A SIMULATION STUDY TO EVALUATE OPTIMAL STRATEGIES FOR SELECTION ON A QUANTITATIVE TRAIT USING MAJOR GENE INFORMATION.

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ABSTRACT

A SIMULATION STUDY TO EVALUATE OPTIMAL STRATEGIES FOR SELECTION ON A QUANTITATIVE TRAIT USING MAJOR GENE INFORMATION

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Previous studies have shown that Marker-Assisted Selection (MAS) based on a known major gene and genotypic selection can increase response to selection in the short term but reduce longer-term response to selection. The criterion for genotypic selection is:

$$I = g + h^2(P - G)$$

were g is the breeding value for the major gene and $h^2(P - G)$ is the animal's polygenic EBV based on phenotype (p) adjusted for major genotype (G). Recently, Dekkers and van Arendonk (1998) developed methods to optimize the use of a known major gene in selection to maximize response over a planning horizon.

The objective of this study was to use stochastic simulation to evaluate the optimal strategies developed by Dekkers and van Arendonk (1998) under a model in which genetic variance declined as a result of selection (Bulmer effect). A population with discrete generations, fixed size and equal selection among males and females

was considered.

Resulting strategies maximized cumulative response to selection for a pre-specified planning horizon. Results show that optimal strategies that are derived under a model with constant genetic variance may not result in greater responses to selection for all situations. Further improvements in optimal strategies are under development.

Advisory Committee: Dr. I. McMillan (advisor)

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Dr. A. Gibbins

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Chapter 1

Introduction

Although animal breeders can not ignore natural selection, the type of selection of primary interest to them is artificial selection, which is under human control (Bourdon, 1997). Genetic improvement of livestock for economic performance is based on selection on estimates of breeding values based on performance of the animal itself and its relatives. This type of selection is also known as mass selection. Selection methods based on phenotypic data rely on accurate estimates of breeding values of individuals or groups of animals. Breeding values can be estimated on phenotypic information of the animal itself and its relatives, using Best Linear Unbiased Prediction (BLUP) procedures (Henderson, 1988).

Advances in the technologies of molecular genetics have greatly increased the information available on individual genes for quantitative traits. Molecular techniques have enabled researchers to identify genetic markers that can be used to evaluate animals more precisely for selection and thus increase efficiency of production. Breeders can benefit from results produced by molecular geneticists on aspects

such as the location, effect and frequency of a major gene, a gene with large effect, for genetic improvement in their breeding programs. Breeders can also improve the accuracy of their selection by using information that is obtained from molecular genetic markers that are closely linked to a quantitative trait locus (QTL). This approach has been named Marker Assisted Selection (MAS).

Genetic marker information may be used to detect a QTL having a large effect on phenotype (Clarke et al., 1998). As more genes with major effects are being discovered, it is possible to incorporate them into selection programs by directly selecting on their genotypic values. This would be an improvement in the accuracy of selection over traditional selection programmes (Kennedy et al., 1990). Hence, by integrating marker information into artificial selection for quantitative traits, the efficiency of selection can be increased substantially, as shown by Lande and Thompson (1989).

There are a number of selection strategies that use information from molecular genetics that can be used to increase the efficiency of selection, such as major gene selection and MAS. Major gene selection depends on the availability of information on genes with major effects on traits of interest. MAS depends on the linkage between markers and loci, including QTLs, affecting relevant traits, and requires linkage disequilibrium (Muir, 1994; Fairfull, 1995).

Candidate gene and comparative gene mapping approaches have been successfully applied in identifying major genes affecting various traits. To date, several

important major genes have been found using the candidate gene approach. Comparative gene mapping is used to find "positional candidate genes" in the regions associated with possible QTL. For the improvement of dairy cattle, it is common to use a progeny test of sires to estimate their breeding values more accurately. The data records from progeny tests and the genotypic information on markers are useful for detection of major genes (Roy et al., 1989).

There are several methods for finding a QTL based on genetic markers or for estimating the effects of a QTL, such as mixed model methodology for analysis of data on multiple genetic markers (Goddard, 1992), a simple regression method for mapping QTL in line crosses (Haley and Knott, 1992), the maximum likelihood methodology (Bovenhuis and Weller, 1994), a random model approach to interval mapping of QTL (Shizhong and Atchley, 1995), or in outbred populations (Liu and Dekkers 1996), and mixed inheritance analysis methods (Hoeschele et al., 1993; Hoeschele, 1994; Uimari et al., 1996a). McMillan and Robertson (1974) studied the power of methods for the detection of major genes affecting quantitative characters.

Bovenhuis et al. (1997) gave an overview of the main characteristics and differences between methods in this area.

Soller (1978) combined marker information and phenotypic information based on selection index principles, to obtain genetic evaluations for selection. Fernando and Grossman (1989) presented methodology for the application of BLUP to estimation of breeding values based on molecular and phenotypic data. The authors showed

that there is additional genetic progress expected from MAS by using BLUP to estimate the breeding value.

To assess the relative advantage of directly incorporating major gene information into a breeding program as compared to conventional phenotypic selection, it is important to examine how successful a selection program could be, using information from a major gene. Ruane and Colleau (1995) used Monte Carlo simulation to evaluate the benefits of MAS in a small population with one marker for a bi-allelic QTL. They concluded that MAS resulted in substantially higher QTL responses (4-54%), especially for low heritability traits, than conventional selection based on BLUP for breeding values, but lower polygenic responses (up to 4%), so that the overall effect on the total genetic response was relatively small.

Gibson (1994) simulated selection on a known major gene using an additive infinitesimal model, which is based on the assumption of an infinite number of loci with very small effects on the quantitative trait, plus a single bi-allelic QTL. The results of this simulation showed that use of information on a QTL in selection gives more rapid short-term response but less long-term response than if the QTL were ignored. This study showed that current strategies for MAS may not maximize response to selection in the longer term.

Dekkers and Van Arendonk (1998) tried to optimize selection for a quantitative trait over multiple generations with information on a major gene. This was based on a deterministic simulation. Their results agreed with those of Gibson (1994), i.e.

that mass selection, which is selection based on phenotype, had greater selection response in the longer term than genotypic selection, which is selection based on the sum of the estimated additive polygenic breeding value and the known breeding value at the major gene locus, according to the known genotype of the candidate. They defined "optimal selection", as an index selection similar to genotypic selection but with a weight assigned to the breeding value for the major gene, such that cumulative gain at the end of a planning horizon is maximized, and showed that optimal selection achieved greater cumulative total response over the planning horizon than genotypic or mass selection. This work addressed the lack of knowledge on the optimal use of a QTL in Gibson's work.

The important issue that was considered by Dekkers and Van Arendonk (1998) was how to optimally combine the information from the polygenic breeding value with than from the major genes, such that a better response could be achieved compared to mass and genotypic selection. In their deterministic simulation, however, they did not consider the impact of gametic phase disequilibrium among polygenes and only considered gametic phase disequilibrium between the major gene and polygenes.

In this present study the effect is taken into account of gametic phase disequilibrium on the reduction in polygenic variance as a result of selection (Bulmer 1971).

This study will use a stochastic model to evaluate the optimal strategies of

Dekkers and Van Arendonk (1998) for selection on a quantitative trait using major gene information, and will compare response from the deterministic model with stochastic simulation.

1.1 Objectives

The objectives of this study were, using a stochastic computer simulation model of a breeding population, to:

- Compare the responses from mass and genotypic selection with the response to optimal strategies for selection on a major gene, as defined by the deterministic model of Dekkers and Van Arendonk (1998)
- Compare the response to selection from the deterministic model with the selection response using stochastic simulation
- Examine the effects on selection response and on the comparison between mass, genotypic, and optimal selection of
  - heritability
  - size of the effect of the major gene
  - degree of dominance at the major gene

Chapter 2

Literature Review

Most of quantitative genetic theory applications to animal breeding are based on the assumption that the traits of interest in animal production are influenced by alleles at many loci, each contributing a small effect to the expression of the phenotype. Not all quantitative traits of interest do, however, owe their expression to the exclusive action of many genes of small effect (polygenes), but instead may be influenced by a limited number of genes of large effect (major genes), along with polygenes.

It is not presently known how commonly QTLs are involved with a major effect. At present, there are 1774 loci mapped in the pig mapping database. This includes 507 genes and 1201 microsatellites markers. The number of genes and microsatellites markers on genetic linkage maps for cattle are 534 and 1219, respectively (August, 1998; http://www.ri.bbsrc.ac.uk/cgi-bin/arkdb). However, as mentioned previously, only a few of these genes are major genes that affect a quantitative trait. The coverage on these maps is now sufficient to allow researchers to

conduct quantitative trait loci linkage analysis.

The first important major genes identified in domestic animals that affect a quantitative trait were revealed when Shultz and Briles (1953) investigated the relation between blood group genes and performance of laying hens. They studied genes affecting the antigenic structure of erythrocytes. Thoday et al. (1964) had considerable success in the detection and location of loci affecting QTLs. The double-muscled condition in cattle is a good example of a major gene for variation in muscle development. Back-crossing F_1 females to a double-muscled sire gave a result that was compatible with the segregation of a major gene (Hanset, 1982). Other examples of continuous traits that are influenced by a major gene are the double muscling gene in pigs (Ollivier, 1980), the callipyge gene in sheep (Cockett et al., 1994), dwarfism in poultry (Merat and Ricard, 1974), the Booroola gene affecting ovulation rate in sheep (Piper and Bindon, 1982), the halothane sensitivity gene in pigs (Smith and Bampton, 1977), the rapid postweaning growth gene in mice (Bradford and Famula, 1984), the high milk protein content gene in goats (Grosclaude et al., 1987), the high milk flow gene in goats (Ricordeau, 1982), the gene for low technological yield for cooked ham in pigs (Roy et al., 1990), and a major gene affecting litter size in pigs (Rothschild et al., 1994).

The basic theory for incorporating a specific gene with a direct effect on a quantitative character into a selection index was derived by Neimann-Sorensen and Robertson (1961). Using blood group data, Neimann-Sorensen and Robertson concluded

that the difference in performance may have two genetic causes: they may be directly due to the gene (the blood group) or to genes closely linked to the blood group gene.

It has been proposed that genotypic information on marker loci that are linked to QTLs can be combined with phenotypic information to maximise genetic responses to selection (Neimann-Sorensen and Robertson, 1961; Smith, 1967; Soller, 1978).

Smith and Simpson (1985) showed that any genotypic information on QTLs can increase the accuracy of selection. This may be particularly useful when the phenotypic information can not be measured directly on the live animals (such as for carcass traits) or when phenotypic information is expensive to collect, or is sex limited (such as milk yield in females) (Smith and Simpson, 1986).

Meuwissen and Goddard (1995) used information on marker haplotypes to increase rates of genetic gain in closed nucleus breeding schemes. They concluded that the extra genetic gain decreases with the number of generations of MAS, as the variance of the QTL becomes more and more exploited. In this study, the marked QTL was assumed to explain 33% of the genetic variance. They also showed that the extra rates of gain from MAS can be large when there is a continuous detection of a new QTL. In the case of a carcass trait, extra response rates were up to 64%.

Spelman (1998) showed that MAS can increase the rate of genetic gain, but the degree of improvement in genetic gain is extremely variable and greatly depends on the size of the QTL and on the genetic model simulated. The larger the QTL size

and the more QTL alleles simulated, the greater the genetic response.

To date, MAS has not been used or tested on a wide scale in practice. The only reported attempt to actually use MAS was that of Dunnington et al. (1992), who used appropriate family structure in chickens to search for sire-specific DNA fingerprint bands associated with QTLs, and to test by MAS the effectiveness of genetic marker as a potential selection tool. Their results indicated that use of DNA fingerprint bands can be an aid to classical selection for improving quantitative traits of economic importance.

Some quantitative geneticists have presented an overly optimistic scenario for MAS. For example, Lande and Thompson (1990) showed theoretically that selection efficiency can be increased by over 400% with MAS. Because numerous simplifying assumptions were made in this study, Zhang and Smith (1992) developed a simulation model to investigate the effects on selection response of a genetic markers linked to a QTL with gametic phase disequilibrium generated by a cross between individual lines. Results showed that selection on phenotype always gave greater response than selection on markers alone. According to Gibson (1994), this may not be expected. The use of marker quantitative trait locus (MQTL) effects and the phenotypic information in combined selection gave greater response than selection on the phenotype or marker. However, the improvement was much less than the 100-200% improvement predicted by Lande and Thompson (1990).

When phenotypic selection is effective (high heritability), further information

on a major gene will add little to the rate of improvement (Muir and Stick, 1998). If phenotypic selection is not effective, as for traits with low heritability, indirect selection must be used, and selection on the major gene can add significantly to the rate of genetic improvement (Smith and Webb, 1981).

Saefuddin (1991) used stochastic computer simulations of populations of finite size to examine the behaviour of a transgene in a population under selection for a single trait. In all cases of transgene effect, genotypic selection, in which the candidate animals were evaluated and selected on the sum of estimated breeding value for the quantitative trait and their expected value at the transgene, reached fixation for the transgene much faster than phenotypic selection. Genotypic selection led to enhanced rates of genetic gain, but only in the early generations.

Van Arendonk et al., (1994) simulated MAS for a trait which was not sex-limited. An animal model was used to estimate BLUP, of additive effects at the marker QTL and of additive effects of polygenes. The cumulative genetic gain due to using markers diminished over time, giving an initial 12-19 % advantage, which reduced to -1 to +5 % by the 12^{th} generation. They explained this decline as being due to a large reduction in variance of allelic effects at the QTL, when markers are used. It must be noted that 12 generations is considered equivalent to a long period of time for livestock species such as cattle.

Gibson(1994) reported on a simulation experiment, which indicated that use of information on a QTL in selection gives greater selection response in the short-

term, compared to phenotypic selection, but less response in the long term. Gibson (1994) simulated selection on the sum of the breeding value for the major gene and an estimated breeding value for polygenes.

Most comparisons between MAS and phenotypic selection have been based on the infinitesimal model except those of Zhang and Smith (1992) and Muir and Stick (1997), who used a gene level simulation program.

The objective of the Muir and Stick (1997) study was to examine, through use of a Monte Carlo gene level simulation program, the potential relative advantage that direct selection on the genotype adds to a breeding program. They showed that selection directly on the QTL was disadvantageous in both the short term and the long term for heritabilities larger than 1%. For heritabilities less than 1%, they showed that direct selection on the QTL was always more advantageous that selection on phenotype alone. These researchers did not use genotypic selection, and put more weight on the major gene than did others, so it is difficult to compare their study to other studies using major gene information.

The Larzul et al. (1997) study was based on two indices. The first index did not consider the major genotype and information whereas the second index used this information. The model for the estimation of genetic progress into account took overlapping generations with infinite population size. A constant selection pressure of 80% was assumed. They showed that information about the major gene in breeding value estimation should be incorporated in selection, when the

heritability is low, and the major gene effect is high and its initial frequency small, in particular for a recessive major gene. They showed that including major gene information is valuable in limited circumstances. The value of including the major gene information in selection may be very high in the most favourable case. When the favourable allele was recessive, a 200% increase of the genetic response after 25 generations of selection was observed (Larzul et al., 1997). Obviously 25 generations is considered a long time.

Fournet et al., (1997) performed a stochastic simulation to examine the effect of including major gene information in genotypic selection. They concluded that the inclusion of major gene information can provide extra gain in the medium and long-term, when the favourable allele at the major locus is rare and recessive. Their results gave good agreement with the results of Larzul et al. (1997). Their results agreed with those of Gibson (1994) for the additive case where, in the long term, mass selection was always superior to genotypic selection.

Muir and Stick (1998) developed a simulation program to evaluate the advantage of combining major gene information in breeding programs. In this study the authors concluded that, with a very low heritability(1%), using the major gene is superior to phenotypic selection but, with a heritability of 10% and higher, phenotypic selection was superior to selection on an index that included a high weighting on major gene information. They also showed that placing too much emphasis on the major genes is disadvantageous to the breeding program.

Dekkers and Van Arendonk (1998) used information on a major gene to optimize selection for a quantitative trait. This was based on a deterministic simulation model. They used optimal control theory to derive weights for an index of major gene effects and estimates of polygenic breeding values that maximized cumulative response over a given number of generations of selection. Genotypic selection resulted in greater response than mass selection in the short term but lower response in the longer term, which is similar to the results of Gibson (1994). The second conclusion to be draw from their study was that optimal selection achieved greater cumulative total response over the planning horizon than genotypic and mass selection. They examined models with and without gametic phase disequilibrium between the major gene and polygenes. Gametic phase disequilibrium among polygenes was not modelled (constant polygenic variance). Without gametic phase disequilibrium between the major gene and polygenes, optimal selection achieved 0.4%, 2.2%, and 2.1% higher cumulative responses than genotypic selection for planning horizons of 5, 10, and 15 generation, respectively. When gametic phase disequilibrium between the major gene and polygenes was taken into account, cumulative response was reduced less in the initial generations for optimal selection compared to genotypic selection; the extra response at the end of 5 and 10 generation planning horizons was 0.58% and 1.98%, respectively. In this study, stochastic simulation were used to evaluate the results of a deterministic model for optimization of quantitative trait loci.

Chapter 3

Materials and Methods

3.1 Assumptions and general description of the simulation model

A stochastic computer simulation of a population under selection for a quantitative trait was constructed by a program developed using Fortran 77. The program was developed with the facilities available at Iowa State University and the Centre for Genetic Improvement of Livestock (CGIL) at the University of Guelph. The program does not require machine dependent subroutines. Also, in order to avoid portability problems, standard forms of Fortran programming were applied as much as possible.

The population under selection was assumed to be large with no accumulation of inbreeding (constant Mendelian sampling variance over time), with discrete generations. Selection was considered for a hypothetical quantitative trait, which is controlled by a major gene and polygenes. It was assumed that a single gene, the " major gene ", had been detected and that it was possible to determine the genotype

of each individual at the major gene. The major gene had two alleles (B and b) and, therefore, three genotypes BB, Bb and bb with average genotypic value of a, d and -a, respectively. The individual genotypes at the major gene and the effects of each possible genotype on the trait were assumed to be known without error. The polygenic part consisted of many genes, each with a small additive effect, and was modelled following the infinitesimal model. The base generation was in genetic gametic phase equilibrium between the major gene and polygenes, as well as among polygenes.

3.2 Model and simulation procedures

The general model used for this trait, with characteristics as in Table 3.1, was:

$$y_{ik} = mg_k + A_i + e_i$$

where:

- y_i = Phenotypic value of individual i with major genotype k.
- mg_k = effect of the major genotype k on the individual's phenotype.
- A_i = collective effect of the polygenes on the individual's phenotype.
- e_i = random error.

3.2.1 Base population

True breeding values A_i for the polygenic effect of base population animals were

simulated according to the formula:

$$A_i = v_i \times \sigma_a$$

were v_i is a random normal deviate drawn from a standard normal distribution, N(0,1), with zero mean and variance one, and σ_a is the additive genetic standard deviation in the base population.

The genotypic value for the major gene was calculated based on the genotype of each individual and the value of the favourable allele (a and d). To simulate the major genotype of an individual, a random number was drawn from a uniform distribution (URN). If the random number was smaller than or equal to the frequency of the BB genotype (p^2), the animal was assigned genotype BB. If the random number was between p^2 and $p^2 + 2pq$, the animal was assigned genotype Bb. If the random number was greater than $p^2 + 2pq$, then the animal was assigned genotype bb. Table 3.3 shows the genotypic value associated with each major genotype. Considering a single locus with two alleles, B and b, the genotypic value of the favourable homozygote (BB) was set equal to $+a$, that of the unfavourable homozygote(bb) was set equal to $-a$ and that of the heterozygote (Bb) equal to d (Falconer and Mackay 1996).

The random error were simulated according to the formula:

$$e_i = v_i \times \sigma_e$$

were v_i is a random normal deviate sampled from a standard normal distribution,

with mean zero and variance σ_e^2 (residual variance).

Adding the effects from the major gene's genotypic value (mg_k) to the polygenic breeding value (A_i) gives the total genetic value of an individual. The phenotype is determined by adding the genotypic value and the random deviation (e_i).

3.2.2 Progeny population

The breeding values for polygenes of progeny were generated as follows:

$$A_i = 0.5 \times (A_{si} + A_{di}) + \phi_i$$

Where A_i, A_{s_i} and A_{d_i} are the polygenic breeding values of progeny i and of its sire and dam, respectively, and ϕ_i is the Mendelian sampling contribution, which was generated as:

$$\phi_i = v_i \times \sqrt{0.5 \times \sigma_a^2}$$

were v_i is a random normal deviate drawn from a standard normal distribution. It was assumed that Mendelian sampling contributions follow a normal distribution with zero mean and variance $0.5\sigma_a^2$. To generate the genetic value of the major gene for a progeny, a random number sampled from a uniform distribution (0,1) was used to determine which alleles were transmitted from heterozygous (Bb) sires and dams. If the random number was smaller than or equal to 0.5, B allele was passed to the progeny, otherwise the b allele was inherited (Table 3.4).

The phenotypic value of a progeny was the sum of the polygenic breeding value, the major gene genotypic value, and the random error. Environmental effects were

sampled from a normal distribution, with mean of zero and variance σ_e^2.

