AN ANIMAL BREEDERS VIEW OF UNDER-UTILIZED TOOLS TO IMPROVE FERTILITY IN BEEF HERDS

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Introduction

Fertility traits have generally been estimated to be lowly heritable, and consequently ignored by some cattle producers in the list of criteria to improve via genetic selection. However, genetic selection represents a cumulative and permanent means of changing phenotypic levels of performance and thus the return on investment can be substantial. Moreover, commercial cattle producers have the ability to exploit the advantages of non-additive genetic effects through the use of well-structured crossbreeding systems, and although not a "free lunch", heterosis has well-documented favorable impacts on female fertility. Although newer applications of technology such as lower-cost genotyping platforms for commercial animals and gene-editing offer opportunity to further enhance genetic changes for fertility, the largest industry-wide changes in beef cattle would arguably come from simply adopting the tools that have been readily available for decades. Although improvement in fertility can have a substantial economic impact for commercial cattle enterprises, it is critical to understand the profit drivers of the enterprise and to place emphasis on these key traits proportional to their economic value.

Foundational Principles

Identifying breeding objectives: A breeding objective is an objective list of traits that are economically relevant (Golden et al., 2000) to an enterprise. This should include traits that are directly related to a source of cost or a source of revenue. Consequently, to form a breeding objective there are key management questions that need to be answered including:

1) How do I intend to generate replacement females? If females are to be produced within-herd, then maternally expressed traits (e.g., female fertility, mature cow feed intake, maternal weaning weight, maternal calving ease) become important in making sire selection decisions. If replacements are to be purchased, then sire selection decisions can ignore maternal traits and focus on terminal traits (growth, carcass merit) exclusively.
2) How, and when, do I plan to market cattle? The sale point of terminal calves (i.e., weaning, after backgrounding, after the finishing phase) dictates the terminal traits that are most economically relevant for the enterprise.
3) Are there labor or environmental constraints? Labor, environmental, and land constraints become economic constraints. For example, additional labor to help during calving (when dystocia is of concern) is likely available but the cost may not be economically justifiable. Similarly, in environments where forage availability is limited, purchased feed can be acquired but the cost might not be worth the added performance of the cattle. Additional land resources, to support more cows or larger cows, is available as well but the purchase price might exceed any revenue the cattle enterprise could generate.

Once the three general questions above are answered, identification of economically relevant traits is possible. For the traits of economic importance, quantifying current levels of herd performance is important (e.g., Enns et al., 2006). For example, if current heifer pregnancy rates are exceptionally high, then there is less economic incentive to increase it relative to other traits in the breeding objective.

Breeding systems. Before selecting individuals (sires) within breed, producers must first select the breeds that they plan to use. Note breed is plural. There is no logic in commercial producers confining themselves to a singular breed and in the process forfeiting the benefits of heterosis and breed complementarity. There is a reason other industries adopted very well-structured crossing designs decades ago—it is profitable.

Unfortunately, objective breed differences for female fertility traits are not available either in published literature or from the U.S. Meat Animal Research Center (USMARC). However, to the extent that maternal weaning weight and mature cow weight impact environmental fitness and are useful to develop maternally focused breeding systems, producers can find contemporary breed differences (Kuehn and Thallman, 2020; Riberio et al., 2022). Importantly, producers should choose breeds that complement each other relative to the identified breeding objective. Defining a well-structured, and maintainable, crossbreeding program enables the continued exploitation of non-additive genetic effects to capture heterosis. For producers that produce their own female replacements this includes creating heifers that have a high-degree of retained heterozygosity to capture maternal heterosis. Heritability and the proportional benefit of heterosis are inversely related (Table 1) meaning that among the methods beef cattle producers have to improve fertility a well-structured crossbreeding system is critical. The impact of heterosis on female fertility traits (calving rate, sustained fertility) have been well documented (Tables 2-5) as summarized by Weaber (2021), with larger estimates coming from crosses between taurine and indicine animals. Although crossbreeding, and the benefits of it, have been promoted by academicians for decades it remains underutilized and this lack of adoption is a substantial competitive disadvantage to the beef industry.

