PHYSIOLOGICAL BREEDING VALUES: RETHINKING THE WAY WE EXPRESS GENETIC VALUES FOR IMPROVING PRODUCTION SYSTEMS

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SUMMARY

Bio-economic simulation is the most promising technology for evaluating production systems. The genetic inputs to simulation models should satisfy two criteria: (1) they must indicate underlying genetic potential—genetic potential that is not compromised by the constraints commonly found in field data—and (2) they must measure traits that are logical inputs for mechanistic modeling. Physiological breeding values (PhBVs) are such inputs. They are the conceptual offspring of a marriage of statistical and biological approaches. Researchers need to develop methods for translating current genetic predictions to PhBVs, likely using an assortment of techniques, some purely statistical, some deterministic.

Keywords: breeding value, genetic prediction, production systems, simulation.

INTRODUCTION: A SLOBOVIAN CASE STUDY

The problem. You are an academic animal breeder, and you have been given the task of optimizing management and determining breeding objectives for CIC Inc., a large commercial beef cattle enterprise in Lower Slobovia. It is not a simple job. CIC's owners want you to examine a variety of crossbreeding systems, supplementation schemes, marketing alternatives, and other management options. And there is the question of what bulls to use. You will need to estimate typical production for each management scenario/biotype combination and calculate income, costs of production, and net returns. You must be careful to abide by constraints on available land, capital, and labor, steer clear of biotypes that are not well adapted in high-stress years, make sure that the production system is sustainable—for example, if you opt for larger cattle, you should avoid overgrazing by reducing herd size. The owners have high expectations of you and not a lot of time.

The solution. You need a tool and a powerful one. You need a bio-economic computer model that will simulate the many combinations of management scenarios and biotypes, allowing you, in effect, to co-optimize all these elements. Such models exist. Researchers have been working on them for years (Sanders and Cartwright 1979; Keele *et al.* 1992; Baker *et al.* 1992; Tess and Kolstad 1993; Williams and Jenkins 1996; Williams and Jenkins 1997). You review the literature, ask around, and choose a model that can simulate the kinds of systems you are interested in, has a reputation for sound biology, and is well documented and user friendly. The acronym for this particular model is BFBM (Big Friendly Beef Model), and it is state-of-the-art, the Cadillac of beef production models. It effectively simulates the influence of environment on forage quantity and quality and on animals' feed intake, energy partitioning, growth, body composition, lactation, fertility, and death loss. It can handle any and all cattle

biotypes and accounts for the effects of hybrid vigor. Besides being biologically sophisticated, BFBM is an individual animal model capable of simulating cattle populations with appropriate amounts of randomly generated genetic and environmental variation. It is just the model you need to determine the impact of specific sires on the CIC herd.

Using EPDs as genetic inputs. *Issue 1: traits.* One of your first tasks is to genetically characterize the existing CIC herd in order to establish a benchmark for future comparisons. Luckily, CIC has kept immaculate records over the years, and you have access to the EPDs of all sires and maternal grandsires of CIC cows. With a little arithmetic, you are able to build a genetic profile of the herd based on EPDs.

There is a problem, however. Some of the traits for which you have EPDs—traits like birth weight and mature weight—are listed as genetic inputs to the simulation model. But other traits are not. Where you have an EPD for the maternal component of weaning weight (measured in kg of weaning weight), the model asks for peak milk production potential (measured in kg of milk per day); where you have a prediction of fertility in the form of an EPD for stayability, the model wants a value for interval from calving to first heat and for probability of conception. The traits required by the model do not match the traits with available EPDs.

Issue 2: means. There is another problem with EPDs. EPDs (or, if you double them, EBVs) are expressed as deviations from means. They have values such as +5 and −14. The simulation model requires genetic potentials that have the appearance of phenotypic values, i.e., values that include a mean. An appropriate input value for mature weight would not be −18 kg, but rather 507 kg.

