

GENETIC CONSEQUENCES OF CROSSBREEDING^{1, 2}

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CROSSBREEDING involves the mating of two or more breeds. In most species of domestic livestock, crossbreeding has some desirable consequences, especially in the production of market stock. These consequences are the production of heterosis, the opportunity to incorporate desirable genetic material quickly, and the chance to combine several desirable traits into a market animal. The consequences of crossbreeding depend on gene frequency differences among the breeds with the resulting increase of heterozygotes in the cross and the degree of dominance. For the crossbreeding to be utilized commercially in a class of livestock, there either must be a source of distinct genetic groups or the production of such groups must be economically possible, and the resulting crosses must have a distinct economic advantage over conventional market stock. Species having low reproductive potentials, such as cattle, must rely on exploiting the existing genetic differences among groups like breeds. Lucky is the species in which crosses among existing breeds have an economic advantage.

The purpose of this paper is to describe the consequences of crossbreeding in genetic terms by using a simple model. This is done so that the factors influencing the consequences can be specified and used to develop crossbreeding programs that maximize the advantage.

Theory

Consider a single locus with two alleles, A_1 and A_2 , and two breeds, H and A, that have gene frequencies $p:q$ and $p+\Delta p:q-\Delta p$. All parameters are expressed relative to breed H. The breed means and the cross are symbolized by μ_{ij} where i represents

the sire breed and j the dam breed. The means are

$$\begin{aligned}\mu_{HH} &= (p-q)a + 2pqd, \\ \mu_{AA} &= \mu_{HH} + 2\Delta pa - 2(\Delta p)^2d \\ \text{and } \mu_{AH} &= \mu_{HA} = \mu_{HH} + \Delta pa.\end{aligned}$$

The notation of Falconer (1960) is followed where the genotypic values of A_1A_1 , A_1A_2 and A_2A_2 are $+a$, d and $-a$, respectively. The d is the deviation of A_1A_2 from the midpoint between $+a$ and $-a$. When $d=a$ dominance is complete. The a represents the average effect of substituting the A_1 gene for the A_2 gene in breed H.

The means of the two breeds differ as a function of the gene frequency difference, Δp . The difference exists in two parts. The first involves the average effect of the gene and the second the dominance deviation. The gene frequency difference is involved in the additive part while the square of the gene frequency difference is involved in the dominance part. Even when dominance is complete, the additive part predominates. For $p=1/2$, $\Delta p=1/4$, and $a=d=1$ the additive part is $1/2$ and the dominance portion only $1/8$ or when $\Delta p=1/8$ the additive part is $1/4$ and the other part $1/32$.

Heterosis

The crossbred mean is increased by an additive part, Δpa , when a random set of males having gene frequency, $p+\Delta p:q-\Delta p$, are mated with a random set of females having gene frequency, $p:q$. Heterosis is defined as the difference between the mean of the cross and the average of the parents. The heterosis is

$$(\Delta p)^2d$$

for the A-H cross. It depends on the squared difference in gene frequency between the breeds and the degree of dominance. When either is zero there is no heterosis. This result suggests that to maximize heterosis in

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the offspring of a cross between breeds, the breeds crossed should be as genetically divergent (differ in gene frequency) as possible and the favorable gene must exhibit some dominance. Over-dominance ($d > a$) is not necessary for heterosis. This genetic divergence can be carried too far. When a deterioration of adaptive epistatic combinations of each breed occurs, then there are problems.

Further study of the mean difference result is informative. We have assumed that both breeds were random mating, but such is not true for the cross. There is an increase in the fraction of heterozygotes when compared with the average genotypic frequency of the two parents. The change is

$$\begin{aligned} A_1A_1 & - (\Delta p)^2/2, \\ A_1A_2 & + (\Delta p)^2 \\ \text{and } A_2A_2 & - (\Delta p)^2/2. \end{aligned}$$

Multiplying the changes by their respective genotypic values gives

$$(\Delta p)^2d$$

since the homozygotes cancel.

The cross mean is only increased by an additive part, Δp_a . This can be written as

$$\mu_{AH} = \mu_{HA} = \mu_{HH} + \Delta p(a - \Delta p d) + (\Delta p)^2d$$

since the contribution of say sires to their own breed relative to the other breed is

$$\Delta p(a - \Delta p d).$$

The AA breed is then

$$\mu_{AA} = \mu_{HH} + \Delta p(a - \Delta p d) + \Delta p(a - \Delta p d)$$

where the first term is the sire contribution and the second the dam one. These formulae apply equally well to the situation where Δp rather than being present is produced by selection. The difference between Δp_a found when one sex is selected and $\Delta p(a - \Delta p d)$ when the same sex is selected along with the other sex also or Δp^2d could be termed dominance slippage.

