A COMPARISON OF MASS SELECTION WITH INBRED LINES AND LINE CROSSES IN THE LABORATORY RAT

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY

David Richard Pratt

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This is to certify that the

thesis entitled

A COMPARISON OF MASS SELECTION
WITH INBRED LINES AND LINE CROSSES
IN THE LABORATORY RAT

presented by

David Richard Pratt

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Animal Husbandry

William T. Magee
Major professor

Date 1-15-60

O-169

A COMPARISON OF MASS SELECTION WITH INBRED LINES AND LINE CROSSES IN THE LABORATORY RAT

By

David Richard Pratt

AN ABSTRACT

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Animal Husbandry

1960

Approved William T. Magee

ABSTRACT

A COMPARISON OF MASS SELECTION
WITH INBRED LINES AND LINE CROSSES
IN THE LABORATORY RAT

By David Richard Pratt

Inbred lines of rats were developed from each of two heterozygous populations of the laboratory rat by mating sons, double sons, and triple sons back to their dams. Four lines were developed from a two-strain base population and four lines from a three-strain base population. A mass selected group was developed from each of the base populations.

Selection was made on the basis of weight gain from the twenty-first to fiftieth day of age. Crosses were made between the inbred lines within each of the populations and comparisons of the inbred lines and the line crosses were made with the mass selected groups of each population.

Inbred males gained an average of 40 grams more than the inbred females. In the mass selected groups, males outgained females by 54 grams.

As inbreeding increased, average weight gain of the inbred animals decreased, and the difference between the mass selected and inbred groups increased from 4 to 34 grams in the three-strain population and from 12 grams to 21 grams in the two-strain population.

Crosses between the inbred lines restored part of the loss in weight gains which was incurred during inbreeding; however, no hybrid vigor in excess of the mass selected group was observed in either the 2-I or 3-I line crosses (2-I and 3-I represent the inbred lines developed from the two-strain and three-strain base populations), although there was less difference between the average gain of the mass selected group and the line crosses than between the mass selected groups and the inbred groups the previous generations.

Average litter size at birth in the fourth generation was significantly higher in both the 2-S and 3-S groups (2-S and 3-S represent the mass selected groups developed from the two-strain and three-strain base populations) than in the corresponding inbred group and in the 2-S group in the fifth generation also. As inbred dams were used in both these generations, it was concluded that inbreeding of the dam had more influence on the size of the litter at birth than did the inbreeding of the litter itself.

Litter size at weaning was significantly larger in the 3-S group than in the 3-I group in the fourth generation, and it was also larger in the 2-S group than in the 2-I group in the fifth generation. An analysis of the average litter death loss showed no difference in birth to weaning livability between the mass selected and inbred groups.

Estimates of the variance components for weight gains between litters within lines were smaller than the between litter estimates for the mass selected groups. Variance of weight gain within inbred litters in the 2-I group tended to be reduced as inbreeding progressed.

The amount of heterozygosity in the base population apparently had no effect on the selection in either the mass selected or the inbred groups. Average weight gains, litter size at weaning and at birth, and livability from birth to weaning were similar for both mass selected groups and for both inbred groups including the line crosses.

One of the major drawbacks to the development of superior inbred lines by the son-to-mother matings system used in this experiment was the reduced prolificacy of the inbred dams. Reduced prolificacy, in addition to the already restricted size of the inbred lines, increased the necessity of developing more lines if this system were to be used to its best advantage.

Another drawback to the development of inbred lines by a strict method of son-to-dam matings was the small number of animals available for maintenance of the individual lines and for making line crosses. Expansion of the lines by brother-sister matings earlier in the development of the lines, perhaps even as early as the first generation of inbreeding, along with continued son-dam matings is recommended to allow sufficient numbers to maintain the proposed lines in each group as well as supply sufficient number of females for more complete testing of the better lines in line crosses.

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ACKNOWLEDGEMENTS

The author wishes to express his deepest appreciation to Dr. William T. Magee, under whose guidance and supervision this work was done, for his interest, encouragement, and help throughout the course of study. His patience, willingness to offer assistance, and inspiration will always be remembered.

Sincere thanks are also expressed to the other members of the guidance committee - Dr. W. D. Baten, Dr. Lois Calhoun, Dr. A. S. Fox, Dr. L. D. McGilliard, and Dr. J. E. Nellor - for their willing assistance, advice, and encouragement throughout the course of study. The association with the entire committee and the opportunity to have known each of them as a scientist, teacher, and friend will be cherished always.

Grateful appreciation is extended to Dr. R. H. Nelson, head of the Department of Animal Husbandry, and to Michigan State University for provision of the facilities and materials necessary for this study and for financial aid in the form of an assistantship.

The author wishes to express special appreciation to his wife, Billye, for her inspiration, patience, and encouragement and for an excellent typing of the manuscript. Sincere gratitude is expressed to all his

family whose encouragement, sacrifices, and faith made the study possible.

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FINAL EXAMINATION: November 15, 1960, 3:00 p.m.
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INTRODUCTION

A program has been in operation with swine at Michigan State University to test the feasibility of developing inbred lines on the basis of mating sons to outbred dams. This system would delay any detrimental effects of inbreeding in the dams but would allow a rather rapid increase in the inbreeding of the offspring in each generation.

More use of laboratory animals to check logical statistical conclusions to learn the differences between observation and expectation has been advocated (Craft *et al.*, 1951). The use of laboratory animals has also been suggested as an aid in solving theoretical problems in livestock selection.

The purpose of this study with the laboratory rat has been as a pilot study of the program with swine. The similarities of swine and the rat as to nutrition requirements, litter size, and growth pattern after weaning allow valid comparisons. The reproductive habits of the rat make it possible to observe many more numbers than with swine in a much shorter time. The size of the rat allows these numbers to be kept for observation at a much lower expense than would be possible for swine.

The true value of an inbred line must be determined from its value in crossing (Craft _et al_., 1951). A method of improving swine, based on a comparison of performance of crossbreds within and between breeds with the performance of selected, well-bred, and well-managed non-inbreds, was advocated by Winters _et al_. (1944). Thus this project was designed to study the performance of the crosses between inbred lines compared to that of animals produced by mass selection.

OBJECTIVES

The objectives of this study were:

(1) To compare mass selection with selection among inbred lines as a method of increasing rate of gain;

(2) To determine if the amount of heterozygosity in the base population affects the results of selection;

(3) To test for general and/or specific combining ability in the crossing of inbred lines;

(4) And to indicate possible guides in the breeding systems to be used in swine breeding.

REVIEW OF LITERATURE

From the observations of 15 generations of brother-sister matings of the laboratory rat, King (1918) found that the inbred rats, both male and female, were heavier in body weight than stock albino rats. Also, she found that the variability of the body weights decreased as the inbred generations advanced.

In additional work King (1919) observed that in 10 more generations the inbred strains were lighter in body weight than earlier generations. However, the inbred strains were still much superior to the stock albino strains reared under the same conditions. The results of 25 generations of brother-sister matings showed that no deterioration of rate or extent of growth in body weight had been produced.

Body weight in 13-week-old rats was found to average significantly heavier in crossed progeny than in the component inbred lines from which the crosses were derived (Craig and Chapman, 1953). This hybrid vigor observed in cross progenies was apparently due to dominance and/or overdominance. The performance of inbred lines was used to predict the relative value of the lines for crossing with other inbred lines.

Jones (1918) recognized that the effect inbreeding would have on any organism would depend on the hereditary constitution of that organism at the time inbreeding began. He further found that inbreeding generally led to the elimination of undesirable characters which are controlled by one pair of genes by recognition of these characters as they were expressed through homozygous recessives and the culling of the affected animals. However, inbreeding was usually accompanied by a loss of size, vigor, and productiveness, which was generally returned with the crossing of the inbred strains.

