a one unit increase in the mean for trait \( i \), and \( c_i \) is the extra cost associated with a one unit increase in the mean for trait \( i \). For example, considering milk yield for dairy cattle, \( r_i \) is the return per kg increase in milk yield, and \( c_i \) is the extra feed cost associated with a one kg increase in milk yield. In this accounting procedure, it is important to avoid double counting. For example, when fat and protein yield are also included in the aggregate genotype, extra returns and costs associated with a one kg increase in milk yield must be computed while keeping the means for fat and protein yield constant, even though in practice an increase in milk yield tends to be associated with increases in fat and protein yield because of positive correlations between these traits. Not doing so would result in double counting because the economic effect of increasing fat and protein yield are already accounted for in the economic values of these respective traits.

In addition, it is important to realize that \( r_i \) and \( c_i \) are **marginal** rather than average returns and costs. Thus, they must be evaluated on the basis of a marginal increase of the trait value.

2) **Profit function**: in general, a profit function is a single equation that describes the change in net economic returns as a function of a series of physical, biological and economic parameters. As will be shown in section 7.3, the economic value of trait \( i \) can be obtained as the first partial derivative of the profit function evaluated at the current population mean for all traits.
The profit function method avoids double counting because of the use of partial derivatives. In addition, because of their mathematical properties, profit functions facilitate theoretical derivations of economic values and has been used extensively for that purpose, as will be demonstrated in subsequent sections.

3) **Bio-economic model**: production systems are complex and can often not be described by a single profit function. In a bio-economic model, relevant biological and economic aspects of the production system are described as a system of equations. Examples of bio-economic models are in the Tess et al. (1983, J. Anim. Sci. 56:354) for pigs and Van Arendonk (1985 Agric. Systems 16:157) for dairy cattle. Both these models describe the life cycle of a pig cq. dairy cow, including inputs and outputs, as a function of biological traits and economic parameters.

Bio-economic models can be used to derive the economic value of trait \(i\) in the following manner:

1° Run the model for current population means for all traits, including the current mean for trait \(i\), \(\mu_i\), and record the average profit per animal: \(P_{\mu_i}\)

2° Increase the mean of trait \(i\) by \(\Delta\) to \(\mu_i+\Delta\), while keeping the means of other traits at their current values; run the model and record the average profit per animal: \(P_{\mu_i+\Delta}\)

3° Derive the economic value for trait \(i\) as:

\[
v_i = \frac{P_{\mu_i+\Delta} - P_{\mu_i}}{\Delta}
\]

### 7.3 Deriving Economic Weights from Profit Functions

The use of the profit function in animal breeding is principally to define economic weights of traits contributing to economic genetic improvement, i.e. traits in the aggregate genotype. Profit should therefore be defined as a function of genetic performance of aggregate genotype traits. In some cases, all other inputs such as management contributions and economic parameters are considered as fixed, so that

\[
P = f(y_1, y_2, y_3 \ldots y_n)
\]

where \(y_i\) is the genetic performance of the individual for trait \(i\). This need not be so, and profit could be defined as a function of management variables, genetic variables and economic variables as

\[
P = f(m_1, m_2 \ldots m_n, g_1, g_2 \ldots g_n, \pi_1, \pi_2 \ldots \pi_s)
\]

But for simplicity, and because it does not affect initial results (see later for extended discussion), we will assume here that profit is a function of genetic performance for a given set of management and economic parameters.

Since \(y_i\) is defined as the genetic performance of trait \(i\), it can be rewritten as \(y_i = \mu_i + g_i\), where \(\mu_i\) is the mean of the population for trait \(i\). Thus, the profit function can be rewritten as:

\[
P = f(\mu_1+g_1, \mu_2+g_2, \ldots, \mu_n+g_n) = f(\mu + \mathbf{g})
\]
where $\mu$ and $g$ are vectors of population means and additive genetic values, respectively, for the $n$ traits.

### 7.3.1. Linear Profit Functions

Given the aggregate genotype as a linear function of genetic deviations,

$$H = v_1 g_1 + v_2 g_2 + \ldots + v_n g_n$$

assume that the profit equation is also a linear function of phenotypic values of traits:

$$P = \pi_1 y_1 + \pi_2 y_2 + \ldots + \pi_n y_n$$

$$= \pi_1 g_1 + \pi_2 g_2 + \ldots + \pi_n g_n + \pi_1 \mu_1 + \pi_2 \mu_2 + \ldots + \pi_n \mu_n$$

Since $\mu_i$ are constants, it is obvious that for this case the economic weights defining the aggregate genotype are simply $v_i = \pi_i$.

### 7.3.2 Non-Linear Profit Functions

In most realistic situations, $P$ is not likely to be a linear function of performance traits. In general, $P$ might be any more or less complex function of performance traits,

$$P = f(y_1, y_2 \ldots y_n)$$

and the general solution to $v_i$ with a linear aggregate genotype is the partial derivative of profit with respect to $y_i$ evaluated at the current mean for all traits:

$$v_i = \frac{\partial f}{\partial g_i}[\mu]$$

where $\frac{\partial f}{\partial g_i}[\mu]$ is the partial derivative of the profit function with respect to $g_i$ evaluated at the current mean, $\mu$. This partial derivative is the rate of change in profit as genetically controlled performance of trait $i$ changes, when all other traits remain unchanged. In other words it is the (linear) tangent to the profit curve with respect to $y_i$, at the mean performance of all other traits (see Figure 7.1). Substituting these economic values in the aggregate genotype results in:

$$H = \frac{\partial f}{\partial g_1}[\mu] g_1 + \frac{\partial f}{\partial g_2}[\mu] g_2 + \ldots + \frac{\partial f}{\partial g_n}[\mu] g_n$$

This shows that the aggregate genotype is a first order Taylor series approximation of the profit function evaluated at current population means.

Use of first partial derivatives evaluated at the current population mean requires that genetic change is sufficiently small so that second order effects can be ignored. Illustrative examples are given below. Exact solutions, not requiring genetic change to be very small, are given later.
The situation is illustrated graphically in Figure 7.1, which shows a curvilinear profit function of a single trait, \( y \), where the rate of increase of profit decreases as the trait mean increases. The economic weight of \( y \) is the slope of the tangent to the profit curve at the current population mean, \( \mu \), shown by the straight line. It is clear from this figure that using this tangent to the profit curve in a linear prediction of aggregate genotype should be a reasonable representation of the true curve, if the range of genotypes being considered is small relative to the curvature of the graph.

![Figure 7.1: Generalized curvilinear relationship between trait yield, \( y \), and profit, showing the tangent, ab, to the profit curve at the population mean, \( \mu \).](image)

In most cases, the profit function is described in terms of population means:

\[
P = f(\mu_1, \mu_2, \ldots, \mu_n) = f(\mu)
\]

and economic values are derived as partial derivatives with regard to the population mean:

\[
v_i = \frac{\partial f}{\partial \mu_i}[\mu]
\]

Under certain assumptions, which will be discussed later,

\[
\frac{\partial f}{\partial \mu_i} = \frac{\partial f}{\partial g_i}
\]

### 7.3.3. Examples of Linear Indexes for Dairy Cattle

**Example 1.**

Consider the following simplified profit function for dairy cattle, where the breeding objective is profit per cow per lactation:

\[
P = \frac{\mu_L (r_M \mu_M + c_M \mu_M - C_L) - C_R}{\mu_L} = r_M \mu_M + c_M \mu_M - C_L - \frac{C_R}{\mu_L}
\]
where $\mu_L$ is the genetic level for number of lactations, $\mu_M$ the genetic level for milk yield, $r_M$ and $c_M$ the marginal returns and costs per kg of milk, $C_L$ the maintenance cost per lactation (maintenance feed and housing), and $C_R$ is the rearing cost. An important feature of this profit function is that rearing costs are spread over $y_L$ lactations.

Using partial derivatives, the economic value of milk yield is:

$$v_M = \frac{\partial P}{\partial \mu_M} [\mu_M, \mu_L] = r_M - c_M$$

Note that the economic value of milk yield does not depend on population means and is the same as what would be derived using the accounting approach.

The economic value of number of lactations is:

$$v_L = \frac{\partial P}{\partial \mu_L} [\mu_M, \mu_L] = \frac{C_R}{\mu_L^2}$$

Thus, the economic value of number of lactations depends on the number of lactations. A graph is shown in Figure 7.2.

![Figure 7.2: Economic value of herd life as a function of mean herd life](image)

**Example 2.**

Another reasonably realistic example is illustrated graphically here, with data adapted and simplified from an economic analysis of milk production in Canadian dairy cattle (Gibson, Graham and Burnside, 1992). The price of milk was 0.479 $/kg, with estimated marginal costs of production (feeding and management) of 0.093 $/kg and an annual maintenance cost (feeding and management) of 1457 $ per cow. There are quotas on milk production so that as milk production per cow increases, the number of cows must decrease. Imagine a herd with a quota, $Q$, of 300,000 kg milk and average production $y$ kg per cow. Then the profit function from the herd can be written as

$$P = (0.479 - 0.093)Q - 1457 n$$

where $n$ is the number of cows, and $n = \frac{Q}{y}$, so that $P = 115,800 - \frac{4.371 \times 10^6}{y}$.  

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This markedly non-linear profit function is shown graphically in Figure 7.3. The tangent to the profit function at a mean yield of 3500 kg has a much higher slope than that at 6500 kg. Since the economic weight in a linear index is given by the slope of the tangent to the profit curve, the economic weight for improving milk yield falls markedly as the mean yield increases from 3500 to 6500 kg. Quite clearly, if the range of breeding values between candidates for selection were very large (say 3000 or 4000 kg), as might happen when comparing breeds, these tangents to the profit function would do a poor job of estimating economic breeding merit. In general, linear indexes will often be poor approximations of non-linear profit functions when comparing genetic differences and should not generally be used in breed comparison work. The range of genotypes encountered in within line selection will, however, be much smaller, as illustrated below.

![Figure 7.3: Profit per herd vs. milk yield per cow with 300,000 kg quota.](image)

At any point in time, the range in estimated transmitting abilities (ETA = \( \frac{1}{2} EBV \)) for milk yield between the top 5% and bottom 5% of bulls will be approximately \( 4\sigma_{\text{ETA}} \). Assuming bulls are accurately evaluated, with \( r_{HI} = 1 \), that \( h^2 = 0.25 \), and \( CV = 0.18 \), then, approximately, \( \sigma_{\text{ETA}} \) is given by

\[
\sigma_{\text{ETA}}^2 = 0.25 \cdot r_{HI}^2 \cdot \sigma_{s_i}^2
\]

\[
= 0.25 \cdot h^2 \cdot (CV \cdot \bar{y})^2
\]

\[
= 0.25 \cdot 0.25 \cdot (0.18 \cdot \bar{y})^2
\]

\[
= 0.002025 \cdot \bar{y}^2,
\]

giving

\[
\sigma_{\text{ETA}} = 0.045 \bar{y}.
\]

(In practice \( \sigma_{\text{ETA}} \) will be lower than this because \( r_{HI} < 1 \) and sires and dams of sires are intensely selected so that \( \sigma_{s_i}^2 < h^2 \cdot \sigma_p \).)
Thus at \( y = 3500 \) kg, 95% of sire ETA will fall within the range \( \pm 1.96 \times 0.045 \times 3500 = 309 \) kg and at \( y = 6500 \) kg, the range of sire ETA is 573 kg. These ranges are indicated by the bounds \( a,b \) and \( c,d \) on the two tangents to the profit curve in Figure 7.3.

It is now quite clear that the linear approximation given by the slope of the tangent to the profit curve gives a very good approximation to the profit function over the range of ETA encountered in practice. Indeed, Figure 7.3 gives an exaggerated example since profit is expressed at the herd level whereas it would be more realistic to express it per breeding animal (i.e. per cow) since this is the unit of genetic improvement. In this case \( v = \frac{1}{n} \frac{\partial P}{\partial y} \), where \( n \) is the number of cows rather than \( \frac{\partial P}{\partial y} \) as in Figure 7.3. In this case, since \( n = \frac{g}{y} \), economic weights change at about half the rate as in the example above and the linear approximation will be an even better fit.

A (slightly) more formal argument for the use of linear indexes is as follows. In general, taking into account the non-linearity of the profit function by constructing a non-linear index, is to take into account not only the slope of the tangent to the profit curve but also the rate of change of that slope, i.e. including both \( v = \frac{\partial P}{\partial y} \) and \( \frac{\partial v}{\partial y} = \frac{\partial^2 P}{\partial y^2} \). In most situations \( \frac{\partial^2 P}{\partial y^2} \) is a second order effect to \( \frac{\partial P}{\partial y} \) so that for relatively small changes in \( y \), \( \Delta y \), \( \frac{\partial^2 P}{\partial y^2} \) may be ignored. However, it doesn’t appear that any formal investigation has been made of the conditions under which ignoring terms in \( \frac{\partial^2 P}{\partial y^2} \) would cause serious losses of economic progress.

