SELECTION INDICES FOR NON-LINEAR BREEDING OBJECTIVES, SELECTION FOR OPTIMA

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Abstract

Linear selection index assumes that the objective function is a linear function of the trait values. In actual commercial breeding populations this is rarely the case. For non-linear profit functions there is no uniformly "best" solutions. Maximum genetic progress will always be achieved by a linear index, but for a non-linear profit function, the index that results in maximum genetic gain in the future will be a function of the selection intensity. For traits which are non-linear in the objective function, it should be possible to increase the mean value of the objective function in the progeny by planned matings. The advantage of planned matings will be greatest for traits with high heritability and population mean close to the economic optimum. Results of a simulation based on 1006 cows and 20 sires in the Israeli population showed that planned matings increased the mean profit value of the progeny by only 0.4% even though the population was close to the optimum value for somatic cell score, and heritability was 0.15.

1. Introduction

In nearly all animal breeding situations, the objective function consists of several traits, each with its own economic value. Hazel (1943) defined the aggregate genotype, H, for a given individual as a'y where a is the vector of economic values of the traits included in the objective function, and y is the vector breeding values for these traits for the individual considered. The elements of a are the partial derivatives of the objective function with respect to each trait included in this function. Generally, only the vector a can be directly observed, while y can be estimated from phenotypic values on the individual and his relatives on the traits included in the objective function and for additional correlated traits. In the most general terms, the goal of breeding is to increase the population mean of H in future generations, by selecting the "best" individuals as parents for the next generation. However, as will be seen below, "The devil is in the details!"

If the objective function is a linear function of all traits, then a will be a vector of constants. In this case, linear selection index first derived by Hazel (1943) is clearly the optimum solution. In linear selection index all candidates for selection are ranked on an index, $I = b'x$, where b is a vector of index values and x is a vector of records for the traits included in b.

Under the condition that a is a vector of constants equal for all individuals, linear selection index as formulated by Hazel (1943) also has several desirable properties in addition to being the optimum criteria for ranking candidates. However, in the "real world" the conditions assumed by linear selection index for a are never completely met, and for all other situations there is no uniformly "best" solution, although numerous alternatives have been proposed. Linear selection index is least appropriate when the objective function is maximum at an intermediate trait value, close to the population mean.

To explain why no uniformly "best" solution is possible for nonlinear objective functions, we will first summarize the important properties of linear selection index. In the interest of brevity, these properties will be presented without proof, although references will be provided. We will then explain why a is generally not a function of constants, and the different types of functions that can be encountered in this vector. Finally, we will consider the different solutions that have been proposed for nonlinear objective functions, and discuss the strengths and weaknesses of each alternative. Within this context we will consider the specific questions of mate selection within the context of breeding for an optimum. An example will be given based on milk production traits and somatic cell concentration in the Israeli Holstein population. Notation throughout will be consistent with Weller (1994).

2. Properties of linear selection index

If the candidates for selection are also those animals recorded for the traits included in the objective function, then b, the vector of index weights for the optimum selection index is computed as follows:

$$b = P^{-1}Ga \qquad [1]$$

where P is the phenotypic variance-covariance matrix, G is the genetic variance-covariance matrix, and the other terms are as defined previously. $P^{-1}G'x$ will be the estimated breeding values for the individual traits, with x measured relative to the trait means. If a is a vector of constants then the selection index has the following important properties, summarized by Henderson (1973) and Brascamp (1984).

1. Define H_a = mean for the aggregate genotype of the selected individuals. If individuals are selected by ranking on I = b'x, then $E(H_a)$ will be maximum as compared to any other group of individuals of equal number.

2. Of all possible linear functions of x, I = b'x gives the maximum correlation with H computed over all individuals used to compute P and G.

