MATE SELECTION IN PARENTAL LINES TO EXPLOIT KNOWN DOMINANT QTL IN CROSSES

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INTRODUCTION
Line crossing is a common way of crossbreeding to exploit heterosis in animal breeding operations. Development of parental lines and crossing strategies to exploit these lines are a key issue. Crossbreeding programs may vary in many aspects, such as objectives or gene actions of the trait of interest. Optimal line development for different situations is of importance, e.g. for utilizing dominance effects. Selection based on breeding value will not optimally exploit non-additive genetic effects. However, mate selection can be a powerful tool for this purpose by finding optimal mating pairs (Hayes and Miller, 2000; Hayes et al., 1997), and accounting for different factors simultaneously (Kinghorn and Shepherd, 1990). The aim of this paper is to demonstrate the use of mate selection as a natural way for line development in crossbreeding programs. We will use a very simple model based on one single identified quantitative trait loci (QTL) in a two-way crossing system.

MATERIALS AND METHODS
Two-way crossing system. An unselected base population and selection with discrete generations was assumed. A sire-line and a dam-line were developed from two base populations that had either the same or different initial allele frequencies (IAF). The term allele used here and below refers to the favourable allele of the QTL concerned. Selection occurred within lines for purebred and crossbred performance. Males from the sire-line were crossed with females from the dam-line. Purebred offspring were selected for pure breeding or crossbreeding. The remaining purebreds and all crossbreds were sold to market. The numbers of sires and dams in the sire- and dam-lines depended on the number of crossbreds, the reproductive rate of dams (rrd) and dams mated per sire (dps). In our example, rrd was 5 and dps was 30.

Genetic model. Phenotypes were based on one bi-allelic QTL. No polygenic effects were included. QTL genotypes were identified without error in all individuals prior to selection. The QTL had three genotypes, aa, Aa and AA, with genotypic values -a, d×a and a (where a was additive effect and d degree of dominance of the QTL). a was 1.0, and d was 1.0 or 2.0 for fully- or over-dominant QTL, respectively. IAF of the QTL at the base populations were 0.05 or 0.5. The populations were simulated deterministically, considering only cohorts as defined by sex and destiny of their progeny (parental lines and crossbreds). Cohorts were characterised by their size (total number of animals) and allele frequency.

Selection methods. Two selection methods, mate selection and index selection, were compared in this paper. Mate selection was based on the same principle as the one proposed by Kinghorn (1998) and extended to multiple generations. It was implemented to determine an
optimal solution that maximises an objective function. The objective function used here was cumulative discounted performance (CDP) of animals sold over 5 generations. Discount rate was 10%. Either CDP of total progeny sold (total progeny merit, TPM) or CDP of crossbreds (crossbred merit, CBM) was used to optimise CDP of different animal groups. The parameters to be optimised were the number of animals selected for pure breeding and crossing in each genotype and the number of matings in the 9 possible mating combinations for each line and cross. A Differential Evolution Algorithm (Price and Storn, 1997) was used to find the optimal number of animals selected and optimal mating combinations in different cohorts.

Index selection was based on breeding values (BV) of QTL genotypes. BV was the sum of the average effects of genes. BV of a genotype for pure breeding (BVpb) depended on allele frequency in the purebred lines and that for crossbreeding (BVcb) on the frequency in the line to be crossed to. Index selection was used to select the best animals in each generation for pure breeding and subsequently the next best for crossbreeding. Selected animals were mated randomly. The selection criterion used was calculated as $k \cdot \frac{n_1 \cdot BV_{pb}}{n_2} + BV_{cb}$, where $n_1$ was the number of animals culled from pure breeding, $n_2$ was the number of crossbreds, and $k$ was equal to 0 when selection was based on CBM and 1 for selection on TPM.

RESULTS AND DISCUSSION

Superiority of mate selection over index selection. Table 1 shows superiority of CDP in mate selection over index selection with fully- and over-dominant QTL in different IAF for different optimisation objectives. The superiority was 5-28% and 11-81% for fully- and over-dominant QTL, respectively.

