SELECTION FOR BODY WEIGHT IN SYNTHETIC MONOPAROUS POPULATIONS OF MICE

by

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A THESIS

submitted to

OREGON STATE COLLEGE

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1959

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Date thesis is presented May 8, 1959

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ACKNOWLEDGEMENTS

The following people have contributed efforts, ideas and knowledge to the planning, execution, analysis and interpretation of this experiment: Dr. Ralph Bogart, Professor of Animal Husbandry; Dr. Hugo Krueger, Professor of Physiology; Dr. Lyle Calvin, Professor of Statistics; R. C. DeBaca, H. H. Nicholson, Frank Hudson and Stewart Floyd, Research Fellows, all at Oregon State College; and Dr. Paul Stratton, Professor of Animal Production, University of Wyoming.

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INTRODUCTION

Cattle are mainly monoparous in their reproduction, i.e., the females generally produce not more than one offspring per mating. Due to failure of fertilization, losses in the uterus, and death of some of the young, the net final reproduction rate is less than one offspring per mating. Therefore, it can be considered that if the number of offspring produced is 80 per cent of the females in any one mating group, the mating group is average or above in fertility (1) (17).

An important factor in practical management of beef cattle is the greater economic value at slaughter of steers as compared with bulls. The problem of selecting bulls within a herd is eliminated if all of the male calves are castrated and the bulls are purchased from purebred breeders. However, some ranchers find considerable personal satisfaction and economic advantage in breeding and developing their own herds closed to other genetic material but at the same time obtaining income from selling castrate males for beef production. In order to obtain a high selling price, there is a need to castrate males at one to three months of age in order to have steers of satisfactory appearance to meet market competition. There is also a need not to castrate males until all have had a chance to develop and express their individual economic and aesthetic values as breeding animals. In this case there is an economic barrier to selection of males which needs to be broken either by removing the need for early castration of market animals or by providing a satisfactory basis of decision as to which animals should be retained for breeding and hence not castrated at an early age.

A possible method of deciding which animals should not be castrated at an early age would be to select males because they were sons of females with sufficient genotypic information available to estimate satisfactorily the performance of the son. The purpose of this investigation was to select males for breeding purposes solely on the basis of the phenotypic merit of their dams and to compare the effectiveness of the selection with selection of males on their own phenotypic merit in a monoparous population. For this purpose a synthetic monoparous population of mice was designed to approximate the situation existing in a breeding program with beef cattle. In order to facilitate the interpretations, selection was practiced for large and for small 45-day body weights.

MATERIALS AND METHODS

Experimental Animals: Source and Statistical Description

The animals for this experiment were obtained by mating together mice of the four strains O, V, A, and C which have been partially described by Bogart et al. (2) and by Mason et al. (15). The 45-day body weights of these strains and the F_1 crosses produced simultaneously by a diallel mating plan are presented in table 1. The plan for producing the F_1 offspring was to mate each of seven males from each of the four strains to four females, one from each of the four strains, i.e., four litters would have been produced from each male or 112 litters from 112 females of which 28 were from strain O, 28 from strain V, 28 from strain C, and 28 from strain A. Actually 113 litters were produced from 29 sires and 105 females. There was differential fertility in the strains which resulted in disproportionate numbers of offspring in the 32 groups of table 1. Therefore the analysis presented in table 2 for general combining ability, specific combining ability, etc., was run on the means according to the method of Snedecor (19, p. 385-387) using the within subclass sum of squares divided by the harmonic mean of subclass numbers as the error sum of squares. The harmonic mean of the subclass numbers was 10.59. The general plan

Table 1

Average 45-Day Body Weights of Mice Produced by Crossing the Four Strains A, C, O and V

Strain of Male Parent	Strain of Female Parent and Sex of Offspring									
	O		V		A		C		Ave.	
	M	F	M	F	M	F	M	F	M	F
O	24.5	21.9	18.5	18.1	22.0	19.2	18.2	16.9	20.8	19.0
Ave.	23.20		18.30		20.60		17.55		19.91	
V	22.5	20.2	19.2	17.5	18.5	17.3	17.1	15.9	19.3	17.7
Ave.	21.35		18.35		17.90		16.50		18.53	
A	23.5	20.7	22.1	18.8	21.2	18.0	13.8	17.2	20.2	18.7
Ave.	22.10		20.45		19.60		15.50		19.41	
C	23.5	18.8	21.9	18.7	21.9	19.4	19.5	16.2	21.7	18.3
Ave.	21.15		20.30		20.65		17.85		19.99	
Ave.	23.5	20.4	20.4	18.3	20.9	18.5	17.2	16.6	20.5	18.4
Ave.	21.95		19.35		19.69		16.85		19.46	

TABLE 2
Analysis of Variance of 45-Day Body Weights of Mice Produced by Crossing the Four Strains A, C, O and V

Source of Variation	Degrees of Freedom	Mean Square
general combining ability	3	18.8261
specific combining ability	6	1.0911
reciprocal effects	6	11.9963
sex	1	34.2378
sex x general combining ability	3	0.2544
sex x specific combining ability	6	1.5261
sex x reciprocal effects	6	2.4329
strain of dams	3	34.8695
strain of sires	3	3.6253
sire strain x dam strain	9	2.1686
sex x sire strain	3	1.6653
sex x dam strain	3	4.2357
sex x sire strain x dam strain	9	0.7571
error	405	0.5569

of the analysis was method 1, Model 1 outlined by Griffing (8).

An attempt was made to produce all of the 256 varieties of crosses, reciprocal crosses and back crosses in the F_2 generation, and from these the four-way crossbreds were to be used for this experiment. Because of low fertility in some of the crosses, not enough four-way crossbred mice were produced to form the foundation stock and therefore, three-way crossbreds were used to complete the numbers required. The three-way crossbreds were chosen so that the qualitative contribution of each of strains O, A, V and C to each treatment was equalized, and in addition, pure strain mice were excluded as the parents of the three-way crossbreds used for the experiment. For example, a three-way cross of OVC was used if it was produced by mating an OV crossbred mouse with a VC crossbred mouse, but was not used if it was produced by mating an OV crossbred mouse with a pure C strain (CC) mouse.

Five groups of 20 females each were formed from forty litters of 3 and 4-way crossbred mice which were divided within litters so that the groups were as similar as possible from the standpoint of their genetic history. The treatments were assigned five 4-way crossbred males in a manner similar to that described for assignment of the females to each treatment. In an attempt to reduce random genetic drift, the fifth treatment or control group was assigned 20 males, of which 7 were 4-way crossbreds. These 3 and 4-way crossbred mice were the offspring in "mating year" zero and the parents in "mating year" one. The term "mating year" is defined on page 9.

The five treatments of this experiment were: I, selection of large males and large females according to individual 45-day body weights; II, selection of small males and small females according to individual 45-day body weights; III, selection of males whose mothers had large 45-day body weights together with selection of females which had large individual 45-day body weights; and IV, selection of males whose mothers had small 45-day body weights coupled with selection of females which had small individual 45-day body weights; and V, no intentional selection for either large or small body size.

Experimental Plan:

Selection for large 45-day body weight was practiced in treatments I and III and for small 45-day body weight in treatments II and IV. Treatment V was the control. Breeding groups of all selection treatments consisted of 20 females and 5 males. Five males were used in order to minimize inbreeding which would be consistent with a large beef operation. However, breeding groups of the control contained 20 males as well as 20 females in an attempt to further minimize random genetic drift. It is recognized that genetic drift might be expected in the selected lines in which only 5 males were used. It was considered that selection in these lines would largely control the direction and amount of genetic change.

In the selection treatments, 20 females which had either the largest (treatments I and III) or smallest (treatments II and IV) body weights at 45-days of age were used for breeding. There was no intentional selection for any inherited characteristic other than 45-day weight and all animals not selected for breeding at the beginning of a mating year were discarded. There was, as will be described below, minor selection of younger animals in favor of older ones. Henceforth, whenever body size is mentioned it refers to 45-day body weight.

Individual selection of males for large 45-day weights was practiced in treatment I and individual selection of males for small 45-day body weights was practiced in treatment II. In individual selection, the 5 males were used for breeding which had the largest or smallest 45-day body weights.

Mother selection of males was practiced in treatments III and IV. In mother selection the 5 males were used for breeding whose mothers had either the largest (treatment III) or smallest (treatment IV) 45-day body weights. The individual 45-day body weights of males were disregarded in mother selection.

Every attempt was made in the experimental plan to mimic the conditions of a beef cattle population. Beef cattle are generally managed so that events are repeated yearly. For instance the breeding season is limited to a certain period and consequently calves are weaned on approximately the same date each year, etc. A "mating year" of 81 days and allowing for 15 days for mating, 21 days for gestation, 21 days for lactation and 24 days for post-weaning growth was devised to correspond to a calendar year in beef cattle. Mating years were simultaneous for all five treatments.

