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Asymmetrical correlated responses to selection under an infinitesimal genetic model

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Summary. Asymmetry in correlated responses to selection is expected when more than one cycle of selection is practised due to changes in genetic parameters produced by selection. In large populations, under the infinitesimal model these changes are due to linkage disequilibrium generated by selection and not to gene frequency changes. This study examines the conditions under which asymmetrical correlated responses are to be expected when an infinitesimal model is considered. Asymmetrical correlated responses in two traits in respect to which trait is selected are expected if the two traits have different heritabilities. Predicted asymmetry increases with the absolute value of the genetic correlation between the two traits, the difference between the two heritabilities, the intensity of selection and the number of generations of selection. Linkage disequilibrium generated by selection should be taken into account in explaining asymmetrical correlated responses observed in selection experiments.

Key words: Asymmetry – Correlated response – Selection – Infinitesimal model – Heritability

Introduction

Asymmetrical correlated responses occur either when correlated responses for one trait from selection in two directions (high and low) on another trait differ or when standardized correlated responses to selection of two different traits differ (Bohren et al. 1966). Asymmetry in correlated responses to selection has been observed in several selection experiments. In some cases, correlated responses in two traits differed depending on the trait subjected to selection (Falconer 1960; Abplanalp et al. 1962; Siegel 1962; Bell and McNary 1963; Bradford 1969; Sorensen et al. 1980; Baker et al. 1984; Fuente et al. 1986; Nielsen and Andersen 1987; Mrode et al. 1990). In other cases, differences occurred depending on the direction of selection (Clayton et al. 1957; Synenki et al. 1972; Hanrahan et al. 1973; Nordskog et al. 1974; Baptist and Robertson 1976; Atchley et al. 1982). Several studies have reported both types of asymmetry (e.g. Festing and Nordskog 1967; McCarthy and Doolittle 1977).

Bohren et al. (1966) explained asymmetry in correlated responses in terms of changes in gene frequencies of loci affecting the traits. They showed that in the first generation of selection, standardized correlated response in trait 2 from selection on trait 1 is expected to be the same as that in trait 1 from selection on trait 2, i.e. no asymmetry occurs, and correlated responses in trait 2 from selection on trait 1 in opposite directions are also expected to be symmetric. Asymmetry can result, however, after more than one cycle of selection because of the changes in genetic variances and covariances from gene frequency changes. The analysis of Bohren et al. (1966) was limited to diallelic loci. A more general analysis was carried out by Turelli (1988). Since these theoretical works, experimental observations of asymmetry in correlated responses have often been attributed to changes in gene frequencies (Festing and Nordskog 1967; Bradford 1969; Synenki et al. 1972; Hanrahan et al. 1973; Nordskog et al. 1974; McCarthy and Doolittle 1977; Sorensen et al. 1980; Atchley et al. 1982; Baker et al. 1984; Nielsen and Andersen 1987). Change in gene frequency is a plausible explanation for observed asymmetry of response, but other explanations are also possible.

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Selection produces changes in genetic parameters not only by changing gene frequencies, but also by generating linkage (gametic phase) disequilibrium (Bulmer 1971). In an infinite population, Bulmer (1971, 1980) has shown that changes in gene frequencies can be ignored if an infinitesimal genetic model (infinite number of loci each with infinitely small effect) is assumed. With this model, the only cause of changes in genetic parameters is linkage disequilibrium induced by selection. The purpose of this study is to show that asymmetry in correlated responses can be expected under an infinitesimal genetic model due to differential reductions in responses by linkage disequilibrium generated under selection.

Model

Consider two traits each controlled by an infinite number of loci of infinitely small effect: the infinitesimal model (Fisher 1918; Bulmer 1980). There is no physical linkage, and genes act additively (no dominance or epistasis). Environmental deviations are normally distributed. The initial population is in Hardy-Weinberg and linkage equilibrium. The size of the population is infinite. Repeated cycles of selection with a constant selection intensity are practised. The selection criterion is individual phenotypic performance, and selection is by truncation. Individuals with the highest phenotypic value are selected and mated at random to produce the next generation. Environmental variances of the two traits are constant across generations. Generations are discrete.

