

AN ABSTRACT OF THE THESIS OF

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Title Selection for Hybrid Female Reproductive Performance in
the Mouse

Abstract approved

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The design of this study was suggested by the following observations: (1) the successful application of recurrent selection techniques in obtaining improvement of hybrid performance in corn and Drosophila, (2) the increased production realized by rotational crossbreeding, and (3) the expression of a relatively large degree of hybrid vigor in traits of reproductive performance. On the basis of these observations, a rotational recurrent selection scheme was proposed as a means of improving the reproductive performance of females in a rotational crossbreeding program.

In this study recurrent selection was conducted in three strains of mice for hybrid female reproductive performance (10-day litter weight). Selection in each strain was based upon the average litter weight at 10 days of a sire's interstrain hybrid daughters. Hybrid daughters were obtained from a rotational pattern of interstrain top-cross matings in which males of strain

#20 were mated to strain BCX females, BCX males were mated to females of strain BCL and BCL males were mated to #20 females. The traits of litter size at one and 10 days were also examined.

A comparison of the hybrid and purebred reproductive performance indicated hybrid females were superior in performance to purebred sibs and dams in generation I. A change from harems to the colony groups method of mating caused a decline in the litter size at one-day of generation II hybrids, but the 10-day weight of their litters was still comparable to the 10-day litter weights of their purebred dams.

Because the change in environment was correlated with generations the evaluation of selection was based upon a comparison of selected and realized divergence between high and low classes of two-way selection. The response to selection was positive in strains #20 and BCL but slightly negative in BCX. The pooled response was positive. On the basis of the positive response in two strains and in the pooled data it was concluded that selection had been effective.

Predictions of response, based upon the assumption that differences between sire families were additive, were made from components of variance derived from sib analyses. The ratio of expected response and realized response for litter weight at 10 days in the pooled data was 0.835. When the comparisons were

made by strains, only strain #20 showed a positive correspondence between predicted and realized divergence between high and low classes.

An examination of the data by strains suggested that the following factors should be considered in evaluating the response to selection: (1) the genetic foundation of each sire strain, (2) the genetic foundation of the dam's strain, (3) the presence and influence of maternal effects by the dams of hybrid daughters, and (4) the relative degree of sampling error which influenced selections and predictions of response in generation I.

In strain BCL the realized response was positive but the expected response was zero. The lack of sire variability and consequently the estimated response of zero was attributed to sampling error and the inbred foundation of BCL. The realized divergence between high and low classes in generation II of BCL hybrid daughters was ascribed to the effectiveness of high and low grouping of the dams from strain #20.

Two possible reasons for the negative response in BCX were discussed. First, a higher degree of inbreeding occurred in the intrastrain matings of generation I than in either #20 or BCL. Second, a misclassification of the BCL dams of generation II BCX hybrids may have occurred. The second factor was suggested by the negative relationship between generation I hybrid and purebred

performance in the high and low classification.

On the basis of the correspondence between hybrid and purebred selection differences in strains #20 and BCX, the response to selection in strain #20 and the agreement between the expected and realized divergence in the pooled data it was concluded that selection for 10-day litter weight had acted primarily upon additive genetic variation.

As a consequence of repeated interstrain matings, an additional component of variation between litters in dams was included in the sib analyses of generation II. In strain #20 hybrids, the relative size of the component of variance due to litters indicated that the influence of inbred BCX dams was more variable between successive litters than the influence of less inbred dams of #20 and BCL. Repeatability estimates of litter size performance further indicated that BCX dams were more variable in performance than were purebred dams of #20 and BCL.

The implication that selection had acted largely on additive genetic variation suggested that females within a rotational crossbreeding program could be utilized as dams to obtain hybrid progeny for sire evaluation. The greater variability of dam influence of inbred BCX dams indicated that the use of crossbred dams would lead to a more uniform dam influence in a sire's progeny.

SELECTION FOR HYBRID FEMALE REPRODUCTIVE
PERFORMANCE IN THE MOUSE

by

VERNE MERRILL CHAPMAN

A THESIS

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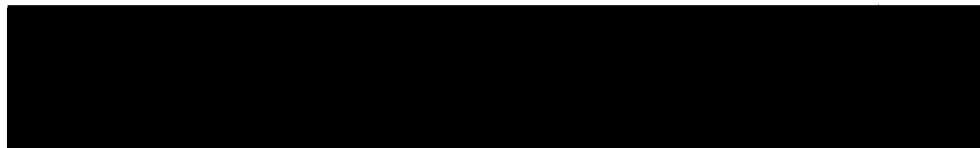
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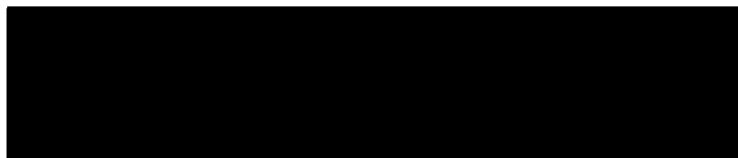
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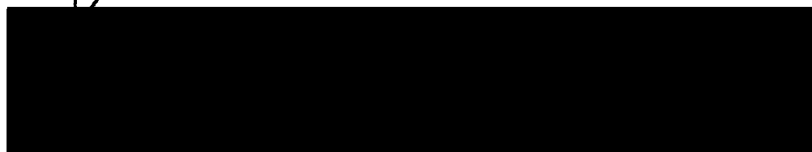
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SELECTION FOR HYBRID FEMALE REPRODUCTIVE PERFORMANCE IN THE MOUSE

INTRODUCTION

The discovery of Mendelian principles of heredity and the subsequent expansion of these concepts to the genetics of populations and quantitative characters have provided the framework of a basic model which describes the effects of selection. The application of quantitative genetic principles to plant and animal breeding has provided a scientific basis on which the effectiveness of different systems of mating and selection can be evaluated and the predicted results submitted to experimental verification.

Experiments designed to test the validity of the quantitative model have been conducted (Clayton, Morris and Robertson, 1957 and Kyle and Chapman, 1953) and the response to selection on a short term basis has been shown to follow expectations of the model.

On a long term basis, however, numerous observers have encountered the situation of a plateau in response to selection; indeed, selection pressure is necessary to retain the level of performance previously achieved by selection (reviewed by Lerner, 1954 and Allard, 1960). Once a selection plateau has been achieved in a population, it does not necessarily mean that genetic fixation has occurred or that the genetic variation has been exhausted. The

presence of genetic variation is indicated by findings that selection in the reverse direction or relaxation of selection pressure alone results in a change in performance toward the mean of the original base population (Falconer, 1955). Renewed selection efforts have frequently been successful in moving the mean level of performance past the level of the original plateau before a second plateau of response is encountered (Allard, 1960). The nature of the selection plateau phenomenon suggests that the intensity of selection exceeds the ability of the genotype to effectively adapt to the change through recombination. This is essentially one of the basic postulations upon which Lerner (1954) developed his proposal of genetic homeostasis.

One of the central points to Lerner's theory is the superiority of the heterozygote in viability and in reproductive success of fitness. The evidences in support of this point presented by Lerner (1954) as well as the body of evidence that has been published since his proposal was published (Falconer, 1960; Spiess, 1962; King, 1961) suggest that the phenomenon of heterozygote superiority is widespread throughout many classes of organisms.

The general superiority of heterozygotes, heterosis, and the converse phenomenon, inbreeding depression, are phenomena which are central issues in genetical research. A number of gene action models and systems have been proposed, but as yet there is

little positive evidence which favors or nullifies completely any of the alternatives suggested. In a recent review of the genetics of heterosis, Bowman (1959) concluded, "It seems highly probable that there is no single genetical explanation of heterosis but that dominance, whether partial or complete, and all types of genetic interaction combined in different proportions in different situations result in heterosis."

In spite of the lack of a general genetic model to explain the phenomenon of heterosis, plant and animal breeders have developed various means of exploiting heterosis in production agriculture.

One of the most striking uses of heterosis has been in the hybrid corn programs initially developed by Hayes in 1909 (Hayes, 1952) who proposed the production of homozygous inbred lines for seed production from which selected crosses could be made to utilize the F_1 in commercial production. In addition to hybrid vigor, the producer would have genotypic uniformity throughout his crop and the assurance of genotypic uniformity between seasons. A number of factors impeded the initial success of hybrid corn, especially the poor viability of inbred lines and the expense of using these lines for large scale seed production. The difficulty was overcome by the modification of using a double cross, i. e., a cross between two unrelated F_1 single crosses, proposed by Jones in 1917 (Allard, 1960).

At the outset, acceptance of hybrid corn was rather limited; however, by 1940 more than half of the corn acreage of the United States was planted to hybrid varieties, and by 1944 the acreage had increased to over 80 percent (Allard, 1960). The increased use of hybrid corn has been accompanied by significant increases in yield by as much as 20 percent in the corn belt states.

With the accent upon the production of hybrids, much effort by plant breeders has been expended upon producing superior hybrid combinations. Early in the development of hybrids it became obvious that the number of inbred lines that could be produced and the possible combinations of these lines were almost infinite and that more efficient methods of screening and testing lines were needed.

One of the general methods which has been used to improve hybrid yield in corn is recurrent selection for combining ability where selection is based upon the performance of tester or line cross progeny. There are three modifications of recurrent selection which have been devised. One method is recurrent selection for general combining ability. In this method, progeny used for evaluating the male parent are derived from top crosses between the selection lines and a wide genetic base. This wide base is usually made up of a number of other lines so that selection for general combining ability acts upon the additive portion of the

genetic variance.

A second method is recurrent selection for specific combining ability (Hull, 1945). In this method tester progeny are derived from a top cross of the selection line to an inbred line. This method was proposed on the assumption that overdominance gene action is largely responsible for heterosis and that selection for specific combining ability would develop an inbred line with a large number of homozygous loci which are directly complementary to those already homozygous in the tester line.

The third method is essentially a mixture of the first two methods. In this method, selection is conducted in two segregating lines where each is used as a tester line for the other in a reciprocal fashion; hence, the name "reciprocal recurrent selection" (Comstock, Robinson and Harvey, 1949). Specifically, if the lines are designated as line A and line B, then line A males (or parent plants in corn) are selected on the basis of hybrid progeny derived from a top-cross with line B, and line B males are selected on the basis of progeny derived from a top-cross with line A. Selection is followed by intermating of selects within lines. Theoretically, response to selection should be obtained where either overdominance or partial dominance gene models account for heterosis.

Experimental evidence evaluating the various methods comes largely from corn and Drosophila studies. The most extensively

studied method of the three is recurrent selection for general combining ability. Since variability of general combining ability is largely additive, there should be a positive correlation between the phenotypic values of parents and tester progeny.

The positive correlation of parent and tester progeny performance was observed in a study with corn (Lonnquist, 1961). In three cycles of recurrent selection for general combining ability for yield, the synthetic populations improved almost proportionately to the increase observed in intercrosses of synthetic lines. In this study improvement was determined by comparing the performance of synthetic lines undergoing selection and their intercross tester progeny with a standard hybrid variety. The selection was shown to have increased the yields of the synthetic intercrosses by almost 20 percent in comparison with the standard hybrid while the parental synthetics showed an improved yield of about 16 percent.