So, add a mean, you say. But what mean? Means vary for the different breeds because either the breeds are genetically different, their genetic bases or zero values are defined differently, or both. Luckily, Slobovian geneticists have created a breed table that allows you to locate the genetic bases used by Slobovian breed societies on a single scale. The Slobovian breed table also ties in nicely with a similar American table, making it possible to compare Slobovian bases with the bases from which most imported sires deviate. Now the problem is reduced to finding a single constant for each trait. Add these constants to breed adjusted EBVs, and you have the kind of genetic inputs needed by the simulation model. You can estimate the constants through a process of trial and error, inputting different sample values until the performance of simulated animals mirrors historical performance. The issue of means looks tractable.

Issue 3: G × G interactions. A more subtle problem. Some Slobovian breeds—the Slobovian White, for example—were once dual purpose breeds and milk heavily. Breeds like the Slobovian Red, on the other hand, were bred to be draft animals and produce little milk. Assuming both breeds are managed similarly, Slobovian Whites, on average, experience more lactation stress than Slobovian Reds, and are phenotypically less fertile as a result. The range of stayability EPDs is greater for Whites than Reds, and estimates of genetic variance and heritability of stayability are greater for Whites as well. But are Whites truly more genetically

variable than Reds for the underlying trait of fertility? Could it be that the stressful "environment" experienced by Whites causes them to express their potential for fertility to a degree that the less stressful environment experienced by Reds does not? Viewing the matter from a different perspective, does a 1-percent change in stayability EPD in Slobovian Whites indicate the same difference in underlying genetic potential for fertility as a 1-percent change in stayability EPD in Slobovian Reds? Are stayability EPDs for the two breeds expressed on the same scale? These questions are important because if you are to simulate crosses of Slobovian Reds and Whites and predict weaning performance of crossbred calves and production of crossbred daughters, you need comparable genetic inputs from both breeds.

From a statistical standpoint—that is to say, from a traditional animal breeding standpoint—the issue is one of genotype by genotype interaction. Differences in realized fertility between animals differing in genotype for fertility depend on their genotypes for milk production. When milk levels are low, almost all cows breed back; measurable differences in fertility between inherently highly fertile females and inherently lowly fertile females are likely to be small. But at high levels of milk production, these differences are larger. The potential interaction is depicted schematically in Figure 1(a).

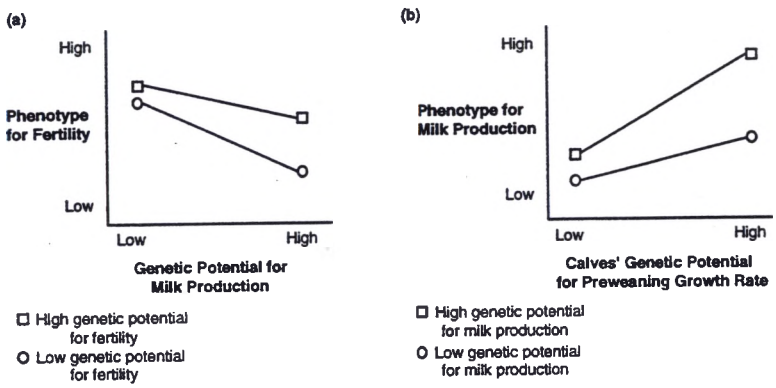

Figure 1. Schematic diagrams of potential $G \times G$ interactions affecting (a) fertility and (b) milk production.

A similar $G \times G$ interaction affects milk production. Differences in actual milk production between dams differing in genetic potential for milk production depend on their calves' genotypes for preweaning growth rate. When calves' potentials for growth rate are low, measurable differences in milk production between females with high genetic potential for milk production and females with low milk potential are small. But at high levels of calf growth potential, these differences are larger (Figure 1(b)). The $G \times G$ interaction affects the relationship between EPDs for the maternal component of weaning weight and underlying genetic potential for milk production. The relationship is stronger in breeds with high growth and low milk production and weaker in breeds with low growth and high milk production.

