Maximizing genetic gain for the sire line of a crossbreeding scheme utilizing both purebred and crossbred information

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Abstract

A selection index procedure which utilizes both purebred and crossbred information was developed for the sire line of a three-path crossbreeding scheme in pigs, to predict response to best linear unbiased prediction (BLUP) selection with an animal model. Purebred and crossbred performance were treated as correlated traits. The breeding goal was crossbred performance but methods can be applied to other goals. A hierarchical mating structure was used. Sires were mated to purebred dams to generate replacements and to F_1s from the dam line to generate fattening pigs. Generations were discrete, inbreeding was ignored. The selection index included purebred and crossbred phenotypic information of the current generation and estimated breeding values for purebred and crossbred performance of parents and mates of parents from the previous generation. Reduction of genetic variance due to linkage disequilibrium and reduction of selection intensity due to finite population size and due to correlated index values was accounted for. Selection was undertaken until asymptotic responses were reached. The index was used to optimize the number of selected parents per generation and the number of offspring tested per litter, and to make inferences on the value of crossbred information when the breeding goal was crossbred performance. It was optimal to test a maximum number of offspring per litter, mainly due to increased female selection intensities. Maximum response reductions due to linkage disequilibrium and correlated index values were 32% and 29% respectively. Correcting for correlated index values changed ranking of breeding schemes. Benefit of crossbred information was largest when the genetic correlation between purebred and crossbred performance was low. Due to high correlations between index values in that case, the optimum number of selected sires increased considerably when crossbred information was included.

Introduction

In animal breeding, optimization of breeding schemes is an important activity of breeding organizations. This optimization is complicated by several factors, like for example the use of family information, reduction of genetic variance due to linkage disequilibrium (Bulmer, 1971) and correlation between index values of selection candidates. Because of this complexity, stochastic simulation is often used to optimize breeding schemes. However, stochastic simulation is often computationally demanding. In this study, deterministic methods are applied in order to allow for a large number of alternative schemes to be investigated with limited computing time.

Breeding value estimation using best linear unbiased prediction of breeding values (BLUP-EBV) under an animal model is a common procedure for genetic evaluation nowadays (Kennedy *et al.*, 1988). A deterministic method for predicting response to selection on BLUP-EBV under an animal model was presented by Wray and Hill (1989). A multitrait extension of this method was presented by Villanueva *et al.* (1993). The method accounted for reduction of genetic variance due to gametic phase disequilibrium induced by selection (Bulmer, 1971), which is often referred to as the Bulmer effect. Wray and Hill (1989) and Dekkers (1992) found that ranking of breeding schemes was little affected by the Bulmer effect when selection was on BLUP-EBV under an animal model and when generations were discreet. However, as shown by Meuwissen (1991), ranking of breeding schemes can change due to reduction of selection intensity when index values of selection candidates are correlated.

In pig and poultry breeding, information from crossbred animals is becoming available which has increased the interest of utilizing crossbred information in genetic evaluation. To optimize breeding schemes utilizing both purebred and crossbred information, methods to predict response under combined crossbred purebred selection (CCPS) are crucial. In these methods, purebred and crossbred performance should be treated as genetically different traits, because empirical evidence for differences between purebred and crossbred genetic parameters has been found (e.g. Brown and Bell, 1980; van der Werf, 1990; Wei and van der Steen, 1991). Theoretical explanations of this phenomenon based on one and two locus models were given by Wei et al. (1991a and b) and Baumung et al. (1997). Differences between purebred and crossbred traits can also arise from genotype X environment interaction, especially for carcass traits (Merks, 1986). Wei and van der Werf (1994) described a selection index procedure for crossbreeding, which utilizes CCPS information. They showed that this index resulted in higher response than pure line selection (PLS) or reciprocal recurrent selection only. However, their index is not expected to predict response to selection on BLUP-EBV under an animal model accurately, because the index did not include pedigree information and the Bulmer effect was ignored.

The set-up of this paper is three-fold. First, a selection index procedure that predicts response to selection on BLUP-EBV under an animal model, is presented for the sire line of a three-path crossbreeding scheme in pigs. Purebred and crossbred performance were treated as genetically correlated traits. The procedure accounts for reduction of the selection intensity due to finite sample size and due to correlated index values, and also the Bulmer effect is taken into account. Secondly, breeding schemes were optimized for different fixed test capacities in order to make optimum use of the available test capacity. Finally, inferences were made on the effect of utilizing crossbred information on the response and on the lay-out of optimum breeding schemes.

Methods
Breeding scheme
An index was derived for selection in the sire line of a three-path crossbreeding scheme in pigs. A hierarchical mating structure was assumed, generations were discrete and inbreeding was ignored. Sires from the sire line were mated to n_{pd} purebred dams from the sire line to produce n_{po} purebred offspring per dam. Sires were also mated to n_{cd} F_1-dams from the multiplier level of the dam line, to produce n_{co} crossbred fattening pigs per F_1-dam.

Dams produced only one litter. Sires were used simultaneously for the production of pure line replacements and for the production of crossbred fattening pigs. Purebred performance was measured on animals within the sire line, crossbred performance was measured on fattening pigs. Purebred and crossbred information was assumed to be available at the same time. The traits were measured on both sexes and each sire had the same number of offspring tested. Each generation, n_s males and $n_s n_{pd}$ females were selected among the $n_s n_{pd} n_{po}$ purebred selection candidates of the current generation of the sire line, to become sires and dams of the next generation. Selected proportions in males and females were calculated as $p_s = n_s / \frac{1}{2}(n_s n_{pd} n_{po})$ and $p_d = n_s n_{pd} / \frac{1}{2}(n_s n_{pd} n_{po})$. Selection was performed by truncation on a selection index.

Breeding goal
The breeding goal (H) was defined as breeding value for crossbred performance. However, because both purebred and crossbred breeding values were needed as information sources in the selection index, the breeding goal included both purebred and crossbred breeding values and zero economic weight was given to purebred breeding value. Therefore, the breeding goal was:

$$H = \mathbf{a'u}$$

where $\mathbf{a'} = (0\ 1)$, which is a vector of economic weights, and $\mathbf{u}$ is a 2×1 vector containing the breeding value for purebred and crossbred performance. Including both traits in $\mathbf{u}$ also allows for the use of other economic values without having to change the selection index equations.

Selection index
An individual animal model was used with one record per animal. Phenotypic observations consisted of additive genetic, common environmental and individual environmental effects, $X = A + C + E$. Maternal effects were not considered. Phenotypic (co)variances were the sum of additive genetic, common environmental and individual environmental (co)variances. Each generation (t), breeding values were predicted for every purebred individual of the current generation, using the following selection index:

$$I_{(t)} = \mathbf{b'}_{(t)}\mathbf{x}$$

where $\mathbf{b}_{(t)}$ is a vector of weighting factors, and $\mathbf{x}$ is a vector of information sources. When the genetic correlation between purebred and crossbred performance is non-zero, purebred information can contribute to estimation of crossbred breeding values. Therefore, both purebred and crossbred

information sources were included in $I_{(t)}$, although the breeding goal only consisted of crossbred performance. Ten information sources were included in x: (1) individual phenotypic record; (2) purebred full-sib phenotypic mean; (3) purebred half-sib phenotypic mean; (4) crossbred half-sib phenotypic mean; (5) estimated purebred breeding value sire; (6) estimated purebred breeding value dam; (7) average of estimated purebred breeding values of n_{pd} purebred dams mated to the sire; (8) estimated crossbred breeding value sire; (9) estimated crossbred breeding value dam; (10) average of estimated crossbred breeding values of n_{cd} F_1-dams mated to the sire.