3. Of all possible linear functions of x, I minimizes $E(H-I_a)^2$, where I_a is any alternative linear function of x.

4. Of all possible functions of x, ranking individuals on I maximizes the probability of correct pairwise ranking on H.

5. Define f(x) = the objective function. For a given selection intensity, f(E(x)) of the progeny will be greatest if their parents are selected based on I.

6. E(f(x)) of the progeny will also be greatest with selection of parents on I. Although properties 5 and 6 appear very similar they are not the same, as noted by Itoh and Yamada (1988). In property 5 the objective function is maximized for the population mean in the next generation. In property 6 the mean of the objective function for each individual is maximized.

7. The optimum selection index is independent of the selection intensity. Thus the same selection index will result in optimum gain over the short- and long-term.

8. If the breeding values are computed by selection index with known trait means, or by Best Linear Unbiased Prediction (BLUP) methodology for unknown trait means, then the optimum selection index can be computed as g'a, where g is the vector of estimated breeding values.

9. If BLUP genetic evaluations are computed for all candidate for selection for all traits, then the optimum index will be g'a for all individuals, even if selection intensities and accuracies are different for different groups of

animals, for example males and females.

As will be seen below, if a is not a vector of constants, no single criteria will have all these properties. As noted by Itoh and Yamada (1988) the main objective of selection is to maximize E(f(x)) in future generations. However, property 7 holds only for linear objective functions. It will be demonstrated that for non-linear profit functions, the index that maximizes E(f(x)) will be a function of the selection intensity.

3. Non-linear objective functions

Various criteria have been suggested to determine objective functions for agricultural breeding. The most widely considered criteria are maximum outputs less inputs (profit), minimum inputs per unit outputs (efficiency), maximum outputs per unit inputs (return on investment) on either an economic or biological basis (Harris, 1970). The relative merits of these criteria were discussed in detail by Groen (1989). In the remainder of this study it will be assumed that profit, defined as income less expenses is the objective function for agricultural breeding, although nearly all of the following also holds for alternative objective functions. Nearly all multitrait profit functions are non-linear. Three type of non-linearity will be defined:

Type 1: Traits with different economic importance for different groups of animals. For example, dystocia is generally only a serious problem for heifer calvings, while growth traits are generally important only for male calves and surplus females calves that are sold for beef.

Type 2: The profit function is maximum at an intermediate trait value. In dairy cattle some conformation traits are of this type, as is somatic cell concentration, for which either too low or too high a value is desirable (Coffey et al., 1986).

Type 3: Traits for which profit is a monotonic function, but not a linear function. The situation that comes first to mind is payment as joint function of two traits, for example payment for milk with a price differential for fat or protein percent. However, even for traits which seem to be linear in profit, this will generally not be the case over the long-term. Consider the following simple situation based on Moav (1973). Farmers are paid a constant price per kg milk. A simple function of profit per cow can be written as follows:

$$f(x_c) = x(i_m - c_m) - c_f \qquad [2]$$

where $f(x_c)$ is profit per cow, x is milk production per cow, i_m is income per kg milk, c_m is costs of production per kg milk, chiefly food, milking costs, storage, transport and refrigeration, and c_f is fixed costs per cow not related to the quantity of milk produced. The

derivative of this profit function with respect to x is $i_m - c_m$, which is a constant. Now assume that the farmer has a milk quota, and that rather than computing profit per cow, he is interested in profit per kg milk. Profit per kg milk, $f(x_m)$ is derived by division of equation [2] by x as follows:

$$f(x_m) = i_m - c_m - c_f/x \qquad [3]$$

Now the derivative of $f(x_m)$ with respect to x is c_f/x^2. As long as x is positive, profit is still a monotonic function of x, but no longer linear, and the economic value of x is a function of x. Since production quotas is apparently the natural state of nature, economic values will not be constants even for production traits. (However, as noted by Brascamp et al. (1985) in the situation of "zero profit", the economic value of x will again be a constant).

