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A note on the formation of optimal composite populations

B. P. Kinghorn, R. K. Shepherd and R. G. Banks

Department of Animal Science, University of New England, Armidale, NSW 2351, Australia

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Summary. Two recently proposed methods for predicting the optimal breed contributions to a new composite breed are discussed. It is shown that these can both lead to incorrect solutions, and a reliable method is proposed.

Key words: Composite breed – Optimisation – Crossbreeding

Introduction

Crossbreeding has become an important method of achieving improved genetic merit in most livestock industries. However, the cost of maintaining purebred units to supply parental stocks for crossbreeding can be high, especially in species with low fecundity. This is a major reason for the development of self-replacing composite breeds, each containing genetic material from a number of pure breeds.

MacNeil (1987) reviews one method (Kinghorn 1982) of predicting the optimal breed contributions to a new composite breed (the set of breeds and their relative contributions which give the highest predicted genetic merit at equilibrium). Both Kinghorn and MacNeil state that this method, termed the backward elimination method by MacNeil, can give rise to a sub-optimal solution. MacNeil proposes a forward-stepwise method, which he claims will ensure that the optimal breed composition is found. Unfortunately, the example he uses to contrast the methods involves arithmetic rounding errors which give rise to an incorrect conclusion.

This note will briefly demonstrate that both methods can, in fact, arrive at a sub-optimal solution, and that a more exhaustive approach must be used for reliability. This note will not describe the two methods involved. The reader is directed to MacNeil (1987) and Kinghorn (1982) for each description. A brief discussion on the utility of knowing the "best" breed composition of a composite breed will be given.

MacNeil's example

In the example given by MacNeil (1987), the "net returns through slaughter" for breeds I, II and III are 89, 93 and 69, respectively, presumably in units of dollars per breeding female, and heterosis is 30 units for all breed pairs.

In his use of the forward-stepwise method, MacNeil arrives at a perceived optimal composite including breed I (proportion of breed I, $p_I = 0.467$) and breed II ($p_{II} = 0.533$), with a calculated merit of 107 units. A more accurate calculation using, e.g., MacNeil's Eq. (2) follows:

$$Merit = (89 \times 0.467) + (93 \times 0.533) + 30\,(1 - (0.467^2 + 0.533^2)) = 106.07$$

In his use of the backward elimination method, MacNeil arrives at a composite between breed I ($p_I = 0.422$), breed II ($p_{II} = 0.489$), and breed III ($p_{III} = 0.089$), with a calculated merit of 106 units. These calculated breed proportions appear correct, but a more accurate calculation of merit using MacNeil's Eq. (2) follows:

$$Merit = (89 \times 0.422) + (93 \times 0.489) + (69 \times 0.089) + 30\,(1 - (0.422^2 + 0.489^2 + 0.089^2)) = 106.42$$

Contrary to MacNeil's claim, the backward elimination method has not given a solution with more breeds used than is optimal. In fact, a proper application of the forward-stepwise method would have progressed to use

Table 1. Calculation of optimum proportional contributions of three parental breeds (1, 2 and 3) to a new composite breed. Four examples are given, each defined by a G matrix. G is a square matrix with dimensions equal to the number of breeds involved, and elements $g_{i,j}$, $i=1$ to n and $j=1$ to n, where $g_{i,j}$ is the genetic value of the F_1 cross between breeds i and j, or the genetic value of pure breed i if $i=j$ (Kinghorn 1982). Genetic value can here relate to either a single trait or an index of traits, and can include both direct effects as expressed in an F_1 cross and maternal effects as expressed in the progeny of an F_1 cross. The forward-stepwise method and the backward elimination method are applied for each example (see MacNeil 1987 and Kinghorn 1982, respectively, for descriptions of method implementation). For each round of each method, the calculated breed proportions are shown as a column of three figures, breed 1 at the top. To the right of each column is the predicted genetic merit of the resulting composite. * Denotes an optimal result. For the first example, in which both methods fail, the optimal composite has proportions 0, 0.545, 0.455 with a predicted merit of 102.73 units

G matrix			Round	Forward-stepwise		Backward elimination	
100	90	90		1		0.560	
90	80	130	1	0	100	0.240	95.60
90	130	70		0		0.200	
			2	No change		No change	
110	110	121		1		0.043	
110	101	130	1	0	110	0.478	115.26*
121	130	100		0		0.478	
			2	No change		No change	
120	90	90		1		0.298	
90	80	130	1	0	120*	0.383	98.94
90	130	70		0		0.319	
			2	No change		No change	
110	130	130		1		0.424	
130	101	130	1	0	110	0.293	121.51*
130	130	100		0		0.283	
				0.592			
			2	0.408	118.16	No change	
				0.000			
				0.424			
			3	0.293	121.51*		
				0.283			

of all three breeds, giving a predicted merit of 106.42 units. Thus, properly applied, both methods will give the optimal result for this example.

Other examples

Table 1 illustrates the application of both the forward-stepwise and the backward elimination methods to four examples. Both methods fail to find the optimum composite in the first example. The forward-stepwise method fails in the second example, the backward elimination method fails in the third example, but both succeed in the fourth example.

Both methods can be used with confidence when F_1 dominance is positive and equal for each pair of parental breeds (such that the matrix G described in Table 1 is negative definite), as for example in MacNeil (1987). However, under less simple circumstances, solutions can represent other types of stationary points, such as saddles or local maxima. It is clear that better methods are required for the general case.

More reliable methods

The determination of the optimal composite breed can be considered as a special case of the quadratic programming problem (Gill et al. 1981). Algorithms designed for the solution of the general quadratic programming problem can be used. For example, the routine E04NAF in the Fortran subroutine library NAG (1987) will obtain the global maximum when the G matrix (as defined in Table 1) is negative definite or negative semi-definite; otherwise the solution obtained will be a local maximum (which may or may not be a global maximum). A grid of starting values can be used when the matrix is indefinite, so as to increase the chance of finding the global maximum. This grid procedure was used successfully in each of the examples discussed in this note.

A method which is completely reliable under the dominance model of heterosis involves finding every possible stationary point by applying, e.g., Eq. (5) of Kinghorn (1982) to each possible set of breeds. The feasible stationary point with the highest genetic merit is the global maximum. As the number of candidate breeds is not usually large, this method should be of use in practice. For example, with five breeds there are 31 possible stationary points to be found – this is the sum of ${}^5C_x$ for $x=1$ to 5.

Where epistasis is important in the expression of heterosis, the problem of predicting the optimal composite becomes complex, and this is not addressed here.

Utility of knowing "best" breed proportions

Whatever method is used, the value of developing an "optimal" set of breed contributions to aim at can be questioned. What mating strategy should be used to approach this state? Factors such as cost of breeding stocks and exploitation of within-breed genetic variation should affect the strategy adopted.

Kinghorn (1982, 1986) attempts to do this by incorporating crossbreeding effects and certain aspects of running costs into the selection index framework. Elzo and Famula (1985) present a multibreed sire evalution procedure which enables prediction of the total genetic value of progeny. In this case, the between-breed and within-breed genetic effects are integrated with environmental fixed effects to give a practical model.

These approaches can be applied in breeding programs if a suitable mate allocation algorithm is used. Simulation studies have shown that where the development of a composite breed results from such application, breed proportions approach the theoretically optimum set (Kinghorn 1986). This takes place while simultaneously exploiting within-breed genetic variation and accounting for certain costs.

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