

Effect of selection on genetic parameters of correlated traits

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Summary. Changes in genetic parameters of correlated traits due to the buildup of linkage (gametic phase) disequilibrium from repeated truncation selection on a single trait are studied. After several generations of selection, an equilibrium is approached where there are no further changes in genetic parameters and limiting values are reached. Formulae are derived under an infinitesimal model for these limiting values of genetic variances and covariances, heritabilities, and genetic correlations between traits directly and indirectly selected. Changes from generation zero to the limit in all these parameters become greater as heritability of the trait under direct selection increases and, to a lesser extent, as intensity of selection increases. Change in heritability of a trait under indirect selection also increases as the absolute value of the correlation between the trait under indirect and the trait under direct selection increases. The change is maximum when the initial value of heritability is close to 0.5 and insignificant when the initial value is close to zero or one. Change in the genetic correlation between the trait under direct selection and the trait under indirect selection is maximum when its initial value is close to ± 0.6 and insignificant when its initial value is close to zero or ± 1 . Heritability of the trait indirectly selected and genetic correlation between that trait and the trait directly selected always decrease in absolute value, whereas genetic correlation between two traits indirectly selected can either decrease or increase in absolute value. It is suggested that use be made of formulae at selection equilibrium in the prediction of correlated responses after several generations of selection.

Key words: Selection – Linkage disequilibrium – Correlated response – Genetic correlation

Introduction

Directional selection causes negative linkage disequilibrium (Felsenstein 1965), which results in a reduction of the genetic variance of the trait under selection, its heritability, and response to selection. In an infinite population, Bulmer (1971) showed, assuming the “infinitesimal model”, that any change in the variance will be due to linkage disequilibrium. He also showed that with repeated cycles of selection, an equilibrium situation is eventually achieved in which the genetic variance lost by selection is regenerated by recombination. He obtained the expression to compute the limiting value of the disequilibrium contribution, assuming that selection intensity is constant across generations.

Selection not only produces changes in the genetic variance of the trait directly selected, but genetic variances of and covariances between other correlated traits are also affected. Changes in population genetic parameters of traits indirectly selected as a consequence of the generation of linkage disequilibrium after repeated selection have been considered previously by Fimland (1979), Bennett and Swiger (1980), Tallis (1987), Zeng (1988), and Wray and Hill (1989). These changes should be taken into account in the prediction of correlated responses in long term selection programs.

The objective of this paper is to show the effect of selection on genetic parameters of correlated traits when truncation selection is carried out on a single trait. We give expressions for the limiting values of these parameters and examine prediction of correlated response to selection.

Model

Consider three traits that are determined by an infinite number of unlinked loci, each with infinitely small addi-

tive effect (Fisher 1918). Environmental effects are assumed to be normally distributed. There is no dominance, no epistasis, and no correlation or interaction between genotype and environment. The population is of infinite size and in Hardy-Weinberg and linkage equilibrium prior to the start of selection.

Selection is practiced on a single trait and the selection criterion is the phenotypic performance of the candidate for selection. Selection is directional and by truncation. Selected individuals are randomly mated to produce the next generation and they all have the same probability of having offspring. Repeated cycles of selection are practiced and selection intensity is constant across generations. Also, environmental variances for the three traits are constant. Departures from normality induced by selection are ignored. Generations do not overlap.

Genetic (co)variances in the base population

Assume that phenotypes (P_1 , P_2 , and P_3) and genotypes (A_1 , A_2 , and A_3) are multivariate normal random variables. Selection is based only on phenotypic values for trait 1. Individuals with the largest P_1 are selected as parents of the next generation and the rest are discarded.

The genetic variance for trait i ($i=1, 2, 3$) in the selected group of parents ($\sigma_{A_i}^2$) can be obtained from principles of conditional variance. It is well known that

$$\sigma_{A_i}^2 = \text{Var}(A_i|P_{1s}) + \text{Var}[E(A_i|P_{1s})],$$

where the subscript s refers to selected individuals, $\text{Var}(A_i|P_{1s})$ is the conditional variance of A_i given P_{1s} , and $E(A_i|P_{1s})$ is the conditional expectation. From linear regression theory,

$$\sigma_{A_i}^2 = \sigma_{A_i}^2 [1 - h_1^2 r_{1i}^2 k],$$

where $\sigma_{A_i}^2$ is the additive genetic variance of trait i in the whole population before selection, h_1^2 is the heritability of the trait directly selected, r_{1i} is the genetic correlation between traits 1 and i , and $k=i(i-x)$, where i is the standardized deviation of the mean of the selected group from the population mean, and x is the standardized deviation of the truncation point from the population mean for the trait directly selected. Thus, directional selection, which decreases the variance of the trait directly selected, also decreases the variance of a correlated trait, whether the correlation between them is positive or negative. This well-established result is due to Pearson (1903).

