CHARACTERISTICS OF A GOOD (SIMULATED) CONTROL POPULATION IN STUDIES OF ASSORTATIVE MATING

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SUMMARY
Some properties of the Hardy-Weinberg model and the Infinitesimal model with regard to the design of control populations is discussed. Attempts have been made to quantify the minimum required population size and the minimum required number of loci to fulfill the conditions set forth by the Hardy-Weinberg and the Infinitesimal model.

INTRODUCTION
The role and significance of the control populations have been discussed many times (e.g. Hill 1972a,b). The main purpose of having control populations are to separate observed changes in phenotypic values into its environmental and genetic components e.g. to correct for environmental fluctuations or time trends in conjunction with selection experiments or breeding programs. In this respect, any population with minimal inbreeding has been considered good enough for most purposes. Furthermore, for the best utilization of the breeding facilities it has been desirable to increase the effective size (N_e) of population over the actual size by decreasing variation of family size. Hence, single pair matings of parents each producing only one male and one female offspring has been considered to be the best.

For a population to be considered as a good control population in simulation studies certain requirements of basic quantitative genetic models must be fulfilled. There are two such models: Hardy-Weinberg model and Infinitesimal model.

**Hardy-Weinberg model:** This model basically states that in the absence of mutation, migration and selection the only force causing any change of gene frequency in a random mating population is random drift. To counteract the effects of random drift one must have a 'large' population. Avoidance of mutation, migration and selection in simulation studies poses no problem, but the question is how large a population must be to be considered as 'large'? Since apart from computing time and resources that are both important and expensive there is no upper limit to the size, we can reformulate this question and ask how small a population can be to be considered as 'large'?

**Infinitesimal model:** Due to the continuous distribution of most of the traits considered in quantitative genetics, and the great genetic variability found for these traits even after some generations of selection and for the sake of mathematical simplicity the infinitesimal model has been the model of convenience in the quantitative genetic theory. In this model each trait is considered to be controlled by a large number of genes each having a very minute effect on the expression of the trait under consideration. The question is, therefore, how many loci are necessary for a simulated trait to behave according to the requirements of the infinitesimal model.

In addition to these two criteria, control populations must be able to answer some other relevant questions pertaining to the actual investigations they are designed for. In the present paper the purpose is to discuss the control populations in studies of 'Joint effects of assortative mating and selection in small populations', so the control populations must be in perfect 'random mating'.

MATERIALS AND METHODS
A series of computer programs have been used in this study to simulate animals from a diploid species, each having a finite number of unlinked loci with equal gene effect. In the results presented here average gene frequency in the base population is 0.5 for all loci. The genetic value of each locus is determined by the
genotype according to the specified additive genetic input values. Dominance and epistasis were assumed not to play an important role in the problem of concern and were accordingly ignored. The individual’s phenotypic value is the sum of the genetic value and a random normal environmental deviation $N(0,0.5)$. Additive genetic value for each locus was chosen in such a way that the additive genetic variance ($VA$) in the base population became 0.5, irrespective of the number of loci. Therefore, the initial heritability is 0.5 in the various models. Expected and realized inbreeding coefficients are calculated from effective population size ($N_e$) and pedigree information for each individual, respectively. Individuals were mated randomly in a single pair mating scheme. Each mating produced equal number of male and female offspring.

A non-selection model with only one locus was used for quantification of the required minimum population size in the Hardy-Weinberg model. Two selection models, one with 10% and the other with 50% of the population selected were used for quantification of the required minimum number of loci in the Infinitesimal model. Each parameter combination was replicated 40 times.

RESULTS

Population size: To quantify the required minimum population size in the Hardy-Weinberg model inbreeding coefficient was used as an indicator of random drift. The average inbreeding coefficients for populations of various sizes are shown in Fig. 1. Fig. 2 shows product-moment correlation between phenotypic values of mated individuals in a population of size $N_e = 800$, for three replicates. As regards to the randomness of matings, individual lines (replicates) show much fluctuations. Phenotypic correlations between mates are customarily used to show the assortative mating. Since the matings in this study were supposed to be random, the arisen phenotypic correlations are a measure of unplanned assortative mating.

Fig. 1. Expected and realized inbreeding coefficients in populations of various size.

Fig. 2. Phenotypic correlation of mates’ in three randomly mated populations of size $N_e = 800$.
Number of loci: In order to quantify the required minimum number of loci in the infinitesimal model, one has to consider the effects of selection on the gene frequency and genetic variation. Fig. 3 and Fig. 4 show the effect of selection on genetic variance with 10% and 50% selection intensity, respectively. Fig. 5 and Fig. 6 show the effect of selection on the frequency of the favorable allele with 10% and 50% selection intensity, respectively.

Fig. 3. Effect of number of loci on the genetic variance under selection when 10% of the population is selected (N_e=1400).

Fig. 4. Effect of number of loci on the genetic variance under selection when 50% of the population is selected (N_e=1400).

Fig. 5. Effect of number of loci on the frequency of the favorable allele under selection when 10% of the population is selected (N_e=1400).
As is shown in Fig. 1 expected and realized inbreeding coefficients are in good agreement with each other. Although, inbreeding coefficients are negligible in populations of \( N_e = 800 \) or larger, effects of chance events are still large enough to concern us in the studies of mating effects. This shows that the inbreeding coefficients are not sensitive after a certain population size and another method of measuring the effects of chance events must be used, i.e. the degree of assortative mating. The reason can be explained as follows. In small populations and in the early generations of a breeding experiment individuals’ inbreeding coefficients could fluctuate between certain fractions, i.e. 0, \( \frac{1}{2} \), \( \frac{1}{4} \) and so on, and population’s inbreeding coefficient as an average of the individuals’ inbreeding coefficients is a good enough measure of the chance events, if we look at \( F \) as a measure of the variance of gene frequency between sub-populations \( (\sigma^2_F = \sigma^2_q F) \). However, in larger populations and in later generations of a breeding experiment individuals’ inbreeding coefficients are more uniform and demonstration of chance events requires another method that mathematically is more elaborate than simple averaging. That is why correlation coefficients are more capable of revealing the chance events. Fig. 2 shows that unplanned assortative mating sets a higher demand on the required minimum size of a population \( (N_e > 1400) \); results not shown) to fulfill Hardy-Weinberg conditions.

Under the assumptions of the Infinitesimal model, changes occurring in the population’s phenotypic mean is the outcome of a covariance between loci (Bulmer, 1971). Furthermore, model the gene frequencies are considered to be affected very little by selection in the short term (Crow and Kimura, 1970). However, the matter is complicated by two factors. First is the fact that ‘short term’ is a rather vague and subjective term. The same applies to the second factor, i.e. the selection pressure. If we assume that any change in gene frequency change less than 10% of the initial gene frequency (i.e. 0.5) is negligible, then in the data presented here a gene frequency of 0.55 for the favorable allele constitutes the border between the infinitesimal and non-infinitesimal model. Accordingly, the minimum required number of loci to satisfy the infinitesimal model very much depends on the selection pressure and duration of selection.

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REFERENCES