

SYMPOSIUM: SELECTION INDEX THEORY

The Selection Index—Then, Now, and for the Future¹

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ABSTRACT

When improvement is desired for several traits that may differ in variability, heritability, economic importance, and in the correlation among their phenotypes and genotypes, simultaneous multiple-trait index selection was more effective than independent culling levels or sequential selection. Such comparisons required definition of aggregate breeding value determined jointly by breeding values and the economic importance of the component traits. The economic weight should approximate the partial regression of cost per unit of enterprise output value on breeding value for each trait. These can vary with production and marketing system, with performance of traits, and with breed role (i.e., paternal, maternal, or general) in crossbreeding systems. Genetic gains desired to maintain competitive ranking also may define the relative importance of traits. Because information available to estimate breeding values varies among the ages and categories of individuals under selection and because means are unknown, regressed (BLUP) predictions

of trait breeding values are useful. They allow appropriate economic weights to be applied as the last step for predicting aggregate breeding values for individuals of different age classes, and they simplify choosing the proportions of selected breeders from each age class that maximize rate of change in aggregate breeding values. Inappropriate economic weights or errors in the parameters used to predict trait breeding values overestimate realized response in true aggregate breeding value.

(Key words: selection index, multiple-trait selection, selection criteria, animal breeding methods)

Abbreviation key: a_i = economic weight for trait i , G_i = breeding value for trait i , H =

aggregate breeding value = $\sum_{i=1}^n a_i G_i$, I =

$\sum_{i=1}^n (b_i X_i)$ where b_i is a selection index weight, X_i is phenotypic measure, and n = number of traits, i = selection differential in standard deviation units.

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²Dr. Hazel had prepared initial notes for his invited paper in July 1992, which constitute substantial portions of this text, but ill health prevented further direct involvement before his death in October 1992.

INTRODUCTION

The Program Committee of the American Dairy Science Association invited L. N. Hazel to review the early development of the selection index approach to simultaneous improvement of multiple-trait components of performance, which he began some 50 yr ago (25). They also asked for his evaluation of the pres-

ent and possible future usefulness of selection index methodology. Before his death in 1992, Hazel prepared a brief draft of his recollections and thoughts, which have been supplemented by the coauthors. The text written by L. N. Hazel appears in quotation marks.

"The subject of selecting simultaneously for several traits arose at an informal coffee session of J. L. Lush with several of his graduate students in 1940 when Lush suggested that this subject would make a good thesis topic." Before that time, Lush had spent several summers at Kimber Farms in Niles, California, working with W. F. Lamoreux on problems of breeding for improvement of many different traits of poultry, including age at sexual maturity, rate of egg production, egg size, shell strength, internal egg quality, and viability under differing exposures to disease vectors. Lush also was involved in a large experiment to select for growth rate, conformation, and reproductive rate of swine as part of the Cooperative Regional Swine Breeding Laboratory effort. These traits differed not only in economic importance, but also in variability, heritability, and genetic and phenotypic correlations. Clearly a need existed for someone to quantify the influence of these factors on the weighting for each trait of selection that would produce maximum genetic change in the economic merit of the selected population. This was the challenge Hazel accepted for his thesis project.

HAZEL'S DEVELOPMENT OF MULTIPLE-TRAIT INDEX SELECTION

"As it turned out, most of the important principles and concepts required to maximize expected genetic improvement were already being taught in courses of animal breeding, statistics, and genetics. For example, a course in statistics showed how the multipliers of independent variables could be chosen so as to result in a maximum correlation with a dependent value (65). Genetics courses included sections on pleiotropic and linked gene effects that might cause simultaneous effects upon two traits. In animal breeding courses, Wright's (75) research on the biometrical relationship between genotype and phenotype was discussed. Problems of evaluating the transmitting ability of dairy cows and their sires were illustrated (39), and heritabilities of a few traits, such as growth rate and milk fat produc-

tion, were appearing in journal articles (40). Thus, most of the necessary ingredients for an organized plan to optimize multiple-trait selection had been developed, but no one had taken the time or trouble to complete that plan. Apparently, Hazel did not discover the parallel work of Fairfield Smith (64) on plant selection until he was preparing his thesis work for publication in *Genetics*."

Hazel described the plan as follows:

"First, the purpose of index selection should be to achieve maximum genetic progress toward a stated economic goal.

Second, economic return to the livestock enterprise should be of primary importance, requiring the expected independent monetary return from a unit of change in each trait (a) wherein change was sought. Thus, gain from change in all individual traits included could be summed into that for an aggregate genotype

$(\Delta H = \sum_1^n a_i \Delta G_i)$, where H is aggregate breeding value, a_i is the economic weight for trait i , and G_i is the breeding value for trait i .

Third, the biometrical relationships between genotypes and phenotypes should indicate the relative amounts of change expected from selection (i.e., among the ΔG_i).

The remaining problem was that of genetic and environmental correlation between traits and its role in selection index construction. Pleiotropic gene effects, imbedded in a mixture of genetic and environmental variation, eventually were estimated by comparing traits of animals related by descent (76), just as were the biometrical relationships between genotype and phenotype of the same trait (75). Each offspring (o) and parent (p) comparison yielded two regression estimates, that of trait X_o on Y_p and that of Y_o on X_p , which relative to corresponding regressions of X_o on X_p and Y_o on Y_p , became an estimator of the genetic correlation (r_G):

$$\sqrt{(b_{X_o Y_p} b_{Y_o X_p}) / (b_{X_o X_p} b_{Y_o Y_p})} = r_{G_{xy}}$$

The remainder of the analyses consisted of using multiple regression techniques except that each partial regression coefficient was divided by its standard deviation (65), thereby expressing each trait in units of its standard deviation. The solution of the simultaneous

equations, which maximized the correlation between aggregate genotype and the phenotypic index (I), provided the unknown multiplier (b_i) for each of the traits ($i = 1 \dots n$) in the

$$\text{index, } I = \sum_{i=1}^n (b_i X_i).$$

In writing theses, a customary procedure was to develop certain theoretical principles and to apply them to suitable experimental data. In this case, as in many others 50 yr ago, entirely suitable data did not exist. But three traits had been measured on most pigs in a cooperative breeding experiment started in 1936 between the then Iowa Agricultural Experiment Station and the Regional Swine Breeding Laboratory (USDA) to study effects of selection and different rates of inbreeding in Poland China pigs. There were 12 separate inbred lines, and inbreeding varied from 0 to 40% between 1936 and 1940. Use of the standardized regression coefficients minimized effects of seasonal variations, selection of parents, and different levels of inbreeding. The "flip-flop" manual calculator and the one motorized Monroe calculator were available to graduate students with priority, amounting to fairly full usage from 10 p.m. to 7 a.m., when most estimates of heritabilities and genetic correlations were made!

Thanks to Frances Hazel, who was assistant bulletin editor of the Iowa Agricultural Experiment Station and a good typist as well, little rewriting and no major changes were necessary. Publication of Hazel's was accepted promptly by *Genetics* (25)."

Total Score, Tandem, or Independent Culling Level Selection

Hazel's work on multiple-trait selection was divided between two publications. The first one compared selection for several traits based on a total score; selection was based on independent culling levels or on one trait at a time (29). For n independent traits of the same variability, heritability, and economic importance, combined response from selection on total score (ΔH_2) is expected to average $\sqrt{n}$ times larger than that from tandem selection for one trait each generation (ΔH_1), so that response in each of the n traits from total score selection would average $1/\sqrt{n}$ of that from selecting for only one trait.