4. Non-linear profit functions, linear vs. non-linear indices

If the objective function is non-linear, then question arises as to which criteria should be used to rank candidates for selection? Several alternatives have been considered, and these were summarized by Goddard (1983). The first alternative he considered was to compute the derivatives of objective function setting the traits values at the current population means. By definition the economic values will then be constants. This will work reasonably well if changes in the population mean due to selection are small relative to the value of the derivative, and are frequently updated (Groen et al., 1994; Dekkers et al, 1995). However, this will not be the case if the population is close to optimum for some of the traits. Consider the following theoretical profit function:

$$f(x) = -(x-a)^2 \qquad [4]$$

The derivative of $f(x)$ with respect to x is $-2(x-a)$, and $f(x)$ will be maximum when $x = a$. If $x < a$ then the derivative is positive and profit is increased by increasing x, while if $x > a$ then the derivative is negative and profit is increased by decreasing x. If selection intensity is high, and the population is close to optimum, ranking individuals on a selection index computed using the current mean trait value can result in a *decreased* mean profit value in the next generation. A somewhat realistic example was presented by Dekkers et al. (1995) for poultry egg production with an economic optimum egg weight. Once the population is close to the optimum, an index based on the differentials computed at the current population mean in each generation will result in oscillation of mean egg weight around the optimum.

Probably the most intuitive answer would be to maximize $E(H_a)$, the expected mean aggregate genotype of the selected individuals. If the objective function is non-linear, then the index that maximizes $E(H_a)$ will also be non-linear. There is no general analytical solution for all possible objective functions, but solutions have been derived for the case of quadratic and cubic objective functions (Wilton et al., 1968; Ronningen, 1971). Although this solution is intuitively appealing, neither $f(E(x))$ or $E(f(x))$ of the progeny will be maximized if their parents are selected by $E(H_a)$. This was explained by Goddard (1983), who used the following example. Assume that $f(x) = x^2$, and that the population mean for $x = 0$. Then the individuals with the highest genetic merit will be those with highly positive and negative values for x. If these individuals are selected as parents and mated randomly, there will be no genetic progress for x. However progress could be achieve by selection for either high or low x.

Another alternative that has been proposed is restricted selection indices (Brascamp, 1984). Although we often have only a vague idea of the profit function, and over the long-term the function will change; the breeder does know that over the long-term certain results are undesirable, for example a genetic reduction in fertility. Thus, a linear index can be devised that results in the desired change, or no change, in certain traits and maximum increase in others. However, as noted previously (Gibson, and Kennedy, 1990; Groen et al., 1994), restricted indices will generally not be economically optimal for any criteria.

We will now consider properties 5, 6, and 7 in detail. Goddard (1983) following Moav and Hill (1966) assumed that property 5, maximizing $f(E(x))$ of the progeny should be primary criteria for selection. In this case, as Goddard (1983) noted, a linear selection index will always be optimum. Genetic progress with a linear index for a given selection intensity is defined by a multidimensional ellipse. For a given selection intensity and any direction of genetic progress, this ellipse defines the maximum genetic change possible for the population mean, and will always be greater than genetic progress with a non-linear selection index. This is analogous to the shortest distance between two points being a straight line. Goddard also considered the possibility that there is a optimum value for $f(x)$ within the selection ellipse (Type 2 non-linearity). In this case he argued that since selection costs money, the optimum solution would be to decrease the selection intensity and thus reach the optimum population mean with a linear index and a lower selection intensity.

