Theor Appl Genet (1995) 91: 776–779

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The effect of simultaneous selection on the genetic correlation

Received: 31 November 1994 / Accepted: 21 April 1995

Abstract The theoretical effect of simultaneous selection on the genetic correlations between two traits over 20 generations was examined using simulation. For each generation, a population of 50 male and 50 female diploid genotypes with 15 loci, each with two alleles, was synthesized. None of the loci exhibited dominance. Five loci affected only trait 1, 5 loci only trait 2 and 5 were pleiotropic (affected both traits). Initial allelic frequencies were equal at each locus. Phenotypes were created by adding a random normal deviation for each trait to the genotype. The size of this deviation for each trait determined its heritability (h^2). Index selection with h^2 combinations of (0.15, 0.15), (0.15, 0.45) and (0.45, 0.45) and relative economic weights of (1, 1) and (1, 3) for each h^2 combination was employed. In each generation, the highest ranking 25 genotypes of each sex were used to generate the next generation with single-pair matings, each producing two male and two female offspring. One hundred replicates were run for both negative and positive correlations. With a positive initial value, the genetic correlation tended to decline (toward zero). The rates of change were moderately affected by index weights and h^2. With a negative initial value, the genetic correlation tended to decrease (towards –1). However, unequal heritabilities and unequal relative economic weights slowed the rate of change with the greatest imbalances tending to hold the correlation constant or move it toward zero. These simulations illustrate that changes in parameters over time can affect the selection practiced. Under some of the conditions simulated, the use of initial genetic parameter values without change could have potentially negative effects on overall genetic gain.

Key words Index selection · Genetic correlation · Simulation · Heritability · Economic weight

Introduction

The genetic correlation exhibited between two or more traits in a population can be caused either by the linkage disequilibrium of genes affecting the traits independently or by the pleiotropic effects of single loci. Since the effect of linkage disequilibrium is dissipated as the population approaches equilibrium, pleiotropism is probably the more relevant of the two mechanisms for applied study.

Much work has been done on the sensitivity of estimation procedures for the genetic correlation coefficient (Reeve 1955; Robertson 1959) and on the behaviour of the genetic correlation in single trait selection (Parker et al. 1969, 1970), but little attention has been given to the behaviour of the genetic correlation under simultaneous selection for more than one trait. Lerner (1950) suggested that simultaneous selection for two characters would cause a reduction in their genetic correlation, and just such a decline was observed by Friars et al. (1962) while selecting in poultry. However, the trend in genetic correlations between traits under selection was dependent on the environment (Friars et al. 1973). Since the genetic correlation between traits x_i and x_j can be expressed as,

$$r_G = \frac{\sigma_{ij}}{\sigma_i \sigma_j} \tag{1}$$

where σ_{ij} is the genetic covariance of x_i and x_j and σ_i and σ_j are their respective genetic standard deviations, a decline in the absolute value of r_G implies that σ_{ij} is being reduced in relation to $\sigma_i\sigma_j$.

Letting the effect of a gene substitution at locus k affecting trait x_i be α_{ik}, the genetic variances and covariances

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Communicated by E. J. Eisen

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of traits x_i and x_j can be expressed as

$$\sigma_i^2 = 2\sum_{k=1}^{m} a_{ik}^2 \, q_k (1-q_k) \qquad (2)$$

$$\sigma_{ij} = 2\sum_{k=1}^{m} a_{ik} \, q_{jk} \, q_k (1-q_k) \qquad (3)$$

where q_k is the frequency of the + allele at the k^{th} locus and m is the total number of loci affecting either or both traits. After one generation of selection, the change in these parameters can be expressed as a function of the change in q;

$$\Delta\sigma_i^2 = 2\sum_{k=1}^{m} a_{ik}^2 \, \Delta q_k (1-2q_k+\Delta q_k) \qquad (4)$$

$$\Delta\sigma_{ij} = 2\sum_{k=1}^{m} a_{ik} \, a_{jk} \, \Delta q_k (1-2q_k+\Delta q_k) \qquad (5)$$

To find the rate of change of these parameters, it is necessary to express Δq in terms of the selection pressure at each locus. If traits x_i and x_j are given equal economic weights, then under simultaneous selection,

$$\Delta q_k = \bar{\imath}\left\{\frac{a_{ik}}{V_i^{1/2}} + \frac{a_{jk}}{V_j^{1/2}}\right\} q_k \, s(1-q_k) \qquad (6)$$

where $\bar{\imath}$ is the standardized selection differential and $V_i^{1/2}$ is the phenotypic standard deviation of trait x_i.