Another important characteristic of a beef cattle population is that it is monoparous and therefore, in mating year one and subsequently, each litter was adjusted at birth to contain four individuals and one of these, chosen at random, was identified by removing one toe. This marked individual was the only one which could represent the litter following weaning. Thus a monoparous situation was simulated in all treatments except in the controls. In the controls another of the opposite sex was randomly chosen at weaning. The purpose for intentionally retaining a member of each sex within each litter in the controls was to minimize the probability of genetic drift so that better estimates of selection response in the selection treatments could be obtained.

Each mouse previously selected randomly at birth was assigned a number for identification when weaned from its mother at 21 days of age and then kept in an individual cage until mating at 45 to 60 days of age. Forty-five-day body weights were recorded to the nearest one-half gram. At the beginning of mating year two and all subsequent mating years, mice in treatments I, II, III, and IV were ranked within sex by 45-day body weight from largest to smallest or from smallest to largest according to the treatment requirements and females ranking within the desired 20 or males ranking within the desired 5 were kept, and all other animals were discarded. Of course, in treatments III and IV the males were not ranked; instead the mothers of the males were ranked and the males whose mothers ranked within the desired 5 were kept, and the remaining ones were discarded.

In ranking the animals, whenever analogous weights occurred, the younger animal was ranked higher than the older animal. Thus, if the duplicate weights were such that there was a tie for twentieth place in the females or for fifth place in the males, the older animal was discarded. If the tie involved two animals of the same age, i.e., those born in the same mating year, the decision as to which to save was made by the toss of a coin.

Subsequent to mating year one, there were, at the beginning of each mating year, about 30 females in each of treatments I, II, III, and IV from which to select 20 for the breeding group. These approximately 30 females were made up of the surviving females of the 20 in the breeding group of the previous mating year in addition to about 10 virgins ageing from 45 to 60 days. Likewise there were about 15 males, 5 older ones plus 10 younger ones from which to select 5 for the breeding group. In the same way there were, in treatment V, about 40 mice of each sex, 20 older ones plus about 20 younger ones, from which to obtain at random 20 of each sex for the breeding group.

Matings, which were simultaneous for all treatments, were made within treatments by randomly assigning four selected females to each selected male, or in the control, one female was randomly assigned to each male. The time of mating was when the youngest mouse born in the particular mating year had reached 45 days of age. Males and females were left together for two weeks; therefore, age at first mating ranged from 45 to 60 days.

<u>Environment</u>:

The animals were housed in an insulated quonset hut with windows on the east side only. During the winter months the temperature in the building was thermostatically controlled at approximately 70°F. During the warmer months there was no temperature control.

Each mouse was caged individually from weaning at 21 days of age until mating at 45 to 60 days of age. During the mating period four females were placed with a single male in one cage for two weeks or in the control line one female was placed with a single male. Following the mating period of two weeks the males and females were separated and each was placed in an individual cage. After the weaning of the litters, adult females were kept together in pairs for 24 to 39 days until the next mating period. Except during the mating period of each mating year, all males were kept in individual cages.

The cages were made from one pound coffee cans and wire screen. Wood shavings were used for bedding. At least once daily all water bottles were checked and those which were empty were refilled. A diet purchased from Crown Mills, Portland, was fed free choice during the first five mating periods. This diet consisted of the following ingredients in the indicated proportions:

Wheat mill run	70 lbs.
Ground yellow corn	50 lbs.
Dehydrated alfalfa meal	10 lbs.
Dried skim milk	20 lbs.
Herring meal (70%)	20 lbs.
Irradiated yeast	4 lbs.
Wheat germ meal	4 lbs.
Ground limestone	1 lbs.
Iodized salt	1 lbs.

During the period which should have been the sixth mating year, a ration purchased from a different mill was fed. This ration supposedly consisted of these same ingredients and was thus supposedly identical, but it resulted in complete failure of reproduction as well as some death loss of mature animals. Therefore, the matings of the sixth mating year were repeated, with some missing pairs, after changing the diet to the Rockland mouse diet which was fed free choice for the remainder of the experiment.

Analysis of the Data:

In order to facilitate analysis and interpretation of the data and to provide a means whereby data on the two sexes could be combined, 45-day body weights were adjusted to a mid-sex basis according to the method of Mason *et al.* (14). These workers have shown that differences between the sexes are not constant, as the differences become more marked in larger mice than in smaller ones. After making this adjustment, sex was ignored as a variable.

Mason *et al.* (14) adjusted females to a male basis on the assumption that females and males were genetically equivalent in terms of standard deviations from their respective means. In other words a female one standard deviation below the mean of females was considered equivalent to a male one standard deviation below the mean of males. In converting male and female values to a mid-sex basis, males and females of the same standard measure are also considered equivalent. The absolute value assigned to a particular male (female) in terms of grams of body weight was the average of his (her) actual 45-day body weight and the body weight of females (males) the same number of standard deviations away from the mean of females (males). The assumed relationships between males and females are derived from the data presented in table 3. For example, a male weighing 27.29 grams (24.51 + 2.78) was considered equivalent to a female weighing 22.79 grams (20.72 + 2.07). The value assigned to the 27.29 gram male for analysis of the data was 25.04 grams or (27.29 + 22.79) / 2. Likewise, a female whose actual 45-day body weight was 22.79 grams was assigned a value of 25.04 grams for analysis of the data.

It was considered necessary to make the adjustment for sex because the number of animals in the subclasses, i.e., the number of animals of a particular sex, in a given treatment in a given mating year, was small (table 7). Adjusting for sex essentially doubled the number of animals in a subclass and did reduce the number of subclasses by half.

Heritability was determined in two ways: (1) from

TABLE 3

Average 45-Day Body Weights, and Sums of the Squared Deviates for Males and Females of the Unselected Treatment

Mating Year	n	Males Average	Males Sum of Squares	Females Average	Females Sum of Squares
1	13	22.12	45.08	19.04	56.23
2	16	22.75	266.50	19.91	73.61
3	15	24.70	67.90	20.13	47.23
4	11	23.82	18.14	20.23	26.68
5	14	25.32	124.30	21.64	74.71
6	8	26.00	38.50	22.00	17.50
7	12	26.83	72.67	22.08	55.42
Total	89	171.54	633.09	145.03	351.38
Average*		24.51		20.72	
Standard Deviate**			2.78		2.07

* 171.54 / 7 and 145.03 / 7

** The square roots of 633.09 / 82 and 351.38 / 82 the regression of the 45-day body weight of the offspring on the average 45-day body weight of the parents (10, p. 291-292) and (2) from the two-way selection differentials and responses (6, p. 478).

Since breeding groups were composed of 20 females and since fewer than 20 females in each breeding group produced offspring, there existed a possibility of natural selection within breeding groups for either large or small 45-day body weights coinciding with low fertility. The extent of this type of natural selection was evaluated by comparison of the actual parental means with the expected parental means had all 20 females in each breeding group reproduced. Failure to have differential fertility within groups does not imply that all groups are equal in fertility. Fertility of the groups can be obtained directly from table 7 where the number of offspring are recorded, and from Appendix tables 4-8 where the numbers of females which were mated are recorded. Fertility in a monoparous population is all or none, therefore the number of offspring and the number of females which reproduced are the same. A female was not considered to have reproduced unless her offspring reached 45 days of age.

In other words, for the purposes of this investigation, a female, or a mating, was considered unsuccessful and therefore infertile, unless the offspring which was chosen randomly at birth reached 45-days of age. The proportion of females, or matings, in a given treatment-mating year breeding group which was fertile can be obtained by dividing the number of offspring recorded in table 6 for that treatment and that mating year by the number of females in the corresponding breeding group. For example, the number of females in the breeding group in treatment IV, mating year seven, was 13 (from either table 4 or Appendix table 7) and the number of offspring produced by this breeding group was 2 (from table 7); division of 2 by 13 gives 0.154, the proportion of females in the breeding group which were considered fertile. There is a discrepancy for the controls, treatment V, between the number of offspring recorded in table 7 and the number of females which were considered fertile. This discrepancy is partially due to the fact that one mouse of each sex was not always present in the litter at weaning, in which case two of the same sex were kept, and partially due to the fact that occasionally one mouse only reached 45 days of age. The number of females which were considered fertile in treatment V in mating years 1-7 inclusive are respectively: 16, 17, 18, 15, 17, 14 and 16.

Five kinds of two-way selection differentials are considered. These are designated as (1) maximum expected; (2) attempted phenotypic; (3) realized phenotypic; (4) attempted standard; and (5) realized standard.

