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HISTORY OF GENETIC EVALUATION METHODS IN DAIRY CATTLE I. DAUGHTER-DAM COMPARISONS

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Abstract

The procedures used on genetic evaluation in dairy cattle are presented, during the last century. These procedures have evolved greatly over the years, from the simple dam-daughter comparison to animal model, from single trait to multiple trait analysis, and from lactation to test-day model. Nowadays, more emphasis is put on the incorporation marker genetic information, in order to get so named GEVB-genomic breeding value.
From historical point of view, there are four category of methods: 1) Methods based on averages (1902-1952); 2) methods based on selection index procedure (B.L.P;1952-1970.); 3) Methods based on mixed model equations (B.L.U.P.; 1971-2000) and 4) Methods based on BLUP and Genomics (2001-present).
The aim of this paper is to give an overview of the genetic evaluation methods in dairy cattle, starting with first category of methods: "the Methods based on averages" or Daughter-Dam Comparisons.
This group of methods cover the period 1906-1950, and take in account the following 12 indexes. For each index the formula is given and also the main advantages and disadvantages are presented.

Key words: *Selection index, daughter-dam comparison, heritability, regression.*

INTRODUCTION

The idea to use the best animals for reproduction is rather old, being mentioned by VARRO, 2000 B.C. The same idea was resumed under different forms in the 18th and 19th centuries. Thus, H. BRANTH (cit. by BONNIER, G., 1936), a Danish farmer, said (1891) that "*the ability of a cow to produce more or less milk fat, from the feed it eats, depends on heredity*".

BRANTH's ideas have been further developed by SEDELHOLM (cit. by BONNIER, G., 1936), who verified them in his own farm (1900). Practically, Sedelholm compared the daughters with the dams in terms of milk fat, proving that the bulls have a variable influence on daughter records. Historically, this was *the first real attempt to apply selection by progeny in cattle*.

After 1920, the research to identify the best animals in a dairy cattle population entered a new stage with the focus on the genetic evaluation of the bulls.

Several indexes were developed during this period for the genetic evaluation of dairy bulls, most of them being variations of the basic method (dam-daughter comparison). Most indexes rely on the average record of the daughters and dams and on a linear regression which can take values from 0 (Daughter - mean index) to 0.5 (Intermediate index).

A general approach of the selection indexes that have as variables both dam records ($\bar{Y}$) and daughter records ($\bar{X}$) was proposed by LUSH (1933;1944). Within this context he presented a new formula and showed how an index can be obtained starting from the general formula:

$$\hat{I} = a + c \cdot \left(\bar{X} - b \cdot \bar{Y}\right)$$

where a , b and c are constants; $\bar{X}$ = average record of bull's daughters; $\bar{Y}$ = average record of the dams.

The main objective of all indexes proposed by the different authors was to eliminate dam influence and to highlight the genetic potential of the bulls. No index is perfect because the sources of error cannot be removed completely, just minimized. Therefore, the genetic potential of a bull can only be estimated, within predictable limits. The bulls can be classified on the basis of their genetic potential and retained for breeding depending on the present intensity of selection.

In order to obtain an acceptable precision of the bull index one of the first recommendations was that the bull has to be evaluated on the basis of several dam-daughter couples. As an overview, in table 1 are enumerated the most important indexes, frequently cited in the literature.

The Högström′s index was formulated in base of GALTON′s idea, namely that each progeny inherits ¼ from each parent, the rest coming from other ancestors.

Hansson (1913) continued the investigations in the same farm which Högström had analyzed and proposed a new formulation to estimate the genetic value of bulls for milk fat.

The same Index has been proposed later by YAPP (1925) and mentioned in the literature as YAPP′s index. Because Hansson was the first to propose this index, it was referred in literature as HANSSON-YAPP′s index, as the "index of parental equality", as the "intermediary index" or as the "American index". This index has been used for the genetic evaluation of the Ayrshire and Holstein breeds and by the American Club for Dairy Cattle.

From the early stages of genetic evaluation of bulls, farmers noticed that the average record of a sufficiently large number of daughters can be used to measure the genetic potential of bulls. At least six daughters must be used to obtain an acceptable accuracy (Davidson, 1925; Lush, 1931). R. R. Graves (1925) seems to be the first to present how the index is calculated and to use it under USA conditions.

Based on the study of Gowen (1930) regarding the crosses in cattle, Goodale (1927) proposed the Mount Hope index. In his study, Gowen reached the conclusion that in the first generation of crosses between a breed with higher milk yield and a breed with lower milk yield, the average daughter production is not half way between the parental breeds but closer to the level of the higher parental breed, while the fat percentage is closer to the level of the lower parental breed.

The results of these experiments lead to the conclusion that when animals with different production levels are mated, the average production of milk is about seven tenths of the difference between the parental levels above the level of the higher parent; the fat percentage is about four tenths of the difference above the lower parent.

Gifford (1930) showed that the average record of the progeny is a sufficiently accurate indicator of the bull′s genetic transmission ability (1/2 of the breeding value). The main attribute of GIFFORD′s method is that it allows using the records of all the daughters of a bull, even if their dams have not been tested.

