STRATEGIES AND PROBLEMS RELATIVE TO GENETIC IMPROVEMENT IN A MULTIBREED POPULATION

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SUMMARY

The importance of crossbreds in commercial beef production has increased. Consequently, genetic improvement in crossbred performance is of concern to producers and breeders. In current beef cattle breeding programs, genetic improvement is carried out mainly by selection within breed. The genetic correlation between purebred and crossbred performance (r_{pc}) may be less than one and within-breed selection may not be optimal for crossbred improvement. In current beef production, two alternative breeding goals can be considered, i.e., the improvement of 'general combining ability' across breeds and genetic improvement for specific types of crossbreds. To improve 'general combining ability', breed and heterosis effects have to be accounted for in evaluation models, and crossbred information can be used. However, methods to properly account for heterosis effects are not available. Also, the breeding goal should be specific to the type of crossbred, and an approach to achieve genetic progress in specific types of crossbreds is discussed. By this approach, the value of a purebred animal should be determined by both its purebred and crossbred progeny performance. The breeding scheme has to be designed in such a way that both purebred and crossbred information can be collected and properly weighed in a genetic evaluation model. Rotational and terminal crossing systems are two alternatives assuming that mating within breeds is always needed to maintain purebred populations. An evaluation method was discussed for a terminal crossing scheme to achieve optimal crossbred improvement. For a rotational cross, a proper evaluation method has yet to be established. Application of either crossbreeding scheme may result in decreasing the number of breeds, i.e., less efficient breeds in the production system will gradually disappear. For the short term, decreasing of number of breeds may be economically efficient. For the long term, we may lose valuable genetic resources and the question is how we can balance the short and long term interests.

INTRODUCTION

As the importance of crossbred animals increases in commercial animal production, breeding strategies face new challenges in terms of breeding goal, genetic evaluation and breeding scheme. For example, what should be the breeding goal in a multibreed population? How should crossbred performance records be incorporated into a genetic evaluation program? How will crossbred and purebred animals be compared and will crossbreds be used as breeding animals? This paper presents some strategies to meet these challenges and discusses relevant problems in achieving genetic improvement in a multibreed population.

STRATEGIES AND PROBLEMS

1. Breeding Goal. Breeding goal in this paper is defined as what types of animals (purebred, crossbred or both) breeding program aims to improve, and not as it is commonly defined as a combination of traits. As crossbred performance has become more important in commercial beef production, and crossbred performance records become more abundant, a re-examination of breeding goals becomes essential. Theoretically, three breeding goals can be classified for a multibreed population. The first one is classic, genetic improvement within breeds/lines. The methodology to achieve this goal is well established. This breeding goal is generally applied in beef cattle breeding. For example, in North America, genetic improvement is mainly achieved within breeds (Nunez-Dominguez et al., 1993). Organization and supervision of breeding programs are often by breed associations. Crossbreds are not included in evaluation, and crossbred improvement depends on purebred progress.

To use crossbred performance records and compare animals across breeds and crossbred types, attention is paid to 'general combining ability' of animals. Here, 'general combining ability' is defined as the additive genetic effect of an animal as evaluated by all possible purebred and crossbred progeny. In this context breeding animals should be good not only to produce purebred progeny but also crossbred progeny. The improvement of 'general combining ability' can be defined as another breeding goal. For example, in Ontario, Canada, an across breed comparison index (ABC) is being used to compare animals across breeds and crossbred types.

The improvement of general combining ability may not be completely sufficient when breeders and producers are interested mainly in specific types of crossbred. A third breeding goal can be introduced as the genetic improvement for a specific crossbred type (Wei and Van der Werf, 1993). Without non-additive genetic variation, the three breeding goals are equivalent, i.e., when $r_{pc}=1$ (Wei, et al., 1991). However, existence of non-additive genetic variation in most economical traits requires consideration of alternative breeding goals.