Purebred and crossbred estimated breeding values refer to estimated breeding values for purebred and crossbred performance. Estimated breeding values of sires and dams were included in x in order to utilize pedigree information. Estimated breeding values of sires and dams were equal to their index in the previous generation, i.e. when they were still an 'individual'. Therefore, estimated breeding values of parents did not include progeny information, but this information is included in the index for the individual via full-sibs and half-sibs. This index is comparable with index ISD of Wray and Hill (1989). It is assumed to approximate selection on BLUP-EBV under an animal model because pedigree information is included in sire and dam EBV and phenotypic records of paternal half-sibs are corrected for the genetic level of their dams by including information sources 7 and 10.

Each generation, index weights were calculated according to:

$$b_{(t)} = P^{-1}{}_{(t)}G_{(t)}a$$

where $P_{(t)}$ is the 10 × 10 variance-covariance matrix between information sources in x, and $G_{(t)}$ is a 10 × 2 matrix of covariances between information sources in x and breeding values in u. For each generation, $P_{(t)}$ and $G_{(t)}$ are given by:

$G_{(t)} =$

$$\begin{bmatrix} G_0(1,1)_t & G_0(1,2)_t \\ G_1(1,1)_t & G_1(1,2)_t \\ G_2(1,1)_t & G_2(1,2)_t \\ G_3(1,2)_t & G_3(2,2)_t \\ S(1,1)_t/2 & S(1,2)_t/2 \\ D(1,1)_t/2 & D(1,2)_t/2 \\ D(1,1)_t/2n_{pd} & D(1,2)_t/2n_{pd} \\ S(1,2)_t/2 & S(2,2)_t/2 \\ D(1,2)_t/2 & D(2,2)_t/2 \\ 0 & 0 \end{bmatrix}$$

where indices 1 refer to the purebred trait and indices 2 refer to the crossbred trait. Notation follows as closely as possible that of Villanueva et al. (1993). Generally speaking, three types of covariance elements can be distinguished in $P_{(t)}$ and $G_{(t)}$; covariances between phenotypic information sources denoted by $P.(i,j)_t$, covariances involving estimated breeding values of sires and dams denoted by $S(i,j)_t$ and $D(i,j)_t$ and covariances between phenotypic information sources and breeding values of the individual denoted by $G.(i,j)_t$, where i and j can take the value 1 or 2, i.e. refer to the purebred or the crossbred trait. Because sires and dams were assumed to be unrelated, and because F_1-dams were not related to pure-bred animals, $P_{(t)}$ and $G_{(t)}$ contain zeros at the corresponding positions. In $P_{(t)}$, element $G_3(1,2)_t$ is denoted with a G because it is identical to element $G_3(1,2)t$ in $G_{(t)}$. Elements of $P_{(t)}$ and $G_{(t)}$ that do not contain crossbred components are identical to the corresponding elements of $P_{(t)}$ and $G_{(t)}$ derived by Villanueva et al. (1993).

Predicted breeding values for trait j were obtained from the index:

$$I_{j(t)} = b'_{j(t)}x$$

where

$$b_{j(t)} = P^{-1}{}_{(t)}g_{j(t)}$$

where $g_{j(t)}$ is the column of $G_{(t)}$ corresponding to the jth trait.

$P_{(t)} =$

$$\begin{bmatrix} P_0(1,1)_t & P_1(1,1)_t & P_2(1,1)_t & G_3(1,2)_t & S(1,1)_t/2 & D(1,1)_t/2 & D(1,1)_t/2n_{pd} & S(1,2)_t/2 & D(1,2)_t/2 & 0 \\ & P_1(1,1)_t & P_2(1,1)_t & G_3(1,2)_t & S(1,1)_t/2 & D(1,1)_t/2 & D(1,1)_t/2n_{pd} & S(1,2)_t/2 & D(1,2)_t/2 & 0 \\ & & P_2(1,1)_t & G_3(1,2)_t & S(1,1)_t/2 & D(1,1)_t/2n_{pd} & D(1,1)_t/2n_{pd} & S(1,2)_t/2 & D(1,2)_t/2n_{pd} & 0 \\ & & & P_3(2,2)_t & S(1,2)_t/2 & 0 & 0 & S(2,2)_t/2 & 0 & D_{F1}(2,2)_t/2n_{cd} \\ & & & & S(1,1)_t & 0 & 0 & S(1,2)_t & 0 & 0 \\ & & & & & D(1,1)_t & D(1,1)_t/n_{pd} & 0 & D(1,2)_t & 0 \\ & & & & & & D(1,1)_t/n_{pd} & 0 & D(1,2)_t/n_{pd} & 0 \\ & & & & & & & S(2,2)_t & 0 & 0 \\ & & & & & & & & D(2,2)_t & 0 \\ & & & & & & & & & D_{F1}(2,2)_t/n_{cd} \end{bmatrix}$$

Matrix elements

For the calculation of elements of $P_{(t)}$ and $G_{(t)}$, total phenotypic (co)variances between trait i and j ($\text{Cov}(X_i, X_j)_t$) were partitioned into additive genetic (co)variances ($\text{Cov}(A_i, A_j)_t$), common environmental (co)variances ($\text{Cov}(C_i, C_j)$) and individual environmental (co)variances ($\text{Cov}(E_i, E_j)$) between trait i and j. Additive genetic (co)variances between trait i and j were further partitioned into between sire family (co)variances ($\text{Cov}_s(A_i, A_j)_t$), between dam family (co)variances ($\text{Cov}_d(A_i, A_j)_t$) and within family (co)variances ($\text{Cov}_w(A_i, A_j)$) between trait i and j. Elements of $P_{(t)}$ and $G_{(t)}$ were calculated as:

$$G_0(i,j)_t = \text{Cov}(A_i, A_j)_t$$

$$G_1(i,j)_t = \text{Cov}_s(A_i, A_j)_t + \text{Cov}_d(A_i, A_j)_t + \text{Cov}_w(A_i, A_j) / n_{po}$$

$$G_2(i,j)_t = \text{Cov}_s(A_i, A_j)_t + \text{Cov}_d(A_i, A_j)_t / n_{pd} + \text{Cov}_w(A_i, A_j) / n_{po} n_{pd}$$

$$G_3(i,j)_t = \text{Cov}_s(A_i, A_j)_t$$

$$P_0(i,j)_t = \text{Cov}(X_i, X_j)_t$$

$$P_1(i,j)_t = G_1(i,j)_t + \text{Cov}(C_i, C_j)_t + \text{Cov}(E_i, E_j) / n_{po}$$

$$P_2(i,j)_t = G_2(i,j)_t + \text{Cov}(C_i, C_j) / n_{pd} + \text{Cov}(E_i, E_j) / n_{po} n_{pd}$$