Correlated responses in the first generation of selection

The expected genetic correlated response in a trait j when selection is applied to another trait i $(i=1, 2; j=1, 2; i \neq j)$ after one generation of selection $(CR_{j.i(1)})$ is

$$CR_{j.i(1)} = z_i \, h_{i(0)} \, h_{j(0)} \, r_{A(0)} \, \sigma_{P_j(0)}$$

where subscripts in brackets refer to generation number, z_i is the selection differential for trait i in standard units, i.e. the selection intensity, h_i and h_j are the square roots of heritabilities of traits i and j, respectively, r_A is the genetic correlation between both traits and σ_{P_j} is the phenotypic standard deviation of trait j (Falconer 1989).

Correlated response in standard deviations in trait j for each standard deviation of selection in trait i, in the first generation of selection, is

$$CR'_{j.i(1)} = \frac{CR_{j.i(1)}}{z_i \, \sigma_{P_j(0)}} = h_{i(0)} \, h_{j(0)} \, r_{A(0)}$$

(Bohren et al. 1966). Thus, after one cycle of selection, the standardized correlated response in trait 2 from selection on trait 1 is expected to be equal to the response in trait 1 from selection on trait 2,

$$CR'_{2.1(1)} = CR'_{1.2(1)} = h_{1(0)} \, h_{2(0)} \, r_{A(0)} \, .$$

Similarly, symmetric responses in trait 2 are expected from selection on trait 1 in the two directions (Bohren et al. 1966).

Correlated responses after repeated cycles of selection

As selection continues for more than one generation, standardized responses $CR'_{2.1}$ and $CR'_{1.2}$ are no longer expected to be equal due to changes in genetic parameters. Under the infinitesimal model, directional selection changes genetic variances and covariances by the generation of linkage disequilibrium. Change is maximum in the first generation and declines with subsequent generations. After about four generations of selection genetic parameters approach limiting values after which no further change occurs (Bulmer 1971, 1980).

If it is assumed that selection intensity is constant across generations, the expected genetic correlated response per generation in trait j from selection on trait i in the limit, $(CR_{j.i(L)})$ is

$$CR_{j.i(L)} = z_i \, h_{i(L)} \, h_{j(L)} \, r_{A(L)} \, \sigma_{P_j(L)}$$

where $h_{i(L)}$ and $h_{j(L)}$ are the limit values for the square roots of heritabilities for traits i and j, respectively, $r_{A(L)}$ is the limit for the genetic correlation between both traits and $\sigma_{P_j(L)}$ is the limit for the phenotypic standard deviation of trait j. Expressions for limiting values of genetic parameters have been given by Gomez-Raya and Burnside (1990) and by Villanueva and Kennedy (1990a). Standardized correlated response in trait j from selection on trait i in the limit, $(CR'_{j.i(L)})$ is

$$CR'_{j.i(L)} = \frac{CR_{j.i(L)}}{z_i \, \sigma_{P_j(L)}} = h_{i(L)} \, h_{j(L)} \, r_{A(L)} \, .$$

Under directional selection, the genetic variances of traits directly and indirectly selected always decrease. Also, the genetic correlation between both traits decreases in absolute value (Fimland 1979; Tallis 1987; Villanueva and Kennedy 1990a). Therefore, correlated responses at the equilibrium are always smaller than those expected in the first generation of selection. The percentage of decrease in $CR'_{j.i}$ at the equilibrium relative to that obtained in the first generation of selection is

$$PR'_{j.i} = \left[1 - \frac{CR'_{j.i(L)}}{CR'_{j.i(1)}}\right] \times 100 = \left[1 - \frac{h_{i(L)} \, h_{j(L)} \, r_{A(L)}}{h_{i(0)} \, h_{j(0)} \, r_{A(0)}}\right] \times 100$$

and substituting values of $h_{j(L)}$ and $r_{A(L)}$ given by Villanueva and Kennedy (1990a),

$$PR'_{j.i} = 1 - \left[\sqrt{\frac{h^2_{i(L)}}{h^2_{i(0)}\,[1 + h^2_{i(L)}\,k_i\,[1 - h^2_{j(0)}\,r^2_{A(0)}]]}} \right] \times 100$$

where k_i is $z_i(z_i - x_i)$, and x_i is the standardized deviation of the truncation point from the population mean for trait i. The limiting value of heritability of the trait directly selected ($h^2_{i(L)}$) depends on its initial value in the base population and to a lesser extent on k_i (Gomez-Raya and Burnside 1990). Therefore, in the last term, the percentage reduction in standardized correlated response in a trait indirectly selected depends on the initial heritabilities of both traits, the initial squared value of the genetic correlation and the intensity of selection. If the same selection intensity is applied on both traits, asymmetry in correlated responses is expected if the two traits have different heritabilities. On the other hand, correlated responses in one trait from upward and downward selection on another trait are always symmetric.

