RESPONSE TO DIVERGENT SELECTION FOR HINDLEG MUSCLE SYSTEM WEIGHT IN MICE

By

C. REID McLELLAN, JR.

Bachelor of Science
Louisiana State University
Baton Rouge, Louisiana
1967

Master of Science
Oklahoma State University
Stillwater, Oklahoma
1970

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
DOCTOR OF PHILOSOPHY
May, 1972

RESPONSE TO DIVERGENT SELECTION FOR HINDLEG MUSCLE SYSTEM WEIGHT IN MICE

Thesis Approved:

Richard R Frahm
Thesis Adviser

Joe W Whitman

Irvin T. Omtvedt

Lyle D. Brumeling

Laval M. Verhalen

D D Dunham
Dean of the Graduate College

ACKNOWLEDGMENTS

Sincere appreciation is extended to Dr. Richard R. Frahm, Associate Professor of Animal Science, for his suggestions, encouragement and counsel during the course of this study and in the preparation of this thesis.

The author also extends thanks to Dr. Irvin T. Omtvedt and Dr. Joe V. Whiteman, Professors of Animal Science; Dr. Lyle D. Broemeling, Associate Professor of Statistics; and Dr. Laval M. Verhalen, Associate Professor of Agronomy, for their suggestions and contributions to this study and for critiquing the manuscript of this thesis.

The author is deeply indebted to the mouse lab technicians, particularly Mike Brown, Jodena Netherton and Brenda Bright, for their tireless efforts in the collection of the data.

Grateful acknowledgment is also made of the contributions of the author's fellow graduate students.

Most special appreciation is extended to the author's wife, Lana, who typed the rough drafts of this thesis and without who's help, understanding and encouragement this thesis would not have been possible. Thanks are also due to two people who don't know how much help they were: the author's daughter Noelle, and son, Bucky.

...

TABLE OF CONTENTS

Chapter		Page
I.	INTRODUCTION	1
II.	REVIEW OF LITERATURE	3
	Divergent Selection	5
	Measurement of Selection Response	7
	Correlated Selection Responses	10
	Related Studies in Farm Animals	11
III.	MATERIALS AND METHODS	13
	Selection Procedure	15
	General Procedure and Husbandry	17
	Response to Selection	18
	Body Composition Analysis	22
	Variance-Covariance Analysis of Genetic Parameters in the Base Population	23
	Statistical Analysis	23
IV.	RESULTS AND DISCUSSION	27
	Estimation of Genetic Parameters in the Base Population	27
	Direct Response to Hindleg Muscle Weight Selection	32
	Correlated Selection Responses	39
	Weight at 84 Days	41
	Ratio of Hindleg Muscle Weight to 84-Day Weight	50
	Correlated Response in Reproduction Performance	50
	Twelve-Day Litter Weights	54
	Weight at 21 Days	58
	Average Daily Gain from 21 to 42 Days of Age and 42-Day Weight	61
	Asymmetry of Direct and Correlated Selection Responses	67
	Unsuitable Scale of Measurement	67
	Genetic Asymmetry	69
	Maternal Influence	69
	Inbreeding Depression	71
	Crosses Between Selection and Control Lines	73
	Body Composition Analysis	75

Chapter Page

V. SUMMARY 79

LITERATURE CITED 83

APPENDIX 87

LIST OF TABLES

Table		Page
I.	Number of Males Weighed and Slaughtered at 84-Days in Each Line Each Generation	20
II.	Total Number of Males and Females on Which Performance to 56-days was Measured in Each Line Each Generation	21
III.	Sources of Variation, Degrees of Freedom for Each Source and Expected Mean Squares and Products for Analysis of Variance and Covariance	28
IV.	Components of Variance by Source for Nine Traits Measured for Variance-Covariance Analysis of Control Line	29
V.	Estimates of Heritability, Genetic Correlation and Phenotypic Correlation from Variance-Covariance Analysis of Control Line	31
VI.	Mean Hindleg Muscle Weight by Line and Generation	33
VII.	Cumulative Selection Differentials for Hindleg Muscle Weight and Subsequent Response as Deviations from Control Line.	36
VIII.	Estimates of Genetic Correlation Between Hindleg Muscle Weight and Selected Performance Traits from Selection Responses and Variance-Covariance Analysis	43
IX.	Cumulative Consequential Selection Differentials (CSD) and Subsequent Responses in 84-Day Live Weight	45
X.	Spearman's Rank Correlation Coefficients Between Ranking Based on Muscle Weight and Ranking Based on 84-Day Weight	48
XI.	Comparison of Actual Selection Differentials (SD) for Hindleg Muscle Weight with Consequential Selection Differentials (CSD) for Hindleg Muscle Weight Obtained from Selection Based on 84-Day Weight	49
XII.	Hindleg Muscle Weight as Percent of 84-Day Weight by Line and Generation	52
XIII.	Total Number of Matings and Percent Litters Born in Each Line and Generation	53

