The University of Manitoba

AN EXAMINATION OF THE EFFICIENCY OF A REPEAT MATING DESIGN

FOR THE SEPARATION OF GENETIC AND ENVIRONMENTAL TRENDS IN

A SELECTION EXPERIMENT AND ITS RELATIVE

EFFICIENCY FOR THE GENERATION OF

RESPONSE TO SELECTION

IN MICE

By

Tsang Kay Cheung

A Thesis

Submitted to

The Faculty of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree of

Doctor of Philosophy

Department of Animal Science

Winnipeg, Manitoba

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ABSTRACT

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Doctor of Philosophy

February, 1975

Supervisor: Dr. R. J. Parker

The efficiency of a repeat mating design for the
separation of genetic and environmental trends, and its
effectiveness in achieving response to selection were
observed during eight cycles of directional selection for
large 12th day litter weight in mice. A control group was
used to monitor the accuracy of the repeat mating group in
estimating environmental trend. Two further groups under
two different levels of mass selection were used to compare
the relative success of the repeat mating group in
achieving selection response.

From the 3rd cycle to the 8th cycle, the
estimated genetic gain in 12th day litter weight in the

repeat mating group was 0.89 ± 0.25 gm per cycle. The selection response was lower than in M_2 mass selection group and higher than in the M_1 mass selection group. The estimate of environmental trend was -0.79 ± 0.78 gm per cycle which was in close agreement with the value of -0.88 ± 0.55 gm per cycle estimated from the control group.

ACKNOWLEDGEMENT

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INTRODUCTION

Quantitative geneticists have long been aware of the importance of an accurate separation of genetic and environmental trends in breeding programs and in selection experiments. Many methods have been developed to assess genetic and environmental trends, especially in the fields of poultry breeding and dairy cattle breeding. A repeat mating design has been proposed as a scheme to separate these trends and has received considerable theoretical treatment with regard to its advantages and efficiency. However, little or no major research work has been published where the repeat mating design has been subjected to an experimental test.

The present investigation was to examine the efficiency of the repeat mating design for the separation of genetic and environmental trends under directional selection for large 12th day litter weight in mice. Also of interest was the effectiveness of repeat mating under selection in achieving response to selection relative to two different intensities of mass selection.

REVIEW OF LITERATURE

The aim of artificial selection is to produce some change in the genetic structure of the population in question. The separation of observed change into its environmental and genetic components is an important part of the analysis of selection experiments or breeding programmes. Unless the environment can be maintained constant over the period of the experiment, a simple measure of genetic response using phenotypic change cannot be used. For some traits that are sensitive to environmental variation, a close to constant environment is not sufficient. Kojima and Kelleher (1963) reported that egg production in D. pseudoobscura showed marked fluctuations over a period of generations, even when the flies were maintained at constant temperature. Furthermore, except for laboratory animals, to provide a sufficiently constant environment for many generations is very difficult if not impossible.

Attempts have been made to compare different genotypes at the same time in the same environment. The use of control populations to provide material for the evaluation of the level of management and in monitoring the genetic improvement in selection programmes has proved its value. Control strains have been used extensively in laboratory investigations and in poultry breeding over a long period of time, but there have been few reports on

the genetic consistency of the control strains used. The
first detailed analysis of one particular control flock
over a short period was presented by Gowe et al. (1959a).
Their objective was to describe the performance over six
generations of a random bred control strain in poultry and
to indicate the value of the strain in interpreting a
selection experiment. The random-bred control strain of
S.C. White Leghorns consisted of an average mating popula-
tion of 47 males and 182 females in each of six genera-
tions. The effective number of parents per generation was
estimated at 146 and there was no evidence of any signifi-
cant change in the genetic value of the strain over the
six generations when tested on six farms. The performance
of the control strain was compared with that of two other
strains on test in the same environment. Comparisons of
the effects of selection on increased hen-housed egg
production, survivor egg production, viability during
fertility and hatchability measured in the two selected
strains were made, based on the absolute trends in these
flocks over the six generations and also on deviations
from the performance of the control strain. The results
indicated that this control strain could be used for the
efficient separation of genetic and environmental effects.

Genetic changes in a control population may
consist of both random drift and directional changes due
to natural selection. From the point of view of genetic
constancy, it is clear that a control population of

unlimited size is the ideal case. The practical task is
to specify the mating design which will maximize efficiency
in the sense that genetic drift is reduced to a minimum
under the given circumstances of resources and labor.
Gowe et al. (1959b) compared the theoretical efficiency of
a pedigreed control population to a random bred control
population in maintaining genetic constancy with care being
taken that within the limit of the design each member of
the population contributed equally to the next generation.
With the same number of breeding parents in each generation
for both kinds of control populations, genetic sampling in
the pedigreed population was reduced to minimum and the
effective number of parents was larger than in the random
bred control population. It was concluded that the
pedigreed control population was better than the random
bred population in reducing the magnitude of genetic drift
and was a more efficient control population for a selection
programme.

Hill (1972), in discussing the design of control
populations, has emphasized that efforts should be made to
minimize genetic drift and has shown that if steps are
taken to keep family size equal, both drift variance and
possible directional selection effects are minimized. But
the magnitude of the effects of natural selection and of
genotype-environment interactions are difficult to quantify
from theoretical arguments and estimates of their real
importance in practical situations can only be obtained

from experimental analysis of field data.