$$P_3(2,2)_t = \text{Cov}_s(A_2, A_2)_t + [\tfrac{1}{2}\text{Cov}_{F_1,B}(A_2, A_2)_{eq} + \text{Cov}(C_2, C_2)] / n_{cd}$$
$$+ [(\tfrac{1}{4}\text{Cov}(A_2, A_2)_{t=0} + \tfrac{1}{4}\text{Cov}_{F_1}(A_2, A_2)_{t=0} + \text{Cov}(E_2, E_2)] / (n_{cd} n_{co})$$

$$S(i,j)_t = \text{Cov}(A_i, I_j)_{t-1} - \frac{\text{Cov}(A_i, I)_{t-1}\, \text{Cov}(I_j, I)_{t-1}}{\sigma^2_{I(t-1)}} k_s$$

$$D_{F_1}(2,2) = r^2_{IHeq}\, \text{Cov}_{F_1}(A_2, A_2)_{eq}.$$

Where $\text{Cov}_{F_1,B}(A_2, A_2)_{eq}$ is the between-family component of additive genetic variance for crossbred performance among F_1-dams in equilibrium, $\text{Cov}_{F_1}(A_2, A_2)_{t=0}$ is the total additive genetic variance for crossbred performance among F_1-dams in the base generation, $\text{Cov}_{F_1}(A_2, A_2)_{eq}$ is the total additive genetic variance for crossbred performance among F_1-dams in equilibrium and r^2_{IHeq} is the accuracy of breeding value estimation of F_1-dams in equilibrium. The element $D_{F_1}(2,2)$ represents the variance in indexes of F_1-dams, and was calculated as the squared accuracy times the additive genetic variance in equilibrium. It was assumed that F_1-dams had equilibrium genetic parameters. Therefore, all covariance components concerning F_1-dams were constant. If it is assumed that there is no breeding value estimation on F_1-dams, the last row and column of $P_{(t)}$ are removed, and $P_{(t)}$ becomes a 9 $\times$ 9 matrix and $G_{(t)}$ becomes a 9 $\times$ 2 matrix.

Every generation t, the total phenotypic (co)variance was calculated as the sum of additive genetic, common environmental and individual environmental (co)variance. The total additive genetic (co)variance was calculated as the sum of sire, dam and within-family component of additive genetic (co)variance. The common environmental and individual environmental (co)variances were assumed to be constant over time. $\text{Cov}(C_1, C_1)$ and $\text{Cov}(C_2, C_2)$ were calculated as: $c^2_1 \sigma^2_{p1(t=0)}$ and $c^2_2 \sigma^2_{p2(t=0)}$ respectively, where c^2_1 and c^2_2 are the common environmental variance between full-sibs as a proportion of the total phenotypic variance for purebred and crossbred performance in the base generation respectively, and $\sigma^2_{p(t=0)}$ is the total phenotypic variance in the base generation. Because inbreeding was ignored, the within-family component of additive genetic variance ($\text{Cov}_w(A_i, A_j)$) was equal to $\tfrac{1}{2}\text{Cov}(A_i, A_j)_{t=0}$, and was constant over time. The between sire family component of additive genetic variance was calculated every generation as:

$$\text{Cov}_s(A_i, A_j)_t = \tfrac{1}{4}\, \text{Cov}(A_i, A_j)_{t-1} - \frac{\text{Cov}(A_i, I)_{t-1}\, \text{Cov}(A_j, I)_{t-1}}{\sigma^2_{I(t-1)}} k_s$$

where:

$$\text{Cov}(A_i, I)_t = \mathbf{b}'_{(t)} \mathbf{g}_{i(t)}$$

$$\sigma^2_{I(t-1)} = \mathbf{b}'_{(t)} \mathbf{P}_{(t)} \mathbf{b}_{(t)}$$

where $\sigma^2_{I(t-1)}$ is the variance in the index, $k_s = i_s(i_s - x_s)$, and i_s is the selection intensity and x_s is the corresponding standardized truncation point for sires. $\text{Cov}_d(A_i, A_j)_t$ was calculated in the same way as $\text{Cov}_s(A_i, A_j)_t$, but k_d was used instead of k_s. $\text{Cov}(A_i, I_j)_t$ and $\text{Cov}(I_j, I)_t$ were calculated as:

$$\text{Cov}(A_i, I_j)_t = \mathbf{b}'_{j(t)} \mathbf{g}_{i(t)}$$

$$\text{Cov}(I_j, I)_t = \mathbf{b}'_{j(t)} \mathbf{G}_{(t)} \mathbf{a}.$$

Elements $D(i,j)_t$ were calculated similar to $S(i,j)_t$, but k_d was used instead of k_s.

The sire line heritability for crossbred performance was defined as:

$$h^2_c = \text{Cov}(A_2, A_2)_{t=0} / \sigma^2_{p2(t=0)}$$

where $\sigma^2_{p2(t=0)}$ is the phenotypic variance among crossbreds in the base population. The genetic covariance between purebred and crossbred performance, $\text{Cov}(A_1, A_2)_{t=0}$, was defined as four times the covariance between purebred and crossbred half-sibs. The purebred-crossbred genetic correlation was defined as:

$$r_{pc} = \frac{\text{Cov}(A_1, A_2)_{t=0}}{\sqrt{\text{Cov}(A_1, A_1)_{t=0}\, \text{Cov}(A_2, A_2)_{t=0}}}$$

Selection intensity

Approximate selection intensities corrected for correlated index values and for finite sample size were calculated using the method suggested by Meuwissen (1991):

$$i_r(t_{fs}, t_{hs}) = i_r(0,0)\{1 - t_{av}(t_{fs}, t_{hs})\}^{u(t_{fs}, t_{hs})}$$

where $i_r(0,0)$ is the selection intensity for uncorrelated index values corrected for finite sample size, t_{av} is the correlation between index values averaged over all selection candidates, t_{fs} is the correlation between index values of full-sibs, t_{hs} is the correlation between index values of half-sibs and $u(t_{fs}, t_{hs})$ is a weighting factor. This method is a three-dimensional application of Rawlings' (1976) method, and performs well for nested full-half-sib family structures (Meuwissen, 1991; Phocas and Colleau, 1995). The approximation of Burrows (1972) was used to calculate selection intensities for uncorrelated index values corrected for finite sample size ($i_r(0,0)$). The correlation between index values averaged over all selection candidates was calculated as (Meuwissen, 1991):

$$t_{av} = \frac{(n_{po} - 1)t_{fs} + n_{po}(n_{pd} - 1)t_{hs}}{n_s n_{pd} n_{po} - 1}.$$

Correlations between selection index values of relatives, i.e. between full-sibs (t_{fs}) and between half-sibs (t_{hs}), were calculated as (de Boer and van Arendonk, 1991):

$$t_{rel} = b'_{(t)} R_{(t)} b_{(t)} / b'_{(t)} P_{(t)} b_{(t)}$$

where $R_{(t)}$ is a 10 × 10 variance-covariance matrix between information sources of two relatives in generation t.

Selection response

Because the breeding goal only consisted of crossbred performance, response in crossbred performance was identical to response in aggregate breeding goal. The expected response was calculated as:

$$R_{(t)} = i_{(t-1)} \sigma_{I(t-1)}$$

where $i_{(t)}$ is $(i_{s(t)} + i_{d(t)})/2$. $i_{s(t)}$ and $i_{d(t)}$ are the selection intensities for sires and dams in generation t, corrected for finite sample size and correlated index values. Because the same index was used for males and females, $\sigma_{I(t)}$ was the same for both sexes. Throughout the results and discussion - section, response refers to genetic response for crossbred performance.