Moav and Hill (1966) derived a graphic method to determine the vector of index coefficients, b, that maximize $f(E(x))$ for two traits and a given selection intensity. If the profit function is non-linear, then b will be a

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function of the selection intensity. For more than two trait, b, can be derived from the vector of expected genetic gains, ϕ, which is also a function of the selection intensity. ϕ can be computed iteratively (Itoh and Yamada, 1988; Pasternak and Weller, 1993) as follows:

$$\phi^{k+1} = \frac{GP^{-1}G\{\delta[f(x + \phi^k)]/\delta\phi\}i}{(\{\delta[f(x + \phi^k)]/\delta\phi\}'GP^{-1}G\{\delta[f(x + \phi^k)]/\delta\phi\})^{1/2}} \quad [5]$$

where ϕ^{k+1} is the vector of genetic gains at the k+1 iteration, $\delta[f(x + \phi^k)]/\delta\phi$ is the vector of partial derivatives of the objective function with respect to the individual traits with the population mean set at $x + \phi^k$ for all traits included in the index, i is the selection intensity, and the other terms are as defined above. The vector of index coefficients can then be derived as follows.

$$b = (\sigma_1/i)G^{-1}\phi^* \quad [6]$$

where σ is the standard deviation of the index, and ϕ^* is the solution for ϕ at convergence. Note that both ϕ^* and b are functions of the selection intensity.

Although both Moav and Hill (1966) and Goddard (1983) considered this solution to be the optimum solution for nonlinear objective functions, several recent studies disagree. The reasons are as follows:

1. This solution maximizes the objective for a specific vector of genetic gains determined by the population mean prior to selection and the selection intensity. Thus, the optimum selection index will be different for each generation, and different from the selection index that would maximize the gain in the objective function over several generations. Dekkers, Birke, and Gibson (1995) suggested maximizing total profit up to the profit horizon, discounting expected profit in each subsequent generation relative to the time until the expected gain is realized. They also developed numerical methods to solve for the index coefficients. They found that the net present value of profit could be significantly lower for an index that maximizes f(E(x)) after ten generations of selection as compared to an index that maximizes net present value of profit over ten generations. The problems with this solution are first, that both the profit horizon and the discounting rate are generally arbitrary. Second, the solution presented is only valid for a situation of discrete generations, which is definitely not the case for dairy cattle. Third, past experience shows that objective functions tend to change over time. Fourth, as noted by Groen et al. (1994) genetic and phenotypic variance matrices will change over time due to selection and other factors. Finally, economic values tend to change over time. Thus, selection for maximum f(E(x), or maximum net present value, for several generations into the future for dairy cattle, under the assumption that the objective function remains constant, would seem to be rather fool-hardy.

2. As noted by Itoh and Yamada (1988) with a non-linear profit function, maximization for f(E(x)) is not the same as maximization for E(f(x)). Equations [5] maximize the profit of the expected mean trait values for the progeny, while the objective of selection is to maximize the expected mean profit of the progeny. Itoh and Yamada (1988) were not able to analytically derive the b vector that maximizes E(f(x)) for any function; but did derive approximate methods. However, they also note that for quadratic as well as linear profit functions maximizing f(E(x) is equivalent to maximizing E(f(x)). Since a wide range of profit functions can be approximated by either linear or quadratic functions, this problem is probably not serious under realistic situations.

3. As first noted by Moav (1973) for animal breeding in general and by Allaire (1977) for the specific case of dairy cattle, with a non-linear profit function, E(f(x)) will also depend on the specific mating combinations. Generally for profit functions with an optimum value with respect to certain traits, disassortative mating will result in greater mean profit than assortative mating. We will now consider in detail the question of mate selection within the context of non-linear profit functions.

5. Mate selection for non-linear profit functions

Moav (1966) first noted that one of the causes of heterosis for profit is that profit is not linear on the additive genetic scale. Once the parents for the next generation have been selected, in theory it should be possible with a non-linear profit function to plan matings so that the expected mean value of the objective function in the next generation is greater than the expectation by random mating. The following example was given by Moav (1966) for the case of swine, and corresponds to Type 3 non-linearity defined above.