Selection for increased hybrid yield utilizing recurrent selection for specific combining ability has been tested by Sprague, Miller, and Penny (1959). This experiment was also designed to test whether overdominance gene models accounted for heterosis. Selection was conducted in two varieties, Lancaster Sure Crop and Kolkmier Reid. Selection in each variety was based upon tester performance with the same inbred line. It was reasoned that if selection were effective in building up frequencies of complementary

alleles of genes which accounted for heterosis by overdominance, the frequencies of these alleles would be increased in the same manner in both varieties; therefore, an intercross between the two selected varieties would be expected to show a decrease in heterosis after selection was conducted.

The results showed the performance of the selected populations did not change with selection, but the yield of the test cross improved with each succeeding cycle. Furthermore, intercrosses between the populations also revealed an improvement in successive cycles of selection. On the basis of improved intercross performance it was concluded that dominance or partial dominance gene models accounted for observed heterotic effect.

In the evaluation of evidence of the nature presented by Sprague, Miller, and Penny (1959), it is imperative that underlying assumptions be examined with respect to conclusions reached. In the study by Sprague, Miller, and Penny (1959), the assumption was that the original genotypes of the two varieties were segregating at the same loci and selection effects were similar in the two lines. If this assumption were valid then the explanation of dominance and partial dominance may have value; however, alternative conclusions cannot be excluded in interpreting these results since this assumption has not been subjected to test.

Bowman (1962) conducted a recurrent selection study in mice

in which an inbred line was used as the maternal parent. Selection was based upon the size of litters by crossbred females derived from matings of outbred sires with inbred dams. In this experiment, selection was conducted in an outbred stock (M) which had been previously maintained as a control strain. The average inbreeding coefficient of M was estimated to be 20 percent. The inbred line (I) which had been previously mated full sib for 16 generations, was estimated to be 96 percent inbred. Both populations, I and M, were originally derived from the same base population.

Twenty-one M males were harem bred to I females to produce hybrid (X) daughters. These daughters were mated and the size of their litters recorded. Each M male was then evaluated on the basis of litter size records of six X daughters. The 14 males with the lowest X daughter performance were discarded and the M line was continued by keeping three M males and nine M females out of the remaining seven sires. The experiment was conducted over four cycles of selection. The reasons for stopping the selection program were the following: (1) It was difficult to raise the X progeny on I dams and (2) the level of performance of X was considerably below either parent and showed no heterosis.

The lack of heterotic effect upon performance in this study makes the results of questionable value in assessing the effectiveness of selecting for superior hybrid performance; however,

estimates of expected response to selection were compared with the average deviation of X performance from the mid-parent value. A difference of -1.02 young was found between the X and mid-parent value in the first cycle and -0.12 was the corresponding value in the fourth cycle which represented an increase of 0.9 young between the beginning and end of the program. A comparison of this value with a pooled estimated improvement of 0.71 young derived from within cycle mean square estimates was in fair agreement; however, the data would be of a completely different nature if similar computation had been done on the first three cycles where no improvement was observed. Because of the apparent high degree of variability between selection cycles and the limitation of poor hybrid performance, the study was not an adequate test of this mating system.

A second experiment for low abdominal bristle number in Drosophila was conducted in a similar manner to the preceding mice experiment (Bowman, 1962). The inbred line (L5/1) was derived from the same parental stock as the line (R) used for selection; however, line L5/1 had earlier been selected for low bristle number over 33 generations. Following this period of selection, line L5/1 was inbred by full sib matings for 15 generations.

Selection for low bristle number in R was based upon the number of bristles on abdominal sternites four and five of a sample

of ten female progeny (T) obtained from mating R males to ten L5/1 females. Selection was conducted over a period of 14 generations.

Correlations between a sire's T progeny and R progeny were found to be generally positive but showed a marked decline as selection proceeded.

The data showed the numerical value of the T progeny was consistently greater than the mid-parent value throughout the study and the decline of bristle number in T corresponded with the decline of bristles in R. This observation suggested that the variation observed among T progeny means was largely additive and that selection had not been effective in exploiting non-additive mechanisms in effecting a change in bristle number in T populations.

In both of the studies by Bowman (1962), the evaluation of recurrent selection was seriously hindered by the lack of any real heterotic response, and it must be concluded that the effectiveness of recurrent selection for specific combining ability in animal populations has not been adequately tested.

Experiments comparing conventional selection with reciprocal recurrent selection (RRS) in Drosophila have been conducted in which selection was practiced for traits of various heritabilities and for traits which displayed varying degrees of heterosis (Bell, Moore and Warren, 1955; Rasmuson, 1956; and Kojima and Kelleher, 1963).

One of the first studies reported on RRS was that of Bell, Moore and Warren (1955). In their study, RRS was compared with (1) conventional within line selection, (2) recurrent selection for specific combining ability and (3) inbreeding followed by line crossing.

The foundation material of Experiment I consisted of eight random mating laboratory stocks of Drosophila melanogaster. In the purebred or closed population selection, the eight foundation stocks were combined into one composite. This composite was also utilized for recurrent selection, but subsequent selection was based upon the performance of top-cross progeny with an inbred line. In the reciprocal recurrent selection, the eight lines were divided into two groups of four from which two segregating composites were made.

In Experiment II the foundation consisted of the closed population of Experiment I, an unselected non-inbred stock, and two inbred lines. As in Experiment I, the closed and recurrent selection populations were derived from a composite of all four lines while each of the segregating reciprocal lines was a composite of one outbred and one inbred line.

The effectiveness of selection by these methods was compared with the performance of single crosses of inbred lines derived from the eight original lines. In Experiment II additional

inbred lines were developed from the material used as the foundation.

The first experiment was carried for 16 generations and ended with a performance test over a six week period. Selection in this experiment was based upon an index giving equal weight to fecundity (number of eggs laid in a four day period) and egg size.

In the second experiment, selection was conducted for fecundity alone over a 39 generation period and was terminated with a seven week performance test period.

Bell, Moore and Warren (1955) concluded that the closed population method seemed to be most advantageous for traits of medium to high heritability, but they suggested that in traits of low heritability, such as egg counts, RRS may be of greater advantage in long term response. In light of the differences in the genetic bases of the populations used in these two methods, the possible advantage of RRS may have been overshadowed. The closed populations in both experiments were made up of a broader sampling than either of the reciprocal populations and should have had a greater degree of genetic variability than either of the reciprocal populations.

Rasmuson (1956) reported a study comparing the effectiveness of RRS with a half sib selection in Drosophila. While she concluded that RRS resulted in an improved performance, especially for

egg production and hatchability, her findings were based upon a comparison of the overall mean response of 20 generations of RRS vs. half sib families and were not fully indicative of the presence of actual selection change.

In the study of Kojima and Kelleher (1963), RRS was compared with purebred selection or full sib family selection (FFS) for the character of egg production. Egg production was averaged over three days between the 12th and 14th day of adult life. Two separate base populations of Drosophila pseudoobscura which had been collected from separate localities of the same region were taken from random mating cage populations. A preliminary examination of these populations indicated additive genetic variation to be very low for the character under selection.

In FFS selection a deliberate attempt was made to keep the rate of inbreeding low and the variation of inbreeding within lines as low as possible. After 13 cycles of selection, a heritability estimate was calculated from the cumulative response to selection in both lines. The results indicated that the response to selection was essentially zero.

In the RRS populations, the cumulative response adjusted to control values was linear to the 11th cycle after which it appeared to cease. The slope of the response in the first 10 cycles was 0.16 ± 0.03 . A half sib analysis produced an estimate of 0.13 which was

within one standard error of the slope measured.

In a comparison of F_1 crosses of a random sample of 12 inbred lines derived from the same base population with the RRS performance, it was found that the average performance of RRS hybrids was equivalent to the level of the top four percent of 96 F_1 combinations of the inbred lines.

The above study represents possibly the strongest experimental evidence in animal populations that RRS can be effective in changing the level of performance of hybrid populations.

Although the studies discussed here are not a complete coverage of the work reported concerning the effectiveness of selection for combining ability, they are representative of the work conducted testing recurrent selection methods, especially in animals. With the exception of one study (Kojima and Kelleher, 1963), many workers have found the method of RRS to be of questionable value in comparison with more conventional selection techniques. Nevertheless, the number of studies conducted and the incompleteness of many of the experimental situations attest to the need of more experimental evidence from a wider variety of sources.

In evaluating the application of recurrent selection methods to animal populations, it should be understood that one of the goals the animal breeder expects to achieve with these methods is improvement of hybrid or crossbred performance. With this in mind,

a brief examination of the manner in which heterosis is exhibited will be made, accompanied by a review of prominent methods used to exploit heterosis in animal populations, especially in farm animal populations.

Traits which exhibit prominent heterosis or conversely inbreeding depression have two characteristic qualities. Firstly, they are usually of low heritability; secondly, they are features of the whole organism rather than its component traits. A rather striking example of the latter was shown by Roberts (1961) in a comparison of the lifetime reproductive performance of mice strains with the performance of an intercross of strains.

One of the strains (RCL) was a stock which had been previously selected for high six week weight. A second strain (MS) was a small stock which had resulted from extensive selection for small body size. A reciprocal intercross of these two strains resulted in F_1 hybrids (MXR).

The character of reproduction, as well as body size, differed markedly between the two parental strains. Strain RCL had a larger average litter size than strain MS, 7.1 young vs. 4.6 young; however, MS had an average of 10.6 litters per female as opposed to only 3.4 litters in RCL. Thus on a lifetime basis the small strain MS had an average of 49.0 young per female while RCL averaged 24.2 young. The interstrain F_1 females, MXR, showed

an average litter size of 9.3 young per litter and averaged 11.0 litters per female which amounted to an average total number per female of 102.5 young. The comparison of MXR performance with parental performance for either of the two characters showed some heterosis, but the difference expressed by the total was the most significant expression of heterosis. An examination of the average total weight of offspring weaned revealed the same picture. RCL weaned a total weight of young of 198.99 gms., MS weaned a total weight of 205.70 gms., and MXR weaned 847.24 gms. of young per female. Obviously, the total advantage of MXR was due to a multiplicative effect of improvement of several traits, i. e., high average number of young per litter x increased average number of litters.

The hybrid vigor expressed by MXR in the study by Roberts (1961) was an example of similar results attained in crossbreeding experiments with both laboratory and farm animals. Exceptions to the general finding that the performance of crossbreds, i. e., crosses of breeds, strains or lines, exceeds the performance of parents have been reported by Bowman (1962) and Mason et al. (1961). In the mouse study conducted by Bowman (1962), the hybrid daughters had litter sizes which were below either of the parental lines. Mason et al. (1961) found that hybrid daughters of a specific strain intercross in mice were below the mean of parental strains for litter size and litter weight at 12 days. Dobzhansky (1952) also

reported findings of a similar kind in Drosophila experiments and has proposed that such results are due to a lack of co-adaptation between parental genotypes which is the outcome of divergent selection pressures in the parental stocks. The observation made by Bowman (1962) and Mason et al. (1961) of "negative" heterosis, perhaps better termed genetic incompatibility, implies that heterozygosity per se as suggested by King (1961) may not be the entire solution to understanding heterosis.

The attempts to systematically utilize heterosis in livestock production have been considerably influenced by the results obtained with hybrid corn and the methods utilized by corn breeders. Many of these attempts have been impaired, however, by the economic restriction resulting from the lower rate of reproductivity of individual breeding units in livestock.

