PERIODIC ROTATIONAL CROSSES. II. OPTIMIZING BREED AND HETEROSIS USE

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ABSTRACT

Choice of the optimal number and sequence of breeds in a periodic cross was determined by comparing the trade-off between increased utilization of breed differences and decreased utilization of heterosis. It was shown that the change in mean efficiency resulting from adding the next best breed to the best conventional n-breed rotation is always less than the change in efficiency predicted from the increase in heterosis. Periodic rotations were generally optimized by decreasing the proportion of poorer performing breeds in the rotation. However, efficiency of periodic rotations can exceed that of the better breed even when the difference in additive breed effects for efficiency is almost twice the effect of heterosis on efficiency. The periodic rotation that was optimal also tended to have the lowest inter-generational variance. It was suggested that inter-generational variances of component traits, which are not necessarily minimized when crosses are selected on a combined efficiency trait, can be considered by including inter-generational variance in an index or by introducing maximum thresholds.

(Key Words: Crossbreds, Breeding Programs, Heterozygosity, Breed Differences.)

Introduction

Some periodic rotational crosses have been shown to use 70 to 95% as much heterosis as conventional rotations (Bennett, 1987). Along with this reduction in heterosis comes the opportunity to allow some breeds to contribute more to the weighted average breed composition. This can allow some periodic rotations to exceed the efficiency of conventional rotations (Bennett, 1987) depending on breed differences and heterosis.

Comparisons of breeding systems are usually based on the mean level of performance or efficiency (Dickerson, 1973). However, it has been recognized that variability among generations may be a problem with rotational crosses. This had led to the suggestion (Gregory and Cundiff, 1980) that rotational crossing among breeds with greatly different birth weights, or other attributes where divergent dam and offspring genotypes may be incompatible, should be avoided. In addition, rotations may be inappropriate when a mixture of diverse genotypes from different generations may cause management problems, such as pasture allocation, or increased variability in a bulked product, such as wool.

Optimizing productivity or efficiency from periodic rotational crosses consists of trading off increased breed utilization for decreased heterosis utilization. In this paper, conditions required for the efficiency of one cross to exceed that of another are determined. Methods of accounting for inter-generational variance in combination with average breed and heterosis utilization are proposed.

Materials and Methods

Definitions. As in the previous paper (Bennett, 1987), periodic rotations will be identified by a letter sequence representing the sequence of sire breeds used. Capital letters will be used both to identify the breeds and to represent their additive breeding values. For this paper only, the letters will represent breeds ordered for the trait of interest; i.e., A = best breed, B = second best breed, etc. An appropriate trait for comparing rotations is an efficiency or other net merit measure (Bennett, 1986).

A simple model of heterosis will be used to determine optimal rotations. Heterosis is assumed to arise from dominance among alleles that are homozygous and unique to each breed.
Useful quantities for comparing rotations are the scaled breed differences $\Delta X_i = (A - b)/H$, where $A$ and $b$ represent the additive breed effects of the first and the $i$th ordered breed, respectively, and $H$ is heterosis. For the general solutions presented in this paper, heterosis will be considered equal for all possible crosses. For ease in discussing results, it will also be assumed that heterosis is positive and that the difference between the first and last ordered breed is greater than or equal to zero. These assumptions force $\Delta X_1$ to be greater than or equal to zero and $\Delta X_2 \leq \Delta X_3 \leq \Delta X_4$, etc. The formulas also apply to situations where both heterosis and desirable breed effects are negative.