Values for the percentage reduction in $CR'_{2.1}$ ($PR'_{2.1}$) and $CR'_{1.2}$ ($PR'_{1.2}$) from the first generation to the equilibrium are shown in Table 1 for several combinations of initial heritabilities of both traits and genetic correlation in absolute value. Selection intensity applied on the two traits was the same and corresponded to selected proportions of 1%, 20% and 50%. Percentage reduction in standardized correlated response increases with heritability of the trait under direct selection and with selection intensity and decreases with heritability of the trait indirectly selected and genetic correlation. No asymmetry is observed ($PR'_{2.1} = PR'_{1.2}$) when the two traits have the same heritability, but asymmetry occurs ($PR'_{2.1} \neq PR'_{1.2}$) if they have different heritabilities. The absolute difference between $PR'_{2.1}$ and $PR'_{1.2}$ increases with decreasing proportion selected (i.e. the higher the intensity of selection, the greater the asymmetry in correlated responses) and increases slightly with an increase in the genetic correlation. For a given heritability of one of the traits, the more the other heritability is different the more $PR'_{2.1}$ and $PR'_{1.2}$ differ; i.e. asymmetry increases with the difference between initial heritabilities.

From the equilibrium onwards, rates of response remain constant across generations since there are no further changes in genetic parameters. However, asymmetry can increase as selection proceeds because the rate of response continues to differ for the two traits if heritabilities differ. Cumulated standardized correlated response in trait 2 from selection on trait 1 and the difference between that response and the corresponding response in trait 1 from selection on trait 2 after four generations of selection (at about when equilibrium is approached) are given in Table 2 and after ten generations in Table 3. The difference between $CR'_{2.1}$ and $CR'_{1.2}$ is taken as a measure of asymmetry. Genetic parameters

Table 1. Percentage reduction from first generation to equilibrium in standardized correlated response of trait 2 from selection on trait 1, $PR'_{2.1}$, and in standardized correlated response of trait 1 from selection on trait 2, $PR'_{1.2}$, for several combinations of initial heritabilities of trait 1, $h^2_{1(0)}$, and trait 2, $h^2_{2(0)}$, genetic correlation in absolute value, $|r_{A(0)}|$, and selected proportion of individuals, p

$\|r_{A(0)}\|$	$h^2_{1(0)}$	$h^2_{2(0)}$	p = 1%		p = 20%		p = 50%	
			$PR'_{2.1}$	$PR'_{1.2}$	$PR'_{2.1}$	$PR'_{1.2}$	$PR'_{2.1}$	$PR'_{1.2}$
0.2	0.2	0.2	12.54	12.54	11.17	11.17	9.45	9.45
		0.5	12.46	21.86	11.10	19.80	9.39	17.12
		0.8	12.39	26.37	11.04	24.02	9.34	20.91
	0.5	0.5	21.73	21.73	19.68	19.68	17.01	17.01
		0.8	21.60	26.20	19.56	23.85	16.90	20.76
	0.8	0.8	26.02	26.02	23.69	23.69	20.61	20.61
0.5	0.2	0.2	12.28	12.28	10.94	10.94	9.25	9.25
		0.5	11.82	21.40	10.52	19.37	8.89	16.73
		0.8	11.35	25.76	10.10	23.44	8.53	20.38
	0.5	0.5	20.57	20.57	18.59	18.59	16.03	16.03
		0.8	19.70	24.63	17.79	22.36	15.32	19.39
	0.8	0.8	23.44	23.44	21.24	21.24	18.38	18.38
0.8	0.2	0.2	11.80	11.80	10.51	10.51	8.88	8.88
		0.5	10.59	20.53	9.41	18.56	7.94	16.01
		0.8	9.32	24.58	8.27	22.32	6.97	19.35
	0.5	0.5	18.26	18.26	16.46	16.46	14.13	14.13
		0.8	15.79	21.42	14.18	19.34	12.13	16.66
	0.8	0.8	17.82	17.82	16.00	16.00	13.67	13.67

