ESTIMATION OF RESPONSE TO SELECTION IN BEEF CATTLE

By

Pedro Franklin Barbosa

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Prof. Dr. Charles R. Long

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Introduction

Several selection experiments and breeding programs have been established in different parts of the world. Both purebred and crossbred populations of beef cattle have been selected for different traits of economic importance. With some exceptions, the general rule in projects of that nature has been the absence of appropriate methods in the design of the experiment to measure the selection response after some generations of selection, that is, once established there is no possibility to evaluate the selection program in an experimentally critical manner.

However, due to the development of facilities for processing large volumes of data and adequate statistical methodology, a large number of attempts has been made in order to estimate changes that have occurred in populations submitted or not to artificial selection, even if the data had been collected in the absence of a specific experimental design for this purpose. The primary objective of this type of analysis has been the separation of the observed change into its environmental and genetic components. The results of these studies have demonstrated the validity of the retrospective evaluation of selection programs in progress.

The objective of this paper is to discuss methods that can be used to estimate phenotypic, genetic and environmental changes and to present some results of selection in beef cattle.

Genetic Change

The genetic change, determined by the selection of sires and dams, is reflected on the phenotypic average of the progeny from selected parents. The phenotypic average constitutes the observational components or the basis for the evaluation of selection programs in domestic animals. Usually, a set of annual phenotypic averages of the different characters considered in the selection program is available to the researcher for estimation of the genetic and environmental changes in the average of a given character. However, due to the fact that it is rarely possible to conduct experiments in uniform conditions over periods of several generations, the annual variation in the phenotypic averages cannot be attributed to the exclusive effects of selection of parents since other factors can also affect the changes in the average of a character.

Therefore, it is much more realistic to assert that the observed annual phenotypic change in the average of a character is due to the entire collection of effects from genetic and non-genetic changes. This change can be expressed as:

$$p = g + e \qquad \text{where:}$$

p = observed annual phenotypic change in the average of the character being considered;

g = proportion of the annual phenotypic change due to the selection of parents;

e = proportion of the annual phenotypic change due to environmental changes occurred during the period considered.

Among the environmental changes the most common are: 1) annual variations in the external environment, including changes in feeding, management, sanitation and climatic conditions; 2) annual variations in the internal environment including the effects associated with the age of the individuals, mainly if an unequal distribution occurs in the different age classes, and 3) changes that eventually occur in the selection criterion, data collection system and also those consequent of changes in the staff in charge of the program (Packer, 1976).

In any selection program, it is probably that the majority, otherwise all these variables, affect the annual change in the average of a character. Moreover, as several of these causes act simultaneously, it is reckless to attribute the annual variation observed in the average of a character to this or that cause specifically. On the other hand, because of this confounding of effects, the separation of the phenotypic change into its environmental and genetic components is fundamental to the analysis of selection experiments or breeding programs (Hill, 1972a).

In general, the estimation of genetic change in beef cattle populations has been made to accomplish one or more of the following objectives: 1) to evaluate selection response within herds, 2) to compare results of breeding programs, 3) to estimate and eliminate or reduce the error introduced by genetic change in the process of sire evaluation, and 4) to obtain correction factors for the age of dam adjusted for the effects of genetic change.

Methods of Estimating Genetic Change

Several methods of estimating genetic changes have been devised. Many of them have been considered in review papers by Dickerson (1969), Hill (1972a) and Syrstad (1974). A brief description of each method and its limitations, as well as some results of application in beef cattle are given here.

Constant Environment

If the environment can be maintained constant over a long period of time an unselected population would not undergo any fluctuation in its annual phenotypic mean; on the other hand, if selection is applied, the genetic change can be estimated directly from phenotypic change (Hill, 1972a).

However, the assumption that the environment remains constant over time is not valid either for animals under range conditions or at performance test stations. Even in selection experiments carried out in laboratories, where efforts were made in order to maintain a constant environment, fluctuations in performance due to the environment have been observed (Hill, 1972a; Syrstad, 1974). Therefore, unless there is a clear evidence that a particular trait measured in a specific environment is not affected by environmental variations, an estimate of genetic change directly derived from the phenotypic change cannot be obtained.

Despite its limitations, this method was used by Politiek and Vos (1965), cited by Syrstad (1974), to estimate the genetic gain in milk production, considering records of cows of the same age and lactation period obtained in two different periods twenty years apart, assuming that the environment had not changed in that period. Apparently there has been no reports of genetic change estimation using this method in beef cattle.