Inbreeding experiments in other species generally have shown a decrease in productivity with an increase in inbreeding.

Hybrid mice were found by Chai (1956) to be no more superior for bioassay than an inbred parental line. One line of inbred mice showed a greater response of the seminal vesicles to androgen than did another inbred line or the F_1 hybrid of these two lines. The nature of the stimulus and the genetic constitution of the test animal was shown to have a great influence on the usefulness of a line or line-cross used for bioassays.

Tantawy (1957) observed a decline in wing length and thorax due to inbreeding by mating sibs and first cousins in Drosophila melanogaster. He also found (1956) the coefficient of variation declined in brother-sister matings but increased over the controls mated by a systematic cyclic method of outbreeding, designed to keep inbreeding at a minimum.

Brother-sister matings of guinea pigs have produced a decline in all measures of vigor. Eaton (1932) showed these changes took place uniformly rather than suddenly.

A decline in vigor in all characteristics studied, particularly in frequency and size of litter, was observed by Wright (1922a) after 13 years of brother-sister matings of guinea pigs. The most marked decline was in frequency and size of litter. He also found a greater decrease in gains after birth than in birth weight. Also, the decrease in the per cent raised of the young born alive was greater than the decrease in the number born alive.

Improvement over parental stocks of animals produced by crossing inbred families of guinea pigs was reported by Wright (1922b). This improvement was found in each trait studied and apparently was manifested most for adult weight and disease resistance in the progeny of the first cross females mated to inbred males. Mortality at birth, mortality between birth and weaning, and size and frequency of litters each were improved somewhat when both sire and dam were crossbred. Although the improvement in each factor was small, the combined improvement resulted in superiority greater than that of random bred stocks over the inbreds.

Greenwood and Blyth (1951) showed that superiority of inbred line crosses in poultry depended on the characteristics measured. In crosses between inbred lines, egg size and body weight were intermediate between parents; but winter egg production was superior to that of the parents. Viability in the crosses was similar to viability in the best inbred lines.

Reproductive fitness in line crosses of domestic fowl, measured by the number and weight of November eggs, was generally superior to contemporary inbreds (Shultz, 1953). However, this superiority was not over the production-bred flock from which the inbred lines were developed. The superior crosses tended to be those between lines selected differently rather than between those selected similarly.

In a herd of Holstein-Friesian cattle, an average decrease in birth weight of about one-eighth of a pound was reported for each one per cent increase in inbreeding of a calf itself (Nelson and Lush, 1950). They found a slightly smaller effect due to the inbreeding of the dam.

Regan et al. (1947) observed increased total mortality in dairy calves with increased inbreeding. His data included abortions, stillbirths, and postnatal deaths to four months of age.

Tyler et al. (1947) reported an average decrease in birth weight of 0.28 pounds for each one per cent increase in the inbreeding of calves. However, the inbred calves of the sires transmitting genes for heavy birth weights tended to be heavier than outbred calves. This was due to their having more of their sires desirable genes for birth weight which cancelled part of the reduction in birth weight due to homozygosity of undesired recessive genes for birth weight.

The result of inbreeding of 362 litters of Chester White swine was a downward trend in litter size at birth, 28 days of age, and at 70 days of age (Hetzer et al., 1940). Litter size seemed to be more affected by the differences of inbreeding of the litters themselves than by the inbreeding of the sires and dams.

An increase of 10 per cent in the inbreeding of dams resulted in a decrease of about 0.6 pig per litter at farrowing time (Stewart, 1945). However, the litter size at birth was apparently not affected by the inbreeding of the litter itself.

Godbey and Starkey (1932) reported a negative correlation between degree of inbreeding and weaning weight of Berkshire swine.

A decrease in fertility and very high mortality in the second generation of brother-sister mating of Poland China swine caused McPhee et al. (1931) to discontinue their experiment with swine sib matings.

Half-sib swine matings resulted in a decrease in the number of pigs farrowed as reported by Willham and Craft (1939). A gradual decrease in the average number of pigs weaned per litter as well as the per cent of pigs raised to weaning occurred as inbreeding increased. The coefficient of inbreeding in the eighth generation was 45.6 per cent.

Craft (1953) observed that for each 10 per cent increase in inbreeding there was a decrease in number of pigs farrowed of approximately one-third of a pig per litter and about one-half pig per litter for number weaned. He also found an apparent reduction in strength and liveliness of pigs at birth as inbreeding was increased. Litter size was much more difficult to maintain in inbred lines than was growth rate.

Previously Craft (1943) had reported that, although there might be slight decreases in fertility, vitality and growth rate with inbreeding, the rate of inbreeding in swine could be increased five to ten times as fast as that rate commonly practiced by pure bred breeders without loss of individual merit.

Maintenance of litter size in inbred lines of swine was found by Comstock and Winters (1944) to be much more difficult than maintenance of growth rate. They therefore emphasized the necessity for maximum attention to selection for fertility in the development of inbred lines.

Single crosses between inbred (F=.42) lines of swine showed that inbreeding had a greater effect on viability than on rate of growth (Dickerson _et al._, 1946).

Winters _et al._ (1944) obtained a degree of increased vigor from crossing inbred lines of swine in keeping with the decrease of inbreeding of the crossbreds. Also, the increased vigor was greater in line crosses between breeds than within breeds; thus, the increase in vigor was apparently affected by the genetic diversity of the parental stocks. Vigor was based on measurements of fertility, litter size, survival, rate and economy of gain, and score for body conformation. They also found a tendency for the superior lines to produce the superior crossbreds.

Sierk (1948) reported an increase in vigor of approximately 15 per cent for the best crosses between inbred lines compared with non-inbred crosses and non-inbred swine. The best line crosses were between lines having the greatest genetic diversity in the foundation animals. Thus, this indicated the importance of genetic diversity for heterosis (Sierk and Winters, 1951).

Inbred line crosses of Duroc swine resulted in an increase in both number of pigs per litter and litter birth weights (Chambers and Whatley, 1951). Hybrid vigor as expressed in the increase in viability of the pigs and productivity of the two-line cross gilts was greater than

hybrid vigor expressed as increased growth rate in individual pigs. Two-line cross litters raised by inbred dams performed equally as well as outbred litters for the same reason. Two-line cross gilts, mated to an inbred boar of a third line, produced three-line cross litters which were superior to both two-line cross and outbred Duroc litters for most of the characteristics studied. In most cases the increased number of pigs per litter accounted for a large percentage of increase in total litter weight.

An inbred line of Chester White swine with an average inbreeding coefficient of .4 in the sixth generation, which had a satisfactory reproductive rate and no important defects, was found by Warwick and Wiley (1950) to perform well in line crosses. When the inbred Chester gilts were mated to inbred boars of Landrace x Duroc foundation stock, the resulting cross line pigs were heavier at birth; had superior gaining ability, longer carcasses, and a larger average number of pigs per litter; and required less feed per unit of gain than the conventionally bred purebred and crossbred swine.

Garwood (1956) analyzed data collected from Duroc swine at experiment stations in Ohio, Oklahoma, and Nebraska. He found that hybrid vigor in general was more evident when two-line crosses were compared with inbreds than when two-line and three-line crosses were compared.

