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The effect of index selection on allele frequencies and future genetic gains when traits are correlated

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Abstract The application of the selection index in the case of an additive two-trait model in which the genetic effect on each trait is determined by a finite number of loci is examined. Simulation results indicate that the direction of change in the frequency of favourable alleles is not necessarily in the positive direction at all loci when index selection is used as the basis for truncation selection. When the genetic correlation was positive (or favourable with respect to the economic weights), there was little difference (< 5%) in genetic gain over 20 generations and no difference in the direction of change in allele frequencies or genetic correlation whether or not updated values for the genetic (co)variances were used in constructing the selection index. However, when the genetic correlation was negative or unfavourable, the effect of using genetic parameters which were not updated had unexpected effects on the allele frequencies and genetic correlation and reduced the genetic gain by a greater amount (< 12%).

Key words Correlation · Genetic gain · Allele frequency · Index weight

Introduction

The selection index method has been the basis of truncation selection in artificial selection programmes for the last 60 years (Bulmer 1985) in which it is used to discriminate between individuals as to the relative economic merit of their offspring (breeding value). Only those individuals predicted to have offspring with economic merit above a given value reproduce, and reproductive rate is assumed to be the same for all these individuals.

When economic merit is a linear function of one or more traits, the economic merit of an individual's offspring may be predicted, using multiple regression, from one or more relevant sources of information (phenotypic records). The partial regression coefficient corresponding to each information source determines the relative weight placed on that source. Truncation selection based on this predicted value yields the largest expected response to selection when the regression of genetic merit on phenotype is linear for all traits, and the relationships among the different sources of information are also linear (Bulmer, 1985), as is the case under the multivariate infinitesimal model. By implication, under this model, inheritance is additive (there is no effect due to dominance or epistasis) and the genotypic expression of a trait is determined by a very large number (conceptually infinite) of unlinked loci, all of which make a similar (infinitesimally small) contribution to the genotypic value of the trait (Bulmer 1985). Changes in allele frequencies are not described by a model of this type.

The objective of this paper is to assess the impact of truncation selection on the basis of a selection index in a finite population under a finite locus model. In particular, we will study the changes in allele frequencies as well as response to selection over multiple generations since these affect the factors used in the choice of selection/evaluation strategy. Although predicted response to selection is usually the main criterion used in the decision, there are three additional considerations.

Future genetic gains

In finite populations, the selection intensity and method of evaluation which yields the greatest response in a selection programme is very much dependent on the number of generations involved (Quinton and Smith 1995). This is rarely predetermined exactly in practice, and comparisons of response to selection under different intensities at a given generation number are often made

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at the same level of inbreeding in order to standardise the potential future response to selection (Quinton et al. 1992). Under the finite locus model, the change in genetic (co) variance cannot be described sufficiently well by the average level of inbreeding in the population since allelic frequencies have also changed. Future genetic gains can be affected by changes in allelic frequencies, firstly since favourable alleles can be subject to negative selection pressure and may be lost from the population and, secondly, genetic correlations can be changed (Bohren et al. 1966; Villanueva and Kennedy, 1990) and may become more or less favourable with respect to an objective function.

Variance in response due to changes in economic weights

Response due to index selection, particularly when selection is conducted over several generations, must be robust to economic weights since these may be incorrectly estimated or may change with time. Young (1961) and Smith (1983) found response after a single generation of index selection to be adversely affected by the use of incorrect economic weights, especially when the product of the economic weight and heritability is high for some traits, and increasingly so when such traits are negatively correlated.