The Δp or difference in gene frequency between the breeds can be partitioned into the average difference between the breeds and that produced by selection of the particular parents. One runs the risk of decreasing the total difference in gene frequency and thus reducing measurable heterosis, but not the mean response.

In mammals, maternal heterosis especially for reproductive traits is expected. Consider the three breed cross where breed C has a gene frequency difference from breed A of

$\Delta p'$. The gametic array of the crossbred HA is

$$(p + \frac{\Delta p}{2}) A_1 + (q - \frac{\Delta p}{2}) A_2.$$

The mean of the three breed cross is:

$$\mu_{C \cdot HA} = \mu_{HH} + \Delta p'a + \frac{\Delta p}{2} a - 2\Delta p' \frac{\Delta p}{2} d.$$

The heterosis of the offspring, excluding maternal heterosis of the cross HA, is predictable from the average of the heterosis in cross CH and CA. The heterosis of the offspring, figured as the difference between the three way cross and the parent breeds is

$$1/2 (\Delta p')^2d + 1/2 (\Delta p - \Delta p')^2d$$

where $(\Delta p - \Delta p') = p_C - p_A$ since the heterosis is between C with H and C with A. Note that when p_C is most divergent with p_A and p_H maximum heterosis will occur. On top of this heterosis can be added that for maternal heterosis in the HA cross. The backcross or mating among the first cross halves the heterosis.

Incorporation

But crossbreeding has advantages besides the generation of heterosis. By crossbreeding, desired genes can be incorporated into a market animal faster than by conventional selection procedures within a breed. Suppose a group of breed H females are bred to bulls of breed H that have been selected for the trait of interest. Then the resulting offspring have a mean,

$$\mu_{HHS} = \mu_{HH} + \Delta p_s a,$$

where

$$\Delta p_s = \frac{pq a}{\sigma_p^2} \cdot S.$$

The first term of Δp_s is the regression of gene frequency change on selection differential (S) where σ_p^2 is the phenotypic variance. Suppose $p = 1/2$, $a = 1$, $\sigma_p = 100$, and $S = 100$. Then $\Delta p_s = .005$ and $\mu_{HHS} - \mu_{HH} = .005$. Now suppose that a group of breed H females are mated to bulls of breed C. Then

$$\mu_{CH} = \mu_{HH} + \Delta p'a$$

where $\Delta p'$ is the difference in average gene frequency between the breeds C and H. Since p in the selection example was $1/2$ the difference could be as large as $1/2$ giving the mean change of .5 rather than .005. Indeed, crossbreeding can be used to introduce new genes

into the combination that breed H does not have. Then $\Delta p_s = 0$ and $\Delta p'$ would be 1. Frequently, the introduction of new genes or the rapid increase in the frequency of desired genes is more important than the extra achieved by heterosis.

Suppose one wishes to incorporate desired genes by crossbreeding and selecting among the crossbreds say for a new breed. Market animal production has been considered to this point. One way to illustrate the response to selection in the crossbred context is by examining the covariance between gene frequency change and the selection differential as illustrated previously. This covariance is pqa in the H breed and $(p + \Delta p')(q - \Delta p')(a - 2\Delta p'd)$ in the C breed. Mating of CH crossbreds and selection among these offspring (F_2) gives a covariance for the locus of $(p + \frac{\Delta p'}{2})(q - \frac{\Delta p'}{2})(a - \Delta p'd)$ since random mating is returned. However, for selection among individuals of the CH cross the relationship of Δp_s to S is altered by there being an excess of heterozygotes. Relative to the F_2 covariance the covariance differs by

$$-\frac{(\Delta p')^2}{4} (a - d (q - p - \Delta p')).$$

Table 1 illustrates this lowering of selection response in the crossbreds when compared with the response in the F_2 . The first two examples are for genes being absent in one breed but fixed in the other. All crossbreds are A_1A_2 so no covariance exists. The other two examples involve intermediate frequencies. The results are those found in Lush (1945, p. 123) for Δp per generation when selection is for a gene with no dominance and with dominance. Obviously, this is oversimplified since several loci, linkage, et cetera are not considered. But, it does show the basic problem of selection among crossbreds.