Independent culling level selection for n traits was less efficient than total score selection in allowing superiority in one trait to compensate for inferiority in another trait because the total proportion selected (p) for all n traits must be the product of the n effective proportions (q_i) selected for each trait (i.e., $p = q_1 q_2 \dots q_n$). This result limits total response from equal culling levels for all n traits to

$$\sqrt{n} \frac{Z_{q_i} Z_p}{q_i p} \text{ or } \sqrt{n} \frac{Z_q}{Z_p} q^{n-1} \text{ of that from total}$$

score selection [Figure 11 in (29)]. The advantage of total score over independent culling level selection increases sharply with number of traits and with larger total proportion (p) saved for breeding [Figure 12 in (29)].

When the traits selected are uncorrelated but differ in the product of economic importance, heritability, and variation (79), the optimal proportion to be culled ($1 - q_i$) for two traits under culling level selection differs by at least the squared ratio, $(a_i g_i^2 \sigma_i / a_j g_j^2 \sigma_j)^2$, and needs to be determined by trial and error. Here, a_i and a_j are economic weights, g_i^2 and g_j^2 are heritabilities, and σ_i and σ_j are phenotypic standard deviations for traits i and j . If the traits included in independent culling level selection are correlated, the optimal standardized selection differential ($i x_i$) for each trait is proportional to the $\sigma_{x_i} b_{HX_i}$ or to the β_{HX_i} for each trait [as computed for index selection], but again subject to the restriction that the combination of the n corresponding q_i fractions chosen must equal the total fraction (p) selected (72).

Optimal Index Selection

For his thesis research (25), Hazel addressed the broader problem of genetic improvement of several traits (X_i) that differ in economic importance, variability, heritability, and degree of genetic and environmental correlation. He first defined the overall breeding objective or aggregate breeding value as the sum of the n trait breeding values, each weighted by its

$$\text{relative economic importance, } H = \sum_{i=1}^n (a_i G_i),$$

and then derived the index weightings (b_i) of the respective phenotypes that would max-

imize the multiple correlation of a phenotypic total score or I with H . The R_{IH} determines the potential improvement of H from the possible standardized selection differential (i_I) for the index, $E\Delta H = i_I R_{IH}\sigma_H$. The biometrical relationships between the X_i and H , as illustrated in Hazel's path diagram (Figure 1), must be known to derive the optimal weightings of phenotypic traits.

Relative Economic Importance

When genetic correlation exists among the traits in which improvement is sought, the relative economic values should represent the direct or partial regressions of H (or net economic return) on G_i for each trait when G_j for the other traits are unchanged. For his pig examples, Hazel used the approximations of a_i values for growth, conformation score, and

sow productivity reported by Lush (41). In Hazel's later (26) example for index selection in beef cattle, roughly independent values were assigned to weaning weight (\$.30/lb for extra feed), weaning score (\$2.00 per point), post-weaning feed efficiency (-\$.15 per unit lb of feed/lb of gain), slaughter grade (\$10 per unit), and rate of daily feedlot gain (\$16/lb) for fewer days in feedlot.

When not measured, feed intake remains in the definition of H , but selection index weightings for the remaining traits, particularly daily gain, are adjusted to maximize index prediction of H (R_{IH}). Hazel recognized that more precise estimates of relative economic importance could be obtained through production system simulation and that these relative economic weights would change with the differences in production and marketing systems among regions and over time.

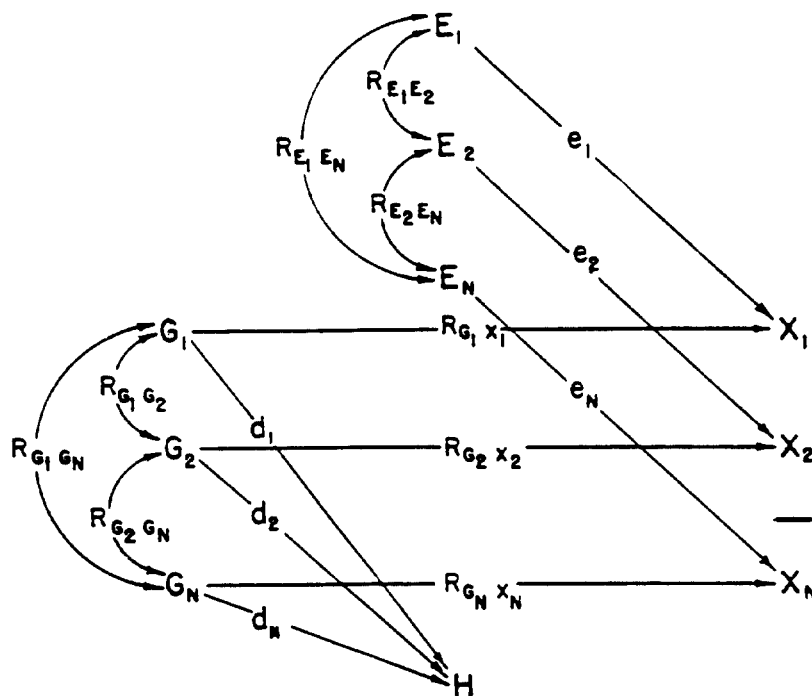


Figure 1. Path coefficient diagram showing the relationship between phenotypic measurements (X_i) and the aggregate genotype (H). e_i and $R_{G_i X_i}$ are correlations of E_i (environmental effect for trait i) and G_i (breeding value for trait i) with X_i ; d_i are standard partial regressions of H on G_i ; $R_{E_i H}$ and $R_{G_i H}$ are correlations of E_i with H and G_i with H . From Hazel (25).

Role of Genetic Parameters

As indicated in Figure 1, the heritabilities and the genetic (r_G) and total phenotypic (r_X) correlations among the several traits included in H are needed to solve the n equations of correlation between H and each trait (X_i) for the standard partial regression (β_i) of index (I) on each of the trait phenotypes (X_i) that maximize R_{IH} .

$$\begin{aligned} r_{X_1H} &= \beta_1 + r_{X_1,2}\beta_2 + \dots + r_{X_1n}\beta_n \\ &\vdots \\ r_{X_nH} &= r_{X_n1}\beta_1 + r_{X_n2}\beta_2 + \dots + \beta_n \end{aligned}$$

where

$$\begin{aligned} r_{X_iH} &= h_i(d_1 + r_{G_{1,2}}d_2 + \dots + r_{G_{1n}}d_n), \\ &\text{etc., and} \\ d_i &= \frac{a_i\sigma_{G_i}}{\sigma_H}, \\ h_i &= \frac{\sigma_{G_i}}{\sigma_{X_i}}, \\ H &= \sum_1^n (a_iG_i), \end{aligned}$$

and

$$\sigma_H = \sqrt{\sum_1^n a_i^2 \sigma_{G_i}^2 + 2 \sum_1^{n(n-1)/2} (a_i a_j \sigma_{G_i} \sigma_{G_j} r_{G_{ij}})}.$$

In terms of variances and covariances, the r_{X_iH} equations for n traits reduce to the form:

$$\sigma_{G_iH} = b_{HX_1}\sigma_{X_1}^2 + b_{HX_2}\sigma_{X_2}^2 + \dots + b_{HX_n}\sigma_{X_n}^2 \quad [2]$$

where the n values for σ_{G_iH} are obtained from

$$\sigma_{G_iH} = a_1\sigma_{G_i}^2 + a_2\sigma_{G_{i,2}}^2 + \dots + a_n\sigma_{G_{i,n}}^2.$$

These equations can then be solved directly for the partial regression (b_{HX_i}) index weightings per phenotypic unit of each trait. The

corresponding standard partial regression, $\beta_{HX_i} = b_{HX_i}(\sigma_{X_i}/\sigma_H)$, better indicates the relative importance of each trait for predicting H.