Table		Page
XIV.	Average Number of Live Mice Per Litter at Three Days by Line and Generation	55
XV.	Mean Twelve-Day Litter Weights by Line and Generation	56
XVI.	Mean 21-Day Weights by Line and Generation	59
XVII.	Average Daily Gain from 21 to 42 Days of Age by Line and Generation	62
XVIII.	Mean 42-Day Weights by Line and Generation	65
XIX.	Phenotypic Variances and Coefficients of Variation (CV) of Hindleg Muscle Weight by Line and Generation	68
XX.	Average Inbreeding by Line and Generation	72
XXI.	Mid-parent and Progeny Means for Crosses Between Selection Line Males and Control Line Females	74
XXII.	Body Composition Analysis for Each Line After Five Generations of Selection	76
XXIII.	Generation Means by Line and Sex for Performance to 56 Days	88
XXIV.	Means, Standard Deviations (SD) and Coefficients of Variation (CV) for Nine Traits Studied in Variance-Covariance Analysis of Control Line	90
XXV.	Estimates of Heritability, Genetic Correlation and Phenotypic Correlation for Variance-Covariance Analysis of Males and Females Separately	91

LIST OF FIGURES

Figure		Page
1.	Establishment of Selection and Control Lines	14
2.	Selection Procedure Used in Both Selection Lines Each Generation	16
3.	Responses to Selection for Total Hindleg Muscle Weight Plotted on Generations	35
4.	Responses to Selection as Deviations from the Control Line Plotted on Cumulative Selection Differential (CSD)	37
5.	Total Divergence in Hindleg Muscle Weight Between Heavy and Light Muscle Lines Plotted on Cumulative Selection Differential (CSD) for Divergence	40
6.	Correlated Responses in 84-Day Weight Plotted on Generations	42
7.	Correlated Responses in 84-Day Weight as Deviations from the Control Line Plotted on Consequential Cumulative Selection Differential (CCSD)	46
8.	Correlated Responses in Ratio of Hindleg Muscle Weight to 84-Day Weight (Percent Muscle)	51
9.	Correlated Responses in 21-Day Weight Plotted on Generations	60
10.	Correlated Responses in Average Daily Gain from 21 to 42 Days of Age Plotted on Generations	63
11.	Correlated Responses in 42-Day Weight Plotted on Generations	66

CHAPTER I

INTRODUCTION

Selection studies involving the livestock species have traditionally attempted to increase total muscling through selections based on live weights and/or gain per unit of time. An important factor contributing to the emphasis placed on these studies has been the increased consumer demand for retail cuts with a higher proportion of muscle to bone and fat (Brackelsberg et al., 1971; Palsson, 1955). The object of a practical program of animal breeding is to improve quantitative characters of economic importance such as total carcass muscle. Consequently, basic information relative to the genetic control of muscle weight should increase the effectiveness of selection to improve carcass merit.

Falconer (1953) suggested that selection is an effective method of verifying existing hypotheses as to the genetic basis for a particular trait as well as disclosing new phenomena relative to the inheritance of the trait. The information obtained from selection experiments with large meat animals (cattle, swine and sheep) is limited primarily because of the extensive facilities required for adequate animal numbers and the relatively long time required to obtain conclusive information as to the inheritance of quantitative traits. Selection studies of carcass traits in the livestock species are further limited since direct measures of carcass merit are not easily obtained on the

prospective parents of the next generation.

To obtain sufficient observations in as short a time as possible, mice were chosen as the experimental unit for a selection study in which direct selection pressure was applied to the weight of a muscle system. The purpose of this experiment was to study the genetic basis of muscle weight by observing the response to divergent selection for hindleg muscle system weight in mice.

CHAPTER II

REVIEW OF LITERATURE

Laboratory animals as experimental units for studies of quantitative inheritance have several advantages over the larger farm animals. More precise estimates of genetic parameters are more easily obtained since a relatively large population of laboratory animals can be maintained in a comparatively small space at a much lower cost per unit. Furthermore, genetic information is obtained more rapidly with laboratory species due to their considerably shorter generation intervals. Many other advantages such as the ease of obtaining measurements and the ability to control the environment add to the desirability of these species for genetic studies (Chapman, 1951; Staats, 1966).

One important question concerns the validity of using the results from experiments with laboratory animals to describe genetic situations which actually exist in the same or similar traits in the livestock species. In this regard, an important factor to consider is the repeatability of the results since, as Falconer (1953) pointed out, the validity of general conclusions rests on repeatability and the contribution of laboratory experiments to practical problems of livestock improvement is through the establishment of general principles of quantitative inheritance. Robertson (1955) stated that comparisons of data from unrelated forms such as Drosophila, mice and poultry enabled the animal geneticist to broaden the theoretical basis of quantitative

inheritance and lead to more confident generalizations than were obtained from studies with large animals alone. Bell, Moore and Warren (1955) pointed out that many of the concepts in quantitative genetics were theoretical studies and not necessarily designed for any particular species of animals. The concepts should then be expected to be equally valid in laboratory and livestock species.

Another problem is that of deciding which laboratory organism should be used. Dobzhansky, in the discussion after the presentation of the paper by Bell et al. (1955) emphasized that Drosophila were used in genetic studies because they yielded to more penetrating genetic analyses than did other materials. But, are the conclusions obtained from an organism with four pair of chromosomes valid for animals with larger numbers of chromosomes? Tribolium castaneum, a flour beetle with ten pairs of chromosomes, has been used (Bell et al., 1955; Englert and Bell, 1969) to study the effects of selection for growth traits in a laboratory species with a larger number of chromosomes than Drosophila. Falconer (1953) pointed out that since the principle animals involved in the practical application of quantitative genetics were mammals, selection experiments with mice were easily justified.

