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The effect of positive assortative mating on genetic parameters in a simulated beef cattle population*

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Summary. Two simulated data sets, representing random mating and positive assortative mating in a beef cattle population over 10 rounds of mating, were each composed of 100 replicates. Three correlated traits were considered; calving ease (CE), 200 day weight (WW) and postweaning gain (PG). All selection practiced in the simulation was random. Positive assortative mating, which was based on parental WW phenotypic records, increased the progeny additive genetic variance of WW. The absolute values of genetic covariances and correlations between WW with CE and PG were also increased by positive assortative mating. Variances or covariances did not reach their expected equilibrium values due to overlapping generations, low replacement rates and only 10 rounds of mating.

Key words: Simulation – Positive assortative mating – Beef cattle population

Introduction

Positive assortative mating involves individuals that are more alike phenotypically than they would be if the mating pair were chosen at random from a population.

Effects of assortative mating have been studied for a single locus, two allele model (Jennings 1916; Wentworth and Remick 1916) and for a multi-locus model (Fisher 1918; Wright 1921; Crow and Felsenstein 1968; Bulmer 1980). Positive assortative mating causes an increase in homozygosity, population variance (Crow and Felsenstein 1968) and genetic variance (Bulmer 1980). The increase in homozygosity is very small with a multifactorial model unless the number of loci is small and the phenotypic correlation between mates is very nearly unity (Lush 1948; Crow and Felsenstein 1968). In the case of non-overlapping generations, the equilibrium values in homozygosity and genetic variance are reached rapidly. The majority of the increase in genetic variance occurs within the first few generations following positive assortative mating (Bulmer 1980). The large increase in genetic variance can be explained by an association of genes of like effect which results in gametic phase (linkage) disequilibrium (Crow and Felsenstein 1968). Gianola (1982) determined that positive assortative mating increases the genetic correlation between two traits but does not change the sign of correlation.

Little consideration has been given to the effects of positive assortative mating on genetic parameters in livestock populations, where breeding animal replacement rates are low and generation overlap exists. Therefore, this study examines the effect of positive assortative mating on the genetic variances, covariances and correlations of three correlated traits in a simulated beef cattle population.

Simulation

The assumption that the genetic variance is composed of equal effects from an infinitely large number of unlinked loci is invoked for the complete simulation. Two sets of replicated data were used to compare random and positive assortative mating. Each data set was composed of 100 replicates. Each replicate consisted of a base population and 10 rounds, or cycles, of mating. The base population is assumed to be in Hardy-Weinberg and linkage equilibrium, i.e. zero covariance within and between chromosomes. Breeding values were simulated for three traits: calving ease (CE), 200 day weight (WW) and postweaning gain (PG). Breeding values of base population animals, 20 sires and 500 dams all unrelated, were

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simulated according to an additive genetic model following a method described by Schaeffer (1982). Given $\mathbf{w}$, a vector of independent pseudorandom normal deviates, then $\mathbf{w} \sim N(\mathbf{0}, \mathbf{1})$ and given $\mathbf{V} = \mathbf{TT}'$ where $\mathbf{T}$ is a lower triangular matrix, then $E(\mathbf{Tw}) = \mathbf{T}(E(\mathbf{w})) = \mathbf{0}$ and $V(\mathbf{Tw}) = \mathbf{T}(V(\mathbf{w}))\mathbf{T}' = \mathbf{TT}' = \mathbf{V}$. The matrix $\mathbf{V}$ is the additive genetic variance-covariance matrix among the traits (Table 1). $\mathbf{Tw}$ represents a vector of simulated breeding values for the traits. The elements of $\mathbf{T}$ were computed using a Cholesky decomposition of $\mathbf{V}$ (e.g. Goult et al. 1974) and the elements of $\mathbf{w}$ were generated using the IMSL (1979) subroutine RANDOM.