Genetic correlations initially were estimated from offspring-parent regression. However, Hazel (28) recognized the potential biases arising from genetic and environmental maternal influences on progeny performance that are often involved in both heritabilities and genetic correlations when estimated from regression of offspring on parent. He then extended the estimation of heritability from paternal half-sib correlation to use of sire components of (co)variance to estimate correlation for average (additive) gene effects, which was a major and much emulated contribution (27).

Hazel's original publication (25) examined the potential improvement in accuracy from including the full-sib family means in addition to individual performance in selection index. Addition of full-sib performance improved accuracy but also showed that important common maternal environment for full sibs could lead to negative weighting of the family (litter) mean as a correction for common environmental influences. Hazel's use of family means preceded later extensions to use of sire family means (52) and, then, to use of the more complete relationship matrices (31, 32).

LATER REFINEMENTS OF THE SELECTION INDEX

As with any other major advance, selection index theory has been further improved and extended by others.

Hazel's Perspective

"Because livestock producers in 1943 were only beginning to take records of performance on their livestock, few applications of the concept were immediately possible. There was time for colleagues to investigate and study the theory, and even a few experiments that involved certain concepts of the selection index were undertaken.

In the meantime, rapid developments continued to enhance the usefulness of index selection:

1. The cooperative collection of production records by dairy herd improvement as-

- sociations, breed associations, livestock recording associations, and artificial breeding organizations.
2. The development of high speed electronic computers to process masses of numerical records.
 3. The development of computer programs, which provided access to the stored records and accurate answers to estimates of heritability, and genetic correlations.
 4. Systems approach to production problems do and will give more accurate cost-return figures upon which economic values can be based.
 5. Access to the mammalian genome will provide more accurate information concerning the roles of heredity in animal development. Animals can be given credit or debit more accurately for known genes or sections of genes."

Separation of Trait Breeding Value Estimation

One very useful modification was developed by one of Hazel's own graduate students, C. R. Henderson [1951 mimeo publication, Cornell University, Ithaca, NY (31)], and first applied by students of A. B. Chapman (8, 35). This modification separated application of the selection index into two steps. The first step is estimation of individual breeding values for each trait included in the definition of aggregate breeding value. The second step is application of the relative economic weights, H

$$= \sum_{i=1}^n a_i \hat{G}_i.$$

This separation has two important advantages. It permits use of the most complex and accurate BLUP techniques to estimate individual breeding values for each index trait, including adjustment for differing amounts of information (31, 32), and it then allows the economic weightings applied to vary with differing selection objectives, depending upon how different breeds are used in a breeding system or the particular production and marketing system, without recalculating breeding values.

Henderson (31) showed that, when assumptions of known means and unequal information were accounted for, the resulting equations were what is now known as the mixed model

for estimation of fixed effects and prediction of random variables, such as the trait breeding values, $\hat{G}_i$, for individual animals. Henderson (31) had not yet shown the properties of the equations he derived to be best linear unbiased estimator (BLUE) or BLUP. Henderson (32) later showed the Hazel (25) index to be in the class of best linear predictors when means and variances are known. Even with BLUP estimation of the G_i and weighting the G_i predictions with the economic values to obtain H , the Hazel definition of H is still appropriate and useful.

Because the BLUP estimation of G_i also allows comparison of individuals from different age classes, BLUP facilitates optimal choice of the proportions of selected young and progeny-tested sires that will maximize expected rate of genetic change per year, as shown by Dickerson and Hazel (16, 17).

Effect of Errors in Genetic Parameters

Several researchers have examined the potential overestimation of expected response in H from index selection, which can arise from sampling error of the genetic parameters used in constructing an index (12, 22, 67, 69, 74) as well as from failure to adjust for changes in parameters during the course of a selection program (71). The latter also illustrated how very much the advantage of index over tandem selection increases with change from positive to negative genetic correlation between selected traits, even though actual total response in H declines.

Relative Economic Importance of Traits

"The importance of transportation, temperature, humidity, availability of feedstuffs, and geopolitical factors, such as national habits and pride, and trade restrictions, illustrated vividly how genetic populations can be made to differ in response to the economic values placed on different traits of the same species. Dual purpose breeds have in general been quite successful in Europe, but much less so in the United States. A breed developed for the triple purpose of providing meat, milk, and draft could be justified for an isolated mountain village.

The intense concentration on livestock production systems research that is presently

For breeding female		For her progeny	
$\frac{\text{Expense per year}}{\text{Product per year}} = \frac{(A/Y) + (I_d + B_d \bar{F}_{md} + \bar{F}_{pd}) + N D(I_o + B_o \bar{F}_{mo} + F_{po}) + S_o }{P_d V_d + N P_o V_o} [1]$			
A/Y	= (Cost, young female:value, old female) per year in production.	B_o	= Mean postweaning metabolic body size for individual, relative to population mean.
I_d	= Yearly fixed costs per female, including labor, housing.	$\bar{F}_{mo}$	= Mean daily maintenance feed cost per animal for population.
B_d	= Metabolic body size of female relative to population mean.	F_{po}	= Mean daily feed costs above maintenance for individual.
$\bar{F}_{md}$	= Yearly maintenance feed costs per female for population.	S_o	= Fixed costs per animal including marketing, slaughter, and vaccines.
$\bar{F}_{pd}$	= Yearly feed cost above maintenance per female.	P_d	= Yearly volume of product per female.
N	= Yearly number progeny marketed per female.	V_d	= Value per unit of female product.
D	= Days from weaning to market weight for individual.	P_o	= Live weight of meat animal when marketed.
I_o	= Daily mean fixed costs per animal.	V_o	= Value per unit of live weight.

Figure 2. Diagram of major variable controlling input costs per unit of output value from an animal production enterprise. From Dickerson (14).

occurring is providing excellent examples of changing economic values and what they may be in the future. Can specialized female lines bred for reproduction and mated to specialized male lines for a final terminal cross be more profitable than straight or rotational cross-breeding production, as it has been for broiler production?

Useful economic values must, of necessity, be based upon conditions likely to exist sometime in the future, because several generations are required for appreciable genetic change, even after the opportunity is generally recognized. Selection indexes are well-adapted to such situations because they provide a logical method of changing goals gradually as developing situations indicate the need and the direction of change."

Hazel (25) defined the relative economic importance of a trait as the net increase in profit of the production enterprise for a unit of change in one trait, independent of effects from genetic changes in other traits included in the definition of aggregate breeding value. This definition of unit of change in profit assumes no effect of genetic reduction in production cost per unit on the market price received for the output, but actual profit depends upon supply and demand and may even be a reduction in loss. Thus, some workers

define relative economic importance in terms of expected reduction in cost per unit of equivalent output value rather than an increase in profit [Figure 2, from Dickerson (14, 15)]. Production costs tend to govern future market prices received for animal products, and thus, their impact on costs to consumers. Effects of genetic change in performance traits are also more meaningful and stable as a proportion of production costs than of profit. However, Smith et al. (63) have shown that the two approaches lead to essentially the same relative economic weights if price per unit output was assumed constant.

