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by

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DOCTORAL THESIS, GENETICS

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Abstract

The effects of intentional inbreeding on the response to selection for a low-heritability quantitative character manifesting itself in one sex were studied using simulation and numerical methods. In simulation the character was determined by 32 or 108 loci with two alleles, whereas in the numerical models genetic change at a single locus was calculated. There were no epistatic interactions. In regard to the response to selection, various methods of inbreeding with alternating random mating and full-sib mating periods were compared with random mating in all generations.

When there was between-family selection in the inbreeding periods of three generations and combined selection in the random-mating periods of three or six generations, in populations of 1500 the advantage of inbreeding in the response to selection of 30 generations compared with random mating depended on the number of families selected to inbreed and on the effects of loci. For loci with large standardized effects the advantage of inbreeding was small, even in the case of a lot of families and high degrees of dominance.

When there was random mating and full-sib mating in alternate generations and phenotypic selection of females, in populations of 400 with a 50 % proportion selected the time saved due to inbreeding compared with random mating in reaching a given proportion of the maximum response was 10-20 %. For deterministic single-locus models the corresponding time saved was 20-40 %. The advantage of the inbreeding system in the rate of response was somewhat larger for weak selection than for stronger. In simulation the time saved due to inbreeding until fixation at all loci was 12-43 %, increasing mainly with the degree of dominance. In general, both systems of breeding resulted in the same ultimate response to selection.

Using a deterministic model, it was found that for an additive locus some advantage of the alternating mating system in the response to selection of 20-100 generations could be expected if the loss in the selection differential due to inbreeding remained clearly below 20 % and selection was not very strong. In strong selection the corresponding loss is below 15 %.

It was concluded that the best prospects for the successful use of inbreeding to increase the response to selection are in a large population with a relatively high proportion selected. The main problem in using an inbreeding system is the decrease in selection intensity due to the effects of inbreeding on fitness.

CONTENTS

This thesis is principally based on the following publications and manuscripts, which are referred to by their Roman numerals in the text:

I Sirkkomaa, S. and Maijala, K. 1980.
A simulation study on intensive selection and inbreeding in laying hens. Hereditas 92: 331-334.

II Sirkkomaa, S. 1984.
Effects of inbreeding on the response to selection in a simulated population. Hereditas 100: 233-241.

III Sirkkomaa, S. 1986.
Long-term response to selection with inbreeding in alternate generations. In: Dickerson, G.E. and Johnson, R.K. (Eds) 3rd World Congr. Genet. Appl. Livestock Prod. XII. Biotechnology, selection experiments, parameter estimation, design of breeding systems, management of genetic resources. University of Nebraska, Lincoln, pp. 297-302.

IV Sirkkomaa, S.
Ultimate response to selection with alternate random and full-sib mating generations. Submitted to Theor. Appl. Genet.

V Sirkkomaa, S.
Use of inbreeding to increase the responses to various intensities of selection. Submitted to Theor. Appl. Genet.

Introduction

Mating schemes in which the population is no longer a single panmictic unit but is divided into separate breeding groups have been recognized as important factors in evolution, and possibly also in animal breeding, in increasing the response to selection (e.g., Wright 1922, 1939, 1951, 1977; Lush 1945).

One possible breeding system with subdivided population structures is to divide a population into L small, isolated sublines of size N, to select within lines for some generations (usually 4-8), and then to select the best lines for intercrossing to produce a new set of sublines. The response to selection obtained in this kind of system is compared with that in a single population of size LN with the same selection intensity as in each subline. The results have been largely negative, i.e., there has been no extra selection gain due to the subdivision (for increased pupa weight in Tribolium Enfield (1970), Goodwill (1974), Katz and Enfield (1977); for reduced sternopleural bristle number in Drosophila Madalena and Robertson (1974); for increased abdominal bristle number in Drosophila Rathie and Nicholas (1980)). Madalena and Hill (1972) found in their simulation study with non-epistatic models that there was some advantage of the subdivided mating structure in the selection response when the recessive allele with a low initial frequency was favoured. By using a simulation model very closely resembling that of Madalena and Hill (1972), Enfield and Anklesaria (1986) found that a breeding scheme with subdivision can be more effective than breeding in a single population if there is multiple peak epistasis in the character selected for. However, the advantage of subdivision in the selection response was critically dependent on many parameters.

Wright (e.g., 1939, 1977) suggested, on the basis of his shifting balance theory of evolution, that a breeding programme with a subdivided structure might be fairly effective if epistatic gene interactions are important and there is migration between the sublines (demes). In an experiment of Katz and Young (1975) concerning increased adult body weight in Drosophila, there was regular, cyclical migration of individuals between demes in each generation. The response to selection in this subdivided structure was significantly larger than that in a single large population.

In assortative mating the individuals chosen as parents are more similar for some phenotypic character than if they were sampled at random from the population. In truncation selection this means that the selected group is not a panmictic breeding unit and can be considered as a subdivided structure, especially if the ranked individuals are divided into isolated breeding subgroups. There is quite a large increase in the variance of a multifactorial character due to assortative mating, but only a slight increase in homozygosity unless the number of loci is small (e.g., Crow and Felsenstein 1968; Crow and Kimura 1970). In addition, assortative mating affects only the loci controlling the character in question, and the increase in variability increases with the number of loci.

The increased additive genetic variance caused by assortative mating has drawn attention to the possibility of enhancing the selection response by using this mating system (Breese 1956; James and McBride 1958). A superiority of assortative mating over random mating with respect to the response to selection has been found in experiments (for abdominal chaeta score in Drosophila McBride and Robertson (1963); for pupa weight in Tribolium Wilson et al. (1965), Mwenya et al. (1983)). The same kind of superiority has also been observed in simulation experiments (Rico et al. 1973; DeLange 1974; Fernando et al. 1983; Fernando and Gianola 1986). In the latter three simulations, it has been verified that a higher proportion selected increases the advantage of assortative mating over random mating, which was a theoretical result of Baker (1973). The simulation study of DeLange (1974) showed that the advantage from assortative mating increases with the number of loci. This was also the result obtained by Fernando and Gianola (1986) with a theoretical model. Moreover, it has been shown that the advantage of assortative mating over random mating increases with the initial heritability (DeLange 1974; Fernando and Gianola 1986), as expected by McBride and Robertson (1963) and Baker (1973).

With regard to natural selection, on the basis of their results, Fernando and Gianola (1986) suggested that a population with assortative mating could potentially displace one with random mating if the two populations were competing for scarce resources.

When using inbreeding, the selected group is divided into completely isolated subgroups (families), in which the matings take place at random. The theory of inbreeding has been thoroughly studied and summarized by numerous authors (e.g., Wright 1921; Fisher 1949; Crow and Kimura 1970). Inbreeding causes an increase in homozygosity at all segregating loci, and the increase in the variability of a character compared with random mating is independent of the number of loci involved. The increase in homozygosity brings about inbreeding depression, especially concerning fertility and viability (fitness), so behaviour patterns exist in nature which reduce the probability of matings between close relatives (e.g., Greenwood and Harvey 1976; Feldman and Christiansen 1984). However, it has been shown theoretically that enhancing the degree of inbreeding can increase the rate of change in the frequency of an altruistic allele (Wade and Breden 1981).

The use of the increased additive genetic variance and heritability caused by inbreeding to improve the selection response in animals has received continued interest (e.g., Lush 1945; Dickerson 1973; Dickerson and Lindhé 1977). On the basis of the selection theory, the expected response per generation in inbred populations is larger than that in random-bred populations (e.g., Wright 1942). However, for the successful use of inbreeding, large problems with the selection intensity and with the effective population size must not occur (Dickerson and Lindhé 1977). Bereskin (1972) concluded from a simulation experiment that moderate inbreeding through selection may not reduce genetic gains. In developing inbred lines three generations of full-sib mating and intense selection between lines have been proposed (Warren 1950; Abplanalp 1974). Dickerson (1973) suggested recurrent cycles of inbreeding, between-line selection and combination of the best lines to increase the response to selection. The experimental results on the use of inbreeding to improve the selection response have been largely negative (for litter size in mice Bowman and Falconer (1960); for a biomass index in Japanese quail MacNeil et al. (1984a,b); for pupa weight in <u>Tribolium</u> Dion and Minvielle (1985)).

In animal breeding research the comparisons between different schemes of mating and selection can be made in four principal ways (Rasch and Herrendörfer 1972):

1) pure theoretical-mathematical analysis (deduction);
2) simulation experiments;
3) experiments with model populations (experimental animals);
4) experiments with the populations of domestic animals (induction).

Numerical methods can be included in 1. The development of computers created opportunities for the use of simulation and numerical methods. Since the work of Fraser (1957a,b), many computer simulations have been made to clarify various problems in quantitative population genetics and breeding planning. Due to the complications caused by finite population size, linkage, dominance and epistasis, precise analytical treatment is extremely difficult (e.g., Robertson 1970a).

The purpose of the present investigation was to study the effects of inbreeding on genetic gain in selecting for a low-heritability character manifesting itself in one sex only. The methods used were simulation and numerical models.

Methods

1. Simulation model

The method of simulation was outlined in I-IV. Some details on the procedures concerning genetic structures and phenotypes are given here because they were not completely described in I-IV.

1.1. Production of random numbers

Pseudo-random numbers of uniform distribution (U) were generated using the linear congruential method (function subprogram RNDM, programmed for UNIVAC 1100 Series by the Computing Centre, University of Helsinki). Poisson-distributed random variates were produced using the U numbers in a subprogram written by the author according to Knuth's algorithm (Yakowitz 1977). Random deviates of normal distribution were obtained using the U numbers in a subprogram written by the author according to the Box-Muller method (Yakowitz 1977).

1.2. Genetic structures

1.2.1. General

The main storage of a computer consists of bits, which can be in two different states representing 0 or 1. Several bits are grouped to form one word. In UNIVAC 1100 one word is equal to 36 bits, whose states can be switched by function FLD of FORTRAN V (SRC 1971). If diallelic loci with alleles A_1 and A_2 are simulated, two bits are required to represent the state of one locus in a diploid individual (homologous chromosomes = words 1 and 2):

genotype	A_1A_1	A_1A_2			A_2A_2
word 1	1	1	or	0	0
word 2	1	0		1	0

Thus, for a quantitative character controlled by L loci, 2L bits are required to represent the genotype of one diploid individual, the bits being divided into two bit strings which represent two haploid sets of chromosomes.

1.2.2. Forming of the initial population

Let the population size and the initial frequency of A_1 be T and p, respectively. Thus, in the whole population there must be 2Tp A_1 alleles at a particular locus.

Procedure for one locus:

a) setting all the 2T bits to be 0;

b) random drawing of an individual i (i=1,...,T, probability of 1/T for every individual);

c) random drawing of a chromosome j (j=1,2, probability of 1/2 for each homologue);

d) if the bit corresponding to ij is 1, returning to b, else setting this bit to be 1;

e) if fewer than 2Tp bits are in state 1, returning to b, else proceeding to fill the next locus.

Using this procedure, the expected genotype frequencies are:

A_1A_1	$p^2-p(1-p)/(2T-1)$
A_1A_2	$2p(1-p)(1+1/(2T-1))$
A_2A_2	$(1-p)^2-p(1-p)/(2T-1)$,

which are the random-mating proportions in a finite population (Crow and Kimura 1970). The states of the loci in an individual are generated independently, so the expected initial state concerning all loci is linkage equilibrium.

1.2.3. Forming of the linkage groups

In reality the loci are scattered over several chromosomes (linkage groups). Let the length of the i^{th} chromosome be q_i ($i=1,\ldots,K$, where K is the number of chromosome pairs), and suppose that the loci are randomly distributed among chromosomes. Then, the probability that there are n_i loci on the i^{th} chromosome ($i=1,\ldots,K$) is:

$$\frac{L!}{n_1!\ldots n_K!} \quad q_1^{\,n_1} \ldots q_K^{\,n_K} \, (1/Q)^L,$$

where $n_1+\ldots+n_K = L$ = number of loci
$n_i=0,\ldots,L \quad (i=1,\ldots,K)$
$q_1+\ldots+q_K = Q.$

The sites of the n_i loci on chromosome i were determined by drawing at random n_i even-numbered, mutually exclusive integers from an interval $1,\ldots,Z$, where Z is a large integer. The numbers and sites of loci on every chromosome were generated at the beginning of each replicate run and stored as vectors in a COMMON area for further use in the forming of gametes.

The number of chromosome pairs (K) was 39. Most of the total length of the genome was shared by 9 macrochromosomes (70 %). The remaining 30 chromosomes (microchromosomes) shared only 30 % of the total length.

1.2.4. Forming of the gametes

The genome of a gamete is a kind of sample from the genetic structure of a diploid individual. The sampling is realized in meiosis, in which the number of chromosomes is halved and recombination takes place. In this process new genetic arrangements are generated by the independent assortment of chromosome pairs in prophase I and by crossing-over events between the maternal and paternal strands of bivalents.

There are two bit strings corresponding to the genetic structure of every individual (1.2.1). The length of each string is L bits. The distribution of the L loci along chromosomes is represented by other vectors (1.2.3). The first step in the formation of a gamete is duplication of the two strings. The result is matrix F(4,M), where M is the number of words required to represent a string of L bits. Matrix F corresponds to that stage of meiosis in which the homologous chromosomes have been duplicated and paired. The main principle in the formation of a gamete is that from the four bit strings of matrix F a bit string is recombined. The result is vector G(M). There are all the bivalents with their four chromatids in matrix F. The task is to sample one from the four alleles of every locus.

If there is no crossing over, one can proceed in the Mendelian way (recombination only between chromosomes). If there is crossing over, the situation is more complicated (recombination both between and within chromosomes). The subprogram GAMETE produces a gamete by copying a part of matrix F into vector G. GAMETE, which handles matrix F as successive bivalents, contains four subprograms:

1) POISSO: generates a Poisson-distributed random number (P) with parameter a_i (i=1,...,K). P represents the number of chiasmata (crossing-over points) in the i^{th} bivalent. The value of parameter a_i is directly proportional to the length of the i^{th} bivalent (1.2.3).
2) KIASMA: generates mutually exclusive locations of the P chiasmata along the bivalent. These locations are drawn at random from the set of odd-numbered integers between 1,...,Z (the same Z as in 1.2.3) and are stored in a vector so that they can be compared with the locus points in the crossing-over process.
3) CROSSO: copies from matrix F a bit string representing one chromatid into vector G. First, CROSSO draws at random those two chromatids between which the chiasma is formed at each location of crossing-over, separately and independently for each of the P locations. Thus, there is no chromatidal interference. The chiasmata occur between non-sister chromatids only. Second, CROSSO draws at random a chromatid (1-4) and begins to copy it. If a chiasma is encountered CROSSO skips to another chromatid and continues copying.
4) MENDEL: copies from matrix F into vector G always an intact chromatid which is drawn at random (1-4) from the bivalent. MENDEL is used only if no chiasmata have been formed or if the formed chiasmata have no recombinational effect.

Thus, for every bivalent, GAMETE uses either CROSSO or MENDEL (Fig. 1). The latter route is faster because there is no need to make comparisons between the points of loci and chiasmata. After GAMETE has been performed, there is a haploid genome in vector G, containing one intact or recombinant chromatid from each chromosome pair. The genotypic structure of a new individual consists of two gametes, generated from a female and from a male.

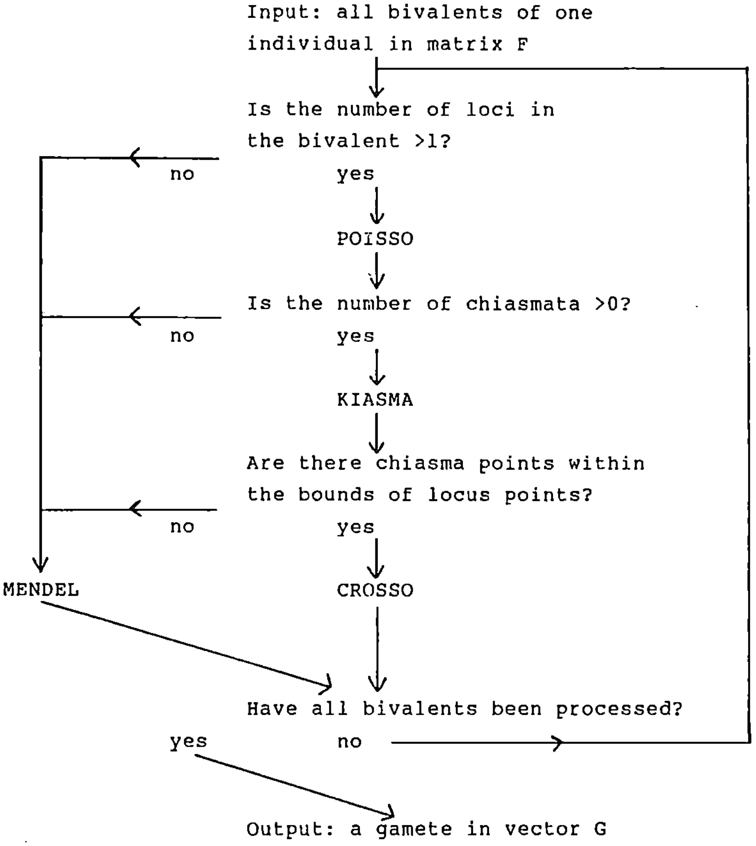

Fig. 1

The operation of subprogram GAMETE with its subprograms (POISSO, KIASMA, CROSSO, MENDEL).

1.3. Forming of the phenotypic value

The values of the three possible genotypes (A_1A_1, A_1A_2 and A_2A_2) at each locus were determined on the basis of the values of initial parameters (heritability (h^2), phenotypic variance (V_P), frequencies of A_1 at loci (p)). If L equivalent loci with equal degrees of dominance (d) are assumed to control the genetic variation of the character and there is initially Hardy-Weinberg equilibrium at every locus, without interactions the additive genetic variance (V_A) and the dominance variance (V_D) are:

$V_A = 2p(1-p)(a+ad(1-2p))^2\ L$ and

$V_D = (2p(1-p)ad)^2\ L$,

where a is the value of A_1A_1 (e.g., Falconer 1981). The values of A_2A_2 and A_1A_2 are -a and ad, respectively. Without epistasis V_A+V_D is the total genotypic variance. Because $V_A=h^2V_P$,

$$a = \left(\frac{h^2V_P}{2p(1-p)(1+d(1-2p))^2\ L} \right)^{1/2}$$

When determining the genotypic value of an individual, the states of all the L loci are examined and the values of individual loci are summed up. The result is the total genotypic value (G_T).

The forming of the phenotype (P) can be described as $P = G_T+E$, where E is the influence of environment on phenotype (environmental deviation). In the present study E was independent of G_T and was sampled from the normal distribution with an expectation of 0 and variance V_E. V_E was calculated from initial variances, i.e. $V_E = V_P-V_A-V_D$, and was kept constant.

2. Markov chain model

The method of successive multiplication of transition probability matrices for calculating genetic changes at one diallelic locus in a finite population was described in IV.

3. Deterministic models

Some methods of calculation which assume an infinite population were used to clarify theoretical courses of selection in gene frequency at one diallelic locus. These methods involved both simple models for gene frequency change (described in III and IV) and a more complicated mating-type model (described in V).

Results and discussion

I: simulation, 108 loci, population size 1400, initial heritability 0.25, initial phenotypic variance 49.0, initial frequency of the favourable allele 0.5.

In I various systems of inbreeding with alternating full-sib mating periods of three generations and random-mating periods of six generations were compared with random mating in all generations. There was between-family selection in inbreeding generations.

For the selection intensity S_a ((10♂+100♀)/1400), all the inbreeding systems resulted in a better response to 30 generations of selection than the random-mating system, when the degree of dominance (d) was 0.20. For the selection intensity S_b ((5♂+50♀)/1400), the result was almost the reverse. In general, the responses obtained by S_a were larger than those obtained by S_b. In S_a the highest response was attained when the first phase of inbreeding occurred in generations 7-9. To begin inbreeding earlier or later than this was less advantageous. The method with the first phase of inbreeding in generations 7-9 was also studied for degrees of dominance of 0.05 and 0.50 in S_a. For d=0.05, the response was about the same as that without inbreeding. For d=0.50, the response with inbreeding was about 20 % greater than that without inbreeding.

II: simulation, 32 loci, population size 1500, initial heritability 0.075 or 0.250, initial phenotypic variance 49.0, initial frequency of the favourable allele 0.5.

In II the alternating mating structure was the same as in I, except that the random-mating periods lasted either three or six generations.

For the selection intensity S_c ((100♂+100♀)/1500), the unfavourable allele A_2 was fixed at only a few loci until the 30th generation. In the inbreeding systems the fixation of the favourable allele A_1 was faster than that in random mating. For the selection intensity S_d ((50♂+50♀)/1500), this difference was small, and the use of inbreeding clearly accelerated the fixation of A_2.

For S_d with inbreeding the final response to selection in the 30th generation was 3-5 % lower than that for S_d without inbreeding. There was no advantage of inbreeding at any stage. For S_c the final responses in the systems with inbreeding were only marginally larger than those without inbreeding, when the initial heritability (h^2) was 0.250. There was no clear advantage from inbreeding at the earlier stages of the selection process either. When h^2 was 0.075, however, the final responses to selection in the inbreeding systems were 4-8 % higher than those in random mating.

In general, a larger final response was attained for S_c than for S_d. There was a much higher variability in the final response for S_d than for S_c. For S_d this variability was remarkably larger in the systems with inbreeding than in random mating. For S_c there were no corresponding differences in the variability of the final response.

On the basis of the simulation method and assuming random mating with no selection, for a breeding group of 10♂+100♀ an effective population size (N_e) of 33.6 was calculated (II). With these assumptions N_e for 100♂+100♀ is 133.8. For h^2=0.250 in the case of 108 loci (I), the standardized effect of each locus (Falconer 1981) is about 0.136, whereas, for h^2=0.075 in the case of 32 loci (II), the standardized effect is about 0.137. These nearly equal standardized effects increase the validity of comparison of the results, which is not perfect due to the differences in the selection intensity and in N_e. For a degree of dominance of 0.5, the extra genetic gain due to inbreeding periods was about 5 % (II), whereas in the earlier study it was about 20 % (I). The main reason for this difference is probably that in II the parental group was 100♂+100♀ in every generation. In I the parental group was of this size in the inbreeding generations only; in other generations it was 10♂+100♀ . Thus, with regard to N_e the system without inbreeding was in a worse position than the inbreeding system in I than in II. In addition, there were only 6 replicate runs in I compared with 25 in II, which may be an important reason for the difference (sampling effects).