In order to get some idea of the amount of progress that would have been possible under ideal conditions, the maximum expected selection differentials under a constant environment were calculated on the basis of: (1) 80% fertility which was determined from the number having litters compared with the number bred in the controls over the time of the experiment; (2) a sex ratio of 1 male to 1 female which was close to the average sex ratio of 1.03 males to 1 female over the time of the experiment for the selection treatments; (3) a regression coefficient of male 45-day body weights on their mothers' 45-day body weights of 0.2 which is near the common regression coefficient calculated by Mason _et al._ (13) and is also about one half of the heritability estimates in mating years 0-3 inclusive; (4) a variance of 5.68 for offspring born in all mating years and which was calculated from the offspring born in mating years 0-2 inclusive; (5) no loss of animals from death or other causes after they once reached 45 days of age; and (6) a heritability of 0.40. All of these conditions are ideal. The detailed calculations are given in the Appendix.

Attempted phenotypic two-way selection differentials were calculated by subtracting the average 45-day body weight of the mice in a small selected breeding group of either individual or mother selection from the average 45-day body weight of the corresponding breeding group selected for large size.

Realized phenotypic two-way selection differentials were calculated by subtracting the average 45-day body weight of the mice in a small selected parent group of either individual or mother selection from the average 45-day body weight of the corresponding parent group selected for large size. Parent groups are derived from a breeding group; they may be the same as the breeding group, but most often are not because fewer animals become parents than are bred. In this experiment, fewer females reproduced than were bred in each and every breeding group.

Standard selection differentials corresponding to attempted and realized phenotypic selection differentials were calculated in terms of standard deviations of each animal from the mean of the animals born in the same treatment-mating year class. The standard deviations were then altered up or down according to the number of standard deviations a treatment-mating year offspring mean was expected to deviate from the original mean of the foundation animals on the basis of 40% heritability and the selection differential of the parents. The standard deviation values calculated in this way approximate deviations from the original mean had the environment been constant. These values are not free from environmental influences. They contain unmeasured amounts of any effects on the 45-day body weight of the offspring which are associated with the age or the generation of the mother. There was not enough information to get any estimation of the magnitude of these effects and neither was it possible, because of small numbers, to calculate standard selection differentials within mating years, within treatments, within age of dam, within generation of dam. These values may be taken as a better estimate of an animal's relative genetic worth than an animal's actual 45-day body weight, and perhaps more important, although not necessarily for this investigation, they provide a means of estimating the effective amount of selection practiced in each treatment. The selection differentials, in standard deviations, were converted to grams by the standard deviation of 2.38 which was the pooled estimate of the population standard deviation calculated from the offspring born in mating years 0-2 inclusive. These selection differentials are henceforth called standard selection differentials.

The effectiveness of mother selection as compared with individual selection can be stated in terms of two-way selection differentials and also in terms of differences in 45-day body weights of contemporary offspring. Effectiveness was calculated for the maximum expected two-way selection differentials, the attempted and realized phenotypic two-way selection differentials, and the attempted and realized standard selection differentials. Attempted selection differentials are based on the animals in the breeding group, whereas the realized ones are based on the animals which were actually parents. Effectiveness was also calculated for differences between the 45-day body weights of the offspring. Effectiveness is simply the two-way selection differential in mother selection, for a given mating-year, divided by the corresponding two-way selection differential in individual selection. In the case of the offspring, effectiveness is simply the average 45-day body weight of the offspring born from mice selected for large size minus the 45-day body weight of the offspring born from mice selected for small size in mother selection in a given mating year divided by the corresponding difference in individual selection.

DATA; INFERENCE; DISCUSSION

The Breeding Groups:

All 45-day body weights referred to henceforth have been adjusted to a mid-sex basis.

The average 45-day body weights of the mice in the breeding groups and the standard selection differentials which are presented in table 4 are weighted for the number of times each mouse was expected to be a parent. Since this was a monoparous population, except in mating year zero, the expected number of times that any female would be a parent in any mating year is one, but each male in treatments I through IV inclusive was used four times. In the control, treatment V, each mouse, male or female, was expected to leave two offspring and therefore no weighting was required. The variances given in table 4 are those of the expected parental mean values. An expected parental mean value is obtained whenever a female is mated, by averaging her 45-day body weight with that of the male. The number of such values is indicated in the table and it is the variance of n such observations which is given in conjunction with the weighted mean of any breeding group.

It is obvious that over the mating years the 45-day body weights of the mice in the selected breeding groups increased or decreased in accord with the direction

TABLE 4

Averages and Variances of the Average 45-Day Body Weights of Pairs of Mice in the Breeding Groups[1] and Standardized Values of the Mean[2] in Grams

Mating Year	Treatment I		Treatment II		Treatment III		Treatment IV		Treatment V	
	$\bar{y}$	s^2	$\bar{y}$	s^2	$\bar{y}$	s^2	$\bar{y}$	s^2	$\bar{y}$	s^2
0*	19.7	4.6	20.1	3.7	20.2	2.5	19.7	3.2	19.5	4.9
1**	19.9	4.8	20.7	8.6	18.0	4.6	18.2	4.0	19.7	6.9
	0.36		1.13		-1.62		-1.43		0.15	
2**	21.7	1.8	18.4	5.6	21.1	2.9	19.3	3.1	20.2	6.2
	1.59		-1.76		1.02		-0.81		0.02	
3**	22.9	0.7	18.0	4.1	21.5	1.2	19.0	3.1	21.3	5.1
	2.71		-2.57		1.67		-1.07		0.36	
4**	24.3	0.8	17.3	3.6	22.4	1.4	18.4	1.5	22.0	5.0
	3.52		-3.28		0.93		-2.24		0.67	
5**	24.8	0.7	17.4	2.4	23.0	0.6	18.6	1.3	21.9	3.7
	4.07		-3.43		2.38		-2.48		0.43	
6	25.4[c]	0.5	17.8[a]	4.1	23.6[b]	0.5	19.1[d]	1.6	22.6[b]	1.9
	3.55		-3.78		1.95		-5.28		0.07	
7	25.2**	0.4	18.6[a]	7.3	23.0**	1.0	19.0[e]	0.9	23.4**	2.8
	2.93		-3.67		1.07		-5.36		0.24	

*n = 25 for all five groups **n = 20 for all five groups [a]n = 16 [b]n = 17 [c]n = 19 [d]n = 14 [e]n = 13

1 The number of pairs in the various groups of mating years 6 and 7 was not constant but footnotes a to e are used to show the number, n, for each group.

2 Standardized attempted selection differentials from 19.56 grams, the unweighted mean of all animals in the breeding groups of mating year one.

selection was being practiced. This is even more striking when one observes the standardized values. In all of the treatments, except treatment II where selection was individually for small size, the variance of the selected breeding groups also decreased as would be expected. The variance in treatment II was large because two extremely small males weighing 11.3 and 12.6 grams were used in all mating years. No such extremes were involved in the other breeding groups.

A remarkably unexpected happening was the continuing increase in the 45-day body weights of the control mice. This appears to be largely an accumulation of the effects of reducing the litters to 4 in number at birth since the standard selection differentials, both the attempted ones, table 4, and especially the realized ones, table 5, were essentially zero in the control.

> At the conclusion of the selection experiment in October 1957, all mice in the selected treatments were discarded. However, the mice in control were kept and have been maintained continuously by mating 20 males with 20 females every 81 days. Beginning with the first litters born after the conclusion of the selection experiment, reduction to four in number at birth was no longer practiced and the females have been allowed to raise all mice to which they gave birth. Replacements have been chosen so that all litters have been represented in the next generation. No intentional selection for any characteristic has been practiced. The average 45-day body weight of 104 mice which descended from the controls

of this experiment and which were measured between November 1, 1958 and March 1, 1959 was 21 grams. The average of the F_1 and F_2 generations, in which all mice born were raised was 19.7 grams, a difference of 1.3 grams between the two periods.

It is noteworthy that the O strain mice measured from November 1, 1958 to March 1, 1959 averaged 22.6 grams in 45-day body weight as compared with 23.2 grams in 1955; the strain V mice now weigh 20.1 grams as compared with 18.4 grams in 1955; the A strain now weighs 23.2 grams as compared with 19.6 grams in 1955. The C strain has been lost in the interim due to its low fertility. At no time have litter numbers been reduced in these strains and from September, 1955 to date the strains A, V and O have been maintained by keeping about 10 females and 10 males to mate together frequently to avoid the loss of genetic material due to death losses from old age or the infertility accompanying old age. Since September 1958, 30 males and 30 females have been maintained in each strain. Matings have been made between 10 of each sex every three weeks and the mice have averaged about 60 days of age when they were first mated. Females which did not raise a litter have been kept and remated to minimize genetic drift.

Both the V and the A strains are larger than previously and it is proposed that the change to the Rockland mouse diet has led to this increase in 45-day body weights through alleviation of some of the inherited vitamin deficiency syndromes reported by Mason <u>et al</u>. (12). It is also proposed that some of the 1.3 grams difference between the 45-day body weights of the controls now and of the F_1 and F_2 generations is due to the change in ration.