Moav and Moav (43), Cartwright (10), and Cartwright et al. (11) were pioneers in their use of production and marketing simulation to derive economic weights for components of performance. Harris (23) and Harris and Newman (24) have defined relative economic weights in terms of simulated profit functions that include the nonlinear economic effects of genetic changes in component traits on the H for individual candidate breeders. Production system simulation is highly useful to estimate the independent effects of unit changes in each component trait on cost per unit output over ranges of performance and for differing breed roles (i.e., paternal, maternal, or general) and for differing production and marketing sys-

TABLE 1. Standard partial regression coefficients of profit per year of herd life with their standard errors and probabilities of Type I error.¹

Variable	Standard partial regression coefficients	Standard errors of coefficients	Type I error <i>P</i>
Milk production	.64	.07	.0005
Mastitis	-.38	.06	.0005
Milk fat test	.31	.06	.0005
Calvings per year	.22	.07	.002
Herd life	.10	.08	.179
Body weight	.09	.07	.190
Milking time	.03	.06	.581

¹From Andrus and McGilliard (1).

tems. Similar efforts have been made for dairy cattle, as shown in Table 1 (1, 20). Smith et al. (62) have shown how greatly the importance of genetic changes in components of swine performance is affected by the definition of breeding objectives, market endpoint, and breed role.

As Hazel (26) had done for beef cattle, Nordskog (48) suggested assigning economic weights only to the minimum number of (primary) traits most directly controlling efficiency of production and then using the genetic and phenotypic parameters of other (secondary) traits and their genetic correlations with the primary traits to derive the optimal weighting for the traits to be included in a composite selection index. If a primary trait (e.g., feed consumption) is not measured directly, production system simulation may be required to estimate independent economic weightings for the observed predictive traits.

The desired gains approach (54, 77) is just another way to assign relative economic importance for alternative genetic changes. Some rational basis is needed for assessing equivalent value of unit genetic changes in several components of performance. Ranking in relation to competing commercial breeding stocks for particular traits is sometimes more important to a breeder than the general goal of improved efficiency of production and is used to define genetic goals (58). Breeders also must be wary of potential loss in components of genetic merit from genetic antagonism (pleiotropy) between a selected and an impor-

tant but possibly unselected trait (e.g., growth rate with excess fat, lower egg production, or leg weakness in broilers or turkeys; rate of production with egg size and shell strength in layers). Restricted selection indexes (37) are intended to maintain optimal levels for some traits while improving other traits with which they have some degree of genetic antagonism.

PRESENT AND FUTURE USE OF INDEX SELECTION IN LIVESTOCK IMPROVEMENT

Except for large corporate breeding organizations, it generally is not feasible for individual breeders to develop their own selection indexes, because these involve not only the relative economic weightings for component traits, but also accurate estimates of variability, heritability, and genetic and phenotypic correlation. For this reason, it is very helpful for an animal breeding enterprise to be part of a larger organization that can facilitate data recording and can compute individual breeding values for the traits considered important, using information on relationships and on the genetic parameters appropriate for the management system. The breeder can then apply the economic weights considered to be most appropriate for the breed role and for the production and marketing system to be served to obtain individual selection indexes. If the breeder's enterprise is part of a larger group with similar breeding goals, all members of the group can use the same economic weights to provide a selection index for each candidate breeding animal. Each breeder then can limit added inputs to adjusting index rankings to fit special concerns or to include other traits or more current information.

The use of index selection for livestock breeding programs was reviewed comprehensively in the *Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production* (18). Only a brief summary of present and potential future use of index selection approaches for several livestock species is attempted here.

Dairy Cattle

Rates of genetic improvement for yield of milk, fat, and protein have increased dramatically (Figure 3) in recent decades in the United

TABLE 2. Statistical information required (arbitrary values) for example of selection index for beef cattle.¹

Character	Economic value	Standard deviation	Heritability	Phenotypic correlation				Genetic correlations			
				2	3	4	5	2	3	4	5
1. Weaning weight	.3	40.0	.25	.4	.1	.0	.2	.2	.2	-.1	.3
2. Weaning score	2.0	1.0	.35		.0	.2	.0		.0	.6	-.2
3. Feed efficiency	-15.0	.5	.50			.0	-.3			.3	-.5
4. Slaughter grade	10.0	1.0	.40				-.2				-.3
5. Rate of gain	16.0	.3	.65								

¹From Hazel (26).

States (49). This increase is attributed to the greater accuracy of estimating transmitting abilities from mixed model analysis, which uses information from all relatives (70) and permits direct comparison of genetic merit among age groups of candidate breeders to maximize annual rate of improvement. Continued improvements are anticipated, especially for multiple-trait index selection and for optimal balance between individual and progeny-test selection for both milk and beef production of dual purpose cattle (55).

For specialized dairy cattle populations in temperate climatic zones, breeding objectives for dairy cattle now include such traits as milk composition, herd life, and perhaps somatic cell count (a measure of current infectious state of the udder) in addition to milk volume. Rogers (56) developed an index using milk yield, udder depth, teat placement, foot angle, and somatic cell score that increases the gain in aggregate genotype by 1 to 4% over milk

yield alone. Schutz (59) discussed sire evaluation for somatic cell score that is planned to be implemented on a national basis. The traits included in any index depend upon the market served and the levels of performance and costs of production (21, 53). Selection indexes are also useful to adjust for changing relative prices for milk fat and protein and feed costs (21).

In regions where feed costs and land prices are high and beef production is largely limited to that from dual purpose cattle, growth and body composition also have significant economic importance. Here, both individual and progeny testing for growth and carcass traits is justified (47). In tropical environments, where nutrition is marginal, exposure to tick-borne diseases is common, and income from both milk and meat is desired, the economic importance of cow and calf survival and calf growth is increased relative to milk output and milk composition (42). In tropical environments, genetic improvement also depends heavily upon more complete pedigree and performance recording and planned structure of cattle populations (38).

Beef Cattle

The earliest selection index for beef cattle was one proposed by Hazel (26) at the 1951 meeting of NC-1 Regional Beef Cattle Breeding Committee to illustrate the application of selection index principles. Approximate relative economic weights and estimates of population parameters (Table 2) were assigned for weaning weight and score, postweaning feed efficiency, daily gain, and slaughter grade. These were then used to define aggregate

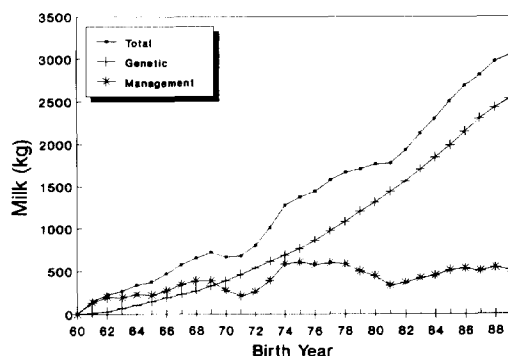


Figure 3. Trends in milk production of Holstein cows in the US. From Norman and Powell (49).

TABLE 3. Matching genetic potential for different traits to varying production environments¹.

