M. Wei

COMBINED CROSSBRED AND PUREBRED SELECTION IN ANIMAL BREEDING

Promotor:	**dr. ir. E.W. Brascamp** **hoogleraar in de veefokkerij**
Co-promotor:	**dr. ir. J.H.J. van der Werf** **universitair docent in de veefokkerij**

Ming Wei

Combined Crossbred and Purebred Selection in Animal Breeding

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. H.C. van der Plas,
in het openbaar te verdedigen
op maandag 14 december 1992
des namiddags te vier uur in de Aula
van de Landbouwuniversiteit te Wageningen.

CIP-GEGEVENS KONINKLIJKE BIBLIOTHEEK, DEN HAAG
ISBN 90-5485-056-6

Wei M., 1992. **Combined crossbred and purebred selection in animal breeding.** *The aim of this thesis is to study the selection methods to optimize genetic response in crossbreds by combining both crossbred and purebred information in selection. (1) The locus model study clarified theoretically the meaning and use of genetic parameters related to crossbreds, which are generally not a function of parameters in parental lines. (2) Additive and dominance variances were estimated for egg production traits using linear mixed models and a restricted maximum likelihood. Sire-dam model, additive animal model and dominance animal model were compared in estimating heritability. (3) A combined crossbred and purebred selection method (CCPS) was developed to optimize crossbred response. The method was compared with the pure line selection and crossbred selection methods. Robustness of the method against inappropriate values of genetic parameters was studied. A linear mixed model was presented to apply CCPS. (4) The application of CCPS in animal breeding was extensively discussed.* **Doctor Thesis**, Department of Animal Breeding, Wageningen Agricultural University, P.O.Box 338, 6700 AH Wageningen, The Netherlands.

STELLINGEN

1. To obtain genetic progress in crossbreds, combined crossbred and purebred selection (CCPS) is always more optimal than pure line selection (PLS) or reciprocal recurrent selection (RRS).

   This thesis

2. Most models for analysis of crossbred data incorrectly assume that variances and covariances related to crossbreds are a linear function of variances in the purebred populations.

   This thesis

3. In contrast to the statement of Pirchner and Mergl (1977), the genetic correlation between purebred and crossbred performance (r_{pc}) can be smaller than unity in case of partial dominance.

   Pirchner and Mergl, J. Anim. Breed. Genet. 94:151

4. To optimize the genetic progress in crossbreeding systems, the breeding goal should be based on the breeding values for purebred, as well as for crossbred performance.

   This thesis

5. Selection for litter size in crossbred pigs should be based on combining selection for high ovulation rate at the level of parental populations, with selection for high survival of the crossbred embryo.

6. The availability of genetic markers increases the value of genetic conservation for animal improvement.

7. In the expression of a quantitative trait the interaction among genes is unjustifiably ignored in studies searching for the effect of quantitative trait loci.

8. Making a decision is easier than providing alternatives. However, the people who make decisions are often more rewarded than those providing alternatives.

9. There is no paradise unless you make one for yourself.

10. You can enjoy a grander sight, by climbing to a greater height.

    Wang Zhihuan (Poet of Tan Dynasty)

M. Wei
Combined Crossbred and Purebred Selection in Animal Breeding.
Wageningen, The Netherlands, 14 December 1992.

Preface

First, I would give my thanks to my promoter, Prof. Dr. ir. Pim E.W. Brascamp, for his strategic and insightful guidance, and to my co-promoter, Dr. ir. Julius H.J. van der Werf, for his supervision on a daily basis and for his friendship and help which has contributed not only to the success on my thesis but also to my enjoyment of stay in the Netherlands.

I would like to thank Dr. ir. Hein A.M. van der Steen for being my supervisor during the first period of my study when we together initiated this research topic, and for his continuous interest in my work. Prof. Dr. ir. Politiek is acknowledged for his accepting me as a visiting scholar which lead to the chance for my Ph.D study later on.

I very much appreciated sharing office space with Dr. ir. Huub A. Huizinga, Ir. Chris Schrooten, Dr. ir. Henk Bovenhuis, Dr. ir. Ron Hovenier and Ing. Esther J.M. Verstege etc. They have given me a lot of help as both colleagues and friends. I enjoyed very much all those talks, discussions, daily greetings, social activities and fun ⋯⋯ made together with them, which are unforgettable.

I wish to thank Prof. Dr. Michael Grossman from whom I learned a lot about locus model theory which directly contributed to Chapters 2 and 3, and to thank Prof. Dr. W.G. Hill for his comments on Chapter 2 and for his encouragement of my research ideas at the very beginning.

The department of animal breeding is acknowledged for being a nice environment for my study and for providing me the last two years' financial support. I am greatly indebted to all department members and foreign visitors for various kinds of help and friendship. Specifically, the secretaries, Ms. Ada G.L.M. Wiggerman, Ms. Petra de Jong and Ms. Karen den Outer-Sieverts gave me a lot of extra helps due to me being foreigner. Ing. Egbert M. Urff and Ing. Arnoud W. van der Lugt, and Ing. Hendrik Klompmaker gave me assistance with computers and computer programs. Dr. ir. Ella Luiting gave her comments on Chapters 5 and 6. Ir. Cees van Drunen of Euribrid B.V. provided the chicken data and related help for dominance variance estimation (Chapter 5). Ir. Pieter Knap gave his comments on Chapters 6 and 7, and specifically contributed to making a clear outline for writing Chapter 7 through the discussion with him. Dr. ir. Ab Groen gave his comments on the economical aspects of CCPS method applying to animal breeding in Chapter 7. Dr. Sara Knott corrected the English in Chapters 3 and 4. Dr. Chris Davies corrected my English for Chapter 5. I also remember that a lot of colleagues and friends whose names are not mentioned here, both from this department as well as out of the department, have given me help in one way or another. Here, I express my appreciation to all of them.

My acknowledgement also goes to Waginingen Agricultural University (international education office) for financially supporting me in the second year, and to the Education Ministry of the Netherlands for providing the first year fellowship when I was a visiting scholar.

I very much appreciate all of the Dutch people who spoke English to me, this created an opportunity for me to communicate with them, and understand them, their culture and daily life. I have, and shall keep, a very good memory about my experiences here in the past years.

At last, I deeply appreciate my wife, Huajie Chen, besides all other contributions to the success of my Ph.D study, specially due to her creating an excellent environment for us to communicate with Dutch people, and understand them and their culture.

Contents

Chapter 1. General introduction 1

Chapter 2. Comparison of reciprocal recurrent selection with pure-line selection systems in animal breeding (A review) 7

Chapter 3. Relationship between purebred and crossbred parameters. I. variances and covariances under the one-locus model 39

Chapter 4. Relationship between purebred and crossbred parameters. II. genetic correlation between purebred and crossbred performance under the model with two loci 55

Chapter 5. Animal model estimation of additive and dominance variances in egg production traits of poultry 69

Chapter 6. Maximizing genetic response in crossbreds using both purebred and crossbred information 87

Chapter 7. General discussion 107

Appendix. A linear mixed model for combined crossbred and purebred selection 139

Summary 147

Dutch summary 153

Glossary 159

Chinese summary 161

Curriculum vitae 163

Chapter 1

General Introduction

Ming Wei

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

The aim of this thesis is:

"to study the selection methods to optimize genetic response in crossbreds by combining both crossbred and purebred information in selection."

General Introduction

Ming Wei

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

Crossbreeding is intensively applied to produce commercial animals in almost all species of livestock, especially in poultry and swine (Arthur, 1986; Lasley, 1987; Legates, 1988). The advantage of using crossbreds is mostly based on the appearance of heterosis which is a general phenomenon for most commercially important traits (Orozco, 1986). Moreover, crossbreeding enables to combine different traits from more than one population (Smith, 1964; Moav and Hill, 1966). Based on the fact the final commercial products are crossbred animals, it is believed that the breeding goal should be set at the level of crossbred performance rather than purebred (Comstock, 1961; Orozco, 1986; Hartmann, 1992). However, most selection methods are optimal for improving animals within purebred populations (Legates, 1988). Genetic evaluation in crossbreeding systems may not be optimum if it relies on purebred selection theory.

In the analysis of data on crossbreds, attention has been primarily paid to the additive breed or line effects, and an interaction between lines as heterosis or recombination. The relevant theory on analyzing crossbreeding experiments and genetic effects is well presented by Dickerson (1973), Hill (1982) and Kinghorn (1982). Relatively, little attention has been given to genetic variation within a line for the crossbred performance, i.e., for the breeding value of animals that are crossed to other lines.

Two selection methods to improve crossbred performance in animal breeding have generally been used, (1) pure-line selection (PLS) which uses information from purebred animal and/or their relatives within populations, and (2) crossbred selection (CS), such as recurrent selection (Hull, 1945) and reciprocal recurrent selection (RRS) (Comstock et al., 1949). These methods uses crossbred progeny or crossbred sib information as selection criteria. However, selection methods for optimizing crossbred improvement by using both purebred and crossbred information have rarely been studied.

The genetic improvement with regard to crossbreds is characterized by the utilization of both additive and non-additive variances in traits. Therefore, to obtain a maximum genetic progress in crossbred performance, both kinds of genetic variance have to be exploited efficiently (Siegel, 1988). There is a marked difference between pure line selection and crossbred selection methods in utilizing the genetic variances. Under a PLS program, purebred animals are improved by efficiently exploiting additive variance. Through PLS the breeding goal aims at improving purebred performance within populations and crossing these populations causes an amount of heterosis which has not been selected for. Theoretically, a PLS scheme can maximize the purebred response. In fact, the success of this approach in practice has always been with the continuous utilization of additive variance. However, both theory and experiments have failed to prove that PLS can maximize crossbred response if non-additive variance is involved (Bell, 1982; Hill, 1971). For example, in some experiments RRS effectively improved crossbred performance when the purebred lines did not respond to PLS any more (Kojima and Kelleher, 1963).

The CS method was designed to maximally exploit both general and specific combining abilities (Comstock et al., 1949). Orozco and Bell (1974) showed that the CS can exploit nonadditive variation better than PLS. The crossbred animals were faster improved than the purebreds through a RRS scheme (Saadeh et al., 1968). The experiments on comparison of PLS with RRS methods have shown that most experiments were in favour of PLS when comparisons were based on the crossbred response (Bowman, 1959; Bell, 1982). However, several shortcomings of RRS are known and they are not always due to inefficient selection but moreover a result of the design of selection program. For example, a progeny test is mostly used resulting in a longer generation interval and realised selection intensity for CS is often not equal to PLS given a limited number of total progeny.

This thesis starts with a critical review on theoretical and experimental comparison of pure-line selection with reciprocal recurrent selection systems and the emphasis will be on the reasons why different selection schemes have different effects on crossbred animal improvement (Chapter 2).

Combining purebred and crossbred information seems to be a logical way to achieve maximum genetic progress in crossbreds. However, a method with optimal weighing both types of information to maximize crossbred progress has not been established. In poultry breeding, both crossbred and purebred information are used to some extent to achieve genetic progress of crossbreds under crossbreeding systems (Arthur, 1986 and Flock, 1988), for instance by means of independent culling. But, this method has no properties of optimality.

Still, several aspects of such an "optimal" procedure are unanswered. For example, to optimize crossbred response to selection, genetic parameters related to crossbreds should be known. Some selection experiments have demonstrated the difference between purebred and crossbred parameters. For instance, the crossbred and purebred heritabilities were not equal (Louca and Robison, 1967; Pirchner and von Krosigk, 1973). To obtain a better theoretical understanding of reasons for such differences, a locus model was used to study the genetic parameters related to crossbreds (Chapter 3 and 4). Chapter 3 aims at developing knowledge on the sire component of variance in crossbreds, the heritability for crossbreds, the genetic covariance between purebred and crossbred half-sibs, and relationships among these parameters. Chapter 3 concentrates on how the dominance effects and gene frequencies in parental populations influence the genetic correlation between purebred and crossbred performance (r_{pc}).

The increasing value of crossbred information in relation to purebred information is greatly dependent on the nonadditive variance. In Chapter 4, the dominance variance is estimated for egg production traits in poultry using a restricted maximum likelihood (REML) method to allow for data on several generations. The estimates of dominance variance were compared with crossbreeding parameters, e.g., r_{pc}, heterosis, and inbreeding depression, to test the theory on dominance. Also, three models (i.e., sire-dam model, additive animal model and dominance animal model) are compared in estimating heritability in order to examine the effect of dominance on heritability estimation.

In chapter 5, selection index theory is applied to establish a combined purebred and crossbred selection method (CCPS). It aims at solving the problem how to construct a selection index for a CCPS scheme once both purebred and crossbred information, and relevant genetic parameters are available. The CCPS is compared with PLS and CS methods in terms of crossbred response under different circumstances. Moreover, it is studied how robust the methods are against inappropriate genetic parameters, because an objection against using combined information might be that the crossbred parameters are unknown or not estimated very precisely and accurately.

In the final chapter (Chapter 7), implications of the CCPS methods for practical crossbreeding programmes were thoroughly discussed. Some relevant problems which have not been solved in this study and some prospects for applications of the results on this topic were presented. In the appendix, an animal model applying mixed model methodology was given for an implication of the proposed genetic evaluation method when data is on several generations.

REFERENCES

Arthur, J.A., 1986. An evaluation of industry breeding programmes for egg type chickens. Proc. 3rd World Cong. Genet. Appl. Livest. Prod. 10:325-335.

Bell, A.E., 1982. Selection for heterosis - results with laboratory and domestic animals. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. 6:206-227.

Bowman, J.C., 1959. Selection for heterosis. Anim. Breed. Abstr. 27:261-273.

Comstock, R.E., Robinson, H.F., and Harvey, P.H., 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agronomy Journal 41:360-367.

Cunningham, E.P., 1990. Quantitative approaches for animal improvement. Proc. 4th World Cong. Genet. Appl. Livest. Prod. XIII:4-14.

Dickerson, G.E., 1973. Inbreeding and heterosis in animals. Proc. Anim. Breed. Genet. Symp. in Honour of Dr. J.L. Lush. ASAS, Champaign, IL. pp54-77.

Flock, D.K., 1988. An assessment of progress with different stocks and methods of selecting in egg layers. In: Animal Breeding Opportunities. BSAP Occas. Pub. 12:189-201.

Hartmann, W., 1992. Evaluation of the potentials of new scientific developments for commercial poultry breeding. World's Poult. Sci. J. 48:17-27.

Hill, W.G., 1971. Theory of limits to selection with line crossing. In: Kojima, K. (ed.) Mathematical Topics in Population Genetics. Berlin, German Federal Republic, Springer-Verlag.

Hill, W.G., 1982. Dominance and epistasis as components of heterosis. J. Anim. Breed. Genet. 99:161-168.

Hull, F.H., 1945. Recurrent selection for specific combining ability in corn. J. of American Society Agronomy. 37: 134-145.

Kinghorn, B.P., 1982. Genetic effects in crossbreeding. 1. models of merit. J. Anim. Breed. Genet. 99:59-68.

Kojima, K.; Kelleher, T.M., 1963. A comparison of purebred and crossbred selection schemes with two populations of Drosophila pseudoobscura. Genetics 48:57-72.

Lasley, J.E., 1987. Genetics of Livestock Improvement (4th Ed.). Prentice-Hall, Inc. Englewood Cliffs, New Jersey.

Legates, J.E., 1988. Development in theory and application of animal breeding. In: Korver, S. et al. (ed.) Advances in animal breeding - Proceedings of the World Symposium in honour of Professor R.D. Politiek. Wageningen, The Netherlands. Pudoc. 11-14 Sept. 1988. pp15-26.

Louca, A.; Robison, O.W., 1967. Components of variance and covariance in purebred and crossbred swine. J. Anim. Sci. 26:267-273.

Moav, R.; Hill, W.G., 1966. Specialised sire and dam lines IV. Selection within lines. Anim. Prod. 8:375-390.

Orozco, F.; Bell, A.E., 1974. Reciprocal recurrent selection compared to within-strain selection for increasing rate of Tribolium under optimal and stress conditions. Genetics 77:143-161.

Orozco, F., 1986. Crossbreeding and heterosis. U.S.-Spain joint seminar on sheep breeding. Zaragoza, 10-15 Nov. 1986.

Pirchner, F.; von Krosigk, C.M., 1973. Genetic parameters of cross- and pure-bred poultry. Br. Poult. Sci. 14:193-202.

Saadeh, H.K.; Craig, J.V.; Smith, L.T.; Wearden, S., 1968. Effectiveness of alternative breeding systems for increasing rate of egg production in chickens. Poult. Sci. 47:1057-1072.

Siegel, P.B., 1988. Future breeding programmes in poultry. In: Korver, S. et al. (ed.) Advances in Animal Breeding: Proceedings of the World Symposium in Honour of Professor R.D. Politiek. Wageningen, Netherlands. Pudoc. 11-14 Sept. 1988. pp.107-115.

Smith, C., 1964. The use of specialised sire and dam lines in selection for meat production. Anim. Prod. 6:337-344.

Chapter 2

Comparison of Reciprocal Recurrent Selection with Pure-line Selection Systems in Animal Breeding (a review)

Ming Wei and H.A.M. van der Steen

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

Published in: ***Animal Breeding Abstracts 59:281-298 (1991)***.
Reproduced by permission of CAB International, U.K.

"Maximum selection response in crossbreds may be obtained only when proper weighing parameters are given to purebred and crossbred performance in a selection index designed to aim at the best hybrids."

Comparison of Reciprocal Recurrent Selection with Pure-line Selection Systems in Animal Breeding (a review)

Ming Wei and H.A.M. van der Steen

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

I. ABSTRACT. Comparisons between reciprocal recurrent selection (RRS) and pure-line selection (PLS) in both theory and experiments were reviewed. The relative importance of additive and non-additive genetic variance is important to predict the effectiveness of RRS and PLS. RRS is more efficient than PLS to improve a heterotic trait. RRS obtains its highest selection response when overdominance genes exist. On the other hand, PLS is better than RRS to improve a trait whose heritability (h^2) is high. The genetic correlation between means of purebred and means of crossbred half-sib (r_{pc}) is a reliable indicator for evaluation of RRS and PLS. The experimental comparisons are basically in agreement with theoretical results. PLS is better than RRS to exploit additive variance, while RRS, which makes use of both additive and non-additive gene effects, is more efficient to exploit non-additive variance. A RRS scheme is very suitable for a long-term selection programme. During the initial generations of RRS, selection response is usually low. After the "lag" period, RRS gain will be faster. Experiments showed that RRS always obtained higher selection response than PLS in an adverse environment. Modified RRS schemes have some advantages over RRS. An important point is that PLS and RRS are not contradictory but complementary selection methods. Thus, the combination of them is expected to be successful. Some forms of the combination and their merits are discussed here. It is concluded that the optimal selection response may be obtained only when optimal weighing parameters are available for the purebred and crossbred performance in a selection index.

II. INTRODUCTION

The reciprocal recurrent selection procedure (RRS) was proposed by Comstock et al. (1949) for using specific combining ability in plant breeding. It was introduced into animal breeding by Bell et al. (1950). Since then, many RRS experiments have been done in animals, including laboratory animals (Drosophila, Tribolium and mice) and domestic animals (poultry and pig). The main objective of the experiments was to determine the effectiveness of selection based on (1) crossbred progeny performance in RRS and (2) purebred performance under pure-line selection (PLS). The results have been rather conflicting. Although slightly more comparisons were in favor of PLS, results did not indicate that PLS is a better method in general, as RRS is significantly more efficient in exploiting non-additive variance in selected traits.

Today, when almost all commercial breeding animals are highly selected under PLS, crossbreeding to exploit non-additive variance can be more important (Barker, 1974). Legates (1988) pointed out that the utilization of hybrid vigor has been a major component of applied breeding programs. Especially, Arthur (1986) pointed out that modern breeding systems in poultry generally use reciprocal recurrent selection or some modifications of that system to improve the performance of the cross.

Bowman (1959), King (1971), Bell and Moore (1972), Bell (1982) and Sellier (1970 and 1982) reviewed crossbreeding, including experiments on RRS. However, the studies on comparing RRS with PLS have not been comprehensively reviewed. Therefore, the present paper will focus on the comparison of RRS with PLS systems, in theory and practice. The merits existing in the two selection systems, and some possible further studies to improve them, are discussed.

III. SELECTION METHODS

Before discussing the comparison of PLS with RRS, several selection methods concerned will be described.

1. Pure Line Selection

PLS can be defined as selection based on the performance of individuals (and/or relatives) within a certain population (Legates, 1988; Siegel, 1988). PLS used in animals includes independent culling, mass selection, family selection, progeny testing, index selection and the BLUP method. As a breeding system, PLS is frequently combined with line (strain or breed) crossing (Legates and Politiek, 1971; Cahaner and Siegel, 1986).

2. Recurrent Selection

Recurrent selection for specific combining ability (RS) was proposed by Hull (1945 and 1952), and is basically a system of progeny testing. It involves (1) a segregating population and (2) a constant tester line. The segregating population can be a breed, strain or line. The constant tester might be an inbred line or a single cross of two inbred lines. Both males and females from the segregating population are crossed to the constant tester. Selection is based on performance of the test-cross progeny. Proven males and females of the segregating population are mated together to reproduce the population. Selection may be continued until individuals of the segregating population uniformly combined well with the tester line.

In animal breeding, RS is not practicable, as it involves maintaining a tester line without selection. There are only quite rare reports about its use in animals (Andrews and Stephenson, 1970; Bell et al., 1955; Bowman, 1959 and 1962; Hansson and Lindkvist, 1962; Hupp, 1977).

3. Reciprocal Recurrent Selection

In general, RS has been replaced by RRS (Comstock et al., 1949) to select for specific combining ability. RRS was an extension of RS. Application of RRS to animals was first discussed by Bell et al. (1950) and Heisdorf (1950). RRS differs from RS only in that segregating populations (A and B) are utilized on both sides of the cross. The selection of purebred animals is based on the performance of A*B (and/or B*A) hybrids. Selected individuals are mated at random within each population to form new A and B populations. RRS is a kind of progeny-testing system and each selection cycle covers 2 generations (Comstock et al., 1949; Jull, 1952).

4. Modified RRS Methods

Because RRS did not achieve the goals expected in theory, some modified RRS methods were developed improve it by shortening generation interval, using purebred performance or considering environmental effects (Sellier, 1982). Main types of them are described below.

(a). Half-sib RRS scheme (HS-RRS). HS-RRS is suggested to shorten selection interval. Under HS-RRS, selected pure-line animals produce the next purebred generation and the crossbred progeny simultaneously. The selection is based on the performance of half-sib crossbred. Selection cycle takes only one generation. (b). M-RRS. M-RRS is based on the mean performance of purebred and crossbred animals in order to use both purebred and crossbred information. Krehbiel et al. (1971a and 1971b) and Hetzer et al. (1977) carried out M-RRS experiments.

(c). PC-RRS. PC-RRS is based on purebred and crossbred performance in two-stage selection with independent culling levels for purebred and crossbred progeny performance. The purebred selection in PC-RRS precedes each cycle of crossbred selection (Brown and Bell, 1980). Schnell (1961) also suggested the scheme.

(d). Environmental RRS (E-RRS). A significant higher selection response in stress environments from RRS than from PLS has been described (Krause et al., 1964; Kincaid and Touchberry, 1970; Orozco, 1974; Barlow, 1981). E-RRS is based on the mean performance of crossbred and purebred in an adverse and optimal environment respectively (Orozco, 1974). Moreover, Moreno-Gonzàlez (1986) suggested a method called dual-environment RRS (DE-RRS). Progeny from line A and B are evaluated in two different environments. DE-RRS would provide a wider range of genes under selection if different sets of genes were operating in different environments.

(5). Others. Moreno-Gonzàlez and Grossman (1976) proposed a modified RRS scheme in order to use overdominant gene effects.

IV. THEORETICAL COMPARISON OF RRS WITH PLS

The first theoretical comparison of RRS with PLS was made by Crow (1953). Later, Griffing (1962), Hill (1970), McNew and Bell (1976) and some others compared the two systems with respect to genetic gain and selection limits. In general, two models described below were used in the comparison.

1. One Locus Model

The study was based on a simple model of a single locus with two alleles with specific degree of dominance. Gene epistasis and linkage are not relevant in the model. Here the comparison model proposed by Hill (1970) will be described.

Considering an autosomal locus with alternative alleles A_1 and A_2, the average genotypic values of A_1A_1 and A_2A_2 were assumed to be a_2 and a_1, respectively. The frequency of A_1 is q, and q' is defined as $a_2/(a_1+a_2)$. Since only differences in genotypic value are important, the genotypic value of heterozygote is assumed to be $a = a_1+a_2$. There are,

Genotype	A_1A_1	A_1A_2	A_2A_2
Genotypic value	$(a_1+a_2)-a_1$	a_1+a_2	$(a_1+a_2)-a_2$
=	aq'	a	a(1-q')

The alternative types of gene action can be summarized as follows,

A_1 overdominant	$1/2<q'<1$
A_1 completely dominant over A_2	$q'=1$
A_1 partially dominant over A_2	$1<q'<\infty$
Additive	$q' \longrightarrow \pm\infty$ (but aq' is finite)
A_2 partially dominant over A_1	$-\infty<q'<0$

A_2 completely dominant over A1	$q'=0$
A_2 overdominant	$0<q'<1/2$

If truncation selection is practised on individual phenotypes in a large single population, the change in gene frequency in one generation is, approximately,

$$D_q = \frac{-ia}{\sigma} q(1-q)(q-q') \qquad [1]$$

where i is the selection differential in standard units and σ is the phenotypic standard deviation. Formulae similar to equation (1) have been derived by various authors, notably Comstock et al. (1949), Crow (1953), and Griffing (1960). Equation (1) holds only if gene effects are small such that terms in $(a/\sigma)^w$ can be ignored relative to a/σ for $w>1$. If progeny testing, for example, is practised in a pure line, the response becomes,

$$D_q = -\frac{1}{2}\frac{ia}{\sigma_f}(1-q)(q-q') \qquad [2]$$

where σ_f is the standard deviation of progeny test means. More generally, the response will be proportional to the average of i/σ_f for two sexes, if, as is probable, they are not tested with exactly the same design. The relative response with different schemes, such as individual selection and progeny testing is well known (Falconer, 1981). The formula can be simplified below if $s = ia/\sigma_f$. s may be regarded as a selective value.

$$D_q = -\frac{1}{2}sq(1-q)(q-q') \qquad [3]$$

In a RRS scheme, the individuals with the highest average crossbred progeny test are assumed to be chosen as parents of the next generation. Two populations X and Y are assumed; p and q are the frequencies of allele A_1 for X and Y, respectively; r and s are respective selective values (i.e. the mean over sexes of ia/σ_f). Predictions of changes in gene frequency in a RRS programme have been given by Comstock et al. (1949) and Dickerson (1952). The changes in gene frequency will be,

$$\begin{aligned} &\text{Population X:} \quad D_p = -\frac{1}{2}rp(1-p)(q-q') \\ &\text{Population Y:} \quad D_q = -\frac{1}{2}sq(1-q)(p-q') \end{aligned} \qquad [4]$$

In a RRS programme, r and s are expected to be equal, but this would not be the case if no reciprocal crosses are made. When comparing PLS with RRS schemes the selection value, s, may not be assumed to be the same for both systems because the selection intensities may not be the same.

If random mating is practised between individuals of both strains, the mean, μ, of the crossbred progeny for the quantitative trait is:

$$\mu = a[1-q'(1-q') - (p-q')(q-q')] \tag{5}$$

This mean is maximized with overdominance if $p=1$ and $q=0$ or vice versa, with complete dominance of A_1 if $p=1$ or $q=1$, and with partial dominance or additivity if $p=q=1$. The change in the mean with one cycle of selection is:

$$D_\mu = -a[(q-q')D_p + (p-q')D_q + D_pD_q] \tag{6}$$

Thus, if the product term D_pD_q is ignored, which should introduce little error if changes in gene frequency are small each generation, the responses to a single cycle of selection for the alternative schemes are as follows,

System	D_μ
PLS	$\frac{a}{2}(p-q')(q-q')[rp(1-p)+sq(1-q)]$
RRS	$\frac{a}{2}[rp(1-p)(q-q')^2+sq(1-q)(q-q')^2]$

In the PLS system, selection is carried out independently in the two populations, and r and s refer to population X and Y, respectively.

After the theory above is expanded to finite populations, the comparison of two methods is made in terms of the parameters Mr and Ns (mainly the case Mr=Ns was studied) where M and N are the effective population sizes for X and Y, respectively. Conclusions summarized by Hill (1970) were: (1) with complete dominance RRS is more effective than PLS; (2) with partial dominance RRS and PLS have similar efficiency; and (3) with overdominance PLS is not useful and RRS is much better than PLS.

2. Quantitative Genetic Theory

Comparisons between RRS and PLS from Griffing (1962), McNew and Bell (1976) and Bell (1982) are summarized here. Assuming equal selection intensity and equal phenotypic variance among purebred and crossbred lines, the formulae to compare RRS with PLS in selection gain are,

$$\text{Comparison 1:} \quad \frac{\sigma^2_{Ax1}+\sigma^2_{Ax2}}{(\sigma^2_{Ap1}+\sigma^2_{Ap2})/2}\left(\frac{nd}{nd+n+2}\right) \qquad [7]$$

$$\text{Comparison 2:} \quad \frac{\sigma^2_{Ax1}+\sigma^2_{Ax2}}{Cov_1+Cov_2}\left(\frac{nd}{nd+n+2}\right) \qquad [8]$$

where, σ^2_{Ap} = additive variance in purebred; $(Cov)_i$ = covariance of additive effects of alleles between purebred line i and crossbred; $(\sigma^2_{Ax})_i$ = variance of additive effects of alleles in crossbred contributed by line i; n = number of offspring in purebred full-sib family; d = number of purebred dams mated to a male; i = purebred population 1 or 2.

Comparison 1 is a direct comparison of purebred response to PLS with crossbred response to RRS. In the case of purely additive gene action, $2\sigma^2_{Ax}$ and σ^2_{Ap} are equal for any population and PLS excels over RRS, which reflects the increased efficiency of family selection over sib selection. When mass selection is applied in addition to family selection, the superiority of PLS over RRS is increased even more (this happened in the Tribolium experiment of Bell and Moore, 1972). When non-additive gene effects are present, the ratio of $2\sigma^2_{Ax}$ to σ^2_{Ap} is primarily a function of previous selection history. With unselected base populations, σ^2_{Ap} and $2\sigma^2_{Ax}$ are not greatly different, and PLS frequently excels in early generations. But when $2\sigma^2_{Ax}$ become significantly larger than σ^2_{Ap}, the outcome favors RRS as happened in the experiment of Orozco and Bell, 1974.

For the comparison of RRS with PLS for crossbred selection response, comparison 2 is applicable. In this case, the covariance between purebred and crossbred (Cov) becomes of major importance. For a simple case of additive gene action, 2Cov is equal to σ^2_{Ap}, and PLS excels as for comparison 1. However, when non-additive gene effects exist and population 1 and 2 do not have identical gene frequencies, Cov will be smaller. It is obvious that Cov term does not need to be negative, as for over-dominance, for RRS to excel over PLS. When Cov becomes negative, RRS certainly excels over PLS (Bell, 1982).

Another comparison formula is described by Sellier (1982) as,

$$\frac{PLS}{RRS} = r_{pc}\frac{i_p}{i_c}\,\frac{t_c}{t_p}\,\frac{\alpha h_p}{\beta h_c} \qquad [9]$$

where, PLS/RRS = ratio of "correlated" response in crossbred from PLS to "direct" response from RRS per year; r_{pc} = purebred and crossbred genetic correlation, and the method to estimate r_{pc} is proposed by Henderson (1953); i_p and i_c = selection intensities in PLS (p) and RRS (c), respectively; t_p and t_c = selection generation intervals in PLS and RRS respectively; $2h_p$ and h_c = square roots of heritability in purebreds and crossbreds; α and β = coefficients depending on specific methods used as PLS and RRS, respectively. For example, α is simply equal to 1 when mass selection is applied in PLS. If RRS is based on progeny testing males with n crossbred offspring (paternal half-sibs) per sire, ß is given by $\{n/[4+(n-1)h^2_c]\}^{½}$.

Among the 9 parameters to determine PLS/RRS, three (r_{pc}, h_p and h_c) strictly depend on the genetic properties of the trait in particular populations. If assuming $\alpha = 1$, $\beta = \surd\{n/[4+(n-1)h^2_c]\}$, $t_c/t_p = 2$, $h_p = h_c$, and $i_p = i_c$, formula (9) becomes,

$$\frac{PLS}{RRS} = 2r_{pc}\sqrt{\frac{[4+(n-1)h_c^2]}{n}} \qquad [10]$$

PLS/RRS depends greatly on r_{pc}. When r_{pc} is near 1, PLS/RRS is larger than one and PLS usually is better than RRS (Dunn et al., 1970; Standal, 1968). When r_{pc} is low or even negative, RRS will be more efficient. The last part of the formula, $\surd[4+(n-1)*h^2_c]/\surd n$, is favorable to RRS when n is large.

Comstock (1961) proposed a comparison formula which is,

$$\frac{PLS}{RRS} = 4\frac{i_p}{i_c}\frac{\sigma_c}{\sigma_p}\frac{Cov_{pc}}{\sigma^2_{cc}} \qquad [11]$$

where, i_c, i_p and PLS/RRS have the same meaning as in formula 9; σ_p and σ_c are phenotypic standard deviation of individuals in purebred and crossbred population, respectively; σ^2_{cc} is the sire component of variance in crossbred progeny; Cov_{pc} is the sire component of covariance between purebreds and crossbreds. Comstock (1961) suggested i_c/i_p between 0.4 and 0.8, being larger when population size is large. The formula has been used by Stanislaw et al. (1967) and Wong et al. (1971).

3. Selection Limit

The selection limits on RRS and PLS are also important for breeders. Under a single locus model with two genes (A_1 and A_2), the efficiency of RRS and PLS at the selection limit in crosses is strongly determined by the level of dominance and initial allelic frequencies in the two lines. When dominance is zero, partial or complete, the effect of RRS as well as PLS is to lead both lines towards fixation for the favorable allele, A_2. They have the same selection limit (Bell et al., 1952). On the contrary, at loci with overdominance effects, the frequencies of favorable alleles tend toward fixation in one purebred line and toward zero in the other under RRS. For overdominance loci, frequencies of heterozygosis tend to move toward one in crossbred progenies (Comstock et al., 1949). The selection limit under RRS is reached when lines 1 and 2 are fixed for the A_1 and A_2 alleles, respectively. The selection limit under PLS is still the fixation for the A_2 in lines, or the maintenance of a certain frequency of gene A_1 and A_2 in both lines.

4. Epistasis

Epistatic gene effects (nonallelic interaction effects) sometimes are involved in discussing the comparison of RRS with PLS. With epistasis, the frequencies of alleles in the entire interacting system in two purebred lines are changed due to RRS in such a way that the frequency of the best gene combinations tends to 1 in crossbred. When the best genotype is heterozygous at some loci, the allelic frequencies at these loci tend to unity in one purebred line and zero in the other. With respect to the loci which are homozygous in the best genotype, the fixation of these homozygosis will result in both purebred lines. PLS is much less efficient in using epistatic gene effects. Bell et al. (1952) pointed out that RRS provide an opportunity for increasing the frequency of those genes which would combine for superior epistatic combinations in the strain-cross progeny, but, no detailed study on this was found.

5. Others

Dickerson (1952) reported that when both lines involved in RRS are initially at equilibrium frequencies for the same overdominant loci, and the cross progenies display the same gene frequency, RRS is likely to have little effect in the first few generations. Further studies were done by computer simulation (Arthur and Abplanalp, 1964 and 1970). RRS was used, starting with two lines each at an initial equilibrium for overdominant loci due to previous PLS. Under RRS, there was an initial lag period of 4 to 5 cycles during which little or no response occurred. But when disequilibrium was created in one of the lines by putting it through a bottleneck of 1, 2 or 3 generations of sibbing, it resulted in immediate response. The second study showed that reducing one line to a bottleneck of two individuals for one generation or more before initiating RRS was very effective in overcoming the equilibrium. RRS with prior recurrent inbreeding was not effective in overcoming the unstable equilibrium, but yielded greater response per cycle after selection response began.

V. EXPERIMENTAL COMPARISON OF RRS WITH PLS

1. Comparison of RRS with PLS

The first experiment to compare RRS with PLS in animals (Drosophila) was reported by Bell et al. (1955). Since then, many reports on this topic have appeared. Twenty two experiments, specially designed to compare RRS with PLS in animals, are outlined in Table 1.

Experimental results about the comparison are still conflicting, and similar to those reviewed by Bowman (1959), Hale and Clayton (1965) or Sellier (1970; 1982). More experiments were favorable to PLS than RRS (Table 1).

TABLE 1. A list of experiments comparing RRS with PLS.

Species	Reference	Cycles	Traits	Comparison[*]
Poultry	Krueger et al., 1961.	3	9-week weight	PLS>RRS
			Hatchability	PLS>RRS
	Saadeh, 1968.	7	Egg number	PLS>RRS
	Calhoon and Bohren, 1974.	6	Survivors egg production	PLS>RRS
Pigs	Stanislaw et al., 1967	10 years	56-day weight	PLS>RRS
			Postweaning mean daily gain	RRS>PLS
			Probed backfat thickness	PLS>RRS
	Biswas et al., 1971	7 PLS	Litter size	RRS>PLS
		5 RRS	Mean pig weight per litter	PLS>RRS
			Litter weight	RRS>PLS
	Krehbiel et al., 1971[a,b]	5 RRS	Preweaning litter size	RRS>PLS
		9 PLS	Litter size	RRS>PLS
			Postweaning gain	RRS>PLS
	Wong et al., 1971	9	Litter size	PLS>RRS
			Daily gain	PLS>RRS
			Backfat thickness	PLS>RRS
			Feed efficiency	RRS>PLS
			Index (4 traits)	PLS>RRS
	Dickerson et al., 1974	7 RRS	Preweaning litter size	RRS>PLS
		14 PLS	Litter weight	PLS>RRS
			Postweaning litter growth	RRS>PLS
	Hetzer et al., 1977	6 RRS	Preweaning litter growth	RRS>PLS
		12 PLS	Litter size	RRS>PLS
Mice	Hansson and Lindkvist, 1962	7	Body weight at 6-week	RRS>PLS
	Vinson et al., 1969	2	Body weight	PLS>RRS
			Litter size	RRS>PLS
	Bell, 1982	8	60-day body weight	RRS>PLS

(continued Table 1)

Drosophila	Bell et al., 1955	16 (1)	Egg production + egg size	RRS > PLS
	(2 experiments)	39 (2)	(index)	
			Egg production	RRS > PLS
			Egg size	PLS > RRS
	Rasmusan, 1956	20 (1)	Egg production	RRS > PLS
	(3 experiments)	13 (2)	Hatchability	RRS > PLS
		6 (3)	Body weight	RRS > PLS
	Kojima and Kelleger, 1963	16 RRS	Egg number	PLS > RRS
		13 PLS		
	Kincaid & Touchberry, 1970	30	Thorax length	
	(2 experiments =		(1) Normal environment	PLS > RRS
	2 environments)		(2) X-ray environment	RRS > PLS
	Brown and Bell, 1980	10	Egg number	RRS > PLS
Tribolium	Bell and Moore, 1958	16	Body weight	PLS > RRS
	(2 experiments)			
	Bell and Moore, 1972	24 (1)	Pupal weight	PLS > RRS
	(2 replications)	17 (2)		
	Orozco and Bell, 1974		Egg number	
			(optimum and mild stress)	PLS > RRS
			(severe stress)	RRS > PLS
	McNew and Bell, 1976	11	3-day larval weight	PLS > RRS
	Orozco et al., 1979	9	Adult weight (in logarithms)	PLS > RRS
			Egg number	

[*] **RRS and PLS methods are compared with respect to the selection response per year.**

The effectiveness of RRS and PLS greatly depends on the trait selected. For highly heritable traits primarily governed by additive genes, RRS does not lead to as high performance as PLS (Bowman, 1959). For lowly heritable and heterotic traits, PLS loses its superiority over RRS (King, 1971). For example, egg production in Drosophila, a heterotic trait (Robertson, 1957), was improved by RRS more quickly than PLS (Bell et al., 1955; Rasmuson, 1956; Brown and Bell, 1980). For the same reason, RRS was more efficient in improving litter size in pigs (Biswas and Craig, 1969; Krehbiel et al., 1971a and 1971b; Dickerson et al., 1974; Hetzer et al., 1977) and also in mice (Vinson et al., 1969).

Conversely, for the body weight, which usually has high h^2, RRS is less efficient than PLS (Bell and Moore, 1958 and 1972; Krueger et al., 1961; Stanislaw et al., 1967; Vinson et al., 1969; Wong et al., 1971; Biswas et al., 1971; Robertson, 1971; Orozco, 1972; Dickerson et al., 1974; McNew and Bell, 1974 and 1976).

RRS can more efficiently exploit non-additive genetic variance than PLS. The experiment by Kojima and Kelleher (1963) showed that RRS was effective in improving a quantitative trait on a hybrid basis, even when purebred lines did not respond to PLS because of the lack of additive variance within lines. In the experiment, egg production of crossbred Drosophila under RRS increased about 25% but the trait of purebred under PLS showed almost no change. In an experiment with fowls (Saadeh et al., 1968), cross performance (egg production) was improved under RRS, but parental strains showed less improvement. An experiment was designed by Richardson and Kojima (1965) to determine the genetic structure of two pairs of populations which had experienced earlier selection. They concluded that crossbred selection (RRS) must have exploited the new genetic variation (non-additive variance) existing in crosses in such a way that crossbred fecundity increased considerably.

RRS can exploit not only non-additive variance but also additive variance as expected in theory (Cress, 1966; Vinson et al., 1969; Bell and Moore, 1972; Orozco, 1974; Hill, 1971). As pointed out by Orozco and Bell (1974), the evidence from realized h^2 and genetic correlations suggested that RRS had utilized both additive and dominance effects, but PLS response was limited to additive effects. In almost all experiments, the purebred performance from RRS was improved when the performance of crossbred was. As an example, RRS brought about a increase in body weight of both purebred and crossbred broilers (Griesbach, 1962). The purebred broilers from selected strains increased in weight as the experiment progressed, at approximately the same rate as their crossbred. The selection apparently resulted in an accumulation of genes having an additive favorable effect on body weight. RRS failed to improve combining ability because the trait, body weight, was primarily controlled by additive genes. Krosigk et al., (1973) reported a RRS experiment in fowls using an index designed to maximize net profit. The selection responses indicated an increase of 1.5%, or about 5.5 eggs per generation in purebred for 5 generations.

When comparing RRS with PLS in using additive variance, PLS is more efficient than RRS. In almost all experiments, the improvement of purebred to RRS was lower than that to PLS (Richardson and Kojima, 1965; Saadeh et al., 1968; Bell, 1972; Calhoon and Bohren, 1974; McNew and Bell, 1976).

As expected by Comstock et al. (1949) and others, RRS is especially efficient for using overdominant gene effects. In some experiments, negative genetic change occurred in pure lines submitted to RRS, whereas crossbred from RRS exhibited genetic gain. The egg production of poultry (Calhoon and Bohren, 1974) and the postweaning growth in pigs (Bereskin and Hetzer,1981) showed this. It indicated that overdominance controlling traits had been exploited. According to Richardson and Kojima (1965), the final populations under RRS were being fixed in a complementary fashion with respect to these overdominant and/or dominant alleles. In maintaining genetic variance of traits, RRS has a certain advantage over PLS (Al-Murrani, 1974). In some experiments, additive variance of crossbreds was higher than that of purebreds (Comstock and Robinson, 1957; Stanislaw et al., 1967; Taran et al., 1971; Pirchner and Krosigk, 1973; Brown and Bell, 1980; López-Fanjul and Villaverde, 1989). A Tribolium experiment showed that h^2 of purebred (egg number) declined under PLS, but that of crossbred under RRS showed no decline. Calhoon and Bohren (1974) reported that the lines under RRS had a slightly larger realized h^2, as expected in the presence of non-additive variance.