Heterosis in the two-line crosses over the inbreds was measured as the increase in performance of the reciprocal crosses over the average of the parental lines. Heterosis was determined by the mean estimations of inbreds and two-line crosses which were unadjusted for differences in effects of litter inbreeding. Heterosis was determined in the Ohio two- and three-line crosses on the basis of the mean estimation of the crosses which were adjusted for difference in the inbreeding of the dam. In the two- and three-line crosses at Nebraska and Oklahoma, general means were used to calculate heterosis. The heterotic effect was taken as the increase in production of three-line crosses over the two-line crosses. Specific combining ability was found in two of the four Nebraska lines.

Garwood also reported no differences between outbreds and three-line crosses at Oklahoma or between the Ohio outbreds, rotational crosses, or three-line crosses.

MATERIALS AND PROCEDURES

Method of Developing Inbred Lines Using Outbred Dams

Inbred lines can be developed by the mating of females to their full brothers. A male offspring of this mating can be mated back to his dam. A son in this double son litter can be mated back to his dam to produce triple sons. These triple sons can be mated to their dams and also to full sisters to produce enough females available for the crossing between lines.

The Foundation Stock Rats

Three inbred strains of rats were used: a strain of hooded rats, an albino strain from the Michigan State University Chemistry Department referred to as the Hoppert strain, and an albino strain from the University Isotope Laboratory. The average inbreeding coefficient of each of the original inbred strains was estimated to be .80.

Management Procedures

Matings were made by placing the female(s) and a male in the breeding cages for 14 days, a period long enough to include at least two estrous cycles for each female. When it was evident that reproductive failures might limit numbers too greatly, the females were left in the breeding cages an additional three to five days. This additional period would permit time for three estrous periods.

Upon removal of the females from the breeding cages, they were placed in individual littering cages until the litters were born and weaned. During the littering period close daily observations of the females were made, and birth dates and litter size at birth were recorded.

Until the birth of the first three-way inbred litters, the dams were allowed to keep all the rats in their litters and to raise as many as possible. However, beginning with the first inbred litters, all litters of over eight rats were reduced to eight at five days of age. The heaviest four females and four males were saved as far as was possible. If there were not four of one sex in litters of eight or more, five or more of the majority sex were retained so that there would still be eight in the litter. It was considered that maintenance of litters not larger than eight would tend to reduce any effect that larger litter numbers might have on growth rate. Since there is a limit to the amount of milk produced by a dam and this factor would naturally affect growth rate in the litter, it was thought that by limiting litter size to a moderate number each rat would have adequate nutrition for maximum growth before weaning.

Where there was opportunity to do so, the males and females saved were also selected for color pattern. Males and females representing each color pattern - hooded, self, or albino - in the litter were saved if possible. The primary interest, nevertheless, was to save as equal a number of both sexes as possible and still keep only eight. This reduction in litter size to eight was done in all litters of both groups after it was started.

During the suckling period the dam was self-fed, and no attempt was made to prevent the young rats from free access to the dam's feed. The rats generally began to consume feed between sixteen and eighteen days of age. No attempt was made to estimate the effect of the feed on weaning weights, but it was thought that these few days of feed helped to prevent any setback at weaning and thus gave a clearer indication of the growing ability.

At 21 days of age the litters were weaned, earnotched, and weighed. They were placed in feeding cages and fed as a litter. Depending on size of litter and availability of cages, the litters were separated by sex either at weaning or within the next 21 days to prevent overcrowding and to insure virginity in the females. At 50 days of age they were again weighed and the gain in the 29-day feeding period after weaning was used as the basis for selection.

The ration fed the first generation was a standard commercial laboratory animal ration. After the first generation the rats were fed a similar ration which was formulated and prepared at Michigan State University. The formula for this latter ration appears in the Appendix on page 52.

To give all rats equal opportunity to utilize the ration and to avert possible errors in feeding, the same ration was fed to all groups of rats <u>ad libitum</u>; and no attempt was made to adjust the ration to compensate for either age or weight of the rats.

Weaning weights for the first four generations were recorded to the nearest .2 gram. The 50-day weights were recorded to the nearest gram. Between the weaning of the fourth and fifth generations, the scales normally used were broken; and the scales substituted for the fifth generation weights were accurate only to the nearest .5 gram. Therefore, the weaning weights of the fifth and succeeding generations were recorded only to the nearest .5 gram.

Development of the Heterogenous Base Populations of Rats

In January 1957 two inbred hooded male rats were each mated with two inbred albino female rats. The female offspring of the resulting four litters were divided into two groups so that each litter was represented in each group. One group of females was mated back to the hooded males, care being taken that no female was mated with her sire. This group was then closed to outside matings and was called the two-way group.

An additional selected mating was made prior to the start of the inbred lines. The fastest gaining male and female of each litter were selected, and matings were made with the restriction that no sibs be mated together. This additional mating provided a base population which had a family structure. Without the additional mating of the selected group, the relationship between sibs would have been virtually no higher than that between non-sibs because of the high degree of inbreeding (F=.8) in the original lines.

The other group of females was mated to males from a second inbred albino strain. This group was then closed to outside matings and was called the three-way group.

Both the two-way and the three-way groups were subsequently divided into an inbred and a selected group.

Development of the Inbred Lines of Rats

Essentially the same pattern was used in developing the inbred line of both the two-way and three-way groups. From the heterogenous base population, two females and a male from each litter were selected on the basis of gain during the feeding period. One female was mated to her full brother to begin an inbred line; the other female was used in the development of a selected group. It was not expected that the high gaining females in a litter would have the same rate of gain; therefore, the selection of one for the inbred group and one for the selected group was made at random. This random selection was to minimize any bias which might influence later comparisons of the inbred group with the selected group.

The fastest gaining male in the litter produced by the brother-sister mating was mated with his dam. The procedure previously mentioned of mating sons, double sons, and triple sons back to the dam was followed in developing the inbred line of rats. The use of the same females, which were mated to their youngest son each generation, allowed the inbreeding of a line to be increased as rapidly as possible without the influence or variation which more than one dam might cause.

In the two-way group full sib matings to begin the inbred lines were made among the offspring of the generation in which the covariance coefficient between litters was equal. At a particular season the two-way inbred group (designated 2-I) was a generation behind the three-way inbred group (3-I), which was begun with the full sib matings among the offspring of the first three-strain cross.

Development of the Selected Groups of Rats

The same males used in the brother-sister matings to develop the inbred lines were used to develop the mass selected groups. Each male was mated to a high gaining female non-sib from a litter of the same generation and group, with the restriction that inbreeding be kept at a minimum. In a population closed to outside breeding, an increase in inbreeding is inevitable; thus, it was necessary to impose this restriction on all matings of this group to minimize the inbreeding. Twelve litters were represented in this initial generation.

In the succeeding generation of the mass selected groups, the eight fastest gaining females from a group representing the fastest gaining female of each litter was chosen to be dams of the next generation. From the eight litters thus represented, the next four fast gaining females were chosen as dams for reserve litters in case of reproductive failures, with the restriction that no more than two of the 12 females would be from the same litter.

In the same manner the four high gaining males from a group representing the fastest gaining male of each litter were selected as sires of the next generation. Each male was mated to three females, one of which was the reserve mating. The four reserve females were mated with the additional restriction that no two litter mates would be mated to the same male.

Adjustment of Data for Sex

Because of a large difference between the weight gains of the males and females in the first generation, an adjustment was made in the data. The average difference between the male and female weight gains on a within litter basis was found for the combined selected groups and for the inbred group in the first generation. The average difference of 54 grams in the selected groups was added to the observed weight gain of each female in the selected groups to remove differences due to sex. The average difference of 40 grams in the inbred group was added to the observed weight gain of each female in the inbred groups.

An analysis of variance showed no significant differences between these adjustment factors and actual differences between sexes in the other generations of inbreeding; thus, it was concluded that the factors of 54 grams for females in the selected groups and 40 grams for females in the inbred groups were valid factors for all generations of inbreeding. Reference for statistical procedure was made to Snedecor (1956).