Production environment		Traits					
Feed availability	Environmental stress ²	Milk production	Mature size	Ability to store energy ³	Adaptability to stress ⁴	Calving ease	Lean yield
High (H)	L	M to H	M to H	L to M	M	M to H	H
	H	M	L to H	L to H	H	H	M to H
Medium (M)	L	M+	M	M to H	M	M to H	M to H
	H	M-	M	H	H	M	M
Low (L)	L	L to M	L to M	H	M	M to H	M
	H	L	L	H	H	H	L to M
Breed role in terminal crossbreeding systems							
Maternal		L to H	L to M	M to H	M to H	H	L to M
Paternal		L to M	H	L	M to H	M	H

¹From Beef Improvement Federation (4).²Heat, cold, parasites, disease, mud, and altitude.³Ability to store fat and regulate energy requirements with changing (seasonal) availability of feed.⁴Physiological tolerance to heat, cold, parasites, disease, mud, and other stresses.

breeding value (H) and to solve for the optimal (maximum R_{IH}) selection index weightings of phenotypes for each trait in the index, using only weaning weight and score (I_1), all five traits (I_3), or all traits but feed efficiency (I_2). Hazel (26) then showed how much genetic change would be expected per standard deviation of selection differential for each of these indexes for each of the five traits (ΔG_i) and for overall breeding values (ΔH), which illustrated the principle that selection for H could be based upon partial information that was genetically correlated with the breeding goal. The most obvious omissions in this proposed index were the economic importance of reproductive rate, as influenced by fertility, calf survival, herd life, and the effect on cow size and maintenance costs from increased growth rate.

Cartwright's (10) comprehensive description of traits desired for the beef cow, bull, and market progeny (steers) to improve economic efficiency of beef production indicated antagonism between effects of rapid growth rate on cow versus contributions of calf and bull to efficiency. The production system simulation of Notter et al. (50) showed that, for terminal crossbreeding, the major economic traits for maternal breeds include components of reproductive rate and weaning weight (milk), but that only growth rate, mature size, calving ease, and carcass composition are primary for terminal sire breeds. For straight breeding or

rotational crossbreeding systems, however, maternal and market animal performance are both important; emphasis is less clear for growth rate and associated mature size. Because beef cattle are used to harvest a wide variety of forages under diverse climatic, management, and marketing systems, the relative importance of performance traits for selection can differ greatly among breeds and breeders (Table 3). Thus, the current general approach of pedigreed cattle breeds is to report breeding values for the traits considered important and only to suggest how breeders choose the relative emphasis on performance traits best suited to their individual breeding objectives [e.g., (4, 5)].

The genetic trends of widely used maternal breeds in the US indicate major past emphasis on increased yearling weight and associated mature size and birth weight [e.g., American Angus Association, (2)], probably because these breeding values are so readily available and moderately heritable. Estimation of breeding values and genetic trends has become routine for some beef breeds for both sire and dam effects on calving ease, weaning weights, maternal milk, and yearling weights. Some breeds (Figure 4 for Simmental) show desired increases in growth without loss of calving ease from increased birth weight (61). However, the progeny tests required for accurate breeding values on cow reproductive traits,

except calving ease, and on calf carcass traits are only beginning to be obtained in the US (4, 9). More emphasis has been placed on carcass traits of dual purpose breeds in Europe breeds (60) and on cow reproductive performance for tropical cattle breeding (51).

Pigs

Hazel's (25) original publication on the selection index used swine improvement as an example. Applications to multiple-trait selec-

tion for swine breeding during the last 50 yr have included refinements in both the relative economic importance of traits and the estimation of trait breeding values. Hazel's live backfat thickness (28) and later ultrasound composition measurement have replaced conformation score, and feed efficiency plus daily gain, or days to market weight, have replaced 180-d weight (45).

Production system simulation has provided more precise estimates of relative economic importance of component traits and demon-

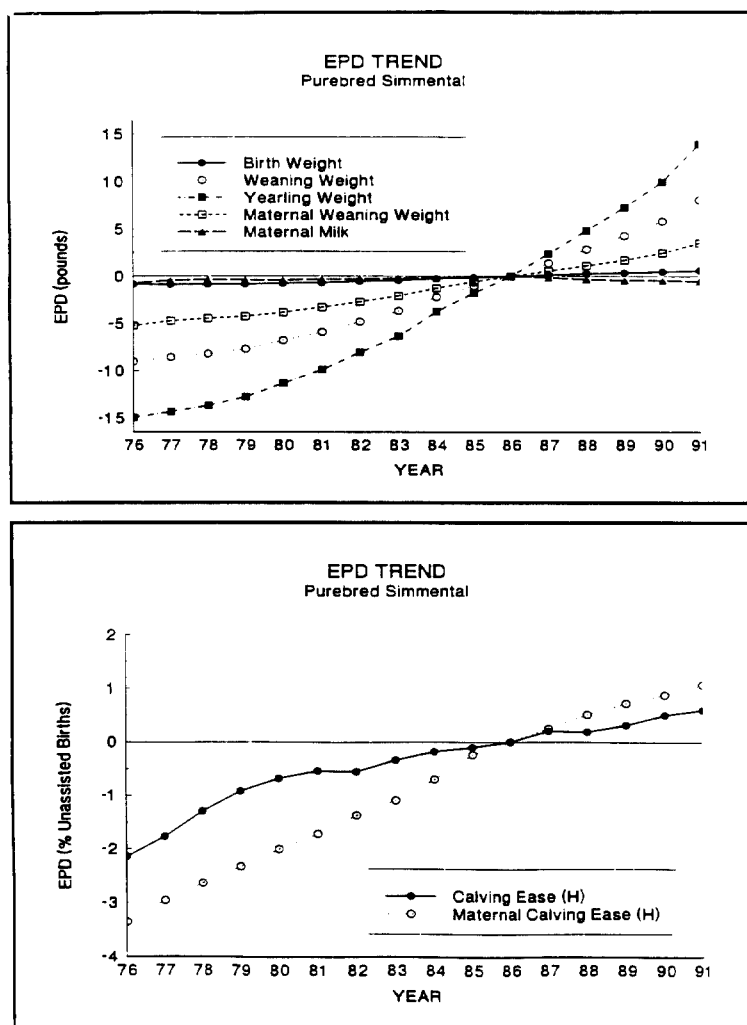


Figure 4. Estimated genetic trends in purebred American Simmental cattle as deviation from mean for 1986. From 1992 *Sire Summary* (61).