Chapman (1951) in an early review of the effectiveness of selection in laboratory animals summarized that there were no obvious inconsistencies between the results from selection in laboratory animals and genetic theory. Therefore, it would appear that studies concerning the inheritance of muscle weight in mice would provide some indication as to the basic genetic controls involved and would, as a result, be of practical value in developing efficient selection programs designed to increase total muscle product in the livestock species.

Divergent Selection

Heritability (h^2) estimated from the resemblance between relatives is a parameter that can be used to approximate the expected average response to divergent selection. However, the use of these estimates for predicting progress under selection is dependent on the symmetry of the response in both directions. If the response is asymmetrical, predicted response in one direction will be overestimated whereas it will be underestimated in the opposite direction when based on this average heritability. In most divergent selection studies in mice in which some measure of size was used as the selection criteria, asymmetrical responses were observed in which selection in the downward direction was more effective (Falconer, 1953 and 1960a).

In experiments designed to study a trait which had not been the subject of previous selection, evaluation of the response to divergent selection for that trait would give a more complete picture of the h^2 in the base population than would response to selection in only one direction. Furthermore, comparisons of correlated responses between lines selected in opposite directions should indicate the traits most influenced by the selection employed (Fowler, 1958).

The literature does not contain reports of experiments in which the selection criteria was muscle weight per se. However, much work has been done on selection for high and low body weight in mice at different ages, and muscle composition in the selection lines was evaluated in several of these studies. Luff and Goldspink (1971) reported a significant ($P < .05$) positive phenotypic correlation between weights of various muscles and body weight within unselected strains of mice. Robinson and Bradford (1969) found that selection for rapid

postweaning growth rate in mice resulted in a higher total amount of DNA, RNA and protein in muscle tissue. Timon, Eisen and Leatherwood (1970) proposed that effective selection for increased weight gain inevitably resulted in a genetically controlled change in the deposition rate of protein. Robinson and Lambourne (1970) and Masters (1963) pointed out that muscle mass formed the major protein store of the body. Natural variation in body size is partly heritable (Fowler, 1958) and the genetic variation of body weight in mice has been observed to be primarily additive (Lang and Legates, 1969). Selection for muscle weight, therefore, should be effective since there is a definite positive relationship between body size and muscle size.

Asymmetry of response to divergent selection has a direct influence on the interpretation of the genetic control of the trait being selected (Falconer, 1953 and 1960a). Englert and Bell (1969) reported asymmetry of response to selection for growth complexes in Tribolium, and they proposed that this asymmetry gave evidence of different genetic mechanisms being activated in response to different directions of selection. Robertson (1955) observed asymmetry of response to selection for size in Drosophila. Frahm and Kojima (1966) reported a similar asymmetric response to divergent selection for body weight in Drosophila. Several examples of asymmetrical responses to selection for size in mice have been reported (MacArthur, 1944; Falconer, 1953 and 1955) and several researchers have observed asymmetry of response to selection in swine (Hetzer and Harvey, 1967; Krider et al., 1946) and poultry (Festing and Nordskog, 1967).

Falconer (1953, 1955 and 1960a) proposed the following as possible causes of asymmetrical response in mice:

(1) Genetic asymmetry

  (a) Directional dominance

  (b) Directional gene frequencies

(2) Unsuitable scale of measurement

(3) Maternal influences

(4) Inbreeding depression.

Each of these possible causes will be examined in more detail in the discussion of the asymmetry observed in the present study.

In addition to asymmetry found in direct response to selection, asymmetry has also been observed in correlated responses in Tribolium (Englert and Bell, 1969), Drosophila (Robertson, 1955) and mice (Falconer, 1953 and 1960b; Fowler, 1958). Englert and Bell (1969) suggested that this asymmetry of correlated responses may be indicative of the activation of different genetic mechanisms in response to selection based on different criteria.

Measurement of Selection Response

The measurement of response in selection experiments provides information as to the genetic basis of the trait being selected. Response to selection is measured as the difference between the mean phenotypic value of the offspring of the selected parents and the mean phenotypic value of the parental generation before selection (Falconer, 1960a). Mather (1955) concluded that the response of a population to selection depended on three sets of factors:

(1) Types and strengths of selective forces

(2) Actions and interactions of genes

(3) Amount, distribution and system of genetic variability in the population.

According to Falconer (1955) the practical method of presenting response to selection has been to plot the mean value of the selected character against the number of selected generations. Although this shows progress in a practical way, Falconer pointed out that this method of presenting response did not reveal much about the genetic situation because the intensity of selection was not considered. A more informative method would be to plot the response against cumulative selection differential. Falconer further suggested that this method of plotting the response would eliminate the need to make scale transformations. The slope of the regression line for the points thus plotted would be an estimate of realized heritability which is influenced very little by scale transformations.

Robertson (1955) indicated that a logarithmic or multiplicative scale transformation should be most satisfactory since it eliminates the differences in variance between sexes. Frahm and Kojima (1966) observed a curvilinear response to divergent selection for size in Drosophila and fit an exponential curve to their data. These workers suggested that a curve such as theirs had a biological meaning since it reflected a gradual decrease in selection response which would be expected if the initial genetic variability in a closed population was high and tended to be depleted as selection proceeded. The transformation to a logarithmic scale does not greatly affect the analysis of size differences according to Robertson (1955) who concluded that this lack of effect provided an empirical justification for the use of

the ordinary linear scale in the comparison of means. James (1965) also demonstrated that the logarithmic transformations were more impressive in Drosophila experiments than in experiments with mice and that the transformations were more important as the response to selection approached the biological limits.