$$P_1 = K_1 - K_2x_2 - K_3/x_1 \quad [7]$$

Where P_1 is profit per pig marketed, x_1 is number of pigs weaned per sow per year, x_2 is age to a fixed market weight, K_1 is income less costs independent of x_1 and x_2, K_2 is costs dependent on x_2, and K_3 are fixed costs (feed and non-feed) per sow. Assuming complete heritability, the parental mean for profitability, P_{pm}, can be computed as follows:

$$P_{pm} = (P_s + P_d)/2 = K_1 - K_2(x_{2s}+x_{2d})/2 - K_3(x_{1s}+x_{1d})/(2x_{1s}x_{1d}) \quad [8]$$

Where the subscripts "s" and "d" refer to the sire and dam values, respectively. Assuming

additivity of the scale of measurement, the profit value of the offspring, P_o will be:

$$P_o = K_1 - K_2(x_{2s} + x_{2d})/2 - 2K_3/(x_{1s} + x_{1d}) \quad [9]$$

The difference between P_o and P_m is a measure of the "non-linearity heterosis", H_{nl}, and can be computed as follows:

$$H_{nl} = P_o - P_{pm} = \frac{K_3(x_{1s} - x_{1d})^2}{2x_{1s}x_{1d}(x_{1s} + x_{1d})} \quad [10]$$

Heterosis due to non-linearity was simulated for dairy cattle by Allaire (1973), and summarized recently by Allaire (1993). Thus, by mate selection it should be possible to increase $E(f(x))$ in the next generation over the expectation with random mating. However, it is very difficult to achieve this objective for dairy cattle. The reasons are as follows:

1. We generally only have a vague idea of the actual profit function, especially with respect to those traits with maximum profit at intermediate values, such as conformation traits.

2. If the mean of the population is not near the optimum, profit will generally be close to a linear function of the trait value, and the "heterotic" gain possible by planed matings will be minimal.

3. Heritability of nearly all economic traits in dairy cattle is low to moderate. The expected value from a specific mating will be the mean of the parental breeding values. The female breeding value, based chiefly on her own phenotype, will have low reliability, and is therefore highly regressed. Thus, even if the putative dam is phenotypically extreme for a particular trait, the expectation for the progeny will be close to the mean with a prediction error variance only marginally less than the phenotypic variance. This is not the case for Type 1 non-linearity defined above. If either the objective function or the mean trait values are significantly different for different groups of animals, then it is analogous to a situation of complete heritability.

4. The number of possible matings in a population of any reasonable size is enormous and constantly in flux. It is therefore not generally practical to test all combinations to determine the "economically best" mating strategy. Several techniques have been proposed to minimize this problem, such as linear programming (Jansen and Wilton, 1985) and Bayesian methods (Smith and Allaire, 1985).

In addition, as noted by Weller (1994), unlike selection, any gain obtained by planned matings is not permanent and cumulative. Planned mating among a given group of putative parents does not change the gene pool of the population, and specific advantageous genetic combinations, if achieved, "break down" each generation. Thus, over the long-term, any gain obtained by a specific mating strategy is worth much less then the same nominal gain obtained by index selection. With a discount rate of 0.03, corrected for inflation, and an infinite profit horizon, the "nominal gain" from planned matings is only worth 3% of the same nominal annual gain from selection (Weller, 1994). It should also be noted that disassortative mating will decrease genetic variances, but under realistic conditions, the effect will be insignificant.

Despite these considerations, there is considerable interest in planned matings. On the positive side, it should be note that the cost of a planned matings program is insignificant, unless additional traits are measured specifically for the program. Second, it is not necessary to achieve the "economically best" strategy, just a strategy better than the alternative of random mating. Furthermore, if the strategy is based on only one or two traits that are strongly nonlinear in profit, it is not necessary to test all possible combinations, but only to consider gradients.

In general, planned mating in dairy cattle has been phrased in terms of finding the "best" sire for each dam. This solves the problem of evaluating all possible matings, but will generally not produce an optimum solution. Even if a single sire is best for all dams, several sires will be used even in a relatively small population, if for no other reason than to minimize inbreeding. Thus, semen from the best sires can be considered a limited resource, and, in theory, systems analysis techniques can be used to optimize allocation of this resource, subject to the qualifications given above, and considerations of inbreeding (Jansen and Wilton, 1985).