More importantly, a 1-kg difference in milk EPD in high growth, low milk breeds connotes a considerably smaller difference in true milk production potential than a 1-kg difference in EPD in low growth, high milk breeds (Enns 1995). Maternal EPDs for the two types of breeds are expressed on different scales.

Issue 4: $G \times E$ and $G \times G \times E$ interactions. And then there are genotype by environment interactions. You have worried about these for some time—ever since you read the paper by Frisch (1981). He suggested that the set of genes responsible for growth in a feedlot environment is different from the set of genes responsible for growth in a nutritionally stressful range environment. His work implied that the individuals that grow fastest in the feedlot do so because of their inherent propensity for growth, while those that grow fastest on range do so because of inherently low maintenance requirements or better genotypes for other adaptability traits. Because there are no feedlots in Lower Slobovia—young animals are grown out on grass—this particular $G \times E$ interaction concerns you. Will growth EPDs published in American sire summaries be useful indicators of growth under harsh Slobovian conditions?

The deeper you investigate, the more complex the interactions you discover. The magnitude of $G \times G$ interactions often depends on environment, creating $G \times G \times E$ interactions. Furthermore, these interactions involve only the transmittable portion of genetic potential. In simulating crossbreds, you must also be concerned with interactions involving hybrid vigor (HV). There are potential $G \times HV$, $G \times G \times HV$, and $G \times G \times HV \times E$ interactions, any of which can make prediction of phenotype more difficult.

The classical genetic model implies that a 1-unit change in genetic value results in a similar 1-unit change in phenotypic value. The model holds reasonably well when applied to a single population in a single environment. But mix genetically diverse populations and (or) place them in substantially different environments, and interactions cause the model to lose validity. A 1-unit change in a sire's EPD may result in considerably more or less than a 1-unit change in his offspring's performance.

Inevitably, $G \times G$, $G \times E$, and $G \times G \times E$ interactions and many of the interactions involving hybrid vigor are caused by the inability of animals to completely express their genetic potential for a trait. Sometimes the physical environment is limiting, as in the case of growth rate on range. Other times the physiological environment is limiting. Cows with little milk may not express their genetic potential for fertility. Cows with low-growth calves may not express their genetic potential for milk production. Whatever the constraint, the inability of animals to express genetic potential distorts the relationship between measures of breeding value—i.e., EPDs—and true genetic potential. This distortion causes EPDs from different populations to mean different things. And combining EPDs from different sources in a simulation model can be, in some cases, like mixing apples and oranges.

Why biological models require the genetic inputs they do. Good biological models are largely mechanistic, that is, they use equations designed to reflect fundamental biological

processes. For example, tissue growth is typically modeled as a function of energy intake, current body composition, physiological maturity, and associated requirements for maintenance, fat and lean growth, and so on. Sometimes, particularly when our understanding of a biological process is weak, these models rely on empirical relationships, often regression equations derived from one or more data sets. If a model is to be applied broadly, however, empirical relationships are risky; they work well under conditions similar to those of the original data sets but not so well under other conditions. Given a choice, modelers generally prefer mechanistic relationships.

For a mechanistic model, the only workable genetic inputs are those that represent an animal's genetic *potential*—its maximum performance given optimal conditions. The model begins with these values, then adjusts them downward (if necessary) to reflect the effects of a less than perfect environment. For the model to work correctly, its genetic inputs must have consistent, universal meaning. EPDs, of course, do not represent genetic potential in this sense because they are derived from populations in which certain genotypes never have the opportunity to achieve their potential, populations affected by the interactions mentioned earlier. And for the same reason, EPDs do not have universal meaning.

The idea behind a mechanistic model is to start with genetic potentials, add environmental conditions, and reconstruct via the deterministic equations of the model the biological relationships that cause differences in animal performance. If all works well, these differences will often form the patterns of data that, when analyzed statistically, are interpreted as interactions. We will have recreated something very similar to real data, and if our model is good enough—i.e., sufficiently correct and sufficiently mechanistic—we can recreate realistic data under a variety of genetic and environmental conditions.