If it is accepted from the above analysis that an increase of 1.3 grams in the controls in mating year seven is due to the better ration, then the remaining increase in 45-day body weights of 3.2 grams (from table 8) could be ascribed to the reduction in litter size. No other explanation seems feasible. Thus there were two apparent factors, reduction of litter size and a change of ration, operating upon all mice to increase 45-day body weights, and there is evidence, from the fact that the O strain is slightly smaller but the A and V strains are larger at the present time than when they were fed the original ration, that the ration change interacted with the genotypes undergoing selection.

The Parent Groups:

The data presented in table 5 require little elucidation in light of the above discussion on average 45-day body weights of the mice in the breeding groups. These data, table 5, are the weighted averages of the 45-day weights of the mice which were successful in reproduction, and the variances associated with the means are, in contrast to those in table 4, variances of actual parental mean values. The mean and variance of any mating year-treatment class are based on the total number of offspring for that class or the sum of the male and female offspring,

TABLE 5

Averages and Variances of the Average 45-Day Body Weights of the Pairs of Mice in the Breeding Groups Which Were Successful in Reproduction[1] and Standardized Values of the Mean[2] in Grams

Mating Year	Treatment I $\bar{y}$	I s^2	II $\bar{y}$	II s^2	III $\bar{y}$	III s^2	IV $\bar{y}$	IV s^2	V $\bar{y}$	V s^2
0	19.7	4.6	20.1	3.7	20.2	2.5	19.7	3.2	19.5	4.9
1	20.1+	5.0	20.9+	10.0	19.1+*	1.7	18.5+	4.1	20.5+	4.6
	0.50+		1.40+		-0.26+*		-0.93+*		0.83+	
2	21.8+	1.5	18.7+	5.1	21.1	2.8	19.3	3.7	20.5+	5.0
	1.74+		-1.29+		0.93-		-0.81		0.31+	
3	22.9	0.7	18.2+	5.5	21.7+	1.2	19.2+	3.5	21.7+	4.5
	2.67-		-3.07-*		0.98-*		-1.07		0.48+	
4	24.1-	0.4	17.1-	3.1	22.4	1.8	18.6+	1.3	21.8-	4.0
	3.26-		-3.26+		1.19+		-2.17+		0.48-	
5	24.4-	0.6	17.2-	1.7	23.0	0.6	18.2-	1.3	22.0+	3.8
	3.81-		-3.62-		1.43-*		-2.38+		0.48+	
6	25.4	1.0	16.9-*	3.4	23.9+	0.4	19.5+	0.5	22.6	1.9
	3.57+		-4.83-*		1.93-		-2.21+*		0.00-	
7	25.0	0.8	18.7+	9.7	23.3+	0.9	18.5-	0.3	23.5+	2.2
	3.28+		-3.67		1.17+		-3.24+*		0.14-	

1 For the value of n associated with each mean see table 7 and sum respective values for males and females.

2 Realized Standard selection differentials in grams from 19.56 grams, the mean of all animals in the breeding groups of mating year one.

* See text

the numbers of which are presented in table 7. The average 45-day body weights of the mice which were successful in reproduction, or the standard values of these averages, differ little from those of the mice in the breeding groups. In only three mating year-treatment classes is the difference in average 45-day body weight more than 0.5 grams and the standard values of these means differ by this much in only 8 such classes. In table 5 the means that differ from the respective means in table 4 are indicated by + or - signs and those which differ by more than 0.5 grams are indicated by asterisks. Since the plus and minus signs are about the same in number, differential fertility within groups seems to have been minor.

<u>Selection Differentials</u>:

The maximum expected two-way selection differentials (table 6) are different for mother selection and for individual selection.

As would be expected, from comparison of the means in table 4 with the respective means in table 5, realized phenotypic two-way selection differentials differed little from attempted ones or from the standard ones. If a realized two-way selection differential is less than the corresponding attempted one, this is indicated by a minus sign in table 6, and likewise if a realized two-way

TABLE 6

Expected Maximum (EMSD), Attempted Phenotypic (APSD), Realized Phenotypic (RPSD), Attempted Standard (ASSD) and Realized Standard (RSSD) Two-way Selection Differentials in Grams in Individual Selection (I-II and in Mother Selection (III-IV)

Mating Year	I-II Individual Selection					III-IV Mother Selection				
	EMSD	APSD	RPSD	ASSD	RSSD	EMSD	APSD	RPSD	ASSD	RSSD
1	0.00	-0.86	-0.86	-0.77	-0.90+	0.00	-0.19	0.61+*	-0.19	0.67+*
2	3.48	3.25	3.07	3.35	3.03-*	1.52	1.76	1.82+	1.83	1.74-
3	5.20	4.94	4.74-	5.28	5.74+*	2.34	2.42	2.52+	2.74	2.05-*
4	6.38	7.00	7.04+	6.80	6.52-	2.96	3.98	3.79-	3.17	3.36+
5	7.26	7.35	7.20-	7.50	7.43-	3.46	4.44	4.19-	4.86	3.81-*
6	8.02	7.60	8.53+*	7.33	8.40+*	3.86	4.59	4.47-	7.23	4.14-*
7	8.60	6.63	6.34-	6.60	6.95+*	4.22	4.00	4.82+*	6.43	4.41-*

* See text.

selection differential is greater than the attempted one, this is indicated by a plus sign. In only three cases is the difference between the attempted and the realized phenotypic two-way selection differential greater than 0.3 grams and these three cases are indicated by asterisks. Nine of the realized standard two-way selection differentials differ from the attempted ones by more than 0.3 grams and these are also indicated by asterisks.

It is necessary, in individual selection, to consider departure of the attempted or realized two-way selection differentials from the expected ones only in the last mating year, whereas, in mother selection, similar departures over the entire experiment need to be considered. Referring to table 4, it is obvious that in individual selection for small size (treatment II), further phenotypic progress was not made after the fourth mating year. Reasons for this are: (1) with two factors acting to increase 45-day body weights, young mice were larger than their parents and (2) death of some of the older, smaller animals forced the use of more of the young. Standard selection in treatment II, however, continued to be effective through mating year six. Phenotypic selection in treatment I was effective through mating year six, but standard selection was decreased in mating years six and seven. Thus the failure to reach the expected selection differentials was due to the experimental plan, which failed to recognize in any way possible environmental variation affecting the values of the animals selected, and partially because the method of calculating the maximum selection differentials ignored death loss.

In all of the selection treatments, the attempted selections in mating year seven were less than those of the previous mating year. The reason for this is that it was necessary to use all of the offspring born in mating year six to (1) replace the mice that died from the ration change and (2) to replace some of the remaining foundation females which were too old to breed. Replacement of old females by younger ones was made in treatment III, where selection was for large size. In treatments II and IV, where selection was for small size, the death losses were so great and the fertility was so low in mating year six that it was even impossible in mating year seven to bring the number of females in the breeding groups up to 20. Both the death losses and the low fertility in these treatments in mating year six could be a consequence of old age (Appendix tables 4-8) as well as small size.

The foundation females in treatment IV were, by chance, smaller than average (table 4). Many of the foundation females in treatment IV, where selection was for small size, were kept for several mating years and full advantage was taken in treatment III of the increasing body size which was apparently caused by ration change and litter size adjustment. Thus the expected phenotypic selection differentials were exceeded. As a consequence of using the older females longer and saving a smaller proportion of the young females born each mating year, the standard selection differentials in treatment IV where selection was for small size were much greater than expected. The standard selection differentials in treatment III where selection was for large size were, as a consequence of saving too many young females, less than expected, but the net result in mother selection was to increase the standard selection differentials since the increase in treatment IV was of greater magnitude than the decrease in treatment III. The number of animals born in each mating year which were used in succeeding mating years are presented in Appendix tables 4-8.

Forty-five Day Body Weights of the Offspring:

The 45-day body weights of the mice in the various treatments which are presented in table 8 appear to have responded fairly well to selection as indicated by divergence between the large and small selection treatments.