Variance in response due to changes in (co)variances

Genetic components of variance are generally difficult to estimate and the sampling error of these estimates is large. Recent work by Koots and Gibson (1994) casts doubt on estimates of genetic correlation by suggesting that the sampling variance associated with these estimates may be even larger than expected. Harris (1964) found predictions of genetic gain to be poor when sample estimates of (co)variances are used in constructing the index. Hayes and Hill (1980) suggest the use of a transformation of the variance-covariance matrix in order to compute the sampling properties of weights applied to the traits in the index in a single generation of selection. In addition, these (co)variances may change with time, due to sampling losses and/or selection and must be re-estimated. Breeding values calculated on the basis of a selection index which incorporates all relevant pedigree information and data take into account changes in (co)variance due to selection over multiple generations (Kennedy and Sorensen 1988) caused by the accumulation of inbreeding and linkage disequilibrium under the assumption of an infinitesimal model (Bulmer 1985) but do not account for the effect of changing allele frequencies.

McMillan et al. (1973, 1995) found, using stochastic simulation, that the direction and rate of change of the genetic correlation and allele frequencies, when truncation selection on an index is applied over 20 generations, depends on the initial heritabilities, genetic correlation and economic weights of the traits. Villanueva and Kennedy (1990), in examining the effect of indirect selection in a finite locus model over ten cycles of selection, found changes in genetic parameters due to linkage disequilibrium to be important in early generations, but those due to changes in allele frequencies more important in later generations. De Koning and Weller (1994) found response to index selection over 15 generations was in some cases less than the economic optimum because the less favourable genotype reached fixation for some loci.

As an illustration of the unpredictability of changes in genetic parameters as a result of index selection, this paper discusses a simple case in which economic merit is a linear function of two traits which are inherited additively. Genetic correlation is assumed to be caused by pleiotropic loci, or equivalently, pairs of single-trait loci with vanishingly small probability of bracketing a recombination event, in which the direction of the correlation is the same.

Theory

Selection index weights in the two-trait case

The genetic and phenotypic variance-covariance matrices between two economically important additive traits can be written as

$$G = \begin{pmatrix} \sigma_1^2 & \sigma_{12} \\ \sigma_{12} & \sigma_2^2 \end{pmatrix} \tag{1}$$

and

$$P = \begin{pmatrix} V_1 & V_{12} \\ V_{12} & V_2 \end{pmatrix}. \tag{2}$$

When there is no environmental covariance,

$$V_{12} = \sigma_{12} = r_G \sqrt{\sigma_1^2 \sigma_2^2} \tag{3}$$

where r_G is the genetic correlation between the two traits.

Assume that the objective of the selection programme is to maximise the value of a linear function $a'Y$ where Y is a vector of the average breeding values of each trait in the selected population. The vector of selection index weights is calculated from

$$b = P^{-1} Ga \tag{4}$$

where $a' = (a_1\ a_2)$ is the vector of economic weights. The index weights are

$$b_1 = \frac{1}{|P|}(-a_1\sigma_{12}^2 + a_2(V_2 - \sigma_2^2)\sigma_{12} + V_2\sigma_1^2 a_1) \tag{5}$$

and

$$b_2 = \frac{1}{|P|}(-a_2\sigma_{12}^2 + a_1(V_1 - \sigma_1^2)\sigma_{12} + V_1\sigma_2^2 a_2) \qquad (6)$$

where $|P|$ is the determinant of P. If inheritance is additive, truncation selection on the basis of an index

$$I = b_1 y_1 + b_2 y_2$$

where y_1 and y_2 are the phenotypic values of the traits, expressed as deviations from the population means, will maximise the expected value of the index of the selected individuals, providing that the correct value of G is used in calculating the index weights.