Base generation animals had no family information and were selected on their own phenotype only. Subsequent generations were selected on the above described index. Selection was undertaken until constant selection responses per generation were obtained (equilibrium). Dekkers (1992) distinguished two equilibria. The first equilibrium is due to build up of pedigree information. The second equilibrium arises from reduction of additive genetic variance due to selection (Bulmer, 1971). To distinguish between reductions due to the Bulmer effect and due to effects of correlated index values, responses were calculated for three equilibria. First, pedigree equilibrium response (R_{ped}) ignoring the Bulmer effect and correlated index values was calculated. Secondly, correlated index values were also taken into account (R_{int}), and finally, equilibrium response taking both effects into account, i.e. the asymptotic response (R_{as}), was calculated. Therefore, reductions in response due to correlated index values are expressed by differences between R_{int} and R_{ped}, and due to the Bulmer effect by differences between R_{as} and R_{int}.

Optimization of number of selected parents

The selection index was used to optimize selection in the sire line, given a fixed test capacity. For a fixed test capacity, the number of selected boars and sows and the number of offspring tested per litter was optimized, keeping the amount of crossbred information per sire constant. Test capacity refers to the total number of purebred animals (boars + gilts) from the sire line that were tested on their purebred performance per generation. Test capacities were: N = 96, 192, 384, 768, 1536 and 3072 animals per generation. The number of selected sires varied from generation. The number of selected sires varied from n_s = 2, 4, 6, 8, 12, 24. From all litters, an equal number of animals was tested. The number of tested animals per litter was: n_{po} = 2, 4, 6 or 8. Testing eight animals per litter was assumed to be the biological maximum. In the basic scheme, equal numbers of boars and gilts were tested. The number of selected dams was calculated as N/n_{po}. The amount of crossbred information was kept constant at 64 crossbred offspring tested per sire, i.e. the total crossbred offspring tested per sire, i.e. the total number of tested crossbreds varied with the number of sires. Purebred and crossbred heritabilities were assumed to be equal. Heritability alternatives were: h^2 = 0·15, 0·25 and 0·40. Phenotypic variance was 1, r_{pc} was 0·7, and c_1^2 and c_2^2 were 0·1. Sensitivity of the optimum number of selected parents to the value of r_{pc} and to the amount of crossbred information included was investigated in the section on benefit of including crossbred information.

Benefit of including crossbred information

The selection index was also used to make inferences on the potential benefit of using crossbred

information. Genetic responses in crossbred performance under PLS (i.e. no crossbred information) were compared with maximum responses in crossbred performance that were obtained when a large amount of crossbred information was included. The effect of crossbred information on response depends on assumptions about breeding values of F_1-dams, crossbred litter size and on the existence of common environmental effects among crossbred full-sibs. Inferences about the effect of including crossbred information were made assuming unknown breeding values of F_1-dams, a crossbred litter size of eight and absence of common environmental effects among crossbreds.

Results

Optimization of the number of selected parents

Optimum number of offspring tested. Table 1 shows the optimum number of selected sires and the corresponding asymptotic selection response in crossbred performance, for a varying number of offspring tested per litter and for different test capacities. Given the fixed test capacity, less litters had to be produced and fewer dams were selected when the number of tested animals per litter increased. For example, for $N = 768$ and $n_{po} = 8$, $768/8 = 96$ dams had to be selected from $768/2$ selection candidates, and the selected proportion equalled 0·25. When $n_{po} = 4$, $768/4 = 192$ dams had to be selected from $768/2$ selection candidates and the selected proportion equalled 0·5. For this reason selection intensity in dams increased when more animals per litter were tested and highest responses were always obtained when the maximum number of eight animals per litter was tested. Selection response increased with increasing test capacity. However, the increase in response was rather low compared with the increase in test capacity. This was because the proportion of females selected was independent of N. When eight animals per litter were tested, one out of four females was needed for replacement. For this reason, the selected fraction in females was always 25% regardless of N. Therefore, increase in response with increasing test capacity was mainly due to higher selection intensities in sires. When the number of offspring tested per litter was below the optimum, i.e. n_{po} was lower than eight, the optimum numbers of selected sires also decreased.

Table 1 *Optimum number of selected sires ($n_{s,opt}$) and corresponding asymptotic response in crossbred performance (R_{as}) for a varying number of offspring tested per litter (n_{po}) and different heritabilities (h^2) and test capacities (N)*†

N	$h^2 = 0.15$			$h^2 = 0.25$			$h^2 = 0.40$		
	n_{po}	$n_{s,opt}$	R_{as}	n_{po}	$n_{s,opt}$	R_{as}	n_{po}	$n_{s,opt}$	R_{as}
3072	2	6	0·224	2	4	0·324	2	4	0·459
3072	4	8	0·250	4	6	0·361	4	6	0·513
3072	6	12	0·267	6	8	0·385	6	6	0·546
3072	8	12	**0·278**	8	8	**0·400**	8	6	**0·566**
1536	2	6	0·209	2	4	0·302	2	4	0·428
1536	4	8	0·237	4	6	0·342	4	6	0·485
1536	6	8	0·253	6	8	0·365	6	6	0·518
1536	8	12	**0·264**	8	8	**0·381**	8	6	**0·538**
768	2	4	0·194	2	4	0·280	2	4	0·369
768	4	6	0·222	4	6	0·321	4	4	0·457
768	6	8	0·239	6	6	0·345	6	6	0·489
768	8	8	**0·250**	8	8	**0·360**	8	6	**0·509**
384	2	4	0·176	2	4	0·255	2	2	0·364
384	4	6	0·207	4	4	0·299	4	4	0·427
384	6	6	0·224	6	6	0·323	6	4	0·458
384	8	8	**0·234**	8	8	**0·337**	8	4	**0·480**
192	2	4	0·158	2	2	0·229	2	2	0·331
192	4	4	0·190	4	4	0·276	4	4	0·393
192	6	6	0·207	6	6	0·299	6	4	0·425
192	8	8	**0·217**	8	6	**0·314**	8	4	**0·446**
96	2	2	0·138	2	2	0·204	2	2	0·294
96	4	4	0·173	4	4	0·251	4	4	0·355
96	6	4	0·188	6	4	0·273	6	4	0·387
96	8	6	**0·198**	8	4	**0·288**	8	4	**0·409**

† For $r_{pc} = 0.7$ and 64 crossbreds tested per sire. Optimum parameters and maximum responses are printed bold.