The inbreeding depression in the character selected for, but also the advantage of inbreeding periods in the response, were larger for a parental group of 100♂+100♀ than of 50♂+50♀ (II). This probably occurred because in the inbreeding generations the variance of gene frequency (V_b) between the full-sib families of the selected group is larger for a less intense selection pressure than for a stronger one. In the case of 100 full-sib families, the average number of selected families is 13.3, whereas in the case of 50 full-sib families on an average only 3.3 families are selected. It is quite natural that V_b is larger in the former case. Of course, there will be no difference between full-sib mating and random mating with regard to genotype frequencies in the progeny population if there is no variation in gene frequency among the full-sib families of the parental group. Evidently, for a breeding structure of 50♂+50♀, V_b did not become large enough to make selection with inbreeding more effective than that with random mating (II).

For a population in which there is a departure from the random-mating proportions of genotypes due to inbreeding and the number of gametes contributed per parent to the breeding group of the next generation does not follow a binomial distribution, the variance effective size (N_e) can be smaller than for a population with random-mating proportions (Crow and Kimura 1970). As a result of a reduction in N_e, the expected ultimate selection response diminishes and its variability increases (e.g., Robertson 1960, 1970b; Nicholas 1980). When comparing the selection responses obtained by inbreeding with those obtained by random mating, these effects of finite size were clearly seen when the number selected was 50♂+50♀ (II). On the other hand, when the number selected was 100♂+100♀, inbreeding did not increase either the rate of fixation of the unfavourable allele A_2 or the variability of the response very much, so there is not inevitably a larger variability associated with the larger response obtained by inbreeding.

On the basis of the methods and values used in I and II, the advantage of inbreeding in the genetic progress in comparison with random mating seems to depend on the number of families selected to inbreed and on the effects of loci. For loci with large standardized effects, the advantage of inbreeding is small, although there would be a lot of families and a high degree of dominance. Dickerson and Lindhé (1977) pointed out that the extra genetic gain attainable with cyclical inbreeding and between-family selection compared with random mating might be largest when the character has low heritability and the phenotypic correlation between family members is low. Deductions of this kind had been made already by Lush (1945), and the results of I and II support them.

In a breeding programme of only a few generations the expected response is maximized by selecting quite intensely, the optimum proportion selected depending on the number of generations and on the size of the population (Robertson 1970b). Because there seems to be some advantage of inbreeding in the selection response only if the proportion selected is not very small (I and II), any kind of extra genetic gain in comparison with random mating cannot be attainable in a short-term programme. For instance, suppose that until generation t the expected response in breeding with random mating is maximized by selecting N_f females + N_m males from M_f females and M_m males in each generation (if $N_f+N_m=N$ and $M_f+M_m=M$, for individual selection there must be $N_f=N_m=N/2$ and $M_f=M_m=M/2$ (Jódar and Lopéz-Fanjul 1977)). If there is some advantage of inbreeding only if N/M is not small, a sensible value for t inevitably is relatively large.

In I and II there was combined selection among females in random-mating generations. Robertson (1960) showed that it is best to use phenotypic selection alone if the aim is to maximize the expected long-term genetic progress. To maximize the expected limit of response, half the population should be selected (Dempster 1955; Robertson 1960; Jódar and López-Fanjul 1977). In a simulation study using the present model, combined and phenotypic selection were compared (Sirkkomaa and Lindström 1981). In certain cases the responses in phenotypic selection were larger than those in combined selection, even in a programme of only 20 generations for a low-heritability character.

III: simulation, 32 loci, population size 400, initial heritability 0.075 or 0.250, initial phenotypic variance 49.0, initial frequency of the favourable allele 0.5;

two deterministic models, one locus, initial frequency of the favourable allele 0.5.

In III there was random mating in all generations or random mating and full-sib mating in alternate generations among the selected individuals. In simulation females were selected by using phenotypic values. The males chosen to breed were full-brothers of the selected females. In simulation 100 females and 100 males were selected in each generation.

The response in gene frequency for the deterministic models was more rapid than that for simulation. The deviations from the results of simulation were lowest in the random-mating system. For the deterministic models the time saved due to inbreeding compared with random mating in reaching a given proportion of the maximum response (50, 75 and 90 %) was about 20-40 %, increasing with the degree of dominance and with the proportion of the maximum response. For simulation with approximately the same selection pressures as in deterministic calculation, the corresponding time saved was about 10-20 %. The advantage of inbreeding in the rate of response was somewhat larger for weak selection than for stronger.

IV: simulation, 32 loci, population size 400 or 60, initial heritability 0.075 or 0.250, initial phenotypic variance 49.0, initial frequency of the favourable allele 0.25, 0.50 or 0.75;

deterministic model, one locus, initial frequency of the favourable allele 0.5;

Markov chain model, one locus, initial frequency of the favourable allele 0.5.

In IV the selection and mating systems were the same as in III. In simulation the replicate runs were continued up to fixation at all loci.

For initial frequencies (p) of 0.50 and 0.75 of the favourable allele A_1, there was no fixation of the unfavourable allele A_2 at any locus in simulation, and the maximum response (all loci fixed for A_1) was attained in all cases. For p=0.25, allele A_2 was fixed at some loci. The differences in U (proportion of loci fixed for A_2) between inbreeding and random mating were small, yet for a degree of dominance (d) of 0.2, U was somewhat higher with inbreeding. The differences in U between the two systems decreased with an increasing d, which is understandable because the rate of response in an inbred population relative to that in a random-bred population increases with d (e.g., III). However, there should be an increase in the expected rate of response due to inbreeding for any value of d used. Therefore, there has been a decrease in the variance effective size (N_e) due to inbreeding. If p is low, the larger rate of response per generation with inbreeding cannot compensate for the decrease in N_e, especially at low values of d. As a result, there will be a decrease in the probability of fixation of allele A_1.

The time saved (D) due to inbreeding until fixation at all loci was 12-43 %, depending mainly on d. In general, D for d=0.8 was much larger than D for d=0.2. In most cases the coefficient of variation of the number of generations until fixation at all loci was smaller with inbreeding than with random mating. In general, for the parameter combinations studied in a fairly large population (proportion selected (100♀ +100♂)/400) both systems of breeding resulted in the same ultimate response to selection. The use of full-sib matings remarkably accelerated fixation: the time saved in comparison with random mating was 21-43 % for d=0.8.

The case of initial gene frequencies of 0.5 at each locus was also studied by selecting 15♀ +15♂ from a population of 60 individuals, because there was no fixation of A_2 for a proportion selected of (100♀ +100♂)/400. For an initial heritability (h^2) of 0.075 with d=0.8, the final response with inbreeding was 8.4 % larger and was reached 10.8 % faster than with random mating.

For p=0.5, the deterministic change in gene frequency was calculated up to a frequency of 0.975. In early generations the rate of response using calculation was higher than that using simulation. At later stages the situation was reversed, and, for d=0.8, the goal in gene frequency was attained remarkably earlier in simulation. To study these differences between the simulated and calculated results, the rate of response per generation in the mean gene frequency at several loci was compared with that in gene frequency at one locus. In these calculations the effects of finite population size were not taken into consideration, albeit they are an important reason for the discrepancies between the simulated and calculated results. For d=0.8, the rate of response calculated with 32 loci exceeded that with one locus at a lower level of gene frequency than for smaller degrees of dominance. This accords with the result that the given frequency of allele A_1 (0.975) was attained for d=0.8 earlier in simulation with 32 loci than in deterministic calculation with one locus.

In simulation the time saved due to inbreeding in attaining a given response was somewhat higher for $h^2=0.075$ than for $h^2=0.250$. This accords with the result that the use of full-sib mating in alternate generations should save more time in weak selection than in stronger (III).

A simulation experiment was also performed to study the decrease in N_e due to inbreeding in the present mating system. For a population structure of (10♀ +10♂)/60 without the phenotypic selection of females, the mean time until the fixation of either one of the two alleles at all 32 loci (initial gene frequencies 0.5) with inbreeding was about 90 % of that with random mating. Thus, the representative variance effective size in the alternating mating system would be roughly 90 % of N_e in random mating if the time until fixation is linearly dependent on N_e, as it is in the case of one locus (Kimura and Ohta 1969).

In the Markov chain calculation on the change of gene frequency for a breeding group of 10♀ +10♂ , the probability of fixation of A_1 was clearly smaller with inbreeding than with random mating when the decrease in N_e due to inbreeding was assumed to be 20 %. This result shows that for small numbers the advantage of inbreeding in the ultimate response is very sensitive to a possible decrease in N_e. However, for a decrease of 10 % in N_e, the response with inbreeding was somewhat higher than that with random mating, and fixation was reached 12.3-17.6 % faster.

The Markov chain method was also used to evaluate the optimum number selected for maximizing the expected response to 30 generations of selection in a finite population (Table 1) (not included in IV).

Table 1. The optimum number selected (females+males, equal numbers of both sexes) for maximizing the expected response to 30 generations of selection with random mating. The size of the unselected female population is 100. There is full-sib selection of males.
p: initial frequency of the favourable allele
stef: standardized effect of the locus

		Degree of dominance			
p	stef	0.0	0.2	0.5	0.8
0.25	0.05	24	24	26	26
	0.10	24	24	22	22
	0.15	22	22	20	18
0.50	0.05	22	22	20	20
	0.10	20	20	18	16
	0.15	18	18	14	12
0.75	0.05	22	20	18	14
	0.10	18	18	14	12
	0.15	16	14	12	10

Table 2. The expected response in gene frequency (R), the coefficient of variation of the response (CV) and the increase in R due to inbreeding (I) in 10 generations of selection for the optimum numbers selected (Table 1).

A: random mating in all generations

B: random mating and full-sib mating in alternate generations

			Degree of dominance											
			0.0			0.2			0.5			0.8		
p	stef		R	CV	I(%)	R	CV	I(%)	R	CV	I(%)	R	CV	I(%)
0.25	0.05	B	.180	1.95	17.3	.187	1.86	15.8	.197	1.68	13.8	.208	1.57	12.2
		A	.153	2.26		.162	2.13		.173	1.89		.185	1.75	
	0.10	B	.395	0.86	15.7	.405	0.81	14.4	.417	0.77	12.8	.426	0.72	11.6
		A	.342	1.02		.354	0.95		.370	0.90		.382	0.82	
	0.15	B	.583	0.45	11.3	.588	0.42	10.4	.591	0.41	9.5	.589	0.41	9.1
		A	.524	0.57		.533	0.53		.539	0.50		.540	0.49	
0.50	0.05	B	.198	1.60	14.5	.196	1.60	14.6	.193	1.66	14.9	.190	1.67	15.1
		A	.173	1.88		.171	1.88		.168	1.95		.165	1.96	
	0.10	B	.358	0.66	10.7	.353	0.66	11.1	.344	0.70	11.8	.335	0.75	12.4
		A	.324	0.81		.317	0.81		.308	0.86		.298	0.92	
	0.15	B	.451	0.30	6.2	.444	0.31	6.8	.434	0.38	7.8	.423	0.44	8.8
		A	.424	0.41		.416	0.42		.403	0.50		.389	0.57	
0.75	0.05	B	.126	1.73	12.3	.121	1.89	13.9	.113	2.14	16.5	.105	2.56	18.8
		A	.112	2.05		.106	2.28		.097	2.62		.088	3.19	
	0.10	B	.201	0.70	8.0	.195	0.75	9.4	.185	0.94	11.8	.175	1.11	14.1
		A	.186	0.87		.178	0.95		.165	1.20		.153	1.44	
	0.15	B	.235	0.31	4.1	.231	0.38	5.4	.223	0.48	7.4	.215	0.62	9.6
		A	.226	0.43		.219	0.52		.208	0.67		.196	0.84	

The responses corresponding to these optimum numbers selected were compared with the responses obtained by using the alternating mating system with the same numbers selected (Table 2). The advantage of inbreeding in the selection response was 4.1-18.8 %, being highest for small standardized effects (Table 2). For p=0.50, the advantage of inbreeding was only weakly dependent on the degree of dominance. It has to be pointed out that in these calculations the effective population sizes were assumed to be identical for both systems of mating. Moreover, despite the small numbers of parents and selection, the departures from Hardy-Weinberg proportions in random-bred and inbred generations were assumed to be exactly 0 and 1/4, respectively. Because the same intensities of selection were used for both mating systems, the calculated increases in response due to inbreeding must be close to the maximum values attainable in the breeding plans in question.

In the selection experiment of MacNeil et al. (1984a,b) with Japanese quail, there was no advantage of the alternating mating system in the total response to selection of 16 generations for a biomass index. This is understandable, because there were severe effects of inbreeding on fertility and viability, and the selection differentials in the inbreeding system were significantly lower than those in the random-mating system. In the present study it was supposed that a population can be purified of some detrimental genes in the course of time. MacNeil et al. (1984a,b) found that the rate of response in later generations in the alternating system became higher than that in the random-mating system, due to adaptation to inbreeding.

Dion and Minvielle (1985) selected for pupa weight in Tribolium. There was no significant difference between the random-mating and alternating systems in the response to selection of 15 generations, despite the fact that the average selection differential over generations was slightly larger with inbreeding. Unfortunately, the populations were small (15 pairs of parents selected from 55-70 individuals), and there were only two replicates for both systems of mating. There were no detrimental effects of full-sib mating on reproductive performance. The authors believed that gene frequencies in the base population were close to 0.5. In the present simulation experiment with a similar proportion selected and certainly without any problems in regard to fertility and viability, the response of 15 generations in the alternating system was only 3.4 % higher than that in the random-mating system (population size = 400, d=0.2, p=0.5, h^2=0.25). In spite of differences in the methods of selection and mating, on this basis the results obtained by Dion and Minvielle (1985) are not very surprising.

V: deterministic model, one locus, various combinations of the initial frequency of allele A_1 (p), degree of dominance (d) and selection coefficient among females (s).

In V there was random mating in all generations or random mating and full-sib mating in alternate generations among the selected individuals. The breeding males were full-brothers of the selected females.

The responses to selection of 20, 50 and 100 generations were calculated for both systems of mating. In general, for weak selection (s=0.01) at an additive locus (d=0.0), the increase in response due to inbreeding (I) was 23-31 %. For s=0.01 at a locus with complete dominance (d=1.0), the results were much more variable, the increases in response being 14-18 %, 25-27 % and 68-71 % for initial frequencies of 0.2, 0.5 and 0.8, respectively. However, for p=0.5 in weak selection I was 24-27 %, fairly independently of d and of the number of generations in the breeding programme. The value of I increased with d, apart from weaker selection pressures (s=0.01,0.10,0.20) for p=0.2, especially in the short term.

The numbers of generations required for the inbreeding system to attain the responses reached by the random-mating system in 20, 50 and 100 generations were also determined. For d=0.0, the results were very uniform for all the initial frequencies and the coefficients of selection, the decrease in time due to inbreeding (D) being 15-21 %. In addition, for p=0.5 in weak selection (s=0.01) D was independent of d, being 15 % in the short term (20 generations) and 21-23 % in the long term (100 generations). In weak selection at a locus with d=1.0, for initial frequencies of 0.2 and 0.8, the decreases in time were 10-13 % and 35-44 %, respectively. In general, D increased with the number of generations in the breeding programme, with d and with s. In a programme of 100 generations, for the strongest selection pressure (s=0.8) at a locus with d=1.0 the values of D were 71 %, 73 % and 77 % for initial frequencies of 0.2, 0.5 and 0.8, respectively.

In real populations, s might not be the same for the two systems of breeding. For instance, MacNeil et al. (1984a,b) found in Japanese quail that the average selection differential (SD) for a biomass index in the alternating system was smaller than that in the random-mating system. As a result, s would diminish because of the dependence on SD. For a small standardized effect of a locus, s is even a linear function of SD (Haldane 1931; Kimura and Crow 1978; Falconer 1981) if the character in question is normally distributed. On the other hand, in any breeding programme there is no constant s at a locus because the gene frequency changes at all of the loci affect the variability of the quantitative character selected for. In the present calculations it was simply supposed that s in the alternating system is smaller than s in the random-mating system, due to various effects of inbreeding on fertility and viability. A constant decrease in s with respect to generations was assumed, although it is probable that the difference in s between the two systems of breeding will diminish in the course of generations as the population practicing inbreeding is purified of many harmful recessive genes. This kind of change was observed by MacNeil et al. (1984a,b).

On the basis presented above, ML was evaluated for a comparison between the two systems of mating (ML = the maximum loss of s for which the response in the alternating system is still at least equal to that in the random-mating system). The results for an additive locus were fairly independent of the number of generations and of p. In weak selection (s=0.01), ML was 19-21 %, whereas for s=0.8 ML was 14-18 %. For medium coefficients of selection (s=0.1,0.2,0.5) at an additive locus ML was 16-20 %. Thus, for an additive locus we could expect some advantage of the alternating system, if the loss in SD due to inbreeding remains clearly below 20 % and selection is not very strong. In strong selection the bearable loss in SD is below 15 %.

With increasing degrees of dominance the results were more variable, and, in the case of complete dominance, much larger values of ML were obtained for p=0.8 than for p=0.2. In general, ML increased with d (except in weak selection for p=0.2) and with the number of generations. ML also increased with s, apart from degrees of dominance of 0.0 and 0.25. For strong selection at a locus with complete dominance, losses of 70-80 % in s might be bearable in a long-term programme.

In the selection experiment of 16 generations by MacNeil et al. (1984a,b), the average SD over generations in the alternating system was 18.4 % lower than that in the random-mating system, and there was no advantage of inbreeding in the total response to selection. This result accords with the present calculations, unless a high average degree of dominance over loci is assumed.

General conclusions

In addition to the dependence on the genotypic effects at loci, the possibilities of the use of intentional inbreeding to enhance the response to selection are dependent on the changes in effective population size and in selection intensity. Fluctuations may occur in the total population size and in the size of the breeding group (N) due to the harmful effects of inbreeding on fertility and viability. In addition, even if N remained constant, there might be a considerable increase in the variance of the number of gametes (v) contributed per parent to the breeding group of the next generation. In these cases inbreeding would lessen the variance effective size (N_e), and there would be an increase in the variance of gene frequency change.

In an inbreeding system (IS), v might be considerably larger than v in the random-mating system. For instance, in the inbred generations of some IS, there may be an increase in v if the expected number of gametes to the breeding group of the next generation is not the same for each parent. In the random-bred generations of the IS, viability disturbances are probably produced for the next generation if there is inbreeding in the selected group. The magnitudes of the disturbances in fertility and viability are not predictable in detail because they depend heavily on the genetic composition of the base population and on the dominance relations at loci. In a small population a decrease in N_e has catastrophic consequences for the long-term response to selection. On the other hand, in a large population with a large number selected, a decrease in N_e is perhaps not very serious if the reduced value of N_e still is high.

The best prospects for the successful use of inbreeding in selection are in a large population with a relatively high proportion selected. It is evident that the main problem in using inbreeding is the dependence of the selection intensity on the degree of inbreeding in most populations. There is not much use for the increased genetic variance created by inbreeding if the group chosen as parents does not sufficiently differ from the population mean with respect to the character selected for. The problem with the intensity of selection concerns both small and large populations.

The relevant problems with the use of inbreeding are summarized in Fig. 2. In addition, there are the probable economic losses which would be encountered by an animal breeder using an inbreeding system, due to depression in production traits. In practical animal breeding the long-term goal alone is not most important, but rather the economic gains in every generation or over some other period of time.

The results of the present study are not directly applicable to the breeding of any domestic species. First, in breeding planning it is not common to take into account the long-term response to selection. Second, if both sexes are selected on the basis of phenotype, the advantage of inbreeding in the response will be less than in the system of the present study. Third, the total economic benefit from an inbreeding programme is question-

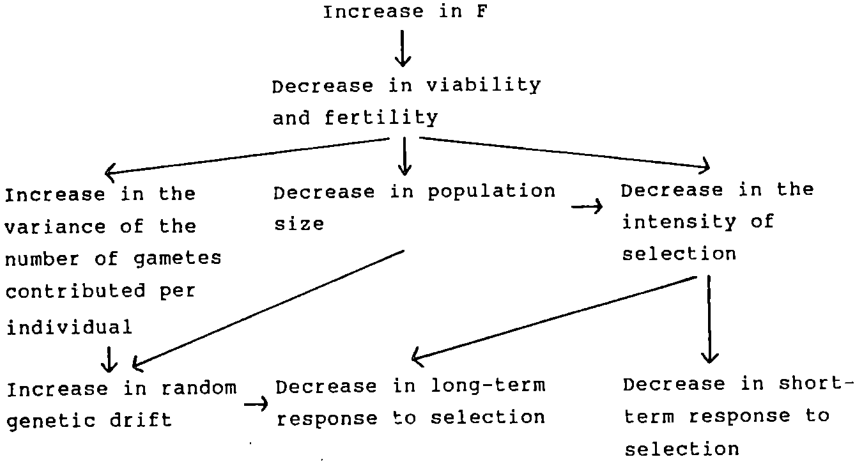

Fig. 2

The problems associated with an increase in F (degree of inbreeding).

able, in spite of the possible increase in the response. Nevertheless, the pronounced effect of inbreeding on increase and redistribution of variance presents a challenge to animal breeders to develope methods for its utilization (Pirchner 1985).

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A simulation study on intensive selection and inbreeding in laying hens

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The effects of temporary inbreeding and between-line selection phases on genetic advances for poultry egg mass production were studied by computer simulation. In the case of many full-sib lines, a better selection response was attained in a periodically subline-divided population than in one large population, provided that there was a reasonable degree of dominance at the loci influencing on the selected trait.

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In animal breeding research, one aim is to find a mating and selection system that will maximize the genetic progress. The approximate mathematical method created by ROBERTSON (1960) is based on the theory of fixation of mutant genes in a finite population (KIMURA 1957). Because of the complexity of the problem, many computer simulations have been made to solve various situations in quantitative population genetics since the work of FRASER (1957a, b).

One possible breeding system is to divide the population into sublines and try to use the variation which will be generated between the lines. The advantage with regard to genetic progress is questionable in a trait without dominance variation (MADALENA and HILL 1972). For poultry breeding, it has been suggested (e.g. WARREN 1950; DICKERSON 1973; ABPLANALP 1974) that it would be best for genetic progress in egg production traits to alternate full-sib mating periods (2–3 generations, with strong between-line selection) and selection periods without intentional inbreeding. Due to very many crossing and inbreeding experiments it is a well-known fact that there is dominance variation in egg number and in other egg production traits (e.g. egg mass production).