2. Evaluation Methodology. The evaluation method to achieve genetic improvement within breed /line has become sophisticated, i.e., animal model BLUP (Henderson, 1984; Kennedy, 1989) which uses all possible animal information, accounts for all possible animal relationships and fixed effects. The basic evaluation model (model 1) is $y_1=a_1+e_1$ (ignoring fixed effects), where y_1 is the phenotypic value, a_1 is the additive genetic effect, and e_1 is the residual effect. A better estimate of a_1 may be obtained when the model includes non-additive genetic effects (e.g., dominance effect) if non-additive variation is important (Van der Werf, 1990). When crossbreds constitute a major part of commercial production and the genetic correlation between purebred and crossbred (r_{pc}) significantly differs from one, evaluation model 1 is not optimal. In some beef cattle experiments (Cunningham and Magee, 1986; Massey and Benyshek, 1986; Garrick et al., 1989; Tilsch et al., 1989; Nunez-Dominguez et al., 1993), r_{pc} was found to be .57-.76 for pre-weaning gain, .52-.85 for post-weaning gain, and .68-.76 for 365-day body weight. In this case there is great potential for improvement through use of crossbred information (Wei and Van der Werf, 1993).

Crossbreds are dominant in commercial animal production. Setting improvement of general combining ability as a breeding goal allows all crossbred performance records to be included in evaluation. The purpose is to evaluate how good an animal is to produce its purebred and crossbred progeny. To use both crossbred and purebred information in one evaluation, breed and heterosis effects should be included in the model. The basic theory on heterosis was described by Dickerson (1969) and Hill (1983). The evaluation model (model 2) is: $y_2=b_2+h_2+a_2+e_2$, where y_2 is the phenotypic value of purebred or crossbred, b_2 is the breed effect, h_2 is the heterosis effect, a_2 is the additive genetic effect, and e_2 is the residual effect. This model provides a reasonable way to use crossbred information and to compare animals among breeds. Some details on model 2 are given in Arnold et al. (1992). Following Dickerson (1969), Gomez-Raya (1993) presented formulas to calculate coefficients for heterosis effects resulting from dominance. The coefficients can be used in the model to account for heterosis of any type of crossbreds. This approach makes the crossbred information in the evaluation comparable to the purebred information. In this model, EBV of an animal is a_2, which is used for selection within breeds. Another index is $(b_2+h_2+a_2)$, which predicts average progeny performance of any type of crossbred where b_2 and h_2 are relevant to the type of crossbred to be expected. When heterosis effects are properly corrected, crossbred information adds to accuracy of EBV estimation of purebreds. Model 2 is equivalent to model 1 but includes breed and heterosis effects. To meet the need of breeders and producers, we suggest to publish all solutions on b_2, h_2 and a_2, and then $(b_2+h_2+a_2)$ can be calculated by breeders and producers for selection concerning their specific purposes.

The model 2 can be criticized in several aspects. Heterosis may not be explained generally by a dominance model (Hill, 1982). Also genetic variance and covariance related to crossbreds may not be a linear function of the relevant purebred parameters (Wei et al., 1991). These variance and covariance estimates relative to crossbreds are not often available. Simply deriving these variances and covariances from purebred genetic parameters will result in some bias. General combining ability is less informative in terms of selection criteria when breeders and producers are interested in breeding animals who produce specific types of progeny but not all types of progeny. Moreover, EBV of a crossbred seems to be of little use in selection. A crossbred EBV would not inform you of the expected progeny performance because progeny performance depends on what type of animals the crossbred is crossed to. A crossbred

EBV is just informative, for example, of what progeny is expected from its purebred parents in the case of two-way crossing. Therefore, crossbred EBVs may not be taken as selection criteria. Studies are needed on how to evaluate crossbreds as breeding animals.

To account for breed effects, a standardization has been suggested to put phenotypic values of all breeds and crossbred types on the same base, (normal, 0,1) (Wei, et al., 1994). It is specifically useful for beef cattle within herd evaluation and station-tested bull evaluation where the number of animals of any genotype is small.