For producers that purchase replacement females, sourcing females that are crossbred and come from a program that places selection pressure on female fertility and decreased mature weight makes sense. The purchasing of replacement females can aid female fertility in other, perhaps latent, ways. If the source of such females truly prioritizes “maternal” traits then it is likely that purchased females would have greater genetic values for such traits compared to those produced from a system that places selection emphasis across a much wider range of traits. Additionally, if replacement females can be purchased that are already bred with their 2^{nd} or later calf, re-breed rates should be higher overall.

Table 1. Summary of heritability and level of heterosis by trait type.[a]

Trait	Heritability	Level of Heterosis
Carcass/end product Skeletal measurements Mature weight	High	Low (0 to 5%)
Growth rate Birth weight Weaning weight Yearling weight Milk production	Medium	Medium (5 to 10%)
Maternal ability Reproduction Health Cow longevity Overall cow productivity	Low	High (10 to 30%)

[a]Adapted from Kress and MacNeil. 1999.

Table 2. Units and percentage of heterosis by trait for *Bos taurus* crossbred calves.

	Heterosis	
Trait	**Units**	**Percentage (%)**
Calving Rate, %	3.2	4.4
Survival to Weaning, %	1.4	1.9
Birth Weight, lb.	1.7	2.4
Weaning Weight, lb.	16.3	3.9
Yearling Weight, lb.	29.1	3.8
Average Daily Gain, lb./d	0.08	2.6

Table 3. Units and percentage of heterosis by trait for *Bos taurus* crossbred dams.

	Heterosis	
Trait	**Units**	**Percentage (%)**
Calving Rate, %	3.5	3.7
Survival to Weaning, %	0.8	1.5
Birth Weight, lb.	1.6	1.8
Weaning Weight, lb.	18.0	3.9
Longevity, years	1.36	16.2
Lifetime Productivity		
Number of Calves	.97	17.0
Cumulative Weaning Wt., lb.	600	25.3

Table 4. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred calves.[1]

Trait	Heterosis Units
Calving Rate, %[1]	4.3
Calving Assistance, %[1]	4.9
Calf Survival, %[1]	-1.4
Weaning Rate, %[1]	1.8
Birth Weight, lb. [1]	11.4
Weaning Weight, lb. [1]	78.5

[1]Adapted from Franke et al. 2005; numeric average of Angus-Brahman, Brahman-Charolais, and Brahman-Hereford heterosis estimates.

Table 5. Units and percentage of heterosis by trait for *Bos Taurus* by *Bos indicus* crossbred dams.[1,2]

Trait	Heterosis Units	Percentage (%)
Calving Rate, %[1]	15.4	--
Calving Assistance Rate, %[1]	-6.6	--
Calf Survival, %[1]	8.2	--
Weaning Rate, %[1]	20.8	--
Birth Weight, lb. [1]	-2.4	--
Weaning Weight, lb. [1]	3.2	--
Weaning Wt. per Cow Exposed, lb.[2]	91.7	31.6

[1]Adapted from Franke et al. 2005; numeric average of Angus-Brahman, Brahman-Charolais, and Brahman-Hereford heterosis estimates.
[2]Adapted from Franke et al. 2001.

Sire selection. Once a breeding system and breeds have been chosen, individuals within those populations (breeds) can be chosen. Perhaps not immediately intuitive, but sire selection drives progress made for all traits including those related to female fertility. Admittedly the list of fertility traits with available Expected Progeny Differences (EPD) is limited compared to other trait complexes (e.g., growth), but tools do exist. These traits vary among breed associations and are listed below as summarized by Spangler (2021).

- Scrotal Circumference (SC)—Scrotal circumference is another indicator trait. The EPD for this trait is used as an indicator for the fertility of a bull's progeny through his sons' scrotal circumference and his daughters' age at puberty. The Scrotal Circumference EPD is expressed in centimeters with a larger number being more desirable. SC EPD is of use only in situations in which male calves are retained as bulls. Given the availability of female fertility EPD, the utility of SC as a proxy for female fertility is diminished.

- Heifer Pregnancy (HP)—Heifer pregnancy is an ERT. Heifer Pregnancy EPD reports differences in the probability of bulls' daughters' ability to conceive and calve at two years of age. HP EPD is also reported as a percentage where a higher value indicates progeny with a higher probability of conceiving to calve at two years of age.

- Age at First Calf (AFC)—This trait is defined as the age of a female when she has her first calf. A lower value is more desirable. Differences between sires' EPD reflect differences in the average age at which their daughters will have their first calf.

