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.
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 ≠ j) after one generation of selection (CR_{j,i}^{(1)}) is

\[ CR_{j,i}^{(1)} = z_i h_i(0) h_j(0) r_A(0) \sigma_p(j) \]

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 \( \sigma_p(j) \) 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

\[ CR_{j,i}^{\ast,(1)} = \frac{CR_{j,i}^{(1)}}{\sigma_p(j)} \]

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 (Finland 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 \( CR_{j,i}^{\ast,(1)} \) at the equilibrium relative to that obtained in the first generation of selection is

\[ PR_{j,i}^{\ast} = \left[ \frac{1}{\frac{CR_{j,i}^{\ast,(1)}}{CR_{j,i}^{(1)}}} \right] \times 100 \]

Correlated responses after repeated cycles of selection

As selection continues for more than one generation, standardized responses \( CR_{j,i}^{(L)} \) and \( CR_{i,j}^{(L)} \) 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

\[ CR_{j,i}^{(L)} = z_i h_i(L) h_j(L) r_A(L) \sigma_p(j) \]

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 \( \sigma_p(j) \) 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 Burns-side (1990) and by Villanueva and Kennedy (1990a). Standardized correlated response in trait j from selection on trait i in the limit, \( CR_{j,i}^{\ast,(L)} \) is

\[ CR_{j,i}^{\ast,(L)} = \frac{CR_{j,i}^{(L)}}{\sigma_p(j)} \]

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 (Finland 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 \( CR_{j,i}^{\ast,(1)} \) at the equilibrium relative to that obtained in the first generation of selection is

\[ PR_{j,i}^{\ast} = \left[ \frac{1}{\frac{CR_{j,i}^{\ast,(L)}}{CR_{j,i}^{(L)}}} \right] \times 100 \]