Following Crow and Kimura (1970), assume the probability distribution of $I, f(I)$, can be considered normal with mean $\bar{I}$ and variance σ_I^2. Let I_A be the average index value of an individual with one A allele, and I_a the average index value of an individual with one allele other than A. Providing the effect of A on I is small relative to σ_I^2, the probability density function of the index value of the individuals with one A allele is approximately

$$f_A(I) = f(I)(1 + \alpha_A y + \ldots)$$

where $\alpha_A = (I_A - \bar{I})/\sigma_I$ is the average effect of A on I, and $y = (I - \bar{I})/\sigma_I$. If the proportion of the whole population selected is Q, the proportion, P_A, of the individuals with one A allele that is selected will be

$$\begin{aligned} P_A \approx \int_T^{\infty} f_A(I)dI &= \int_T^{\infty} f(I)dI + \alpha_A \int_T^{\infty} \frac{I - \bar{I}}{\sigma_I} f(I)dI \\ &= Q(1 + \mathfrak{I}\alpha_A) \end{aligned}$$

where T is the truncation point and $\mathfrak{I}$ is the standardised selection differential.

The change in the frequency of A, p_A, from the parent to the offspring population, assuming the Hardy-Weinberg equilibrium holds, is

$$\Delta p_A = \mathfrak{I} p_A \alpha_A.$$

Expressed in terms of the effect of allele substitution,

$$\alpha = \alpha_A - \alpha_a$$

where $\alpha_a = (I_a - \bar{I})/\sigma_I$ is the average effect of any allele other than A on I, then

$$\Delta p_A = \mathfrak{I} p_A (1 - p_A)\alpha.$$

When the population is in linkage equilibrium,

$$I_A = \frac{b_1\alpha_1 + b_2\alpha_2}{\sigma_I}$$

where α_i is the effect of allele substitution of A on trait i, $(i = 1, 2)$. In this case,

$$\Delta p_A \propto \begin{cases} \mathfrak{I} p_A(1 - p_A)(b_1\alpha_1) & \text{when trait 2 is not affected} \\ \mathfrak{I} p_A(1 - p_A)(1 - p_A)(b_1\alpha_1 + b_2\alpha_2) & \text{when both traits are affected} \\ \mathfrak{I} p_A(1 - p_A)(b_2\alpha_2) & \text{when trait 1 is not affected} \end{cases}$$

Clearly, the direction of the change in p_A depends on the signs of the b_i. For example, when $b_1 < 0$, negative selection pressure is applied to the favourable alleles affecting only trait 1.

The genetic (co)variances are dependent on the allele frequencies in the following way. Assume trait i is controlled by n loci, at each of which a distinguished allele acts additively, and providing that the loci are in linkage equilibrium, the variances can be expressed by

$$\sigma_i^2 = 2\sum_{k=1}^{n} \alpha_{ik}^2 p_k(1 - p_k)$$

and the covariance by

$$\sigma_{ij} = 2\sum_{k=1}^{n} \alpha_{ik}\alpha_{jk} p_k(1 - p_k) \quad (i \neq j)$$

where α_{ik} is the effect of allele substitution on trait i of locus k (McMillan et al. 1995). The (co)variances are therefore changed in the offspring population due to the change in allele frequencies.

Prediction of the signs of the index weights in the two-trait case

Even when the values used in calculating the index for the economic weights are positive for both traits, and the value used for the genetic correlation is positive, both index weights may not necessarily be positive when there is an additional environmental correlation.

For simplicity in the following discussion, we will assume that there is no environmental correlation between the traits and that both economic weights are positive.

When the genetic correlation used in calculating the index, r_G, is positive, from Eqs. 5 and 6, $b_1 > 0$ and $b_2 > 0$ whenever $\sigma_1^2 > 0$ and $\sigma_2^2 > 0$.

For some values of $r_G < 0$, depending on other factors in the model, b_1 or b_2 may be zero, and any stronger negative genetic correlation used will give a negative value to b_1 or b_2.