**Results**

**Conventional Rotations.** Considering only conventional rotations, it is well known that increasing the number of breeds in a rotation increases heterosis (Carmon et al. 1956). It is also recognized that the difference between the best and worst conventional rotation of $n$ breeds decreases as the number of breeds ($n$) in the rotation increases (Bennett, 1986) when there are more than $n$ breeds available. The trade-off between increased heterosis and decreased intensity of breed selection with increasing number of breeds included in the rotation can be evaluated by comparing the best rotations for each number of breeds. The best conventional rotation with $n$ breeds has the following predicted value ($P_n$):

$$P_n = A + \left[ -\sum_{i=2}^{n} \Delta X_i/n + (2n - 2)/(2n - 1) \right] \times H.$$ 

Therefore, the marginal difference between the best rotations with $n$ and $n - 1$ breeds is:

$$P_n - P_{n-1} = \left\{ \left[ (\sum \Delta X_i) - n \Delta X_n \right]/[n(n - 1)] \right\} +$$

$$\left(2^n + 2^{1-n} - 3\right)^{-1} \times H.$$ 

Obviously, this difference must be positive if the best $(n - 1)$-breed rotation is to be improved by the addition of another breed. The marginal increase in heterosis utilization must exceed the decrease in average breed performance.

Two other results can be shown from the marginal differences of adding another breed to the rotation. Since $\sum_{i=1}^{n} \Delta X_i = n \Delta X_n$ is always undesirable if at least one breed is better than any other $(\Delta X_2 > 0)$, the net improvement ($P_n - P_{n-1}$) from adding another breed to the best $(n - 1)$-breed rotation is always less than the gain $[(2^n + 2^{1-n} - 3)^{-1} \times H]$ in heterosis. It can also be shown that if the addition of the best remaining breed to the best $(n - 1)$-breed rotation does not result in a net improvement, then the addition of any number of remaining breeds will also not result in an improvement. These results, of course, depend on heterosis being equal among all crosses.

**Net difference over the best breed in units of heterosis for the best two- and three-breed rotations relative to differences among the best three breeds is shown in figure 1. The figure illustrates that the best two-breed rotation exceeds the best single breed if the breed difference is less than 4/3 heterosis. If there is no difference between the second and third breed, then the best three-breed rotation exceeds the best two-breed rotation as long as the difference between the first and second breeds is less than 1.14 heterosis. When the difference between the first and third breed increases to 1.6 and 2.2 times the difference between the first and second breed, three-bred rotations exceed two-breed rotations when the difference between the first two breeds is less than .52 and .34 times heterosis, respectively (figure 1).**

**Periodic Rotations.** The marginality concept can be extended to periodic rotations. The increase in weighted additive breed effects must be greater than the decrease in heterosis utilization if one periodic rotation is better than another. The breed difference, or differences at which two rotations are equal, can be found by equating their expected breed composition and heterosis as determined by Bennett (1987).

Table 1 shows the range in scaled breed difference over which some two-breed periodic rotations exceed the best breed. Also shown in table 1 is the range in scaled breed difference over which each two-breed periodic rotation exceeds the other two-breed periodic rotations considered. These relationships are illustrated in figure 2. As determined earlier, the conventional rotation exceeds the best breed only if the breed difference is less than 4/3 heterosis. However, periodic rotations can extend this range up to twice heterosis by using a greater proportion of the best breed while giving up some heterosis.
utilization. Even for breed differences of less than 4/3 heterosis, periodic rotations using two breeds unequally can exceed the conventional two-breed rotation. Over a wide range of scaled breed differences there is little difference between conventional and periodic rotations of similar breed composition, e.g., AB and ABA.

Similar relationships for some three-breed periodic rotations are graphed in figures 3a, 3b and 3c for differences between the second

### TABLE 1. BREED DIFFERENCE RANGES OVER WHICH SOME TWO-BREED PERIODIC ROTATIONS EXCEED THE BEST BREED AND ALL OTHER ROTATIONS CONSIDERED

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Exceeds best breed</th>
<th>Exceeds other rotations</th>
</tr>
</thead>
<tbody>
<tr>
<td>AB</td>
<td>0 - 1.33</td>
<td>.0 - .57</td>
</tr>
<tr>
<td>ABA</td>
<td>0 - 1.71</td>
<td>.57 - 1.26</td>
</tr>
<tr>
<td>ABAA</td>
<td>0 - 1.87</td>
<td>1.26 - 1.59</td>
</tr>
<tr>
<td>ABAAAA</td>
<td>0 - 1.94</td>
<td>1.59 - 1.94(^b)</td>
</tr>
<tr>
<td>ABA..A(^c)</td>
<td>0 - 2.00</td>
<td>1.94(^b)-2.00</td>
</tr>
</tbody>
</table>

\(^a\)(A-B)/heterosis.