TABLE 7

The Number of Offspring by Sex, Treatments, and Mating Years and the Total Number of Offspring in Each Treatment Each Mating Year

Mating Year	Treatment and Sex														
	I			II			III			IV			V		
	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
1	5	9	14	10	6	16	2	10	12	11	6	17	17	14	31
2	8	9	17	4	6	10	12	5	17	6	11	17	18	16	34
3	9	9	18	7	8	15	7	9	16	10	6	16	19	17	36
4	5	11	16	9	4	13	6	9	15	8	6	14	17	12	29
5	6	8	14	6	7	13	6	8	14	9	6	15	17	16	33
6	7	4	11	3	3	6	4	4	8	3	0	3	15	10	25
7	8	7	15	6	3	9	7	4	11	1	1	2	16	14	30

TABLE 8

Averages ($\bar{y}$) and Variances (s^2) of 45-Day Body Weights in Grams of the Offspring in the Various Treatments by Mating Years and the Amount in Grams by Which the Averages are Expected to Deviate From the Controls on the Basis of the Standard Selection Differential of the Parents and 40 Per Cent Heritability

Mating Year	Treatment I[1] $\bar{y}$	I s^2	II $\bar{y}$	II s^2	III $\bar{y}$	III s^2	IV $\bar{y}$	IV s^2	V $\bar{y}$	V s^2
0	20.5	13.8	21.1	12.8	18.0	7.3	18.4	11.5	19.7	11.8
1	21.2	5.3	20.7	14.1	22.0	4.6	20.8	4.3	21.0	5.1
	-0.23		0.23		-0.44		-0.74			
2	20.9	3.8	21.2	3.3	22.0	2.7*	20.9	3.2	21.5	9.9
	0.57		-0.64		0.25		-0.45			
3	23.0	4.8**	19.5	5.8	22.6	4.4	21.6	9.5	22.1	4.4
	0.88		-1.42		0.20		-0.64			
4	22.5	4.1**	21.0	4.7	22.4	4.2	21.8	6.7	22.2	3.2
	1.11		-1.50		0.28		-0.83			
5	24.5	5.4	22.2	4.2	23.2	2.7	22.1	4.7	23.6	6.5
	1.33		-1.64		0.38		-1.02			
6	24.0	2.9	23.0	28.4	22.9	6.8	19.9	1.0	24.4	4.3
	1.43		-1.93		0.77		-1.02			
7	23.5	7.1	21.7	4.6	23.3	3.0	22.9	0.9	24.2	5.6
	1.26		-1.52		0.41		-1.08			

* P less than 0.05

** P less than 0.01

1 Contemporary means in treatment I have been compared with those in treatments II and III, and contemporary means in treatment II have also been compared with those in treatment IV. No comparable differences exist between treatments I and III or between treatments II and IV. Contemporary differences which are recognized between treatments I and II and between treatments III and IV are indicated by asterisks.

Comparison of the 45-day body weights of the contemporary offspring in treatments I and III with those of the controls indicate no differences, i.e., selection for large 45-day body weights appears to have been ineffective. The offspring in treatments II and IV were generally well below those of the controls or of the large selected lines, i.e., selection for small size appears to have been effective. If the control data (table 8) are used as standards it seems that no progress was made toward increasing 45-day body weights but that all of the response was in the small selection lines. This may be the same type of asymetric response encountered by Falconer (7, p. 180-181), i.e., higher heritability for small body size than for large body size; however, since the standard selection differentials for small body size (table 5) were generally greater than those for large body size, the offspring in the small selected treatments (II and IV) would be expected to show a greater response. Unfortunately, since the controls increased in 45-day body weight, even in the virtual absence of selection, it is impossible to make any decision as to the differential responses because the main environmental factor which seems to be involved is associated with the age and generation of the mother, and neither the average age nor the distribution of the ages of the mothers in any mating year-treatment class are sufficiently similar to those of the respective control class for comparison.

The object, here, is not, however, to be concerned with whether selection for large size is more or less effective than selection for small size, but to compare mother selection with individual selection. For this comparison it is only necessary to be able to assume that heritability for large size was the same in both treatments where selection was for large size and that the heritability was the same in both treatments where selection was for small size. Selection differentials have been established, and it is necessary to determine whether differences in the offspring were realized. Differences between offspring groups can be obtained from table 8, and the differences pertinent to evaluating mother selection are presented in table 9 together with 95 per cent confidence limits.

The differences in average 45-day body weight of the contemporary offspring in mother selection are not expected to become great enough to reach statistically significant levels. On the basis of 16 offspring per treatment per mating year and a variance of 5.68, a difference between offspring in a large selected treatment and a small selected treatment of 1.79 grams would be required for statistical significance at the 0.05 level. The maximum difference expected (Appendix table 3) between treatments III and IV is 1.76 grams. In individual

TABLE 9

Regression of 45-Day Body Weights of Offspring on Mid-Parental Average 45-Day Body Weights, or Heritability Estimates

Mating Year	Treatment I	II	III	IV	V	Common Estimates and 95% Confidence Limits
0	0.57	0.31	0.49	-0.04	0.54*	0.40 ± 0.18
1	0.42	0.57*	0.07	0.05	0.48**	0.35 ± 0.20
2	0.78*	0.49	0.46*	0.57*	0.28	0.42 ± 0.24
3	0.62	-0.48*	0.25	0.87*	0.09	0.11 ± 0.26
4	0.36	-0.41	0.42	-0.16	0.49**	0.25 ± 0.28
5	1.56*	0.44	0.59	-0.77	0.18	0.19 ± 0.34
6	0.44	-2.42*	-0.53	1.50	-0.10	-0.54 ± 0.58
7	-0.54	0.21	0.89	-1.68	-0.21	0.03 ± 0.30
Common or Pooled for Mating Years 2-7 Inclusive	0.55*	-0.17	0.43*	0.44**	——	—— ——

* P less than 0.05

** P less than 0.01

selection, statistically significant differences or differences exceeding 1.79 grams were expected between the offspring of treatments I and II which were born in mating year three and in all subsequent mating years. At no time were statistically significant differences expected between either treatments I and III, the treatments where selection was for large size or between treatments II and IV where selection was for small size.

Statistically significant differences were observed between the offspring of treatments I and II (individual selection) in each of mating years three, four and five. On the basis of the standard selection differentials and 40 per cent heritability significant differences should also have been observed in mating years six and seven. Heritability will be considered below; the differences between the average 45-day body weights of the offspring in the comparable groups are about as expected (table 9). However, non-genetic effects associated with the age and generation of the dam may be important in the differences between contemporary groups selected for large and small body size since the tendency was to keep young females in selection for large 45-day body weight and older females in selection for small 45-day body weight (Appendix tables 4-8).

<u>Heritability</u>:

Heritability and the regression coefficient of offspring values on the mid-parental average values are one and the same (10, p. 291-292). The regression coefficients or heritability estimates within each treatment, each mating year, are presented in table 9 together with common estimates for each mating year and for each treatment over the last five mating years. Very few of the within treatment-within mating year values are statistically significantly different from zero.

Heritability within treatment I was not different than heritability within treatment III, i.e., heritability was the same for large size in individual selection as in mother selection, the common estimate with 95 per cent confidence limits being 0.48 ± 0.30. Heritability within treatment IV was significantly greater than heritability within treatment II, i.e., heritability was higher in mother selection for small size than in individual selection for small size. As noted previously, two extremely small males were used extensively in treatment II. One male was used throughout the experiment and another one was used in the latter six of the eight mating years. These two mice were extremely valuable phenotypically but as breeding animals they were useless for reproducing their valuable phenotypes. Theoretically, it was not known that these two were undesirable males to use because supposedly the females were mated randomly to the males as would be done in a large commercial cattle operation where several bulls roam freely with a large number of cows. Under these conditions it is impossible to know which calf is sired by which bull. The dogged use of these two males with the consequent negative heritabilities and failure to make progress toward the intended goal is a good example of the fallacy of making too much use of bulls of superior phenotypes unless it is known that the calves sired are inheriting the superior phenotypes.

Heritability was significantly greater in treatments I and III where selection was for large size than in treatments II and IV where selection was for small size. As mentioned above, the common estimate for heritability for the large selection treatments was 0.48 ± 0.30. The common estimate with 95 per cent confidence limits for the small selection treatments was 0.04 ± 0.24, but of course the difference between the estimates for large and small selection was entirely due to treatment II, as can be observed from table 9. The heritability estimate in mother selection together with 95 per cent confidence limits was 0.44 ± 0.26 and this was significantly greater than the estimate of -0.02 ± 0.26 for individual selection, but again the low estimate for individual selection was entirely due to treatment II. A common estimate of heritability was also calculated by pooling all of the data for mating years 0-2 inclusive. This estimate together with its 99 per cent confidence limits was 0.39 ± 0.15.

Heritability estimates obtained from the two-way selection differentials and responses are presented in table 10 for mating years two to seven inclusive. The arithmetic averages of these estimates for mother selection and for individual selection are also given together with their 95 per cent confidence limits. In each comparison, eg., mother selection (III-IV) versus individual selection (I-II) under R/ASSD (response divided by attempted standard selection differential) or mother selection (III-IV) versus individual selection (I-II) under R/RSSD (response divided by realized standard selection differentials), the heritability estimate is significantly greater (P less than 0.05) in mother selection than in individual selection. That is, $0.31 > 0.25$; $0.40 > 0.24$; $0.36 > 0.26$; and $0.36 > 0.27$.