The present study is an attempt to clarify the genetic gain in poultry egg mass selection. The special object of this simulation experiment is to study the effect of temporary inbreeding and between-line selection phases on genetic advance.

Methods

A Fortran program was written to simulate the desired processes of artificial selection in a diploid Mendelian population. Pseudo-random numbers were generated by using a linear congruential method appropriate to the length of memory word of UNIVAC 1108. Two gene alternatives were simulated for each locus by using the bit structure of computer storage. The influences of the three possible genotypes at loci were calculated on the basis of certain initial parameters (heritability, phenotypic standard deviation, gene frequency, degree of dominance and number of loci) so that the effects of the loci are equal. The number of loci was set to be 108 rather arbitrarily. The haploid number of chromosomes was 39, which is nowadays the generally accepted number for *Gallus domesticus* (e.g. POLLOCK and FECHHEIMER 1976).

The following random processes are operating in simulation:

1. Forming of the structure of the genome. This is performed at the beginning of each replicate, and it includes the generation of the genetically active lengths of chromosomes, distribution of loci among chromosomes and scattering of loci to places in chromosomes. Because of the peculiar structure of the genome of *Gallus domesticus* (macrochromosomes and microchromosomes), a special procedure is made in the generation of chromosomal lengths. Due to this procedure about 70 % of the loci will fall into 9 chromosomes. This

distribution is in agreement with the observations of Shoffner and Krishan (1965) on the relative lengths of the bivalents of *Gallus domesticus*. In general, however, linkage has only a small effect on genetic advance in the case of many chromosomes (Robertson 1970).

2. At the beginning of each replicate (in generation zero) the loci are filled with the two gene alternatives according to the initial frequency (0.5) so that the expected state of every locus is the Hardy-Weinberg equilibrium. In addition the loci are filled independently of each other. The validity of these assumptions is of course not completely clear, but we can expect to get some kind of general understanding of the situation.

3. Generation of gametes, which includes the imitation of the Mendelian mechanisms and the forming of chiasmata. The number of chiasmata is a Poisson-distributed variate; the expected value is 3 for the longest bivalent. The crossing-over processes are, however, not described in detail because the role of linkage is not important with regard to the comparison of simulation results in this chromosomal situation, especially as a reasonable amount of crossing over is generated.

4. Mating is accomplished by sampling a mate from the selected male group for each selected female. Full-sib mating is avoided in the non-inbreeding generations. In the inbreeding generations each selected female is mated with a full-brother.

5. The relevant number of progeny (1400) is uniformly distributed among selected dams (d) so that the expected number of progeny per dam is 1400/d.

6. The sex of each individual is generated with equal probability for male and female.

7. A normally distributed deviate (mean 0, variance V_E) is added to the total genotypic value of each female for the creation of phenotype. V_E is the pertinent environmental variance calculated from known initial parameters.

The heritability of the selected trait (daily egg mass production) was estimated in every generation according to Becker (1967, p. 15–23). If the estimate of heritability was not between zero and one in some generation, then the last sensible estimate was used in the calculation of breeding values. In the non-inbred generations, the breeding value for each male was calculated on the basis of full-sib average and half-sib average; in the case of females, the phenotype was also taken into account. The weighting factors for combined selection presented by Osborne (1957a, b) were used. In the inbred generations, the breeding values were calculated only for the full-sib lines. In addition, the females were sorted inside the lines on the basis of phenotype.

The population size (1400) is typical of the Finnish breeding populations of poultry. Two strengths of intensive selection were used: (10♂ + 100 ♀)/1400 and (5♂ + 50 ♀)/1400. In the inbred phases these intensities correspond to selection among 100 or 50 full-sib lines so that the desired number of females is picked beginning with the best phenotype of the best line. Six systems of mating with alternating inbreeding and non-inbreeding phases were used (Table 1). In the generation zero, the females were selected according to phenotypes and mated with sampled males.

The selected trait was set to correspond to daily egg mass production according to the variation estimates obtained from the Finnish breeding populations of poultry. Thus, the initial narrow sense heritability was 0.25, phenotypic standard deviation 7 g. The initial mean, however, was not transformed to correspond to the real situation (about 40 g). Consequently, the initial mean is completely determined by the genotypic influences and Hardy-Weinberg state at loci.

Because of computing time, the number of replicate runs for each parameter combination was only 6, and in each run 30 generations were proceeded. The results are given only with regard to the replicate averages.

Results and discussion

In general, the less intensive selection S_a has led to a better genetic gain than the strong selection S_b (Table 2). This result is predictable on the basis of

Table 1. The mating systems (A–F)

	Avoidance of full-sib mating in generations	Full-sib mating in generations
A	1–29	
B	4–9, 13–18, 22–29	1–3, 10–12, 19–21
C	1–3, 7–12, 16–21, 25–29	4–6, 13–15, 22–24
D	1–6, 10–15, 19–24, 28–29	7–9, 16–18, 25–27
E	1–9, 13–18, 22–29	10–12, 19–21
F	1–12, 16–21, 25–29	13–15, 22–24

Table 2. Population mean ± standard error of the mean in the 30th generation (A–F are the mating systems, Table 1). The degree of dominance is 0.2. The initial population mean was 5.2

	Proportion selected	
	(10♂ + 100 ♀)/1400 S_a	(5♂ + 50 ♀)/1400 S_b
A	29.5 ± 1.0	30.3 ± 1.0
B	31.8 ± 1.3	25.1 ± 1.1
C	31.2 ± 0.6	28.1 ± 0.7
D	34.7 ± 1.5	28.5 ± 1.2
E	31.7 ± 0.8	31.4 ± 1.2
F	31.9 ± 1.3	28.3 ± 1.7

the theories of Kimura (1957) and Robertson (1960). By using strong selection the effective population size is smaller than for a less intensive selection, so the strong selection cannot compensate the random fixation of undesirable alleles at loci.

The standard errors of the obtained population means at the 30th generation are 0.6–1.7 (Table 2), for which reason it is not possible to draw very sure conclusions from the comparison of the mating systems. In any case, it is noteworthy that for the selection intensity S_a all of the runs with inbreeding (B–F) have produced a better response than the non-inbreeding run (A). For the selection intensity S_b the situation is almost reverse. In Fig. 1 the comparison is presented with regard to the whole breeding process. Evidently, it is disadvantageous to start the first phase of inbreeding too early (B–C, Fig. 1a) or to retard it too long (E–F, Fig. 1a). In the case of the selection intensity S_b, the result is not so clear. It is noticeable, however, that the very early use of inbreeding (B, Fig. 1b) has caused a breakdown for the genetic advance.

Because of the remarkable difference between the mating systems A and D for the less intensive selection (Fig. 1a), the runs were also performed at two other degrees of dominance. When the degree of dominance is 0.05, the difference between A and D is very small (Fig. 2). The difference is clear, however, when there is a larger degree of dominance (0.50, Fig. 2). One can easily identify the phases of inbreeding depression (generations 8–10, 17–19, 26–28) and the phases of heterosis (generations 11, 20, 29) on the curve D. The better selection response in a subline-divided population than in one large population is in agreement with the results of Madalena and Hill (1972).

The results of the present study give support to some early ideas (e.g. Wilson 1948; Warren 1950) on the use of inbreeding in poultry selection. Be-

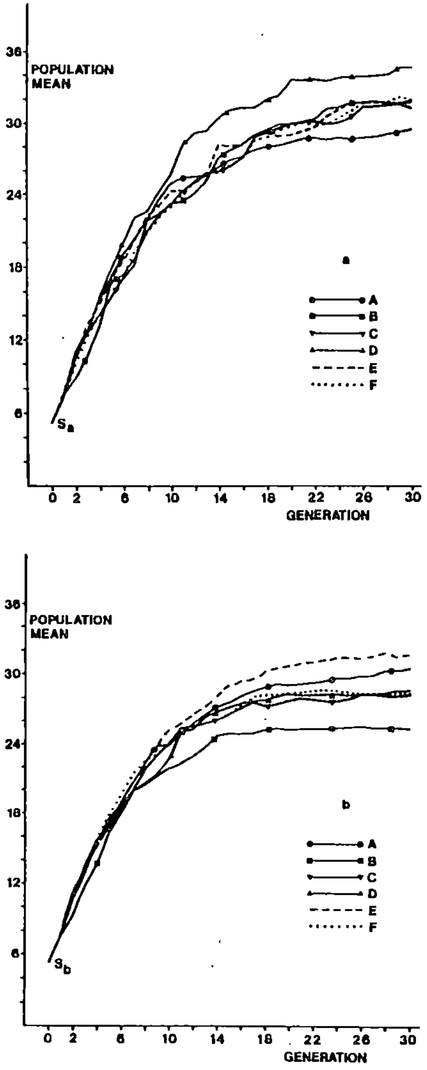

Fig. 1a–b. Progress in the selected trait. A–F are mating systems (Table 1). The degree of dominance is 0.20.

S_a: proportion selected (10♂ + 100 ♀)/1400
S_b: proportion selected (5♂ + 50 ♀)/1400

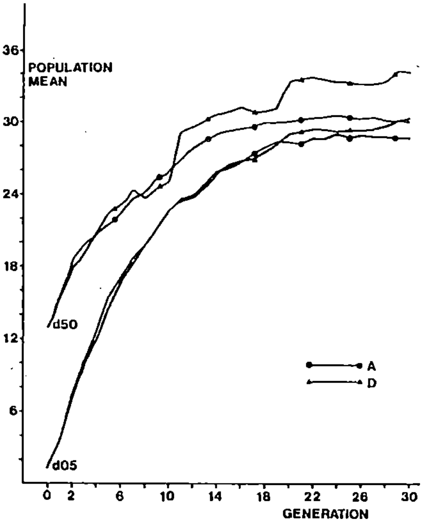

Fig. 2. Progress in the selected trait. A and D are mating systems (Table 1). The proportion selected is (10♂+100 ♀)/1400.

d05: degree of dominance 0.05
d50: degree of dominance 0.50

fore the first inbreeding phase one has to select a good genetic material, and one has to develop many lines during inbreeding for a successful between-line selection. By proceeding so, it is possible to attain more genetic gain in a periodically subdivided population than in one large population. One serious problem is the decreasing fertility during inbreeding periods. As a result the selection intensity will go down, so in reality it is perhaps not possible to use the inbreeding method very successfully.

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II

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Effects of inbreeding on the response to selection in a simulated population

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Simulation experiments were performed to clarify the effect of cyclical full-sib mating on the response to selection for a low-heritability character ($h^2 = 0.075$ o 0.250) without male phenotypes. There were 32 two-allelic loci affecting the trait, partial dominance over the unfavourable allele at each locus, but no epistasis. In the initial population linkage equilibrium and Hardy-Weinberg genotype frequencies with a gene frequency 0.5 at each locus were generated.

The population size was 1500, and in each of the 30 generations 50♂ + 50♀ or 100♂ + 100♀ were selected. In the inbreeding periods (3 generations) selection between full-sib families was employed, whereas in other periods (3 or 6 generations) there was combined selection.

For the selected number 50♂ + 50♀ there was no short-term advantage to progress from inbreeding and a loss of 3–5 % in the cumulative response relative to the response with avoidance of full-sib mating. The variation of the final response was larger for selection with inbreeding than for that without inbreeding. For the selected number 100♂ + 100 ♀ there was some short-term advantage from inbreeding and an extra gain of 4–8 % in the final response when h^2 was 0.075, but only a marginal advantage when h^2 was 0.25. The variation of response for selection with inbreeding was about the same as for that without inbreeding. It was concluded that the appearance of genetic defects and the decline in fertility might render the selection with inbreeding an unattractive proposal.

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The use of inbreeding in improving the cumulative response to selection is a problem receiving continued interest (e.g., LUSH 1945; DICKERSON 1973; DICKERSON and LINDHÉ 1977). On the basis of the selection theory it is clear that the expected response per generation (M) is larger in populations with inbreeding than in panmictic populations (WRIGHT 1942). However, if there is a departure from the random-mating frequencies of genotypes among the parents the effective population size is smaller than that in panmictic populations with the same number of parents (CROW and KIMURA 1970). Accordingly, there is an increase in the variance of the response per generation (V) and the cumulative response after several generations can be smaller than that obtained by random mating among the selected individuals in each generation.

The process of genetic progress with inbreeding in some generations is not time-homogeneous because both M and V depend on the time parameter in addition to the dependence on the gene frequencies (CROW and KIMURA 1970). Thus, there are difficulties in studying the process by the Kolmogorov equations. Moreover, due to the complications caused by dominance, linkage and other factors the precise analytical treatment is extremely difficult.

In developing inbred lines for crossing, three generations of full-sib mating and strong selection between lines have been proposed as an appropriate method for poultry (e.g., WARREN 1950; ABPLANALP 1974). DICKERSON (1973) suggested recurrent cycles of inbreeding, between-line selection and combining the best lines for enhancing the genetic progress in egg production traits.

In a previous simulation study intended to clarify the usefulness of temporary inbreeding and between-line selection cycles in improving poultry egg mass production, a better response after 30 generations was attained in a population with periodic full-sib mating and selection between many full-sib families than in a population without intentional inbreeding (SIRKKOMAA and MAIJALA 1980). There were 108 loci with two alleles influencing on the selected trait and some dominance over the unfavourable allele at each locus. However, the number of the selected males was smaller in the generations without inbreeding than in the generations with full-sib mating. Consequently, the comparison of the mating structures with regard to the cumulative response was not quite unbiased. In addition, there was a need to study the process with a smaller number of loci and with a larger number of replicate runs. The purpose of the present study is not to find the best mating and selection method for the long-term progress, but to elucidate the effect of temporary inbreeding phases on the genetic gain in selecting for a low-heritability trait without male phenotypes (e.g., egg mass production in poultry).

Methods

A simple model with 32 two-allelic loci equally and additively affecting the selected character was used. The initial frequency of the desirable allele was 0.5 at each locus. In the initial population (generation zero) the Hardy-Weinberg frequencies of genotypes at loci and linkage equilibrium were generated. The initial phenotypic standard deviation of the trait was 7.0. Thus, for the initial heritabilities 0.075 and 0.250 the standardized effects of the loci (FALCONER 1981, p. 187) were 0.137 and 0.250, respectively. Because of the apparent inbreeding depression found in a variety of studies for the egg production traits of poultry, two degrees of dominance (0.5 and 0.8) over the undesirable allele at each locus were used.

The forming of the structure of the genome by taking, to some extent, into account the chromosomal composition of *Gallus domesticus*, the production of gametes and other random processes of the simulation program in question were the same as described in an earlier study (SIRKKOMAA and MAIJALA 1980). The estimation of the heritability of the selected trait and the calculation of breeding values in combined selection were also described in the above study. The combined selection is always more efficient than phenotypic or family selection (OSBORNE 1957a, b), and in the selection of males for egg production characters it is very natural to use combined full-sib and half-sib averages. In the inbreeding generations the selection was performed among the full-sib families by using weighted family averages.

The total number of progeny (population size) produced by the selected individuals was 1500. The mating was accomplished by sampling, with replacement, a mate from the selected male group for each selected female. In the non-inbreeding generations max. 1000 samples were drawn for finding a male other than a full-brother (avoidance of full-sib mating). Correspondingly, in the inbreeding generations a full-brother was sampled (favouring of full-sib mating). The number of progeny individuals (1500) was multinomially distributed among the selected dams (D) so that the expected number of progeny per dam was 1500/D. The sex of each individual was generated with equal probability for male and female.

In individual selection the proportion selected that maximizes the response after a finite number of generations is below 50 %, depending on the number of generations and the number of measured individuals (SMITH 1969; ROBERTSON 1970). In addition, one should score and select equal numbers of males and females in each generation (JÓDAR and LÓPEZ-FANJUL 1977). In the present study no attempt was made to reveal the selection intensity that would maximize the genetic gain after 30 generations. The sizes of the selected groups in each generation were 50♂ + 50♀ and 100♂ + 100♀.

Inbreeding periods of three generations were used, interrupted by non-inbreeding periods of three or six generations. At every combination of parameters 25 replicate runs were performed. The average of the replicate runs was calculated for each desired variable. All the results given in the present study are those averages.

The initial mean of the character selected for (egg mass production in poultry) was set to be 40 g.

Results

In comparing the responses attained by different breeding programmes, one has to consider, also, the genetic variation remaining in the final generation. The possibilities for further responses are strictly dependent on the allelic variation at loci. The fixation of both alleles has been more rapid in the strong selection (50♂ + 50♀) than in the less intensive selection (100♂ + 100♀) for all parameter combinations (Table 1). In the less intense selection there is practically no fixation of the undesirable allele. Regularly, the fixation of the desirable allele has been more rapid in selection with inbreeding (B_1, B_2, B_3) than in selection

Table 1. The percentage of fixed loci in the 30th generation

A: avoidance of full-sib mating in all generations

B: favouring of full-sib mating in generations
4–6, 13–15, 22–24 (B_1)
7–9, 16–18, 25–27 (B_2)
7–9, 13–15, 19–21, 25–27 (B_3)

d_y: degree of dominance is y

h^2_z: initial heritability is z

			Proportion selected					
			(50♂ + 50♀)/1500			(100♂ + 100♀)/1500		
			Desirable allele fixed	Undesirable allele fixed	Neither allele fixed	Desirable allele fixed	Undesirable allele fixed	Neither allele fixed
$h^2_{0.250}$	$d_{0.5}$	B_1	98.0	1.3	0.7	96.8	0.1	3.1
		A	98.6	0.1	1.3	92.0	0.0	8.0
	$d_{0.8}$	B_1	97.5	0.6	1.9	92.8	0.0	7.2
		A	95.8	0.0	4.2	74.3	0.0	25.7
$h^2_{0.075}$	$d_{0.5}$	B_2	91.3	3.5	5.2	82.1	0.0	17.9
		B_3	91.6	3.9	4.5	85.8	0.2	14.0
		A	87.0	2.4	10.6	58.5	0.0	41.5
	$d_{0.8}$	B_2	89.5	2.5	8.0	70.1	0.0	29.9
		B_3	89.2	2.8	8.0	74.5	0.1	25.4
		A	82.2	0.8	17.0	48.9	0.0	51.1

without inbreeding (A) for the selected number 100♂ + 100♀ (Table 1). For the selected number 50♂ + 50 ♀ this difference is small, and the use of inbreeding has clearly accelerated the fixation of the undesirable allele. Evidently, for the selected number 50♂ + 50♀ the increase of response caused by inbreeding has not been large enough to compensate the reduction of effective population size.

In the absence of complete fixation at all loci the comparison of responses is not possible on the basis of Table 1. The final mean frequency of the desirable allele at loci indicates a lower genetic gain in selection with inbreeding (B_1, B_2, B_3) than in selection without inbreeding (A) for the selected number 50♂ + 50♀ (Table 2). In the less intensive selection (100♂ + 100♀) the situation is reverse, and for the initial heritability 0.075 the best response for both degrees of dominance has been produced by this selection intensity with inbreeding (Table 2). For the initial heritability 0.25 these differences are marginal. The same kind of observations on responses can be made by considering the obtained phenotypic population means (Table 3).

Table 2. The mean frequency of the desirable allele at the selected loci in the 30th generation. The initial frequency is 0.5.

A: avoidance of full-sib mating in all generations

B: favouring of full-sib mating in generations
4–6, 13–15, 22–24 (B_1)
7–9, 16–18, 25–27 (B_2)
7–9, 13–15, 19–21, 25–27 (B_3)

d_y: degree of dominance is y

h^2_z: initial heritability is z

			Proportion selected	
			(50♂ + 50♀)/1500	(100♂ + 100♀)/1500
$h^2_{0.250}$	$d_{0.5}$	B_1	0.984	0.996
		A	0.996	0.996
	$d_{0.8}$	B_1	0.989	0.995
		A	0.993	0.979
$h^2_{0.075}$	$d_{0.5}$	B_2	0.950	0.976
		B_3	0.948	0.979
		A	0.955	0.952
	$d_{0.8}$	B_2	0.952	0.962
		B_3	0.949	0.963
		A	0.951	0.926

In general, the standard errors of the replicate averages are much larger for the strong selection than for the less intensive selection (Table 3). For the selected number 50♂ + 50♀ with inbreeding (B_1, B_2, B_3) the standard errors are considerably larger than for that without inbreeding (A). For the selected number 100♂ + 100♀ these differences are not obvious, indicating that in enhancing genetic progress by inbreeding there is not inevitably an increase in the variability of re-

Table 3. The population mean of the selected trait in the 30th generation. The initial population mean is 40 g.

$\bar{x}$: average of the 25 replicate runs (g)

$s_{\bar{x}}$: standard error of $\bar{x}$

A: avoidance of full-sib mating in all generations

B: favouring of full-sib mating in generations:
4–6, 13–15, 22–24 (B_1)
7–9, 16–18, 25–27 (B_2)
7–9, 13–15, 19–21, 25–27 (B_3)

d_y: degree of dominance is y

h^2_z: initial heritability is z

			Proportion selected	
			$(50♂+50♀)/1500$	$(100♂+100♀)/1500$
			$\bar{x}$ $s_{\bar{x}}$	$\bar{x}$ $s_{\bar{x}}$
$h^2_{0.250}$	$d_{0.5}$	B_1	60.15±0.22	60.84±0.11
		A	60.75±0.09	60.81±0.04
	$d_{0.8}$	B_1	56.25±0.15	56.73±0.04
		A	56.75±0.05	56.50±0.06
$h^2_{0.075}$	$d_{0.5}$	B_2	50.07±0.23	51.04±0.06
		B_3	50.00±0.25	51.20±0.10
		A	50.39±0.19	50.65±0.06
	$d_{0.8}$	B_2	48.08±0.19	48.91±0.07
		B_3	47.89±0.19	48.66±0.06
		A	48.34±0.11	48.25±0.06

sponse (Table 3). The same ranking as in standard errors can be seen in the coefficients of variation of the final response (Table 4).

The extra genetic gain obtained by the inbreeding method for the selected number 100♂ + 100♀ is marginal when the initial heritability is 0.25 (Table 4). For the initial heritability 0.075 the extra gain due to inbreeding is 4–8 % (Table 4). For the selected number 50♂ + 50♀ there is a loss of 3–5 % caused by inbreeding, and the use of an additional inbreeding period in B_3 has increased the loss and the coefficient of variation a little (Table 4).