### 7.3.4. Development of Profit Equations

A profit function should include all the traits that are included in the breeding goal. Therefore, the same criteria as those set out for development of breeding goals hold. In general, two approaches have been used to derive the parameters of profit a function.

a) as a single-equation bio-economic model (see below)

b) empirical, using field data by multiple regression of profit on recorded traits. A problem with this approach is that it is restricted to recorded traits and, thereby, confuses the breeding goal and the selection criterion, and that relationships are phenotypic, rather than genetic.

For the profit equation to be useful in animal breeding the following minimum criteria must be met:

1. Change in profit should be a function of genetic change, not other changes of phenotype.

2. Management conditions assumed must be relevant to the population in which and at the time when the genetic change will be expressed.
3. Economic parameters should reflect the marketing and management system in which genetic improvement is to be used and at the time the genetic improvement will be expressed.

These criteria, which also hold for derivation of economic values using the accounting and bio-economic model methods, are discussed in more detail below.

7.3.4.1 Genetic versus Phenotypic Change
It is a key point of profit equations for animal breeding that they describe the relationship between profit and genetic change. Yet this point is easily forgotten when profit equations are constructed, and relationships between profit and nutritional or management derived changes in performance are often used instead.

Consider as an example a profit equation for dairy cows based on the genetic value for milk production where feed intake is treated as a cost item, which is entirely dependent on milk production (and other traits). As milk yield per cow increases so does feed intake. In order to estimate the cost associated with increased production, we need to know the relationship between genetic increases in production and increases in feed intake. It is tempting to take such relationships directly from relationships between production level and intake recommended by NRC or ARC, or other feeding guidelines. But, the vast majority of the data on which such guidelines are based come from experiments where cows are fed differing diets or amounts of feed. Analyses of such data treat cows as random effects so that the resulting relationship between nutritional intake and performance is evaluated at constant genotype. By definition, such data conveys no information about the relationship between genotype and intake. Other data contributing to publication of nutritional guidelines come from experiments where cows of differing initial performance levels (phenotype) receive different nutritional treatments. One problem with such data is that it is often difficult to decide the extent to which imposed differences in diets across performance levels pre-determine the observed relationships. Also, since $h^2$ is around 0.25 for milk yield, (i.e. 75% of the variation is not additive genetic), the relationship between performance and intake is dominated by non-genetic relationships.

In general, there is very little direct data on the relationships between genetic changes in performance and returns and costs. What data there are is often, necessarily, derived from relatively small experiments and estimated relationships consequently have high errors. Thus, constructing genetic based profit equations will often involve intelligent interpretation (guess work?) of the results of the largely non-genetic investigations available to us.

However, one can in principle utilize estimates of genetic correlations between traits to determine the impact of a genetic change in one trait on the genetic change in another. Referring to the previous example of milk yield and feed intake in dairy cows, the genetic effect of a change in milk yield ($M$) on feed intake ($I$) can be estimated from the genetic regression of feed intake on milk yield, which is equal to:

$$b_{g_Mg_I} = r_{g_MI} \frac{\sigma_{g_M}}{\sigma_{g_I}}$$

Expanding this to multiple traits, consider the following two aggregate genotypes for dairy cattle, with milk yield ($M$), fat yield ($F$), protein yield ($P$), and feed intake ($I$):
\[ H_1 = v_M \hat{g}_M + v_F \hat{g}_F + v_P \hat{g}_P \]
\[ H_2 = v_M^* \hat{g}_M + v_F^* \hat{g}_F + v_P^* \hat{g}_P + v_I \hat{g}_I \]

For \( H_1 \), economic values are typically derived as: \( v_i = r_i - c_i \)

Considering only extra feed costs, \( c_i \) can be derived as the product of the price per unit of feed, \( \pi_i \), and the extra amount of feed required for one additional unit of production of trait \( i, f_i \), i.e.:
\[ c_i = \pi_i f_i \]

Extra feed required for an additional unit of \( i, f_i \), is typically derived using feeding norms.

For aggregate genotype \( H_2 \), economic values for production traits should not consider the impact of increasing production on feed intake because feed intake is included as a separate trait. Thus, economic values are simply equal to price per unit: \( v_i^* = r_i \). The economic value of feed intake is equal to the price per unit of feed: \( v_I = \pi_I \).

Now, consider an index that includes multiple-trait EBV for milk, fat, and protein:

\[ I = b_M \hat{g}_M + b_F \hat{g}_F + b_P \hat{g}_P \]

Then, based on \( H_1 \), index weights are equal to the economic values \( v_i \):
\[ I_1 = v_M \hat{g}_M + v_F \hat{g}_F + v_P \hat{g}_P \]

Without loss of information in relation to index \( I \), aggregate genotype \( H_2 \) can be reduced to an aggregate genotype based on production traits alone following section 6.3 as:
\[ H_2^{**} = v_M^{**} \hat{g}_M + v_F^{**} \hat{g}_F + v_P^{**} \hat{g}_P \]

\[
\begin{bmatrix}
  v_M^{**} \\
  v_F^{**} \\
  v_P^{**}
\end{bmatrix} = \mathbf{b}_{H_2^I} \begin{bmatrix}
  v_M^* \\
  v_F^* \\
  v_P^*
\end{bmatrix} = \mathbf{C}_{H_2^I} \begin{bmatrix}
  v_M^* \\
  v_F^* \\
  v_P^* \\
  v_I^*
\end{bmatrix}
\]

with
\[
\begin{bmatrix}
  v_M^{**} \\
  v_F^{**} \\
  v_P^{**}
\end{bmatrix} = \mathbf{b}_{H_2^I} \begin{bmatrix}
  v_M^* \\
  v_F^* \\
  v_P^* \\
  v_I^*
\end{bmatrix} = \mathbf{C}_{H_2^I} \begin{bmatrix}
  v_M^* \\
  v_F^* \\
  v_P^* \\
  v_I^*
\end{bmatrix}
\]

This results in the following index:
\[ I_2 = v_M^{**} \hat{g}_M + v_F^{**} \hat{g}_F + v_P^{**} \hat{g}_P \]

Note that the derivation of economic values in \( H_2^{**} \) did not utilize feeding norms. Instead, relationships between production traits and feed intake were quantified by the genetic parameters included in matrices \( \mathbf{C}_I \) and \( \mathbf{C}_{H_2^I} \).
Veerkamp (1996) compared the economic values from these two approaches using UK data and obtained the following results:

\[
\begin{bmatrix}
  v_M \\
  v_F \\
  v_P 
\end{bmatrix} = \begin{bmatrix}
  -0.03 \\
  +0.66 \\
  +3.84 
\end{bmatrix} \quad \text{and} \quad \begin{bmatrix}
  v_M^* \\
  v_F^* \\
  v_P^* 
\end{bmatrix} = \begin{bmatrix}
  +0.02 \\
  +0.32 \\
  +3.12 
\end{bmatrix}
\]

These two set of economic values and their resulting indexes are clearly different, in particular the sign of the weight on milk yield. This illustrates that the two approaches can provide rather different answers. Given the inaccuracy of genetic parameters, it is not obvious that the economic values derived using breeding goal $H_2$ are better.

### 7.3.4.2 Appropriate Management Systems

In most species, there is a wide range of possible management systems, often leading to a wide range of production levels. Profit equations are often formed to represent a particular management system. In other cases one has the option to represent a range of management systems by including appropriate management variables or parameters (represented by vector $\mathbf{m}$):

\[
P = f(\mu, \mathbf{m})
\]

Economic values are then derived as partial derivatives evaluated at current means and for a particular management situation:

\[
v_i = \frac{\partial f}{\partial \mu_i} [\mu, \mathbf{m}]
\]

Obviously the management parameters that should be used should be for the appropriate management system. The question is what is appropriate? The following alternatives exist for choice of management systems or variables to derive economic values:

1) Current (average) management.
2) Management expected when the genetic improvement is expressed.
3) Optimal management for the current genetic level.
4) Optimal management for the genetic level when the genetic improvement is expressed.

These alternatives will be discussed further below.

### Future vs. Current Management Systems

One school of thought would say that the appropriate management system is that which will be (or is most likely to be) in place when genetic improvement is utilized or expressed. This recognizes that there is considerable time lag between when a selection decision is made and when improved animals resulting from that decision enter the production system. For example, with swine in a breeding company, a selected boar will have progeny in the nucleus next year which will pass genes through one or two levels of multiplier herds over the next year or two and will finally result in genetic improvement in a commercial herd anything from 2 to 4 years hence. Also, a farmer choosing an AI bull for use in his dairy herd today, will see replacement heifers starting their first lactation about 3 years from now, and they will (hopefully) stay in the herd for 4 or 5 years. So his decision today results in improved profitability over the period from 3 to 8 years from now. On the other hand, the sire-selector, setting up matings to produce a young bull for progeny testing, should be looking over 10 to 15 years ahead (see Table 7.1).

Imagine a profit equation for dairy production, which showed that the relationship between profit and genetic improvement for milk production per cow is dependent on the initial production
level of the herd (a simple example is given in section 7.3.3, example 2). If the current rate of increase in yield per cow is 2% per annum, due to both genetic and management improvement, then the expected production level 13 years from now will be proportionately \((1.02)^{13} = 1.29\) (i.e. +29%) higher than today. From Table 7.1, the sire selector’s decision results in genetic improvement at an average of about 13 years from now, and so his profit equation, used to derive economic weights, should be evaluated at an average herd production level that is 29% higher than the present level. If the economic value of yield is linear (as in the above examples) herd level has no impact but it will for traits with a non-linear economic value.

**Table 7.1** Approximate time scales of genetic improvement in dairy cattle.

<table>
<thead>
<tr>
<th>Event</th>
<th>Time from previous event (yr)</th>
<th>Cumulate time (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mating to produce young bulls</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Young bull born</td>
<td>0.75</td>
<td>0.75</td>
</tr>
<tr>
<td>Young bull 1(^{st}) service to produce daughters for progeny test</td>
<td>1.25</td>
<td>2.0</td>
</tr>
<tr>
<td>Progeny test daughters born</td>
<td>0.75</td>
<td>2.75</td>
</tr>
<tr>
<td>Progeny test daughters complete 1(^{st}) lactation; 1(^{st}) proof on bull available</td>
<td>3.0</td>
<td>5.75</td>
</tr>
<tr>
<td>Average time for widespread use of proven sire; 2 years of use</td>
<td>1.0</td>
<td>6.75</td>
</tr>
<tr>
<td>Main crop daughters born</td>
<td>0.75</td>
<td>7.5</td>
</tr>
<tr>
<td>Main crop daughters start 1(^{st}) lactation</td>
<td>2.25</td>
<td>9.75</td>
</tr>
<tr>
<td>Main crop daughters complete average lactation (assume average herd life of 3 yr)</td>
<td>3.0</td>
<td>12.75</td>
</tr>
</tbody>
</table>

In some cases, impending technologies can radically affect profit equations by eradicating or perhaps creating opportunities for genetic improvement. A good example might be disease resistance. Imagine a particular viral disease of swine, say, which is estimated to cost an average of $4 per slaughter pig in terms of prophylactic treatments and reduced performance. Genetic resistance to this disease could appear in the profit equation and might potentially be an important component of profit. However, if an effective vaccine is discovered which costs, say, $0.2 per pig to administer and which completely prevents the disease, then the potential value of complete genetic disease resistance falls from $4.00 per pig to $0.2 per pig, the value of not having to vaccinate pigs. In this situation a great deal of effort and expense might be wasted in selecting for resistance if in the interim an effective and cheap vaccine is discovered.

**Optimal Management Systems**

A variant on the perspective of profit equations for future management systems, is profit equations for optimal management systems. The argument is that genetic improvement is a slow but cumulative process and consequently works most effectively when the direction of change is consistent over long periods. It is important therefore not to breed for sub-optimal management systems, since non-genetic improvements in management are generally made more rapid and easier than genetic improvements. We should therefore breed only for those aspects of improvement that cannot be made by other management improvements. This argument will be
discussed in more detail in relation to the work of Smith, James and Brascamp (1986) later in this Chapter.

**Optimal management for the current vs. future genetic level**

Accepting economic values must be derived using optimal management and using management that is appropriate to the genetic level when the genetic gain is expressed, it appears logical that economic values must be derived for the management system that is optimal for the future rather than the current genetic level. Goddard (1983), however, showed that, provided genetic change is small, economic values derived based on the future genetic level are equal to those derived based on the current genetic level, provided current management is optimal. Therefore, economic values can be derived based on current management, as long as that management is optimal.