The number of selection cycles and the base populations are important factors affecting the comparison. Theoretical studies (Dickerson, 1952; Schnell, 1961; Arthur and Abplanalp, 1964 and 1970) showed that a slow initial response could happen under RRS in certain cases. On the other hand, in theory, the larger the allelic frequency difference between the two populations, the more efficient RRS is in exploiting non-additive effects. At the same time, the larger the allelic frequency difference between the two lines, the greater the superiority of PLS over RRS in utilizing additive effects (Orozco, 1973). The lack or low magnitude of initial response under RRS may indeed be predicted when base populations have similar gene frequencies and/or the additive genes are dominant. Evidence supporting the "delayed" response is found in the same successful RRS experiments which clearly gave greater crossbred response than PLS in late generations of RRS, for example in two Drosophila experiments (Bell et al., 1955), two Tribolium experiments (Bell, 1972; Orozco and Bell, 1974) and one poultry study (Saadeh et al., 1968). In the poultry experiment, selection involving a heterotic trait (egg production) was initiated from heterogeneous base populations. The initial responses in all three cases were in favor of PLS, yet RRS cumulative response had overcome the initial lag when the experiment was terminated after 7 generations of selection. In the two Drosophila experiments, in which selection was extended to 16 and 35 generations respectively, the early advantage of PLS was lost by the 12th generation, with RRS response continuing to a higher level. Moreover, a long-term RRS experiment (Flock, 1974) indicated that replicate breeding programs based on the same source lines, with different or even identical breeding goals, may produce genetic diversification of the sub-lines which can be utilized to achieve greater over all progress.

2. Environment relative to the comparison of RRS and PLS

The relation between heterosis and environment was discussed by Lerner (1954), Sang (1956), Young (1971), Orozco (1976), Barlow (1981), Sheridan (1981) and Velasco et al. (1987). Lerner (1954) proposed the concept of genetic homeostasis, in which heterozygoses are expected to be less influenced by environmental effects than homozygoses.

Young (1971) reported that the amount of heterosis for weight of Drosophila was dependent upon both temperature and larval density. The hybrid advantage was least under optimum conditions and greatest under less desirable conditions. Krause et al. (1964) reported a RRS experiment in poultry in 3 diversified environments, and demonstrated that the genotype (crossbred and purebred) by environment interaction variance component (as a percentage of total variance), which were 10% for sexual maturity and 8% for egg production, were significant sources of variation. Another poultry experiment (Hull et al., 1963) also showed this.

Kincaid and Touchberry (1970) compared RRS with PLS in different environments. In two environments (2 levels of X-irradiations, zero and 500R), two groups of Tribolium were selected for thorax length for 30 generations. The interaction of selection method with irradiation level on genetic gain was highly significant. PLS yielded 11.9% more genetic gain per generation than RRS in the non-irradiated environment, and RRS yielded 105.8% more gain than PLS in the irradiated environment. Later, Orozco and Bell (1974) reported an experiment with Tribolium in 3 environments (optimum, mild stress or severe stress environment). Only in severe stress did RRS response significantly exceed that of PLS. They concluded that PLS response was limited to additive gene effects, but RRS had utilized both additive and dominant effects because crosses combining non-additive gene effects from RRS had a ability to resist severe stress environments. The experiment by Carbonell-Guevara (1974) further demonstrated that RRS was very efficient in building up non-additive genetic complexes to resist stress in the line selected in the stress environment.

3. Genetic correlation between purebred and crossbred performance (r_{pc})

An important genetic parameter in discussing the merits of PLS and RRS is the genetic correlation between purebred and crossbred performance (r_{pc}). The reports about r_{pc} are summarized in Table 2. Bell (1982) suggested r_{pc} as the most reliable indicator of the relative emphasis to give to purebred versus crossbred information when selecting for crossbred performance.

Most of r_{pc} values are moderate to high positive. A high positive r_{pc} indicates the relative higher importance of additive variance (Biswas and Craig, 1969). It suggests that the performance of crossbred can efficiently be improved as a correlated response to PLS for purebred improvement, because the crossbred response to PLS is dependent upon the genetic covariance between additive effects in purebred and crossbred (Griffing, 1962; Hale and Clayton, 1965; Salah et al., 1969; Dunn et al., 1970; Wong et al., 1971; Bell and Moore, 1972; Singh and Dev, 1974; Ayyagari et al., 1982; Brah et al., 1987). Some experiments showed a low positive r_{pc} for some traits (Krause et al., 1965; Taylor et al., 1965; Biswas and Craig, 1969; Pirchner and Mergl, 1977; Singh et al., 1983). A negative r_{pc} was found in some studies (Bowman, 1960; Enfield and Rempel, 1962; Wilson et al., 1962; Taylor et al., 1965; Pirchner and Mergl, 1977; Brown and Bell, 1980). A low and negative r_{pc} is favorable

TABLE 2. A list of experimental values of r_{pc}.

Species	References	Methods	Traits	r_{pc}
Poultry	Comstock and Robinson, 1957	RRS	8-week weight	0.6 (average)
	Hale and Clayton, 1965	Diallel crossing	Egg production	0.87
			Pullet weight	0.88
			Age at 1st egg	0.92
			Egg weight	0.79 (average)
	Krause et al., 1965	RRS	Sexual maturity	0.17 (& 0.24)
			Egg percentage production	0.26
	Biswas and Craig, 1969	RRS	Rate of laying to 260 days	0.92-0.96
			Age at first egg	0.70-0.89
	Taran et al., 1971	RRS	Egg number	0.66
			Egg weight	0.70
			Body weight	0.71
	Pirchner and Krosigk, 1973	PLS & crossing	Body weight	0.88-0.97
			Age at 1st egg	0.55-0.79
			Egg number	0.32-0.72
			Egg weight	0.77-0.99
	Singh and Dev, 1974	Crossing test	Age at 1st egg	0.78
			Egg production	0.85
			Egg weight	0.81
			Body weight	0.64
	Pirchner and Mergl, 1977	RRS	Egg production	-0.10 to 0.38
	Rabsztyn, 1979	Crossing	Body weight	0.92
			Egg weight	0.49
			Egg production	0.46
	Singh et al., 1983	Diallel cross	10-day body weight	0.36
			Shank length	0.17
			Keel length	0.10
			Breast angle	0.15
	Mielen and Muller, 1989	RRS	Egg production	0.38-0.63
			Egg weight	0.62-0.96
			Body weight	0.68-0.94

(continued Table 2)

Sheep	Salah et al., 1969	PLS & crossing	Weaning weight	0.82
	Hupp, 1977	RS	Growth rate	0.0 (realized)
Pigs	Robinson et al., 1964	Crossing	140-day weight	0.22 & 0.72
			140-day backfat thickness	0.21 and >1
			Litter size	-0.74
			Number of pigs raised	< -1.0
	Taylor et al., 1965			
			Litter size and litter weight at birth and weaning	0 & negative for 4 traits
	Stanislaw et al., 1967	RRS & PLS		
			56-day weight	1.61*
			Daily gain	0.0013*
			Backfat thickness	0.0023*
	Standal, 1968	Cross progeny test		
			Birth weight	0.70
			Daily gain	1.33
			Backfat thickness	0.41
			3-week weight	0.83
	Biswas et al., 1971	RRS & PLS		
			Litter size	Low, negative
			Litter weight	Low, negative
			Mean pig weight per litter	<0.44
	Wong et al., 1971	RRS & PLS		
			Litter size	0.74
			Daily gain	0.55
			Backfat probe	> 1
			Feed efficiency	0.09
			Index (4 traits)	0.47
Tribolium	Wong and Boylan, 1970	PLS & crossing	Pupa weight	0.40
	Bell and Moore, 1972	RRS & PLS	Pupa weight (2 replicates)	>0.9
Drosophila	Orozco, 1974	RRS & PLS	Rate of egg laying	0.53
	Brown and Bell, 1980	RRS & PLS	Egg number	-0.32 to -0.85 (2 populations)
Mice	Vinson et al., 1969		Body weight	around 0.7-1.0
			Litter size	negative

*** refers to Cov.**

to RRS, especially negative r_{pc} which may show overdominant gene effects in the selected trait (Bowman, 1960; McNew and Bell, 1971). Bichard and Yalcin (1964), Biswas and Craig (1969) concluded that when r_{pc} is low, PLS is not likely to improve crossbreds. Comstock (1960) pointed out that if negative r_{pc} is important, the effective genetic variance among crossbred sire families may be considerably greater than that within the populations.

When considering r_{pc} and the comparison together, it can be found out that r_{pc} is a satisfying indicator for predicting the effectiveness of RRS versus PLS. As expected in theory, a moderate to high r_{pc} is favorable to PLS. In the experiment of Bell and Moore (1972), a near perfect genetic correlation existed between purebred and crossbred (pupa weight), as evidence by purebred response, with the reciprocal lines paralleling those observed for RRS crossbred. PLS was significantly more efficient than RRS in two replications (Tables 1 and 2). In a pig experiment, Wong et al. (1971) reported r_{pc} for litter size, daily weight gain, backfat probe, feed efficiency and index (4 traits) to be 0.74, 0.55, >1, 0.09, and 0.47, respectively. Except for the feed efficiency, all other r_{pc} were moderate and high, and thus the response to PLS was higher than to RRS for the 4 traits. But for the feed efficiency (r_{pc} was low), RRS obtained a higher selection gain. In an experiment in Drosophila (Brown and Bell, 1980), values of r_{pc} in egg number were negative (-0.85 and -0.32) for the two base populations. RRS showed its advantages over PLS. In a mouse experiment (Vinson et al., 1969), the same phenomena was found.

Many authors have reported a decrease of r_{pc} after long-term PLS. Comstock and Robinson (1957) reported r_{pc} for body weight of broilers to decrease from 0.67 to 0.25 after several generations of selection. In the study of Pirchner and Von Krosigk (1973), r_{pc} appeared to decrease over a span of five generations ($b = -0.11 \pm 0.08$ and -0.16 ± 0.06, respectively in two lines). In a report on poultry (Pirchner and Mergl, 1977) r_{pc} also declined over 12 generations of RRS.

VI. DISCUSSION

1. Theory

In the early years after RRS was proposed by Comstock et al. (1949), main emphasis was on the theoretical comparison of RS with RRS (Comstock et al., 1949; Bell et al., 1952; Dickerson, 1952; Schnell, 1961; Griffing 1962 and 1963; Cress, 1966). Later, many studies comparing RRS with PLS were reported.

With regard to the limitations of these studies based on the locus model, Bowman (1959) and Hill (1970) have pointed out that the theoretical calculations at the locus level are generally based on 4 assumptions, (1) no epistasis; (2) no more than two alleles per locus; (3) linkage equilibrium; (4) an infinitely large population. It is no doubt that these assumptions decrease the practical values of the theory.

In the analysis based on quantitative genetics at animal level (Formula 9, 10 and 11), the effectiveness of RRS versus PLS depends greatly on additive and non-additive variance, and also r_{pc}. Generally, theoretical results on comparing RRS with PLS are in agreement with experiments. McNew and Bell (1976) reported that realized response rates under RRS (and PLS) were similar to those predicted in theory. In the experiment of Brown and Bell (1980), the difference between predicted and realized response in crossbred under RRS and PLS was quite small (about 20%). However, the present theory on crossbreeding such as RRS is effective only for short term selection. Up to now, all theory on RRS is based on an additive effect model (Orozco and Bell, 1974). In these selection formula for RRS and PLS (McNew and Bell, 1976), non-additive effects (dominance and epistasis) are ignored. So the theoretical discussion above is limited to an additive selection theory for a short-term response. Bell (1982) and Brown and Bell (1980) pointed out that a predictive model for the total genetic variation may not be feasible without a better understanding of the kinds and amounts of non-additive gene effects. Almost no studies on the theory of a long-term crossbred selection are to be found. Some basic concepts, such as r_{pc}, crossbred h^2, heterosis and the response to crossbred selection, still need more theoretical understanding. Krause et al. (1965) reported that the additive variance observed among crossbred progeny might contain both the additive variation found in pure-lines and the purebred's non-additive variance which was observed as additive variation in the crossbred. More authors reported that crossbreds had higher h^2 than parental purebred lines (Stanislaw et al., 1967; Vinson et al., 1969; Wong and Boylan, 1970; Orozco and Campo, 1974 and 1975; Pirchner and Mergl, 1977; Rabsztyn and Nowak, 1978). Especially when RRS continues for many cycles, the genetic parameters like h^2 and r_{pc} will obviously change in a different way from PLS (Sellier, 1982). As reported by Taran et al. (1971), the h^2 of various traits was higher when calculated on the basis of crossbred offspring than when calculated on the basis of purebred offspring. López-Fanjul and Villaverde (1989) reported that inbreeding converted a fraction of non-additive variance into additive variance.

2. Experiments

Bowman (1959), Hale and Clayton (1965) and Sellier (1982) concluded that the actual merit of breeding schemes such as RRS, relatively to PLS, appears to be questionable except in a few cases. Experiments showed that these general remarks are not adequate judgement to the two methods, because each of them has its own advantage in the use of either additive or non-additive gene effects.

There are some reasons which result in the fact that more experiments were favorable to PLS. First, RRS does not utilize additive variance as efficiently as PLS. Second, realized selection intensity could be higher in PLS than RRS. For a given total number of animals, family selection, as compared to mass selection, is known to reduce selection intensity. The selection intensity ratio of RRS/PLS is lower than 1, namely 0.4-0.8 proposed by Comstock (1961) and 0.3-0.8 by Robertson (1957). When PLS was designed as half-sib selection, RRS could give a higher response (in pig, Stanislaw et al., 1967 and Standal, 1968; in mice, Vinson et al., 1969). Third, when RRS is carried out as a progeny testing, its generation interval is twice as long as in PLS. Fourth, the selection in some experiments lasted on only for few generations. During the short period, RRS might not have showed its advantage as an effective long-term selection scheme. Finally, the population size in some experiments was not large enough for RRS. As described previously (Formula 10), when population size is small, the accuracy to select animals is lower for RRS. From formula 9, it can be seen that the effectiveness of RRS and PLS can increase by raising population size. Moreover, the purebreds under RRS have lower performance (Bell, 1972).

RRS has some advantages appealing to animal breeders. The inbreeding coefficient in purebreds under RRS is smaller than under PLS, because progeny testing makes the selection cycle twice as long as for PLS. RRS increases h^2 of the selected trait because the additive variance of crossbred may contain some non-additive variance (Comstock and Robinson, 1957; Krause et al., 1965; Stanislaw et al., 1967; Taran et al., 1971; Pirchner and Krosigk, 1973; Orozco and Bell, 1974; Orozco and Campo, 1974 and 1975; Brown and Bell, 1980; López-Fanjul and Villaverde, 1989). In the absence of linkage or negative pleiotropic effects with fitness, the ultimate effect of PLS is to exhaust additive variance (Enfield, 1979). The populations of domestic animal usually have a long PLS history. Additive variance in the populations has greatly been exploited. So, RRS can increase the variation of traits by using non-additive variance. Schell (1961) suggested that RRS should not be regarded as a shortcut, but as a way to enhance the genetic diversity of breeding stocks for the future.

Importantly, the breeding goal of RRS, selecting for hybrids, is more suitable for a commercial breeding because almost all commercial animals are crosses. Comstock (1960) pointed out that as long as our market hogs are crossbreds, the primary criterion of genetic value in breeds should be the performance of the crossbred offspring of purebreds rather than that of purebreds themselves. Also, Brascamp (1985) pointed out that the breeding goal should be defined at the level of commercial growing in pig breeding program. The studies of Merks (1988) supported the conclusion. Under PLS hybrids are only the result of commercial crossing and not the result of selection for this goal. After a long-term PLS, the crossbred response to PLS may decrease or stop because PLS cannot use non-additive genes efficiently. For example, in the Tribolium PLS experiment (Wong and Boylan, 1970), continued purebred response in pupal weight was predicted while cross response appeared to be ceasing after 22 generations of PLS.

Some mistakes in the comparison are worthy of being mentioned. First, a comparison should be based on the crossbred under RRS and PLS because the breeding goal is to improve crossbreds (Calhoon and Bohren, 1974). In fact, some experiments were designed to compare crossbred under RRS with purebred under PLS. Second, to keep the comparable basis both types of populations should be derived from a common base population. This design can decrease the error from different base populations. In fact, almost no experiment was available on this point except one reported by Hetzer et al. (1977). Limited number of selection generations and population size also reduces the effectiveness of these experiments. In the experiments (Krueger et al., 1961; Hansson and Lindkvist, 1962; Saadeh et al., 1968; Vinson et al., 1969; Biswas et al., 1971; Krehbiel et al., 1971a and 1971b; Calhoon and Bohren, 1974), the selection was made only for 2 to 7 cycles.

3. Environment

Experiments demonstrated that environment*selection-method interaction is significant, and RRS is more efficient in achieving a response than PLS in adverse environments. This was explained by the assumption that hybrids have a higher ability against an adverse condition than purebreds (McDowell, 1982). Orozco (1974) proposed the E-RRS method, in which crossbreds are tested in an adverse condition and purebreds in optimal conditions. So, the use of E-RRS should depend on the breeding goal and the existing environment-genotype interaction. It is reasonable to look for effective heterozygous combinations for traits through RRS in adverse environments, such as a tropic area.

4. Genetic correlation between purebred and crossbred performance (r_{pc})

For the traits with high r_{pc}, their h^2 usually was high because large additive variance (Wilson et al., 1962; Robinson et al., 1964; Vinson et al., 1969; Robertson, 1971; Ameli, 1989). Many authors indicated that crossbred selection schemes are not necessary when r_{pc} is positive and high, and PLS followed by crossing is a better scheme (Biswas and Craig, 1969; Robertson, 1971; Bell, 1982; Sellier, 1982). But, experimental evidence does not completely support this view because r_{pc} may change (usually decrease) during long-term selection (Comstock and Robinson, 1957; Pirchner and Krosigk, 1973; Pirchner and Mergl, 1977). Wong and Boylan (1970) found out that, after a long-term PLS in two lines, the improvement of crossbreds might not continue, even when improvement continued within the lines. During the initial PLS period, the additive genes are more rapidly approaching fixation, and non-additive gene effects become important for the trait later. Thus, r_{pc} will be decreased by PLS. Pirchner and Mergl (1977) reported that the decline of r_{pc} indicates overdominance as a cause of heterosis. Pirchner and Krosigk (1973) stressed that if r_{pc} changes over relatively short periods, as appears possible, indices would have to be frequently reconstructed.

Moreover, some estimates of r_{pc} were not so accurate due to the limits of experiments, such as population size (Robertson, 1959). Biswas et al. (1971) used only 3 - 4 breeding sires; Krause et al. (1965) 22 and 24 sires for two lines; Salah et al. (1969) fewer than 10 sires on average.

5. Modified RRS methods

There are several modified RRS methods, each of which has its own advantages. To a great extent, modified RRS is more efficient than RRS (Krause et al., 1964; Kincaid and Touchberry, 1970; Krehbiel et al., 1971; Orozco, 1974; Moreno-Gonzàlez and Grossman, 1976; Hetzer et al., 1977; Brown and Bell, 1980; Moreno-Gonzàlez, 1986). Especially, the modified RRS experiments, in which both purebred and crossbred performance were considered, all showed higher response than RRS and/or PLS (Krehbiel et al., 1971; Hetzer et al., 1977; Brown and Bell, 1980).

6. Combining PLS with RRS

An important finding is that RRS and PLS are not contradictory but complementary selection methods, because they are efficient in using different variances (Hansson and Lindkvist, 1962; Vinson et al., 1969). According to Bell (1982), during the past 25-30 years there has been an enormous increase in the use of controlled hybridization for improving commercial livestock and poultry. While animal breeders agree that an optimum combination of individual and family selection provides maximum genetic gain in purebreds, there is no agreement as to the most effective method of improving crossbreds. Many scientists have tried to combine purebred with crossbred selection scheme for improving hybrids. The basic principle of this has been considered by Hill (1971) and Sellier (1982). There are essentially two "families" of breeding programme for obtaining good hybrids. In the first family, emphasis is given on selection within lines. In the second family, in the simplest case, one starts with a pair of lines known to be a good cross combination, and then selection is made within the lines with the objective to improve their crosses. The two approaches are not entirely independent of each other, and, in real situations, mixture of the two generally occurs. Bichard et al. (1986) also mentioned the combination of breeds or lines into an optimum crossbreeding system to exploit both the strengths of each line and the heterosis expressed in some traits. So hybrid breeders can continue to exploit both between- and within-line variation. Ameli (1989) pointed out this idea based on a long-term RRS experiment. The main types of the combination are discussed below.

(a) Method 1: The combination of PLS with crossing is a popularly used breeding scheme (Legates and Politiek, 1971; Cahaner and Siegel, 1986). During the period of PLS, additive variance is well exploited, and in the final phase, non-additive variance is used through crossing. The breeding scheme utilizes non-additive and additive variance in separated periods. Clearly, it is not an optimum strategy to exploit non-additive variance because, during a long period of PLS, no consideration is given to non-additive variances. It can be imagined that many valuable non-additive genes are lost during the PLS period. Commercial crossing utilizes only a limited part of non-additive genes. Tijen (1976) emphasized that capitalising on heterosis is only possible if one selects at the same time. Similarly, the scheme is not very efficient for a trait primarily governed by non-additive genes, such as litter size in pigs (Wilson et al., 1962; Robinson et al., 1964; Louca and Robison, 1967) and egg production in poultry (Goto and Nordskog, 1959; King, 1961; Wearden et al., 1965; King, 1971; Sato and Nordskog, 1977; Rabsztyn and Nowak, 1978).

(b) Method 2. In the system, RRS is used to improve those traits in which non-additive genes play an important role, and PLS to improve other traits in which additive genes are significant. Over a number of generations, good crosses may be produced through crossing the two lines. This scheme has not been carried out in practice. King (1961) suggested that selection should be for specific combining ability for egg production and viability, and with most of the selection for other traits within lines involved. Here, the consideration is given to both additive and non-additive effects. A heterotic trait indicates only that additive variance is relatively less important. It is still necessary to pay an attention to additive effects, even when the emphasis is given to non-additive effects.

(c) Method 3 (Modified RRS Method 2, M-RRS). Under M-RRS, additive and non-additive variance are both considered, and with the expectation that they can be utilized at the same time. Tow experiments (Krehbiel et al., 1971; Hetzer et al., 1977) showed that the response to M-RRS was higher than that to PLS. In theory, the mean of crossbred and purebred performance is not an optimal index. When a trait has extremely high h^2 and is almost completely governed by additive genes, the information from crosses should be less important than that from purebreds. As an example, Ameli et al. (1988) used M-RRS to replace RRS in the last period of a long-term RRS experiment. They reported that the change from RRS to M-RRS had decreased heterosis for egg production. This result was in agreement with the thinking that M-RRS decreased the selection power for non-additive variance relative to RRS.

(d). Method 4 (Modified RRS Method 4, PS-RRS). PC-RRS is also designed to consider both additive and non-additive variance. The experiment of Brown and Bell (1980) showed that PC-RRS was better than both PLS and RRS in improving hybrids. However, with this scheme, it is not altogether clear as to the kind of gene effects involved, or how they are utilised.

Moreover, some authors tried to combine both purebred and crossbred information into a selection index (Henderson, 1963; Jakubec et al., 1974) in order to obtain the highest response. The index has been used in some experiments. Singh and Dempfle (1989) included the information on individual, dams, purebred full- and half-sibs and crossbred paternal and maternal half-sibs. This idea is valuable, and should be developed. Information is needed on the genetic parameters to be used in a selection index to improve crossbreds, and how the parameters should be used. Also, the following questions need to be answered. What is the result when comparing the two selection indices (with and without crossbred information) in theory and experiments ? Is it correct to derive a selection index including crossbred information by the method as described by Hazel (1943) ?

VII. CONCLUSION

In comparison of PLS and RRS, (1) Slightly more experiments favored to PLS; RRS was better than PLS when they were both designed as a progeny test. (2) PLS is better for using additive variance. RRS can exploit both additive and non-additive variance, and is more efficient for using non-additive variance. So, the 2 selection methods are not contradictory but complementary. A combination of RRS with PLS could be the most efficient method. (3) RRS is suitable for long-term selection programmes. During the initial few generations of RRS, the response is usually slow. After a "lag" period, the genetic gain will increase. (4) The effectiveness of RRS and PLS greatly depends on the amounts and kinds of genetic variance. The h^2 and r_{pc} are suitable parameters for evaluating the effectiveness of the 2 methods. (5) Almost all experiments showed that purebreds under RRS had poorer performance than under PLS. This can be explained on the basis that RRS uses less additive variance and/or RRS uses overdominant effects, and makes the lines diversify. (6) In an adverse environment RRS is more efficient the PLS in making selection response. (7) After long-term selection, r_{pc} may change (usually decrease) after long-term selection. (8) Modified RRS schemes have shown an advantages over RRS. (9) The current theory on RRS is based on an additive model, and is suitable only for a short-term selection. RRS theory to deal with long-term selection has not yet been developed. (10) Information from both purebreds and crossbreds is important for improving crosses. Maximum selection response in crossbreds may be obtained only when proper weighing parameters are given to purebred and crossbred performance in a selection index designed to aim at the best hybrids.

ACKNOWLEDGEMENT

We are indebted to Prof. E.W. Brascamp and Ir. J.H.J. van der Werf with whom we discussed this paper, and also Prof. W.G. Hill who read this review and gave his valuable comments.

REFERENCES

Al-Murrani, W.K. (1974). The limits to artificial selection. Animal Breeding Abstracts 42,587-592.

Ameli, H. (1989). Inzucht-und heterosiseffekte sowie genetische parameter in zwei langjährig reziproker rekurrenter selektion unterworfenen weissen leghornlinien (LSL) und ihren reziproken kreuzungen. [Inbreeding and heterosis effects and genetic parameters in two White Leghorn (LSL) lines and their reciprocal crosses after long-term reciprocal recurrent selection]. Ph.D Dissertation, Aus dem Institut für Tierzucht und Haustiergenetik der Georg-August-Universität Göttingen, Göttingen.

Ameli, H.; Flock, D.K.; Glodek, P. (1988). Inbreeding and heterosis in SC white leghorns after long-term reciprocal recurrent selection. Proceedings of the 18th World Poultry Congress, Nagoya, Japan, 1988, S,369-371.

Andrews, L.D.; Stephenson, A.B. (1970). Recurrent selection in the domestic fowl. Poultry Science 49,361-368.

Arthur, J.A. (1986). An evaluation of industry breeding programs for egg type chickens. Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production 10,325-335.

Arthur, J.A.; Abplanalp, H. (1964). Studies using computer simulation of reciprocal recurrent selection. Genetics 50,233.

Arthur, T.A.; Abplanalp, H. (1970). Computer simulation of reciprocal recurrent selection with overdominant gene action. Animal Production 12,639-649.

Ayyagari, V.; Mohapatra, S.C.; Renganathan, P.; Johri, D.C.; Thiagasundaram, T.S.; Panda, B.K. (1982). Cross performance as influenced by selection in pure lines. British Poultry Science 23,469-479.

Barker, J.S.F. (1974). The state of information concerning deviations from additivity of gene effects. Proceedings of the 1st World Congress on Genetics Applied to Livestock Production 1,373-383.

Barlow, R. (1981). Experimental evidence for interaction between heterosis and environment in animals. Animal Breeding Abstracts 49,715-737.

Bell, A.E. (1972). More on reciprocal recurrent selection. Proceedings of the 21st national Breeders' Roundtable, Kansas City, 1972, pp.18-51.

Bell, A.E. (1982). Selection for heterosis--results with laboratory and domestic animal. Proceedings of the 2nd World Congress on Genetics Applied to Livestock Production 6,206-227.

Bell, A.E.; Moore, C.H. (1958). Further comparisons of reciprocal recurrent selection with conventional methods of selection for the improvement of quantitative characteristics. Proceedings of the Xth International Congress of Genetics 2 (Abstracts), 20-21.

Bell, A.E.; Moore, C.H. (1972). Reciprocal recurrent selection for pupal weight in Tribolium in comparison with conventional methods. Egyptian Journal of Genetics and Cytology 1,92-119.

Bell, A.E.; Moore, C.H.; Bohren, B.B.; Warren, D.C. (1952). Systems of breeding designed to utilize heterosis in the domestic fowl. Poultry Science 31,11-22.

Bell, A.E.; Moore, C.H.; Warren, D.C. (1950). Systems of breeding designed to give maximum heterosis in chickens. Poultry Science 29,749.

Bell, A.E.; Moore, C.H.; Warren, D.C. (1955). The evaluation of new methods for the improvement of quantitative characteristics. Cold Spring Harbor Symposia on Quantitative Biology 20,197-212.

Bereskin, B.; Hetzer, H.O. (1981). Reciprocal recurrent selection in swine: postweaning growth. Journal of Animal Science 53,1446-1457.

Bichard, M.; David, P.J.; Bovey, M. (1986). Selection between and within lines and cross-breeding strategies for worldwide production of hybrids. Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production 10,130-142.

Bichard, M.; Yalcin, B.C. (1964). Crossbred sheep production. III. Selection for growth rate and carcass attributes in the second-cross lamb. Animal Production 6,179-182.

Biswas, D.K.; Chapman, A.B.; First, N.L.; Self,H.L. (1971). Intrapopulation versus reciprocal recurrent selection in swine. Journal of Animal Science 32, 840-848.

Biswas, D.K.; Craig, J.V. (1969). Relationship between purebred and crossbred paternal half-sisters' performance in chickens. Poultry Science 48,524-526.

Bowman, J.C. (1959). Selection for heterosis. Animal Breeding Abstracts 27,261-273.

Bowman, J.C. (1960). Recurrent selection. I. The detection of overdominance. Heredity 14, 197-206.

Bowman, J.C. (1962). Recurrent selection. II. An experimental study with mice and Drosophila. Genetical Research 3,333-351.

Brah, G.S.; Chaudhary, M.L.; Sandhu, J.S. (1987). Cross-line productivity in relation to selection in pure-line White Leghorns. Journal of Animal Breeding and Genetics 104,391-396.

Brascamp, E.W.; Merks, J.W.M.; Wilmink, J.B.M. (1985). Genotype environment interaction in pig breeding programmes: methods of estimation and relevance of the estimates. Livestock Production Science 13,135-146.

Brown, W.P.; Bell, A.E. (1980). An experimental comparison of selection alternatives to plateaued response. Genetics 94,477-496.

Cahaner, A.; Siegel, P.B. (1986). Evaluation of industry breeding programs for meat-type chickens and turkeys. Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production 10,337-345.

Calhoon, R.E.; Bohren, B.B. (1974). Genetic gains from reciprocal recurrent and within-line selection for egg production in the fowl. Theoretical and Applied Genetics 44,364-372.

Carbonell-guevara, E. (1974). Reciprocal recurrent selection in Tribolium: problems of long term selection. Proceedings of the 1st World Congress on Applied Livestock Production 3,533-539.

Comstock, R.E. (1960). Problems and evidence in swine breeding. Journal of Animal Science 19,75-83.

Comstock, R.E. (1961). Reciprocal recurrent selection with reference to swine breeding. 22nd Annual Report, Regional Swine Breeding Lab., U.S.D.A., Ames, Iowa.

Comstock, R.E.; Robinson, H.F. (1957). Findings relative to reciprocal recurrent selection. Proceedings of International Genetics Symposium. Science Council of Japan, Tokyo, pp.461-464.

Comstock, R.E.; Robinson, H.F.; Harvey, P.H. (1949). A breeding procedure designed to make maximum use of both general and specific combining ability. Agronomy Journal 41,360-367.

Cress, C.E. (1966). A comparison of recurrent selection systems. Genetics 54,1371-1379.

Crow, J.F. (1953). Theoretical considerations of reciprocal recurrent selection and recurrent selection compared to other breeding methods. Proceedings of American Poultry Breeders' Roundtable, 1953.

Dickerson, G.E. (1952). Inbred lines for heterosis ? In: Heterosis. (Edited by J.W. Gowen). Iowa State College Press. Iowa, USA. pp.330-351.

Dickerson, G.E.; Hetzer, H.O.; Krehbiel, E.V.; Flower, A.E. (1974). Effectiveness of reciprocal selection for performance of crosses between Montana No. 1 and Yorkshire swine. III. Expected and actual response. Journal of Animal Science 39,24-41.

Dunn, R.J.; Magee, W.T.; Gregory, K.E.; Cundiff, L.V.; Koch, R.M. (1970). Genetic parameters in straightbred and crossbred beef cattle. Journal of Animal Science 31,656-663.

Enfield, F.D. (1979). Long term effects of selection: The limits to response. In: Selection Experiments in Laboratory and Domestic Animals (proceedings of a symposium held at Harrogate). (Edited by A.F.R.S.Robertson). UK, 1979, pp.69-80.

Enfield, F.D.; Rempel, W.E. (1962). Covariance of sire effects in purebred and crossbred populations of swine. Journal of Animal Science 21,971 (abstract).

Falconer, D.S. (1981). Introduction to Quantitative Genetics. New York, USA. Longman Group Limited, 1981.

Flock, D.K. (1974). Recent results on advantages of reciprocal recurrent selection (R.R.S) within split populations of White Leghorn strains. Proceedings of the 1st World Congress on Genetics Applied Livestock Production 1,925-930.

Goto, E.; Nordskog, A.W. (1959). Heterosis in poultry. IV. Estimation of combining ability variance from diallel crosses of inbred lines in the fowl. Poultry Science 38,1381-1388.

Griesbach, L. (1962). A test of the reciprocal recurrent selection technique with chicken broilers. Canadian Journal of Animal Science 42,145-157.

Griffing, B. (1960). Theoretical consequences of truncation selection based on the individual phenotype. Australian Journal of Biology Science 13,307-343.

Griffing, B. (1962). Prediction formulae for general combining ability selection methods utilizing one or two random-mating populations. Australian Journal of Biology Science 15,650-665.

Griffing, B. (1963). Comparisons of potentials for general combining ability selection methods utilizing one or two random-mating populations. Australian Journal of Biology Science 16,838-862.

Hale, R.W.; Clayton, G.A. (1965). A diallel crossing experiment with two breeds of laying fowl. British Poultry Science 6,153-174.

Hansson, A.; Lindkvist, G. (1962). Selection for general and specific combining ability with regard to body weight in mice. Kungl. Lantbrukshögskolans Annaler 28,215-233.

Hazel, L.N. (1943). The genetic basis for constructing selection indexes. Genetics 28,476-490.

Heisdorf, A. (1950). Reciprocal recurrent selection. Proceedings of the 3rd Pacific Northwest Poultry Breeders' Roundtable. Vancouver,B.C., Canada.

Henderson, C.R. (1953). Estimation of variance and covariance components. Biometrics 9, 226-252.

Henderson, C.R. (1963). Selection index and expected genetic advance. In: Statistical Genetics and Plant Breeding. (Edited by W.D. Hanson and H.F. Robinson). National Academy of Science--National Research Council, Publication 982, Washington D.C. pp.141-163.

Hetzer, H.D.; Miller, R.H.; Kling, R.C. (1977). Effectiveness of RRS for improving preweaning performance in swine. Journal of Animal Science 45,989-1009.

Hill, W.G. (1970). Theory of limits to selection with line crossing. In: Mathematical Topics in Population Genetics. (Edited by K.Kojima). Berlin, Heidelberg, New York. Springer-Verlag. 1970, pp.210-245.

Hill, W.G. (1971). Theoretical aspects of crossbreeding. Annales Génétique et de Sélection Animale 3,23-34.

Hull, F.H. (1945). Recurrent selection for specific combining ability in corn. Journal of the American Society of Agronomy 37,134-145.

Hull, F.H. (1952). Recurrent selection and overdominance. In: Heterosis. (Edited by J.W. Gowen). Iowa State College Press. Iowa, USA. pp.451-473.

Hull, P.; Gowe, R.S.; Slen, S.B.; Crawford, R.D. (1963). A comparison of the interaction, with two types of environment, of pure strains or strain crosses of poultry. Genetical Research 4,370-381.

Hupp, H.D. (1977). Recurrent selection for increased growth rate in Hampshire sheep. Dissertation Abstracts International B. 38,977.

Jakubec, V.; Podebradsky, Z.; Pichova, J.; Hyanek, J. (1974). Construction and use of selection indices for populations in broiler production. Proceedings of the Working Symposium on Breed Evaluation and Crossing Experiments with Farm Animals, Zeist, 1974, pp.55-66.

Jull, M.A. (1952). Reciprocal recurrent selection. In: Poultry Breeding (3rd edition), New York, 1952, pp.375-376.

Kincaid, H.L.; Touchberry, R.W. (1970). Long term RRS selection study in D. Melanogaster. Journal of Animal Science 31,165.

King, J.W.B. (1971). Crossbreeding of pig and poultry. Proceedings of the Xth International Congress on Animal Production, Paris-Versaillers, pp.117-130.

King, S.C. (1961). Inheritance of economic traits in the regional cornell control population. Poultry Science 40,975-986.

Kojima, K.; Kelleher, T.M. (1963). A comparison of purebred and crossbred selection schemes with two populations of Drosophila Pseudoobscura. Genetics 48,57-72.

Krause, E.; Yamada, Y.; Bell, A.E. (1964). An evaluation of genotype by environment interaction in populations of chicks under reciprocal recurrent selection. Genetics 43,1334-1335.

Krause, E.; Yamada, Y; Bell, A.E. (1965). Genetic parameters in two populations of chickens under reciprocal recurrent selection. British Poultry Science 6,197-206.

Krehbiel, E.V.; Hetzer, H.O.; Flower, A.E.; Dickerson, G.E.; Harvey, W.R.; Swiger, L.A. (1971a). Effectiveness of reciprocal selection for performance of crosses between Montana No. 1 and Yorkshire swine. I. Preweaning traits. Journal of Animal Science 32,191-210.

Krehbiel, E.V.; Hetzer, H.O.; Flower, A.E.; Dickerson, G.E.; Harvey, W.R.; Swiger, L.A. (1971b). Effectiveness of reciprocal selection for performance of crosses between Montana No. 1 and Yorkshire swine. II. Postweaning traits. Journal of Animal Science 32,211-224.

Krosigk, C.M. von.; Havenstein, G.B.; Flock, D.K.; McClary, C.F. (1973). Estimates of response to selection in populations of White Leghorns under reciprocal recurrent selection. Proceedings of the 4th European Poultry Conference, London, pp.265-271.

Krueger, W.F.; Ryan, C.B.; Williams, J.D.; Quisenberry, J.H. (1961). Three cycles of intra and cross-line selection for a high and a low heritability trait. Poultry Science 40,1422 (abstract).

Legates, J.E.; Politiek, R.D. (1971). Optimum utilization of genetic material, with special reference to crossbreeding in relation to other methods of genetic improvement. Proceedings of the 10th International Congress on Animal Production. pp.83-91.

Legates, J.E. (1988). Developments in theory and application of animal breeding. In: Advances in Animal Breeding: Proceedings of the World Symposium in Honour of Professor R.D. Politiek. (Edited by S. Korver et al.). Wageningen Pudoc, Netherlands, 1988, pp.15-26. Lerner, I.M. (1954). Genetic Homeostasis. Edinburgh and London, UK. Oliver and Boyed. 1954.

López-Fanjul, C.; Villaverde, A. (1989). Response to artificial selection for a non-additive trait in inbred and non inbred lines of Drosophila. The 40th Annual Meeting of the European Association for Animal Production, Dublin, Ireland, 1989, 1 (summaries),223.

Louca, A.; Robison, O.W. (1967). Components of variance and covariance in purebred and crossbred swine. Journal of Animal Science 26,267-273.

McDowell, R.E. (1982). Crossbreeding as a system of mating for dairy production. Southern Cooperative Series Bulletin No.259, July 1982.

McNew, R.W.; Bell, A.E. (1971). The nature of the purebred-crossbred genetic covariance. Genetical Research 18,1-7.

McNew, R.W.; Bell, A.E. (1974). Crossbred response from purebred selection, an experimental check on selection theory with Tribolium. Theoretical and Applied Genetics 44,100-105.

McNew, R.W.; Bell, A.E. (1976). Comparison of crossbred and purebred selection for a heterotic trait in highly selected populations of Tribolium. The Journal of Heredity 67,275-283.

Merks, J.W.M. (1988). Genotype * Environment interactions in pig breeding programmes. PhD thesis, Wageningen Agricultural University, The Netherlands.

Mielenz, N.; Müller, J. (1989). Schätzung genetischer Korrelationskoeffizienten zwischen Reinzucht- und Kreuzungsleistungen bei Legehennen. [Estimation of genetic correlations between performances of purebred and crossbred laying hens]. Archiv für Tierzucht 32,79-91.

Moreno-Gonzàlez, J. (1986). Choice of environments in reciprocal recurrent selection programs. Theoretical and Applied Genetics 71,652-656.

Moreno-Gonzàlez, J.; Grossman, M. (1976). Theoretical modifications of reciprocal recurrent selection. Genetics 84,95-111.

Orozco, F. (1972). Influence of fitness deterioration on selection limits. Annales de Génétique et de Sélection Animale 7,569-592

Orozco, F. (1973). Additive gains in reciprocal recurrent selection. Genetics 74, s204-s205(abstract).

Orozco, F. (1974). Selection for egg production and related economic traits. Proceedings of the 1st World Congress on Genetics Applied to Livestock Production 1,941-949.

Orozco, F. (1976). Heterosis and genotype-environment interaction: theoretical and experimental aspects. Animal

Breeding Abstracts 45,449.

Orozco, F.; Bell, A.E. (1974). Reciprocal recurrent selection compared to within-strain selection for increasing rate of egg lay of Tribolium under optimal and stress conditions. Genetics 77,143-161.

Orozco, F.; Campo, J.L. (1974). A comparison of purebred and crossbred genetic parameters in layers. Proceedings and Abstracts of the 15th World's Poultry Congress and Exposition, pp.161-162.

Orozco, F.; Campo, J.L. (1975). A comparison of purebred and crossbred genetic parameters in layers. World's Poultry Science Journal 31,149-153.

Orozco, F.; Campo, J.L.; Fuentes, M.C.; Lopez-Fanjul, C.; Tagarro, P. (1979). A comparison between crossbreeding and index selection for the simultaneous improvement of two traits in Tribolium Castaneum. In: Selection Experiments in Laboratory and Domestic Animals: Proceedings of a Symposium held at Harrogate. (Edited by A.F.R.S. Robertson). UK, 1979, pp.37-52.

Pirchner, F.; von Krosigk, C.M. (1973). Genetic parameters of cross- and pure-bred poultry. British Poultry Science 14,193-202.

Pirchner, F.; Mergl, R. (1977). Overdominance as cause for heterosis in poultry. Journal of Animal Breeding and Genetics 94,151-158.

Rabsztyn, A. (1979). Genetic correlations between sire's purebred and crossbred progeny performance for the same trait in chickens. Genetica Polonica 20,425-429.

Rabsztyn, A.; Nowak, J. (1978). A comparative study on genetic, environmental and phenotypic variances and on heritability of some performance traits in purebred hen strains and their reciprocal crosses. Genetica Polonica 19,193-199.

Rasmuson, M. (1956). Recurrent reciprocal selection: Results of three model experiments on Drosophila for improvement of quantitative characters. Hereditas 42,397-414.

Richardson, R.H.; Kojima, K. (1965). The kinds of genetic variability in relation to selection responses in Drosophila fecundity. Genetics 52,583-598.

Robertson, A. (1959). The sampling variance of the genetic correlation coefficient. Biometrics 15,469-485.

Robertson, A. (1971). Optimum utilization of genetic material, with special reference to cross-breeding in relation to other methods of genetic improvement (Introduction report). Proceedings of the Xth International Congress on Animal Production. Paris-Versaillers, pp.57-68.

Robertson, A. (1957). Optimum group size in progeny testing and family selection. Biometrics 13,442-450.

Robertson, F.W. (1957). Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production in Drosophila melanogaster. Journal of Genetics 55,428-443.

Robinson, O.W.; Louca, A.; Legales, J.E. (1964). Purebred and crossbred performance of paternal half-sibs of swine. Journal of Animal Science 23,854 (abstract).

Saadeh, H.K.; Craig, J.V.; Smith, L.T.; Wearden, S. (1968). Effectiveness of alternative breeding systems for increasing rate of egg production in chickens. Poultry Science 47,1057-1072.

Salah, E.; Galal, E.; Hazel, L.N.; Sidwell, G.M.; Terrill, C.E. (1969). Correlation between purebred and crossbred half-sibs in sheep. Journal of Animal Science 30,475-480.

Sang, J.H. (1956). Hybrid vigour and animal production. Animal Breeding Abstracts 24,1-6.

Sato, M.; Nordskog, A.W. (1977). On estimating components of genetic variance in Diallel matings. British Poultry Science 18,699-704.

Schnell, F.W. (1961). On some aspects of reciprocal recurrent selection. Euphytica 10,24-30.

Sellier, P. (1970). Hètèrosis et croisement chez le porc. [Heterosis and crossbreeding in swine]. Annales de Génétique et de Sélection Animale 2,145-207.

Sellier, P. (1982). Selecting populations for use in crossbreeding. Proceedings of the 2nd World Congress on Genetics Applied to Livestock Production 6,15-49.

