The Value of Phenotypes

Dorian Garrick
Department of Animal Sciences, Colorado State University, Fort Collins, CO 80523

Introduction

Most livestock breeders gain satisfaction from breeding, performance recording and selling seedstock animals. Not all livestock breeders rely on profits from the operation to support their lifestyle –for some it is a form of recreation. Such breeders may collect phenotypes simply for enjoyment and interest. However, the framework for this paper is limited to the business viewpoint of investing financial resources in the collection of phenotypes in order to achieve cost-effective genetic improvement. The approach that will be described applies to measurement of economically-relevant traits (e.g., carcass attributes), indicator traits (e.g., live animal ultrasound measures), on individuals of interest (e.g., potential sale bulls) or relatives (e.g., offspring in a progeny). In this context, characterization of DNA (or RNA) can mostly be considered in the same manner as a conventional phenotype.

Increasing Accuracy

In theory, collection of additional information cannot reduce the accuracy of evaluation. In this paper, accuracy is defined as the correlation between true and estimated genetic merit, rather than the related definition of accuracy used by BIF and routinely published on sire summaries. Some performance information will not contribute to an increase in accuracy. For example, information on characteristics that are not correlated to the trait or objective targeted for selection is of no value as is information collected in the absence of meaningful contemporaries. This can occur in several circumstances: when an animal has no contemporaries; or in the case of sires, when a contemporary group contains no offspring of other sires; or in threshold traits, when an entire contemporary group has the same observed score. Apart from these exceptions, collection of additional phenotypes provides an opportunity to *purchase* an increase in accuracy.

Increasing accuracy usually exhibits the phenomenon of diminishing returns – the higher the accuracy, the more expensive it is to achieve further increases. For example, in a progeny test, each additional progeny has a lesser impact on increasing accuracy, with accuracy approaching an asymptote of one.

Genetic Progress

Increasing accuracy does not in itself guarantee an increase in genetic progress. First, accuracy in relation to selection age must be considered. This will be further considered in following paragraphs. Provided selection is not delayed in order to collect more information and increase accuracy, gain will be increased if an objective basis is used for selection, whereby animals with highest index or EPD values are chosen as parents. It is important in practice that additional information is only used in the prediction of overall merit, and not also considered separately, as that practice can lead to reduced selection advance.

It must be recognized that a unit increase in accuracy will not, in livestock, typically lead to a unit increase in genetic gain per generation. This occurs because genetic gain is the result of more than just one pathway of selection. In the simplest selection scheme, gain depends upon the sum of genetic advance from selection of males to be sires and the selection advance of

females to be dams. In more realistic selection schemes, different strategies are used to select sires of sires than are used to select sires of dams and different strategies are used to select dams of sires compared to dams of dams. The influence on genetic gain of an increase in accuracy in one of these four pathways will be diluted by selection on the other three pathways. Furthermore, the benefit in terms of selection advance from an increase in accuracy will also depend upon the intensity of selection. It is the selection intensity in product with the accuracy that dictates the advance in any one pathway. Increasing accuracy will be more beneficial in paths with intense selection (e.g., sire pathways) than in paths with low selection intensity (e.g., dams to breed dams).

Accuracy can often be increased by delaying selection until more information on the individual of interest or its relatives is available. However, any increase in the average age of parents when offspring are born will erode the annual rate of genetic gain, unless the genetic advance per generation increases proportionately more than the generation intervals. For example, progeny testing can always be used to increase accuracy. The delay in waiting for progeny to be produced and measured is usually only beneficial in traits that have low heritability, are sex-limited, or can be measured with little impact on generation intervals.

Industry Structure

Increasing accuracy is seldom free, but may or may not be expensive. If increased accuracy results in faster genetic progress, then this should generate increased benefit. The value of benefit from genetic gain depends enormously on industry structure. In an unstructured industry, the benefit of genetic improvement might be limited to the increased performance of the herd subjected to selection. In the simplest two-tiered industry, the seedstock herd would incur the costs of collecting information,

and the so-called *commercial* herd(s) that use sires from the seedstock sector would represent the major beneficiary. The relative size, in terms of breeding females, of the commercial vs. seedstock sector dictates the number of phenotypic expressions that enjoy improved performance in relation to the number of individuals that incur measurement costs. An industry with 1% breeding females in the seedstock sector will get much greater relative benefit from gain than an industry with 10% breeding females in the seedstock sector.