A number of simplified programs for utilization of heterosis have been used with success in livestock production, especially the systematic crossing of breeds which include the following: (1) the single cross in which crossbred progeny are not kept for reproduction, (2) a crisscross or backcross mating program involving two breeds in which crossbred females are kept and bred alternately to purebred males of each breed in successive generations, and (3) the rotational cross in which daughters of a cross between two breeds are mated to males of a third breed. Crossbreeding is

continued by mating the daughters of the second cross to males of a fourth breed, or back with a male of one of the original parental breeds and thus establishing a rotational system.

The initial testing of the rotational crossbreeding scheme by Winters et al. (1935) with swine yielded significant improvement in the performance of crossbred sows over purebred parents for litter size at birth, liveability of pigs to weaning, and weaning weight of litter. Again, as in the case demonstrated with Roberts' (1961) study with mice, the crossbred advantage became greater as the traits measured approached the total female performance.

The results of the studies by Roberts (1961) and Winters et al. (1935) as well as numerous other studies concerning the effects of inbreeding and crossbreeding have clearly shown that hybrid vigor in mammals is especially important for maternal traits. Thus, if selection for heterosis is to be effective, it must be based upon those traits which show the most significant expression of this phenomenon, namely, traits of reproduction.

The applications of recurrent selection techniques in corn (Lonnquist, 1962) and in Drosophila (Kojima and Kelleher, 1963) have shown success in the improvement of hybrid performance. Accordingly, the success of recurrent selection and the improved production observed in rotational crossbreeding suggest that the application of a modified reciprocal recurrent selection program

might be an effective means of developing improved hybrid performance, especially when applied to the characters of female reproductive performance.

In view of the success of rotational crossbreeding and considering the possible application of recurrent selection techniques, the following breeding program is offered as a potential means of improving the performance of crossbred females in a rotational crossbreeding program.

Rotational Recurrent Selection

The proposed program is an expansion of the reciprocal recurrent selection scheme of Comstock, Robinson, and Harvey (1949) to include three or more segregating lines. The basic purpose of such a program is to develop males that will sire daughters of improved reproductive merit in a rotational crossbreeding program.

When three closed segregating breed populations are used, designated as A, B, and C, selection would be conducted between males on the basis of the mean reproductive performance of hybrid daughters which have been derived from interbreed top crosses in the following manner:

- (1) Breed A males are selected on the basis of A-B crossbred daughter performance,

(2) Breed B males are selected on the basis of B-C crossbred daughter performance, and

(3) Breed C males are selected on the basis of C-A crossbred daughter performance.

Selected males are then mated to unselected females of the same breed to perpetuate the breed. For the purposes of this program, the tester females and their litters would be discarded after each generation of sires was evaluated.

Progeny of intrabreed matings are used as the parents of the next generation. Sons of selected males are also incorporated as sires in rotational crossbreeding programs in a complementary manner to the selection procedure, i. e., A males would be used where crossbred females were sired by B males, B males mated to crossbred females sired by C males, and C males used where crossbred females were sired by A males. The selected sires themselves could be used directly after they had produced the following generation of purebreds.

A mating system comparable to the one described here was suggested in published literature after the present study was initiated. In a study with mice, Hansson and Lindkvist (1962) proposed essentially the same outline except they proposed to test purebred sires within the rotational crossbreeding system itself. Males were evaluated on the basis of the performance of hybrid daughters

which resulted from matings of purebred males to crossbred females which were sired by males of the complementary line, i. e., A males were mated to crossbred females sired by B males, B males were mated to crossbred females sired by C males, and C males were mated to crossbred females sired by A males.

In the system proposed by Hansson and Lindkvist (1962), it should be noted that in testing sires for selection only 56 percent of the heredity of the crossbred females used to produce tester progeny is that of the complementary breed. Since the remaining 44 percent of the genotypic make-up will, in the long run, be an average of 28 percent of the third breed and 16 percent of the sire's breed, selection by this method will tend to be less effective for specific combining ability than the selection method outlined in this thesis study.

In the study by Hansson and Lindkvist (1962) selection in the conventional method was conducted by keeping nine males out of 27 males, and in each of the three recurrent selection lines three of nine males were selected. Thus, while intensity of selection appeared equal, a disparity in the rate of inbreeding occurred between the two selection methods so that the effects of selection were directly confounded with differential rates of inbreeding.

In the proposed system of rotational recurrent selection, it should be noted that recurrent selection was to be conducted on the

basis of hybrid or crossbred female reproductivity. However, a number of modifications could be included within the framework of this system. For example, selection for traits which readily respond to mass selection methods could be conducted on a phenotypic basis of the entire population so that only a select group would be used in the progeny evaluation. Such a modification is essentially a tandem type of selection method, and it would be especially apropos to classes of animals with a high rate of reproduction. Certainly other factors such as family selection methods could be easily incorporated within the structure of the proposed recurrent selection program.

The purpose of this study was to examine whether a rotational recurrent selection system of mating would be of value in improving the reproductive performance of hybrid females. Mice were used as the experimental animal, and selection was based upon first litter reproductive performance of strain cross females as indicated by the total weight of a dam's litter at ten days post partum. The specific purposes of this study were the following:

- (1) to examine the extent and character of differences between sire families for reproductive performance and
- (2) to determine whether the rotational recurrent selection method would effectively select for differences between sire family means.

PROCEDURE

Three separate mouse populations, which are referred to as strains, were obtained from the stocks of the Oregon State University Small Animal Laboratory. The mice strains used in this project were identified as BCX, BCL, and #20. The following is a general description of each of these strains.

(1) Strain BCX. Strain BCX was a heterogeneous population composed of unidentified stock obtained from the University of British Columbia in 1961 and wild stocks which had been incorporated into stocks of the Oregon State University facility. This strain was characterized by numerous hair coat colors, especially black, agouti, and white. During the course of the project, a number of other colors such as pale brown or cinnamon, grey, and dark brown were also observed. This strain had been maintained in colony mating groups previous to the time the study was initiated. The size of the breeding colony was estimated to be between 20 and 40 females; therefore, a relatively low rate of inbreeding was assumed.

(2) Strain BCL. Strain BCL was the inbred stock LG of the University of British Columbia which had previously been selected for large body size, approximately 40 gms., and had been inbred for 10 to 15 generations. This strain was obtained by the Oregon State University Small Animal Laboratory in the fall of 1961. The fertility of BCL was the poorest of the strains used in this study.

(3) Strain #20. The stocks designated as #20 in the study were partially derived by crossing #20 males with females of #6 in the foundation matings. This crossing was necessary because of an insufficient number of #20 females. The original Strain #20 was derived from a composite of the strains O, C, and V used in the study reported by Mason et al. (1960). The strain #6 was the strain designated as V in Mason's work. Prior to this study, both strains #6 and #20 had been maintained with small population sizes, probably about five to 10 females and five males, and generation time had been delayed by replacing females only as they became too old to breed. The composite #20 in the study was of moderate fertility and somewhat smaller in adult body size than the other strains used. An earlier description of these stocks given by Ray (1959) cited that strain #6 was degenerating in body size, litter size, and vigor; however, since Ray's study some conscious selection for fertility has probably been practiced which has counteracted this condition.

In the present experiment, sire selection within each of the strains was based upon the reproductive performance of hybrid daughters obtained from intercrossing strains in the following manner:

BCX males x BCL females

BCL males x #20 females

#20 males x BCX females

Three kinds of matings were necessary in each cycle or generation of the breeding program: (1) an interstrain mating to produce hybrid females (as illustrated) (2) mating of hybrid females, and (3) an intrastrain mating to produce purebred stocks of the succeeding generation.

Pedigree diagrams of inter- and intra-strain matings in this study are given in Appendix A. For interstrain matings, the diagrams show identity of sires and dams and the number of fertile hybrid daughters which came from each mating. Only matings which had one or more fertile daughters are shown. In the intrastrain matings, the identity of fertile offspring as well as parental identity are shown.

Because of the limited numbers of breeding adults available from laboratory stocks, it was necessary to make an initial intra-strain mating to increase the numbers in each strain. In each case three males were mated to harems of three to five females. As it was previously noted, this procedure of matings within strains was modified in #20 where #6 females were used.

Three males were kept from each of the original sires so that in the first generation of testing and selection each strain consisted of nine sire groups. Two way selection for high and low hybrid female reproductive performance was conducted in the first generation by selecting males from the two highest and two lowest

sires. Inasmuch as females were retained from all the sires whenever possible, the designation of "high" and "low" for females was based upon sires above the mean and below the mean, respectively.

Originally, three males were kept from each sire so that each strain subdivision of "high" and "low" consisted of six sire groups. However, the expansion of the population to this size exceeded the capacity of the facility and following the first interstrain mating in generation II each of the sub-groups was reduced by half. This reduction was done by discarding the least fertile males in each group so that each sub-group was composed of three sire groups.

At the completion of the first interstrain mating in generation II, the decision was made to replicate the interstrain matings to produce additional hybrid daughters. This decision was based partly upon the fact that the BCL x #20 matings had been low in fertility which made evaluation and selection impossible. A second factor influencing this decision was the inadequacy of the numbers of daughters available for evaluation in the remainder of the sire groups in view of the amount of sampling variation observed within sire groups.

The data of this study include testing and selection in one generation and three replicates of sire progeny testing in the second generation.

Husbandry

Breeding was conducted by mating sires with harems of from three to six females in both inter- and intra-strain matings. The first parity matings were made when the females were about six weeks of age. The harem mating scheme was used in evaluation of the first generation hybrids by mating them with purebred males of the nonrelated third strain; however, the increased number of daughters evaluated in the second generation necessitated two changes in procedure. First, the number of pure strain males was insufficient to mate the available hybrid females, and because of the greater number of hybrid females, it was necessary to mate them to two-strain intercross males which had been kept as part of laboratory colony. Second, the increased number of hybrid females could not be accommodated in harem breeding groups, so they were bred under colony conditions. Groups of about 15 females were mated with two or three males which had been previously raised together.

All breeding groups were checked daily for pregnant females starting at the 16th or 17th day post-mating. When females appeared to be pregnant, they were removed to individual cages where they were kept until the litter was weaned at 21 days of age.

At weaning the young were identified by a system of ear notching and toe clipping. Hybrid females were identified on the

basis of litter group while all of the purebred offspring were individually identified.

The system of identification developed for this study included the following:

1. Ear notches were used to identify strains, i. e., strain BCX was notched in the right ear, strain BCL was notched in the left ear, and strain #20 received no notch. Code letters of R for BCX, L for BCL, and N for #20 were derived from right, left, and no notch respectively.

2. All four feet were used in toe clip identification. Since three males were kept from a sire, the forefeet were used to identify both sire and grandsire origin, i. e., a front left toe clip indicated a particular grandsire and a right front toe clip indicated which of his three sons was the sire.

The ten hind toes were used for individual identification in purebreds and litter identification in hybrids.

The weaned young were sexed and placed in separate cages of 25 to 30 mice where they were kept until breeding groups were established.

Harem mating groups were kept in round, wire bottomed, cages, nine inches in diameter and nine inches deep. Feed cubes were placed in wire mesh cylinders which were hung on the inside of the cages.

Individual cages were made by inserting a cylinder of wire mesh eight to ten inches high and four inches in diameter inside a 505 can (one pound coffee can). These cages were bedded with an inch of wood shavings. Cubed feed was provided in a wire mesh cylinder placed inside the cages.