Sheridan, A.K. (1981). Crossbreeding and heterosis. Animal Breeding Abstracts 49,131-144.

Siegel, P.B. (1988). Future breeding programs in poultry. In: Advances in Animal Breeding: Proceedings of the

World Symposium in Honour of Professor R.D. Politiek. (Edited by S. Korver et al.). Wageningen Pudoc, Netherlands, 1988, pp.107-115.

Singh, B.P.; Chaudhary, R.P.; Ahlawat, S.P.S.; Singh, R.V. (1983). A note on the estimate of genetic correlations between purebred and crossbred half-sibs for some broiler characters. Avian Research 67,60-61.

Singh, H.; Dev, D.S. (1974). Genetic correlation between performance of purebred White Leghorn pullets and their paternal half-sisters from Rhode Island Red dams. British Poultry Science 15,513-515.

Singh, R.P.; Dempfle, A.L. (1989). Optimising multistage selection in a modified reciprocal recurrent selection program considering cost and rate of genetic progress. The 40th Annual Meeting of the European Association for Animal Production. Dublin, Ireland, Volume 1 (summaries),167.

Standal, N. (1968). Studies on breeding and selection schemes in pigs I. Selection on performance of purebred versus crossbred progeny. Acta Agriculturae Scandinavica 18,222-232.

Stanislaw, C.M.; Omtvedt, I.T.; Willham, R.L.; Whatley Jr, J.A. (1967). A study of some genetic parameters in purebred and crossbred populations of swine. Journal of Animal Science 26,16-20.

Taran, M.; Gabriel, E.; Moses, E.; Soller, M. (1971). Performance of purebred and crossbred progeny of White Leghorn and New Hampshire sires. British Poultry Science 13,331-339.

Taylor, J.C.; Miller, R.H.; Hetzer, H.O. (1965). Genetic correlations between straightbred and crossbred swine. Journal of Animal Science 24,852.

Tijen, W.F. van. (1976). Crossbreeding in poultry. World's Poultry Science Journal 33,105-110.

Velasco, T.; Toro, M.A.; Fuentes, M.C. (1987). Heterosis and genotype-environment interaction: an experimental study with Tribolium castaneum. Journal of Animal Breeding and Genetics 104,273-282.

Vinson, W.E.; Eisen, E.J.; Robison, O.W. (1969). Predicted response to selection for crossbred performance in mice. Journal of Animal Science 28,725-733.

Wearden, S.; Tindell, D.; Craig, J.V. (1965). Use of a Full Diallel Cross to estimate general and specific combining ability in chickens. Poultry Science 44,1043-1053.

Wilson, S.P. van; Whatley Jr, J.A.; Whiteman, J.V.; Morrison, R.D. (1962). Influence of sire and line of breeding on sow productivity. Journal of Animal Science 21,119-122.

Wong, W.C.; Boylan, W.J. (1970). Intrapopulation selection and correlated response in crossbreds of Tribolium Castaneum. Genetics 64,69-78.

Wong, W.C.; Boylan, W.J.; Rempel, W.E. (1971). Purebred versus crossbred performance as a basis of selection in swine. Journal of Animal Science 32,605-610.

Young, S.S.Y. (1971). The effects of some physical and biotic environments on heterosis of direct and associate genotypes in Drosophila melanogaster. Genetics 67,569-578.

Chapter 3

Relationship between Purebred and Crossbred Parameters. I. Variances and covariances under the One-locus Model

M. Wei [a], H.A.M. van der Steen [b], J.H.J. van der Werf [a]
and E.W. Brascamp [a]

[a] Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

[b] Pig Improvement Company Ltd., Fyfield Wick, Abingdon,
Oxfordshire OX13 5NA, United Kingdom

Published in: ***Journal of Animal Breeding and Genetics 108:253-261 (1991).***
Reproduced by permission of Verlag Paul Parey, Hamburg and Berlin.

"Sire and dam component of variance in a crossbred population are generally unequal to each other in the case of unequal gene frequency of parental lines, and they are not a function of additive variances in parental populations."

Relationship between Purebred and Crossbred Parameters. I. Variances and Covariances under the One-locus Model

M. Wei[a], **H.A.M. van der Steen**[b], **J.H.J. van der Werf**[a]
and E.W. Brascamp[a]

[a] Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

[b] Pig Improvement Company Ltd., Fyfield Wick, Abingdon,
Oxfordshire OX13 5NA, United Kingdom

SUMMARY: *A one-locus model with two alleles was used to study the relationship between purebred and crossbred parameters. Sire and dam lines contribute a different amount of additive variance for their crossbreds if there is a gene frequency difference between sire and dam lines. An estimate of the heritability for a crossbred population using four times the sire component of variance does not give the ratio of additive genetic to total variance for the crossbreds. In the case of dominance, the additive variance for the crossbreds can be higher than both the variances in the parental populations because of the different gene frequencies in the two populations. The sire component of covariance between purebreds and crossbreds is not always equal to one quarter of the additive variance in sire line. The genetic regression of sires' crossbred progeny on purebred progeny depends on gene frequency and dominance effect. The absolute value of the regression is positively related to the additive variance for crossbreds contributed by the sire line. The genetic correlation between purebreds and crossbreds could not be adequately studied under the one-locus model and a study with a two-loci model will be undertaken.*

---

1. INTRODUCTION

The genetic correlation between purebred and crossbred half-sibs (r_{pc}), the regression of crossbred on purebred half-sibs (b) and the additive genetic variance for crossbreds are important parameters to optimize purebred and crossbred selection schemes in animal breeding (Bell, 1982; Sellier, 1982). They are needed to predict the selection response in a crossbred population and to evaluate different purebred and crossbred selection methods (McNew and Bell, 1971; Pirchner, 1974; Wei and Van der Steen, 1990).

Wei and Van der Steen (1990) reviewed theoretical and experimental results on the comparison of reciprocal recurrent selection with pure-line selection. Experimentally obtained values for crossbreeding parameters could not always satisfactorily be explained by theory. Firstly, many experiments have shown a higher heritability in crossbreds than in the constituting purebreds (Krause et al., 1965; Stanislaw et al., 1967; Taran et al., 1971; Pirchner and Von Krosigk, 1973; Orozco and Bell, 1974; Brown and Bell, 1980; Van der Werf, 1990). Secondly, the additive genetic variance for crossbreds was often estimated as four times the sire component of variance in the crossbred population (Hale and Clayton, 1965; Krause et al., 1965; Louca and Robison, 1967; Stanislaw et al., 1967; Standal, 1968; Vinson et al., 1969; Orozco and Campo, 1975). This procedure seems debatable because the sire component and the dam component of variance in the crossbred population are often not equal. A more theoretical basis to understand estimation of the genetic parameters in crossbreeding was felt to be lacking.

The objectives of this paper were to study the relationships between purebred and crossbred parameters, as affected by gene frequencies in the constituting purebreds and the magnitude of dominance. A one-locus model with two alleles was used.

2. METHODS

The genetic model used in this study was based on Griffing (1960 and 1962), Stuber and Cockerham (1966) and Grossman and Fernando (1989).

2.1. Model of genetic effects

One locus with 2 alleles (A_1 and A_2) was assumed. The frequency of A_i in population k is f_{ki}. The frequency of genotype A_iA_j in population k is f_{kij}. The value of genotype A_iA_j in population k is y_{kij}. The subscript k refers to population 1, 2 or 3. Population 3 is crossbred between sires of population 1 and dams of population 2. Random mating and infinite population size are assumed. Environmental effects are not considered.

The values of genotypes A_1A_1, A_1A_2 (= A_2A_1) and A_2A_2 are defined as 1, d and -1, respectively, and d is the dominance level.

The model of genotypic effects under the assumptions is,

$$y_{kij} = y_{ij} = \mu_k + \alpha_{kip} + \alpha_{kjm} + \delta_{kij} = \mu_k + A_{kij} + \delta_{kij} \qquad [1]$$

where, y_{kij} = value of genotype A_iA_j (with y_{kij} equal for all k); μ_k = population mean; α_{kip}

= additive effect of gene A_i from the sire; α_{kjm} = additive effect of gene A_j from the dam; A_{kij} = additive value of genotype A_iA_j; and δ_{kij} = dominance effect. These effects are calculated as follows,

$$\mu_k = \sum_{i=1}^{2} \sum_{j=1}^{2} \left(f_{kij} y_{ij}\right)$$

$$\alpha_{kip} = \frac{\sum_{j=1}^{2} \left(f_{kij} y_{ij}\right)}{\sum_{j=1}^{2} \left(f_{kij}\right)} - \mu_k$$

$$\alpha_{kjm} = \frac{\sum_{i=1}^{2} \left(f_{kij} y_{ij}\right)}{\sum_{i=1}^{2} \left(f_{kij}\right)} - \mu_k$$

$$\delta_{kij} = y_{ij} - \mu_k - \alpha_{kip} - \alpha_{kjm}$$

2.2. Model of genetic variances

The variance of genetic effects defined in (1) is represented as,

$$V_{yk} = V_{\alpha kp} + V_{\alpha km} + V_{\delta k} = V_{Ak} + V_{\delta k} \qquad [2]$$

where, V_{yk}, $V_{\alpha kp}$, $V_{\alpha km}$, V_{Ak} and $V_{\delta k}$ are the variance of y_{kij}, α_{kip}, α_{kjm}, A_{kij} and δ_{kij}, respectively. These variances are calculated as,

$$V_{\alpha kp} = \sum_{i=1}^{2} \left[\left(\sum_{j=1}^{2} \left(f_{kij}\right) \right) \left(\alpha_{kip}\right)^2 \right]$$

$$V_{\alpha km} = \sum_{j=1}^{2} \left[\left(\sum_{i=1}^{2} \left(f_{kij}\right) \right) \left(\alpha_{kjm}\right)^2 \right]$$

$$V_{\delta k} = \sum_{n=1}^{2} \sum_{w=1}^{2} \left[\left(\sum_{j=1}^{2} f_{knj} \right) \left(\sum_{i=1}^{2} f_{kiw} \right) \left(\delta_{knw}\right)^2 \right]$$

$$V_{Ak} = V_{\alpha kp} + V_{\alpha km}$$

It should be noted that V_{A3} is the additive genetic variance in the parental purebred lines for crossbred performance. The value of V_{A3} is equal to the sum of $V_{\alpha 3p}$ and $V_{\alpha 3m}$ which are the additive variances for crossbreds contributed by sires and dams, respectively. This parameter will be called shortly crossbred additive variance or additive variance for crossbreds.

2.3. Sire component of covariance between purebreds and crossbreds (Cov_{pc})

There are four different genotypes (A_1A_1, A_1A_2, A_2A_1 and A_2A_2) in the sire line. Sires of one particular genotype (A_iA_j) and dams of another (A_wA_n) have a progeny mean of $(1/4)(y_{iw}+y_{in}+y_{jw}+y_{jn})$. Sires of the particular genotype (A_iA_j) mated with a random sample of the dams have purebred and crossbred half-sib means (M_{1ij} and M_{3ij}), respectively, as follows,

$$M_{1ij} = \sum_{w=1}^{2}\sum_{n=1}^{2}\left[f_{1wn}\left(\frac{1}{4}\right)(y_{iw}+y_{in}+y_{jw}+y_{jn})\right]$$

$$M_{3ij} = \sum_{w=1}^{2}\sum_{n=1}^{2}\left[f_{2wn}\left(\frac{1}{4}\right)(y_{iw}+y_{in}+y_{jw}+y_{jn})\right]$$

The sire component of covariance between purebreds and crossbreds (Cov_{pc}) in this case can be calculated by the covariance between purebred and crossbred half-sib means as,

$$Cov_{pc} = \sum_{i=1}^{2}\sum_{j=1}^{2}\left[f_{1ij}(M_{1ij}-\mu_1)(M_{3ij}-\mu_3)\right] \qquad [3]$$

2.4. Correlation and regression

The sire components of variance in sire line (V_{hs_p}) and crossbred population (V_{hs_c}) have to be derived to calculate the genetic correlation between purebred and crossbred half-sibs (r_{pc}). Here, V_{hs_p} and V_{hs_c} can be calculated by the variances of paternal purebred and crossbred half-sib means, respectively, as,

$$V_{hs_p} = \sum_{i=1}^{2}\sum_{j=1}^{2}\left[f_{1ij}(M_{1ij}-\mu_1)^2\right]$$

$$V_{hs_c} = \sum_{i=1}^{2}\sum_{j=1}^{2}\left[f_{1ij}(M_{3ij} - \mu_3)^2\right]$$

The genetic correlation between purebred and crossbred half-sibs (r_{pc}) and genetic regression of crossbred progeny on purebred progeny (b) are,

$$r_{pc} = \frac{Cov_{pc}}{\sqrt{V_{hs_p} * V_{hs_c}}} \qquad [4]$$

$$b = \frac{Cov_{pc}}{V_{hs_p}} \qquad [5]$$

The correlation and regression coefficients are based on the sire component of variance and covariance, and therefore do not contain any other non-genetic components of variance.

3. RESULTS AND DISCUSSION

3.1. Additive variances for pure lines (V_{A1} and V_{A2}) and crossbred population (V_{A3})

In the absence of dominance, the crossbred additive variance (i.e., additive variance for crossbred performance in parental purebreds) is the average of the additive variances in the parental populations, i.e., $V_{A3} = (V_{A1} + V_{A2})/2$ (Table 1; Fig. 1a). With dominance, V_{A3} can be larger than $(V_{A1} + V_{A2})/2$ and sometimes larger than both V_{A1} and V_{A2} (Fig. 1b and 1c). This effect is stronger with overdominance (Fig. 1b and 1c).

In some experiments, h^2_c calculated from the sire variance in crossbreds was larger than that for the parental lines (Miquel and Cartwright, 1963; Bassett and Shelton, 1966; Wong and Boylan, 1970; Orozco and Campo, 1975; Pirchner and von Krosigk, 1973; Pirchner, 1974; McLaren, et al., 1985). This has been explained by a higher additive variance among the crossbreds containing both additive and non-additive variance found in the purebreds (Krause et al. 1965; Pirchner, 1974; Brown and Bell, 1980). This study shows that these differences in variance are due to the different gene frequencies in parental lines in combination with dominance.

3.2. Sire component of variance in crossbred population (V_{hsc})

Twice the sire component of variance in a crossbred population ($2*V_{hs_c}$) represents the crossbred additive variance contributed by sires (V_{Ap1}), and also for dam line $2*V_{hs_p} = V_{Am2}$ holds (Table 1). Four times the sire component ($4*V_{hs_c}$) has been used to estimate the additive variance for the crossbred population (Miquel and Cartwright, 1963; Hale and Clayton, 1965; Louca and Robison, 1967; Stanislaw et al., 1967; Standal, 1968; Salah et al., 1969; Wong and Boylan, 1970; Pirchner and Von Krosigk, 1973; Koger et al., 1975; Orozco and Campo, 1975; Brown and Bell, 1980). In this study, the additive variance for crossbreds (V_{A3}) was found to be equal to the sum of the additive variances contributed by sires and dams ($V_{Ap1} + V_{Am2}$). However, these contributions, V_{Ap1} and V_{Am2}, are different when the gene frequency differs between sire and dam lines (Fig. 2a, 2b and 2c). The sire component of variance estimated from crossbreds is, therefore, not an appropriate estimator of the additive variance for crossbred population. Furthermore, the additive variances for crossbreds contributed by parental lines (V_{Ap1} and V_{Am2}) are not proportional to the additive variances of the parental lines (V_{A1} and V_{A2}) (Table 1), i.e., V_{A1}/V_{A2} generally is not equal to V_{Ap1}/V_{Am2}. Additive variance in purebred lines, therefore, is not a measure of the contribution from the pure lines to the crossbred additive variance.

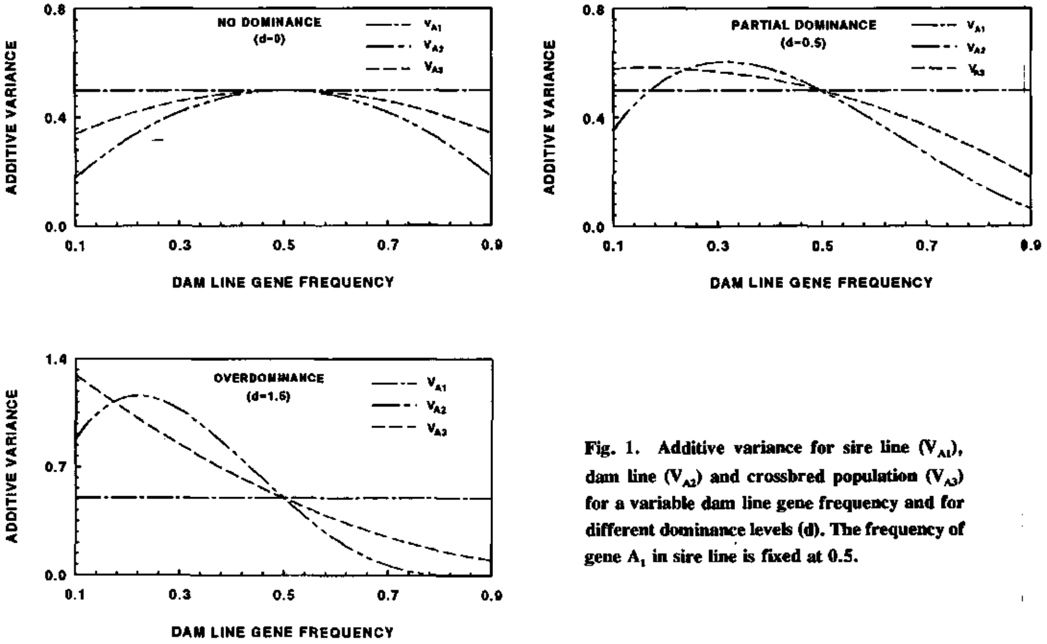

Fig. 1. Additive variance for sire line (V_{A1}), dam line (V_{A2}) and crossbred population (V_{A3}) for a variable dam line gene frequency and for different dominance levels (d). The frequency of gene A_1 in sire line is fixed at 0.5.

Experimental results confirm that the values of h_c^2 (or additive variance) calculated by sire and dam component of variance differ (Hale and Clayton, 1965; Pirchner and Von Krosigk, 1973; Louca and Robison, 1967; Vinson et al., 1969; Wong and Boylan, 1970; Biswas et al., 1971; Wong et al., 1971). Biswas et al. (1971) explained this as either caused by a maternal effect or a higher non-additive genetic variance. This study shows that also the unequal gene frequency in the parental lines is a cause for the difference between sire and dam component, irrespective of dominance level.

The definition of h^2_c as $4*V_{hs_c}$ may be used to predict the crossbred response to the selection in the sire line. However, this h^2_c could not be used to predict the crossbred response to selection in the dams or in both sire and dam lines. To predict the crossbred response, the dam component in crossbreds is needed. It should be kept in mind that both of the two components should properly be considered to obtain the crossbred response to selection in both sire and dam lines because the sire and dam components in crossbreds are generally not equal.

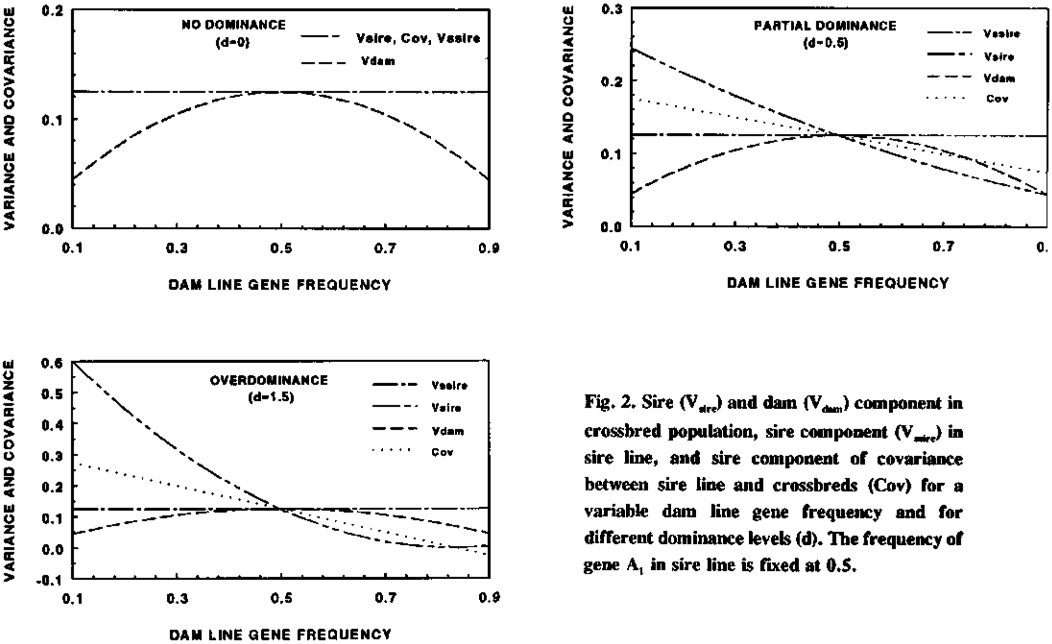

Fig. 2. Sire (V_{sire}) and dam (V_{dam}) component in crossbred population, sire component (V_{ssire}) in sire line, and sire component of covariance between sire line and crossbreds (Cov) for a variable dam line gene frequency and for different dominance levels (d). The frequency of gene A_1 in sire line is fixed at 0.5.

3.3. Sire component of covariance between purebreds and crossbreds (Cov_{pc})

Without dominance, the value of Cov_{pc} depends on the gene frequency in the sire line but not on the dam line gene frequency. And, 4*Cov_{pc} is equal to the additive variance of the sire line (V_{A1}) (Fig. 2a). Cov_{pc} changes with the gene frequencies in both sire and dam lines if dominance is involved. In the case of partial dominance, Cov_{pc} is always positive. With overdominance ($d=1.5$), Cov_{pc} becomes negative when the gene frequencies in parent populations appear in one of the following situations, (1) $f_{11} < 5/6$ and $f_{21} > 5/6$, or (2) $f_{11} > 5/6$ and $f_{21} < 5/6$, where 5/6 represents the genotypic maximum for a population (see Pirchner and Mergl, 1977, for more detail). It means that in the case of $f_{11} < 5/6$ and $f_{21} > 5/6$, the ranks of sires evaluated by progeny mean in purebreds are the opposite of those in crossbreds.

It should be noted that unless f_{11} is equal to f_{21}, Cov_{pc} is equal to neither 1/4 of the additive genetic variance of the sire line nor to 1/4 of the additive variance for crossbred population (Fig. 2a, 2b and 2c).

3.4. Genetic correlation between purebred and crossbred performance (r_{pc})

The results on r_{pc} are the same as found by Pirchner and Mergl (1977). In the case of partial or no dominance, r_{pc} is equal to 1. With overdominance, r_{pc} becomes -1 when the gene frequencies in parental lines give rise to a negative Cov_{pc}, i.e., when sire and dam gene frequencies are on either side of the equilibrium frequency given by $(a+d)/(2d)$, where a indicates the value of favourable gene A_1.

Experimental estimates for r_{pc}, which were reviewed by Wei and Van der Steen (1990), varied over all values between -1 and 1. In the one-locus model, there are only three genotypes used to calculate purebred or crossbred half-sib means, and the breeding values of sires change with gene frequency from one extreme to another. Therefore, the one-locus model is not suitable to study r_{pc}, and a model with more loci will be needed.

3.5. Genetic regression of crossbred progeny on purebred progeny (b)

Results on b show that both gene frequencies in parental lines and dominance level affect b. First, b is always equal to 1 when parental lines have equal gene frequency or when there is no dominance. Second, with partial dominance, b is positive. For a constant gene frequency of A_1, ($=f_{11}$), b decreases with increasing f_{21} (Fig. 3a and 3b). For a constant f_{21}, b increases with decreasing f_{11} (Table 1). Generally, the larger the difference of gene frequency between parental lines is, the more b deviates from 1 (Fig. 3a and 3b). Third, when overdominance exists, the change in b behaves similarly to the situation with partial dominance. The value of b becomes negative when the gene frequencies in parental lines give rise to a negative

Cov_{pc}. Fourth, b has no particular relationship with the sire component in the sire line, but the absolute value of b has a positive relation with the additive variance (V_{Ap1}) contributed by sires to crossbreds (Table 1, Fig. 3a and 3b).

The indirect response in crossbreds (R_c) to selection in parental purebred populations when selection is based on individual phenotypes is,

$$R_c = \frac{1}{2}\left(i_1 h_1 \sigma_{A1} b_1 + i_2 h_2 \sigma_{A2} b_2\right) \qquad [6]$$

where, the subscript 1 and 2 refer to sire and dam line, respectively; i_i = selection intensity; h_i = square-root of heritability; σ_{Ai} = square-root of additive variance; b_i = genetic regression of crossbred progeny on purebred progeny. Notice that the b values calculated for the parental lines are generally not equal to each other.

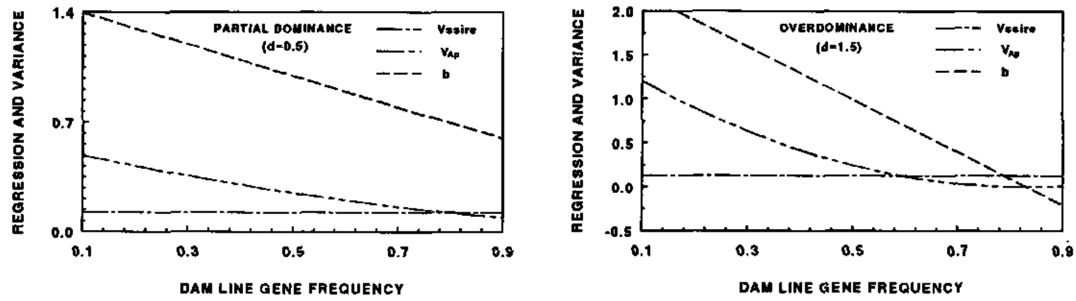

Fig. 3. Genetic regression of crossbred progeny on purebred progeny (b), additive variance for crossbreds contributed by sire line (V_{Ap}), and sire component in sire line (V_{sire}) for a variable dam line gene frequency and for different dominance levels (d). The frequency of gene A_1 in sire line is fixed at 0.5.

4. CONCLUSION

The present study indicates that some genetic parameters of the crossbred population can be obtained only when the crossbred information is available.

(1). In case of dominance, the additive variance for crossbred population (V_{A3}) can not be predicted by the average of additive variances in parental populations (V_{A1} and V_{A2}). V_{A3} can be larger than both V_{A1} and V_{A2}. It implies that crossbreds could have a higher heritability than both parental lines.

(2). Sire and dam component of variance in a crossbred population are generally unequal to each other in the case of unequal gene frequency of parental lines, and they are not a function of additive variances in parental populations. The estimation of crossbred additive variance (V_{A3}) using the sire component is not appropriate. To predict crossbred response when selection happens in both sire and dam lines, both sire and dam components should be considered. Alternatively, when using crossbred data from relatives from more generations, an animal model could be considered. Such a model should allow for heterogeneous additive variances, e.g. the variance contributed from sire and dam lines is not necessarily equal.

(3). The sire component of covariance between purebreds and crossbreds (Cov_{pc}) is not a function of the variances within the sire line. Cov_{pc} can not be replaced by one quarter of the additive variance in the sire line.

(4). The genetic regression of crossbred progeny on purebred progeny is a suitable term to predict the crossbred response from pure-line selection. Its magnitude depends on the crossbred additive variance contributed by the sire line. The regression coefficients generally differ between parental lines. It seems appropriate to choose as a sire line the one with higher regression because of higher selection intensity.

(5). In the case of no interaction among loci, the results on variances and covariances can be extended to a more loci case. Results on genetic correlation between purebred and crossbred performance could not be appropriately studied with a one locus model and a model with more loci is needed.

ACKNOWLEDGEMENT

Prof. M. Grossman is gratefully acknowledged for his contribution in the discussion about the genetic model.

TABLE 1. Genetic parameters under a one-locus model in case of different dominance levels (d).

		d = 0.0				d = 0.5						d = 1.5					
f_{11}	f_{12}[a]	V_{A1}[b]	V_{A2}	V_{A3}	V_{hs_c}	V_{A1}	V_{A2}	V_{A3}	V_{hs_c}	Cov_{pc}	b	V_{A1}	V_{A2}	V_{A3}	V_{hs_c}	Cov_{pc}	b
.1	.3	.18[c]	.42	.30	.045	.353	.605	.541	.065	.076	.86	.871	1.075	1.247	.115	.158	.73
	.5	.18	.50	.34	.045	.353	.500	.580	.045	.063	.71	.871	.500	1.300	.045	.009	.46
	.7	.18	.42	.30	.045	.353	.269	.469	.029	.050	.57	.871	.067	1.031	.007	.040	.18
	.9	.18	.18	.18	.045	.353	.065	.209	.016	.038	.43	.871	.007	.439	.002	-.020	-.09
.3	.1	.42	.18	.30	.105	.605	.353	.541	.206	.176	1.17	1.075	.871	1.247	.508	.370	1.38
	.5	.42	.50	.46	.105	.605	.500	.570	.105	.126	.83	1.075	.500	.473	.105	.168	.63
	.7	.42	.42	.42	.105	.605	.269	.437	.067	.101	.67	1.075	.067	.571	.017	.067	.25
	.9	.42	.18	.30	.105	.605	.065	.205	.038	.076	.50	1.075	.007	.239	.004	-.034	-.13
.5	.1	.50	.18	.34	.125	.500	.353	.580	.245	.175	1.40	.500	.871	1.300	.605	.275	2.20
	.3	.50	.42	.46	.125	.500	.605	.570	.180	.150	1.20	.500	1.075	.850	.320	.200	1.60
	.7	.50	.42	.46	.125	.500	.269	.370	.080	.100	.80	.500	.067	.250	.020	.050	.40
	.9	.50	.18	.34	.125	.500	.065	.180	.045	.075	.60	.500	.007	.100	.005	-.025	-.20
.7	.1	.42	.18	.30	.105	.269	.353	.469	.206	.118	1.75	.067	.871	1.031	.508	.092	5.50
	.3	.42	.42	.42	.105	.269	.605	.437	.151	.101	1.50	.067	1.075	.571	.269	.067	4.00
	.5	.42	.50	.46	.105	.269	.500	.370	.105	.084	1.25	.067	.500	.250	.105	.042	2.50
	.9	.42	.18	.30	.105	.269	.065	.133	.038	.050	.75	.067	.007	.023	.004	-.008	-.50
.9	.1	.18	.18	.18	.045	.065	.353	.209	.088	.038	2.33	.007	.871	.439	.218	-.020	-11.0
	.3	.18	.42	.30	.045	.065	.605	.205	.065	.032	2.00	.007	1.075	.239	.115	-.014	-8.0
	.5	.18	.50	.34	.045	.065	.500	.180	.045	.027	1.67	.007	.500	.100	.045	-.009	-5.0
	.7	.18	.42	.30	.045	.065	.269	.133	.029	.022	1.33	.007	.067	.023	.007	-.004	-2.0

[a] f_{11} and f_{21} = frequency of gene A_1 in line 1 and 2, respectively.

[b] V_{Ak} = additive variance for population k (=1, 2, 3). V_{hs_c} = sire component of variance in crossbreds. Cov_{pc} = sire component of covariance between sire line and crossbreds. b = genetic regression of crossbred progeny on purebred progeny.

[c] Without dominance, b=1 and $V_{hs_c}=Cov_{pc}$. With equal gene frequency in parental lines, $V_{A1}=V_{A2}=V_{A3}$ and $V_{hs_c}=Cov_{pc}$.

REFERENCES

Bassett, J.W.; Shelton, M., 1966: Crossbreeding influence on heritability estimates. J. Anim. Sci. 25,877.

Bell, A.E., 1982: Selection for heterosis——results with laboratory and domestic animal. Proc. 2nd World Congr. Genet. Appl. Livest. Prod. 6,206-227.

Biswas, D.K.; Chapman, A.B.; First, N.L.; Self, H.L., 1971: Intrapopulation versus reciprocal recurrent selection in swine. J. Anim. Sci. 32, 840-848.

Brown, W.P.; Bell, A.E., 1980: An experimental comparison of selection alternatives to plateaued response. Genetics 94,477-496.

Griffing, B., 1960: Theoretical consequences of truncation selection based on the individual phenotype. Aust. J. Biol. Sci. 13,307-343.

Griffing, B., 1962: Prediction formulae for general combining ability selection methods utilizing one or two random-mating populations. Aust. J. Biol. Sci. 15,650-665.

Grossman, M.; Fernando, R.L., 1989: Covariance between relatives for X-chromosomal loci in a population in disequilibrium. Theor. Appl. Genet. 77, 311-319.

Hale, R.W.; Clayton, G.A., 1965: A diallel crossing experiment with two breeds of laying fowl. Br. Poult. Sci. 6, 153-174.

Koger, M.; Jilek, A.F.; Burns, W.C.; Crockett, J.R., 1975: Sire effects for specific combining ability in purebred and crossbred cattle. J. Anim. Sci. 40,230-234.

Krause, E.; Yamada, Y.; Bell, A.E., 1965: Genetic parameters in two populations of chickens under reciprocal recurrent selection. Br. Poult. Sci. 6,197-206.

Louca, A.; Robison, O.W., 1967: Components of variance and covariance in purebred and crossbred swine. J. Anim. Sci. 26,267-273.

McLaren, D.G.; Buchanan, D.S.; Hintz, R.L., 1985. Sire ranking based upon purebred versus crossbred progeny performance in swine. J. Anim. Sci. 60,902-912.

McNew, R.W.; Bell, A.E., 1971: The nature of the purebred-crossbred genetic covariance. Genet. Res. camb. 18,1-7.

Miquel, C.; Cartwright, T.C., 1963. Comparison of heritabilities in crossbred and purebred cattle. J. Anim. Sci. 22, 821.

Orozco, F.; Bell, A.E. 1974: Reciprocal recurrent selection compared to within-strain selection for increasing rate of egg lay of Tribolium under optimal and stress conditions. Genetics 77,143-161.

Orozco, F.; Campo, J.L., 1975: A comparison of purebred and crossbred genetic parameters in layers. World's Poult. Sci. J. 31,149-153.

Pirchner, F., 1974: Genetic correlations between pure-line and cross-line performance in poultry. Proc. 23rd Nat. Poultry Breeders' Roundtable. May 2-3, 1974. Kansas City, Missouri. pp202-230.

Pirchner, F.; von Krosigk, C.M., 1973. Genetic parameters of cross- and pure-bred poultry. Br. Poult. Sci. 14,193-202.

Pirchner, F.; Mergl, R., 1977: Overdominance as cause for heterosis in poultry. J. Anim. Breed. Genet. 94,151-158.

Salah, E.; Galal, E.; Hazel, L.N.; Sidwell, G.M.; Terrill, C.E., 1969: Correlation between purebred and crossbred half-sibs in sheep. J. Anim. Sci. 30,475-480.

Sellier, P., 1982: Selecting populations for use in crossbreeding. Proc. 2nd World Congr. Genet. Appl. Livest. Prod. in Madrid. 6,15-49.

Standal, N., 1968: Studies on breeding and selection schemes in pigs. I. Selection on performance of purebred versus crossbred progeny. Acta Agric. Scand. 18,222-232.

Stanislaw, C.M.; Omtvedt, I.T.; Willham, R.L.; Whatley Jr, J.A., 1967: A study of some genetic parameters in purebred and crossbred populations of swine. J. Anim. Sci. 26,16-20.

Stuber, C.W.; Cockerham, C.C., 1966: Gene effects and variances in hybrid populations. Genetics 54,1279-1286.

Taran, M.; Gabriel, E.; Moses, E.; Soller, M., 1971: Performance of purebred and crossbred progeny of White Leghorn and New Hampshire sires. Br. Poult. Sci. 13,331-339.

Van der Werf, J.H.J., 1990. Models to estimate genetic parameters in crossbred dairy cattle populations under selection. Doctoral Thesis, Wageningen Agri. Univer., Wageningen, The Netherlands.

Vinson, W.E.; Eisen, E.J.; Robison, O.W., 1969: Predicted response to selection for crossbred performance in mice. J. Anim. Sci. 28,725-733.

Wei, M.; van der Steen, H.A.M., 1990: Comparison of reciprocal recurrent selection with pure-line selection systems in animal breeding. Anim. Breed. Abstr. 59,281-298.

Wong, W.C.; Boylan, W.J., 1970: Intrapopulation selection and Correlated response in crossbreds of Tribolium Castaneum. Genetics 64,69-78.

Wong, W.C.; Boylan, W.J.; Rempel, W.E., 1971: Purebred versus crossbred performance as a basis of selection in swine. J. Anim. Sci. 32,605-610.

Chapter 4

Relationship between Purebred and Crossbred Parameters. II. Genetic correlation between Purebred and Crossbred Performance under the Model with Two Loci

M. Wei, J.H.J. van der Werf and E.W. Brascamp

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

Published in: ***Journal of Animal Breeding and Genetics 108:262-269 (1991)***.
Reproduced by permission of Verlag Paul Parey, Hamburg and Berlin.

"In general, r_{pc} decreases with increasing dominance level or gene frequency difference between parental lines."

Relationship between Purebred and Crossbred Parameters. II. Genetic Correlation between Purebred and Crossbred Performance under the Model with Two Loci

M. Wei, J.H.J. van der Werf and E.W. Brascamp

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

SUMMARY: *The present study under the model with two loci showed that the genetic correlation between purebred and crossbred performance (r_{pc}) reflects not only dominance levels at loci but also the gene frequency difference between parental populations. The value of r_{pc} was found to vary over all values between -1 and 1 depending on dominance and gene frequency difference between parental populations. The r_{pc} is 1 in the case of no dominance or with equal gene frequencies in parental lines. It is positive in any case of partial dominance, and becomes negative only in some cases of overdominance. In general, r_{pc} decreases with increasing dominance level or gene frequency difference between parental lines. With a high r_{pc}, it is generally impossible to distinguish whether the gene frequency difference between parental lines is large or dominance effects are small. It was concluded that r_{pc} is a reliable indicator for the effect of selection method on genetic response. For a long term selection, r_{pc} is expected to increase with no or partial dominance, but with overdominance r_{pc} decreases after crossbred selection.*

---

1. INTRODUCTION

The genetic correlation between purebred and crossbred performance (r_{pc}) can be used to predict selection response in crossbreds based on pure line selection (McNew and Bell, 1971; Pirchner, 1974; Bell, 1982; Sellier, 1982). Wei et al. (1990) argued that a one-locus model is sufficient to understand the behaviour of the relevant covariances and variances. To understand the nature of the genetic correlation the model with two-loci is needed because in the one-locus model only +1 and -1 are occurring to the value of r_{pc}. This is in agreement with Pirchner (1974) and Pirchner and Mergl (1977), who concluded by extrapolation to more loci that $r_{pc} < 1$ would occur only in the case of overdominance. This is a somewhat surprising result because in most experiments estimates of r_{pc} are smaller than 1 (Wei and van der Steen, 1990) and overdominance is expected not to occur very often.

The aim of this paper is therefore to study the behaviour of the genetic correlation between purebred and crossbred performance under the model with two-loci, in dependency of gene frequencies and degree of dominance. Furthermore, the effects of selection in relation to r_{pc} and dominance are discussed.

2. METHODS

2.1. Basic assumptions

It is assumed that there are two loci (L=1, 2), each with two alleles (A_{L1} and A_{L2} for locus L). The frequency of allele, A_{Li}, in population p is f_{pLi}. The frequency and value of genotype, $A_{Li}A_{Lj}$, in population p are f_{pLij} ($= f_{pLi}f_{pLj}$) and y_{PLij} ($y_{Lij} = y_{PLij}$), respectively. The subscript p refers to populations 1, 2 and 3. The population 3 is the crossbreds from crossing sires of population 1 with dams of population 2.

For each locus, the values of homozygote, $A_{i1}A_{i1}$ and $A_{i2}A_{i2}$, are defined as 1 and -1, respectively. The value of the heterozygote $A_{i1}A_{i2}$ ($=A_{i2}A_{i1}$) is defined as d_i which is dominance level.

The mean of population p (μ_p) is as,

$$\mu_p = \sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{u=1}^{2}\sum_{v=1}^{2}\left[f_{p1ij}f_{p2uv}\left(y_{1ij}+y_{2uv}\right)\right]$$

No interaction effect between loci, no environmental effects, random mating and infinite population size are assumed. More details on the genetic model with one locus were described by Wei et al. (1990).

2.2. Sire component of covariance between purebreds and crossbreds (Cov_{pc})

There are 16 different genotypes possible in each population. Sires of one particular genotype ($A_{1i}A_{1j}A_{2u}A_{2v}$) have a purebred progeny family mean (M_{1ijuv}) and a crossbred progeny family mean (M_{3ijuv}) as,

$$M_{1ijuv} = \sum_{n=1}^{2}\sum_{m=1}^{2}\left[f_{11n}f_{12m}\frac{1}{4}\left[\left(y_{1in}+y_{2um}\right)+\left(y_{1in}+y_{2mv}\right)+\left(y_{1nj}+y_{2um}\right)+\left(y_{1nj}+y_{2mv}\right)\right]\right]$$

$$M_{3ijuv} = \sum_{n=1}^{2}\sum_{m=1}^{2}\left[f_{21n}f_{22m}\frac{1}{4}\left[(y_{1in}+y_{2um})+(y_{1in}+y_{2mv})+(y_{1nj}+y_{2um})+(y_{1nj}+y_{2mv})\right]\right]$$

The sire component of covariance between purebreds and crossbreds (Cov_{pc}), in this case, is calculated by the covariance between sires' purebred (p) and crossbred (c) half-sib means as,

$$Cov_{pc} = \sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{u=1}^{2}\sum_{v=1}^{2}\left[f_{11ij}f_{12uv}(M_{1ijuv}-\mu_1)(M_{3ijuv}-\mu_3)\right] \qquad [1]$$

2.3. Correlation

The sire components in the sire line (V_{hs_p}) and crossbred population (V_{hs_c}) are determined to calculate the genetic correlation between purebred and crossbred half-sibs (r_{pc}). In this case, V_{hs_p} and V_{hs_c} are calculated as the variances of paternal purebred and crossbred half-sib family means, respectively, as follows,

$$V_{hs_p} = \sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{u=1}^{2}\sum_{v=1}^{2}\left[f_{11ij}f_{12uv}(M_{1ijuv}-\mu_1)^2\right]$$

$$V_{hs_c} = \sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{u=1}^{2}\sum_{v=1}^{2}\left[f_{11ij}f_{12uv}(M_{3ijuv}-\mu_3)^2\right]$$

The genetic correlation between purebred and crossbred performance (r_{pc}) is, therefore, calculated as,

$$r_{pc} = \frac{Cov_{pc}}{\sqrt{V_{hs_p} * V_{hs_c}}} \qquad [2]$$

3. RESULTS AND DISCUSSION

3.1. Effect of dominance and gene frequency on the genetic correlation between purebred and crossbred performance (r_{pc})

The genetic correlation between purebred and crossbred performance (r_{pc}) are shown in Table 1 and Figs. 1 and 2 for different levels of dominance and gene frequency difference in parental populations. The r_{pc} takes all values between -1 and 1 depending on dominance levels and gene frequencies. The r_{pc} is always equal to 1 in the case of no dominance or with equal gene frequencies in parental populations. It is positive in any case of partial dominance, and becomes negative in some cases of overdominance.

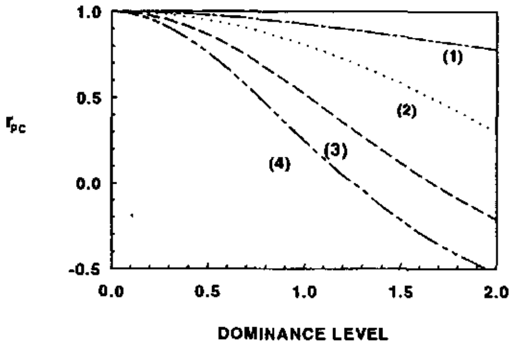

Fig. 1. Relationship between genetic correlation between purebred and crossbred performance (r_{pc}) and dominance levels. The gene frequency difference between parental lines at locus 1 and 2 for lines 1, 2, 3 and 4 are defined as (1) small and small; (2) medium and small; (3) medium and medium; and (4) large and large, respectively (definitions of small, medium and large are in Table 1).