Table 2. Cumulative standardized correlated response in trait 2 from selection on trait 1 in absolute value, $|CR'_{2.1}|$, and difference between $|CR'_{2.1}|$ and the corresponding response in trait 1 from selection on trait 2, Asymm. = $|CR'_{2.1} - CR'_{1.2}|$, after four generations of selection for several combinations of initial heritabilities of trait 1, $h^2_{1(0)}$, and trait 2, $h^2_{2(0)}$, genetic correlation in absolute value, $|r_{A(0)}|$, and selected proportion of individuals, p

$\|r_{A(0)}\|$	$h^2_{1(0)}$	$h^2_{2(0)}$	p = 1%		p = 20%		p = 50%	
			$\|CR'_{2.1}\|$	Asymm.	$\|CR'_{2.1}\|$	Asymm.	$\|CR'_{2.1}\|$	Asymm.
0.2	0.2	0.2	0.15	0.00	0.15	0.00	0.15	0.00
		0.5	0.23	0.02	0.24	0.02	0.24	0.02
		0.8	0.30	0.04	0.30	0.03	0.30	0.03
	0.5	0.5	0.34	0.00	0.35	0.00	0.36	0.00
		0.8	0.43	0.02	0.44	0.02	0.45	0.02
	0.8	0.8	0.52	0.00	0.53	0.00	0.55	0.00
0.5	0.2	0.2	0.37	0.00	0.37	0.00	0.38	0.00
		0.5	0.59	0.05	0.59	0.04	0.60	0.04
		0.8	0.74	0.09	0.75	0.08	0.76	0.07
	0.5	0.5	0.86	0.00	0.87	0.00	0.90	0.00
		0.8	1.09	0.05	1.11	0.04	1.14	0.04
	0.8	0.8	1.33	0.00	1.36	0.00	1.40	0.00
0.8	0.2	0.2	0.59	0.00	0.60	0.00	0.61	0.00
		0.5	0.95	0.08	0.95	0.06	0.96	0.05
		0.8	1.21	0.16	1.22	0.14	1.23	0.12
	0.5	0.5	1.40	0.00	1.42	0.00	1.45	0.00
		0.8	1.80	0.09	1.83	0.08	1.86	0.06
	0.8	0.8	2.23	0.00	2.27	0.00	2.32	0.00

Table 3. Cumulative standardized correlated response in trait 2 from selection on trait 1 in absolute value, $|CR'_{2.1}|$, and difference between $|CR'_{2.1}|$ and the corresponding response in trait 1 from selection on trait 2, Asymm. = $|CR'_{2.1} - CR'_{1.2}|$, after ten generations of selection for several combinations of initial heritabilities of trait 1, $h^2_{1(0)}$, and trait 2, $h^2_{2(0)}$, genetic correlation in absolute value, $|r_{A(0)}|$, and selected proportion of individuals, p

$\|r_{A(0)}\|$	$h^2_{1(0)}$	$h^2_{2(0)}$	p = 1%		p = 20%		p = 50%	
			$\|CR'_{2.1}\|$	Asymm.	$\|CR'_{2.1}\|$	Asymm.	$\|CR'_{2.1}\|$	Asymm.
0.2	0.2	0.2	0.36	0.00	0.36	0.00	0.37	0.00
		0.5	0.57	0.06	0.57	0.05	0.58	0.04
		0.8	0.72	0.11	0.73	0.10	0.74	0.09
	0.5	0.5	0.81	0.00	0.83	0.00	0.85	0.00
		0.8	1.03	0.06	1.05	0.05	1.08	0.04
	0.8	0.8	1.23	0.00	1.27	0.00	1.31	0.00
0.5	0.2	0.2	0.90	0.00	0.91	0.00	0.92	0.00
		0.5	1.42	0.14	1.44	0.13	1.46	0.11
		0.8	1.81	0.27	1.83	0.24	1.86	0.22
	0.5	0.5	2.05	0.00	2.10	0.00	2.16	0.00
		0.8	2.62	0.15	2.67	0.13	2.75	0.12
	0.8	0.8	3.17	0.00	3.25	0.00	3.36	0.00
0.8	0.2	0.2	1.44	0.00	1.46	0.00	1.48	0.00
		0.5	2.30	0.23	2.33	0.21	2.36	0.18
		0.8	2.95	0.45	2.98	0.41	3.01	0.35
	0.5	0.5	3.36	0.00	3.43	0.00	3.51	0.00
		0.8	4.36	0.26	4.44	0.24	4.53	0.20
	0.8	0.8	5.39	0.00	5.50	0.00	5.64	0.00