Another way to present response to selection is as deviations from an unselected control population being maintained in a manner similar to the selected population. Dickerson (1955) stated that a genetically constant control population was necessary in order to make precise estimates of the genetic trends. The control population would, ideally, allow the separation of the genetic and environmental components of the response. Falconer (1960a) suggested that a more accurate measurement of the response could be obtained if the control was not an unselected population, but was a population selected in the opposite direction. His reasoning was that the variation between generations would be reduced to the extent that environmental changes affected both lines to the same degree. If, however, the response is asymmetrical, an unselected control population should be maintained in order to ascertain the response in each direction.

For response to selection to indicate the possible genetic mechanisms involved, measures of the intensity of selection must be obtained. Although selection differential has been defined as the difference between the mean of the selected animals and the mean of the population to which they belong, Falconer (1953 and 1960a) emphasized that the "effective selection differential" must be the deviation of the selection parents weighted by the number of offspring of these selected parents measured in the next generation.

Cumulative selection differential is the sum of the selection differentials obtained each generation (Falconer, 1953). The use of cumulative selection differential rather than generation number as the ordinate on which response is plotted gives a more complete picture of the genetic properties of the trait under selection.

Correlated Selection Responses

Selection for a particular trait changes the frequencies of the genes affecting that trait. If any of these genes have pleiotropic effects (i.e., they affect other traits in addition to the one being selected), corresponding changes in these traits will be observed. These corresponding changes are referred to as correlated responses.

One of the more frequently studied correlated responses to body weight selection in mice has been body composition. Timon, Eisen and Leatherwood (1970) emphasized that effective selection for increased weight gain would inevitably result in a genetically controlled change in the deposition rate for protein, ether extract, water and ash. Selection studies in mice based on weight gains or live weights at a given age have generally indicated that significant increases or decreases in the primary trait were accompanied by corresponding increases or decreases in the total weights of the compositional components (Biodini, Sutherland and Haverland, 1968; Fowler, 1958; Lang and Legates, 1969; Robinson and Bradford, 1969). Bailey, Kitts and Wood (1960) reported results on the chemical composition of mice during growth which demonstrated that, on the average, the composition of the dry, fat-free carcass remained relatively constant with increasing body weight. Hull (1960) found significant differences in proportion

of fat between lines of mice selected at different ages. Lassiter, Cullison and Carmon (1960) showed significant differences in percent ether extract among groups of mice with different average daily gains. Most of these compositional studies have found no significant changes in the composition of the fat-free carcass. However, the general trend was for proportion of fat to increase as body weight and/or rate of gain increased (Timon et al., 1970).

Other correlated responses reported in mice include reproductive performances. Fertility as a function of number of matings, number of ovulations and fertilization rate decreased in mice selected for small body size at 42 days-of-age (Elliott, Legates and Ulberg, 1968). Moore, Eisen and Ulberg (1970) examined the correlated response in prenatal and postnatal maternal influences on growth and found that maternal ability remained relatively constant in a line selected for increased 42-day weight and decreased rapidly in a line selected for decreased 42-day weight. Correlated responses in such traits as tail length (Falconer, 1953), 12-day litter weight, litter size and live weights at 21, 42 and 56 days of age (Falconer, 1953; MacArthur, 1949) have also been studied.

Related Studies in Farm Animals

Joubert (1956) reported breed differences for muscle size in chickens which almost paralleled differences in body size. Festing and Nordskog (1967) reported asymmetry of direct response to selection for body weight in poultry and of correlated response in egg production.

Blunn and Baker (1947) found a significant ($P < .05$) positive phenotypic correlation of 0.18 between gain from 56 days of age to

slaughter and the circumference of the ham in swine. These workers also reported a significant ($P < .01$) negative correlation of -.36 between gain and length of the hindleg. The genetic correlations, although not significant, were in the same direction. Hetzer and Harvey (1967) observed asymmetry of response to selection for high and low fatness in swine in favor of high fatness, and Krider et al. (1946) reported asymmetrical response to selection for rapid and slow growth rate in swine in favor of slow growth rate.

Cundiff et al. (1969) presented the results of a detailed analysis of beef cattle carcass components which demonstrated that growth of retail product was highly (0.44 to 0.68) heritable while variation in proportion of retail product was moderately (0.31 to 0.42) heritable. Furthermore, selection for growth of the round would result in increased weight of the round and other cuts, but proportion would be changed very little. According to these workers, selection for retail product in the round (adjusted for weight of carcass) would be as effective in increasing the proportion of retail product in the carcass as would selection based on complete carcass cut-out.

Brackelsberg et al. (1971) also reported that selection for increased porportions of round and loin in cattle would be effective since the heritability of percent round and loin was very high (0.81). These workers also reported a heritability estimate of 0.70 for "round value" (weight X price per pound) and an estimate of -.75 for r_g between proportion of round and loin and carcass fatness. Butterfield (1965) and Orme et al. (1960) reported high phenotypic correlations (0.95 to 0.98) between the weight of a single muscle or group of muscles and the total muscle content of cattle carcasses.