In the base population a difference of 37 grams was found between male and female weight gains on a within litter basis. As there was no inbreeding that generation and no real advantage in using an adjustment factor constant for other generations, a 37 gram factor was added to the observed female weight gains to equalize sex influence.

Making Inbred Line Crosses

When the 3-I dams were about a year old and had produced three litters, the third generation males were mated to two sisters as well as their dams. The lines were thus increased in numbers, and possible loss of lines through reproductive failure was averted. The additional litters provided a larger number of females for making the line crosses.

In order to make the 2-I line crosses at the same season as the 3-I crosses, the 2-I males in generation 3 were mated to two sisters as well as their dams. Generation 3 was the third generation of inbreeding in the 3-I group but only the second generation of inbreeding in the 2-I group.

From among the expanded inbred lines of the fourth generation, four lines were used in both the 2-I and 3-I groups for making line crosses. The original intent of the experiment was to select the four superior lines in each group on the basis of gain for making line crosses, but the lack of sufficient numbers in all the lines prohibited selection for gain among the eight original lines in each group. The four lines used in each group were used because of the numbers in the line and not because they had been selected for their superior gains.

The fastest gaining male in each line of the resulting fourth generation was mated to females from each of the other lines and, where it was possible, to a female from each litter in that line. The same procedure which was used for the 3-I line crosses was used for making the line crosses among the litters of the expanded 2-I lines.

RESULTS AND DISCUSSION

Total Gain as a Measure of Performance

Selection for Gain in the Mass Selected Groups

A comparison of the group generation averages for total gain in weight from the twenty-first to the fiftieth day in the two-strain and three-strain selected groups (2-S and 3-S) revealed similar trends for both groups. Little increase in total gain was made in either group until the fourth generation, at which time the average gain in both groups increased. The increases in average gain in the first generation of selection over that of the base population can best be explained as a result of a change in management procedure. It was in this generation that litter numbers were restricted to eight, apparently causing a more desirable pre-weaning period that resulted in a more favorable post-weaning period.

In the fifth generation the average gain of both groups decreased to a level below the previous generation levels. Table 1 shows the group average gain for each generation.

Apparently several generations of selection were needed to accumulate enough genes for gain to change gene

TABLE 1. Average gain (in grams) of the groups each generation and differences between the groups

Generation	3-S	3-I	High 3-I[b]	3-S Minus 3-I	3-S Minus High 3-I[b]	2-S	2-I	High 2-I	2-S Minus 2-I	2-S Minus High 2-I[c]
Base	160					146				
1	169	165	159	4	10	165	a			
2	168	149	168	19	0	165	153	185	12	-20
3	171	153	156	18	15	165	146	163	19	2
4	181	147	155	34	26	169	148	155	21	14
5	154	138	144	16	10	156	144	147	15	9
6	123	124		-1		159	135		24	

[a]Inbreeding of the two-strain group did not begin until a generation after the beginning of the three-strain inbred group.

[b]The average for 3-IC for first four generations and the average of crosses of Line $3\text{-}I_D$ in the fifth generation.

[c]The average for $2\text{-}I_B$ for generation 2, 3, and 4 and the average of the crosses of $2\text{-}I_C$ in the fifth generation.

frequency enough to increase the mean gain. It has been shown (Lush, 1958) that a slow rate of increase in the mean under selection could be due to either a low heritability or a small selection differential or both.

The decrease in the average gain in the fifth generation of selection was not expected if previous increases had been due to an increase in frequency of genes with additive effects. If the decrease in gain in the fifth generation were due primarily to environmental factors, it is probable that a large part of the increase in the mean gain made in the previous generations was environmental. The fact that all groups did poorly in the fifth generation indicated an extremely poor average environment during that time. Average environment is used to denote the gross environmental conditions which affect the complete population that generation in contrast to environment which is used in the classical animal breeding concept to denote the non-genetic factors which affect the individual animals within the population. The group averages were actually averages of gains incurred in two seasons, the second season being a repeat mating of the first.

The average number of rats weaned per litter in the fifth generation (Table 7, page 41) decreased as did the average gain. Some factor, possibly a viral disease, which reduced the litter size may also have inhibited growth rate or gain. Identification of the factor(s) was not feasible. The small number of rats in the sixth generation with essentially no increase in gain further indicated some relationship between small litter size and decreased growth rate.

The reach of the selected rats and generation gains in averages which were actually obtained for the selected groups are shown in Tables 2 and 3. The reach ranged from 11 grams to 24 grams in the 2-S group and from 5 grams to 20 grams in the 3-S group. Reach was defined as the difference between average gain of those males and females which had offspring that lived to 50 days of age and the average gain of all animals in the generation from which the parents were selected.

A comparison of the observed reaches with the expected reaches computed by the method outlined by Lush (1948) revealed a rather close agreement between the two values. Generally the reach obtained was less than the estimated reach. The selected animals in the base population were divided into the inbred group foundation and the selected group foundation. This division was taken into account, and the large differences between the observed reach and the estimated reach in the base generation and in the first generation of the 2-S group can best be explained as sampling errors. The reason for the observed reaches in the fifth

TABLE 2. The expected and observed reach in weight gains for males and females with the resulting "gain" in 2-S group[a]

Generation	Average Gain of Group	Expected Reach in Males	Expected Reach in Females	Observed Reach in Males	Observed Reach in Females	Selected Males Minus Selected Females	"Gain"[b]	"Gain"/Reach	Estimated Average Reach	Observed Average Reach
Base	146	28.9	17.5	6.0	14.0	- 8.0			23.2	11
1	165	24.9	15.6	12.0	11.0	1.0	19	1.72	20.1	12
2	165	21.6	13.6	23.2	8.5	14.7	0	.00	17.6	16
3	165	22.6	17.4	19.6	9.1	10.5	0	.00	20.0	14
4	169	18.5	10.6	18.1	13.0	5.1	4	.29	14.5	16
5	156	34.3	31.6	21.3	25.7	- 4.4	-13	-.81	32.9	24
6	159						3	.13		

Average $\frac{\text{"Gain"}}{\text{Reach}}$ = .22

[a]Expected reach (selection differential) is based on standard deviation, proportion of males and females selected, and *z* of normal curve.

[b]"Gain" equals present generation average minus previous generation average.

TABLE 3. The expected and observed reach in weight gains for males and females with the resulting "gain" in 3-S group[a]

Generation	Average Gain of Group	Expected Reach in Males	Expected Reach in Females	Observed Reach in Males	Observed Reach in Females	Selected Males Minus Selected Females	"Gain"[b]	"Gain"/Reach	Estimated Average Reach	Observed Average Reach
Base	160	16.2	13.2	7	3.0	4.0			14.7	5
1	169	25.7	16.4	26	4.0	22.0	9	1.80	21.1	15
2	168	21.1	14.2	21	2.5	18.5	1	.07	17.6	12
3	171	21.3	13.4	22	5.0	17.0	3	.25	17.3	14
4	181	18.5	10.6	25	12.0	13.0	10	.71	14.5	19
5	154	19.9	15.0	21	31.0	-10.0	-27	-1.42	17.5	26
6	124									
Average	$\frac{\text{"Gain"}}{\text{Reach}}$ = .26						-30	-1.15		

[a]Expected reach (selection differential) is based on standard deviation, proportion of males and females selected, and <u>z</u> of normal curve.

[b]"Gain" equals present generation average minus previous generation average.

and sixth generations being larger than the estimated reaches was also best explained as sampling errors.