Let r_G' be the value of r_G at which $b_1 = 0$, if such a value exists between -1 and $+1$, and let r_G'' be the value of r_G at which $b_2 = 0$. Setting $b_1 = 0$ in Eq. 5,

$$\sigma_{12} = \frac{-a_2(V_2 - \sigma_2) \pm (a_2^2(V_2 - \sigma_2^2)^2 + 4a_1^2 V_2\sigma_1^2)^{0.5}}{-2a_1}. \qquad (7)$$

Solving for $r'_G = \sigma_{12}/(\sigma_1\sigma_2)$,

$$r'_G = ak_1 - (a^2k_1^2 + 1/h_2^2)^{0.5} \tag{8}$$

where $a = a_2/a_1$, $h_2^2 = \sigma_2^2/V_2$ and $k_1 = (\sigma_2/2\sigma_1)(1/h_2^2 - 1)$. The positive root of the discriminant is required for $0 \geq r'_G \geq -1$ since $k \geq 0$ and $a > 0$.

Since $-1 \leq r_G \leq 1$, r'_G can only exist when

$$ak_1 - (a^2k_1^2 + 1/h_2^2)^{0.5} \geq -1.$$

Therefore,

$$-(a^2k_1^2 + 1/h_2^2)^{0.5} \geq -(1 + ak_1)$$

$$1/h_2^2 \leq 1 + 2ak_1 = 1 + \frac{\sigma_2}{\sigma_1}(1/h_1^2 - 1)$$

$$\frac{\sigma_1}{\sigma_2} \leq \frac{a_2}{a_1}.$$

Similarly, setting $b_2 = 0$ in Eq. 6,

$$r''_G = k_2/a - (k_2^2/a^2 + 1/h_1^2)^{0.5} \tag{9}$$

where $h_1^2 = \sigma_1^2/V_1$ and $k_2 = (\sigma_1/2\sigma_2)(1/h_1^2 - 1)$. $-1 \leq r''_G \leq 1$ will only exist when

$$k_2/a - (k_2^2/a_2 + 1/h_1^2)^{0.5} \geq -1.$$

Hence, if

$$a_2\sigma_2 > a_1\sigma_1 \tag{10}$$

$b_1 < 0$ whenever $r_G < r'_G < 0$. Similarly, if

$$a_2\sigma_2 < a_1\sigma_1 \tag{11}$$

$b_2 < 0$ whenever $r_G < r''_G < 0$.

Effect of selection index weights on allele frequencies in the two-trait case

Let the frequency of the most favourable allele at locus i be p_i.

When r_G is assumed to be positive, both $b_1 > 0$ and $b_2 > 0$ and all loci are subject to positive selection pressure, the pleiotropic loci being subject to greater pressure, as the McMillan et al. (1995) simulations indicate. In this case, p_i increases after selection at all loci.

This situation is more complicated when r_G is assumed to be negative. When $a_2\sigma_2 \neq a_1\sigma_1$, one of the following two situations will apply.

1) For some value of r_G, say r'_G, b_1 will be zero, and whenever $r_G < r'_G$, b_1 will be less than zero.
2) For some value of r_G, say r''_G, b_2 will be zero, and whenever $r_G < r''_G$, b_2 will be less than zero.

When $b_1 > 0$ and $b_2 > 0$, McMillan et al. (1995) found that those loci affecting only one of the two traits will be subject to more selection pressure than the pleiotropic loci. This is because, for the pleiotropic loci, when $r_G < 0$, the selection pressure induced by b_1 on a favourable allele for either trait is in the opposite direction to that induced by b_2. Therefore, p_i is increased by a greater amount at any locus which affects only one trait than at a pleiotropic locus.

If $b_1 < 0$, negative selection pressure is applied to any locus affecting only trait 1, and p_i is decreased at this locus. Similarly, if b_2 is negative, p_i is decreased at any locus affecting only trait 2. The pleiotropic loci will not be subject to conflicting pressure as in the case where $b_1 > 0$ and $b_2 > 0$, and p_i at these loci will change by a greater amount than those at loci affecting a single trait. The direction of change will be to increase the frequency of those alleles which are most favourable for the trait with the positive index weight.