Colony groups were kept in stainless steel dishpans 15 inches in bottom diameter bedded with an inch layer of wood shavings. Feed cubes were placed loose on top of the shavings. The pans were covered with lids of expanded metal.

All of the mice received fresh water daily, and feed cubes were given ad libitum. The diet given to all the mice was a commercial preparation. The animals were transferred to clean cages weekly or as the need dictated.

All stocks were maintained in the mouse room of the Oregon State University Small Animal Laboratory. In the cold seasons, the temperature was maintained between 65 - 75° F, and in hot weather air conditioning usually kept the room below 80 - 85° F. Ventilation and temperature control were not completely automatic, however, and there were occasions when temperatures fluctuated above or below the given values.

Data

The data in this study were the first parity reproduction

records of females collected on the date of littering and at 10 days post partum. Included in these records is the following information:

(1) the size of the litter, i. e., number of young at birth or first day and at 10 days, and

(2) the weight of the litter at birth and 10 days.

Weight data were taken to the nearest .05 grams. First day data were collected during the first day post partum and included litters which were born during the 24 hour period between daily inspections.

Ten day litter weights were used as the criterion of a dam's mothering ability. The 10-day weight rather than weaning weight at 21 days was used because the size of the individual cages was not completely adequate, imposing a greater environmental restriction upon large litters than upon small ones. The cage size became more restrictive as the activity of the young increased. Ten-day weights were also chosen because most of the post-natal mortality had occurred by this time, and 10 day litter sizes were usually representative of the size of the litter at weaning. An additional reason for using 10-day weights was the young have not opened their eyes at that time, and they can be handled for weighing more easily than the young at the later stages of suckling.

The primary characters which were examined in detail in this study include the following: (1) size of litter at birth, (2) size

of litter at 10 days and (3) weight of the litter at 10 days. In the generation II data, an additional component of milking ability was also examined. Suckling ability for a given dam was expressed by

$$Wt. 10 - \bar{Wt. 10}_x$$

where: $Wt. 10$ is the weight of the dam's litter at 10 days and $\bar{Wt. 10}_x$ is the strain average 10 day weight of litters of size x .

Analysis of Data

The data were arranged by classes of progeny groups of dams within respective sire groups in each strain. In generation II where three replicates of interstrain matings were conducted, an additional grouping by replicates was made. A hierarchical analysis of variance was conducted on each set of intercross and intracross daughter groups in generation I and on the pooled data of the three replicates in generation II. The generation II data were also tested for differences between replicates in litter size at one and 10 days and for litter weight at 10 days.

Because replicate matings in generation II resulted in more than one litter group by the same sire and dam, an additional classification of "litters within dams" was added to these analyses of variance.

Estimation of mean square values for sib analyses was complicated by unequal numbers of observations in subclasses;

therefore, it was necessary to use an adjusted mean of subclass numbers derived from the formula by Warren and Dickerson (1952)

$$K = \frac{\sum \left(\frac{\sum K^2}{\sum K} \right)_c - \sum \left(\frac{\sum K^2}{\sum K} \right)_g}{N_c - N_g}$$

where: K = number of observations in a set which have identical deviations from the source concerned.

N_c = number of groups

N_g = total number of subclasses within all of the N_c groups.

RESULTS AND ANALYSIS

The basic purpose for conducting selection for hybrid female reproductive performance was to capitalize the advantage of hybrid vigor; therefore, the first factor examined was whether hybrid females were superior to purebred females in the trait under selection. The character of the design used in this program offered two modes of comparison in assessing hybrid vigor which included the following: (1) a comparison of the performance of contemporary purebred and hybrid females and (2) a comparison of hybrid female performance with that of purebred females of the parental generation. The latter case was somewhat hindered, however, by apparent environmental changes between generations.

The mean performance by strain of sire for hybrid and purebred females is shown in Table 1. The code letters of daughter identity were those used in Appendix A, where N, R and L designated sire strain #20, BCX and BCL respectively and the use of a double letter code indicated strain parentage of hybrid daughters from interstrain matings. The data listed in each row were the performance of the daughters indicated by the code. It should be noted that generation F females were the dams of both the hybrid and purebred females of generation I. The purebred females of generation I were the dams of generation II hybrid females.

Table 1. Mean performance of generation F purebred females, generation I hybrid (NR, RL and LN) and purebred (N, R, and L) females and generation II hybrid females by strain of sire and pooled over all strains.

Sire	Dam	Daughter Code	Gen.	No. of Sires	n1 ¹	Size 1	n10 ²	Size 10	Weight 10
#20	#20	N	F	3	16	7.12	16	6.69	38.17
	BCX	NR	I	8	50	8.70	37	7.73	42.20
	#20	N	I	6	25	8.16	23	7.74	39.29
	BCX	NR	II	6	202	7.68	207	7.11	36.93
BCX	BCX	R	F	3	29	7.21	28	7.04	40.84
	BCL	RL	I	9	86	8.71	60	7.97	41.86
	BCX	R	I	7	42	7.07	40	6.52	33.90
	BCL	RL	II	6	144	7.25	145	6.71	35.08
BCL	BCL	L	F	3	32	7.72	32	7.28	41.53
	#20	LN	I	8	32	8.39	26	7.73	41.06
	BCL	L	I	6	37	8.00	36	7.39	36.58
	#20	LN	II	6	124	7.65	122	7.09	36.32
Pooled									
	Purebred		F	9	77	7.40	76	7.07	40.57
	Hybrid daughters		I	25	168	8.65	123	7.80	41.79
	Purebred daughters		I	19	104	7.66	99	7.13	36.12
	Hybrid daughters		II	18	470	7.54	474	6.98	36.10

¹n1 = number of observations at one day.
²n10 = number of observations at 10 days.

An examination of the data pooled over all strains showed a decline in litter weight of 4.45 grams between generation F and generation I purebred females and a similar decrease of 5.56 grams was noted between generations I and II hybrid female performance. Some factors which appeared to be associated with the changes in performance between generations included the following: (1) environmental changes caused by expanding the population size,

(2) the effects of inbreeding in generation I purebreds and (3) genetic change resulting from selection. In this study seasonal conditions influenced the laboratory environment but no data were available to verify the significance of this variable as a factor which accounted for the observed changes in level of performance.

The expansion of population sizes caused a general lowering of the level of cleanliness that could be maintained in the individual cages where females littered and raised their young. The decreased adequacy of the individual cage environment was evidenced by the decline in the average weight per young, i. e., the litter size to litter weight relationship, between generation F and generation I. In generation II the change in the method used for breeding hybrid females from harem mating groups to larger breeding colonies was previously mentioned. Although colony cages used for colony breeding provided what appeared to be a better physical environment than the wire bottomed cages used for harem mating, the use of multiple males and the increased numbers of females resulted in increased social agitation. The decrease in the litter sizes at birth in generation II hybrid females as compared with all other groups indicated the adverse effects of the change in the breeding environment between generations I and II.

Part of the decline in performance of litter weight at 10 days in generation I purebreds as compared with generation F was due

to the effect of inbreeding. The inbreeding effect in generation I was especially indicated in BCX where the highest degree of inbreeding occurred and the greatest decline in performance was observed. The high rate of inbreeding in BCX was the result of mating within half sib families so that generation I purebred females were inbred 12.5 percent and in some cases 25.0 percent. In strains #20 and BCL the dams of generation I purebreds were randomly allotted to sires but sib matings were avoided as much as possible.

Although the data were confounded with a number of factors the expression of hybrid vigor, at least for generation I, can be inferred from a comparison of generation I hybrid performance with the performance of purebred females in generation F and generation I. Where the mating conditions were similar for all three of these groups, the hybrids had an average litter size at one day of 8.65 young as compared with average litter sizes of 7.40 young for generation F females and 7.66 young for generation I purebred females. At 10 days the litter weight of the generation I hybrids exceeded that of generation F by 1.22 grams and the weight of litters by generation I purebred females by 5.67 grams.

The superiority of generation I hybrid female performance over the performance of either generation F or generation I purebred females was consistent for all strains. In #20 the hybrid and

purebred females of generation I had the same mean litter size at 10 days but the hybrids showed an average superiority of 1.91 grams in litter weight. In BCX where the purebreds of generation I were inbred the difference between the hybrids and purebreds of generation I was especially pronounced for litter size and weight.

A comparison of generation II hybrid performance with that of the parental strain was confounded by the change in the mating method which appeared to adversely affect litter size in the hybrids of generation II. Where the data were pooled, the litter weight for the hybrid group was essentially the same as that of the generation I purebred group; the size of litter however was .15 young greater for purebred females. Thus, even though hybrids of generation II were subjected to what the decline in litter size at birth indicated to be less desirable environment, the overall performance of generation II hybrids was the same as parental purebred performance.

In each of the strains the comparison of generation II hybrids with parental purebred performance was not always consistent with the pooled comparison. In #20 the purebred production in generation I had improved in litter size over generation F and exceeded the performance of hybrid daughters by 2.34 grams at size 10. This was probably due, in part, to the expression of some intra-strain hybrid vigor which resulted from the initial matings (generation F) of strain #6 to #20.

In BCX the situation was reversed from #20 due to the inbreeding in generation I purebreds so that the difference between generation I purebreds and generation I hybrids was 1.18 grams.

In BCL the performance of generation I purebreds and generation II hybrids was essentially the same.

The degree of hybrid vigor expressed cannot be measured with accuracy from these data, but it may be inferred, especially from generation I hybrid data, that the hybrid female was superior to purebred contemporaries and parents.

Generation I Sire Performance

The performance of generation I sire families by strains is shown in Appendix B, Tables 2, 3, and 4. Both purebred and hybrid daughter means are shown for each sire, although sire family selection was based entirely upon the latter. Two-way selection was conducted by keeping three males from one or two sires with the highest family means of litter weight to make a high class, and three males were kept from the two sires with the lowest family average litter weight. The selected sires and the number of sons kept is indicated by the key 1L, 2L, 1H, and 2H where the number indicates the number of sons kept and L and H refer to the low and high classifications respectively.

A summary of selection differentials for each class, high and

low, in strains and averaged over all strains is shown in Table 2. The selections for litter size at one and 10 days which accompanied selection for litter weight are also shown. Due to the decreased performance of generation II hybrids which was assumed to be largely due to change in environment, the evaluation of selection was based upon a comparison of the divergence between high and low classes in the selected families and the difference between high and low classes in generation II hybrids.

Table 2. Generation I high and low class hybrid family means, selection differentials of sire family means (S. D.) and divergence between class means (D) for litter size at one day (size 1) and 10-day litter size (size 10) and weight (weight 10) by strains and pooled over all strains.

Strain	Class	Size 1			Size 10			Weight 10		
		Mean*	S. D.**	D***	Mean	S. D.	D.	Mean	S. D.	D.
#20	High	8.67	0.06		9.47	1.57		47.48	4.13	
	Low	8.73	0.12	-.06	7.13	-.77	2.34	40.79	-2.56	6.69
BCX	High	9.63	1.20		8.70	1.14		45.19	6.19	
	Low	8.20	-.23	1.43	7.30	-.26	1.40	33.73	-5.27	11.46
BCL	High	7.90	-.47		8.00	0.24		47.35	5.60	
	Low	6.70	-1.67	1.20	6.50	-1.26	1.50	40.27	-1.48	7.08
Pooled	High	8.73	0.25		8.73	0.99		46.67	5.18	
	Low	7.88	-.60	0.85	6.98	-.76	1.75	38.26	-3.23	8.41

*Mean = mean of sire family means.