3.2.3 Selection

Three selection methods were applied in this study, depending on whether and how the major gene information was included in the selection criterion. After selecting animals as breeding sires and dams, selected animals were mated at random.

3.2.3.1 Mass selection:

Candidate animals were selected on the basis of their phenotypic performance, with the best ones being selected as breeders. Although information from the major gene was not included directly, the implicit model for this selection criterion was:

$$\mathbf{I_i = h^2 \times P = h^2(g_m) + h^2(P - g_m)}$$

Selection on phenotype does result in indirect selection for the major gene.

3.2.3.2 Genotypic selection:

Here the value of the major gene is known and included in the selection criteria. The candidate animals were evaluated based on an index that was the sum of the estimated breeding value for polygenes, which was based on phenotype only, and on the average breeding value at the major gene locus, according to the known genotype of the candidate.

The model for this selection criterion is:

$$I_i = Mg_k + h^2(P_i - gm_k)$$

- I_i = Selection criterion for individual i.
- Mg_k = Average breeding value for major genotype k.
- P_i = Phenotypic value of individual i.
- h^2 = Heritability of the trait.
- gm_k = Average genotypic value for major genotype k.

Under gametic phase disequilibrium between the major gene and polygenes, the breeding value for the major gene, Mg_k, takes values of $2q\alpha$, $(q-p)\alpha$, and $-2q\alpha$ with frequencies p^2, 2pq, and q^2 for the BB, Bb, and bb genotypes, respectively. Where α is average effect of gene substitution : $\alpha = a + d(1-2p)$ (Falconer and Mackay 1996). In the stochastic and deterministic models, breeding values for the major gene were reparameterized by taking each different genotypic value as a deviation from the breeding value for the heterozygote, in which case breeding values for BB and bb were equal to α and $-\alpha$, respectively. Gametic phase disequilibrium between major gene and polygenes which is equivalent to using gene frequency, was calculated based on following formula (Falconer and Mackay 1996):

$$0.5(\bar{A}_{BB} - \bar{A}_{bb})$$

and, with the average polygenic breeding value of each genotype was added to α. Alternatively, the value for α was calculated as follows:

$$\alpha = a + d(1 - 2p) + 0.5(\bar{A}_{BB} - \bar{A}_{bb})$$

where:

$\bar{A}_{BB}$ and $\bar{A}_{bb}$ are average polygenic values of gametes.

gm_k is the average genotypic value for the major gene, which is **a** for BB, **d** for Bb, and **-a** for bb, where a is the additive genetic value and d is the dominance effect of the single locus. The average polygenic breeding values for the major gene, with linkage disequilibrium between the major gene and polygenes, were calculated for different genotypes as shown in Table 3.6.

3.2.3.3 Optimal selection:

Optimal selection was selection based on an index of the breeding value for the major gene and on estimates of the breeding value for polygenes, similar to genotypic selection but with a weight assigned to the breeding value for the major gene. Here different index weights were considered, according to what genotype animals carried at their known major gene locus:

$$\mathbf{I_i = b_1 \times Mg_1 + h^2(P_i - gm_1)} \ \textit{for the BB Genotype}$$

$$\mathbf{I_i = b_2 \times Mg_2 + h^2(P_i - gm_2)} \ \textit{for the Bb Genotype}$$

$$\mathbf{I_i = b_3 \times Mg_3 + h^2(P_i - gm_3)}\ \textit{for the bb Genotype}$$

- I_i = Index for individual i.
- Mg_k = Average breeding value for major genotype k.
- P_i = Phenotypic value of individual i.
- h^2 = Heritability of the trait.
- b_1 = Index weight on the major gene for genotype BB.
- b_2 = Index weight on the major gene for genotype Bb.
- b_3 = Index weight on the major gene for genotype bb.

Since in this study Mg_k was reparameterized as deviations from the heterozygote, weight b_2 is immaterial because Mg_2 is equal zero.

Weights for the optimal index were derived from optimal control theory to maximize cumulative response after a given number of generations (from the deterministic model by Dekkers and Van Arendonk (1998), as described in Chapter one.

3.2.3.4 Use of actual heritability:

In the previous study, it was assumed that heritability used to calculate the selection criteria was unaffected by selection and was constant over generations. Heritability will, however, be reduced over generations as a result of gametic phase disequilibrium (Bulmer 1971). We also examined the effect of using the reduced heritability

in the criteria for genotypic and optimal selection on selection response. In this case, the genetic variance was calculated for each generation based on the formula of Gomez-Raya and Burnside (1990) :

$$\sigma_A^2 = (1 - \frac{1}{2} * K * Oldh^2)\sigma_{At-1}^2 + (\frac{1}{2})(\sigma_{A_o}^2 - \sigma_{At-1}^2)$$

where:

$K = i * (i - x)$, i=2.063 (selection intensity) and x=1.645 (truncation point).

The corresponding heritabilities were derived accordingly, based on the following formula:

$$New\ h^2 = \frac{new\ \sigma_A^2}{new\ \sigma_A^2 + \sigma_e^2}$$

The new h^2 was used in the following general selection indexes for genotypic and optimal selection.

3.3 Statistical methods

The phenotypic means were compared using the student t-test with the two levels of significance, 0.05 and 0.10. Estimates of response to mass, genotypic, and optimal selection are based on the mean responses observed over 1000 replicates of simulation.

Let mean responses be X_1 and X_2 , with variances S_1^2 and S_2^2 respectively. The

resulting t-test for differences in the means is:

$$t = \frac{(X_1 - X_2)}{\frac{\sqrt{(S_1^2 + S_2^2)}}{\sqrt{1000}}}$$

3.4 Deterministic and stochastic modelling of animal breeding programs

A selection system is composed of several components which have functional relationships with each other. These relationships are generally composed of both deterministic and stochastic elements. In deterministic relationships, variables are related to each other algebraically such that, for a certain set of inputs, a single output is always obtained (Dent and Blackie, 1979). In stochastic relationships, random elements are involved such that a unique result is obtained every time such a stochastic model is run with a different seed number. Stochastic models are often working at the level of the individual animal, and generally do not require knowledge of algebraic relationships that describe expected selection response. Therefore, stochastic simulation is often preferred over deterministic simulation for complex systems. This is due to the consideration of inherent complexities that might not be possible to take into account in deterministic simulations. The principles of model building can be better taught using deterministic models initially and then introducing stochastic elements where deterministic models appear inadequate. In this study, a stochastic simulation model was used as well as a deterministic model. The deterministic model is based on that of Dekkers and Van Arendonk (1998)

and was used in their study to find strategies for selection on a major gene that maximized response over a planning horizon. This will be described below.

3.4.1 Deterministic model

A deterministic model to maximize cumulative selection response for a quantitative trait over multiple generations with information on a major gene was developed by Dekkers and Van Arendonk (1998). The quantitative trait was affected by a major gene and polygenes. Models with and without gametic phase disequilibrium (gpd) between the major gene and polygenes were used. The authors showed that optimal use of information on the major gene in selection programs required development of selection criteria that combine information from single genes with phenotypic information in an optimal manner. Therefore, they developed selection criteria that maximized cumulative response over a planning horizon. This involved optimization of relative weights in an index of major gene effects and the polygenic estimated breeding value.

Dekkers and Van Arendonk (1998) simulated a population of infinite size with discrete generations and equal selection among males and females. They assumed that polygenic heritability is constant over generations.

3.4.1.1 A deterministic model for predicting genetic gain in a population

Optimization was based on a deterministic model of genetic improvement. Dekkers and Van Arendonk (1998) described equations that model how gene frequency

changes from one generation to the next and equations that describe how the average polygenic breeding values change. The authors referred to these as the state equations in their paper. State equations, which were formulated for each generation t, describe the passage of state variable from one stage to another, i.e. from generation t to generation t+1. This model essentially involves truncation selection across three normal distributions, as illustrated in Figure 4.1 for $\sigma_{mt} = \sigma$, where x_{mt} is the standard normal truncation point for genotype m, i_{mt} is the selection intensity and f_{mt} is the proportion selected from genotype m. The average polygenic values of animals in generation t with major genotype BB, Bb, and bb is $2\bar{A}_{B,t}$, $\bar{A}_{B,t} + \bar{A}_{b,t}$, and $2\bar{A}_{b,t}$, respectively. As shown in Figure 4.1, with selection among animals in generation t, parents selected from major genotype class BB have average polygenic breeding value equal to $2\bar{A}_{B,t} + i_{1t}$ and produce 100% B gametes with an average polygenic breeding value equal to $\bar{A}_{B,t} + \frac{1}{2}i_{1t}$. Also parents with the major gene genotype bb produce 100% b gametes with an average polygenic value equal to $\bar{A}_{b,t} + \frac{1}{2}i_{1t}$. Parents with major genotype Bb produced 50% B gametes and 50% b gametes. The average polygenic value of both types of gametes is equal to $\frac{1}{2}(\bar{A}_{B,t} + \bar{A}_{b,t} + i_{2t})$. The following state equations can then be set up for $\bar{A}_{B,t}$ and $\bar{A}_{b,t}$, respectively:

$$\bar{A}_{B,t+1} = \frac{f_{1t}P_t^2(\bar{A}_{B,t} + \frac{1}{2}i_{1t}) + f_{2t}P_t(1 - P_t)\frac{1}{2}(\bar{A}_{B,t} + \bar{A}_{b,t} + i_{2t})}{f_{1t}P_t^2 + f_{2t}P_t(1 - P_t)}$$

$$\bar{A}_{b,t+1} = \frac{f_{3t}P_t^2(\bar{A}_{b,t} + \frac{1}{2}i_{3t}) + f_{2t}P_t(1-P_t)\frac{1}{2}(\bar{A}_{B,t} + \bar{A}_{b,t} + i_{2t})}{f_{3t}(1-P_t)^2 + f_{2t}P_t(1-P_t)}$$

3.4.1.2 The optimal control method for obtaining optimal index weights

The second part of the model deals with deriving optimal index weights using optimal control, based on this deterministic model.

Dekkers and Van Arendonk (1998) applied truncation selection on an index that combines the value of the major genotype with an estimate of the polygenic breeding values for animal i.

The optimal selection index was;

$$\mathbf{I_i = b_k \times Mg_k + h^2(P_i - gm_k)}$$

Weights b_{1t} and b_{3t} in the index are equal to the truncation points for each distribution based on :

$$b_{1t} = \frac{\sigma(x_2 - x_1)}{(a + \bar{A}_{1t} - \bar{A}_{2t})}$$
$$b_{3t} = \frac{\sigma(x_3 - x_2)}{(a + \bar{A}_{2t} - \bar{A}_{3t})}$$

Based on this, index weights b_k affect truncation points x_{mt} which affect proportions selected, f_{mt}.

Optimizing proportions selected, f_{mt}	$\Rightarrow$	Optimizing truncation points, x_{mt}	$\Rightarrow$	Optimization of weights, b_k

Therefore, optimizing proportions selected from the three distributions of estimated breeding values for each generation t results in optimizing truncation points. Optimizing truncation points is equal to the optimization of weights b_k. The authors showed that the fraction selected from each genotype, f_{mt}, can be derived based on the iterative procedure of Ducrocq and Quaas (1988), and based on the overall fraction selected, Q, and the differences between truncation points. An iterative procedure was derived to obtain optimal weights.

3.5 Parameters and structure of the simulated populations

A population of 2000 individuals (half males, half females) was simulated. A fraction Q=20% of males and females was selected each generation, with each dam producing 5 sons and 5 daughters as candidates for the next generation. Alternative simulation programs accommodate any percentage selected as well as different selection intensities for males and females. Simulations were restricted, however, to equal selection for males and females because the optimal strategies have been developed only for that simulation. Mating was at random among selected parents. Truncation selection was practised for 3, 5, 10 or 15 generations. Parameters used in the base population are summarized in Table 3.1. One thousand replicates were run for each parameter set.

The initial polygenic heritability and phenotypic standard deviations were 0.3

and 1, respectively. Three selection schemes were examined: mass, genotypic, and optimum selection. The ranking of selection methods was studied for alternative scenarios as shown in Table 3.2.

Table 3.1: Parameters in the base population

Parameter	
Population size	2000
Number of selected males (N_m)	200
Number of selected females per male (N_f)	1
Number of progeny per female	10
Starting Gene Frequency	0.05, 0.5
Number of generations of selection	3, 5, 10, 15

Table 3.2: Alternative scenarios considered

Additive effect of the major gene (a)	0.1	0.25	0.5	1
Degree of dominance (d)	d=-a	d=0.0	d=a	
heritability (h^2) (Adjusted for polygenes)	0.1	0.3	0.5	

Table 3.3: Assignment of genotype and genotypic values for the major gene for animals in the base population. Considering a single locus with two alleles, B and b, at frequencies p and q, the genotypic value of BB individuals is $+a$, that of the other homozygote $-a$ and that of the heterozygote d.

	Selected random number (URN)		
	$URN \leq p^2$	$p^2 < URN < p^2 + 2pq$	$p^2 + 2pq \leq URN$
	$\Downarrow$	$\Downarrow$	$\Downarrow$
Genotype $\rightarrow$	BB	Bb	bb
	$\Downarrow$	$\Downarrow$	$\Downarrow$
Major gene $\rightarrow$ genotypic value	a	d	-a

Table 3.4: Assigning genotype to progeny and calculating the genotypic value on that basis.

Parent's Genotype		Parent's Genotype
BB Bb bb		BB Bb bb
⇓ ⇓ ⇓		⇓ ⇓ ⇓
	If random number	
$0.5 \leq URN$		$URN < 0.5$
⇓ ⇓ ⇓		⇓ ⇓ ⇓
Allele Passed to Progeny		Allele Passed to Progeny
B b b		B B b

Genotypic value for major gene

If progeny's genotype is		
BB	Bb	bb
⇓	⇓	⇓
a	d	-a

Table 3.5: Reparameterized average breeding values for major genotypes(Mg) as deviations from the heterozygote (Bb). with linkage disequilibrium between major gene and polygenes.

Genotype G	Mg (Breeding Value for Major Gene)				
BB	$2q\alpha$	$\rightarrow$	$2q\alpha - (q-p)\alpha$	$\rightarrow$	α
Bb	$(q-p)\alpha$	$\rightarrow$	$(q-p)\alpha - (q-p)\alpha$	$\rightarrow$	0
bb	$-2p\alpha$	$\rightarrow$	$-2p\alpha - (q-p)\alpha$	$\rightarrow$	$-\alpha$

Table 3.6: Average polygenic breeding value for major gene with linkage disequilibrium between major gene and polygenes.

	genotype		
	BB	Bb	bb
	$\Downarrow$	$\Downarrow$	$\Downarrow$
$gm \rightarrow$	$a + \bar{A}_{BB}$	$d + \bar{A}_{Bb}$	$-a + \bar{A}_{bb}$

Chapter 4

Results and Discussion

4.1 Comparison between a deterministic and stochastic model for mass and genotypic selection on an additive major gene

Genetic response is affected by selection intensity, the accuracy of selection and additive genetic variance (Falconer et al., 1996) . With mass selection, the accuracy of selection is the square root of heritability. With genotypic selection, the accuracy is 100% for the major gene. This will result in a higher overall accuracy of genotypic selection versus mass selection. The greater the effect of the major gene on the trait, the greater will be the accuracy of genotypic selection.

Bulmer (1971) showed that selection causes a reduction in the additive genetic variance, due to gametic phase disequilibrium. The reduction of variance has to be taken into account, otherwise the expected genetic progress will be overestimated. Bulmer (1971) also showed that, in the infinitesimal model, the reduction in genetic variance is due to covariances generated between the genotypic values of different

loci. He showed that directional selection introduces a negative covariance until a limiting value is reached in about five generations. The population then remains in a steady state gametic phase disequilibrium provided that the breeding structure and selection intensity remain constant. Based on computer simulation, Bulmer (1976) concluded that changes in gene frequencies and gametic phase disequilibrium are the two most important components that affect the changes in genotypic variance. He also concluded from simulation that, for a quantitative trait, the effect of gametic phase disequilibrium will be more important than the effects due to changes in gene frequencies. This section will compare the results from selection on a quantitative trait that is affected by a major gene through mass or genotypic selection, based on a deterministic and a stochastic model. In contrast to the stochastic model, the deterministic model does not take reductions in polygenic variance due to selection into account.

4.1.1 Total genetic response for mass versus genotypic selection

Figure 4.2 presents the cumulative total genetic response (as affected by the major gene plus polygenes) for mass and genotypic selection in the deterministic and the stochastic models. Figure 4.3 presents cumulative responses for mass selection as a percentage of genotypic selection response for the stochastic and deterministic models.

The simulation results presented in Figures 4.2 and 4.3 confirm the conclusion

reached by Gibson (1994), pertaining to a situation in which QTL information on a major gene was either included or not included in selection. The genetic gain with genotypic selection was greater in the short-term (i.e., in the simulation illustrated in Figure 4.3 for the stochastic model, genotypic selection exhibited up to 4.15 % greater cumulative selection response during generations 1 through 10), but lower in the long-term (0.72 % lower response at generation 15). In other words, mass selection tended to supersede genotypic selection as the number of generations increased.

4.1.2 The polygenic variance

Figure 4.4 compares changes in variance among polygenes for mass and genotypic selection between the stochastic and deterministic model. In the stochastic model the effect of gametic phase disequilibrium, which occurs as a result of selection, is taken into account. As illustrated in Figure 4.4, the polygenic variance declined in the first generation of selection for both genotypic and mass selection, continued to decrease for a few cycles of selection, and then stabilized. Dekkers and Van Arendonk (1998) did not consider the impact of gametic phase disequilibrium among polygenes in their deterministic simulation. Therefore, the variance among polygenes remained constant (0.3) over generations. The dotted line in Figure 4.4 shows the expected reduction in polygenic variance over generations.

Since no reduction in genetic variance was taken into account in the determin-

istic model, the total response was greater for the deterministic model than for the stochastic model, as shown in Figure 4.2. Results from Table 4.1 show that the deterministic model predicted 15.67% and 16.11% greater cumulative selection response after 10 generations of selection compared to the stochastic model for genotypic and mass selection, respectively.

4.1.3 Gametic phase disequilibrium between the major gene and polygenes

Figure 4.5 shows the amount of gametic phase disequilibrium between the major gene and polygenes. The deterministic model of Dekkers and Van Arendonk (1998) took into account the impact of gametic phase disequilibrium between the major gene and polygenes but not among polygenes. Graphically the results were similar for both models except after generation 9 where the amount of gametic phase disequilibrium increased linearly for genotypic selection using the stochastic model. The increase can be explained due to the various methods of averaging the results of iteration. Any iterations containing fixed genes were removed. The amount of gametic phase disequilibrium calculated was based, therefore, upon the average of the replicates in which the gene was not fixed.

4.1.4 Frequency of the major gene

Figure 4.6 shows how the major gene is approaching fixation with genotypic selection and mass selection for the deterministic and the stochastic models. Fixation occurred by generation ten with genotypic selection, whereas fixation did not occur

with mass selection by generation 15. The initial gene frequency was 0.05 for both situations. The deterministic model showed similar trends to those of the stochastic model.

Smith (1982) found that the change in frequency of the major gene was slower for a trait that is controlled by polygenes (many genes with small effect) and a major gene than for a trait that is controlled only by a major gene. This arises because in the former case selection pressure is placed on the other loci affecting the trait and, in the latter situation, a disequilibrium between the major gene and polygenes is induced.

4.1.5 Response in polygenes

The effect of genotypic versus mass selection on response in polygenic effects is shown in Figure 4.7 for the stochastic and deterministic models. The stochastic model followed the same trend as the deterministic model. It is evident that mass selection put more selection pressure on polygenic effects than did genotypic selection. As a result, higher rates of response were achieved for polygenic effects under mass selection.

4.2 Comparison of mass and genotypic selection with optimal selection

4.2.1 Index weights on the major gene for optimal selection

The differences between mass, genotypic and optimal selection are the differences

in weights exerted on the major gene and polygenes, which is illustrated in Figure 4.9.

Index weights for optimal selection on the additive major gene changed over generations and were greater when the individual had the unfavourable (bb) major genotype. As a result, there was more selection pressure against (bb) than on selection in favour of (BB) genotypes. Optimal weights were lower than weights under genotypic selection (b=1) and closer to implicit weights for mass selection ($b = h^2 = 0.3$). In the last generation of selection, the optimal weights were equal to weights under genotypic selection for the additive major gene.

4.2.2 Frequency of the major gene

Optimal selection after 10 generations of selection led to changes in frequency of the major gene that were intermediate between genotypic and mass selection, as is illustrated in Figure 4.10. Results from the deterministic model were similar to those from the stochastic model.

4.2.3 Response in polygenes

As the results for the stochastic and deterministic models show in Figure 4.11, both optimal and mass selection achieved higher rates of response for polygenic effects than genotypic selection, which is due to the greater selection pressure than mass and optimal selection put on polygenic effects. Figure 4.11 shows that under the stochastic model, polygenic response was 6.3%, and 2.85% greater than for

genotypic selection for mass and optimal selection, respectively, after 10 generations of selection.