Ontario beef evaluation model is a modification of model 2, i.e., $y_o=a_o+e_o$, where a_o is the additive genetic effect, e_o is the residual effect, y_o is the phenotypic value pre-adjusted for the difference of phenotypic variances among breeds and heterosis effects (i.e., using a fixed heterosis value to adjust for crossbreds assuming heterosis is linearly correlated with breed combinations). The evaluation program provides EBV and ABC (Across Breed Comparison) for purebreds and only ABC for crossbreds. Breed basis (breed effect) is calculated from the average additive effect by breed. EBV is the deviation of additive effect from breed basis. The breed basis for a crossbred is calculated from its breed composition. ABC is (breed-basis + EBV)/2. ABC of a crossbred indicates the additive genetic effects plus breed effects explained in terms of its purebred ancestors. Use of ABC allows all animals across breeds and crossbred types to be comparable on an additive genetic effect basis.

EBV and ABC of a purebred are easy to understand, but must be interpreted carefully for a crossbred. First, ABC of a purebred is equivalent to the breed mean plus within-breed EBV. A crossbred ABC is the additive genetic effect in terms of breed composition, and can not be used as a selection criterion because it would not generally predict the progeny performance of this crossbred. Interpreting a crossbred ABC as a selection criterion depends greatly on what type of animal (e.g., breed) the crossbred animal is going to cross to. A fixed heterosis adjustment for all crossbreds may cause some bias. The breed basis for a crossbred calculated from its breed composition may be biased when non-additive variation exists (Van der Werf, 1990). Moreover, it may be biased to derive variances and covariances related to crossbreds as a linear function of relevant variances and covariances in purebred populations (Wei et al., 1991; Swan, 1992).

Another evaluation method is to estimate the breeding values of purebred animals for specific types of crossbred, named crossbreeding value (Wei and Van der Werf, 1993). The crucial point of this approach is to consider purebred and crossbred performance as different traits with a genetic correlation (r_{pc}). A multiple trait model (model 3) has been proposed as $\mathbf{y}_3 = \mathbf{a}_3+\mathbf{e}_3$, where $\mathbf{y}_3$ is the vector of phenotypic values of purebreds and crossbreds, $\mathbf{a}_3$ is the vector of animal genetic effects for purebred and crossbred performance (i.e., purebreeding and crossbreeding values), and $\mathbf{e}_3$ is the vector of residual effects. Model 3 provides not only the crossbreeding values which are used to achieve crossbred improvement, but also the breeding value within breeds to be used for purebred improvement. In terms of estimation of EBV, this model is better than model 1 since additional crossbred information is used. It is better than model 2 since heterosis effects need not to be corrected because they are accounted in the multiple trait model. This approach requires estimates of all variance/covariance related to crossbreds, and a terminal crossing system. This approach is suggested to maximize selection response in crossbreds, but has yet to be used in practice (Wei and Van der Werf, 1993).

3. <u>Breeding Schemes</u>. In beef cattle breeding, within-breed mating and rotational crossing are the most important mating schemes although terminal crossing is in use also. Assuming that mating within breeds is always needed to keep purebred populations, emphasis should be paid to the merits of rotational and terminal crossing systems under various breeding goals and evaluation methods.

An advantage of using rotational cross is that breeders or producers always maintain their own crossbred female population and purchase only purebred sires. This system benefits from about 67-85% maternal and individual heterosis for a 2-way or 3-way rotational cross. In practice, sires used in this system are evaluated within breeds. Use of the bull does not match to the goal of evaluation. Selection of dams by producers is not very efficient. Also, how to properly evaluate crossbred dams as breeding animals is still a unsolved problem. As a result, genetic improvement in the system is mainly from the selection of sires based on within-breed EBV. If crossbred progeny information is used to estimate crossbreeding values for sires, the generation interval may get longer. Rotational crossing system is not optimized for crossbred improvement. Studies should be conducted to improve rotational crossing as a breeding scheme, not simply a mating strategy. Here, breeding scheme is defined as the mating scheme considering selection and evaluation.