For each trait, phenotypic records were the sum of a fixed mean effect plus the breeding value of the animal plus a random residual effect. The random residual effects for each trait were generated using the same method that was used to generate the breeding values. The residual variances and covariances used in this procedure are in Table 1. The fixed mean values were 94 pts, 208 kg and 137 kg for CE, WW and PG, respectively and remained constant for the entire simulation. Each round of simulation included determination of mates, mating, computation of progeny breeding values, random culling of parents and random selection of replacement progeny. Mating was either random or positive assortative. Each male parent was mated to 25 female parents each round. Random mates were chosen using pseudo-random variables from a uniform distribution.

Given the assumption of a large number of unlinked loci with free recombination, the additive genetic model used in this simulation produces normally distributed genotypic values under random mating (Sorensen and Kennedy 1984). The phenotype will also be normally distributed because the phenotype was the sum of the genotype and a normally distributed environmental effect. Bulmer (1971) demonstrated that changes in genetic variance due to directional selection, were due to the generation of gametic disequilibrium among loci and not changes in gene frequencies. Bulmer (1980) also showed that, given this model, the genotypic values following selection and mating were of approximately multivariate normal distribution. Therefore, as discussed by Sorensen and Kennedy (1984), the genetic model and simulation procedures for random or positive assortative mating used in this study simulate the Mendelian process. In this study positive assortative mating was based on phenotypic 200 day weight records of parent animals. The sires and dams were ranked separately for WW from the highest to lowest. The top ranking sire was mated to the top 25 ranking dams, the second ranking sire to the next 25 ranking dams, etc., until all matings were completed.

Table 1. Variances and covariances used in simulation[a]

Trait	Trait[b]		
	Calving ease (CE)	200 day weight (WW)	Postweaning gain (PG)
CE	24.8 257.0	− 10.4	− 9.3
WW	− 38.6	122.6 591.0	30.7
PG	0.0	− 51.5	77.7 457

[a] Genetic variances and covariances above diagonal, residual below diagonal as estimated for the Hereford breed by Schaeffer and Wilton 1981

[b] Variance for CE in pts², WW and PG in kg²

Progeny breeding values were the average of the sire and dam breeding values plus a Mendelian sampling term (E). The Mendelian sampling term was generated in the same manner as the breeding values of parent animals as described previously. The Mendelian sampling variances and covariances, in the absence of inbreeding, are equivalent to one-half the additive genetic variances and covariances (Table 1). Inbreeding was ignored because the average inbreeding coefficient at equilibrium would be negligible (Crow and Felsenstein 1968). The progeny phenotypic records for each trait were computed as the sum of the fixed mean effect plus the progeny breeding value plus a random residual term. The sex of the progeny was determined using an independent pseudo-random normal deviate ($X \sim N(0, 1)$), such that if $X \geq 0.0$ the animal was a male, otherwise, the animal was a female.

Four sires and 50 dams were randomly culled each round, which represented 20 and 10% replacement rates, respectively. Replacement animals were randomly chosen from the progeny of the current round. Culled animals and progeny not selected as replacement animals were considered removed from the simulation.

Results and discussion

The mean variances and covariances of progeny breeding values were computed separately for each round of each data set. Mean variances and covariances of progeny breeding values with random mating are listed in Table 2 and with positive assortative mating in Table 3. Mean variances and covariances with random mating were not significantly different from the initial values (Table 1) for any of the traits. Positive assortative mating did not significantly affect the variances of CE or PG nor the covariance between CE and PG over 10 rounds (Table 3). However, the variance of WW and covariances between WW with CE and PG were increased (in absolute measures) over the initial values. These increases in the additive genetic variance and covariance agree with Crow and Felsenstein (1968), Bulmer (1980) and Gianola (1982). But, the increases did not meet the expected equilibrium variance-covariance values (Table 4) which were computed using formulae described by Gianola (1982). The phenotypic correlation between mates for WW was 0.97. The mean progeny variances and covariances between WW and PG or CE never reached their expected equilibrium values after 10 rounds of positive assortative mating. A probable explanation for this results from overlapping generations with only 20 and 10% of the sires and dams being replaced each round.