\(^b\)Depends on the number of generations in ABA..A.

\(^c\)Indicates an unrepeated cross of B onto A.
and third breed of 0.3 and 0.6 times heterosis, respectively. As the difference between breeds increases, periodic rotations that decrease the use of poorer breeds and increase the use of better breeds (e.g., ABACAB) exceed the conventional three-breed rotations. When the breed differences A-B and B-C are about half heterosis, the performance of ABC, ABCAB, ABAC, and ABACAB are similar.

**Inter-generational Variance.** Bennett (1987) derived coefficients of breed differences and heterosis products and cross-products that predict inter-generational variance of selected periodic rotations. The relationships between scaled breed difference and inter-generational variance (in units of heterosis squared) for some two-breed periodic rotations are shown in figure 4. As the difference between breeds increases, inter-generational variance of the conventional rotation increases. Inter-generational variance initially decreases for other periodic rotations before eventually starting to increase. Comparing figure 4 with figure 2 shows that the best rotation at any breed difference also tends to have a low inter-generational variance, although this relationship is not exact. Inter-generational variance for some three-breed rotations are shown in figures 5a and 5b. The relationship between high means and low variances is reduced in three-breed periodic rotations.

The trait used to select among periodic rotations, e.g., efficiency, will have low inter-generational variance because of the preceding observed relationship between high means and low variances. However, there is more interest in reducing inter-generational variance of component or secondary traits such as birth weight, mature size or milk production. Selection of a periodic rotation on the basis of a combined efficiency trait does not ensure low variance for component or secondary traits.

One method of accounting for inter-generational variation in component or secondary traits is to calculate the variation of these traits for each periodic rotation considered. These variances can then be weighted and added to the mean efficiency to evaluate each rotation. Weighting of variances is needed because the
Figure 3. Comparison of four three-breed periodic rotations for net difference in heterosis units from the best breed (A) relative to the scaled breed difference (A-B)/heterosis when breed B exceeds breed C by a) 0, b) .3 or c) .6 times heterosis.
additive breed and heterotic effects on efficiency would usually assume no inter-generational variation. The weightings would account for the possible reduction in efficiency caused by the effects of inter-generational variation of traits such as birth weight, milk production and wool diameter which can result in increased dystocia, inappropriate feed allocation and reduced wool price, respectively. Alternatively, threshold values for maximum inter-generational variance of each trait can be used to eliminate some rotations when weightings are unavailable.

Discussion

Periodic rotations can improve performance over conventional rotations by giving an optimal balance to breed and heterosis effects. The primary question is whether the increase in utilization of breed offsets the loss in heterosis. Periodic rotations can also reduce inter-generational variance and are one way of managing rotations among breeds with greatly different trait breeding values.

Kinghorn (1982, 1983) has shown that periodic rotational crosses may be established by selection of sires on "breed breeding value," a combination of additive breed effect and expected heterosis when mated to females of a given breed composition. However, the best periodic rotation will not necessarily be established. Breed breeding value selection can be shown to establish AB, ABA and ABAA rotations at the following scaled breed difference ranges: 0 to .67, .67 to 1.43 and greater than 1.43, respectively. Correspondingly ranges over which these periodic rotations result in the best mean performance are: 0 to .57, .57 to 1.26 and greater than 1.26, respectively. Breed breeding value methods fail to anticipate possible future increases in heterosis by having a relatively lower-performing generation in the rotation. However, there is little practical difference between a periodic rotation generated by breed breeding values and one selected on mean performance, because over the small ranges where the two methods select different periodic rotations, their mean performances are similar.
Figure 5. Inter-generational variance for four three-breed periodic rotations relative to the scaled breed difference (A-B)/heterosis when breed B exceeds breed C by a) 0 or b) .6 times heterosis.
The two examples used in the first paper of this series (Bennett, 1987) help illustrate the optimization of breed and heterosis. In the swine example based in Wilson and Johnson (1981), the difference between the breeds producing the most and next largest number of pigs was .875 times average heterosis. At this breed difference, an ABA rotation yields the largest average mean. The difference between the breeds producing the first and third largest number of pigs was 1.03 times average heterosis. Increasing the best breed and reducing the second and third breeds equally by using an ABAC rotation resulted in the largest number of pigs/sow because there was only a small difference between the second and third breeds.