Aside from laboratory animal research and poultry breeding, few selection programs with domestic animals can have a satisfactory control population in terms of size and design efficiency because of the prohibitive monetary expense involved. Even in poultry breeding, new mating designs with the purpose of separating genetic and environmental trends have been proposed in order to bypass the expense of maintaining control populations.

In breeding programs with farm animals, methods have been developed to estimate genetic and environmental trends based on the analysis of field records. The contemporary comparison procedure of Robertson and Rendel (1954), which compares all A.I. and non-A.I. first lactation daughters in the same herd-year-season, estimates the superiority of A.I. progeny over their non-A.I. contemporaries by means of least squares analysis of the field records. Van Vleck and Henderson (1961) modified this method to accomodate the estimation of genetic trend of the A.I. population by adding the seasonal estimates of contemporary comparison superiority to the estimates of trend in the non-A.I. population. Henderson et al. (1959) developed a maximum likelihood procedure to estimate genetic change in herds of species that have repeated records of production and are subject to culling. They showed that the classical least squares approach will give a biased estimate of environmental effect when culling is

practised. The statistical model provides estimates of both heritability and repeatability of the trait under analysis.

Smith (1962) proposed an analysis to estimate genetic change in a pig herd. The method depended upon the difference in the rate of change of performance in the population as a whole and in the successive progenies of individual sires. An estimate of genetic change from the regression of performance on time is given by twice the pooled within-sire regression on time of the difference between the population and individual sire means.

Burnside and Legates (1967) used records from full sisters and paternal half-sisters to estimate genetic trends in a population of Holstein-Friesians. All records were analyzed to obtain least-squares constants for year of calving. A weighted regression of these constants on years provided an estimate of the annual trend, genetic plus environmental. Full sisters were analyzed to obtain least-squares year constants adjusted for sire and dam effects and corrected for selection. Weighted regression of these constants on year indicated the environmental trend in the population, and comparison with the genetic plus the environmental trend provided an estimate of annual genetic trend. A second estimate of the annual genetic trend was obtained by comparing the over-all trend with one-half the genetic, plus the environmental trend estimated from records of paternal half-sisters adjusted

for sire effects. The authors reported a close agreement of estimates obtained by the two methods.

A formalized method for estimating environmental and genetic trends is the repeat mating design proposed primarily for poultry by Goodwin et al. (1960) and further elaborated by Giesbrecht and Kempthorne (1965). The terminology used is appropriate to poultry breeding but can be given general application. The plan of this design depends essentially on the use of matings which are repeated identically during two successive breeding seasons. Inter-year comparisons of progeny groups of the same generation measure environmental changes, and intra-year comparisons of progeny groups of two successive generations measure genetic changes.

Hickman (1958) designed a repeat mating system for use with dairy cattle on experimental farms. All virgin heifers and first lactation cows would be mated to young pedigree-selected bulls and all older cows would be mated to proven bulls. Bulls would be selected for use as proven sires at eight years of age and used as such for three years. As the same proven bulls would sire daughters from the same group of cows in successive years, the correlated array of genotypes over the two years would be the required subpopulations, and from them environmental differences in consecutive years, and age and genetic effects could be isolated.

Hickman and Freeman (1968) suggested that the

reports on repeat matings by Hickman (1958), Goodwin
et al. (1960) and Giesbrecht and Kempthorne (1965) had
included both male and female parents. Consequently, they
were confronted with accounting for maternal effects.
They proposed a design for dairy cattle selection with
attempts to avoid confounding with maternal effects by
repeating the use of only the male parents in a random
fashion across all possible mates, to balance the maternal
effects in comparisons of progeny of bull groups. Young
bulls would be selected each year on pedigree performance
using paternal half-sib and maternal information. After
the progeny tests were completed, the bulls which sired
the best progeny would be used to breed nominated cows
which would become dams of a new group of young bulls.
Such a group of young bulls would be introduced every year
for two years' use, with each group being mated at random
across all females except the nominated cows. The average
difference in phenotype between daughters of successive
bull groups provides an unbiased estimate of differences in
genotype created by selection. If bulls are selected in
the same direction each year, the average difference
between successive bull groups is efficiently estimated by
the regression of daughter performance on bull group
number. Year effects can be simultaneously estimated by
least squares analysis.

Krehbiel et al. (1969) used the repeat mating
scheme proposed by Goodwin et al. (1960) to maintain a

control line of Montana No. 1 swine in order to monitor the effectiveness of reciprocal selection for performance of crosses between Montana No. 1 and Yorkshire swine. They reported that the repeat mating group was an adequate control population. The yearly environmental changes estimated from repeat matings in the control line were used to adjust the time trend to provide a better estimate of genetic improvement.

The few repeat mating schemes which have been developed have received considerable theoretical treatment, but no comprehensive research data have been published to verify experimentally the efficiency of a repeat mating design in estimating environmental and genetic trends. Whether the repeat mating group can replace the control group in practice in assessing environmental trend is still unclear. Also the effectiveness of the repeat mating group under selection in achieving response to selection has not been determined.

Growth of mammals during their suckling period is influenced by their own genes as well as by postnatal environmental influences, a portion of which would be due to the influence of the genotype of the dam. Twelve day litter weight in mice, as a preweaning trait, has received considerable attention in this regard. Falconer (1947) suggested that 12th day litter weight of nursing young may provide a useful measure of milk yield in dams. The sources of variation in 12th day litter weight were

examined by Bateman (1954) using a cross-fostering technique to partition the variation in maternal effects on 12th day litter weight into prenatal and postnatal components. This analysis indicated that only 32 percent of the variation in 12th day litter weight of eight mice was postnatal in origin. However, subsequent studies (Cox et al. 1959; Young et al. 1965) using similar cross-fostering techniques showed that postnatal maternal influences accounted for 70 to 80 percent of the variance in 12th day litter weight of six mice. El Oksh et al. (1967) reported similar results for 14th day litter weight of six mice. Nagai (1971) reported that in six-young and eight-young groups, the postnatal maternal influences accounted for 65 percent and 66 percent of the variance in 12th day litter weight respectively.