CHAPTER III

MATERIALS AND METHODS

Three inbred lines, AKR/J, SLJ/J and BALB/C, and one non-inbred line, ICR, of albino mice were intermated to produce a four-way cross population (Figure 1). This population was randomly intermated for one generation to form the base population from which two selection lines and two random-mating control lines were initiated. The control lines of 20 litters each were being maintained in the laboratory for other selection experiments as well as for the present one. The genetic control used in this study was the average performance of the two control lines.

Selection was based on the weight of the muscle system dissected from the hindlegs of 84-day old males. The selection lines, designated heavy-muscle line (HML) and light muscle line (LML), were selected on the basis of heavy and light hindleg muscle weight, respectively. To obtain measurement of the muscle system weight, both hindlegs were skinned and dissection of the hindleg was initiated by an incision along the dorsal midline. The removal of each leg was completed by scraping the pelvic bone and separating the femur from the ballsocket joint of the pelvic girdle. The subcutaneous fat generally adhered to the hide during skinning of the leg. Any fat remaining on the leg was scraped off with a scapel. The foot was removed at the tibio-tarsal joint, and the intact hindleg was weighed. The muscle was then

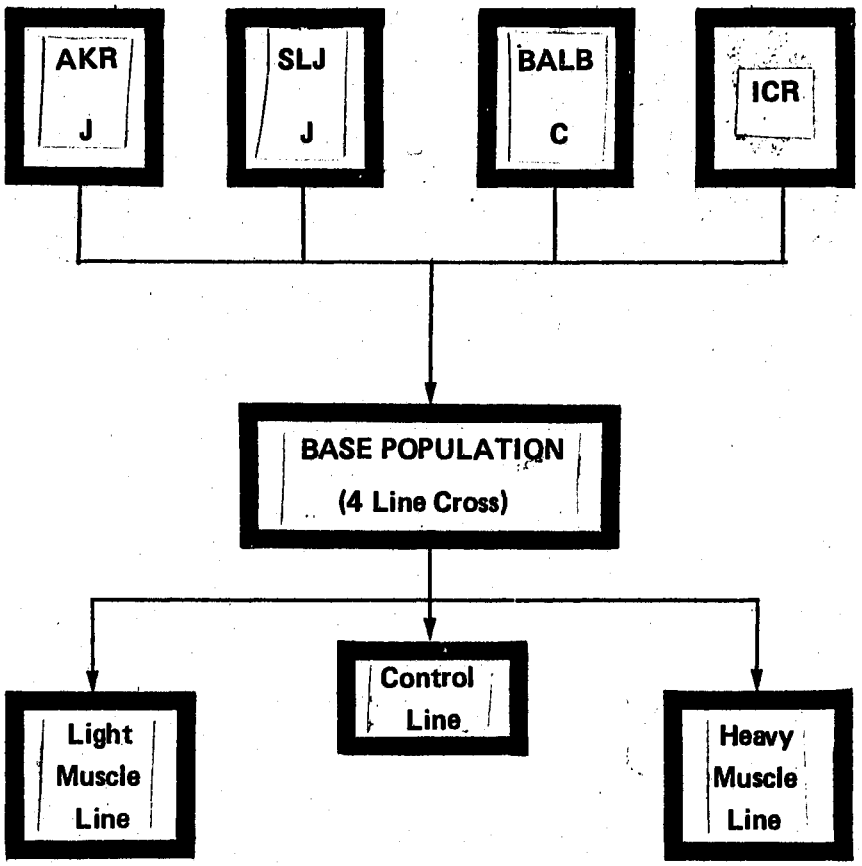

Figure 1. Establishment of Selection and Control Lines

separated from the bone and weighed. Differences between intact hindleg weight and the sum of the weights obtained for the muscle and bone portions were due primarily to moisture evaporation and any muscle lost during dissection. These errors were of the same general magnitude in each line and ranged from one to five percent during the experiment. The combined weight of the muscle systems from both hindlegs was used as the selection criteria.

Selection Procedure

In both selection lines the selection procedure for each generation was the same except for the direction of selection. The selection procedure followed each generation is illustrated in Figure 2.

In each line 24 males (which had been previously mated to two females each) were weighed at 84 days of age and immediately sacrificed in a carbon dioxide chamber. Each mouse was placed in a polyethelene bag, stored at $1^{o}C$ overnight and dissected the following day (when possible). When circumstances prohibited dissection on the day following sacrifice, the mice were frozen at $-18^{o}C$ until the day before dissection at which time they were placed in a $1^{o}C$ cooler and allowed to thaw overnight. The hindlegs of each male were dissected, and the muscle was separated from the bone and weighed as previously described. The half-sib families from these sires were ranked from one to 24 based on the muscle system weight of the sire and the respective selection criteria in each line. From each of the six highest ranking half-sib families, four males (two from each litter when possible) were selected at random to obtain the 24 males for the next generation. All of the females from the six highest ranking families were saved, and additional

