

Formation of optimal composite populations

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Summary. The optimal breed composition of a composite population is derived from straightbred and average heterotic effects. It is demonstrated that there is a unique breed composition which maximizes a bioeconomic objective for a composite of m breeds. A forward stepwise approach for determination of the number of breeds to include in the composite population is advocated. Two examples of optimal composite populations are presented and briefly discussed using simulated net returns to weaning and through slaughter as objectives.

Key words: Breed use $-$ Composite populations $-$ Heterosis - Breed effects

Introduction

According to the U.S. Department of Commerce (Anonymous 1984), the majority of the U.S. beef breeding herd is contained in production units of 100 or fewer cows. Furthermore, these production units comprise the vast majority (93%) of all beef producers. Gregory and Cundiff (1980) advocated use of composite populations as a pragmatic means to exploit breed differences and heterosis in beef production units which are too small to effectively implement rotational crossbreeding systems. Composite populations are also advantageous if variation across generations in levels of performance are problematic in rotational crossbreeding systems (Gregory and Cundiff 1980).

Kinghorn (1980) devised a strategy for grading up an existing population through annual introductions of novel breeds to an improved composite population.

The objective in the grading up process was taken as annual maximization of genetic gain after consideration of operating costs. Later, in development of methodology to jointly consider inter- and intrabreed selection in the formation of composite populations, Kinghorn (1982) proposed a stepwise elimination approach to the breed selection problem. Addressed herein is formation of composite populations which at equilibrium maximize a bioeconomic objective, for example maximizing net return from the sale of weaned calves produced by the cows supported on a fixed resource base. The proportion of genes from each breed and the number of breeds to employ are specific questions which require solutions. Skjervold (1982) has discussed the practical importance of this problem for the development efficient breeding programs.

Theory

Proportional representation of breeds

Let the available populations of straightbreds be ordered 1 to n by their ranking for the bioeconomic objective and the economic value of the additive genetic effects of the ith straightbred be abbreviated gi for $i = 1$ to *n*. The representation of genes from each of the m breeds $(m \le n)$ to be included in a specific composite is abbreviated p_i for $i = 1$ to m, subject to:

$$
\sum_{i=1}^{m} p_i = 1 \tag{1}
$$

where m is the number of breeds to be used in the composite. Finally, let the economic value of total heterosis as it is expressed in composite populations at equilibrium be abbreviated H, and let H be assumed

positive and constant across the m breeds considered. The extension to consider breed-specific effects of heterosis would parallel Kinghorn (1982). In application, estimates of heterotic effects for all feasible pairs of beef breeds may not be known at all or with sufficient accuracy to distinguish between breedspecific and average effects on the bioeconomic objective. This lack of information necessitates use of the average effects.

After Dickerson (1973), the predicted value of the bioeconomic objective (Y) of an m breed composite is:

$$
Y = \sum_{i=1}^{m} g_i p_i + H \left(1 - \sum_{i=1}^{m} p_i^2 \right).
$$
 (2)

Equation 2 can be rewritten using equation 1 as:

$$
Y = \sum_{i=1}^{m-1} g_i p_i + g_m \left(1 - \sum_{i=1}^{m-1} p_i \right)
$$

+
$$
H \left[1 - \sum_{i=1}^{m-1} p_i^2 - \left(1 - \sum_{i=1}^{m-1} p_i \right)^2 \right].
$$
 (3)

To find the optimum set of p_i , the partial derivatives of Y (equation 3) with respect to each p_i are taken and the resulting set of differential equations are set equal to zero and solved simultaneously. The general form of $\partial Y/\partial p_i$ is shown in equation 4. The form of the solution for p_i is shown in equation 5.

$$
\frac{\partial Y}{\partial p_i} = g_i - g_m + 2 H \left[1 - \sum_{j=1}^{m-1} p_j | j \neq i - 2_{p_i} \right],
$$
 (4)

$$
p_i = \left[m g_i - \sum_{j=1}^{m} g_j \right] \left[2 m H \right]^{-1} + m^{-1} . \tag{5}
$$

It can be seen from equation 5 that the optimal composite population is composed of m breeds used in equal frequency only when the g_i for $i = 1$ to m are all equal. However, as H increases (ceteris paribus), the p_i approach m^{-1} ; that is the greater the magnitude of heterosis, the less important are the g_i's and the more important it is to have equal p_i 's to maximize the expression of H in the composite. The derivative of equation 4 with respect to p_i is:

$$
\frac{\partial^2 Y}{\partial p_1^2} = -4H
$$
 (6)

for all p_i . Since the equations typified by 2, 4 and 6 are all continuous and since equation 6 is negative for any value of i, there exists for a given value of m, a unique set of p_i which maximize Y. That set of p_i can be found as indicated above. Notice that the procedure presented here will yield the same set of optimum breed fractions in a composite of m straightbreds as Kinghorn's (1982) if the heterotic effects are different for all breed combination and the economic values are the same for the additive genetic effects of all breeds and the heterotic effects of all breed combinations.