The negative changes in average gain in the 2-S group in the fifth generation and in the 3-S group in the fifth and sixth generations indicated that average environmental influence was so large and poor that an increase in gene frequency for desired genes was not expressed. Generation heritability estimates calculated as $\frac{\text{change in mean}}{\text{reach}}$ ranged from numbers greater than one to negative numbers, with an average of .22 for the 2-S group and .26 for the 3-S group. Estimates of heritability of gain for each generation, based on reach and change in generation means, are also found in Tables 2 and 3.

The differences in total gain of the 2-S and 3-S groups were relatively small but were consistently in favor of the 3-S group in the early generations. In the later generations the advantages of the 3-S group became smaller and even reversed.

Selection for Gain in the 3-I Group

The average gain of the 3-I group increased in the first generation of inbreeding; however, this increase was probably due to a large extent, if not entirely, to the previously mentioned change in management procedure during this generation. Thereafter there was a general decline in performance in the inbred group as a whole. The large decline in the second generation indicates that the slight recovery made in the third generation was primarily an average environmental recovery.

Inbreeding progressed at a rapid rate as shown in Table 4, and selection in the group was not sufficient to maintain the average performance of the inbred group. Performance of the high producing line declined in keeping with the group average and was only slightly superior to the average of the group. As there was only one litter per line in each generation from which to select, a decline in performance was expected.

TABLE 4. Average coefficient of inbreeding (F) of the inbred litters each generation

Group	Generation				
	Base	1	2	3	4
3-I	0	.25	.38	.44	.50
2-I	0	.00	.25	.38	.45

There was an average decline in total gain of 2.53 grams for each 10 per cent increase in inbreeding. The average inbreeding coefficient, which was calculated by Wright's method (1922c), was .50 at the time line crosses were made.

The reach expressed in the high producing line of the 3-I group averaged 7.1 grams per generation. The decline in gain of the high producing line averaged

8 grams per generation. The low producing line had an average reach of 8.7 grams per generation, and the average change in gain per generation was 0 grams. The level of performance of the low line was very low and variable, ranging from 125 grams to 156 grams. The level of performance of the high performing line ranged from 155 grams to 168 grams. Table 5 shows the weight gains and reach for the high and low inbred lines.

Selection for Gain in the 2-I Group

The average total gain of the 2-I group declined fairly consistently each generation. The slight increase which occurred in the fourth generation was considered to be more a result of average environmental nature or of sampling error than a result of genic improvement. Actually the increase occurred in the third generation of inbreeding of this group, as inbreeding in the 2-I group began a generation later than in the 3-I group.

The average decrease in gain, as shown by the regression of gain on inbreeding coefficient, was 4.4 grams for each 10 per cent increase in inbreeding. The average inbreeding coefficient of this group was .45 at the time line crosses were made.

The actual reach which was practiced in Line B of the 2-I group averaged 7.7 grams per generation. The line had an average net loss in performance of 10 grams. Line B was consistently the high performing line. The

TABLE 5. The observed reach in weight gains for males and females with the resulting "gain" in the high and low lines of the inbred groups

Generation	Average Gain of Line	Reach in Males	Reach in Females	"Gain"[a]
		2-I High Line (2-IB)		
Base (1)	165	38	-3	
2	185	9	0	20
3	163	1	1	-22
4	155			- 8
		2-I Low Line (2-IE)		
Base (1)	145	52	7	
2	153	2	0	8
3	118	41	0	-35
4	144			26
		3-I High Line (3-IC)		
Base	163	25	1	
1	159	11	0	- 4
2	168	15	0	9
3	156	0	5	-12
4	155			- 1
		3-I Low Line (3-IA)		
Base	137	0	2	
1	156	0	0	19
2	125	29	0	-31
3	148	16	5	23
4	137			-11

[a]Gain equals present generation average minus previous generation average.

consistently low performing line (Line E) averaged 17 grams per generation for the reach, and the average performance decreased only .3 gram per generation. However, the level of performance in Line E was quite low, ranging from a low average of 118 grams to a high of 153 grams.

Average performance for Line B averaged from 155 grams to 185 grams. The reach and weight gains of the high and low lines each generation are shown in Table 5.

Comparison of 3-I with 2-I

Certain similarities in performance of gain were noticeable between the two inbred groups. There was a decline in performance in both groups as inbreeding increased, and this decline existed in each line. When compared on the basis of equal or near equal amounts of inbreeding, the similarities were even more striking than when compared on a seasonal basis. Both groups had a slight recovery in the second generation of inbreeding. One explanation for this recovery was that the dams had an increased milk production or some other increased mothering ability during their second lactations and thus afforded their offspring a better pre-weaning environment. In addition to this, there had to be a positive correlation between the pre-weaning period and the post-weaning period which caused a higher post-weaning gain due to better pre-weaning environment. If, in fact, there were factors which caused better post-weaning performance in second litters because of better pre-weaning conditions, there should have been an increase in the performance of the cross-line rats from the repeat matings over that of first matings. However, a decrease rather than an increase in performance of the cross-line repeat matings occurred, thus tending to repudiate any tendency for second litters to perform differently from first litters.

Comparison of 3-I Group with 3-S Group

The average gain of the 3-S group was greater than that of the 3-I group in each generation except the sixth, in which both groups did extremely poorly. There was a trend for the difference between the average gain of the two groups to become larger as inbreeding progressed. Table 1 shows a comparison of the two groups. In the first generation of inbreeding there was only an insignificant difference of four grams in the averages of the groups. However, an analysis of variance showed the differences of 19, 18, and 34 grams in the second, third, and fourth generations, respectively, to be highly significant ($P < .01$).

The high producing inbred line, 3-IC, had an average gain below the 3-I group average in the first generation and, consequently, a larger difference (10 grams) in the average gain from the 3-S group. In subsequent generations, the 3-IC line average gain had smaller differences from the average gain of the 3-S group than did the 3-I group as a whole. However, in only one generation (the second) did the average of the high producing inbred line equal that of the selected group.

Line crosses in the 3-I group recovered part of the loss in productivity which occurred in the inbred

group. Although there was no cross which surpassed the selected group in performance, the inbred group as a whole increased in performance when compared to the selected group. The difference in average gain between the selected group and the line crosses was reduced to 16 grams, less than one-half the difference between the selected group and the 3-I group the previous generation. The difference between the average of the selected group and the highest performing line cross (Line D x Line C) was 9 grams.

In the sixth generation the average of the 3-I group was one gram more than the average of the 3-S group. Although the performance of both groups was greatly reduced, this insignificant difference indicated that performance of the three-line crosses equalled that of the selected group. There was only a four gram difference between the high and low producing 3-I three-line cross. As only three of the three-line crosses were available, and only one litter per cross, no one cross was considered better than the others.

Comparison of the 2-I and 2-S Groups

The average gain of the 2-S group was larger each generation than the average gain of the 2-I group. The difference between the average gain in the two groups tended to become larger as inbreeding progressed, just as it did with the three-strain groups. Crossing of the inbred lines apparently restored some of the productivity lost during inbreeding, as the difference between the gain averages of the 2-I and the 2-S groups in the fifth generation was smaller than in the two previous generations.

The high producing line of the 2-I group, Line 2-IB, exceeded the 2-S group average by 20 grams in the first generation of 2-I inbreeding. In the third generation the average of Line 2-IB was only two grams less than the 2-S group. In the fourth generation Line B had an average of 14 grams less than the 2-S group.

None of the 2-I lines produced crosses which surpassed the average of the selected group. The average gain of the highest producing line cross (Line C x Line B) was 151 grams, which was only five grams less than the average of the 2-S group. The average gain of all crosses of Line 2-IC was only nine grams less than the average of the selected group.