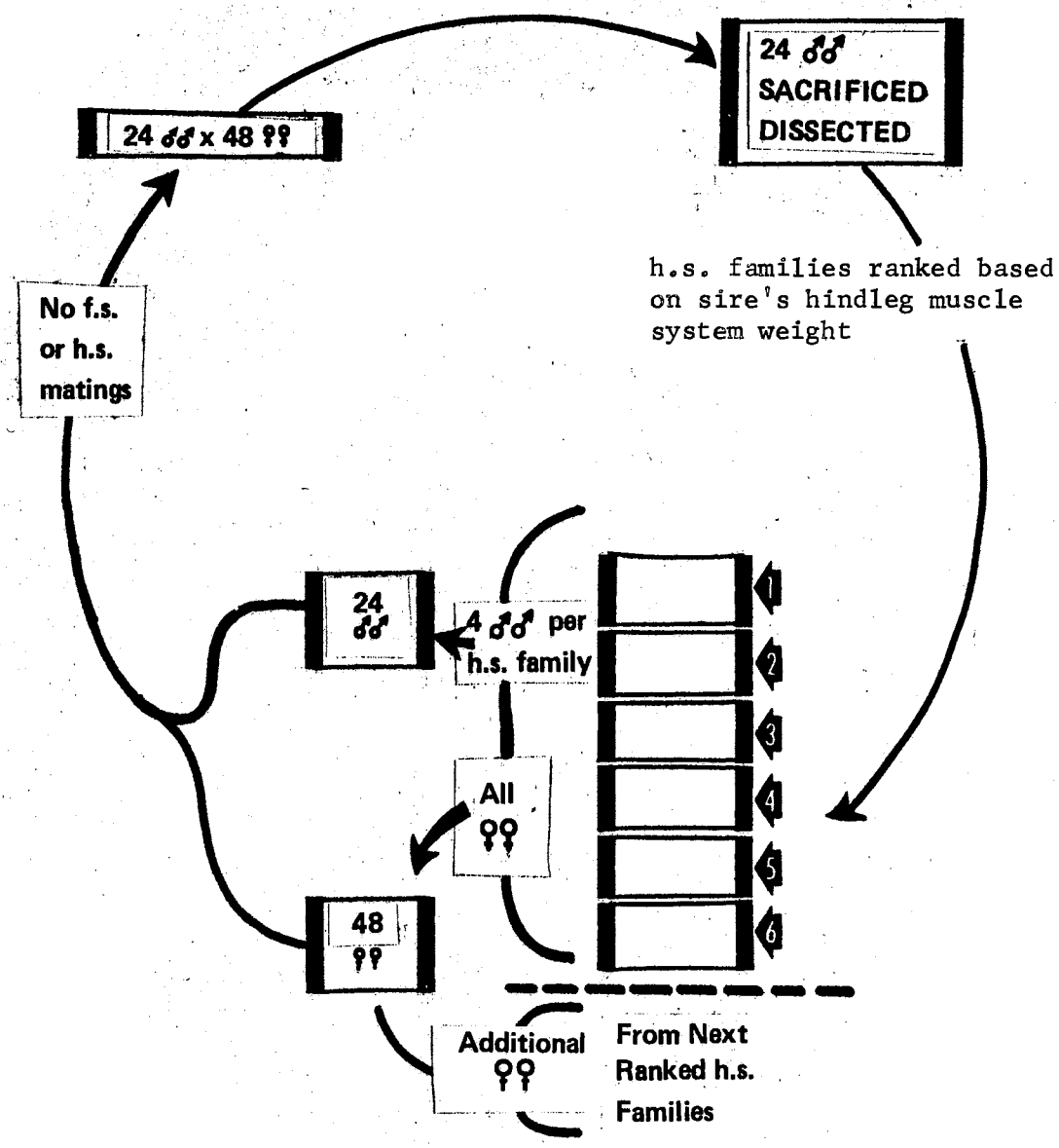

Figure 2. Selection Procedure Used in Both Selection Lines Each Generation

females were selected (as necessary) from the next ranking half-sib families to obtain the 48 females required for the next generation. In general, these additional females were obtained from the next two half-sib families. Each of the 24 males was mated at random to two females with matings between half-sib or closer relatives prohibited.

Live performance measures to 56 days in the selection lines were obtained on all progeny from the half-sib families contributing potential parents of the next generation.

From the random sample of 20 males used to perpetuate each control line, 12 were randomly selected from each line to obtain the 24 males for muscle weight determinations each generation.

General Procedure and Husbandry

The same general procedure was followed in all lines each generation. Individuals selected as parents of the next generation were placed together in mating cages at an average age of approximately 63 days. Matings for each generation were made on the same date for all lines. Males were removed from the mating cages 14 days later and litters were born when the females averaged 84 days of age. Litters were generally born within 19 to 23 days after males and females were placed together in mating cages, and all litters used in the analyses of the data were born within 32 days.

At three days of age litters were standardized to eight mice by removing excess mice from litters with more than eight and cross-fostering mice into litters with less than eight. Fostering was done only between litters of the same line born in the same 24-hour period. Cross-fostered mice were identified by clipping a portion of the tail.

Litters were weighed at 12 days of age and individual offspring were identified by toe-notching and classified as to sex.

At 21 days of age offspring were weaned and individually weighed. Males and females were separated and placed in cages for post-weaning growth with no more than four mice per cage. Normally, mice of the same sex and litter were placed in the same cage. When necessary, individuals from different litters in the same line born within a 24 -hour period were placed together so that each individual was ordinarily raised with three contemporaries. Each mouse was weighed at 42 and again at 56 days of age. Matings were made during the ninth week after littering began at which time nearly all of the mice were at least 56 days old.