Table 2 *Pedigree equilibrium response* (R_{ped}), *corrected intensity response* (R_{int}) *and asymptotic response* (R_{as}) *in crossbred performance for different numbers of sires selected* (n_s) *and for different test capacities* (N) *and heritabilities* (h^2)†

N	n_s	$h^2 = 0.15$			$h^2 = 0.25$			$h^2 = 0.40$		
		R_{ped}	R_{int}	R_{as}	R_{ped}	R_{int}	R_{as}	R_{ped}	R_{int}	R_{as}
3072	2	**0·472**	0·339	0·229	**0·658**	0·493	0·351	**0·902**	0·708	0·526
	4	0·451	0·378	0·266	0·629	0·541	0·391	0·863	0·760	0·562
	6	0·437	0·384	0·273	0·611	0·547	0·397	0·838	**0·764**	**0·566**
	8	0·427	**0·387**	0·277	0·598	**0·548**	**0·400**	0·820	0·764	0·565
	12	0·413	0·385	**0·278**	0·579	0·544	0·399	0·794	0·755	0·559
	16	0·402	0·381	0·277	0·565	0·539	0·396	0·775	0·746	0·552
	24	0·387	0·373	0·274	0·544	0·528	0·389	0·747	0·729	0·540
768	2	**0·427**	0·308	0·211	**0·598**	0·448	0·322	**0·820**	0·643	0·480
	4	0·402	0·341	0·423	0·565	0·488	0·356	0·775	**0·685**	**0·509**
	6	0·387	0·344	0·248	0·544	**0·490**	0·359	0·747	0·684	0·509
	8	0·375	**0·344**	**0·250**	0·529	0·489	**0·360**	0·726	0·681	0·506
	12	0·359	0·339	0·248	0·506	0·481	0·355	0·696	0·666	0·496
	16	0·346	0·333	0·246	0·489	0·472	0·350	0·673	0·653	0·486
	24	0·328	0·320	0·238	0·465	0·454	0·338	0·640	0·627	0·468
96	2	**0·346**	0·246	0·176	**0·489**	0·360	0·266	**0·673**	0·517	0·394
	4	0·315	**0·269**	**0·198**	0·446	**0·387**	**0·288**	0·614	**0·541**	**0·409**
	6	0·295	0·265	0·198	0·418	0·379	0·285	0·576	0·527	0·399

† For $n_{po} = 8$, $r_{pc} = 0.7$ and 64 crossbreds tested per sire. Maximum responses are printed bold.

Response in different equilibria. Table 2 shows selection responses for different equilibria, for a varying number of selected sires and eight animals tested per litter. As expected, first generation (not shown) and pedigree equilibrium responses (R_{ped}) were always highest when only two sires were selected due to highest selection intensities. Benefits in response from pedigree information (not shown), i.e. differences between first generation and pedigree equilibrium response, were largest when heritability was low. For this reason, pedigree equilibrium responses increased less than linearly with heritability, whereas first generation responses increased linearly with heritability.

Contrary to R_{ped}, responses corrected for correlated index values (R_{int}) were highest when more than two sires were selected. This means that accounting for reduction of selection intensity due to correlated index values, altered the ranking of breeding schemes. The effect of correlated index values on selection response increased with decreasing heritability. When heritability was low, information of relatives contributed more to EBV of selection candidates and correlations between index values increased. Therefore, relative reductions in response due to correlated index values were highest for low heritabilities. Maximum relative reduction in response due to correlated index values was 29% for the scenario of $h^2 = 0.15$, $N = 96$ and $n_s = 2$. Differences between R_{int} and asymptotic responses (R_{as}) represent reductions due to the Bulmer effect.

Relative reductions due to the Bulmer effect increased slightly with decreasing heritability. This result seems to be in contradiction with results of Dekkers (1992), who showed that relative reductions due to the Bulmer effect are only dependent on the selection intensity and not on the heritability. However, in the present study, reduction of between-family variance due to the Bulmer effect changed the correlation between index values, and therefore affected the selection intensity. When correlated index values were ignored, the heritability did not influence relative reductions of response due to the Bulmer effect. Compared with R_{int}, the Bulmer effect had little influence on the ranking of breeding schemes in general. Maximum reduction in response due to the Bulmer effect was 32%, for the scenario of $h^2 = 0.15$, $N = 3072$ and $n_s = 2$. Maximum overall reduction in response compared with pedigree equilibrium response was 51% for the scenario of $h^2 = 0.15$, $N = 3072$ and $n_s = 2$. Because reductions in response increased with decreasing heritability, the optimum number of selected sires increased when heritability decreased (see also Table 1).

When the test capacity decreased, the optimum number of selected sires decreased only slightly. Compared with maximum pedigree equilibrium response, maximum asymptotic response increased slightly more with increasing test capacity. For example, for a heritability of 0·15, the ratio between maximum pedigree equilibrium response for N = 3072 and N = 96 equalled: 0·472/0·346 = 1·364,

whereas for maximum asymptotic response, the ratio equalled: $0{\cdot}278/0{\cdot}198 = 1{\cdot}404$. This means that the benefit of having a large test capacity is larger than judged by maximum pedigree equilibrium response.

Testing different numbers of males and females. To investigate whether it is beneficial to test different numbers of males and females, the number of males and females tested per litter was varied. Testing more offspring from a certain sex per litter results in more selection candidates of this sex. Therefore, selection intensity increases for this sex. Testing on average four animals of the same sex per litter was assumed to be the biological maximum. For this reason, a total of six animals per litter was tested, and the number of males tested per litter varied from 2 to 4, i.e. the number of females tested varied from 4 to 2. The number of selected sires per generation was varied from $n_s = 4$, 6, 8 or 12, except for $N = 96$, where n_s was 2, 4, 6, or 8.

Table 3 shows the optimum number of selected sires and the corresponding asymptotic responses for a varying number of males tested per litter and for different test capacities and heritabilities. Highest responses were obtained when only two males per litter were tested, and therefore four females per litter were tested. This was because female selection intensity increased relatively more than male selection intensity decreased when going from 2 to 4 females tested and from 4 to 2 males tested. Differences between responses for two and three

males tested were small. Differences between responses for three and four males tested were larger because reductions in selection intensity due to correlated index values were more severe for small proportions selected. Responses with six progeny tested were always lower than responses with eight progeny tested per litter with equal proportions tested for males and females (see Table 1). This indicates that it is optimal to test the maximum number of offspring per litter, and especially the maximum number of female offspring per litter.

Benefit of crossbred information
When the amount of crossbred information per sire increased, response increased until there was no additional benefit in extra crossbred information. The response predicted for this situation is referred to as maximum response. Figure 1 shows the ratio of asymptotic maximum response over the asymptotic response obtained without crossbred information, i.e. under PLS, as a function of the purebred-crossbred genetic correlation and for a test capacity of $N = 768$ purebred offspring. The response in both cases is calculated for the optimum number of selected sires under PLS and under CCPS respectively, and the ratio expresses the maximum superiority of CCPS over PLS. The optimum number of selected sires differed between PLS and CCPS (see Table 4). As expected, the benefit of crossbred information increased rapidly when the purebred-crossbred genetic correlation decreased, and approached infinity when r_{pc} approached zero. Apart

Table 3 *Optimum number of selected sires* ($n_{s,opt}$) *and corresponding asymptotic response in crossbred performance* (R_{as}) *for a varying number of males tested per litter* (n_{mt}) *and for different test capacities* (N) *and heritabilities* (h^2)†

