

Combined Selection for the Beef Cattle Industry

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Introduction

The production of beef cattle can be categorized by operations that breed purebred cattle, and operations that produce crossbred cattle. Less than 5% of beef cows are used to produce seedstock bulls (Garrick and Golden, 2008), with that small fraction of the industry typically consisting of registered purebred cattle. Product quality and efficiency of commercial crossbred herds can be improved through selection and use of high merit purebred stock in designed crossbreeding systems. Traditionally, performance data used in genetic evaluation programs has been collected in purebred herds on potential selection candidates (Garrick and Golden, 2008). Therefore purebred selection becomes extremely important for the long-term success of crossbred herds (Dunn et al., 1970), especially when such a small proportion of producers are developing the purebred genetics.

Commercial herds typically use crossbreeding to capitalize on the benefits that heterosis and breed complementarity offer (Cundiff, 1970). Comstock (1960) suggested that if the majority of livestock produced are crossbred, performance information on those animals should be considered in the selection of their purebred sires. With the predominance of crossbreeding in beef cattle, large amounts of information could be made available for this purpose.

The question becomes, “Are we better served in utilizing purebred information alone, or a combination of purebred and crossbred information, in our genetic evaluation programs?” If our breeding goal is to optimize crossbred performance this question becomes even more relevant (Wei and van der Werf, 1994). Since the backbone of beef cattle production is the crossbred herd, defining the aim of beef breeding programs in terms of crossbred performance would seem sensible. At present, only limited amounts of crossbred information are being utilized in formal genetic evaluation programs. The focus of this review is to consider the potential

benefits and drawbacks of formally incorporating crossbred performance data into genetic evaluations of their purebred parents.

Review of Literature

Crossbred Selection

Two methods in achieving crossbred improvement for a given trait have been established (Wei and van der Werf, 1994). The first method, pure line selection (**PLS**), utilizes data from purebred animals and their relatives within a population. The implementation of PLS takes several forms: mass selection, family selection typically utilizing an index, or best linear unbiased prediction (**BLUP**) (Wei and van der Steen, 1991). The extent of crossbred improvement depends on a correlated response to the selection in the purebred.

The second method, reciprocal recurrent selection (**RRS**), was established by Comstock et al. (1949). It is based on comparing the performance of crossbred progeny based on the combining ability of different purebred parental stocks. The selection of purebred animals to use in producing crossbreds is based on comparing reciprocal crosses of different pairs of breeds (Wei and van der Steen, 1991).

Combined crossbred purebred selection (**CCPS**), which merges the performance information of purebred animals with that of their crossbred relatives, was proposed by Wei and van der Steen (1991). The use of CCPS involves evaluating phenotypic measurements for a given trait, collected in purebreds and their crossbred relatives, as separate yet genetically correlated traits (Wei and van der Werf, 1994; Jiang and Groen, 1999). The genetic correlation reveals the strength and direction of the relationship between breeding values for the two defined traits. The effectiveness of CCPS depends on family structure, the selection procedures employed, and the heritabilities and genetic correlations among the traits considered (Jiang and Groen, 1999).

In swine and poultry production, large amounts of crossbred data are available to supplement genetic evaluations. In operations that already utilize structured crossbreeding and collect performance records as their norm, CCPS can easily be implemented (Wei and van der Werf, 1994). Utilizing information on crossbred

performance contributes to genetic gain in purebreds by increasing selection accuracy (Jiang and Groen, 1999). Even when the amount of crossbred information is limited, CCPS still proves effective when purebred sires themselves have few purebred progeny (Bijma and van Arendonk, 1998). Genetic gains in poultry can be increased especially when a higher number of crossbred progeny are tested per purebred female (Jiang and Groen, 1999). Since poultry and pigs have much larger family sizes, unsurprisingly CCPS were first introduced into these species.

An example of CCPS from Bijma et al. (2001) involves a three-way crossbreeding system. Sires from a sire line are either mated to dams from that sire line, or to dams from the first cross (F_1) of two dams lines. In that instance, sires from the sire line produce two types of offspring: purebred offspring within the sire line, which are the selection candidates for the next generation, and commercial crossbred offspring which provide information on crossbred performance.

In illustrating CCPS, a selection index based on the theory of Hazel (1943) was developed involving the following sources of information: crossbred paternal half-sib family mean (X_1), purebred paternal half-sib family mean including the animal to be selected and its full-sibs (X_2), purebred full-sib family mean including the animal to be selected (X_3), and the animals' own performance (X_4) (Wei and van der Werf, 1994). The phenotypic information on the crossbred half-sibs of the selection candidate makes CCPS unique (Wei and van der Werf, 1994). Three selection indices were proposed:

$$I_{CCPS} = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$$

$$I_{PLS} = b_2X_2 + b_3X_3 + b_4X_4$$

$$I_{CS} = b_1X_1$$

where CS refers to an index based on crossbred information alone.

