

QUANTITY, QUALITY AND THE CONSUMER: LIMITATIONS TO BREEDING OBJECTIVES

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SUMMARY

Since Robert Bakewell made the observation that like begets like, animal breeders have been attempting to better define what we like. For the most part, we have divided selection into two parts, genetic prediction of breeding values for individual traits and combining those predictions into multi-trait selection criteria to maximize progress towards the breeding objective. Technology is well advanced in predicting the transmittable genetic component of traits. Given a database of pedigree information and observed phenotypic performance, we can predict accurate and unbiased breeding values. Through the use of profit functions, we have effective tools to describe selection objectives. Procedures have been developed to consider complicating issues such as opportunity costs, genetic lag, market elasticity, non-linear values, restrictions to change, risk and competition. We can even integrate mating systems and use of multiple genetic lines in mating programs into our objectives. A summary of selection criteria being applied around the world is presented. What is obvious as the limitation in those applied programs is our lack of data recording programs for all traits of economic importance. For some traits, such as reproductive efficiency and longevity, it is just a simple matter of more comprehensive data recording. But for other traits, such as carcass quality, we do not fully understand the biological processes that control and define the trait or have accurate phenotypic measures of the trait. Therefore can not access the trait in sufficient numbers of selection candidates to generate reasonable selection intensities. And ultimately, genetic improvement is dependent on how much selection intensity we generate and where we direct it.

Keywords: Selection, Swine, Pigs, Limitations

INTRODUCTION

In the beginning, Robert Bakewell (1725-1795) said, "like begets like" and animal breeding moved into the modern era. In the interim, we have been trying to determine how much of the like we truly beget, and do a better job of deciding what we like. We have even come to understand that two unlikes can beget better.

The next major event in genetic selection to come along (besides Mendel's peas and Fisher's heritability) was when Hazel (1943) said $b=P^{-1}Ga$, and the selection index was born. We moved from single traits to multiple traits in defining what we liked, the breeding objective.

Since 1943, we have been refining the techniques we use to develop selection indexes. Work for the most part can be divided into two areas of development. The $P^{-1}G$ bit is handled by genetic prediction of breeding values, which deals with parameter estimation and utilization of phenotypic information on relatives to predict the genetic value of animals for multiple traits.

The “a” bit, determining the relative economic weightings, is handled through the definition and parameterization of the breeding objective which describes the bioeconomic relationships between traits and the net output (\$) of the production system.

GENETIC PREDICTION

Henderson (1984) said BLUP and things really got a whole lot easier. We have rapidly progressed from estimating breeding value (EBV) being a simple function of h^2 and phenotypic deviations, through the Sire, RAM (Reduced Animal Model), AM (Animal Model) and Multitrait-AM models. The current status of methodology to predict genetic value for traits is far ahead of our ability to observe traits and knowledge of genetic variance-covariance structures. We have progressed from Least Squares to Maximum Likelihood (both ML and REML, Method R and even Gibbs Sampling) in our quest to be more efficient and accurate in our estimation of genetic parameters. The revolution in computing since 1983 has facilitated the adoption of BLUP methodologies in applied breeding programs. We have ready access to technology to maximize the accuracy of predictions incorporating varying amounts of phenotypic information, heterogeneous variation, multiple environments and even multiple breeds (depending on your views of Genotype-Environment Interactions).

Given phenotypic observations, the task of predicting breeding values on a group of animals and their relatives is relatively simple. The limitations are in the phenotypic data. While we have a large number of data sets, we are plagued with poorly defined contemporary groups in terms of uniform environmental conditions, adequate numbers of sires and progeny within groups and proper genetic ties among groups. Figure 1 demonstrates the relationship between accuracy of estimation and data structure as described by sires per group and numbers of contemporary groups for a sire family (Lofgren and Stewart 1994). Secondly, we will show in our discussion of the “a” bit (economic values) that we do not have information on many of the traits important to our breeding objectives.