**SD = Selection differential.

***D = Divergence between high and low class means.

The high selection differentials for litter weight were similar for all strains. The selection differentials were 4.13 grams in #20, 5.80 grams in BCX and 5.60 grams in BCL. The low selection differentials were much more variable and ranged from -2.56 grams for #20, -5.66 grams for BCX to -1.48 grams for BCL. The divergence between classes was 6.69 grams for #20, 11.46 grams for BCX and 7.08 grams for BCL. Pooled over all strains the high selection was 5.18 grams, the low selection differential was -3.23 grams with a total difference of 8.41 grams between high and low class means.

The selection for litter size at 10 days which accompanied the classification by litter weight varied between strains but followed the general pattern seen for litter weight.

In #20 and BCX the high selection differential was larger than the low selection differential which corresponded to the pattern in the selection for litter weight in these strains.

In the selection for litter size at 1 day which resulted from the selection for litter weight, only one of the strains (BCX) retained a consistent relationship with 10-day litter size and weight. In #20 the amount of selection practiced was slightly negative but essentially zero. In BCL both high and low class selection differentials were negative but the divergence between class means was still positive.

Response to Selection

A summary of generation II class means and the divergence between classes by strains is shown in Table 3 for litter weight and litter size at one and 10 days. The individual sire means for the data in Table 3 are shown in Appendix B, Table 5.

Table 3. Generation II high and low class hybrid family means and divergence (D) between class means for litter size at one day (size 1) and 10-day litter size (size 10) and litter weight (weight 10) by strains and pooled over all strains.

Strain	Class	Size 1		Size 10		Weight 10	
		Mean*	D**	Mean	D	Mean	D
#20	High	8.08		7.43		37.89	
	Low	7.17	0.91	6.77	0.66	35.16	2.73
BCX	High	6.73		6.17		34.62	
	Low	7.67	-.94	7.07	-.90	35.47	-.85
BCL	High	7.87		7.50		38.35	
	Low	7.47	0.40	6.83	0.67	35.08	3.27
Pooled	High	7.57		7.03		36.95	
	Low	7.43	0.14	6.89	0.14	35.23	1.72

*Mean = mean of sire family mean.

**D = divergence between high and low class means.

The response to selection for 10-day litter weights was positive for #20 and BCL but negative for BCX. This same pattern of response was also observed for litter size at one and 10 days.

The evaluation of the response to selection is shown by the

ratios of observed response to selection difference. These ratios or realized heritabilities are summarized in Table 4. The ratios in BCX were listed as zero although they were actually negative. The selection difference was negative for size 1 of #20, but because of the positive divergence of 1.01 young in generation II the realized heritability was listed as zero.

Table 4. Ratios of divergence between classes in generation II (Response) to divergence between class means of generation I (Selected) for litter size at 1 day and litter size and weight at 10 days by strains and pooled over all strains.

Strain	Size 1	Size 10	Weight 10
#20	0	0.2863	0.4080
BCX	0	0	0
BCL	0.3333	0.4187	0.4618
Pooled	0.1647	0.0786	0.2092

To determine the predictability of the observed results sib analyses were conducted on the data of generation I hybrid sire families within each strain and pooled over all strains. On the assumption that the variance among sires is additive, Bowman (1962) shows that genetic change can be predicted by the following:

$$\Delta G = \bar{I} \sqrt{\left(\sigma_s^2 + \frac{n}{p} \sigma_d^2 + \frac{1}{Kp} \sigma_w^2 \right)}$$

- where ΔG = the genetic change;
- \bar{i} = the selection differential between sire families
in phenotypic standard deviations;
- σ_s^2 = the component of variance due to differences be-
tween sires;
- σ_d^2 = the component of variance due to differences be-
tween dams mated to same sire;
- σ_w^2 = the component of variance due to differences be-
tween full sibs;
- n = number of sires;
- p = number of full sib groups;
- Kp = number of offspring in any one full sib group.

The mean square values and the corresponding degrees of freedom of the sib analyses are shown in Table 5 for litter weight and litter size at one and 10 days by strains and pooled over all strains. The estimated components of variance for sires, dams and full sibs derived from these mean square values are given in Table 6. Adjustments for unequal subclass sizes were made by the method of Warren and Dickerson (1952). Because of the zero or negative sire components in litter size at one day the above analysis model was modified by eliminating the dam component so that the analysis included between sires and within sires.

The ratios of expected response and observed response are given

Table 5. Mean squares (M.S.) and degrees of freedom (d.f.) from analyses of variance of generation I hybrid sire families for litter size at 1 day and litter size and weight at 10 days for strains #20, BCX, and BCL and pooled over all strains.

Traits	Source of Variation	NR ¹		RL ²		LN ³		Pooled	
		d. f.	M. S.	d. f.	M. S.	d. f.	M. S.	d. f.	M. S.
Size 1	Strains							2	0
	Sires in strains	7	4.3690	8	8.1137	6	4.9060	21	5.9489
	Dams in sires	13	5.8205	20	7.7897	5	11.6377	38	7.6223
	Progeny in dams	29	2.2155	57	4.8601	20	4.1125	106	3.9955
Size 10	Strains							2	0.5416
	Sires in strains	7	8.5424	8	7.8100	6	4.3884	21	7.0765
	Dams in sires	11	8.5606	17	5.2141	5	2.2428	33	5.8794
	Progeny in dams	18	2.7407	34	3.3768	14	4.3511	66	3.4100
Weight 10	Strains							2	10.2989
	Sires in strains	7	214.6350	8	178.5365	6	40.2203	21	151.3361
	Dams in sires	11	113.4994	17	66.2122	5	77.6666	33	83.7101
	Progeny in dams	18	80.1253	34	48.5272	14	62.8754	66	60.1884

¹NR = #20

²RL = BCX

³LN = BCL

Table 6. Component of variance estimates by strains and pooled over all strains for litter size at 1 day and litter size and weight at 10 days in generation I hybrid sire families.

Trait	Component of Variance	NR ¹	RL ²	LN ³	Pooled
Size 1	Sires	0	0	0	0
	Dams in sires	1.7519	1.1291	3.4415	1.5385
	Full sibs	2.2155	4.8601	4.1125	3.9955
Size 1 ⁴	Between sires	0.1705	0.2682		0.1457
	Within sires	3.3313	5.6210		4.9526
Size 10	Sires	0	0.3260	0.0085	0.1426
	Dams in sires	3.0364	0.8777	0	1.2486
	Full sibs	2.7407	3.3768	4.3511	3.4100
Size 10 ⁴	Between sires	0.8011	0.5916		
	Within sires	4.9482	3.9892		
Weight 10	Sires	22.3027	16.6616	0	12.6284
	Dams in sires	17.4123	8.4487	8.6045	11.8934
	Full sibs	80.1252	48.5272	62.8754	60.1884

¹NR = #20

²RL = BCX

³LN = BCL

⁴Effect of dams omitted.

in Table 7. For litter weight the ratios between expected and observed response were not as close to unity as the pooled data. In BCL no predictions of results were possible because of the zero sire component in the sib analyses for all traits.

Table 7. Expected divergence between generation II class means (Expected) and ratios of observed divergence between class means (Observed) to expected divergence for litter size at one day and litter size and weight at 10 days by strains and pooled over all strains.

Strain	Size 1		Size 10		Weight 10	
	Expected	$\frac{\text{Observed}}{\text{Expected}}$	Expected	$\frac{\text{Observed}}{\text{Expected}}$	Expected	$\frac{\text{Observed}}{\text{Expected}}$
#20	0	0	0.9845 ¹	0.6703	2.046	1.3343
BCX ²	0.4400 ¹	0	0.2010	0	3.7979 ¹	0.7188
BCL	0	0	0	0	4.4368	0
Pooled	0.1423 ¹	0.9838	0.1048 ¹	1.3358	0	0
			0.7031 ¹	0.199	2.171	0.835

¹ Estimate based upon σ_s^2 from analyses without dam.

² All observed responses were negative.

Two estimations of expected response for litter weight were determined for #20. In the analysis which excluded the effects of dam the estimated response exceeded the observed response as indicated by the ratio of 0.7188. When the sire component in #20 was based upon a sib analysis which included the effects of dams the estimated response was less than the observed response as indicated by the ratio 1.3343 of observed to expected response.

The expected responses of litter weight and size at 10 days in BCX were based upon sib analyses which contained the effects of dam while the estimated sire component for litter size at one day was obtained from the simplified analysis. The ratios of observed to expected response were recorded as zero although the observed response was negative for all three traits.

The agreement between the expected and observed response for 10-day litter weight in the pooled data and the inconsistency of agreement within strains suggested that the variance between all sire families was to a large extent additive but that the sampling error within each of the strains impaired the accuracy of predictions within strains.

A further evaluation of the effect of selection and the variation of litter weight was made by conducting sib analyses on the performance of generation II hybrid females. The mean square values and corresponding degrees of freedom for analyses of litter

size at one and 10 days, litter weight at 10 days and for an index of suckling ability are given for each strain and pooled over all strains in Table 8. These analyses were subdivided by classes in strains, sires in class, dams in sires, litters in dams and within progeny. The component of litters in dams was a result of repeated inter-strain matings. To estimate the total amount of variability between sires the source of variation due to class was ignored. Components of variance were obtained by using the adjustment for unequal subclass numbers and solving for a series of linear equations. The estimates for components of variance within each analyses are given in Table 9.

The analysis of litter weight at 10 days for the pooled data showed a significant difference between classes which indicated that selection for 10-day litter weight was effective. This difference was evident in hybrid daughters of #20 and BCL, but not in BCX. The mean square values of class differences in Table 8 were in agreement with the responses noted earlier in Table 3.

A comparison of the sib analyses of generation II (Tables 8 and 9) with those of generation I hybrids in Tables 5 and 6 showed that the effects of sire in generation I tended to become progressively greater from litter size at one day, to litter size at 10 days and that the effects of sire were most prevalent for 10-day litter weight. In generation II the effects were reversed, that is, the

Table 8. Means squares (M. S.) and degrees of freedom (d. f.) from analyses of variance of litter size at 1 day, litter size and weight at 10 days and suckling ability by strains and pooled over all strains for generation II hybrid females.