Genetic covariances between traits i and j ($i=1, 2, 3$; $j=1, 2, 3$; $i \neq j$) among the selected parents ($\sigma_{A_i A_j}$) can be obtained following the same principles as before, namely,

$$\sigma_{A_i A_j} = \sigma_{A_i A_j} - h_1^2 r_{1i} r_{1j} \sigma_{A_i} \sigma_{A_j} k,$$

where $\sigma_{A_i A_j}$ is the additive genetic covariance between traits i and j in the unselected population (Pearson 1903).

The genetic covariance between the trait under direct selection and another trait under indirect selection in the selected group of individuals is always reduced in absolute value, i.e., the genetic covariance moves towards zero. Also, the covariance is reduced proportionally by the same amount as the genetic variance of the trait directly selected. In the case of the covariance between two traits indirectly selected ($\sigma_{A_2 A_3}$), either if r_{12} and r_{13} have the same sign and $\sigma_{A_2 A_3}$ is negative or if r_{12} and r_{13} have opposite signs and $\sigma_{A_2 A_3}$ is positive, the covariance in the selected group of individuals increases in absolute value, i.e., the genetic covariance moves away from zero. Otherwise, the covariance can either increase or decrease in absolute value in the selected group, i.e., the genetic covariance can either move away from or towards zero.

Genetic (co)variances in the first generation following selection

Bulmer (1971) showed that if loci are unlinked and individuals mate at random after selection, then the reduction in genetic variance among the progeny is half the reduction among parents. The same principle applies to covariances. Therefore, genetic (co)variances in the first generation after selection can be obtained from

$$\sigma_{A_i A_j(1)} = \sigma_{A_i A_j(0)} - 0.5 h_{1(0)}^2 r_{1i(0)} r_{1j(0)} \sigma_{A_i(0)} \sigma_{A_j(0)} k,$$

where the subscripts in parentheses represent generation number.

Genetic (co)variances in subsequent generations of selection

If no further selection is practiced, one-half the lost genetic (co)variances will be regenerated each generation (assuming no linkage), and in the limit these parameters will return to their original values. However, if selection is continued, there will be a further reduction in the (co)variances in subsequent generations, as a consequence of the new disequilibrium introduced by the action of selection (Bulmer 1980). The genetic (co)variances at any generation t , are given by

$$\begin{aligned} \sigma_{A_i A_j(t)} = & \sigma_{A_i A_j(t-1)} \\ & - 0.5 h_{1(t-1)}^2 r_{1i(t-1)} r_{1j(t-1)} \sigma_{A_i(t-1)} \sigma_{A_j(t-1)} k \\ & + 0.5 [\sigma_{A_i A_j(0)} - \sigma_{A_i A_j(t-1)}]. \end{aligned} \quad (1)$$

An equivalent result was obtained by Tallis (1987) using an alternative statistical argument. The second summand on the right-hand side in Eq. 1 corresponds to the new disequilibrium induced by selection in generation $t-1$. The third summand corresponds to the recovery of the (co)variation due to free recombination (only half the

disequilibrium contribution present in the previous generation is preserved). If different selection pressures are applied in the two sexes, then $k = 0.5(k_m + k_f)$, where subscripts m and f refer to males and females, respectively.

Genetic (co)variances, heritabilities, and genetic correlations in the limit

After a few generations of selection the genetic (co)variance asymptotes to a limiting value. At this point, the (co)variance lost by selection is recovered by recombination. Limiting values for genetic (co)variances, denoted by the parenthesized subscript L , can be obtained from Eq. 1 by putting $\sigma_{A_i A_j(t-1)} = \sigma_{A_i A_j(t)} = \sigma_{A_i A_j(L)}$. Thus,

$$\sigma_{A_i A_j(L)} = \sigma_{A_i A_j(0)} - h_{1(L)}^2 r_{1i(L)} r_{1j(L)} \sigma_{A_i(L)} \sigma_{A_j(L)} k. \quad (2)$$