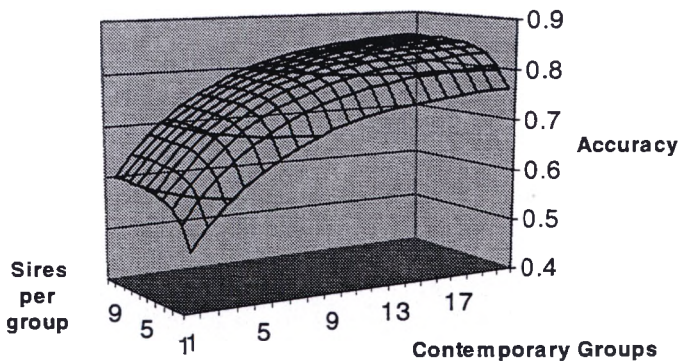


Figure 1 Accuracy of Genetic Prediction for a moderately heritable trait.

Closely related to the limitations we have in phenotypic observations is our knowledge base of the Covariance structure among traits. Covariance structures impact our selection programs both in the genetic prediction of correlated traits and in the correlated response to selection for multiple traits of economic importance. If we categorize traits into production, reproduction and end product traits, our knowledge of co-variation decreases as we move from production to end products and our knowledge between categories is more limited than that within categories. I will not review the literature on co-variation but rather refer you to Hermes (1996).

RELATIVE ECONOMIC VALUES (“a”)

The adoption of selection indexes had been hampered by confusion over the economic part of the equations. For the most part, determining relative economic values for the traits has been viewed as a stressful decision for practicing breeders. The tool we use to determine economic weighting is a profit function. And here is where the problems start. First, with whose profit are we concerned; the farm, the industry or the consumer? Should profit be measured per farm, per animal, per unit output or per unit input? Are we concerned with absolute profit (Return-Cost) or profit ratio R/C? Are we concerned with short-term or long-term gains, which introduces the consideration of discount rates? Then when you introduce the reality that both biological and economic relationships are frequently non-linear, you bring in the concept of differential economic values depending on where production occurs relative to optimal levels and scale of operations. I will attempt to outline the resolution to these and related issues that have been presented in the literature.

Who’s profit might at first seem to be a more philosophical than economic debate. But in reality, differing perspectives in assessing profit can impact the relative value among traits. Moav (1973) demonstrated that when economic weights were derived per breeder, per individual or per unit product, the relative values of component traits differed by more than the scalar differences of number of offspring per breeder and amount of product per individual (Table 1). Brascamp et al (1985) noted that when profit is zero, then the differences between economic weightings disappear and the relative values are the same regardless of the perspective. Zero profit can be achieved by including a “normal” profit as a cost of production.

Table 1 Profit equations and relative economic weights for three basis of comparison

Basic of Evaluation	Profit Equation	Economic Weight		
		$\delta\pi/\delta n$	$\delta\pi/\delta d$	$\delta\pi/\delta w$
Per Female	$P_1 = nwV - nC_1d - C_2$	$wV - C_1d$	$-nC_1$	nV
Per Individual	$P_2 = wV - C_1d - C_2/n$	C_2/n^2	$-C_1$	V
Per Unit Product	$P_3 = V - (C_1d/w) - (C_2/nw)$	C_2/n^2w	$-C_1/w$	$w^2(C_1d + C_2/n)$

n = number offspring/female/year, w = weight of product/individual, d = days to market, V = value/unit of product, C_1 = cost/individual/day, C_2 = cost/female/year. Brascamp et al. (1985)

The point of zero profit per unit for an enterprise is better defined as when the enterprise is at the optimal point of production relative to the input (MC=MR, the point where marginal cost =

marginal return). So, we can eliminate the problem of whose profit do we consider as long as the enterprise is optimized for production. This introduces a complicating issue. Optimum production is determined by the relative output per unit input. As we change the genetic potential for alternative traits, we change the input/output relationships and the point of optimum production shifts. When the optimum shifts, the total profit for the enterprise shifts. Thus, what do we do with the added (or reduced) profit? McArthur (1987) suggests that the profit for the enterprise should be determined for the optimal points of production for t_0 and $t_0+\Delta t$ and the value of the trait is the change in value/ Δt . Smith et al (1986) suggested that profit that can be derived by simply rescaling an enterprise to achieve the same level of output as the genetic improvement should not be included in the value of the genetic change. McArthur argues that if increased profit could occur by rescaling then the enterprise was not optimized prior to the genetic improvement. So another perspective is introduced into the optimization problem: what constraints are placed on the optimization of the enterprise?