The mice were kept in 4.53 x 2.95 x 1.97cm polypropolene cages with metal tops which provided a place for feed and a water bottle. Sterilized sugarcane bagasse was shredded and used as bedding. Cages were changed weekly. Temperature in the laboratory was controlled between 20 and 22°C and relative humidity was maintained at 50% or higher. Lighting was automatically controlled on a 12-hour on-off cycle. Throughout the life cycle all mice were fed ad lib. on Purina Lab Chow. The selection lines were maintained during every phase of the cycle on the same rack in the stock room. The lines were rotated to the opposite side of the rack each generation. The two control lines were placed in two of eight random locations in the laboratory with the restriction that they were not placed adjacent to each other.

Response to Selection

Selection line performance is presented as generation means and as

deviations from the control line mean. Eighty-four day weight means and hindleg muscle weight means in each line were based on data from 21 to 24 males except in generations zero and six as shown in Table I. In the selection lines in generation six, all extra males from selected half-sib families were measured. The 118 males measured in the control line at generation six were used in a half-sib analysis of variance and covariance to obtain estimates of the genetic parameters in the control line.

Selection differentials were calculated by subtracting the mean of all males measured in one generation from the mean of the sires contributing offspring to the next generation. Weighted selection differentials were calculated based on the proportion of offspring measured in the next generation. In all generations each selected sire contributed at least three and most contributed four individuals to the next generation, so weighted selection differentials were essentially the same as the unweighted selection differentials. As a result, unweighted values were used in this study.

Weights of litters were obtained at 12 days of age and weights were taken at 21, 42 and 56 days on all individuals in litters contributing to the generation mean for each line. The total number of individuals on which these traits were measured in each line each generation is presented in Table II. Appendix Table XXIII presents the generation means by line and sex for the live weights and average daily gain from 21 to 42 days of age. Visual examination of the data in this Table indicated that the trends in all lines were similar for the two sexes. Since the trends were similar for the two sexes, the simple average of the sex means was used for analysis of the

TABLE I

NUMBER OF MALES WEIGHED AND SLAUGHTERED AT 84-DAYS IN EACH LINE EACH GENERATION

Generation	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		50	
1	24	24	23
2	21	24	22
3	22	24	22
4	24	24	22
5	24	24	24
6	35	118	33

TABLE II

TOTAL NUMBER OF MALES AND FEMALES ON WHICH PERFORMANCE TO 56 DAYS WAS MEASURED IN EACH LINE EACH GENERATION

Generation	Heavy-Muscle Line		Control Line		Light-Muscle Line	
	Males	Females	Males	Females	Males	Females
0			150	150		
1	65	55	169	141	64	56
2	50	52	146	124	59	44
3	77	60	157	153	57	69
4	50	53	146	146	53	52
5	31	48	152	160	70	52
6	35	35	294	311	33	26

correlated responses in the live performance traits.

Body Composition Analysis

Body composition analyses were conducted on all males dissected in generation five to see what changes in moisture, protein, ether extract and ash had occurred as a result of selection for hindleg muscle weight. Duplicate determinations of moisture, protein and ether extract were taken on samples of the whole ground mouse. Ash was determined by difference.

Mice slaughtered in generation 5 were dissected in the prescribed manner with care taken to identify the legs removed so that they could be placed with the corresponding mouse for storage. All parts of each mouse were placed together in a polyethelene bag and frozen at -18°C until time for grinding.

To prepare for sampling, the mouse to be ground was placed in liquid nitrogen for a minimum of two minutes. Each mouse was then ground coarsely with a mortar and pestle which had been pre-cooled with solid carbon dioxide (dry ice). Half of this coarsely ground mouse was then finely ground for approximately 15 seconds in a high speed cryogenic mill which had also been pre-cooled with dry ice. The resulting powder was scraped into a sample bottle, and the second portion of the mouse was ground and placed in the same sample bottle. Each sample was identified and stored at -18°C until time for chemical analysis. For protein analysis the samples were removed from the freezer and stirred with a spatula until a pasty consistency was obtained. Duplicate four-gram subsamples were weighed out and nitrogen determinations were made using Kjeldahl procedures. Samples were refrozen until all

nitrogen determinations had been completed. The samples were again taken from the freezer and stirred, and duplicate four-gram subsamples were weighed out for moisture determination. Ether extract was determined from these same subsamples after drying. The total of percent protein, percent moisture and percent ether extract was subtracted from 100 percent to arrive at percent ash.

Variance-Covariance Analysis of Genetic Parameters in the Base Population

A hierarchal design involving half-sib and full-sib families from generation five control line mice was used to estimate the genetic parameters in the base population. Initially, 48 males were mated to two females each. Of these, 25 produced two litters with at least two male offspring in each litter. Six sires produced one litter with two or more male progeny with the other litter having only one male progeny. Consequently, a total of 118 male progeny from 31 sires were weighed and slaughtered at 84 days.

Statistical Analysis

From the variance-covariance analysis of the base population, heritabilities (h^2) and genetic correlations (r_g) were calculated using the half-sib intrclass correlation. Heritabilities were estimated as four times the half-sib intraclass correlation coefficient. Estimation of r_g from variance-covariance analysis was shown by Hazel, Baker and Reinmiller (1943) as:

$$r_g = \frac{COV\ (i,j)}{\sqrt{V_g(i)\ V_g(j)}}$$

where:

r_g = estimate of genetic correlation between traits "i" and "j"

COV (i,j) = estimate of genetic covariance between traits "i" and "j"

V_g(i or j) = estimate of genetic variance of trait "i" or "j".