In generation zero only phenotypic selection of females could be accomplished, and they were mated with sampled males. The consequence is observable as slow first-generation responses (Fig. 1a–b, Fig. 2a–b). In considering the rate of genetic progress over the whole breeding process, for the selected number 100♂ + 100♀ there has been only a minor advantage from the periods of inbreeding and between-family selection when the initial heritability is 0.25 (Fig. 1a–b). For the selected number 50♂ + 50♀ any kind of advantage from inbreeding is non-existent (Fig. 1a–b).

Table 4. The response after 30 generations of selection (R), its coefficient of variation (CV), and the response with inbreeding / the response without inbreeding (R_B/R_A)

A: avoidance of full-sib mating in all generations

B: favouring of full-sib mating in generations
4–6, 13–15, 22–24 (B_1)
7–9, 16–18, 25–27 (B_2)
7–9, 13–15, 19–21, 25–27 (B_3)

d_y: degree of dominance is y

h^2_z: initial heritability is z

			Proportion selected					
			$(50♂ + 50♀)/1500$			$(100♂ + 100♀)/1500$		
			R	CV (%)	R_B/R_A (%)	R	CV (%)	R_B/R_A (%)
$h^2_{0.250}$	$d_{0.5}$	B_1	20.15	5.4	97.1	20.84	2.6	100.1
		A	20.75	2.3		20.81	1.1	
	$d_{0.8}$	B_1	16.25	4.7	97.0	16.73	1.3	101.4
		A	16.75	1.5		16.50	1.7	
$h^2_{0.075}$	$d_{0.5}$	B_2	10.07	11.3	96.9	11.04	2.8	103.7
		B_3	10.00	12.5	96.2	11.20	4.5	105.2
		A	10.39	8.9		10.65	2.9	
	$d_{0.8}$	B_2	8.08	11.7	96.9	8.91	4.0	108.0
		B_3	7.89	11.9	94.6	8.66	3.7	105.0
		A	8.34	6.4		8.25	3.6	

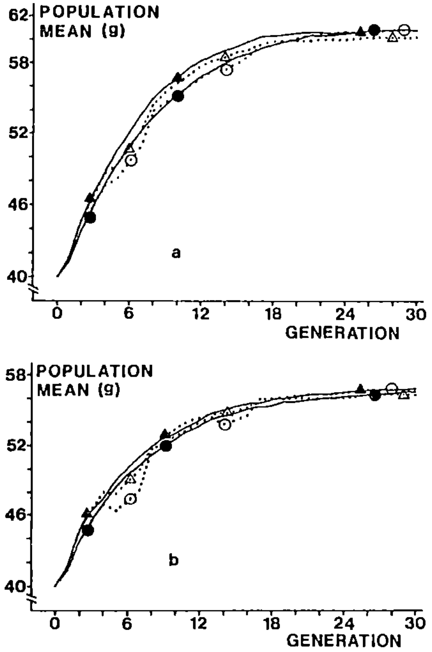

Fig. 1a and b. Progress in the selected trait. The initial heritability is 0.25. **a** degree of dominance 0.5. **b** degree of dominance 0.8.

Avoidance of full-sib mating in all generations (A):

—▲— proportion selected (50♂ + 50♀)/1500

—●— proportion selected (100♂ + 100♀)/1500

Favouring of full-sib mating in generations 4–6, 13–15, 22–24 (B_1):

···△··· proportion selected (50♂ + 50♀)/1500

···○··· proportion selected (100♂ + 100♀)/1500

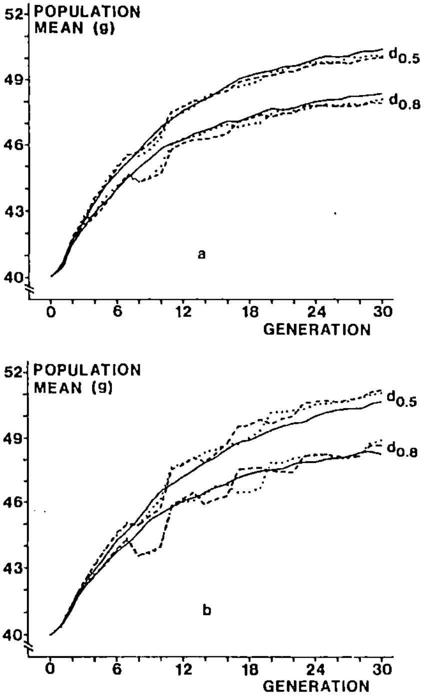

Fig. 2a and b. Progress in the selected trait. The initial heritability is 0.075. **a** proportion selected (50♂ + 50♀)/1500. **b** proportion selected (100♂ + 100♀)/1500.

d_y: degree of dominance is y

——— avoidance of full-sib mating in all generations (A)

······· favouring of full-sib mating in generations 7–9, 16–18, 25–27 (B_2)

– – – favouring of full-sib mating in generations 7–9, 13–15, 19–21, 25–27 (B_3)

Likewise, for the initial heritability 0.075 there has been no advantage from using inbreeding in the strong selection (Fig. 2a). This result is very uniform for both degrees of dominance, in spite of the larger inbreeding depression for the degree of dominance 0.8. For the degree of dominance 0.8 inbreeding in the less intensive selection has not been advantageous before generations 13–15 (Fig. 2b). For the degree of dominance 0.5 already an earlier use of inbreeding (generations 7–9) seems to have been of some advantage to progress.

Discussion

The results obtained in the present study for the initial heritability 0.075 are fairly similar to those in an earlier study for the initial heritability 0.25 (SIRKKOMAA and MAIJALA 1980). In that earlier study with 108 loci the standardized effect of each locus (r) was 0.136. In the present study with 32 loci it is nearly the same (0.137) because the phenotypic standard deviation is 7.0 in both cases. The coefficient of selection (s) against the inferior homozygote at each locus is approximately ir, where i is the intensity of selection (e.g., FALCONER 1981). Thus, for the proportion selected (10♂ + 100♀)/1400 used in the earlier study and for the proportion selected (100♂ + 100♀)/1500 of the present study the coefficients of selection are about 0.28 and 0.22, respectively. In the inbreeding generations of the earlier study the proportion selected was (100♂ + 100♀)/1400, corresponding to the coefficient of selection 0.21. For the degree of dominance d (favourable allele A_1 partially dominant over A_2) the relative fitnesses of the genotypes A_1A_1, A_1A_2 and A_2A_2 are 1, 1-s(1-d)/2 and 1-s, respectively. In random mating the expected frequencies of A_1A_1, A_1A_2 and A_2A_2 in the progeny population are p^2, $2p(1-p)$ and $(1-p)^2$, respectively (p is the frequency of A_1 in the selected group of the previous generation). As a result of inbreeding among selected individuals the corresponding genotype frequencies in the progeny population are $(\bar{p}^2 + V_p)(1-F) + F\bar{p}$, $2(\bar{p}(1-\bar{p}) - V_p)(1-F)$ and $((1-\bar{p})^2 + V_p)(1-F) + F(1-\bar{p})$, where F is the inbreeding coefficient ($\bar{p}$ and V_p are the mean and the variance of the frequency of A_1 among possible subgroups in the selected group of the previous generation). On the basis of the frequencies and the fitnesses of genotypes the expected change of gene frequency per generation can be calculated (e.g., FALCONER 1981). Assuming individual selection and $V_p = 0$, the expected change of the frequency of the favourable allele A_1 in an inbred population was compared with that in a population with random-mating proportions (Fig. 3a–b). In spite of being calculated for a special case, this picture shows the magnitude of the expected superiority of selecting in an inbred population. The absolute difference in the amount of gene frequency change is highest at frequencies 0.6–0.7 (Fig. 3b), suggesting that the optimum time for the first phase of inbreeding is not too late in the selection process. This was an observation in the previous study (SIRKKOMAA and MAIJALA 1980).

The inbreeding coefficient (F) produced by random mating of t generations and after that by inbreeding is:

$$F = 1-(1-1/(2N_e))^t\,(1-f),$$

where f is the inbreeding coefficient achieved by consanguineous mating and N_e is the effective population size during random mating (e.g., CROW and KIMURA 1970). In the present simulation model the mating is accomplished so that in the absence of selection the number of gametes contributed per female to the group of breeding individuals of the next generation would be binomially distributed with mean N/N_0 and variance $N(1-1/N_0)/N_0$, where N_0 is the number of females and N is the total size of the group of breeding individuals ($N = N_0+N_1$, where N_1 is the number of males). However, in the present simulation the number of gametes per male is not binomially distributed. The number of females mated per male (X) has the binomial distribution with mean N_0/N_1 and variance $N_0(1-1/N_1)/N_1$. The number of gametes per male (Y) has the following conditional distributions given X=x:

$$P(Y=y|X=x) = \binom{N}{y}(x/N_0)^y\,(1-x/N_0)^{N-y}$$

$$y=0,\ldots,N \qquad \text{if } 0<x<N_0$$

$$P(Y=0|X=0) = 1$$

$$P(Y=N|X=N_0) = 1.$$

The mean of Y is simply N/N_1, but the variance is $N/N_1 + N(N-1)(N_0(1-1/N_1)/N_1 + N_0^2/N_1^2)/N_0^2 - N^2/N_1^2$. Assuming random mating and no selection, for the breeding numbers 10♂ + 100♀ and 100♂ + 100♀ the effective sizes 33.6 and 133.8 were calculated, respectively. If full-sib mating is avoided the effective sizes are somewhat larger (JACQUARD 1971). In artificial selection the effective population size can be smaller, especially if selection is strong and much weight is given to the family averages, as is the case in combined selection for a low-heritability character with a small phenotypic intra-family correlation (ROBERTSON 1961).

It was calculated that for the effective size 33.6 the inbreeding coefficients produced by one, two and three generations of full-sib mating after seven generations of random mating are about 0.325, 0.437 and 0.550, respectively. These coefficients are relevant to the first period of inbreeding in the earlier study (Fig. 2, SIRKKOMAA and MAIJALA 1980). For the effective size 133.8 the corresponding inbreeding coefficients are about 0.269, 0.391 and 0.513, being relevant to the present study (Fig. 2b). The extra gain in cumulative response due to inbreeding is about 5 % for the degree of dominance 0.5 (Table 4). In that earlier study the extra gain was about 20 % for the degree of dominance 0.5 (Fig. 2, SIRKKOMAA and MAIJALA 1980). Compared to the present investigation the larger relative superiority of the selection with inbreeding over selection without inbreeding (20 %) is only to a minor extent due to the more rapid increase of the inbreeding coefficient described above, because the effect of a

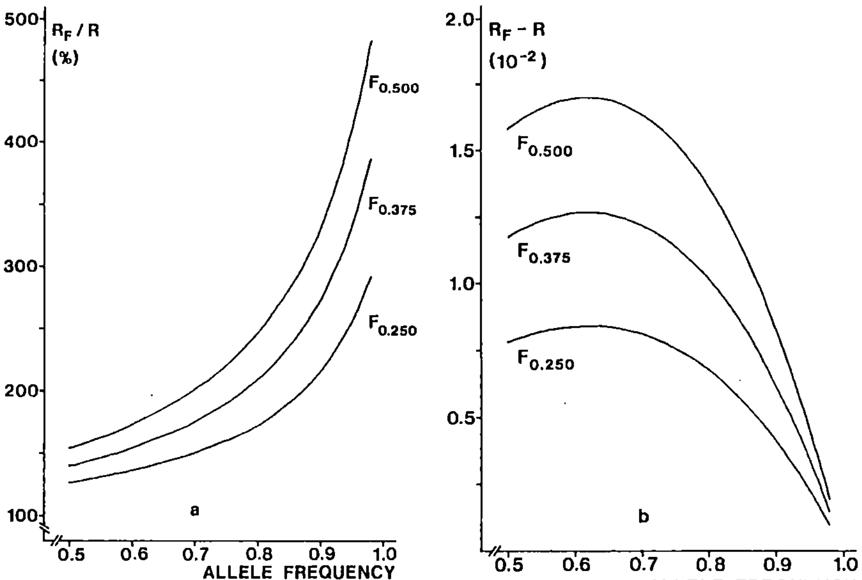

Fig. 3 a and b. The expected change of gene frequency in an inbred population (R_F) compared with that in a random-bred population (R) as a function of the frequency of the favourable allele and the coefficient of inbreeding. The degree of dominance over the unfavourable allele is 0.8. The coefficient of selection against the recessive homozygote is 0.22. a proportion of responses (R_F/R). b difference of responses (R_F–R). F_x: coefficient of inbreeding is x.

small difference in F is not large (Fig. 3a). The main reason for the discrepancy is that in the present study the breeding group was 100♂ + 100♀ in each generation, whereas in the earlier study the breeding group was 10♂ + 100♀ in the non-inbreeding generations, resulting in a severe loss of the cumulative response for the selection with avoidance of full-sib mating in each generation.

For the breeding number 50♂ + 50♀ the effective population size in the present simulation is about 67.1, if random mating and no selection are assumed. The inbreeding coefficients produced by one, two and three generations of full-sib mating after seven generations of random mating with the effective size 67.1 are about 0.288, 0.407 and 0.526, respectively. These coefficients differ only slightly from 0.269, 0.391 and 0.513, which are relevant to the effective size 133.8 of the breeding number 100♂ + 100♀. The inbreeding depression observed in the total progeny population in generations 8–10 and in other inbred phases is larger for the selected number 100♂ + 100♀ than for 50♂ + 50♀ (Fig. 2a–b). This is probably mainly due to differences in the variance of gene frequency (V_b) among the full-sib families of the group selected in the previous generation, because F and $\bar{p}$ are approximately the same for both intensities of selection. The same kind of considerations with respect to inbreeding depression apply to the initial heritability 0.25 (Fig. 1a–b). In the inbreeding generations there are, on an average, 3.3 and 13.3 full-sib families selected from 50 and 100 families for the strong selection and for the less intensive selection, respectively. It is quite natural that V_b is larger in the latter case. The superiority of the between-family selection with inbreeding over the selection without inbreeding depends on the genetic variance among the full-sib families of the progeny population. The results indicate that the extra response due to inbreeding is smaller than that calculated for individual selection (Fig. 3a). An explanation for this is that the combined selection of high efficacy was used in the selection without inbreeding.

The variance of the change of gene frequency per generation is increased if there is an inbreeding departure from random mating proportions in the group of breeding individuals and the number of gametes contributed per parent is not binomially distributed (CROW and KIMURA 1970). As a result the cumulative response is lowered and its variability is increased. In comparing the results obtained by selection and inbreeding with those obtained by selection without inbreeding these effects are clearly seen for the selected number 50♂ + 50♀ (Tables 1, 3 and 4). The variation of the final response is an important factor in planning breeding programmes (e.g., NICHOLAS 1980). In reality only one experiment is often performed. Thus, for a large variation of response the gain in the last generation of the programme can be almost anything regardless of the expected result.

The breeding method of the present study can be considered as an example of subdivision in selection. In some earlier studies on the use of subdivided population structures in improving the response to selection, a population was divided into small isolated sublines, and there was within-line selection interrupted cyclically by one generation with selection between lines and with crossing the best lines for a new subdivision (animal experiments, e.g. MADALENA and ROBERTSON 1974; KATZ and ENFIELD 1977; RATHIE and NICHOLAS 1980). The selection response of several generations in a subdivided population was in no case better than that in one large population with the same intensity of selection. However, MADALENA and HILL (1972) found in their simulation study that in the case of complete dominance there is some advantage to response in intermediate generations from between-line selection performed at later times in the process, provided that the recessive allele is at a low initial frequency. In the present study with intermediate initial allele frequencies at loci the selection was performed between full-sib families in each inbreeding generation, in other generations there was combined selection and no subdivision in the group selected for breeding. The superiority in using this method seems to depend on the number of families selected for inbreeding and on the effects of loci. In the present method the between-line selection in early generations is of no use either. For a trait affected by loci with large standardized effects there is practically no use of the method in question even in the case of a considerable degree of dominance. DICKERSON and LINDHÉ (1977) pointed out that the expected gains from cyclical selection between inbred families are larger for traits with a low heritability and when there is little environmental correlation among family members. Deductions of this kind were made earlier by LUSH (1945), and the results of the present simulation study support them.

Because the results suggest that a rather weak selection is needed for the inbreeding method to be better than selection without inbreeding, the extra gain in genetic progress is not attainable in a short-term breeding programme. In a selection programme of only a few generations the expected gain is maximized by a small proportion selected, in which case inbreeding is not beneficial according to the present results. This means that similar short-term gains as in a structured population can be obtained simply by using more intense selection in one large population (MADALENA and HILL 1972). However, the variability of response can be large in such a very intense selection. In addition to the considerations above, ROBERTSON (1970) showed that in individual selection it would be possible to increase the advance at intermediate generations by allowing the proportion selected to decline with time. The extra gain with respect to the optimum fixed proportion selected is around 4 % in many cases and is never more than a few percent.

In the simulation the decline in fertility and the appearance of genetic defects due to inbreeding were ignored. In reality all the deterioration caused by inbreeding will not be associated with the individuals which are culled from the breeding group on the basis of their low performance in the character selected for. The problem is expected to diminish if this character is closely correlated to fertility. Epistatic models would be worth studying, especially as Sewall Wright has repeatedly considered the importance of epistasis to selection response in subdivided population structures (e.g., WRIGHT 1977).

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III

LONG-TERM RESPONSE TO SELECTION WITH INBREEDING IN ALTERNATE GENERATIONS

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SUMMARY

The rate of genetic progress in selecting for a character with female phenotypes only was studied using two single-locus deterministic models and one simulation model with 32 loci (two alleles with initial frequencies of 0.5 at each locus). There was random mating in all generations or random mating and full-sib mating in alternate generations among the selected individuals.

For deterministic models the saving of time due to inbreeding in reaching a given proportion of the maximum response (50, 75 and 90 %) was about 20-40 %, increasing with the degree of dominance and with the proportion of the maximum response. For simulation the corresponding saving of time was about 10-20 %. It was concluded that the models generally exaggerate the advantage from the inbreeding method in real populations, the success depending decisively on the genetic composition of the base population.

INTRODUCTION

In animal breeding it is a common procedure to use random mating or to avoid matings between close relatives among the individuals selected to produce the next generation. However, if only genetic variation and the response to selection are considered, it has been known for a long time that some form of inbreeding might be of use (e.g. Wright 1942, Lush 1945). For instance, full-sib mating and random mating (or outbreeding) in alternate generations has been proposed (Dickerson 1973, Dickerson and Lindhé 1977). Recently, this kind of method has been studied in Japanese quail by MacNeil et al. (1984a,b), and in flour beetles by Dion and Minvielle (1985). They found no advantage of the inbreeding method to the total response to selection. The present study compares some results on the subject got by deterministic models with those of simulation for a character manifesting itself in one sex only.

METHODS

Deterministic course of selection at one locus.

Model 1. The frequencies and the relative fitnesses of the genotypes in an arbitrary inbred generation t-1 are (fitness values of males are approximate in the full-sib selection based on sisters):

Genotype	Frequency	Fitness		Frequency in the selected group	
		Females	Males	Females	Males
A_1A_1	P_1	1	1	$P_{f1}=P_1/\overline{W}_f$	$P_{m1}=P_1/\overline{W}_m$
A_1A_2	P_2	1-hs	1-hsr	$P_{f2}=P_2(1-hs)/\overline{W}_f$	$P_{m2}=P_2(1-hsr)/\overline{W}_m$
A_2A_2	P_3	1-s	1-sr	$P_{f3}=P_3(1-s)/\overline{W}_f$	$P_{m3}=P_3(1-sr)/\overline{W}_m$

where $h=(1-d)/2$ (d is the degree of dominance in terms of Falconer (1981)), s is the coefficient of selection and r is the coefficient of relationship by Wright. $\overline{W}_f$ and $\overline{W}_m$ are the mean fitnesses of females and males, respectively. The coefficient r between full-sibs was assumed to be a constant of 0.6 because each inbred generation was produced by full-sib mating (in fact there will be a slight increase in r in the course of generations).

In random mating among the selected individuals of generation t-1 the frequencies of different mating combinations (MC) and the genotype distribution in the progeny population t are:

MC in generation t-1	Frequency	Genotype distribution in generation t		
$A_1A_1 \times A_1A_2$	$Q_1=P_{f1}P_{m2}+P_{f2}P_{m1}$	1/2 A_1A_1	1/2 A_1A_2	
$A_1A_1 \times A_2A_2$	$Q_2=P_{f1}P_{m3}+P_{f3}P_{m1}$		A_1A_2	
$A_1A_2 \times A_2A_2$	$Q_3=P_{f2}P_{m3}+P_{f3}P_{m2}$		1/2 A_1A_2	1/2 A_2A_2
$A_1A_1 \times A_1A_1$	$Q_4=P_{f1}P_{m1}$	A_1A_1		
$A_2A_2 \times A_2A_2$	$Q_5=P_{f3}P_{m3}$			A_2A_2
$A_1A_2 \times A_1A_2$	$Q_6=P_{f2}P_{m2}$	1/4 A_1A_1	1/2 A_1A_2	1/4 A_2A_2

In the selected female group of generation t the proportions of the progeny of different mating combinations and the gene frequencies are:

MC in generation t-1	Proportion of progeny in the selected females	Frequency of allele A_1 in the selected females
$A_1A_1 \times A_1A_2$	$Q_{f1}=Q_1(1-hs/2)/\overline{W}_f$	$p_{f1}=1/2(1+(1-hs)/2)/(1-hs/2)$
$A_1A_1 \times A_2A_2$	$Q_{f2}=Q_2(1-hs)/\overline{W}_f$	$p_{f2}=1/2$
$A_1A_2 \times A_2A_2$	$Q_{f3}=Q_3(1-s(h+1)/2)/\overline{W}_f$	$p_{f3}=1/4(1-hs)/(1-s(h+1)/2)$
$A_1A_1 \times A_1A_1$	$Q_{f4}=Q_4/\overline{W}_f$	$p_{f4}=1$
$A_2A_2 \times A_2A_2$	$Q_{f5}=Q_5(1-s)/\overline{W}_f$	$p_{f5}=0$
$A_1A_2 \times A_1A_2$	$Q_{f6}=Q_6(1-s(h+1/2)/2)/\overline{W}_f$	$p_{f6}=1/4(2-hs)/(1-s(h+1/2)/2)$

In the selected male group of generation t the corresponding frequencies of A_1 are: $p_{m1}=3/4$, $p_{m2}=1/2$, $p_{m3}=1/4$, $p_{m4}=1$, $p_{m5}=0$ and $p_{m6}=1/2$.