<u>Effectiveness of Mother Selection versus Individual Selection</u>:

In order to be able to compare the two methods of selection it was necessary to determine (1) whether responses to selection could be expected, i.e., was there sufficient genetic variation present; (2) whether

TABLE 10

Heritability Estimates (R/APSD; R/ASSD; R/RPSD and R/RSSD) in Individual Selection (I-II) and in Mother Selection (III-IV) Based on Attempted Selection Differentials (ASSD, APSD) Realized Selection Differentials (RSSD, RPSD) and Responses (R)

Mating Year	R		R/ASSD		R/RSSD		R/APSD		R/RPSD	
	I-II	III-IV	I-II	III-IV	I-II	III-IV	I-II	III-IV	I-II	III-IV
2	-0.22±1.55	1.09±0.84	-0.07	0.60	-0.07	0.63	-0.07	0.62	-0.07	0.60
3	3.44±1.65	0.95±1.90	0.65	0.35	0.60	0.46	0.70	0.39	0.73	0.38
4	1.51±1.60	0.61±1.78	0.22	0.19	0.23	0.18	0.22	0.15	0.21	0.16
5	2.25±1.75	1.04±1.48	0.30	0.21	0.30	0.27	0.31	0.23	0.31	0.25
6	1.13±2.98	3.09±3.62	0.15	0.42	0.13	0.75	0.15	0.67	0.13	0.69
7	1.77±2.17	0.44±2.86	0.27	0.07	0.25	0.10	0.27	0.11	0.28	0.09
Average			0.25	0.31	0.24	0.40	0.26	0.36	0.27	0.36
95 Per Cent Confidence Limits			±0.25	±0.20	±0.23	±0.28	±0.26	±0.25	±0.28	±0.25

substantial or expected selection differentials were established; (3) whether the responses to selection were reasonable, i.e., were the differences established between offspring groups reasonable.

The genetic variation was initially and on the average comparable to that reported by Falconer (6, p. 479). With this level of heritability he was able to bring about considerable differences between lines selected for large and for small size. Maximum expected selection differentials were for the most part exceeded. The differences established in the offspring were not disappointing, although the catastrophe of mating year six may have disturbed things to such an extent that evaluation in the last two mating years may be questionable. The fact that the controls increased in size in the absence of selection is also cause for caution, but since the ages of the mothers in treatment II and IV are not too different and likewise since the ages of the mothers in treatments I and III are similar, comparisons of mother versus individual selection seem to be in order, since it is not expected that the mice in the treatments would be effected as much as the controls by the accumulation of the effects of the reduction in litter size as there were fewer generations involved.

In general, mother selection was a bit more effective in creating a selection differential than was expected (table 11). In creating a difference between offspring born from large selected and from small selected parents, mother selection was often less effective than expected, but when the values under response in table 11 are averaged, mother selection appears more effective than expected, which is consistent with the higher heritability in mother selection and also with the greater than expected selection differentials in mother selection. However, it must be remembered that the experimental error involved with differences between offspring groups is large (table 10).

TABLE 11

Effectiveness of Mother Selection as a Fraction of Individual Selection in Creating the Indicated Selection Differentials and in Creating Responses or Differences Between Offspring Born from Parents Selected for Large and for Small Size

		Type of Selection Differential				
Mating Year	Expected Effectiveness	Attempted Phenotypic	Realized Phenotypic	Attempted Standard	Realized Standard	Response
2	0.44	0.54	0.59	0.55	0.57	*
3	0.45	0.49	0.53	0.52	0.36	0.28
4	0.46	0.57	0.54	0.47	0.52	0.40
5	0.48	0.60	0.58	0.65	0.51	0.46
6	0.48	0.60	0.52	0.99	0.49	2.73
7	0.49	0.60	0.76	0.97	0.63	0.25
Average	0.467	0.567	0.587	0.692	0.513	0.824

* A negative response to selection was observed in individual selection in mating year 2.

GENERAL DISCUSSION

Considerations for Synthesizing a Monoparous Population of Mice:

The analysis presented in table 2 would indicate the litters should not be adjusted to a common size in experiments where synthetic monoparous populations are used. The only necessary criterian for synthetic monoparous population is that one mouse be randomly selected and identified at birth. The mother could just as well be allowed to raise the entire litter as to be allowed to raise only four. Further,the remaining members of the litter could be used to advantage for such things as: (1) determining the degree to which the chosen individual represented the litter from which it came or in other words, how well it represented the heritable portion of its parents phenotype or genotype; (2) obtaining estimates of actual genetic variation; (3) making more reliable sex adjustments; (4) determining the effects of the age and the generation of the dam; and (5) in general, verifying and investigating problems that arise in selection in a monoparous population.

The works of Falconer (5) (7, p. 191-194), MacDowell et al. (11), Parkes (16), Chai (4), and Butler and Metrakos (3) indicate that alteration of litter size might cause an increase in 45-day body weight as was encountered in this experiment. In general these people have shown that larger females have larger litters and produce more milk than smaller females; and that reduction of the number of mice in the litter results in the remaining members being larger than they otherwise would have been and consequently females raised in reduced litters tend to have larger litters and to produce greater amounts of milk than they otherwise would. From this investigation it appears that repeated reduction of litters in succeeding generations results in further gain. It is not known how many generations of raising mice in reduced litters would be required before a new steady state was reached, but it would appear from this investigation that several generations might be involved.

A final consideration is that there is a possibility that after several generations of management of mice under monoparous conditions, the number of mice born per litter would become fewer since litters of only one or two have an equal chance of representation in the next generation with litters of, for example, ten or twelve. The consequences of this, through genetic association with other characteristics such as 45-day body weight, might be important.

<u>Inference to Beef Cattle Populations:</u>

This experiment was designed with the thought that the environmental effects would be randomly distributed, a condition which was not fulfilled. It is doubtful whether environmental effects are, in fact, randomly distributed in any beef cattle herd. For instance, the science of nutrition is continually operating to drive the phenotypes of beef cattle in the same direction as is the science of genetics. Of course, the commercial rancher has to take advantage of all scientific advances and, therefore, cannot maintain a constant environment. It is, therefore, desireable to devise some plan which will allow for making genetic gains while at the same time capitalizing on other scientific advances. As indicated from this experiment, strict selection on phenotype can cause difficulty, eg., low standard selection differentials in treatment III, and negative heritability in treatment II. In beef cattle or synthetic monoparous populations a more suitable method of selection might be to select about one-half of the heifer calves, or females, born each year. Bull calves, or males, could, at least initially, as indicated from this investigation, be chosen solely on the basis of their dams' records. This would easily reduce the number of males that would have to be kept to older ages for evaluation on their own merit, or might even render individual evaluation of males not worth while. Of course, the success of mother selection of males depends upon how well the record of the dam predicts the breeding value of her son. In general the higher the heritability of the trait, the better this prediction will be. For certain characteristics which are important in a beef cattle operation, such as mothering ability, mother or daughter selection of males is a necessity.

An animal selected solely because of an outstanding phenotype need not necessarily have a good genotype, as borne out by this investigation, especially in treatments II and III. However, the chances that an animal with a very outstanding phenotype, in relation to the phenotypes of comparable animals, would also have a very poor genotype are probably small. Consequently, in a herd of beef cattle in which it is not known which bull sired which calf, that is, where it is impossible to know the genotype, the overuse of bulls with outstanding phenotypes but poor genotypes can be avoided by rapid turnover of bulls.

Although another investigation with laboratory animals would be desirable for verification, since the results of the present investigation are only indicative, it is proposed that genetic progress in a closed commercial herd of beef cattle can be made if bull calves are selected from the most outstanding young cows, and for greater assurance of success it is proposed that each bull should be used for only one or two years.

SUMMARY

A selection experiment was conducted with synthetic monoparous populations of mice for the purpose of inferring as to the relative effectiveness of two methods of selecting bulls for breeding purposes. One method of selection, designated as individual selection, incorporated the selection of males on their own merit, whereas the other method of selection, designated as mother selection, incorporated selection of males solely on their mothers' merit. Selection was practiced by both methods for large and for small 45-day body weights for the equivalent of six years in a beef cattle operation.

With 99 per cent confidence, heritability of 45-day body weights expressed as the regression coefficient of offspring on mid-parent was, initially, 0.39 ± 0.15. The corresponding heritability estimates (pooled for the six years of selection) were: 0.55 for individual selection of males for large 45-day body weights; -0.17 for individual selection of males for small 45-day body weights; 0.43 for mother selection of males for large 45-day body weights; and, 0.44 for mother selection of males for small 45-day body weights. Expected maximum selection differentials, under ideal conditions, were estimated and reasonably approximated the realized selection

differentials. However, slightly greater than expected selection differentials were attained in mother selection

The responses to selection indicated by the observed differences in 45-day body weight between offspring born from large and from small selected parents in individual selection, and also in mother selection, were reasonably close to the differences expected on the basis of the estimated maximum selection differentials and a heritability of 40 per cent.

Realized heritability, based on two-way standard selection differentials and responses, averaged 0.24 in individual selection and 0.40 in mother selection.

The expected effectiveness of mother selection, relative to individual selection under ideal conditions, was estimated to average 0.48 over the six mating years of selection. The observed effectiveness in terms of standard selection differentials averaged 0.69, whereas the observed effectiveness in terms of responses averaged 0.82.

Although the results of the present investigation are only indicative, it is proposed that genetic progress in any trait of sufficiently high heritability could be made in a closed commercial herd of beef cattle if bull calves were selected from the most outstanding young cows, and for greater assurance of success, it is proposed that each bull should be used for only one or two years.