4.2.4 Total genetic selection response

Figure 4.12 shows that optimal selection on an additive major gene over 10 generations, with optimal weights derived from the deterministic model, also achieved greater cumulative response than mass and genotypic selection at the end of the planning horizon under the stochastic model. Optimal selection achieved 2.82% and 1.23% greater response after 10 generations than mass and genotypic selection, respectively, for the stochastic model, and 1.81% and 1.84% greater response for the deterministic model.

The results in Figure 4.12 illustrate cumulative response to mass and optimal selection over 3, 5 and 10 generations of selection. Under the deterministic model, optimal selection achieved 0.13%, 0.21% and 1.88% greater cumulative responses than genotypic selection for planning horizons of 3, 5 and 10 years, respectively, and 0.21% and 1.23% greater cumulative responses under the stochastic model for 5 and 10 generation planning horizons, respectively, but 0.59% less response than genotypic selection after 3 generations of selection. The results of the stochastic simulation confirmed the results of the deterministic model simulation, except for the short planning horizon, for which the optimal strategy did not give greater final cumulative response than genotypic selection. This is likely due to the assumption

that polygenic variance was constant for the deterministic model that was used to derive the optimal strategies. Under the deterministic model, the optimal strategies of Dekkers and Van Arendonk (1998), resulted in a higher response to selection over the specified planning horizon, regardless of length of the planning horizon (see also Table 4.1).

4.3 The effect of size of the effect of an additive major gene on response to selection

Figure 4.13 shows the effect of the major gene on selection response under the stochastic model for 15 generations of selection under different selection regimens (mass and genotypic selection). The difference in total response between genotypic selection and mass selection increased proportionally to size of the effect of the major gene. The largest difference was when size of the effect of the major gene was one σ_p, and the smallest difference was when the major gene had an effect equal to 0.1 σ_p. When the effect of the major gene was 0.25, 0.5, or 1 σ_p, mass selection superseded genotypic selection at generations 12, 6, and 4 respectively (Figure 4.13). When the major gene effect was 0.1 σ_p, the behaviour of the mass selection curve was irregular and mass selection did not achieve a greater response than did genotypic selection even after 15 generations of selection. As the results show, with increasing size of the effect of the major gene from 0.25 to 1 σ_p, response to mass selection increased from 1.2 % to 4.25 % relative to genotypic selection.

Figure 4.14 shows the effect of different sizes of effect of the major gene of mass, and optimal selection relative to genotypic selection for planning horizons of 3, 5 and 10 generation under the stochastic and deterministic models. Numeric results are given in Tables 4.2 and 4.3. As the results show, optimal selection under the deterministic model achieved greater cumulative selection response compared to mass and genotypic selection for all different sizes of effect of the major gene considered for 3, 5 and 10 generation of planning horizons.

Table 4.4 illustrates the extra total response for mass and optimal selection as a percentage of genotypic selection response: under the stochastic model, optimal selection did not achieve greater cumulative selection response compared to mass and genotypic selection for a major gene with small effect (i.e. 0.1 σ_P) for any planning horizon tested, including a short planning horizon with a major gene with size of 0.25 σ_P. In addition, Table 4.4 shows that as the size of the effect of the major gene increased, the superiority of optimal selection over genotypic selection increased for all planning horizons (3, 5 and 10 generations of selection).

4.4 The effect of different levels of heritability on selection response, with and without major gene information.

A simulation was conducted with three different heritabilities in the base population (0.1, 0.3 and 0.5) for three planning horizons (3, 5 and 10 years generations of selection). The results from stochastic and deterministic models are summarized

in Table 4.5. Obviously, higher response rates were achieved when heritability was higher.

Figure 4.15 shows that as the amount of heritability in the base population increased, the magnitude of the difference in response between mass and optimal selection with genotypic selection decreased.

Table 4.6 illustrates the extra total response for mass and optimal selection as a percentage of genotypic selection response for 3, 5 and 10 generations of selection under the stochastic and deterministic models for different levels of heritabilities. Under the deterministic model, extra total response for optimal selection relative to genotypic selection increased with a decreasing heritability levels in the base population for all planning horizons (3, 5 and 10 generations of selection) and for all different initial levels of heritabitilies tested (Table 4.6). The results also show that superiority of genotypic selection over mass selection increased at the end of the planning horizons (3, 5 and 10 generations of selection) when heritability of the base population declined.

Comparisons between different levels of heritability under the stochastic model show that with decreasing heritability in the base population the superiority of optimal selection response over genotypic selection increased for 5 and 10 generations of selection. Also, optimal selection achieved higher selection response compared to mass selection at the end of the planning horizon. For all planning horizons (3, 5 and 10 generation of selection), with decreasing heritability the inferiority of

mass selection over genotypic selection increased. Optimal selection did not achieve better selection response compared to genotypic selection for heritability equal to 0.3 and 0.5 after 5 generations of selection.

Table 4.6 illustrates extra total response for optimal selection over genotypic selection increased from 0.01% to 7.38% with decreasing heritability from 0.5 to 0.1 over a planning horizon of 10 generations of selection under the stochastic model. But mass selection response after 10 generations of selection was 4.19% and 5.38% lower than genotypic selection response with changing levels of heritability from 0.5 to 0.1 under the stochastic and deterministic models, respectively (See also Figure 4.15).

The results of this study emphasize that selection on a major gene only should not be used for traits of higher heritability, as previously observed by Smith (1967); Lande and Thompson (1989); Ruane and Colleau (1995); and Meuwissen and Goddard (1995). Larzul et al. (1996) also concluded that the genetic gain of selection response decreases when the heritability increases, and showed that the more the genetic variation may be explained by a major gene, the more it becomes worthwhile to include the corresponding information in the breeding evaluation.

4.5 The effect of using actual heritability on the selection criterion.

After a few cycles of selection (four to five generations) on individual phenotype,

the genetic variance decreases until a steady state is attained. This is illustrated in Figure 4.16. The reduction in variance results in lower heritability in later generations. The genetic variance of a quantitative trait decreases under directional selection due to gametic phase disequilibrium (Falconer et al., 1996).

Under mass selection, individuals are selected according to their phenotypes, whereas under genotypic and optimal selection the selection criterion is calculated based on the heritability and different weights are placed on the major gene.

Figure 4.17 shows that optimal selection achieved 1.34% and 1.17 % extra total response over genotypic selection when using the constant heritability of the base population or the actual heritability of the current generation, respectively. The results show that use of the actual heritability had no significant effect ($P < 0.05$) on genotypic and optimal selection response.

4.6 The effect of dominance at the major gene on selection response

Index weights for mass, genotypic and optimal selection for a gene with complete dominance are illustrated in Figure 4.18. Optimal weights were lower than weights under genotypic selection(b=1) and mostly lower that weights under mass selection ($b = h^2 = 0.3$).

The effects of complete dominance at the major gene on responses to mass, genotypic and optimal selection are shown in Figure 4.19 for the deterministic and

stochastic models.

Figure 4.20 provides a comparison between mass and genotypic selection under two different gene actions for the deterministic model. When there was no dominance, (d=0.0), genotypic selection achieved greater selection response than mass selection up to generation 11. Under complete dominance (d=a=0.25 σ_p), mass selection produced greater selection response than genotypic selection after about the 4th generation. At the end of the planning horizon (11th generation), superiority of mass selection over genotypic selection was 3.51% under complete dominance as shown in Figure 4.20.

As shown in Figure 4.21 for the stochastic model, without dominance, genotypic selection was superior to mass selection up to generation 11. Although not shown here, mass selection superseded genotypic selection beyond generation 13. Under complete dominance (d=a=0.25 σ_p) , mass selection started to produce more response than genotypic selection from generation 4, the greatest extra response being 9% in generation 7. From generation 7, the difference between genotypic selection and mass selection decreased, but mass selection maintained a superiority over genotypic selection. At generation 11, the difference between mass and genotypic selection under complete dominance was about 7.02% in favour of mass selection. Without dominance, the difference was 1.57% in favour of genotypic selection.

Comparisons of both mass and genotypic selection with optimal selection under no dominance and complete dominance are shown in Figure 4.20 for the determin-

istic model. These results show that, with complete dominance, mass and optimal selection achieved more selection response than genotypic selection at about generation 4, and mass and optimal selection achieved 3.51% and 4.03% greater response than genotypic selection at the end of the planning horizon. Optimal selection achieved 0.49% greater response than mass selection after 10 generations of selection under the deterministic model (Table 4.7).

The comparison of mass and genotypic selection with optimal selection under no dominance and complete dominance for the stochastic model is shown in Figure 4.21. Mass selection and optimal selection produced more response than genotypic selection under complete dominance after generation 4, with optimal selection eventually out performing genotypic selection by 7.5%.

Comparisons between extra total response for optimal, mass, and genotypic selection as a percentage of response to genotypic selection for 3, 5 and 10 generations of selection for a major gene with complete dominance under the stochastic and deterministic models are shown in Figure 4.22. Under the deterministic models, optimal selection achieved 2.95%, 4.36% and 4.03% greater selection response than genotypic selection when optimizing for 3, 5 and 10 generations of selection, respectively. Also, optimal selection produced 4.21%, 1.43% and 4.9% greater selection response than mass selection for 3, 5 and 10 generations of selection, respectively. Under the stochastic model, optimal selection produced 8.43% and 7.53% greater

response after 5 and 10 generations of selection, respectively than did genotypic selection. Optimal selection achieved 1.6% greater selection response than mass selection after 5 generations of selection, but for 10 generations of selection, mass selection achieved 7.53% and 0.52% greater selection response than genotypic and optimal selection under the stochastic model (see also Table 4.8).

4.6.1 The effect of negative dominance on selection response

Optimal weights for the favourable allele (BB) were higher than weights under mass selection but lower than weights under genotypic selections except for generation 9. Optimal index weights for the unfavourable allele (bb) were lower than weights for mass and genotypic selection (results not shown here).

Figure 4.23 shows that responses to optimal and mass selection significantly ($p< 0.05$) differed from those for genotypic selection for a major gene with negative dominance under the stochastic models.

As results in Table 4.10 show, optimal selection produced 1.42%, 2.33% and 2.52% greater selection responses than genotypic selection under the deterministic model, and 0.92%, 0.43% and 0.93% greater selection response relative to genotypic selection for the stochastic model for 3, 5 and 10 generations of selection, respectively. Results also showed that optimal selection achieved greater selection response compared to mass selection for 3, 5 and 10 generations of selection under both the deterministic and the stochastic models.

It can be concluded that optimal strategies derived using the deterministic model, which includes constant variance, prove to be less than optimal when tested using the stochastic model. But in all cases, results from the stochastic model depend on population parameters. As shown in Figure 4.24, starting at a higher gene frequency (0.5) and with less selection intensity (25%), optimal selection achieved greater selection response relative to genotypic selection for a gene with negative dominance under the stochastic model (see also Table 4.9).

Figure 4.1: Selection on an index of major genotype value and estimates of polygenic breeding values in the form of truncation selection.

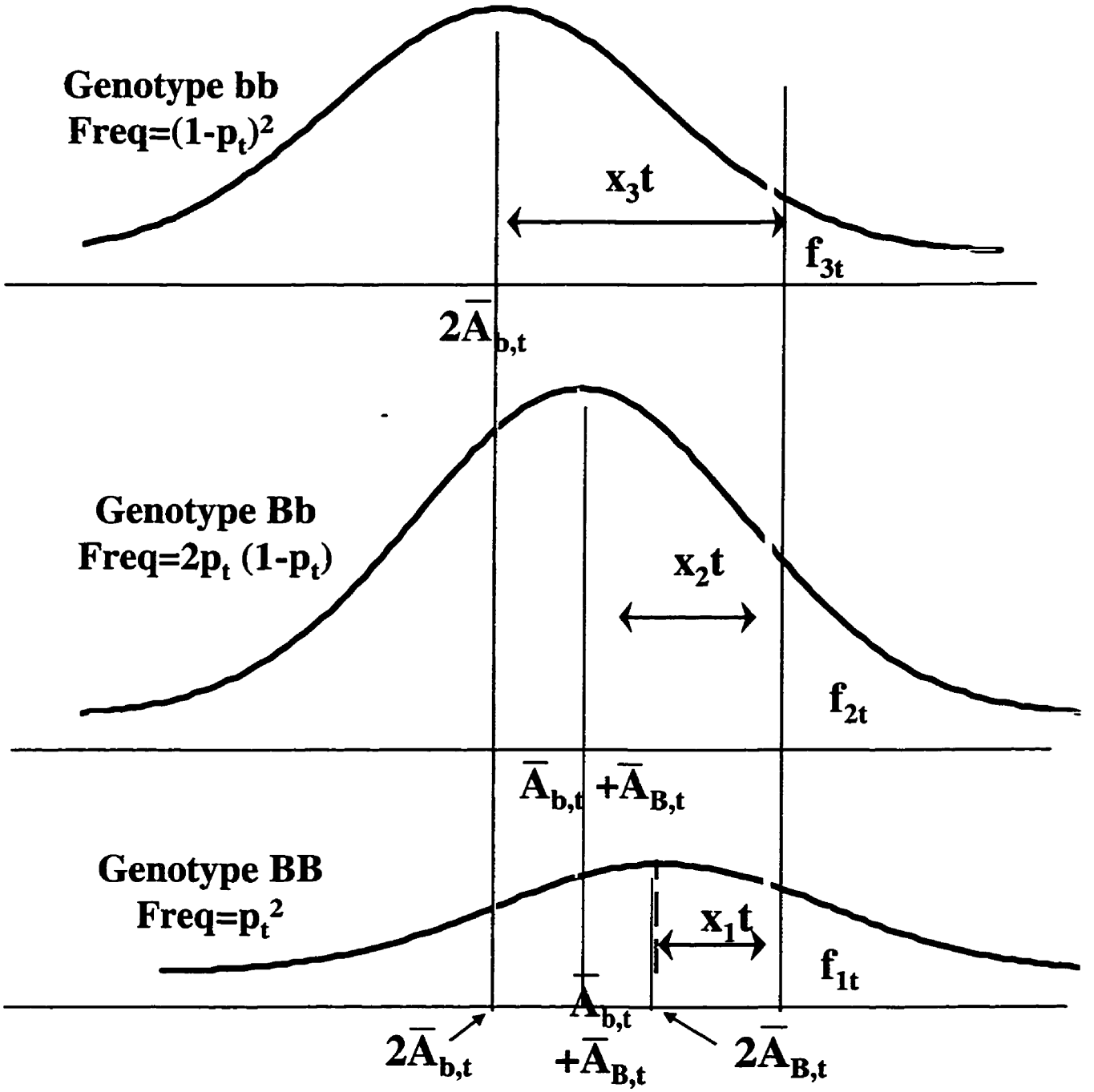
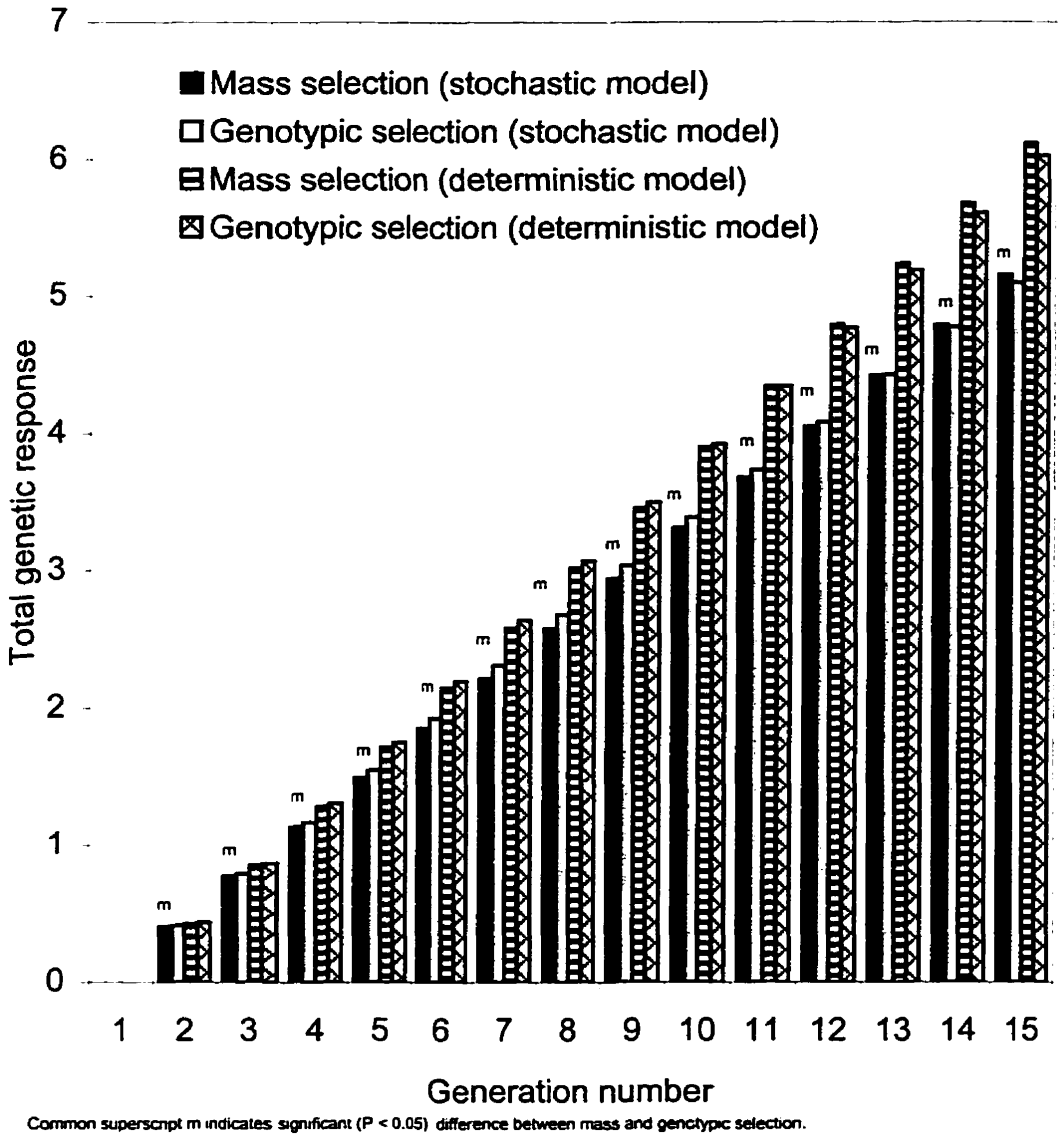


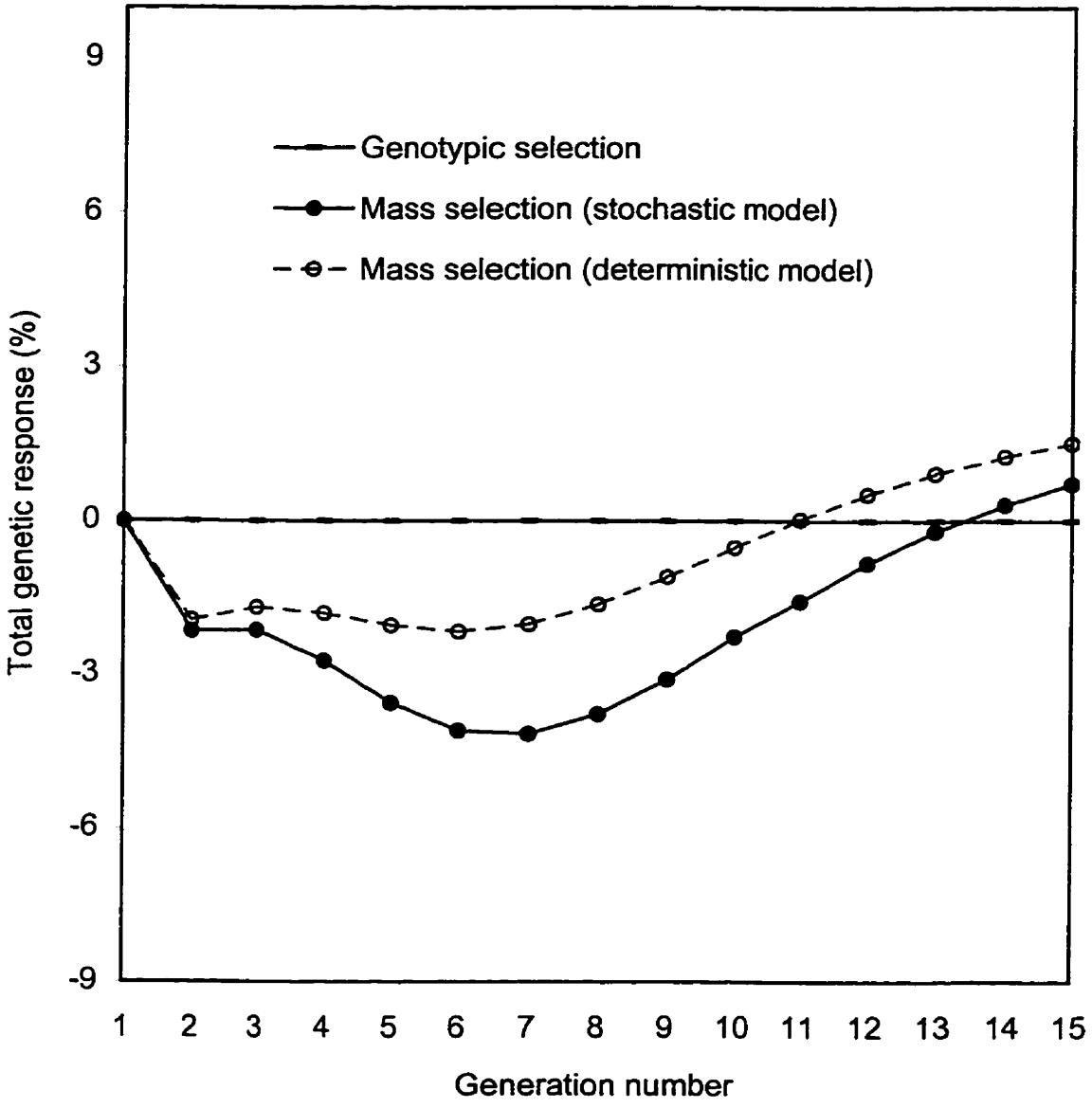
Figure 4.2: Comparison between the stochastic and deterministic models for cumulative total response (major gene plus polygenes) for mass and genotypic selection for a major gene with additive effects.