Methods

The simulations described by McMillan et al. (1995) were repeated, using a value for G in calculating the index which was estimated from the true (known) genetic values of the individuals in each generation in order to account for changes in G due to selection in previous generations. In addition, in order to compare these results with those using a value of G which does not account for such changes, the same initial set of populations was subject to truncation selection on an index calculated in each generation with the base population value of G for 20 generations. Each population simulated consisted of 50 male and 50 female diploid genotypes with two alleles segregating at each of 15 unlinked loci. Twenty-five males and 25 females were chosen as parents in each generation and were mated randomly to produce two offspring of each sex. Generations were non-overlapping.

The phenotypic expression of each of two traits was determined by the sum of equally weighted contributed froms each of 10 loci, 5 of which affected one trait and 5 of which affected both traits, plus a normally distributed environmental term. There was no correlation between the environmental terms or between either environmental term and any genetic effect. Both traits are measured on all individuals in the population, and each individual's own phenotypic records are the only source of information used in predicting the economic merit of its offspring. The contribution of a heterozygote was intermediate between the two homozygotes. For populations sampled from a base population with a genetic correlation of 0.5, the sign of the contributions of the loci which affected both traits was the same for both traits; for those sampled from a base population with a genetic correlation of -0.5, the sign was opposite. Heritabilities of 0.15 and 0.45 were simulated by changing the environmental variance for the trait in question.

Allele frequencies were all 0.5 in the base population, so that the genetic variances were both at their maximum value (5 in this case). Although this situation is highly artificial, the intention of this paper is to illustrate the fact that the changes in allele frequencies are not homogeneous among loci under selection. In addition, the use of initial frequencies less than 0.5 would illustrate other differences between the finite locus and infinitesimal model, such as an increase in genetic variance after selection, that are not the focus of this paper.

All populations were replicated 100 times.

Results

When the sample populations were drawn from a base population with a genetic correlation of 0.5 and were

Table 1 Value of objective function after 20 generations of selection

Base r_G	a_1	a_2	h_1^2	h_2^2	Updated G	Constant G
−0.5	1	1	0.15	0.15	7.25	7.19
				0.45	8.47	7.78
			0.45	0.45	9.64	9.58
	1	3	0.15	0.15	21.36	20.82
				0.45	25.90	24.48
			0.45	0.45	27.06	23.69
0.5	1	1	0.15	0.15	16.66	16.60
				0.45	17.97	17.01
			0.45	0.45	19.32	19.30
	1	3	0.15	0.15	33.54	33.45
				0.45	36.86	36.29
			0.45	0.45	38.74	38.73

Table 2 Average allele frequencies at generation 20 (base population $r_G = -0.5$)

				G updated			G constant		
				Alleles affecting			Alleles affecting		
a_1	a_2	h_1^2	h_2^2	Only trait 1	Only trait 2	Both	Only trait 1	Only trait 2	Both
1	1	0.15	0.15	0.86	0.86	0.49	0.86	0.86	0.51
			0.45	0.88	0.97	0.21	0.79	0.99	0.04
		0.45	0.45	0.98	0.98	0.53	0.98	0.98	0.50
1	3	0.15	0.15	0.50	0.93	0.07	0.39	0.93	0.05
			0.45	0.65	0.99	0.02	0.47	1	0
		0.45	0.45	0.79	0.99	0.03	0.39	0.99	0

subject to index selection using an updated value of G, b_1 and b_2 were both positive. The allele frequencies, p_i, (favourable for both traits) in the pleiotropic loci increased more rapidly then those in the single trait loci. Genetic (co)variances and genetic correlations declined to zero. The rate of change depended on the heritabilities and ratio of economic weights. When G was not updated, the changes in allele frequencies and genetic correlations were similar to the changes for the case where G was updated. These results are not shown since they were similar to those of the simulations described by McMillan et al. (1995). The improvement in the objective function as a result of selection was reduced by at most 5% when G was not updated. The average value of the objective function over the 100 replicates after 20 generations of selection are shown in Table 1.