Bohren et al. (1966) pointed out that, for genes exerting pleiotropic effects, those for which α_i and α_j are of the same sign would contribute most to the change in genetic variance and covariance parameters. That is, the selection pressure on these loci is greater than the selection pressures that act separately on the non-pleiotropic loci. This is because the average effect of a gene substitution when using an index is the summed contribution of the locus to both traits. Therefore, the gene frequency at the pleiotropic loci will be changing more rapidly than at the non-pleiotropic loci causing σ_{ij} to change more rapidly than $\sigma_i\sigma_j$. Conversely, if α_i and α_j are equal but of opposite sign at the pleiotropic loci, σ_{ij} will change more slowly than $\sigma_i\sigma_j$. How these changes in gene frequency affect the genetic correlation depends upon the gene frequencies themselves and the direction of selection. Both genetic variance and covariance parameters are maximized at q=0.5 and decrease as q moves away from 0.5 in either direction.

There are an infinite number of possible combinations of correlations, selection methods and gene frequencies. We have chosen to examine a rather simple case where all gene effects are equal and additive, all initial gene frequencies are 0.5 and selection is by the index method.

Methods

A computer programme was written to create, by simulated random mating, a population of 50 male and 50 female diploid genotypes, each having 15 loci. All 15 loci had two alleles that exhibited no dominance, and each locus controlled one or both of two traits, x_1 and x_2. For both traits, the homozygous values were –1 and 1, while the heterozygote value was 0. Five of the loci controlled only trait x_1, 5 controlled only x_2 and the remaining 5 were pleiotropic.

The weights (b_i) used for constructing the index of each phenotype in the population were calculated in each generation from

$$\boldsymbol{b} \times P^{-1} \, G\boldsymbol{a} \qquad (7)$$

where P and G are the phenotypic and genotypic variance-covariance matrices calculated in each generation and **a** is the vector of relative economic weights. The indices were ordered in the population, and the 25 largest of each sex were selected to generate the next generation of genotypes. Single pair matings were randomly made, each producing two males and two females.

A genetic correlation of 0.5 was simulated by $\alpha_1=\alpha_2$ for all pleiotropic loci, while $\alpha_1=-\alpha_2$ at these same loci allowed for $r_G=-0.5$. Genetic effects were additive, and phenotypes were created by adding a random normal deviation for each trait to the genotypes. The size of this deviation in relation to the genetic values determined the heritabilities of the two traits.

Different combinations of two heritabilities (0.15 and 0.45) and two economic weights (1 and 3) were employed, and 100 replicate runs were done for each combination using different initial populations for each run. Selection was continued over 20 generations, and the genetic correlation in each generation was obtained as the product-moment correlation of the recalculated genetic values of traits x_1 and x_2. The change in correlation from initial to final generation was calculated for each combination of heritabilities and economic weights.

Results and discussion

Table 1 summarizes the computer simulation results for the change in r_G across 20 generations of selection for each set of parameter combinations. When the initial genetic correlation was positive, r_G showed a decline towards zero for all combinations of heritabilities and economic weights. As expected, the rate increased as h^2 increased for one or both traits. For an initial genetic correlation of –0.5, r_G declined towards zero when the economic weights were unequal, but increased in absolute magnitude and moved towards –1.0 when the economic weights were equal. The interpretation of these observations relates directly to the relative changes in gene frequency at the various loci.

When the economic weights are equal and r_G is initially positive, the selection pressure is greater on pleiotropic loci than on non-pleiotropic loci, and σ_{ij} is declining at a greater rate than $\sigma_i\sigma_j$. When r_G is initially negative, the opposite situation arises. Now the pleiotropic loci tend to change more slowly in gene frequency than non-pleiotropic loci, and σ_{ij} declines more slowly than $\sigma_i\sigma_j$. To verify that this is the case, we show the average gene frequencies at each set of 5 loci in generation 20 in Table 1 for each combination of parameter values used. The gene frequencies appearing in the table are for those alleles being selected at each locus. For the pleiotropic loci, the gene frequencies are for the allele favouring trait x_1 when $r_G=-0.5$.