Common superscript m indicates significant ($P < 0.05$) difference between mass and genotypic selection.

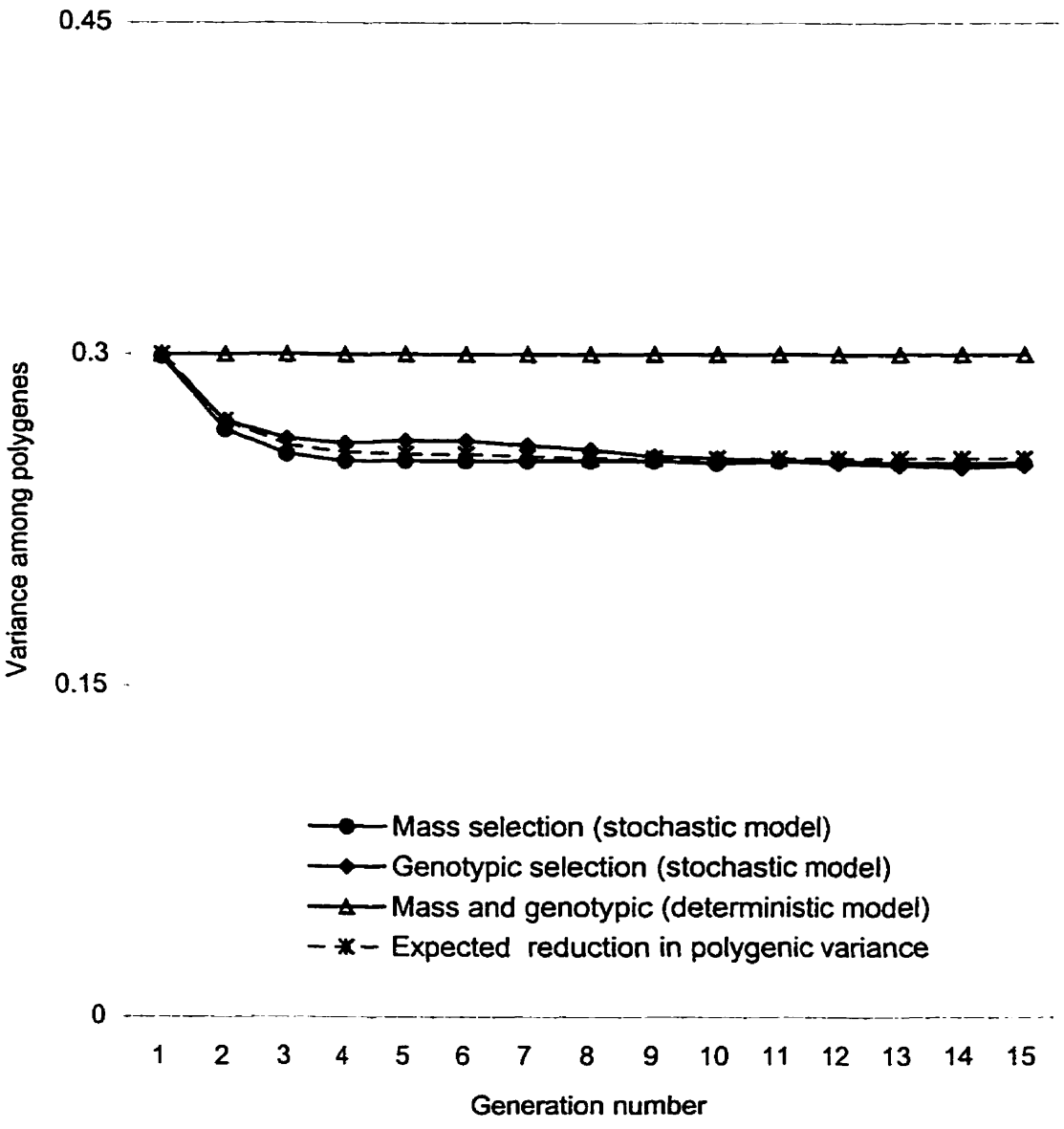
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.3 : Comparison between the stochastic and deterministic models for cumulative total response for mass selection on an additive major gene as a percentage of genotypic selection.



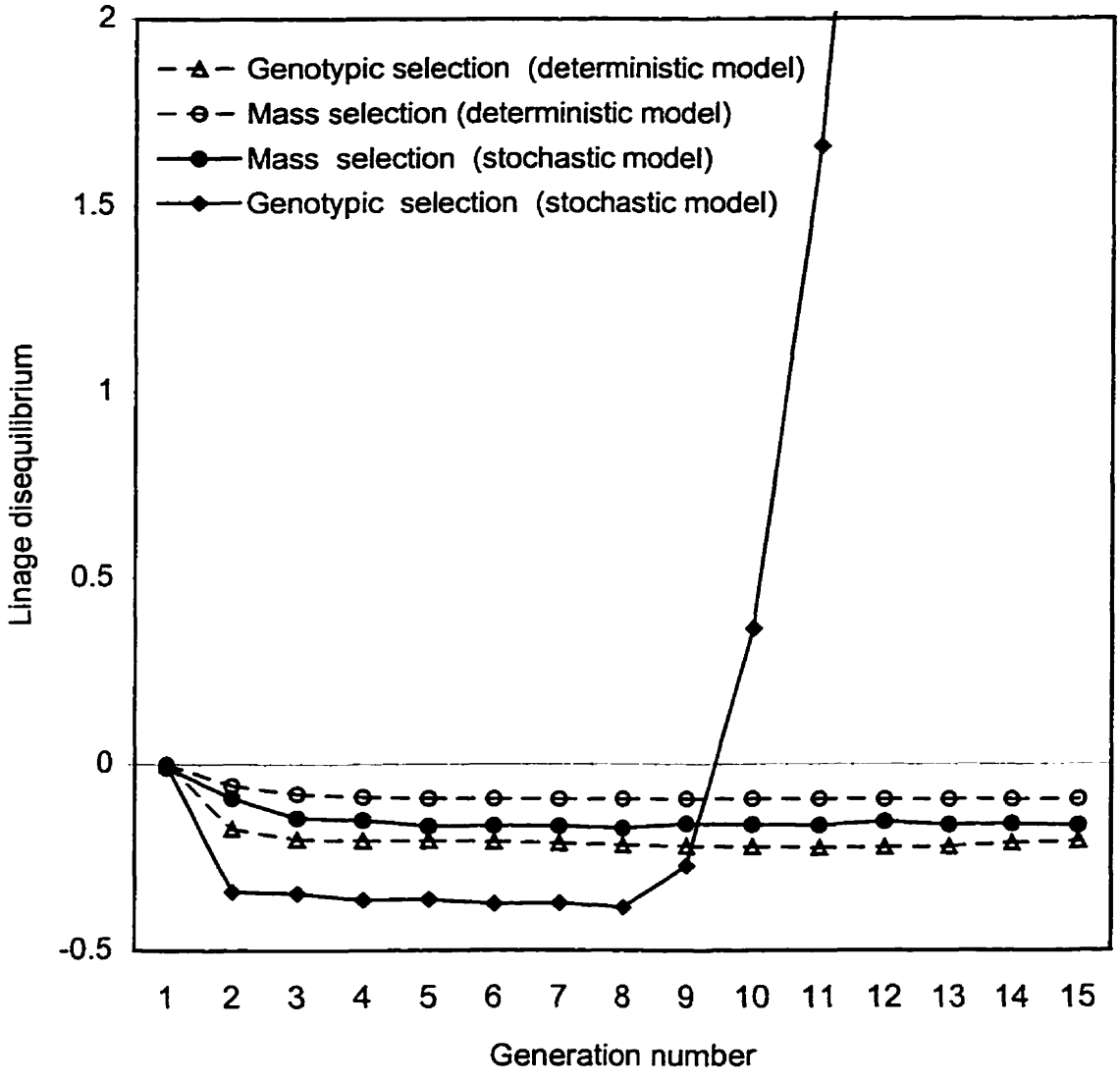
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.4: Comparison between the stochastic and deterministic models for variance among polygenes for mass and genotypic selection for a major gene with additive effects.



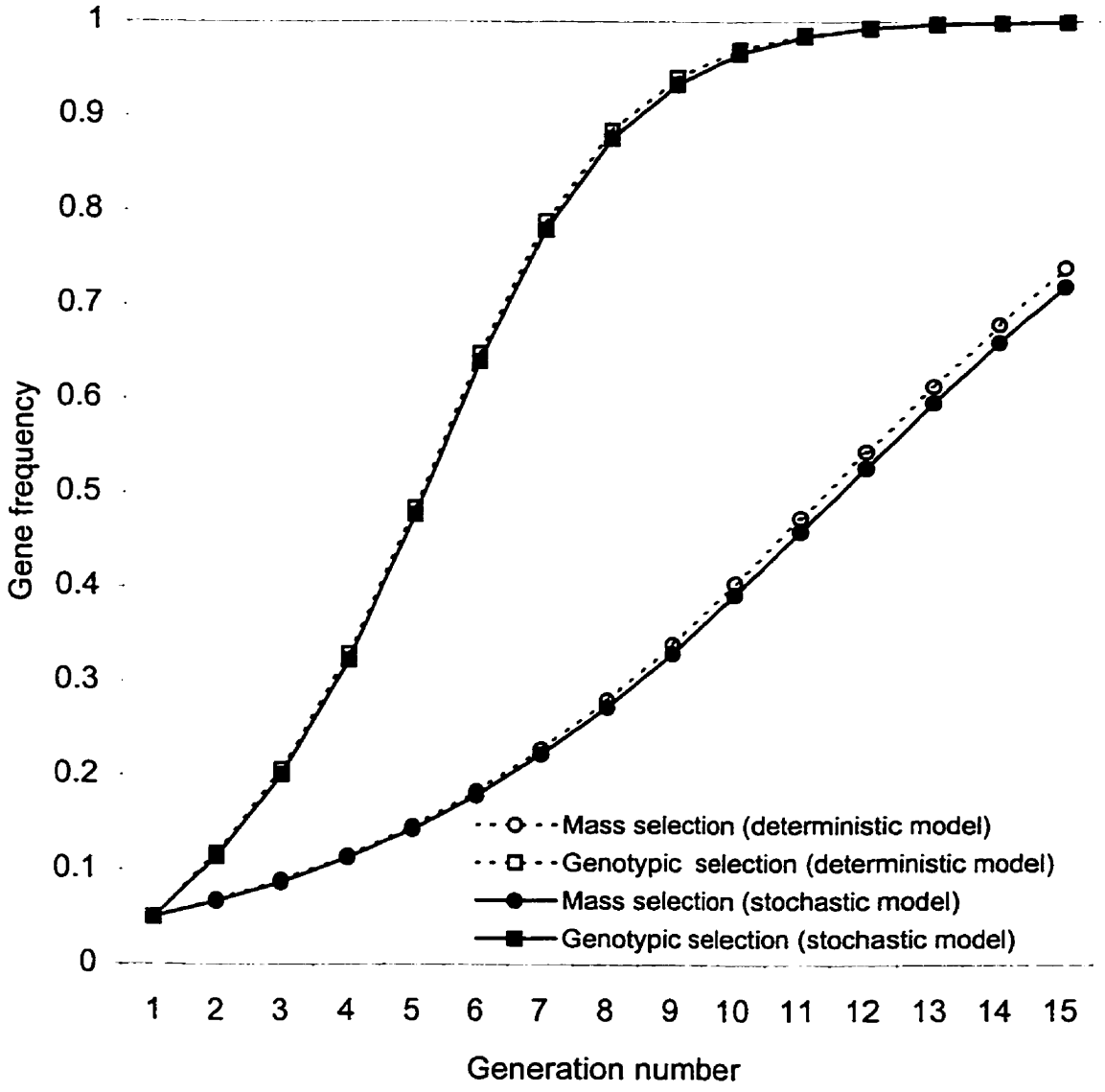
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.5: Comparison between the stochastic and deterministic models for linkage disequilibrium between the major gene and polygenes for a major gene with additive effects.



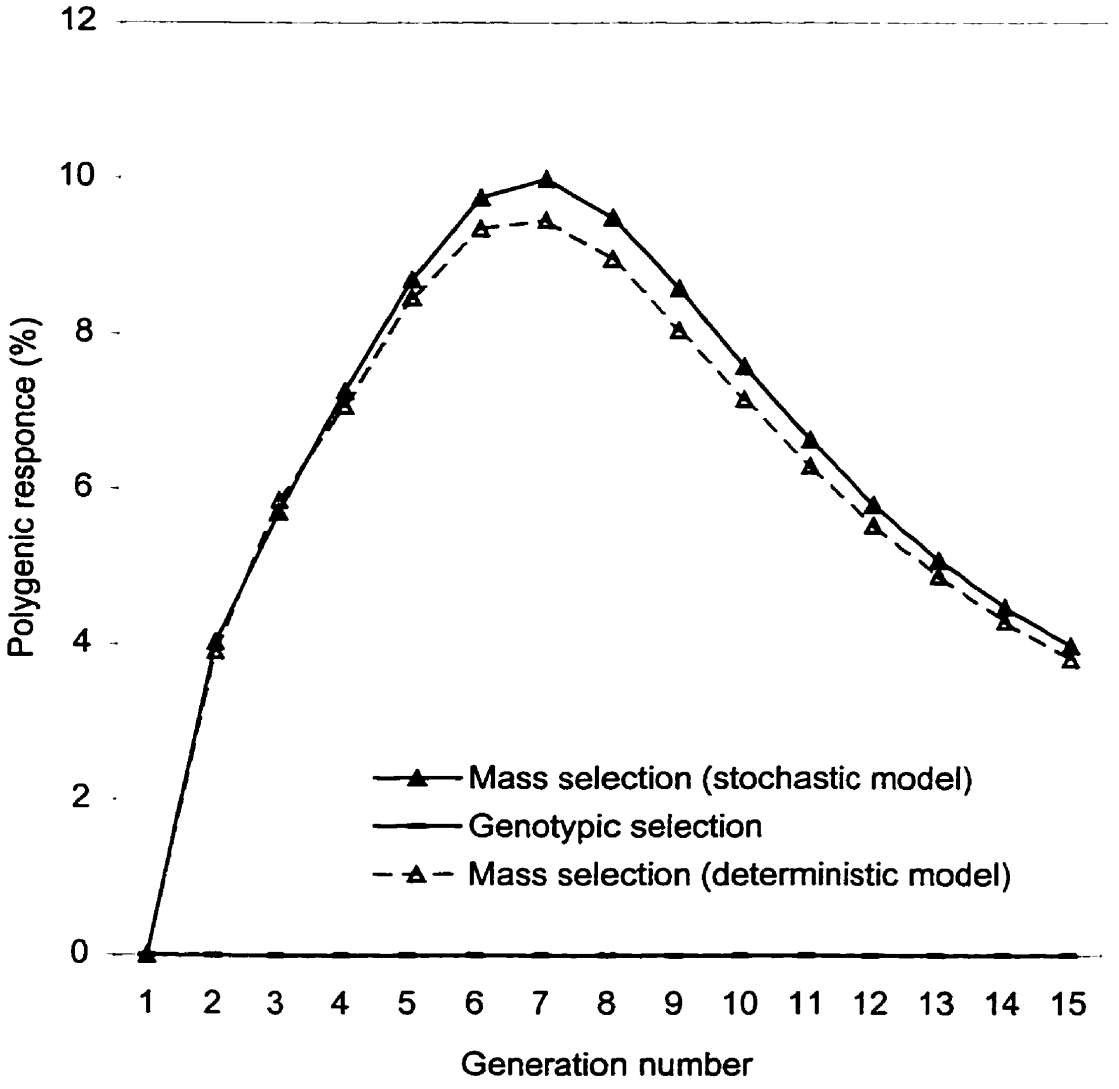
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.6: Comparison between the stochastic and deterministic models for the effect on gene frequency of mass or genotypic selection on an additive major gene.



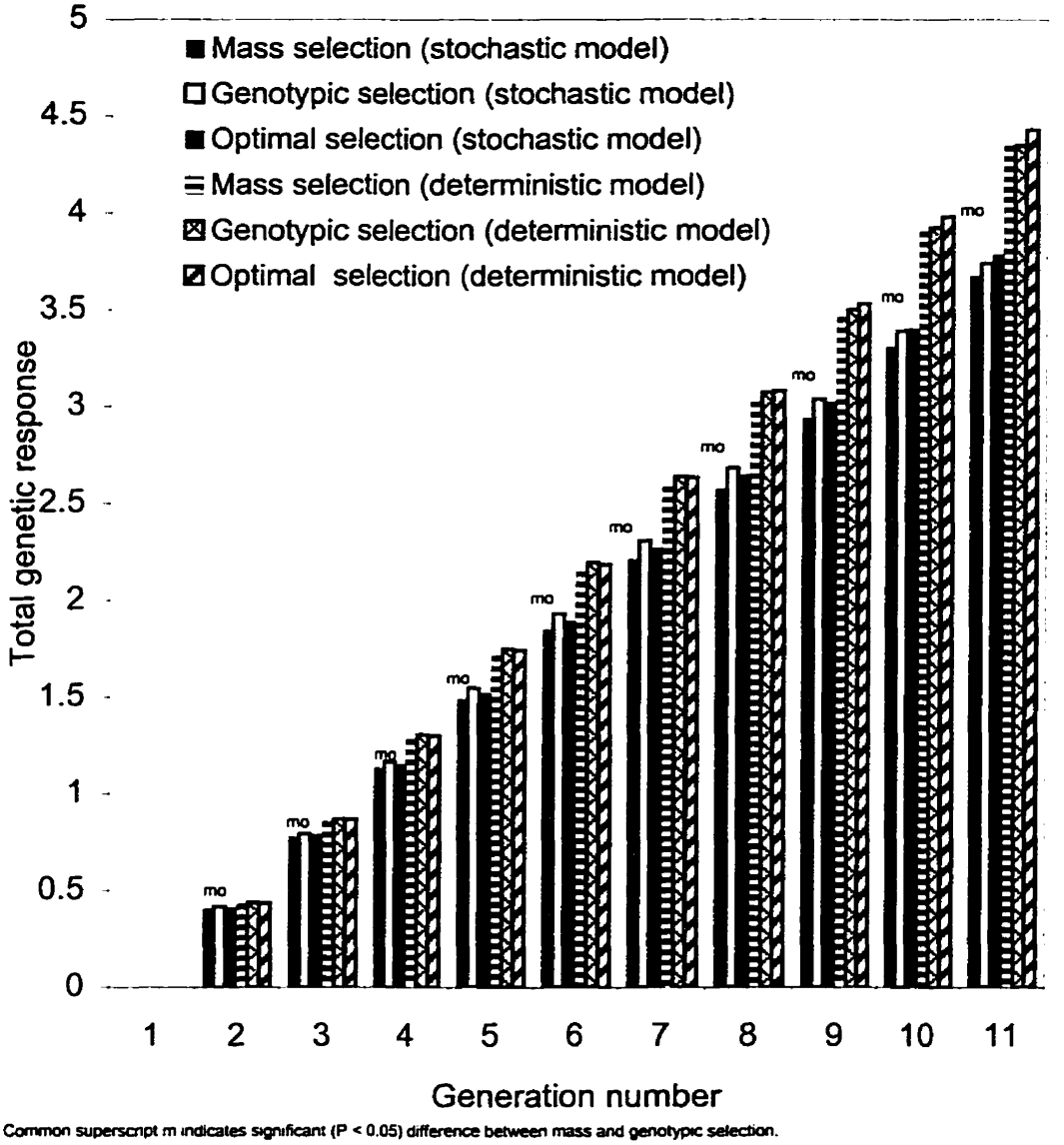
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.7: Comparison between the stochastic and deterministic models for cumulative polygenic response for mass and genotypic selection on an additive major gene, as a percentage of genotypic selection.



Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

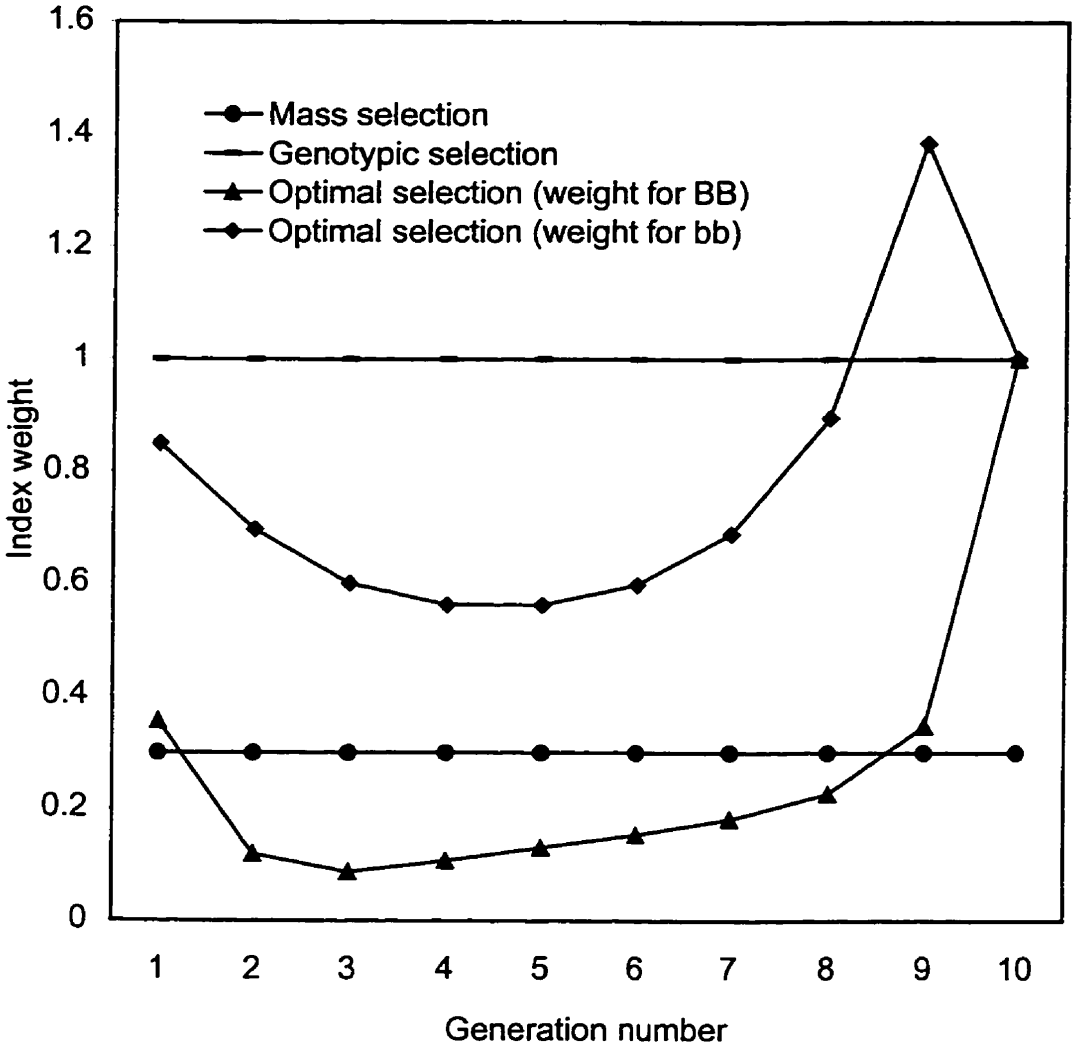
Figure 4.8: Comparison of total genotypic response for mass and genotypic selection with optimal selection over 10 generations for an addititve major gene, under the deterministic and stochastic models.



Common superscript m indicates significant ($P < 0.05$) difference between mass and genotypic selection.
Common superscript o indicates significant ($P < 0.05$) difference between optimal and genotypic selection.

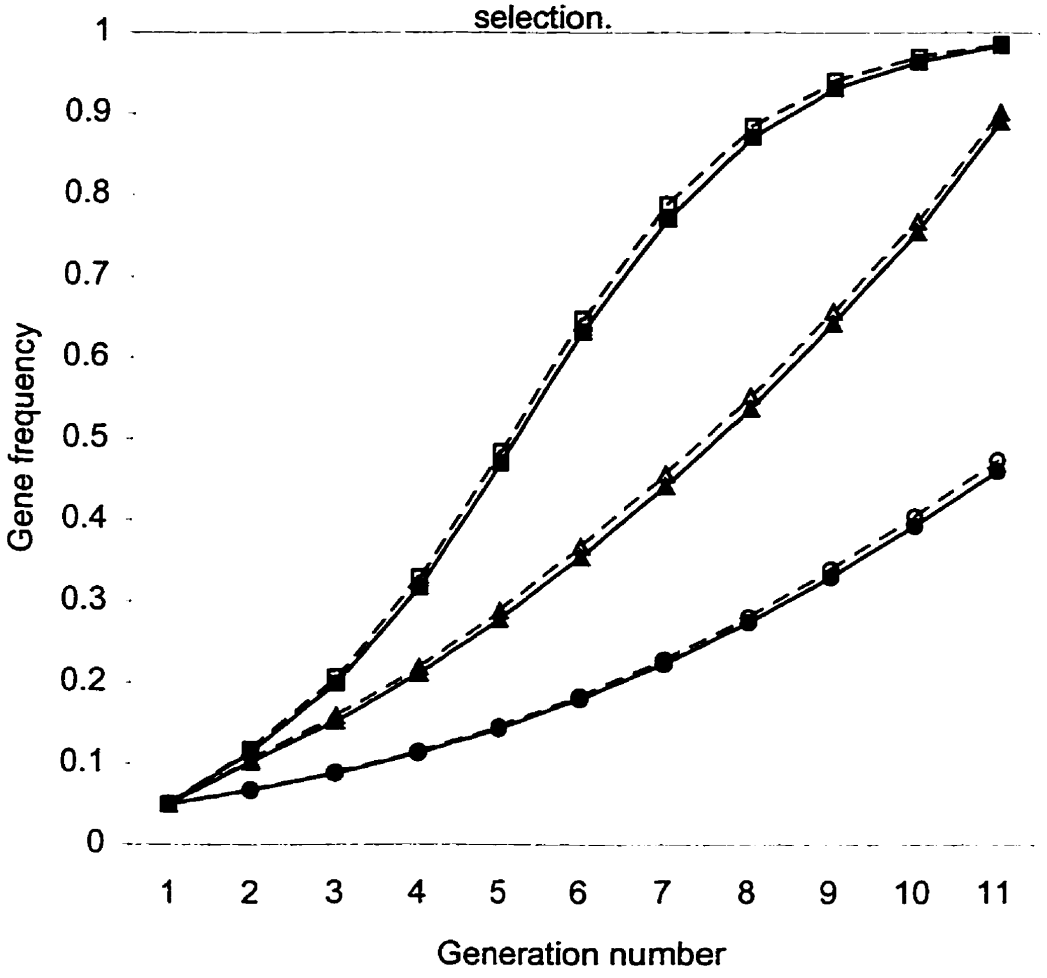
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.9: Index weights on the major gene for optimal (10 generation) mass and genotypic selection for an additive major gene.



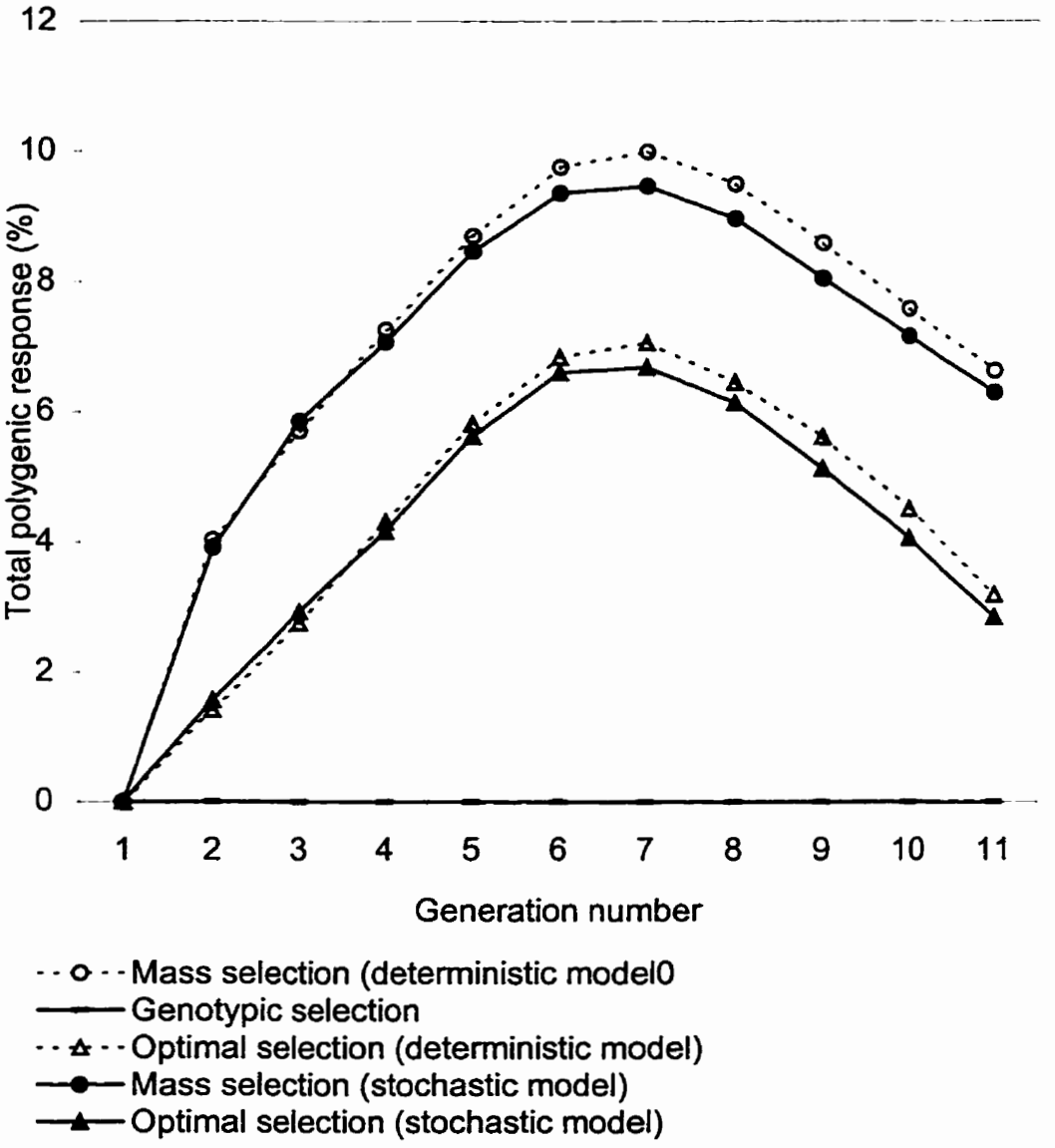
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.10: Comparison between the stochastic and deterministic models for changing gene frequency for a major gene with additive effects after 10 generations of selection.



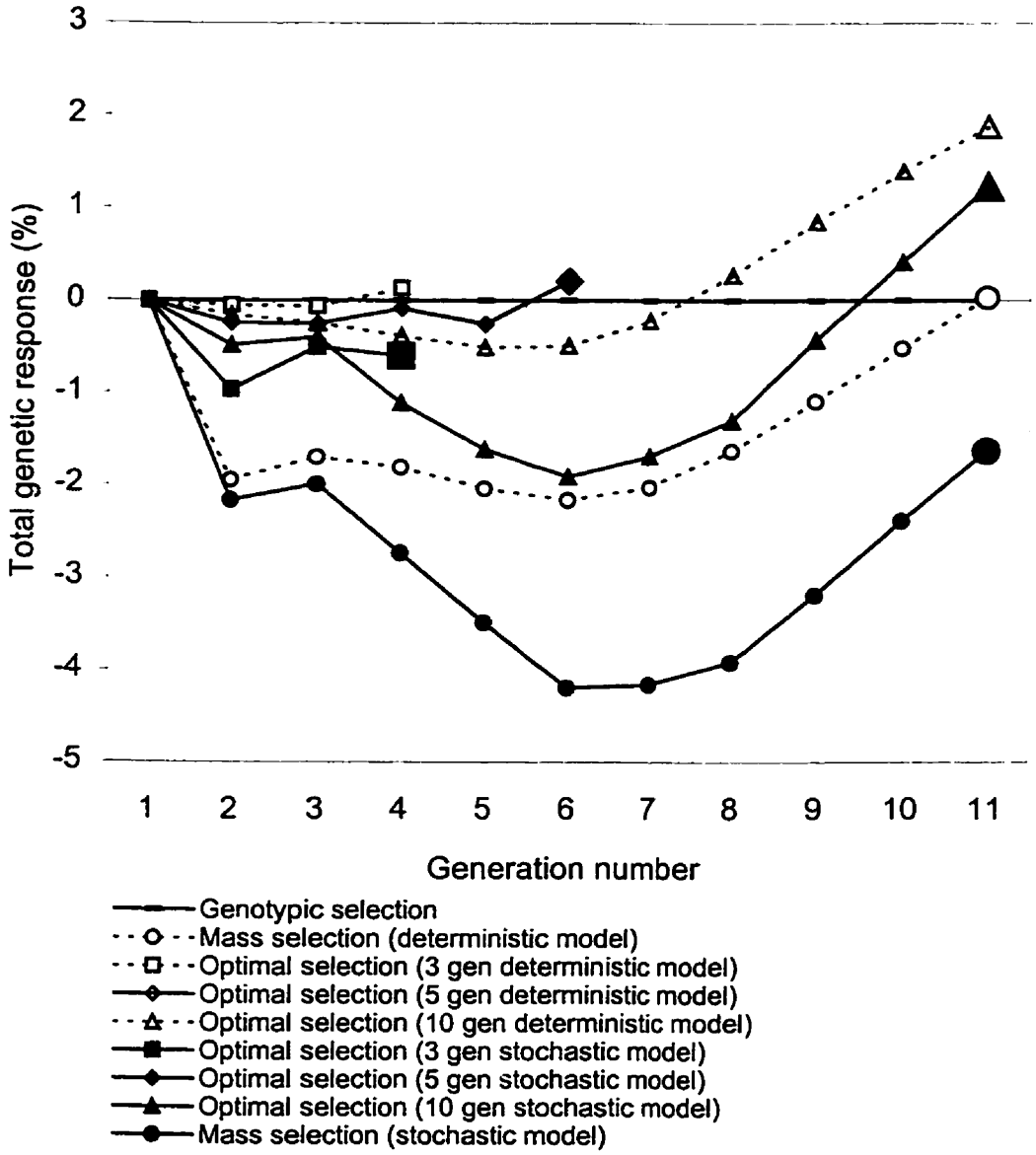
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.11: Comparison between the stochastic and deterministic models for mass and genotypic selection with optimal selection for total cumulative polygenic response, as a percentage of genotypic selection.



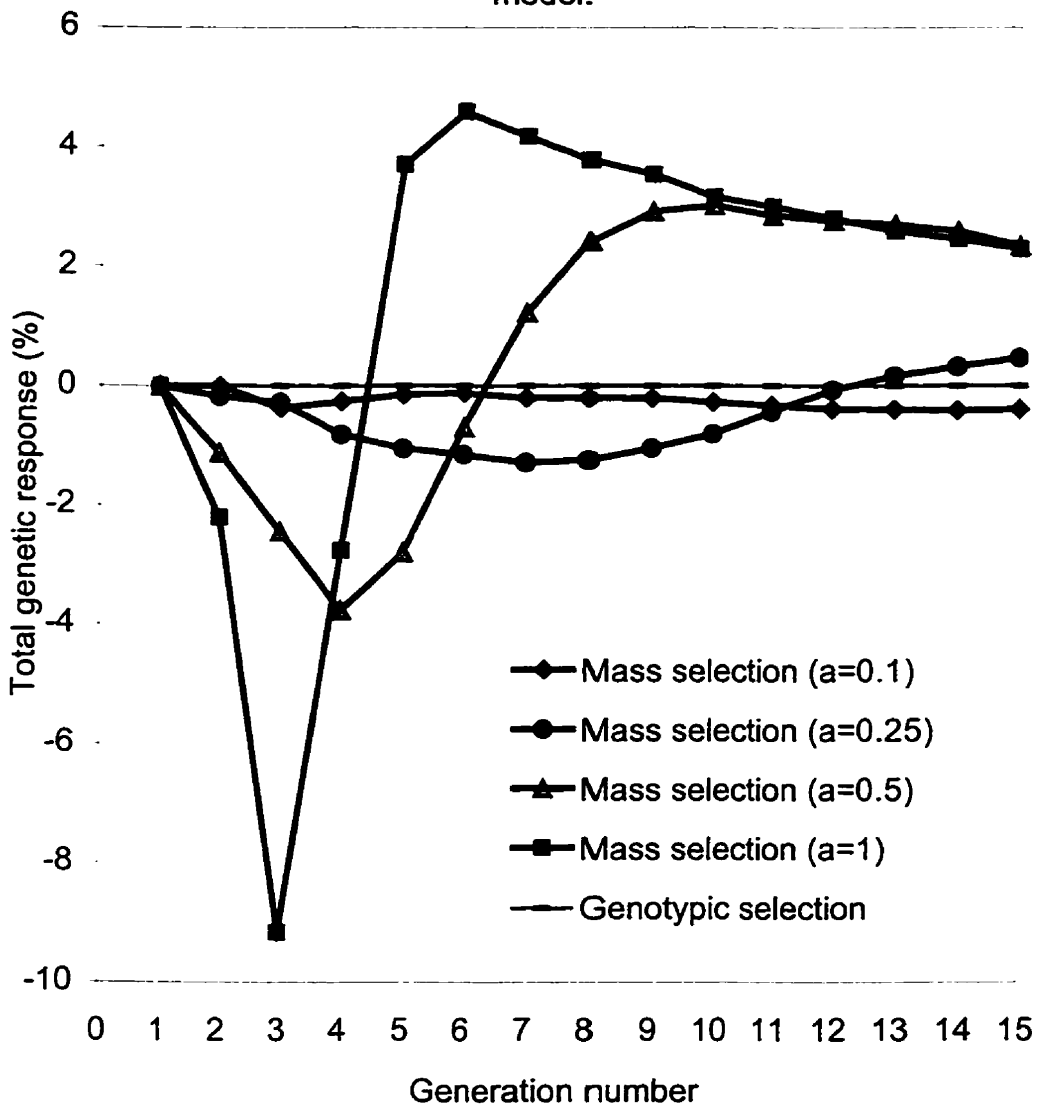
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	$a=0.25\ \sigma_p$

Figure 4.12: Comparison of total response for mass and optimal selection as a percentage of genotypic selection over 3, 5 and 10 generations for an additive major gene, under the deterministic and stochastic models.



Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.13: The effect of the size of the effect of an additive major gene on cumulative response after 15 generations of mass and genotypic selection as a percentage of genotypic selection under the stochastic model.



Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.14: The effect of size of the effect of an additive major gene on cumulative response after 3, 5 and 10 generations of mass, genotypic and optimal selection under the stochastic and deterministic models (h2=0.3, starting gene frequency =0.05, major gene with additive effect=0.25 σ_p, males and females selected = 20%).