Combination

By crossbreeding desired combinations of traits can be incorporated into the phenotype

TABLE 1. SELECTION RESPONSE IN THE CROSSBRED CONTEXT COMPARED

p	Δp	a	d	Covariance			
				HH	CC	HC _{F1}	HC _{F2}
0	+1	1	0	0	0	0	1/4
0	+1	1	1	0	0	0	1/4
1/4	+1/2	1	0	3/16	3/16	3/16	8/16
1/4	+1/2	1	1	9/32	3/32	6/32	8/32

of market animals. Also, desirable genes at different loci influencing the same trait can be incorporated. Consider two loci, one for trait X and one for trait Y each with two alleles. Then the breed means are

$$\begin{aligned}\mu_{HH} &= \mu_{AA} \\ \mu_{AA} &= \mu_{HH} + 2\Delta p a_X + 2\Delta p a'_Y \\ &\quad - 2(\Delta p)^2 d_X - 2(\Delta p')^2 d_Y\end{aligned}$$

where the primes denote the frequency difference for Y. Then the cross is

$$\mu_{HA} = \mu_{HH} + \Delta p a_X + \Delta p' a_Y.$$

Suppose that the frequency of the desired gene for X is 1 in breed H, that it is 0 in breed A, and that the reverse is true for Y. The $\Delta p = -1$ and $\Delta p' = +1$, so

$$\mu_{HA} = \mu_{HH} - a_X + a_Y.$$

When dominance is complete or $d = a$ we have

$$\begin{aligned}\mu_{HH} &= \mu_{HH} \\ \mu_{HA} &= \mu_{HH} + 2a_Y \\ \mu_{AA} &= \mu_{HH} + 2a_Y - 2a_X\end{aligned}$$

where μ_{HA} is greater than either parent breed. Even when dominance is not complete, the cross will be better for the combination of X and Y than either breed. This possibility for combining useful traits quickly in a market product is a primary consideration for crossbreeding.

Discussion

These simple examples using one and two loci, each with two alleles and no epistasis, serve to illustrate the consequences of crossing genetically divergent populations such as breeds. The consequences are

1. The production of heterosis. This depends on the degree of dominance and the square of the gene frequency difference between the populations crossed.
2. The incorporation of desired genes into a population at a faster rate than increasing the frequency of the genes by selection within the population. This depends on the gene frequency difference between populations relative to the gene frequency change possible by selection.
3. The incorporation of a combination of desirable traits into a population. This depends on the degree of dominance and the gene frequency difference.

In all three, the amount of genetic divergence (as measured by gene frequency differences)

influences the amount of response. In 1 and 3, the degree of dominance is important, but even complete or overdominance is not required for a response.

In general, the simple example lays bare the essential elements and consequences. The concept of dominance is described statistically as an interaction. The definition of heterosis is, in fact, a definition of interaction. Interaction is the failure of an additive scheme to describe the facts. Thus, the use of dominance serves to illustrate what occurs genetically upon crossing populations. Epistasis or the interaction among nonallelic genes is a contributing factor to heterosis, but its inclusion in the deliberations would be essentially like those of the dominance deviations. More than two alleles does complicate the theory somewhat because more than one dominance deviation per locus is possible. But if one gene of several at a locus is favored, then this gene can be used along with the rest lumped together, and the two-allele system is preserved. The inclusion of many loci rather than one or two is a simple additive process unless epistasis is considered. The simple example, although not nearly descriptive of a real situation, does serve as a model to use in the design of breeding programs and in the study and analysis of crossbreeding experiments.

Since the additive genetic variance equals $2pq\alpha^2$ for the example and since the heritability of a trait in general is $\Sigma 2pq\alpha^2/\sigma^2$,

where the sum denotes adding up all loci, the heritability of a trait provides a guide as to the amount of response to expect from crossbreeding. Usually, traits of high heritability show little evidence of heterosis. But for the other consequences, the desired response may not depend on the heritability of the trait, especially when an intermediate is desired. Crossbreeding studies themselves yield the best result as to whether there is enough dominance and epistatic variance to produce heterosis since the dominance variance, $(pqd)^2$ is illusive to estimate.

Summary

Crossbreeding produces some desirable consequences. They are the production of heterosis, the opportunity to incorporate desirable genetic material quickly, and the chance to combine several desirable traits into a market animal. The primary factor involved in each consequence is genetic divergence as measured by gene frequency difference among the groups. The degree of dominance is important in the production of heterosis and combining several desirable traits.

Literature Cited

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