N	n_{mt}	$h^2 = 0{\cdot}15$		$h^2 = 0{\cdot}25$		$h^2 = 0{\cdot}40$	
		$n_{s,opt}$	R_{as}	$n_{s,opt}$	R_{as}	$n_{s,opt}$	R_{as}
3072	2	12	0·272	8	0·392	6	0·554
	3	12	0·267	8	0·385	6	0·546
	4	8	0·255	8	0·370	6	0·525
1536	2	8	0·258	8	0·372	4	0·526
	3	8	0·253	8	0·365	6	0·518
	4	8	0·242	6	0·350	6	0·497
768	2	8	0·243	6	0·351	4	0·497
	3	8	0·239	6	0·345	4	0·489
	4	8	0·228	6	0·330	4	0·469
384	2	6	0·227	6	0·328	4	0·466
	3	6	0·224	6	0·323	4	0·458
	4	6	0·213	6	0·308	4	0·439
192	2	4	0·209	4	0·304	4	0·431
	3	6	0·207	4	0·299	4	0·425
	4	6	0·196	4	0·285	4	0·406
96	2	4	0·191	4	0·277	4	0·391
	3	4	0·188	4	0·273	4	0·387
	4	4	0·179	4	0·261	4	0·370

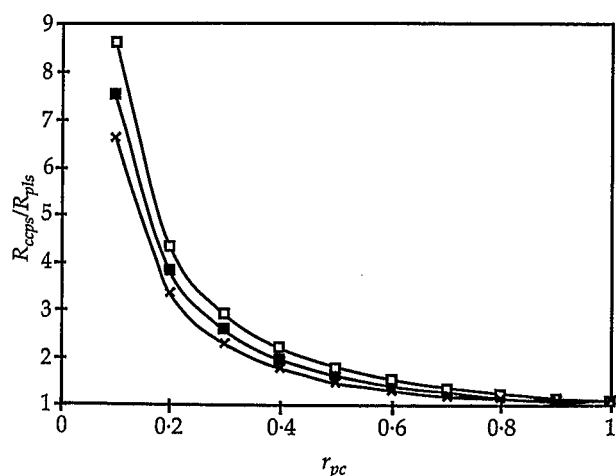† For $r_{pc} = 0{\cdot}7$, $n_{po} = 6$ and 64 crossbreds tested per sire.

Figure 1 Ratio of asymptotic maximum response (R_{ccps}) over asymptotic response under pure line selection (R_{pls}) for different purebred-crossbred genetic correlations (r_{pc}) and heritabilities (h^2) and for a test capacity (N) of 768 pure bred offspring. —— □ —— $h^2 = 0.15$; —— ■ —— $h^2 = 0.25$; —— × —— $h^2 = 0.40$.

from the fact that crossbred information is measured directly on the trait in the breeding goal, it can also be regarded as an increase of the amount of sib

information. For this reason, there was still a small benefit of using crossbred information when r_{pc} equalled unity, and the benefit of crossbred information was highest for low heritabilities, because low heritable traits benefit more from sib information. For example, for $h^2 = 0.15$ and $r_{pc} = 1$, the ratio R_{ccps}/R_{pls} equalled 1.05.

At low values of r_{pc}, the question arises if there is any benefit of including purebred information when the breeding goal is crossbred performance. However, when only crossbred information is used, there is no possibility to distinguish between purebred full-sib, because they all have exactly the same information, i.e. the crossbred breeding value of sire and dam, and the crossbred half-sib performance. For this reason, accuracy decreases and also selection intensity decreases due to higher correlations between index values when only crossbred information is used. For example, for $r_{pc} = 0.4$, $h^2 = 0.25$, $N = 768$, $n_s = 12$ and information on 25 crossbred litters per sire, response with and without utilizing purebred information was 0.334 (Table 4) and 0.308 (not shown) respectively.

Figure 2 shows the effect of the amount of crossbred information on the asymptotic response for a

Table 4 Pedigree equilibrium response (R_{ped}), corrected intensity response (R_{int}) and asymptotic response (R_{as}) in crossbred performance, when information on 25 crossbred litters of litter size eight is included, and asymptotic response under PLS (R_{pls}), for a varying number of selected sires (n_s) and a range of purebred-crossbred correlations (r_{pc}) and heritabilities (h^2)†

r_{pc}	n_s	$h^2 = 0.15$				$h^2 = 0.25$				$h^2 = 0.40$			
		R_{ped}	R_{int}	R_{as}	R_{pls}	R_{ped}	R_{int}	R_{as}	R_{pls}	R_{ped}	R_{int}	R_{as}	R_{pls}
0.4	2	0.433	0.285	0.170	0.111	0.585	0.394	0.245	0.170	0.769	0.534	0.348	0.253
	4	0.409	0.331	0.220	**0.121**	0.552	0.453	0.306	**0.178**	0.726	0.605	0.419	**0.256**
	6	0.394	0.338	0.231	0.120	0.532	0.461	0.320	0.176	0.700	0.613	0.433	0.252
	8	0.383	0.342	0.239	0.119	0.518	0.465	0.328	0.174	0.681	0.617	0.441	0.248
	12	0.367	0.341	0.244	0.115	0.496	0.463	0.333	0.168	0.652	0.611	**0.444**	0.239
	16	0.355	0.338	**0.245**	0.112	0.480	0.458	**0.334**	0.163	0.631	0.603	0.443	0.233
	24	0.338	0.328	0.242	0.105	0.456	0.443	0.327	0.155	0.599	0.583	0.432	0.222
0.7	2	0.460	0.326	0.219	0.195	0.631	0.466	0.330	0.297	0.853	0.660	0.488	0.443
	4	0.434	0.365	0.257	**0.211**	0.596	0.512	0.370	**0.310**	0.806	0.708	0.524	**0.448**
	6	0.418	0.369	0.264	0.210	0.575	0.515	0.375	0.307	0.776	0.708	**0.525**	0.440
	8	0.407	0.371	0.267	0.208	0.559	0.515	**0.377**	0.303	0.755	0.705	0.522	0.433
	12	0.389	0.366	**0.267**	0.201	0.536	0.507	0.374	0.293	0.723	0.691	0.513	0.418
	16	0.377	0.361	0.266	0.194	0.518	0.499	0.369	0.285	0.700	0.677	0.504	0.406
	24	0.358	0.349	0.259	0.184	0.492	0.481	0.357	0.271	0.665	0.651	0.485	0.387
0.9	2	0.489	0.362	0.257	0.250	0.678	0.526	0.391	0.381	0.931	0.759	0.582	0.569
	4	0.461	0.396	0.287	**0.271**	0.640	0.564	0.418	**0.399**	0.879	0.794	**0.598**	**0.575**
	6	0.443	0.398	0.291	0.270	0.617	0.563	**0.418**	0.394	0.848	0.788	0.592	0.565
	8	0.431	0.398	**0.291**	0.266	0.599	0.560	0.416	0.389	0.824	0.781	0.584	0.555
	12	0.412	0.391	0.288	0.257	0.574	0.549	0.408	0.376	0.790	0.761	0.569	0.536
	16	0.399	0.384	0.284	0.249	0.556	0.538	0.400	0.365	0.764	0.744	0.555	0.521
	24	0.378	0.370	0.275	0.235	0.528	0.517	0.385	0.347	0.726	0.713	0.533	0.496