The average gain of the 2-I three-line crosses in the sixth generation was 24 grams less than the 2-S group, and none of those crosses were superior to the average of the selected group. The average of the best three-line cross was only five grams less than the selected group, and it was produced by mating a sire of Line A to cross-line dams of Line B x Line C.

Litter Size as a Measure of Performance

Litter Size at Birth

During the generations that inbreeding was practiced, average litter size at birth (Table 6) was larger in the selected groups than in the inbred groups. The difference in litter size averages between the selected group and the inbred group ranged from a low of .3 rat in the three-strain group to a high of .8 rat in the two-strain groups. The differences which were non-significant were apparently random, as no trend toward either increased or decreased differences was observed in the first three generations.

TABLE 6. Average litter size at birth for each group by generations

Generation	2-S	2-I	3-S	3-I
1	11.6		12.0	9.3
2	10.8	10.3	10.7	10.4
3	11.8	9.0	9.6	8.6
4	10.9*	8.2	10.3*	8.7
5[a]	12.0**	5.6	7.4	8.3
6	11.3	10.6	8.5	8.8

*Significant at $P<.05$

**Significant at $P<.01$

[a]Data from repeat mating only

The first significant difference ($P<.05$) came in the fourth generation. It was in this generation that inbred females were first used as dams; and, in both the two-strain and three-strain groups, the selected group average litter size was significantly higher than the inbred group. Thus, inbreeding of the dam and litter combined appeared to produce a significant decrease in number of offspring born.

In most of the generations only one litter per line was represented, and for this reason no meaningful comparison could be made of the separate lines with the selected group.

The 2-I line crosses, as a group, had a significantly (P .01) lower average litter size than did the 2-S group. Data on the litter size at birth were incomplete on the first line cross litters produced. Therefore, the data used for litter size in the line cross litters were only from those litters produced from the repeat matings. The difference of .9 rat larger litter size in the 3-I than the 3-S group in this same generation was not significant at P=.05.

On the basis of both the two-strain and the three-strain groups, it appeared that the single cross litters out of inbred dams had a smaller litter size at birth than the litters in the mass selected groups.

No significant differences were found in litter size between either the 2-S and 2-I groups or the 3-S and 3-I groups in the sixth generation. This indicated that, if the reductions in litter size were brought about through inbreeding, these reductions were restored in the three-line crosses in which outbred dams were used.

In both the 2-I and the 3-I groups, the only generations in which litter size was significantly different from the selected group were those generations in which inbred dams were used. The 3-I inbred dams in the fifth generation did not produce cross-line litters significantly different in size from the 3-S group that generation; nevertheless, in three of the four possible comparisons, significant differences did occur.

Although inbreeding of the litters reached its maximum in the fourth generation in each group, the change from the previous generation in the inbreeding coefficient of the litters was much less than the change in the inbreeding coefficient of the dams. That larger change in the inbreeding of the dams, in addition to the fact that there were differences in litter size at birth in the only generations in which inbred dams were used, lends support to the conclusions that litter size is more affected by the inbreeding of the dam than by the inbreeding of the litter itself.

Litter Size at Weaning

It has already been indicated that litter size at weaning was not an absolute measure of the performance of a dam. There were two reasons for this. In the first place, the attempt to equalize the numbers in each litter by reducing the litters to eight eliminated some of the variation among litters which would normally be expected. Secondly, the dams used in developing the inbred lines were used as dams for several generations. Thus, the variation of maternal influence on litter size at weaning was considerably reduced between generations. The exact effect of maternal influence on litter size at weaning is unknown, but it was assumed to be somewhat constant, especially in the inbred groups, and at least to average nearly the same each generation in each of the selected groups.

Table 7 shows the average number of rats weaned per litter in each generation. These averages were computed from among those litters which actually had rats born and no attempt was made to consider those females which were exposed to the male but did not produce a litter. The selected groups generally, although not always significantly, had larger litters at weaning than did the inbred group counterpart. The 3-I line cross litters of the fifth generation were non-significantly larger than the 3-S litters. The 2-S litters, in contrast, were significantly ($P < .05$) larger than the 2-I line cross litters.

In the line cross litters of the 3-I group a recovery of the loss of litter size at weaning was made when compared with the selected group. It was recognized that litter size at weaning was not used as a criteria for selection; and thus, unless there was genetic correlation between litter size at weaning and post-weaning gains, the primary cause of any difference between the

groups would be produced by mothering ability of the dams. It appeared more likely that sampling errors rather than poor mothering ability made the 3-S litter size small in the fifth generation.

TABLE 7. Average litter size at weaning for each group by generations

Generation	2-S	2-I	3-S	3-I
1	7.87		7.75	6.83
2	7.63	7.75	7.73	7.00
3	8.00	6.63	7.52	6.29
4[b]	6.91	6.11	6.90*	5.60
5	6.47*	4.66	4.09	5.77
a				

[a]Data on generation 6 not used because of small number of litters weaned

[b]Average of first and second (repeat) matings

*Signigicant at P<.05

A reduction in litter size at weaning in the inbred groups could have occurred as a result of reduced litter size at birth or from reduced livability from birth to weaning or a combination of those factors. Because litter size was restricted to a maximum of eight rats, an analysis was made of the differences between the number allowed to live and the number actually weaned. That difference was taken as the best estimate of pre-weaning death loss or, the reverse, livability to weaning. Table 8 shows the average litter death loss.

The analysis of litter death loss showed no significant difference between either the 2-S and 2-I groups or the 3-S and 3-I groups. Thus the significant differences found in litter size at weaning between the inbred and selected groups were apparently the result of the differences in litter size at birth.

TABLE 8. Average litter death loss of the groups by generations[a]

Generation	2-S	2-I	3-S	3-I
1				.50
2	.13	.25	.09	.70
3		.50	.18	.57
4	1.00	.83	1.00	1.30
5[b]	1.60	2.00	4.20	2.10

[a]Calculated as the difference between the number of rats allowed to live and the number weaned

[b]Based on repeat mating only

Variance of Weight Gains as a Measure of Performance

Variance Components of Weight Gains Between Litters

The variance components of weight gains between litters are shown in Table 9. The components for the inbred group in generations 1, 2, and 3 were actually components between lines as there was only one litter per line in those generations. The variance component between lines was expected to be larger than that between litters of the selected group the same generation. In one generation of the 2-I group and in two of three generations of the 3-I group, the between litter (line) components were larger that the between litter components of the respective selected groups.

TABLE 9. Variance components of weight gains between litters of the group by generations

Generation	2-S	2-I	3-S	3-I
1	95		80	158[a]
2	53	163[a]	38	369[a]
3	114	115[a]	49	26[a]
4	74	27[b]	93	59[b]
5A	4	2	94	131
5B	472	121	41	110
6	49	47	c	c

[a]Between lines (one litter to each line)

[b]Between litters within lines

[c]A negative component was calculated.

The between litter within line variance components of the fourth generation were smaller in both the 2-I and the 3-I groups than the between litter components in the selected groups, which was expected. As inbreeding in a line increases, genetic differences between animals in that line decrease. Thus, the variance between individuals is reduced. The variance between litters within that line is also reduced, as the differences between non-sibs tend to become no greater than differences between sibs.

The variance components between litters in the fifth generation of the two-strain group were not consistent with those of the three-strain group. The variance component of both matings of the 2-I group was smaller than the 2-S group; whereas, the component of both matings in the 3-I group was larger than that of the 3-S group.

The very small components in both the 2-S and 2-I groups the first mating and the very large components of the 2-S group in the repeat mating indicate that environment or sampling errors, or both, had a large influence.