- Stayability (STAY)—Stayability, also called Sustained Cow Fertility (SCF), reflects the longevity of a bull's daughters in the cow herd. This EPD predicts differences in the probability of bulls' daughters having additional calves during their lifetime or remaining in the herd through extended ages.

Admittedly there is room for improvement in fertility traits with EPD, both in availability among breed associations and in trait definitions. Part of the underlying issue is data availability in the seedstock sector. The development of EPD rely on phenotypic records, and if beef breed associations do not capture relevant phenotypes, or if seedstock producers do not record or submit them, EPD cannot be developed. Snelling et al. (2019) reported genetic parameter estimates for cumulative weight weaned using a random regression model as a suggestion for a new cumulative measure of female productivity. Such a trait relies on data that would be routinely recorded currently, namely unadjusted weaning weight of calves and cow age, and accounts for genetic differences in sustained fertility over time and for the ability to conceive earlier in the breeding season. The fact that a random regression model was used means that published EPD could be projected to any cow age within the range of available data.

Female fertility traits have generally been estimated to by lowly heritable ($h^2 <0.20$; Koots et al., 1994). However, this does not mean that genetic gain, and ultimately phenotypic changes, cannot be achieved for these traits. To understand why this is true first requires a high-level understanding of what heritability is and how it is estimated. Most would recognize heritability as the fraction of phenotypic variation that can be explained by additive genetic variation (narrow sense heritability; additive genetic variance divided by phenotypic variance). This leads to a common misbelief that management factors that contribute to overall phenotypic variance must explain more variation than do additive genetic effects. This is not necessarily true. Commonly, heritability is estimated from models that include contemporary group (as a fixed effect) and covariates, as appropriate, for age, weight, breed proportions, and retained heterozygosity. Consequently, the phenotypes are adjusted for these effects and the heritability estimate is simply the additive genetic variance divided by the sum of the additive genetic variation and the residual variation (think of it as an adjusted phenotypic variance). Low heritability does not necessarily mean that the amount of additive genetic variation is small but rather that the amount of additive genetic variation in relation to the residual variance, or the variation in phenotype that cannot be explained by the model, is small. Generally, the contemporary group effect would be relatively large but it is important to keep in mind that a contemporary group is the concatenation of several factors. Contemporary groups are defined as animals given an equal opportunity to perform, or in the case of fertility and equal opportunity to conceive. A reasonable grouping would include herd-year of birth-breeding pasture. The contemporary group effect then includes the main effect of each of these factors and all interactions (2-way and 3-way in this example). There is obviously considerable year-to-year variation and variation in forage availability and quality among breeding pastures. The point being that although heritability is low, considerable genetic variation in female fertility does exist and can be exploited. Furthermore, there is considerable residual variation meaning that there are environmental effects acting on fertility that we do not observe.

The accuracy associated with EPD increase as more data is acquired, and for lowly heritable traits the accumulation of accuracy can take a long time. However, with the inclusion of genomic data in the calculation of EPD accuracy can increase much faster for non-parent animals than during the pre-genomic period. This should enable faster rates of genetic gain given accuracy increases and the average age of parents (in seedstock herds) should decrease, two key components of the breeders' equation that determines the rate of genetic gain. This also means that commercial bull (or semen) buyers should observe more differentiation among candidate sires for numerous traits and can buy bulls with greater confidence. A more tangible way to think of this increase is in terms of progeny equivalents. A progeny equivalent value is the number of offspring a parent would need to have to equate to the same level of accuracy as if they were genotyped and did not have offspring. An example of progeny equivalents for female fertility traits comes from International Genetic Solutions (IGS) who estimates that genotyping a non-parent animal is equivalent to that animal having 15 daughter records for stayability.

Despite the importance of female fertility to commercial breeding programs, it is not the only trait that impacts profitability. Simultaneous selection for a multitude of traits is need to advance a breeding objective. The most efficient method of selecting for multiple traits simultaneously is a selection index. The notion of economic selection indexes is far from new (Hazel, 1943), but still largely underutilized in beef cattle selection. The majority of U.S. beef breeds that conduct a genetic evaluation publish one or more economic selection indexes. Key to the use of these tools is to use an index that best matches the defined breeding objective. For example, if a producer retains replacement females then an index that is completely terminal (i.e., does not contain EPD for maternal traits) would be a mistake. Given each enterprise has unique circumstances, some enterprises may wish for greater customization in the index used to select sires or semen. Spangler et al. (2022) describe a web-based decision aid (iGENDEC) that enables user input to construct economically optimal selection indexes. The iGENDEC software is currently hosted by the Beef Improvement Federation to enable industry-wide access for a fee to support routine maintenance and server capacity.