With the exception of Bateman's report (1954), all reports have indicated that 12th day litter weight is a trait influenced by a major maternal component. Willham (1963) has suggested that such a trait has additional complexity added to the characterization of genetic variability and response to selection. Few studies have been carried out specifically to examine the response to selection of 12th day litter weight in mice and conflicting results among these reports make the picture far from clear. Bateman, cited by Falconer (1955), reported on two experiments where selection was made for standardized 12th day litter weight of eight mice. The first experiment

showed no increase in 12th day litter weight. However, no control line was maintained so that environmental effects were confounded with selection for 12th day litter weight. Upward selection yielded small progress with realized heritability of 0.14. The realized heritability from downward selection was fully five times that from upward selection. This decline in 12th litter weight in the low line might be augmented by inbreeding depression. Since the total range covered by the response to selection amounted to only twice the original genetic standard deviation, it was suggested that only a few genes were concerned with the major part of the response.

Legates and Farthing (1962) reported a two-way selection experiment for standardized 12th day litter weight of six mice. The realized heritability of 12th day litter weight was 0.04 and 0.18 for the upward and downward selection lines respectively. Response to selection was distinctly asymmetrical with little response in the upward selection line and decline of 12th day litter weight in the downward selection line augmented by in-breeding depression. Dalton and Bywater (1963) selected for high 25th day litter weight of mice on two different diets. The report showed no significant response to selection. However, failure to standardize litters re-sulted in confounding of litter size and litter weight, and a meaningful interpretation of response to selection for litter weight was not possible. Eisin et al. (1970)

reported a positive linear response of standardized 12th day litter weight of six mice under upward selection. The cumulated pooled estimate of genetic advance of all four replicates was 2.52 gm. over the ten generations of selection. The direct additive genetic variance for growth rate in the young accounted for approximately 22 percent of the variation in individual 12th day litter weight. The replicate lines of the experiment were examined for correlated responses in lactational performance by Hanrahan and Eisin (1970a) and by Eisin and Hanrahan (1970). They reported no significant changes in milk yield, percent fat or percent protein. Eisin (1972) reported that the long term response to selection for 12th day litter weight in mice under upward selection stopped at generation 17 although genetic variation was still present and the finding could not be interpreted conclusively. Eisin (1973) evaluated the response to selection for 12th day litter weight in mice in terms of average direct and average maternal genetic responses. Comparisons were made among selected and control parental lines, reciprocal F_1 crosses, F_2's and backcrosses. It was found that selection response for 12th day litter weight was due primarily to average direct genetic effects with an almost complete absence of the average maternal variance for preweaning body weight found in cross-fostering experiments within random-bred lines (Young et al., 1965; El Oksh et al., 1967; Nagai, 1971;).

It would appear from the information available the 12th day litter weight is a complex reproductive trait with a rather low heritability. However, most reports do indicate that moderate additive genetic variance is present and that the trait will respond to selection.

MATERIALS AND METHODS

Breeding Stock

The mice used in the experiment were from a line obtained from the Agriculture Canada Research Station, Lacombe, Alberta. The line was based on eight inbred strains which had been combined through crossing, and random mated without selection as an outbred population for 20 generations. The line has been subsequently maintained as a control line with no selection of any kind and had been random mated for a further 12 generations prior to the start of the experiment. This strain provided a broad genetic base for the selection experiment.

General Selection Criteria

The trait selected for was large 12th day litter weight and first parity litters were used exclusively. Litters were standardized to eight mice at three days of age to remove the effect of number suckled on lactation output. Standardization at three days instead of at birth was to avoid the possible high postnatal mortality shortly after birth if the dams are disturbed. Litters consisting of five, six or seven mice at three days were augmented to eight by choosing foster young of the same age, group, and of similar weights from litters having more than eight mice. Litters with less than five mice were discarded. On the 12th day of age the litter weight was recorded to the

nearest one-tenth of a gram. In litters where only seven
mice survived to 12th day of age, litter weight was
adjusted to an eight-mouse equivalent by multiplying
average individual weight by eight (Eisin et al. 1970). No
adjustment for differences in litter weight due to diffe-
rences in sex ratio was made since the difference between
male and female weights has been found to be negligible at
the 12th day of age (Eisin et al. 1970; Nagai 1971). Sub-
sequent selection was applied only among litters which had
eight or more mice at three days of age because the
fostered young mice were not identified.

Mating and Selection Scheme

The random mated base population available at the
start of the experiment was subdivided into four different
groups. These four groups consisted of a control population,
a group in a repeat mating design (RM) and two mass selec-
tion groups (M_1 and M_2), each under a different level of
mass selection. The mating and selection scheme for each
of these groups is described in detail below.

Control Group

The control group in the 1st and 2nd generations
comprised 30 females and 15 males chosen at random and
mated at random (one male mated to two females) to produce
the next generation with the restriction of no full sib
mating. From the 3rd generation to the last generation the

control group was expanded to consist of 40 females and 20 males.