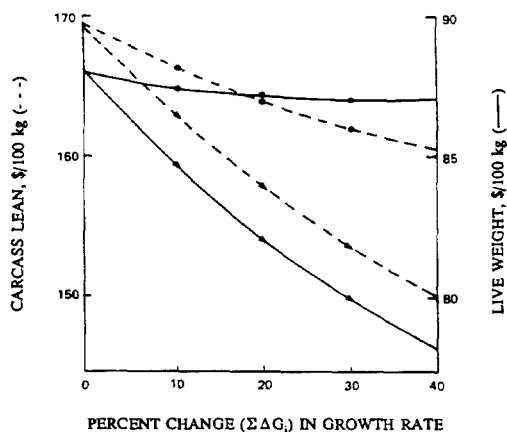


Figure 5. Pig model. Predicted reduction in dollars per 100 kg of carcass lean (---) and in dollars per 100 kg of live weight (—) for pigs marketed at constant live weight (●) or age (→). From Tess (68).

strated their sensitivity, especially to the breed role in crossbreeding systems (7), degree of pricing market hogs according to lean retail value, age versus weight market endpoints (Figure 5), and costs of feed versus other inputs (68). For cost per unit of lean output value in straight breeding, rotation crossbreeding, and maternal breeds in crossbreeding, the descending order of importance was greater litter size, leanness, viability, and conception rate, plus some for milk production and earlier puberty. For terminal sire breeds, the important traits were only leanness, growth rate, and pig viability (7). Only recently has payment for leanness by US processors even begun to approach the actual lean retail value used in the simulation work cited. This change now justifies roughly twice the economic importance for backfat probe that was recommended by The National Swine Improvement Federation (45) and has stimulated initiation of a Terminal Sire Testing Program by the National Pork Producers Council (44) to provide unbiased data on growth and carcass traits, including backfat and meat quality.

Estimation of the individual breeding values for traits used to calculate selection indexes has gradually become more systematic and accurate, utilizing information on all relatives within and, to lesser degree, across herds of the same breed (57). Such a swine testing and

genetic evaluation system (STAGES) is being used by the Yorkshire (78) and several other breed associations. The appropriate economic values are then used to weight the relevant trait breeding values for predicting genetic deviation in net income for candidate breeders being selected within a terminal sire, a maternal or a general purpose (rotation crossing) breed (66). Parallel procedures are now used by major pig breeding companies, the Nebraska Specific Pathogen-Free Program (46), and to evaluate results from US national test station data.

Sheep and Goats

After completing his graduate program with Lush (25, 29) at Iowa State University, Hazel collaborated with Clair Terrill in applying index selection at the US Sheep Experiment Station at Dubois, Idaho. This effort required development of numerous adjustments for environmental effects and estimates of heritability, genetic correlation, and relative economic importance for components of lamb and wool production (see their publications in Volumes 4 and 5 of *Journal of Animal Science*). During 1946, work of Hazel and Terrill (30) culminated in a proposed multiple-trait index for selection of range Rambouillet lambs. The relative economic importance of traits included was estimated as the standard partial regressions on each component: .40 for face covering, .39 for neck folds, .38 for body weight, .16 for body condition, .14 for staple length, and .01 for body type. Compared with selection on general appearance, use of the index shifted emphasis to the more important and highly heritable traits and greatly increased selection differentials for the more important traits, especially in the less intense selection for ewes than for rams.

Both the relative economic importance of component traits and the application of multiple-trait selection for diverse industry breeding programs were reviewed comprehensively in *Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production* (18). The excellent review of economic breeding objective for sheep and goats (18) illustrated the major effect of the enormous range among world production-marketing environments on the relative economic importance of such traits as reproduc-

tive rate, viability, growth rate, body composition, fiber quantity, and quality. The review of costs and benefits of differing breed utilization strategies emphasized the vital rate of production system simulation to include effects on real economic efficiency of traits that are difficult to measure on all animals, such as nutrient intake and body composition. An example of the wide differences in economic importance and in sensitivity to mean genetic levels among component traits is given in Figure 6 (73) for efficient lamb and wool production under semi-intensive management in the US.

Other reviews (18) emphasized the substantial potential gains in selection response from more complete recording of both primary performance traits and pedigrees and from accurate estimates of the genetic parameters needed to predict breeding values for the primary traits. Complete pedigree information allows use of information on all relatives to rank more accurately animals differing in both ages and amounts of information (31, 32) and thus achieves optimal age composition and maximal rate of selection response. This BLUP (31) procedure also simplifies use of relative economic weights by applying them to the updated individual animal breeding values for primary traits as the last step for ranking candidate breeders.

The continuing refinement of breeding objectives and methods of selecting for those objectives under diverse world environments for sheep and goat production is described further by many papers in *Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding* (34) and the *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production* (33).

Poultry

Because of the small value of individual birds, their high reproductive rate, and their adaptability to mass production systems, most genetic selection programs of poultry are now conducted by separate breeding organizations rather than as a cooperative effort of many independent breeders. The number of economically important traits is large for poultry, and more so for egg-producing stocks than for meat-producing stocks. Arthur (3) presents an

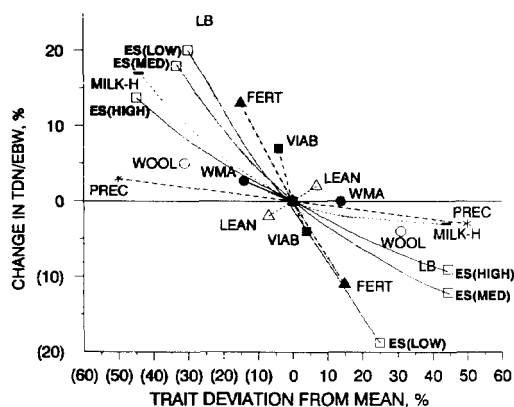


Figure 6. Change in TDN input (percentage) per unit (percentage) change in trait deviation from population mean; for precocity (PREC); fertility (FERT); lambs born (LB); viability; length of estrus season (ES) for high, medium, and low reproductive rates; growth rate (WMA); percentage of lean content; rate of wool growth; and milk production for high lambing rate. From Wang and Dickerson (73).

excellent review of industry programs for egg-producing stocks.

The relative economic importance of component traits has been used in several different ways to determine the selection index weightings of traits that are expected to maximize desired genetic improvement. For comparisons among commercial breeding stocks, random sample performance testing provided useful information on income over feed and chick costs for egg-laying stocks and broiler stocks of chickens during an early period of the poultry breeding industry (13). For individual breeders, one alternative has been to estimate the independent (partial regression) effect per unit of genetic change for all traits that influence economic efficiency (36). The economic weights used at Kimber Farms (Table 4) were an early example. As with other meat-producing species, the goals for genetic stocks used only as male parents of market meat chickens or turkeys are quite different from the goals for strains used to produce the strain-cross female parents of the market birds. This divergence in goals of paternal and maternal crossing stocks tends to minimize selection problems from genetic antagonism of growth and carcass traits with reproductive performance.

TABLE 4. Example of economic value per unit and per genetic standard deviation of change for egg production traits.¹

	Genetic variation (σ_G)	Economic value per unit	Economic value per σ_G
Fertility, ² %	.95	.008	.008
Hatch, ² %	1.6	.008	.013
Normal, ² %	1.7	.008	.014
Early viability, %	4	.012	.05
Adult viability, %	7	.025	.18
Egg production to 72 wk, %	3.84	.110	.42
Age first egg, d	7.9	.023	.18
Calmness score, 0 to 1	.128	.500	.06
At 32 wk			
Body weight, kg	.133	.772	.10
Egg weight, g	2.41	.085	.21
Specific gravity score (.004)	.75	.080	.06
Shape 10 L/W, 0 to 1	.26	.050	.013
Albumen, Haugh units	3.35	.020	.07
No blood, 1%	1.28	.040	.05
No color ³	.20	.50	.10
Shell smoothness ³	.056	.50	.03

¹From Bennett et al. (6) and Emsley and Dickerson (19).²For eggs or progeny from breeding female over an 8-wk laying period.³Score, 0 to 1.