The proof provided by Goddard (1983) is as follows:

Given the profit function $P = f(\mu, m)$, and defining $m_o(\mu)$ as the optimal level of management variables as a function of the population mean, the profit function under optimal management is equal to:

$$P = f(\mu, m_o(\mu))$$

Let $m^c_o$ be the optimal level of the management variables associated with the current genetic level $\mu_c$. The optimal level of management variables for a given population level, $m_o(\mu)$, can be derived by setting the first derivative of the profit function with regard the management variable equal to zero:

$$\frac{\partial f (\mu, m)}{\partial m} = 0 \Rightarrow m_o(\mu)$$

Then, the economic value under optimal management can be derived as the partial derivative of the optimal profit function evaluated at the current population mean, $\mu_c$, and optimal management, $m^c_o$, taking into account both the direct effect of genetic change on profit, as well as its indirect impact through changes in optimal management:

$$v_i = \frac{\partial f (\mu, m_o(\mu))}{\partial \mu_i} [\mu_c, m^c_o]$$

$$= \{ \frac{\partial f (\mu, m^c_o)}{\partial \mu_i} + \frac{\partial m_o(\mu)}{\partial \mu_i} \frac{\partial f (\mu, m)}{\partial m} \} [\mu_c, m^c_o]$$

where the first term corresponds to the effect on profit of changing the population mean, while keeping management constant, and the second term to the indirect effect of a change in the population mean on profit through the associated change in optimal management. However, since with optimal management $\frac{\partial f (\mu, m)}{\partial m}$ is by definition equal to zero, the second term drops out and the economic value simplifies to:

$$v_i = \frac{\partial f (\mu, m^c_o)}{\partial \mu_i} [\mu_c, m^c_o]$$

Without re-optimization, management is set to a constant, $m^c_o$ (optimal management for current genetic means), and economic weights would also be equal to $\frac{\partial f (\mu, m^c_o)}{\partial \mu_i} [\mu_c, m^c_o]$. Thus, to a first order approximation (i.e. assuming very small genetic changes) economic weights can be estimated without re-optimization of the enterprise and can be derived using partial
derivatives evaluated at current parameters, provided that profit is a continuous function of genetic and management traits.

As an example, consider the following simple profit function for beef cattle, after Wilton and Goddard (1996):

$$P = w - 2.5f - 0.5d$$

where $w =$ weight at slaughter (price per unit weight = $1)
$f =$ fat thickness ($2.50$ penalty per unit increase in fat thickness)
$d =$ age at slaughter ($0.50$ cost per day)

Now, assume weight is a linear function of the genetic variable growth rate per day, $g_w$, such that:

$$w = g_w d$$

and that fat thickness is defined by

$$f = g_f d^2$$

where $g_f$ is a genetic variable related to rate of fat deposition.

Then, the profit function can be written as:

$$P = g_w d - 2.5 g_f d^2 - 0.5d$$

The management variable is $d$, age at slaughter.

Derivation of the economic values results in:

$$v_{gw} = \frac{\partial P}{\partial g_w} = d$$

and

$$v_{gf} = \frac{\partial P}{\partial g_f} = -2.5d^2$$

Thus, economic values clearly depend on the management variable age at slaughter.

Optimal management, i.e. optimal age at slaughter, can be derived by setting the derivative of $P$ with regard to variable $d$ equal to zero:

$$\frac{\partial P}{\partial d} = g_w - 5g_f d - 0.5 = 0$$

Solving for $d$ gives the optimal age at slaughter as a function of genetic variables:

$$d_o = \frac{-0.5 + g_w}{5g_f}$$

For current means of $g_w=1$ and $g_f=0.001$, optimal age at slaughter is equal to 100. Evaluating economic values at the current optimal management by substituting 100 for $d$, results in economic values of:

$$v_{gw} = 100$$
$$v_{gf} = -25,000$$

Choice of Management Variables
In the previous, age at slaughter was defined as the management variable. Using a constant age at slaughter would, however, result in different weights and fat thickness at slaughter, and may not be the most desirable endpoint. Alternatives are to market cattle at a constant fat thickness or at constant weight. If fat thickness is used as endpoint, fat thickness, rather than age at slaughter becomes the management variable. Since different producers may chose different endpoints, an important question then becomes which endpoint to use for derivation of economic values. This issue was examined by Wilton and Goddard (1996) using the profit function described in the previous section.
Using weight as the management variable, age at slaughter can be expressed as: \( d = \frac{w}{g_w} \)

Substituting into the profit function gives:

\[
P = w - 2.5g_f \frac{w^2}{g_w^2} - 0.5 \frac{w}{g_w}
\]

And economic values are equal to:

\[
v_{g_w} = \frac{\partial P}{\partial g_w} = 5 \frac{g_f w^2}{g_w^3} + 0.5 \frac{w}{g_w^2}
\]

and

\[
v_{g_f} = \frac{\partial P}{\partial g_f} = -2.5 \frac{w^2}{g_w^3}
\]

Now, the economic values depend on the management variable weight at slaughter.

Deriving optimal management gives:

\[
\frac{\partial P}{\partial w} = 1 - 5 \frac{g_f w}{g_w^2} - 0.5 \frac{1}{g_w} = 0
\]

Solving for \( w \) gives the optimal weight at slaughter as a function of genetic variables:

\[
w_o = \frac{g_w^2 - 0.5g_w}{5g_f}
\]

Substituting current means of \( g_w = 1 \) and \( g_f = 0.001 \), optimal weight at slaughter is equal to 100.

Evaluating economic values at the current optimal management by substituting 100 for \( w \), results in economic values of:

\[
v_{g_w} = 100
\]

\[
v_{g_f} = -25,000
\]

Thus, economic values do not depend on choice of endpoint, provided the chosen endpoint is optimized.

### 7.3.4.3 Appropriate Economic Environments

The argument here is analogous to the previous in that the profit equation should reflect the economic environment in which genetic improvement is to be applied. In this case, apart from targeting the appropriate market, the principal concerns are the likely returns and costs of products and inputs at the point in the future when genetic improvement appears in the production system. This necessarily involves the sometimes-difficult task of predicting future prices for products and inputs.

A good example of rapid change in prices is the shift in milk payment over the past decade in many western countries from a volume or volume and fat basis, to a system based primarily on protein with lesser payment for fat and little or no payment on volume. This change, reflecting changing consumer preferences, could reasonably have been predicted 10 to 20 years ago, but with very few exceptions, breeding programs were based on current profits not future profits.

An example in the making is the continued practice of paying pork producers in the USA primarily by lean weight with little incentive for meat quality, despite overwhelming demand by consumers for quality pork. Almost certainly future payments will have to give a heavy incentive for meat quality, and profit equations for genetic improvement should be anticipating these changes.
7.3.5 Linear Indexes With Finite Genetic Change

Derivations in the previous section assumed the amount of genetic change was small relative to the non-linearity of the profit function, such that second-order effects could be ignored. In that case, economic values can be derived as partial derivatives $v_i = \frac{\partial P}{\partial \mu_i}$ evaluated at the current population mean and the associated (optimal) management system. However, as genetic change becomes larger and/or the profit function more nonlinear, these economic weights. The problem is illustrated in Figure 7.4. Imagine two traits, in this case with equal $h^2$ and $\sigma_p = 1$. For a given intensity of selection, a response ellipse (in this case a circle) defines all possible combinations of change in the genetic means of the population for traits 1 and 2, a result of selection as the index weights are varied. Figure 7.4 shows three response ellipses (circles), which correspond to selection intensities of $i = 1, 2$ or 3, for all indexes that would give a positive change in both traits. The broken lines on Figure 7.4 are curves of equal profit (iso-profit contours), corresponding a nonlinear profit function, $P = f(x, y)$. The point on the response ellipse which touches the maximum iso-profit contour shows the direction of selection which will maximize profit. For selection intensities of $i = 1, 2$ and 3, the profit maximizing response occurs at points $a$, $b$, and $c$. It is quite clear that the optimum direction of selection changes with selection intensity. Economic values derived based on partial derivatives evaluated at the current mean optimize response when selection intensity is infinitely small.

![Figure 7.4: Plot for iso-profit contours (broken lines) for a non-linear profit function of two traits, and response ellipses (solid lines) for three intensities of two-trait selection. Heritabilities = 0.5; $r_g=0$; $i = 1,2,3$](image-url)
7.3.5.1 Maximizing response over a single generation of selection

Moav and Hill (1966) and Goddard (1983) proposed finding the optimal index weights graphically (Figure 7.4). This has obvious limitations when more than two traits are involved. Pasternak and Weller (1991) and Dekkers et al. (1995) showed that linear index weights for an index $I = \mathbf{b}'\mathbf{x}$ that maximize response in profit from generation $t$ to generation $t+1$ can be derived by solving the following constrained optimization problem for the profit function $P_t = f(\mu_t)$:

\[
\begin{align*}
\text{Maximize} & \quad f(\mu_{t+1}) \\
\text{subject to} & \quad \mu_{t+1} = \mu_t + \mathbf{b}_t'\mathbf{G}/c \\
& \quad \mathbf{b}_t'\mathbf{P}_t = c^2
\end{align*}
\]

where $\mu_t$ is the vector of trait means in generation $t$, $\mathbf{G}$ and $\mathbf{P}$ are the usual variance-covariance matrices for index derivation, and $\mathbf{b}_t$ is the vector of index weights.

Note that the first constraint in this optimization problem is simply the equation for predicting responses to selection based on index selection, with $c$ defined as the standard deviation of the index. The constant $c$ can be set to any number and reflects that linear indexes are scaleable. I.e. selection on $cI$ gives the same ranking of animals and response to selection as selection on $I$.

Note that in Chapter 3 we forced the scale of the index such that the index is unbiased and $b_{II} = 1$. That constrained is not imposed here but, instead, the standard deviation of the index is constrained to a constant $c$.

This constrained optimization problem can be solved using Lagrange Multipliers (Pasternak and Weller, 1991; Dekkers et al., 1995), resulting in the following equation for the optimal index weights:

\[
\mathbf{b}_t = \frac{c}{\sqrt{\lambda_t'\mathbf{G}^{-1}\lambda_t}} \mathbf{P}^{-1}\mathbf{G}\lambda_t,
\]

where $\lambda_t$ is a vector of Lagrange multipliers and equal to the vector of partial derivatives of the profit function with regard to each of the traits, evaluated at the mean in generation $t+1$:

\[
\lambda_t = \frac{\partial f(\mu)}{\partial \mu} [\mu_{t+1}]
\]

Notice that, apart from a scaling constant, $k = \frac{c}{\sqrt{\lambda_t'\mathbf{G}^{-1}\lambda_t}}$, this equation is identical to the selection index equation $\mathbf{b}_t = k \mathbf{P}^{-1}\mathbf{G}\lambda_t$ when the economic values $\mathbf{v}_t$ are set equal to $\lambda_t$. Thus, economic values for a non-linear profit function that maximizes the increase in profit from generation $t$ to $t+1$ are equal to partial derivatives of the profit function evaluated at the mean of the progeny ($\mu_{t+1}$), rather than partial derivatives evaluated at the current mean ($\mu_t$):

\[
\mathbf{v}_t = \frac{\partial f(\mu)}{\partial \mu} [\mu_{t+1}]
\]

Unfortunately, economic values thus defined cannot be obtained analytically. The reason is that economic values depend on population means in the next generation, $\mu_{t+1}$, which in turn depend on the selection that is being practiced (i.e. on the economic values $\mathbf{v}_t$). Thus, economic values must be obtained numerically, which can be done by the following iterative process:

1° Set starting values for $\mathbf{v}_t$, e.g. partial derivatives at the current mean: $\mathbf{v}_t = \frac{\partial f(\mu)}{\partial \mu} [\mu_t]$
Compute index weights using
\[ b_t = \frac{c}{\sqrt{v_t^* G' P' G v_t}} \]

Compute the vector of genetic levels in generation t+1,
\[ \mu_{t+1} = \mu_t + \hat{b} G v_t/c \]

Compute a new vector of economic values \( v_t^* \) using
\[ v_t = \frac{\partial f(\mu)}{\partial \mu} [\mu_{t+1}] \]

To enable convergence, restrict changes in economic values from one iteration to the next by setting the new vector of economic values equal to:
\[ v_t^* = v_t + \alpha(v_t^* - v_t) \]
where \( \alpha \) is a relaxation factor < 1.

Set \( v_t = v_t^* \) and continue with 2° until convergence (i.e. economic values or response changes by less than a pre-specified amount from one iteration to the next).