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APPENDICES

DESCRIPTION AND EXPLANATION OF APPENDIX TABLES 1 TO 3, AND DETAILS OF CALCULATIONS

In appendix table 1, under selection of mothers, the number of females supposedly available from which to select the 20 for a breeding group are given under the heading "Total". For example, 20 unselected females were randomly assigned to each treatment in mating year one. From these 20 females, 16 offspring were expected to be produced, of which 8 were expected to be females. These 8 are tabulated under the heading "Increase" for mating year 2. There were expected to be 28 females, the 20 older ones plus the 8 younger ones, available in mating year two, from which to select 20. The fraction 20/28 is recorded under the heading "Fraction" for mating year two. This represents the expected proportion of the females available which were selected for any breeding group in mating year two. If the per cent of the total animals which were selected is known, the mean of the selected group in standard deviations, or in other words, the standard selection differential, can be obtained (6, p. 475-477) (9, p. 112). The standard selection differential of 0.47 which is associated with the fraction 20/28 is recorded under the heading "Average". Eight more females were expected to be born in mating year two, making a total of 36 from which to select 20 in mating year three for a standard selection differential 0.71, etc., through mating year seven.

The only difference from the above for obtaining the expected standard selection differentials for males in individual selection is that only 5 males were made available in mating year one, thus making the "Total" 15 less for males than for females in each mating year, and of course, since only 5 males were used each mating year, the fractions are 5/x rather than 20/x, where x represents the expected total in each mating year.

In mating year one, 5 unselected males were mated to 20 unselected females, therefore the average expected deviation of the matings was 0.00 which is recorded in Appendix table 1 under the heading "Matings". In mating year two, females expected to average 0.47 standard deviations were mated to males which were expected to average 0.99 standard deviations, and the average of the matings was expected to be 0.73 standard deviations above or below the mean depending upon the direction of selection.

In mother selection of males, five males were initially assigned to the treatments. Twenty unselected females were mated to unselected males. From these 20 females 8 males were expected to be produced. Thus a total of 13 males were expected from 25 females; the 20 in the breeding group plus the 5 mothers of the foundation males These 13 males were expected to distribute evenly as sons from the top ranking female to the bottom ranking female, and it was expected that 5 males would be born from the top 9.6 females; thus the expected standard selection differential for the mothers of the males selected in mother selection in mating year two is based on the fraction 9.6/25. On the basis of a heritability of 40 per cent or regression coefficient of male offspring 45-day body weights on the mother's 45-day body weights of 0.20, only two tenths of the selection differential in the mothers is expected in sons which were actually saved for breeding. Thus the expected selection differential of the males used for breeding in mother selection in mating year two was 0.20 standard deviations, and the expected average selection differential of the animals in the breeding group was 0.34, or 0.47 plus 0.20 divided by 2. In mating year three 33 possible mothers were considered, of which only the highest ranking 20 were mated. The 33 possible mothers consist of the mothers of the 5 foundation males, the 20 foundation females, and the 8 females supposedly born in mating year one. Of the 20 which were mated, only 16 were considered, on the basis of 80 per cent fertility, to have reproduced, and, on the basis of a 50 per cent sex ratio, only 8 male offspring were considered to have been produced. These 8 male offspring were considered to have been equally distributed from the highest ranking to the lowest ranking of the 20 females which were mated. In this way, on the average, 5 males could have been chosen from the top 12.5 of the considered 33 females. The same considerations apply to mating years four through seven, except that more possible mothers are considered in each succeeding mating year.

In Appendix table 2 the expected maximum selection differentials in grams, the expected deviation in grams of the offspring born, and the expected deviation in grams of the accumulated population from the original mean of the foundation animals, are given for each mating year for individual selection of males. The foundation population consisted of 25 animals with a mean, u. The matings were made without selection, therefore the expected mean of the selected animals and offspring born was also u. On the basis of 80 per cent fertility, 16 offspring with the mean of u were expected to be added to the original 25 with a mean of u. Thus there were expected to be 41 animals with a mean of u in the accumulated population at the beginning of mating year two. From Appendix table 1, under the column headed "Matings" and under individual selection of males it is found that the expected selection differential in standard deviations in mating year two is 0.73. Multiplication of 0.73 by 2.38 grams, the standard deviation of the population, gives a value of 1.74 grams for the amount by which the mean of the animals selected for a breeding group in individual selection in mating year two is expected to be greater than u. Of course, if selection was for small size the mean breeding group would be expected to be 1.74 grams less than u. On the basis of 40 per cent heritability the offspring produced by the mating group would be expected to average 0.70 grams above the mean, u, or in the case of small selection, that much below u. On the basis of 80 per cent fertility, 16 offspring averaging u + 0.70 grams are expected to be produced. Thus, average 45-day body weight of the 57 animals in the accumulated population at the beginning of mating year three is u + 0.20 grams and the details for obtaining this value are, as in Appendix table 2, $\frac{41\,u + 16(u + 0.70)}{57}$. Referring again to Appendix table 1, it is found that animals selected for a breeding group in mating year three are expected to average 1.01 standard deviations above the mean, u + 0.20, for all in the accumulated population. As above, 1.01 is multiplied by 2.38 to give 2.40 grams as the amount by which the animals selected for a breeding group are expected to deviate from the mean of the accumulated population at the beginning of mating year three. Thus, since the mean of the accumulated population is u + 0.20, the average 45-day body weight of the animals in a breeding group in individual selection in mating year three is expected to be u plus 2.60 grams, etc., through mating year seven. Exactly the same procedures were followed in obtaining the values in Appendix table 3, except that in obtaining the selection differentials in standard deviations, Appendix table 1 was entered under mother selection of males.

Only positive values are given in Appendix tables 1-3 inclusive, therefore, where selection is for large size, these values can be taken at face value; but where selection is for small size, the standard deviations in Appendix table 1 are negative rather than positive, as are gram deviations in Appendix tables 2 and 3.

APPENDIX TABLE 1

The Number of Animals One Mating Year of Age (Yearlings) the Total Numbers of Animals Available From Which Selection Can Occur (Total), the Fraction of the Available Total Which is Selected (Fraction), the Average Standard Deviation Value of the Fraction Saved (Ave.), 0.2 Times the Average Standard Deviation in the Case of Mother Selection of Males, and the Average Standard Deviation Value of the Elected Males and of the Selected Females (Matings) for Each Mating Year (Year), and for Each Method of Selecting Males

Selection of Mothers

Year	Yearlings	Total	Fraction	Ave.	0.2xAve.	Matings
1	-	20	20/20	0.00	--	--
2	8	28	20/28	0.47	--	--
3	8	36	20/36	0.71	--	--
4	8	44	20/44	0.87	--	--
5	8	52	20/52	0.99	--	--
6	8	60	20/60	1.09	--	--
7	8	68	20/68	1.17	--	--

Individual Selection of Males

Year	Yearlings	Total	Fraction	Ave.	0.2xAve.	Matings
1	-	5	5/5	0.00	--	0.00
2	8	13	5/13	0.99	--	0.73
3	8	21	5/21	1.30	--	1.01
4	8	29	5/29	1.48	--	1.18
5	8	37	5/37	1.60	--	1.30
6	8	45	5/45	1.70	--	1.40
7	8	53	5/53	1.76	--	1.47

Mother Selection of Males

Year	Yearlings	Total	Fraction	Ave.	0.2xAve.	Matings
1	-	5	5/5	0.00	0.00	0.00
2	8	25	9.6/25	0.99	0.20	0.34
3	8	33	12.5/33	1.00	0.20	0.46
4	8	41	12.5/41	1.15	0.23	0.55
5	8	49	12.5/49	1.26	0.25	0.62
6	8	57	12.5/57	1.34	0.27	0.68
7	8	65	12.5/65	1.42	0.28	0.73

APPENDIX TABLE 2

Maximum Expected Selection Differentials in Grams in Individual Selection of Males for Large Size, the Expected Average of all Animals Born in all Time, and the Expected Average Deviation From the Original Mean (u) of all Animals Born in Each Mating Year. Individual Selection of Males for Small Size is Expected to Cause Deviations Below the Mean by Like Amounts

Mating Year	n	Mean of all Animals Born in all of the Time	Mean of the Animals Selected	Mean of the Animals Born
1	25	u	u	u
2	41	u	u + 1.74	u + .70
3	57	$\frac{41u + 16(u+.70)=u+.20}{57}$	(u+.20)+2.40=u+2.60	u + 1.04
4	73	$\frac{57(u+.20)+10(ul.04)=u+.38}{73}$	(u+.38)+2.81=u+3.19	u + 1.28
5	89	$\frac{73(u+.38)+16(u+1.28)=u+.54}{89}$	(u+.54)+3.09=u+3.63	u + 1.45
6	105	$\frac{89(u+.54)+16(u+1.45)=u+.68}{105}$	(u+.68)+3.33=u+4.01	u + 1.60
7	121	$\frac{105(u+.68)+16(u+1.60)=u+.80}{121}$	(u+.80)+3.50=u+4.30	u + 1.72