All indexes presented so far relied on the phenotypic difference of the dam and daughter average records without explicitly taking into account the number of dam-daughter pairs (n). In order to eliminate this deficiency, Wright (1932) proposed a new index which takes this aspect into consideration and incorporated the number of daughter-dam pairs (n) per bull.

Bonnier (1936) showed that by using this index, Wright intended to give a higher weight to the bulls with a higher number of daughters. Thus, two bulls with the same phenotypic differences of the daughters, but with a different number of daughters, will have different genetic values, the bull with more daughters having a higher value.

First index proposed by Bonnier (1936) was the ″*regression index*″ with variable coefficients. The regression coefficient (b) was estimated with the least squares method, by minimizing the difference of the potential yield of a cow and its actual yield.

When the regression has an intermediate value ($b = 0.5$), the regression index coincides with the Hansson-Yapp index. When b is variable, therefore different from 0.5, the values of the two indices are no longer similar. This shows that the Hansson-Yapp index is a particular case of the regression index, the latter having a wider scope.

HÖGSTRÖM's INDEX (1906)	Finnaly, the formula proposed for the evaluation of bulls was: $\hat{I} = 4 \cdot \bar{X} - \bar{Y} - 2 \cdot A$, where A is the breed average.
PEARL 's INDEX (1919)	When a=0; b=c=1, the dam-daughter comparison index is obtained: $\hat{I} = \bar{X} - \bar{Y}$
HANSSON-YAPP INDEX (1913; 1925)	$\hat{I} = 2 \cdot \bar{X} - \bar{Y}$ which is equivalent with the fact that the value of an average progeny will always be half way between its parents. According to Lush (1944) the same formula is obtained when a=0; b=0.5 and c=2.
MOUNT HOPE's Index (1927)	a) When daughter average is above dam average: $\hat{I}_{Milk} = \bar{X} + 0.429 \cdot (\bar{X} - \bar{Y})$; $\hat{I}\_\%\_Fat = (\bar{X} + 1.5 \cdot (\bar{X} - \bar{Y})$ b) When daughter average is below dam average: $\hat{I}_{Milk} = \bar{X} - 2.333 \cdot (\bar{Y} - \bar{X})$; $\hat{I}\_\%\_Fat = (\bar{X} - 0.667 \cdot (\bar{Y} - \bar{X})$ The total Index: $\hat{I}_{Total} = \hat{I}_{Milk} \times \hat{I}_{Fat}$
GIFFORD's INDEX (1930)	When constants a and b are null, and constant c is 1, an index relying only on daughters' average is obtained: $\hat{I} = \bar{X}$
WRIGHT's Index (1932)	$\hat{I} = A + \frac{n}{n+2}\left(2 \cdot \bar{X} - \bar{Y} - A\right)$
NORTON' Index (1933)	$\hat{I} = \bar{X} + (\bar{X} - e) \Leftrightarrow I = 2 \cdot \bar{X} - e$
BONNIER's Indexex (1936)	a) ''regression index'' : $\hat{I} = \frac{\bar{X} - b \cdot \bar{Y}}{1-b}$ b) '' Index of minimal variance'': $\hat{I} = a \cdot \bar{Y} + (1-a) \cdot \bar{X}$
LUSH's Index (1941)	$\hat{I} = (2 \cdot \bar{X} - A) - Average\left(\frac{n \cdot h^2}{1+(n-1) \cdot R}\right) \cdot (\bar{Y} - A)$ $\hat{I} = (2 \cdot \bar{X} - A) - Average\left(\frac{\bar{Y} - A}{2}\right)$
RICE's Index (1944)	$\hat{I} = A + (\bar{X} - e)$
ALLEN's Index (1944)	$\hat{I} = A + 2 \cdot (\bar{X} - e)$

Figure 1. Proposed Daughter-Dam Indexes (Table 1)

The second index proposed by Bonnier (1936) was '' *Index of minimal variance'' to* minimize the difference between the true genetic value of a bull (I) and the estimated genetic value of that bull.

Finally, in order to obtain an index with the lowest variance, constant a is incorporated in