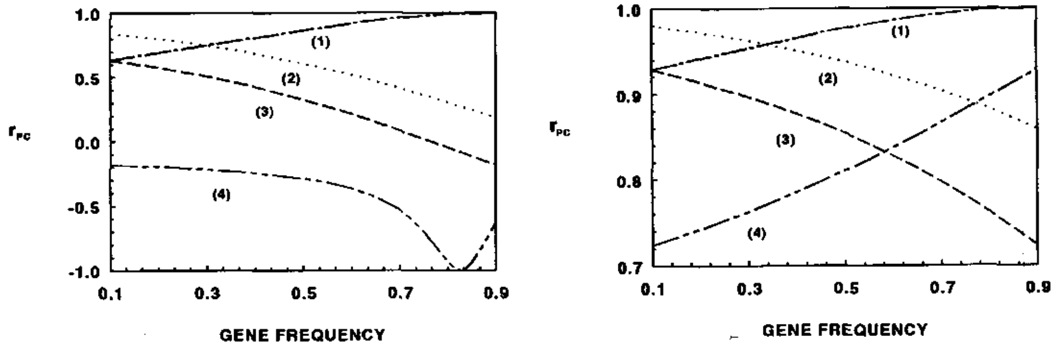

Fig. 2. Genetic correlation between purebred and crossbred performance (r_{pc}) in dependency of gene frequency (f_{22}), under different dominance levels ($d_1=d_2=0.5$ for Fig. 2a; $d_1=d_2=1.5$ for Fig. 2b). The gene frequencies, f_{11}-f_{21} and f_{12}, are fixed for 4 lines as (1) .1-.1 and .9; (2) .7-.3 and .1; (3) .9-.1 and .1; and (4) .1-.9 and .9, respectively. f_{pL} is the frequency of favourable gene, A_1, at locus L of population p. d_L is the dominance level at locus L.

The value of r_{pc} generally decreases with increasing dominance levels. Fig. 1 shows the decline of r_{pc} with dominance levels at various gene frequency combinations. The decline of r_{pc} with dominance is also dependent on the gene frequency difference between parental populations (Fig. 1 and Table 1). The larger the gene frequency difference is between parental lines, the lower is r_{pc}.

Fig. 2 illustrates the effect of the gene frequency difference on r_{pc} under partial dominance and overdominance. The curves of r_{pc} increase with decreasing gene frequency difference between parental lines (Lines 1 and 4 in Fig. 2a), and vice versa (lines 2 and 3 in Fig. 2a).

The effect of gene frequencies on r_{pc} increases dramatically with overdominance compared to partial dominance (comparing Fig. 2a with 2b). Under certain conditions, r_{pc} becomes negative. These conditions were studied by Pirchner and Mergl (1977) under the one-locus case. With overdominance, r_{pc} generally changes similarly as with partial dominance (lines 1, 2 and 3 in Fig. 2b), but in some cases, r_{pc} changes differently (e.g. line 4 in Fig. 2b). This marked difference is determined by an equilibrium point, given by $(a+d_L)/(2d_L)$, where the population obtains its maximum value, as discussed by Dickerson (1952), Arthur and Abplanalp (1964 and 1970), and Pirchner and Mergl (1977).

In the case of one locus with partial dominance combined with another locus with overdominance, r_{pc} is more affected by the change of the gene frequency difference at the locus with overdominance (Table 1 and Fig. 3). The higher the dominance level, the more the gene frequency difference at that particular locus contributes to the change (decline) of r_{pc}.

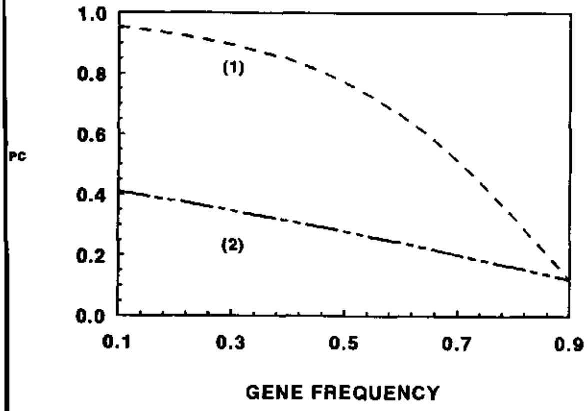

Fig. 3. Genetic correlation between purebred and crossbred performance (r_{pc}) in dependency of gene frequency (f_{22}) in the case of one locus with partial dominance and another one with overdominance, $d_1=0.5$ and $d_2=1.5$ for (1); $d_1=1.5$ and $d_2=0.5$ for (2). The gene frequencies, f_{11}-f_{21} and f_{12}, are fixed at .9-.1 and .1. f_{Pl} and d_L are defined as in Fig. 2.

Pirchner and Mergl (1977) extended the result under the one-locus model to the more loci situation by adding the effect from each locus, and proposed a formula for r_{pc}, i.e., $r_{pc} = (s+s'-x)/(s+s'+x)$. In the formula, s' represents the number of loci with overdominance and gene frequencies in both populations to cause $r_{pc}=1$ for each single locus; x refers to the number of loci with overdominance and gene frequencies causing $r_{pc}=-1$; s refers to the number of loci with partial or no dominance (also leading to $r_{pc}=1$). Consequently, they concluded that any value of $r_{pc} < 1$ indicates overdominance at $x=(1-r_{pc})/2$ loci. However, it is shown in Table 1 that r_{pc} can be smaller than 1 even with only partial dominance at both loci.

TABLE 1. Genetic correlation between purebred and crossbred performance (r_{pc}) for the change of dominance and gene frequency under the model with two loci.

Gene Freq. Dif.[a]		Gene frequency		r_{pc}[b] at various dominance levels			
Locus 1	Locus 2	f_{11}[c] - f_{21}	f_{12} - f_{22}	d_1[d] = .5 d_2 = .5	d_1 = .5 d_2 = 1.5	d_1 = 1 d_2 = 1	d_1 = 1.5 d_2 = 1.5
small	small	.3-.1	.3-.5	0.986	0.953	0.962	0.936
		.3-.1	.5-.7	0.984	0.907	0.951	0.920
		.3-.1	.7-.9	0.983	0.894	0.957	0.944
		.5-.3	.5-.7	0.981	0.894	0.929	0.858
		.5-.3	.7-.9	0.980	0.876	0.931	0.894
		.7-.5	.7-.9	0.970	0.789	0.832	0.555
small	medium	.3-.1	.1-.5	0.977	0.905	0.939	0.903
		.3-.1	.3-.7	0.965	0.797	0.894	0.822
		.3-.1	.5-.9	0.955	0.627	0.857	0.767
		.7-.5	.1-.5	0.963	0.885	0.868	0.752
		.7-.5	.3-.7	0.953	0.747	0.811	0.586
		.7-.5	.5-.9	0.936	0.406	0.658	0.136
		.9-.7	.1-.5	0.964	0.918	0.909	0.891
		.9-.7	.3-.7	0.966	0.779	0.884	0.789
		.9-.7	.5-.9	0.946	-.049	0.586	-.727
medium	medium	.5-.1	.3-.7	0.939	0.755	0.818	0.692
		.5-.1	.5-.9	0.929	0.600	0.781	0.640
		.7-.3	.5-.9	0.905	0.438	0.611	0.214
medium	large	.5-.1	.1-.7	0.933	0.730	0.810	0.687
		.5-.1	.3-.9	0.897	0.451	0.692	0.493
		.5-.1	.1-.9	0.902	0.534	0.727	0.559
		.7-.3	.1-.7	0.904	0.661	0.678	0.420
		.7-.3	.3-.9	0.868	0.294	0.520	0.120
		.7-.3	.1-.9	0.859	0.388	0.535	0.188
		.9-.5	.1-.7	0.882	0.603	0.971	0.286
		.9-.5	.3-.9	0.872	-.056	0.380	-.369
		.9-.5	.1-.9	0.811	0.069	0.303	-.284
large	large	.7-.1	.3-.9	0.838	0.316	0.493	0.154
		.7-.1	.1-.9	0.837	0.402	0.517	0.210
		.9-.3	.1-.9	0.763	0.101	0.250	-.213

[a] Small, medium and large refer to the gene frequency difference between parental populations as 0.2, 0.4 and 0.6-0.8 at locus, respectively.

[b] $r_{pc}=1$ with $d_1=d_2=0$ or with equal gene frequencies in parental populations.

[c] f_{pl} refers to the frequency of favourable gene, A_1, at locus L of population p.

[d] $_L$ refers to dominance level at locus L (L = 1, 2).

With no interaction between loci, the value of r_{pc} under the n-loci case (r_{pcn}) can be computed as,

$$r_{pc_n} = \frac{Cov_{pc_n}}{\sqrt{V_{hsp_n} * V_{hsc_n}}} = \frac{\sum_{L=1}^{n} \left(Cov_{pc_L}\right)}{\sqrt{\left(\sum_{L=1}^{n} V_{hsp_L}\right) * \left(\sum_{L=1}^{n} V_{hsc_L}\right)}} \qquad [3]$$

where Cov_{pcn} and Cov_{pcL} are the sire component of covariance between purebreds and crossbreds calculated from n loci and single locus L, respectively; V_{hspn} and V_{hspL} are the sire component in sire line calculated from n loci and single locus L, respectively; V_{hscn} and V_{hscL} are the sire components in crossbreds from n loci and single locus L, respectively; L is the Lth locus (L = 1, 2, ... n); n is the total number of the loci concerned. Comparison of (3) with the formula proposed by Pirchner and Mergl (1977) shows that the latter approach only holds when the gene frequencies are equal at all loci for each line.

The estimates for r_{pc} in experiments ranged all values between -1 and +1 (Bowman, 1960; Wilson et al., 1962; Krause et al., 1965; Biswas and Craig, 1969; Pirchner, 1974; Rabsztyn and Nowak, 1978; Ayyagari et al., 1982; Brah et al., 1987). A high positive r_{pc} has been explained by a high additive variance; a low r_{pc} was assumed to be due to a large component of non-additive variance; and a negative r_{pc} was attributed to overdominance (Robinson et al., 1964; Biswas and Craig, 1969; Salah et al., 1969; Vinson et al., 1969; Wong et al., 1971; Singh and Dev, 1974; Ameli, 1989). These results were supported by the present theoretical study. Moreover, this study also clarified the experiments showing a high r_{pc} for a trait with large non-additive effects (Wong et al., 1971; Rempel, 1974) because of the gene frequency difference between parental lines being small.

Table 2 summarizes the results in Table 1 showing that a high r_{pc} can occur with overdominance if gene frequency difference between parental populations is small. When r_{pc} is low, large dominance and big gene frequency difference between parental populations can be expected. In case of a high r_{pc} it is not possible to distinguish between gene frequency difference and dominance levels. Some authors (e.g. Hill, 1970) suggested that traits with overdominance could profit from crossbred selection. The interesting question arises if selection based on crossbred performance is to be preferred in case of overdominance even if the value of r_{pc} is high. The thought behind this is that gene frequency difference might increase as a consequence of selection, which justifies selection on crossbred performance in later generations.

TABLE 2. Genetic correlation between purebred and crossbred performance in the case of high or low dominance levels combined with large or small difference of gene frequencies between parental populations.

Dominance levels		Overdominance	Partial dominance
Gene freq. diff. [a]:			
	Large	low or negative	high
	Small	high	very high

[a] **the difference of gene frequency between parental purebred populations.**

3.2 Response to purebred and crossbred selection in relation to r_{pc} and dominance

We compared the effect of purebred (PS) and crossbred selection (CS) on selection response and gene frequency change.

Responses to selection based on purebred or crossbred progeny means are shown in Fig. 4. Selection based on purebred performance (PS) is better (Fig. 4a) to improve purebreds. On the other hand, selection based on crossbred performance (CS) is more efficient to improve crossbred response (Fig. 4b). Crossbred response to CS and PS is in the same direction in the case of a positive r_{pc}. Note that response of PS relative to CS is similar for two levels of dominance but with equal r_{pc} (case 1 and 2 in Fig. 4). With a negative r_{pc}, the selection response for purebreds and crossbreds has a different sign (case 3 in Fig. 4b). The same phenomenon was also found in some experiments (Calhoon and Bohren, 1974; Bereskin and Hetzer, 1981). Results illustrate that r_{pc} rather than dominance level is a good indicator for the effect of selection method on purebred and crossbred response.

The change of gene frequencies after selection is illustrated in Fig. 5. It is shown that both CS and PS increase the frequency of favourable genes if the r_{pc} is positive (case 1 and 2 in Fig. 5). PS and CS change the gene frequencies in different direction with a negative r_{pc} (case 3 in Fig. 5).

The change of gene frequencies after selection will inevitably cause a change of r_{pc}, which should be considered for a long-term crossbreeding program. In the case of no overdominance, PS and CS have the same effect on the change of gene frequencies, i.e., increasing favourable gene frequencies. In the case of overdominance, CS results in the frequencies of favourable genes towards fixation in one line and towards zero in another line, whereas PS results in frequencies towards the equilibrium point (Comstock et al., 1949; Bell et al., 1952; Dickerson, 1952). It should therefore be expected that in the case of no overdominance r_{pc} will increase after a long-term PS or CS whereas with overdominance the

r_{pc} will decrease after a long-term crossbred selection. This supports the conclusion made by Pirchner and Mergl (1977) that the decline of r_{pc} after reciprocal recurrent selection (RRS) indicates overdominance. The implication is that in the case of overdominance with a high r_{pc}, crossbred selection should still be considered for a long-term breeding program although the response on a short-term is similar to purebred selection.

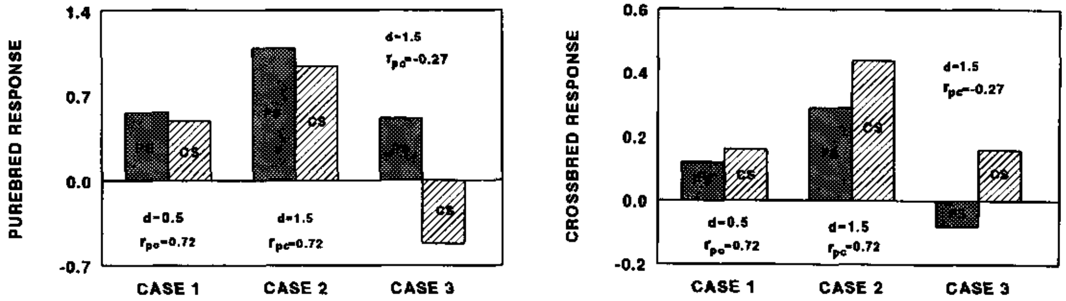

Fig. 4. Purebred (Fig. 4a) and crossbred (Fig. 4b) response to selection based on purebred (PS) and crossbred (CS) progeny mean. The gene frequency sets, f_{11}-f_{21} and f_{12}-f_{22}, for case 1, 2 and 3 are .1-.9 and .9-.1; .1-.1 and .3-.8; .5-.9 and .9-.1, respectively. Top 20% of sires are selected, no selection in dams.

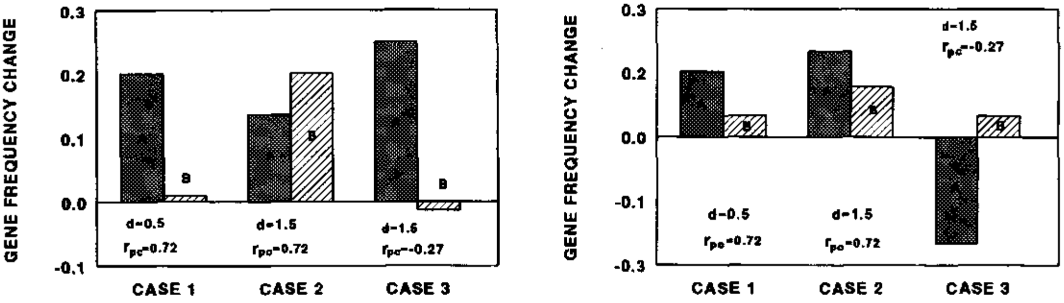

Fig. 5. Change of favourable gene frequency at locus A and B by selection based on purebred (Fig. 5a) and crossbred (Fig. 5b) progeny mean. The gene frequency sets for case 1, 2 and 3 are the same as in Fig. 4. Top 20% of sires are selected, no selection in dams. f_{pi} and d_L are defined as in Fig. 2.

4. CONCLUSION

The present study shows that in addition to dominance the gene frequency difference between parental populations is an important factor to affect the genetic correlation between purebred and crossbred performance (r_{pc}). Some implications from this study are described. (1) The value of r_{pc} can be lower than 1 in the case of partial dominance. (2) Because r_{pc} is better indicator than dominance to reflect the effect of selection method on response r_{pc} should be the indicator for the usefulness of crossbred selection, at least for a short term. (3) The change of r_{pc} after a long-term selection will depend on dominance effect and selection method. In the case of partial dominance, the value of r_{pc} will increase after either purebred or crossbred selection. However, in the case of overdominance r_{pc} will decrease after a long-term crossbred selection. The optimal selection strategy in case of partial dominance would be to combine crossbred and purebred information in an index. In the case of overdominance crossbred selection is to be preferred on a long term because of a higher selection limit (Hill, 1970).

REFERENCES

Ameli, H., 1989: Inbreeding and heterosis effects and genetic parameters in two White Leghorn (LSL) lines and their reciprocal crosses after long-term reciprocal recurrent selection. Ph.D Dissertation, University Göttingen, Göttingen, Germany.

Arthur, J.A.; Abplanalp, H., 1964: Studies using computer simulation of reciprocal recurrent selection. Genetics 50,233.

Arthur, J.A.; Abplanalp, H., 1970: Computer simulation of reciprocal recurrent selection with overdominant gene action. Anim. Prod. 12,639-649.

Ayyagari, V.; Mohapatra, S.C.; Renganathan, P.; Johri, D.C.; T.S. Thiagasundaram, T.S.; Panda, B.K., 1982: Cross performance as influenced by selection in pure lines. Br. Poult. Sci. 23,469-479.

Bell, A.E.; Moore, C.H.; Bohren, B.B.; Warren, D.C., 1952: Systems of breeding designed to utilize heterosis in the domestic fowl. Poult. Sci. 31,11-22.

Bell, A.E., 1982: Selection for heterosis——results with laboratory and domestic animal. Proc. 2nd World. Congr. Genet. Appl. Livest. Prod. 6:206-227.

Bereskin, B.; Hetzer, H.O., 1981: Reciprocal recurrent selection in swine: postweaning growth. J. Anim. Sci. 53, 1446-1457.

Biswas, D.K.; Craig, J.V., 1969: Relationship between purebred and crossbred paternal half-sisters' performance in chickens. Poult. Sci. 48,524-526.

Bowman, J.C., 1960: Recurrent selection. I. The detection of overdominance. Heredity 14,197-206.

Brah, G.S., Chaudhary M.L.; Sandhu, J.S., 1987: Cross-line productivity in relation to selection in pure-line Whit Leghorns. J. Anim. Breed. Genet. 104,391-396.

Calhoon, R.E.; Bohren, B.B., 1974: Genetic gains from reciprocal recurrent and within-line selection for egg production in the fowl. Theor. Appl. Genet. 44,364-372.

Comstock, R.E.; Robinson, H.F.; Harvey, P.H., 1949: A breeding procedure designed to make maximum use of both general and specific combining ability. Agronomy J. 41,360-367.

Dickerson, G.E., 1952: Inbred lines for heterosis ? In: Heterosis (Edited by J.W. Gowen). Iowa State College Press. Iowa, USA. pp330-351.

Hill, W.G., 1970: Theory of limits to selection with line crossing. In: Mathematical Topics in Population Genetics (Edited by K. Kojima). Berlin. Springer-Verlag. New York, 1970, pp.210-245.

Krause, E., Yamada, Y.; Bell, A.E., 1965: Genetic parameters in two populations of chickens under reciprocal recurrent selection. Br. Poult. Sci. 6,197-206.

McNew, R.W.; Bell, A.E., 1971: The nature of the purebred-crossbred genetic covariance. Genet. Res.,camb.18,1-7.

Pirchner, F., 1974: Genetic correlations between pure-line and cross-line performance in poultry. Proc. 23rd Nat. Poultry Breeders' Roundtable. May 2-3, 1974. Kansas City, Missouri. pp202-230.

Pirchner, F.; Mergl, R., 1977: Overdominance as cause for heterosis in poultry. J. Anim. Breed. Genet. 94,151-158.

Rabsztyn, A.; Nowak, J., 1978: A comparative study on genetic, environmental and phenotypic variances and on heritability of some performance traits in purebred hen strains and their reciprocal crosses. Genetica Polonic 19,193-199.

Rempel, W.E., 1974: Selection for crossbred performance in pigs. Proc. 1st World Congr. Genet. Appl. Livest. Prod. 1,849-858.

Robinson, O.W.; Louca, A.; Legates, J.E., 1964: Purebred and crossbred performance of paternal half-sibs of swine. J. Anim. Sci. 23,854 (abstr.).

Salah, E.; Galal, E.; Hazel, L.N.; Sidwell, G.M.; Terrill, C.E., 1969: Correlation between purebred and crossbred half-sibs in sheep. J. Anim. Sci. 30,475-480.

Sellier, P., 1982: Selecting populations for use in crossbreeding. Proc. 2nd World Congr. Genet. Appl. Livest. Prod.

6,15-49.

Singh, H.; Dev, D.S., 1974: Genetic correlation between performance of pure-bred White Leghorn pullets and their paternal half-sisters from Rhode Island Red dams. Br. Poult. Sci. 15,513-515.

Vinson, W.E.; Eisen, E.J.; Robison, O.W., 1969: Predicted response to selection for crossbred performance in mice. J. Anim. Sci. 28,725-733.

Wei, M.; Van der Steen, H.A.M., 1990: Comparison of reciprocal recurrent selection with pure-line selection systems in animal breeding. Animal Breeding Abstracts 59,281-298.

Wei, M.; Van der Steen, H.A.M.; Van der Werf, J.H.J.; Brascamp, E.W., 1990: Relationship between purebred and crossbred parameters. 2. variances and covariances under the one-locus model. J. Anim. Breed. Genet. 108,253-261.

Wilson, S.P.; Whatley Jr., J.A.; Whiteman, J.V.; Morrison, R.D., 1962: Influence of sire and line of breeding on sow productivity. J. Anim. Sci. 21,119-122.

Wong, W.C.; Boylan, W.J.; Rempel, W.E., 1971: Purebred versus crossbred performance as a basis of selection in swine. J. Anim. Sci. 32,605-610.

Chapter 5

Animal Model Estimation of Additive and Dominance Variances in Egg Production Traits of Poultry

Ming Wei and J.H.J. van der Werf

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

To be published in ***Journal of Animal Science*** (in press)
Reproduced by permission of American Society of Animal Science

"Significant dominance variation was found for all egg production traits, especially egg number. ... To improve performance of commercial laying hens, crossbred information should be considered so that dominance can be exploited in the selection program."

Animal Model Estimation of Additive and Dominance Variances in Egg Production Traits of Poultry [1]

Ming Wei and J.H.J. van der Werf

Department of Animal Breeding,Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

ABSTRACT: *An animal model analysis was used to estimate simultaneously additive (σ_a^2) and dominance (σ_d^2) variances for egg production traits within three White Leghorn lines. The data consisted of information for three generations on egg number (EN) produced at 18 to 25 (EN1), 26 to 65 (EN2), and 18 to 65 wk of age (EN3); egg weight (EW) measured at 30 to 35 (EW1) and 40 to 45 wk (EW2); and egg specific gravity (ESG) measured at 30 to 35 (ESG1) and 40 to 45 wk (ESG2). A transformation was used for EN2 and EN3 because of a skewed distribution. In total, 813 sires, 2,575 dams, and 28,649 daughters were involved in the analyses. Three genetic models (sire-dam, additive, and dominance) were compared in estimating heritability (h^2). The sire-dam model underestimated h^2 because it ignored animal relationships. The h^2 estimates from the additive model were approximately 9 to 52% higher for EN and 2 to 18% higher for EW and ESG than those from the dominance model. The differences between the h^2 estimates from the additive and dominance models were increased for larger dominance variance (σ_d^2). Ratios of σ_d^2 to total variance were high for EN (10 to 20%) and low for EW and ESG (1 to 13%). Ratios of σ_d^2 to total genetic variance for EN1, EN2, EN3, EW1, EW2, ESG1, and ESG2 were 18 to 36, 29 to 43, 29 to 56, 1 to 26, 3 to 8, 20 to 27, and 2 to 14%, respectively. The results on dominance were in good agreement with heterosis and inbreeding depression for these egg production traits described previously.*

Key Words: *Animal Models, Dominance Variation, Egg Production, Heritability, Model Comparison, Poultry*

---

[1] *The authors express their appreciation to Cees P. van Drunen of Euribrid for providing us the data and relevant information, to Karin Meyer for using her DFREML program, and to Ina Hoeschele and Paul VanRaden for using their program to calculate the inverse of dominance relationship matrix.*

Introduction

There are several reasons for estimating dominance variation: an unbiased estimation of heritability in the narrow sense, more precise prediction of additive effects, and usage of dominance effects through a crossbreeding or special mating strategy. Dominance influences all genetic parameters related to crossbreeding (Wei et al., 1991a,b).

Recently, mixed models including additive and nonadditive genetic effects have been developed (Henderson, 1988; Meyer, 1989; Hoeschele and VanRaden, 1991). The method of choice for estimating variance components is REML using a mixed linear model including matrices for additive genetic and dominance animal relationships. The advantage of this methodology is that data from several generations can be used so that dominance is no longer confounded with maternal or common environmental effects to full sibs.

Dominance variation estimation using the described methodology has not been reported in poultry, even though egg production is influenced by dominance (Fairfull and Gowe, 1990). VanRaden (1989), Hoeschele (1991), and Tempelman and Burnside (1991) have, however, reported such estimation of dominance variance for dairy cattle traits.

The objective of this study was to estimate additive and dominance variances for egg production traits of three lines of laying hens using an animal model analysis. Estimates from a full model were compared to those from an additive animal model and a commonly used sire-dam model.

Materials and Methods

Data

The data consisted of records on egg number (EN), egg weight (EW), and egg specific gravity (ESG) for three generations of three White Leghorn lines. Data were obtained by Euribrid between 1987 and 1989. Lines 2 and 3 had been selected mainly for EN and EW for many generations, but Line 1 had only a short history of selection. Line 3 is used as a dam line and Lines 1 and 2 as sire lines in a crossbreeding system. All hens were moved to a laying house at approximately 16 wk of age (ranged from 15 to 17 wk), where they were raised in individual cages under a well-controlled environment. In each line, each sire was mated to approximately five dams and each dam produced approximately 20 to 25 progeny (i.e., approximately 12 daughters). Within line and generation, the hens were distributed over groups (one to four groups per line and generation) to facilitate management and prevent inbreeding. In total, > 2,500 full-sib families and 28,000 records were used in the analyses (Table 1). Every record contained information on 1) early egg production defined as egg number laid between 18 and 25 wk of age (EN1); 2) main period egg production between 26 and 65 wk (EN2); 3) total egg production between 18 and 65 wk (EN3); 4) egg weight measured at 30 to 35 wk (EW1); 5) egg weight at 40 to 45 wk (EW2); 6) egg specific gravity measured at 30 to 35 wk (ESG1); and 7) egg specific gravity at 40 to 45 wk (ESG2). The ESG was defined as follows: ESG = 10,000 × [EW in air/(EW in air - EW in water) - 1], where EW in air and EW in water refer to normal egg weight and the weight measured in water, respectively.

Table 1. Number of sires, dams, and daughters (with records) of three laying hen lines used in analyses

	Line 1			Line 2			Line 3		
Generation	Sire	Dam	Daughter	Sire	Dam	Daughter	Sire	Dam	Daughter
1	31	139	1,552	84	370	3,084	49	149	1,703
2	99	238	3,199	216	578	5,658	91	377	4,910
3	42	106	1,250	136	367	3,868	65	251	3,425
Total	172	483	6,001	436	1,315	12,610	205	777	10,038

Because laying hens were hatched in different weeks and the recording of their EN ended at the same time, the following formula was used to correct EN into a standard 65-wk egg number (EN_{65}): $EN_{65} = EN_m + (65 - m)EN_n/n$, where EN_m is the actual EN produced until the mth wk of age, EN_n is the EN produced in the last period of recording (last n weeks), n is the number of weeks for the last period of recording (approximately 10 wk), and m is the age (in weeks) of a laying hen at the end of EN recording.

The EN traits, EN2 and EN3, showed a negatively skewed distribution. A transformation of these data was therefore carried out following the empirical method suggested by Ibe and Hill (1988) as follows:

$$z(t) = \frac{(y^t - 1)}{tG_y^{t-1}} \qquad [1]$$

where y is an original untransformed observation, z(t) is the standardized transformed variate, G_y is the geometric mean of the original observations, and t is the value obtained by maximizing the log likelihood of Equation [2].

The variables, z(t), were used to calculate the log likelihood, $L_{max}(t)$, for trial values of t, which is as follows:

$$L_{max}(t) = -\frac{n}{2}\log_e[\frac{S_r(t)}{n}] \quad [2]$$

where n is the total number of observations and $S_r(t)$ is the residual sum of squares from analysis of the standardized dependent variable [1] using the linear model [3] described later as a sire-dam model. This procedure treats sire and dam as fixed effects in model [3]. A more complete methodology for estimating transformation parameters simultaneously with other parameters in a mixed model was proposed by Gianola et al. (1990).

The optimal t value is empirically chosen in such a way that the log-likelihood $L_{max}(t)$ was maximum and $\log_e[S_r(t)/n]$ minimum. The values of t used for EN2 and EN3 in Lines 1, 2, and 3 were 4.7 and 2.7, 6.1 and 4.0, and 8.8 and 5.4, respectively.

Both the transformed and untransformed data were used in estimating variance components on EN2 and EN3 under all models.

Models

Sire-Dam Model. Sire and dam components were first calculated by a sire-dam model that did not account for animal relationships other than sire-progeny and dam-progeny. Such a model is usually applied for analyzing poultry data and it was used here for comparison with other methods. The linear model to analyze data for each line is expressed as follows:

$$y_{ijklmn} = \mu + G_i + GROUP_{ij} + HW_{ijk} + s_{ijl} + d_{ijlm} + r_{ijklmn} \quad [3]$$

where y_{ijklmn} is the ijklmnth observation on EN, EW, and ESG; μ is the common mean; G_i is the fixed effect of the ith generation (i = 1, 2, or 3); $GROUP_{ij}$ is the fixed effect of the ijth group within generation; HW_{ijk} is the fixed effect of the ijkth hatch week within group and generation; s_{ijl} is the random effect of the ijlth sire within group and generation following *NIID*$(0, \sigma^2_{sire})$ (*NIID* stands for normal, independent, and identically distributed); d_{ijlm} is the random effect of the ijlmth dam within sire, group, and generation, *NIID*$(0, \sigma^2_{dam})$; and r_{ijklmn} is the residual effect, *NIID*$(0, \sigma^2_r)$.

Estimates of variance components were obtained using the REML method in the VARCOMP procedure of SAS (1989). Heritability (h^2) was estimated from the sire component, $h^2_s = 4\sigma^2_{sire}/(\sigma^2_{sire} + \sigma^2_{dam} + \sigma^2_r)$, as well as from the sire-plus-dam component, $h^2_{s+d} = 2(\sigma^2_{sire} + \sigma^2_{dam})/(\sigma^2_{sire} + \sigma^2_{dam} + \sigma^2_r)$.

Additive Model. The estimation of additive genetic variances for egg production traits in each line was based on the following linear model:

$$y_{ijkl} = \mu + GROUP_i + HW_{ij} + a_{ik} + e_{ijkl} \quad [4]$$

where y_{ijkl} is the ijklth observation for EN, EW, or ESG; μ is the common mean; $GROUP_i$ is the fixed effect of the ith group; HW_{ij} is the fixed effect of the ijth hatch week; a_{ik} is the random additive effect of the ikth animal; and e_{ijkl} is the error effect.

The model above is expressed in matrix notation as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \qquad [5]$$

where **y** is the vector of observations, **b** is the vector of fixed effects, **a** is the vector of random additive animal effects, and **X** and **Z** are the incidence matrices relating the observations to the respective fixed and random effects. **Z** is partitioned into a null matrix for base animals without records and an identity matrix for animals with records.

The means and variances for the model are assumed to be as follows:

$$E\begin{bmatrix}\mathbf{y}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{Xb}\\ 0\\ 0\end{bmatrix}, \qquad V\begin{bmatrix}\mathbf{y}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{V}_{add} & \mathbf{ZA}\sigma_a^2 & \mathbf{I}\sigma_e^2\\ \mathbf{AZ}'/\sigma_a^2 & \mathbf{A}\sigma_a^2 & 0\\ \mathbf{I}\sigma_e^2 & 0 & \mathbf{I}\sigma_e^2\end{bmatrix}$$

where $\mathbf{V}_{add} = \mathbf{ZA}\sigma_a^2\mathbf{Z}' + \mathbf{I}\sigma_e^2$, **A** is the additive animal relationship matrix, **I** is an identity matrix, and σ_a^2 and σ_e^2 are the additive genetic and error variances.

Dominance Model. The linear dominance model was as follows:

$$y_{ijkl} = \mu + GROUP_i + HW_{ij} + a_{ik} + d_{ik} + e_{ijkl} \qquad [6]$$

where d_{ik} denotes the random dominance effect of the ikth animal, and other variables are the same as explained in the additive model [4].

The model is expressed in matrix notation as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Zd} + \mathbf{e} \qquad [7]$$

where **d** refers to the vector of random dominance effects, and other variables are the same as explained in model [5]. The means and variances in the dominance model are assumed to be as follows:

$$E\begin{bmatrix}\mathbf{y}\\ \mathbf{a}\\ \mathbf{d}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{Xb}\\ 0\\ 0\\ 0\end{bmatrix}, \qquad V\begin{bmatrix}\mathbf{y}\\ \mathbf{a}\\ \mathbf{d}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{V}_{dom} & \mathbf{ZA}\sigma_a^2 & \mathbf{ZD}\sigma_d^2 & \mathbf{I}\sigma_e^2\\ \mathbf{AZ}'/\sigma_a^2 & \mathbf{A}\sigma_a^2 & 0 & 0\\ \mathbf{DZ}'/\sigma_d^2 & 0 & \mathbf{D}\sigma_d^2 & 0\\ \mathbf{I}\sigma_e^2 & 0 & 0 & \mathbf{I}\sigma_e^2\end{bmatrix}$$

where $\mathbf{V}_{dom} = \mathbf{Z}(\mathbf{A}\sigma^2_a + \mathbf{D}\sigma^2_d)\mathbf{Z}' + \mathbf{I}\sigma^2_e$, σ^2_d is the dominance genetic variance, and **A** and **D** are the additive and dominance animal relationship matrices.

The method of estimating variance components under both the additive and the dominance models was based on the derivative-free REML algorithm for animal models (Graser et al., 1987). The simplex method was used to maximize the likelihood functions. The DFREML program of Meyer (1989) was used for all animal model analyses. The rapid method for calculating the inverse of **D**, developed by Hoeschele and VanRaden (1991), was used in the analysis. This method partitions dominance effects into sire-dam subclass effects and constructs the inverse of the relationships matrix among both dominance and subclass effects. We obtained the relationships defined in $\mathbf{D}^{-1}$ by absorbing the subclass coefficients into the dominance effects, a principle proposed by Henderson (1976). Asymptotic standard errors of h^2 and d^2 (ratio of dominance variance to total phenotypic variance) estimates were approximated using a Taylor's series.

Results and Discussion

Heritability Estimation Under Three Models

Heritability estimates (h^2) calculated from three different models are presented in Tables 2, 3, and 4. Based on the sire-dam model the h^2 estimates were high for EW (.43 to .56), intermediate for EN1 (.41 to .49) and ESG (.34 to .40), and relatively low for EN2 and EN3 (.21 to .40). It is noted that only the h^2_{s+d} estimates based on sire plus dam component are discussed here. The h^2 estimates calculated by the sire-dam model (Tables 2, 3, and 4) were similar to those found in the literature (Fairfull and Gowe, 1990). The h^2 estimates observed in Line 1 are the largest, and h^2 estimates in Line 2 are bigger than those in Line 3. One explanation may be that Line 1 has had only a short history of selection.

Data transformation always resulted in higher estimates of h^2 for EN traits under all three models (i.e., 13 to 18% higher for EN2 and 5 to 8% higher for EN3) (Tables 2 and 5). Similar results were found by Ibe and Hill (1988) and Besbes et al. (1991a). In fact, data transformation decreased the error (σ^2_e) or residual (σ^2_r) variance estimates in relation to additive variance (σ^2_a) or sire and dam variances (σ^2_{sire} and σ^2_{dam}), respectively, under the animal model or the sire-dam model. Results for untransformed data are shown only for Line 1 (Table 5), but the differences between the estimates based on transformed and untransformed data were similar for Lines 2 and 3.

Because relationships were assumed to account for selection over generations, a generation effect was omitted from the animal models [5] and [7]. However, the effects of generation were explained by group effects in the animal model and did not significantly influence the variance estimation.

Table 2. Estimates of genetic parameters[a] under three models in hen Line 1

Models	Trait[b]	h^2	± SE	d^2	± SE	σ^2_a	σ^2_d	σ^2_e
Dominance model	EN1	.52	.057	.11	.046	30.50	6.67	21.65
	EN2	.35	.051	.15	.055	41.06	17.13	59.43
	EN3	.36	.058	.15	.051	66.87	27.84	89.86
	EW1	.55	.056	.01	.045	4.272	.039	3.440
	EW2	.63	.048	.06	.038	6.379	.565	3.118
	ESG1	.31	.043	.08	.046	427.4	105.7	855.3
	ESG2	.39	.048	.01	.042	474.9	11.9	723.0
Additive model	EN1	.60	.038			34.89		23.84
	EN2	.44	.042			52.86		68.53
	EN3	.45	.046			84.98		104.16
	EW1	.59	.043			4.745		3.339
	EW2	.66	.042			6.527		3.411
	ESG1	.38	.035			562.5		943.8
	ESG2	.40	.042			496.8		740.1
		h^2_s	± SE	h^2_{s+d}	± SE	σ^2_{sire}	σ^2_{dam}	σ^2_r
Sire-dam model	EN1	.37	.076	.47	.042	5.09	7.92	41.90
	EN2	.39	.075	.40	.038	11.27	11.55	91.98
	EN3	.41	.075	.40	.039	18.26	17.00	143.05
	EW1	.52	.094	.49	.047	.952	.849	5.567
	EW2	.63	.093	.56	.045	1.432	1.105	6.548
	ESG1	.42	.070	.36	.037	145.8	104.8	1,142.1
	ESG2	.50	.076	.38	.040	153.3	80.4	980.7

[a] σ^2_a, σ^2_d, and σ^2_e are estimates of additive, dominance, and error variances. h^2 is the heritability. d^2 is the dominance variance as a proportion of total variance. h^2_s and h^2_{s+d} are the h^2 estimated by sire and sire-plus-dam components. σ^2_{sire}, σ^2_{dam}, and σ^2_r are the sire, dam, and residual variances.

[b] EN1, EN2, and EN3 are transformed egg numbers produced between 18 and 25, 26 and 65, and 18 and 65 wk of age. EW1 and EW2 are egg weights measured at 30 to 35 and 40 to 45 wk. ESG1 and ESG2 are egg specific gravities measured at 30 to 35 and 40 to 45 wk.

Within each line, the estimates of h^2 from the additive animal model were higher than those (h^2_{s+d}) from the sire-dam model (i.e., 3 to 28% higher for EN, 6 to 20% higher for EW, and 3 to 8% higher for ESG). The additive model had a lower σ_e^2 and a higher σ_a^2 than the sire-dam model. A sire-dam model is expected to underestimate h^2 because it ignores animal relationships (van der Werf and de Boer, 1990). The additive animal model, therefore, yielded higher h^2 estimates than those found in the literature (Fairfull and Gowe, 1990).

Table 3. Estimates of genetic parameters[a] under three models in hen Line 2

Models	Trait[b]	h^2	± SE	d^2	± SE	σ_a^2	σ_d^2	σ_e^2
Dominance model	EN1	.48	.043	.10	.054	27.17	5.89	23.60
	EN2	.28	.039	.20	.060	28.71	20.42	52.00
	EN3	.35	.040	.18	.057	58.75	29.67	79.99
	EW1	.41	.047	.07	.040	3.986	.693	5.033
	EW2	.52	.039	.02	.046	6.403	.214	5.779
	ESG1	.34	.040	.11	.054	607.7	191.1	999.5
	ESG2	.40	.039	.05	.053	734.0	93.6	1,003.3
Additive model	EN1	.53	.025			29.99		26.36
	EN2	.37	.023			36.86		63.30
	EN3	.40	.024			66.66		101.75
	EW1	.47	.028			4.729		5.320
	EW2	.53	.025			6.721		5.930
	ESG1	.38	.024			636.50		1,033.3
	ESG2	.43	.024			767.40		1,033.7
		h_s^2	± SE	h_{s+d}^2	± SE	σ_{sire}^2	σ_{dam}^2	σ_r^2
Sire-dam model	EN1	.53	.054	.49	.030	7.339	6.175	42.17
	EN2	.34	.043	.35	.034	8.539	8.930	82.28
	EN3	.42	.047	.39	.025	17.285	14.858	132.94
	EW1	.51	.061	.43	.031	1.238	.843	7.555
	EW2	.61	.058	.50	.029	1.841	1.173	9.075
	ESG1	.36	.045	.37	.025	159.2	166.8	1,451.7
	ESG2	.46	.046	.40	.026	206.9	155.2	1,444.4

[a] σ_a^2, σ_d^2, and σ_e^2 are estimates of additive, dominance, and error variances. h^2 is the heritability. d^2 is the dominance variance as a proportion of total variance. h_s^2 and h_{s+d}^2 are the h^2 estimated by sire and sire-plus-dam components. σ_{sire}^2, σ_{dam}^2, and σ_r^2 are the sire, dam, and residual variances.

[b] EN1, EN2, and EN3 are transformed egg numbers produced between 18 and 25, 26 and 65, and 18 and 65 wk of age. EW1 and EW2 are egg weights measured at 30 to 35 and 40 to 45 wk. ESG1 and ESG2 are egg specific gravities measured at 30 to 35 and 40 to 45 wk.

Table 4. Estimates of genetic parameters[a] under three models in hen Line 3

Models	Traits[b]	h^2	± SE	d^2	± SE	σ_a^2	σ_d^2	σ_e^2
Dominance model	EN1	.33	.048	.19	.055	14.16	8.10	20.30
	EN2	.15	.031	.11	.046	16.08	11.93	77.12
	EN3	.12	.031	.16	.050	20.90	27.14	123.81
	EW1	.38	.048	.13	.053	4.250	1.468	5.552
	EW2	.48	.049	.04	.046	6.875	.539	6.769
	ESG1	.33	.043	.13	.049	481.1	177.6	805.5
	ESG2	.32	.037	.05	.044	683.4	107.3	1,319.9
Additive model	EN1	.47	.030			20.76		23.14
	EN2	.23	.024			25.75		86.38
	EN3	.25	.023			41.59		128.67
	EW1	.46	.029			5.481		6.370
	EW2	.52	.034			7.405		6.924
	ESG1	.37	.029			518.9		890.6
	ESG2	.36	.030			758.4		1,373.0
		h_s^2	± SE	h_{s+d}^2	± SE	σ_{sire}^2	σ_{dam}^2	σ_r^2
Sire-dam model	EN1	.35	.052	.41	.027	3.695	4.932	33.06
	EN2	.18	.032	.22	.019	5.032	7.034	98.10
	EN3	.12	.030	.21	.019	5.008	12.335	147.49
	EW1	.47	.058	.43	.030	1.341	1.137	8.991
	EW2	.50	.067	.44	.034	1.715	1.308	10.590
	ESG1	.39	.050	.35	.027	135.3	101.7	1,135.8
	ESG2	.41	.056	.34	.029	215.8	140.6	1,748.0

[a] σ_a^2, σ_d^2, and σ_e^2 are estimates of additive, dominance, and error variances. h^2 is the heritability. d^2 is the dominance variance as a proportion of total variance. h_s^2 and h_{s+d}^2 are the h^2 estimated by sire and sire-plus-dam components. σ_{sire}^2, σ_{dam}^2, and σ_r^2 are the sire, dam, and residual variances.

[b] EN1, EN2, and EN3 are transformed egg numbers produced between 18 and 25, 26 and 65, and 18 and 65 wk of age. EW1 and EW2 are egg weights measured at 30 to 35 and 40 to 45 wk. ESG1 and ESG2 are egg specific gravities measured at 30 to 35 and 40 to 45 wk.