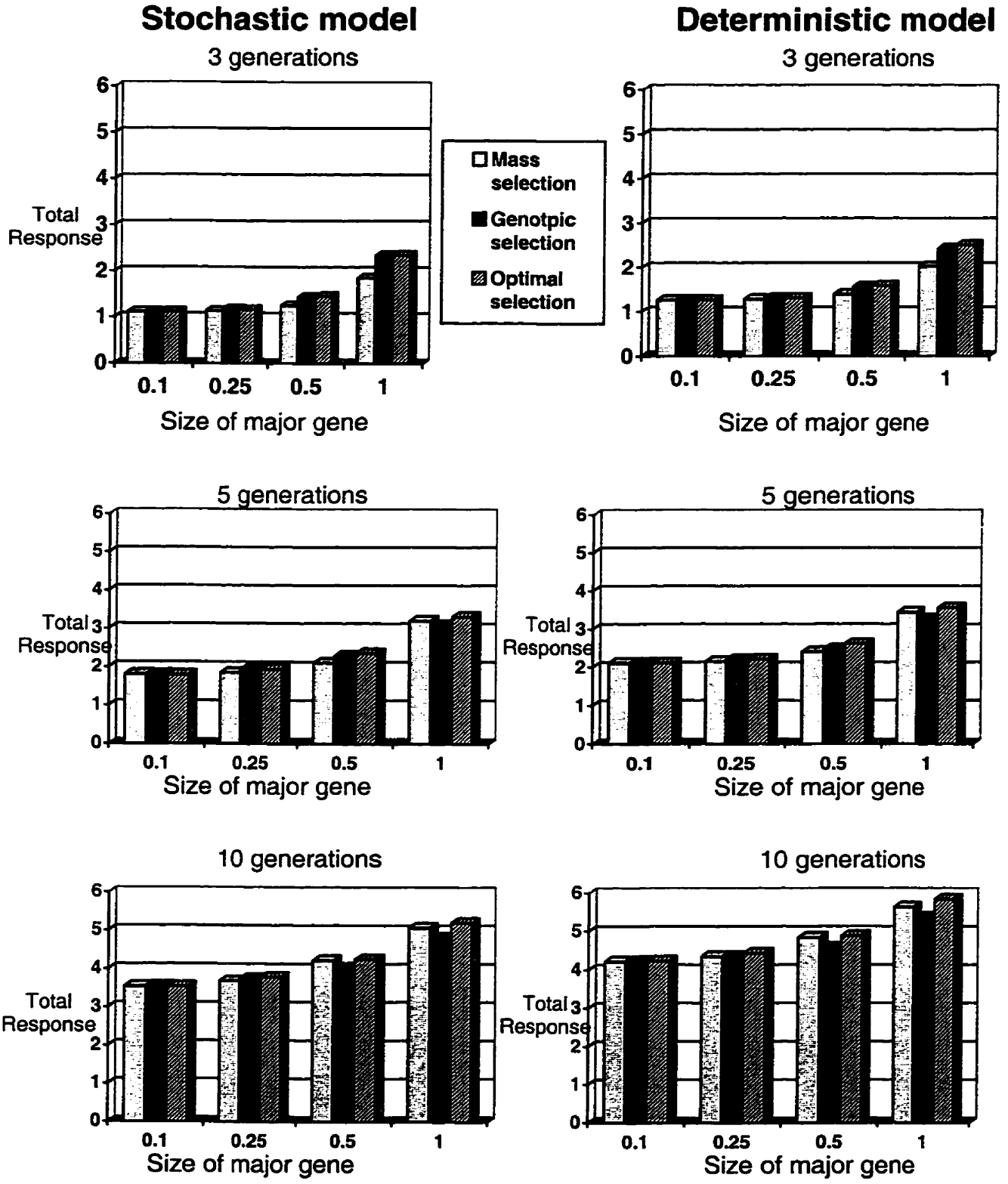
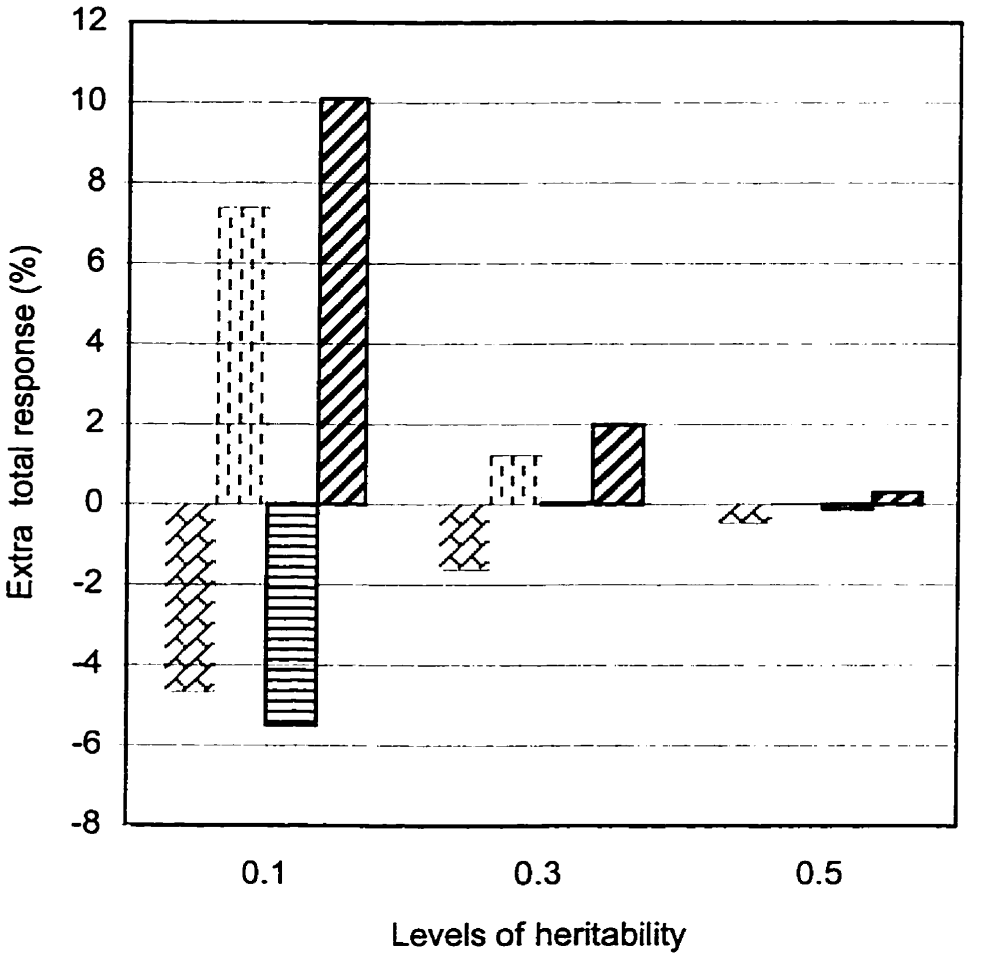
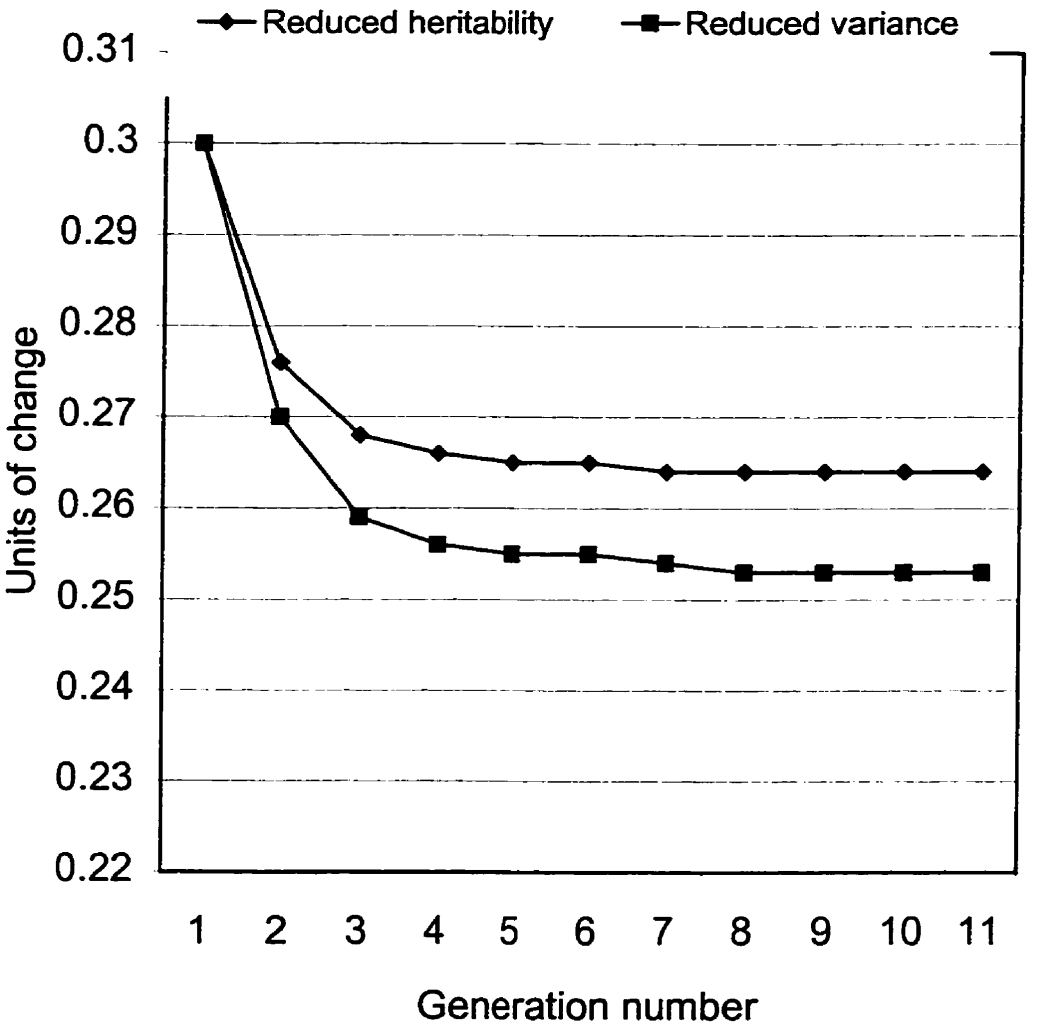


Figure 4.15: The effect of levels of heritability on extra total response for mass and optimal selection as a percentage of genotypic selection after 10 generations of selection under the stochastic and deterministic models.



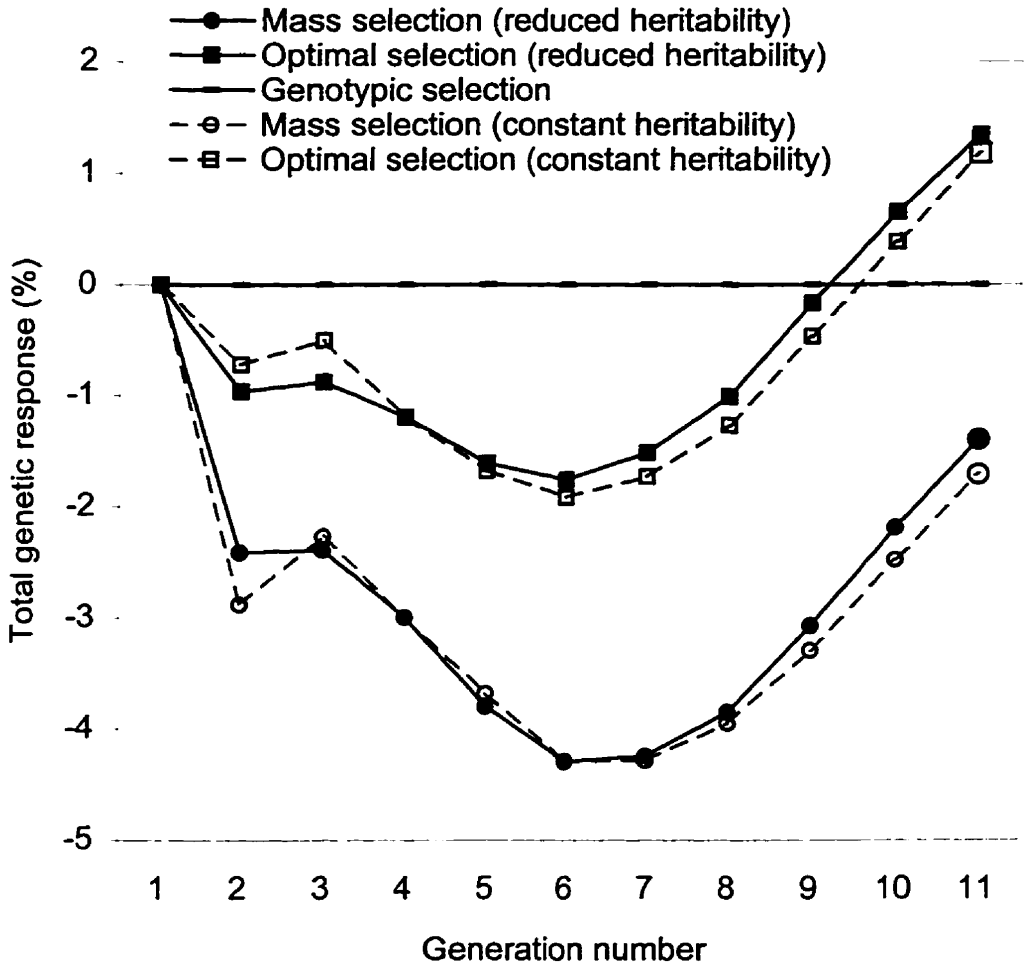
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	$a=0.25\sigma_p$

Figure 4.16: Changing variance and heritability over generations for an additive major gene under the stochastic model.



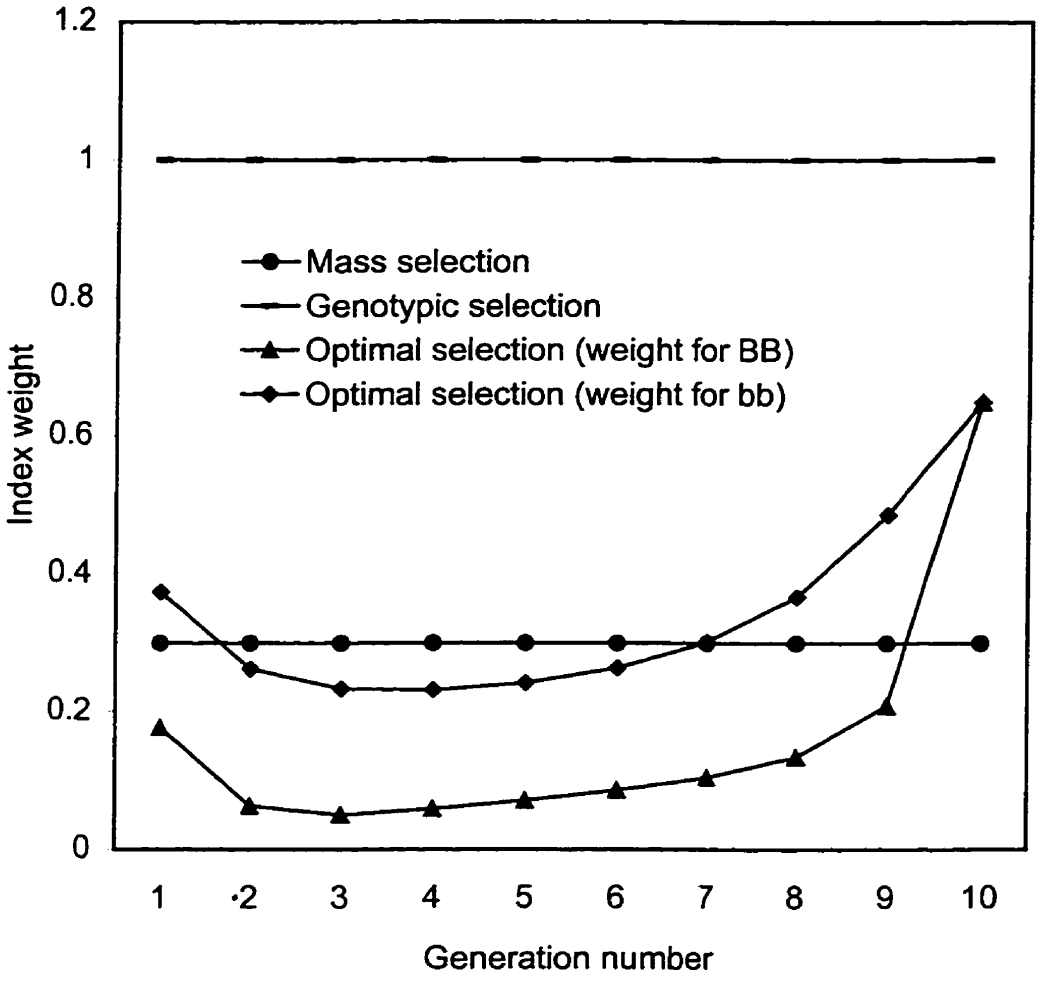
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.17: Comparison of mass and optimal selection with genotypic selection as a percentage of genotypic selection when using actual heritability in selection criteria after 10 generations of selection under the stochastic model.



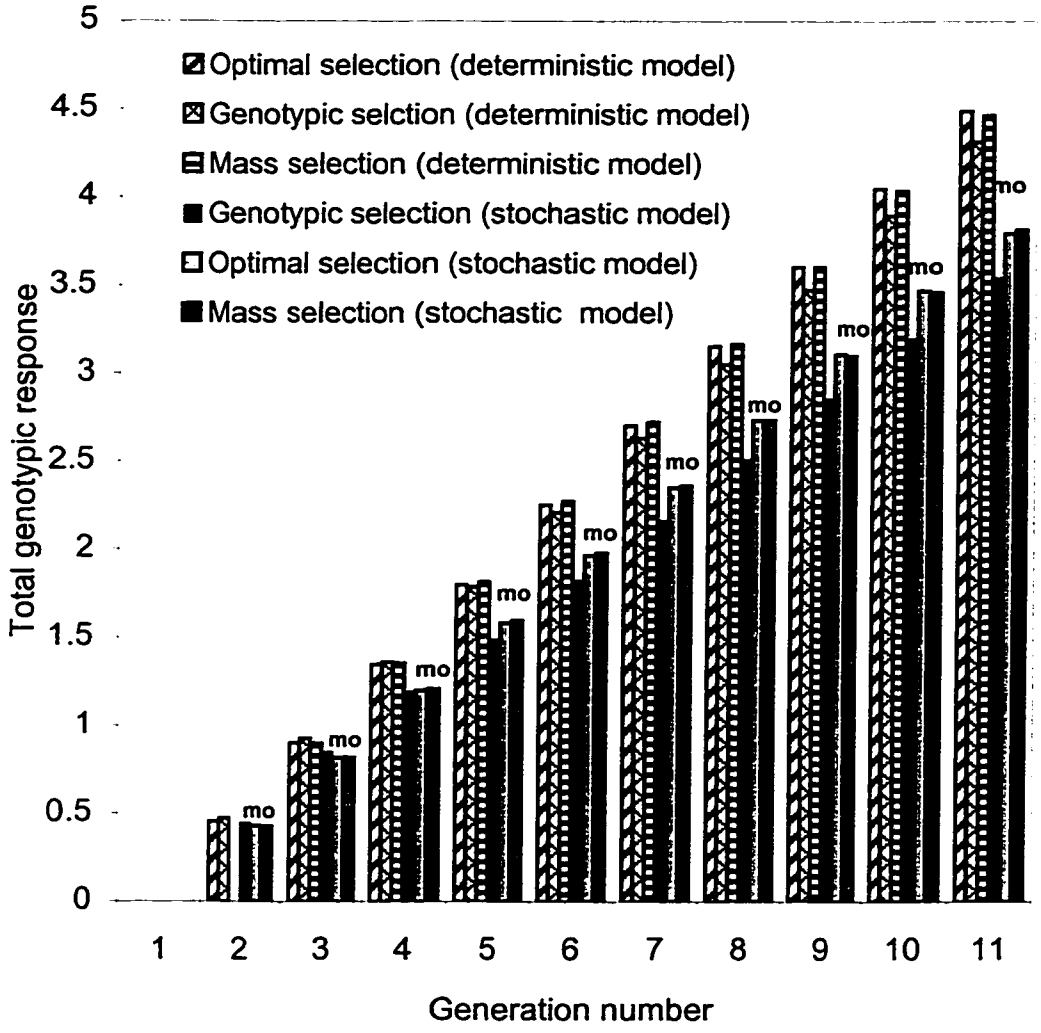
Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	10	2000	1000	0.05	0.30	(d=0.0)	a=0.25 σ_p

Figure 4.18: Comparison of mass and genotypic selection with optimal selection for changing index weights over generations for a complete dominance effect.