Livestock industries often have more than two tiers. More commonly, a multiplier tier makes up most of the seedstock sector, the nucleus that drives genetic gain being a small component. This adds further complexity as the value of increased information is quite different in nucleus compared to multiplier herds. Nucleus herds include those that produce sires of sires, whereas multiplier herds use *outside* sires bred in other herds. This further complicates the formal consideration of valuing the collection of phenotypic information.

An appropriately-structured industry can afford to pay more to increase accuracy than a poorly-structured industry. However, industry structure is not easy to quantify, nor does it usually come about by design, except in some vertically-integrated industries. The structure of the beef industry is the collective result of selection decisions in every seedstock and commercial herd.

Example Calculation

The above principles can be quantified by considering some scenario and evaluating the costs and benefits from different levels of information collection. However, creating such an example is problematic because so many assumptions must be made. Accordingly, the interested reader really needs to seek professional help in such analysis in their own circumstances. Factors that will alter the

outcome include: aspects of the breeding scheme (current selection accuracy, generation intervals, selection pathways and annual genetic gain), the industry structure (seedstock, multiplier, commercial), and economic factors (costs of measurement, value of benefits, transfer of benefits). The following scenario concerning selection for increased marbling is therefore designed for illustrative purposes, rather than attempting to represent a definitive analysis.

Assumptions. The goal is to increase carcass marbling in a vertically-integrated beef production system. The seedstock tier consists of a closed nucleus of 1,000 breeding females. Bulls are made available to the commercial sector as yearlings, where they are used as terminal sires in an extensive ranching system for an average of 3 years at a mating ratio of 1:20. Suppose the calving percentage in product with survival to sale is 90%. Each bull therefore sires $3 \times 20 \times 0.9 = 54$ harvested offspring over its lifetime. Note that this number is very sensitive to the number of offspring produced by each sire over its lifetime. In an intensive natural mating situation, each bull might easily produce 200 rather than 60 conceptions.

Suppose a unit change in marbling score increases carcass value by $10/cwt. If average carcass weights were 700 lb, the value of a one unit change in bull marbling EPD would be $54 \times 7 \times 10 = \$3,780$. Note this figure would be different in self-replacing herds for two reasons. First, less offspring would be harvested as some heifers would be retained as replacements. Second, the cow herd would annually increase in merit for marbling such that harvested offspring would exhibit twice the rate of improvement that would occur in a terminal sire system.

The seedstock herd of 1,000 cows might produce 450 bull calves at weaning each year. Suppose 200 of these are used as sires in the commercial sector. On average one sire

produces $3,780 in additional carcass value (through a unit increase in marbling score) over its lifetime, therefore 200 bulls would generate $200 \times \$3,780 = \$756,000$ additional income per unit marbling. Assume these rewards are to be equally partitioned between the seedstock sector, cow-calf sector and feedlot/packer. This would generate added revenue of around $250,000 per unit marbling score for increased seedstock margin plus costs of phenotypic collection.

Suppose it costs $7 to measure carcass marbling and $20 to obtain parentage information in an outcross progeny test through a co-operating herd. It costs $25 to measure ultrasound IMF% in the seedstock herd as an indicator trait.

Suppose the bull breeding herd uses a team of 40 sires with just two pathways of selection. Bulls are used in the seedstock herd an average of two breeding seasons, with the best 20 bulls being selected each year from 450 available. This gives a selection proportion of $20/450 = 0.045$ with corresponding selection intensity of 2.1. The cows in the seedstock herd have an average generation interval of 5 years from a replacement rate of 20%, equivalent to a standardized selection differential of around 1.4. The bull generation interval will depend upon the selection strategy. In the case of ultrasound measures or genotypes, we will assume this could be achieved prior to mating the bulls as yearlings, so their first offspring would be born when the bulls are two yr old. If the bulls are used for two breeding seasons to provide good linkage across years, the average bull generation interval would be 2½ years. In the case of an outcross progeny test, yearling bulls would be used in an outside population, with offspring born when the bulls were two yr old. The bulls would be 3 yr old when the progeny test offspring were yearlings, and four yr old when the progeny test offspring had been harvested and the bulls ranked. The selected elite bulls would be five yr old when their first progeny were born in the bull breeding herd. If these

bulls are also used for two breeding seasons, the bull generation interval would be 5½ years.