† For a test capacity of 768 purebred animals $(N = 768)$ and a purebred litter size of eight $(n_{po} = 8)$. Maximum responses are printed bold.
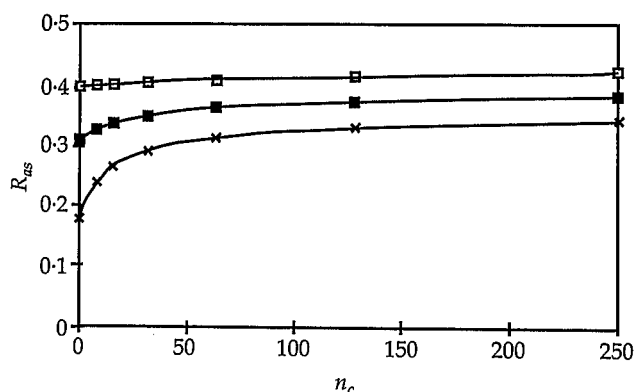
Figure 2 Asymptotic (R_{as}) achieved with optimum numbers of sires for different numbers of crossbred offspring included in the index (n_c) and different purebred-crossbred genetic correlations (r_{pc}) for $N = 768$ and $h^2 = 0.25$. ——×—— $r_{pc} = 0.4$; ——■—— $r_{pc} = 0.7$; ——□—— $r_{pc} = 0.9$.

heritability of 0·25 and a crossbred litter size of eight. In this Figure, n_c is the number of crossbred offspring per sire included in the selection index. The assumptions used were that crossbred litter size was eight, breeding values of F_1-dams were unknown and there was no common environment between crossbred half-sibs. When n_c equalled zero, the PLS response was obtained, when n_c was large, response approached the maximum crossbred response. Under PLS, $(n_c = 0)$, the ratio of responses for different values of r_{pc} equalled the ratio of r_{pc}-values because the purebred response was not influenced by r_{pc}. For low values of r_{pc}, the response increased rapidly when the number of crossbred offspring increased. For $r_{pc} = 0.4$, 22 litters were needed to obtain 90% of the maximum extra response attainable by including crossbred information. For higher values of r_{pc}, larger amounts of crossbred information were needed to obtain a certain percentage of the attainable extra response. For example, for $r_{pc} = 0.7$, more than 64 crossbred litters were needed to obtain 90% of the potential extra response. Large amounts of crossbred information could not completely compensate for low values of r_{pc}, i.e. the PLS response with $r_{pc} = 0.9$ could not be reached with $r_{pc} = 0.7$ and a large amount of crossbred information. This is because crossbred half-sibs do not provide information on within family deviations, i.e. information of crossbred half-sibs is common to all purebred offspring of a sire. The only within family information source is the individual (purebred) record, and its contribution increases with increasing r_{pc}.

As to be expected, knowledge about breeding values of F_1-dams increased response, whereas presence of

common environmental effects decreased response. For a fixed total number of crossbred half-sibs included in the index, it was most efficient to measure only one half-sib per litter, i.e. having a maximum number of F_1-dams. However, when breeding values of F_1-dams were known without error and common environment was absent, responses were the same for testing one or eight crossbred half-sib per litter given a fixed total number of crossbred half-sibs. In practice, all offspring of a litter will probably be tested because this is cheaper than testing only one offspring per litter and a large number of litters.

Effect of crossbred information on optimum number of selected parents. Table 4 shows responses for different equilibria and optimum numbers of selected sires when including information on 25 crossbred litters of eight offspring each. For comparison, the asymptotic response obtained under PLS, denoted as R_{pls}, is also included in Table 4. By comparing R_{as} and R_{pls} for different values of r_{pc}, it can be seen that the benefit of crossbred information increased when r_{pc} decreased, which is in agreement with Figure 1. Inclusion of crossbred information increased the correlation between index values of relatives, because the crossbred information is common to all half-sibs. For example, for $r_{pc} = 0.4$, $h^2 = 0.25$ and 16 sires selected, the average correlation between index values equalled 0·0294 under PLS, whereas it equalled 0·0522 when crossbred information was also included. This resulted in a considerable decrease in the selection intensity, which can be seen from the large differences between R_{ped} and R_{int} especially for low values of n_s. For this reason, the optimum number of selected sires increased considerably when crossbred information was incorporated. Under PLS, the optimum number of selected sires always equalled four, whereas it ranged between 16 and 4 when crossbred information was included. The optimum number of selected sires was largest for $r_{pc} = 0.4$ and $h^2 = 0.15$, because correlations between index values were largest for this situation.

The results in Table 4 are for a situation where information on a fixed number of crossbred litters per sire was included in the index. Therefore, the total amount of crossbred information varied with the number of sires. To make a comparison at the same level of cost, it is interesting to fix the total amount of crossbred information, instead of fixing it per sire. Results of a comparison are listed in Table 5, for of total of 96 and 384 crossbred litters tested respectively. Results are for $h^2 = 0.15$ and $r_{pc} = 0.4$, and can be compared with results for these parameters in Table 4. Compared with Table 4 $(\max(R_{as}) = 0.245 \rightarrow n_s = 12)$, the optimum number of sires under CCPS decreased when the total amount

Table 5 *Asymptotic responses for a fixed total number of 96* (R_{96}) *and 384* (R_{384}) *crossbred litters tested, for different numbers of selected sires* (n_s)*, and for a heritability of 0·15 and a purebred crossbred genetic correlation* (r_{pc}) *of 0·4†*

n_s	R_{96}	R_{384}
2	177	182
4	220	233
6	**224**	243
8	**224**	**248**
12	218	**248**
16	210	245
24	193	232

† For a test capacity of 768 pure-bred animals $(N = 768)$. Purebred and crossbred litter size equalled eight $(n_{po} = 8, n_{co} = 8)$. Maximum responses are printed bold.

of crossbred information was fixed. This is to be expected, because when the total amount of crossbred information is fixed, the amount per sire will decrease when the number of sires increases, which reduces the accuracy of the selection index. Especially for low total amounts of crossbred information this effect is important, because the benefit of additional crossbred information is limited when the amount of information is already high. This fact is illustrated by the comparison at a low (R_{96}) and a high (R_{384}) total amount of crossbred information. The optimum number of sires was highest for 384 crossbred litters tested (8 to 12 v. 6 to 8), and closer to results for 'fixed per sire' schemes (Table 4, $n_s = 16$). Differences of optimum numbers of sires between 'fixed total' and 'fixed per sire' schemes will decrease when r_{pc} and h^2 increase, because for these situations the optimum numbers of sires are already closer to PLS optima and because benefit of large sib groups is lower for high heritabilities.

Discussion

In the present study, a selection index was developed, which approximates selection on BLUP-EBV for a crossbreeding situation. This index was used to optimize the selected number of parents and the number of purebred offspring tested per litter, and to make inferences on the potential benefit of including crossbred information in the selection index. Wray and Hill (1989) showed that an index including phenotypic records on an individual and its sibs, and estimated breeding values of parents and of mates of parents can be used to approximate selection on BLUP-EBV under an animal model when generations are discrete. Compared with the index of Wray and Hill (1989), the index in this paper also includes phenotypic information on crossbred half-sibs and estimated crossbred breeding values of

parents and of mates of parents. Wray and Hill (1989) found good agreement between response obtained from stochastic simulation and prediction from their selection index. For this reason, it is expected that the index used in the present study will also provide a good approximation of response on BLUP selection, and that there is little benefit in checking the results by means of stochastic simulation. As recommended by Wray and Hill (1989), ranking of breeding schemes was based on asymptotic response. Because asymptotic responses were reached in five generations and more than 95% of the reductions in response due to the Bulmer effect and due to correlated index values occurred in the first two generations, asymptotic response is a suitable measure for ranking breeding schemes in the present study. An assumption in the prediction method used here is that fixed effects are known without error. This is not true in practice as fixed effects are estimated from the data simultaneously with the breeding values. For this reason, the test capacity has to be regarded as effective test capacity, i.e. it is corrected for the distribution of observations over fixed effect classes, and it is therefore smaller than the actual number of test places.