Repeat Mating Group

The mating and selection procedure for the repeat mating group (RM) is presented schematically in Table 1. Two sire groups, group 1 and group 11, were chosen at random with each group consisting of 15 males. Each sire was mated to five randomly chosen dams to produce the first cycle progeny. For the second cycle mating, Sire Group 11 was used again with a new Sire Group 111 selected at random from male progeny of the first cycle. Both Sire Group 11 and Group 111 were mated to randomly chosen female progeny of the first cycle. At the same time, the two sires from Sire Group 1 and 11 with the best 12th day litter weight average were chosen as nominated sires. One female from each of the 16 heaviest litters were chosen at random to be the nominated females and the two nominated sires were used to breed the nominated females (one male to eight females). The average 12th day litter weight of these 16 litters was calculated. Enough males were selected at random from litters that had an above average weight to form a new group of young sires (Group 1V) to be used in 3rd cycle mating. New sire groups from then on were formed similarly and each new sire group was introduced for two cycles' use.

Table 1. Mating scheme of the repeat mating group.

Cycle	Sire Group No.		Female		Origin of Sire Group No.
1	1	15 ♂	150 ♀	Progeny	1 Random
	11	15 ♂			11 Random
2	11	$15-x_1$ *♂	150 ♀	Progeny	111 Random
	111	$15+x_1$ ♂			IV 2♂ (Top 2♂ among the 30)
					16 ♀ (One ♀ from each of the top 16 heaviest litters)
3	111	$15+x_1-x_2$ *♂	150 ♀	Progeny	V 2♂ (Top 2♂ among the 30)
		$15-x_1+x_2$ ♂			16 ♀ (One ♀ from each of the top 16 heaviest litters)
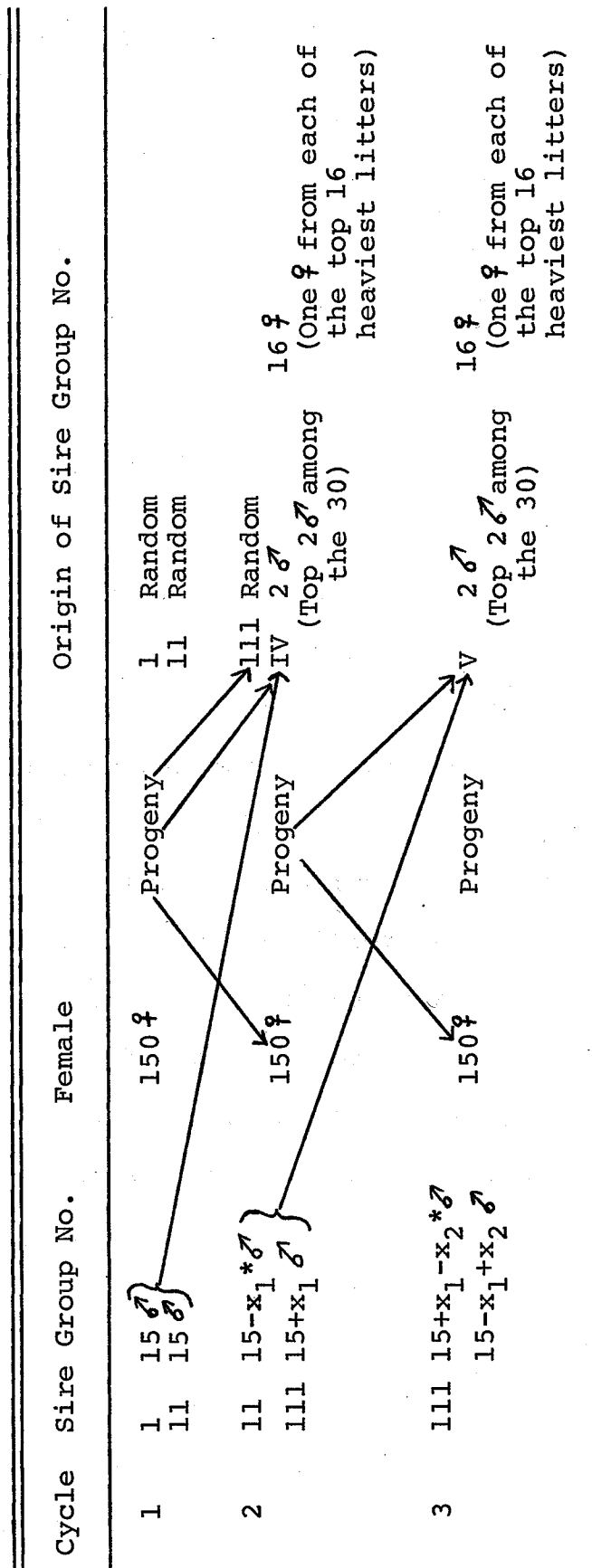
* x_1 and x_2 = 0, 1 or 2, depending upon whether 0, 1 or 2 sires were nominated from that group.

Mass Selection Groups

Two mass selection groups were used to monitor the selection response of the RM group. In the first mass selection group (M_1), 50 litters were chosen at random from the base population to form the first generation population. The top 30 litters in rank in 12th day litter weight were selected. Out of each of these 30 selected litters one male and three females were randomly chosen to provide 30 males and 90 females which then became the parents of the second generation. Mating was at random (one male mated to three females) with the restriction of no full sib mating. The mating and selection scheme was the same throughout the rest of the experiment. In the second mass selection group (M_2), 100 litters were chosen at random to form the first generation population. The top 30 litters in rank in 12th day litter weight were selected and from each selected litter one male and four females were randomly chosen to be parents of the next generation. Mating was at random (one male to four females) with the restriction of no full sib mating. The mating and selection scheme was the same throughout the rest of the experiment.