Divergent Selection

Selection in opposite direction in two contemporaneous lines at the same location can be applied for a certain period of time, and an estimate of response to selection which is not confounded by environmental effects can be obtained (Hill, 1972a). However, a limitation of this method is that the lack of symetry of response cannot be precisely estimated and a comparison of results and predictions of response is not possible.

In terms of application to beef cattle selection experiments, mainly those designed for comparing alternative methods of improving the same trait, it appears that this method would have some value because the differences in response can be estimated without using control populations. However, only the reports by Seifert (1975a, 1975b) used this procedure to estimate genetic changes in beef cattle.

Results of selection for growth in crossbred populations of beef cattle were reported by Seifert (1975a, 1975b). The project has been carried out in Australia, where four crossbred populations were generated by crossing Africander x Hereford, Africander x Shorthorn, Brahman x Hereford, and Brahman x Shorthorn; the F_2 generations were obtained by inter se mating of individuals within each of the four F_1 types, with the populations being closed after that. In these four populations, sires and dams were selected for high and low weight per day of age at 24 months of age. Matings were based on the phenotypic similarity of the individuals. Therefore, two lines were selected in each population. Progenies from the lines selected for high weight per day of age were heavier at birth and maintained this superiority for all measures to weaning when compared with progeny from lines selected for low weight. Most of the superiority up to weaning was attributed to the higher weight of dams in the lines selected for high weight. Postweaning daily gain was evaluated only in the heifers, and those from the line selected for high weight were significantly heavier at 26 months of age than those from the low weight lines. This advantage was due to the higher birth weight, as well as to the greater pre and postweaning daily gains of the lines selected for high weight per day of age.

Control Population

As implied by the denomination of the method, a control population is simultaneously maintained with the selected population, with the objective of estimating the changes in the environment. For that to be possible there should not occur genetic change in the control population (Dickerson, 1969), i.e., the same set of genotypes should be repeated in successive generations (Hill, 1972a). However, several sources of error can affect the estimate of genetic change, which is expressed as a deviation from the control population. Among them the most important are: (a) random genetic drift in the control, (b) genetic change in the control due to natural selection and/or to non-intentional artificial selection, (c) differential response of control and selected lines to environmental changes (genotype-environment interaction), and (d) error in the estimation of genotypic mean from phenotypic mean in both populations, even more important in the control due to the usually smaller number of individuals in that population. The first three sources of error tend to be cumulative, whereas the fourth one, besides being of a non-cumulative nature in the various generations, can be minimized by defining the optimum size of the control population (Hill, 1972a).

Estimation of genetic gain through the method of control populations has been used in laboratory animals and in poultry breeding experiments. However, despite the cost of maintaining a control population in beef cattle, this method has been used in several experiments as those reported by Newman _et al_ (1973), Anderson _et al_ (1974), McPeake _et al_ (1976), Thrift _et al_ (1981) and Frisch (1981) for which the following discussions are given.

Results of ten years of selection for yearling weight in two replicated herds of beef shorthorn cattle in Canada were reported by Newman _et al_ (1973). Genetic gains of 4.8 ± 3.1 and 4.1 ± 3.0 kg/year in males and 3.3 ± 2.7 and 2.3 ± 1.5 kg/year in females were estimated for both herds resp. These changes were measured as deviations from an unselected control line mean and accounted for 40-45% of the increase in yearling weight that occurred during the period considered. The correlated responses in other characters, in the same experiment, were reported by Anderson et al (1974). The differences from the control line were 3.6 and 3.0 kg for birth weight, 16.2 and 7.8 kg for weaning weight, and 104 and 118 g for daily gain from birth to 10 months of age in both herds resp. However, indirect effects on carcass merit were not in the desirable direction because a higher percentage of bone ($P \leq 0.01$) and a reduced lean/bone ratio ($P \leq 0.05$) were observed. Also, the change in birth weight due to its association with yearling weight, ranged from 0.6 to 0.7 kg/year during the most recent 5 years of the experiment.

McPeake et al (1976) reported the results over a 4 year period of a breeding program in Michigan, where 4 groups of 50 cows each were submitted to one of the following selection criteria: 1) unselected group, Hereford, 2) Hereford selected for final weight, 3) three-breed rotation of Hereford, Angus and Charolais, and 4) three-breed rotation of Hereford, Angus and Holstein. Sires used in groups 2,3 and 4 were selected primarily on yearling weight. Adjusted weaning weight was 193, 215, 241 and 256 kg for groups 1 to 4, resp. The crossbred steers had a higher marbling score than the Hereford selected for yearling weight (13.8 vs. 11.8) and the differences among the four groups were significant ($P \leq 0.05$).