In the cattle example based on MacNeil et al. (1986), the breed differences between the breed producing the most weight of calf weaned and the second and third breeds were .33 and .59 times average heterosis. This resulted in a conventional rotation of the two best breeds exceeding other two-breed periodic rotations. All three-breed rotations considered resulted in about the same predicted weight of calf weaned/cow exposed, since breed differences were about one-half heterosis. Considering only the Angus and Shorthorn breeds, the Angus-Shorthorn and Angus-Shorthorn-Angus rotation were nearly equal because the scaled breed differences were close to the point where ABA begins to exceed AB.

In both the swine and cattle examples, use of specific heterosis altered conclusions based on use of average heterosis. When only two breeds are considered, use of specific heterosis for average heterosis will determine the appropriate two-breed periodic rotation. Considering specific heterosis among three or more breeds is more complicated. However, increases in breed utilization must still offset heterosis losses. As noted previously (Bennett, 1987), some periodic rotations alter the ratio of heterozygosity due to one particular breed combination relative to total heterozygosity. Periodic rotations can be used to increase the proportion of total heterozygosity arising from breeds that show high heterosis and minimize the proportion of heterozygosity arising from breeds that show low heterosis.

Hypothetical cattle breeds characterized for birth weight, milk production and efficiency were used to illustrate the consideration of inter-generational variance of component traits in selection of periodic rotations. Table 2 gives trait ratios (percentage units) for the component and efficiency traits of the hypothetical breeds. Forty-six rotations with an average efficiency of 130 or greater were found. The five best rotations ignoring variances are shown in table 3. Using arbitrary thresholds of 5 and 10% for inter-generational variances of birth weight and milk production, respectively, the two rotations exceeding mean efficiencies of 130 are also shown in table 3. The five best rotations using arbitrary weighting factors of -.15 and -.02 for inter-generational variances of birth weight and milk production are also shown in table 3 for comparison. Selection among rotations with maximum thresholds for birth weight and milk production inter-generational variances reduced the mean efficiency by 5.32%.

The use of periodic rotations to control inter-generational variances of component and sec-

### Table 2. Additive Breed Effects and Heterosis for Seven Hypothetical Breeds of Cattle

<table>
<thead>
<tr>
<th>Breed</th>
<th>Birth wt, %a</th>
<th>Milk production, %a</th>
<th>Efficiency, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>73</td>
<td>150</td>
<td>117</td>
</tr>
<tr>
<td>B</td>
<td>100</td>
<td>105</td>
<td>110</td>
</tr>
<tr>
<td>C</td>
<td>107</td>
<td>111</td>
<td>110</td>
</tr>
<tr>
<td>D</td>
<td>96</td>
<td>102</td>
<td>101</td>
</tr>
<tr>
<td>E</td>
<td>111</td>
<td>111</td>
<td>96</td>
</tr>
<tr>
<td>F</td>
<td>115</td>
<td>43</td>
<td>85</td>
</tr>
<tr>
<td>G</td>
<td>99</td>
<td>78</td>
<td>84</td>
</tr>
<tr>
<td>Heterosis</td>
<td>3</td>
<td>7</td>
<td>27</td>
</tr>
</tbody>
</table>