When the samples were drawn from a population with a genetic correlation of -0.5, the results were less consistent. Overall improvement in the objective function as a result of selection was less than that attained when the initial genetic correlation was positive, and was further reduced by up to 12% when the value of G was not updated.

For some populations, the use of a selection index based on a value for G which was not updated altered the direction of change of some allele frequencies and the genetic correlation from the case in which G was updated. Average allele frequencies at generation 20 for populations with initial $r_G = -0.5$ are shown in Table 2.

Although there was no environmental correlation in the simulations, when incorrect values of G were used, the average value of $V_{12} \neq \sigma_{12}$, where V_{12} is the sample phenotypic covariance of the population, and σ_{12} the fixed base population genetic covariance.

The critical values r'_G and r''_G must be calculated from the parameters used in calculating the index weights. In this case, after the first generation, from Eq. 5,

$$r'_G = \frac{V_{12}sa - V_{22}/s}{V_{22}a - V_{12}} \tag{12}$$

and from Eq. 6

$$r''_G = \frac{V_{12}/s - V_{11}sa}{V_{11}a - V_{12}} \tag{13}$$

where $s = \sigma_2/\sigma_1$ is the ratio of genetic standard deviations used in G. These values are shown in Table 3 for the cases where either one of r'_G or r''_G exist between -1 and $+1$. This situation did not occur in any population with a positive initial genetic correlation.

Since the base population values of G were used in all generations when G was held constant, the values of b_1 and b_2 in the first generation were generally similar to those when G was updated. After repeated cycles of selection, these values differed substantially for some populations.

Table 3a Genetic correlation, value of the correlation used in the index at which either index weight changes sign and index weights for equal economic weights

					G updated					*G* constant				
a_1	a_2	h_1^2	h_2^2	Gen.	r_G[a]	r'_G	r''_G	b_1	b_2	r_G[a]	r'_G	r''_G	b_1	b_2
1	1	0.15	0.15	0	−0.49			0.08	0.08	−0.49			0.08	0.08
				1	−0.51			0.08	0.08	−0.51			0.08	0.09
				2	−0.51			0.08	0.07	−0.50			0.09	0.08
				5	−0.53			0.07	0.07	−0.53			0.09	0.09
				10	−0.55			0.06	0.06	−0.56			0.08	0.09
				15	−0.60			0.05	0.05	−0.61			0.09	0.09
				20	−0.67			0.03	0.04	−0.68			0.09	0.09
			0.45	0	−0.49			0.10	0.25	−0.49			0.10	0.26
				1	−0.50		−0.97	0.09	0.23	−0.51			0.10	0.26
				2	−0.51		−0.95	0.09	0.21	−0.51			0.09	0.26
				5	−0.52		−0.95	0.08	0.19	−0.52			0.10	0.29
				10	−0.55		−0.88	0.07	0.12	−0.53			0.10	0.33
				15	−0.61		−0.84	0.05	0.07	−0.49			0.09	0.38
				20	−0.70		−0.86	0.03	0.04	−0.41			0.09	0.40
		0.45	0.45	0	−0.49			0.30	0.29	−0.49			0.30	0.30
				1	−0.53			0.27	0.28	−0.54			0.31	0.32
				2	−0.54			0.26	0.25	−0.55			0.32	0.31
				5	−0.58			0.23	0.22	−0.59			0.33	0.33
				10	−0.68			0.15	0.15	−0.68			0.36	0.36
				15	−0.80			0.08	0.07	−0.83			0.39	0.39
				20	−0.92			0.03	0.03	−0.92			0.41	0.41

b Genetic correlation, value of the correlation used in the index at which either index weight changes sign and index weights for equal economic weights