Table 4. Limiting values for heritabilities of trait 1, $h^2_{1(L)}$, and trait 2, $h^2_{2(L)}$, and genetic correlation in absolute value, $|r_{A(L)}|$when selection is on trait 1, ST1, or on trait 2, ST2, for several combinations of initial heritabilities of trait 1, $h^2_{1(0)}$, and trait 2, $h^2_{2(0)}$, and genetic correlation in absolute value, $|r_{A(0)}|$. Selected proportion of individuals is 20%

$\|r_{A(0)}\|$	$h^2_{1(0)}$	$h^2_{2(0)}$	ST1			ST2		
			$\|r_{A(0)}\|$	$h^2_{1(L)}$	$h^2_{2(L)}$	$\|r_{A(0)}\|$	$h^2_{1(L)}$	$h^2_{2(L)}$
0.2	0.2	0.2	0.19	0.18	0.20	0.19	0.20	0.18
		0.5	0.19	0.18	0.50	0.17	0.20	0.43
		0.8	0.19	0.18	0.80	0.16	0.20	0.72
	0.5	0.5	0.17	0.43	0.50	0.17	0.50	0.43
		0.8	0.17	0.43	0.80	0.16	0.80	0.72
	0.8	0.8	0.16	0.72	0.80	0.16	0.80	0.72
0.5	0.2	0.2	0.48	0.18	0.20	0.48	0.20	0.18
		0.5	0.48	0.18	0.49	0.45	0.19	0.43
		0.8	0.48	0.18	0.79	0.42	0.19	0.72
	0.5	0.5	0.45	0.43	0.48	0.45	0.48	0.43
		0.8	0.45	0.43	0.79	0.42	0.48	0.72
	0.8	0.8	0.42	0.72	0.78	0.42	0.78	0.72
0.8	0.2	0.2	0.78	0.18	0.19	0.78	0.19	0.18
		0.5	0.78	0.18	0.48	0.76	0.17	0.43
		0.8	0.78	0.18	0.79	0.73	0.16	0.72
	0.5	0.5	0.76	0.43	0.46	0.76	0.46	0.43
		0.8	0.76	0.43	0.77	0.73	0.43	0.72
	0.8	0.8	0.73	0.72	0.75	0.73	0.75	0.72

needed to compute responses were obtained each generation by recurrently using expressions described by Villanueva and Kennedy (1990a). Intensity of selection was the same for the two traits and corresponded to proportions of selected individuals of 1%, 20% and 50%. Different initial heritabilities and genetic correlation were considered. Asymmetry in standardized correlated responses increased with the absolute value of the genetic correlation, with the difference between both heritabilities and with the number of cycles of selection.

Asymmetry in predicted correlated responses after repeated cycles of selection is a consequence of the asymmetry in genetic parameters involved in such predictions. Selection on trait 1 can result in different equilibrium heritabilities and genetic correlation than selection on trait 2. Equilibrium values for heritabilities of the two traits and the genetic correlation between them when selecting for trait 1 or trait 2 are shown in Table 4. Selection intensity corresponded to a proportion of individuals saved of 20%. Combinations of initial genetic parameters considered were the same as in previous tables. At the limit the genetic correlation is asymmetric when the two traits have different heritabilities. This is due to the fact that change in the genetic correlation from generation zero to the equilibrium increases with heritability of the trait directly selected and does not depend on the heritability of the trait indirectly selected (Villanueva and Kennedy 1990a). Not only is the genetic correlation asymmetric when the two initial heritabilities differ, but so is the product of both heritabilities in the limit.