the general equation established by BONNIER (1996).
Historically, the index proposed by J. L. Lush is the first one to take into consideration the heritability and repeatability as genetic parameters to calculate the breeding value.
Another improvement of the index is the term of comparison used for the daughters. Thus, Lush proposed to replace the dam average by the farm average, which seems to be an advantage because the daughters whose dams had not been tested could not be included in the calculations for the candidate bulls.
Given the average productive life of the dams, the number of dam records (n) usually varies between 2 and 4. In this case, the value of the heritability of the average, varies between 0.39 (n=2) and 0.49 (n=4), considering a heritability of 0.28 and a repeatability of 0.43 (Lush, 1941). In base of these values, Lush rewrites initial formula. Dam selection was an important source of errors which affects the breeding value of the candidates for selection. This happens when the dams are not a representative sample of the population. In other words, some bulls are mated to better (selected) dams, which will shift the breeding values of these bulls.
When the dams are not selected, and each one has one record, the daughters will exceed their mothers by $(\bar{Y} - A)\cdot(1-0.5\mathrm{h}^2)$. At the same time, the average daughter record is shifted in an opposite direction, by an amount of $(\bar{Y} - A)\cdot(0.5\mathrm{h}^2)$, which will also favor the bulls mated with superior dams (Lush, 1941).
If the dams have several records, the heritability of a single record is replaced by the heritability of multiple records (h_m^2). The amount of shift generated by dam selection is also affected by the level of heritability and by the number of records; the shift will increase with the decrease of n and of the heritability. Therefore, one way to dampen dam selection effect, which shifts the breeding values of candidate bulls, is to take into consideration several records (lactations), while heritability should tend as much as possible towards the level of the repeatability (Lush, 1941).
H. W. Norton Jr. (1933, cit. by LUSH, 1933) suggested an index based on daughter records regressed towards dam records (Allen, 1944; Rice, 1944). In his study, Norton relied on the records extracted from the genetic registry of the Holstein breed. He analyzed daughters whose dams were recorded in the registry. After grouping the dams by classes of production, Norton calculated the average yield of the daughters, which he called "the expected average daughter record" (e). He also proposed a modification of the Hanson-Yapp index, replacing the average dam records with the expected average daughter record.
V. A. RICE (1944), suggested a new method to evaluate bulls based on the expected daughter average record and the breed average record. The method compares the average daughter record with their expected average record and the difference is added to the breed average record. His index was officially adopted in the United States in 1945, and allowed comparing bulls within the breed, not just within the farm(s) where the daughters were; this enabled a better classification of the candidates for selection.
Allen (1944) proposed a modification of Norton's index, by which twice the deviation between the average progeny record and the expected record (e) is added to the population (breed) average.
Allen's index with Rice's index does not double the deviation between the average progeny record and the expected record. However, by definition, the genetic value of a bull is double the deviation of its progeny from the population average, doubling the deviation proposed by Allen's index seems appropriate. Allen's index is identical with the Hansson-Yapp index, but the similarity is valid only when the regression has the value of 0.5. Therefore, the additional accuracy of Allen's index appears only when the value of the regression is different from 0.5.
Over the years, this index have been subjected to rigorous comparative analysis in order to highlight the merits or shortcomings.
Gowen (1930) studied the agreement between the breeding value of the bulls calculated with the selection indices available at his time (Gifford, Pearl, Wright, Mount Hope) and the daughter records, used the correlation method to measure the agreement between the breeding value of the bulls and the average records of their future daughters.
The results showed that the highest agreement was obtained with the Gifford index, while the

lowest concordance was noticed for the Pearl index. On the basis of these results, Gowen proposed a new index to calculate the breeding value of the bulls on the basis of two sources of information: average daughter records corrected for the age at calving, combined with mother records.

Edwards (1932) based on the idea that an ideal index should not change bull classification irrespective of the dams, made a comparison of five indices (Pearl, Hansson-Yapp, Wright, Mount Hope, Gifford), in terms of accuracy of breeding value estimation. First, he calculated the value of each type of index using the three types of averages (general, low production, high production) average, and after determines the differences between indices calculated using the low and high averages and the index inferred from the general average. Thus, Edwards noticed that Gifford′s index, in based of the lowest average difference was considered to be the best. Edwards justified this by Galton′s theory according to which the average daughter records are expected to vary less around the population (breed average) than the dam average records. Edwards reached two important conclusions for the genetic evaluation of the bulls:

a) if the purpose is to achieve stability in bull ranking as new data are added to the evaluation process, the best method was the index with minimal variance;

b) if the purpose is to predict with the highest accuracy the records of the future daughters, the Hanson-Yapp index is the best Rice (1933) conducted an analysis of three indices, (Hansson-Yapp, Mount Hope, Gifford), conclude that any index must meet at least three criteria in order to be useful:

a) it must be readily understandable by the user. If an index is too complex and the users have problems understanding, its utility will be hampered;

b) the index must include both dam and daughter records;

c) by its numerical value the index must state clearly how much it can improve the production level of the evaluated trait

These results show that no index is universally valid. Therefore, adequate indexes must be used for different objectives of selection.

The main disadvantage of the Daughter-Dam Indexes is the fact that the daughters are not contemporary with their dams when records are produced. For instance, there is a gap in excess of 2.5 years between the first lactation of the dams and of their daughters. Changes in the environmental factors can appear in this interval, even within the same farm, which may alter the expression of the genetic potential of the animals. Even more drastic changes may occur if the dams and daughters perform under different environments (farms/production units).

Environmental differences between farms also have an influence on breeding values of candidate bulls. The selection methods most affected by the environmental differences are the Gifford index (average records of the daughter), and the Pearl index (dam-daughter comparison). The other indices are less affected.

In order to overcome the problem of the adverse environmental influences, the USDA decided in the early 60s to replace the dam-daughter comparison by the herdmate comparison.

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