Trait	Source of Variation	NR ¹		RL ²		LN ³		Pooled	
		d. f.	M. S.	d. f.	M. S.	d. f.	M. S.	d. f.	M. S.
Size 1	Strains							2	8.8110
	Class	1	66.7432	1	26.0258	1	3.4210	3	32.0633
	Sires	5	26.5391	5	15.5556	5	5.8516	15	*15.9821
	Sires in class	4	*16.4881	4	12.9379	4	6.4593	12	11.9618
	Dams in sires	28	4.8364	23	7.0275	16	*8.4426	67	*6.4497
	Litters in Dams	31	5.1283	25	4.0802	21	3.0729	77	4.2274
	Progeny in litters	137	4.0045	90	4.0398	81	3.3767	308	3.8497
Size 10	Strains							2	7.6623
	Class	1	46.0210	1	29.0991	1	10.7266	3	*28.6155
	Sires	5	19.6285	5	13.0171	5	3.5965	15	*12.0807
	Sires in Class	4	*13.0304	4	8.9966	4	1.8140	12	7.9470
	Dams in sires	28	4.3210	24	5.4149	16	6.7457	68	5.2776
	Litters in dams	31	4.8045	25	3.4635	21	3.1986	77	3.9311
	Progeny in litters	142	3.6590	90	3.4087	79	2.6192	311	3.3334
Wt. 10	Strains							2	145.2252
	Class	1	290.5051	1	33.6881	1	348.5491	3	*224.2474
	Sires	5	89.7364	5	48.3166	5	122.4967	15	86.8499
	Sires in class	4	39.5442	4	51.9737	4	65.9836	12	52.5005
	Dams in sires	28	110.2635	24	74.6399	16	*129.6072	68	102.2419
	Litters in dams	31	85.7835	25	65.5301	21	52.5975	77	70.1570
	Progeny in litters	142	72.6808	90	57.0613	78	46.7178	310	61.6135
S. A.	Strains							2	0
	Class	1	39.8167	1	158.6365	1	59.3117	3	85.9216
	Sires	5	95.6086	5	65.6037	5	43.1394	15	*68.1172
	Sires in class	4	109.5566	4	42.3455	4	39.0963	12	*63.6661
	Dams in sires	28	50.7825	24	17.6212	16	22.7648	68	*32.3391
	Litters in dams	31	17.0824	25	19.2119	21	19.9393	77	18.6828
	Progeny in litters	142	24.5617	90	12.5973	78	16.4079	310	19.0365

*Significance at P of .05

¹NR = #20

²RL = BCX

³LN = BCL

Table 9. Component of variance estimates by strains and pooled over all strains for litter size at 1 day, litter size and weight at 10 days and suckling ability for generation II hybrid females.

Trait	Component of Variance	NR ¹	RL ²	LN ³	Pooled
Size 1	Class	0.5008	0.1795	0	0
	Sires	0.6421	0.3452	0	0.3588
	Sires in class	0.3458	0.2352	0	0.2001
	Dams	0	0.6053	0.9180	0.4015
	Litters	0.3858	0.1690	0	0.1500
	Full Sibs	4.0045	4.0398	3.3767	3.8497
Size 10	Class	0.3200	0.2998	0.0593	0
	Sires	0.4291	0.3062	0	0.2512
	Sires in class	0.2397	0.1387	0	0.0927
	Dams	0	0.4159	0.5955	0.2258
	Litters	0.3890	0.0221	0.2760	0.2333
	Full Sibs	3.6590	3.4087	2.6192	3.3334
Weight 10	Class	1.6722	0	3.8448	1.5032
	Sires	0	0	0	0
	Sires in class	0	0	0	0
	Dams	4.0175	1.7956	12.7488	5.6000
	Litters	4.4498	3.4233	2.8015	3.3948
	Full Sibs	72.6808	57.0613	46.7178	61.6135
S. A.	Class	0	1.7545	0.3162	0.2615
	Sires	1.0452	1.8683	1.0099	1.2867
	Sires in class	1.5020	0.8930	0.8230	1.1332
	Dams	4.5970	0	0.0958	2.4939
	Litters	0	2.6738	1.6826	0
	Full Sibs	24.5617	12.5973	16.4079	19.0365

¹NR = #20

²RL = BCX

³LN = BCL

sire effects were most prominent for litter size at one day and become progressively smaller at litter size at 10 days and zero throughout all strains for litter weight at 10 days. The decreased variation between sires for 10-day litter weight can be attributed to the intensity of selection in generation I for this trait.

The increased sire component of variance for litter size at one day in generation II (Table 9) as compared to the relative size of the sire component in generation I (Table 6) was to be expected where family sizes were increased and the sampling error reduced. The lack of a similar increase in the sire component for litter size at 10 days as a result of a decrease in sampling error can be attributed to the effects of selection for 10-day litter weight which had reduced the variance between sires.

The analyses of suckling ability are also included in Tables 8 and 9. The index of suckling ability was the grams deviation that a female's litter weight differed from the average litter weight of litters of the same size. Thus, in each strain the sum of the differences in litter weights for each litter size group and over all groups was zero.

Since the indices of suckling ability within a litter size group summed to zero, there was an increased probability that the sum of indices for sub-class groups composed of observations of similar litter size would also be near zero. The confounding of litter size

and suckling ability was most apparent in the "litters in dams" and the "dams in litter" subclassifications of the component analyses given in Table 9.

In #20 the covariance of litter size within litter groups exceeded the covariance of litter size for dams. The reverse effect was noted for suckling ability where the covariance of litters was less than the covariance of dams. Similar patterns, especially, for the dam and litter components, were observed in BCX and BCL. The character of the confounding of suckling ability and litter size observed suggested that the value of the index of suckling ability used in this study depended upon the size of sub-classes and the degree of intraclass correlation for litter size.

The divergence between high and low sire means for suckling ability is shown in Appendix B, Table 5. The consistent positive divergence throughout all strains indicated that selection for 10-day litter weight resulted in positive selection for suckling ability.

DISCUSSION

There were two stated objectives of this study. The first objective was to determine the extent and character of variation between sire families for hybrid daughter reproductive performance. Particular attention was given to litter weight at 10 days. The specific purposes of these objectives were to determine the additivity of the variance among sire families and whether predictions could be derived for accurately estimating the genetic change that would be accomplished by selection.

The second objective was to determine whether selection based upon sire family performance in a rotational mating scheme would be effective.

Ideally, the most useful demonstration of the effectiveness of selection is the mean change in performance between generations; however, when a change in generations is correlated with a change in environment other methods of evaluating the response to selection must be employed. In this study the environmental change between generations I and II necessitated the use of the divergence between high and low classes in a two-way selection scheme for the evaluation of the effectiveness of selection. The use of the two-way selection scheme in overcoming the difficulty of environmental change has a serious limitation; namely, only the divergence

between the two directions of selection can be measured. The response measured in terms of divergence will only express the average of the response in the separate directions and unless information is available for estimating the symmetry of response, the response to selection in either direction cannot be accurately predicted.

An example of asymmetry of response to selection was shown by Falconer (1955) in selection for lactation in mice. In one experiment no progress was realized for upward selection. In this case a realized heritability for divergence of 50 percent was found in two-way selection which indicated that the heritability of the downward selection practiced was 100 percent. In a second experiment, the overall realized heritability was again about 50 percent with 14.5 percent occurring for the upward selection and 84 percent for the downward selection.

In the present study two-way selection was conducted in generation I and the divergence between high and low selection classes was compared with the observed divergence in generation II. These comparisons were made by strains and on the pooled data.

In assessing the effectiveness of selection practiced in this study one of the important considerations is the relative value of the evaluation by strains as compared with the evaluation based

upon the pooled data. When the evaluation was based upon the pooled data a comparison of expected and observed response showed a ratio of 0.835. This agreement suggests that the overall variation among sire families was additive.

The evaluation by strains showed a positive response to selection in strains #20 and BCL but a slightly negative response in BCX (Table 3). A positive ratio of expected and observed response was achieved only in strain #20 (Table 7). Thus, while the data by strains generally support the effectiveness of selection, the inconsistency of the expected and realized divergence between strains does not support the conclusion that the variability between sire families was additive.

In view of the unique characteristics of the strains utilized, evaluation of the response to selection in this study should be based upon a consideration of the following:

- (1) the genetic foundation of each sire strain,
- (2) the genetic foundation of the dam's strain,
- (3) the presence and influence of maternal effects by the dams of hybrid daughters, and
- (4) the relative degree of sampling error which influenced selections and predictions of response in generation I.

Sire variability was observed in strains #20 and BCX in both generations I and II (Tables 6 and 9). In BCL, however, the

estimated sire component of variance was positive in only one analysis, suckling ability in generation II. The absence of sire variability in BCL was probably the result of a combination of factors. Firstly, BCL was an inbred strain and the amount of genetic variability relative to the other strains would be expected to be low. Secondly, the number of observations per sire in generation I was smaller than in either of the other two strains which could lead to a greater degree of sampling error. Thirdly, the relationship between sires in generation II was closer than in the other strains; in the high group all three sires were half sibs and two of them were full sibs.

When the above factors are considered, the high realized heritabilities (Table 4) in BCL are almost surprising. In considering the lack of sire variability in either generation I or II it seems likely that the divergence attributed to BCL males was partly the result of high and low grouping of the #20 dams to which BCL males were mated. The effectiveness of high and low grouping of #20 dams was indicated by the positive response to selection for #20 males (Table 3). A second factor was the positive divergence between the performance of high and low groups in #20 (Appendix B, Table 2).

The negative response in generation II in BCX is difficult to explain since the sampling error which influenced sire evaluation

and selection should have been the lowest of the three strains. Part of the negative response in BCX may have been due to the effects of the greater amount of inbreeding which resulted from mating within sib families. A second factor which may have been responsible for the negative response was the sampling error in classifying BCL females into high and low groups. The error in classification is suggested by the performance of purebred daughters of generation I sires which is shown in Appendix B, Tables 2, 3 and 4. In both #20 and BCX the selection differences between high and low classes were similar for hybrids and purebreds, while in BCL the divergence based upon purebred value was negative and contradictory to the positive difference between hybrid classes based upon the same sire groups. A misclassification of dams could have resulted in high BCX males being mated to low BCL females or low BCX males being mated with high BCL females.

The second factor above seems plausible although when the lack of genetic variability in BCL sires is considered it detracts from the soundness of basing the negative response completely on the misclassification of BCL dams.

The selection (Table 2), response (Table 3), and prediction of response (Table 7) in #20 was the most consistent with the pooled data. The results of the selection in this strain are perhaps the best indication of the manner in which populations in the proposed

selection program should be conducted. In the foundation matings the genetic variability was increased by intermating #20 males with #6 females; also in the intrastrain matings of generation I inbreeding was minimized as much as possible.

An interesting relationship concerning the effects of inbreeding is suggested by the character of the sib analyses of strain #20 where the BCX dams were inbred 12.5 to 25.0 percent. In the analyses of #20 (Tables 8 and 9) the relative variability between litters exceeded the variability of dams for litter size at one and 10 days and litter weight. In the other strains the general case observed was the opposite, that is, the dam component usually exceeded the litter component. The increased litter component in #20 hybrid females suggests that the depressed level of performance in generation I BCX purebreds (Table 1) which were the dams of #20 hybrid females, was accompanied by a greater variability of performance between litters.

A more direct measure of the variability of dam performance was made by estimating the repeatability of litter size performance of the purebred dams used in the replicated interstrain matings. The estimates of repeatability were derived from a component analysis of the variation between and within dams (Table 10). The estimate of repeatability of 0.111 for BCX as compared with the estimates of 0.185 for #20 and 0.192 for BCL females were in

agreement with the implications of the sib analyses in Table 9.

Table 10. Mean squares (M. S.) and degrees of freedom from analyses of variance of generation I purebred dam litter size performance, and estimates of repeatability of litter size performance in repeated interstrain matings.