Discussion

Traditionally, asymmetry in correlated responses in two traits observed in selection experiments has been explained by changes in gene frequencies (Festing and Nordskog 1967; Bradford 1969; McCarthy and Doolittle 1977; Sorensen et al. 1980; Baker et al. 1984; Nielsen and Andersen 1987). Bohren et al. (1966) and Turelli (1988) outlined the conditions in which asymmetry can be expected based on gene frequency changes, and Bohren et al. (1966) concluded that correlated responses are very sensitive to such changes and that frequent asymmetry is to be expected in practice. However, if the number of loci controlling the traits under consideration is very large, changes in gene frequencies can be ignored (Bulmer 1971, 1980). In this study it has been shown that under the asssumptions of an infinitesimal genetic model it is still possible to expect asymmetry due to changes in genetic parameters by linkage disequilibrium. Asymmetry is expected when the heritabilities of the traits involved are different.

Under the infinitesimal model, correlated response is reduced in the same proportion as the direct response (Villanueva and Kennedy 1990a). In other words, the ratio $CR_{j.i}/R_i$ (where R_i is the direct response of the selected trait i) remains constant across generations. This would not necessarily be the case if a model with finite number of loci is assumed. Standardization of correlated responses in terms of direct responses could be useful to help distinguish between both models.

The build-up of asymmetry by linkage disequilibrium is in the early generations of selection. After about four cycles of selection, genetic parameters and rates of responses approach equilibrium values. However, if the two traits differ initially in heritability, their respective rates of response at equilibrium also differ. Asymmetry then accumulates and increases with the number of generations of selection. Therefore, although linkage disequilibrium generated by selection mostly occurs in the early generations, its effect in producing asymmetry in correlated responses remains important in the long term.

The interpretation of observed asymmetrical responses in selection experiments is difficult. In some experiments asymmetry occurred according to the magnitudes of initial heritabilities; i.e. correlated response was smaller for the trait with the smaller heritability (McCarthy and Doolittle 1977; Fuente et al. 1986). However, in other experiments asymmetry occurred in the opposite direction to what is expected under the infinitesimal model; i.e. correlated response was smaller for the trait with the higher heritability (Sorensen et al. 1980; Baker et al. 1984). In still other studies, asymmetrical correlated responses were found although heritabilities of the two traits considered did not differ significantly (Bell and McNary 1963; Festing and Nordskog 1967).

Several factors may explain the observed results in selection experiments. Firstly, in practice population size is finite, and random fluctuations due to genetic drift can occur. Secondly, in selection experiments, estimates of base population parameters can have large sampling errors. Also, with a finite number of loci, selection can induce simultaneously changes in gene frequencies and linkage disequilibrium. Finally, other assumptions of the model studied in this work (normality of the traits, additive gene action, equal selection intensity on both traits, absence of natural selection) may not hold in practice.

In order to evaluate the efficiency of indirect selection, a simulation study of selection on two traits with different heritabilities (0.1 versus 0.5) was carried out by Villanueva and Kennedy (1990b). The genetic correlation between traits was 0.5. The genetic model was the same as in the present work except that the number of loci controlling the traits was finite (10 or 30). Therefore, both effects of selection (changes by linkage disequilibrium and gene frequency changes) were accounted for. One thousand individuals were simulated so rate of inbreeding was small. Only responses for one of the traits were reported (Villanueva and Kennedy 1990b), but responses for the other trait were also obtained. Standardized correlated responses in the first generation of selection were equal to 0.11 for both traits in both 10- and 30-loci experiments. However, after ten generations of selection cumulative standardized correlated responses showed asymmetry (0.50 versus 0.89 with 10 loci and 0.72 versus 0.97 with 30 loci), with the greater response being in the trait with the higher heritability. These results agree well with theoretical expectations of the present work. Reduction in correlated response was greater for the trait with lower heritability.

Different possible causes of asymmetry in correlated responses such as assortative mating (Gianola 1982), gene frequency changes by selection (Bohren et al. 1966; Turelli 1988) or linkage disequilibrium produced by selection can interact and make the interpretation of experimental results difficult.

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