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<thead>
<tr>
<th>IAF</th>
<th>Fully-dominant</th>
<th>Over-dominant</th>
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<tbody>
<tr>
<td></td>
<td>TPM</td>
<td>CBM</td>
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<tr>
<td>0.5</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>0.5</td>
<td>12</td>
<td>17</td>
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<td>0.05</td>
<td>19</td>
<td>28</td>
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</table>

Allele frequency fixation patterns in index selection. Allele frequency fixation patterns in index selection are shown in Figure 1. For $d=1$ (shown in Figure 1a), allele frequency in the higher IAF line was fixed faster than that in the lower IAF line for both selection based on CBM and TPM. Allele frequency in the higher IAF line increased to fixation, and that in the lower IAF line was fixed later for selection based on TPM or it stabilized at about 0.8 for selection based on CBM. When the two lines had the same IAF, the allele frequency fixation patterns were the same (results not shown). With overdominant QTL ($d=2$) allele frequency fixation patterns were the same for both selection based on TPM and CBM. Again, when IAF was equal in both lines, allele frequency fixation patterns were the same in both lines, with oscillation leading to fixation at generation 5. This is because genotype AA has the highest BV when allele frequency < 0.75 and lowest BV when allele frequency > 0.75. When $d = 2$ and IAF were unequal between lines, allele frequencies in the two lines diverged, increasing in the higher IAF line and decreasing (excepting generation 1) in the lower IAF line.

Allele frequency fixation pattern in mate selection. Allele frequency fixation patterns in mate selection are shown in Figure 2. For $d=1$, allele frequency in the sire-line was fixed...
earlier than that in the dam-line for optimising either TPM or CBM, when IAF was unequal. For optimising TPM, the allele frequency in the dam-line increased and fixed two generations after the sire-line when the sire-line had high IAF (0.5), and stayed at about 0.75 when the sire-line had low IAF (0.05). For optimising CBM, allele frequency in the dam-line was increased before the sire-line was fixed and unstable after fixation in the sire-line. This is because the dam-line allele frequency affects crossbred merit if allele frequency in the sire-line is fixed.

For d=2 and optimising TPM or CBM, allele frequencies diverged in the sire- and dam-line. Frequency in the sire-line decreased and that in the dam-line increased in most of cases (continuous line in Figure 2b). When optimising TPM for d=2, allele frequency in the dam line increased to about 0.95 and then decreased to 0.75, which ensured that the dam-line could produce the necessary AA females for crossing and maximize number of Aa males for market. The allele frequency fixation pattern was reverse if IAF in the dam-line was below 0.15 and IAF in the sire-line was over 0.35 (dotted line in Figure 2b). The dam-line increased to about 0.44 and then decreased to 0.25, which ensured that the dam-line could produce the maximum number of aa females for crossing and maximum number of Aa males for market. The value of culled purebred animals contributes to profit and as many more purebreds are culled from the dam-line than from the sire-line, it is more optimal to have a high frequency of the favourable
allele in the dam-line. Larger differences in allele frequency between the two lines were observed for optimising CBM than optimising TPM because CBM is affected only by genotypes resulting from the crossing of the two lines.

The superiority of CDP in mate selection over index selection results from exploitation of non-additive genetic effects in the line development where mating pairs and partitioning of animals among pure breeding, crossing and selling are optimised. The superiority depends on the difference of allele fixation patterns between the two selection methods. The more difference in the pattern exists the more superiority over index selection is observed. For an over-dominant QTL, the biggest superiority was observed when both lines had the same IAF (0.5), where index selection did not lead to divergence of allele frequencies in the lines whereas mate selection did. When IAFs in the two lines were different, divergence occurs in index selection but not in an optimal way. For a fully-dominant QTL, the biggest superiority was observed when IAF of the sire-line was lower than that of the dam-line. The allele frequency in the dam-line is fixed earlier than that of the sire-line in index selection whereas optimal patterns for this case are opposite. When IAFs in the sire- and dam-line were 0.5 and 0.05, respectively, the superiority declined because the allele frequency fixation patterns are closer.

This paper demonstrates that mate selection naturally optimises genotypic selection for an identified QTL in the development of crossing lines for a two-way crossing system. Mate selection utilizes dominance effects more effectively than index selection in crossbreeding as it is based on expected genetic value of offspring. The index selection is based on additive genetic value, leading to fixation of the favourable allele and loss of heterozygosity. The effectiveness of mate selection is achieved by selecting and mating animals simultaneously, which ensures favourable mating pairs are produced, and by considering multiple generations. The mate selection algorithm used here is easily extended to a two QTL model. If genotypes of QTL are not perfectly known, QTL genotype probabilities can be used in the mate selection algorithm.

In optimising CDP of the two-way crossing system, the optimal strategy of line development depended not only on the genetic model of QTL and breeding objective but also on starting allele frequencies. If we would be concerned about performance of the crossing system in the long-term, the optimal configuration of crossing lines should not be influenced by the starting situation.

REFERENCES