From this general expression the genetic variance ($\sigma_{A_1(L)}^2$) and heritability ($h_{1(L)}^2$) of the trait directly selected in the limit can be derived:

$$\sigma_{A_1(L)}^2 = \frac{\sigma_{A_1(0)}^2}{1 + h_{1(L)}^2 k} \quad (3)$$

and

$$h_{1(L)}^2 = \frac{-1 + \sqrt{1 + 4h_{1(0)}^2 k[1 - h_{1(0)}^2]}}{2k[1 - h_{1(0)}^2]}.$$

These formulae were first given by Gomez-Raya and Burnside (1990). Also, special cases of Eq. 2 are the limiting values for the genetic variance of an indirectly selected trait ($\sigma_{A_j(L)}^2$, $j = 2, 3$):

$$\sigma_{A_j(L)}^2 = \frac{\sigma_{A_j(0)}^2}{1 + h_{1(L)}^2 r_{1j(L)}^2 k}, \quad (4)$$

and for the genetic covariance between the trait under direct and the trait under indirect selection ($\sigma_{A_1 A_j(L)}$):

$$\sigma_{A_1 A_j(L)} = \frac{\sigma_{A_1 A_j(0)}}{1 + h_{1(L)}^2 k}. \quad (5)$$

Assuming an additive genetic model and constant environmental variance across generations ($\sigma_{E_j(t-1)}^2 = \sigma_{E_j(t)}^2 = \sigma_{E_j}^2$), the limiting value of the heritability of trait j is given by:

$$h_{j(L)}^2 = \frac{\sigma_{A_j(L)}^2}{\sigma_{A_j(L)}^2 + \sigma_{E_j}^2},$$

and substituting $\sigma_{A_j(L)}^2$ for its value found in Eq. 4:

$$h_{j(L)}^2 = \frac{h_{j(0)}^2}{1 + h_{1(L)}^2 r_{1j(L)}^2 k[1 - h_{j(0)}^2]}. \quad (6)$$

The value of the genetic correlation between the trait directly selected and a second trait indirectly selected in the limit can be obtained from Eqs. 3, 4, and 5. Working

from

$$r_{1j(L)} = \frac{\sigma_{A_1 A_j(L)}}{\sigma_{A_1(L)} \sigma_{A_j(L)}},$$

it can be shown that the genetic correlation in the limit is:

$$r_{1j(L)} = \frac{r_{1j(0)}}{\sqrt{1 + h_{1(L)}^2 k[1 - r_{1j(0)}^2]}}. \quad (7)$$

Thus, the limiting value of the genetic correlation depends only on its initial value, the initial value of heritability of the trait under selection, and the intensity of selection (because $h_{1(L)}^2$ only depends upon initial value and selection intensity). The following can be stated from this equation:

1. $r_{1j(L)} = 0$ if $r_{1j(0)} = 0$;
2. $r_{1j(L)} = r_{1j(0)}$ if $r_{1j(0)} = \pm 1$;
3. $|r_{1j(L)}| \leq |r_{1j(0)}|$ since $\sqrt{1 + h_{1(L)}^2 k[1 - r_{1j(0)}^2]} \geq 1$.

Therefore, selection causes the genetic correlation to move towards zero.

Figure 1 shows limiting values of the genetic correlation ($r_{1j(L)}$) as a function of the correlation in the base population ($r_{1j(0)}$) for several values of initial heritability of the trait under selection ($h_{1(0)}^2$). Three selection intensities have been considered, corresponding to selected proportions of individuals of 1% (Fig. 1 a), 20% (Fig. 1 b), and 50% (Fig. 1 c). It can be observed that:

1. the change in r_{1j} from generation zero to the limit increases with $h_{1(0)}^2$ and with selection intensity, but effects of the different intensities of selection examined were not large;
2. the change in genetic correlation is greatest when $r_{1j(0)}$ is close to ± 0.6 (values of initial correlation for which difference between initial and limiting value is maximum ranged from ± 0.58 to ± 0.63 for the different $h_{1(0)}^2$ and selection intensities examined);
3. for values of $r_{1j(0)}$ close to zero or ± 1 , change in the genetic correlation is very small even if $h_{1(0)}^2$ is relatively large.

Now, substituting Eq. 7 in Eq. 6 gives

$$h_{j(L)}^2 = h_{j(0)}^2 \frac{1 + h_{1(L)}^2 k[1 - r_{1j(0)}^2]}{1 + h_{1(L)}^2 k[1 - h_{j(0)}^2 r_{1j(0)}^2]}.$$

Thus, the limiting value of heritability of the trait indirectly selected depends on the intensity of selection, the initial heritability of that trait, the initial squared value of the genetic correlation between both traits, and the limiting value of the heritability of the trait directly selected. The latter depends only on the intensity of selection and its initial value.