Estimates of genetic parameters based on selected and control beef cattle populations in the Southern Region were reported by Thrift et al (1981). Heritability estimates for various characters were higher for control than for selected populations, whereas phenotypic correlations were similar and genetic correlations were more inconsistent than those obtained for the heritabilities. These results are an indication that genetic changes occurred in the selected populations, more in males than in females.

Results of 12 years of selection for growth rate in a closed line of Hereford x Shorthorn cattle under conditions of moderate to high environmental stress at the National Cattle Breeding Station, 'Belmont', Queensland, Australia, were measured over the most recent 6 year period as differences from an unselected control line and reported by Frisch (1981). The response to selection for growth rate, expressed as the difference between selected and control lines; was -8.3 and 66.7% under the low and high level of environmental stress, resp. As pointed out by the author, these results suggested that selection for production in stressful environmental conditions would be in fact selection for resistance to those stresses which affect production.

Repeated Matings

With the objective of creating an internal control within the selected line itself through the repetition of genotypes over time, this technique was proposed by Goodwin et al (1955) and described in more details by Goodwin et al (1960). The procedure requires the use of identical matings during two breeding seasons. The environmental change is estimated by the comparison between pairs of progenies of the same generation in successive years, whereas the genetic change is estimated by comparing individuals of successive generations in the same year. It also provides an estimation of any change in maternal effects with aging, where the separation of the environmental change from maternal influence changes with aging can be accomplished by adding to the repeated matings females of different age classes from that one of the particular mating.

Responses to selection for weaning weight and postweaning daily gain in three lines of Hereford cattle were reported by Flower et al (1964). A fourth line was used to test the performance of linecrosses. Other three lines were developed by crossing line 4 with lines 1, 2 and 3, resp. The phenotypic change was negative in all lines for birth and weaning weights. Environmental changes were -0.821 and -0.490 kg/year for birth and weaning weights, resp. However, genetic changes were 0.43 and 2.07 kg/year for both characters, resp. Chapman et al (1968) estimated the genetic change for birth weight, weaning weight and average daily gain from birth to weaning in Hereford cattle obtaining the following values: 0.0, 1.23 kg/year and 9 g/year, resp.

Repeated matings procedure was used in order to estimate phenotypic, genetic and environmental changes in inbred and linecross groups of Hereford cattle at the San Juan Basin Research Center, Hesperus, Colorado. Phenotypic changes were variable for the different traits in the inbreds and mostly negative, whereas they were upward in most of the traits in the linecrosses. Estimated genetic gain per generation due to within-line selection was negative for almost all of the traits in the inbreds, while a considerable genetic progress for the linecrosses was estimated for all traits except heart girth circumference at birth, weaning score and feed efficiency (Nwakalor, 1976). The same data were analyzed by Nwakalor et al (1976) with reference to weaning weight. The estimated environmental change was -1.52 kg/year and the genetic change in the period of 1946 - 1971 for weaning weight was 1.17, 1.87 and 2.09 kg/year in the inbred lines, inbred lines adjusted for inbreeding of calf and of dam, and linecrosses, resp. Brow (1977) compared 4 methods of estimating phenotypic, genetic and environmental changes using data collected during 1957 - 1975 on an Aberdeen-Angus herd. The techniques compared were: sires-over-time, repeat-mating, dams-over-time, and sires-and-dams-over-time, where each performance record was expressed as a deviation from the annual population mean. The sires-over-time estimator was superior to the others for it was minus twice the pooled within-sire regression of the deviation of performance on time.

Comparison of Contemporary Animals from Different Generations

An estimate of genetic change per generation can be obtained by comparing performance records of animals raised at the same period on the same environment but belonging to different generations (Syrstad, 1974). The genetic gain can be estimated directly through the regression of the average performance within years on the generation number of the individuals. In beef cattle, Koch et al (1974) estimated the genetic change of various characters through this procedure and a brief discussion of their results follows.

Selection response in three lines of Hereford cattle selected for weaning weight (Line 1), yearling weight (Line 2) or an index of yearling weight and muscling score (Line 3) was reported by Koch et al (1974). Selection response was estimated by several measures of offspring regression on selection in parents. Average estimated responses, expressed in standard deviation units per generation, in the three lines, were: 0.22, 0.28 and 0.28 for birth weight; 0.20, 0.13 and 0.12 for weaning daily gain; 0.23, 0.17 and 0.15 for weaning weight; 0.28, 0.42 and 0.33 for post-weaning daily gain; 0.36, 0.43 and 0.33 for yearling weight and -0.03, 0.01 and 0.24 for muscling score, resp. Responses per unit of selection applied were 0.47, 0.37 and 0.48 for birth weight, postweaning gain and yearling weight, which can be considered relatively large, and 0.11 and

0.13 for weaning daily gain and weaning weight, which can be considered a small response per unit of selection applied. The observed responses in the three lines evidenced the existence of an intense genetic association among the characters measured. Therefore, various selection criteria could yield improvement in the economic traits of Hereford cattle under similar conditions to the experiment reported.