7.3.5.2 Maximizing response over multiple generations of selection
Since genetic responses are additive over time, the three response ellipses in Figure 7.4 would also apply to response after 1, 2 and 3 generations of selection with intensity \( i = 1 \), when the same index is used in each generation. Thus, the direction of selection would depend on whether profit after 1, 2 or 3 generations was the goal. In general, with non-linear profit functions, the direction of selection in one generation affects the maximum possible profit achievable in all future generations. The goal of selection will generally be to maximize an aggregate profit over a planning horizon of \( T \) generations, which can be written as:
\[ \text{maximize } P = \sum_{t=1}^{T} w_t P_t \]
where \( w_t \) is a weighting factor for profit at time \( t \) and could, e.g., represent a discount rate (see Chapter 8). A solution to finding economic weights for each generation that maximize \( P \) over a defined time horizon was given by Dekkers et al. (1995). Optimal economic values for derivation the index for selection in generation \( t \) were found to equal:
\[ v_t = \sum_{u=t+1}^{T} w_u \frac{\partial f(\mu)}{\partial \mu} \left[ \mu_u \right] \]
Thus, economic values are equal to a weighted sum of partial derivatives of the profit function evaluated at population means in the remaining generations of the planning horizon, as illustrated in Figure 7.5.

A similar iterative program as specified in the previous section can be utilized to derive these economic values (Dekkers et al., 1995). Note that maximization of profit in the next generation is a special case, with \( T=1 \) and \( w_t=1 \).

This method was illustrated in Dekkers et al. (1995) with a real life egg-laying poultry example with a goal of improving net discounted profit over a 10-generation time horizon. Performance was compared to use of economic weights derived as partial derivatives of the profit function evaluated at the current generation mean or at the progeny generation mean. Optimizing index weights over all generations simultaneously gave about 0.1% higher profit than using economic weights based on progeny generation means, which gave about 2.0% higher profit than the standard economic weights based on partial derivatives using current generation means.
The example chosen by Dekkers et al. (1995) was for a rather extreme practical situation, with a highly nonlinear profit function involving an optimum (for egg weight). Thus, it seems likely that multiple generation optimization of index weights would rarely, if ever, be necessary in practice. The simpler recursive procedure to derive economic weights based on progeny generation performance might give one or two percent extra gains in some practical situations. But in most situations, the classical approach of using partial derivatives of profit based on current generation means, will be sufficiently accurate, rarely giving more than one or two percent less gain in profit than an optimized procedure.

7.3.6 Non-Linear Indexes for Non-Linear Profit Functions

Although most profit functions are non-linear, in the previous we only considered linear indexes. At first glance, it seems reasonable to assume that a non-linear index would be better than a non-linear index. In this section, non-linear indexes will be introduced, followed by a discussion of using linear versus non-linear indexes.

Wilton et al. (1968) showed that with quadratic profit functions, quadratic indexes of quadratic aggregate genotypes can be defined that are maximum likelihood solutions to maximizing economic genetic progress.

For example, if the profit function took the form $P = \pi_1y + \pi_2y^2$
then the aggregate genotype could be defined as $H = v_1(\mu_g + g) + v_2(\mu_g + g)^2$. 

Figure 7.5 Economic values for multiple generation selection

The 1-st derivative for the graph is shown as a dotted line, and the economic value is shown as a solid line.
and the selection index as

\[ I = b_1 x_1 + b_2 x_2 \]

where \( \mu_g \) is the mean genotypic value of the trait, \( x_1 \) is an observation (e.g. phenotype, full-sib mean, etc.) based on \( y \), and \( x_2 \) is the equivalent observation based on \( y^2 \) (e.g. mean phenotype squared, full-sib mean of squared phenotypes, etc.). The term \( \mu_g \) is introduced into \( H \) because the economic merit of an animal relative to other animals is now, because of the quadratic profit relationship, dependent on the population mean. With a linear aggregate genotype, relative economic values are independent of the mean genotypic value. Optimal weights for the quadratic index were derived by minimizing the sum of squared differences between the index and genetic merit of selection candidates for the profit function. Solutions to the problem were given by Wilton et al. (1968) and are not dealt with here.

Given that we have phenotypic and genetic variances and covariances for \( y \), it is straightforward to derive them for \( y^2 \) and to derive covariances between \( y \) and \( y^2 \) (see Appendix B). And hence it is straightforward, though obviously a little more tedious, to derive quadratic indexes. However, if the initial variance/covariance matrixes are close to being non-positive definite, adding the additional terms for \( y^2 \) will often cause the matrixes to become non-positive definite. This may sometimes happen when the initial matrixes are not close to being non-positive definite.

Ronning (1971) extended the method of Wilton et al. (1968) to derive a cubic index for a cubic profit function.

In several practical applications, a non-linear index is developed by substituting multiple trait EBV directly into the profit function.

E.g., for a profit function \( P = f(\mu + g) \) the selection index is \( I = f(\mu + \hat{g}) \).

7.3.7 Non-Linear vs. Linear Indexes for Non-Linear Profit Functions

Goddard (1983) argued that the quadratic index of Wilton et al. (1968) does not maximize profit of progeny. The reason is that the index is derived to maximize the correlation of the index with genetic merit for profit of the selection candidates. This does not necessarily maximize the correlation of the index of selection candidates and genetic merit for profit of their progeny.

To illustrate the inadequacy of a quadratic index, Goddard (1983) used an example of a profit function \( P = y^2 \), where \( y \) is an additive trait with heritability 1.0 and \( \bar{y} = 0 \). For this case, the index is \( I = y^2 \). As illustrated in Figure 7.6, selection on this index would select individuals with high \( y \), as well as individuals with low \( y \). Mating the selected parents (at random), would result in a progeny generation for which the genetic mean for the trait still is zero. Thus, there is no response to selection.
The reason for the lack of response to selection on the quadratic index is that, although all variation in profit is genetic, additive genetic variance for profit is zero. In fact, all genetic variance for profit is epistatic (additive x additive), which is not inherited from parents to progeny. This despite the fact that all genetic variance for the trait $y$ is additive. The presence of non-genetic variance is a general property of non-linear profit functions and forms the basis of the concept of profit heterosis of Moav (1966). Presence of non-additive variance for profit also implies that mean profit can be increased by assortative mating. And indeed, when selecting individuals based on the quadratic index, mean profit of the progeny will be increased if individuals with high negative trait values for $y$ are mated to each other and, similarly, individuals with high positive trait values are mated. Ultimately, this would result in the development of two separate lines, one with high $y$ and one with low $y$.

For the example of $P = y^2$, the first derivative of the profit function evaluated at the current population mean (=0) is equal to zero. Thus a linear index $I = by$ that is derived based on the current population mean would have $b=0$ ($b$ can be set equal to $v = 0$ because heritability = 1) and would therefore be equal to zero for all individuals and result in no response to selection. However, when the linear index is derived based on the first derivative of the profit function at the mean of the progeny, as in section 7.3.5.1, the index weight $b$ will be non-zero. In this case, the linear index will either select individuals with high negative values for $y$, if $b<0$, or select individuals with high positive values, if $b>0$, but not both. This will result in a change in the population mean and an increase in mean profit.

More generally, Meuwissen and Goddard (1997) explained the sub-optimality of a non-linear index that is developed by substituting multiple trait EBV in the profit function, i.e. $f(\mu + \hat{g})$, as follows: if the genetic traits are additive and distributed multivariate normal, $\hat{g}$ are maximum likelihood estimates of the genetic value of the individual for component traits and, therefore, $f(\mu + \hat{g})$ provides a maximum likelihood estimate of the genetic value of the animal for profit. If profit is a non-linear function and, therefore, includes non-additive genetic variation, $f(\mu + \hat{g})$ is not guaranteed to provide a maximum likelihood estimate of the genetic value of the progeny.
Although the previous illustrates that the quadratic index of Wilton et al. (1968), and non-linear indexes in general, do not maximize response in profit, it does not imply that the best index is a linear index. To pursue this, it is important to distinguish between the following two selection objectives:

a) maximize profit of an average progeny, i.e. Max[f(\bar{y}_{r+1})]

b) maximize the average profit of progeny, i.e. Max[\bar{f}(y_{r+1})]

Note that in section 7.3.5.1, the first objective was used to derive the optimal linear index.

For a linear profit function, it is clear that f(\bar{y}_{r+1}) = \bar{f}(y_{r+1}) and the same index maximizes both objectives. The same holds for a quadratic profit function if genetic traits are distributed multivariate normal. To see this, consider the following general quadratic profit function:

P = f(y) = a'y + y'Ay

where a and A are a vector and matrix of constants. Then

E[f(y)] = E[a'y + y'Ay] = a'E[y] + E[y']A'E[y] + tr(AV)

where tr is the trace operator, and V is the variance-covariance matrix of y.

Now, since tr(AV) is equal to a constant, E[f(y)] = f(E[y]) + constant

Thus, for a quadratic profit function with multi-variate normal variables, E[f(y)] and f(E[y]) only differ by a constant and, thus, maximizing f(\bar{y}_{r+1}) is equivalent to maximizing \bar{f}(y_{r+1}) and the two objectives are equivalent. For profit functions with higher degrees of non-linearity, however, the two objectives are not equivalent.

We will first consider the first objective, i.e. maximizing profit of an average progeny, for which the optimal linear index was derived in section 7.3.5.1. Goddard (1983) provided an intuitive proof that for the index that maximizes profit of an average progeny is a linear index regardless of the degree of non-linearity of the profit function if the traits that contribute to profit are additive. Itoh and Yamada (1988) provided a formal proof. The intuitive proof is based on the fact that the greatest genetic change in any direction in the multi-dimensional space of population trait means will be achieved by a linear index when the traits are additive. Referring to Figure 7.4, the origin is the current combination of population means for the two traits and the circles represent the response circle for all possible linear indexes for a given selection intensity. Consider the second response circle. As suggested, a linear index will result in the greatest change in the combination of population means in any direction and thus in the greatest distance of any point on the circle from the current population mean A. Any non-linear index will result in a combination of population means that lies within the response circle. Then, when the objective is to maximize f(\bar{y}_{r+1}), two possibilities exist:

1) The profit function has no maximum within the response circle. In this case there will be a point on the response circle that will result in greater f(\bar{y}_{r+1}) than any other point on or within the response circle. In Figure 7.4 this is represented by point b on the second response circle, for which the response circle is tangent with the furthest profit contour.
2) The profit function has a maximum within the response circle. In this case we can reduce the selection intensity such that the maximum falls on the response circle for linear indexes. Now situation 1) applies and, thus, a linear index results in at least as much gain as a non-linear index.

Thus, if the objective is to maximize profit of an average progeny, a linear index derived as described in section 7.3.5.1 is optimal.

When the objective is to maximize average profit of the progeny, rather than profit of an average progeny, the linear indexes derived above will also maximize the objective for linear and quadratic profit functions because, as shown above, $E[f(y)]$ and $f(E[y])$ only differ by a constant.

Itoh and Yamada (1988) argued that most higher-order profit functions can be approximated reasonably well by a quadratic profit function. Although this may not hold for the entire range of a profit function, this will indeed most often hold for the range of EBV present in any given generation. If the quadratic approximation is accurate, we are again back to the situation of a quadratic profit function, for which a linear index derived based on maximizing profit of an average progeny is optimal.

One can also argue whether the objective should indeed be to maximize the average profit of progeny instead of maximizing the profit of an average progeny. Profit of an average progeny, $f(\bar{y}_{t=1})$, is determined by progeny means for the genetic traits in $y$. In general, the difference between $f(\bar{y}_{t=1})$ and $f(y_{t=1})$ depends on the nature of the profit function and on the distribution of traits among the progeny. Selection has a direct effect on population means for the genetic traits, i.e. on $\bar{y}_{t=1}$. Apart from the effects of selection on genetic variance, as described in Chapter 3, selection does not affect the distribution of traits among the progeny. The distribution of traits among progeny can, however, be affected to some degree by mating, independent of selection, by capitalizing on profit heterosis (Moav and Hill, 1966). This means that for selection purposes, the main objective should be to improve population means for biological traits and, as a result, prime emphasis should be on improving the profit of an average progeny, while the mating strategy can focus on improving distribution aspects. This is in particular true if longer-term objectives are considered, e.g. maximizing cumulative discounted profit over a planning horizon, because mating will only have a temporary effect, whereas changes in population means are permanent and passed on from generation to generation.

The previous assumes selection and mating strategies are independent. Ideally, however, selection and mating should be combined into mate-selection strategies (Kinghorn, 1997). These strategies are, however, beyond the scope of this course.

Meuwissen and Goddard (1997) compared by simulation the performance of alternative selection indexes with regard to profit obtained after 10 generations of selection. Their profit function included non-linear economic, as well as non-linear genetic relationships between traits. The latter caused genetic parameters to change as population means changed. In this case, derivation of the optimal linear index also involved updating genetic parameters. They showed that, in general, the difference between the optimal linear index and a non-linear index created by
substituting multiple-trait EBV in the profit function, i.e., \( f(\mu + \hat{g}) \), was small. The optimal linear index was, however, more difficult to derive and required updating of genetic parameters, whereas genetic parameters were not updated for the non-linear index. If parameters were not updated for the linear index, the non-linear index was slightly better. Thus, the non-linear index appeared quite robust to non-linearities in genetic parameters. Thus, a ‘simple’ non-linear index may be slightly better than a ‘simple’ and, therefore, sub-optimal linear index. The same held true for selection on direct EBV for profit (Meuwissen and Goddard, 1997).