CONCLUSIONS

The basic purpose of the selection index of Hazel (25) was to maximize economic response from multiple-trait selection. This goal is accomplished by first weighting the unit of genetic change in each component trait according to its independent effect on potential net profit. Then, the genetic and phenotypic parameters are used to find the index weightings of trait phenotypes of individuals and relatives that maximize correlation of index with genetic variation in net profit. Because selection objectives for domestic animals almost always include several genetic traits, the concept of index selection has received continuing attention in both theory and application. Application of relative economic values of traits as a separate last step for index selection simplifies continuous updating of trait information on all relatives and the direct comparison of animals with unequal information to be used for selection and allows for variation in the relative economic weights most appropriate for individual breeds or breeders. Simulation of production systems is useful in clarifying the relative economic importance of traits as influenced by trait performance, breed

roles in breeding systems, and production and marketing environments. Desired or intended genetic changes in traits to maintain or to improve the competitive position of a genetic stock also defines the relative importance of traits.

REFERENCES

- 1 Andrus, D. F., and L. D. McGilliard. 1975. Selection of dairy cattle for overall excellence. *J. Dairy Sci.* 58: 1876.
- 2 American Angus Association. 1992. Angus EPD trends. Page 4 in *Sire Evaluation Report*. Anim. Dairy Sci. Dep., Univ. Georgia, Athens.
- 3 Arthur, J. A. 1986. An evaluation of industry programs for egg type chickens. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:325.
- 4 Beef Improvement Federation. 1990. Guidelines for Uniform Beef Improvement Programs. 6th ed. Beef Improve. Fed., Univ. Georgia, Athens.
- 5 Beef Improvement Federation. 1992. *Proc. Res. Symp. 24th Annu. Mtg. Beef Improv. Fed.*, Univ. Georgia, Athens.
- 6 Bennett, G. L., G. E. Dickerson, and T. S. Kashyap. 1981. Effectiveness of multiple-trait index progeny test selection for field performance of strain-cross layers. *Poult. Sci.* 60:22.
- 7 Bennett, G. L., M. W. Tess, G. E. Dickerson, and R. K. Johnson. 1983. Simulation of breed and cross-breeding effects on costs of pork production. *J. Anim. Sci.* 56:801.

- 8 Bernard, C. S., A. B. Chapman, and R. H. Grammer. 1954. Selection of pigs under farm conditions: kind and amount practiced and a recommended selection index. *J. Anim. Sci.* 13:389.
- 9 Bolze, R. 1992. What's new in national sire evaluation/national cattle evaluation. Page 36 in *Proc. Tri-State Cow/Calf Symp. Coop. Ext., Univ. Nebraska, Lincoln*.
- 10 Cartwright, T. C. 1970. Selection criteria for beef cattle for the future. *J. Anim. Sci.* 30:706.
- 11 Cartwright, T. C., H. A. Fitzhugh, and C. R. Long. 1975. Systems analysis of sources of genetic and environmental variation in efficiency of beef production and mating plans. *J. Anim. Sci.* 40:433.
- 12 Cochran, W. G. 1951. Improvement by means of selection. Page 449 in *Proc. 2nd Berkeley Symp. Math. Stat. Prob., Univ. California Press, Berkeley*.
- 13 Dickerson, G. E. 1965. Random sample testing performance of poultry in USA. *World's Poult. Sci. J.* 21:345.
- 14 Dickerson, G. E. 1970. Efficiency of animal production—molding the biological components. *J. Anim. Sci.* 30:849.
- 15 Dickerson, G. E. 1982. Principles in establishing breeding objectives in livestock. *Proc. 1st World Congr. Sheep Beef Cattle Breeding. Vol. 1(Tech):9*.
- 16 Dickerson, G. E., and L. N. Hazel. 1944. Effectiveness of selection on progeny performance as a supplement to earlier culling in livestock. *J. Agric. Res.* 69:459.
- 17 Dickerson, G. E., and L. N. Hazel. 1944. Selection for growth rate of pigs and productivity of sows. *J. Anim. Sci.* 3:201.
- 18 Dickerson, G. E., and R. K. Johnson. 1986. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod. Vol. IX, Breeding Programs for Dairy and Beef Cattle, Water Buffalo, Sheep and Goats, and Vol. X, Breeding Programs for Swine, Poultry and Fish. Univ. Nebraska, Lincoln*.
- 19 Emsley, A., and G. E. Dickerson. 1974. Predicting 12-trait aggregate breeding value from indexes composed of fewer than 12 traits in egg production chickens. Page 157 in *Proc. XV World Poultry Congr., New Orleans, LA*.
- 20 Gill, G. S., and F. R. Allaire. 1976. Genetic and phenotypic parameters for a profit function and selection method for optimizing profit in dairy cattle. *J. Dairy Sci.* 59:1325.
- 21 Harris, B. L., and A. E. Freeman. 1993. Economic weights for milk production traits and herd life under various economic conditions and production quotas. *J. Dairy Sci.* 76:868.
- 22 Harris, D. L. 1964. Expected and predicted progress from index selection involving estimates of population parameters. *Biometrics* 20:46.
- 23 Harris, D. L. 1970. Breeding for efficiency in livestock production: defining the economic objectives. *J. Anim. Sci.* 30:860.
- 24 Harris, D. L., and S. Newman. 1992. How does genetic evaluation become economic improvement? Paper presented Symp. Appl. Expected Progeny Differences Livest. Improve. Am. Soc. Anim. Sci., Pittsburgh, PA.
- 25 Hazel, L. N. 1943. The genetic basis for constructing selection indexes. *Genetics* 28:476.
- 26 Hazel, L. N. 1951. Construction and use of selection indexes in beef cattle. Page 34 in *Annu. Rep. NC-1 Reg. Coop. Res. Project Improvement of Beef Cattle Through Breeding. Univ. Nebraska, Lincoln*.
- 27 Hazel, L. N., M. L. Baker, and C. F. Reinmüller. 1943. Genetic and environmental correlations between growth rates of pigs at different ages. *J. Anim. Sci.* 2:118.
- 28 Hazel, L. N., and E. A. Kline. 1951. Mechanical measurement of fatness and carcass value on live hogs. *J. Anim. Sci.* 11:318.
- 29 Hazel, L. N., and J. L. Lush. 1942. The efficiency of three methods of selection. *Jour. Hered.* 33:393.
- 30 Hazel, L. N., and C. E. Terrill. 1946. The construction and use of a selection index for range Rambouillet lambs. *J. Anim. Sci.* 5:412.
- 31 Henderson, C. H. 1963. Selection index and expected advance. Page 141 in *Statistical Genetics and Plant Breeding. Natl. Acad. Sci./Natl. Res. Council. Publ. No. 982. Natl. Acad. Sci., Washington, DC*.
- 32 Henderson, C. H. 1972. Sire evaluation and genetic trends. Page 10 in *Proc. Anim. Breeding Genet. Symp. in Honor of Dr. J. L. Lush. Am. Soc. Anim. Sci., Am. Dairy Sci. Assoc., Champaign, IL*.
- 33 Hill, W. G., R. Thompson, and J. A. Woolliams. 1990. *Proc. 4th World Congr. Genet. Appl. Livest. Prod., Edinburgh, Scotland. XV:*
- 34 Institut National de la Recherche Agronomique. 1988. *Proc. 3rd World Congr. on Sheep and Beef Cattle Breeding. June 19–23, 1988, Vol. 1 and 2. Inst. Natl. Res. Agron. Paris, France*.
- 35 Karam, H. A., A. B. Chapman, and A. L. Pope. 1953. Selecting lambs under farm conditions. *J. Anim. Sci.* 12:148.
- 36 Kashyap, T. S., G. E. Dickerson, and G. L. Bennett. 1981. Effective use of progeny test, multiple-trait index selection for field performance of strain-cross layers. *Estimated responses. Poult. Sci.* 60:1.
- 37 Kempthorne, O., and A. W. Nordskog. 1959. Restricted selection indices. *Biometrics* 15:10.
- 38 Kunzi, N., and W. Kropf. 1986. Genetic improvement for milk and meat production in the tropics. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod., Lincoln, NE XII:165*.
- 39 Lush, J. L. 1937. *Animal Breeding Plans. Collegiate Press, Inc., Ames, IA*.
- 40 Lush, J. L. 1940. Intra-sire correlation or regression of offspring on parent as a method of estimating heritability of characteristics. Page 293 in *Proc. 32nd Annu. Mtg., Am. Soc. Anim. Prod.*
- 41 Lush, J. L. 1940. Relative importance of dams productivity, pigs own market score and pigs own growth rate in selecting young boars and gilts for breeding. *Mimeo, Res. Item No. 18 Reg. Swine Breeding Lab., Ames, IA*.
- 42 Madelena, F. E. 1986. Economic evaluation of breeding objectives for milk and beef production in tropical environments. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod., Lincoln, NE XII:33*.
- 43 Moav, R., and J. Moav. 1966. Profit in a broiler enterprise as a function of egg production of parent stock and growth rate of their progeny. *Br. Poult. Sci.* 7:5.