Source of Variation	N ¹		R ²		L ³	
	d. f.	M. S.	d. f.	M. S.	d. f.	M. S.
Between dams	19	7.8708	28	10.3151	22	9.7734
Within dams	27	5.1358	47	7.7730	37	6.0315
Repeatability	0.185		0.111		0.192	

¹N = strain #20

²R = strain BCX

³L = strain BCL

The decreased repeatability of performance in BCX females corresponds with the general evidence that inbreeding is associated with greater phenotypic variation (Lerner, 1954; Falconer, 1960 and King, 1961). The results of King's (1961) study are especially relevant where he measured the relative phenotypic stability of individual Drosophila females in successive measurements. The trait studied was the hatchability of eggs laid on each of five consecutive days. King found that the variation of repeated measurements was lower in random bred stock than in inbred stocks.

The importance of the above finding with respect to the

selection program proposed in this study is two fold. First, where the individual is inbred, the phenotypic expression of that individual's performance becomes less reliable as a measure of the genetic differences between individuals in the population. Second, the maternal influence upon offspring becomes more variable between dams and between successive litters from the same dam. The effect of the second point may impair the predictive value of the sib analysis.

The effect of dam upon hybrid female performance has been discussed with reference to the negative response observed in BCX and the inconsistency of performance between litter groups in full sib families in strain #20. In the first case the effect suggested was of a genetic nature and in the second case the effect was more of a non-genetic character. The performance of BCL in generation II was also suggestive of the genetic influence of dams. The relative effects of the maternal influence and the genetic contribution by strains, however, could not be readily measured.

Falconer (1955) found that the factor of maternal effect, expressed as litter size, can negate selection for litter size because of a negative relationship between a dam's litter size and the weight of the daughter at six weeks. As a result of this correlation, Falconer found that daughters of larger litters tended to be smaller and have smaller litters than larger daughters from small litters.

The maternal effect observed by Falconer should have been

relatively unbiased in the selection program of this study where selection was based upon the mean performance of a sire's progeny.

In this study the selection of purebred females of generation I, which were the dams of generation II hybrids, are shown by sires in Appendix B, Tables 2, 3, and 4. The fact that females were kept from a greater number of sires and the overall ratio of about five females mated to each male indicates that the genetic variability between dams was greater than the genetic variability between sires. Therefore, the dam component of variance for each analysis of generation II was influenced by the greater degree of genetic variability between dams as well as differences in maternal effects. The additional theoretical presence of 1/4 of the genetic variance due to dominance in the dam component further confounds the interpretations concerning the nature of genetic variability associated with the traits under study.

The number of studies which were directly related to the system of mating employed in this study and for the same traits was limited. The study by Bowman (1962) previously discussed was hindered by a lack of heterotic response in the performance of hybrid progeny. In an assessment of the genetic mechanisms which influenced hybrid performance, Bowman regressed hybrid daughter performance on the performance of purebred dams and concluded that the gene mechanisms underlying the expression of heterosis

were either dominant or partially dominant.

Comparable regressions of daughter on dam were not conducted in this study; however, some inference of the general nature of the genetic variability can be derived from the corresponding positive selection values in strains #20 and BCX for purebred progeny which resulted from the classification of sires on the basis of hybrid progeny performance (Appendix B, Tables 2, 3, and 4). The correspondence between hybrid and purebred selection differences in generation I, the response to selection in strain #20 and the close agreement between the pooled values of expected and realized divergence imply that the selection conducted in this study acted upon genetic variation of an additive nature.

One study which was pertinent to the trait under selection in the present study was a selection study for lactation in mice (Falconer, 1955). Lactation data in Falconer's study was the weight of the litter at 12 days with the units being percentages of a certain weight. Litters were standardized to eight young at birth or appropriate corrections were made for the number in litters which were less than eight.

In the first experiment no response to selection was realized after the second generation in an upward selection program. In generations 7 and 8, two-way selections were made which yielded significant differences between high and low groups. The realized

heritability was 50 percent and in view of the lack of upward response it was concluded that the response to low selection was nearly 100 percent.

In the second experiment, two-way selection was conducted by simple mass selection. Inbreeding was minimized by avoiding sib and first cousin matings. The averaged realized heritability based upon the divergence was 49 percent. In this experiment, however, a steady upward response of about 14.5 percent was realized. The downward selection showed a realized heritability of 84 percent for the first six generations but the response ceased after six generations.

The total divergence produced by two-way selection in Falconer's study was about 1.5 phenotypic standard deviations. Even though an upward selection limit was not reached in the second experiment, Falconer concluded that relatively few genes contributed to the additive genetic variance of lactation.

In the present study the trait selected (10-day litter weight) was similar but not directly comparable to lactation in Falconer's study since the 10-day litter weight was an aggregate of the dam's milking ability and the size of the litter. The character of the sib analyses between generations (Tables 6 and 9) was suggestive that the character of response to selection in this study may be similar to the response observed by Falconer. It was previously noted that

in generation I the sire component became more distinctive from litter size at one day to litter size at 10 days and the most distinctive sire variation was noted for litter weight. In generation II, however, the reverse trend was noted with the sire component of variance being zero in all strains for litter weight at 10 days. The occurrence of variation among sires (sires in class) for litter size at one and 10 days indicates that the absence of sire variability for litter weight cannot be entirely attributed to the relatedness among sires in classes and the intensity of selection.

Although the similarity with Falconer's results is evident, a conclusion concerning the number of genes which contributed to the genetic variation of litter weight should be withheld in consideration of the limitation of one generation of selection.

The trait of suckling ability in this study is more comparable to the trait of lactation in Falconer (1955), but the index used in this study should be considered with caution in view of the confounding effects with litter size.

One study with swine (Wilson, et al., 1962) was reviewed which compared the performance of crossbred and purebred daughters of the same sires. The low number of daughters per sire (2.8 crossbreds and 3.5 purebreds) and the significant environmental effects resulted in inconclusive findings with regard to sire differences in daughter productivity and the relationship between

hybrid and purebred performance.

The asymmetry of the response to selection for lactation observed by Falconer (1955) advise against conclusions concerning the progress which would be achieved for increased litter weight by the selection program used in this study. In the present study a number of factors which indicated that the observed variation between sire families was additive included the following:

- (1) the correspondence between the expected response and realized response in the pooled data and in strain #20.
- (2) the response to selection, and
- (3) the correspondence between the hybrid and purebred class differences in generation I for strains #20 and BCX.

On the basis of additive variation the application of this selection method could be simplified in the manner suggested by Hansson and Lindkvist (1962).

In the design proposed in the study by Hansson and Lindkvist (1962) hybrid progeny were obtained by mating purebred males to crossbred females in a rotational crossbreeding system. Thus, instead of mating A males to B females to obtain hybrid progeny, A males would be mated to crossbred females which had been sired by B males. The same pattern would be followed throughout the remaining strains.

An additional advantage of using hybrid dams is suggested

by the observation in this study that inbred dams were more variable in performance than less inbred females. The use of hybrid females in the system of mating proposed by Hansson and Lindkvist should, therefore, offer a greater uniformity of dam influence within sire families than more homozygous purebreds.

SUMMARY AND CONCLUSIONS

In this study recurrent selection was conducted in three strains of mice for hybrid female reproductive performance. Selection in each strain was based upon the average litter weight at 10 days of a sire's interstrain hybrid daughters. Hybrid daughters were obtained from a rotational pattern of interstrain top-crossing in which #20 males were mated to females of BCX, BCX males were mated to females of BCL and BCL males were mated to females of #20.

The presence of hybrid vigor in the reproductive performance of hybrid females was indicated by the greater performance of generation I hybrid females as compared with the performance of purebred dams of generation F and purebred sibs of generation I. A change from harem to colony group mating caused a decline in litter size in generation II hybrids, but their 10-day litter weights were the same as the 10-day litter weights of purebred dams.

The effectiveness of selection was evidence by the positive divergence realized between high and low selection classes in strains #20 and BCL and in the data pooled over all strains.

Predictions of response were made from components of variance derived from sib analyses. The ratio of expected to realized divergence between classes for litter weight at 10 days was 0.835 for the pooled data. By strains, however, only strain #20 showed

a positive correspondence between the expected and realized divergence.

In strain BCL the realized response was positive but the expected divergence was zero. The lack of sire variability which led to the zero expected response was attributed to sampling error and the inbred foundation of BCL.

The negative response realized in strain BCX may have been caused by (1) a misclassification of the BCL dams of BCX hybrid females or (2) the effects of inbreeding of generation I intrastain mating of BCX.

On the basis of the correspondence between hybrid and purebred selection differences in strains #20 and BCX, the response to selection in strain #20 and the agreement between expected and realized divergence in the pooled data it was concluded that selection for 10-day litter weight had acted primarily upon additive genetic variation.

In strain #20 hybrids, the relative size of the component of variance due to litters in dams indicated that the influence of inbred BCX dams was more variable between successive litters than the influence of less inbred dams of #20 and BCL. Repeatability estimates of litter size performance further indicated that BCX dams were more variable in performance than were purebred dams of #20 and BCL.

The implication that selection had acted largely on additive genetic variation suggested that females within a rotational crossbreeding program could be utilized as dams to obtain hybrid progeny for sire evaluation. The greater variability of dam influence of inbred BCX dams indicated that the use of crossbred dams would lead to a more uniform dam influence in a sire's progeny.

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APPENDICES

APPENDIX A

APPENDIX A. Strain Pedigree diagrams of (1) interstrain matings and number of hybrid daughters which littered and (2) intrastrain matings and fertile progeny used in subsequent matings.

Key to diagram charts

1. Male identification

The foundation of each strain is based upon three sires which were numbered in the following manner:

Sire Number	Strain
1, 2, 3	#20
4, 5, 6	BCX
7, 8, 9	BCL

Subsequent male offspring are denoted by the addition of digits to the original sire's numerical identity, e. g., sons of sire 4 are males 41, 42, and 43.

2. Female identification

a. Strains

Strains are coded by the following prefix letters:

Code	Strain
N	#20
R	BCX
L	BCL

b. Interstrain hybrid females are coded by code letters of both parental strains as follows:

Code	Parental Strain
NR	#20 x BCX
RL	BCX x BCL
LN	BCL x #20

c. Purebred females of each strain are identified individually, and by sires so that:

- (1) the first number(s) following the strain letter code denote the individual's identity.
- (2) the second series of numbers preceded by a dash (-) indicate sire, e. g., daughter 13 by sire 5 is R13-5.

3. Outline of mating scheme

- a. Mating F -- Initial intrastrain crosses to expand the population size.
- b. Generation I -- (1) Interstrain topcross to produce hybrid females -- number of hybrid females of a mating which littered are shown under coded column.
(2) Intrastrain matings to produce generation II purebreds.
- c. Generation II -- Interstrain topcross replicated in three mating sets.