There were, of course, some selected litters which deviated from the desired sex ratio (less than three or four females in the two mass selection groups) and more than three or four females had to be chosen from other selected litters but the selection scheme remained

essentially the same. Restriction of levels of selection to 30 percent and 60 percent for M_2 and M_1, respectively, were considered and would be desirable. However, it was obvious that practical considerations such as fertility, number of litters born having eight or more mice and number of litters having seven or more mice at 12th day would not ensure the maintenance of the specified selection levels, especially the 30 percent selection level. It was, therefore, decided to select the top 30 litters among the total number of litters eligible for selection in each of the two mass selection groups. The actual percent saved for breeding in each generation and the effective cumulated selection differential in groups M_1 and M_2 are presented in Table 4.

Analysis of Data

Standard statistical procedures were employed in the estimation of all parameters. Heritability of 12th day litter weight was estimated both from parent-offspring covariance and regression and as realized heritability. Inbreeding coefficients were calculated from covariance tables within each group for each generation. Estimations of genetic and environmental trends in the repeat mating group were by means of standard least squares analysis.

a) Sire-offspring covariances and regressions:

Heritability was estimated from the regression of offspring on sire. In any sire offspring regression the form of the analysis is similar to the following:

$$b = \frac{\text{Cov } xy}{\sigma_x^2}$$

where twice b value is an estimate of heritability, Cov xy is the covariance between the phenotype of sire (x) and the phenotype of the offspring (y) and σ_x^2 is the phenotypic variance of sires. The standard error of the estimate of heritability was estimated according to Becker (1967) as

$$\text{S.E. } (h^2) = 2 \sqrt{\frac{S_b^2}{\Sigma x^2}}$$

where S_b^2 is the mean square deviation from regression, and Σx^2 is the corrected sum of squares of sires.

Realized heritability was estimated from regression of generation means on accumulated selection

differential (Falconer 1960).

b) Calculation of inbreeding coefficient:

A computer program was specially written to calculate the inbreeding coefficient from covariance tables within each group for each generation. This computer program can be used to calculate both the inbreeding coefficient of the over-lapping generations (repeat mating group) and non-overlap generations (Control, M_1, M_2) populations. The details of this computer program are presented in the appendix.

c) Least squares analysis*:

The analysis is a statistical estimate of the consequences of selection operations measured within time period. This appears justified, in that selection is based on phenotype, which is assumed to be an unbiased estimate of genotype. The average difference in phenotype between litters of successive sire groups is, consequently, an unbiased estimate of differences in genotype created by the selection operation. If sire groups are selected in the same direction each year, an average difference between successive sire groups is efficiently estimated by the regression of progeny litter weight on sire group number. Generation or time period effects can be simultaneously estimated. The statistical model is as follows:

$$Y_{ijk} = y_i + b\,G_{ij} + e_{ijk}$$

where Y_{ijk} = 12th day litter weight of individual litter of kth dam mated to j^{th} sire group in the ith cycle.

y_i = average 12th day litter weight of all litters in the ith cycle.

G_{ij} = $-\frac{1}{2}$ if sire group j is being repeated.

$+\frac{1}{2}$ if sire group j is being used for the first time.

b = average difference in 12th day litter weight of litters produced from consecutive sire groups within the same cycle (i.e., regression on G_{ij} as defined in the model).

e_{ijk} = random error assumed being normally and independently distributed.

An example of a least squares analysis based on this model is given in Table 2, where X_i for y_i is 1 for observations in cycle i (i = 1 to 3) and zero otherwise.

Table 2. Least squares analysis with assumed data.

	Y_1	Y_2	Y_3	b	12 day litter weight
Cycle 1					
Sire Group I					
Y_{111}	1	0	0	$-\frac{1}{2}$	50 gm
Y_{112}	1	0	0	$-\frac{1}{2}$	50 gm
Sire Group II					
Y_{121}	1	0	0	$+\frac{1}{2}$	52 gm
Y_{122}	1	0	0	$+\frac{1}{2}$	52 gm
Y_{123}	1	0	0	$+\frac{1}{2}$	52 gm
Cycle 2					
Sire Group II					
Y_{221}	0	1	0	$-\frac{1}{2}$	52 gm
Y_{222}	0	1	0	$-\frac{1}{2}$	52 gm
Y_{223}	0	1	0	$-\frac{1}{2}$	52 gm
Sire Group III					
Y_{231}	0	1	0	$+\frac{1}{2}$	54 gm
Y_{232}	0	1	0	$+\frac{1}{2}$	54 gm
Y_{233}	0	1	0	$+\frac{1}{2}$	54 gm
Cycle 3					
Sire Group III					
Y_{331}	0	0	1	$-\frac{1}{2}$	54 gm
Y_{332}	0	0	1	$-\frac{1}{2}$	54 gm
Y_{333}	0	0	1	$-\frac{1}{2}$	54 gm
Sire Group IV					
Y_{341}	0	0	1	$+\frac{1}{2}$	56 gm
Y_{342}	0	0	1	$+\frac{1}{2}$	56 gm
	$n_1 = 5$	$n_2 = 6$	$n_3 = 5$		

The procedure for the calculation of ΔG (genetic trend) was then as follows:

a) Set up least squares equations as follows:

$Y_1 \qquad Y_2 \qquad Y_3 \qquad\qquad b$

$$n_1 \qquad\qquad\qquad\qquad \Sigma\, G_{1j} X_1 = \sum_j \sum_k\ Y_{1jk}$$

$$n_2 \qquad\qquad\qquad \Sigma\, G_{2j} X_2 = \sum_j \sum_k\ Y_{2jk}$$

$$n_3 \qquad \Sigma\, G_{3j} X_3 = \sum_j \sum_k\ Y_{3jk}$$

$$\Sigma\, G_{1j} X_1 \quad \Sigma\, G_{2j} X_2 \quad \Sigma\, G_{3j} X_3 \quad \sum_i \sum_j G_{ij}^{\,2} = \sum_i \sum_j \sum_k G_{ij}\, Y_{ijk}$$

b) For the numerical example the equations are:

$Y_1 \qquad Y_2 \qquad Y_3 \qquad\qquad b$

Y_1	Y_2	Y_3	b		
5			$+\frac{1}{2}$	=	256
	6		0	=	318
		5	$-\frac{1}{2}$	=	274
$+\frac{1}{2}$	0	$-\frac{1}{2}$	4	=	$+6$

These simultaneous equations can be solved to estimate y_i and b. In the example:

$$Y_1 = 51$$

$$Y_2 = 53$$

$$Y_3 = 55$$

$$b = 2$$

$$\nabla^2_b = c'' \nabla^2_y \quad \text{where } c'' \text{ is the inverted matrix,}$$

∇^2_y is the phenotypic variance of the trait selected for.

The estimate of genetic change per cycle, ΔG, is b. The total trend is that represented by the successive y_i's. The coefficient for the regression of successive y_i's on cycle number minus b provides an estimate of average environmental trend.

RESULTS AND DISCUSSION

Response to Selection

The phenotypic means for 12th day litter weight for each of the four groups are presented in Table 3 for all eight cycles of selection. The cycle means of each group showed wide fluctuation, but there was an apparent response to selection in all selection groups (M_1, M_2 and RM) when compared to the control group. In group M_1 the mass selection level ranged from 39 percent to 68 percent of offspring saved in any cycle and the mass selection level for group M_2 ranged from 29 percent to 42 percent. The effective cumulated selection differential for mass selection group M_2 was larger than that of group M_1 (Table 4). The regression of cycle mean on cycle number showed that the more intense mass selection group, M_2, had a selection response rate of 0.90 ± 0.49 gm per cycle; the milder mass selection group, M_1 and RM group, had selection response rates of 0.38 ± 0.49 gm and 0.42 ± 0.41 gm per cycle respectively; while the response rate of the control group was -0.04 ± 0.42 gm which was close to zero (Table 3). None of these regression coefficients was significantly different from zero. Responses to selection are also presented as durations from the control population in appendix Table 3.

Fertility and Litter Size

The total number of litters born and the average

Table 3. Generation means and standard deviations for 12th day litter weight of all groups for each of eight generations of selection

Generation	Control	M_1	M_2	Repeat Mating Group
1	52.8 ± 5.6 *(24)	50.2 ± 5.3 (44)	50.4 ± 6.4 (93)	50.8 ± 6.3 (114)
2	56.9 ± 6.4 (20)	58.5 ± 6.5 (58)	60.5 ± 6.8 (105)	58.2 ± 6.0 (115)
3	58.4 ± 5.3 (34)	59.8 ± 6.9 (77)	59.5 ± 6.8 (90)	55.9 ± 6.4 (101)
4	57.3 ± 7.9 (21)	52.1 ± 6.9 (62)	56.7 ± 6.5 (78)	55.3 ± 6.6 (118)
5	55.6 ± 7.4 (35)	54.4 ± 6.0 (55)	58.3 ± 7.0 (72)	55.2 ± 5.5 (109)
6	60.5 ± 7.0 (35)	59.0 ± 6.7 (69)	62.0 ± 6.7 (82)	60.9 ± 5.2 (121)
7	57.0 ± 6.8 (23)	58.0 ± 6.7 (73)	63.5 ± 5.7 (80)	57.7 ± 7.4 (104)
8	51.5 ± 6.7 (31)	55.0 ± 6.9 (46)	57.8 ± 5.6 (59)	54.0 ± 6.3 (58)
	**b=-0.045 ± 0.42	b=0.38 ± 0.49	b=0.90 ± 0.48	b=0.42 ± 0.41
	***b=-0.875 ± 0.55	b=-0.046 ± 0.65	b=0.45 ± 0.54	b=0.11 ± 0.53

* Figures in bracket indicates the number of observations.
** Regression of cycle mean on cycle numbers 1 to 8.
*** Regression of cycle mean on cycle numbers 3 to 8.

Table 4. The actual percent saved for breeding in each generation and the effective cumulated selection differentials for groups M_1 and M_2.

Generation	M_1		M_2	
	Percent Saved	Cumulated Selection Differential	Percent Saved	Cumulated Selection Differential
1	68	0 gm	.32	0 gm
2	52	2.57 gm	.29	7.13 gm
3	39	7.09 gm	.33	14.23 gm
4	48	13.04 gm	.38	20.05 gm
5	55	17.72 gm	.42	26.22 gm
6	43	22.71 gm	.37	32.16 gm
7	41	28.22 gm	.38	38.71 gm
8	--	33.94 gm	--	43.54 gm

Table 5. The average litter size and standard errors of all four groups for each of eight cycles of selection.