Parameters in Population							
No. of Sires	No. of Dams	Total No. of Progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	2000	1000	0.05	0.30	complete (d=0.25)	$a = 0.25\sigma_p$

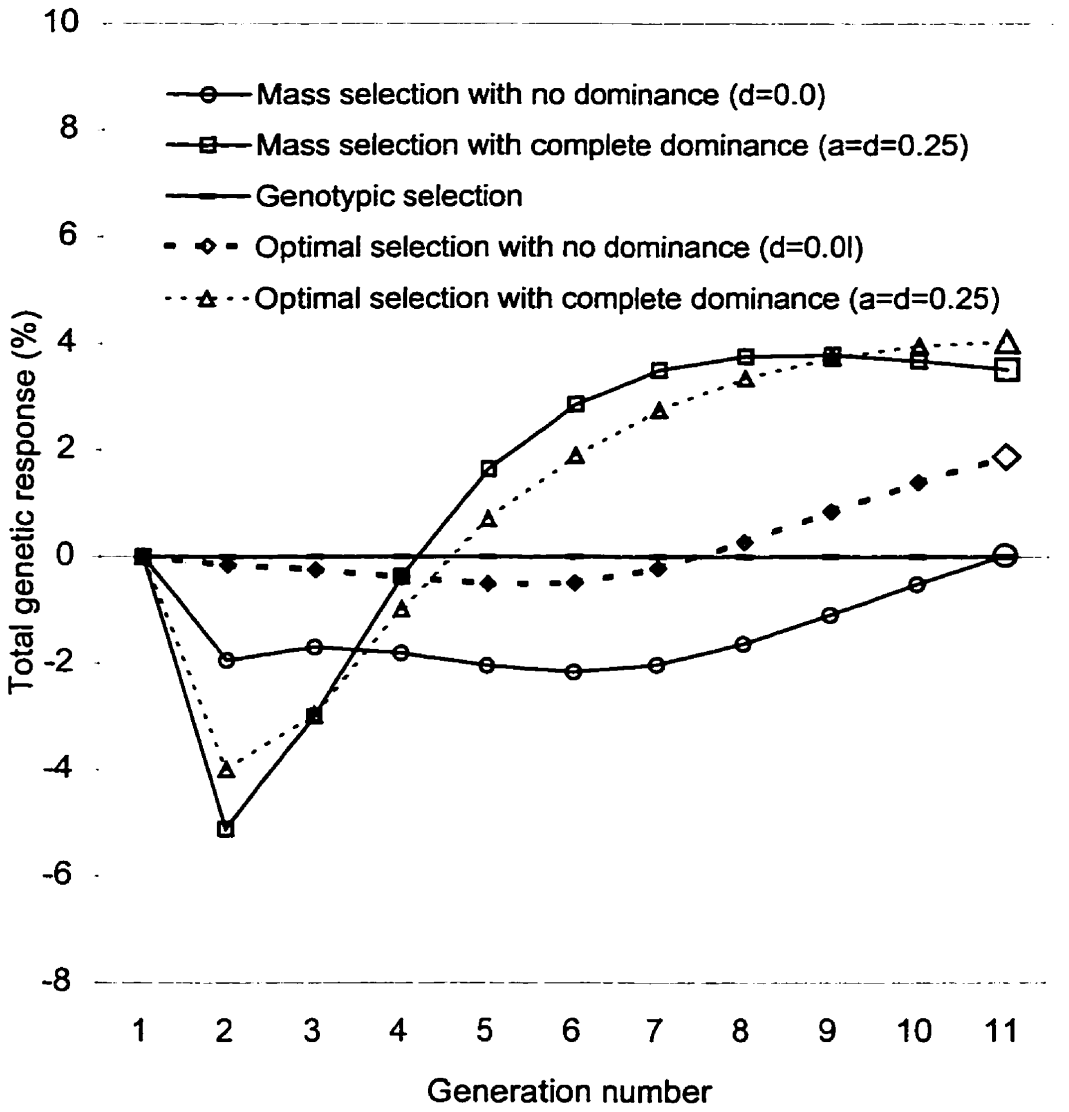
Figure 4.19: The effect of complete dominance at the major gene on cumulative response after 10 generations of mass, genotypic and optimal selection under the stochastic and deterministic models .



Common superscript m indicates significant (P < 0.05) difference between mass and genotypic selection.
Common superscript o indicates significant (P < 0.05) difference between optimal and genotypic selection.

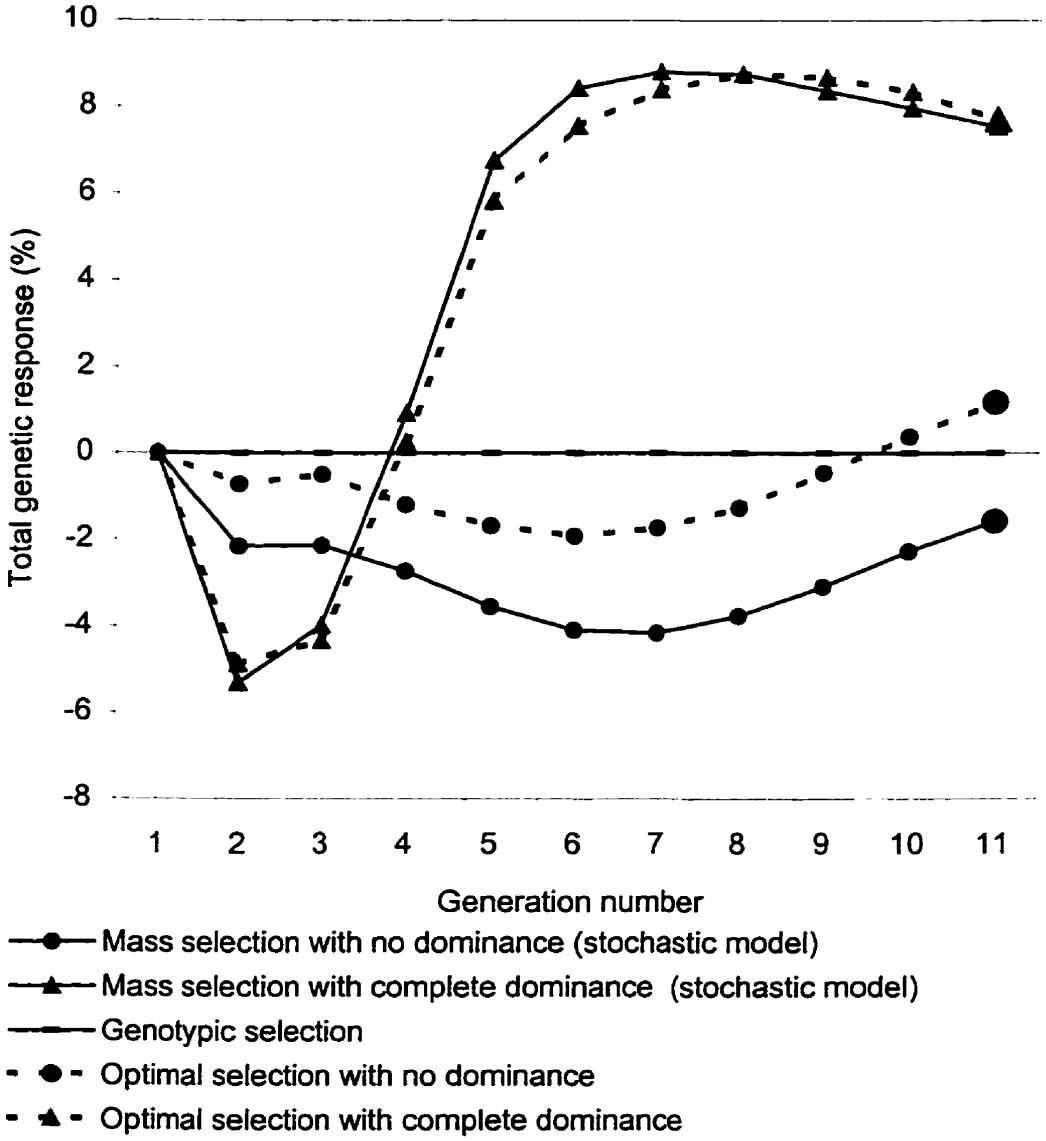
Parameters in Population							
No. of Sires	No. of Dams	Total No. of Progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	2000	1000	0.05	0.30	complete (d=0.25)	$a = 0.25\,\sigma_p$

Figure 4.20: The effect of complete dominance at the major gene on cumulative response after 10 generations of mass and optimal selection as a percentage of genotypic selection under the deterministic model.



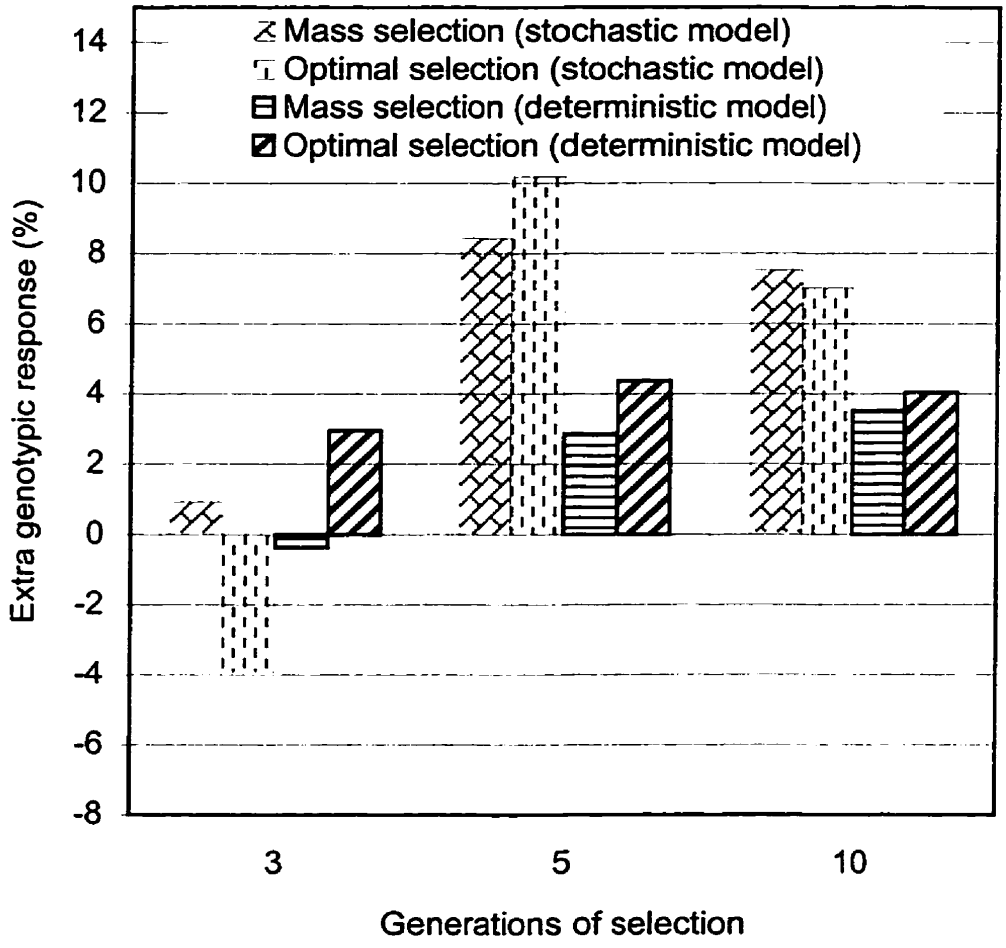
Parameters in Population							
No. of Sires	No. of Dams	Total No. of Progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	2000	1000	0.05	0.30	complete (d=0.25)	$a = 0.25\sigma_p$

Figure 4.21: The effect of complete dominance at the major gene on cumulative response after 10 generations of mass and optimal selection as a percentage of genotypic selection under the stochastic model.



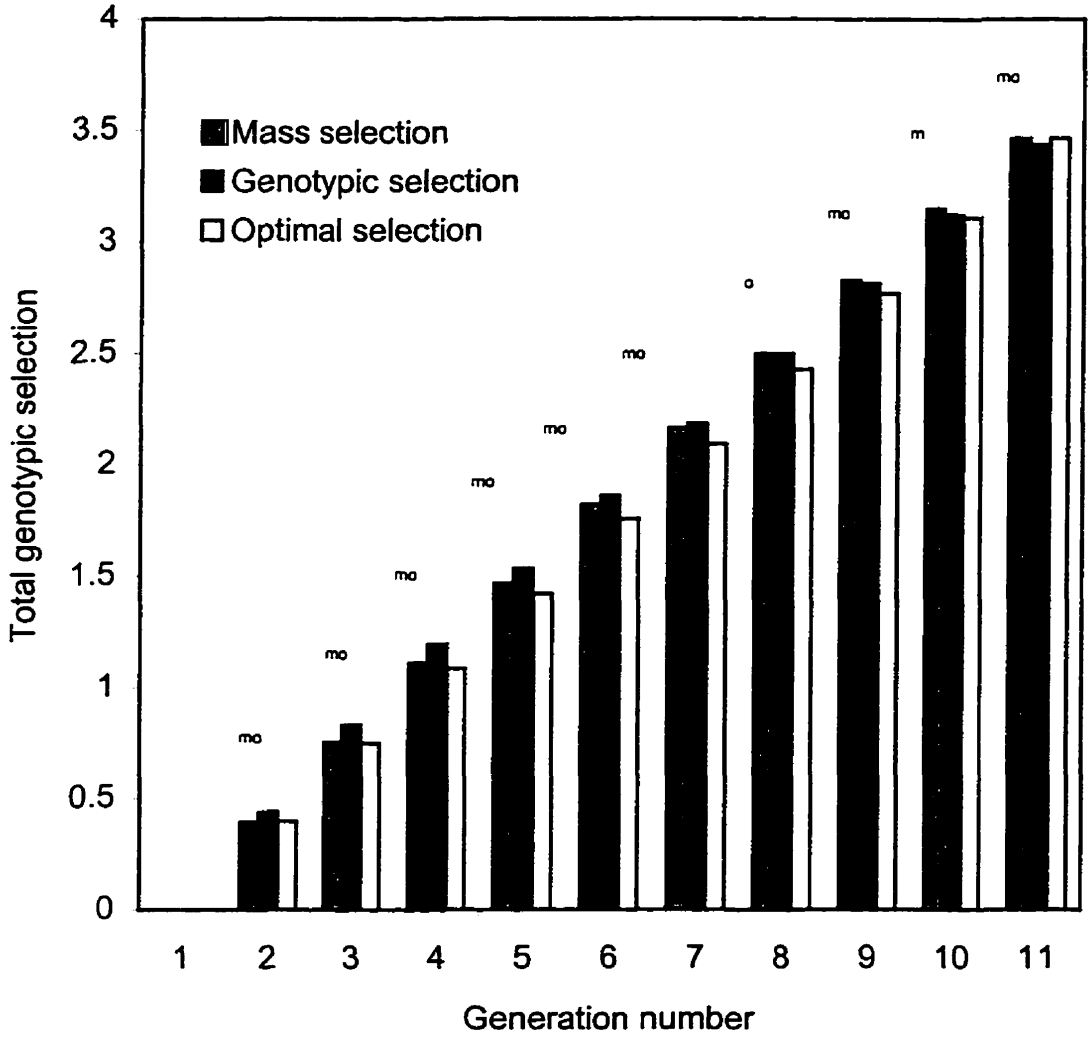
Parameters in Population							
No. of Sires	No. of Dams	Total No. of Progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	2000	1000	0.05	0.30	complete (d=0.25)	$a = 0.25\,\sigma_p$

Figure 4.22: The effect of complete dominance on extra genotypic selection response for mass and optimal selection as a percentage of genotypic selection after 3, 5 and 10 generations of selection under the stochastic and deterministic models.



Parameters in Population							
No. of Sires	No. of Dams	Total No. of Progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
200	200	2000	1000	0.05	0.30	complete (d=0.25)	$a = 0.25\,\sigma_p$

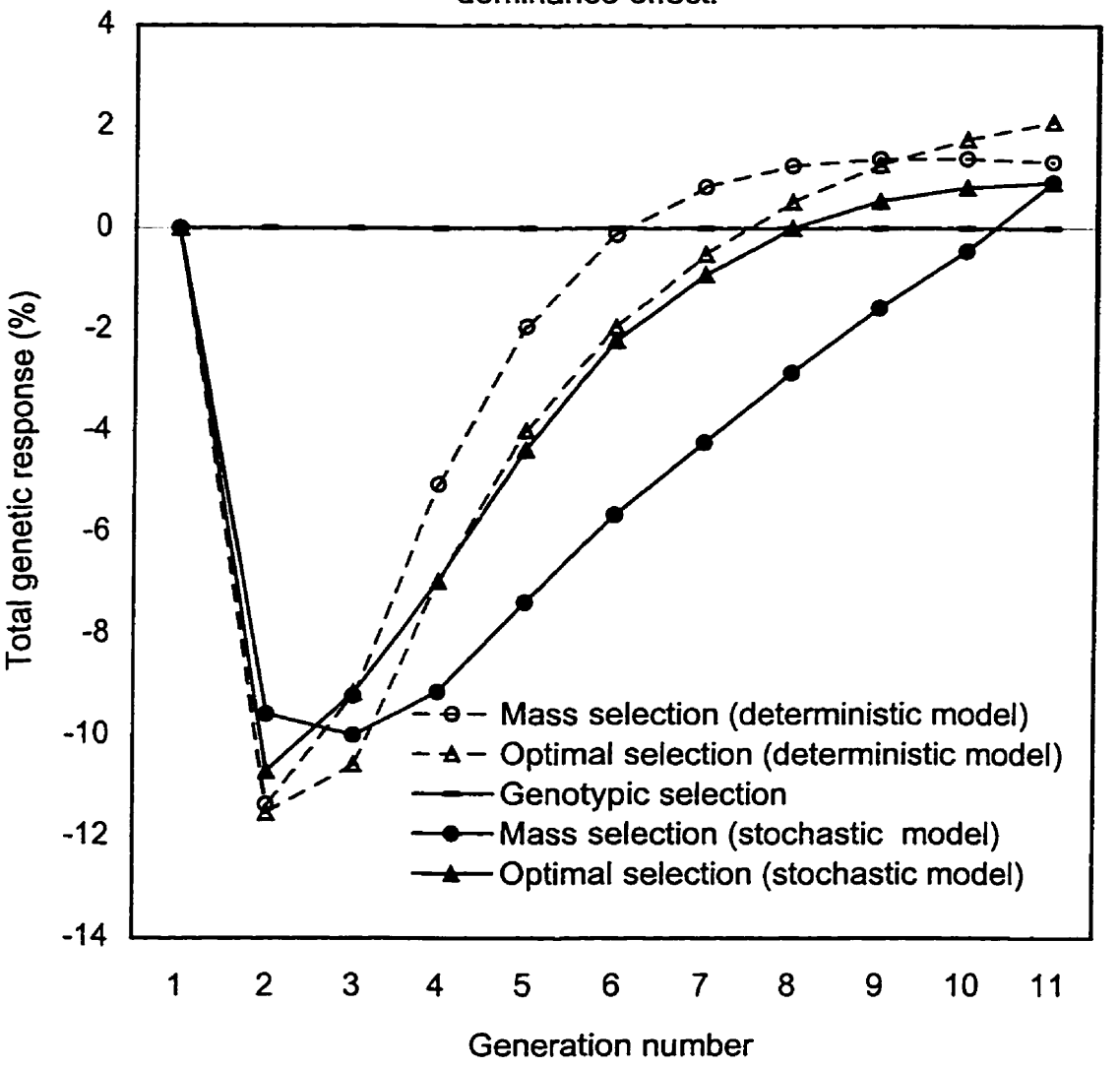
Figure 4.23: Comparison of mass and genotypic selection with optimal selection for total genotypic response (major gene plus polygenes) in the case of a negative dominance effect.



Common superscript m indicates significant (P < 0.05) difference between mass and genotypic selection.
Common superscript o indicates significant (P < 0.05) difference between optimal and genotypic selection.

Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
250	250	8	2000	1000	0.5	0.30	(d=-a=-0.25)	$a=0.25\sigma_p$

Figure 4.24: Comparison of the stochastic and deterministic models for mass and genotypic selection with optimal selection as a percentage of genotypic selection for a negative dominance effect.



Parameters in Population								
No. of Sires	No. of Dams	No. of Progeny	Total No. Of progeny	No. of Replicates	Starting Gene Frequency	h2	dominance effect	Additive Effect of Major gene
250	250	8	2000	1000	0.5	0.30	(d=-a=-0.25)	a=0.25 σ_p

Table 4.1: Comparison of mass and genotypic selection with optimal selection over 3, 5 and 10 generations of selection for a major gene with additive effects under the stochastic and deterministic models.

Stochastic Model

	Generation of Selection								
	3			5			10		
	M	G	O	M	G	O	M	G	O
Polygenic Response Mean	1.107	1.037	1.040	1.786	1.637	1.653	3.473	3.272	3.364
Polygenic Response Variance	0.253	0.261	0.261	0.252	0.261	0.259	0.252	0.250	0.254
Total Response Mean	0.914	0.946	0.935	1.626	1.706	1.710	3.452	3.513	3.559
Total Response Variance	0.961	0.968	0.969	0.964	0.968	0.967	0.970	0.950	0.958
Gene Frequency	0.112	0.318	0.293	0.179	0.637	0.616	0.460	0.984	0.890
Number of Genes Fixed	0	0	0	0	0	0	0	168	0

Deterministic Model

	Generation of Selection								
	3			5			10		
	M	G	O	M	G	O	M	G	O
Polygenic Response Mean	1.252	1.168	1.178	2.081	1.896	1.916	4.136	3.879	4.003
Total Response Mean	1.059	1.083	1.0849	1.923	1.971	1.982	4.123	4.122	4.203
Gene Frequency	0.115	0.329	0.313	0.183	0.648	0.631	0.473	0.985	0.901

M: Mass selection

G: Genotypic selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	(d=0.0)	0.3	0.25 σ_P

Table 4.2: The effect of size of the effect of an additive major gene on cumulative responses after 3, 5 and 10 generations of mass, genotypic and optimal selection under the stochastic model.

Size of the Effect of Major Gene	Generation	*Mass Selection*		*Genotypic Selection*		*Optimal Selection*	
		Total response		Total response		Total response	
		Mean	Variance	Mean	Variance	Mean	Variance
0.1	3	1.115	0.953	1.112	0.952	1.11	0.953
0.1	5	1.811	0.952	1.805	0.951	1.801	0.952
0.1	10	3.537	0.952	3.542	0.953	3.534	0.951
0.25	3	1.137	0.96	1.169	0.968	1.161	0.969
0.25	5	1.853	0.964	1.932	0.969	1.938	0.967
0.25	10	3.682	0.972	3.741	0.952	3.785	0.958
0.5	3	1.245	1.015	1.438	1.019	1.455	0.996
0.5	5	2.109	1.038	2.284	0.96	2.356	0.969
0.5	10	4.218	0.972	4.023	0.948	4.249	0.955
1	3	1.857	1.339	2.341	0.988	2.349	1.012
1	5	3.201	1.069	3.082	0.952	3.307	0.958
1	10	5.067	0.95	4.809	0.952	5.198	0.952

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	(d=0.0)	0.30	0.1 σ_P - 1 σ_P

Table 4.3: The effect of size of the effect of an additive major gene on cumulative responses after 3, 5 and 10 generations of mass, genotypic and optimal selection under the deterministic model.