Some possible selection scenarios are:

1. Measure carcass marbling on progeny test offspring of young bulls bred in the nucleus, prior to their selection in the bull breeding herd.
2. Measure ultrasound IMF% in all yearling males in the bull breeding herd.
3. Measure ultrasound IMF% in all offspring bred in the nucleus herd.
4. Genotype all young males in the bull breeding herd.
5. Genotype and measure IMF% on males in the bull breeding herd.

Many other possible scenarios are available, most notably two-stage options. For example, the first-stage might use ultrasound scanning on all bull calves and the second stage involve genotyping a subset of the bulls with the best EPDs predicted from the ultrasound data. Such two-stage scenarios will not be considered in this illustrative context.

Assume the heritability of carcass marbling is 0.54 and phenotypic and genetic s.d. are 0.88 and 0.65, respectively. The heritability of ultrasound IMF% is 0.50 and the genetic correlation with carcass marbling is 0.72.

Genetic Gain in the Various Scenarios. The annual rate of genetic gain can be computed from the following formula

$$\Delta G = \frac{(ir_{TI})_M + (ir_{TI})_F}{L_M + L_F} \sigma_g,$$

where *i* are selection intensities, r_{TI} are selection accuracies, *L* are generation intervals, *M* and *F* subscripts refer to male and female selection, and σ_g is the genetic standard deviation of the objective.

Scenario 1. The rates of gain with progeny testing of five offspring from every young bull for carcass marbling are

$$\Delta G = \frac{(2.1 \times 0.66)_M}{5.5 + 5} 0.65 = 0.09 \quad \text{marbling}$$

scores per year.

This gain increases to 0.11 or 0.13 scores per year when 20 or 100 offspring are measured per sire, demonstrating the diminishing returns from measuring additional offspring in a progeny test.

Scenario 2. The rates of gain using ultrasound measures on males alone are given by

$$\Delta G = \frac{(2.1 \times 0.5)_M}{2.5 + 5} 0.65 = 0.09 \quad \text{marbling}$$

scores per year. Although the selection accuracy is reduced, the reduction in generation interval results in the same response as can be achieved by progeny testing with five offspring per bull.

Scenario 3. Faster gain can be achieved by scanning bulls and heifers.

$$\Delta G = \frac{(2.1 \times 0.5)_M + (1.4 \times 0.5)_F}{2.5 + 5} 0.65 = 0.15$$

marbling scores per year.

Scenario 4. Genetic gain from DNA genotyping is sensitive to the proportion of genetic variation in marbling that can be accounted for by the markers. Given 10% variation accounted for by markers, the gains from bull selection alone would be

$$\Delta G = \frac{(2.1 \times \sqrt{0.1})_M}{2.5 + 5} 0.65 = 0.06 \quad \text{marbling}$$

scores per year. The gain increases to 0.08, 0.13 or 0.18 for 20%, 50% or 100% variation accounted for by markers.

Scenario 5. Markers that account for less than 100% genetic variation provide opportunities to increase accuracy by collecting phenotypic as well as genotypic information. Either ultrasound IMF% or carcass marbling phenotypes would improve accuracy. Using

ultrasound and DNA on bulls with 10, 20 or 50% variation accounted for by markers gives gains of 0.11, 0.12 or 0.14 marbling scores per year.

The benefits of genetic change for a single crop of bulls can be assessed by multiplying the industry improvement from one year of selection by the number of sale bulls times the number of harvested offspring per bull. For example, a one-third share of the benefits from the lifetime use of one crop of bulls given a gain of 0.1 marbling scores is worth some $25,000. However, genetic gain is permanent, so one round of selection would result in all successive crops of bulls being better by an average of 0.1 marbling scores. In practice, discounting procedures should be used to discount a stream of future returns and derive the net present value

of a particular selection scenario. Suppose we only value the benefit of say 5 successive crops of bulls, and ignore the discounting, the one-third share would be worth $125,000.