Cycle	Control	M_1	M_2	Repeat Mating Group
1	8.47 ± 0.39 *(30/30)	7.90 ± 0.24 (50/50)	8.32 ± 0.16 (100/100)	8.21 ± 0.18 (125/150)
2	8.17 ± 0.36 (24/30)	8.96 ± 0.22 (67/90)	9.03 ± 0.20 (109/120)	8.36 ± 0.17 (121/150)
3	8.50 ± 0.40 (37/40)	9.25 ± 0.26 (88/90)	9.14 ± 0.27 (111/120)	8.77 ± 0.19 (132/150)
4	11.39 ± 0.33 (28/40)	8.95 ± 0.24 (83/90)	9.07 ± 0.19 (116/120)	9.26 ± 0.21 (129/150)
5	9.53 ± 0.34 (38/40)	8.57 ± 0.23 (77/90)	8.59 ± 0.20 (102/120)	9.54 ± 0.20 (119/150)
6	9.82 ± 0.32 (34/40)	9.79 ± 0.29 (87/90)	9.69 ± 0.25 (100/120)	10.30 ± 0.23 (122/150)
7	9.41 ± 0.44 (32/40)	9.74 ± 0.28 (81/90)	11.59 ± 0.27 (97/120)	9.06 ± 0.16 (123/150)
8	9.48 ± 0.43 (40/40)	8.78 ± 0.25 (76/90)	9.11 ± 0.27 (109/120)	8.69 ± 0.19 (123/150)
	**b= 0.18 ± 0.13	b= 0.13 ± 0.08	b= 0.23 ± 0.12	b= 0.14 ± 0.08

* numerator is the number of litters born, denominator is the number of litter possible.

** regression of litter size on cycle number.

litter size for each of the four groups in each cycle are shown in Table 5. Fertility was generally high in all four groups. When the number of litters born in each group is compared to the number of litters that met the described selection criteria at 12th day (Table 3) there was an overall reduction of 15 to 20 percent except in the last cycle. In the last cycle, a sharp increase in cannibalism was observed and consequently resulted in lower numbers of available data in groups M_1, M_2 and RM. This occurrence justified the precaution of selecting the top 30 litters among the total a available litters in the two mass selection groups rather than adhering to a rigid restriction of levels of selection at 30 percent and 60 percent. It clearly indicated that a 30 percent level cannot be maintained consistently, and if what happened in the last cycle had occurred in an intermediate cycle the mass selection groups might have been decimated to the extent that no selection could have taken place.

The average litter size in each group showed an apparent increase over the eight cycles, although the regression coefficients listed in Table 5 are not significantly different from zero. The increase in litter size in the control group was comparable to the other groups, however, and there was no indication that selection for 12th day litter weight had resulted in a correlated response in litter size.

Estimates of Heritability

The estimates of heritability of 12th day litter

Table 6. Heritability estimates (h^2) obtained from sire-
offspring regression for groups M_1, M_2 and
Control; and realized heritability estimates for
groups M_1 and M_2.

	Control	M_1	M_2
h^2 from sire-offspring regression	0.06 ± 0.14	0.28 ± 0.17	0.19 ± 0.16
h^2 (realized heritability)	$-\,-$	0.06 ± 0.10	0.15 ± 0.08

weight in Groups M_1, M_2 and Control were obtained by regression of offspring on sire from data pooled from cycle 2 to cycle 8. For Groups M_1 and M_2 the realized heritability was also calculated (Table 6).

As can be seen from Table 6, the estimates of heritability obtained from regression of offspring on sire were on the whole higher than the realized heritability estimates, although all have large standard errors. The realized heritability estimate from Group M_1, a value of 0.06 ± 0.10, is in close agreement with the estimate of 0.04 obtained from upward selection for 12th day litter weight reported by Legates and Farthing (1962), while the realized heritability of Group M_2, a value of 0.15 ± 0.08, is in close agreement with the value of 0.14 reported by Falconer (1955).

Since 12th day litter weight is a trait influenced by maternal effect, heritability estimates obtained from regression of offspring on dam and sib analysis of variance would not be valid and are not presented.

Estimates of Inbreeding Coefficient

The inbreeding coefficient of every group in each cycle are presented in Table 7. The magnitude of inbreeding in every group in the last cycle ranged from five to seven percent. It is doubtful that inbreeding at this low level could cause inbreeding depression on 12th day litter weight. There was no indication that the level of inbreeding adversely affected fertility in terms of number of litters

Table 7. Inbreeding coefficients for all four groups in
          each cycle.

Cycle	M_1	M_2	Control	Repeat Mating
1	0	0	0	0
2	0.007	0.009	0	0.005
3	0.008	0.013	0.004	0.007
4	0.017	0.022	0.007	0.021
5	0.022	0.028	0.017	0.022
6	0.035	0.043	0.024	0.025
7	0.047	0.068	0.029	0.024
8	0.062	0.069	0.046	0.059
Expected F_x	0.050	0.042	0.080	0.035

born and average litter size of any group.

Estimation of Genetic and Environmental Trends in the Repeat Mating Group

The cycle mean of 12th day litter weight and sire group means for each cycle of the RM group are presented in Table 8.

In the first and second cycle, the sire groups (I, II and III) were formed randomly with no selection, therefore, it is not valid to include them in the least squares analysis model. With data from 3rd to 8th cycles only included in the analysis, the estimated genetic gain was 0.89 $\pm$ 0.25 gm per cycle; the overall trend was 0.10 $\pm$ 0.53 gm and the environmental trend was -0.79 $\pm$ 0.78 gm.