The only previous report on estimation of h^2 for egg production traits using an additive animal model and REML was published by Besbes et al. (1991b). Their h^2 estimates for EW (.47) and ESG (.34) are similar to the results of this study. However, their h^2 estimates for EN between 19 and 26, 26 and 38, and 26 and 54 wk of age were .25, .09, and .18, respectively. These estimates are rather low compared with our corresponding estimates for EN1, EN2, and EN3.

Consistently lower h^2 estimates were obtained under the dominance model than under the additive model (Tables 2, 3 and 4) (i.e., 9 to 30, 20 to 38, 13 to 53, 7 to 17, 2 to 8, 11 to 18, and 3 to 11% lower for EN1, EN2, EN3, EW1, EW2, ESG1, and ESG2, respectively). This was caused by the extraction of σ^2_d from σ^2_e and σ^2_a components, which consequently decreased σ^2_e and σ^2_a estimates and kept total variance almost unchanged in the dominance model. Larger dominance variance (σ^2_d) estimates were accompanied by a bigger difference between h^2 estimates from additive and dominance models. Resemblance between relatives is partly due to dominance effects. Under an additive model, part of the resemblance between related animals due to dominance is contained in the estimated additive effect, hence overestimating additive variance (σ^2_a). In this study, an intermediate to high negative approximate sampling correlation between h^2 and d^2 (ratio of σ^2_d to total phenotypic variance) estimates was found for all traits (-.55 to -.86). This indicates that estimation of dominance and additive effects was largely based on the same comparisons of sibship leading to correlated estimates.

Table 5. Estimates of genetic parameters[a] for the untransformed egg number data under three models in hen Line 1

Models	Trait[b]	h^2 ±	SE	d^2 ±	SE	σ^2_a	σ^2_d	σ^2_e
Dominance model	NEN2	.31	.051	.12	.053	42.52	17.15	78.38
	NEN3	.34	.057	.13	.055	61.89	24.24	95.56
Additive model	NEN2	.38	.045			54.11		86.65
	NEN3	.43	.047			84.32		112.37
		h^2_s ±	SE	h^2_{s+d} ±	SE	σ^2_{sire}	σ^2_{dam}	σ^2_r
Sire-dam model	NEN2	.33	.065	.34	.035	10.77	11.51	108.93
	NEN3	.37	.070	.37	.037	17.31	16.84	150.68

[a] σ^2_a, σ^2_d, and σ^2_e are estimates of additive, dominance, and error variances. h^2 is the heritability. d^2 is the dominance variance as a proportion of total variance. h^2_s and h^2_{s+d} are the h^2 estimated by sire and sire-plus-dam components. σ^2_{sire}, σ^2_{dam}, and σ^2_r are the sire, dam, and residual variances.

[b] NEN2 and NEN3 refer to the untransformed EN2 and EN3.

With regard to the effect of dominance on estimation of additive variation under an additive model, van der Werf and de Boer (1989a,b) reported that h^2 was slightly overestimated by an additive model for milk production traits because of a heterotic effect between breeds. In this study, it was found that within lines dominance variation was a much more important cause of a biased estimation of h^2. Consequently, estimation of additive effects is biased (de Boer and van Arendonk, 1992), and selection accuracy is reduced under an additive model in the case of dominance (Uimari and Mäki-Tanila, 1991).

A sire-dam model overestimates h^2 because it ignores dominance and underestimates h^2 because it ignores animal relationships. Coincidentally, the two biases that affect the estimation of h^2 under a sire-dam model cancel each other out to some extent, especially for EN2 and EN3.

Estimation of Dominance Variance

The estimates of σ_d^2 and d^2 for egg production traits are presented in Tables 2, 3, and 4 for Lines 1, 2, and 3, respectively. The d^2 estimates were high for EN (10 to 20%) and low for EW and ESG (1 to 13%). Estimates for σ_d^2 and d^2 for all traits were similar for the three lines. The trait EN1 is a combination of two traits, early egg laying rate and the age at first egg, and it is dominated by the second one (Fairfull and Gowe, 1990). Thus, EN1 should be considered mostly the age at first egg.

These findings on σ_d^2 for egg production traits were consistent with parameters attributed in the literature to these traits, such as heterosis and inbreeding depression. It is well known that dominance is an important cause of both heterosis and inbreeding depression. In different populations, EN has shown a consistently high heterosis (10 to 20%), EW consistently low heterosis (0 to 5%), ESG no or small heterosis (0 to 5%), and age at first egg low heterosis (0 to -9%) (Fairfull and Gowe, 1986; Fairfull, 1990). Inbreeding depression has been found to be high for EN and relatively low for EW, ESG, and age at first egg (Foster and Kilpatrick, 1987; Abplanalp, 1990; Flock et al., 1991). Flock et al. (1991) recently reported that the inbreeding depression associated with 10% inbreeding was 3% for EN and only 1% for EW and shell quality.

Data transformation resulted in an increase (15 to 25%) in the d^2 estimates mainly because it led to a decrease in the σ_a^2 estimates. This was also the case for h^2 estimation (Tables 2 and 5).

A comparison of variance components for the different models revealed that the variance attributed to σ_d^2 under the dominance model was attributed in part to both σ_a^2 and σ_d^2 under the additive model (Tables 2, 3, and 4).

The percentage of total genetic variance (d_g^2) accounted for by σ_d^2 was 29 to 56% for EN2 and EN3, 18 to 36% for EN1, and 1 to 27% for EW and ESG (Table 6). The findings on d_g^2 can be compared with the theoretic results for a single-locus, two-allele model where d_g^2 is given by the formula (Falconer, 1989) as follows:

$$d_g^2 = \frac{2pqw^2}{2pqw^2 + [1 + w(q - p)]^2} \qquad [9]$$

where p refers to the frequency of a favorable allele, q is the frequency of a recessive allele, the value of half the difference between homozygotes is assumed to be 1, and w is the value of the heterozygote defined as d by Falconer (1989). If one is willing to ignore the interaction of genes of different loci, the formula [9] can be used for a multilocus situation. In the case in which $w = .5$, the value of d_g^2 reaches its maximum at 14.3% for $p = .75$. Even if $w = .8$, d_g^2 will never be larger than 44%. In this study, d_g^2 for EN reached 29 to 56%, indicating that dominance effects were large and overdominance should not be excluded. For EW and ESG, the dominance effects were significant but relatively low.

Simultaneous estimation of σ_a^2 and σ_d^2 using REML and an animal model has not been reported for poultry. However, a few estimates of σ_d^2 for dairy cattle have recently been published. A low σ_d^2 for milk and fat yield was reported by VanRaden (1989) using a tilde hat approach. In contradiction to this, Tempelman and Burnside (1991) found a significant σ_d^2 for fat yield. Hoeschele (1991) found the σ_d^2 for female fertility traits to be small and roughly as large as σ_a^2 under a sire-maternal grandsire model.

Table 6. The dominance variance as a proportion of genetic variance (d_g^2) in three hen lines

Traits[a]	Line 1	Line 2	Line 3
EN1	.18	.18	.36
EN2	.29	.42	.43
EN3	.29	.34	.56
EW1	.01	.15	.26
EW2	.08	.03	.07
ESG1	.20	.24	.27
ESG2	.02	.11	.14

[a] **EN1, EN2, and EN3 are transformed egg numbers produced between 18 and 25, 26 and 65, and 18 and 65 wk of age. EW1 and EW2 are egg weights measured at 30 to 35 and 40 to 45 wk. ESG1 and ESG2 are egg specific gravities measured at 30 to 35 and 40 to 45 wk.**

A comparison of our results from a typical poultry breeding structure with those from dairy cattle (Tempelman and Burnside, 1991) reveals a few interesting points. First, the approximate standard errors for d^2 estimates for dairy production traits (.15 to .20) were much larger than those for laying hens (.04 to .06). The reason for this might be that there were many more dominance animal relationships involved in poultry. Second, the σ_e^2 estimates under the dominance model in this study decreased by approximately 9 to 37% for EN and by 2 to 10% for EW and ESG compared with the additive model; σ_a^2 decreased by approximately 9 to 50% for EN and by 2 to 24% for EW and ESG. In the dairy cattle study, the σ_a^2 estimates under the additive and dominance models were almost the same (1 to 10% difference). Surprisingly, the σ_e^2 estimate under the dominance model decreased by 60 to 80% (except in one case by 14%). The estimates of d^2 (14 to 55%) in the study of Tempelman and Burnside (1991), however, seem to be rather high compared to literature values for heterosis (Turton, 1981; McAllister, 1986; van der Werf and de Boer, 1989b).

Dominance Variance and the Difference Between Sire and Dam Components

The difference between sire and dam components, (σ_{dam}^2 - σ_{sire}^2), has been used to estimate dominance variance under the assumption that maternal, common environmental and epistatic effects are negligible and not important. The question arises how this estimate, (σ_{dam}^2 - σ_{sire}^2), compares to the σ_d^2 estimated under a dominance model. The full-sib covariances contain not only 1/2 additive and 1/4 dominance variances, but also epistatic (σ_{epi}^2), maternal (σ_m^2), and common environmental (σ_{cc}^2) variances or covariances (Falconer, 1989). Theoretically, σ_{dam}^2, and therefore σ_d^2, can be overestimated due to each of these effects if they exist.

In this study, common environment effects for full sibs can be ignored because full sibs were randomly distributed across cages. Maternal effects can also be ignored because they are not important for EN (Fairfull and Gowe, 1986). When such effects would be important, a mixed model using data on more than one generation could possibly correct for such effects by including them in the model.

Epistatic interactions have been found to be a significant effect on EN in line-crossing experiments (Sheridan and Randall, 1977; Fairfull and Gowe, 1986). Therefore, the value of (σ_{dam}^2 - σ_{sire}^2) could result from dominance, and possibly epistatic, effects. Also, the value of σ_d^2 could be due to epistatic effects.

The results presented contradict the method that estimates dominance variance on the basis of (σ_{dam}^2 - σ_{sire}^2). The σ_{sire}^2 was found to be larger than the σ_{dam}^2 for most of the EW and ESG traits, and also for EN1 in Line 2 and for EN2 in Lines 1 and 2 (Tables 2, 3, and 4). This phenomenon has also been described in the literature, especially for EW (van Tijen, 1977; Poggenpoel and Duckitt, 1988; Mou, 1991). For most traits at the same time that a significant σ_d^2 was found under the dominance model, σ_{sire}^2 was larger than or similar to σ_{dam}^2 (Tables 2 and 3). Larger estimates for σ_{sire}^2 than for σ_{dam}^2 may be caused by an additional variation among sires (e.g., due to sex-linked effects, which leads to increased σ_{sire}^2 estimates).

However, this point needs further study.

Implications

A commonly used sire-dam model led to two biases in estimating heritability due to ignoring the dominance effect and animal relationships other than parents-progeny. An additive model including all animal relationships overestimated heritability because it ignored dominance effects. Significant dominance variation was found for all egg production traits, especially egg number. An animal model accounting for additive and dominance effects and REML should be used in analyzing laying hen data to obtain unbiased estimates of heritability and dominance variance. To improve performance of commercial laying hens, crossbred information should be considered so that dominance can be exploited in the selection program.

Literature Cited

Abplanalp, H. 1990. Inbreeding. In: R. D. Crawford (Ed.) Poultry Breeding and Genetics. p 955. Elsevier, Amsterdam, The Netherlands.

Besbes, B., V. Ducrocq, A. Tavernier, and J. L. Foulley. 1991a. Estimation of genetic parameters of egg production traits of laying hens by restricted maximum likelihood applied to a multiple-trait reduced animal model. In: Proc. 42nd Annu. Mtg. of the EAAP, Sept. 8-12, 1991, Berlin, FRG.

Besbes, B., V. Ducrocq, A. Tavernier, J. L. Foulley, M. Boichard, C. Beaumont, and M. Protais. 1991b. Estimation of genetic parameters of egg production traits of laying hens by restricted maximum likelihood applied to a multiple-trait reduced model. In: Proc. 42nd Annu. Mtg of the EAAP, Sept. 8-12, 1991, Berlin, FRG.

de Boer I.J.M., and J.A.M. van Arendonk. 1992. Prediction of additive and dominance effects in selected and unselected populations with inbreeding. Theor. Appl. Genet. 84:451.

Fairfull, R. W. 1990. Heterosis. In: R. D. Crawford (Ed.) Poultry Breeding and Genetics. p 913. Elsevier, Amsterdam, The Netherlands.

Fairfull, R. W., and R. S. Gowe. 1986. Use of breed resources for poultry egg and meat production. Proc. 3rd World Congr. Genet. Appl. Livest. Prod. XII:242.

Fairfull, R. W., and R. S. Gowe. 1990. In: R. D. Crawford (Ed.) Poultry Breeding and Genetics. p 705. Elsevier, Amsterdam, The Netherlands.

Falconer, D. S. 1989. Introduction to Quantitative Genetics (3rd Ed.). Longman Sci. & Tech., New York.

Flock, D. K., H. Ameli, and P. Glodek. 1991. Inbreeding and heterosis effects on quantitative traits in a White Leghorn population under long-term reciprocal recurrent selection. Br. Poult. Sci. 32:451.

Foster, W. H., and D. J. Kilpatrick. 1987. Inbreeding in poultry: Genetic drift and inbreeding depression. Record of Agricultural Research. Vol. 35. Dept. of Agric., Northern Ireland.

Gianola, D., S. Im, R. L. Fernando, and J. L. Foulley. 1990. Mixed model methodology and the Box-Cox theory of transformation: A bayesian approach. In: D. Gianola and K. Hammond (Ed.) Advances in Statistic Methods for Genetic Improvement of Livestock. p 15. Springer-Verlag, New York.

Graser, H.-U., S. P. Smith, and B. Tier. 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. J. Anim. Sci. 64:1362.

Henderson, C. R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. Biometrics 32:69.

Henderson, C. R. 1988. Theoretical basis and computational methods for a number of different models. J. Dairy Sci. 71(Suppl.2):1.

Hoeschele, I. 1991. Additive and nonadditive genetic variance in female fertility of Holsteins. J. Dairy Sci. 74:1743.

Hoeschele, I., and P. M. VanRaden. 1991. Rapid inversion of dominance relationship matrices for noninbred populations by including sire by dam subclass effects. J. Dairy Sci. 74:557.

Ibe, S. N., and W. G. Hill. 1988. Transformation of poultry egg production data to improve normality, homoscedasticity and linearity of genotypic regression. J. Anim. Breed. Genet. 105:231.

McAllister, A. J. 1986. The role of crossbreeding in breeding programs for intensive milk production in temperate climate. Proc. 3rd World Congr. Genet. Appl. Livest. Prod. IX:47.

Meyer, K. 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. Genet. Sel. Evol. 21:317.

Mou, L. J. 1991. Effects of different environments and selection for persistency in laying hens. III. Genetic and phenotypic parameters of egg production. Norw. J. Agric. Sci. 5:273.

Poggenpoel, D. G., and J. S. Duckitt. 1988. Genetic basis of the increase in egg weight with pullet age in a White Leghorn flock. Br. Poult. Sci. 29:863.

SAS. 1989. SAS/STAT® User's Guide (Version 6). Vol. 2. SAS Inst. Inc., Cary, NC.

Sheridan, A. K., and M. C. Randall. 1977. Heterosis for egg production in White Leghorn Australorp crosses. Br. Poult. Sci. 18:69.

Tempelman, R. J., and E. B. Burnside. 1991. Additive and dominance genetic variation for dairy production traits under an animal model. J. Anim. Breed. Genet. 108:330.

Turton, J. D. 1981. Crossbreeding of dairy cattle - a selective review. Anim. Breed. Abstr. 49:293.

Uimari, P., and A. Mäki-Tanila. 1991. Utilization of dominance genetic variation in selection. p 93. In: Proc. 42nd Annu. Mtg. of the EAAP, Sept. 8-12, 1991, Berlin, FRG.

van der Werf, J.H.J., and W. de Boer. 1989a. Influence of non-additive effects on estimation of genetic parameters in dairy cattle. J. Dairy Sci. 72:2606.

van der Werf, J.H.J., and W. de Boer. 1989b. Estimation of genetic parameters in a crossbred population of Black and White dairy cattle. J. Dairy Sci. 72:2615.

van der Werf, J.H.J., and I.J.M. de Boer. 1990. Estimation of additive genetic variance when base populations are selected. J. Anim. Sci. 68:3124.

VanRaden, P. M. 1989. Estimates of nonadditive genetic variation for milk and fat yields of Holsteins. J. Dairy Sci. 72(Suppl. 1):59 (Abstr.).

van Tijen, W. F. 1977. Shell quality in poultry as seen from the breeders' viewpoint 3. Heritabilities: expected versus accomplished response. Poult. Sci. 56:1121.

Wei, M., H.A.M. van der Steen, J.H.J. van der Werf, and E. W. Brascamp. 1991a. Relationship between purebred and crossbred parameters. I. Variances and covariances under the one-locus model. J. Anim. Breed. Genet. 108:253.

Wei, M., J.H.J. van der Werf, and E. W. Brascamp. 1991b. Relationship between purebred and crossbred parameters. II. Genetic correlation between purebred and crossbred performance under the model with two loci. J. Anim. Breed. Genet. 108:262.

Chapter 6

Maximizing Genetic Response in Crossbreds Using both Purebred and Crossbred Information

Ming Wei and Julius H.J. van der Werf

Department of Animal Breeding, Wageningen Agricultural University
P.O.Box 338, 6700 AH Wageningen, The Netherlands

Submitted for publication to ***Animal Production***.

"The CCPS method is optimal for obtaining genetic response in crossbreds."

Maximizing Genetic Response in Crossbreds Using Both Purebred and Crossbred Information

Ming Wei and Julius H.J. van der Werf

Department of Animal Breeding, Wageningen Agricultural University
P.O.Box 338, 6700 AH Wageningen, The Netherlands

ABSTRACT: *A combined crossbred and purebred selection (CCPS) method, i.e., using crossbred and purebred information, was proposed to achieve genetic response in crossbred animals (R_c). Selection index theory was applied to establish a CCPS index. The CCPS was compared on R_c with pure-line selection (PLS) and crossbred selection (CS) assuming a constant number of total progeny. The CCPS was better than PLS or CS under all circumstances. The genetic correlation between purebred and crossbred performance (r_{pc}) and crossbred heritability (h_C^2) are crucial factors in the comparison. The CCPS was a little better than PLS with a high r_{pc}, and than CS when r_{pc} was small. The PLS crossbred response decreased and the CS response is closer to the CCPS response as h_C^2 increased. The robustness of CCPS against inappropriate assumptions on r_{pc} and h_C^2 was investigated. The expected response (EXP) was always an overestimate, and the actual response (ACT) was smaller than the optimal response (OPT) when r_{pc} was assumed one, but the true r_{pc} was smaller. The difference between ACT and OPT increased as r_{pc} decreased but was small for large r_{pc} values (e.g., $<7\%$ for $r_{pc}>.7$). When the h_C^2 was assumed equal to purebred heritability (h_P^2) and the true h_C^2 varied, the ACT was always smaller than OPT. The EXP was higher than ACT except for a large r_{pc} together with $h_C^2>h_P^2$. Finally, the ACT to CCPS was compared with the R_C to PLS. With any positive r_{pc}, the ACT was always bigger than PLS R_C. The crossbred response to PLS became larger than ACT only under negative r_{pc}. The main conclusions, therefore, are (1) the CCPS method is optimal for obtaining genetic response in crossbreds; and (2) the CCPS with inappropriate assumptions on r_{pc} and h_C^2 (i.e., recognizing crossbreds as purebreds) achieves always more genetic response in crossbreds than PLS for a common value of r_{pc} and crossbred heritabilities.*

Key words: *Breeding scheme, Crossbreeding, Crossbred response, Selection index, Selection method*

---

1. INTRODUCTION

The question that has been arising for a long time is how to maximize genetic response to selection in crossbreds (Hill, 1971; Bell, 1982; Sellier, 1982; Wei and Van der Steen, 1991). A lack of the solution to this problem may be attributed to the fact that the breeding goal in a crossbreeding system should be defined at the commercial crossbred level (Comstock, 1961; Orozco, 1986; Hartmann, 1992) whereas the selection methods used are optimized to improve animals within lines or breeds.

In practice, selection criteria are generally based on either purebred or on crossbred information but not both. Only in poultry breeding, especially in layers, both types of information are sometimes considered in selection (Arthur, 1986), for instance, by means of independent culling. However, procedures to optimally weigh purebred and crossbred information have not been developed (Wei and van der Steen, 1991).

Two approaches have basically been used to achieve crossbred improvement. First, pure line selection (PLS) is based on the breeding animal or its relatives' information within populations. Under this approach, the accomplished genetic gain in crossbreds arises from the regression on purebred response. Alternatively, recurrent selection (RS) proposed by Hull (1945) and reciprocal recurrent selection (RRS) proposed by Comstock et al. (1949) are based on the breeding animals' crossbred information. The last methods have shown their advantage to improve traits with low heritability and large nonadditive variation. However, both theoretical and experimental studies showed that neither PLS nor RRS is generally optimal to improve crossbred performance (Wei and Van der Steen, 1991). Both purebred and crossbred information should be weighted appropriately to maximize genetic progress of crossbreds (Wei and Van der Steen, 1991).

Selection methods combining both purebred and crossbred information in selection have not been evaluated although several authors have mentioned this possibility (Hill, 1971; Jakubec et al., 1974; Sellier, 1982; Bichard et al., 1986; Orozco, 1986; Singh and Dempfle, 1989). A straightforward way of combining performance on purebred animals with information from crossbred relatives would be to consider purebred and crossbred performance as two different traits with a genetic correlation between them. An interesting question is, how much additional genetic gain a selection method combining purebred and crossbred information would yield when compared with PLS and CS methods.

Genetic parameters involving crossbreds can not generally be derived from purebred parameters (Wei et al., 1991a,b). For example, heritabilities were found to be generally different for crossbreds and purebreds (Pirchner and von Krosigk, 1973; Biswas et al., 1971), and the genetic correlation between purebred and crossbred performance (r_{pc}) has to be known. The sire component in crossbreds reflects how much genetic variance existing in purebreds influences the crossbred progeny. This is not generally equal to the dam component or one quarter of additive variance in the sire population (Wei et al., 1991a). The r_{pc} is equal to 1 in case of no dominance or equal gene frequencies in parental populations, and decreases with increasing dominance or gene frequency difference between parental populations (Wei et al., 1991).

Since crossbred parameters might not always be accurately known, breeders might not feel comfortable using such parameters in the CCPS method. Therefore, an additional question would be whether such a combined selection method is robust against inappropriately assumed values of genetic parameters.

This study presents a selection index combining crossbred and purebred information (CCPS) to maximize genetic response in crossbreds under a two-way crossing system. The CCPS method is evaluated in comparison with PLS and CS, and the robustness of the CCPS method against inappropriate assumptions on r_{pc} and crossbred heritability (h_C^2) will be examined.

2. METHODS

A two-way crossing system is assumed, in which both purebred and crossbred information is available. Selection occurs within the sire line, and is aimed at improving crossbred performance. Alternative selection methods are pure line selection (PLS), crossbred selection (CS) and combined crossbred and purebred selection (CCPS), i.e., using as selection criterion either purebred or crossbred information or both. All symbols used are explained in Table 1.

2.1. Construction of selection indices for three selection methods.

The aggregate genotype (**H**) of a purebred animal is expressed as $\mathbf{H} = \mathbf{g}$, where **g** is the true breeding value of the animal for crossbred performance, i.e., crossbreeding value. The selection index is $\mathbf{I} = \mathbf{b'X}$ with vector **b** optimally weighing the different sources of information in **X** (Hazel, 1943; Henderson, 1963). Selection index theory is applied for (1) CCPS, (2) PLS, and (3) CS.

Four types of information (observations) are assumed to be available: 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 animals' own performance (x_4). The selection index ($\mathbf{I}_j$) for different methods (j=1, 2 and 3 for CCPS, PLS and CS) includes different sources of information,

$$\mathbf{I}_1 = \mathbf{b}_1\mathbf{X}_1+\mathbf{b}_2\mathbf{X}_2+\mathbf{b}_3\mathbf{X}_3+\mathbf{b}_4\mathbf{X}_4 \qquad [1\text{-}1]$$

$$I_2 = b_2X_2+b_3X_3+b_4X_4 \qquad [1\text{-}2]$$

$$I_3 = b_1X_1 \qquad [1\text{-}3]$$

The genetic response in crossbreds to index selection (R_{Cj}) is as follows,

$$R_{Cj} = i_j r_{IH} C = i_j(G_j' P_j^{-1} G_j)^{.5} \qquad [2]$$

where, i_j is the selection intensity under selection method j; and C is genetic variance of true crossbreeding value (g).

TABLE 1. Symbols and definitions.

Symbols	Definition
n_{Pd}, n_{Po}	number of dams (d) mated to a sire, and number of offspring (o) produced by a dam in pure lines
n_{Cd}, n_{Co}	number of dams (d) mated to a sire, and number of offspring (o) produced by a dam in crossing lines
$\mathbf{b}$	vector of fixed index weights (b_i is element in $\mathbf{b}$)
$\mathbf{X}$	vector of phenotypic values (normally distributed)
x_i	an element in $\mathbf{X}$, i.e., i = 1, 2, 3 and 4 for crossbred half-sib family mean, purebred half-sib family mean, purebred full-sib family mean and individual information, respectively
$V(x_i)$	variance of variable x_i
$Cov(x_i,x_j)$	covariance between variable x_i and x_j
a_{ij}	additive genetic relationship between animal i and j
t	intraclass correlation between full-sibs (t_{fs}) or half-sibs (t_{hs})
$\mathbf{I}_j$	total index, $\mathbf{I}_j = \mathbf{b}'\mathbf{X}$ (j = 1, 2 and 3 for CCPS, PLS and CS)
g	crossbreeding value of animal (breeding value for crossbred progeny)
$\mathbf{H}$	breeding goal (here, equal to g)
$\mathbf{P}$	phenotypic variance-covariance matrix of $\mathbf{X}$
$\mathbf{C}$	genetic variance of g
$\mathbf{G}$	vector of covariances between g and x_i
r_{pc}	genetic correlation between purebred and crossbred performance
σ_{pc}	sire covariance between purebred and crossbred performance
h_p^2, h_c^2	purebred and crossbred heritability estimated as four times sire variance in purebred and crossbred populations
σ_{PT}^2, σ_{CT}^2	phenotypic variance in purebred and crossbred populations

The variances and covariances with respect to x_i and g, the elements of $\mathbf{P}_j$, $\mathbf{G}_j$ and $\mathbf{C}_j$ matrices, are described as follows. For explanation of symbols see in Table 1. The theoretical aspects of genetic parameters involving crossbreds were described by Wei et al. (1991a,b).

$$V(x_1) = \sigma^2_{CT}[1+(n_{Co}-1)t_{Cfs}+n_{Cd}(n_{Co}-1)t_{Chs}]/(n_{Co}n_{Cd})$$
$$V(x_2) = \sigma^2_{PT}[1+(n_{Po}-1)t_{Pfs}+n_{Po}(n_{Pd}-1)t_{Phs}]/(n_{Po}n_{Pd})$$
$$V(x_3) = \sigma^2_{PT}[1+(n_{Po}-1)t_{Pfs}]/n_{Po}$$
$$V(x_4) = \sigma^2_{PT}$$

$$Cov(x_1,x_2) = Cov(x_2,x_1) = (1/4)r_{pc}\sigma_{PT}h_p\sigma_{CT}h_c$$
$$Cov(x_1,x_3) = Cov(x_3,x_1) = (1/4)r_{pc}\sigma_{PT}h_p\sigma_{CT}h_c$$
$$Cov(x_1,x_4) = Cov(x_4,x_1) = (1/4)r_{pc}\sigma_{PT}h_p\sigma_{CT}h_c$$
$$Cov(x_2,x_3) = Cov(x_3,x_2) = \sigma^2_{PT}[1+(n_{Po}-1)t_{Pfs}+n_{Po}(n_{Pd}-1)t_{Phs}]/(n_{Po}n_{Pd})$$
$$Cov(x_2,x_4) = Cov(x_4,x_2) = V(x_2) = \sigma^2_{PT}[1+(n_{Po}-1)t_{Pfs}+n_{Po}(n_{Pd}-1)t_{Phs}]/(n_{Po}n_{Pd})$$
$$Cov(x_3,x_4) = Cov(x_4,x_3) = V(x_3) = \sigma^2_{PT}[1+(n_{Po}-1)t_{Pfs}]/n_{Po}$$

$$Cov(x_1,g) = (1/4)h^2_C\sigma^2_{CT}$$
$$Cov(x_2,g) = r_{pc}\sigma_{PT}h_p\sigma_{CT}h_c[1+(n_{Po}-1).5+n_{Po}(n_{Pd}-1).25]/(n_{Pd}n_{Po})$$
$$Cov(x_3,g) = r_{pc}\sigma_{PT}h_p\sigma_{CT}h_c[1+(n_{Po}-1).5]/n_{Po}$$
$$Cov(x_4,g) = r_{pc}\sigma_{PT}h_p\sigma_{CT}h_c$$

$$V(g) = V(H) = h^2_C\sigma^2_{CT}$$

For purebreds, the intraclass correlation, t, is equal to ($a_{ij}h^2_p + c^2_p$), where a_{ij} is the degree of additive genetic relationship between animals i and j, and c^2_p is the variance due to common environment as a fraction of total phenotypic variance. In this study, c^2_p is assumed to be zero, and then $t_{Pfs} = .5h^2_p$ for full-sibs and $t_{Phs} = .25h^2_p$ for half-sibs. In crossbreds, $t_{Chs} = a_{ij}h^2_c + c^2_c$, where $a_{ij} = .25$ for half-sibs and c^2_c is assumed to be zero, i.e., $t_{Chs} = .25h^2_c$. And, $t_{Cfs} = a_{ij}h^2_{csire} + a_{ij}h^2_{cdam} + c^2_c = .25h^2_{csire} + .25h^2_{cdam}$, where h^2_{csire} and h^2_{cdam} are the crossbred heritability concerning sire and dam populations, respectively, and they are usually unequal (Wei et al., 1991a). In this study, h^2_{cdam} is assumed to be equal to h^2_{csire}. Moreover, it is assumed that the environmental covariance between purebred and crossbreds is zero.

2.2. Robustness of CCPS against inappropriate values for r_{pc} and h_c^2.

Harris (1963) and Sales and Hill (1976) have studied the effect of using parameter estimates on realized response to selection. In practice, breeders might not only use parameter estimates but also ignore the specific nature of crossbred parameters. Here, the second case is considered. The formulas to predict the optimal selection response (R_{opt}) assuming true genetic parameters, the expected response (R_{exp}) and actual response (R_{act}) in case of inappropriately assumed values of r_{pc} and h_c^2 are presented as follows,

$$R_{opt} = i(\mathbf{b}'\mathbf{P}\mathbf{b})^{.5} = i(\mathbf{G}'\mathbf{P}^{-1}\mathbf{G})^{.5} \qquad [3\text{-}1]$$

$$R_{exp} = i(\mathbf{b}_W'\mathbf{P}_W\mathbf{b}_W)^{.5} = i(\mathbf{G}_W'\mathbf{P}_W^{-1}\mathbf{G}_W)^{.5} \qquad [3\text{-}2]$$

$$R_{act} = i\mathbf{b}_W'\mathbf{G}(\mathbf{b}_W'\mathbf{P}\mathbf{b}_W)^{-.5} = i\mathbf{G}_W'\mathbf{P}_W^{-1}\mathbf{G}(\mathbf{G}_W'\mathbf{P}_W^{-1}\mathbf{P}\mathbf{P}_W^{-1}\mathbf{G}_W)^{-.5} \qquad [3\text{-}3]$$

where, $\mathbf{b}_W$, $\mathbf{G}_W$ and $\mathbf{P}_W$ are the **b**, **G** and **P** matrices using inappropriate genetic parameters (r_{pc} and h_c^2).

Two assumptions on r_{pc} and h_C^2 are interesting to be made. (1) the true h_C^2 is known, and the true r_{pc} is unknown (varying between -1 and 1) but assumed to be unity. (2) the true r_{pc} is unknown but assumed to be 1, and h_C^2 is unknown but assumed to be equal to h_P^2.

2.3. Study design.

2.3.1. Comparison of crossbred responses of CCPS, PLS and CS.

It is assumed that selection takes place only in the sire line, and selection intensities are equal for the three selection methods.

Two comparisons were made. In comparison 1 (fixed total progeny), the total number of progeny (including purebreds and crossbreds) per sire is fixed at 100 for the three methods (Table 2). A sire mates to n_{Pd} dams from the same line (pure-breeding) and n_{Cd} dams from another line (crossing). A dam produces either 10 purebred or 10 crossbred progeny.

In comparison 2 (fixed purebred progeny), the total number of purebred progeny per sire is fixed at 50 for the three methods (Table 2). Crossbreds provide extra information in CCPS

TABLE 2. The family structure under three selection methods[a].

	Fixed total progeny		Fixed purebred progeny	
Selection Methods[b]	n_{Cd}[c]	n_{Pd}	n_{Cd}	n_{Pd}
CCPS	5	5	0 → 10[d]	5
PLS		10		5
CS	5	5	0 → 10	5

[a] A dam always produces 10 progeny (i.e., $n_{C_o}=n_{P_o}=10$).

[b] CS, PLS and CCPS denote crossbred, pure-line and combined selection methods, resp.

[c] see Table 1 for further explanation of symbols.

[d] "0→10" denotes a varying number from 0 to 10 with increments of 1.

and CS schemes. The number of dams crossed to a sire (n_{Cd}) varies from 0 to 10. These are realistic assumptions for pig and poultry breeding (Table 2).

The genetic parameters used in the three selection indices are listed in Table 3. Two sets of values for h_P^2 and h_C^2 are assumed. The genetic correlation, r_{pc}, is varied ranging from -1 to 1. The total phenotypic variances in purebreds and crossbreds, σ_{PT}^2 and σ_{CT}^2, are both assumed to be 1 for all cases.

TABLE 3. Genetic parameters assumed for comparisons.

Set	h_P^2 [a]	h_C^2	r_{pc}
1. h_P^2 is equal to h_C^2	.2	.2	-1 → 1[b]
2. h_P^2 is not equal to h_C^2	.2	.0 → .5	-1 → 1

[a] see Table 1 for the meanings of symbols.

[b] The range was covered by .1 increments.

2.3.2. Applying inappropriate genetic parameters in the CCPS index.

When genetic parameters related to crossbreds are unknown, some simple assumptions are likely to be made, which consequently influences the actual (R_{act}) and expected (R_{exp}) crossbred responses to CCPS. In this case, crossbred half-sib information may be treated as information on purebred half-sib (i.e., assuming $r_{pc}=1$). A true h_C^2 may be used when it is known (case 1, Table 4). Otherwise, the values of h_P^2 and h_C^2 may be assumed equal although the true values are not (case 2, Table 4). The n_{Cd}, n_{Co}, n_{Pd}, and n_{Po} are assumed as the same

TABLE 4. The genetic parameters used to study the robustness of CCPS against wrong assumptions on r_{pc} and h_C^2

	True genetic parameters[a]			Assumed genetic parameters		
Case	r_{pc}	h_P^2	h_C^2	r_{pc}	h_P^2	h_C^2
1	-1.0 → 1.0	.2	.2	1	.2	.2
2	-1.0 → 1.0	.2	.0 → .5	1	.2	.2

[a] For symbols, see Table 1.

as in the comparison 1 (Table 2).

For practical implications, it is relevant to compare the actual crossbred response between CCPS with suboptimal parameters and PLS with optimal parameters, which is the commonly-used selection strategy. We compared these methods for the equal total progeny.

3. RESULTS

3.1. Comparison of genetic responses of three selection methods in crossbreds.

Fixed Total Progeny: effect of r_{pc} on comparison among selection methods

Figure 1 presents the percentage ratio of crossbred response of PLS and CS to CCPS for fixed total progeny. This figure is symmetric around the point of $r_{pc}=0$, and therefore the results are sufficiently described with r_{pc} between 0 and 1. The CCPS method always achieves equal or larger crossbred response than other methods (Figure 1).

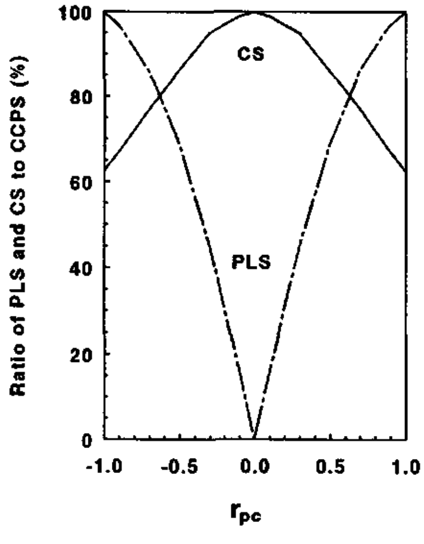

Figure 1. Relative merits of three different methods of selection assuming fixed total progeny and $h_P^2=h_C^2=.2$. Crossbred responses from PLS and CS are given as a percentage of response from CCPS. Results are plotted as a function of r_{pc}. See Table 1 for symbols.

The PLS obtains the same crossbred response as CCPS when r_{pc} is one, and no response when r_{pc} is zero. This reflects that purebred information is just as valuable as crossbred information in case $r_{pc}=1$, and does not contribute to response in case $r_{pc}=0$. Crossbred response to PLS increases with increasing the value of r_{pc} but is always smaller than the CCPS response, which indicates the smaller efficiency of indirect PLS compared with CCPS. Under $r_{pc}=.7$ and $h_P^2=h_C^2=.2$ which may reflect a realistic animal breeding situation, CCPS can obtain approximately 16% more crossbred response than PLS (Figure 2; Table 5).

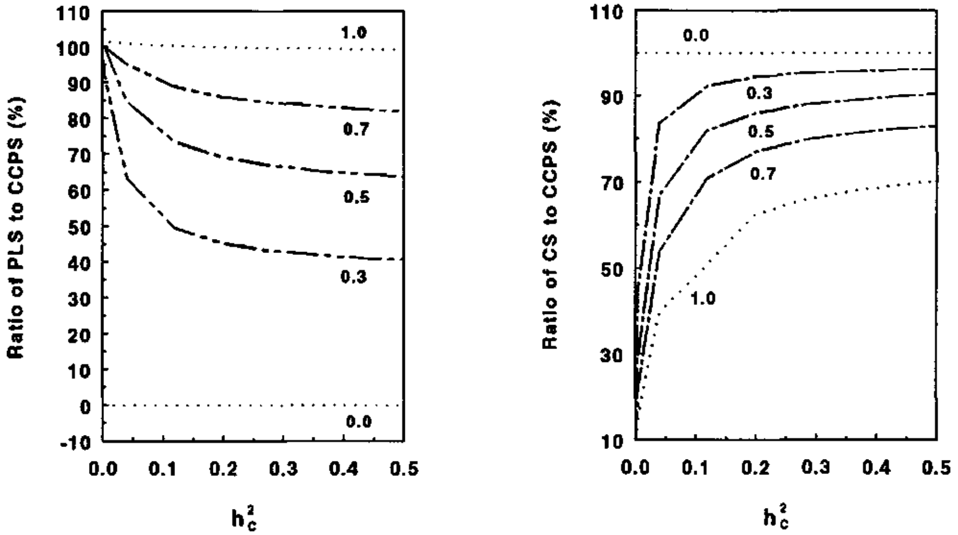

Figure 2. Relative merits of three different methods of selection assuming fixed total progeny for all methods. Crossbred responses from PLS and CS are given as a percentage of response from CCPS. Results are plotted as a function of h^2_C. The different lines refer to different values for r_{pc}. The h^2_P is .2. See Table 1 for explanation of symbols.

The CS reaches the same amount of response as CCPS when r_{pc} is zero, as in that case purebred information has no value. The CCPS obtaining more genetic response than CS when $r_{pc}=1$ indicates that CCPS uses additional purebred information. The crossbred response to CS decreases with increasing r_{pc} until about 63% of the CCPS response. This relative reduction of crossbred response to CS is due to the increasing importance of purebred information with a larger r_{pc}.

The crossbred response to PLS is equal to that of CS when r_{pc} is approximately .6 in our data structure. The PLS has a larger crossbred response than CS when r_{pc} is higher, and has a smaller response when r_{pc} is lower.

Fixed Total Progeny: effect of h^2_C on comparison among selection methods

The PLS obtains almost the same crossbred response as CCPS when h^2_C approaches zero or r_{pc} is one (Figure 2). The h^2_C equal to zero indicates that crossbred information contributes nothing to the crossbred response. When $r_{pc}=1$ the crossbred response to PLS is only equal to CCPS if h^2_C is equal to h^2_P. With $h^2_C<h^2_P$, and $r_{pc}=1$, PLS achieves a little more response

than CCPS, which indicates that crossbred information is less valuable than purebred information. On the other hand, with h_C^2 larger than .2, CCPS obtains more response than PLS. In general, the ratio of PLS to CCPS decreases with increasing h_C^2 except the case with r_{pc}=0 (Figure 2). With r_{pc}=0 where purebred information has no value, CCPS is just equivalent to CS, and the ratio of CS to CCPS is not affected by h_C^2 (Figure 2). With r_{pc} values larger than 0, the ratio of CS to CCPS increases as h_C^2 increases. The ratio becomes zero when h_C^2 is zero because CS makes no genetic response. In general, the advantage of CCPS related to PLS increases but the advantage related to CS decreases with increasing h_C^2 (Figure 2). The change of h_C^2 between 0 and .2 (=h_P^2) has more influence on the comparison of crossbred response among CCPS, PLS and CS than when h_C^2 is larger than h_P^2. Apparently, the exact value of h_C^2 is not important for the comparison among CS, PLS and CCPS if h_C^2 is about equal to or bigger than h_P^2.

TABLE 5. Ratio (%) of CCPS optimal (OPT) and actual (ACT) crossbred responses to actual PLS crossbred response under different assumed r_{pc}[a]

			True h_C^2		
True r_{pc}[b]	Assumed r_{pc}	Ratio (%)	.1	.2	.3
.9[c]	.9	OPT/PLS	101.5	103.1	104.1
.7	.7		110.6	116.0	118.5
.5	.5		132.6	144.5	150.1
.9	1.0	ACT/PLS	101.2	102.4	103.1
.7			105.8	108.8	110.5
.5			113.1	119.0	122.7
.9	.7	ACT/PLS	98.9	101.2	102.3
.7			110.3	116.0	118.7
.5			130.0	141.3	147.6

[a] Comparison of crossbred response between CCPS and PLS was based on the same condition as comparison 1 in Table 2, i.e., fixed total progeny.

[b] see Table 1 for the explanation of symbols used here.

[c] True r_{pc} varies at .5, .7 and .9. True h_C^2 varies at .1, .2 and .3.

Fixing Purebred Progeny: comparison among selection methods

The ratio of PLS to CCPS crossbred response decreases with increasing the number of dams crossed to a sire (n_{Cd}) (Figure 3). The ratio changes faster under a smaller r_{pc}. When r_{pc} is one, increasing n_{Cd} has a very small influence on the ratio. The CCPS achieves a larger response than PLS even when $r_{pc}=1$ because all crossbred information is used as additional information for CCPS in this comparison.

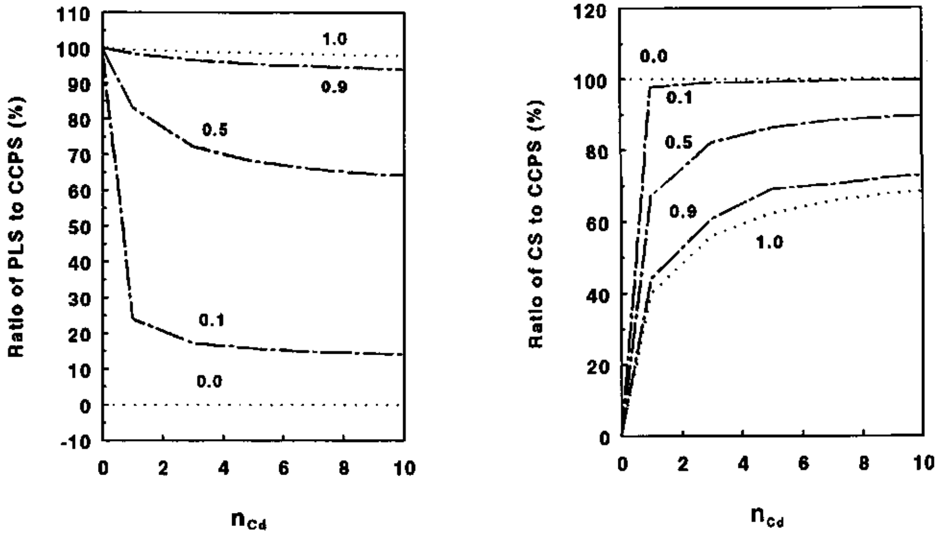

Figure 3. Relative merits of three different methods of selection for varying number of dams that a sire is crossed to (n_{Cd}), under assuming fixed purebred progeny and $h_P^2=h_C^2=.2$ for the three methods. Crossbred responses from PLS and CS are given as a percentage of response from CCPS. Results are plotted as a function of n_{Cd}. The number of dams mated to a sire within population (n_{Pd}) is 5 for the three methods. The different lines refer to different values for r_{pc}. See Table 1 for explanation of all other symbols.