It is apparent from Table 1 that when r_G is initially positive, the alleles at the pleiotropic loci are moving towards fixation more rapidly than are alleles at the non-pleiotropic loci. When r_G is initially negative and the economic weights and heritabilities are equal, alleles at pleiotropic loci maintain intermediate frequencies while alleles at non-

Table 1 Initial values for each set of parameters and mean changes in r_G (Δr_G) with its standard deviation ($\sigma_{\Delta r_G}$) over 20 generations of selection. Frequencies of alleles averaged over five loci favouring trait 1 ($\bar{p}_1$), ($\bar{p}_{12}$) and trait 2 ($\bar{p}_2$)

Initial values							Generation 20		
r_G	a_1	a_2	h_1^2	h_1^2	Δr_G[a]	$\sigma_{\Delta r_G}$	$\bar{p}_1$	$\bar{p}_2$	$\bar{p}_{12}$
0.5	1	1	0.15	0.15	−0.35	0.17	0.853	0.849	0.976
0.5	1	1	0.15	0.45	−0.46	0.17	0.815	0.975	0.997
0.5	1	1	0.45	0.45	−0.49	0.15	0.966	0.968	1.000
0.5	1	3	0.15	0.15	−0.33	0.17	0.777	0.891	0.973
0.5	1	3	0.15	0.45	−0.45	0.15	0.763	0.989	0.997
0.5	1	3	0.45	0.45	−0.49	0.16	0.929	0.983	1.000
−0.5	1	1	0.15	0.15	−0.17	0.11	0.867	0.873	0.475
−0.5	1	1	0.15	0.45	−0.17	0.16	0.877	0.976	0.198
−0.5	1	1	0.45	0.45	−0.42	0.08	0.983	0.982	0.510
−0.5	1	3	0.15	0.15	0.16	0.15	0.519	0.936	0.070
−0.5	1	3	0.15	0.45	0.31	0.18	0.671	0.992	0.014
−0.5	1	3	0.45	0.45	0.14	0.17	0.791	0.993	0.033

[a] Each Δr_G is significantly different from 0 ($P < 0.05$)

pleiotropic loci move towards fixation. When the economic weights are equal and h_2^2 is greater than h_1^2, the loci change in frequency more rapidly for trait 2 than trait 1, and the pleiotropic loci exhibit a change in favour of the allele favouring trait 2. With unequal economic weights, the change in gene frequency, whether heritabilities are equal or not, is more evident for loci controlling trait 2 than for those controlling trait 1, and the frequencies of alleles at pleiotropic loci become very much in favour of the allele for trait 2.

The direction of change in the genetic correlation when it is initially negative depends upon the balance of selection pressures at the pleiotropic loci. When the economic weights and heritabilities for each trait are equal, the selection pressures at pleiotropic loci for each trait tend to cancel one another. When this balance is upset by unequal heritabilities, r_G continues to move towards −1.0, but at a slower rate than expected, as can be seen from the values in Table 1. When the economic weights are unequal, r_G shows a small positive change in value. When both heritabilities and economic weights are unequal, r_G moves towards zero more rapidly than when only heritabilities differ. The way in which the heritabilities and economic weights exert their influence on r_G can be seen from an examination of the index weights (b_1).

From,

$$\boldsymbol{b} \times P^{-1}\, G\boldsymbol{a} \tag{7}$$

solving for **b** we have.

$$b_1 = \frac{\sigma_1 \sigma_2}{|P|}\left\{V_2\left(\frac{\sigma_1}{\sigma_2} a_1 + r_G\, a_2\right) - V_{12}\left(\frac{\sigma_2}{\sigma_1} a_2 + r_G\, a_1\right)\right\} \tag{8}$$

$$b_2 = \frac{\sigma_1 \sigma_2}{|P|}\left\{V_1\left(\frac{\sigma_2}{\sigma_1} a_2 + r_G\, a_1\right) - V_{12}\left(\frac{\sigma_1}{\sigma_2} a_1 + r_G\, a_2\right)\right\} \tag{9}$$

where |P| is the determinant value of the phenotypic variance-covariance matrix, σ_i is the genotypic standard deviation of trait i, r_G is the genetic correlation coefficient and V_i and V_{12} are the phenotypic variances and covariances. The ratio of b_1/b_2 is shown to generation 15 for each of the variable combinations simulated in Figs. 1 and 2.

When $\sigma_{12}=V_{12}=0$, these expressions reduce to the familiar $b_i=h_i^2a_i$. When $\sigma_1=\sigma_2$, $r_G=-0.5$ and $a_1=a_2$ then,

$$b_1 = \frac{\sigma_1 \sigma_2}{|P|}\{0.5(V_2 - V_{12})\} \tag{10}$$

$$b_2 = \frac{\sigma_1 \sigma_2}{|P|}\{0.5(V_1 - V_{12})\} \tag{11}$$

If $V_1=V_2$ then $b_1=b_2$, but if $V_1 \neq V_2$ then $b_1 \neq b_2$. This inequality in the index weights was seen to be sufficient to change the progress of r_G from −0.5 towards 0 instead of −1.0.