Figure 2 shows limiting values of the heritability of a second trait ($h_{j(L)}^2$) as a function of its initial value ($h_{j(0)}^2$),

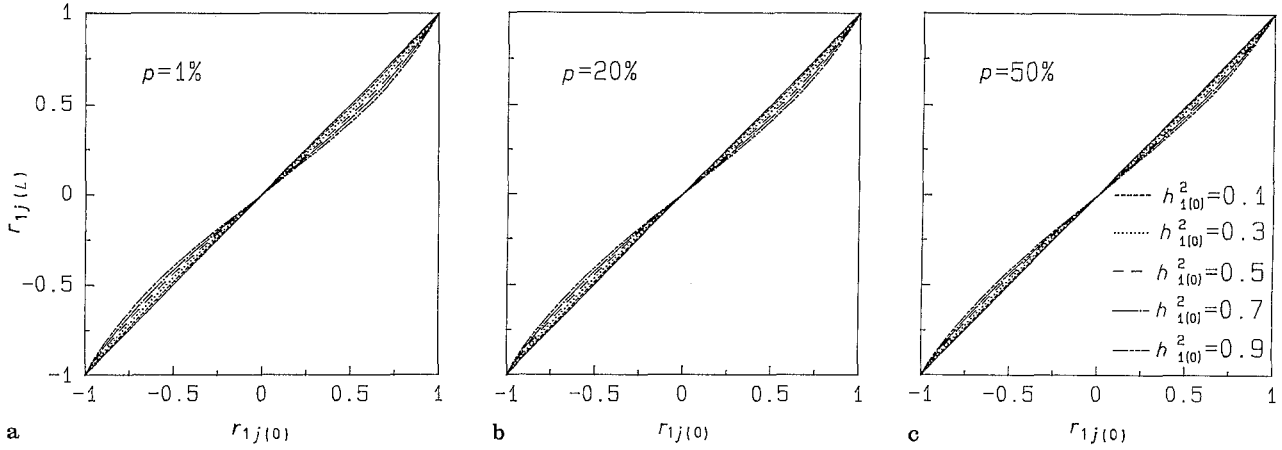


Fig. 1 a-c. Change in genetic correlation between the trait under direct selection and another trait indirectly selected. As a reference, the diagonal straight line is $r_{1j(L)} = r_{1j(0)}$