The ratio of CS to CCPS response increases with increasing n_{Cd} (Figure 3). The lower r_{pc} is, the faster the ratio increases as n_{Cd} increases. For low r_{pc} values, adding crossbred information quickly leads to CS response being close to CCPS response. When r_{pc} is zero, purebred information in CCPS is useless, and therefore, CCPS and CS obtain the same response. When r_{pc} is one, CCPS achieves the greatest response compared with CS because of the contribution of extra purebred information which is equivalent to information from crossbreds.

3.2. Robustness of CCPS against inappropriate values of r_{pc} and h^2_C.

Assuming $r_{pc}=1$ whereas the true r_{pc} is lower, the expected response (R_{exp}) always is larger than the actual response (R_{act}) (Figure 4). The overestimation increases rapidly with decreasing r_{pc} values. The optimal response (R_{opt}) is always between R_{exp} and R_{act} (Figure 4). The difference between R_{act} and R_{opt} is small for a large r_{pc} (>.7). With lower r_{pc} (<.6), the R_{opt} could be much higher than the R_{act}.

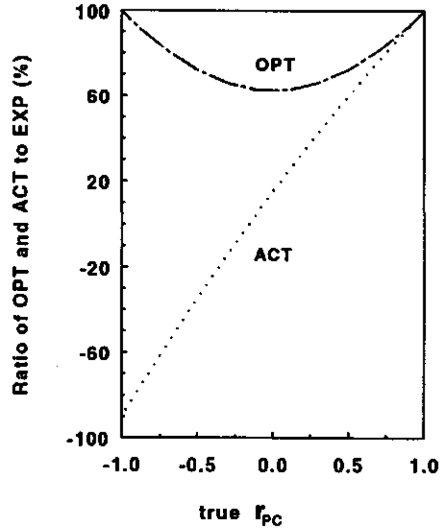

Figure 4. Optimal (OPT) and actual (ACT) response relative (%) to expected response (EXP) to CCPS when assuming inappropriately $r_{pc}=1$, for different values of true r_{pc}. Both h^2_P and h^2_C are .2.

The ratio of R_{act} to R_{exp} increases with increasing h^2_C in case of positive r_{pc}, and decreases in case of negative r_{pc} (Figure 5). The R_{act} is smaller than R_{exp} in most cases (i.e., for $h^2_C < h^2_P$), and is bigger only when both r_{pc} is close to one and h^2_C is larger than h^2_P as illustrated in Figure 5.

The ratio of R_{act} to R_{opt} decreases with increasing h^2_C with a positive r_{pc}, and increases in case of a negative r_{pc} (Figure 5).

3.3. Comparison of actual CCPS response with PLS crossbred response.

Figure 6 presents the ratio of CCPS R_{act} to PLS R_C (crossbred response to PLS) for different r_{pc} and h^2_C values. The CCPS always obtains a larger R_{act} than PLS for positive values of r_{pc} and $h^2_C > h^2_P$. It obtains a smaller R_{act} than PLS in most cases of negative r_{pc}. The PLS crossbred response is close to zero with r_{pc} close to zero, and consequently the ratio of R_{act} to PLS R_C becomes infinitely large. As an example, assuming $r_{pc}=.7$ and $h^2_P=h^2_C=.2$, about 9% more genetic response in crossbreds can be achieved by CCPS than PLS although

16% more can be obtained using correct parameters (Figure 5).

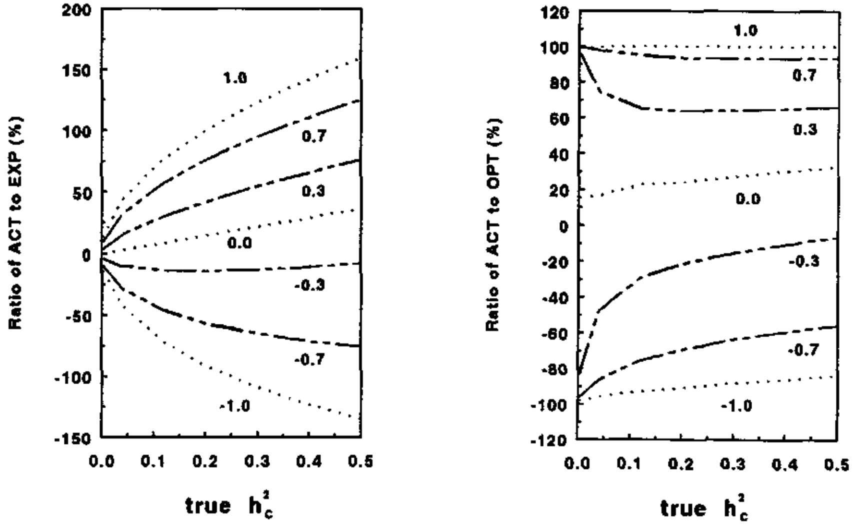

Figure 5. Optimal (OPT) and actual (ACT) crossbred response relative (%) to expected crossbred response (EXP) to CCPS when assuming inappropriately $r_{pc}=1$ and $h_C^2=h_P^2=.2$, for different values of true h_C^2. The different lines refer to different value of true r_{pc}. See Table 1 for other symbols.

4. DISCUSSION

4.1. The merits of the CCPS method in comparison with PLS and CS.

Purebred information always contributes considerably to selection accuracy if r_{pc} is not very small which is often the case in animal breeding practice. On the other hand, the crossbred information measures the breeding goal trait directly and its use always leads to response. The marginal benefit of using crossbred data is only small if a lot of purebred information is used and if r_{pc} is large. Therefore, to improve crossbred performance it always makes sense to include both crossbred and purebred information of any crossbreeding system in selection criteria. A CS method, such as current selection or reciprocal recurrent selection, should always be replaced by a CCPS.

The CCPS is generally suggested to replace the commonly-used PLS method. Conservatively speaking, CCPS would bring about 10% more genetic progress in crossbred performance than the PLS for most reproduction and fitness traits (e.g., in case of r_{pc} = .7 and h_P^2 = h_C^2 = .2). The CCPS can be easily applied already in the case where a crossbreeding structure exists and crossbred information is collected for management purpose. Otherwise, some additional investment may be needed for collecting and processing crossbred data. In pig breeding, electronic identification, use of sow management systems, availability of data collected at slaughter houses and increased computer capacity is making it feasible and relatively cheap to collect and use large crossbred and purebred data sets (Van der Steen and Wei, 1991). It should be stressed that the CCPS is much better than the PLS if crossbreds provide an additional information.

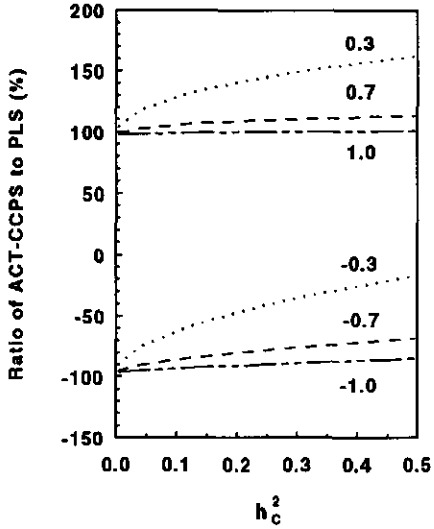

Figure 6. Actual crossbred response of CCPS (ACT-CCPS) (assuming inappropriately $r_{pc}=1$ and $h_C^2=h_P^2=.2$) relative (%) to crossbred response of PLS with fixed total progeny for two methods. Ratios (%) of ACT-CCPS to PLS are plotted as a function of true h_C^2. The different lines refer to different values for r_{pc}. h_P^2 is .2. See Table 1 for other symbols.

The comparison of genetic response in crossbreds between PLS and CS methods has been studied by Comstock (1961), McNew and Bell (1976), Sellier (1982), Harvey (1992, cited by Hartmann, 1992). The results on the comparison of PLS and CS found here are similar to what Comstock (1961) described. The parameters, r_{pc} and h_C^2, play an important role in the relative merits of different methods. In our data structure, PLS is better than CS in case of r_{pc} larger than approximate .6, and worse otherwise (Figure 1).

Setting the breeding goal at the level of commercial crossbreds has been claimed by several authors (Comstock, 1961; Orozco, 1986; Hartmann, 1992). In our CCPS approach, the breeding goal is defined as crossbred improvement so that crossbred response is optimized. However, optimization of crossbred response is not equivalent to optimizing the entire breeding system if purebred performance still contributes considerably to the production system. Experiments have shown that purebred performance was improved slower than crossbred performance or sometimes even obtained a negative response under crossbred selection, the last being explained by the existence of overdominance (Wei and Van der Steen, 1991). For species with low reproductive rates, such as cattle and sheep, purebred performance is important and a loss in purebred response may not be desirable. For species with high reproductivity (pig and poultry), the performance of commercial crossbreds is much more important and less weight should be given to purebreds.

Theoretically, a solution of this problem is to optimally weigh the breeding values of purebreds for purebred and crossbred performance (i.e., purebreeding and crossbreeding values, BV_p and BV_c) and calculate a combined breeding value ($BV_{combined}$) as follows,

$$BV_{combined} = w_pBV_p + w_cBV_c \qquad [4]$$

where w_p and w_c are relative weights of breeding values for purebred and crossbred performance. Such weights can be derived from the relative magnitude of cumulative discounted expressions of each trait in the breeding scheme, e.g., using the gene flow method (Hill, 1974; Brascamp, 1978), multiplied by the economic value of the moment of expression. Moreover, breeding companies might have the tendency to give additional weight to purebred performance because for their primary concern is not the final product but a acceptability of their breeding stock at the multiplier level.

The CCPS approach described in this study optimizes crossbred response only for one generation of selection. Long term effects of the CCPS method are dependent on the change of genetic parameters. A change of r_{pc} due to selection was observed in some experiments (Comstock and Robinson, 1957; Pirchner and von Krosigk, 1973; Pirchner and Mergl, 1977). Theoretically, the change of r_{pc} depends on gene frequency changes due to selection (Wei et al., 1991b). After selection, the value of r_{pc} will increase and eventually get close to one after a long term in case of no or partial dominance, but get smaller after a long term CS or CCPS with overdominance (Wei et al., 1991b; Swan, 1992). An increase of r_{pc} reduces the advantage of CCPS over PLS.

A possible increase of generation interval in applying crossbred selection was discussed by Van der Steen and Wei (1991). This increase can be avoided by producing crossbred and purebred progeny simultaneously or using sib information. The culling and selection moments should be kept unchanged compared with PLS scheme, but merely the available crossbred information should be used.

In this study, the selection intensity is assumed to be the same for the three methods. In animal breeding practice, compared with PLS, the crossbred response to CCPS may be somewhat reduced by the possible lower selection intensity if the total progeny is fixed. However, crossbred information is usually available in crossbreeding systems. If field crossbred data, e.g., data from slaughter house or commercial farms, can be collected, the selection intensity in CCPS does not decrease compared with a PLS scheme.

4.2. Robustness of CCPS against inappropriate values of r_{pc} and h_C^2

The genetic parameters related to crossbreds, especially r_{pc}, are not routinely estimated in animal crossbreeding systems. A good estimation of h_C^2 and r_{pc} needs a good family structure, e.g., reasonable data and family structures, a reasonable number of dams per sire and of progeny per dam. Performance and pedigree records are needed for both purebreds and crossbreds.

The expected crossbred response to CCPS (R_{exp}) is overestimated in case of inappropriate assumptions on r_{pc} and h_C^2, which gives a possible reason for disappointing crossbred responses in animal breeding. The actual crossbred response (R_{act}) is always lower than the optimal one (R_{opt}) although the difference between R_{act} and R_{opt} is small when r_{pc} becomes larger.

Application of CCPS may meet reluctancy due to using inaccurate crossbreeding parameters, i.e., r_{pc} and h_C^2. The comparison of the R_{act} to CCPS with PLS shows that adding crossbred information in selection is always profitable in case of a positive r_{pc} (Table 5). For example, when true $r_{pc}=.7$ and $h_C^2=.2$, CCPS obtains 8.8% more response than PLS although it will be 16% more when using true parameters. Obviously, there is no risk in integrating crossbred information into current animal breeding program even when r_{pc} is not available or not very accurately estimated.

In the previous parts, only the assumption on $r_{pc}=1$ is discussed. However, breeders might think about other values for r_{pc} instead of 1 due to the fact that r_{pc} was found to be generally lower than 1, especially for reproduction or fitness traits (Wei and Van der Steen, 1991). The assumption $r_{pc}=.7$ was used to compare actual crossbred responses between CCPS and PLS with varying r_{pc} by .9, .7 and .5 (Table 5). In general, the outcome for CCPS depends on greatly on the difference between true and assumed r_{pc}, being larger for the smaller ratio of OPT to PLS. The ratio of OPT to PLS under assuming $r_{pc}=.7$ is close to the optimal ratio when true r_{pc} is .5. Therefore, values of r_{pc} from literature should be considered in CCPS models to obtain a reasonable crossbred response rather than simply assuming r_{pc} equal to 1.

The implications to animal breeding can, therefore, be put forward from this study, (1) the CCPS is optimal to achieve genetic response in crossbreds; and (2) crossbred information should be generally used in current animal crossbreeding programmes even when crossbreeding parameters, r_{pc} and h_C^2, are unknown or imprecise estimated because the CCPS is robust against inappropriate values of r_{pc} and h_C^2.

ACKNOWLEDGEMENT

We thank Dr. ir. P. Luiting and Ir. P.W. Knap for useful discussions.

REFERENCES

Bell, A.E.; 1982. Selection for heterosis - results with laboratory and domestic animals. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. 6:206-227.

Bichard, M.; David, P.J.; Bovey, M., 1986. Selection between and within lines and cross-breeding strategies for worldwide production of hybrids. Proc. 3rd World Cong. Genet. Appl. Livest. Prod. 10:130-142.

Brascamp, E.W., 1978. Methods on economic optimization of animal breeding plans - notes for Scandinavian post-graduate course in economic breeding planning, University of Helsinki, Department of Animal Breeding, Helsinki. Aug. 28-Sept. 8. 1978. IVO report B-134. Zeist, the Netherlands.

Comstock, R.E., 1961. Reciprocal recurrent selection with reference to swine breeding. The 22nd Ann. Report, Regional Swine Breeding Lab., USDA, Ames, Iowa.

Comstock, R.E.; Robinson, H.F., 1957. Findings relative to reciprocal recurrent selection. Proc. of Intern. Genet. Symp. Sci. Council of Japan. Tokyo, pp.461-464.

Comstock, R.E.; Robinson, H.F.; Harvey, P.H., 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agronomy J. 41:360-367.

Harris, D.L., 1963. The influence of errors of parameter estimation upon index selection. In: W.D. Hanson and H.F. Robinson (eds.) Proc. Statistical Genetics and Plant Breeding. NAS-NRC publication 982. Washington DC. pp491-500.

Hartmann, W., 1992. Evaluation of the potentials of new scientific developments for commercial poultry breeding. World's Poult. Sci. J. 48:17-27

Hazel, L.N., 1943. Genetics basis for selection indices. Genetics 28:476-490.

Henderson, C.R., 1963. Selection index and expected genetic advance. In: W.D. Hanson and H.F. Robinson (eds.) Proc. Statistical Genetics and Plant Breeding. NAS-NRC Publication 982. Washington DC. pp141-163.

Hill, W.G., 1970. Theory of limits to selection with line crossing. In: Kojima, K. (ed.) Mathematical Topics in Population Genetics. Berlin, Germany Federal Republic, Springer-Verlag. pp210-245.

Hill, W.G., 1971. Theoretical aspects of crossbreeding. Annales de Génétique et de Sélection Animale 3:23-34.

Hill, W.G., 1974. Predication and evaluation of response to selection with overlapping generations. Anim. Prod. 18: 117-139.

Hull, F.H., 1945. Recurrent selection for specific combining ability in corn. J. Amer. Soc. Agro. 45:989-1009.

Jakubec, V.; Podebradsky, Z.; Pichova, J.; Hyanek, J., (1974) Construction and use of selection indices for populations in broiler production. Proc. Working Symp. Breed Evaluation and Crossing Exper. with Farm Anim. Zeist, 1974. pp55-66.

McNew, R.W.; Bell, A.E., 1976. Comparison of crossbred and purebred selection for a heterotic trait in highly selected populations of Tribolium. J. Heredity 67:275-283.

Orozco, F., 1986. Crossbreeding and heterosis. U.S.-Spain joint seminar on sheep breeding. Zaragoza, 10-15 Nov. 1986.

Pirchner, F.; von Krosigk, C.M., 1973. Genetic parameters of cross- and pure-bred poultry. Bri. Poult. Sci. 14:193-202.

Pirchner, F.; Mergl, R., 1977. Overdominance as cause for heterosis in poultry. J. Anim. Breed. Genet. 94:151-158.

Sales, J.; Hill, W.G., 1976. Effect of sampling errors on efficiency of selection indices. 1. use of information from relatives for single trait improvement. Anim. Prod. 22:1-17.

Sellier, P., 1982. Selecting populations for use in crossbreeding. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. 6:15-49.

Singh, R.P.; Dempfle, A.L., 1989. Optimising multistage selection in a modified reciprocal recurrent selection programme considering cost and rate of genetic progress. 40th Ann. Meeting of the EAAP, Dublin, Ireland. Vol. 1 (Summaries):167.

Swan, A.A., 1992. Multibreed evaluation procedures. Ph.D Thesis, University of New England, Australia.

Van der Steen, H.A.M.; Wei, M., 1991. Reciprocal recurrent versus pure line selection. British Poultry Breeders' Round Table. 17 Sept. 1991. Edinburgh, U.K.

Wei, M.; Van der Steen, H.A.M., 1991. Comparison of pure-line selection with reciprocal recurrent selection systems in animal breeding (a review). Anim. Breed. Abstr. 59:281-298.

Wei, M.; Van der Steen, H.A.M.; Van der Werf, J.H.J.; Brascamp, E.W., 1991a. Relationship between purebred and crossbred parameters. 1. variances and covariances under the one-locus model. J. Anim. Breed. Genet. 108: 253-261.

Wei, M.; Van der Werf, J.H.J.; Brascamp, E.W. 1991b. Relationship between purebred and crossbred parameters. 2. genetic correlation between purebred and crossbred performance under the model with two-loci. J. Anim. Breed. Genet. 108:262-269.

Chapter 7

General Discussion

Ming Wei

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

General Discussion

Ming Wei

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

I. INTRODUCTION

The main objective of this thesis was to develop the selection theory for maximizing genetic progress in crossbreds under a two-way crossbreeding system. It is emphasized in a literature review (Chapter 2) that both purebred and crossbred information should be used to improve crossbred performance. The study at the locus level was conducted to investigate the genetic parameters related to crossbreds, such as crossbred heritability (h_c^2), genetic covariance (Cov_{pc}) and genetic correlation (r_{pc}) between purebred and crossbred performance (Chapters 3 and 4), which are important parameters in organizing crossbreeding programmes. Results from the locus model were used to derive optimal selection strategies for combined crossbred and purebred selection using the information on purebreds and crossbreds.

In this chapter the theory at the locus level and possible problems with extrapolating results to the level of the quantitative expression of the traits will be discussed. Also, the theoretical results and the assumptions on parameter values, e.g., for dominance, will be compared with evidence from literature of the existence of nonadditive genetic variation. Our models used for genetic evaluation and selection in a crossbreeding scheme will be compared with other genetic models proposed in literature for analyzing crossbred data. A linear mixed model to estimate simultaneously purebreeding and crossbreeding values, which are necessary for optimizing crossbred response, are in the appendix.

The second part of the discussion will focus on the breeding goal in crossbreeding systems. It is questioned whether the assumption that the breeding goal should be at the level of the crossbreds is always sufficient. In practice there may be reasons for breeders to put some emphasis on the performance of the purebred lines. Furthermore, discuss will focus on the problem of defining the breeding goals in crossbreeding systems that are more complicated than a two way crossing system.

In chapter 6 an optimal method for improving crossbred performance was derived basically following selection index methodology. However, such methods optimize selection for one round only. Optimal selection strategies when selection is expected to be optimized for response after several generations will be discussed. In addition, it will be discussed whether a long term horizon would be affected by changes of crossbreeding parameters that were derived in our theoretical model.

Then, discussion will focus on some considerations about practical aspects of applying the CCPS method in animal crossbreeding systems. Although we have proposed an optimal method to combine crossbred and purebred information, it is up to the breeders to implement it. In this aspect breeders have to make important decisions, e.g., on the testing facilities they make available for crossbred and purebred information collection, and the optimal ratio between those two types of animals in the test. Furthermore, they will have to use genetic parameters for the crossbreeding system. The relevant discussion will be on how to obtain and to interpret such parameters. For example, I shall discuss the common breeding practice where nucleus purebreds and commercial crossbreds are kept in different environments such that genotype by environment interaction effects are confounded with crossbreeding parameters.

Finally, this chapter will end with recommendations drawn from this general discussion for the animal breeding practice.

II. THE GENETIC BASIS OF MODELS OF CROSSBREEDING

Several different models have been proposed to analyze data from crossbreeding experiments and to evaluate animals under crossbreeding systems (Wei and Van der Steen, 1991; Swan, 1992). These models will be compared and discussed here in terms which will be most useful for genetic evaluation and selection in crossbreeding systems to optimize crossbred response. Furthermore, the relevance of nonadditive effects to practical animal crossbreeding programmes will be discussed.

2.1. Genetic theory derived from the locus model.

In this study, locus models were used to generate knowledge about the genetic parameters related to crossbred populations (Wei et al., 1991a,b). Locus models have been proven useful for generating quantitative genetic theory, e.g., Mather and Jinks (1971) and Falconer (1989). However, locus models are simplifications of the true genetic model and it should be questioned whether they are always sufficient. In fact, even the parameters on the locus level can be questioned.

The extrapolation of the results on the locus model to the quantitative level of aggregated loci is based on the assumption that the gene interaction effects among different loci is ignorable. So, the effect of nonadditive variation from epistatic effects on crossbreeding parameters has not been considered in this thesis. However, the concept of homeostasis given by Lerner (1954) would be helpful to understand the meaning and importance of epistasis for a functioning organism. It is logical that genes at different loci always influence each other in one or another way and to a different degrees in terms of balancing an organism and further influencing traits of interest. In fact, epistatic effects have been found to be important for some traits, e.g., egg production and milk production (Fairfull and Gowe, 1986; Bosch, 1990; Cunningham, 1990). Usually, the two-loci interaction model is used in understanding and analyzing epistasis (Willham and Pollak, 1985; Falconer, 1989). However, as pointed out by Cunningham (1990), epistasis is difficult to measure in reality because it is by definition an infinitely expandable category of gene action. Exploiting epistasis seems to be impossible even applying any crossbreeding program (Cunningham, 1990) although it is believed that crossbreeding might take some advantage of epistasis (Bell et al., 1952). How to exploit epistasis in breeding programs will be a challenge for quantitative geneticists.

Recently, Orozco (1983, 1986 and 1989) gave an alternative explanation for heterosis. The theory mentioned above is based on the assumption that heterosis expressed in a certain trait is related to the genes which are directly responsible for the trait. But, according to Orozco (1986) the heterosis does not come from an action of the genes responsible for the character of interest, but from the genes responsible for the vigour or general resistance of the individual. So, the genes controlling the vigour or general resistance serve indirectly to increase the performance of crossbreds because the crossbreds are more vigorous, healthy, and stronger, and consequently are more likely to show their genetic potential and perform better than purebreds. This theory would be supported by the fact, that heterosis varies depending on environments (Barlow, 1981; Fairfull and Gowe, 1986).

According to Orozco's theory, the improvement of final crossbreds for a certain environment should be based on simultaneous selection for the desirable genotype responsible for the trait of interest and for another type of desirable genotypes responsible for the vigour, which allows animals to express their genetic potential. Theoretically, the genetic models, which treat two sets of genes separately, could be established for animal evaluation if both purebred information from central test station and crossbred information from commercial environment are available.

2.2. Models for analyzing crossbreeding experiments.

Several statistical-genetic models have been established to analyze diallel cross experiments (Gardner and Eberhart, 1966; Eisen et al., 1983; Henderson, 1977; Komender, 1988). Most important aspect of this design is to partition the variance into general and specific combining abilities (GCA and SCA) (Griffing, 1956). GCA denotes the average performance of a breed in crossing, which is assumed to be controlled by additive genetic variation. SCA is the performance in a specific cross, reflecting the nonadditive genetic variation. More general models to deal with crossbred data are also introduced by Gardner

(1966), Dickerson (1973), Sheridan (1980 and 1981), Kinghorn (1980), Hill (1982) and Fimland (1983), where additive, dominance and epistatic effects are taken into account. These models were designed to estimate crossbreeding parameters, e.g., additive effects, dominance and epistatic deviations, heterosis or recombination loss (Kinghorn, 1982; Swan, 1992).

These models are useful in determining the additive and nonadditive effects influencing crossbreds from various lines, in predicting the performance of crosses which are not in the design, and in finding out the best combination of lines for specific purposes (Dickerson, 1969; Bell, 1982). However, these between line effects do not constitute the breeding values of animals within a specific line. Therefore, these models are not directly relevant to the within line selection to optimize crossbred response under a given crossbreeding system.

2.3. Multibreed evaluation procedures.

To simultaneously use within and between breed selection in a structured way, Kinghorn (1982, 1983 and 1984) developed a "Multibreed Selection Index" (MSI). The index consists of two basic components. First, a crossbreeding component contains a breed difference and a heterosis effect, which is determined by breed genotype of the animal and the mating genotype. Another component is the breeding value (i.e., additive effect) of the animal within lines. This method has been applied to estimate breeding values and crossbreeding parameters simultaneously by Elzo and Jamula (1985), Komender and Hoeschele (1989), and Van der Werf and de Boer (1989a,b). The MSI has been applied in beef cattle breeding (Notter, 1989a,b). However, as pointed out by Swan (1992) the MSI approach is based on the assumption that the crossbred improvement is paralleled with the purebred improvement by means of the selection within breeds, i.e., according to estimates of breeding values within breeds. These models treat the breed differences and heterosis as fixed effects, and an animal's breeding value is expressed for any type of mating (Komender and Hoeschele, 1989). Once nonadditive variation exists and genetic correlation between purebred and crossbred is not unity, the breeding value of the animal varies depending on the line that is mated to (Wei et al., 1991b). Therefore, the MSI is not the optimal method for achieving crossbred improvement. Elzo and Famula (1985) and Elzo (1986 and 1990) proposed a method to account for the interaction between breeding values of animals estimated in different populations. However, their derivation on variances and covariances involving crossbreds (Elzo, 1986), treats additive genetic variance in a crossbred population as a linear function of variances in parental populations, which has been proven not to be true under the locus model with nonadditive genetic effects (Griffing, 1956; Wei et al., 1991a; Swan, 1992).

Swan (1992) and Swan and Kinghorn (1992) developed a multibreed evaluation models using a multi-trait approach under linear mixed model framework in which both purebred and crossbred information can be used. Their model is similar to the model presented in the

Appendix and is applicable for practical animal crossbreeding programmes. It has to be noted that an animal evaluation in complicated crossbreeding systems involving several lines and several generations of crossbreds many genetic parameters are to be involved and have to be estimated reducing the efficiency for selecting animals within lines. Also, the breeding value estimation for crossbred animals are not assumed to be relevant under the CCPS method.

2.4. Evidence of nonadditive genetic variation on the quantitative level.

Direct estimation of dominance, i.e., dominance variation within lines, were done for egg production traits in poultry (Wei and Van der Werf, 1992a), and for dairy cattle traits (VanRaden, 1989; Tempelman and Burnside, 1990a,b and 1991; Hoeschele, 1991; Lawlor and Short, 1992). A significant dominance variance was found for egg production traits and fat yield.

Indirect evidence of nonadditive genetic variance is usually shown through heterosis, inbreeding depression, genetic correlation between purebred and crossbred performance (r_{pc}) being smaller than unity, difference between purebred and crossbred heritabilities (h_c^2 and h_p^2) (Mather and Jinks, 1971; Wright, 1977; Willham and Pollak, 1985; Wei et al., 1991a,b). Evidence for dominance can be seen shown in an overview of literature values (Tables 1, 2, and 3). The estimates of r_{pc} are reviewed in detail by Wei and van der Steen (1991) and Swan (1992).

Nonadditive variation was also found through analyzing selection or crossbreeding experiments. First, experiments have shown that PLS and RRS exploited different genetic variances controlling the trait as reviewed by Wei and Van der Steen (1991). In two extreme cases, performance in crossbreds did not respond to PLS but could still be improved by RRS (Kojima and Kelleher, 1963; Saadeh et al., 1968). Second, long term selection experiments with laboratory animals have shown dominance and epistatic interaction to be widespread (Falconer, 1989). Third, many crossbreeding experiments have shown dominance and epistasis as the cause of heterosis (Sheridan and Randall, 1977; Sheridan, 1981; Authur, 1986; Lechner et al., 1986; Fairfull et al., 1987; Bosch, 1990; Sharma and Pirchner, 1991; Ahlborn-Breier and Hohenboken, 1991; Brade, 1990).

All these results generally prove the existence of nonadditive genetic variance among most of the commercially important traits in farm animals, which reflects the possibility and necessity of using both types of genetic variation to maximize crossbred performance. An integrated picture relating together all these parameters (heterosis, inbreeding depression, genotype by environment interaction, nonadditive genetic variances) can be drawn for two categories of commercially important traits, (1) production traits, e.g., growth, body weight; and (2) reproduction and fitness traits, e.g., litter size, fertility and egg number. The later group of traits is related to vigour and largely influenced by environmental effects. They usually have a small heritability but a relatively large nonadditive variance. They tend to show

TABLE 1. Heterosis for commercially important traits in different species.

Species	Traits	%	absolute value	References
Pig	Litter size	3→10	.3→1.3 piglets	Sellier, 1970 and 1976. Glodek, 1982. Buchanan, 1988. Bidanel et al, 1988 & 1991a,b. Baas et al., 1992a,b.
	(Maternal heterosis)	(8→20)	(.5→2.4 piglets)	
	Backfat	5→10		
	Body weight (154 days)	5→13	16 kg	
	Average daily gain	2→10.6	.04→.13 kg/day	
	Lean gain/day	1-3	.03→.04 kg/day	
	Little weight at birth	5	1.5→2.6 kg	
	(Maternal heterosis)	(26→50)	(3.9 kg)	
	Conception	5-18		
Laying chicken	Egg production	4→45	2→40 eggs/year	Ayyagari et al., 1982. Fairfull & Gowe, 1986. Hartmann, 1989. Lee & Huang, 1989. Fairfull, 1990; Flock et al., 1991.
	Egg weight	1→4		
	Age at 1st egg	-4→-5		
	Viability	1→17		
	Body weight	0-5		
Broilers	Body weight (8-10wk)	1.7→10		Merritt & Gowe, 1960. Fairfull & Gowe, 1986.
	Feed conversion	3→16		
	Viability	17→22		
Sheep	Birth weight	2→17	.11→.25 kg	Singh et al., 1967. Ghoneim et al., 1968. Terrill, 1974. Wiener & Hayter, 1974 & 1975. Nitter, 1978. Hickman, 1982.
	Body weight (100 days)	0→7	1.3→3.2 kg	
	Reproduction traits	2→17		
	(maternal heterosis)	(3→26)		
	Survival rate	3→40		
Beef cattle	Birth weight	.1→3.1	.9→2.7 kg	Flower et al., 1963. Gregory et al., 1965. Long & Gregory, 1974. Knapp et al., 1980. Peacock et al., 1981. Kress et al., 1990. Gregory et al., 1991.
	(maternal heterosis)	6.3		
	Daily gain	1→8.2	.05→.084 kg	
	Weaning weight	1.1→4.6	2.3→20 kg	
	(maternal heterosis)	7.6	(16→29 kg)	
	Body weight at 200-day	7.2	10.9 kg	
Dairy cattle	Milk yield	0→25	0→540 kg	Schulte-Coerne & Boie,1986. Ericsson et al.,1986. Pedersen & Christensen, 1986. Baumung & Panicke,1986. Turton,1981. McAllister,1986. McDowell,1985. Sharma & Pirchner, 1990. Ahlborn-Breier & Hohenboken, 1991. Touchnerry, 1992. Van der werf and de Boer, 1989a.
	Fat yield	0→12	0→8 kg	
	Protein yield		0→20 kg	
	Calf survival rate	2→18		
	Reproductivity			
	(maternal heterosis)	2→3		

Note: Data presented above refer to individual heterosis. The data in brackets refers to maternal heterosis. The heterosis expressed as a percentage and as absolute value are possibly from different literature sources.

TABLE 2. Purebred and crossbred heritabilities (h_p^2 and h_c^2).

Species	Traits	h_p^2	h_c^2	Authors
Poultry	Egg production	.19	.48	Rabsztyn & Nowak, 1978
		.12	.37	Orozco & Campo, 1975
		.14	.18	Taran, 1971
		.24	.11	Hale & Clayton, 1965
		.34	.36	Hale & Clayton, 1965
		.08	.14	Pirchner, 1973
		.15 (.09)	.17 (.16)	Pirchner & Mergl, 1977
		.08→.15	.16→.26	Mergl, 1977a,b
		.22	.95	Rabsztyn, 1990
		.19 (.20)	.20 (.21)	Pirchner & Krosigk, 1973
	Egg weight			
		.74	.66	Rabsztyn & Nowak, 1978
		.35	.51	Orozco & Campo, 1975
		.29	.57	Taran, 1971
		.46	.42	Hale & Clayton, 1965
		.96	.88	Hale & Clayton, 1965
		.46	.48	Pirchner, 1973
		.22	.51	Rabsztyn, 1990
		.49 (.58)	.58 (.37)	Pirchner & Krosigk, 1973
Pig	Body weight (finished)	.49	.85	Standal, 1968
	Daily gain (20-90 kg)	.30	.30	
	Backfat	.68	.82	
	Body weight (42-day)	.77 (.86)	.60 (.28)	McLaren et al. 1985
	Daily gain (postweaning)	.39 (.52)	.42 (.52)	
	Backfat	.49 (.61)	.57 (.29)	
	Body weight (56-day)	.03	.19	Stanislaw et al., 1967
	Daily gain (postweaning)	.28	.39	
	Backfat	.55	.47	
	Body weight (154 days)	.73	.03	Louca, 1967
	Backfat	.24	.16	
	Weaning weight	.28 (.08)	.20 (.20)	Rempel, 1969.
	Daily gain	.52 (.28)	.58 (.50)	
	Feed efficiency	.43 (.14)	.85 (.27)	
	Litter size	.36	.50	
Sheep	Birth weight	.60	.24 (.03)	Bassett & Shelton, 1966
	Body at 120-day	.47 (.39)	.25 (.45)	
	Weaning weight	.26	.12	Galal et al., 1970
	Weaning weight	.26	.12	Salah et al., 1969

TABLE 3. Inbreeding depression per 10% increasing inbreeding coefficient.

Species	Traits	Inbreeding depression		References
		%	absolute value	
Pig	Little size (alive)	3→4	.06→.39 piglets	Leymaster & Swiger, 1981. Young et al., 1983 a,b.
	Body weight (154d)	3→5	2→3 kg	
	Daily gain		.006→.02 kg	
	Backfat		.0025→.015 cm	
Laying chicken	Egg production	3→4	6→9.5 eggs	Abplanalp, 1974 & 1990. Foster & Kilpatrick, 1987. Flock et al., 1991.
	Egg wight	0→1	.5→3.2 gram	
	Age at 1st egg	0→1	6.8 days	
	Viability	2-2.4		
	Body weight	1-1.5		
	Hatchability	4-7%		
Dairy cattle	Milk yield		226 kg	Short et al., 1992.
	Fat yield		7.8 kg	
	Protein yield		8.5 kg	
Sheep	Ewe survival	7-70		Lamberson & Thomas, 1984; Ercanbrack & Knight, 1991; Wiener et al., 1992.
	Birth weight		.05-.29 kg	
	Weaning weight	3-5	.3-1.8 kg	
	Body weight (6 months)		.5-2.5 kg	
	Body weight (13 months)		1.2-2.7 kg	
	Reproduction rate/ewe	10		
	Fertility	11-16		

a considerable amount of heterosis and inbreeding depression. Also, these traits can be efficiently improved by crossbred selection schemes. The production traits have the opposite properties to reproduction traits, i.e., lower heterosis and inbreeding depression, higher heritability and less dominance variance.

III. THE BREEDING GOAL IN CROSSBREEDING SYSTEMS

In a crossbreeding system, we have distinguished breeding values of purebred breeding animals for purebred and crossbred performance, i.e., purebreeding and crossbreeding values. Also, we have generally assumed that crossbreeding values are the most suitable selection criteria because it is the crossbred performance that is most expressed in commercial animals as mentioned by Orozco (1986) and Hartmann (1990) for poultry breeding. However, could the purebred response be ignored at all ? Would breeders have arguments to also consider purebred breeding values in selection ?

Another point is that selection methods have been studied for a two-way crossbreeding system, i.e., recurrent selection (RS, Hull, 1945), reciprocal recurrent selection (RRS, Comstock, 1949), and CCPS. However, how would the breeding goal look like in more complex crossbreeding systems such as three- or four-way crossing systems ?

Only two-, three- and four-way crossbreeding systems (Table 4), are considered here because they are expected to be the most important in the animal breeding of the future (Orozco, 1986; Webb, 1989). Other crossbreeding systems, such as rotation cross, two-way crisscross systems, diallel cross, back cross, grading up, crossing for forming a synthetic line (Terrill, 1974; Cartwright and Fitzhugh, 1978) are not considered in this discussion although they are applied in animal breeding practice. The reason is that under these systems no breeding value for improving certain final crossbreds can be consistently estimated over generations. These systems are not suitable to simultaneously exploit genetic variation within and between populations, or say selection effects and heterosis as defined by Orozco (1986) and Swan (1992).

Discussion will first focus on the breeding goal under a two-way crossbreeding system which is the most basic form of crossbreeding systems. Then, more complex crossbreeding breeding systems as 3-way and 4-way crosses will be discussed. The terminology and the symbols for different lines used are in Table 4.

TABLE 4. Crossbreeding systems.

	Genotypes		
Crossbreeding systems	Sire population	Dam population	Final crossbred
Two-way cross	A	C	AC
Three-way cross	A	CD	A(CD)
Four-way cross	AB	CD	(AB)(CD)

Note: A, B, C and D denote four different populations (breeds or lines).

3.1. Breeding goal in a two-way crossbreeding system.

As argued in Chapter 6, optimization of crossbred response is not necessarily equivalent to optimizing the entire crossbreeding system if purebred performance still has a significant contribution to this system. In fact, experiments and theory showed that purebred performance is improved slower and sometimes reduced during crossbred selection (Wei and

Van der Steen, 1991), which might be seen as a disadvantage of CS or CCPS (Van der Steen and Wei, 1991) when purebred performance is of any importance. Therefore, breeders often have to consider both crossbred and purebred performance.

Rather than using the breeding value for crossbred performance as a selection criteria, it can be proposed to use the combined breeding value ($BV_{2\text{-way}}$) in selection of purebred animals from sire and dam lines, which is calculated as follows,

$$BV_{2\text{-way}} = w_P BV_P + w_C BV_C \qquad [1]$$

where BV_p and BV_c are the purebreeding and crossbreeding values of the animal; w_p and w_c are the relative weights of breeding values for purebred and crossbred performance. Here, the same character expressed in purebreds and crossbreds is considered two different traits.

The BV_p and BV_c can be estimated by relevant selection indices (Wei and Van der Werf, 1992b) or with a mixed model method (Appendix). The latter method is appropriately corrected for fixed effects in unbalanced cases, and uses information from relatives over more than one generation.

The weights in [1] can be derived from the relative magnitude of cumulative discounted expressions of each trait (purebred and crossbred performance) in the breeding programme, e.g., using the gene flow method (Hill, 1974; Brascamp, 1978), multiplied by the economic value of the moment of expression. It is interesting to determine the factors that have significant influence on these weights.

At the national level or at the level of the total production chain, discounted expressions depend greatly on frequency of expression, i.e., the number of breeding and commercial animals. This is mostly determined by the reproductive rate of the species. For species with high reproductivity like poultry and pig, w_C will be much larger than w_P because the number of breeding animals is relatively very small compared to commercial animals. Conversely, for species with low reproductivity like cattle and sheep, part of selection pressure would be given to improving purebred performance.

At the breeding company level, the profit of companies is directly from selling breeding animals (A sires and C dams) to multipliers. So, the specific demands of multipliers for efficient purebred animals have to be taken into account. Roughly speaking, breeders might want to pay more attention to purebred performance than they should according to discounted expressions, and maximize their profit on a short horizon. However, in the long run final products, AC crossbred performance, are most important because their quality determines the market share.

The breeding goal in formula [1] is the general one to deal with one character expressed in both purebred and crossbred animals (two traits). However, for any crossbreeding system more than one character usually has to be considered. Usually, production traits are important in final products whereas the reproduction traits are of importance in dam lines. Also, specialization of sire and dam lines requires a distinction between reproduction and production traits (Smith, 1964; Knap, 1988 and 1990a,b).

For simplicity, Moav's concept (1966) is used here to distinguish between production and reproduction traits at purebred and crossbred levels. The equation [1] can be rewritten as follows,

$$BV_{2\text{-way}} = (w_{Pp}BV_{Pp}+w_{Pr}BV_{Pr}) + (w_{Cp}BV_{Cp}+w_{Cr}BV_{Cr}) = w_{Pr}BV_{Pr} + w_{Cp}BV_{Cp} \qquad [2]$$

where subscripts p and r denote the production and reproduction traits, respectively. Production traits are important at AC crossbred level, and reproduction traits are important at C purebred level. Therefore, w_{Pp} and w_{Cr} are ignored since they are considered relatively small.

Therefore, the breeding goal in a two-way crossbreeding system is to improve as much as possible the reproduction traits at C level and the production traits at AC crossbred level. It should be stated that these two types of traits can be optimally improved within lines as studied by De Vries (1989).

3.2. Breeding goal in three-way and four-way crossbreeding systems

A four way crossbreeding system (Table 4) is chosen as an example because it is often used in poultry and pig breeding and also because a three-way crossbreeding can be seen as a simplification of it. The breeding goal for a four-way crossbreeding system can be defined as follows. Here, the selection in the line D (grand dam line) is taken as an example.

$$\begin{aligned} BV_{D4\text{-way}} &= (w_{Dp}BV_{Dp} + w_{Dr}BV_{Dr}) + (w_{CDp}BV_{CDp} + w_{CDr}BV_{CDr}) \\ &\quad + (w_{ABCDp}BV_{ABCDp} + w_{ABCDr}BV_{ABCDr}) \\ &= w_{Dr}BV_{Dr} + w_{CDr}BV_{CDr} + w_{ABCDp}BV_{ABCDp} \qquad [3] \end{aligned}$$

where BV_{Dp} and BV_{Dr} are the breeding values for production and reproduction traits, estimated at the level of line A to obtain best animals of line A; BV_{CDp} and BV_{CDr} are the breeding values for production and reproduction traits, estimated under the two-way crossing system to obtain the best CD crossbreds; BV_{ABCDp} and BV_{ABCDr} are the breeding values for production and reproduction traits, estimated at the level of ABCD crossbreds; w_{Dp}, w_{Dr}, w_{CDp}, w_{CDr}, w_{ABCDp} and w_{ABCDr} are the economic weights. It is assumed that for pig and poultry breeding, production traits are important only at the ABCD level, and reproduction traits are important at C and CD levels. Consequently, w_{Dp}, w_{CDp}, and w_{ABCDr} are ignored because they are considered relatively small.

Under considering the line C, w_{Cr} may be assumed to be zero because BV_{Cr} is not economically important when C line provides sires to produce CD animals. In this case, the combined breeding value becomes $BV_{C4\text{-}way} = w_{CDr}BV_{CDr} + w_{ABCDp}BV_{ABCDp}$. Furthermore, the combined breeding value for lines A and B can be simpler assuming that the reproduction traits in the two lines are not important, e.g., $BV_{A4\text{-}way} = w_{ABCDp}BV_{ABCDp}$. Generally speaking, the equation [1] can be extended to a three- or four-way crossing system to obtain a precise relative economic weights for different traits at different levels.