The mean square between litters in both the 3-S and 3-I groups the sixth generation was smaller than the within litter mean square; therefore, the estimate of the variance component would be negative. A negative variance component is impossible; thus, no valid estimate was available.

Examples of analysis of variance tables used in calculating the variance components are shown in Table 10. Tables similar to those in Table 10 were made for each group in each generation. For sake of brevity only three examples are shown, but the results from all the 27 tables used are shown in Table 9. The analysis of variance tables shown are of the 2-I group in generations 3, 4, and 5 and represent each of the types of component estimates.

Variance of Weight Gains Within Litters

A trend was noted in the 2-I group for the variance of gain within litters to be reduced as inbreeding increased, as shown in Table 11. In the 3-I group this trend was not noted; instead, both increases and decreases in the variance occurred without much change. The variance in the fourth generation, in which inbreeding was a maximum, was about the same in both the 2-I and the 3-I

TABLE 10. Analysis of variance tables for weight gains of the 2-I group in generations 3, 4, and 5A, used for making variance component estimates[a]

Generation 3

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square
Between lines	7	944	$\sigma^2 + 6.4\ \sigma_B^2$
Within lines	43	213	σ^2
$\hat{\sigma}^2 = 213$	$\hat{\sigma}_B^2 = 115$		

Generation 4

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square
Between lines	4	1058	$\sigma^2 + 6\ \sigma_L^2 + 11\ \sigma_B^2$
Between litters within lines	5	318	$\sigma^2 + 6\ \sigma_L^2$
Within litters	50	157	σ^2
$\hat{\sigma}^2 = 157$	$\hat{\sigma}_L^2 = 27$	$\hat{\sigma}_B^2 = 68$	

Generation 5A

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square
Between litters	13	320	$\sigma^2 + 5.8\ \sigma_B^2$
Within litters	67	308	σ^2
$\hat{\sigma}^2 = 308$	$\hat{\sigma}_B^2 = 2$		

[a]Estimated variance component for between litters within lines = $\hat{\sigma}_L^2$

Estimated variance component for between lines = $\hat{\sigma}_B^2$

Estimated variance component for within litters = $\hat{\sigma}^2$

group. The variance of the first inbred 2-I group was twice that of the first 3-I group.

TABLE 11. Variance of weight gains within litters of the groups each generation

Generation	2-S	2-I	3-S	3-I
Base	367		156	
1	379		193	150
2	184	318	143	179
3	166	213	138	138
4	150	157	117	155
5A	352	308	950	197
5B	288	180	161	238
6	347	122	521	140

A reduction in the within litter variance occurred in both the 2-S and 3-S groups in the first four generations. The variance in the fourth generation was similar for all groups, and differences in reduction were from differences in the early generations rather than the later generations. Differences between the selected and the inbred groups were the largest in the sixth generation in which the three-line crosses were produced.

The variances within litters indicated that breeders should not expect to get completely uniform litters with regard to growth rate either by inbreeding or by selection.

SUMMARY AND CONCLUSIONS

The heterozygous populations of the laboratory rat were developed from the crosses of two highly (F=.8) inbred lines. The backcross to one of the lines produced the population called the two-strain group. The other population was developed by crossing the offspring of the original line crosses with a third inbred line; thus, it was called the three-strain group.

Both a selected and an inbred group were formed from each of the base populations. Selection was made on the basis of weight gains in a post-weaning feeding period from the twenty-first to fiftieth day of age. Inbred lines were formed by mating sons, double sons, and triple sons, back to their outbred dams. Weight gain of inbred males were found to average 40 grams more than that of inbred females. In the selected groups males were found to average 54 grams more in weight than the females. The differences were based on average differences between the sexes within litters.

A comparison of the weight gains in the selected groups and the inbred groups indicated that as inbreeding increased the difference in average weight gain between the groups increased from 4 grams to 34 grams in the three-strain group and from 12 grams to 21 grams in the two-strain group. Differences in the high producing lines of each group also increased but to a lesser degree.

Crosses between the inbred lines restored part of the loss in weight gains which was incurred during inbreeding; however, no hybrid vigor in excess of the selected group was observed in either the 2-I or 3-I line crosses, although there was less difference between the average gain of the selected group and the line crosses than between the selected groups and the inbred groups the previous generations.

A regression of average weight gain on the inbreeding coefficient indicated a reduction of 4.4 grams for each 10 per cent of inbreeding in the 2-I group and a loss of 2.5 grams for each 10 per cent of inbreeding in the 3-I group.

Average litter size at birth was significantly higher in both the 2-S and 3-S groups in the fourth generation than in the corresponding inbred group and higher in the 2-S group the fifth generation also. As inbred dams were used in both of these generations, it was concluded that inbreeding of the dam had more influence on the size of the litter at birth than did the inbreeding of the litter itself.

Litter size at weaning was significantly larger in the 3-S group than in the 3-I group in the fourth generation,, and it was also larger in the 2-S group than in the 2-I group in the fifth generation. An analysis of the average litter death loss showed no difference in birth to weaning livability between the selected and inbred groups. Thus, it was concluded that the differences in litter size at weaning were due primarily to differences in litter size at birth.

Estimates of the variance components for weight gains between litters within inbred lines were smaller than the between litter estimates for the selected groups.

Variance of weight gain within inbred litters in the 2-I group tended to be reduced as inbreeding progressed. The reduction was from a variance which was larger than the selected group in the early generations to a variance which was apparently equal to the selected group in the fourth generation.

The amount of heterozygosity in the base population apparently had no effect on selection in either the selected or the inbred groups. Average weight gains, litter size at weaning and at birth, and livability from birth to weaning were similar for both selected groups and for both inbred groups including the line crosses.

One of the major drawbacks to the development of superior inbred lines by the son-to-mother matings system used in this experiment was the reduced prolificacy of the inbred dams. Of course it was understood _a priori_ that numbers within the lines would be restricted by the use of a single dam. Reduced prolificacy, in addition to the already restricted size of the inbred lines, increased the necessity of developing more lines if this system were to be used to its best advantage.

Another drawback to the development of inbred lines by a strict method of son-to-dam matings, equally as important as reduced prolificacy, was the small number of animals from which to select for maintenance of the individual lines and for making line crosses. Expansion of the lines by brother-sister matings earlier in the development of the lines, perhaps even as early as the first generation of inbreeding, along with continued son-dam matings would have probably allowed sufficient numbers to maintain all of the proposed eight lines in each group as well as supply sufficient numbers of females for more complete testing of the possible line crosses. Early expansion of the lines would slow the rate of the increase in inbreeding, but selection cannot be effective if there are not sufficient numbers from which to select.

Traditionally the cost of producing inbred lines has been high, and specific or general combining ability had to be found in the inbred lines if inbreeding were to be practical. Thus, it was postulated that this system could be used in swine breeding with the recommendations that many lines be formed and these lines be expanded early to assure a large number of lines from which to select the superior lines and to assure a large number of animals within the lines for testing the line crosses.

APPENDICES

APPENDIX A. Formula for rat feed prepared at Michigan State University

Ingredient	Pounds
Ground shelled corn	960
Sucrose	100
Soybean oil meal (44% protein).	400
Fish meal (58% protein)	200
Alfalfa meal (17% protein, dehydrated).	100
Dried skim milk	200
Corn oil	60
Super trace mineral salt [a]	10
B vitamin supplement [b].	2
Vitamin A and D concentrate	1
Vitamin B_{12} supplement (Pfizer's 9+) [d]	.5

[a]Trace mineral content (per cent): NaCl, 97; I, .007; Fe, .33; Cu, .048; Mn, .40; Co, .022; Zn, .500.