It is interesting to note that b_1 can be negative while b_2 is positive. This occurs when $r_G=-0.5$, $h_1=h_2$, $a_1=1$ and $a_2=3$. Here,

$$b_1 = \frac{\sigma_1 \sigma_2}{|P|}\{-0.5(V_2 + 5V_{12})\} \tag{12}$$

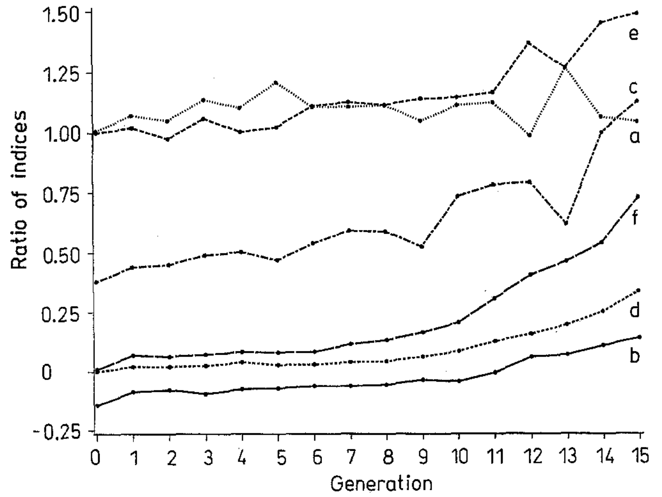

Fig. 1 Changes in b_1/b_2 across generations when the initial r_G is −0.5 for each combination of initial heritability and economic weights. Graph coding is as follows:

	a	*b*	*c*	*d*	*e*	*f*
h^2	(0.15 0.15)	(0.15 0.15)	(0.15 0.45)	(0.15 0.45)	(0.45 0.45)	(0.45 0.45)
Economic weights	(1,1)	(1,3)	(1,1)	(1,3)	(1,1)	(1,3)

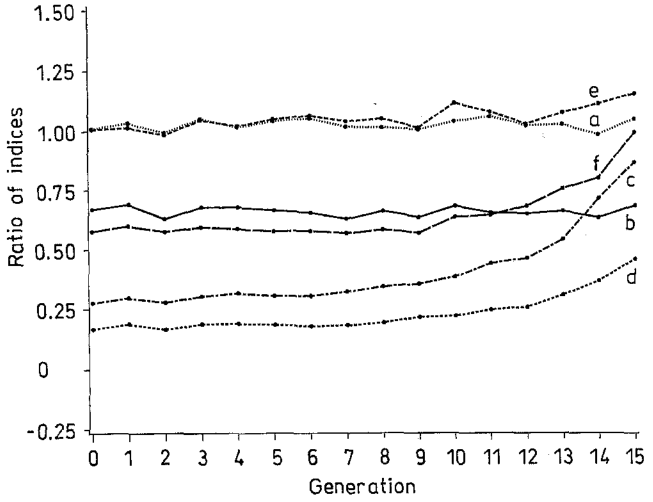

Fig. 2 Changes in b_1/b_2 across generations when the initial r_G is 0.5 for each combination of initial heritability and economic weights. See legend to Fig. 1 for graph coding

Table 2 Values of b1 and b2 across 20 generations for initial values $r_G=-0.5$, $h_1^2=h_2^2=0.15$, $a_1=1$ and $a_2=3$

Generation	b_1	b_2
0	−0.055	0.388
1	−0.033	0.365
2	−0.026	0.350
3	−0.031	0.341
4	−0.023	0.337
5	−0.023	0.316
6	−0.020	0.312
7	−0.020	0.297
8	−0.017	0.277
9	−0.010	0.260
10	−0.013	0.241
11	−0.004	0.217
12	0.008	0.199
13	0.010	0.186
14	0.016	0.167
15	0.017	0.151
16	0.019	0.139
17	0.022	0.134
18	0.023	0.121
19	0.032	0.106

Table 2 lists such results for these values of r_G and a_i with $h_1^2=h_2^2=0.15$. V_{12} is composed of only genetic covariance and will be negative, but if its magnitude is such that V_2+5V_{12} is still positive, then $b_1<0$. This will result in low values of trait x_1 being favoured until V_2 and r_G are changed sufficiently by the selection so that $b_1>0$. If, as is often done in practice, only those values of the index weights calculated in the first generation of selection are used throughout the selection programme, the x_1 trait will reduce in value. This illustrates that unchanging selection weights can be detrimental to the overall genetic gain. However, even when new weights are calculated for each generation, it must be noted that genetic covariances change more rapidly than do variances (Enfield 1980). In fact, long-term selection experiments have found that genetic variance is not exhausted (Enfield 1988; Fairfull and Gowe 1990).

Acknowledgements The authors benefited from comments and suggestions made by Dr. B. Muir.

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