Number of breeds

The performance of the composite for the bioeconomic objective is maximized subject to m being the minimum required to achieve the maximum level of performance. Thus, if the optimal three- and four-breed composites have equal levels of performance then m would be 3. This part of the problem can be approached in a stepwise manner. Breeds are added to the composite in order of rank for the bioeconomic objective. The next step is to identify the optimal twobreed composite and determine whether it exceeds the best straightbred, then continue to identify optimal $(m + 1)$ -breed composites until the optimal $(m + 1)$ breed composite no longer exceeds optimal m-breed composite or one of the p_i becomes negative. If there is more than one breed with equal g_i (i.e., there is a tie in the ranking of breeds), then those breeds should be added to the composite simultaneously. In contrast to the backward elimination procedure wherein infeasible solutions are discarded (Kinghorn 1982), the forwardstepwise approach ensures that the optimal breed composition is found. In addition, if the set of available breeds is large and the gi are diverse relative to H, then fewer sets of breed fractions may need to be examined to find the breed composition of the optimal composite population with a forward-stepwise procedure (Fig. 1).

A limitation

It is unlikely that the true optimal breed composition of a composite population can be achieved directly through the crossing of parental breeds. It can be shown that, in k generations of crossbreeding using straightbred sires, a breed composition can be attained so that each component breed is within $2^{-(k+1)}$ of the optimal proportions. Assume, for instance, that the optimal p_i of a four-breed composite are in the ranges of 0.4375 to 0.3125, 0.3125 to 0.1875, 0.3125 to 0.1875 and 0.1875 to 0.0625 for breeds A, B, C, and D, respectively. A four-breed (3/8A, 2/8 B, 2/8 C, 1/8D) composite can be formed in three generations $(2^{-4} =$ 1/16) as shown in Fig. 2. The sum of squares of deviations of achieved breed composition from optimal breed composition may provide a useful measure of the genetic distance between the achieved and optimal composite populations. This measure of distance can be used to compare alternative achievable

Fig. 1. Distributions of the number of breeds in an optimal composite population as a function of the ratio of the economic value of total heterosis and the standard deviation of economic value of the additive genetic effects (relative heterosis). It was assumed that economic values of the additive genetic effects were distributed normally and that the universe of available breeds numbered 20; 100 pseudorandom replicate samples were drawn for each level of relative heterosis

Table 2. Breed composite of populations which maximize net return to weaning

Breed designation	No. of breeds					
		2		4	5	6
I	0	0	0.322	0.274	0.250	0.236
$\mathbf H$		0.506	0.345	0.298	0.274	0.260
Ш	0	0	0	0	0	0.069
ĨV	0	0	0	0	0.095	0.081
v	0	0	0	0	O	0
VI	0	0	0	0.142	0.119	0.105
VII	0	0		0	0	0
VIII	0	0.494	0.333	0.286	0.262	0.248
Net return:	-19.0	1.5	8.0	9.2	9.6	9.9

Table 1. Sample straightbred effects and heterosis on net returns to beef producers

Fig. 2. Mating plan to develop a 3:2:2: I four-breed composite

3:2:2:1 RBCD COMPOSITE

population

breed compositions of composite populations relative to the optimum composition. It is this distance that will need to be overcome through selection in order to attain the optimal proportion of genes from each breed which contributes to the composite population (Kinghorn 1982).

Examples

The bioeconomic simulation model SIMUMATE (Minyard and Dinkel 1974) estimates net returns to all segments of the beef industry resulting from a variety of breeds and crossbreeding systems. Differences in energy required for maintenance and productive processes of the cow-herd, reproductive rate, growth rate, selling prices and costs of production are accounted for. The model was used to calculate sets of eight straightbred effects and average heterosis effects on net returns to weaning and accumulated through slaughter (Table 1). The methodology presented above was used to generate the breed composition for composite populations which maximize net return to weaning (Table 2) and accumulated through slaughter (Table 3). Even though these sets of net returns have a part-whole relationship and thus are correlated $(r=0.79)$, the optimal composites which maximize

Table 3. Breed composition of populations which maximize accumulated net returns through slaughter

their respective objectives are different. Net return to weaning is maximized with a six-breed composite and accumulated net return through slaughter is maximized with a two-breed composite. The twobreed composite which maximizes accumulated net return through slaughter is also sub-optimal among the two-breed composites at weaning (net return $= 1.0$). These results emphasize the importance of a priori definition of an appropriate objective. The equitable transfer of revenues through segments of the beef industry is also necessary, if cow-calf operators are to produce genotypes that are optimal for the entire industry.

The second example developed here also illustrates a feasible solution with more breeds used than is optimal. The solution $m = 3$ is arrived at using a backward elimination strategy where infeasible solutions are discarded. Both the forward-stepwise strategy and the backward elimination strategy yield the same optimal composite to maximize net return to weaning.

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