In the next generation t+1, after random mating within the six classes of the selected group of generation t (full-sib mating), the genotype frequencies are:

Genotype	Frequency
A_1A_1	$P_1=Q_{f1}p_{f1}p_{m1}+Q_{f2}p_{f2}p_{m2}+Q_{f3}p_{f3}p_{m3}+Q_{f4}+Q_{f6}p_{f6}p_{m6}$
A_1A_2	$P_2=Q_{f1}((1-p_{f1})p_{m1}+p_{f1}(1-p_{m1}))+Q_{f2}((1-p_{f2})p_{m2}+p_{f2}(1-p_{m2}))$ $+Q_{f3}((1-p_{f3})p_{m3}+p_{f3}(1-p_{m3}))+Q_{f6}((1-p_{f6})p_{m6}+p_{f6}(1-p_{m6}))$
A_2A_2	$P_3=Q_{f1}(1-p_{f1})(1-p_{m1})+Q_{f2}(1-p_{f2})(1-p_{m2})+Q_{f3}(1-p_{f3})(1-p_{m3})$ $+Q_{f5}+Q_{f6}(1-p_{f6})(1-p_{m6})$

After this the calculation was continued as in generation t-1. In each generation the frequency of allele A_1 was calculated from genotype frequencies. The departure from Hardy-Weinberg proportions (F) was also calculated from genotype frequencies.

Model 2. In any generation the genotype frequencies and the relative fitnesses are:

Genotype	Frequency	Fitness of females
A_1A_1	$P_1=p_fp_m(1-F)+pF$	1
A_1A_2	$P_2=(p_f(1-p_m)+(1-p_f)p_m)(1-F)$	1-hs
A_2A_2	$P_3=(1-p_f)(1-p_m)(1-F)+(1-p)F$	1-s

where p_f and p_m are the frequencies of allele A_1 among the selected females and males of the previous generation respectively, and $p=(p_f+p_m)/2$.

The difference in the frequency of allele A_1 between the selected female group and the unselected population (Δp_f) is $(P_1+P_2(1-hs)/2)/\overline{W}_f-p$. The corresponding difference with respect to males in full-sib selection (Δp_m) is assumed to be $r\Delta p_f$. In the progeny population the frequency of A_1 is $p+(\Delta p_f+\Delta p_m)/2$. In inbred generations F and r were assumed to be 0.25 and 0.60 respectively, in other generations values of 0.0 and 0.5 were used.

In calculating results for models 1 and 2 there was no selection among males in generation 0 because the initial relationships were assumed to be unknown. In generation 0 the population was in Hardy-Weinberg equilibrium for an initial gene frequency of 0.5. In even generations there was random mating, otherwise full-sib mating (except for the case with random mating in all generations).

Simulation.

The method of simulation was as outlined in previous studies (Sirkkomaa and Maijala 1980, Sirkkomaa 1984). The character selected for was determined by 32 equivalent, practically unlinked loci which were initially in Hardy-Weinberg and linkage equilibrium. In generation 0 the phenotypic variance was 49.0. The initial heritability in the narrow sense was 0.075 or 0.250.

Females were selected by using phenotypic values. The males chosen to breed were full-brothers of the selected females, taken from the relevant sibships as evenly as possible. For maximizing the ultimate response half the population was selected in each generation ((100♂+100♀)/400). In generation 0 males were not selected. In alternate generations full-sib mating was avoided and favoured as completely as possible. A male could mate with several females due to the random drawing of males for mating pairs.

RESULTS AND DISCUSSION

For a weak selection (s=0.02) the rate of change in the departure from Hardy-Weinberg proportions (F) was very similar to the case of a neutral locus (Table 1). During the first 20 generations only a minor increase in the frequency of the favourable allele was obtained (about 0.045). For the higher coefficients of selection the rise in gene frequency was considerably larger than that for the weak selection, being about 0.338 for s=0.20. The rise in F was lower for the strong selection than that for the weak one (Table 1).

A general observation from Table 1 is that for a weak selection F is about 1/3 in inbred generations almost all the time during which p changes from its initial value towards 1. For a strong selection F in inbred generations is clearly below 1/3 most of the time of gene frequency change. Thus, the weaker

Table 1. The departure from Hardy-Weinberg proportions (F) and the frequency of the favourable allele (p). The coefficient of selection is s. The degree of dominance over the unfavourable allele is 0.5. In generation 0 p was 0.5. In odd generations there was full-sib mating, otherwise random mating

		Inbred generation (model 1)					
s		2	4	6	8	10	20
.00	F	.250	.313	.328	.332	.333	.333
.02	F	.249	.311	.326	.330	.331	.332
	p	.503	.508	.512	.517	.522	.545
.11	F	.244	.303	.318	.321	.322	.322
	p	.518	.543	.568	.593	.617	.720
.20	F	.238	.294	.307	.310	.311	.313
	p	.533	.579	.623	.664	.701	.838

Table 2. The number of generations (G) needed to attain a given frequency of the favourable allele and the decrease in time due to full-sib mating (D) for deterministic models with various degrees of dominance (d) and coefficients of selection (s). The relative deviations from the results of simulation (Table 3) are also given (RD). The initial frequency of the favourable allele was 0.5. A: random mating in all generations; B: random mating and full-sib mating in alternate generations (B_1= model 1, B_2= model 2)

			Frequency of the favourable allele								
			0.750			0.875			0.950		
s	d		G	D(%)	RD(%)	G	D(%)	RD(%)	G	D(%)	RD(%)
.02	.2	B_1	121	21.4		218	23.0		337	23.8	
		B_2	131	14.9		238	15.9		368	16.7	
		A	154			283			442		
	.5	B_1	129	23.7		244	27.2		394	30.0	
		B_2	140	17.2		268	20.0		436	22.6	
		A	169			335			563		
	.8	B_1	138	27.0		279	33.9		482	41.6	
		B_2	151	20.1		311	26.3		547	33.8	
		A	189			422			826		
.11	.2	B_1	22	21.4	-21.4	40	21.6	-20.0	61	22.8	-20.8
		B_2	24	14.3	-14.3	43	15.7	-14.0	66	16.5	-14.3
		A	28		- 9.7	51		-12.1	79		-13.2
	.5	B_1	24	22.6	-17.2	45	25.0	-16.7	71	29.7	-16.5
		B_2	25	19.4	-13.8	48	20.0	-11.1	78	22.8	- 8.2
		A	31		- 6.1	60		- 7.7	101		- 1.9
	.8	B_1	26	23.5	-10.3	51	32.9	-15.0	88	40.9	-10.2
		B_2	27	20.6	- 6.9	56	26.3	- 6.7	98	34.2	0.0
		A	34		- 8.1	76		+ 1.3	149		+21.1
.20	.2	B_1	13	13.3	-18.8	22	18.5	-21.4	33	23.3	-21.4
		B_2	13	13.3	-18.8	23	14.8	-17.9	35	18.6	-16.7
		A	15		-16.7	27		-12.9	43		- 6.5
	.5	B_1	13	23.5	-23.5	25	24.2	-16.7	39	29.1	-15.2
		B_2	14	17.6	-17.6	26	21.2	-13.3	43	21.8	- 6.5
		A	17		-10.5	33		- 5.7	55		+ 1.9
	.8	B_1	15	21.1	-16.7	29	29.3	-14.7	49	39.5	- 9.3
		B_2	15	21.1	-16.7	31	24.4	- 8.8	53	34.6	- 1.9
		A	19		- 5.0	41		+ 5.1	81		+20.9

the selection, the larger the advantage from inbreeding to the rate of response might be with respect to random mating in all generations. In general, this reasoning seems to be true in comparing the D values of different strengths of selection within the degrees of dominance (model 1, Table 2), but the differences are not large.

The approximate coefficients of selection at individual loci in simulation (Table 3) were calculated in the common way (e.g. Falconer 1981, p. 186). In general, the progress in gene frequency for the deterministic models was more rapid than that for simulation (RD, Table 2). The deviations from the results of simulation were lowest for random mating, except in the case of long-term response for a degree of dominance of 0.8. The results for model 2 were closer to simulation than those for model 1 (Table 2). The change of F given by model 1 would be realized only in a very large population.

Table 3. The number of generations (G) needed to attain a given mean frequency of the favourable allele at 32 loci and the decrease in time due to full-sib mating (D), results averaged from 50 replicate runs of simulation. The initial frequency of the favourable allele at each locus was 0.5. The proportion selected was (100♂+100♀)/400 in each generation.
d: degree of dominance; h^2: initial heritability; s: coefficient of selection at each locus (approximately)
A: avoiding full-sib mating in all generations
B: avoiding and favouring full-sib mating in alternate generations

			Frequency of the favourable allele					
			0.750		0.875		0.950	
h^2	d		G	D(%)	G	D(%)	G	D(%)
.075	.2	B	28	9.7	50	13.8	77	15.4
(s≈0.11)		A	31		58		91	
	.5	B	29	12.1	54	16.9	85	17.5
		A	33		65		103	
	.8	B	29	21.6	60	20.0	98	20.3
		A	37		75		123	
.250	.2	B	16	11.1	28	9.7	42	8.7
(s≈0.20)		A	18		31		46	
	.5	B	17	10.5	30	14.3	46	14.8
		A	19		35		54	
	.8	B	18	10.0	34	12.8	54	19.4
		A	20		39		67	

An explanation for the discrepancies in G between the calculated and simulated results is, of course, the finite population size existing in simulation. It was calculated in an earlier study (Sirkkomaa 1984) that in the present simulation model the effective population size in random mating and with no selection would be about 134 for a parental group of 100♂+100♀, since the number of gametes contributed per male to the breeding group of the next generation is not binomially distributed. In selection the effective size becomes still smaller (Robertson 1961). In addition, the decrease of effective size in the present simulation is pronounced because the breeding male group is chosen on the basis of relationship with the selected females. The random sampling effect is also increased because of the use of full-sib mating in the inbreeding method. In a simulation experiment using the present model for a population structure of (10♂+10♀)/60 without selection, the mean time until the fixation of either one of the two alleles at all of the 32 loci (initial gene frequencies 0.5) was in mating B about 12 % lower than that in mating A (the average result from 200 replicate runs).

In simulation the coefficient of selection (s) is not a constant over generations because of the random fluctuation in the number of measured individuals (on an average 200 females in each generation) and in the phenotypic variance. In the long term s will change due to the decrease in the phenotypic variance. The average response at several loci cannot be equal to the response at one locus, even in the absence of linkage and epistasis.

The saving of time due to inbreeding in reaching a given gene frequency is about 20-40 % for the single-locus deterministic models (D, Table 2) and about 10-20 % for simulation (D, Table 3). On the basis of the calculated models, in attaining a given response the saving of time due to inbreeding should increase with an increasing degree of dominance and with an increasing magnitude in the response (Table 2). Thus, the advantage from inbreeding should be largest for a degree of dominance of 0.8 in the long-term selection. In general, these predictions are seen in the results of simulation (Table 3). However, there are exceptions from these rules (mainly in the stronger selection). The advantage from inbreeding should be somewhat larger for a weak selection than for a strong one (Table 2). This rule is striking in the results of simulation, with one exception (Table 3).

In the real populations with inbreeding there is usually a decline in the characters concerning fertility and viability, due to increasing homozygosity at all loci. The magnitude of this decline is not predictable in detail, but it depends decisively on dominance relations at loci and on the genetic composition of the base population. All kind of deterioration must have its effects on the efficacy of selection for any trait and on the effective population size. In the experiments of MacNeil et al. (1984a,b) and of Dion and Minvielle (1985) there was no advantage from alternate full-sib mating to the total response. However, these were short-term experiments of 15-17 generations. In the present simulation the responses at generation 20 of the inbreeding method for initial heritabilities of 0.075 and 0.250 were 8-20 % and 9-10 % larger than those of random mating, respectively (depending on the degree of dominance).

It is clear that the results given by most models exaggerate the advantage of inbreeding to the selection response because all the genetic complexity cannot be concerned in affecting them.

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IV

Ultimate response to selection with alternate random and full-sib mating generations

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Summary. The response to selection for a character manifesting itself in females only and the average number of generations until fixation were studied by simulation and by transition probability matrix calculation. Long-term response was also studied by a deterministic model. Females were selected on the basis of phenotypic values, whereas the breeding males were full-brothers of the selected females. There was random mating in all generations (in simulation avoiding full-sib mating), or random mating and full-sib mating in alternate generations (the inbreeding system).

In the simulation of a fairly large population (100 females and 100 males selected from 400 individuals), the ultimate responses for the random-mating and the inbreeding systems were practically the same. However, the fixation at all of the 32 loci initially with two alleles was reached 12-43 % faster in the latter system, depending on the degree of dominance (0.2, 0.5, 0.8), on initial gene frequency at loci (0.25, 0.50, 0.75) and on the initial heritability (0.075, 0.250). Long-term responses in simulation agreed satisfactorily with those in deterministic calculation, and the reasons for the differences were studied. In the transition probability matrix calculation of a small population (effective size ≤ 20), the probability of fixation of the favourable allele for the inbreeding system was about the same as that for the random-mating system, if a reduction of 10 % in the effective size due to inbreeding was assumed. The average calculated time until the fixation of either one of the two alleles was 12-19 % shorter in the inbreeding system than in random mating. The possible decreases in effective population size and in selection intensity due to inbreeding were discussed.

Key words: Inbreeding - Mating system - Selection response - Simulation

Introduction

The use of intentional inbreeding to increase both heritability and the response to selection has not been common in animal breeding, mainly because the increasing homozygosity at all segregating loci causes inbreeding depression in many traits. The interaction between inbreeding and selection has been discussed by several authors (e.g., Wright 1942; Lush 1945). On the basis of a selection experiment for litter size in mice, Bowman and Falconer (1960) concluded that the use of cyclical inbreeding and crossing would not be very promising in the improvement of farm animals. However, Dickerson (1973) and Dickerson and Lindhé (1977) reasoned that a better selection response might be obtained by using full-sib mating and random mating in alternate generations than by using random mating in all generations, if there were no large problems with cycle interval, selection intensity and effective population size. Using this alternating system and individual selection of females for a biomass index, MacNeil et al. (1984a,b) observed no advantage of inbreeding over the random-mating system in Japanese quail. Likewise, Dion and Minvielle (1985) found no advantage of the alternating system in practicing selection for pupal weight in Tribolium.

The use of random mating and full-sib mating in alternate generations might be the best inbreeding method in selecting for a character that does not manifest itself in both sexes, and some form of sib selection is needed. The heritability increases with the coefficient of inbreeding, and the efficacy of sib selection increases with the coefficient of relationship (e.g., Lush 1945; Crow and Kimura 1970). If we consider a large population and exclude selection, the coefficient of inbreeding (F) and the coefficient of relationship between full-sibs (r) in inbred generations of the alternating system rapidly rise to 1/3 and 5/8, respectively (calculated on the basis of Crow and Kimura (1970), p. 69, 87 and 113). In random-bred generations of the alternating system F remains 0, but r rises to 2/3. Thus, F does not rise too high in inbred generations, and r is appreciably larger than 1/2 in all generations. Using random mating in all generations, F and r remain 0 and 1/2, respectively.

In an earlier investigation (Sirkkomaa 1986) the number of generations required to attain a given response in the random-mating and alternating systems was studied by simulation and deterministic calculation. Females were selected on the basis of their own phenotypes, and the breeding males were selected on the performance of their full-sisters. There was some advantage of inbreeding in the rate of response in the long term, mainly for high degrees of dominance in weak selection. In the present investigation long-term and ultimate responses to selection with the random-mating and alternating systems were studied by simulation, by transition probability matrix calculation and by a deterministic model.

Methods

1. Simulation

Individual (phenotypic) selection was used in selecting females. The selected male group was formed by drawing full-brothers of the selected females, as evenly as possible from the relevant sibships containing males.

In each generation a progeny population of T individuals was produced by N_f females and N_m males chosen to breed. In inbreeding generations the mating pairs were formed by sampling at random from the selected male group a full-brother for each selected female. If no full-brothers were available, any male was sampled. In the generations with avoidance of full-sib mating a male other than a full-brother was sampled. In both cases the sampling was with replacement, so a male could mate with several females and paternal half-sibs were produced. Because of the mating method, the effective population size is smaller than N_f+N_m even without selection and for the case of $N_f=N_m$, since the number of gametes contributed per male to the breeding group of the next generation does not follow a binomial distribution (Sirkkomaa 1984).

In the random-mating system (A) there was avoiding full-sib mating in all generations. In the inbreeding system (B) there was avoiding full-sib mating and favouring full-sib mating in alternate generations.

The T progeny individuals were randomly distributed among mating pairs, so that the expected number of progeny per pair was T/N_f. The sex of each individual was generated with a probability of 1/2 for male and female. In forming phenotypes a normally distributed deviate (mean 0, variance V_E) was added to the genotypic value of each female. V_E is the constant environmental variance calculated as the initial phenotypic variance minus the initial genotypic variance.

The expected total response at the limit (fixation at all loci) is maximized by individual selection with a proportion selected of 50 % in each generation, if the loci controlling the genetic variation of the character in question are unlinked (Dempster 1955; Robertson 1960). Moreover, the sex ratio should be 1:1 both in the selected group and in the unselected population (Jódar and López-Fanjul 1977). In the case of skewed phenotypic distributions, the optimum proportion selected may differ from 50 % (Cockerham and Burrows 1980). At intermediate values of linkage the optimum proportion is above 50 %, being 60-70 % in some cases (Robertson 1970).

In the present study there are departures from the conditions for the "50 % rule" in several respects: sex ratio in the unselected population is not a constant of 1:1, males are not selected on the basis of phenotype, and there is some linkage. It would require large-scale simulations with very many replicate runs to determine the precise optimum point for each special case, especially as at large values of T the expected ultimate genetic gain is practically the same for a wide range of proportions around 50 % (Robertson 1960). For these reasons half the population was selected in each generation ($N_f=N_m=100$, T=400, or $N_f=N_M=15$, T=60) to represent the optimum proportion.

There were 32 initially diallelic loci equally affecting the character selected for, an equal degree of dominance (0.2, 0.5 or 0.8) over the unfavourable allele at each locus, but no interactions between genes at different loci (epistasis). In generation zero the genotypes were in Hardy-Weinberg proportions according to the same initial gene frequency (0.25, 0.50 or 0.75) at each locus, and the gametic frequencies were in linkage equilibrium. This kind of situation with gene frequencies of 0.5 might be quite realistic after a few generations of random mating in a large population derived from a cross between inbred lines. The initial heritability of the character was 0.075 or 0.250. The initial phenotypic variance was 49.0. From the parameters and assumptions described above, the values of the three genotypes of each locus were calculated using the well-known formula for the additive genetic variance in a large random-mating population (e.g., Falconer 1981).

At the beginning of each replicate run, the structure of the genome was generated by taking into account some features of the chromosomal composition of Gallus domesticus, as described in an earlier study (Sirkkomaa and Maijala 1980). In these procedures the main principles were the division of the genome into macrochromosomes and microchromosomes (a total of 39) and the random scattering of loci along them from the uniform distribution. However, for comparison there was one simulation in which only one chromosome was generated.

In the production of gametes the number of crossing-over points in a bivalent was a Poisson-distributed random variable truncated to the right at 21. Thus, the occurrence of more than 20 chiasmata in a bivalent was impossible. The locations of crossing-over points were drawn from the uniform distribution without any chiasma interference, and in the tetrad of four strands the chiasmata were formed at random without chromatidal interference. In macrochromosomes the parameter value of Poisson distribution was 2-3; in microchromosomes it was smaller.

Because the effects of varying degrees of linkage and crossing over were not particularly studied, all the procedures described above for the genome and gamete formation were done to create a more real basis for genetic variation than that possible by relying on unlinked loci alone.

2. Deterministic calculation

If one locus is considered, the genotype frequencies in the progeny population are:

A_1A_1: $P_{11} = p_f p_m (1-F) + pF$

A_1A_2: $P_{12} = (p_f(1-p_m) + (1-p_f)p_m)(1-F)$

A_2A_2: $P_{22} = (1-p_f)(1-p_m)(1-F) + (1-p)F$,

where p_f and p_m are the frequencies of the favourable allele A_1 among the selected females and males of the previous generation, respectively, $p=(p_f+p_m)/2$ and F is the coefficient of inbreeding. Consider the selection of females based on phenotypes. The coefficient of selection (s) against the inferior homozygote A_2A_2 is approximately $2ai/\sigma_p$, where a is half the difference between the genotypic values of the two homozygotes, i is the intensity of selection and σ_p is the phenotypic standard deviation (Kimura and Crow 1978; Falconer 1981). For the degree of dominance d, the relative fitnesses of genotypes A_1A_1, A_1A_2 and A_2A_2 are 1, 1-s(1-d)/2 and 1-s, respectively (favourable allele A_1 partially dominant over A_2).

The difference in the frequency of A_1 between the selected females and the unselected population (Δp_f) is:

$$\Delta p_f = \frac{P_{11}+P_{12}(1-s(1-d)/2)/2}{P_{11}+P_{12}(1-s(1-d)/2) \quad +P_{22}(1-s)} - p. \qquad (1)$$

The corresponding difference with respect to selected males (Δp_m) is assumed to be:

$$\Delta p_m = r\,\Delta p_f, \qquad (2)$$

where r is Wright's coefficient of relationship between full-sibs. The frequency of A_1 in the progeny population will be $p+(\Delta p_f+\Delta p_m)/2$.

It can be calculated that in a population of infinite size the value of F in inbred generations will rapidly approach 1/3 if there is random mating and full-sib mating in alternate generations and no selection (see Introduction). Correspondingly, r would approach $2((1+2F)/4)/(1+F) = 0.625$. However, in the present calculations F and r of inbred progeny were assumed to be 0.25 and 0.6, respectively, because there was selection and the matings in the inbreeding generations of simulation were not exclusively between full-sibs, as will be explained in the results. In the random-bred generations of the alternating system values of 0.0 and 0.6 were used for F and r, respectively. In the random-mating system the values of F and r were 0.0 and 0.5, respectively.