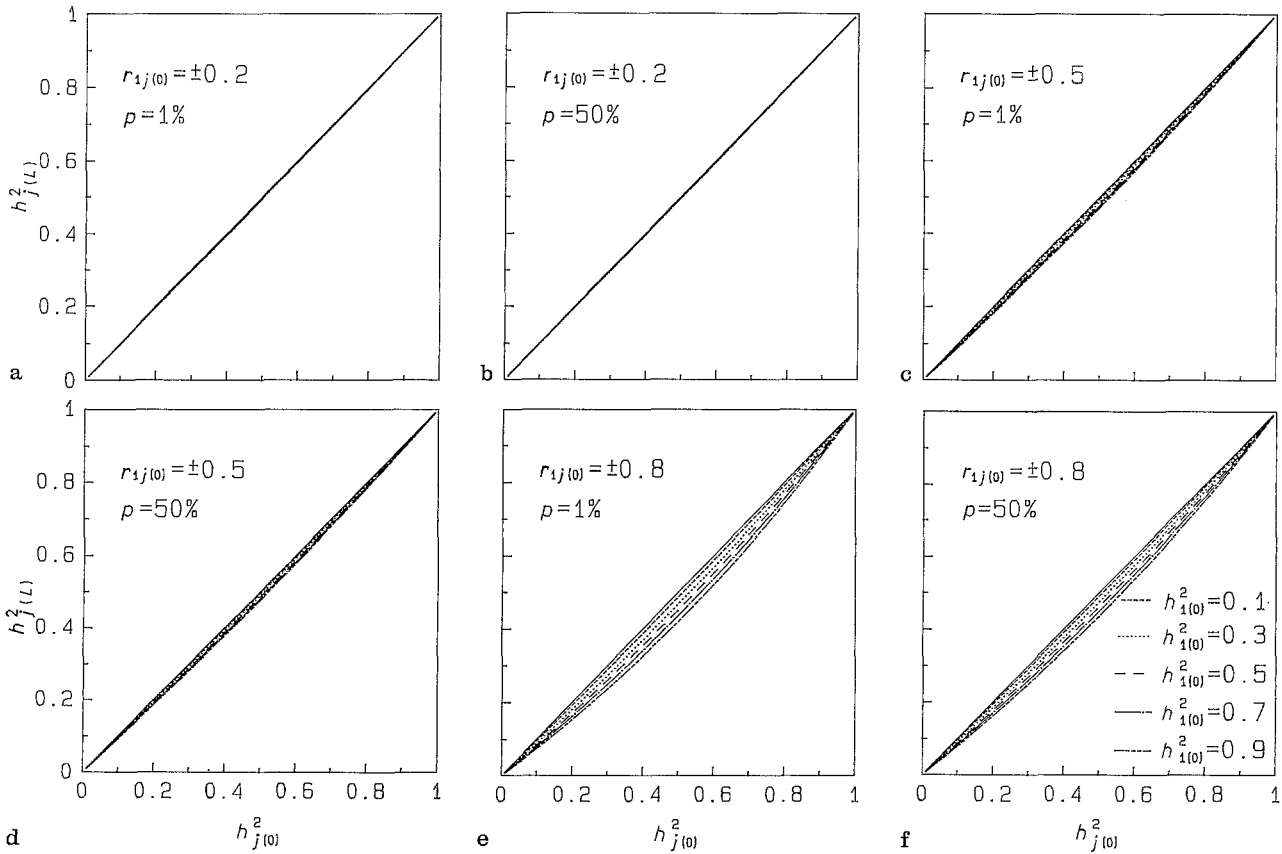


Fig. 2 a-f. Change in heritability of a trait indirectly selected. As a reference, the diagonal straight line is $h^2_{j(L)} = h^2_{j(0)}$

for different values of the initial heritability of the trait directly selected ($h^2_{1(0)}$). Two selection intensities corresponding to selected proportions of individuals of 1% (Fig. 2a, 2c, and 2e) and 50% (Fig. 2b, 2d, and 2f) have been considered. Also, three values for the initial squared genetic correlation are represented, those corresponding to an initial correlation of ± 0.2 (Fig. 2a and 2b), ± 0.5 (Fig. 2c and 2d), and ± 0.8 (Fig. 2e and 2f). The following can be observed.

1. The change in h^2_j from generation zero to the limit increases with the absolute value of $r_{1j(0)}$, $h^2_{1(0)}$, and the intensity of selection. For small values of $|r_{1j(0)}|$ the change is practically nil. Again, different selection intensities lead to similar values of $h^2_{j(L)}$ when the other parameters are held constant.
2. The change in h^2_j is greatest for intermediate values of $h^2_{j(0)}$ (values of initial heritability for which difference between initial and limiting value is maximum ranged

Table 1. Limiting values for the genetic correlation between two indirectly selected traits for several combinations of its initial value, $r_{23(0)}$, the initial values of the genetic correlations between the trait directly selected and the two traits indirectly selected, $r_{12(0)}$ and $r_{13(0)}$, the initial value of the heritability of the trait under direct selection, $h_{1(0)}^2$, and the selected proportion of individuals, p