					G updated					*G* constant				
a_1	a_2	h_1^2	h_2^2	Gen	r_G[a]	r'_G	r''_G	b_1	b_1	r_G	r'_G	r''_G	b_1	b_2
1	3	0.15	0.15	0	−0.49	−0.39		−0.05	0.38	−0.49	−0.39		−0.05	0.39
				1	−0.48	−0.40		−0.04	0.36	−0.48	−0.39		−0.05	0.40
				2	−0.48	−0.39		−0.04	0.35	−0.47	−0.37		−0.06	0.38
				5	−0.46	−0.41		−0.02	0.33	−0.46	−0.38		−0.06	0.40
				10	−0.41	−0.41		0	0.24	−0.42	−0.37		−0.06	0.42
				15	−0.36	−0.45		0.02	0.17	−0.33	−0.36		−0.07	0.43
				20	−0.34	−0.52		0.03	0.11	−0.28	−0.35		−0.07	0.44
			0.45	0	−0.49	−0.49		0	1.14	−0.49	−0.49		0	1.18
				1	−0.48	−0.50		0.01	1.05	−0.47	−0.49		0	1.26
				2	−0.47	−0.50		0.02	0.98	−0.44	−0.47		−0.01	1.28
				5	−0.44	−0.48		0.02	0.86	−0.44	−0.49		0	1.41
				10	−0.37	−0.55		0.04	0.50	−0.34	−0.40		−0.05	1.74
				15	−0.28	−0.76		0.05	0.20	−0.18	−0.34		−0.07	2.00
				20	−0.22			0.05	0.09	−0.09	−0.35		−0.07	2.08
		0.45	0.45	0	−0.49	−0.51		0.03	1.14	−0.49	−0.50		0.01	1.19
				1	−0.46	−0.50		0.05	1.06	−0.47	−0.50		0	1.26
				2	−0.47	−0.50		0.05	0.98	−0.46	−0.48		−0.02	1.27
				5	−0.44	−0.51		0.07	0.86	−0.45	−0.48		−0.02	1.41
				10	−0.40	−0.55		0.11	0.53	−0.31	−0.41		−0.16	1.70
				15	−0.36	−0.66		0.13	0.25	−0.15	−0.36		−0.25	2.00
				20	−0.38	−0.74		0.10	0.13	−0.09	−0.35		−0.28	2.07

[a] Average population genetic correlation. The value of the genetic correlation used in the index was −0.5 in all generations when *G* was held constant

Equal economic weights and negative genetic correlation

When $a_2 = a_1$, $b_1 > 0$ and $b_2 > 0$ in the first generation (Table 3a). This was expected since all the simulated populations were sampled from a base population in which $\sigma_1 = \sigma_2$, and so condition (10) holds only when $a_2 > a_1$.

After selection, the values of p_i at the pleiotropic loci were changed by a smaller amount than at the single trait loci, and the population r_G was more negative.

When $h_1^2 = h_2^2$, index weights were equal and so the changes in σ_1^2 and σ_2^2 after selection were similar since equal selection pressure was applied to both traits. Because of this, neither condition (10) nor condition (11) held after selection. This situation was repeated in subsequent generations. The allele frequencies, p_i, increased at loci affecting only one trait but remained constant (except for sampling) for the loci affecting both traits due to the opposite but equal selection pressure (Table 2). For these populations, the population r_G tends to -1 after repeated cycles of selection (Table 3a).

When $h_2^2 > h_1^2$ then $b_2 > b_1$. After 1 generation of selection, $\sigma_1 > \sigma_2$ since trait two is subject to greater selection pressure. In this case, condition (11) holds, but the value of r_G used in the index was greater than r''_G in all generations, and so $b_1 > 0$ and $b_2 > 0$ (Table 3a). The allele frequencies increased at the single trait loci and decreased at the pleiotropic loci since, in the model used in the simulations, this was the positive direction with respect to the trait with the larger index weight, trait two.