aPercent of mean.
BREED AND HETEROSIS OPTIMIZATION

Primary traits require fortuitous combinations of breed differences and heterosis. In the example (table 2), breed A had very high milk production and very low birth weight. The reason for lower inter-generational variance in periodic rotations where the poorer breeds are used less frequently is that the less-used breeds result in an increase in heterosis in those generations in which they are used. Consequently, increased heterosis compensates for the decreased weighted average breed effect in the generations that a poorer breed is used. If breed A is used often in a rotation, then inter-generational variance in milk production will tend to be reduced because the effects of poorer milk-producing breeds will be associated with increased heterosis. However, using breed A often will increase the inter-generational variance of birth weight since breed A has the lowest birth weight. The probability of fortuitous combinations of breed differences and heterosis is increased by considering a large number of breeds as candidates for rotational crosses, and by focusing on those that have similar breed effects for secondary traits as well as those whose secondary traits deviate from their means in the same (or opposite) direction as heterosis. For instance, breeds G and E, whose deviations for milk and birth weight are in the same direction, are more likely to contribute to periodic rotations with low inter-generational variances of milk and birth weight than are breeds A and F, whose deviations are opposite.

Breed effects and heterosis are rarely known precisely, especially for efficiency of production. The best periodic rotation using breeds unequally can be more efficient than the worst conventional rotation. Misidentification of the best and second best breeds in a periodic rotation can result in reduced average breed effects and reduced heterosis. This same mistake is of no consequence in a conventional two-breed rotation. Breed effects need to be known with a reasonable degree of confidence before implementing unequal use of breeds in periodic rotations.

Literature Cited


TABLE 3. SELECTION OF ROTATIONS FOR AVERAGE EFFICIENCY BY 1) IGNORING INTER-GENERATIONAL VARIANCE, 2) SETTING A MAXIMUM THRESHOLD FOR COMPONENT VARIANCES OR 3) WEIGHTING COMPONENT VARIANCES

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Birth wt</th>
<th>Milk</th>
<th>Efficiency</th>
<th>Birth wt</th>
<th>Milk</th>
<th>Efficiency</th>
<th>Index^a</th>
<th>Selection\textsuperscript{b}</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABC</td>
<td>95.9</td>
<td>128.0</td>
<td>135.47</td>
<td>30.70</td>
<td>56.86</td>
<td>1.56</td>
<td>129.73</td>
<td>I, W</td>
</tr>
<tr>
<td>ABAC</td>
<td>90.7</td>
<td>134.6</td>
<td>135.10</td>
<td>31.29</td>
<td>37.70</td>
<td>5.92</td>
<td>129.65</td>
<td>I, W</td>
</tr>
<tr>
<td>ABCAB</td>
<td>93.0</td>
<td>129.9</td>
<td>134.75</td>
<td>34.28</td>
<td>55.88</td>
<td>4.48</td>
<td>128.49</td>
<td>I</td>
</tr>
<tr>
<td>ACAB</td>
<td>94.4</td>
<td>131.8</td>
<td>134.75</td>
<td>34.40</td>
<td>52.78</td>
<td>4.48</td>
<td>128.53</td>
<td>I</td>
</tr>
<tr>
<td>ACABAC</td>
<td>91.2</td>
<td>134.9</td>
<td>134.34</td>
<td>25.60</td>
<td>57.86</td>
<td>20.42</td>
<td>129.34</td>
<td>I, W</td>
</tr>
<tr>
<td>BCD</td>
<td>103.6</td>
<td>112.0</td>
<td>130.14</td>
<td>2.95</td>
<td>2.00</td>
<td>2.57</td>
<td>129.70</td>
<td>T, W</td>
</tr>
<tr>
<td>BCDBC</td>
<td>104.4</td>
<td>112.5</td>
<td>130.15</td>
<td>2.48</td>
<td>1.37</td>
<td>1.54</td>
<td>129.75</td>
<td>T, W</td>
</tr>
</tbody>
</table>

^aIndex of mean efficiency: \( -0.15 \times \text{variance of birth weight} - 0.02 \times \text{variance of milk} \)

\textsuperscript{b}Selection of five best rotations based on average efficiency by ignoring inter-generational variance (I) or using an index of average efficiency and weighted variance of birth weight and milk (W), or selection of the best two rotations with maximum inter-generational variances below 5 and 10\%\textsuperscript{2} for birth weight and milk, respectively, (T).