The traits simulated in a mechanistic model are those that make mechanistic—as opposed to empirical—sense. From an empirical standpoint, a breeding value for the maternal component of weaning weight is the logical, and perhaps the only possible way of representing milking ability in beef cattle. But it is a totally illogical genetic input to a mechanistic model. The model requires direct information about a cow's potential to produce *milk*, not weaning weight. Similarly, stayability represents a convenient, statistical way of measuring female fertility, but would be cumbersome to deal with in a biological model. Better candidate traits from a mechanistic standpoint are age at puberty, interval from calving to first heat, and probability of conception.

Genetic inputs to biological models should, therefore, meet two conditions. First, they must represent underlying genetic potential—genetic potential that is not compromised by the constraints so commonly found in field data. Second, they must represent traits that are logical inputs for mechanistic modeling. Not all traits we measure are.

PHYSIOLOGICAL BREEDING VALUES

We coined the term physiological breeding value (PhBV) so that there would be a name for the kind of genetic input required by biological simulation models. "Physiological" suggests the

biological, mechanistic roots of such a value, and "breeding value" suggests its statistical counterpart. A PhBV is a lot like our conventional notion of breeding value; it represents the transmittable portion of an individual's underlying genetic potential for a trait. Like breeding values, PhBVs of relatives are correlated, PhBVs for different traits may be correlated as well, and the best prediction of the PhBV of a future offspring is the mean PhBV of its parents. What makes a PhBV different from a breeding value, however, is the way in which genetic potential is defined. In this context genetic potential refers to performance potential *under optimal conditions*. It indicates how an animal might perform if it were given every advantage. A calf's physiological breeding value for weaning weight, for example, is a predictor of its weaning weight if it had the best mother, nutrition, and all-around environment possible.

Unlike conventional breeding values, PhBVs are not population dependent. While an individual's breeding value for a trait depends on the genetic merit of the population that individual belongs to, its PhBV for the trait does not. An Angus cow, when considered a member of the American Angus population, might have a breeding value for mature weight of +46 kg. Considered a member of the Slobovian Angus population, the same cow might have a breeding value of +80 kg. But her physiological breeding value would remain the same—perhaps 590 kg—regardless of the population she belongs to.

PhBVs are also environment independent, that is to say, they do not change under different environmental conditions. As genetic potentials, they predict performance potential in just one environment—the optimal one.

PhBVs are, however, model dependent. Different biological models may define them differently. For example, in one model, PhBV for yearling weight may be defined as genetic potential for empty body weight at a year of age given a certain percentage of chemical fat in the empty body. In another model, the same PhBV may be defined similarly but without any constraint on body condition—i.e., in as fat a condition as possible.

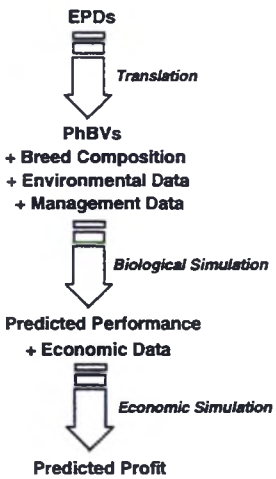

Figure 2. The bio-economic simulation process.

PhBVs alone do not indicate phenotype; they don't tell us how animals will perform in a given environment. But when they are combined with information about breed composition (for calculating hybrid vigor), physical environment, and management in a simulation, the simulation model translates them into performance measures. The entire process, from EPDs to profit prediction, is depicted in Figure 2.

FROM EPDS TO PHBVS

How difficult will it be to transform EPDs to physiological breeding values, to "map" EPDs to a physiological scale? Enns (1995) used the Colorado Beef Cattle Production Model (Bourdon

1992) to simulate 20 years of records from five 300-cow herds representing breeds with low (L), medium (M) or high (H) growth and milk potential (LL, MM, HH, HL, and LH, where the first letter refers to growth and the second to milk). From these five data sets he estimated genetic parameters and predicted within-breed EPDs using Method R and animal-model BLUP. He then developed regression equations to predict physiological breeding values—known values generated by the simulation model—from EPDs.