7.3.8 Some Practical Considerations Regarding Non-linear Profit Functions
(Taken from Dekkers and Gibson, 1997)

In practice, nonlinear relationships are frequently implied in the selection and mating decisions that are made and promoted in the industry. In particular, computerized mating programs, in which mating pairs are arranged or a specific sire is sought for a particular cow, often rely on the concept of corrective mating, which implies existence of nonlinear relationships. Mating strategies often pay particular attention to traits that have or are perceived to have an intermediate optimum. Several conformation traits present examples of such traits, such as set of rear legs when viewed from the side (rear legs that are too curved or too straight are deemed undesirable), teat length, stature, and udder depth (shallow udders are associated with less production, but udders that are too deep are associated with more mastitis). Examples of non-conformation traits that are perceived to have an intermediate optimum are milking speed (slow milkers are associated with increased labor but fast milkers are associated with increased susceptibility to mastitis) and to some extent somatic cell count (SCC) [high SCC is associated with increased susceptibility, but SCC that is too low may also be associated with reduced resistance]. Intermediate optima can relate to traits in the breeding goal or to traits that appear exclusively in the selection index (e.g., conformation traits).

Emphasis by producers on traits with an intermediate optimum or nonlinear relationships, and emphasis on mating in breeding strategies takes away from the use and implementation of the total merit selection strategies that are promoted for genetic improvement of an overall breeding goal. Dealing with these antagonistic perspectives requires a better understanding of the nature of the nonlinear relationships considered by producers and of the role of selection versus mating in genetic improvement strategies.

7.3.8.1 Intermediate optimum traits and non-linear relationships.

A trait can be perceived to have an intermediate optimum because of simultaneous consideration of antagonistic pleiotropic effects of the trait. For traits in the breeding goal, an obvious example is milking speed, which has a positive effect on milking labour but a negative effect on susceptibility to mastitis. Udder depth is a selection index trait that is often perceived to have an intermediate optimum. This is caused by antagonistic relationships that udder depth has with two traits in the breeding goal: udder depth has an undesirable relationship with susceptibility to mastitis but a desirable relationship with production.
For traits with a real, rather than perceived, intermediate optimum, a distinction must also be made between traits in the breeding goal and selection index traits. For traits in the breeding goal, the intermediate optimum relationship between a trait and the overall goal (e.g., profit) can be formulated in terms of a non-linear profit function. Other, less extreme non-linear relationships also fall within this category. Examples of such traits in dairy cattle are conception rate, persistency, and SCC in relation to payment or penalty schemes. Non-linear relationships can also pertain to the relationship between a selection index trait and one or more traits in the breeding goal. An example is set of rear legs, which has an intermediate optimum relationship with longevity. Another example is the assertion that the need for good conformation is more important for cows at high production because better conformation enables the cow to better withstand the stresses of high production (balanced breeding).

Solkner and Furst-Waltl (1996) discussed the potential for non-linear heritabilities and of non-linear genetic correlations for functional traits in dairy cattle. Non-linear genetic relationships can be due to segregation of genes of large effect at low frequency, physiological limits, and others.

7.3.8.2 Nonlinear effects in the formulation of selection and mating strategies.

Three situations can be distinguished with regard to presence or perception of nonlinearity in relation to formulation of selection strategies: antagonistic pleitropic effects, non-linear breeding goal (non-linear profit function), and non-linear genetic parameters. Although, strategies to deal with non-linear effects in genetic improvement programs cannot ignore strategies for mating, in what follows the impact of non-linear relationships on the development and implementation of selection indexes is discussed separately.

**Antagonistic pleiotropic effects.** Antagonistic pleiotropic effects of a trait and the resulting perceived intermediate optimum, can often be resolved through proper formulation of the breeding goal or selection index and through consideration of the role of the trait in the breeding goal or index in relation to other traits that are included. For example, if resistance to mastitis is a trait in the breeding goal, along with milking speed, the economic value of milking speed should only consider the effects of milking speed on milking labour. The negative effect of milking speed on susceptibility to mastitis is accounted for in derivation of the index through the genetic correlation between milking speed and mastitis. With regard to traits in the index, pleiotropic effects of, for example, udder depth are accounted for in formulation of an index for a breeding goal that includes production and mastitis through the genetic correlations among udder depth, production, and mastitis.

**Non-linear breeding goal** This has been discussed previously.

**Non-linear genetic parameters.**

For selection index traits, non-linear relationships with traits in the breeding goal can be caused by or modelled as non-linear genetic correlations (Solkner and Furst 1996). For example, the intermediate optimum relationship between set of rear legs and longevity can be modelled as a non-linear genetic correlation with a positive genetic correlation at low values of the trait (curved), a zero correlation at the intermediate optimum, and a negative genetic correlation at high values of the trait (straight) (Figure 7.7). Similarly, the assertion of the increased importance of conformation
at high production implies that the strength of the relationship between conformation and longevity increases as level of production increases. This relationship can also be modelled as a non-linear genetic correlation, which increases as level of production increases.

Limited research has been conducted on methods for detecting and estimating non-linear genetic relationships. In addition little research has been done on the impact of non-linear relationships on selection strategies. Gowe (1983) suggested that for a trait with a non-linear heritability that is caused by presence of a major gene, selection based on an independent culling level is preferred over inclusion of the trait in a selection index. This advantage, however, was not confirmed in simulation studies by Meuwissen et al. (1995), which suggested the use of an empirical restricted selection index to deal with such traits. Strategies for dealing with this and other types of non-linear genetic parameters require further investigation. Extrapolating from results for non-linear profit functions, linear selection indexes that are derived based on linear genetic parameters evaluated at future rather than current trait means would be expected to be close to optimum for most situations. This situation is illustrated in Figure 7.7 for the non-linear relationship between set of rear legs and profit, for which the genetic correlation evaluated at the mean of progeny would be used to derive an index that maximises profit in the next generation.

For dairy cattle, traits that potentially involve nonlinear genetic relationships have limited economic importance relative to production traits. In addition, although significant nonlinear relationships (e.g., conformation traits and herd life) may be observed at the phenotypic level, as is perceived by breeders, the extent of nonlinearity may be limited at the genetic level. This limitation occurs because the range of breeding values and, especially, the range of estimated breeding values, is much smaller than the range of phenotypic values, in particular for traits with low heritability. Therefore, use of selection indexes derived based on linear genetic parameters estimated at current population means will likely be close to optimum for most applications in dairy cattle.
7.4 Economic Weights for Categorical Traits

7.4.1 A Graphical Illustration

Many traits are either measured on a categorical scale or, although expressed on a linear scale, incur financial rewards or penalties in some stepwise manner. In either case, the relationship between enterprise profit and individual expression of the trait is discontinuous. This does not, however, mean that profit is a discontinuous function of population mean expression for the trait. This is illustrated for the case of calving ease in dairy cattle, which is recorded on a four point scale of decreasing difficulty of calving: S (surgical intervention), H (hard pull), E (easy pull) and U (unassisted). The trait is assumed to operate as a threshold model, which assumes that there is an underlying normal distribution of susceptibility to calving ease. This distribution has a mean of zero and variance of one. Incidences of the categories define the threshold values for susceptibility, as illustrated in Figure 7.8.

An increase in the mean of the population on the underlying scale is illustrated by the broken line in Figure 7.8. The thresholds retain their absolute values but now occur further to the right relative to the mean of the new population. This leads to a decreased incidence of the deleterious calving ease categories.

If the incidence of each category for a given population is \( p_i \), \( i = 1, 4 \), and their respective economic values (i.e. profit) are \( w_i \), then the overall profit is \( P = \sum p_i w_i \). The change in profit with a change in the population mean, \( \mu \), can be found by changing the mean in successive small increments, recalculation incidences \( p_i \) and profit \( P \), and then plotting \( P \) against \( \mu \). For an example situation, the resulting profit function for the population mean of calving ease is shown in Figure 7.8.
in Figure 7.9. The economic weight for calving ease (expressed on the underlying scale) is the tangent to this profit curve at the current population mean. Thus at the current mean of zero, the economic weight is clearly close to zero, and is not much affected by substantial changes on either side of the current mean. But increasing calving difficulties (a decrease in calving ease on the underlying scale) leads to an accelerating increase in the economic weight.

Figure 7.9: Change in average profit with change in genetic mean for calving ease expressed on the underlying (normal) scale

The derivation of profit curves in Figure 7.9 assumes that: 1) variance on the underlying scale is not affected by the mean, and 2) profit per animal associated with each category is not dependent on its incidence. The first assumption can easily be relaxed if there is good reason for doing so, which in most cases there likely would not be. The second assumption may be false in a competitive market between breeding companies where there are acceptable limits for incidence beyond which an increasing proportion of customers would refuse to purchase a particular strain. This situation can be dealt with following the approach of de Vries (1992), after correcting for the errors in his derivations. There may also be direct associations between profit per animal in each category and overall incidence, if increasing incidences make the enterprise increasingly difficult to operate efficiently. If so, the functional relationship between incidence and \( v_i \) can be included directly in the process of constructing the profit curve.

### 7.4.2 An Algebraic Solution

While the graphical approach illustrated above is useful and recommended for exploring the relationship between profit and expression of a categorical trait, economic weights can also be derived directly as follows.

Consider an underlying normally distributed variable with mean \( \mu \) and variance \( \sigma^2 \). Assume the trait is observed in \( n \) categories. Denote the lower and upper thresholds for the normally
distributed underlying variable for category \( i \) by \( x_{U_i} \) and \( x_{L_i} \), the proportion in category \( i \) by \( p_i \), and its value by \( w_i \). Note that \( x_{L_1} = -\infty \) and \( x_{U_n} = +\infty \).

Profit, \( P \), of an average individual is then equal to: \[ P(\mu) = \sum_{i=1}^{n} w_i p_i \]

Assuming small genetic change, the economic weight for this trait expressed on the underlying scale can be derived as the partial derivative of the profit function evaluated at the current population mean:
\[ v = \frac{\partial P}{\partial \mu}[\mu] = \sum_{i=1}^{n} w_i \frac{\partial p_i}{\partial \mu}[\mu] \]

First partial derivatives \( \frac{\partial p_i}{\partial \mu} \) can be derived as follows:

Using properties of the normal distribution, \[ p_i = \int_{x_{L_i}}^{x_{U_i}} N(x|\mu) \, dx \]
where \( N(x|\mu) \) is the normal probability density function, i.e.
\[ N(x|\mu) = \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \]

Then,
\[ \frac{\partial p_i}{\partial \mu}[\mu] = \frac{\partial}{\partial \mu} \int_{x_{L_i}}^{x_{U_i}} N(x|\mu) \, dx \]

Using the rule of Leibnitz, which allows exchange of derivatives and integrals,
\[ \frac{\partial p_i}{\partial \mu}[\mu] = \int_{x_{L_i}}^{x_{U_i}} \frac{\partial}{\partial \mu} N(x|\mu) \, dx = N(x_{L_i}|\mu) - N(x_{U_i}|\mu) \]

Thus the economic value is equal to
\[ v = \sum_{i=1}^{n} w_i \frac{\partial p_i}{\partial \mu}[\mu] = \sum_{i=1}^{n} w_i \{ N(x_{L_i}|\mu) - N(x_{U_i}|\mu) \} \]

Thus, the economic value is equal to a weighted sum over categories of the difference between heights of the ordinates of the Normal distribution at the lower \((N(x_{L_i}|\mu))\) and the upper bound \((N(x_{U_i}|\mu))\) for each category.

The above equation can be compared to the equation describing profit. While profit is a sum of multiple integrations solvable only by methods for numerical integration, the economic weight, expressed on the underlying scale, is a simple algebraic expression.

### 7.5 Economic Values for Infectious Disease Resistance

Genetic improvement of resistance to infectious disease has a direct impact on the improved animal through increased health and performance and through reduced veterinary costs. Genetic improvement of these traits, however, also has an indirect impact on other animals in the herd or population through reduced infection rates because fewer animals transmit the disease, which reduces the probability that non-resistant animals become infected. Both the direct and indirect benefits of increasing resistance must be considered when deriving economic values for these traits. Spread of the disease can be modeled through epidemiological models.
Models that combine genetics and epidemiology were developed by Bishop and Stear (1997 and 1999) to investigate the impact of increasing nematode resistance in sheep. They showed that selection on nematode egg count in faeces results in considerably greater responses in faecal egg count and live-weight gain than expected based on genetic principles when the epidemiological effects through reduced infection pressure were accounted for. These models can also be used as the basis for deriving economic values for infectious disease traits (see 7.6.1).