One obvious constraint that applies to the topic of rescaling enterprises is production quotas. In an example of producing butter fat in New Zealand under two differing quota levels and no quota McArthur (1987) demonstrated a 50% difference in economic value between the two quota levels and a 2 fold difference when no quota was imposed.

Amer and Fox (1992) extended the concepts of utilizing the marginal profits from reoptimized profit functions applied to an industry. They showed that while the economic value of a trait can be equated for differing bases of reference, who benefits from the increase in value (the producer or the consumer) is dependent on the degree of elasticity of demand. In an elastic market, the producer is the primary beneficiary of the genetic improvement but in an inelastic market, the consumer benefits (Figure 2).

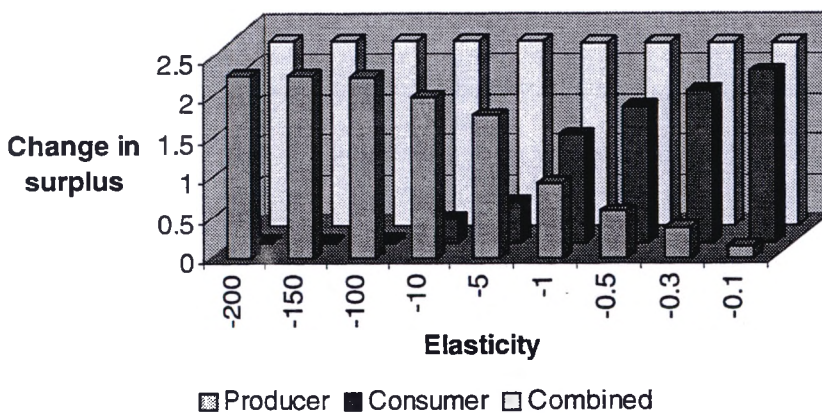


Figure 2. Changes in economic surplus associated with elasticity of market demand, from Amer and Fox (1992).

The need for optimization as part of developing selection indexes was first discussed in reference to non-linear breeding objectives. Frequently, the total merit is non-linear because output is products among traits, values of traits are interdependent and pricing functions may be non-linear. Wilton et al (1968) developed methodology for quadratic objectives as a method to address non-linear objectives. Kempthorne and Nordskog (1959) presented restricted indices as an approach to where one trait could be held to zero, or other level of restricted genetic change, while the remaining traits were improved. Restricted indexes have been used to constrain a trait near its optimal value while correlated traits are altered. While restricted, or constrained or desired gains as are the more contemporary names, indexes are useful when an absolute limit to a change is needed; they do not facilitate identification of economically optimal combinations of change. It may be desirable to have no change in a trait but it may be more economically sensible to allow it to change. Gibson and Kennedy (1990) demonstrated that constrained indexes are equivalent to selection indices with explicitly derived economic weights and their efficacy is determined by the accuracy of the explicit weights relative to the optimal weights derived from a profit function.

Desired gains indexes have been popular applied breeding programs such as Lambplan in recent writings (e.g. Newman and Ponzoni, 1994) because they seemingly avoid the task of a breeder determining the economic values of traits but rather simply describe the changes desired in each trait. The difficulty is in developing the optimal combination of desired changes. It seems implicitly easier to simply develop the profit function and optimize it directly than to attempt to choose the optimal combination of changes without an economic description.