$r_{12(0)}$	$r_{13(0)}$	$r_{23(0)}$	$p = 1\%$			$p = 50\%$			
			$h_{1(0)}^2$: 0.1	0.5	0.9	0.1	0.5	0.9	
0.75	0.75	0.75	0.74	0.70	0.67	0.74	0.71	0.69	
		0.50	0.48	0.41	0.34	0.48	0.43	0.38	
		0.25	0.22	0.11	0.01	0.23	0.14	0.06	
	0.50	0.75	0.74	0.73	0.72	0.75	0.73	0.72	
		0.50	0.49	0.45	0.41	0.49	0.46	0.43	
		0.25	0.23	0.17	0.11	0.23	0.18	0.14	
	0.25	0.00	-0.03	-0.12	-0.20	-0.02	-0.09	-0.15	
		0.75	0.75	0.77	0.78	0.75	0.76	0.77	
		0.50	0.50	0.49	0.49	0.50	0.49	0.49	
	0.50	0.50	0.25	0.24	0.22	0.20	0.24	0.22	0.21
			0.00	-0.01	-0.06	-0.09	-0.01	-0.04	-0.07
			-0.25	-0.27	-0.33	-0.39	-0.27	-0.31	-0.36
0.25		0.75	0.75	0.73	0.72	0.75	0.74	0.73	
		0.50	0.49	0.46	0.44	0.49	0.47	0.45	
		0.25	0.24	0.19	0.16	0.24	0.21	0.18	
0.00		0.00	-0.02	-0.07	-0.12	-0.01	-0.06	-0.10	
		-0.25	-0.27	-0.34	-0.40	-0.27	-0.32	-0.37	
		-0.50	-0.53	-0.61	-0.68	-0.52	-0.59	-0.64	
0.25		0.25	0.75	0.75	0.75	0.75	0.75	0.75	0.75
			0.50	0.50	0.49	0.48	0.50	0.49	0.48
			0.25	0.24	0.23	0.21	0.25	0.23	0.22
	0.00	0.00	-0.01	-0.04	-0.06	-0.01	-0.03	-0.05	
		-0.25	-0.26	-0.30	-0.33	-0.26	-0.29	-0.31	
		-0.50	-0.52	-0.56	-0.59	-0.51	-0.55	-0.58	
	0.00	0.75	0.75	0.75	0.74	0.75	0.75	0.74	
		0.50	0.50	0.49	0.49	0.50	0.49	0.49	
		0.25	0.25	0.24	0.23	0.25	0.24	0.23	
	-0.25	0.00	0.00	-0.02	-0.03	0.00	-0.01	-0.02	
		-0.25	-0.26	-0.27	-0.28	-0.25	-0.27	-0.28	
		-0.50	-0.51	-0.53	-0.54	-0.51	-0.52	-0.53	
-0.75	-0.75	-0.76	-0.78	-0.80	-0.76	-0.77	-0.79		

from 0.50 to 0.54 for the different $h_{1(0)}^2$, $r_{1j(0)}$, and selection intensities examined).

3. For values of $h_{j(0)}^2$ close to zero or one, change in the heritability is very small.

The limiting value of the genetic correlation between two traits indirectly selected ($r_{23(L)}$) can be obtained by substituting Eqs. 4 and 2 in

$$r_{23(L)} = \frac{\sigma_{A_2 A_3(L)}}{\sigma_{A_2(L)} \sigma_{A_3(L)}},$$

which leads to

$$r_{23(L)} = r_{23(0)} \sqrt{[1 + h_{1(L)}^2 r_{12(L)}^2 k] [1 + h_{1(L)}^2 r_{13(L)}^2 k] - h_{1(L)}^2 r_{12(L)} r_{13(L)} k}.$$

It can be observed that:

1. if $r_{23(0)} = 0$, $r_{23(L)}$ will be negative if $r_{12(0)}$ and $r_{13(0)}$ have the same sign and positive if $r_{12(0)}$ and $r_{13(0)}$ have opposite signs;

2. if $r_{12(0)} = r_{13(0)} = 0$, the limiting value of r_{23} will be the same as its initial value;

3. if $r_{1j} = 0$ then $|r_{23(L)}| \geq |r_{23(0)}|$, i.e., r_{23} moves away from zero;

4. if the three initial correlations differ from zero, then either if r_{12} and r_{13} have the same sign and $r_{23(0)}$ is negative or if r_{12} and r_{13} have opposite signs and $r_{23(0)}$ is positive, $|r_{23(L)}| \geq |r_{23(0)}|$, since $\sqrt{[1 + h_{1(L)}^2 r_{12(L)}^2 k] [1 + h_{1(L)}^2 r_{13(L)}^2 k]} \geq 1$; i.e., r_{23} moves away from zero. Otherwise r_{23} can either move away from or towards zero.

Limiting values of the genetic correlation between the two traits indirectly selected appear in Table 1 for different initial values of h_1^2 , r_{12} , r_{13} , and r_{23} . Two different