Now consider the costs of these selection strategies.

1. Progeny testing 450 bulls with n progeny per bull would cost $450 \times n \times (7+20) = \$12,150n$.
2. Ultrasound scanning 450 bulls would cost $450 \times 25 = \$11,250$.
3. Scanning bulls and heifers would cost $22,500.

We can therefore summarize the consequences of the above selection scenarios in the following table (Table 1).

Table 1. Summarization of genetic gain for various selection scenarios[1]

	Genetic gain	Share of revenue	Costs	Net[2]
Scenario 1				
PT *n*=5	0.09	$112,500	$60,750	$51,750
PT *n*=20	0.11	$137,500	$243,000	Loss
PT *n*=100	0.13	$162,500	$1,215,000	Loss
Scenario 2				
IMF% males	0.09	$112,500	$11,250	$101,250
Scenario 3				
IMF% both sexes	0.15	$187,500	$22,500	$165,000
Scenario 4				
DNA 10	0.06	$75,000	Note[3] 1	Note 1
DNA 20	0.08	$100,000	Note 2	Note 2
DNA 50	0.13	$162,500	Note 3	Note 3
DNA 100	0.18	$225,000	Note 4	Note 4
Scenario 5				
DNA 10 & IMF%	0.11	$137,500	+$11,250	+$51,250[2]
DNA 20 & IMF%	0.12	$150,000	+$11,250	+$38,750
DNA 50 & IMF%	0.14	$175,000	+$11,250	+$1,250

[1]*Scenario 1* = Progeny testing *n* offspring of young bulls.
Scenario 2 = Ultrasound IMF% measurements, all yearling males.
Scenario 3 = Ultrasound IMF% measurements, all offspring.
Scenario 4 = DNA genotyping given 10%, 20%, 50%, or 100% of variation accounted for by markers.
Scenario 5 = Ultrasound IMF% measurements in addition to DNA genotyping given 10%, 20%, or 50% of variation accounted for by markers.
[2]Net = Revenue DNA & IMF% – Revenue DNA – IMF% Costs (e.g., +$51,250 = 137,500 – 75,000 – 11,250).
[3]See comments in text below.

Given these various (often unrealistic) assumptions, progeny testing is not worthwhile unless sire parentage is already known or being collected for other purposes and not a cost to the improvement program. Ultrasound scanning of both sexes is well worthwhile.

Note 1. Genotyping using markers that account for 10% variation in marbling, without any phenotypic measurement is less profitable than ultrasound scanning. Measuring IMF% as well as markers would cost an additional $11,250 but bring in an additional $51,250 net of scanning costs. In order for DNA 10 and IMF% to be more profitable than IMF% on bulls alone, the genotyping could not cost more than $25,000 for the 450 bulls or $55 per bull.

Note 2. If DNA accounted for 20% variation in marbling, the test would have to be free to compete with the gains achievable from ultrasound scanning. Nevertheless, measuring ultrasound IMF% would still increase the value of gain, less scanning costs by almost $40,000.

Note 3. A DNA test with 50% variation accounted for was not more profitable than measuring IMF% in both sexes.

Note 4. Genotyping procedures that accounted for 100% variation and only involved measuring bulls could earn $60,000 more than measuring IMF% in both sexes if there were no genotyping costs. The breakeven DNA genotyping cost would be $133 per test, at which point the benefits were the same as ultrasound scanning.

Conclusion

The valuation of alternative scenarios in terms of phenotypes requires a number of assumptions. Investment in the collection of additional phenotypes typically increases accuracy of evaluation and resulting genetic gain. However, the impact on net returns and therefore the role of each scenario must be considered analytically. In general, measurements on the individual are preferable to measurements on progeny because of the time delay associated with progeny testing. Furthermore, conventional phenotypes are typically cost-effective for nucleus breeders even in the presence of good DNA-based tests.