For a proportion selected of 100♀/200♀, the intensity of selection (i) is about 0.795. However, a value of 0.793 was used in the calculation because in simulation the number of females in each generation was not a constant of 200. The theoretical courses of selection in an infinite population were calculated using the same genotypic values as in simulation. Assuming the initial frequency of A_1 to be 0.5 at each locus, approximate coefficients of selection of 0.109 and 0.198 against genotype A_2A_2 were obtained for initial heritabilities of 0.075 and 0.250, respectively. The theoretical progress in gene frequency was calculated up to 95 % of the maximum change.

3. Markov chain calculation

The method of successive multiplication of transition probability matrices was used to calculate the ultimate probability of fixation and the average number of generations until fixation. Hill (1969) used this method exactly by taking into account both the finite number of selected parents and the finite size of the unselected population. He found that the exact calculation of transition probabilities using the theory of order statistics is practically possible only for very small populations and proposed that the model of sampling parents alone is quite sufficient in most cases.

In the present study the transition probabilities were determined by assuming random sampling of 2N gametes from both females and males in the selected group. Suppose that the number of A_1 alleles is i ($i=0,\dots,4N$) among the parents in generation t (N females and N males). In the progeny population produced by them the frequency of A_1 is $i/(4N)=p_i$. Ignoring the effect of different gene frequencies among female and male parents, the genotype frequencies in the progeny population t+1 are:

A_1A_1: $P_{11}= p_i^2(1-F)+p_iF$

A_1A_2: $P_{12}= 2p_i(1-p_i)(1-F)$

A_2A_2: $P_{22}= (1-p_i)^2(1-F)+(1-p_i)F$,

where F is the coefficient of inbreeding. Among the parents in generation t+1, the number of A_1 alleles is Y_f+Y_m, where Y_f and Y_m are the numbers of A_1 among females and males, respectively. The random variable Y_f has the binomial distribution with the following point probabilities, given the number of A_1 is i among the parents in generation t (Δp_{fi} calculated as Δp_f in (1)):

$$P(Y_f=j_f \mid i) = \binom{2N}{j_f}(p_i+\Delta p_{fi})^{j_f}(1-p_i-\Delta p_{fi})^{2N-j_f}$$

$$j_f=0,\dots,2N \quad \text{if } 0<i<4N$$

$$P(Y_f=0 \mid i=0) = 1$$

$$P(Y_f=2N \mid i=4N) = 1.$$

Correspondingly (Δp_{mi} calculated as Δp_m in (2)):

$$P(Y_m=j_m \mid i) = \binom{2N}{j_m}(p_i+\Delta p_{mi})^{j_m}(1-p_i-\Delta p_{mi})^{2N-j_m}$$

$$j_m=0,\dots,2N \quad \text{if } 0<i<4N$$

$$P(Y_m=0 \mid i=0) = 1$$

$$P(Y_m=2N \mid i=4N) = 1.$$

The transition probabilities for $Y=Y_f+Y_m$ are:

$$P(Y=0 \mid i=0) = 1$$

$$P(Y=j \mid i=0) = 0$$

$$j=1,\dots,4N$$

$$P(Y=j \mid i) = \sum_{j_f=0}^{\min(j,2N)} P(Y_f=j_f \mid i)\, P(Y_m=j-j_f \mid i)$$

$$j=0,\dots,4N \qquad i=1,\dots,4N-1$$

$$P(Y=j \mid i=4N) = 0$$

$$j=0,\dots,4N-1$$

$$P(Y=4N \mid i=4N) = 1.$$

Two kinds of transition probability matrices were formed: one for the case F=0 and r=0.5 (Y_1), another for the case F=0.25 and r=0.6 (Y_2). The dimensions of these matrices were (4N+1, 4N+1). Effective population size was assumed to be 2N. To determine the probability of fixation and the average time until fixation, the multiplication was continued 1000 times, using only the Y_1 matrix or using Y_1 and Y_2 alternately. In the latter case N was smaller than in the former in order to represent the decrease in effective population size due to inbreeding in alternate generations. The value used for the intensity of selection was the same in both cases.

The average number of generations until the fixation of either one of the two alleles at 32 equivalent unlinked loci ($\bar{t}_{32}$) was also calculated:

$$\bar{t}_{32} = \sum_{t=1}^{1000} t(Q_t^{32}-Q_{t-1}^{32}) \quad \text{as compared to}$$

$$\bar{t}_1 = \sum_{t=1}^{1000} t(Q_t - Q_{t-1}),$$

where Q_t is the probability of the fixation of either one of the two alleles at one locus in generation t ($Q_0=0$).

For the case of random mating among parents in all generations, the probability of fixation was also calculated using the Kolmogorov backward equation (e.g., Crow and Kimura 1970, p. 423-425). The probability of fixation of a gene with initial frequency p (u(p)) is:

$$u(p) = \int_0^p G(x)dx \Big/ \int_0^1 G(x)dx, \qquad (3)$$

where $G(x) = \exp(-\int 2M_{\Delta x}/V_{\Delta x}\, dx)$.

$M_{\Delta x}$ and $V_{\Delta x}$ are the mean and the variance of the change of gene frequency per generation, respectively. Like in (1):

$$M_{\Delta x} = \frac{x^2+x(1-x)(1-hs)}{x^2+2x(1-x)(1-hs)+(1-x)^2(1-s)} - x$$

$$= \frac{sx(1-x)(1-x+h(2x-1))}{1-s(1-x)(2hx+1-x)},$$

where x is the gene frequency and h=(1-d)/2. For the effective size N_e, the variance $V_{\Delta x}=x(1-x)/(2N_e)$. Thus,

$$2M_{\Delta x}/V_{\Delta x} = 4N_e s \frac{1-x+h(2x-1)}{1-s(1-x)(2hx+1-x)}$$

$$= 2N_e \frac{2s(2h-1)x-2s(h-1)}{s(2h-1)x^2-2s(h-1)x+1-s} \quad \text{and}$$

$$\int 2M_{\Delta x}/V_{\Delta x}\, dx = 2N_e \log(s(2h-1)x^2-2s(h-1)x+1-s)$$

if the integration constant is omitted. This means that

$$G(x) = \exp(-\int 2M_{\Delta x}/V_{\Delta x}\, dx)$$

$$= (s(2h-1)x^2-2s(h-1)x+1-s)^{-2N_e}. \qquad (4)$$

The definite integrals $\int_0^p G(x)dx$ and $\int_0^1 G(x)dx$ were obtained numerically by using the subprogram DCADRE by IMSL, Inc.. The value of s used was 75 % of the coefficient of selection calculated for females in individual selection because male parents were full-brothers of the selected females (the selection coefficient for males is approximately 50 % of that for their full-sisters).

Results

The main aim of simulation was to study the differences between the two mating systems with respect to the selection response and fixation time. For initial frequencies of 0.50 and 0.75 of the favourable allele, there was no fixation of the unfavourable allele at any locus, and the maximum response (all loci fixed for the favourable allele) was attained in all cases (Table 1b,c)(however, see Table 1b'). For an initial frequency of 0.25, the unfavourable allele was fixed at some loci (Table 1a). The differences in U (proportion of loci fixed for the unfavourable allele) between mating systems A and B are small, but, for a degree of dominance of 0.2, U seems to be somewhat higher in the inbreeding system than in A (Table 1a). The differences in U decrease with an increasing degree of dominance (Table 1a), which is understandable because the rate of response in an inbred population relative to that in a random-bred population increases with d (e.g., Sirkkomaa 1986). However, there should be an increase in the expected rate of response due to inbreeding for any degree of dominance used. Therefore, there has been a decrease in the variance effective size due to inbreeding. If the initial frequency of the favourable allele is low, the larger rate of response per generation in the inbreeding system cannot compensate for the decrease in effective size, especially at low degrees of dominance. As a result, there will be a decrease in the probability of fixation.

The time saved (D) until the fixation at all loci was 12-43 %, depending mainly on the degree of dominance (Table 1a,b,c). Only in one case was D for a degree of dominance of

0.2 higher than D for a degree of dominance of 0.8 (h^2=0.075, Table 1b), and in general D for d=0.8 was much larger than D for 0.2. However, the simulation runs made for comparison (Table 1b') show that the result for h^2=0.075 in Table 1b is very probably due to a chance effect. In addition, D clearly increased with d (Table 1b'). The differences in $\bar{G}$ (mean number of generations until fixation at all loci) between systems A and B were fairly large with respect to $S_G/5$ = standard error of $\bar{G}$ (Table 1a,b,c), so the comparisons between the $\bar{G}$ values are sensible. (In Table 1b' the standard error of $\bar{G}$ is $S_G/\sqrt{50}$.) In most cases the coefficient of variation of G was smaller in system B than in system A (Table 1).

In general, for the parameter combinations studied in a fairly large population (Table 1), both mating systems resulted in the same final response to selection (excluding the cases of low degrees of dominance with low initial frequency of the favourable allele). The use of full-sib matings remarkably accelerated fixation, the time saved for a degree of dominance of 0.8 being 21-43 %.

The intermediate case (initial gene frequencies 0.5 at each locus) was also studied by selecting 15♀+15♂ from a population of 60 individuals because there was no fixation of the unfavourable allele for a proportion selected of (100♀+100♂)/400 in Table 1b. Only the case of an initial heritability of 0.075 with a degree of dominance of 0.8 was studied, but the number of replicate runs was 150 (Table 2). In the inbreeding system the final response (P-0.5) was 8.4 % larger and was reached 10.8 % faster than in the other system (Table 2). The coefficients of variation of G were of the same magnitude as for the larger population in Table 1b.

For an initial gene frequency of 0.5, the selection response in simulation (population size 400) and in deterministic calculation were plotted in each generation up to a frequency of 0.975 in order to study the whole process (Fig. 1). The required number of generations up to this frequency and the comparison between simulation and calculation are also presented (Table 3). Two main points are evident in comparing the progress in gene frequency between simulation and calculation (Fig. 1). First, in early generations the rate of response for calculation was higher than that for simulation. This is partly due to the generation of linkage disequilibrium in simulation, especially as the loci were not completely unlinked. Second, at later stages of the progress the situation is reversed, and, for a degree of dominance of 0.8, the goal in gene frequency is attained remarkably earlier in simulation (Fig. 1c, Table 3). To study these findings, some calculations were made of the rate of response in the mean gene frequency at several loci and of that in gene frequency at one locus. The effects of finite population size were not taken into consideration.

Suppose that in some generation the frequencies of genotypes A_1A_1, A_1A_2 and A_2A_2 at each of the 32 unlinked loci are $P_1=p^2$, $P_2=2p(1-p)$ and $P_3=(1-p)^2$, respectively. The total number of different genotypes is 3^{32}, but there are only $\binom{3+32-1}{32}$ = 561 genotypes with different numbers of A_1A_1, A_1A_2 and A_2A_2. The probability of a genotype with n_1 A_1A_1 loci, n_2 A_1A_2 loci and n_3 A_2A_2 loci $(n_1+n_2+n_3=32)$ is

$$\frac{32!}{n_1!n_2!n_3!} P_1^{n_1} P_2^{n_2} P_3^{n_3} = P(n_1,n_2,n_3),$$

if linkage equilibrium is assumed . The value of genotype (n_1,n_2,n_3) is $n_1a+n_2ad-n_3a = v(n_1,n_2,n_3)$, where a is half the difference between the values of A_1A_1 and A_2A_2, and d is the degree of dominance. The mean frequency of gene A_1 in genotype (n_1,n_2,n_3) is $(2n_1+n_2)/64 = m(n_1,n_2)$.

If the environmental deviation is normally distributed with an expectation of 0 and variance V_E (density function $f_N(0,V_E,x)$), on the basis of the theory of mixed distributions, the density function of phenotypic value (f(x)) is:

$$f(x) = \sum_{\substack{n_1,n_2,n_3\\=0\\n_1+n_2+n_3=32}}^{32} P(n_1,n_2,n_3)\, f_N(v(n_1,n_2,n_3),\, V_E,\, x).$$

The response in the mean frequency of the favourable allele A_1 $(\Delta\bar{p})$ was obtained by determining the truncation point (C) that corresponds to the selection of 50 % of the phenotypes, i.e. $\int_C^\infty f(x)dx = 1/2$. Then, the mean fitness $(\bar{W})$ is 1/2 and

$$\Delta\bar{p} = \sum_{\substack{n_1,n_2,n_3\\=0\\ n_1+n_2+n_3=32}}^{32} \left[p(n_1,n_2,n_3)\ m(n_1,n_2\ ) \int_C^{\infty} f_N(v(n_1,n_2,n_3),V_E,x)\,dx \right] / \bar{W} - p.$$

The genotypic values of A_1A_1, A_1A_2 and A_2A_2 and the environmental variances were the same as those calculated in simulation for the three degrees of dominance and for the two initial heritabilities when the initial frequency of A_1 was 0.5. The coefficients of selection in calculating the response at one locus were the same as those used for the theoretical courses of selection. The responses for these two methods of calculation were compared at A_1 frequencies of 0.50, 0.55,..., 0.95 (Fig. 2). The results accord with those in Fig. 1 and Table 3: the rate calculated with 32 loci exceeds that with one locus at a lower level of gene frequency for a degree of dominance of 0.8 than for smaller degrees of dominance. As a result, the given frequency of A_1 (0.975) was attained for d=0.8 earlier in simulation than in calculation at one locus (Fig. 1 and Table 3).

In the calculation for one locus the coefficient of selection (s) was obtained from the product of the intensity of selection and the initial standardized effect of the locus, which is an approximation for small effects (Falconer 1981). In the calculation for 32 loci the mean response was obtained directly from the relevant mixed distribution for each gene frequency, without assuming anything about the values of the coefficients of selection at individual loci. It is evident that with decreasing standardized effects the ratios approach 1.0 (Fig. 2).

In simulation the time saved due to inbreeding in attaining a given response was somewhat higher for an initial heritability of 0.075 than for that of 0.250 (Table 3). This accords with the result that the use of full-sib mating in alternate generations should save more time in weak selection than in a stronger one, because there is a larger coefficient of inbreeding (F) in the former case (Sirkkomaa 1986). In weak selection F in inbred generations rapidly reaches a value of nearly 1/3, if all the matings have been between full-sibs. In strong selection F reaches a lower value.

However, in the deterministic calculation a constant value of 0.25 was used for F in inbred generations. The recurrence relation for F in an infinite population can be expressed (e.g., Crow and Kimura 1970):

$$F_t = R(1+2F_{t-1}+F_{t-2})/4, \qquad (5)$$

where R is the fraction of the population practicing full-sib mating and t is generation. The fraction 1-R is practicing random mating. In the mating method of the present simulation model, R is expected to be less than 1 because in inbreeding generations the females without full-brothers are mated with males sampled at random. Consider numerically only a simple case, in which M females and M males are produced by N_f females (multinomial sampling) in each generation and each female has only one mate. Then, the probability that a randomly chosen progeny female has at least one full-brother is $1-(1-1/N_f)^M = R$. For instance, if $N_f=100$ and $M=200$, R is about 0.866.

Using (5), the equilibrium value of F in inbred generations was studied ($F_0=0$, $F_1=0$, $t=2, \ldots, 50$). At even values of t, F_t was calculated as in (5), whereas, at odd values of t, F_t was set to be 0. An equilibrium value for F was reached rapidly (Table 4). If the relevant value of R is about 0.85, F in a large population might not differ very much from 0.25, being a little bit higher for a weak selection pressure than for a stronger one.

A simulation experiment was performed to study the decrease of the effective population size at small numbers in the present inbreeding system. The breeding structure was (10♀ +10♂)/60 without the phenotypic selection of females, and the initial gene frequencies were 0.5 at each locus. In 200 replicate runs the mean numbers of generations ± standard errors of the means until fixation at all of the 32 loci were 90.06 ± 1.76 for the inbreeding system and 101.96 ± 2.10 for the random-mating system. Thus, the representative variance effective size in the inbreeding system would be roughly 90 % of the variance effective size (N_e) in the random-mating system, if the time until fixation is linearly dependent on N_e as it is in the case of one locus (Kimura and Ohta 1969).

In the Markov chain calculation for the change of gene frequency in a small population the probability of fixation of the favourable allele was clearly smaller in the inbreeding system than in random mating, when the decrease in N_e was assumed to be 20 % (B_1, Table 5). This shows that for small numbers the advantage of inbreeding in the ultimate response is very sensitive to a possible decrease in N_e. However, for a decrease of 10 % in N_e, the response was somewhat higher in the inbreeding system than that in random mating, and the fixation at one locus was reached 12.3-17.6 % faster (B_2, Table 5). For 32 loci the time saved until fixation was 12.8-19.4 %. The probability of fixation for random mating calculated by numerical integration was practically the same as that obtained by the matrix method (Table 5).

In spite of using a constant departure of 0.25 from Hardy-Weinberg proportions for inbred generations and a constant coefficient of selection during the process, the results for 32 loci with s=0.105 and d=0.8 in Table 5 are qualitatively fairly similar to the simulated results in Table 2. The effective population sizes in these two cases are not identical. Using (3) and (4), it was calculated on the basis of the average probability of fixation observed in simulation (Table 2) that N_e without inbreeding must have been only 13-14.

Discussion

In addition to the dependence on the degree of dominance, the possibilities of the use of intentional inbreeding to increase the response to selection are dependent on the changes in effective population size and in selection pressure. Assume a large population with random mating and full-sib mating in alternate generations. The departure from Hardy-Weinberg proportions (F) in inbred generations will rapidly approach an equilibrium value of 1/3 (Table 4). In weak selection there is also approximately the same result in the group selected to breed.

For a monoecious population of constant size the variance effective number (N_e) is (Crow and Kimura 1970):

$$N_e = \frac{2N}{\frac{N}{N-1}\,\frac{V}{2}(1+F)+1-F},$$

where N and V are the actual number of parents in each generation and the variance of the number of gametes contributed per parent to the breeding group of the next generation, respectively. When there are separate sexes with equal progeny distributions, the effective size for large numbers is practically the same as in the case of a monoecious population. In a large population with random mating in all generations (case A), F is approximately 0 and $N_{e(A)} = 4N/(v+2)$, where $v = VN/(N-1)$. If F is 1/3 in inbred generations of the alternating system (case I), $N_{e(I)} = 3N/(v_I+1)$. In random-bred generations of the alternating system (case R), F is 0 and $N_{e(R)} = 4N/(v_R+2)$. The representative variance effective size over two generations ($N_{e(T)}$) in the alternating system is approximately the harmonic mean of $N_{e(I)}$ and $N_{e(R)}$:

$N_{e(T)} = 2/(1/N_{e(I)}+1/N_{e(R)}) = 24N/(4v_I+3v_R+10)$.

The ratio of $N_{e(T)}$ to $N_{e(A)}$ (Q) is:

$Q = N_{e(T)}/N_{e(A)} = (6v+12)/(4v_I+3v_R+10)$.

In the mating method of the present simulation (equal numbers of both sexes in the breeding group, each male can mate with several females) the number of gametes contributed per female without selection follows a binomial distribution, so v for females is 2. The distribution of the number of gametes contributed per male is more difficult to derive because it depends also on the total number of males (the male group chosen to mate is a sample from the set of full-brothers of the selected females). If the size of the breeding group is equal to the total population size, v for males is over 8 for large numbers (a rough calculation by the author). This means that the combined v from females and males is at least 5. Q is about 93 % for $v = v_I = v_R = 5$.

In real populations with inbreeding v_I and v_R might be considerably larger than v, due to inbreeding effects. For instance, in an inbred generation there may be an increase in v_I if the expected number of progeny to the breeding group of the next generation is not the same for each parent. In a random-bred generation with full-sib mating in the selected group, there are probably viability disturbances produced in the next generation. The ratio Q was calculated for some combinations of v, v_I and v_R (Table 6). There is a fairly rapid decrease in Q to 0.5 with increasing v_I and v_R. (However, the limit is not 0.5.)

In strong selection for a character there is an increase in v (Robertson 1961). The diminishing effect of F on N_e increases with v_I. On the other hand, for strong selection, F in the selected group is smaller than for a weaker one, so the decreasing influence of strong selection on N_e diminishes.

A decrease in the variance effective size is not inevitable for inbred populations. If $v_I<2$, there is actually an increase in N_e due to inbreeding. However, this is rather unrealistic because of the apparent disturbances in fertility and viability due to inbreeding in most populations. The magnitudes of these disturbances are not very predictable because they depend heavily on the genetic composition of the base population and on the dominance relations at loci. It can be expected that v_I and v_R are going to decrease if the population is purified of some detrimental genes in the course of generations, and without lowering N_e a higher level of inbreeding could be successfully used than in the early phases of the process. However, in a large population a proportionate decrease in N_e is perhaps not very serious if the reduced number still is high. In a small population a decrease in N_e has catastrophic consequences on the long-term response to selection (Robertson 1970).

It is evident that the worst problem in using an inbreeding system is the dependence of the selection intensity on the degree of inbreeding in most populations. There is not much use of the increased genetic variance created by inbreeding if the group chosen as parents does not positively differ from the population mean with respect to the character selected for. In a selection experiment of MacNeil et al. (1984a,b) with Japanese quail, there was no advantage of the alternating system in the total response to selection of 16 generations for a biomass index. This is understandable because there were severe inbreeding effects in fertility and viability, and the selection differentials in the alternating system were significantly lower than those in the random-mating system. However, the rate of response in the alternating system exceeded that in the random-mating system in later generations, apparently due to adaptation to inbreeding.

Dion and Minvielle (1985) selected for pupal weight in Tribolium. There was no significant difference between the random-mating and alternating systems in the response to the selection of 15 generations, despite the fact that the average selection differential over generations was slightly larger in the inbreeding system. Unfortunately, the populations were small (15 pairs of parents selected from 55-70 individuals), and there were only two replicates for both systems. There were no detrimental effects of full-sib mating on reproductive performance. The authors believe that gene frequencies in the base population were close to 0.5. In the present simulation experiment with a similar proportion selected and certainly without any problems in regard to fertility and viability, the response of 15 generations in the inbreeding system was only 3.4 % higher than that in the random-mating system (degree of dominance 0.2, initial gene frequencies 0.5, initial heritability 0.25). In spite of differences in the parameter values and in the methods of selection and mating, on this basis the results obtained by Dion and Minvielle (1985) are not very surprising. The results of long-term selection experiments (e.g., 30 generations) would be interesting.

Using a deterministic model for the response to selection in an infinite population, the problem of the decreasing selection intensity due to inbreeding will be studied. The question is: how much can the selection pressure at individual loci diminish so that the response after a given number of generations in the inbreeding system still is larger than that in the random-mating system? A proportionate reduction in the coefficient of selection due to inbreeding is assumed in these calculations, which are in preparation.