In every cycle the two best sires were chosen from 30 sires of the two sire groups used in that cycle instead of choosing the two best sires from 15 sires of the sire group after two cycles' service. When sire(s) were chosen from the most recent sire group which had only been used for one cycle's mating, the estimate of genetic gain for the next cycle would be biased upward. The bias would probably be small, however, and the resulting increase in selection intensity probably justified the decision.

Since the inbreeding coefficient of all groups are at the same level the environmental trend estimated from repeat mating group should be comparable to the environmental trend estimated from the control group, if the repeat mating

Table 8. Cycle means, sire group means and standard devia-
tion in each cycle of the repeat mating group.

Cycle	Cycle Mean (gm)	Sire Group	Mean (gm)	No. of Observation
1	50.77 ± 6.3	I	50.39 ± 6.6	57
		II	51.15 ± 5.9	57
2	58.23 ± 6.0	II	57.06 ± 6.3	56
		III	59.35 ± 5.9	59
3	55.91 ± 6.4	III	55.41 ± 6.5	50
		IV	56.41 ± 6.2	51
4	55.25 ± 6.6	IV	54.05 ± 6.5	56
		V	56.34 ± 6.8	62
5	55.24 ± 5.5	V	54.52 ± 6.6	43
		VI	55.72 ± 4.5	66
6	60.94 ± 5.2	VI	61.04 ± 6.2	58
		VII	60.85 ± 4.2	63
7	57.69 ± 7.4	VII	57.33 ± 8.3	45
		VIII	57.96 ± 6.4	59
8	54.04 ± 6.3	VIII	54.06 ± 5.9	29
		IX	54.02 ± 7.0	29

design is efficient in estimating the environmental trend. A simple regression of cycle mean on cycle number from the 3 d to 8th cycle for all groups are presented in Table 1. Since the control group was under no selection, the regression coefficient value should represent the environmental trend. The regression coefficient for the control group was -0.88 ± 0.55 which is in close agreement with the environmental trend estimated from the RM group (-0.79 ± 0.78 gm). The M_2 group still showed the greatest selection response while the M_1 and repeat mating groups showed comparable selection response, with the response of the repeat mating group being a little higher. Again, however, these estimates have large standard errors.

The above results clearly indicate that the repeat mating design can yield accurate estimates of genetic and environmental trends. The way in which new sire groups are formed also yielded fairly intense and effective selection pressure.

SUMMARY AND CONCLUSIONS

A selection experiment was conducted to test the efficiency of a repeat mating design for the estimation of genetic and environmental trends, as well as its effectiveness in applying selection pressure. A control group was included to monitor the accuracy of the repeat mating group in separating these trends. A mild mass selection group, M_1, and a more intense mass selection group, M_2, were used as comparisons to indicate the relative success of selection practised in the repeat mating group. The results clearly indicated that the repeat mating design was efficient in the estimation of genetic and environmental trends. Also, the response to selection in the repeat mating group was encouraging when compared to that in the two mass selection groups.

More research would be desirable to confirm the findings of this experiment in view of the possible important practical application to selection programmes in farm animals. Where a control group is not available or not practical, a repeat mating scheme of this kind with a built-in control mechanism can give accurate assessment of both genetic and environmental trends. Where a control group is available and when the inbreeding level of the control group and the selection groups are the same, the usefulness of the control group in estimating management level and genetic gain can be replaced by the selection

groups in a repeat mating scheme. This repeat mating scheme will make the presence of a control group unnecessary and more resources and facilities can be saved for other uses. When the inbreeding level of the control group and the selection groups are not the same, the environmental trend estimated from the control group would not be valid estimate of environmental trends in the selection groups. Selection groups in a repeat mating design would yield their own estimates of environmental trend under their own level of inbreeding.

In this experiment, the dams in the repeat mating group were replaced randomly each generation without selection. In selection programmes with farm animals, old dams can be culled and new selected dams brought into the herd. This practise of dam culling and selection could increase the selection intensity and as a result increase the selection response.

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Appendix 1. Response to selection for 12th day litter weight of the three groups measured as deviation from the control group.

Cycle	M_1 (gm)	M_2 (gm)	Repeat Mating Group (gm)
1	-2.6	-2.4	-2.0
2	+1.6	+3.6	+1.3
3	+1.4	+1.1	-2.5
4	-5.2	-0.6	-2.0
5	-1.2	+2.7	-0.4
6	-1.5	+1.5	+0.4
7	+1.0	+6.5	+0.7
8	+3.5	+6.3	+2.5
	*b = 0.42 ± 0.19	b = 0.95 ± 0.15	b = 0.46 ± 0.10

* Regression of deviation from the control group on cycle number from 1st to 8th cycle.

Appendix 2. Regression of offspring on sire in control, M_1 and M_2 groups for all cycles, with the cycle effect removed.

	d.f.	Σx^2	Σxy	Σy^2
Control	185	8338.58	235.36	9065.59
M_1	446	5947.57	822.71	20542.47
M_2	559	6164.68	573.27	23750.47

Appendix 3.   Computer program to calculate inbreeding

coefficient.

A computer program using WATFIV language has been
designed to calculate the inbreeding coefficient by
variance - covariance method.   The program can calculate
the inbreeding coefficient of both non-overlapping and
overlapping generations.   At its present form, the input
format can accommodate animal identification tattoo numbers
and alphabets up to ten letters.   The output lists all
parent - offspring groups and the relationship of all
animals.