In the final section we will use the example of somatic cell score (SCS) in the Israeli Holstein population to estimate the expected gain from planned matings relative to random mating with respect to this trait. This example was chosen because the profit function is nonlinear with respect to this trait, heritability is about 15%, which is intermediate for most secondary traits in dairy cattle, and evaluations are available for all individuals.

6. Mate selection relative to scs, an example with Israeli Holsteins

SCS is defined as the log base 2 of cells/(0.01 μl) plus 3. Thus, the SCS of 100,000 cells/ml = 3. LSCS, a lactation measure of SCS was defined as the mean SCS of all records during the lactation corrected for parity, days in milk, and month of test (Weller et al., 1992). LSCS was computed only for cows with at least four valid SCS records during the lactation. Means, phenotypic standard deviations, and

heritabilities for LSCS and milk, fat, and protein production, are given in Table 1. Genetic and environmental correlations are given in Table 2. The genetic correlation between SCS and protein, the main criteria for selection, was positive. Thus, selection for protein will increase SCS. Since farmers in Israel have a milk production quota, the objective function was profit per kg milk in Israeli Shekels (IS), P_m, computed as follows.

$$P_m = [(D_a - 0.18)M + 4.2F + 22.9P - c_f]/M \quad [11]$$

where D_a is the milk price differential for somatic cell concentration; M, F, and P are kg milk, fat, and protein production per cow, and c_f is fixed costs per cow. c_f was set at 5540 IS. The following function, based on the payment scheme for somatic cell concentration was used to approximate P_a.

$$D_a = [0.031 - 0.06(SCS)^{0.5} + 0.039SCS - 0.00382SCS^2] \quad [12]$$

D_a will be maximum with SCS = 2.7, which is only slightly less than the population mean. D_a and the actual payment scheme are plotted as functions of SCS in Figure 1. Although milk price does not decrease with SCS < 2.7 it is assumed that SCS below this level is not desirable (Coffey et al., 1986). Thus, at the population mean P_m was positive, which reflects the current situation.

One thousand and six cows born during 1991 with evaluations for SCS and production traits for two parities were considered for sire selection. The means and standard deviations for the evaluations of these cows are given in Table 3. The base for the evaluations was cows born in 1990. Since there has been positive selection of all of these traits, the means of the evaluations are positive. Twenty sires with the highest evaluations for the index of production traits with P_a set at zero were considered as mating candidates for these cows.

Two mating schemes were evaluated. In both schemes, it was assumed that a single female progeny was produced from each cow, and that each sire was restricted to mating no more than 20% of the cows. In scheme 1, the five best sires were selected by evaluating the expected mean progeny for P_m by mating all 1006 cows to each sire and producing a single female calf. The expected profit in the next generation was estimated from equation [11] using the expected mean trait values, assuming additivity on the scale of the individual traits. That is, the population mean for each trait plus the mean of the sire and dam evaluations. The mean genetic value for the next generation for each trait was estimated as the mean of the progeny evaluations obtained by mating the 1006 cows to the five sires with the highest evaluations. In scheme 2, a linear programing

"transportation" algorithm (Taha, 1976) was used to determine the optimum mating strategy based on the expected progeny profit for each possible mating as computed from equation [11], subject to the restrictions given above.