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Table 1a,b,c

The number of generations (G) until the fixation of either one of the two alleles at all of the 32 loci ($\overline{G}$ = mean of the 25 replicate runs, S_G = standard deviation of G, CV_G = coefficient of variation of G), the decrease in fixation time due to full-sib mating (D), and the mean proportion of loci fixed for the unfavourable allele (U). The initial frequency of the favourable allele at each locus was 0.25 (a), 0.50 (b) and 0.75 (c).

A: random mating in all generations

B: random mating and full-sib mating in alternate generations

d: degree of dominance at each locus

h^2: initial heritability

Table 1a

h^2	d		$\overline{G}$	S_G	CV_G(%)	D(%)	U(%)
0.075	0.2	B	190.64	29.44	15.4	23.9	3.125
		A	250.36	80.15	32.0		2.125
	0.5	B	247.88	47.77	19.3	20.1	1.750
		A	310.36	86.45	27.9		1.750
	0.8	B	278.52	32.12	11.5	32.2	1.000
		A	410.52	87.48	21.3		1.625
0.250	0.2	B	106.72	14.01	13.1	12.1	1.000
		A	121.40	16.38	13.5		0.250
	0.5	B	128.96	20.04	15.5	15.7	0.250
		A	153.00	39.00	25.5		0
	0.8	B	176.72	35.43	20.0	21.4	0.125
		A	224.72	42.35	18.8		0

Table 1b (Initial frequency of the favourable allele is 0.5)

h^2	d		$\overline{G}$	S_G	CV_G(%)	D(%)	U(%)
0.075	0.2	B	157.44	31.99	20.3	25.2	0
		A	210.52	51.77	24.6		0
	0.5	B	206.76	65.52	31.7	14.4	0
		A	241.56	51.93	21.5		0
	0.8	B	240.52	57.72	24.0	21.0	0
		A	304.56	91.06	29.9		0
0.250	0.2	B	95.36	20.24	21.2	12.1	0
		A	108.44	15.87	14.6		0
	0.5	B	113.48	18.52	16.3	12.2	0
		A	129.20	23.64	18.3		0
	0.8	B	126.52	23.22	18.4	30.2	0
		A	181.24	42.48	23.4		0

Table 1b'

As 1b, but all the loci were on the same chromosome (for the number of crossing-over points the parameter value of Poisson distribution was 10.0, see Methods). In addition, the number of replicate runs was 50.

h^2	d		$\overline{G}$	S_G	CV_G(%)	D(%)	U(%)
0.075	0.2	B	177.48	38.89	21.9	11.4	0.125
		A	200.42	34.95	17.4		0.125
	0.5	B	205.62	44.31	21.5	13.8	0
		A	238.60	52.34	21.9		0
	0.8	B	236.04	42.86	18.2	21.6	0
		A	300.94	50.95	16.9		0
0.250	0.2	B	93.62	15.26	16.3	15.2	0
		A	110.46	13.96	12.6		0
	0.5	B	107.82	18.53	17.2	21.5	0
		A	137.30	26.76	19.5		0
	0.8	B	131.00	29.83	22.8	28.7	0
		A	183.72	44.32	24.1		0

Table 1c (initial frequency of the favourable allele is 0.75)

h^2	d		$\overline{G}$	S_G	CV_G(%)	D(%)	U(%)
0.075	0.2	B	110.36	26.86	24.3	14.4	0
		A	129.00	25.62	19.9		0
	0.5	B	114.08	24.42	21.4	23.7	0
		A	149.48	36.02	24.1		0
	0.8	B	115.52	33.42	28.9	30.9	0
		A	167.24	41.65	24.9		0
0.250	0.2	B	54.68	7.26	13.3	25.3	0
		A	73.16	16.47	22.5		0
	0.5	B	66.40	10.06	15.2	26.3	0
		A	90.08	25.09	27.9		0
	0.8	B	64.88	9.96	15.4	43.0	0
		A	113.80	20.54	18.0		0

Table 2

The number of generations (G) until the fixation of either one of the two alleles at all of the 32 loci ($\overline{G}$ = mean of the 150 replicate runs, S_G = standard deviation of G, CV_G = coefficient of variation of G) and the proportion of loci fixed for the favourable allele (P). D and I are the decrease in fixation time and the increase in response due to full-sib mating, respectively. The degree of dominance at each locus is 0.8. The initial heritability was 0.075. The initial frequency of the favourable allele at each locus was 0.5. The proportion selected was (15♂+15♀)/60 in each generation.

	Random mating in all generations	Random mating and full-sib mating in alternate generations
$\overline{G}$	138.44	123.47
S_G	34.15	36.21
CV_G(%)	24.7	29.3
P	0.757	0.779
D(%)		10.8
I(%)		8.4

Table 3

The number of generations (G) required to attain 95 % of the maximum response, the decrease in time due to full-sib mating (D) and the result of simulation compared with that of deterministic calculation (G_{Sim}/G_{Cal}). The initial frequency of the favourable allele was 0.5.

Sim: simulated (change in the mean frequency of the favourable allele at 32 loci, results averaged from 25 replicate runs)

Cal: calculated (change in gene frequency at one locus)

A: random mating in all generations

B: random mating and full-sib mating in alternate generations

d: degree of dominance

h^2: initial heritability

h^2	d		G Sim	G Cal	G_{Sim}/G_{Cal}	D(%) Sim	D(%) Cal
0.075	0.2	B	92	82	1.12	18.6	18.8
		A	113	101	1.12		
	0.5	B	109	100	1.09	18.0	25.4
		A	133	134	0.99		
	0.8	B	115	132	0.87	27.7	39.4
		A	159	218	0.73		
0.250	0.2	B	51	44	1.16	10.5	20.0
		A	57	55	1.04		
	0.5	B	56	54	1.04	16.4	26.0
		A	67	73	0.92		
	0.8	B	66	72	0.92	26.7	39.5
		A	90	119	0.76		

Table 4

The coefficient of inbreeding in generation t (F_t) for various values of R (the fraction of the population practicing full-sib mating). $F_0=F_1=0$, and there are random mating and full-sib mating in even and odd generations, respectively.

R	F_2	F_4	F_{10}	F_{50}
0.60	.150	.173	.176	.176
0.80	.200	.240	.250	.250
0.85	.213	.258	.270	.270
0.90	.225	.276	.290	.290
0.95	.238	.294	.311	.311
1.00	.250	.313	.333	.333

Table 5

The probability of fixation of the favourable allele (P), the number of generations (G) until the fixation of either one of the two alleles ($\bar{G}$ = expectation of G, S_G = standard deviation of G, CV_G = coefficient of variation of G) and the decrease in fixation time due to the B_2 mating (D), Markov chain calculation. The time parameters until the fixation of either one of the two alleles at all of the 32 equivalent unlinked loci are also given. The proportion selected is (10♂+ 10♀)/40 in each generation. The initial frequency of the favourable allele is 0.5.

A: random mating in all generations, effective size assumed to be 20

B: random mating and full-sib mating in alternate generations, representative effective size assumed to be 16 (B_1) or 18 (B_2)

A_I: as A, but calculated by numerical integration

d: degree of dominance

s: coefficient of selection

			Fixation at one locus					Fixation at 32 loci			
s	d		P	$\bar{G}$	S_G	CV_G(%)	D(%)	$\bar{G}$	S_G	CV_G(%)	D(%)
.105	.2	B_1	0.829								
		B_2	0.856	41.33	29.39	71.1	12.3	129.85	36.42	28.0	12.8
		A	0.847	47.15	33.76	71.6		148.91	41.89	28.1	
		A_I	0.844								
	.5	B_1	0.834								
		B_2	0.861	43.36	31.27	72.1	13.5	137.65	38.82	28.2	14.1
		A	0.853	50.10	36.52	72.9		160.32	45.40	28.3	
		A_I	0.852								
	.8	B_1	0.838								
		B_2	0.866	45.55	33.32	73.2	14.6	146.12	41.42	28.3	15.5
		A	0.860	53.35	39.59	74.2		172.95	49.30	28.5	
		A_I	0.860								
.192	.2	B_1	0.956								
		B_2	0.970	30.78	19.39	63.0	14.0	88.19	23.25	26.4	15.2
		A	0.967	35.80	22.97	64.2		103.95	27.65	26.6	
		A_I	0.964								
	.5	B_1	0.961								
		B_2	0.974	33.02	21.28	64.4	15.7	96.12	25.57	26.6	17.2
		A	0.972	39.17	25.86	66.0		116.08	31.25	26.9	
		A_I	0.971								
	.8	B_1	0.965								
		B_2	0.978	35.56	23.49	66.1	17.6	105.39	28.36	26.9	19.4
		A	0.976	43.13	29.39	68.1		130.82	35.75	27.3	
		A_I	0.976								

Table 6

The ratio of the variance effective number of a large population of constant size with random mating and full-sib mating in alternate generations to that with random mating in all generations, as a function of the variance of the number of gametes contributed per parent to the breeding group of the next generation (v). For random mating in all generations, v is assumed to be 5.

v_I: v in inbred generations of the alternating system
v_R: v in random-bred generations of the alternating system

	v_I					
v_R	5	6	7	8	9	10
5	0.93	0.86	0.79	0.74	0.69	0.65
6	0.88	0.81	0.75	0.70	0.66	0.62
7	0.82	0.76	0.71	0.67	0.63	0.59
8	0.78	0.72	0.68	0.64	0.60	0.57
9	0.74	0.69	0.65	0.61	0.58	0.55
10	0.70	0.66	0.62	0.58	0.55	0.53

Fig. 1a,b,c

The change in the mean frequency of the favourable allele at 32 loci (MF) up to 95 % of the maximum response, and the calculated change at one locus. The initial heritabilities were 0.075 (h_1^2) and 0.250 (h_2^2). The degree of dominance (d) is 0.2 (a), 0.5 (b) and 0.8 (c).

Sim: simulated (average of 25 replicate runs)
Cal: calculated (deterministic change at one locus)

——●
random mating in all generations
- - -○

——▲
random mating and full-sib mating in alternate generations
- - -△

Fig. 1a

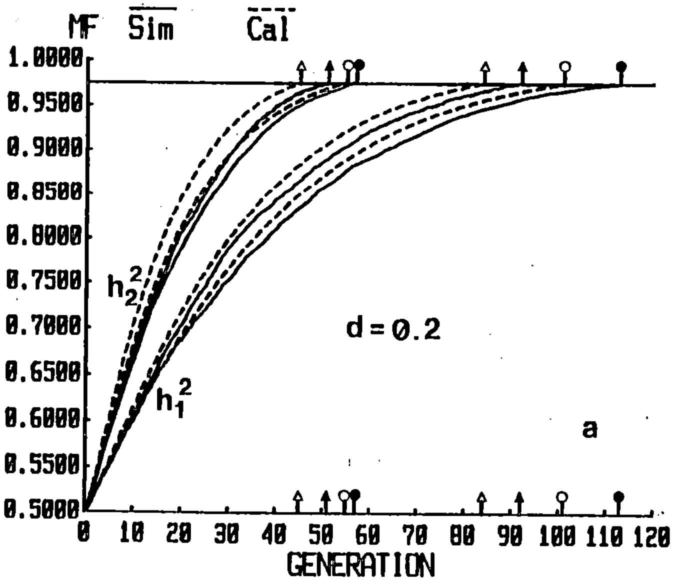


Fig. 1b (degree of dominance is 0.5)

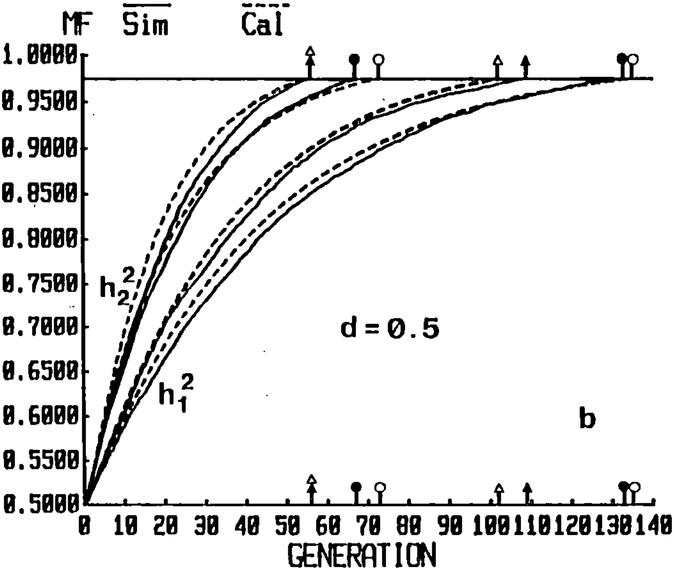
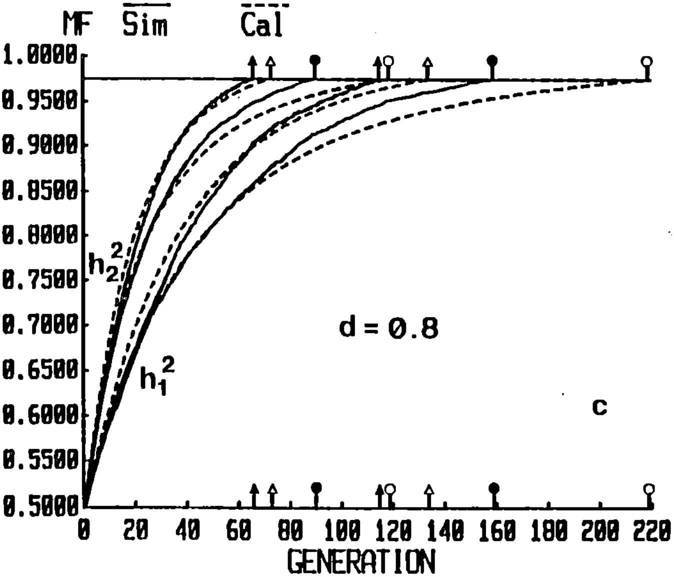


Fig. 1c (degree of dominance is 0.8)



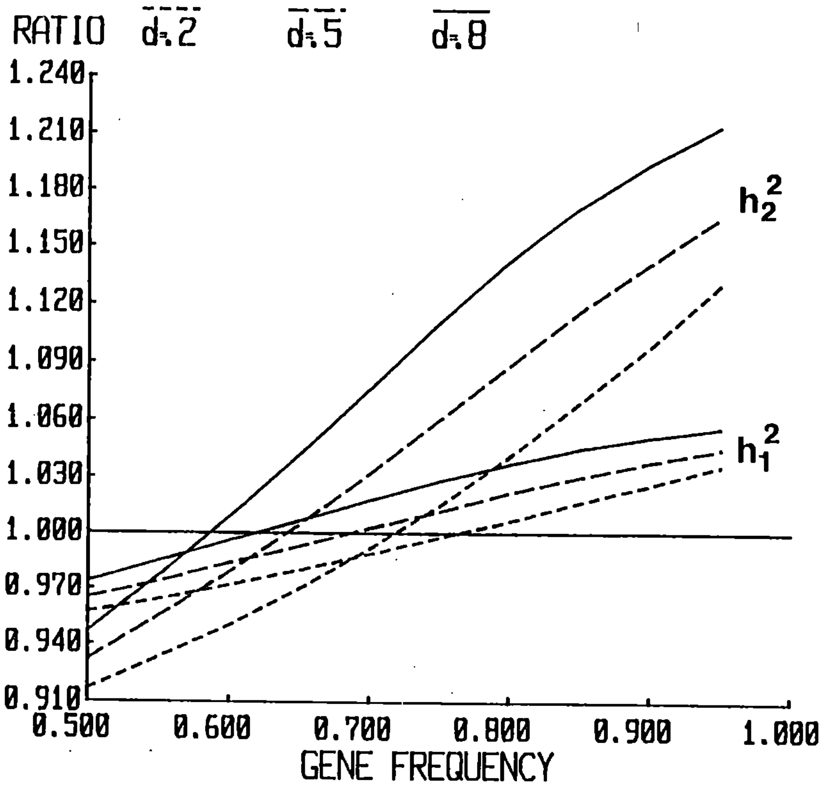


Fig. 2

The ratio of the change of the mean frequency of the favourable allele at 32 loci to the change of gene frequency at one locus as a function of the gene frequency before selection (unselected population in random-mating genotype proportions). In the case of 32 loci exactly the same genotypic values and the same environmental variance were used as in simulation, and half the population was selected. For the change at one locus exactly the same coefficients of selection were used as in calculating the theoretical courses of selection.

d: degree of dominance

h_1^2: calculated for an initial heritability of 0.075

h_2^2: calculated for an initial heritability of 0.250

V

Use of inbreeding to increase the responses to various intensities of selection

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Summary. Effects of inbreeding on the response to selection at a diallelic locus were studied by a deterministic model using varying values of p (initial frequency of the favourable allele), d (degree of dominance over the unfavourable allele), s (selection coefficient in females) and t (number of generations in the breeding programme). The breeding males were full-brothers of the selected females. In the random-mating system (RS) there was random mating among the breeding individuals in every generation. In the alternating system (AS) there was random mating in even generations and full-sib mating in odd generations.

The principal aim of the study was to discover the maximum loss in s (ML) due to inbreeding so that the response for the AS is at least equal to the response for the RS with s. In weak selection (s=0.01) for an additive locus (d=0.0), ML was 19-21 %, nearly independently of p (0.2, 0.5, 0.8) and t (20, 50, 100). In strong selection (s=0.80) for d=0.0, ML was 14-18 %. For larger values of d the results were more variable. In general, ML increased with d, s and t, being 72-79 % for d=1.0, s=0.80, t=100. It was concluded that there might be some use for the AS in increasing the long-term response for a quantitative character controlled by many loci if the loss in the selection differential due to the AS is clearly below 15 %.

Key words: Inbreeding - Mating system - Selection response

Introduction

Inbreeding as a means of increasing genetic variation and heritability has not been a method of practical use in animal breeding. Lush (1945) deduced that there might be some advantage of mild inbreeding in the selection response, especially in family selection. Calculations on the potential use of inbreeding in a large population have shown that the decrease in the intensity of selection due to various inbreeding effects may be the principal difficulty in applying the method (e.g., Dickerson and Lindhé 1977). In a selection experiment with Japanese quail, MacNeil et al. (1984a,b) found that the average selection differential over generations was clearly smaller for the populations with alternate random and full-sib mating generations than for those with random mating alone. This must have been an important reason why the alternating mating system failed to exceed the selection response attained by the random-mating system.

The main purpose of the present study was to evaluate the maximum loss of selection intensity for which the response in the alternating system still is at least equal to that in random mating. Direct selection was on females only, yet there was full-sib selection of breeding males. Only a deterministic model for a single diallelic locus was considered.

Methods

1. General

Consider an autosomal locus with alleles A_1 and A_2. Let the relative fitnesses of genotypes A_1A_1, A_1A_2 and A_2A_2 among females in truncation selection be 1, 1-hs and 1-s respectively, where s is the coefficient of selection and h=(1-d)/2 (d is the degree of dominance). The genotype frequencies within the progeny groups of different mating types (matrix A) and the mean fitnesses of females (matrix B) are:

$$\begin{array}{llccccl}
\text{Mating type} & & \multicolumn{3}{c}{\text{Genotype}} & & \text{Mean fitness} \\
\text{(MT)} & & A_1A_1 & A_1A_2 & A_2A_2 & & \\
1 & A_1A_1xA_1A_2 & 1/2 & 1/2 & 0 & & 1-hs/2 \\
2 & A_1A_1xA_2A_2 & 0 & 1 & 0 & & 1-hs \\
3 & A_1A_2xA_2A_2 & 0 & 1/2 & 1/2 & = A & 1-(h+1)s/2 \quad = B. \\
4 & A_1A_1xA_1A_1 & 1 & 0 & 0 & & 1 \\
5 & A_2A_2xA_2A_2 & 0 & 0 & 1 & & 1-s \\
6 & A_1A_2xA_1A_2 & 1/4 & 1/2 & 1/4 & & 1-(h+1/2)s/2
\end{array}$$

The genotype frequencies among the selected females within the mating types are (matrix C) (the b's are elements of B):

$$\begin{array}{c|ccc|l}
\text{MT} & A_1A_1 & A_1A_2 & A_2A_2 & \\
1 & 1/(2b_1) & (1-hs)/(2b_1) & 0 & \\
2 & 0 & 1 & 0 & \\
3 & 0 & (1-hs)/(2b_3) & (1-s)/(2b_3) & = C. \\
4 & 1 & 0 & 0 & \\
5 & 0 & 0 & 1 & \\
6 & 1/(4b_6) & (1-hs)/(2b_6) & (1-s)/(4b_6) &
\end{array}$$

If there is random mating within the progeny groups of the mating types, on the basis of matrices A, B and C the corresponding mating-type frequencies are (matrix U, which is equivalent to the generation matrix in within-line selection (e.g., Clegg and Kidwell 1974)):

MT in the progeny group

$$\begin{array}{c|cccccc|}
\text{MT} & 1 & 2 & 3 & 4 & 5 & 6 \\ \hline
1 & \frac{1}{2} & 0 & 0 & \frac{1}{4b_1} & 0 & \frac{1-hs}{4b_1} \\
2 & 0 & 0 & 0 & 0 & 0 & 1 \\
3 & 0 & 0 & \frac{1}{2} & 0 & \frac{1-s}{4b_3} & \frac{1-hs}{4b_3} \\
4 & 0 & 0 & 0 & 1 & 0 & 0 \\
5 & 0 & 0 & 0 & 0 & 1 & 0 \\
6 & \frac{1-hs/2}{4b_6} & \frac{1-s/2}{8b_6} & \frac{1-(h+1)s/2}{4b_6} & \frac{1}{16b_6} & \frac{1-s}{16b_6} & \frac{1-hs}{4b_6}
\end{array} = U.$$

2. Calculation of the response

Among the female parents in generation 0 the frequencies of genotypes A_1A_1, A_1A_2 and A_2A_2 are p_1, p_2 and p_3, respectively (matrix $P(1{\times}3)$). The corresponding frequencies among the male parents are q_1, q_2 and q_3 (matrix $Q(1{\times}3)$). Then, the frequencies of the mating types in random mating are (matrix E):

$$\begin{array}{c|c|}
\text{MT} & \text{Frequency} \\ \hline
1 & p_1q_2 + p_2q_1 \\
2 & p_1q_3 + p_3q_1 \\
3 & p_2q_3 + p_3q_2 \\
4 & p_1q_1 \\
5 & p_3q_3 \\
6 & p_2q_2
\end{array} = E'.$$

The genotype frequencies in generation 1 are:

A_1A_1 $\quad e_1/2 + e_4 + e_6/4$

A_1A_2 $\quad e_1/2 + e_2 + e_3/2 + e_6/2$

A_2A_2 $\quad e_3/2 + e_5 + e_6/4.$

The mean fitness ($\bar{W}$) is EB, and the frequencies of the progeny groups of the mating types among the selected females in generation 1 are (matrix V):

$$\begin{array}{cc} \text{MT} & \text{Frequency} \\ \begin{array}{c} 1 \\ 2 \\ 3 \\ 4 \\ 5 \\ 6 \end{array} & \begin{bmatrix} e_1b_1 \\ e_2b_2 \\ e_3b_3 \\ e_4b_4 \\ e_5b_5 \\ e_6b_6 \end{bmatrix} \end{array} \times \frac{1}{\bar{W}} = V.$$

The genotype frequencies among the selected females and among their full-brothers are P=V'C and Q=V'A, respectively. If there is random mating in generation 1, the calculation is continued by computing new values for the elements of E as in generation 0. However, if there is full-sib mating in generation 1, E=V'U and the calculation is continued as described above.