selection intensities corresponding to selected proportions of 1% and 50% are considered. For given values of $r_{12(0)}$ and $r_{13(0)}$, only some values of $r_{23(0)}$ are possible. The genetic variance-covariance matrix has to be non-negative definite (e.g., Seal 1966). A symmetric matrix is non-negative definite if and only if all its principal submatrices have nonnegative determinants (e.g., Anton and Rorres 1987). Thus, the necessary and sufficient condition for the genetic variance-covariance matrix to be non-negative definite is $1 + 2r_{12}r_{13}r_{23} \geq r_{12}^2 + r_{13}^2 + r_{23}^2$ (see Appendix). Given initial values for r_{12} and r_{13} , only initial values of r_{23} that satisfy this inequality are reported. Both positive and negative possible values of $r_{23(0)}$ are considered, but only positive values of $r_{12(0)}$ and $r_{13(0)}$ are tabulated. If $r_{12(0)}$ and $r_{13(0)}$ are both negative, then the value of $r_{23(L)}$ is the same as if $r_{12(0)}$ and $r_{13(0)}$ both had positive signs. If $r_{12(0)}$ and $r_{13(0)}$ have opposite signs, then the value of $r_{23(L)}$ is that corresponding to a $r_{23(0)}$ of opposite sign to its actual value, and the sign of the obtained value must be changed. For example, the limiting value of r_{23} assuming $p=1\%$, $h_1^2=0.9$, $r_{12(0)}=0.75$, $r_{13(0)}=-0.50$, $r_{23(0)}=-0.25$ is obtained from the value corresponding to $r_{12(0)}=0.75$, $r_{13(0)}=0.50$, and $r_{23(0)}=0.25$. From Table 1, this value is 0.11. Then $r_{23(L)}$ in this case will be -0.11 .

The change in r_{23} from generation zero to the limit increases with $h_{1(0)}^2$ and selection intensity. The correlation between two traits indirectly selected can both decrease or increase in absolute value, depending not only on the signs but also on the magnitudes of the parameters involved.

Direct and correlated responses in the limit

The practical effect of the change in the genetic parameters is that related to genetic responses to selection. Both the direct response of the trait on which selection is practiced and the correlated response of a second trait will be altered due to selection.

If we consider a constant selection intensity across generations, i.e., $i_{(0)}=i_{(L)}=i$, the direct response per generation of trait 1 at the limit will be $R_{1(L)}=i h_{1(L)} \sigma_{A_1(L)}$ and the correlated response in a second trait j will be $CR_{j(L)}=i h_{1(L)} \sigma_{A_j(L)} r_{1j(L)}$. Under directional selection, limiting values of h_1 and σ_{A_j} are always smaller than their corresponding initial values. In the same way, the limiting value of r_{1j} is also always smaller in absolute value than its initial value. Therefore, the correlated response per generation in the limit is always less than that obtained in the first generation of selection.

The percentage reduction in correlated response in the limit relative to that obtained in the first generation is:

$$PR_j = \left[1 - \frac{CR_{j(L)}}{CR_{j(1)}} \right] \times 100 = \left[1 - \frac{i h_{1(L)} \sigma_{A_j(L)} r_{1j(L)}}{i h_{1(0)} \sigma_{A_j(0)} r_{1j(0)}} \right] \times 100.$$

Substitution of values of $\sigma_{A_j(L)}$ and $r_{1j(L)}$ obtained in Eqs. 4 and 7 shows that:

$$PR_j = \left[1 - \sqrt{\frac{h_{1(L)}^2}{h_{1(0)}^2 [1 + h_{1(L)}^2 k]}} \right] \times 100,$$

which is the same formula as obtained by Gomez-Raya and Burnside (1990) in relation to direct response. Therefore, as a percentage, correlated response of a second trait is reduced in the same proportion as the direct response of the selected trait. In other words, the genetic regression of trait j on trait 1 is unaffected by selection.

Discussion

Genetic variance, heritability, and response of a trait under direct selection are reduced by generation of linkage disequilibrium (Bulmer 1971). Genetic variances, heritabilities, and genetic covariances and correlations in correlated traits are also affected. After a few cycles of selection, a steady state equilibrium is approached in which the generation of new disequilibrium is compensated for by free recombination. No further changes in genetic variances and covariances occur if selection intensity is kept constant and population size is infinite. Bulmer (1971) has given an expression for the disequilibrium contribution in the limit for the trait directly selected. In this paper, algebraical expressions for the equilibrium values of genetic variances and covariances, heritabilities, and genetic correlations in correlated traits have been derived. These expressions show that: (a) genetic variance and heritability of an indirectly selected trait, as well as the genetic covariance and correlation between that trait and the trait directly selected, are always reduced in absolute value; (b) genetic covariance and correlation between two indirectly selected traits can be either decreased or increased in absolute value; (c) changes in these genetic parameters increase with heritability of the trait under direct selection and with selection intensity, but the effect of the latter is not strong.