7.6 Economic Values for Unpriced Traits

There are several categories of traits that are associated with genetic characteristics that have no direct market value (at present). This can include traits associated with product quality (e.g. meat quality, which may at present not have a direct economic value), quality of production (i.e. traits that are valued by the producer but that have no direct economic value, e.g. temperament of dairy cows), animal welfare, environmental quality, and environmental sustainability.

One approach for such traits would be to use a desired gains index. For example, if temperament is a concern and negatively correlated with, e.g., milk yield, one may want to develop an index that keeps temperament constant. Although this appears to be an attractive alternative, it can also be very dangerous, as discussed in section 6.9. Thus, as a minimum, the impact of restricting change in temperament on change in other traits and quantifiable profit should be evaluated.

Several alternative approaches have been used in the literature to derive economic values for such traits and these will be discussed briefly below.

7.6.1 Economic values for unpriced production traits

For traits that are of importance to the producer because of their inherent impact on the production process (e.g. temperament in dairy cows), one approach to derive an economic value is to evaluate the impact of the trait in relation to traits whose economic value can be quantified. For example, Wickham (1979) regressed survival on milk yield and temperament and used the ratio of the resulting estimates of the regression coefficients ($b_M$ and $b_T$) to quantify the economic value of temperament: when culling cows, the producer values one unit of temperament score as high as $b_T/b_M$ kg of milk. Thus, the economic value for temperament is $b_T/b_M$ times the economic value for milk: $v_T = \frac{b_T}{b_M} v_M$

It is clear that survival is not the only aspect of a cow’s ‘socio-economic’ life on the farm that temperament affects and, for that matter, neither is this the case for milk yield. The method proposed by Wickham (1979) does, however not exclude the potential impact of temperament on aspects beyond culling. However, it does assume that the culling decision provides a good assessment of the relative importance of temperament versus milk yield. To the extent that culling provides a good assessment of a cow’s value to the farmer, this assumption holds. Culling decisions, however, are or should be based on future profit that is expected from a cow
(relative to a replacement), rather than profit over the entire lifetime; although past profit is a
good indicator of expected future profit, other factors, such as health or fertility status are
important determinants of expected future profitability. Thus, the method of Wickham (1979)
will overvalue traits that affect profitability later in life, because those are important determinants
of expected future profitability. In addition, because results are based on field data, the method
assumes that farmer culling decisions are based on sound economic decision making.

Bishop and Nagel (unpublished, as presented in Bishop 2003), estimated a lower bound to the
economic value of nematode egg count in sheep by quantifying the impact of reducing egg count
on live weight, which is one of a number benefits of reducing egg counts – others are enhancing
animal health and reducing anthelmintic costs. The combined genetic – epidemiological model
of Bishop and Stear (1999) was used to quantify the impact of reducing egg count on growth rate
in the flock.

7.6.2 Market surveys

Market surveys can be used to derive economic values for traits that are important to consumers
but that (at present) do not have a direct economic value. Meat quality traits are good examples
of such traits. Such surveys can be conducted at the level of the consumer, processors, or
producers.

Von Rohr et al. (1996) presented a contingent valuation method (Mitchell and Carson 1993) to
derive economic values for meat quality traits in pigs. This method is used to obtain estimates of
costs and benefits for goods and services that are not traded on ordinary markets by presenting
respondents in the survey a market in which the goods under study are treated as if they were
tradable. This obviously requires respondents to be familiar with the goods and services being
evaluated.

In the study of Von Rohr et al. (1996), meat technology experts of several large meat processing
companies were asked to assign price changes from the base market price to a set of hypothetical
carcasses with different quality characteristics (color, drip loss, intramuscular fat, iodine value,
$\text{pH}$, and proportion of premium cuts). Six classes were set up for each quality trait and
hypothetical carcasses consisted in a change from a standard carcass in only one attribute.
Economic values were then estimated using the categorical trait approach described in section
7.4.2.

Melton (1995) and Melton et al. (1996) used the experimental auction method (Shogren 1993)
and the trial/repeat purchasing model to estimate economic values for pork quality traits based on
consumer preferences. In this approach, consumers tasted pork with different quality attributes
and compared it to chicken breast, which they tasted simultaneously. The pork was assigned one
of 5 price levels, in relation to a standard price for chicken, and consumers were then asked
whether they would be more likely to buy this pork, with its specific quality and price attributes,
or the chicken breast. Logistic regression was then used to analyze the probability of purchase
(non-purchase) as a function of pork quality attributes and price:

$$
\text{Prob(pork purchase)} = P_i = \frac{1}{1+e^{\beta'X_i}}
$$
with \( \beta'X_i = \text{fixed effects} + \sum b_{ij}x_{ij} + \frac{pork\text{ price}}{chicken\text{ price}} \)

where \( x_{ij} \) is the value for pork quality attribute \( j \). This model estimates the effect of a change in attribute or price on the probability of purchase. The economic value of a quality attribute was then derived by evaluating the change in price that is needed to keep the probability of purchase constant, when quality is changed by one unit. Algebraically, this can be solved from the above model as follows:

\[
\beta'X_i = \ln \left[ \left( \frac{1}{\text{Prob}(\text{pork purchase})} \right) - 1 \right]
\]

Thus:

\[
pork\text{ price} = \frac{\text{chicken price}}{b_{price}} \left\{ \ln \left( \frac{1}{\text{Prob}(\text{pork purchase})} \right) - 1 \right\} - \text{fixed effects} - \sum b_{ij}x_{ij}
\]

Using a given probability of pork purchase, which was based on current consumption patterns (=0.15), and using parameters estimated from the logistic regression model (i.e. for fixed effects and \( b_{ij} \)), this equation represents a functional relationship between quality characteristics \( x_j \) and price that consumers are will to pay per kg pork. The first derivative of this equation for a given quality trait \( j \), then gives the economic value of that trait on a per kg basis. Multiplying be the kg product per animal, and assuming no costs associated with this change in quality, gives the economic value on a per slaughter pig basis.

### 7.7 Incorporating competitive position in economic values

For breeders that are operating in a competitive market, market share is the driving force behind breeding objectives. De Vries (1989a) argued that in that case, economic values must take into account the competitive position of the company for individual traits. I.e. economic values should be increased for traits for which the company lags behind its competition, and economic values should be reduced for traits for which the company is ahead of the competition. De Vries (1989) used a market model to incorporate the impact of competitive position on profit for the breeder and, consequently, on economic values.

For each trait \( i \) in the breeding goal, an acceptance level \( T_i \) is defined as the minimum level for the breeding stock to be acceptable to the potential buyer. Assuming a normal distribution of acceptance level over all customers, the trait level of a given stock then determines the percentage of the customers that will find the stock unacceptable. The proportion of customers that accepts the trait level for trait \( i \) is equal to the proportion of customers whose acceptance level is below the performance level of the stock. With \( n \) traits, each with acceptance proportions \( p_i \), market share for the stock is:

\[
ms = c (p_1 p_2 p_3 \ldots p_n)
\]

where \( c \) is a constant that depends on the number of competitors.
For stock that is above the acceptance level for trait $i$, it is assumed that price is proportional to the regular economic value of the trait, derived at the producer level, $v_i$.

Then, the economic weight of the trait when taking into account saleability is equal to the regular economic value of the trait for the producer, $v_i$, multiplied by a factor that depends on the acceptance level for trait $i$:

$$v_i^* = \frac{z_i}{p_i} \sqrt{\frac{\pi}{2}} v_i = i \sqrt{\frac{\pi}{2}} v_i$$

Where $p_i$ is the current acceptance level of the stock for trait $i$, $z_i$ the ordinate of the standard normal distribution associated with that proportion, and $i$ the selection intensity associated with proportion $p_i$. Note that the economic value decreases with an increase in the acceptance level for the trait.

Acceptance level for a given trait is related to the level of that trait relative to competitors. Thus, the economic value of trait $i$ for a given stock depends on the genetic level of that trait in that stock relative to competitors; if the genetic level is below that of competitors, the acceptance level will be low and the economic value high; if it is above that of competitors, the acceptance level will by high and the economic value low.

Problems associated with applying this approach were discussed by De Vries (1989b) and include lack of knowledge of the buying behaviour of customers and sub-optimality of resulting indexes for longer-term responses to selection.
7.8 Some practical Considerations
(Taken from Dekkers and Gibson, 1997)

7.8.1 Identification of the Target Group and Intended Use of the Selection Index

The first step in development of breeding goals and selection indexes for practical implementation involves specifying the purpose for which the selection index will be designed. This process includes identification of its target audience, identification of financial and other incentives to which the target audience is exposed which may impact on the perceived importance of traits (Figure 6.2), and consideration of the manner in which the index is to be used. For example, although selection indexes are intended as an initial guide to selection, few breeders would base their entire selection decision on a single overall index. Prior or subsequent selection may be on individual traits, in particular, on conformation traits or individual milk component traits. Consequences of secondary selection decisions on emphasis on traits in the overall selection strategy must be monitored and perhaps incorporated when developing selection indexes.

If selection indexes are made available for cows as well as sires, it must be recognized that selection of dams of cows, which with current female reproductive rates is closely related to culling of cows, should be based on expected profit from the cow herself rather than on a genetic selection index, which is based on expected profit of the descendants. To investigate the potential consequences of implementation of the lifetime profit index (LPI) as criterion for genetic selection of cows in Canada, a study was undertaken (Dekkers and Gibson, 1992, unpublished) to investigate the relative efficiency of culling cows on the index of EBV for milk, fat, and protein that was incorporated in the LPI versus culling cows on an index based on estimated producing abilities for the production traits. Estimated producing ability predicts production of the cow in future lactations and is more appropriate for culling decisions than is EBV. Concern regarding misuse of the LPI for cows was exacerbated by the lack of specific guidelines for culling cows in Canada and implications of the name chosen for the genetic index (Lifetime Profit Index). Results from this study showed that culling on an index of EBV was only 4 to 7% less efficient in improving future production of current cows in the herd than culling on an index of estimated producing abilities. These results alleviated concerns regarding the consequences of potential use of the index for culling rather than genetic selection.

Consideration of the intended use of the index is also important when developing criteria for selection of sires of sons versus for selection of sires of cows. Selection of sires of sons and dams of sons requires a longer planning horizon than selection of sires of cows and selection of dams of cows. In changing markets, the same index may not be appropriate for alternative paths of selection (see subsequent discussion).

In development of breeding goals and selection indexes, a clear distinction must be made between economic traits that are included in the breeding goal and indicator traits that are included in the selection index. With regard to interpretation of the selection index, this involves clarification of the role of indicator traits in relation to the economic traits in the breeding goal. For example, a frequent assertion of breeders is the need to include conformation traits in the breeding goal. Although conformation traits can have a direct economic value for breeders who sell breeding stock, conformation only has an indirect economic value in a commercial milk production.
environment through its relationship with herd life and functionality. In this case, conformation traits should not be in the breeding goal but belong in the selection index as indicator traits for components of the breeding goal.

### 7.8.2 Consideration of Current vs. Future Economic Circumstances and Market Demands

Development of breeding objectives and derivation of economic values must consider future conditions rather than current economic and market conditions because of the delay in the expression of selected genes. The length of the planning horizon depends on the path of selection and is different, for example, for selection of sires of sons than for selection of sires of cows.

Breeders, however, tend to judge the suitability of indexes and economic values primarily in relation to present economic circumstances, perhaps modified by their perception of future trends in consumer demands (Figure 6.2). The latter may be influenced by, for example, media reports on the need for low fat diets. The manner in which producers are paid for milk and its components provides particularly strong economic incentives. In many countries, incentives provided by the pricing system are complicated by the presence of a quota system, which is frequently based on production of one of the components (e.g. fat). This can eliminate the perceived benefits of selection pressure on that trait.

Although payment systems for milk across the world currently tend to converge toward multiple-component pricing, with payments per kg of milk, fat, and protein that are increasingly reflect world market prices, substantial differences remain. Some payment systems lack payment for protein and others base payments for fat and protein on a differential. Pricing systems for milk are typically based on past or current market considerations rather than on anticipated future market conditions. Differences in pricing systems are partly a reflection of regional differences in milk markets and partly a reflection of traditional payment schemes and their inflexibility to change. Economic incentives that are provided to producers through existing pricing systems may, therefore, not promote optimum genetic decisions. Although anticipated future market trends provide indirect incentives that can modify the impact of direct economic incentives on selection decisions (Figure 1), they are often incorporated subjectively. An index that is developed based on economic values that incorporate future market trends (e.g., J. P. Gibson, M. Greimel, and J. C. M. Dekkers, 1996, unpublished) may, therefore, not reflect producer perceptions. Such an index may be difficult to implement. For example, it may be difficult to convince a producer to select for protein yield if the pricing system reflects no payment for protein or if it reflects a protein differential rather than a payment for protein yield.