When G was updated each generation, the population r_G tended to -1. However, when G was held constant over the generations, although $b_1 > 0$ and $b_2 > 0$ and the values of p_i changed in the same direction as the simulations in which G was updated, the ratio of b_1 to b_2 changed differently. The population r_G remained close to the base population value of -0.5 for first 15 generations but after generation 15, r_G increased towards 0.

Unequal economic weights and negative genetic correlation

For populations in which $a_1 = 1$ and $a_2 = 3$, condition (10) holds when $\sigma_1^2 = \sigma_2^2$.

The value of r_G used in the index was more negative then r'_G when $h_1^2 = h_2^2 = 0.15$ in the first 10 generations whether G was updated or not, and so $b_1 < 0$ (Table 3b). (When G was held constant, the value of r_G used in calculating the index was -0.5 in all generations).

In both cases, the allele frequencies, p_i, at the pleiotropic loci changed more rapidly than at the single trait loci (Table 2) and the population r_G increased towards 0.

When $h_2^2 = 0.45$, for both values of h_1^2, the value of r_G used in the index was greater than r'_G in the first two generations whether or not G was updated. For this reason, in both cases, $b_1 > 0$. However, in the following generations the situation was different.

1) When G was updated, $r_G > r'_G$ and $b_1 > 0$. The allele frequencies of the favourable alleles affecting only the first trait were increased over repeated cyces of selection.
2) When G was held constant, using Eq. 12 $r_G = -.5 < r_G$, and $b_1 < 0$. The allele frequencies of the favourable alleles affecting only the first trait were reduced over repeated cycles of selection.

In both cases, the population r_G tended to 0 but at a greater rate when G was constant.

Discussion

Accurate estimation of the genetic (co)variances requires knowledge not only of the number and location of the loci and frequency of alleles at each locus affecting each trait but also of the size of the effect each of these alleles has on each trait. Recent work on the estimation of the location and size of quantitative trait loci (QTLs) has been precipitated by the large number of marker alleles which are now available. Such loci may be found when they are closely linked to a marker locus in a population in linkage disequilibrium with respect to the marker and QTLs (van Arendonk et al. 1994). This type of linkage disequilibrium cannot be assumed across all populations, and the degree of linkage must be estimated within families. Pairs of markers which bracket potential QTL are recommended since they will provide more information than individual markers (Lander and Botstein 1989). The preferred type of population for such analysis would be a cross between two inbred lines (Lander and Botstein 1989). In the ideal situation, it would be possible to assume that one of the lines (the "tester stock") has no allele in a region between a pair of markers which has a greater effect on the quantitative trait than that of any allele which is to be estimated (McMillan and Robertson 1974).

Even in this ideal situation, the estimation of either the location (with respect to a marker) of a QTL or the size of the effect at that locus is subject to bias due to the fact that several distinct QTLs may appear as a single QTL. McMillan and Robertson (1974) have shown that estimates of the effect of major loci may be grossly overestimated due to the presence of undetected loci close to the major locus. These authors illustrate the fact that for a given set of data, the size of an effect which can be detected is inversely related to power of the test to detect that effect. In addition, at a constant probability of detection, the minimum size of the effect which can be detected increases as the distance (recombination rate) between the marker and the QTL decreases.

Multiple trait index selection also requires the estimation of genetic covariances or correlations. The genetic correlation in the model used for the simulations has been assigned to pleiotropy or a tightly linked pair of loci, each of which affects one trait. In general, the degree of linkage between each such pair of loci will vary, and the direction of the correlation may also be different for each pair. For this reason, especially when more than one trait is involved, it is likely that the estimation of genetic (co)variances will always be subject to error.

The results of the simulations illustrate the sensitivity of truncation selection on the selection index to the genetic (co)variances which were used in calculating the index weights. Although the results of selection appear to be fairly robust to these parameters when the genetic correlation is positive, this is not generally the case when the genetic correlation is negative. These results indicate that caution must be used in the application of the selection index when genetic correlation is negative, particularly if selection is intense.

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