[b]Riboflavin, 2000 mg. per pound; pantothenic acid, 4000 mg. per pound; niacin, 9000 mg. per pound; choline (choline chloride equivalent), 10,000 mg. per pound.

[c]Contains 4,450,480 I.U. vitamin A; 1,264,074 I.U. vitamin D per pound.

[d]Pfizer supplement No. 9, containing 9 mg. B_{12} per pound.

APPENDIX B. Litter size and average litter gain of the groups in generation 1.

2-S				3-S				3-I			
Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Weaned Weaned	Gain	Dam	Number Born	Number Weaned	Gain
22-8	10	8	174	21-1	5	5	167	11-1	7	6	156
25-4	11	8	173	11-3	10	8	149	7-3	5	5	150
26-2	14	8	178	10-3	16	8	177	14-3	12	8	159
24-3	13	8	153	16-4	9	8	166	8-1	12	8	183
27-1	11	8	153	7-4	14	8	164	16-1	12	8	155
17-2	7	7	165	14-7	17	8	186	6-2	8	8	173
19-2	14	8	145	9-2	10	8	176	21-2	6	6	180
13-3	13	8	172	8-3	14	8	179	10-2	11	8	170
				6-7	10	8	156	15-2	11	8	146
				15-7	11	8	172	18-3	11	6	174
				12-5	15	8	162	12-8	10	8	174
				20-3	13	8	169	9-3	6	3	135

APPENDIX C. Litter size and average litter gain of the groups in generation 2

2-S				2-I				3-S				3-I			
Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain
67-4	10	8	171	58-1	8	8	143	34-4	13	8	169	11-1	12	8	125
58-4	13	8	158	55-3	10	8	185	51-1	9	8	184	7-3	6	3	139
62-1	12	8	149	62-3	9	8	141	35-2	11	8	174	14-3	13	8	168
65-1	11	8	172	56-1	10	8	153	49-1	13	8	169	8-1	15	8	132
59-1	10	8	171	65-4	10	8	153	44-3	10	8	162	16-1	10	8	149
52-1	11	8	160	59-2	11	7	169	51-2	11	8	169	6-2	9	9	165
56-2	6	5	177	67-2	11	8	135	38-1	8	8	157	21-2	8	8	138
55-1	13	8	164	52-4	13	7	154	28-3	12	8	162	10-2	7	7	150
								49-2	6	6	171	15-2	13	8	133
								34-1	14	8	164	18-3	11	4	164
								44-1	11	8	173				

APPENDIX D. Litter size and average litter gain of the groups in generation 3

2-S				2-I				3-S				3-I			
Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain
109-1	11	8	184	58-1	7	7	144	86-2	11	8	165	11-1	10	7	148
102-3	12	8	163	55-3	5	5	163	74-3	8	8	180	7-3	4	3	148
104-1	8	8	168	62-3	11	7	153	90-1	10	8	178	14-3	4	4	156
104-3	13	8	161	56-1	12	8	149	90-3	11	8	169	8-1	9	8	157
101-1	12	8	139	65-4	5	4	118	76-1	10	8	181	16-1	15	8	143
105-1	13	8	171	59-2	8	8	142	73-1	9	8	177	6-2	9	8	155
108-3	12	8	166	67-2	11	8	137	73-3	12	8	169	21-2	9	6	166
105-3	12	8	167	52-4	13	6	159	72-3	10	8	158				
101-3	13	8	175					77-3	5	5	158				
107-2	9	8	152					87-1	12	8	174				
108-1	12	8	162					74-2	8	6	179				
103-4	14	8	175												

APPENDIX E. Litter size and average litter gain of the groups in generation 4

2-S				2-I				3-S				3-I			
Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain	Dam	Number Born	Number Weaned	Gain
146-4	13	8	171	58-1	4	3	128	126-3	10	8	173	11-1	5	3	153
155-4	11	2	166	143-3	7	7	137	132-3	8	6	184	120-2	9	8	140
148-2	10	8	161	143-4	7	6	143	127-2	7	6	191	120-3	9	7	125
142-4	9	8	166	55-3	11	8	150	130-3	10	8	192	7-3	9	8	154
154-3	6	5	187	140-2	13	8	158	134-4	12	8	176	121-1	8	8	139
153-4	9	7	175	140-1	11	8	157	124-3	8	8	164	14-3	10	8	150
155-1	14	7	149	62-3	7	5	155	125-3	13	8	179	122-1	9	8	161
144-3	11	8	170	141-1	7	7	155	126-2	13	8	182	122-3	11	8	152
				56-1	8	6	137	125-1	13	8	190	8-1	5	2	221
				65-4	5	5	144					158-1	6	3	169
												158-4	11	4	156
												135-1	8	5	150

APPENDIX F. Litter size at weaning and average gain of the 2-I line crosses in generation 5 by line of sire

Line of Dam	Line of Sire											
	A			B			C			D		
	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain
A				41x-2	6	139				34x-3	3	140
B	45x-3	7	138				21x-3	5	162	21x-2	2	130
	21x-1	2	119							45x-1	8	142
	35x-4	8	156									
	21x-1	8	145									
	45x-3	8	126									
C	33x-2	7	150	27x-1	8	125				27x-4	4	154
	33x-2	5	115	27x-2	8	166						
D	40x-3	4	142	40x-6	8	140	40x-2	6	127			
				40x-4	4	132						

APPENDIX G. Litter size at weaning and average gain of the 3-I line crosses in generation 5 by line of sire

Line of Dam	Line of Sire: A			B			C			D		
	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain
A				8x-1	8	137	13x-1	6	134			
							13x-1	1	135			
B	5x-3	4	110									
	14x-2	8	127									
C	17x-3	8	141	17x-1	8	122				17x-2	5	148
	2x-3	7	145	2x-2	8	161				17x-2	8	141
	17x-3	7	151									
	2x-3	8	131									
D				38x-2	8	144						

APPENDIX H. Litter size at weaning and average litter gain of the selected groups in generation 5

2-S			3-S		
Dam	Number Weaned	Gain	Dam	Number Weaned	Gain
31x-3	8	168	18x-4	8	141
32x-3	8	161	16x-4	7	147
28x-2	4	161	4x-1	5	162
25x-1	8	170	6x-1	6	135
29x-1	3	159	7x-2	8	157
36x-2	8	142	12x-2	3	189
30x-3	8	157	6x-1	5	110
24x-1	8	161	1x-2	1	155
25x-4	7	159	9x-4	4	161
31x-4	8	145	16x-4	2	156
28x-3	6	162			
31x-3	6	177			
25x-1	8	175			
36x-2	4	134			
24x-1	7	137			
28x-2	7	174			
30x-3	6	134			
32x-3	7	158			
29x-1	4	113			

APPENDIX I. Litter size at weaning and average litter gain of the three-line crosses in generation 6 by line of sire

2-I

Line Cross of Dam	Line of Sire: A			D		
	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain
B x C	95x-1	8	150			
	92x-3	7	153			
C x D	91x-2	8	135			
	66x-2	8	144			
A x B				94x-4	8	141
A x C				93x-1	7	133

3-I

Line Cross of Dam	Line of Sire: C			D		
	Dam	Number Weaned	Gain	Dam	Number Weaned	Gain
A x C	64x-2	6	123			
C x D	68x-1	8	124			
B x C				58x-3	3	127

APPENDIX J. Litter size at weaning and average litter gain of the selected groups in generation 6

2-S			3-S		
Dam	Number Weaned	Gain	Dam	Number Weaned	Gain
67x-1	8	155	57x-3	6	118
78x-4	4	156	63x-4	3	113
71x-4	4	181	59x-2	3	146

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