In generation 0 the three genotypes were in Hardy-Weinberg proportions according to the initial frequency of allele A_1 (0.2, 0.5 or 0.8). Males were not selected in generation 0. In the alternating system (AS) there was full-sib mating in odd generations and random mating in even generations. In the random-mating system (RS) there was random mating in every generation.

Five coefficients of selection were used (0.01, 0.10, 0.20, 0.50 or 0.80) in order to clarify the differences between weak and strong selection. The degree of dominance over the unfavourable allele A_2 was 0.00 (additive case), 0.25, 0.50, 0.75, or 1.00 (complete or full dominance).

Results and discussion

The responses to 20, 50 and 100 generations of selection were calculated for both methods of mating. In general, for weak selection (s=0.01) at an additive locus (d=0.00), the increase in response due to inbreeding (I) was 23-31 % (Table 1a,b,c). For weak selection at a locus with full dominance (d=1.00), the results were much more variable, the increases in response being 14-18 %, 25-27 % and 68-71 % for initial frequencies of 0.2, 0.5 and 0.8, respectively (Table 1a,b,c). However, for an initial frequency of 0.5 (Table 1b) in weak selection the increase in response was fairly independent of the degree of dominance and of the number of generations in the breeding programme (24-27 %). It is natural that for stronger selection pressures (s=0.10,...,0.80) the differences in response between the two methods of breeding were small because of the approach to the maximum change in gene frequency, especially in the long term (Table 1a,b,c). The increase in response due to inbreeding was an increasing function of the degree of dominance, except for weaker selection pressures (s=0.01,0.10,0.20) for an initial frequency of 0.2, especially in the short term.

The number of generations required for the inbreeding method to attain the response reached by the random-mating method in 20, 50 and 100 generations was also determined. For an additive locus the results were very uniform for all the initial frequencies and the coefficients of selection, the decrease in time due to inbreeding (D) being 15-21 % (Table 1a,b,c). In addition, for an initial frequency of 0.5 (Table 1b) in weak selection (s=0.01), D was independent of the degree of dominance, being 15 % in the short term (20 generations) and 21-23 % in the long term (100 generations). In weak selection at a locus with full dominance, the decreases in time were 10-13 % and 35-44 % for initial frequencies of 0.2 and 0.8, respectively (Table 1a,c).

In general, D increased with the number of generations in the breeding programme, with the coefficient of selection and with the degree of dominance (Table 1). For the strongest selection (s=0.80) in a programme of 100 generations, at a locus with full dominance the decreases in time were 71 %, 73 % and 77 % for initial frequencies of 0.2, 0.5 and 0.8, respectively.

In real populations the coefficient of selection (s) might not be the same for the two methods of breeding. For instance, MacNeil et al. (1984a,b) found in Japanese quail that the average selection differential (SD) for a biomass index in the alternating method was smaller than that in the random-mating method. As a result, s would diminish because of the dependence on SD. For a small standardized effect of a locus, s is even a linear function of SD (Haldane 1931; Kimura and Crow 1978; Falconer 1981), if the character in question is normally distributed. For a general differentiable character distribution, s is linearly dependent on the ratio of the ordinate at the truncation point to the proportion selected, if the standardized effect is small (Kimura and Crow 1978).

In the calculations for Table 2 it was supposed that s will be smaller in the alternating method than in the random-mating method due to various effects of inbreeding on fertility and viability. A constant decrease in s with respect to generations was assumed, although it is probable that the difference in s between the two methods of breeding will diminish in the course of generations as the population practicing inbreeding is purified of many harmful recessive genes. This kind of change was observed by MacNeil et al. (1984a,b). On the other hand, in any breeding programme there is no constant s at a locus because the gene frequency changes at all of the loci affect the variability of the character selected for.

The results for an additive locus were fairly independent of the number of generations in the selection programme and of the initial frequency of the favourable allele (Table 2). In weak selection (s=0.01), a maximum loss of 19-21 % (average 20 %) in s was obtained in order that the response in the inbreeding method was at least equal to that in the random-mating method. In strong selection (s=0.80), the corresponding loss in s was 14-18 % (average 16 %). For medium coefficients of selection (s=0.10,...,0.50) at an additive locus, the maximum loss was 16-20 % (Table 2). Thus, for an additive locus we could expect some advantage from the alternating system if the loss in the selection differential remains clearly below 20 % and selection is not very strong. In strong selection the bearable loss in SD is below 15 %.

With increasing degrees of dominance the results were more variable. In the case of complete dominance, much larger maximum losses in s were obtained for the high initial frequency (0.8) than for the low one (0.2). There was also a tendency that larger maximum losses in s were obtained in the long term than in the short term, especially at high degrees of dominance in strong selection (Table 2).

In the selection experiment of 16 generations by MacNeil et al. (1984a,b), the average SD over generations in the alternating system was 18.4 % lower than that in the random-mating system, and there was no advantage of inbreeding in the total response to selection. This result accords with the calculations of the present study, unless a high average degree of dominance is assumed (Table 2). In a selection experiment of 15 generations for pupal weight in Tribolium, the average SD in the AS was slightly larger than that in the RS (Dion and Minvielle 1985). In spite of this, there was no significant difference in the total response between the two methods of mating. Unfortunately, the numbers of individuals were small in all lines, so there may be large effects of sampling in the results.

In general, the bearable loss in s increased with the degree of dominance (except in weak selection for an initial frequency of 0.2) and with the number of generations in the breeding programme. The bearable loss also increased with the strength of selection, except that there was a slight decrease for degrees of dominance of 0.00 and 0.25. For strong selection at a locus with full dominance, losses of 70-80 % in s might be bearable in a long-term programme (Table 2).

In an earlier study using a deterministic model it was found that the increase in the rate of genetic progress caused by the AS relative to the RS was somewhat larger for weak selection than for stronger (Sirkkomaa 1986). In the AS, for weak selection the departure from random-mating proportions (F) in inbred generations before selection rises rapidly near 1/3, whereas the frequency of the favourable allele rises very slowly. On the other hand, F in inbred generations remains clearly lower for strong selection than for weak selection, and the gene frequencies change rapidly. Thus, Wright's coefficient of relationship between full-sibs (r) in weak selection also reaches a higher level than that in a stronger one. The rise in r is an important aspect in the possible use of inbreeding to increase the responses to family and sib selection, as was pointed out by Lush (1945).

In the present study strong and weak selection were compared with respect to the changes in F and in the efficacy of sib selection. In weak selection (s=0.01), F reached a value of 0.33 in a few generations, while in strong selection (s=0.50) the rise was lower (F_{AS}, Fig. 1). For weak selection the selection differential of males in the random-bred generations of the AS reached about 66 % of that of their full-sisters (SD_{AS}, Fig. 1). In the inbred generations SD_{AS} reached about 62 %. For comparison, in the random-bred and inbred generations of the AS without selection, the coefficients of relationship between full-sibs would be 2/3 (=0.666...) and 5/8 (=0.625), respectively. The cyclical changes in SD_{AS} took place at a lower level for strong selection than for the weak one (Fig. 1). In the RS the differences in the efficacy of full-sib selection between the two strengths of selection were not large (SD_{RS}, Fig. 1). In random mating without selection the coefficient of relationship would be 1/2.

To clarify the possible superiority of weak selection over strong selection with respect to the use of inbreeding, the time in generations required to attain 95 % of the maximum response was determined using the present model. There was a clear decline in the time saved due to inbreeding with increasing coefficients of selection, but in many cases the decrease in D was only marginal (Table 3a,b,c). In reality, the coefficients of selection at individual loci are unavoidably small if many loci contribute to the trait selected for or environmental effects are large. Moreover, the intensity of selection could be deliberately made rather low in order to maximize the long-term response in a finite population (Robertson 1960, 1970). However, in the planning of selection programmes it is not common to consider the time required to attain a given response.

Effective population size (N_e) was not considered in the present study because of the deterministic model. In real populations of finite number there might be fluctuations in the size of the breeding group (N) due to the harmful effects of inbreeding. In addition, even if N would remain constant, there might be a considerable increase in the variance of the number of progeny contributed per parent to the breeding group of the next generation. In these cases inbreeding would lessen the variance effective size, and there would be an increase in the variance of gene frequency change (Crow and Kimura 1970). On the other hand, for a very large population with a large number selected, N_e remains high in spite of the inbreeding effects, and the drift variance can be ignored when considering the responses to selection, even in the long term.

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Table 1a,b,c. The response in gene frequency for random mating in all generations (R), the increase in response due to full-sib mating in alternate generations (I), and the decrease in time due to full-sib mating in reaching R (D). The initial frequency of the favourable allele is 0.2 (a), 0.5 (b) and 0.8 (c).

d: degree of dominance over the unfavourable allele
s: coefficient of selection

Table 1a

		Number of generations								
		20			50			100		
s	d	R	I(%)	D(%)	R	I(%)	D(%)	R	I(%)	D(%)
0.01	0.00	.012	25	15	.032	28	20	.067	31	21
	0.25	.014	21	15	.036	24	18	.077	26	18
	0.50	.016	18	10	.041	21	16	.086	23	16
	0.75	.018	16	10	.046	18	14	.096	20	15
	1.00	.019	14	10	.050	16	12	.105	18	13
0.10	0.00	.155	29	15	.443	24	20	.726	6	21
	0.25	.173	25	15	.457	21	18	.707	8	22
	0.50	.191	21	15	.464	18	18	.684	9	24
	0.75	.206	19	15	.468	16	18	.659	10	27
	1.00	.220	16	10	.468	15	18	.631	11	29
0.20	0.00	.371	25	15	.736	5	20	.799	0	21
	0.25	.388	21	15	.716	7	22	.795	1	24
	0.50	.400	18	15	.692	8	22	.785	2	29
	0.75	.408	16	15	.664	10	26	.762	4	36
	1.00	.413	14	15	.635	11	28	.722	8	43
0.50	0.00	.763	3	15	.800	0	20	.800	0	21
	0.25	.741	5	20	.799	0	24	.800	0	26
	0.50	.713	6	20	.796	0	30	.800	0	33
	0.75	.680	8	25	.780	2	38	.798	0	46
	1.00	.645	9	25	.741	6	46	.772	4	63
0.80	0.00	.799	0	15	.800	0	18	.800	0	19
	0.25	.794	1	20	.800	0	24	.800	0	25
	0.50	.781	2	25	.800	0	30	.800	0	34
	0.75	.752	4	25	.796	0	42	.800	0	49
	1.00	.710	7	35	.765	4	56	.783	2	71

Table 1b (initial frequency of the favourable allele is 0.5)

		Number of generations								
		20			50			100		
s	d	R	I(%)	D(%)	R	I(%)	D(%)	R	I(%)	D(%)
0.01	0.00	.019	24	15	.047	26	20	.093	26	21
	0.25	.018	24	15	.046	26	20	.091	26	21
	0.50	.018	24	15	.046	26	20	.089	27	22
	0.75	.018	25	15	.045	26	20	.087	27	22
	1.00	.018	25	15	.044	27	20	.085	27	23
0.10	0.00	.184	21	15	.374	12	20	.479	3	21
	0.25	.175	22	15	.350	15	22	.462	5	24
	0.50	.167	22	20	.326	17	24	.438	8	29
	0.75	.160	23	20	.302	19	26	.406	13	33
	1.00	.153	23	20	.279	21	30	.370	17	39
0.20	0.00	.332	14	15	.481	2	20	.500	0	21
	0.25	.310	16	20	.465	5	24	.498	0	25
	0.50	.288	17	20	.440	8	28	.492	1	32
	0.75	.268	19	20	.408	12	32	.472	5	41
	1.00	.249	20	25	.371	16	38	.432	12	50
0.50	0.00	.487	2	15	.500	0	20	.500	0	21
	0.25	.472	4	20	.500	0	24	.500	0	26
	0.50	.447	7	25	.497	0	30	.500	0	35
	0.75	.414	10	25	.485	3	42	.499	0	47
	1.00	.375	14	35	.446	10	50	.473	6	67
0.80	0.00	.499	0	15	.500	0	18	.500	0	20
	0.25	.497	1	20	.500	0	24	.500	0	25
	0.50	.487	2	25	.500	0	32	.500	0	35
	0.75	.462	6	30	.497	1	44	.500	0	49
	1.00	.420	11	35	.467	7	58	.483	3	73

Table 1c (initial frequency of the favourable allele is 0.8)

		Number of generations								
		20			50			100		
s	d	R	I(%)	D(%)	R	I(%)	D(%)	R	I(%)	D(%)
0.01	0.00	.012	24	15	.028	25	20	.053	23	21
	0.25	.010	29	20	.024	30	22	.046	29	24
	0.50	.008	36	25	.020	38	28	.038	37	29
	0.75	.006	48	30	.016	50	34	.030	49	35
	1.00	.005	68	35	.011	71	42	.022	71	44
0.10	0.00	.095	17	15	.164	8	20	.195	2	21
	0.25	.082	22	20	.149	13	24	.188	4	26
	0.50	.068	29	25	.129	21	30	.173	10	33
	0.75	.054	40	30	.105	33	38	.149	21	42
	1.00	.039	59	40	.078	54	46	.113	43	54
0.20	0.00	.150	10	15	.195	2	20	.200	0	21
	0.25	.133	15	20	.188	4	24	.199	0	26
	0.50	.113	22	25	.174	9	32	.196	2	35
	0.75	.091	33	35	.149	20	40	.183	8	46
	1.00	.067	52	40	.114	42	52	.146	30	61
0.50	0.00	.196	1	15	.200	0	20	.200	0	21
	0.25	.190	3	20	.200	0	26	.200	0	27
	0.50	.176	8	25	.199	1	34	.200	0	35
	0.75	.151	18	35	.190	5	46	.199	0	50
	1.00	.114	38	45	.155	25	62	.175	14	72
0.80	0.00	.200	0	15	.200	0	18	.200	0	20
	0.25	.199	1	20	.200	0	24	.200	0	26
	0.50	.194	3	25	.200	0	34	.200	0	35
	0.75	.176	10	35	.198	1	46	.200	0	51
	1.00	.138	30	45	.170	17	66	.184	9	77

Table 2. The maximum decrease in s due to inbreeding (%) in order that the selection response for the alternating method is at least equal to that for the random-mating method.

d: degree of dominance over the unfavourable allele
s: coefficient of selection in the random-mating method

		Initial frequency of the favourable allele								
		0.2			0.5			0.8		
		No. generations			No. generations			No. generations		
s	d	20	50	100	20	50	100	20	50	100
0.01	0.00	19	20	21	19	20	21	19	20	21
	0.25	17	18	18	19	21	21	22	24	24
	0.50	15	16	16	19	21	22	27	28	29
	0.75	13	14	15	19	21	22	32	34	35
	1.00	11	13	13	19	21	23	40	43	44
0.10	0.00	18	19	20	18	20	20	19	20	20
	0.25	16	19	22	19	22	24	22	25	26
	0.50	15	19	24	20	24	28	27	30	33
	0.75	14	19	26	21	27	33	34	38	42
	1.00	13	19	29	22	30	39	43	49	55
0.20	0.00	17	19	20	18	19	20	18	20	20
	0.25	16	21	23	20	23	25	23	25	26
	0.50	16	23	29	22	27	31	28	32	34
	0.75	16	25	35	23	32	40	35	41	46
	1.00	16	28	43	25	38	50	45	54	62
0.50	0.00	16	18	19	17	18	19	17	19	19
	0.25	18	22	24	20	24	25	22	24	25
	0.50	20	28	32	24	31	33	29	33	35
	0.75	22	37	45	29	41	48	38	46	50
	1.00	25	47	63	34	53	67	51	64	73
0.80	0.00	14	16	17	15	17	18	16	17	14
	0.25	18	22	23	20	23	24	21	23	24
	0.50	22	30	32	26	31	33	29	33	34
	0.75	28	42	48	33	45	49	40	48	51
	1.00	34	58	72	41	62	75	55	70	79

Table 3a,b,c. The number of generations required to attain 95 % of the maximum response in the random-mating method (G) and the decrease in time due to the inbreeding method (D, %). The initial frequency of the favourable allele is 0.2 (a), 0.5 (b) and 0.8 (c).

d: degree of dominance over the unfavourable allele

Table 3a

		Coefficient of selection				
d		0.01	0.10	0.20	0.50	0.80
0.00	G	1213	118	57	20	11
	D	21.7	21.2	21.1	20.0	18.2
0.25	G	1339	131	63	23	13
	D	24.0	23.7	22.2	21.7	15.4
0.50	G	1561	153	75	28	16
	D	28.3	27.5	26.7	25.0	18.8
0.75	G	2021	199	98	37	22
	D	36.7	36.2	35.7	32.4	31.8
1.00	G	3773	375	186	73	44
	D	58.6	58.1	57.5	56.2	52.3

Table 3b (initial frequency of the favourable allele is 0.5)

		Coefficient of selection				
d		0.01	0.10	0.20	0.50	0.80
0.00	G	975	96	47	17	10
	D	21.7	21.9	21.3	17.6	10.0
0.25	G	1167	115	56	21	13
	D	25.6	25.2	23.2	19.0	23.1
0.50	G	1485	147	72	28	17
	D	31.6	31.3	29.2	28.6	23.5
0.75	G	2156	214	106	41	25
	D	42.3	41.6	40.6	39.0	36.0
1.00	G	5553	554	276	109	68
	D	70.2	69.9	69.2	67.9	66.2

Table 3c (initial frequency of the favourable allele is 0.8)

		Coefficient of selection				
d		0.01	0.10	0.20	0.50	0.80
0.00	G	855	84	42	16	10
	D	21.8	20.2	21.4	18.8	20.0
0.25	G	1093	108	54	21	13
	D	27.0	25.9	25.9	23.8	23.1
0.50	G	1522	151	75	29	18
	D	35.0	34.4	33.3	31.0	27.8
0.75	G	2559	255	127	50	31
	D	49.0	48.6	48.0	46.0	45.2
1.00	G	13093	1308	653	260	162
	D	85.1	84.9	84.8	84.2	83.3

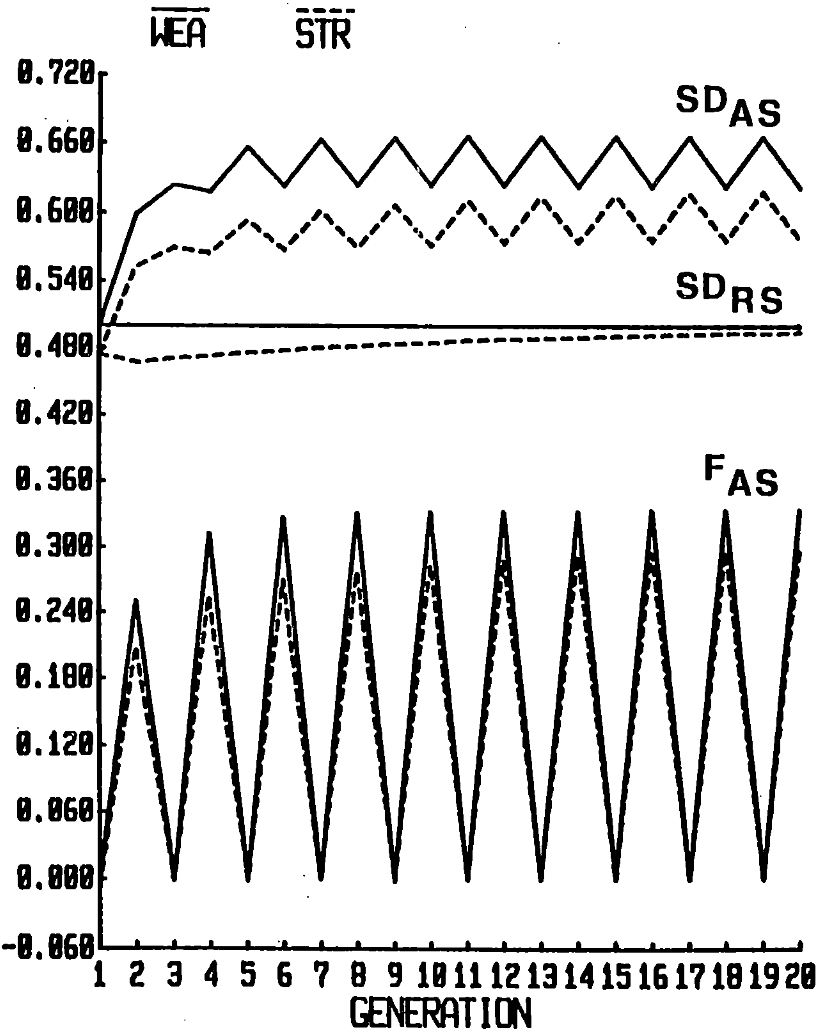

Fig. 1. The selection differential (SD) in gene frequency for sib-selected males relative to that for their full-sisters (AS = alternating system, RS = random-mating system), and the departure from random-mating proportions before selection in the AS (F_{AS}). The initial frequency of the favourable allele is 0.5. The degree of dominance over the unfavourable allele is 0.5.

WEA: weak selection of females (s=0.01)
STR: strong selection of females (s=0.50)

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