This problem of overlapping generations with replacement rates of 20 and 10% for sires and dams is presented in Table 5. The percentage distribution of parents from each round which are still expected to be in the parent population after 10 rounds is determined

Table 2. Mean variances and covariances of progeny breeding values by round with random mating

Round	Mean variances and covariances[a]					
	σ_1^2	σ_2^2	σ_3^2	σ_{12}	σ_{13}	σ_{23}
1	24.4 ± 0.3[b]	123.0 ± 1.3	76.6 ± 0.6	-10.5 ± 0.4	-9.3 ± 0.3	31.6 ± 0.7
2	24.3 ± 0.3	122.3 ± 1.3	76.7 ± 0.8	-10.1 ± 0.4	-9.2 ± 0.3	30.9 ± 0.7
3	24.3 ± 0.3	121.3 ± 1.4	76.4 ± 0.8	-10.5 ± 0.4	-9.5 ± 0.3	30.1 ± 0.7
4	24.2 ± 0.2	122.8 ± 1.3	77.0 ± 0.8	-10.9 ± 0.4	-9.7 ± 0.3	31.1 ± 0.7
5	23.8 ± 0.3	122.4 ± 1.4	77.4 ± 0.7	-10.8 ± 0.4	-9.2 ± 0.3	31.0 ± 0.8
6	24.1 ± 0.3	122.2 ± 1.5	76.3 ± 0.7	-11.0 ± 0.5	-9.1 ± 0.3	30.3 ± 0.9
7	24.2 ± 0.3	120.8 ± 1.4	76.9 ± 0.8	-10.5 ± 0.4	-9.6 ± 0.3	31.0 ± 0.8
8	24.1 ± 0.2	121.0 ± 1.5	76.6 ± 0.8	-10.0 ± 0.4	-9.1 ± 0.3	29.4 ± 0.8
9	24.0 ± 0.3	119.1 ± 1.4	77.2 ± 0.9	-10.0 ± 0.4	-9.2 ± 0.3	29.1 ± 0.9
10	24.1 ± 0.3	118.5 ± 1.1	76.9 ± 0.8	-9.7 ± 0.4	-9.2 ± 0.4	28.8 ± 0.8
Initial values[c]	24.8	122.6	77.7	−10.4	−9.4	30.7

[a] Across 100 replicates where 1, 2 and 3 correspond to calving ease, weaning weight and postweaning gain, respectively

[b] Standard error of the mean

[c] Initial values are those used as parameter inputs to the simulation

Table 3. Mean variances and covariances[a] of progeny breeding values by round with positive assortative mating

Round	Mean variances and covariances[a]					
	σ_1^2	σ_2^2	σ_3^2	σ_{12}	σ_{13}	σ_{23}
1	24.8 ± 0.3[b]	131.3 ± 1.6	77.2 ± 0.8	-10.8 ± 0.4	-9.3 ± 0.4	32.4 ± 0.8
2	24.5 ± 0.3	131.5 ± 1.5	76.4 ± 0.9	-10.7 ± 0.5	-9.1 ± 0.4	33.0 ± 0.9
3	24.4 ± 0.3	130.8 ± 1.5	75.9 ± 0.8	-10.3 ± 0.5	-8.7 ± 0.4	32.6 ± 0.9
4	24.8 ± 0.3	133.6 ± 1.8	76.7 ± 0.9	-11.2 ± 0.5	-9.3 ± 0.4	33.7 ± 0.9
5	24.6 ± 0.3	135.6 ± 1.7	76.1 ± 0.9	-11.7 ± 0.5	-9.0 ± 0.4	33.9 ± 0.9
6	24.4 ± 0.3	135.4 ± 2.0	76.6 ± 0.9	-11.6 ± 0.6	-9.1 ± 0.4	34.0 ± 1.1
7	24.5 ± 0.2	135.2 ± 1.8	75.9 ± 0.9	-11.6 ± 0.6	-9.1 ± 0.3	32.8 ± 0.9
8	23.9 ± 0.3	134.9 ± 1.9	75.5 ± 0.9	-11.6 ± 0.6	-8.7 ± 0.3	32.9 ± 1.1
9	23.8 ± 0.3	135.7 ± 2.1	77.0 ± 0.9	-11.5 ± 0.6	-8.8 ± 0.3	33.5 ± 1.1
10	24.0 ± 0.3	136.4 ± 2.0	76.5 ± 1.1	-11.7 ± 0.6	-9.0 ± 0.3	33.7 ± 1.0
Initial values[c]	24.8	122.6	77.7	−10.4	−9.4	30.7