The purpose of each index was to predict the breeding value of an animal for crossbred performance. First, I_{CCPS} combines information on purebred and crossbred animals to derive the most accurate and comprehensive prediction of breeding value. Second, I_{PLS} includes only purebred information and predicts crossbred performance accurately only when closely related to purebred performance. Third, I_{CS} effectively predicts crossbred breeding value when purebred and crossbred performance is

unrelated, but suffers from low selection intensity due to correlated selection indices within half-sib families (Wei and van der Werf, 1994).

Three crucial population parameters in CCPS include: the genetic correlation between purebred and crossbred performance (r_{pc}), the purebred heritability (h_p^2), and the crossbred heritability (h_c^2). The correlated genetic response expected in the crossbred when selection is practiced in the purebred is defined by r_{pc} (Wei and van der Steen, 1991; Wei and van der Werf., 1995; Besbes and Gibson, 1999). The ratio of additive genetic to total phenotypic variance revealed by h_c^2 is an important factor in optimizing selection using crossbred information (Wei and van der Werf, 1994).

When estimating breeding values for the purebred selection candidates, the information on their crossbred half-sibs can be included in the EBV, which results in a higher accuracy of selection. The construction of these mixed model equations, using BLUP technology, to estimate genetic parameters and breeding values has been demonstrated for CCPS (Wei and van der Werf, 1994; Lo et al., 1997; Spilke et al., 1998).

Genetic Correlation

The r_{pc} is calculated from variances of purebred and crossbred half-sib means and the covariance between them, assuming infinite group sizes (Wei et al., 1991b). The r_{pc} is used to determine weights for the sources of information to be included in CCPS where selection decisions are based on an index (Wei and van der Werf, 1994). Using a two-locus model, r_{pc} was shown to be a function of dominance effects and the difference in gene frequency between parental populations (Wei et al., 1991b). In the case that no dominance effect exists and gene frequencies in parental populations are equal, then r_{pc} equals one. When dominance exists r_{pc} is always positive, but may become negative with overdominance. High positive r_{pc} was associated with a high additive genetic variance, and low r_{pc} with a high non-additive genetic variance (Wei et al., 1991b). In general, r_{pc} decreases when degree of dominance increases (Wei et al., 1991b). Although such studies prove useful in describing the characteristics of parameters at the gene level, in production agriculture most traits of economic

importance involve polygenic gene action with unknown dominance effects and initial gene frequencies.

The benefit of crossbred information increases rapidly when r_{pc} decreases because selection in purebred animals becomes less effective in achieving crossbred genetic gains (Bijma and van Arendonk, 1998). Even when r_{pc} is near unity, crossbred information still proves useful, especially in traits with low heritability due to the additional information on siblings it provides. With low r_{pc} and a breeding objective aimed at crossbred performance, performance information on purebreds is still useful to help differentiate genetic merit among full-sib sires. Typically r_{pc} is estimated more accurately from families of sires as compared to dams, since sires produce a larger number of progeny (Besbes and Gibson, 1999). The optimum number of sires to evaluate as selection candidates increases with lower r_{pc} (Bijma and van Arendonk, 1998).

In swine, r_{pc} estimates between two purebred lines (Landrace, Large White) and their reciprocal crossbred offspring were 0.99 and 0.62 for lifetime daily gain, and 0.32 and 0.70 for backfat (Lutaaya et al., 2001). The departure of these genetic correlations from unity could be attributed to dominance effects and (or) to differences in management between purebred and crossbred lines. Estimates of r_{pc} between purebred Duroc sires and their cross to two different breeds were 0.83 and 0.89 for backfat, 0.78 and 0.80 for muscle depth, 0.53 and 0.80 for body weight, and 0.60 and 0.79 for weight per day of age (Zumbach et al., 2007). The estimates of r_{pc} were generally higher for carcass traits than weight traits, even though carcass measurements on purebreds were ultrasonic based while those on crossbreds were actually measured on carcasses. Feeding regimens were the same in the purebred and crossbred lines, although production environments (housing) differed. Zumbach et al. (2007) explains that low genetic correlations could be attributed to non-additive gene combination effects and genotype by environment interactions.