APPENDIX TABLE 3

Maximum Expected Selection Differentials in Grams in Mother Selection of Males for Large Size, the Expected Average of all Animals Born in all Time, and the Expected Average Deviation From the Original Mean (u) of all Animals Born in Each Mating Year. Mother Selection of Males for Small Size is Expected to Cause Deviations Below the Mean by Like Amounts

Mating Year	n	Mean of all Animals Born in all of the Time	Mean of the Animals Selected	Mean of the Animals Born
1	25	u	u	u
2	41	u	u + .81	u + .32
3	57	$\frac{41u+16(u+.32)}{57} = u+.09$	(u+.09)+1.09=u+1.17	u + .47
4	73	$\frac{57(u+.09)+16(u+.47)}{73} = u+.17$	(u+.17)+1.31=u+1.48	u + .59
5	89	$\frac{73(u+.17)+16(u+.59)}{89} = u+.25$	(u+.25)+1.48=u+1.73	u + .69
6	105	$\frac{87(u+.25)+16(u+.69)}{105} = u+.31$	u + .31+1.62=u+1.93	u + .77
7	121	$\frac{105(u+.31)+16(u+.77)}{121} = u+.37$	u + .37+1.74=u+2.11	u + .84

APPENDIX TABLE 4

Number Females Born in Each Mating Year; the Number From Each Mating Year Which Were in the Breeding Groups (B) of Each Succeeding Year; The Number Which Were Parents in Each Succeeding Mating Year (P); the Number of Death Losses (D) From the Preceeding Mating; the Total Number of Females in the Breeding Groups by Mating Years; the Total Number Which Were Parents by Mating Years; The Total Death Loss by Mating Years; the Average Age in Mating Years of the Females in the Breeding Groups (Average of B); and the Average Age in Mating Years of the Females Which Were Parents (Average of P). Data for Treatment I.

Mating Year	Number of Females Born	Mating Year 1			2			3			4			5			6*			7*		
		B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D
0	20	20	14	1	13	10	0	9	8	0	8	6	0	6	2	1	3	0	0	2	0	0
1	9				7	7	0	5	5	0	2	1	0	2	1	0	0	0	0	0	0	0
2	9							6	5	1	4	4	0	2	2	0	0	0	0	0	0	0
3	9										6	5	0	5	5	0	3	3	0	3	3	0
4	11													5	4	0	5	3	0	5	5	0
5	8																8	5	0	6	5	1
6	4																			4	2	0
Total		20	14	1	20	17	0	20	18	1	20	16	0	20	14	1	19	11	0	20	15	1
Average of B		1			1.65			2.50			2.60			2.85			3.20			3.65		
Average of P		1			1.59			2.17			2.50			2.43			2.82			3.65		

* Females are one mating year older than indicated except for those born in mating year 6.

APPENDIX TABLE 5

Number Females Born in Each Mating Year; the Number From Each Mating Year Which Were in the Breeding Groups (B) of Each Succeeding Year; The Number Which Were Parents in Each Succeeding Mating Year (P); the Number of Death Losses (D) from the Preceeding Mating; the Total Number of Females in the Breeding Groups by Mating Years; the Total Number Which Were Parents by Mating Years; the Total Death Loss by Mating Years; the Average Age in Mating Years of the Females in the Breeding Groups (Average of B); and the Average Age in Mating Years of the Females Which Were Parents (Average of P). Data for Treatment II

Mating Year	Number of Females Born	Mating Year 1			2			3			4			5			6*			7*		
		B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D
0	20	20	16	0	15	7	0	11	9	1	5	4	2	5	2	0	1	0	3	1	0	0
1	6				5	3	0	5	2	0	4	3	1	3	2	0	2	0	1	2	0	0
2	6							4	3	0	3	2	0	3	2	0	2	0	1	2	0	0
3	8										8	4	2	6	5	0	5	2	1	3	1	2
4	4													3	2	0	3	3	0	3	3	0
5	7																3	1	0	3	3	0
6	3																			2	2	1
Total		20	16	0	20	10	0	20	14	1	20	13	5	20	13	0	16	6	6	16	9	3
Average of B			1			1.75			2.35			2.30			3.05			4.00			4.50	
Average of P			1			1.70			2.43			2.85			2.77			3.17			3.11	

* Females are one mating year older than indicated except for those born in mating year 6.

APPENDIX TABLE 6

Number Females Born in Each Mating Year; the Number From Each Mating Year Which Were in the Breeding Groups (B) of Each Succeeding Year; the Number Which Were Parents in Each Succeeding Mating Year (P); the Number of Death Losses (D) from the Preceeding Mating; the Total Number of Females in the Breeding Groups by Mating Years; the Total Number Which Were Parents by Mating Years; the Total Death Loss by Mating Years; the Average Age in Mating Years of the Females in the Breeding Groups (Average of B); and the Average Age in Mating Years of the Females Which Were Parents (Average of P). Data for Treatment III

Mating Year	Number of Females Born	Mating Year 1			2			3			4			5			6*			7*		
		B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D
0	20	20	12	0	10	8	0	6	4	0	3	3	0	2	1	0	0	0	1	0	0	0
1	10				10	9	0	9	7	1	5	3	0	5	4	0	2	0	1	2	0	0
2	5							5	4	0	4	3	1	3	1	0	1	0	2	1	0	0
3	9										8	6	2	4	3	0	3	2	1	3	2	0
4	9													6	5	0	5	2	0	4	2	0
5	8																6	4	1	6	3	0
6	4																			4	4	0
Total		20	12	0	20	17	0	20	15	1	20	15	3	20	14	0	17	8	6	20	11	0
Average of B		1			1.5			2.05			2.15			2.65			3.30			3.65		
Average of P		1			1.47			2.00			2.20			2.50			2.75			2.55		

* Females are one mating year older than indicated except for those born in mating year 6.

APPENDIX TABLE 7

Number Females Born in Each Mating Year; the Number From Each Mating Year Which Were in the Breeding Groups (B) of Each Succeeding Year; the Number Which Were Parents in Each Succeeding Mating Year (P); the Number of Death Losses (D) From the Preceeding Mating; the Total Number of Females in the Breeding Groups by Mating Years; the Total Number Which Were Parents by Mating Years; the Total Death Loss by Mating Years; the Average Age in Mating Years of the Females in the Breeding Groups (Average of B); and the Average Age in Mating Years of the Females Which Were Parents (Average of P). Data for Treatment IV.

Mating Year	Number of Females Born	Mating Year 1			2			3			4			5			6 *			7*		
		B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D
0	20	20	17	0	15	13	0	12	11	0	10	7	0	10	6	0	4	1	5	4	1	0
1	6				5	4	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0	1
2	11							7	5	0	6	5	0	5	5	0	4	0	1	4	0	0
3	6										3	1	0	2	2	1	2	1	0	2	0	0
4	6													2	2	0	2	0	0	2	0	0
5	6																1	1	0	1	1	0
6	0																			0	0	0
Total		20	17	0	20	17	0	20	16	0	20	14	0	20	15	1	14	3	6	13	2	1
Average of B		1			1.75			2.25			3.40			3.95			5.0			6.0		
Average of P		1			1.76			2.38			3.00			3.40			4.33			5.50		

* Females are one mating year older than indicated except for those born in mating year 6.

APPENDIX TABLE 8

Number Females Born in Each Mating Year; the Number From Each Mating Year Which Were in the Breeding Groups (B) of Each Succeeding Year; the Number Which Were Parents in Each Succeeding Mating Year (P); the Number of Death Losses (D) From the Preceeding Mating; the Total Number of Females in the Breeding Groups by Mating Years; the Total Number Which Were Parents by Mating Years; the Total Death Loss by Mating Years; the Average Age in Mating Years of the Females in the Breeding Groups (Average of B); and the Average Age in Mating Years of the Females Which Were Parents (Average of P). Data for Treatment V.

Mating Year	Number of Females Born	Mating Year 1			2			3			4			5			6*			7*		
		B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D	B	P	D
0	20	20	16	0	13	11	1	6	5	0	4	4	1	3	3	0	1	0	0	0	0	0
1	17				7	6	0	2	2	0	2	1	0	1	1	1	1	1	0	1	0	0
2	18							12	11	0	7	4	0	5	3	0	3	2	0	3	1	0
3	19										7	6	0	3	2	0	0	0	0	0	0	0
4	17													8	8	0	2	2	2	1	1	0
5	17																10	9	0	9	8	0
6	15																			6	6	0
Total		20	16	0	20	17	1	20	18	0	20	15	1	20	17	1	17	14	2	20	16	0
Average of B		1			1.65			1.70			2.35			2.40			3.18			3.10		
Average of P		1			1.65			1.67			2.20			2.35			3.86			2.50		

* Females are one mating year older than indicated except for those born in mating year 6.