Given the impact of price incentives on breeding and management decisions, pricing and quota systems must be proactive and aimed toward the future. Ideally, pricing systems are developed in an interactive manner in close relation to anticipated changes in management and genetics that would result from the incentives they provide. This type of development may, however, be unrealistic and would be further complicated by the different planning horizons for management versus genetic decisions. More realistic is the development of pricing systems that reflect the true value of products in the market and that are flexible to accommodate changes in market values.
Breeding goals for production traits should be developed on the basis of fat and protein rather than on their percentages, because component quantities rather than their concentrations in raw milk are the marketable commodities at the level of the processing industry. Many pricing systems at the farm level, however, have traditionally been based on a price per kg of milk and a percentage differential premium based on the fat and protein content of milk. Pricing systems based on fat and protein differentials can be converted to multiple-component pricing systems based on kg of milk, fat, and protein that have an identical payout to the producer. Similarly, for fat and protein differential pricing systems, selection can be based with equal accuracy on an index of milk, fat, and protein yield as on an index that is based on milk yield and fat and protein percentage. An example is given in Table 7.7, in which the 1997 multiple components pricing system in Ontario is converted to an equivalent payment system based on differentials for fat and protein.

The main difference between the two pricing system of Table 7.7 is that the perceived value of milk yield is much higher under the differential pricing system. This is reflected in the economic values and in the resulting index weights. In fact, under the multiple-component pricing system, milk yield has a negative economic value and index weight (Table 7.7). Such an index would be difficult to implement when producers are paid based on a differential pricing system. Ideally the pricing system should be changed to reflect more closely the real economic value of milk and its components. Given the complexities of making such changes, however, the breeding goal and selection index based on milk volume and fat and protein would facilitate their implementation in such situations.

**Table 7.7** Impact of alternative pricing systems, which result in identical payments to producers, on formulation of the breeding goal.

<table>
<thead>
<tr>
<th></th>
<th>Multiple-component pricing</th>
<th>Percentage differential pricing</th>
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<tbody>
<tr>
<td></td>
<td>Milk (kg)</td>
<td>Fat (kg)</td>
</tr>
<tr>
<td>Price, $</td>
<td>0.071</td>
<td>5.31</td>
</tr>
<tr>
<td>Marginal cost, $</td>
<td>0.152</td>
<td>3.11</td>
</tr>
<tr>
<td>Economic value, $</td>
<td>-0.081</td>
<td>2.20</td>
</tr>
<tr>
<td>Index weights$^3</td>
<td>-0.067</td>
<td>2.19</td>
</tr>
<tr>
<td>Standardized$^4</td>
<td>- 4.0</td>
<td>+ 4.9</td>
</tr>
<tr>
<td>Response$^5</td>
<td>+351.07</td>
<td>+14.10</td>
</tr>
</tbody>
</table>

$^1$ Based on 1996 Ontario prices and costs.
$^2$ Includes interest cost on fat quota.
$^3$ Index weights on a per kg basis for sires with 50 daughters.
$^4$ Index weights on a per genetic standard deviation basis.
$^5$ Response in daughter performance to one standard deviation selection in sires on the index.
$^6$ Based on assumed linear relationships between yield traits and % traits.
7.9 Sustainable animal breeding – A European (?) perspective
Incorporating ethical, ecological, and social considerations

We know of several definitions of animal breeding in the scientific literature, since the initial one of Jay Lush in 1945: "the means available for improving the heredity of farm animals". Ollivier (2000) gave a single phrase that encompasses the breadth of the discipline, “animal breeding may be seen as the optimal exploitation of the species' biological variation, under given constraints of reproductive capacity, using appropriate breeding value estimation tools”. "Optimal" in this definition implies some defined criterion of optimality. The term genetic improvement, often considered as synonymous to breeding, also implies that something better is being looked for, and here man is obviously the reference. It is man's welfare that is at stake, though the species being exploited is also expected to preferably enjoy the same state of well being.

Breeding schemes aim at utilization of the between and within breed genetic diversity. Breeding schemes are not aiming at a fixed target; breeding organizations are dynamically searching for improvements. Differences in economic, social and ecological production environment give rise to different desired directions of change. The desired direction of change of a particular breed might differ between regions and change over time. Changes over time are strongly driven by Consumer and Society. Breeding organizations are increasingly aware of this and are changing their breeding objectives by including traits related to animal welfare and quality of product. Reproductive capacities of animals put a major constraint on any animal breeding operation. Reproductive techniques like artificial insemination and embryo transfer can be used to overcome these constraints. These techniques play an important role in the activities of the breeding organization. In essence, the most basic effect of reproductive technologies is to increase fecundity. This means that fewer parents are needed to produce a given number of offspring. The application of reproductive techniques has had a major impact on the structure of breeding programs, the rate of genetic gain and the dissemination of genetic gain in livestock production and aquaculture.

This section provides an overview of current breeding programs in Europe in farm animals and fish

7.9.1 Breeding objective
In general, there seems to be an almost universal agreement that agriculture and animal production like almost all other human activities should become more sustainable (e.g., Heitschmidt et al., 1996; Thompson and Nardone, 1999). In general, resource efficiency, profitability, productivity, environmental soundness, biodiversity, social viability, and ethical aspects are some common elements in published definitions of sustainable agriculture and animal production among those who seek long-term and equitable solutions for food production (Olesen et al., 2000). A whole-system analysis is needed when deciding on the breeding goal for a species in a particular environment. We need to select animals that can contribute to optimizing the system. Olesen et al. (2000) have presented some of the probable characteristics of future agricultural/animal production systems and potential animal breeding strategies to cope with these. Many of their strategies refer to a broader definition of breeding goals, not aiming at higher production levels per animal only, but balancing higher productivity with improved functional traits such as health, fertility and feed intake capacity.
Many practical breeding programs in the past have suffered from the fact that the breeding goals were too narrowly defined. Breeding organizations have become aware of this and are gradually changing their breeding objectives by including traits related to animal welfare and quality of product. The outcome of breeding programs is noticed many years after selection decisions were made. This underlines the need to design breeding objectives for anticipated future circumstances.

The statement of Lush (1945) "Animal breeding is a business" forms the background for breeding plans, particularly when breeding goals have to be defined. It is generally agreed that the ultimate objective is more efficient production and animal products that are better adapted to market conditions. The usual approach has been to maximize the profit of the producer. But we have also seen that efficient production has resulted in lower market prices, which implies that the benefits have essentially been for the consumers, although eating quality may sometimes have deteriorated. According to Harris (1970), breeding goals need to be concerned with the individual producer’s interest, because the producer’s primary reason for buying certain breeding stock at a certain price will be based on an assessment of how the animals will contribute to the efficiency of a farm. A common interest for the society as a whole may not be a sufficient incentive for an individual farmer making breeding decisions (Brascamp et al., 1998). An individual agricultural producer deals with a competitive market, with no individual price setting, and one cannot expect an individual producer not to act according to these (external) prices, even when these prices are misleading from a broader, national perspective. In deciding on their breeding goal, a breeding organization needs to find the right balance between market prices which are relevant in the short term for producers and common interest of society.

<table>
<thead>
<tr>
<th>Species</th>
<th>Priorities</th>
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<tbody>
<tr>
<td>Ruminants</td>
<td>Maintain genetic diversity</td>
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<tr>
<td></td>
<td>Use of land, feed and other resources</td>
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<td></td>
<td>Animal health and welfare</td>
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<td></td>
<td>Food quality and safety</td>
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<td></td>
<td>Use of accepted technologies</td>
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<tr>
<td>Pigs</td>
<td>Maintain genetic diversity</td>
</tr>
<tr>
<td></td>
<td>Animals robust and efficient in different conditions</td>
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<tr>
<td></td>
<td>Animal health and welfare</td>
</tr>
<tr>
<td>Poultry</td>
<td>Efficient production for different markets</td>
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<tr>
<td></td>
<td>Animal health and welfare</td>
</tr>
<tr>
<td></td>
<td>Use of land, feed and other resources</td>
</tr>
<tr>
<td></td>
<td>Current and anticipated future demand for food safety and product quality</td>
</tr>
<tr>
<td>Fish</td>
<td>Minimize environmental impact</td>
</tr>
<tr>
<td></td>
<td>Use of sustainable feed resources</td>
</tr>
<tr>
<td></td>
<td>Safety and consumer acceptability</td>
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<td></td>
<td>Acceptable price</td>
</tr>
<tr>
<td></td>
<td>Maintain animal integrity</td>
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Oleson et al. (2000) suggested to split economic values for traits in the aggregate genotype into non-market values \((NV)\) and market values in the money economy \((ME)\). The latter represent the direct economic value of the trait through increased monetary returns and/or reduced monetary costs. Non-market values refer to the impact of traits on human welfare through ethics (e.g.
ethical values of improved animal welfare), social considerations, (e.g. genetic diversity, impact of animal production on human health), and through the ecosystem (e.g. slower depletion of fossil energy, slower degradation of the atmosphere).

Thus, for a 2-trait aggregate genotype: \[ H = [NV_1 g_1 + ME_1 g_1] + [NV_2 g_2 + ME_2 g_2] \]

Where \( NV_i \) and \( ME_i \) are the non-market and money economy value for trait \( i \). Note that some traits may only have a non-market value or only a money economy value. Olesen et al. (2000) gave several examples of production systems with non-market value considerations and their impact on selection indexes and breeding strategies. Although they showed that consideration of non-market values changes breeding goals and selection strategies, the main problem that remains is how to assign non-market values to individual traits.

7.9.2 Breeding schemes in different species

Product quality, diversity, acceptability, animal welfare and efficiency were listed by breeders as criteria that deserve attention in sustainable breeding schemes (Table 7.8 from Liinamo and Neeteson, 2001). Environmental issues related to sustainability include for example the need to minimize pollution from animal production and to encourage sustainable land use. Efficient use of sustainable feed resources in nutrition is especially important for species such as poultry and pigs that are competing with world human population on cereals as food, or fish that are currently being fed mostly with other fish. Last but not least, no production can be sustainable unless it is economically viable. Efficiency of production and the ability to balance both short term and long term economic gain determine the final success of all and any breeding programs. As stated already by the Brundtland commission in 1987, sustainable development should fulfill the needs of the present generation, without decreasing the possibility for future generations to fulfill their needs. Product quality consists not only of the actual end product quality (organoleptic, nutritional and technological), but is also associated with contaminations from the use of chemical medications and animal-mediated human diseases and with concerns about the production system. Regarding biodiversity, the goal should be the maintenance of current genetic variation in farm animal populations. However, also the adaptability of farm animals to a wide range of diverse production environments, both within Europe (alternative production systems) and outside Europe (competition in breeding stock markets of for example South-East Asia) is of interest in many species. There is a recognized need for the public acceptance of (reproduction) techniques used in breeding. There is growing public concern on issues such as ethics and animal welfare in the whole animal production chain, including breeding and reproduction.

All the above mentioned criteria are not equally important for all farm animal species, as the species differ in both their production circumstances and the length of time they have been within organized animal breeding (e.g., tens of generations in poultry vs. less than two generations in many fish). Some of the criteria can also be contradictory and difficult to take into account at the same time without some compromises. To solve these dilemmas, the criteria need to be arranged according to their priority to each farm animal species.

7.9.2.1 Ruminants

Ruminant production plays an important role in converting local feed resources (including by-products) into animal products (Oltjen and Beckett, 1996). The production systems vary greatly
between regions due to differences in local ecological and climatic conditions. These differences affect the choice of species (sheep, cattle), product (wool, meat, milk) and intensity of production. The differences in production circumstances as well as the increased need to reduce nutrient losses do affect the choice of breeds to be used as well as the desired direction of change within a breed. For example, under the harsh environments in Scotland it is undesirable to increase litter size in sheep, while for sheep kept in the lowlands increased litter size is desirable. The external inputs into production systems could be reduced if we would succeed in improving the efficiency of utilization of locally grown forage (grass, maize silage).

In the past decades, the average milk, fat and protein production per dairy cow per year has increased enormously in Europe due to the increased use of productive breeds (e.g. Holsteins, Brown Swiss), selection within breeds and the need to reduce the number of cows due the implementation of milk-quota system in the EU. This increase in milk production is also a reflection of the fact that productivity has for many years been an important selection criterion, i.e. selection was mainly based on production and type traits as indicators for functional traits. Efficiency of production is, however, influenced by several traits that can be categorized as production traits (milk and beef) and functional traits. The term “functional traits” is used to summarize those characteristics that increase the efficiency not by higher output of products but by reduced costs of input. Major groups of traits belonging to this category are health, fertility, calving ease, efficiency of feed utilization, and milkability (Groen et al., 1997).