The same five sires were selected by both schemes. The mean genetic evaluations of these five sires for the four traits included in the index and the profit function are given in Table 4. The expected means of the progeny obtained by mating these five sires each to 20% of the cows are also given. The sire means are greater than the cow means for all four traits, and for the objective function. By definition, the mean value of the progeny for each trait was the mean of the sire and dam means. However, since the profit function is nonlinear, the mean profit function of the progeny, $E(f(x)) = 0.12296$, was greater than the means of the sire and dams, 0.12155. $E(f(x))$ in this case was also slightly greater than P_m of the expectation of progeny, $f(E(x)) = 0.12251$, computed as P_m for the mean of the sire and dam evaluations for the component traits. The additive gain due to genetic selection of the sires can be computed as $f(E(x))$ of the progeny, less $f(E(x))$ of their dams, or 0.12255 - 0.08071 = 0.04084 IS/kg. The mean value of P_m of the progeny obtain with planned matings was 0.12311, about 0.00015 IS/kg greater than the expectation with random mating, or 0.4% of the gain obtained by selection. This result can be contrasted with the values close to 10% presented by Allaire (1993) for theoretical cases based on complete heritability and extreme non-linearity of the objective function. Since, as noted above this gain is not cumulative and permanent, implementation of a planned mating scheme will be difficult to justify, even if costs will be minimal.

7. Conclusions

For non-linear profit functions there is no uniformly "best" selection index solution. The index that maximizes the expectation of the objective function in future generations will be a function of the selection intensity. Although rather large gains by mate selection have been obtained in theoretical simulations, the results presented indicate that economic gains will be minimal for traits with moderate heritability, even if the population mean is close to the economic optimum.

8. Acknowledgements

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Table 1. Means, phenotypic standard deviations, heritabilities and economic values for the traits included in the index.

Trait	Mean	Standard deviation	Heritability
SCS*	3.12	1.06	0.15
Milk (kg)	9581.	1226.	0.25
Fat (kg)	301.	41.2	0.28
Protein (kg)	289.	32.9	0.23

* Somatic cell score. The mean for this trait is the uncorrected mean of all test records, while the standard deviation and heritability are for LSCS, the lactation measure of SCS.

Table 2. Genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) for the traits included in the index.

Trait	LSCS	Milk	Fat	Protein
LSCS	-	0.182	0.019	0.200
Milk (kg)	-0.065	-	0.416	0.754
Fat (kg)	-0.051	0.603	-	0.596
Protein (kg)	-0.030	0.877	0.672	-

Table 3. Means and standard deviations of 1006 cow evaluations, and correlations among cow evaluations for the trait included in the index, and the objective function.
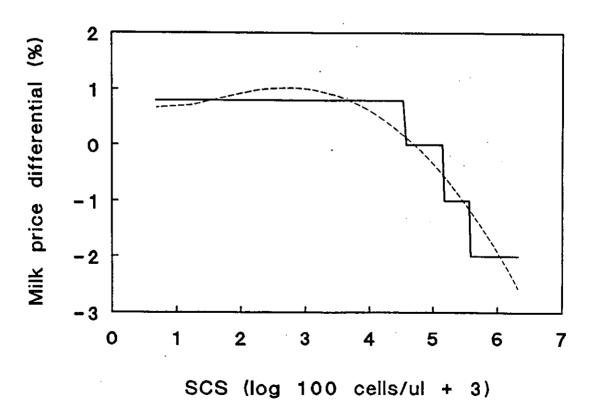
| Trait | Mean | Standard deviation | Correlations | | | P_m |
			Milk	fat	protein	
LSCS	0.039	0.197	-0.062	-0.115	0.130	0.119
Milk (kg)	8.2	414.5		0.492	0.710	0.423
Fat (kg)	4.3	15.3			0.610	0.724
Protein (kg)	2.3	9.7				0.913
P_m	0.08071	0.0214				

Table 4.   Means and standard deviations of the five sires selected and expected means of the progeny for the traits included in the index, and the objective function.

Trait	Mean	Standard deviation	Progeny mean
LSCS	0.102	0.229	0.071
Milk (kg)	322.6	448.4	165.4
Fat (kg)	43.8	14.5	24.1
Protein (kg)	33.8	6.5	18.1
P_m	0.1623	0.0045	0.12296

Figure 1. D_s (—) and the actual payment differential (—) for somatic cell concentration as functions of SCS.