A basic assumption in this study is that both number of loci and population size are infinite. Relaxation of this assumption would result in changes in gene frequencies, which would lead to further changes in genetic variances and covariances. These changes, however, appear to be more important in the long term, whereas changes in genetic parameters due to linkage disequilibrium take place in the early generations (Bulmer 1980; Villanueva and Kennedy 1990).

A practical consequence of reduction in genetic variances and covariances under selection is reduction in direct and correlated responses. An interesting result of this study is that correlated response, as a percentage, is reduced in the limit to exactly the same proportion as

response of the directly selected trait. Formulae commonly used for predicting responses (e.g., Falconer 1981) are only strictly valid for the first generation of selection and overpredict response if used over repeated cycles of selection. Degree of overprediction of response in the limit for the trait directly selected has been considered by Gomez-Raya and Burnside (1990). Equations at the equilibrium are more appropriate to predict responses after several cycles of selection and to compare efficiencies of alternative breeding schemes. An immediate application of these results is related to prediction of efficiency of indirect selection with respect to direct selection. Comparisons between the two methods of selection have been based on expected responses in the first generation (Searle 1965; Falconer 1981). If continued selection is applied, comparisons should be made with the expressions described in this paper. These expressions can also be used when a selection index including several traits is the criterion of selection. The index can be considered as a single trait on which direct selection is practiced, and the traits included in that index are indirectly selected.

Finally, expressions of genetic parameters at the equilibrium could be useful in order to correct for the bias in estimation of these parameters when selection has been practiced.

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Appendix

The genetic variance-covariance matrix considered in this study is

$$\mathbf{G} = \begin{bmatrix} \sigma_{A_1}^2 & \sigma_{A_1 A_2} & \sigma_{A_1 A_3} \\ & \sigma_{A_2}^2 & \sigma_{A_2 A_3} \\ \text{Symmetric} & & \sigma_{A_3}^2 \end{bmatrix}$$

$$= \begin{bmatrix} h_1^2 \sigma_{P_1}^2 & r_{12} h_1 h_2 \sigma_{P_1} \sigma_{P_2} & r_{13} h_1 h_3 \sigma_{P_1} \sigma_{P_3} \\ & h_2^2 \sigma_{P_2}^2 & r_{23} h_2 h_3 \sigma_{P_2} \sigma_{P_3} \\ \text{Symmetric} & & h_3^2 \sigma_{P_3}^2 \end{bmatrix}$$

and principal submatrices of \mathbf{G} are

$$[h_1^2 \sigma_{P_1}^2], \begin{bmatrix} h_1^2 \sigma_{P_1}^2 & r_{12} h_1 h_2 \sigma_{P_1} \sigma_{P_2} \\ \text{Symmetric} & h_2^2 \sigma_{P_2}^2 \end{bmatrix} \text{ and } \mathbf{G}.$$

Matrix \mathbf{G} will be nonnegative definite if and only if all its principal submatrices have nonnegative determinants. The de-

terminants of the principal submatrices are:

a) $|h_1^2 \sigma_{P_1}^2| = h_1^2 \sigma_{P_1}^2$, which is always nonnegative;

$$\text{b) } \begin{bmatrix} h_1^2 \sigma_{P_1}^2 & r_{12} h_1 h_2 \sigma_{P_1} \sigma_{P_2} \\ \text{Symmetric} & h_2^2 \sigma_{P_2}^2 \end{bmatrix} = h_1^2 h_2^2 \sigma_{P_1}^2 \sigma_{P_2}^2 [1 - r_{12}^2],$$

which is always nonnegative since $r_{12}^2 \leq 1$;

$$\text{c) } |\mathbf{G}| = h_1^2 h_2^2 h_3^2 \sigma_{P_1}^2 \sigma_{P_2}^2 \sigma_{P_3}^2 [1 + 2r_{12} r_{13} r_{23} - r_{12}^2 - r_{13}^2 - r_{23}^2],$$

which is nonnegative if

$$1 + 2r_{12} r_{13} r_{23} - r_{12}^2 - r_{13}^2 - r_{23}^2 \geq 0$$

or, equivalently, if

$$1 + 2r_{12} r_{13} r_{23} \geq r_{12}^2 + r_{13}^2 + r_{23}^2.$$

Therefore, the necessary and sufficient condition for \mathbf{G} to be nonnegative definite is $1 + 2r_{12} r_{13} r_{23} \geq r_{12}^2 + r_{13}^2 + r_{23}^2$.

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