Comparison of Contemporary Progenies by Sires of Different Generations

This procedure was devised by Dickerson (1969). It can be considered a variation of the preceeding and appears to be the most viable procedure of estimating genetic and environmental changes in large animals. If sires of a given generation (or semen from these sires) were kept and used after a certain period in comparison to the sires of the most recent generations, then the difference between the performance averages of the contemporary progenies estimates half of the genetic change occurred in the herd during the period considered in the analysis. However, two conditions are required for a correct evaluation of the selection program: 1) both groups of sires must pass through the same selection criterion, since the comparison would be biased if the oldest sires were selected on the basis of their progeny, 2) in both sire groups the cow distribution should be similar as far as age and breeding value are concerned (Syrstad, 1974).

Despite its potential, apparently this procedure has not been utilized to much in beef cattle. However, Newman et al (1973) used this procedure to estimate the genetic change for yearling weight in beef cattle, as already discussed in the control population method due to the fact that the classifications are arbitrary and there is a considerable overlap among them.

Repeated Use of Sires

The successive progeny groups bred by sires (or semen from these sires) used during several years in the population provide a continuity of genotypes over time. The within-sire change in progeny performance from year to year is a measure of the environmental change plus half the genetic change, and has been used in non-experimental selection programs (Smith, 1962). The annual change in the average performance of a given population can be expressed as $(e + g)$ where e is the environmental change and g is the genetic change. Assuming that there is no change in the breeding value of a sire, the average change in the progeny of each sire in successive years would be equal to $(e + 1/2g)$, that is, the contribution of the environmental change plus the genetic change occurred in the female population, which in turn is equal to 1/2 of the total genetic change. Therefore, the difference between the annual change in the population and in the progeny of a sire, namely $(e + g) - (e + 1/2g)$, estimates half of the annual genetic change. However, several sources of error can affect the within-sire progeny performance regression on years. Among them the most important are: (a) sire selection based on its preceeding progeny performance causing a superestimation of the genetic change within-sire over time, (b) age and culling of dams can cause changes in the within-sire distribution of dams age and selection intensity, and (c) the genetic change in the dams can be greater than half of the total genetic change and the estimate would be biased upwards. In beef cattle, this procedure was used by Stewart et al (1974), Packer (1977), and Vanmiddlesworth (1980).

The genetic change over a 15-year period for weaning weight in Brahman cattle was estimated by Stewart et al (1974). The data consisted of progeny records from 484 first-calf heifers and 22 sires, each sire having progenies in at least 2 years. Within-year least-square constants were obtained from models including year, sex and age of calf, with and without sires. The difference between within-year constants of the two models was used as an estimate of half the genetic change for that year. A weighted regression of twice that difference was the estimated genetic change for weaning weight. The phenotypic change showed a curvelinear pattern over time with weaning weight increasing at a decreasing rate. The genetic change was also curvelinear over time with the genetic effect increasing at an increasing rate.

Packer (1977) estimated the genetic change for birth weight and weaning weight of Canchim calves born during 1956 - 1973 by doubling the difference between the linear regression coefficients of calf birth year on year, when sire was ignored and included in the model. Genetic changes were negative for both traits, probably due to the small number of sires which were used more than one year in the herd.

Data collected on 2416 Aberdeen-Angus calves produced in 1955 - 1976 by 667 cows mated to 39 bulls were analyzed by Vanmiddlesworth (1980). Estimates of annual genetic and phenotypic changes were -0.03 ± 0.02 and 0.01 ± 0.01 kg, resp. for birth weight, 0.49 ± 0.10 and 0.30 ± 0.05 kg for 120-day weight, 0.11 ± 0.15 and 0.38 ± 0.07 kg for weaning weight, -0.41 ± 0.17 and 0.63 ± 0.09 kg for 240-day weight, and 0.58 ± 0.30 and 2.18 ± 0.15 kg for 360-day weight. The estimates of environmental change were positive for all traits except for 120-day weight.