The breeding goal in a three-way crossbreeding system (ACD) can be derived from the equation [2] and [3] for a two-way and four-way crossbreeding systems, respectively. The selection in line A follows the method for a two-way crossbreeding systems. The only difference is that the tester for A line is the CD crossbreds instead of C purebreds. The selection in lines C and D follows the four-way approach [3].

3.3. Difficulties on achieving the breeding goals in a three-way or four-way crossbreeding systems and possible solutions.

The breeding goal under a two-way crossbreeding system can be achieved by using the CCPS method as a multitrait breeding goal, i.e., using a combined breeding value ($BV_{2\text{-}way}$ approach). The CCPS method may be applied for a three-way or four-way crossbreeding systems by following the way mentioned above, i.e., estimating combined breeding value under 3-way or 4-way cross system ($BV_{3\text{-}way}$ or $BV_{4\text{-}way}$).

However, there are some difficulties involved in 3-way or 4-way cross systems. The main problem is related to estimating crossbreeding values at ACD and ABCD crossbred level. First, including ABCD information into selection procedure tends to increase generation interval which reduces the genetic gain on the annual basis. In addition, efficiency of ABCD information in selection is largely reduced because of a small coefficient of genetic relationship between A animals and their ABCD grand progeny. Second, the variances and covariances related to ABCD crossbreds have to be estimated, but ABCD crossbred information is not usually available because breeding companies do not test ABCD crossbreds routinely.

Several suggestions may be given to achieve breeding goals in three-way or four-way crossbreeding system. The $BV_{2\text{-}way}$ approach can be directly used to some extent in three-way or four-way crossbreeding systems. With respect to meat-type animal breeding (e.g., broiler and pig), reproduction traits, such as egg production, little size and fertility, are important only at CD level but not at ACD and ABCD level. The $BV_{2\text{-}way}$ approach, therefore, is sufficient to improve these reproduction traits in either three-way or four-way crossbreeding system.

Under a three-way crossbreeding system, the $BV_{2\text{-}way}$ approach is directly applicable for improving the sire line, i.e., line A. In this case, the traits to be improved by $BV_{2\text{-}way}$

approach are only towards production traits at ABC level.

Theoretically, an alternative way to select A purebreds for the best ABCD crossbreds is to have AC and AD or ACD crossbreds tested. Selection of A animals based on the performance of AC and AD or ACD seems to be equivalent to that based on ABCD performance. The reason is that combining ability between A and B is mainly expected to contribute to reproduction at AB level but not to that at ABCD level. Instead, combining ability between A and C, D or CD contributes to the production trait at ABCD level. Therefore, it is logical to hypothesize that testing performance of AC and AD or ACD is a short-cut to test ABCD animals. Practically, it is convenient to test A(CD) crossbreds, and similarly B(CD). Under this hypothesis, $BV_{2\text{-way}}$ approach can be directly used for a whole four-way crossbreeding system.

IV. SHORT-TERM VERSUS LONG-TERM SELECTION FOR CROSSBRED PERFORMANCE

The study described in the previous chapter has provided the selection method to maximize the selection response in crossbreds from one round of selection (Chapter 6). However, the question arises whether selection decisions based on a short term CCPS are also optimal on a longer time scheme. Here, the merits of a long-term CCPS compared for with PLS and CS methods will be discussed on both locus level and quantitative genetic level.

4.1. Locus level.

Genetic progress in crossbreds. An autosomal locus with two alleles (A_1 and A_2) where A_1 is favourable is again considered. The genotypic value of three genotypes, A_1A_1, A_1A_2 and A_2A_2, are assumed to be 1, d and -1, respectively. The d equal to zero indicates pure additive gene effect, the d between 0 and 1 partial dominance, and the d larger than 1 overdominance.

Hill (1971) investigated the selection limit for PLS and RRS schemes under a two-way cross system. PLS is less efficient than RRS to achieve crossbred response with overdominance although PLS and RRS obtain a similar genetic progress under partial dominance. The selection limit is the same for PLS and RRS in case of partial dominance, i.e., fixing genotypes, A_1A_1, in purebred lines. In case of overdominance, applying RRS leads to fixation of the frequency of A_1 in one line and toward zero in the other lines. The PLS method still leads to the fixation of A_1 frequency in both lines (Comstock et al., 1949). Based on Hill's results with partial dominance, all selection methods, also CCPS, lead to the same result in the limit. So, the best one on a short term should be the best in general if overdominance could be ignored.

A simulation study at the locus level (Swan, 1992) showed the different effects of selection methods (PLS and CS) on reaching optimum crossbred genotypes in crossbreds when overdominance exists. In case of overdominance, the CS obtains the maximum crossbred level and heterosis (i.e., fixing A_1 in one line and A_2 in the other line). But the PLS does not reach maximum crossbred genotype and leads to the loss of heterosis. This is in a good agreement with the RRS theory (Comstock et al., 1949) that selection for purebred performance does not naturally improve combining ability but decreases heterosis (Götz et al., 1991; Serrano and Orozco, 1992).

Thus, optimization of crossbred response means not only to obtain maximum crossbred genotype finally but also to obtain the maximum genetic response in crossbred at a short term horizon, e.g., one round of selection. Naturally, it maximizes heterosis (Swan, 1992). The CCPS and CS methods can reach the maximum crossbred genotype but PLS can not. It is shown by Wei and Van der Werf (1992b) that CCPS always results in a larger genetic response in crossbreds, and thus it is the optimal method to obtain crossbred response.

Change of r_{pc} due to selection. The r_{pc} is the most important parameter to optimize crossbred response, and the question is how the value changes in a long-term selection under a crossbreeding program. The r_{pc} value is determined by gene effects and gene frequencies (Wei et al., 1991b). For different selection methods, it can be predicted how gene frequencies change due to selection (Wei et al., 1991b). Without dominance, r_{pc} is unity and never changes under any selection scheme. In case of partial dominance, r_{pc} increases under PLS because the gene frequency difference between parental populations decreases continuously (Wei et al., 1991b). With overdominance, the value of r_{pc} decreases under CS or CCPS but still increases under PLS. Therefore, the behaviour of r_{pc} under a long term CS or CCPS will reflect the gene effects controlling the trait of interest. A simulation study on the behaviour of r_{pc} under selection (Swan, 1992) confirmed these results.

4.2. Quantitative genetic level.

In practical animal breeding, the value of r_{pc} can be estimated, but gene effects and gene frequencies involved are never known, which gives no opportunity for breeders to adjust their breeding schemes based on the information at the locus level. Fortunately, the behaviour of r_{pc} under a long-term CS or CCPS informs us to some extent whether overdominance exists (Wei et al., 1991b), in the sense, that overdominance should be used to explain a decrease of r_{pc} under CS or CCPS. A decrease of r_{pc} was found in several long-term selection experiments (Comstock and Robinson, 1957; Pirchner and Von Krosigk, 1973; Pirchner and Mergl, 1977; Swan, 1992).

Theoretically, it may be expected that crossbred heritability (h_c^2) changes due to changing gene frequency under selection. To obtain an optimum genetic progress, regular estimation of h_c^2 might be needed although the change of h_c^2 has less influence on the efficiency of CCPS method than r_{pc} (Chapter 6). There is no experimental evidence reported on the behaviour of this parameter.

Based on the studies in this thesis (Chapter 6) and those of Hill (1971) and Swan (1992), several hypotheses can be made on the expectation of genetic progress in crossbreds caused by a long term CCPS compared with PLS and CS. An equal total testing capacity for three methods and $h_c^2=h_p^2$ are assumed. Hypothesis one: without dominance (d=0), PLS, CS and CCPS all are able to achieve the maximum crossbred performance, i.e., fixing the A_1 allele. But, PLS achieves the limit faster than CS and CCPS because PLS has a relatively high selection intensity, i.e., with PLS more purebred animals are tested (Figure 1). The CCPS method achieves the limit faster than CS because of using additional purebred information (Figure 1). Hypothesis two: with partial dominance, PLS, CS and CCPS have the same selection limit. But CCPS may obtain a faster progress than CS and PLS (Figure 2). CS may be better or worse than PLS depending on parameters. The r_{pc} increases under all selection schemes and consequently response will decrease under CCPS and increase under PLS. Hypothesis three: in case of overdominance the CCPS achieves a faster and larger crossbred response than PLS. And, CS may reach the selection limit faster or slower than PLS but has definitely at a larger limit (Figure 3). The relative superiority of CCPS and CS over PLS increases because the value of r_{pc} decreases under CCPS and increases under PLS.

The CCPS method is generally preferred. To keep CCPS efficient, r_{pc} should be regularly estimated and genetic models should adopt up-to-date parameters. When r_{pc} becomes larger, purebred information is automatically given more weight in the CCPS method, and also more purebred animals should be tested.

V. EFFECT OF GENOTYPE-ENVIRONMENT INTERACTION ON CCPS SCHEME

Almost all animal breeding programmes face the fact that nucleus purebreds and commercial animals are raised in different environments (Kraus, et al., 1965; Ruvuna et al., 1983; Brascamp et al., 1985; Hartmann, 1989; Sorensen, 1989; Rahnefeld et al., 1991; Sheridan, 1990). To improve the crossbred performance at the commercial environment in a crossbreeding program, the efficiency of selection in nucleus purebreds depends not only on the genetic correlation (r_{pc}) but also on possible genotype*environment (G*E) interaction between nucleus and commercial conditions.

5.1. Nature of G*E interaction and its influence on genetic parameters.

In this paragraph the meaning of the different parameters in a crossbreeding system

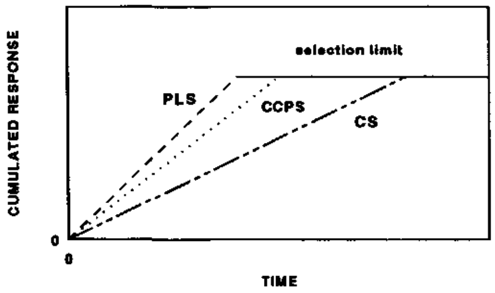

Figure 1. Hypothesis one: relative merits of a long-term CCPS, PLS and CS scheme in case of no dominance. Cumulative genetic responses in crossbreds are plotted against the time.

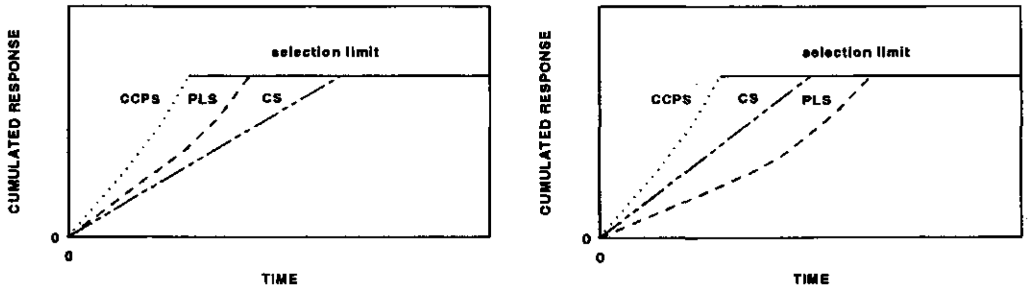

Figure 2. Hypothesis two: relative merits of a long-term CCPS, PLS and CS scheme in case of partial dominance. Cumulative genetic responses in crossbreds are plotted against the time.

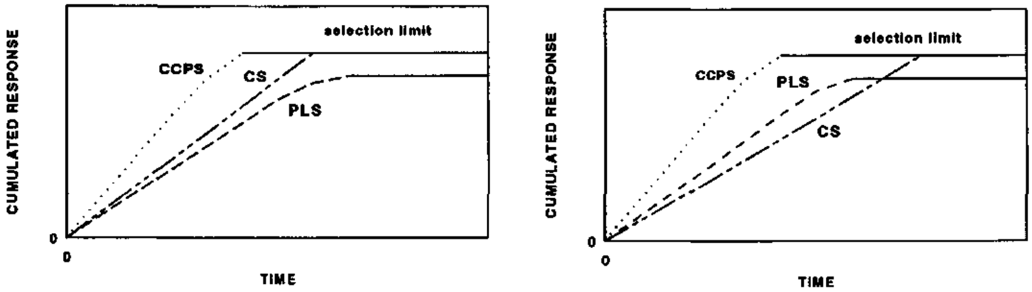

Figure 3. Hypothesis three: relative merits of a long-term CCPS, PLS and CS schemes in case of overdominance. Cumulative genetic responses in crossbreds are plotted against the time.

with different environments is first discussed as well as why those parameters could differ between environments. Subsequently, the consequences for a practical breeding programme will be discussed. Falconer (1952) considered performance in each environment as different traits with a genetic correlation between them. Here, his concept is used to discus G*E interaction related to the CCPS scheme.

The G*E interaction influences the crossbreeding systems because estimates of genetic parameters (variances, covariances and r_{pc}) vary in dependency on environments (Table 5). For example, the crossbred heritability (h_c^2) and genetic correlation between purebred and crossbred performance (r_{pc}) may be smaller when crossbred performance is under a less optimal environment. No environmental effect has usually been taken into account in estimation of r_{pc} as reviewed by Wei and van der Steen (1991) because this is usually confounded with the difference between purebreds and crossbreds.

The experimental way to estimate G*E interaction as well as r_{pc} is to have an appropriate design (Table 5). In such a design, two crossbred heritabilities (h_{c1}^2 and h_{c2}^2) and three genetic correlations (r_{pc1}, r_{pc2} and r_{c1c2}) may be estimated associated with the two relevant environments (Table 5). Theoretically, r_{c1c2} should be unit if there is no G*E interaction because the expectation of sire values is the same in different environments. The r_{c1c2} value is also unity if the G*E interaction is due to a scale effect, thus without affecting the ranking of breeding sires. In this case, G*E interaction does not influence the efficiency of a CCPS program. Another type of G*E interaction, where ranking of genotype varies upon environments, the breeding efficiency will definitely be influenced. The r_{c1c2} smaller than one indicates the existence of this type of G*E interaction. The test for G*E interaction expressed as r_{c1c2} was discussed by Simianer (1991).

TABLE 5. Experimental design of crossbreeding in case of G*E interaction.

	Nucleus Environment (1)	Commercial Environment (2)
Parents	Sire line and dam line	
Progeny	Purebred progeny	
	Crossbred progeny 1	Crossbred progeny 2
Parameters to be estimated	h_p^2, h_{c1}^2, r_{pc1}, Cov_{pc1}	h_{c2}^2, r_{pc2}, Cov_{pc2}, r_{c1c2}, Cov_{c1c2}

Note: r_{pc} is genetic correlation between purebred and crossbred performance; h_c^2 is crossbred heritability; h_p^2 is purebred heritability. r_{c1c2} is genetical correlation between crossbreds in different environments. Cov_{pc} is sire covariance between purebred and crossbred performance. Cov_{c1c2} is sire covariance between crossbreds in two environments. Subscripts 1 and 2 refer to the nucleus and commercial environments.

Crossbred heritabilities estimated in different environments tend to be different depending on the type and degree of G*E interaction, e.g., in poultry (Krause, et al., 1965). They will be equal in case of no G*E interaction. However, the crossbred heritability (h^2_{c2}) in the commercial environment may be smaller or larger than the heritability under the nucleus environment (h^2_{c1}) due to two reasons. First, environmental variance increases in the less controlled environment and consequently decreases the heritability. Second, the genotypes may express themselves differently in different environments, i.e., the ranking of genotype values may change. In practice, h^2_{c1} under the nucleus environment was usually found to be larger than h^2_{c2} under the commercial environment (Pirchner, 1983; Serrano and Orozco, 1992; Merks, 1988).

The difference between r_{pc1} and r_{pc2} depends on G*E interaction. The sire covariances, Cov_{pc1} and Cov_{pc2}, may change according to the type of G*E interaction. Theoretically, Cov_{pc1} can be either larger or smaller than Cov_{pc2}, and consequently r_{pc1} can be larger or smaller than r_{pc2}. For example, G*E interaction was involved in some experiments to compare PLS and RRS schemes (Kincaid and Touchberry, 1970; Orozco and Bell, 1974). As a result, RRS improved crossbreds faster under adverse environment than under optimal environment, and RRS performed better than PLS under adverse environment but worse under the optimal environment. The results implied that r_{pc2} was lower than r_{pc1}, and h^2_{c2} was larger than h^2_{c1}.

Theoretically, two explanations may be given to G*E interaction, (1) the same group of genes express their different genotype value in different environment, and (2) different groups of genes control the trait in different environments. The hypothesis on heterosis theory given by Orozco (1986) might give an explanation on the difference between r_{pc1} and r_{pc2}. In the optimal environment, r_{pc1} is mainly determined by the genes responsible for the trait of interest. Under the commercial environment (less optimal), r_{pc2} is determined not only by the genes responsible for the traits but also by the genes responsible for the vigour. Therefore, the genotypic values are modified and different from those under the optimal environment, which is explained by G*E interaction. This hypothesis is somehow related to the assumption made by Falconer (1952) that the expression of identical traits is not controlled by the same sets of genes when G*E interaction exists. The phenomenon that the degree of heterosis varies upon environments and becomes larger under the less optimal condition, appears to support Orozco's hypothesis. This phenomenon has been first noticed by Barlow (1981), and then by Fairfull and Gowe (1986) and Davis and Lamberson (1991). A poultry crossbreeding experiment of Orozco and Bell (1974) also showed a good example. The *Tribolium* experiment comparing three selection systems for crossbreeding showed that heterosis is not increased by crossbred selection methods in the optimum environment but it is increased in the stress environment (Serrano and Orozco, 1992). An explanation may be that crossbred selection in the optimum environment acts only on the additive genes which are active, but not on the genes responsible for animal vigour. In the stress environment, the genes for animal vigour become active and therefore were selected as well. Paleolog and Maciejowski

(1990) found that in the poor environment selection based on combining ability was more successful than pure line selection, and each of the different selection procedures in each of the different environments lead to different gene combinations. From a crossbreeding experiment of dairy cattle in Denmark, Christensen and Pedersen (1991) concluded that a major part of the heterosis for total merit was due to good stayability and high survival rate of crossbreds, and therefore, crossbreeding is expected to be particularly beneficial in herds with suboptimal environmental conditions. In the tropics, crossbreds from pure European improved breeds and local breeds produced not only more milk than the local breed but also more than the pure European breed (Mason, 1974). Terrill (1974) described the experiment showing no heterosis when well-adapted purebred animals were raised under very good conditions with high production records.

5.2. Crossbreeding strategy in case of G*E interaction.

Breeders have to choose whether to test crossbred animals in central testing station or in the commercial environment. Without eliminating environmental influences, r_{pc2} contains not only genetic but also environmental components, and is expected to be lower than r_{pc1}. For animal breeding, is it necessary to know how the genetic and environmental components affect the genetic correlation ?

The formula on direct and indirect selection (Falconer, 1989) is used here to answer this question. The indirect selection response in crossbreds (CR_C) results from crossbred information that is collected from the nucleus environment. Direct selection response (R_C) is obtained when crossbred information is from the commercial environment. The ratio of CR_C to R_C is expressed by formula [4],

$$\frac{CR_C}{R_C} = r_{c1c2}\frac{i_{c1}a_{c1}}{i_{c2}a_{c2}} = r_{c1c2}\frac{a_{c1}}{a_{c2}} \qquad (\text{assuming } i_{c1} = i_{c2}) \qquad [4]$$

where, i_{c1} and i_{c2} are the selection intensity associated to environment 1 and 2, and they are assumed equal; a_{c1} and a_{c2} are the selection accuracies associated with indirect and direct selection; and r_{c1c2} is the genetic correlation between crossbred animals in two environments. It is clear that a direct selection is more efficient than an indirect selection unless r_{c1c2} becomes smaller than the ratio of a_{c1}/a_{c2}. Usually, a_{c1} is expected to be somewhat larger than a_{c2}, but this does not always compensate for an r_{c1c2} value smaller than one. For example, Mathur and Horst (1991) described a poultry experiment showing a higher direct selection response.

There is no necessity to know the effect of G*E interaction on the value of r_{pc}. In other words, it is not necessary to know why r_{pc2} is different from r_{pc1} because the genotypic values of animals are always associated with a certain environment. Therefore, to optimize the crossbred response for a specific environment, a CCPS system is sufficient when the genetic parameters used in the genetic models are estimated based on information collected in the commercial environment (i.e., r_{pc2}, h^2_{c2}, and Cov_{pc2}). So, the only important thing for breeders is the genotype value under the commercial environment. Moreover, it should be noted that the commercial environment might not be homogeneous. Therefore, the environment where information comes from for parameter and breeding value estimation has to be considered with caution. Crossbred animals should be tested under representable commercial environment.

VII. PRACTICAL CONSIDERATIONS ON APPLICATION OF CCPS METHOD

The application of CCPS in any crossbreeding system will, of course, involve extra efforts mainly in relation to collecting crossbred information, estimating genetic parameters on crossbreds, and organizing matings. It is worthwhile to discuss some practical aspects of the CCPS method in comparison with crossbreeding systems without using crossbred information.

7.1. The design of a CCPS scheme.

Van der Steen and Wei (1991) have stressed two major practical problems for using crossbred information, i.e., first an increased generation interval, and second additional investments in facilities for housing, recording and processing of data.

These problems depend greatly on the species and the design of the breeding program. In poultry and pig breeding, crossbred animals exist anyway. The extra cost is only in recording and collecting the information. Recently, application of advanced management systems provides increasing amount of crossbred data, e.g., electronic identification, sow management systems, and data collection at slaughter house in pig breeding. However, relevant pedigree information has to be obtained as well to be useful for breeding. Integrated identification systems should then be organized for the complete production chain.

To keep the generation interval short, a strategy may be to produce purebred and crossbred progeny simultaneously and thus crossbred sib information may be used in selection. At the moment of selection, the available purebred and crossbred information should be used.

Moreover, when testing capacity has to be allocated for crossbreds to the expense of purebreds, the selection intensity under a CCPS scheme may decrease. If the number of breeding animals is equal in PLS and CCPS systems, there must be some more investment involved in obtaining crossbred information. However, these costs can be minimized by testing crossbreds on the commercial farm but not in the central station. On the other hand, the use of crossbred information may lead to a smaller number of purebred animals to be tested, e.g., in case of small r_{pc}. Consequently, relevant cost is reduced.

7.2. Risk due to applying a long-term CCPS system.

There is an economical risk of applying a long-term CCPS considering the investment. It is up to a breeding company to calculate the investment for developing a CCPS system and the response from the CCPS application in their purebred lines. A possible change in market share has to be determined.

Another worry that might be raised is that a CCPS system might reduce the flexibility of a breeding organization (Van der Steen and Wei, 1991). The CCPS system will have to be restricted to the development of a few lines (2-4 lines). Gradually, these lines are getting more and more dependent on each other because they are the most efficient only when they are combined well to each other. If the product is not competitive or the market changes, there is a risk that these lines have to be culled. This would specifically be a concern when dealing with a quick changing market.

7.3. Estimation of r_{pc} and h_c^2 in animal breeding industry.

Estimation of r_{pc} and h_c^2 should be performed regularly. A good estimation of these parameters basically needs many data and a reasonably balanced design with fair numbers of progeny per dam and dams per sire. Besides this, there are some other difficulties to keep in mind.

First, the r_{pc} and h_c^2 estimated from sire and dam lines are generally different because of the different gene frequencies between lines (Wei and Van der Werf, 1990; Wei et al., 1991a,b). Thus, both r_{pc} and h_c^2 have to be estimated for both sire and dam lines, and different parameters should be used in selection index or BLUP models for selection in sire and dam lines. In animal breeding practice where sire and dame lines are specialized, the r_{pc} and h_c^2 for sire lines can be reasonably estimated, but the estimation of r_{pc} and h_c^2 for dam lines is less accurate or impossible. The h_c^2 may be estimated by the dam component in crossbred population but might be biased by the common environment effects and maternal effects. The r_{pc} for the dam line can not be estimated because a particular dam in a dam line usually has either purebred or crossbred progeny but not both. Reciprocal crossing would be a solution for estimating the reciprocal parameters but this would lead to additional cost for the operation. On the other hand, there should not be too much worry about accuracy of these parameter estimates because the CCPS is robust against the biased estimates (Wei and Van der Werf, 1992b).

Reciprocal crossings are generally not available in animal breeding due to the specialization of dam and sire lines (Smith, 1964; Knap, 1990a,b). Thus, under a CCPS scheme only sires of the sire line and dams of the dam line can be tested for their crossbred performance. The question that could be raised is whether it necessary and possible to select the dams of sire line and sires of dam line based on additional crossbred information. The dams in sire line and the sires in dam line may be selected based on information from relatives, e.g., sib's crossbred progeny. However, if traits are to some extend determined by the sex-linked genes, e.g., egg production in chicken (Merritt and Gowe, 1960; Lowe and Garwood, 1981; Fairfull et al., 1983; Bernon and Chambers, 1985; Fairfull and Gowe, 1986; Brade, 1990), a genetic model is required, which includes the sex-linked gene effects. A specific model should, then, be developed allowing for differences between reciprocal crossings.

VIII. RECOMMENDATIONS

A combined crossbred and purebred selection (CCPS) method, using both purebred and crossbred information, is generally suggested for improving crossbred performance in animal breeding practice because it brings more genetic response in crossbreds in both short term and long term.

The estimation of some genetic parameters such as crossbred heritability (h_c^2) and genetic correlation between purebred and crossbred performance (r_{pc}) are necessary for organizing a CCPS scheme. To have an efficient CCPS program, genetic parameters, especially r_{pc}, should be routinely estimated since they may change due to selection.

Test of crossbred animals can be on the central test station or on the commercial environment. Without genotype and environment interaction, different test places do not make a difference in selection efficiency and therefore testing crossbreds in the commercial environment will be economically advantageous. However, genotype*environment interaction usually is present and genetic parameters or animal ranking changes in dependency on environments. The strategy for commercial animal breeding, is then to test crossbred animals in the commercial environment and the genetic parameters used in CCPS models, r_{pc} and h_c^2, should also be estimated associated with such an environment.

The breeding goal in a crossbreeding system should not only be the improvement of crossbred performance but also of purebred performance because the purebred performance sometimes are commercially important in the production system, especially for the species with low reproductivity like sheep and cattle. A method to optimally weigh breeding values for crossbred and purebred performance was suggested.

IX. REFERENCES

Abplanalp, H.A., 1974. Inbreeding as a tool for poultry improvement. Proc. 1st World Cong. Genet. Appl. Livest. Prod. 1:897-908.

Abplanalp, H.A., 1990. Chapter 39. Inbreeding. In: Crawford, R.D. (ed.) Poultry Breeding and Genetics. Elsevier, Amsterdam, The Netherlands. pp955-984.

Ahlborn-Breier, G.; Hohenboken, W.D., 1991. Additive and nonadditive genetic effects on milk production in dairy cattle: evidence for major individual heterosis. J. Dairy Sci. 74:592-602.

Arthur, J.A., 1986. An evaluation of industry breeding programmes for egg type chickens. Proc. 3rd World Cong. Genet. Appl. Livest. Prod. 10:325-335.

Ayyagari, V.; Mohapatra, S.C.; Renganathan, P.; Johri, D.C.; Thiagasundaram, T.S.; Panda, B.K., Cross performance as influenced by selection in pure lines. Bri. Poult. Sci. 23:469-479.

Baas, T.J.; Christian, L.L.; Rothschild, M.F., 1992a. Heterosis and recombination effects in Hampshire and Landrace swine: I. maternal traits. J. Anim. Sci. 70:89-98.

Baas, T.J.; Christian, L.L.; Rothschild, M.F., 1992b. Heterosis and recombination effects in Hampshire and Landrace swine: II. Performance and carcass traits. J. Anim. Sci. 70:99-105.

Barlow, R., 1981. Experimental evidence for interaction between heterosis and environment in animals. Anim. Breed. Abstr. 49:715-737.

Bassett, J.W.; Shelton, M., 1966. Crossbreeding influence on heritability estimates. J. Anim. Sci. 25:877.

Baumung, A.; Panicke, L., 1986. Heterosis results in dairy cattle. Proc. 37th Ann. Meet. of EAAP, 1986. 1:13.

Bell, A.E., 1982. Selection for heterosis - results with laboratory and domestic animals. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. 6:206-227.

Bell, A.E.; Moore, C.H.; Bohren, B.B.; Warren, D.C., 1952. Systems of breeding designed to utilize heterosis in the domestic fowl. Poul. Sci. 31:11-22.

Bernon, D.E.; Chambers, J.R., 1985. Maternal and sex-linked genetic effects in broiler parent stocks. Poult. Sci. 64:29-38.

Bidanel, J.P.; Caritez, J.C.; Legault, C., 1991a. Studies on the use of Meishan pigs in crossbreeding. 1. Estimation of heterosis for sow productivity traits. Anim. Breed. Abstr. 59:353.

Bidanel, J.P.; Caritez, J.C.; Legault, C., 1991b. Studies on the use of Meishan pigs in crossbreeding. 2. Estimation of crossbreeding parameters for growth traits. Anim. Breed. Abstr. 59:357.

Bosch, A.B., 1990. Nonallelic gene interactions in inbred lines of White Leghorns and their crosses. Anim. Breed. Abstr. 16:367.

Brade, W., 1990. Breeding of laying hens in multi-line projects. Anim. Breed. Abstr. 17:11.

Brascamp, E.W., 1978. Methods on economic optimization of animal breeding plans - notes for Scandinavian Post-graduate Course in economic breeding planning, University of Helsinki, Department of Animal Breeding, Helsinki. IVO report B-134. Zeist, the Netherlands.

Brascamp, E.W.; Merks, J.W.M.; Wilmink, J.B.M., 1985. Genotype environment interaction in pig breeding programmes: methods of estimation and relevance of the estimates. Livest. Prod. Sci. 13:135-146.

Buchanan, D.S., 1988. The crossbred boar. Pig News and Information 9:269-275.

Cartwright, T.C.; Fitzhugh, H.A., 1978. Efficient breeding system for commercial beef production. Proc. 1st World Cong. Genet. Appl. Livest. Prod. I:643-653.

Christensen, L.G.; Pedersen, J., 1991. Crossbreeding of dairy cattle. Anim. Breed. Abstr. 59:17-18.

Comstock, R.E., Robinson, H.F., and Harvey, P.H., 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agronomy Journal 41:360-367.

Comstock, R.E.; Robinson, H.F., 1957. Findings relative to reciprocal recurrent selection. Proc. Intern. Genet. Symp. Science Council of Japan. Tokyo. pp461-464.

Cunningham, E.P., 1990. Quantitative approaches for animal improvement. Proc. 4th World Cong. Genet. Appl. Livest. Prod. XIII:4-14.

Davis, J.A.; Lamberson, W.R., 1991. Effect of heterosis on performance of mice across three environments. J. Anim. Sci. 69:543-550.

De Vries, A.G., 1989. Selection for production and reproduction traits in pigs. Ph.D thesis, Dept. of Anim. Breeding, Wageningen Agri. Univer., The Netherlands.

Dickerson, G.E., 1973. Inbreeding and heterosis in animals. Proc. Anim. Breed. Genet. Symp. in Honour of Dr. J.L. Lush. ASAS, Champaign, IL. pp54-77.

Eisen, E.J.; Horstgen-Schwark, G.; Saxton, A.M.; Bandy, T.R., 1983. Genetic interpretation and analysis of diallel cross with animals. Theor. Appl. Genet. 65:17-23.

Elzo, M.A., 1986. Inverse of single trait additive genetic covariance matrix with unequal variances across additive genetic groups. J. Dairy Sci. 69:569-574.

Elzo, M.A., 1990. Covariances among sire by breed group of dam interaction effects in multibreed sire evaluation procedures. J. Anim. Sci. 68:4079-4099.

Elzo, M.A.; Famula, T.R., 1985. Multibreed sire evaluation procedures within a country. J. Anim. Sci. 60:942-952.

Ercanbrack, S.K.; Knight, A.D., 1991. Effects of inbreeding on reproduction and wool production of Rambouillet, Targhee, and Columbia ewes. J. Anim. Sci. 69:4734-4744.

Ericsson, K.; Banell, B., 1986. Crossbreeding effects between two swedish dairy breeds for production and reproduction traits. Proc. 37th Ann. Meet. of EAAP. 1:17.

Fairfull, R.W., 1990. Chapter 37. Heterosis. In: Crawford, R.D. (ed.) Poultry Breeding and Genetics. Elsevier, Amsterdam, The Netherlands. pp9134-933.

Fairfull, R.W.; Gowe, R.S., 1986. Use of breed resources for poultry egg and meat production. Proc. 3rd World Cong. Genet. Appl. Livest. Prod. 10:242-256.

Fairfull, R.W.; Gowe, R.S.; Emsley, J.A.B., 1983. Diallel cross of six long-term selected Leghorn strains with emphasis on heterosis and reciprocal effects. Brit. Poult. Sci. 24:133-158.

Fairfull, R.W.; Gowe, R.S.; Nagai, J., 1987. Dominance and epistasis in heterosis of White Leghorn strain crosses. Can. J. Anim. Sci. 67:663-680.

Falconer, D.S., 1952. The problem of environment and selection. Amer. Nat., 86:293-298.

Falconer, D.S., 1989. Introduction to quantitative genetics (3rd Ed.). Longman Sci. & Tech., New York.

Falconer, D.S., 1989. Selection experiments and the nature of quantitative variation. In: (Ed. by Hill, W.G. & Mackay, T.F.L.) Evolution and Animal Breeding. C.A.B. International, UK. pp121-127.

Fimland, E., 1983. Methods of estimating the effects of heterosis. J. Anim. Breed. Genet. 100:3-8.

Flock, D.K., 1988. An assessment of progress with different stocks and methods of selecting in egg layers. In: Animal Breeding Opportunities. BSAP Occas. Pub. 12:189-201.

Flock, D.K.; Ameli, H.; Glodek, P., 1991. Inbreeding and heterosis effects on quantitative traits in a White Leghorn population under long-term reciprocal recurrent selection. Brit. Poult. Sci. 32:451-462.

Foster, W.H.; Kilpatrick, D.J., 1987. Inbreeding in poultry: genetic drift and inbreeding depression. Record of Agricultural Research (Dept. of Agri., Northern Ireland). Vol. 35:27-35.

Galal, E.S.E.; Hazel, L.N.; Sidwell, G.M.; Terrill, C.E., 1970. Correlation between purebred and crossbred half-sibs in sheep. J. Anim. Sci. 30:475-480.

Gardner, C.O.; Eberhart, S.A., 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439-452

Ghoneim, K.E.; Aboul-Naga, A.; Labban, F., 1968. Effect of crossing Merino with Ossimi sheep on growth and body weight. J. Anim. Prod., U.A.R. 8:45-56.

Glodek, P., 1982. Experimental results from pigs. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. 6:243-253.

Götz, K.-U.; Glodek, P.; Rapp, K., 1991. Crossbreeding effects after long-term selection for purebred performances: a model experiment with mice 1. Performance of F_1 crosses. Theor. Appl. Genet. 81:720-728.

Gregory, K.E.; Swiger, L.A.; Koch, R.M.; Sumption, L.J.; Rowder, W.W.; Ingalls, J.E., 1965. Heterosis in preweaning traits of beef cattle. J. Anim. Sci. 24:21-28.

Gregory, K.E.; Cundiff, L.V.; Koch, R.M., 1991. Breed effects and heterosis in advanced generations of composite populations for birth weight, birth date, dystocia, and survival as traits of dam in beef cattle. J. Anim. Sci. 69:3574-3589.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9:463-493.

Hale, R.W.; Clayton, G.A., 1965. A diallel crossing experiment with two breeds of laying fowl. Bri. Poul. Sci. 6: 153-174.

Hartmann, W., 1989a. From Mendel to multi-national in poultry breeding. World's Poult. Sci. J. 45:5-26.

Hartmann, W., 1989b. Implications of genotype-environment interactions in animal breeding: genotype-location interaction in poultry. In: Genotype*Environment Interactions in Poultry Production (Ed. by INRA). Jouy-en-Josas, France. pp9-27.

Hartmann, W., 1990. Evaluation of the potentials of new scientific developments for commercial poultry breeding. Proc. of VIII European Poult. Conf. 25-28 June 1990. Barcelona. pp156-164.

Hartmann, W., 1992. Evaluation of the potentials of new scientific developments for commercial poultry breeding. World's Poult. Sci. J. 48:17-27.

Henderson, C.R., 1977. Prediction of the merits of single crosses. Theor. Appl. Genet. 49:273-282.

Hickman, C.G., 1982. Nature and utilization of heterosis: experimental results from sheep and cattle. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. 6:254-261.

Hill, W.G., 1971. Theory of limits to selection with line crossing. In: Kojima, K. (ed.) Mathematical Topics in Population Genetics. Berlin, German Federal Republic, Springer-Verlag.

Hill, W.G., 1974. Prediction and evaluation of response to selection with overlapping generations. Anim. Prod. 18: 117-129.

Hill, W.G., 1982. Dominance and epistasis as components of heterosis. J. Anim. Breed. Genet. 99:161-168.

Hoeschele, I., 1991. Additive and nonadditive genetic variance in female fertility of Hosteins. J. Dairy Sci. 74:1741.

Hull, F.H., 1945. Recurrent selection for specific combining ability in corn. J. of American Society Agronomy. 37: 134-145.

Kincaid, H.L.; Touchberry, R.W., 1970. Long term RRS selection study in D. melanogaster. J. Anim. Sci. 31:165.

Kinghorn, B.P., 1980. The expression of "recombination loss" in quantitative traits. J. Anim. Breed. Genet. 97:138-143.

Kinghorn, B.P., 1982. Genetic effects in crossbreeding. 1. models of merit. J. Anim. Breed. Genet. 99:59-68.

Kinghorn, B.P., 1983. Genetic effects in crossbreeding. III. epistatic loss in crossbred mice. J. Anim. Breed. Genet. 100:209-222.

Kinghorn, B.P., A single approach to genetic improvement which exploits both selection and crossbreeding effects. Proc. 2nd World Cong. Genet. Appl. Livest. Prod. XII:233-244.

Knap, P.W., 1988. Pig herdbook breeding in the Netherlands. 1. Outlines of the breeding structure. World Review of Anim. Prod. Vol. XXIV:43-49.

Knap, P.W., 1990a. Pig Herdbook breeding in the Netherlands. 2. Sire line breeding. World Review of Anim. Prod. Vol. XXV:33-38.

Knap, P.W., 1990b. Pig Herdbook breeding in the Netherlands. 3. Dam line breeding. World Review of Anim. Prod. Vol. XXV:59-64.

Knapp, B.W.; Pahnish, O.F.; Urick, J.J.; Brinks, J.S., 1980. Preweaning and weaning heterosis for maternal effects of beef*beef and beef*dairy crosses. J. Anim. Sci. 50:800-807.

Kojima, K.; Kelleher, T.M., 1963. A comparison of purebred and crossbred selection schemes with two populations of Drosophila pseudoobscura. Genetics 48:57-72.

Komender, P., 1988. Crossbreeding in farm animals III. a general method of comparing models to estimate crossbreeding parameters with an application to diallel crossbreeding experiments. J. Anim. Breed. Genet. *105*:362-371.

Komender, P.; Hoeschele, I. 1989. Use of mixed-model methodology to improve estimation of crossbreeding parameters. Livest. Prod. Sci. 21:101-113.

Krause, E.; Yamada, Y.; Bell, A.E., 1965. Genetic parameters in two populations of chickens under reciprocal recurrent selection. Bri. Poult. Sci. 6:197-206.

Kress, D.D.; Doornbos, D.E.; Anderson, D.C., 1990. Performance of crosses among Hereford, Angus and Simmental cattle with different levels of Simmental breeding: IV. Maternal heterosis and calf production by two-year-old dams. J. Anim. Sci. 68:54-63.

Lamberson, W.R.; Thomas, D.L., 1984. Effects of inbreeding in sheep: a review. Anim. Breed. Abstr. 52:287-297.

Lasley, J.F., 1987. Genetics of livestock improvement (4th ed.). Prentice-Hall, Inc. Englewood Cliffs, New Jersey.

Lawlor, T.J.; Short, T.H., 1992. Estimation of nonadditive genetic variation for milk production within Holsteins. J. Dairy Sci. 75(Suppl. 1):249.

Lechner, G.; Distl, O.; Kräußlich, H., 1986. Estimation of crossbreeding parameters for milk production traits in the Bavarian 'Gelbvieh' population. Proc. 37th Ann. Meet. of EAAP. 1-4 Sept. 1986. Budapest, Hungary.

Lee, Y.P.; Huang, H.H., 1989. Improvement and utilization of genetic resources in native chicken: reciprocal cross between Taiwan county chicken and single comb White Leghorn. Asian J. Anim. Sci. 2:103-114.

Legates, J.E., 1988. Development in theory and application of animal breeding. In: Korver, S. et al. (eds.) Advances in animal breeding - Proceedings of the World Symposium in honour of Professor R.D. Politiek. Wageningen, The Netherlands. Pudoc. 11-14 Sept. 1988. pp15-26.

Lerner, I.M., 1954. Genetic Homeostasis. Edinburgh. Oliver & Boyd.

Leymaster, K.A.; Swiger, L.A., 1981. Selection for increased leanness of Yorkshire swine. III. inbreeding effects on secondary traits. J. Anim. Sci. 53:620-628.

Long, C.R.; Gregory, K., 1974. Heterosis and breed effects in preweaning traits of Angus, Hereford and reciprocal cross calves. J. Anim. Sci. 39:11-17.

Louca, A.; Robison, O.W., 1967. Components of variance and covariance in purebred and crossbred swine. J. Anim. Sci. 26:267-273.

Lowe, P.G.; Garwood, V.A., 1981. Independent effects of K and k$^+$ alleles and maternal origin on mortality and *performance of crossbred chickens.* Poult. Sci. *60*:1123-1126.

Mason, I.L., 1974. Maintaining crossbred populations of dairy cattle in the tropics. World Anim. Rev. 1974(11):36-43.

Mather, K; Jinks, J.L., 1971. Biometrical genetics. Chapman and Hall Ltd. London.

Mathur, P.K.; Horst, P., 1991. Genotype*environment interactions in laying hens as relationship between breeding values of sire. Proc. of 42nd Ann. meeting of EAAP. 8-12 Sept. 1991. Berlin.

McAllister, A.J., 1986. The role of crossbreeding in breeding programs for intensive milk production in temperate climates. Proc. 3rd World Cong. Genet. Appl. Livest. Prod. 9:47-61.

McDowell, R.E., 1985. Crossbreeding in tropical areas with emphasis on milk, health, and fitness. J. Dairy Sci. 68: 2418-2435.

McLaren, D.G.; Buchanan, D.S.; Hintz, R.L., 1985. Sire ranking based upon purebred versus crossbred progeny performance in swine. J. Anim. Sci. 60:902-912.

Merks, J.W.M., 1988. Genotype*environment interactions in pig breeding programmes. Ph.D thesis. Wageningen Agricultural University, Wageningen, The Netherlands.

Mergl, von R., 1977a. Genetische varianz und genetische korrelationen zwischen leistungen von reinzucht- und kreuzungshennen 1. Mitteilung: genetische parameter für zuchthennen. Arch. Geflügelk. 41:92-97.

Mergl, von R., 1977b. Genetische varianz und genetische korrelationen zwischen leistungen von reinzucht- und kreuzungshennen 2. Mitteilung: genetische parameter für Testkreuzungshennen. Arch. Geflügelk. 41:145-148.

Merritt, E.S.; Gowe, R.S., 1960. Combining ability among breeds and strains on meat type fowl. Can. J. Genet. Cytol. 2:286-294.

Moav, R., 1966. Specialized sire and dam lines. I. Economic evaluation of crossbreds. Anim. Prod. 8:193-202.

Nitter, G., 1978. Breed utilisation for meat production in sheep. Anim. Breed. Abstr. 46:131-143.

Notter, D.R., 1989. EPD's for use across breeds. Proc. Beef Improvement Fed. Annu. Convention, pp63-78.

Notter, D.R., 1989. Commercial potential for across-breed EPDs. Proc. Genetic Prediction Workshop. Kansas City, MO., Oct. 16-18, 1989.

Orozco, F.; Bell, A.E., 1974. Reciprocal recurrent selection compared to within-strain selection for increasing rate of Tribolium under optimal and stress conditions. Genetics 77:143-161.