A unique feature of iGENDEC is the opportunity to define a planning horizon. The planning horizon (PH) assumed by an enterprise represents a complex decision that requires consideration of breeding objectives and the need for revenue at alternative points in the future. Philosophically, planning horizon can be thought of as the length of time (years) that the producer wants to consider in determining the economic impact of a genetic selection decision. Using simulation to create a large cowherd that expresses the traits in the breeding objective, as is commonly done in developing selection indexes, PH represents the number of years simulated with the improved genetic merit of bulls. Consequently, PH impacts the number of expressions of traits and thus their economic impact. Valasek et al. (2022) investigated the impact of changing PH when constructing indexes that assumed replacement females were retained and when the sale endpoint was either at weaning or finished animals sold on a carcass basis. Overall the authors noted that as PH increased, the relative emphasis on the sale weight decreased and the relative emphasis on Stayability increased. The authors applied the indexes to a group of approximately 27,000 bulls and quantified the degree of re-ranking due to changes in the PH assumed when constructing the index. The average rank correlation coefficients between indexes with different endpoints was 0.71 (± 0.12) when averaged over different breeding systems and PH lengths. When indexes assumed a finish endpoint, substantial re-ranking (r=0.78 ± 0.09) was observed between the short PH (2, 5, and 10 yrs.) and the longer PH (20, 30, and 50 yrs.). Taken together this illustrates two important points: 1) Aligning the selection index used and the breeding objective an enterprise has is important as illustrated by the re-ranking that would occur if an index that assumed weaned calves were marketed was used to actually produce fed cattle, and 2) Selection to increasing profit in the short-term places more emphasis on sale weights and less emphasis on sustained cow productivity, potentially marginalizing longer-term profitability.

Female Selection. An interestingly common question relates to how best select commercial replacement females. Understandably some selection needs to occur given, hopefully, not all heifers born are needed to replace the mature herd. However, this is an interesting point for an industry to spend considerable time and resources given the limited impact commercial level females have as compared to seedstock parents, particularly sires, and even commercial bulls. In general, there are 3 tiers to think about selecting commercial replacements females as described below.

Tier 1: Select those that are born the earliest in the calving season. There is support for this from the literature (e.g., Cushman et al., 2013; Funston et al., 2012) to promote increased sustained cow fertility. If birth dates are recorded, it also represents the least expensive method.

Tier 2: Select replacements from elite sires. These could be AI sires or natural service sires with higher (maternal) index values. This can be done either through genotyping to confirm paternity or through the use of sexed semen. Note pooled sexed semen with a mixture of terminal and maternally oriented bulls coupled with paternity testing could be an option.

Tier 3: Diagnostic genotyping panels. This represents a higher-cost option, and should only be contemplated if breeding system design and sire selection are well implemented. The economic benefits of breeding system design and sire selection far outweigh the choice of keeping or culling a small fraction of commercial heifers based on additive genetic merit. If genotyping commercial females is conducted , it is important to test all candidate replacement heifers, not just the ones you already decided to keep. It is also critical to ensure that the panel used was designed for the breed composition of the herd it will be used in. There is an abundance of published research that shows SNP effects are sensitive to relationships between the training and target populations, and an extreme example is using a test designed for Angus in Hereford animals where results are expected to be poor and there is evidence that genetic marker effects are not transferable among closely related breeds such as Angus and Red Angus (Kachman et al., 2013). Finally, clearly determining the potential return on investment is important.

Summary

Despite the availability of tools and strategies to genetically improve female fertility and enterprise level (and system wide) profitability the commercial beef industry has elected to largely dismiss them. It is beyond contestation that crossbreeding and within-population selection using EPD work. Newer tools, such as gene editing and exploiting epigenetic variation are indeed exciting. However, their impact is additive relative to currently available tools and methods. In other words, the full benefit of newer technologies will not be captured until breeding systems and sire selection decisions are optimized.

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