Size of the Effect of Major Gene	Generation	*Mass Selection* Total response (Mean)	*Genotypic Selection* Total response (Mean)	*Optimal Selection* Total response (Mean)
0.1	3	1.26305	1.26491	1.26517
0.1	5	2.1052	2.10843	2.10893
0.1	10	4.2126	4.22318	4.22558
0.25	3	1.2845	1.3082	1.30991
0.25	5	2.14825	2.1958	2.2073
0.25	10	4.3482	4.34692	4.42851
0.5	3	1.39259	1.55612	1.58346
0.5	5	2.40053	2.47692	2.6162
0.5	10	4.83711	4.57955	4.88456
1	3	2.01913	2.42057	2.50592
1	5	3.43916	3.26163	3.55644
1	10	5.62936	5.36135	5.83226

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	(d=0.0)	0.30	0.1 σ_P - 1 σ_P

Table 4.4: Extra total response for mass and optimal selection as a percentage of genotypic selection response, for 3, 5 and 10 generations of selection under the stochastic model for an additive major gene with different sizes of effect.

		Generation of Selection					
		3		5		10	
Size of Effect of Major Gene		M	O	M	O	M	O
0.1 σ_P	Extra Genotypic Response (%)	+0.27	-0.18	+0.33	-0.22	+0.14	-0.23
0.25 σ_P	Extra Genotypic Response (%)	-2.74	-0.68	-4.09	+0.31	-1.58	+1.18
0.5 σ_P	Extra Genotypic Response (%)	-13.42	+1.18	-7.66	+3.15	+4.62	+5.62
1 σ_P	Extra Genotypic Response (%)	-20.67	+0.34	+3.86	+7.30	5.36	+8.09

M: Mass selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	(d=0.0)	0.30	0.1 σ_P - 1 σ_P

Table 4.5: The effect of level of heritability on cumulative selection responses, using mass, genotypic and optimal selection after 3, 5 and 10 generations, for an additive major gene with different levels of heritability, under the stochastic and deterministic models.

Stochastic Model

		Generation of Selection								
		3			5			10		
		M	G	O	M	G	O	M	G	O
h^2 (0.1)	Total Response Mean	0.195	0.404	0.465	0.479	0.675	0.741	1.247	1.302	1.433
	Total Response Variance	1.004	1.001	1.002	1.010	0.994	0.995	1.019	0.992	0.992
h^2 (0.3)	Total Response Mean	0.91	0.942	0.929	1.625	1.706	1.669	3.452	3.513	3.559
	Total Response Variance	0.961	0.968	0.966	0.963	0.966	0.970	0.970	0.950	0.958
h^2 (0.5)	Total Response Mean	1.577	1.583	1.585	2.683	2.703	2.700	5.475	5.526	5.506
	Total Response Variance	0.889	0.894	0.891	0.889	0.893	0.892	0.898	0.891	0.893

Deterministic Model

		Generation of Selection								
		3			5			10		
		M	G	O	M	G	O	M	G	O
h^2 (0.1)	Total Response Mean	0.2272	0.4331	0.4534	0.5439	0.71784	0.8024	1.3399	1.4177	1.5608
h^2 (0.3)	Total Response Mean	1.0595	1.0832	1.0849	1.9232	1.9708	1.9823	4.1232	4.1219	4.2035
h^2 (0.5)	Total Response Mean	1.8934	1.8968	1.8977	3.3089	3.3160	3.3185	6.8735	6.8812	6.9016

M: Mass selection

G: Genotypic selection

O: Optimum selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	(d=0.0)	0.1-0.5	$0.25\sigma_p$

Table 4.6: Extra total response for mass and optimal selection as a percentage of genotypic selection response, for 3, 5 and 10 generations of selection for a major gene with additive effects, under the stochastic and deterministic models.

Stochastic Model

		Generation of Selection					
		3		5		10	
		M	O	M	O	M	O
h^2 (0.1)	Extra Total Response (%)	-51.73	+0.25	-29.04	+9.78	-4.66	+7.38
h^2 (0.3)	Extra Total Response (%)	-3.39	+1.38	-4.75	-2.17	-1.63	+1.23
h^2 (0.5)	Extra Total Response (%)	-0.38	+0.18	-0.74	-0.11	-0.47	+0.01

Deterministic Model

		Generation of Selection					
		3		5		10	
		M	O	M	O	M	O
h^2 (0.1)	Extra Total Response (%)	-47.54	+4.69	-24.23	+11.78	-5.49	10.10
h^2 (0.3)	Extra Total Response (%)	-2.19	+0.16	-2.41	+0.58	0.03	1.98
h^2 (0.5)	Extra Total Response (%)	-0.18	+0.05	-0.21	+0.07	-0.11	+0.29

M: Mass selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	(d=0.0)	0.1-0.5	$0.25\sigma_P$

Table 4.7: The effect of complete dominance on cumulative selection response for mass, genotypic and optimal selection for 3, 5 and 10 generations of selection under the stochastic and deterministic models.

		Generation of Selection								
		3			5			10		
		M	G	O	M	G	O	M	G	O
Stochastic Model	Total Response	1.209	1.198	1.151	1.981	1.827	2.013	3.813	3.546	3.793
	Polygenic Response	1.090	0.790	1.076	1.743	1.374	1.616	3.417	3.093	3.347
Deterministic Model	Total Response	1.357	1.362	1.402	2.272	2.209	2.305	4.465	4.313	4.487
	Polygenic Response	1.226	1.006	1.127	2.026	1.793	1.956	4.067	3.868	4.083

M: Mass selection

G: Genotypic selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	complete (d=0.25)	0.3	0.25 σ_P

Table 4.8: Extra total response for mass and optimal selection response as a percentage of genotypic selection response, for 3, 5 and 10 generations of selection for a complete dominance effect, under the stochastic model.

		Generation of Selection					
		3		5		10	
		M	O	M	O	M	O
Stochastic Model	Extra Genotypic Response (%)	+0.918	-3.92	+8.43	+10.18	+7.53	+7.026
Deterministic Model	Extra Genotypic Response (%)	-0.372	+2.945	+2.856	+4.366	+3.51	+4.035

M: Mass selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
200	200	10	2000	1000	0.05	complete (d=0.25)	0.3	0.25 σ_P

Table 4.9: The effect of a major gene with negative dominance effect on cumulative selection response for mass, genotypic and optimal selection for 3, 5 and 10 generations of selection under the stochastic and deterministic models.

		Generation of Selection								
		3			5			10		
		M	G	O	M	G	O	M	G	O
Stochastic Model	Total Response	1.111	1.194	1.205	1.819	1.860	1.868	3.464	3.433	3.465
	Polygenic Response	0.968	0.977	0.899	0.987	1.509	1.547	3.101	3.057	3.128
Deterministic Model	Total Response	1.254	1.334	1.353	2.089	2.103	2.152	4.069	4.001	4.102
	Polygenic Response	1.101	0.977	0.997	1.83	1.728	1.786	3.704	3.634	3.731

M: Mass selection

G: Genotypic selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
250	250	8	2000	1000	0.5	Negative Dominance (d=-0.25)	0.3	0.25 σ_P

Table 4.10: Extra total response for mass and optimal selection response as a percentage of genotypic selection response, for 3, 5 and 10 generations of selection for a major gene with negative dominance effect, under the stochastic model.

		Generation of Selection					
		3		5		10	
		M	O	M	O	M	O
Stochastic Model	Extra Genotypic Response (%)	-6.95	+0.92	-2.2	+0.43	+0.90	+0.93
Deterministic Model	Extra Genotypic Response (%)	+0.6	+1.42	-0.67	2.33	+1.7	+2.52

M: Mass selection

O: Optimal selection

No. of Sires	No. of Dams	No. of Progeny Per Dam	Total No. of Progeny	No. of Replicate	Starting Gene Frequency	Dominance Effect	h^2	Additive Effect of Major gene
250	250	8	2000	1000	0.5	Negative Dominance (d=-a=-0.25)	0.3	0.25 σ_P

Chapter 5

General Discussion and Conclusion

5.1 Discussion

This thesis focuses on using major gene information in selection for a quantitative trait based on different selection methods.

Aspects affecting the outcome include starting heritability in the base generation, the size of the effect of the major gene, the length of the planning horizon simulated, as well as the type of selection strategy used. In this thesis, through use of stochastic simulation, the effect of incorporating a major gene in the selection criteria was evaluated, using several combinations of parameters; alternative scenarios were considered by varying the additive effect of the major gene (0.1, 0.25, 0.5 and 1 phenotypic standard deviation), degree of dominance, and initial heritability (0.1, 0.3 and 0.5). Each scenario was replicated 1000 times. The main objective of this study was to evaluate optimal strategies for selection on a quantitative trait

including major gene information.

A comparison with the optimal strategies of Dekkers and Van Arendonk (1998) confirmed the greater response for optimal selection over genotypic and mass selection for longer planning horizons. Improved responses for optimal selection were not always confirmed for short planning horizons, which is likely due to the constant polygenic variance that was used to derive optimal strategies. The advantage of optimal selection over genotypic selection under the stochastic model with 0.05 frequency for the favourable allele was 0.21% for a planning horizon of 5 generations, and increased to 1.23% for a planning horizon of 10 generations (Figure 4.12). However, optimal selection had 0.59% less response than genotypic selection for a planning horizon of 3 generations.

Results from this study indicate that including the major gene information in the selection criterion based on genotypic selection gives slightly better results in the first few generations than mass and optimal selection. Gibson (1994) and Woolliams and Pong-Wong (1995) also concluded that MAS based on genotypic selection had lower efficiency in the long-term compared to mass selection, when effects of alleles are additive. The authors did not mention the effect of dominance in their study. Muir and Stick (1998), in contrast to Gibson (1995), concluded that mass selection was better than selection on the major gene for both the short and long-term. Muir and Stick did however not use genotypic selection (with weight=1), but put a large weight on the major gene. Therefore it is difficult to compare their results with

those of Gibson (1994) and this study.

Dekkers and Van Arendonk (1998) concluded that benefits of genotypic or optimal selection relative to mass selection were limited, in particular in the long term. Their results show that optimal selection achieved greater cumulative total response over the planning horizon than genotypic or mass selection, although differences were small. They showed that selection index weights are related to the emphasis that is put on the major gene in the selection criterion but they are not related to the effective selection pressure that is put on the major gene, this also depending on variation present at the major gene. For genotypic selection, selection pressure on the major gene changed over generations, although the index weights remained constant(=1). Changes in selection pressure were due to changes in variance contributed by the major gene as its gene frequency changed over generations. Therefore, they concluded that the loss in longer-term cumulative response with genotypic selection compared to mass and optimal selection was not caused by gametic phase disequilibrium between the major gene and polygenes but by unequal selection pressure on the major gene over generations, relative to genetic variance contributed by the major gene.

Dekkers and Van Arendonk (1998) suggested that, although emphasis in their study was on selection for identified major genes, results can be extrapolated to selection on genetic markers. They suggested that the differences between mass or genotypic selection and optimal selection may be smaller with selection on ge-

netic markers that are linked to a major gene, because recombination breaks the relationship between the major gene and genetic markers over generations.

One of the objectives of this study was to examine the relationship of size the of major gene effect with selection response. The conclusion was that a reduced efficiency of mass selection within the very first few generations is observed for the large major gene effects. In other words, the maximal difference between mass and genotypic selection was higher for a major gene with larger effect.

As the results from section 4.5 show, with lower h^2 and higher initial gene frequency of the favourable allele, the efficiency of the method including major gene information is higher for an additive major gene. The greater the proportion of variance that is explained by the major gene, the more worthwhile it becomes to include the corresponding information in the breeding evaluation. Similar results were found by Smith (1967); Thompson (1990); Ruane and Colleau (1995); and Larzul et al. (1997).

Another objective of this study was to examine the changes in selection response for reduction on variance and heritability due to selection. Both the deterministic and stochastic models gave a similar pattern for the effect of using actual heritability to calculate the selection index over generations relative to using a constant heritability. Results show that there is in significant difference on selection response for genotypic and optimal selection for these conditions.

The results of this study indicate that when the major gene shows negative

dominance, the genotypic selection was more efficient in the short term, but from generation 6 this genotypic selection is less efficient than mass and optimal selection under both the deterministic and stochastic models. But when the initial frequency of favourable allele was low (e.g. 0.05), in the case of negative dominance, optimal selection did not achieve higher selection response compared to genotypic selection under the stochastic model after 10 generation of selection (result not shown). A similar result was detailed by Larzul et al. (1997) for the case of negative dominance with an initial frequency of the favourable allele lower than 0.1, for genotypic and mass selection.

Figures 4.19 and 4.23 showed that, under the stochastic model, optimal selection achieved 3% and 7% greater response after 10 generations than mass and genotypic selection, respectively, for a major gene with a complete dominance effect, and 0.5% and 1% greater response for a major gene with negative dominance. Therefore, the superiority of optimal selection over genotypic selection is increased when dominance at the major genes increases, compared to genotypic selection. These results contrast to those of Fournet et al. (1997) for mass and genotypic selection. The authors concluded that the extra genetic gain may be quite important when the favourable allele B is recessive, but decreases when the degree of dominance is increased over b.

Meuwisson and Van Arendonk (1992) and Muir and Stick (1998) concluded that mass selection would be superior to MAS based on genotypic selection in the long-

term because mass selection allocates less selection differentiation to the fixation of major genes and more to selection differential of polygenes with small effects.

Muir and Stick (1998) concluded that, when major genes are identified, the optimal program is not to fix the gene as rapidly as possible. In doing so, animals with many favourable polygenic alleles will be discarded to the overall detriment of the program. The authors showed that a gene should be incorporated into the population over a period of several generations using an index giving a relative weight to the gene proportional to its effect on the overall genetic variance for the trait. Planning horizon of 3, 5, and 10 generations of selection was arbitrary. Obviously 10 generations of selection is considered equivalent to an unacceptably long period of time for livestock species such as cattle.

5.2 Conclusion

The results from this study clearly show that use of a major gene in a selection strategy can be optimized for specific situations. Therefore, each strategy should be based on the mode of action and size of effect of the major gene. Resulting strategies should maximize cumulative responses to selection for a pre-specified planning horizon.

Optimal strategies that are derived under a model with constant genetic variance may not result in greater responses to selection for all situations.

Since using the major gene information requires genotyping animals individually,

which is costly, the advantage of including a major gene in the breeding program may not be worth the cost of genotyping the animals. However, small extra genetic gains can sometimes provide substantial advantages within the context of a breeding program. Using major genotype information can be more useful for sex-limited traits, traits that can not be measured in either sex, and for traits with low heritability.

5.3 Limitations and future research

Several important limitations should be noted in the model developed here. The model presented contains simplifying necessary assumptions to keep the model to a manageable level. Some of the assumptions of this simulation would be impossible to achieve in an actual breeding program, such as the accuracy of the knowledge on the major genotype being assumed to be known without error. If the major genotype had been estimated given major gene information, the extra gain due to the inclusion of this information would be less important if there were a risk of error in the estimation. A large effect could be estimated with relatively high accuracy, but a major gene with smaller effect would require much more data to estimate accurately. How realistic is the infinitesimal model? or do we really have infinite numbers of polygenes? Some of these assumptions could be removed and others modified after future study.

There is a disadvantage in developing a strategy (for the objective of optimal

strategies) which is maximizing response after T generations. Pre-determined information at the base generation is required, which is not practical. A breeding company will be selling breeding stock from its population in each year/generation of the planning horizon. Therefore, they are interested not only in the genetic level at the end of the planning horizon, but in the genetic level in each generation. Also if there is more information, new tools or changes in economic value during planning horizon they would not able to add them in selection program. Ideally, we should maximize some discounted sum of genetic levels in each generation of the planning horizon.

Optimal strategies give optimized index weights only for the deterministic model, which includes constant variance among polygenes. They are not optimized for the stochastic model.

Time did not permit extention to major genes of partial and over dominance and future study is required for this aspect. It would also have been more informative to use a wider range of models and parameters such as unequal selection intensity for male and female, partial and over dominance effects, more than one major gene and errors of estimating the major gene effect.

Further research is needed to derive strategies that optimize marker-assisted selection under alternative genetic models that include such effects as changes in inbreeding, and in genetic variance. The optimal control methods developed by Dekkers and van Arendonk (1998) can provide a useful framework for these further

developments.

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IMAGE EVALUATION
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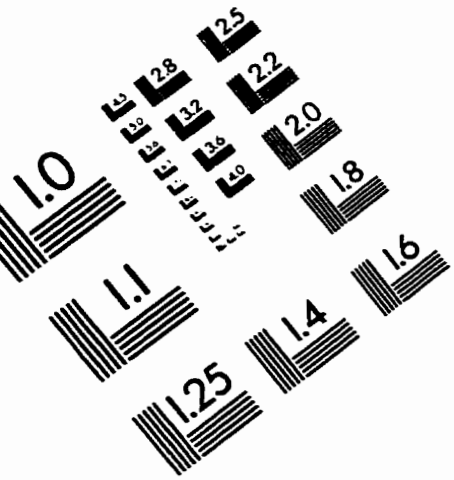

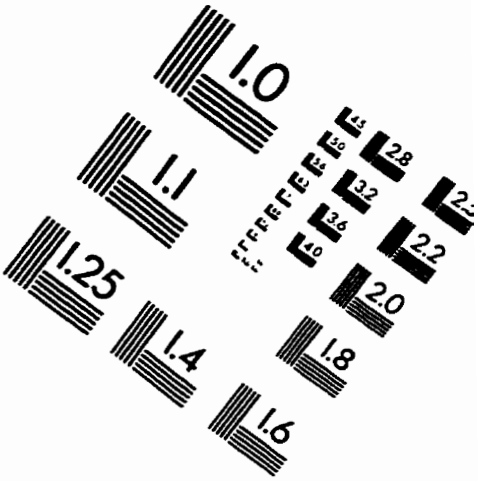

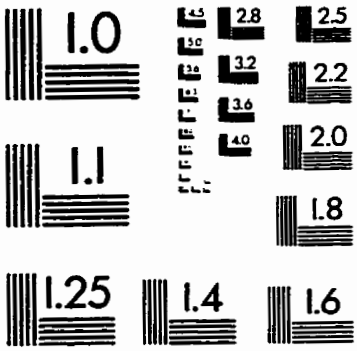

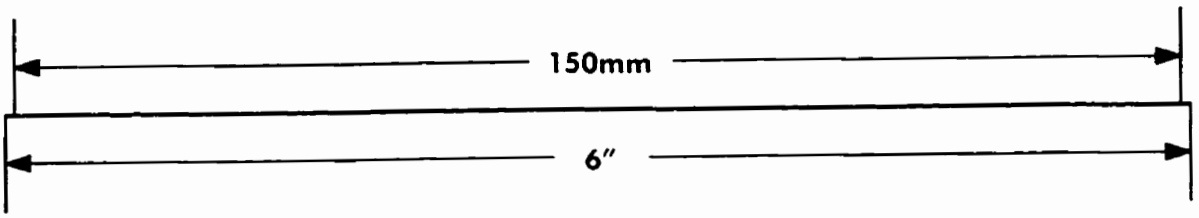

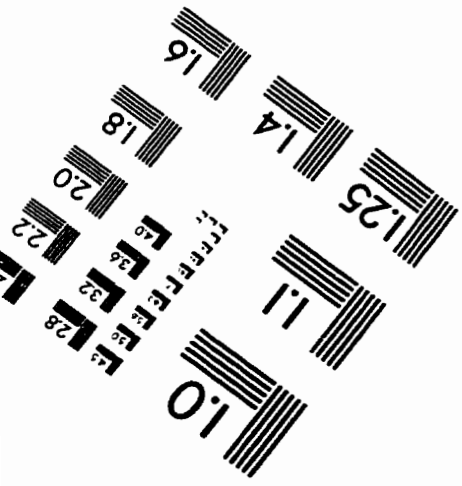

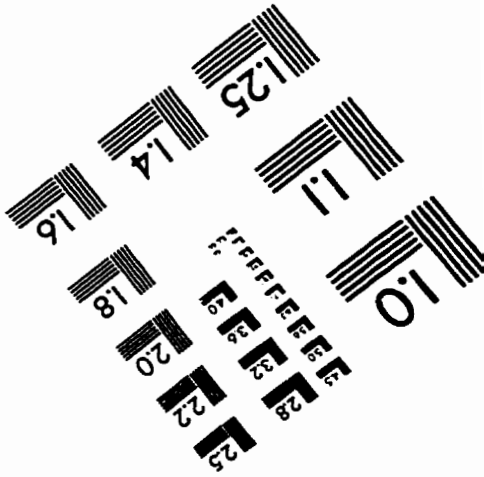

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