Orozco, F., 1983. Selection in crossbreeding. In: RDS summer school - "Modern Techniques in Animal Breeding". Dublin, Ireland.

Orozco, F., 1986. Crossbreeding and heterosis. U.S.-Spain joint seminar on sheep breeding. Zaragoza, 10-15 Nov. 1986.

Orozco, F., 1989. Heterosis as overdominance in animal vigour: heterosis according to environment. In: (Ed. INRA) Genotype*environment interaction in poultry production. Jouy-en-Josas (France), May 9-15, 1989. pp127-135.

Orozco, F.; Campo, J.L., 1975. A comparison of purebred and crossbred genetic parameters in layers. World's Poul. Sci. J. 31:149-153.

Paleolog, J.; Maciejowski, J., 1990. Selection for female fecundity in Drosophila test crosses and lines selected in different environments. I. Response to selection. J. Anim. Breed. Genet. 108:355-362.

Peacock, F.M.; Koger, M.; Olson, T.A.; Crockett, J.R., 1981. Additive genetic and heterosis effects in crosses among cattle breeds of british, european and Zebu origin. J. Anim. Sci. 52:1007-1013.

Pedersen, J.; Christensen, L.G., 1986. Heterosis for milk production traits by crossing Red Danish, Finnish Ayrshire and Holstein-Friesian cattle. Proc. 37th Ann Meet. of EAAP. 1986. 1:7.

Pirchner, F.; von Krosigk, C.M., 1973. Genetic parameters of cross- and pure-bred poultry. Br. Poult. Sci. 14:193-202.

Pirchner, F.; Mergl, R., 1977. Overdominance as cause for heterosis in poultry. J. Anim. Breed. Genet. 94:151-158.

Pirchner, F., 1983. Population genetics in animal breeding (2nd Ed.). Plenum press. New York.

Rabsztyn, A., 1990. Genetic parameters of purebred Rhode Island Red and Bared Rock hen strains and their reciprocal crossbreds. Genetica Polonica 31:129-135.

Rabsztyn, A.; Nowak, J., 1978. A comparative study on genetic, environmental and phenotypic variances and on heritability of some performance traits in purebred hen strains and their reciprocal crosses. Genetica Polonica 19:193-199.

Rahnefeld, G.W.; Weiss, G.M.; Fredeen, H.T.; Mckay, R.M.; Lawson, J.E.; Newman, J.A.; Bailey, D.R.C., 1991. Reproductive efficiency of F_1 and reciprocal backcross beef cows under contrasting environments. Can. J. Anim. Sci. 71:969-985.

Rempel, W.E., 1969. Selection for crossbred performance. Proc. 32nd Ann. Report Regional Swine Breed. Lab., Ames IA. Vol.32:107-126.

Ruvuna, F.; McDaniel, B.T.; McDowell, R.E.; Johnson, J.C.; Hollon, B.T.; Brandt, G.W., 1983. Crossbred and purebred dairy cattle in warm and cool seasons. J. Dairy Sci. 66:2408-2417.

Saadeh, H.K.; Craig, J.V.; Smith, L.T.; Wearden, S., 1968. Effectiveness of alternative breeding systems for increasing rate of egg production in chickens. Poultry Sci. 47:1057-1072.

Salah, E.; Galal, E.; Hazel, N.; Sidwell, G.M.; Terrill, C.E., 1969. Correlation between purebred and crossbred half-sibs in sheep. J. Anim. Sci. 30:475-480.

Schulte-Coerne, H.; Boie, D., 1986. Heterosis in crosses between european and american dairy breeds. Proc. 37th Ann. Meet. of EAAP. 1:21.

Sellier, P., 1976. The basis of crossbreeding in pigs: A review. Livest. Prod. Sci. 3:203-226.

Serrano, M.; Orozco, F., 1992. A comparison of three selection systems for crossbreeding. J. Anim. Breed. Genet. 109:168-179.

Sharma, B.S.; Pirchner, F., 1991. Heterosis in Friesian*Sahiwal crosses. J. Anim. Breed. Genet. 108:241-252.

Sheridan, A.K., 1980. A new explanation for egg production heterosis in crosses between White Leghorns and Australorps. Brit. Poult. Sci. 21:85-88.

Sheridan, A.K., 1981. Crossbreeding and heterosis. Anim. Breed. Abstr. 49:131-144.

Sheridan, A.K., 1990. Chapter 36. Genotype*environment interaction. In: Crawford R.D (ed.) Poultry Breeding and Genetics. Elsevier, Amsterdam, The Netherlands. pp897-912.

Sheridan, A.K.; Randall, M.C., 1977. Heterosis for egg production in White Leghorn-Australorp crosses. Br. Poult. Sci. 18:69-77.

Short, T.H.; Lawlor, T.J., 1992. Inbreeding in U.S. Holsteins and its effect on yield and type traits. J. Dairy Sci. 75(Suppl. 1):154.

Singh, B.P.; Rempel, W.E.; Reimer, D.; Hanke, H.E.; Miller, K.P., 1967. Evaluation of breeds of sheep on the basis of crossbred lamb performance. J. Anim. Sci. 26:261-266.

Simianer, H., 1991. Test for Genotype*environment interaction expressed as a genetic correlation. Proc. 42nd Ann. Meeting of EAAP. 8-12 Sept. 1991, Berlin, Germany.

Smith, C., 1964. The use of specialised sire and dam lines in selection for meat production. Anim. Prod. 6:337-344.

Sorensen, P., 1989. Interaction between genotype and management factors in broilers. In: Genotype*environment Interaction in Poultry Production (Ed. by INRA). Jouy-en-Josas, France. pp67-81.

Standal, N., 1968. Studies on breeding and selection schemes in pigs. I. Selection on performance of purebred versus crossbred progeny. Acta Agri. Scand. 18:222-232.

Stanislaw, C.M.; Omtvedt, I.T.; Willham, R.L.; Whatley, J.A. Jr., 1967. A study of some genetic parameters in purebred and crossbred populations of swine. J. Anim. Sci. 26:16-20.

Swan, A.A., 1992. Multibreed evaluation procedures. Ph.D Thesis, University of New England, Australia.

Swan, A.A.; Kinghorn, B.P., 1992. Evaluation and exploitation of crossbreeding in dairy cattle. J. Dairy Sci. 75:624-639.

Taran, M.; Gabriel, E.; Moses, E.; Soller, M., 1971. Performance of purebred and crossbred progeny of White Leghorn and New Hampshire sires. Brit. Poult. Sci. 13:331-339.

Tempelman, R.J.; Burside, E.B., 1990a. Additive and nonadditive genetic variation for production traits in canadian Holsteins. J. Dairy Sci. 73:2206-2213.

Tempelman, R.J.; Burside, E.B., 1990b. Additive and nonadditive genetic variation for conformation traits in canadian Holsteins. J. Dairy Sci. 73:2214-2220.

Tempelman, R.J.; Burside, E.B., 1991. Additive and dominance genetic variation for dairy production traits under an animal model. J. Anim. Breed. Genet. 108:330.

Terrill, C.E., 1974. Review and application of research on crossbreeding of sheep in North America. Proc. 1st World Cong. Genet. Appl. Livest. Prod. 1:765-777.

Touchberry, R.W., 1992. Crossbreeding effects in dairy cattle: the Illinois experiment, 1949 to 1969. J. Dairy Sci. 75:640-667.

Turton, J.D., 1981. Crossbreeding of dairy cattle - a selective review. Anim. Breed. Abstr. 49:293-300.

Van der Steen, H.A.M.; Wei, M., 1991. Reciprocal recurrent versus pure line selection. British Poultry Breeders' Round-Table. Sept. 17, 1991. Edinburgh

Van der Werf, J.H.J.; de Boer, W., 1989a. Influence of non-additive effects on estimation of genetic parameters in dairy cattle. J. Dairy Sci. 72:2606-2614.

Van der Werf, J.H.J.; de Boer, W., 1989b. Estimation of genetic parameters in a crossbred population of black and white dairy cattle. J. Dairy Sci. 72:2615-2623.

VanRaden, P.M., 1989. Estimates of nonadditive genetic variation for milk and fat yields of Holsteins. J. Dairy Sci. 72(Suppl. 1):59.

Webb, A.J., 1989. Animal breeding practice. In: (Ed. by Hill, W.G. and Mackey, T.F.L.) Evolution and Animal Breeding. C.A.B. International, U.K. pp195-202.

Wei, M.; Van der Steen, H.A.M., 1991. Comparison of reciprocal recurrent selection with pure-line selection systems in animal breeding (A review). Anim. Breed. Abstr. 59:281-298

Wei, M.; Van der Steen, H.A.M.; Van der Werf, J.H.J.; Brascamp, E.W., 1991a. Relationship between purebred and crossbred parameters. I. Variances and covariances under the one-locus model. J. Anim. Breed. Genet. 108:253-261.

Wei, M.; Van der Werf, J.H.J., 1990. Selection methods using purebred and crossbred performance. Proc. 4th World Congr. Appl. Livest. Prod., Edinburgh, Vol.XIII, pp.289-292.

Wei, M.; Van der Werf, J.H.J., 1992a. Animal model estimation of additive and dominance variances in egg production traits of poultry. Accepted for publication in J. Anim. Sci.

Wei, M.; Van der Werf, J.H.J., 1992b. Maximizing genetic response in crossbreds using both purebred and crossbred information. (in preparation).

Wei, M.; Van der Werf, J.H.J.; Brascamp, E.W., 1991b. Relationship between purebred and crossbred parameters. II. Genetic correlation between purebred and crossbred performance under the model with two loci. J. Anim. Breed. Genet. 108:262-269

Wiener, G.; Hayter, S., 1974. Body size and conformation in sheep from birth to maturity as affected by breed, crossbreeding, maternal and other factors. Anim. Prod. 19:47-65.

Wiener, G.; Hayter, S., 1975. Maternal performance in sheep as affected by breed, crossbreeding and other factors. Anim. Prod. 20:19-30.

Wiener, G.; Lee, G.J.; Woolliams, J.A., 1992. Effects of rapid inbreeding and of crossing of inbred lines on conception rate, prolificacy and ewe survival in sheep. Anim. Prod. 55:115-121.

Willham, R.L.; Pollak, E., 1985. Theory of heterosis. J. Dairy Sci. 68:2411-2417.

Wright, S., 1977. Evolution and the genetics of populations. Volume 3. Experimental results and evolutionary deductions. The University of Chicago Press. Chicago.

Young, L.D.; Omtvedt, I.T.; Whatley, Jr. J.A.; Johnson, R.K., 1983. Reciprocal recurrent selection for 21-day litter weight of crossbred gilts. I. selection applied and genetic change in reproduction of crossbred gilts. J. Anim. Sci. 57:1418-1430.

Young, L.D.; Omtvedt, I.T.; Whatley, Jr. J.A.; Johnson, R.K., 1983. Reciprocal recurrent selection for 21-day litter weight of crossbred gilts. II. reproductive performance of purebred females producing purebred and two-way cross litters and performance of purebred and crossbred pigs. J. Anim. Sci. 57:1431-1439.

Appendix

A Linear Mixed Model for Combined Crossbred and Purebred Selection

M. Wei and J.H.J. van der Werf

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

A Linear Mixed Model for Combined Crossbred and Purebred Selection

M. Wei and J.H.J. van der Werf

Department of Animal Breeding, Wageningen Agricultural University,
P.O.Box 338, 6700 AH Wageningen, The Netherlands

INTRODUCTION

The combined crossbred and purebred selection method has been presented using a selection index method (Wei and van der Werf, 1992). It is proved to be optimal method to obtain genetic response in crossbreds. However, optimum efficiency of selection index depends on the assumption of unbiased correction of fixed effects or of balanced data. In animal breeding practice, these conditions are usually not fulfilled. Mixed model methodology, generally applied in animal breeding for genetic evaluations, corrects for fixed effects and treatment of unbalanced data set, and therefore, should also be used in animal crossbreeding schemes.

In this appendix, a multiple-trait mixed model is presented for CCPS to estimate simultaneously purebreeding and crossbreeding values of purebred animals within a line of a two-way crossing system.

MIXED MODEL FOR CCPS

A multiple-trait approach using mixed model methodology is applied to use both purebred and crossbred information. A mixed model expressed in matrix notation is described as follows,

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 & 0 \\ 0 & \mathbf{X}_2 & 0 \\ 0 & 0 & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{Z}_2 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{Z}_3 \end{bmatrix} \begin{bmatrix} \mathbf{g}_{11} \\ \mathbf{g}_{13} \\ \mathbf{g}_{22} \\ \mathbf{g}_{23} \\ \mathbf{g}_{33} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix} \qquad [1]$$

in simpler matrix notation written as: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z}^*\mathbf{g} + \mathbf{r}$

where $\mathbf{y}_i$ is the vector of observations for pure line animals (i = 1, 2 for line 1 and 2) and crossbred animals (i = 3); $\mathbf{b}_i$ is the vector of fixed effects for population i; $\mathbf{g}_{ij}$ is the vector of random animal effects (breeding values), i.e., $\mathbf{g}_{ii}$ refers to the breeding value of animals in population i, and $\mathbf{g}_{i3}$ is the breeding value of animals in population i for the crossbred performance (i = 1 or 2); $\mathbf{e}_i$ is the error term in population i; $\mathbf{X}$ is the incidence matrices relating the observations to the fixed effects. $\mathbf{Z}^*$ is a design matrix that links observation to breeding values. Columns in $\mathbf{Z}^*$ are zero for base animals without records (parents of the animals with records), and for columns referring to the breeding values of purebreds for crossbred performance ($\mathbf{g}_{13}$ and $\mathbf{g}_{23}$). These genetic effects ($\mathbf{g}_{13}$ and $\mathbf{g}_{23}$) would be estimated using crossbred information ($\mathbf{y}_3$) through the genetic correlation (r_{pc}) between purebred and crossbred performance and through their genetic relation with $\mathbf{g}_{33}$ values.

The values of $\mathbf{g}_{33}$ are not of interest because the crossbred animals are not used for breeding. Alternatively, the model can be reduced by writing $\mathbf{y}_3$ as a function of $\mathbf{g}_{13}$ and $\mathbf{g}_{23}$. Using this so-called reduced animal model (Quaas and Pollak, 1980), the equation [1] becomes,

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 & 0 \\ 0 & \mathbf{X}_2 & 0 \\ 0 & 0 & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{Z}_2 & 0 \\ 0 & \mathbf{Z}_{13} & 0 & \mathbf{Z}_{23} \end{bmatrix} \begin{bmatrix} \mathbf{g}_{11} \\ \mathbf{g}_{13} \\ \mathbf{g}_{22} \\ \mathbf{g}_{23} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \boldsymbol{\epsilon}_3 \end{bmatrix} \qquad [2]$$

in simpler notation equal to: $\mathbf{Y} = \mathbf{Xb} + \mathbf{Zg} + \mathbf{e}$

where $\mathbf{Z}_{13}$ and $\mathbf{Z}_{23}$ are the incidence matrices which relate the crossbred animal record to the $\mathbf{g}_{13}$ and $\mathbf{g}_{23}$. The non-zero elements of design matrices $\mathbf{Z}_{13}$ and $\mathbf{Z}_{23}$ are 0.5 instead of 1 because only half of the breeding value is transmitted from parents to progeny. ϵ_3 is the residual effect under the model,

$$y_3 = s_1 + d_2 + \epsilon_3 \qquad [3]$$

where y_3 is the observation of crossbred animal; s_1 is the random effect of sires from line 1; d_2 is the random effect of dams from line 2; ϵ_3 is the residual effects or within full-sib family effect which contains half of the genetic variance (Mendel sampling effects), besides the environmental error. The variance of crossbred observations in linear model [3] is expressed as follows,

$$\sigma^2_{y3} = \sigma^2_{s1} + \sigma^2_{d2} + \sigma^2_{\epsilon 3} = (1/4)\sigma^2_{33a} + (1/4)\sigma^2_{33b} + \sigma^2_{\epsilon 3} \qquad [4]$$

where σ^2_{33a} ($= \sigma^2_{s1}$) and σ^2_{33b} ($= \sigma^2_{d2}$) are the sire and dam variances in the crossbreds under the model [3]; $\sigma^2_{\epsilon 3}$ is the residual variance.

Explaining a record by genetic effects of the parents, the residual variance for that record is no longer assumed to be σ^2_{e3}, rather $\sigma^2_{\epsilon 3} = \sigma^2_{y3} - \sigma^2_{33a} - \sigma^2_{33b}$.

From equation [2], we have three kinds of models, one for purebred of line 1 [5.1], one for purebreds of line 2 [5.2] and one for crossbreds [5.3]

$$(1) \quad \mathbf{y}_1 = \mathbf{X}_1\mathbf{b}_1 + \mathbf{Z}_1\mathbf{g}_{11} + \mathbf{e}_1 \qquad [5.1]$$

$$(2) \quad \mathbf{y}_2 = \mathbf{X}_2\mathbf{b}_2 + \mathbf{Z}_2\mathbf{g}_{22} + \mathbf{e}_2 \qquad [5.2]$$

$$(3) \quad \mathbf{y}_3 = \mathbf{X}_3\mathbf{b}_3 + \mathbf{Z}_{13}\mathbf{g}_{13} + \mathbf{Z}_{23}\mathbf{g}_{23} + \epsilon_3 \qquad [5.3]$$

The variance-covariance matrix of $\mathbf{y} = (\mathbf{y}_1\ \mathbf{y}_2\ \mathbf{y}_3)'$ is,

$$\text{Var}(\mathbf{y}) = \text{Var}(\mathbf{Zg} + \mathbf{r}) = \mathbf{Z}\text{Var}(\mathbf{g})\mathbf{Z}' + \text{Var}(\mathbf{r}) = \mathbf{ZGZ}' + \mathbf{R}$$

where $\mathbf{r} = (\mathbf{e}_1\ \mathbf{e}_2\ \epsilon_3)'$; $\mathbf{Z}$ is the incidence matrix of the reduced animal model; and the covariance between breeding value and residual effects is assumed to be zero.

The variance of residual effects is as

$$\mathbf{R} = var(\mathbf{r}) = var\begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \epsilon_3 \end{bmatrix} = \begin{bmatrix} \sigma^2_{e1}\mathbf{I} & 0 & 0 \\ 0 & \sigma^2_{e2}\mathbf{I} & 0 \\ 0 & 0 & \sigma^2_{\epsilon 3}\mathbf{I} \end{bmatrix} \qquad [6]$$

where $\mathbf{I}$ is identity matrix; $\sigma^2_{\epsilon 3}$ is the residual variance under model [3].

The variance of breeding values is as

$$\mathbf{G} = var\begin{bmatrix} \mathbf{g}_{11} \\ \mathbf{g}_{13} \\ \mathbf{g}_{22} \\ \mathbf{g}_{23} \end{bmatrix} = \begin{bmatrix} \sigma^2_1\mathbf{A}_{11} & \sigma_{13}\mathbf{A}_{11} & 0 & 0 \\ \sigma_{31}\mathbf{A}_{11} & \sigma^2_{3a}\mathbf{A}_{11} & 0 & 0 \\ 0 & 0 & \sigma^2_2\mathbf{A}_{22} & \sigma_{23}\mathbf{A}_{22} \\ 0 & 0 & \sigma_{32}\mathbf{A}_{22} & \sigma^2_{3b}\mathbf{A}_{22} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_{01}\otimes\mathbf{A}_{11} & 0 \\ 0 & \mathbf{G}_{02}\otimes\mathbf{A}_{22} \end{bmatrix} \qquad [7]$$

where $\mathbf{A}_{ii}$ is the animal relationship matrix in population i (i = 1 or 2); $\otimes$ refers to a direct product; $\mathbf{G}_{01}$ and $\mathbf{G}_{02}$ matrices are as follows,

$$\mathbf{G}_{01} = \begin{bmatrix} \sigma_1^2 & \sigma_{13} \\ \sigma_{31} & \sigma_{3a}^2 \end{bmatrix}; \quad \textit{and} \quad \mathbf{G}_{02} = \begin{bmatrix} \sigma_2^2 & \sigma_{23} \\ \sigma_{32} & \sigma_{3b}^2 \end{bmatrix}$$

An important consideration is that genetic variances and covariances related to crossbreds can not be simply derived from the genetic parameters of parental lines when dominance is involved (for details see Wei et al., 1991). There are three categories of variance and covariance included in the equation [2]. First, the variances among the breeding values of purebreds within line 1 and 2, which is usually known, i.e., σ_i^2 refers the genetic variance within line i for i = 1 or 2. The σ_i^2 is simply estimated by the four times sire variance under a sire-dam model or by the additive variance under an animal model in line i. Second, the variances among the crossbred breeding values of purebreds (or purebred breeding value for crossbred) in line i, i.e., σ_{3a}^2 and σ_{3b}^2 refer to the genetic variance among the crossbred breeding values of purebred animals (or purebred breeding value for crossbred) in line 1 and 2, respectively. σ_{3a}^2 is calculated by four times sire variance in the crossbred population with model [3], and σ_{3b}^2 by four times dam variance in model [3]. Notice that the covariance structure of crossbreeding values is assumed linear in the genetic relationship structure. This is justified if traits are regulated by many genes each having a small effect and gene frequency change due to selection is ignorable, giving this two trait approach of crossbreeding a theoretical justification. Third, the genetic covariance between purebred and crossbred breeding values is estimated by four times sire covariance between purebred and crossbreds (σ_{3i}). $\sigma_{3i} = \sigma_{i3} = r_{pc}\sigma_{3a}\sigma_{3b}$ (i = 1 and 2), where r_{pc} is the genetic correlation between purebred and crossbred performance. It should be noted that, usually, σ_{3a} is not equal to σ_{3b}, σ_{i3} or one quarter of σ_i^2.

The mixed model equations (MME) for joint evaluation of purebreeding and crossbreeding values are presented in the equation [8], where $\mathbf{r}^{ii}$ is $1/\sigma^2_{e1}$, $1/\sigma^2_{e2}$ or $1/\sigma^2_{e3}$ for i = 1 ,2 and 3; $\mathbf{A}^{ii}$ is the inverse of $\mathbf{A}_{ii}$; and $\mathbf{g}^{ij}$ is defined as follows,

$$\mathbf{G}_{01}^{-1} = \begin{bmatrix} \mathbf{g}^{11} & \mathbf{g}^{13} \\ \mathbf{g}^{31} & \mathbf{g}^{33a} \end{bmatrix}; \quad \textit{and} \quad \mathbf{G}_{02}^{-1} = \begin{bmatrix} \mathbf{g}^{22} & \mathbf{g}^{23} \\ \mathbf{g}^{32} & \mathbf{g}^{33b} \end{bmatrix}$$

$$\begin{bmatrix} \mathbf{X}_1'\mathbf{r}^{11}\mathbf{X}_1 & 0 & 0 & \mathbf{X}_1'\mathbf{r}^{11}\mathbf{Z}_1 & 0 & 0 & 0 \\ & \mathbf{X}_2'\mathbf{r}^{22}\mathbf{X}_2 & 0 & 0 & 0 & \mathbf{X}_2'\mathbf{r}^{22}\mathbf{Z}_2 & 0 \\ & & \mathbf{X}_3'\mathbf{r}^{33}\mathbf{X}_3 & 0 & \mathbf{X}_3'\mathbf{r}^{33}\mathbf{Z}_{13} & 0 & \mathbf{X}_3'\mathbf{r}^{33}\mathbf{Z}_{23} \\ & & & \mathbf{Z}_1'\mathbf{r}^{11}\mathbf{Z}_1 + \mathbf{g}^{11}\mathbf{A}^{11} & \mathbf{g}^{13}\mathbf{A}^{11} & 0 & 0 \\ & & & & \mathbf{Z}_{13}'\mathbf{r}^{33}\mathbf{Z}_{13} + \mathbf{g}^{33a}\mathbf{A}^{11} & 0 & \mathbf{Z}_{13}'\mathbf{r}^{33}\mathbf{Z}_{23} \\ & & & & & \mathbf{Z}_2'\mathbf{r}^{22}\mathbf{Z}_2 + \mathbf{g}^{22}\mathbf{A}^{22} & \mathbf{g}^{23}\mathbf{A}^{22} \\ & & & & & & \mathbf{Z}_{23}'\mathbf{r}^{33}\mathbf{Z}_{23} + \mathbf{g}^{33b}\mathbf{A}^{22} \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \\ \mathbf{g}_{11} \\ \mathbf{g}_{13} \\ \mathbf{g}_{22} \\ \mathbf{g}_{23} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1'\mathbf{r}^{11}\mathbf{y}_1 \\ \mathbf{X}_2'\mathbf{r}^{22}\mathbf{y}_2 \\ \mathbf{X}_3'\mathbf{r}^{33}\mathbf{y}_3 \\ \mathbf{Z}_1'\mathbf{r}^{11}\mathbf{y}_1 \\ \mathbf{Z}_{13}'\mathbf{r}^{33}\mathbf{y}_3 \\ \mathbf{Z}_2'\mathbf{r}^{22}\mathbf{y}_2 \\ \mathbf{Z}_{23}'\mathbf{r}^{33}\mathbf{y}_3 6 \end{bmatrix} \qquad [8]$$

REFERENCES

Quaas, R.L.; Pollak, E.J., 1980. Mixed model methodology for farm and ranch beef cattle testing programs. J. Anim. Sci. 51:1277-1287.

Wei, M.; Van der Werf, J.H.J., 1992. Maximizing genetic response in crossbreds using both purebred and crossbred information. Submitted to Animal Production.

Wei, M.; Van der Steen, H.A.M.; Van der Werf, J.H.J.; Brascamp, E.W., 1991. Relationship between purebred and crossbred parameters. I. Variances and covariances under the one-locus model. J. Anim. Breed. Genet. 108-261.

Summary

Ming Wei

Department of Animal Breeding, Wageningen Agricultural University
P.O.Box 338, 6700 AH Wageningen, The Netherlands

Summary

Crossbreeding has been extensively used in animal breeding to exploit complementarity of traits from sire and dam lines and heterosis. The genetic improvement under such a system is mostly based on the selection within lines (i.e., pure line selection). It is assumed that the improvement of breeding values within lines is paralleled with those for crossbred performance. However, this assumption is not generally true due to the fact that the genetic correlation between purebred and crossbred performance is usually smaller than one. The question arises which methods are optimal for genetic response in crossbreds. It was stressed in the review on comparison between pure line selection and reciprocal recurrent selection methods (Chapter 2) that crossbred and purebred information should be combined in selection to maximize crossbred response.

To organize breeding programmes using both crossbred and purebred information, relevant genetic parameters on crossbreds should be known. In Chapter 3, the study on one-locus model showed that in case of dominance the genetic parameters related to crossbreds are generally not a function of parameters in parental populations. Crossbred heritability (h_c^2) was defined as four times the sire component of variance in crossbreds. It was shown that h_c^2 is generally different from purebred heritability (h^2). The sire component of covariance between purebreds and crossbreds generally is not equal to one quarter of the additive genetic variance in the sire line. Therefore, these genetic parameters related to crossbreds have to be estimated specifically in crossbreeding schemes.

In Chapter 4, the model with two loci was used to study the genetic correlation between purebred and crossbred performance (r_{pc}). The r_{pc} is unity only when there is no dominance or equal gene frequencies in parental populations, and decreases with increasing dominance and with increasing gene frequency difference between parental populations. It is proven that r_{pc} can be lower than one even when partial dominance is involved. On the quantitative level, it is generally impossible to distinguish whether a high r_{pc} is caused by the small gene frequency differences between parental lines or small dominance effects. This indicates that crossbred selection may be necessary even when r_{pc} is high. The change of r_{pc} by change of the gene frequency due to selection was investigated.

In Chapter 5, a linear mixed model with restricted maximum likelihood method was used to estimate dominance variance for egg production traits within three White Leghorn lines. The ratio of dominance variance to phenotypic variance was found to be high for egg number (10 to 20%) and relatively low for egg weight and egg specific gravity (1 to 13%). Three statistical models (i.e., sire-dam model, additive animal model and dominance animal model) were compared in estimating heritability (h^2). A sire-dam model has two types of biases in the estimation of h^2 caused by ignoring dominance effects and genetic animal relationships other than parents-progeny. An additive animal model overestimated h^2 because

it ignored dominance effects. An animal model accounting for additive and dominance effects and REML should be used in analyzing laying hen data for unbiased h^2. Such a model also should be used for breeding value estimation.

A combined crossbred and purebred selection method (CCPS) was proposed to maximize genetic response in crossbreds (Chapter 6). A CCPS index was established and compared with pure line selection (PLS) and crossbred selection (CS) methods. Carrying out a CCPS scheme will always bring more genetic progress than either PLS or CS schemes. The robustness of CCPS against inappropriate assumptions on r_{pc} and h_c^2 was investigated. An inappropriate value of h_c^2 has less influence on the efficiency of CCPS than r_{pc} especially when the true h_c^2 is approximately equal to or larger than h^2. Inappropriately assumed values of r_{pc} reduces the CCPS efficiency considerably, but the CCPS always obtains larger genetic response than PLS if true r_{pc} is positive.

In Chapter 7, a thorough discussion was given on the application of CCPS methods for practical crossbreeding systems. The breeding goal in a crossbreeding system should be defined as the improvement for the entire breeding system, and the purebred breeding value should sometimes also be given some weight, especially for the species with low reproductivity. An entire genetic improvement under a two-way crossing system can be achieved by optimally weighting purebreeding and crossbreeding values. The breeding goal in a three-way and four-way crossbreeding systems and relevant problems were also discussed. A long term CCPS was discussed on comparison with PLS and CS, which depends greatly on the change of r_{pc} due to selection. This correlation will in most cases increase after pure line selection. With overdominance, it may decrease after crossbred selection. Genotype-environment interaction due to nucleus purebreds and commercial crossbreds being in different environments is usually confounded with purebred and crossbred performance. The strategy suggested is that the genetic parameters should be estimated in the environment of the commercial animals and used in the selection.

In the appendix, a mixed model was presented for the CCPS method. It is a two trait linear mixed model that can be used in practical crossbreeding systems to obtain BLUP crossbred and purebred breeding values through weighing optimally both purebred and crossbred information.

General Conclusions:

1. The genetic parameters related to crossbreds generally are not linear functions of genetic parameters in the parental populations.
2. The genetic correlation between crossbred and purebred performance is equal to unity in case of no dominance or equal gene frequencies in parental populations. It decreases with increasing dominance or with increasing gene frequency difference between parental populations.
3. Dominance variance is a significant source of variance for egg production traits. The animal model accounting for dominance effect and all animal relationships should be used for an unbiased estimation of heritability and breeding values.
4. The combined crossbred and purebred selection method (CCPS) is optimal to obtain genetic response in crossbred performance, therefore is always better than pure line selection and crossbred selection, and in most cases even with incorrect crossbreeding parameters. Therefore, it should be applied to animal breeding practice, especially poultry and pig breeding.

Samenvatting

Ming Wei

Vakgroep Veefokkerij, Landbouwuniversiteit Wageningen

Samenvatting

Kruising wordt in de veefokkerij veelvuldig toegepast voor de benutting van combinaties van kenmerken in vader- en moederlijnen en van heterosis. De genetische verbetering in een kruisingsprogramma is meestal het resultaat van selectie van dieren binnen lijnen (zuivere lijn selectie). De aanname daarbij is dat de verbetering van fokwaarden van dieren binnen lijnen samenvalt met de verbetering van fokwaarden voor de gekruiste lijn. Deze aanname is echter niet geheel terecht aangezien de genetische correlatie tussen zuivere lijn prestaties en prestaties van kruisingsdieren meestal kleiner is dan 1. De vraag is daarbij wat een optimale methode zou moeten zijn om de genetische respons in de kruising te maximaliseren. In een revieuw (hoofdstuk 2) is een vergelijking gemaakt tussen zuivere lijn selectie en reciproke kruisingsselectie waarbij werd geconcludeerd dat informatie aan zowel kruisingsdieren als aan zuivere lijn dieren optimaal zou moeten worden ingewogen voor het maximaliseren van genetische respons in de kruisingspopulatie.

Relevante genetische kruisingsparameters zijn nodig voor het uitvoeren van selectieprogramma's waarbij zowel zuivere lijn informatie als informatie aan gekruiste dieren wordt benut. In hoofdstuk 3 is met behulp van een één-locus model aangetoond dat in geval van dominantie de kruisingsparameters niet een functie zijn van genetische parameters in de ouderpopulaties. De erfelijkheidsgraad voor kruisingsgeschiktheid (h^2_c) was gedefinieerd als vier maal de vadervariantie in gekruiste nakomelingen. Er is aangetoond dat deze erfelijkheidsgraaad meestal verschilt van die voor de zuivere-lijn (h^2). De vadercomponent van de covariantie tussen kruislingen en zuivere-lijn dieren is meestal niet gelijk aan een kwart van de additief genetische variantie in de vaderlijn. Deze kruisingsparameters zullen daarom specifiek geschat moeten worden binnen een kruisingsprogramma.

In hoofdstuk 4 is de genetische correlatie (r_{pc}) tussen fokwaarden voor gekruiste nakomelingen en zuivere-lijn nakomelingen bestudeerd met behulp van een twee-locus model. De r_{pc} is alleen gelijk aan 1 bij afwezigheid van dominantie of bij gelijke genfrequenties in de ouderlijke populaties. De correlatie neemt af bij toenemende dominantie en bij grotere verschillen tussen genfrequenties in de ouderlijnen. Er is aangetoond dat de r_{pc} ook van 1 kan afwijken in geval van partitiële dominantie. In de praktijk is het moeilijk te achterhalen of een hogere waarde voor r_{pc} wordt veroorzaakt door een kleiner verschil in genfrequenties dan wel door kleine dominantie effecten. Dit betekent dat kruisingsselektie ook nog van belang zou kunnen zijn in het geval van een hoge r_{pc} waarde. Veranderingen van de r_{pc} waarde als gevolg van verandering van genfrequenties zijn in dit hoofdstuk onderzocht.

De dominantie variantie voor eiproduktie binnen 3 White Leghorn lijnen zijn geschat met een lineair mixed model en Restricted Maximum Likelihood (hoofdstuk 5). Dominantie variantie als percentage van de fenotypische variantie was hoog voor het kenmerk eiproduktie (10-20%) en relatief lager voor ei-gewicht en het soortelijke gewicht van eieren (1-13%). Drie

statistisch-genetische modellen, nl. het sire-dam model, het additief diermodel en het dominantie-diermodel werden vergeleken voor het schatten van de erfelijkheidsgraad (h^2). Een sire-dam model heeft twee onzuiverheden, nl. als gevolg van het verwaarlozen van genetische relaties over generaties en van de dominantie effecten. Met een additief model werd de erfelijkheidsgraad overschat door de verwaarlozing van het dominantie-effect. Voor een zuivere schatting van erfelijkheidsgraad en fokwaarden bij de analyse van data aan legkippen zou dan ook een diermodel met zowel additief genetische als met dominantie-effecten moeten worden toegepast .

Een gecombineerde kruislings- en zuivere-lijn selectiemethode (CCPS) is voorgesteld voor het maximaliseren van de genetische respons in de gekruiste dieren. Een CCPS index is in een voorbeeld uitgewerkt en vergeleken met selectie op alleen zuivere-lijn informatie (PLS) dan wel op basis van alleen kruisingsinformatie (CS). Een CCPS selectieschema heeft altijd meer genetische vooruitgang in de kruislingen tot gevolg dan het PLS of het CS schema. De robuustheid van het CCPS schema voor incorrecte parameterwaarden voor r_{pc} en h^2_c is onderzocht. Incorrecte waarden voor h^2_c hebben minder invloed op de efficiency van CCPS dan incorrecte waarden voor r_{pc}, zeker indien de werkelijke waarde voor h^2_c niet veel kleiner is dan de erfelijkheidsgraad in de zuivere lijn (h^2). Incorrecte waarden voor de r_{pc} reduceren de efficiëntie van de CCPS in belangrijke mate, maar de CCPS response is altijd hoger dan de response voor PLS in geval van een positieve r_{pc}.

In hoofdstuk 7 wordt in een uitgebreide discussie ingegaan op de toepassing van CCPS in praktische fokprogramma's. Het fokdoel in een dergelijk programma moet gericht zijn op de verbetering van het gehele fokprogramma, en niet alleen op de verbetering van gekruiste dieren. Dit geldt met name voor diersoorten met een lage reproduktiviteit. Er is een methode voorgesteld om vooruitgang voor het gehele fokprogramma te bewerkstelligen. Selectie moet dan plaatsvinden op een combinatie van zowel de zuivere-lijn fokwaarde als fokwaarde voor kruising. Het fokdoel in drie- en vierweg kruisingssysteem is eveneens bediscussieerd. Een vergelijking van de lange termijn selectie respons van CCPS enerzijds en PLS en CS anderzijds zal vooral afhangen van een verandering in r_{pc}. Deze correlatie zal in de meeste gevallen groter worden na selectie. Het effect van genotype-milieu interactie is meestal nog verstrengeld met de vergelijking van zuiver-lijn dieren en gekruiste dieren. Kruisingsparameters moeten daarom geschat worden op basis van prestaties van gekruiste dieren in hun produktieomgeving. In de appendix is de CCPS methode gepresenteerd in termen van een mixed model. Een 2-kenmerkenmodel kan worden toegepast in praktische fokprogramma's waarbij de fokwaarden worden geschat met behulp van informatie aan zowel zuiver-lijn dieren als aan gekruiste dieren.

Algemene Conclusies

1. De genetische parameters die betrekking hebben op gekruiste dieren zijn in het algemeen niet een lineaire functie van de genetische parameters in de ouderlijnen.
2. De genetische correlatie tussen fokwaarden voor de zuiver lijn en fokwaarden voor gekruiste nakomelingen is gelijk aan 1 bij afwezigheid van dominantie of bij gelijke genfrequenties in de beide ouderpopulaties. De correlatie neemt af bij toenemende dominantie en bij toenemende genfrequentieverschillen tussen de ouderlijnen.
3. De dominantievariantie is een significante bron van variatie voor ei-produktie kenmerken. Het diermodel, dat corrigeert voor dominantie effecten en dat rekening houdt met alle genetische relaties tussen dieren, zou moeten worden toegepast voor een zuivere schatting van de erfelijkheidsgraad en de fokwaarden.
4. De gecombineerde kruislings- en zuivere-lijn selectiemethode (CCPS) is een optimale methode voor het verkrijgen van genetische response in gekruiste nakomelingen. De methode is superieur aan de zuivere-lijn en de kruislings-selectie methode, en in de meeste gevallen zelfs als de kruisingsparameters incorrect zijn. De gecombineerde selectiemethode zou dan ook moeten worden toegepast in kruislings-fokprogramma's

GLOSSARY

1. CCPS (Combined crossbred and purebred selection). The CCPS is the selection method suggested in this thesis. Under this scheme, both purebred and crossbred information in a crossbreeding system are optimally weighted in selection criteria aimed at improving crossbred performance. In this thesis, the CCPS method was formulated in a two-way crossbreeding system and compared with PLS and CS methods.
2. h_c^2 and h_p^2 (Crossbred and purebred heritability). h_p^2 is the commonly-used heritability measured within a population. h_c^2 is defined as the heritability of purebred animals measured on the basis of crossbred progeny, and calculated as four times the sire component of variance in the crossbred population. It quantifies how much genetic variance existing in the sire line influences the crossbreds, and therefore can be used for predicting direct crossbred response to crossbred selection.
3. BV_c and BV_p (Crossbreeding and purebreeding values). Purebreeding value is defined as the breeding value of a purebred animal estimated within the population, which is related to twice the deviation of its purebred progeny. Crossbreeding value is the breeding value of a purebred animal estimated in a crossbreeding system, which is related to twice the deviation of its crossbred progeny.
4. CS (crossbred selection). The selection method using only crossbred information. The breeding goal is to improve crossbred performance.
5. PLS (pure line selection). PLS is the selection method using only purebred information as selection criteria, to improve purebred performance within population.
6. h_{csire}^2 (Sire component in crossbreds). h_{csire}^2 is the sire variance estimated in the crossbred population, which indicates the amount of genetic variance in crossbreds influenced by the sire line.
7. r_{pc} (Genetic correlation between purebred and crossbred performance). The r_{pc} denotes the correlation of true breeding values of purebred animals estimated in purebred and crossbred populations. It is calculated by $Cov_{pc}/(\sigma_{Psire}\sigma_{Csire})$, where Cov_{pc} is the sire covariance between the sire line and its crossbred population, σ_{Psire} and σ_{Csire} are sire components in purebred and crossbred population, respectively.
8. $BV_{2\text{-}way}$. $BV_{2\text{-}way}$ approach is an application of the CCPS method in order to optimize the genetic improvement for an entire two-way crossbreeding system. There, the selection of purebred animals is based on the combined breeding value by optimally weighing crossbreeding and purebreeding values.

组合选择理论 (CCPS)

尉 明

荷兰，瓦格宁根农业大学，动物育种系

(1992年 10月)

博士论文摘要

自50年代以来，纯繁选育配以杂交制种已经作为经典育种方法而广泛应用于动物育种实践. 曾几何时，育种工作者设想选择理论已发展到完美的境地. 这一设想的根据是：杂交制种的应用可获得品种或品系间杂交优势效应以及父母品系间性状互补效应，而品系内选育又能促进杂种遗传进展. 这一美好的设想曾被广泛地接受已致于忽视了一个众所周知的事实：纯种与杂种遗传相关系数一般小于壹，即纯种遗传进展并不完全传递给杂种.

在近年来动物选择理论发展进程中，虽然有人偶尔疑问过现行的两种选择方法 - 纯系选育和杂交育种(比如正反反复选择法)，并且试图提出一种新的选择方法，但是，终因无坚固的理论根据而被淹没.

本研究通过理论模拟第一次提出了改良杂种生产性能的最优选择方法，即在选择中合并利用纯种与杂种信息，以获得最大的杂种选择进展. 通过三年来的研究，本博士论文提出了改良杂种性能的最优方法 - 组合选择法 (CCPS)，并为这一方法建立了完整的，系统的理论 - 组合选择理论.

组合选择理论着重阐述了杂交遗传参数的意义及其应用，组合选择指数以及相应动物模型的建立. 论文的七个章节分别叙述了以下几个重点：

一. 通过理论和试验对纯系选择与杂交选择方法的系统比较，指出：一个杂交生产体系中的育种目标应定义为杂种遗传进展；选择应同时利用杂种和纯种信息(第一,二章).

二. 本文应用单位点遗传模型分析了杂交遗传参数，其研究结果表明杂交遗传参数一般不是其父母代遗传参数的线性函数(第三章).

三. 纯杂种遗传关系数在无基因显性效应或父母系基因频率一致时为壹，而随着这两者的增大而减小(第四章).

四. 为了更准确地估计遗传参数及育种值，本文推出了包含显性效应和所有动物加性血缘关系的混合模型. 该模型消除了因基因显性效应与选择所导致的估计误差(第五章).

五. 组合选择方法从理论上证明了能获得最大杂种遗传进展(第六章). 本文还多方面地讨论组合选择方法在动物育种实践中的应用及其前景，并指出此方法应该且将很快应用于动物育种，特别是家禽和猪育种实践中(第七章).

Curriculum vitae

Ming Wei was born on November 17, 1960 in Chengdu, Sichuan, P.R.China. He fulfilled his primary education in two schools, GaogangLi Primary School in Nanjing (two and half years) and Suwa North First Street Primary School (two years) in Chengdu. He spent one year in Suwa North First Street Primary School and two years in Chengdu Eleventh High School to finish his middle school education. Then, he finished his high school education in Chengdu Cultural Palace High School in two years. In the autumn of 1978, he entered Sichuan Agricultural University (Department of Animal Science) to study animal science. After receiving his Bachelor Degree, he immediately started his graduate study majoring in Poultry Breeding and Genetics under the supervision of Prof. Qiu Xiangpin and Prof. Zhen Fantong and obtained his Master Degree in the Summer of 1985. In the autumn of 1985, he started to work in the Poultry Research Unit, Department of Animal Science, Sichuan Agricultural University, first as an assistant and from 1986 as a lecturer. In September of 1987, he started his Ph.D programme majoring Poultry Genetics and Breeding under the supervision of Prof. X.P. Qiu. In November 1988, he went to Wageningen Agricultural University (Department of Animal Breeding) as a visiting scholar funded by the ministry of education of the Netherlands. From the summer of 1989, he started his Ph.D program in the Department of Animal Breeding, Wageningen Agricultural University, the Netherlands. From September of 1992, he was employed by Department of Animal Breeding, Wageningen Agricultural University, for a teaching work. He is going to do his post-doctoral research with the Centre for Genetic Improvement of Livestock and Department of Animal and Poultry Science at the University of Guelph.