The last decade can be characterized by a growing awareness of consumer concern for the suffering of animals from diseases and disorders, and for the use of antibiotics in livestock production systems. Breeding organizations have realized that a single-minded increase of product output per animal will lead to a deterioration of animal health and reproductive performance, and therefore, to increased metabolic stress and reduced longevity. This has resulted in –some cases radical- changes in breeding goals: the emphasis on functional traits has increased whereas less attention is paid to product output. In addition, selection on functional traits is done based on direct recording of these traits rather than by indirect selection through type traits. Breeding values for a wide range of functional traits have been implemented in most countries, which enable breeding organizations and farmers to pay direct attention to these traits in their selection decisions.

Sustainable production systems need to be tailored towards the regional, natural and social conditions. Recognition of differences in cultural and social aspects between regions, but also in natural circumstances, enhances the differentiation in production systems. For breeding organizations this posses the question on whether they should diversify their breeding objective or whether they can breed an animal that will do well under a wide range of production circumstances. At this stage, little is known about the environmental sensitivity of animals. Little is known about genetic aspects of robustness and capacity of adaptation of animals. More knowledge is required on factors contributing to homeostatic imbalance in a given husbandry system or management practice.

There is a clear need for reduced use of chemical medications. This implies that animals are required to have a better resistance in general and tolerance to particular infections and parasites. Breeding can be used to improve disease resistance but knowledge on adequate parameters to measure and genetic parameters is lacking for most cases.

The technology to select animals on a broader range of traits is available. In most countries, for example, systems have been implemented to breed animals with longer productive live. This principle can be extended to other traits as soon as good selection criteria have been developed.
To monitor effects of selection a good monitoring program needs to be implemented in order to see undesired effects of selection at an early stage. This early information should be used to take measures to prevent an undesired genetic trend. Such a monitoring scheme would need to cover a wide range of production environments. In doing so, animals can be selected that perform well under a wide range of production circumstances.

7.9.2.2. Pigs

The pig breeding programs have been very successful in creating genetic improvement of economically important traits, especially daily gain, backfat thickness, feed efficiency and, during the last decade, litter size. However, the present breeding goals are not limited to these traits. Breeding goals have been, or are presently being set up more broadly. Breeding is aiming at efficient production under all relevant circumstances and adequate management. This means finding an adequate strategy for organizations operating on international markets to deal with genotype x environment interaction and to include also selection pressure for traits that are currently of negligible economical importance or of less interest to producers. Examples include piglet survival, interval between weaning and first estrus, longevity of sows, conformation (esp. legs), vitality of pigs until slaughter weight, meat color, and drip loss. Furthermore, due to the concentration and increasing scale of pig production, a good health status of the pigs is becoming more important. This means not only setting up high health breeding farms (minimal disease level) but also selection for general disease resistance under commercial conditions.

Pig breeding has evolved from pure breeding to crossbreeding in the 20th century. With crossbreeding, separate selection pressure can be put in the male and the female lines on reproduction and production traits. The development of Artificial Insemination, mainly introduced to decrease diseases in farm animals, has proved to be a good way to disseminate genetic progress. Non-surgical embryo transplantation is still in the development stage.

There is a need to understand how to balance inputs and outputs for sustainable use of resources and how to improve this balance through breeding. For example, by increasing growth efficiency we can reduce environmental pollution e.g. increased protein growth efficiency reduces nitrogen excretion, but is this sustainable if it relies on imported feed. There is a lack of knowledge on nutrient (e.g. amino acid) requirements for specific genotypes (in order for them to fulfill their genetic potential). In addition, there is a need to understand the capability of different genotypes (breeds) to utilize non-traditional (homegrown or low-value) feeds (e.g. crop residues or edible wastes from the human food chain). This also applies to matching different developmental stages to feeding regimes. There is a lack of knowledge about “genetic plasticity” and the interaction between different breeds and different acceptable environments. It would like to be beneficial breeds and animals within breeds could be evaluated for robustness, as measured by their reaction to differences in environment (G*E, fitness and also reduced susceptibility to disease).

7.9.2.3 Poultry

The poultry industry in Europe until the 2nd World War consisted of a large number of small farms, often part of a mixed farm. The traditional chicken breeds were dual-purpose: the females would be used for table egg production and the males were grown for meat consumption. These days, eggs are produced mainly from special crosses of egg-type chickens, and poultry meat is mainly produced from fast growing meat-type broilers and turkeys. Lately, some slow-growing meat poultry lines, such as “Label Rouge” in France, have also been developed in some
European countries. Other avian species (waterfowl such as ducks and geese, guinea fowl, ostriches, pigeons) serve niche markets.

These days, Europe is the main source of the world’s poultry breeding stock. Continuing concentration has led to the current situation that only three groups of primary breeders account for about 90% of the layers, broilers and turkeys produced annually. Most breeding companies offer several different strain crosses to satisfy a range of customer demands. Primary breeders need to anticipate future market demands, so all keep under development additional experimental lines, which may become useful in the future for specific segments of the market. Breeding programs, thus far, have been based on classical breeding techniques. The selection program is carried out in the nucleus stock i.e. the so-called pedigree stock. In three to five generations, the genetic improvement is then forwarded through multipliers to commercial farmers.

Commercial poultry are a cross between several lines. For example, for meat-producing poultry i.e. broiler chicken, turkeys and ducks, the birds used in the meat producing generation are the result of crossing males from lines which have been selected for growth and conformation, with females from lines where most selection emphasis has been placed on reproductive characteristics with only a minor emphasis on growth and conformation, to maintain existing growth rates and to keep conformation uniform. Which particular lines and breeds are developed and crossed is the “recipe” of the individual breeding company. Today, the main selection criteria in poultry are production quantity (e.g., number of saleable eggs per hen housed per year) and quality (e.g., external and internal egg quality), reduction of health disorders such as leg disorders and cardio-vascular problems, and traits that are of primary importance to processing plants such as uniformity of product. The most difficult challenge for geneticists is the adaptation of specific strain combinations to the wide range of environmental conditions the parents and commercial progeny are likely to encounter in the world-wide market. The definition of sustainability is continuously changing. Essential practical aspects for poultry breeding and reproduction are: (1) production of high quality food for human consumption; (2) from animals kept and selected according to animal welfare regulations; (3) utilizing feed, water and energy resources efficiently; (4) minimizing the pollution of the environment; and (5) maintaining genetic diversity for future selection in a direction which cannot be predicted today. The need for a new balance between health and welfare on one hand and production efficiency and product specifications on the other hand is paramount for the success of European poultry breeding in the future. To determine exactly what this balance should be is the joint responsibility of both breeding companies and society at large. With the present high and ever-increasing efficiencies and highly specific product requirements by consumers (e.g., high demand for specific components of the carcass or the egg), it will be increasingly difficult to maintain this balance. New insights into avian biology are needed to support breeding programs in maintaining and improving this balance in the future. The poultry industry in Europe should make their production as transparent as possible and continue to offer “value for money” from production systems preferred by consumers.

Today, the main selection criteria in laying hens are: (1) number of saleable eggs per hen housed per year, (2) efficiency of converting feed to eggs, (3) external and internal egg quality in line with demand and (4) adaptability to different environments. Egg production is tested in cross-lines and pure-lines and in different environments, with emphasis on persistency. Residual feed consumption, i.e. the deviation from calculated demand to satisfy maintenance and production requirements, is used as a measure of efficiency. The most important external egg quality criteria are shell strength and optimal egg weight. Shell color is also receiving attention, especially in
brown-egg stocks, in response to consumer preferences for uniform, dark brown eggs. Traditional internal quality criteria are albumen height, sometimes converted to Haugh units, and incidence of blood and meat spots, which are to be minimized. With increasing use of eggs for further processing, selection for higher yolk percentage and dry matter has become more important in recent years, whereas selection for lower cholesterol level has proved to be of short-lived interest. The most difficult challenge for geneticists is the adaptation of specific strain crosses to the wide range of environmental conditions the parents and commercial layers are likely to encounter in the world-wide market. In view of current trends in the European market, with growing demand of consumers for eggs from animal-friendly management systems and legal constraints regarding production in cages, breeders of egg-type chickens have been intensifying their efforts to select against feather-pecking and cannibalism, two behavioral problems which are more difficult to control in floor management (large groups) than in cages (small groups). Also, resistance to E. coli infections and other typical ‘floor’ problems is receiving additional attention, whereas selection against osteoporosis may lose its urgency if cages are no longer used in Europe.

In contrast to egg-type chickens, where heterosis effects in multiple strain crosses accounted for a significant portion of the genetic improvement, broiler breeders relied longer on pure-breeding. The development of specialized male and female lines and the introduction of controlled feeding of parents became effective tools to overcome the negative correlation between juvenile growth rate and reproductive traits (egg production and hatchability). With increasing world feed prices during the 1970’s, direct selection for efficient feed conversion was introduced, which also helped to counteract an apparent tendency of fast-growing broilers to over-consume and deposit excessive abdominal fat. During the last two decades, emphasis of selection has shifted more and more to traits which are of primary importance to processing plants: breast meat yield, total carcass value, efficiency of lean meat production, uniformity of product, and low mortality and condemnation rates. In view of current trends in the EU broiler market, consumers being more aware of welfare and food safety issues, geneticists are putting more emphasis on broiler livability and related traits, especially cardio-vascular insufficiency (sudden death syndrome and ascites) and leg disorders. Until these causes of mortality and potential suffering are effectively reduced by selection, they can be alleviated to some extent by improved management. An open question is whether the excessive appetite, which currently requires controlled feeding of broiler breeders, can be overcome in the long run by selection.

The main welfare issues in broilers are leg weakness, sudden death syndrome and ascites. Selection for body weight gain, intensive feeding and some management procedures contribute to these problems. The locomotive activity of commercial broilers is very low (compared to slow growing poultry breeds) and as of the 3rd week of age the birds spend most of their time sitting. The lack of exercise further increases the incidence of leg problems and may cause foot lesions, hock burns and dermatitis under unfavorable climatic conditions and wet litter. Turkeys are more active, but periodically leg problems appear, often associated with digestive upsets to which the turkey is prone. The causes are probably multifactorial and require further research. Breeders of broilers and turkeys are aware of these problems and have increased selection pressure against the incidence of leg disorders and malfunction of the cardio-vascular system since several years.

7.9.2.4 Fish
The breeding of aquaculture species is still in its infancy. In many fish species, domestication has not yet been initiated or has only just started. In only a very few species domestication and
Selection has been in progress for 7 to 8 generations (trout, carp, and salmon). Most of the genetic improvement in fish is based on mass selection without any pedigree information (97% of aquaculture). This is due to the impossibility to physically tag fry at hatching (2 mm to 1 cm). Traits for selection are mostly growth and fillet yield (only available with family selection) and, to a lesser extent, spawning season, age at maturation and morphology. Advances in selection methodologies (e.g. BLUP) developed for livestock animals, have been transferred also to fish (Atlantic salmon, trout, tilapia, Arctic charr). Genetic progress of 10-14% per generation has been obtained for growth rate (2 to 3 times more efficient than selection in domestic livestock animals). Several selection programs (<25), which are currently being executed around the world are based on a combination of family and individual selection for not more than 7 generations and are applied to few species. The high cost of family selection (>10 times as expensive as mass selection) is justified by the need to select broodstock on several traits or on traits that cannot be recorded on live animals and that need collection of data from relatives, e.g. lipid content and color of the meat, yields of viscera and fillet, or disease resistance. The recent development of DNA fingerprinting, allowing parentage recognition, could reduce the costs of such a type of selection program by reducing the time needed for separate tanks for each family up to tagging size. Aquaculture is a relatively recent farming activity, and the feeding and breeding technology used are often adaptations from technologies used in livestock farming. However, several factors make fish decidedly different: many species are carnivorous, fish are more dependent on their environment in terms of water temperature and quality, and while livestock have little chance to breed with wild conspecifics fish have every opportunity to do so. As a consequence, several factors need to be considered for the future development of the industry, such as minimizing genetic interaction with wild stocks, reducing environmental impact, reducing dissemination of diseases, improving use of (vegetarian feed) resources and maintaining animal integrity and reproduction functions. The application of breeding technologies in fish farming is recent. Very few negative effects are documented thus far in cases where modern breeding programs have been developed. The introduction of new traits in future breeding programs is thus considered as a way to better adapt genotypes to new developments in the industry. New objectives, all of which are indirectly related to the improvement of fish welfare, could be for example specialization of genotypes for different farming environments, improvement of meat quality traits, improvement of resistance to specific pathogens, maintenance of animal integrity and functional traits, ability to consume plant ingredients, improvement of feed conversion, and conservation of genetic resources. Domestication of a great number of aquatic species is in progress in Europe and globally. The development of selective breeding programs based on classical selection is expensive and thus is applied to only few species. The application of sophisticated breeding technologies for all species (> 20) seems unrealistic today, and research into reduced costs of such programs is important.