- 44 National Pork Producers Council. 1993. Genetic test starts down long road. *Terminal Sire Program*. Pork 93 (May):38.
- 45 National Swine Improvement Federation. 1988. Guidelines for Uniform Swine Improvement Programs. Natl. Pork Prod. Council, Des Moines, IA.
- 46 Nebraska SPF. 1990. Annual Report. Nebraska SPF Swine Accrediting Agency, Lincoln.
- 47 Niebel, E. 1986. Economic evaluation of breeding objectives for milk and beef production in temperate zones. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:18.
- 48 Nordskog, A. W. 1986. Economic evaluation of breeding objectives in layer-type chickens. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:207.
- 49 Norman, H. D., and R. L. Powell. 1992. Genetic change attained and possible. Page 59 in *Large Dairy Herd Management*. ADSA, Champaign, IL.
- 50 Notter, D. R., J. O. Sanders, G. E. Dickerson, G. M. Smith, and T. C. Cartwright. 1979. Simulated efficiency of beef production for a midwestern cow-calf-feedlot management system. *J. Anim. Sci.* 49:70, 83.
- 51 Ordoñez, J. A. 1990. Breeding beef cattle in Latin American tropics. *Proc. 4th World Congr. Genet. Appl. Livest. Prod.* Edinburgh, Scotland, XV:254.
- 52 Osborne, R. 1957. The use of sire and dam family averages in increasing the efficiency of selective breeding under a hierarchical mating system. *Heredity* 11:93.
- 53 Pearson, R. E. 1986. Economic evaluation of breeding objectives in dairy cattle. Intensive specialized milk production in temperate zones. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:11.
- 54 Pesek, J., and R. J. Baker. 1969. Desired improvement in relation to selection indices. *Can. J. Plant Sci.* 49:803.
- 55 Pirchner, F. 1986. Evaluation of industry breeding programs for dairy cattle milk and meat production. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:153.
- 56 Rogers, G. W. 1993. Index selection using milk yield, somatic cell score, udder depth, teat placement, and foot angle. *J. Dairy Sci.* 76:664.
- 57 Schinckel, A. P., D. L. Harris, T. S. Stewart, and D. L. Longren. 1986. Swine testing and genetic evaluation system for purebred swine associations. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:96.
- 58 Schultz, F. T. 1986. Formulation of breeding objectives for poultry meat production. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:215.
- 59 Schutz, M. M. 1993. Genetic evaluation of somatic cell scores for U.S. dairy cattle. *J. Dairy Sci.* 76: (Suppl. 1):229.(Abstr.)
- 60 Simm, G., D. E. Steane, and N. R. Wray. 1990. Developments in beef cattle breeding programmes in Europe. *Proc. 4th World Congr. Genet. Appl. Livest. Prod.*, Edinburgh, Scotland, XV:231.
- 61 Simmental. 1992. Genetic trends in Simmental. Page 10 in *Sire Summary*. Am. Simmental Assoc., Bozeman, MT.
- 62 Smith, C., G. E. Dickerson, M. W. Tess, and G. L. Bennett. 1983. Expected relative responses to selection for alternative measures of life-cycle economic efficiency of pork production. *J. Anim. Sci.* 56:1306.
- 63 Smith, C., J. W. James, and E. W. Brascamp. 1986. On the derivation of economic weights in livestock improvement. *Anim. Prod.* 43:545.
- 64 Smith, F. 1937. A discriminate function for plant selection. *Ann. Eugen.* 7:240.
- 65 Snedecor, G. W., and W. G. Cochran. 1940. *Statistical Methods*. Iowa State Univ. Press, Ames.
- 66 Stewart, T. S., D. L. Harris, A. P. Schinckel, and D. L. Longren. 1986. A bioeconomic objective for swine improvement. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:87.
- 67 Tallis, G. M. 1960. The sampling errors of estimated genetic regression coefficients and errors of predicted gains. *Aust. J. Stat.* 2:66.
- 68 Tess, M. W. 1986. The impact of production/marketing system on breeding objectives in swine. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:3.
- 69 Vandepitte, W. M., and L. N. Hazel. 1977. The effect of errors in economic weights on accuracy of selection indexes. *Ann. Genet. Sel. Anim.* 9:87.
- 70 Van Vleck, L. D. 1986. Evaluation of dairy cattle breeding programs: specialized milk production. *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE XII:141.
- 71 Villanueva, B., and B. W. Kennedy. 1993. Index versus tandem selection after repeated generations of selection. *Theor. Appl. Genet.* 85:706.
- 72 Vinson, W. E., and A. E. Freeman. 1971. Maximizing genetic gain from selection by independent culling levels for correlated traits. *J. Dairy Sci.* 54:774.(Abstr.)
- 73 Wang, C. T., and G. E. Dickerson. 1991. Simulation of life-cycle efficiency of lamb and wool production for genetic levels of component traits and alternative management options. *J. Anim. Sci.* 69:4324.
- 74 Williams, J. S. 1962. The evaluation of a selection index. *Biometrics* 18:375.
- 75 Wright, S. 1920. The relative importance of heredity and environment in determining the piebald pattern of guinea pigs. *Proc. Natl. Acad. Sci. USA* 6:320.
- 76 Wright, S. 1921. The biometrical relations between parent and offspring. *Genetics* 6:111.
- 77 Yamada, Y., K. Yokouchi, and A. Nishida. 1975. Selection index when genetic gains of individual traits are of primary importance. *Jpn. J. Genet.* 50:33.
- 78 Yorkshire. National Swine Evaluation. 1992. *Trait Leaders*. Am. Yorkshire Club, Dep. Anim. Sci., Purdue Univ., Lafayette, IN.
- 79 Young, S.S.Y. 1961. A further examination of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. *Genet. Res. Camb.* 2:106.