STRAIN BCX

MATING F		GENERATION I				GENERATION II																																																																					
Sire	Dam	Progeny	Interstrain		Intrastrain		Interstrain			Total Sibs																																																																	
			Sire	Dam	RI	RY	Set 1	Set 2	Set 3																																																																		
4	R1	43	L3-9	1	Died	None	412	412	L6-81	2	L6-83	1	L6-83	6	9																																																												
		R0-4	L6-9	1												413	413	L6-72	1	L6-72	3	L6-72	2	6																																																			
		R1-4	L10-9	7																					41	41	L1-7	2	L8-81	1	L8-81	5	6																																										
	R2	42	L5-8	1	R2-4																													R3-41	4	L0-72	4	L0-72	3	7																																			
		R2-4	L10-8	1																																					R5-4	R5-41	3	L2-81	3	L2-81	3	6																											
		R3-4	L13-8	1																																													R6-4	R1-41	4	L8-81	1	L8-81	5	6																			
		R4-4	L6-8	1																																																					R12-5	R8-51	1	L1-72	1	L1-72	2	7											
		R5-4	L1-7	2																																																													R13-5	R9-51	1	L7-81	1	L7-81	1	1			
	R6-4	L8-7	1	51	R10-51																													1	L11-81	4	L11-81	4	8																																				
	5	R3	R12-5																																					L3-7	2	51	51	R11-5	R11-51	R9-5	R0-52	R3-53																									R3-53	R0-5	532
			R13-5																																					L5-7	1								52	52	R9-5	R0-52	R3-53	R3-53	R0-5	532																			
51			L6-7			1	R4-5	R4-52	R7-5	R7-52	R0-53	R2-53	R3-53	R0-5	532																									532	L7-83																2	L7-83	4	L7-83	3	9													
R4		R3-5	L7-8			3										52	52	R4-5	R4-52	R7-5	R7-52	R0-53	R2-53	R3-53																		R0-5	532	532	L7-83	2	L7-83	4															L7-83	3	9										
		R5	R0-5	L14-8	2	53																			53	R5-2	R9-53	R0-53	R2-53	R3-53	R0-5	532	532	L7-83	2	L7-83	4	L7-83	3										9																										
R6		R1-5	L0-8	3	53		53	R5-2	R9-53	R0-53	R2-53	R3-53	R0-5	532	532	L7-83	2	L7-83	4	L7-83	3	9																																																					
		R7	R2-5	L3-7		2																	61	61	R7-7	R3-61	R0-63	R1-63	631	631	L7-93	2	L7-93	1	3																																								
6		R5	R8-5	L5-9	3	53	53	R0-5	532	532	L7-83	2	L7-83	4	L7-83	3	9																																																										
			R9-5	L2-9	3													61	61	R8-6	R5-61	R0-63	R1-63	631	631	L7-93	2	L7-93	1	3																																													
			R10-5	L2-7	7																										63	63	R10-6	R1-63	631	631	L7-93	2	L7-93	1	3																																		
		R11-5	L4-7	2	63	63	R3-6	R4-63	632	632	L3-93	4	L3-93	3	7																																																												
	53	L7-7	2	63												63	R6-6	R7-63	R0-6	R23-62	R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																														
	R7	R4-5	L5-9																											2	62	62	R2-6	R8-62	R9-62	R0-6	R23-62	R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																													
		R8	R5-5		L0-9	5	62	62	R3-6	R7-62	R0-6	R23-62	R1-6	R22-62	622															622																	L0-93	2	L0-93	3	5																								
	R9	R6-5	L9-9	3	62	62										R3-6	R7-62	R0-6	R23-62	R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																															
		R10	R7-5	L8-3			1	62	62	R3-6	R7-62	R0-6	R23-62	R1-6	R22-62														622	622	L0-93	2	L0-93	3	5																																								
	R12	R6-6	L2-8	2	62	62	R3-6									R7-62	R0-6	R23-62	R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																																
		R11	R13-6	L9-8				2	62	62	R3-6	R7-62	R0-6	R23-62	R1-6													R22-62	622	622	L0-93	2	L0-93	3	5																																								
R13	R7-6	L12-8	5	62	62	R3-6	R7-62	R0-6								R23-62	R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																																		
	R12	R8-6	L8-8						2	62	62	R3-6	R7-62	R0-6	R23-62											R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																									
R13	R13-6	L11-8	1	62	62	R3-6	R7-62	R0-6	R23-62							R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																																			
R14	R14-62	L11-8	1							62	62	R3-6	R7-62	R0-6	R23-62										R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																										
R15	R15-62	L11-8	1	62	62	R3-6	R7-62	R0-6	R23-62							R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																																			
R16	R2-62	L11-8	1							62	62	R3-6	R7-62	R0-6	R23-62										R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																										
R17	R3-62	L11-8	1	62	62	R3-6	R7-62	R0-6	R23-62							R1-6	R22-62	622	622	L0-93	2	L0-93	3	5																																																			

APPENDIX B

Averages of sire family performance of litter size at one and 10 days and litter weight at 10 days for generation F (Table 1), Generation I hybrid and purebred families (Tables 2, 3, and 4) and generation II hybrids (Table 5).

Table 1. First parity performance of generation F purebred females by sire families.

Code	Sire	n1	Size 1	n10	Size 10	Weight 10
N	1	4	7.2	4	6.8	37.05
	2	6	7.0	6	6.8	38.48
	3	6	7.2	6	6.5	38.60
	$N\bar{s}^1$		7.13		6.70	38.04
R	4	7	7.1	7	7.0	38.07
	5	10	6.8	10	6.8	41.48
	6	12	7.6	11	7.3	42.02
	$R\bar{s}$		7.17		7.03	40.53
L	7	8	8.4	8	8.1	43.66
	8	13	6.5	13	5.9	36.48
	9	11	8.6	11	8.3	45.95
	$L\bar{s}$		7.83		7.43	42.03
Pooled	\bar{s}		7.38		7.05	40.20

\bar{s}^1 = mean of sire family means.

Table 2. Strain #20 hybrid (NR) and purebred (N) sire family means and classification of progeny used as generation II sires and dams.

Sire	Code	n1	Size		Size		Weight	Male	Female
			1	n10	10	10			
11	N	3	10.3	3	9.7	47.43			
	NR	6	9.2	6	9.0	47.40	IH	H	
12	N	2	7.0	1	10.0	52.40			
	NR	6	9.0	6	8.3	44.84			H
22	N	3	8.0	3	7.3	41.83			
	NR	6	8.4	3	9.7	47.52	2H		H
23	N	7	7.6	6	6.8	37.02			
	NR	12	9.1	8	7.2	39.59	2L		L
24	N	5	8.8	5	7.8	33.33			
	NR	8	8.0	6	7.0	43.18	IL		L
31	N	5	7.6	5	7.4	38.95			
	NR	3	10.0	1	9.0	54.25			L
32	N	-	-	-	-	-			
	NR	6	7.2	4	5.0	28.64			
33	N	-	-	-	-	-			
	NR	3	8.0	3	8.0	41.37			
Sire Mean	N		8.22		8.17	41.83			
	NR		8.61		7.90	43.35			
Selection differentials	N-high		0.55		-.07	1.97			
	N-low		-.22		-1.04	-6.04			
	NR-high		0.06		1.57	4.13			
	NR-low		0.12		-.77	-2.56			
Divergence	N		0.77		0.97	7.01			
	NR		-.06		2.34	6.69			

Table 3. Strain BCX hybrid (RL) and purebred (R) sire family means and classification of progeny used as generation II sires and dams.

Sire	Code	n1	Size		Size	Weight	Male	Female
			1	n10				
41	R	3	7.0	3	7.0	36.62		
	RL	3	8.7	3	7.7	33.64	2L	L
42	R	-	-	-	-	-		
	RL	4	7.2	1	4.0	27.05		
43	R	-	-	-	-	-		
	RL	13	8.9	9	8.3	46.10		
51	R	7	7.7	4	6.1	31.47		
	RL	5	7.6	4	8.3	36.59		L
52	R	3	9.3	2	7.5	33.92		
	RL	15	8.1	6	7.5	44.58		L
53	R	6	6.3	6	6.3	31.42		
	RL	7	7.2	6	6.5	33.91	1L	L
61	R	3	8.3	3	8.0	41.50		
	RL	13	9.2	10	8.1	41.46		H
62	R	15	6.4	15	5.8	30.84		
	RL	12	9.5	11	9.1	46.87	1H	H
63	R	5	8.8	4	8.2	42.51		
	RL	14	9.7	10	8.5	44.35	2H	H
Sire Mean	R		7.69		6.99	35.47		
	RL		8.46		7.56	39.39		
Selection differential	R-high		0.31		0.41	3.15		
	R-low		-.92		-.22	-2.32		
	RL-high		1.17		1.14	5.80		
	RL-low		-.26		-.26	-5.66		
Divergence	R		1.23		0.63	5.47		
	RL		1.43		1.40	11.46		

Table 4. Strain BCL hybrid (LN) and purebred (L) sire family means and classification of progeny used as generation II sires and dams.

Sire Code	nl	Size		nl0	Size	Weight	Male Selects	Female Selects
		l			10	10		
72	L	6	6.7	6	5.7	29.62		
	LN	-	-	-	-	-		L
73	L	5	7.4	5	7.4	37.80		
	LN	4	7.9	4	8.0	47.35	3H	H
81	L	7	8.3	7	7.6	34.62		
	LN	4	7.5	3	7.0	41.05	1L	L
82	L	-	-	-	-	-		
	LN	9	8.8	7	7.6	38.02		
83	L	5	9.6	5	8.4	40.63		
	LN	5	8.8	4	7.2	40.01		L
91	L	-	-	-	-	-		
	LN	4	9.5	4	8.5	45.86		
92	L	3	8.7	2	9.0	47.35		
	LN	3	6.3	3	6.3	39.88	2L	L
93	L	11	7.9	11	7.5	37.34		H
	LN	3	9.7	3	9.7	40.10		
Sire Mean	L		8.10		7.60	37.89		
	LN		8.36		7.76	41.75		
Selection differential	L-high		-.70		-.20	-.09		
	L-low		0.50		0.90	+5.22		
	LN-high		-.47		0.24	5.60		
	LN-low		-1.67		-1.26	-1.48		
Divergence ($H\bar{s} - L\bar{s}$)	L		-1.20		-1.10	-5.31		
	LN		1.20		1.50	7.08		

Table 5. Generation II sire family means by class (H and L) and strain for litter size at one and 10 days, litter weight at 10 days and suckling ability.

Strain	Class	Sire	nl	Size		Weight		S. A.
				1	n10	10	10	
		112	44	8.8	45	7.9	38.19	-1.572
		223	33	7.6	32	7.1	37.68	0.843
		224	43	7.9	46	7.3	37.80	- .018
	H			8.08		7.43	37.89	- .249
		241	12	7.5	12	7.2	33.50	-3.892
		231	41	6.3	41	5.9	34.82	1.968
		233	29	7.7	31	7.2	37.16	0.342
	L			7.17		6.77	35.16	- .527
#20				7.62		7.10	36.52	- .388
		622	23	7.3	22	6.1	33.58	0.717
		631	15	6.4	15	6.1	34.85	1.258
		622	23	6.5	22	6.3	35.42	1.806
	H			6.73		6.17	34.62	1.260
		412	29	8.1	31	7.3	37.38	- .173
		413	24	8.2	24	7.7	34.82	-3.025
		532	30	6.7	32	6.2	34.20	0.096
	L			7.67		7.07	25.47	-1.034
BCX				7.20		6.62	35.04	0.226
		732	10	7.9	10	7.7	37.66	- .360
		733	16	7.7	16	7.3	40.17	2.660
		735	22	8.0	22	7.5	37.22	0.111
	H			7.87		7.50	38.35	0.804
		812	18	6.6	18	6.4	34.15	0.154
		922	20	8.2	20	7.2	37.36	0.666
		924	38	7.6	36	6.9	33.72	-1.595
	L			7.47		6.83	35.08	- .258
BCL				7.67		7.16	36.72	0.531