[a] Across 100 replicates where 1, 2 and 3 correspond to calving ease, 200-day weight and postweaning gain, respectively

[b] Standard error of the mean

[c] Initial values are those used as parameter inputs to the simulation

Table 4. Expected equilibrium variances and covariances with positive assortative mating and non-overlapping generations

	Variances and covariances[a]				
	σ_1^2	σ_2^2	σ_3^2	σ_{12}	σ_{23}
Initial value	24.80	122.64	77.72	−10.36	30.68
Equilibrium value	25.01	152.77	79.54	−11.74	37.70
% increase	0.85	24.6	2.3	13.3	22.9

[a] 1, 2 and 3 correspond to calving ease, 200-day weight and postweaning gain, respectively

by the replacement rates. Table 5 shows that a large percentage, 13.4 and 38.7 of the sires and dams, respectively, from the base population will still be parents after 10 rounds. Since base population animals were not products of positive assortative mating, variances and covariances among them are expected to equal the initial values. As well, parents from other rounds (2–9) are affected by positive assortative mating to a smaller degree than parents from round 10. Therefore, differing replacement rates cause variable changes in genetic variances and covariances which directly affect the response to selection from a breeding program.

Table 5. Percentage of parents at each round which are parents after 10 rounds of simulation

Parents	% by round[a]									
	1	2	3	4	5	6	7	8	9	10
Sires	13.4	3.5	4.0	5.5	6.5	8.0	10.5	13.0	16.0	20.0
Dams	38.7	4.3	4.8	5.3	5.9	6.6	7.3	8.1	9.0	10.0

[a] Assumes random replacement of 20% of sires and 10% of dams each round

The expected equilibrium genetic correlations between WW with CE and PG were computed according to Gianola (1982). The base population genetic correlations were −0.17 and 0.31 for CE and PG with WW, respectively. The genetic correlations following 10 rounds were −0.16 and 0.33 for CE and PG with WW, respectively. The expected equilibrium genetic correlations of CE with WW and PG with WW were −0.19 and 0.34, respectively. The genetic correlation of CE with WW was essentially unchanged given rounding error but the correlation of PG with WW increased by 0.02 compared to the base population values. As with the variances and covariances, the genetic correlations did not reach the expected equilibrium values because of the overlapping generations, too few rounds of mating and low replacement rates in the simulated beef cattle population.

The sign of the base population correlation of PG with WW was the same as the sign of the phenotypic correlation between mates for WW. Therefore, the equilibrium genetic correlation of PG with WW was greater than the base population correlation as predicted by Gianola (1982). The base population genetic correlation of CE with WW was opposite in sign to the phenotypic correlation between mates for WW. This resulted in an equilibrium genetic correlation which was less than the base population genetic correlation of CE with WW which also agrees with the theoretical conclusions made by Gianola (1982).

In conclusion, positive assortative mating increased the genetic variance for WW and the absolute value of the covariances between WW with CE and PG. The variances and covariances did not reach their expected equilibrium levels under positive assortative mating because of overlapping generations, low replacement rates and the number of rounds of mating. Replacement animals have a two year time span per round while breeding animals have one year per round with the replacements used. Each round of mating represents approximately one year. Therefore the total simulation represents about 10 years. The increases in variances and covariances under very strict positive assortative mating were not as large as the theoretical predictions. The problem of low replacement rates in beef cattle populations coupled with overlapping generations reduces the response to positive assortative mating. Therefore, when trying to utilize positive assortative mating in a breeding program for beef cattle one cannot expect the rapid changes in genetic variance and correlations that are predicted by theory.

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