The investigation of r_{pc} in Herefords, Angus and their crosses included ranges of 0.88 to 0.97 for birth weight, 0.55 to 0.94 for weaning weight, and 0.68 to 0.86 for yearling weight (Nunez-Dominguez et al., 1993). Newman et al. (2002) reported r_{pc} in Australian cattle of 0.48 for 400-day weight, 0.48 for carcass weight, 0.83 for

percentage of retail beef yield, 0.95 for percentage of intramuscular fat, 1.0 for subcutaneous rump fat thickness, and 0.78 for pre-slaughter scanned eye muscle. Results of these studies suggest that sire re-ranking may occur when bulls are evaluated based on purebred progeny performance, but not crossbred progeny performance for weight traits and eye muscle area. Evaluating sires only on purebred progeny performance is likely acceptable for rump fat and intramuscular fat.

In analyzing egg production traits, estimates of r_{pc} ranged from 0.56 to 0.73 for egg number, 0.69 to 0.99 for egg weight, and 0.72 to 0.82 for egg specific gravity (Wei and van der Werf, 1995). The departure in unity of these estimates suggests CCPS could be useful in making genetic progress within layer operations.

Heritability

Purebred heritability is the ratio of additive genetic variance to total phenotypic variance. Factors that cause the ratio to be below one include dominance, epistatic and environmental variances, and maternal effects. Crossbred heritability is related to the amount of genetic variation among purebreds for crossbred performance. In a one-locus model Wei et al. (1991a) reported that h_c^2 is not a linear function of the heritabilities in parental lines (h_p^2) if dominance exists, and should be estimated separately for different lines and their crosses. The same study concluded that h_p^2 (or sire component of variance in purebreds) is different from h_c^2 (or sire component in crossbreds) due to larger dominance effects and (or) large gene frequency differences in parental populations. When a crossbred trait is of lower h_c^2 it is more difficult to change genetically (Wei and van der Werf, 1995). Even so, CCPS remains valuable, particularly when h_p^2 and r_{pc} for the trait of interest is low (Bijma et al., 2001).

When fitting both an animal and sire-dam model, the h_c^2 was higher than h_p^2 for egg number, egg weight and shell strength (Besbes and Gibson, 1999). This is generally explained by dominance variance increasing relative to additive variance in h_c^2 as compared to h_p^2 . In a separate poultry study that considered egg number, egg weight and egg specific gravity, estimates of h_c^2 were lower than h_p^2 (Wei and van der

Werf, 1995). These comparatively lower h_c^2 could be partially explained by a more variable housing environment for the crossbred hens.

Estimates of h_p^2 and h_c^2 for swine growth, gain and carcass traits were of similar ranges of magnitude in purebreds and crossbreds, with the exception of 21-day weight where h_p^2 was significantly higher (McLaren et al., 1985). Heritability estimates for lifetime daily gain and backfat of two purebred lines of swine and their reciprocal cross were very similar (Lutaaya et al., 2001). In a cattle study conducted by Newman et al. (2002) h_c^2 was higher than h_p^2 for weight traits. However, this relationship was reversed when considering carcass traits.

The average heritabilities within two pure Duroc lines (h_p^2) and their resulting crossbred (h_c^2), when mated to a Large White x Landrace dam line, were respectively 0.37 and 0.32 for backfat, 0.27 and 0.16 for muscle depth, 0.26 and 0.17 for body weight, and 0.27 and 0.18 for weight per day of age (Zumbach et al., 2007). Heritability estimates in these purebreds were consistently larger than in their crossbred counterparts possibly due to more variable production environment among the crossbreds.

Evaluations of CCPS

The value of CCPS relative to PLS has been considered both through simulation and experimentation. From a simulation, Bijma and van Arendonk (1998) demonstrated that for r_{pc} of 0.4, maximum response under CCPS was approximately twice that under PLS. In a separate study, CCPS offered a 22% increase in response compared to PLS on a phenotypic standard deviation basis (Dekkers, 2007). When evaluating combined improvement in crossbred and purebred performance of broilers, Jiang and Groen (1999) noted that there was no significant genetic improvement resulting from CCPS when r_{pc} was 0.7 or higher.

When assuming that h_p^2 equaled h_c^2 , and with r_{pc} of 0.7, CCPS yielded a 4.8% greater crossbred genetic response than PLS (Wei and van der Werf, 1994). Moreover, when r_{pc} was decreased to 0.5, CCPS yielded 23.6% greater crossbred response than PLS. As r_{pc} approached zero, PLS proved ineffective. Nonetheless PLS resulted in a

higher crossbred response when r_{pc} equaled one due to a shorter generation interval. Purebred information always increases selection accuracy when r_{pc} is large. The benefit of crossbred performance information is only limited if r_{pc} is large and many purebred performance records exist. In cases of fixed numbers of purebred records, then CCPS is superior to PLS.

With stochastic simulation, CCPS was clearly superior to PLS when the trait of interest is controlled by loci with full dominance or overdominance. However, when loci were partially dominant, PLS was adequate (Uimari and Gibson, 1998). The effectiveness of CCPS versus PLS depends primarily on degree of dominance, rather than initial differences in allele frequencies between lines (Uimari and Gibson, 1998).