In crossbreeding, the final aim is to produce high-quality crossbred fattening pigs. For this reason, the breeding goal was defined at the crossbred level. In a boar line, the number of animals is small compared with the number of crossbred fattening pigs, and purebred performance is therefore of minor importance. However, breeding organizations might want to put some weight on purebred performance. In the presented method, this can easily be accommodated by changing the economic values for purebred and crossbred performance.

In the present study, breeding schemes were optimized assuming a limited test capacity within the pure line, whereas the potential amount of crossbred information was assumed to be unlimited. However, at present crossbred information is not directly available to many breeding organizations. In order to use crossbred information, registration at multiplier herds, fattening herds and slaughter houses has to be integrated and data has to be collected. Given the availability of modern information technology, this is possible, but it will take considerable effort. For this reason, it is likely that breeding organizations will contract a limited number of test farms and slaughter houses and crossbred information will be collected only there. (E. Knol, personal communication).

The present study showed, that given a fixed test capacity, especially the maximum number of female offspring per litter should be tested. This means that

the number of selected sows. i.e. the sow capacity, has to be adjusted to the test capacity. When instead of the test capacity, the sow capacity is limited, e.g. because testing is cheap and keeping sows is expensive, testing the maximum number of offspring per litter will obviously result in the highest response and the test capacity is a result of the sow capacity. Therefore, optimum schemes for fixed test capacity and fixed sow capacity are identical, i.e. the highest response for both situations is obtained when the maximum number of offspring per litter is tested. When only two offspring per litter were tested, the selected proportion in females was 100% and selection intensity equalled zero. However, instead of selecting only tested offspring, the best 50% of the tested offspring could be selected supplemented with untested offspring, which would raise the selection intensity to 0·398 in this case (Kirsch et al., 1962). This scheme is however still inferior to testing eight offspring per litter, and in addition it might be undesirable for breeding organizations to supplement the selected group with untested animals for veterinary or management reasons.

Responses obtained when using both purebred and crossbred information were higher than responses under PLS. Especially for low values of the purebred-crossbred genetic correlation (r_{pc}) the benefit of including crossbred information was very clear (see Figure 1). For $r_{pc} = 0·4$, the maximum response under CCPS was approximately twice the response under PLS. When r_{pc} was high, i.e. >0·9, the potential benefit was small (Figure 1) and large amounts of crossbred information were needed to obtain extra response (Figure 2). Wei and van der Werf (1994) also compared selection response under PLS with response under CCPS using selection index theory, but ignored the Bulmer effect and pedigree information. They concluded that CCPS was better under all circumstances, even when large errors in estimates of r_{pc} and h^2 were present. This conclusion is not expected to be affected by the correction for correlated index values and for the Bulmer effect and can therefore be extended to the present study.

De Roo (1987 and 1988) studied breeding schemes for the sire line of a closed pig population using detailed stochastic simulation. The breeding goal consisted of three traits and only own performance was included in the selection index. De Roo (1988) found considerable reductions in response due to the Bulmer effect and due to correlated index values and finite sample size. Maximum overall reduction in short-term response equalled 34% (De Roo, 1988; Table 8). In the present study, overall reduction in response ranged from 27% to 51% (Table 2). Due to the use of sib information, reductions in response due to the Bulmer effect and due to correlated index

values were larger than found by De Roo (1988) in our study. De Roo (1988) found optimum numbers of selected sires around 5 and 15 for time horizons of 5 and 25 years respectively. In the present study, the optimum number of selected sires ranged from 4 to 16 (Table 1 and Table 4) and increased with decreasing heritability and with decreasing purebred-crossbred genetic correlation when crossbred information was included (Table 4). The optimum number of boars for PLS was four (Table 4), which is very close to results of De Roo (1988) for a time horizon of 5 years. For longer time horizons, De Roo (1988) found higher optimum numbers of sires due to accumulated inbreeding and drift variance. In our study, inbreeding was ignored and optimum numbers of selected sires have to be interpreted as giving the maximum response on intermediate time horizons. For longer time horizons, the number of selected boars may need to be larger because of inbreeding. In the present study, correction of the selection intensity for finite population size and correlated index values was based on the total number of animals per generation, i.e. selection took place only once per generation. In practice, selection takes place weekly as simulated by De Roo (1988) and selection intensity is overestimated in the present study. Accounting for correlated index values changed the ranking of breeding schemes considerably, which was also found by Meuwissen (1991). This means that accounting for correlated index values is crucial when comparing breeding schemes.

Discrete generations were used in the present study, whereas in practice generations overlap. Overlapping generations provide opportunity for sequential culling, i.e. animals can be culled if a better replacement is available. Belonsky and Kennedy (1988) found an increased response due to sequential culling of 34% and 57% when selection was on individual phenotype and on BLUP-EBV, respectively. However, sequential culling also increased inbreeding from 0·288 for BLUP selection without sequential culling to 0·383 when sequential culling was practised (Belonsky and Kennedy, 1988; Table 3). For this reason, the benefit of sequential culling would be smaller when responses were compared at the same level of inbreeding. In the present study, selected proportion in females was limited to a minimum of 0·25 because all replacements had to be produced from the current generation. When generations overlap, female selection intensity increases due to an increased number of selection candidates. It is not clear from our study if this would influence ranking of breeding schemes. Further research on the effect of overlapping generations together with crossbred information is needed.

In practice, the number of selected boars is limited by inbreeding constraints. Inbreeding reduces the variance due to Mendelian sampling and is associated with risk due to drift variance and inbreeding depression when dominance effects are lost. For production traits, inbreeding depression is of minor importance in crossbreeding schemes, because dominance effects are regained in the hybrid slaughter pigs. Due to the presence of inbreeding constraints, it is valuable to compare responses at similar rates of inbreeding. An approximation of the benefit of including crossbred information when the number of selected sires is limited by inbreeding constraints can be gained by comparing asymptotic responses at equal numbers of selected sires. It follows from Table 4, that especially for low values of r_{pc} the benefit of including crossbred information is larger when compared at equal numbers of sires than when compared at optimum numbers of selected sires. For example, for $r_{pc} = 0.4$ and $h^2 = 0.15$ the ratio of R_{ns} over R_{pls} for a fixed number of 16 sires selected equalled $0.245/0.112 = 2.188$, whereas the ratio of optimum responses equalled $0.245/0.121 = 2.025$. Therefore, the benefit of including crossbred information seems to be larger than that judged by optimum responses when the number of selected sires is limited by inbreeding constraints. However, inclusion of crossbred information increases the correlation between index values, and might therefore also increase the rate of inbreeding, which hampers the comparison between CCPS and PLS at equal numbers of selected sires. A promising approach seems to be the use of crossbred information together with a selection method that imposes restrictions or a cost factor on the rate of inbreeding (e.g. Wray and Goddard, 1994; Meuwissen, 1997).

Acknowledgements

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