BIOLOGICAL VS ECONOMIC EFFICIENCY

Dickerson (1970) proposed efficiency defined as output to input ratios as the biological objective of breeding programs. Gunsett (1984) showed how the weightings on the components of a ratio were dependent on selection intensity and as selection intensity increased, the relative emphasis placed on the numerator increased over that of the denominator. Melton and Colette (1993) discussed two implications critical to the use of efficiency ratios, one being that ratios are typically not linear over a range of inputs, and secondly biological efficiency is not necessarily reflective to economic profitability of an enterprise. To demonstrate their first point, genotype environment interactions are cited as an example of changing inputs impacting the ratio of output to input. To illustrate their second point, Melton and Colette consider the multi-year, multi-generation aspect of animal production and demonstrate that considering gene flow and discounting outputs to net present value will alter the rankings of individuals or breeds. For the most part, Melton and Colette's arguments can be summarized as a need for complete and comprehensive definitions of inputs and outputs over the full planing horizon. Their argument with ratios really boils down to their being over-simplified rather than being inherently flawed. Gunsett however, points out a problem associated with relative selection pressure placed on the components of the ratio, which is of direct concern to breeders.

SHORT-TERM VERSUS LONG-TERM RESPONSE

With BLUP based selection, there is an increase in the rate of inbreeding relative to mass selection because of the tendency toward family selection. Quinton et al (1992) showed that at equal levels of inbreeding, the increases in response to selection associated with the increased accuracy of BLUP-based selection is negated. Several authors have proposed methods to control the accumulation of inbreeding by restricting the usage of sire or selection of sibs. Alternative methods have been proposed to adjust the breeding value of an individual downward based on their contribution to inbreeding in the next generation. Wray and Goddard (1994) proposed an algorithm to optimize the selection of sires based on EBVs and the contribution to inbreeding but allowing flexibility in the usage of a sire or selection of sibs depending on the genetic merit of the sire and/or family. Based on simulated results, the proposed algorithm would increase the rate of genetic improvement while minimizing the accumulation of inbreeding even using fewer sires.

The status of selection index methodology is good. We have useful tools to estimate genetic values and have the tools to optimize those genetic values to maximize profit. We can discount EBVs for levels of inbreeding to optimize both short-term and long-term selection. Now let's look at the status of applied selection programs.

APPLIED SELECTION PROGRAMS

Table 2 summarizes traits utilized in pig selection indexes from a sampling of countries around the world. The traits common to all indexing systems are growth, fat depth and number born. Traits frequently included are feed conversion, percent lean, litter weights and sizes at weaning. The emerging traits are indicators of carcass quality. While not shown in the table, the weightings applied to the indexes are similar, after adjusting for differences in currency and in some cases standardization. In all systems summarized, the weightings were derived from profit functions that included costs of feed and facilities, and value of pigs associated with carcass quality. The differences in the indices are in the amount of phenotypic information available to predict the genetic values for the traits in the indices. For example feed information ranges from predictions based on growth and backfat to intake measured on sibs to use of electronic feeders to measure individual intake. The other major difference is in carcass premiums. All systems include measures of leanness. Some also include indicators of meat quality. The difficulty is that all the meat quality indicators currently in use are measured on carcasses, not live animals. This leads to reduced accuracy of predictions for selection candidates and to reduced selection intensities because of the smaller number of animals evaluated.

Table 2. Traits used in selection indexes around the world.