Repeated Records by the Same Individual

An early attempt to separate the observed annual phenotypic change into its causal components was made by Lortscher (1937) cited by Syrstad

(1974). Also, Nelson (1943) considered the difference in milk production of the same cow in successive years as an estimate of the environmental change. The basic concept involved is that the genotype of an individual is constant throughout its life, and consequently that any change in performance is of environmental origin (Syrstad, 1974). This procedure, however, presents an error of logic, which biases the results because the performance of the same cow in successive years varies systematically for two reasons: 1) annual changes in management and in other factors of the external environment, and 2) changes in performance associated with the increase in age of the cow (Rendel and Robertson, 1950). An additional problem consists of the culling process of animals in successive years. This situation is likely to occur in beef cattle when selection of cows is based on weaning weight of calves. The data collected consist of performance records of dams in successive years and could be represented by a factorial design including dams and years as factors. However, Henderson (1949) demonstrated that estimates of year effects by least-squares analysis, considering dams as a fixed effect were biased determining an apparent conclusing that the environment gradually deteriorated over years. The same problem was reported by Lush and Shrode (1950). As a solution to this problem, Henderson et al (1959) suggested two methods: 1) estimation of year effects through maximum likelihood, which requires the previous knowledge of the repeatability of the character, or 2) estimation of repeatability and environmental change simultaneously. It has been shown that both methods are equivalent for the same repeatability. Estimates obtained by least-squares analysis are not biased, unless dams are selected based on the previous progeny performance (Henderson, 1958). However, estimates obtained by maximum likelihood would be more efficient because they are based on differences between dams and comparisons within dams.

Estimates of genetic changes in beef cattle through maximum likelihood were reported by Bailey _et al_ (1971), Chevraux and Bailey (1976), and Packer (1977).

Results of selection for postweaning daily gain (Lines 1 and 4), feed efficiency (Lines 2 and 5) and conformation (Line 3) in Hereford cattle at two locations were reported by Bailey _et al_ (1971). Only selection for postweaning gain and the correlated response for feed efficiency in Line 4 were different from zero. Genetic changes observed in the primary characters in Lines 1 to 5 were 1.49 kg of gain in 140 days, 0.18 kg of gain/100 kg of Total Digestible Nutrients (TDN), -0.09 score units (excellent = 100), 2.17 kg of gain in 140 days, and 0.17 kg of gain/100 kg of TDN. Genetic change for final weight after 140 days in test was 1.22 ± 0.90 kg/year (Chevraux and Bailey, 1976).

Working with data on 1818 Canchim calves (5/8 Charolais + 3/8 Zebu Foundation) born during 1956 - 1973 in Sao Carlos, Brazil, Packer (1977) estimated phenotypic, genetic and environmental changes for birth and weaning weights. Phenotypic changes were 0.22 ± 0.04 and 0.63 ± 0.20 kg/year for birth weight and weaning weight resp., whereas environmental changes were 0.16 ± 0.06 and 0.33 ± 0.25 kg/year for both characters resp. Genetic change was non-signficant for birth weight (0.05 ± 0.05 kg/year), and showed a quadratic response over the years for weaning weight.

Genotype Storage

This is a way in which replication of the same genetic material in successive generations can be achieved. The use of frozen embryo panels stored over a long period of time was proposed by Smith (1977) to measure genetic changes in farm animals. With current technology, a simplified method is to use a panel of sires in a rotational manner on each other's daughters, and so develop a frozen embryo panel control line. With the use of frozen embryos the full genetic change is measured, the risks of loss of the control can be minimized, panels can be regenerated at any time from current stock, genetic changes in previously unrecorded traits can be measured, and a series of overlapping frozen embryo panels can be used to cover long periods of time. Also, genetic change in the control would be eliminated by storage of the base material (Hill, 1972a). Two important features of this procedure are its adaptation to either experimental or field use and its relatively low cost of maintaining the panels and of measuring genetic changes with high precision. As discussed by Bradford and Kennedy (1980), the potential of embryo transfer for increasing rate of genetic improvement appears to be greater in beef cattle than in dairy cattle. They also pointed out the possibility of provision of genetically stable control populations, with improved embryo storage capability.

Summary

Several methods of estimating genetic change have been applied to both experimental and non-experimental populations of beef cattle. Various sources of error associated with each method have been identified but not quantified, with the most important being bias and sampling error. Therefore, estimates of genetic change should be interpreted with these problems in mind, because even a consistency among results obtained by various methods would not be an indication of correct estimates. With the development of the frozen embryos technique it appears that most of the problems in estimating genetic changes in beef cattle will be better understood, mainly due to the possibility of identifying and quantifying different types of interactions and other sources of error.

However, an analysis of the results insofar obtained permits to establish the following points: 1) with some exceptions, the majority of the studies used indirect methods to measure genetic changes, 2) most of the studies evidenced positive effects of selection for growth traits in beef cattle, and 3) in general, selection has been applied to purebreds, most of them of European origin, on a within-herd basis.

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