Terminal crossing is an alternative. A two-way crossing system provides 100% individual heterosis but no maternal heterosis. Three-way crossing will give 100% individual and maternal heterosis. An advantage of this system is that specialized sire and dam breeds/lines can be established so that production and reproduction traits (also, maternal and direct effects) can be emphasized in different breeds/lines to achieve the best combination and economic benefit. If breeding goal is defined as crossbred improvement and evaluation model 3 is used, both purebred and crossbred information can be combined to estimate breeding values for purebred and crossbred performance. Selection intensity may increase in this system compared with rotational crossing. When improvement of specific crossbreds is used as the breeding goal in a terminal crossing system, no comparison among breeds and crossbred types are necessary. A disadvantage of this system is that large purebred populations have to be maintained to produce terminal crossbreds (for beef cattle and not for swine and poultry). Producers either have to buy all crossbreds or breed purebred dams themselves to produce commercial animals. Application of this approach tends to decrease the number of breeds in the beef production system since only a small number of breeds which are the best to produce commercial animals will survive. On the one hand, it is economic to use few breeds to achieve faster genetic improvement and more efficient production. On the other hand, there is a risk in losing some breeds which may not be considered to be genetically good at this moment but may be valuable genetic resources in the future.

4. Conclusion and Suggestions. The breeding goal in a multibreed population should be defined at the commercial production level, i.e., genetic improvement of both purebreds and crossbreds. The evaluation model estimating breeding value for crossbred performance should be considered in achieving crossbred improvement. Using ABC or EBV of a crossbred as a selection criterion remains questionable. A terminal crossing system with specialized sire and dam breeds/lines can be an efficient breeding scheme. A re-evaluation of breeding goals, evaluation methods and breeding schemes in a multibreed population should be done in order to find a way to optimize current beef cattle breeding programs.

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REFERENCES

ARNOLD, J.W., BERTRAND, J.K. and BENYSHEK, L.L. (1992) J. Anim. Sci. 70:3322-3332.

CUMMINGHAM, B.E. and MAGEE, W.T. (1986) Proc. Beef Impr. Ann. Meet., p203-206.

DICKERSON, G.E. (1969) Anim. Breed. Abstr. 37:191-202.

GARRICK, D.J., POLLAK, E.J., QUAAS, R.L. and VAN VLECK, L.D. (1989) J. Anim. Sci. 67:2515-2528.

GOMEZ-RAYA, L. (1993) personal communication.

HENDERSON, C.R. (1984) Univer. of Guelph, Guelph, Ontario, Canada.

HILL, W.G. (1982) J. Anim. Breed. Genet. 99:161-168.

KENNEDY, B.W. (1989) Erasmus Lecture Note, Trinity College, Dublin, Northern Ireland.

MASSEY, M.E. and BENYSHEK, L.L. (1986) J. Anim. Sci. 53:940-945.

NUNEZ-DOMINGUEZ, R., VAN VLECK, L.D., BOLDMAN, K.G., and CUNDIFF, L.V. (1993) J. Anim. Sci. 71:2330-2340

SWAN, A.A. (1992) Ph.D. Thesis. Univer. of New England, Armidale, Australia.

TILSCH, K, WOLLERT, J. and BAUMUNG, A. (1989) Livest. Prod. Sci. 21:275-285.

VAN DER WERF, J.H.J. (1990) Ph.D. thesis. Wageningen Agri. Univer., Wageningen, The Netherlands.

WEI, M. and VAN DER STEEN, H.A.M. (1991) Anim. Breed. Abst. 59:281-298.

WEI, M.; VAN DER STEEN, H.A.M.; VAN DER WERF, J.H.J. and BRASCAMP, E.W. (1991) J. Anim. Breed. Genet. 108:253-261.

WEI, M. and VAN DER WERF, J.H.J. (1993) submitted to Anim. Prod.

WEI, M., WILTON, J.W. and KENNEDY, B.W. (1994) Proc. 5th World's Cong.Appl.Livest.Prod. (in press).