Results for yearling weight and milk production are shown in Figure 3. EPDs for the direct component of weaning weight (WW_d) from the five breeds mapped nicely to the physiological scale for yearling weight—the trait determining early growth potential in the simulation model (Figure 3(a)). Regardless of breed, a unit difference in EPD for WW_d translated into a nearly constant difference in physiological breeding value for yearling weight. That suggests that mapping EPDs for growth to a physiological scale is relatively straightforward.

The same may not be said for milk production. The mapping of EPDs for the maternal component of weaning weight (WW_m) to the physiological scale for theoretical peak milk production differed for each breed (Figure 3(b)). For example, a unit difference in EPD for WW_m in the HL breed indicated a much smaller difference in actual potential for milk production than did a unit difference in EPD in the LH breed. Maternal EPDs from the LH breed varied little, ranging from just -.6 to +.5 kg compared to a range of -24.1 to +18.6 kg in the HL breed. Developing good predictions of PhBVs for milk production, especially for breeds like the LH population, will be difficult.

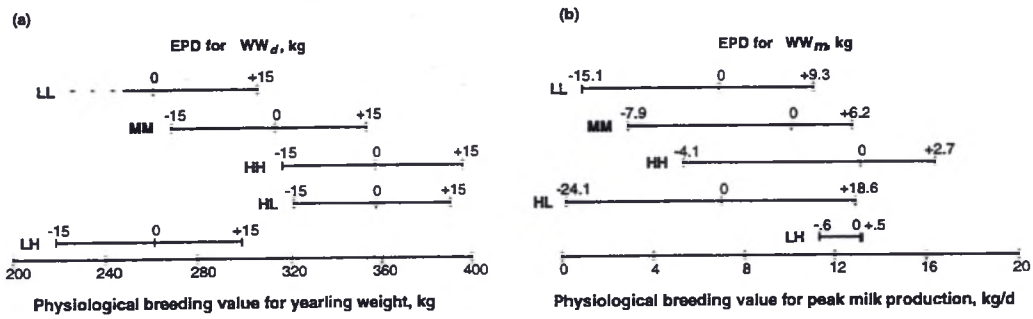

Figure 3. Physiological "map" of EPDs for (a) WW_d and (b) WW_m for five breeds representing different combinations of growth and milk potential. (Adapted from Enns 1995.)

The methodology for translating EPDs to PhBVs is yet to be developed and is a fertile area for future research. The kind of "reverse simulation" technique used by Enns (1995) is one alternative, though a far from perfect one. Purely statistical approaches may work too, especially if they combine purebred and crossbred data. Perhaps physiological maps will be

built much like chromosome maps, rough at first, more precise later as researchers combine information acquired using a variety of techniques.

Should PhBVs replace EPDs as the genetic predictions of choice to be published in sire summaries and sale catalogs? The advantage of PhBVs is their universality; they can be directly compared across breeds and environments. But PhBVs may be too easily confused with phenotypic values, and they may be defined differently depending on the particular model they are designed for. EPDs do not have the universal meaning of PhBVs, but they have the advantage of familiarity, and a unit change in EPD, at least on a within-breed, within-environment basis, does indicate a unit change in actual performance.

IMPLICATIONS

Quantitative geneticists have traditionally relied on statistical tools, particularly for genetic prediction and breeding program design. With the advent of biological simulation models, it may be time to combine statistical and mechanistic methods. Physiological breeding values, with their biological underpinnings and statistical properties, represent a marriage of the two approaches. But PhBVs are just the beginning. In the future, as we learn more about biological relationships, we may use deterministic equations to do many of the jobs that genetic and environmental correlations do now. We may use new tools to move beyond the limitations of the simple, linear genetic model.

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