In an experimental program, purebred breeding values were predicted in swine fitting either a purebred or crossbred model, the latter including both purebred and crossbred observations, to assess differences in reliability of estimates (Lutaaya et al., 2002). The crossbred model was not justified when primary interest was in the evaluation of purebred animals, especially when the number of crossbreds was small relative to purebreds. This was due to modest changes in accuracy of prediction and very high rank correlations (Lutaaya et al., 2002). However, the crossbred model was useful when evaluation of both populations was important, and when crossbred records were more numerous than purebred records with some traits primarily measured on crossbreds. The latter can certainly be the case for many carcass traits.

Challenges and Opportunities

Drawbacks to implementing CCPS in the form of a selection index include selecting animals on an individual basis and only optimizing crossing systems for one future generation, not a more extended period (Li et al., 2006). The application of CCPS has been limited to date, due to the responsibility of commercial producers to maintain pedigree records tying their animals to purebred parents (Dekkers, 2007). Such management restrictions are also apparent in simply recording animal performance at the purebred, commercial and harvest levels (Bijma and van Arendonk,

1998). Alternatively, Wei and van der Werf (1995) suggest the vast volumes of commercial information can be obtained relatively cheap as a tool for selection.

Should genotype by environment interactions exist due to differences in production environment (housing) of the purebred compared to the crossbred, it would be confounded in r_{pc} (Wei and van der Werf, 1994; Uimari and Gibson, 1998). This would be indistinguishable from the non-additive genetic defects contributing to the decreased correlation coefficient (Wei and van der Werf, 1994). This confounding would not need to be distinguished as long as crossbred performance is measured in the same environment for which the breeding goal is defined (Wei and van der Werf, 1995).

Another measure to evaluate CCPS is the ratio of dominance variance to total genetic variance (Uimari and Gibson, 1998). If this ratio exceeds 0.3, then CCPS is more effective than PLS since the trait exhibits a high degree of dominance and the additive effect is unpredictable when comparing purebred and crossbred performance (Uimari and Gibson, 1998). Calculating such dominance variances for egg production traits in three purebred lines of poultry layers, with an animal dominance model, was shown to decrease bias in heritability estimates (Wei and van der Werf, 1994). Still, in most cases r_{pc} is a more useful indicator in determining what information is utilized than the dominance variance (Besbes and Gibson, 1999).

Combined crossbred purebred selection has been compared with pure line selection, evaluated on the basis of genetic gain at constrained levels of inbreeding (Bijma et al., 2001). At fixed levels of inbreeding CCPS is superior to PLS, although in most cases CCPS increases the level of inbreeding due to the dependency on family information for selection (Bijma et al., 2001). Incorporating marker assisted selection with CCPS should deliver optimal selection response, while minimizing CCPS inbreeding effects by revealing mendelian sampling differences between full-sib families (Dekker, 2007).

DNA technology offers advantages over traditional identification methods by maintaining the association of phenotypes, such as carcass measures, with animal records (Heaton et al., 2002). Based on the promise of DNA parentage verification to identify paternity (Heaton et al., 2002; Van Eenennaam et al., 2007), genetic

improvement can be fostered by collecting crossbred phenotypes of economically relevant traits in herds that utilize multiple-sire pasture arrangements.

Conclusions and Implications to Beef Cattle Genetic Improvement

The structure of genetic evaluation in the beef cattle industry analyzes animals, typically purebreds, which make up a very small proportion of the total beef cow population. Traits included in these analyses such as ribeye area, marbling and backfat are usually measured indirectly in purebreds through the use of ultrasound. Improving lowly heritable traits such as calving ease and calving interval involves collecting large numbers of accurately measured records. In addressing such challenges, the opportunity exists to garner large amounts of directly measured performance data, if economically feasible, from the crossbred and commercial beef cattle population. Currently, adoption of CCPS has not been widespread in the beef cattle industry. Advances in DNA technology could stimulate the maintenance of pedigree relationships in large commercial and crossbred operations. This would aid in jointly analyzing purebred and crossbred information, facilitating selection decisions directed toward improving commercial herds. The increased selection accuracy garnered from additional phenotypic records could encourage producers to collect performance measurements. Any genetic improvement CCPS could provide would need to be compared with the cost of time and labor to implement it.

The practice of CCPS offers clear benefits when genetic improvement of crossbred livestock is desired. Utilizing different forms of CCPS selection indices could allow relative economic values and sources of phenotypic information to be weighted according to the optimal production desired by producers. The application of CCPS is likely best achieved through the analysis of training data sets in large crossbred herds with complete pedigree relationships and accurate collection of performance measurements for economically relevant traits.

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