Source	Line	Growth	Feed	Carcass Quality	Reproduction	Other
Sullivan Canada	Sire	D to 100 kg		Fat Depth		
	Dam	D to 100 kg		Fat Depth	N. Born Alive	
Goetz, Bavaria	Sire	Daily Gain	(Omitted to increase intake)	Lean Percentage Conformation		Leg Sound
	Dam	Daily Gain	Feed Conv. on sibs	Lean Percentage Conformation	N. Born Alive	Leg Sound N. of Teats
	Commer	Daily Gain	Feed Conv. on sibs	Lean Percentage		
Hofer Switzer- land	Prod sib test	Daily Gain 30 to 103 kg	Feed Conversion	% Lean Cuts Intram. Fat pH 1 and 24 hr, Color		Leg Weak Osteochon.
	On-Farm Repro	DG to 97.5 kg	Backfat		N. Born Alive Wean -Estrus	
Australia	Com	D to 90 kg	Predicted	Fat Depth	N. Born Alive	
US	Sire	D to 105 kg	Predicted	Fat Depth		
	Dam	D to 105 kg	Predicted	Fat Depth	N. Born Alive Pig survival L. 21-day Wt.	
Short PIC-US	Sire	D to 110 kg	Individual data on Boars	Backfat, Loin Depth, Muscle Conform. Ultimate pH & Color		Leg Score Markers (4)
	Dam	Days to 110 kg	Individual data on Boars	Fat Depth	Litter Size L. Wean Wt. N. of Teats	Leg Score
Rydmer Sweden	Sib test	DG, 35 to 104 kg (scale fed)	Feed Con. 2 sibs avg	Lean Percentage Partial dissection Back Fat Depth		Leg Scores Osteochon.
	On-Farm	DG, Birth to 100 kg				
	Repro				N. Born Alive Farrow Inter.	
Visser S. Africa	Mat. Pat.	.8xSib test + On Farm + Reproduction .8xSib test + On Farm				
	Repro				L. S. Born L. S. Weaned L. Wean Wt. N. Born Alive	
	Stat. Test	Daily Gain 27-86 kg	Individual Intake	% lean Backfat Depth Shoulder dissect. Backfat		Visual appear 14 traits
	Sire, Group	Daily Gain 25 to 99 kg				
	Sire, Indiv.	Daily Gain 25 to 99 kg	Individual intake	Backfat		

CONCLUSIONS

The major limitation to developing effective selection programs is lack of phenotypic information on selection candidates for emerging traits of economic importance. Most obvious in current programs is the lack of observable information on meat quality traits. Meat quality is difficult to accurately assess on carcasses let alone live animals. A few applied breeding programs are utilizing carcass information from sibs or progeny. These programs are too costly relative to the amount of information generated and will be no more successful than the progeny programs used in the 1960s and 70s in an attempt to reduce carcass fat content prior to the development of ultrasonic technologies for accurately assessing fat in live animals. Similarly, information is needed on reproductive efficiency and longevity. However, phenotypic information is more readily available for these traits. What is needed are accurate and effective data recording systems to capture the information. Once the performance records exist, we have the technology to predict genetic merit and combine those predictions into appropriate selection criteria to maximize progress towards the selection objective. Of course, our ultimate limitation to developing long-term selection objectives is our cloudy view of the constraints and products of animal production beyond the next generation or two.

REFERENCES

- Amer, P.R. and Fox, G.C., (1992) *Anim. Prod.* **54**:341
Brascamp E. W., Smith C. and Guy D.R. (1985) *Anim. Prod.* **40**:175
Dickerson, G.E. (1970) *J. Anim. Sci.* **30**:849
Gibson, J.P. and Kennedy, B.W. (1990) *Theor. Appl. Genet.* **80**:801
Gunsett, F. C. (1984) *J. Anim. Sci.* **59**:1185
Hazel, L.N. (1943) *Genetics* **28**:476
Henderson, C. R. (1984) "Application of Linear Models in Animal Breeding. Univ. of Guelph
Hermesch, S. (1996) PhD Thesis, University of New England.
Kempthorne, O. and Nordskog, A. W. (1959) *Biometrics* **15**:10
Lofgren, D. L. and Stewart T. S. (1994) *J. Anim. Sci.* **72**:2254
McArthur, A.T.G. (1987) *6th AAABG* **6**:179
Melton, B.E. and Colette, W.A. (1993) *J. Anim. Sci.* **71**:579
Moav, R. (1973) In "Agricultural Genetics: Selected topics" p319, Wiley, New York
Newman, S. and Ponzoni, R.W. (1994) *5th WCGALP* **18**:217
Quinton, M., Smith C., and Goddard, M. (1992) *J. Anim. Sci.* **70**:1060
Smith, C., James, J. W., and Brascamp, G. L. (1986) *Anim. Prod.* **43**:545
Wilton, J. W. Evans, D. A and Van Vleck, L. D. (1968) *Biometrics* **24**:937
Wray, N., and Goddard, M. (1994) *Genet. Sel. Evol.* **26**:431

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