In the analysis of covariance for traits "i" and "j" the intra-class correlation coefficient (sire component) estimates 1/4[COV(i,j)]. Estimates of the genetic variance for each trait were obtained from the sire component of the analysis of variance for that trait.

The h^2 of muscle weight was also estimated from the regression of response on cumulative selection differential in the selection lines. Genetic correlations were estimated from the selection lines using the correlated response technique as outlined by Clayton et al. (1956) and demonstrated by Falconer (1954). If trait "i" is the trait being selected and correlated response is measured in trait "j", then:

$$r_g = \frac{\overline{CR}_{(j)}\, h_{(i)} S_p(i)}{\overline{R}_{(i)}\, h_{(j)} S_p(j)}$$

where:

$\overline{CR}$ (j) = average correlated response per generation in trait "j"

$\overline{R}$ (i) = average direct response per generation in trait "i"

$h_{(i)}$ = square root of the heritability for trait "i"

$h_{(j)}$ = square root of the heritability for trait "j"

$S_p(i)$ = phenotypic standard deviation of trait "i"

$S_p(j)$ = phenotypic standard deviation of trait "j".

Standard errors for the genetic correlations were computed using the method of Robertson (1959) and Falconer (1960a) for analysis of variance and covariance. The sampling variance of the estimate of r_g is estimated by:

$$V(r_g) = \frac{[1 - r_g^2]^2}{\sqrt{2}} \sqrt{\frac{SE(h_i^2)\ SE(h_j^2)}{(h_i^2)\ \ (h_j^2)}}$$

where:

$SE(h^2)$ = the standard error of the respective heritability.

The standard error of the estimate of r_g is the square root of the sampling variance.

Spearman's rank correlation coefficient (Conover, 1971) was calculated to compare the ranking of the selection line males dissected each generation when the ranking was based on muscle weight versus the ranking based on 84-day weight. Spearman's rank correlation coefficient (r_s) was calculated by:

$$r_s = 1 - \frac{6T}{n(n^2 - 1)}$$

where:

n = number of males ranked

$T = \sum_i [R_i(84) - R_i(M)]^2$

$R_i(84)$ = rank of individual "i" based on 84-day weight

$R_i(M)$ = rank of individual "i" based on hindleg muscle weight.

Differences between mean performances of the lines was determined using the "t" test statistic. Tests for equality of variances among the selection lines were made using the "F" test statistic. Significance levels were obtained from appropriate tables in Steel and Torrie (1960).

CHAPTER IV

RESULTS AND DISCUSSION

Estimation of Genetic Parameters in the Base Population

A sib-analysis was conducted on the progeny of 31 generation-five control-line males for the purpose of estimating genetic variances and covariances of various performance traits. For the live performance traits (21-day weight, 42-day weight, average daily gain from 21 to 42 days of age and 56-day weight) a hierarchal analysis of variance and covariance was conducted separately on 233 male progeny and 222 female progeny and then pooled over sexes. A second analysis was conducted on the 118 males slaughtered to study the genetic parameters of 84-day weight and the "carcass" traits (hindleg weight, bone weight, muscle weight and percent muscle). The "carcass" weights were the sums of the respective parts of the two hindlegs. Percent muscle was the ratio of hindleg muscle weight to 84-day weight.

Means, standard deviations and coefficients of variation for the nine traits studied are presented in Appendix Table XXIV. Table III gives degrees of freedom, expected mean squares and expected mean products for each source of variation in the analysis. The variance components by source for each trait studied are presented in Table IV.

From the values in Table IV it can be observed that for all except bone weight, the dam component of variance was larger than the sire component. The dam component is an estimate of $\frac{1}{4}V_A + \frac{1}{4}V_D + V_{EC}$ where V_A is

TABLE III

SOURCES OF VARIATION, DEGREES OF FREEDOM FOR EACH SOURCE AND EXPECTED MEAN SQUARES AND PRODUCTS FOR ANALYSIS OF VARIANCE AND COVARIANCE[1]

Source	df	Expected Mean Squares	Expected Mean Products[3]
POOLED[1]			
Total	453		
Sires	60	$\sigma_w^2 + 4.087\ \sigma_f^2 + 7.492\ \sigma_s^2$	$(\sigma_1\sigma_2)_w + 4.087\ (\sigma_1\sigma_2)_f + 7.492\ (\sigma_1\sigma_2)_s$
Dams/Sires	62	$\sigma_w^2 + 3.523\ \sigma_f^2$	$(\sigma_1\sigma_2)_w + 3.523\ (\sigma_1\sigma_2)_f$
Progeny/ Dams/Sires	331	σ_w^2	$(\sigma_1\sigma_2)_w$
118 MALES[2]			
Total	117		
Sires	30	$\sigma_w^2 + 1.935\ \sigma_f^2 + 3.805\ \sigma_s^2$	$(\sigma_1\sigma_2)_w + 1.935\ (\sigma_1\sigma_2)_f + 3.805\ (\sigma_1\sigma_2)_s$
Dams/Sires	31	$\sigma_w^2 + 1.871\ \sigma_f^2$	$(\sigma_1\sigma_2)_w + 1.871\ (\sigma_1\sigma_2)_f$
Progeny/ Dams/Sires	56	σ_w^2	$(\sigma_1\sigma_2)_w$

[1] Values for pooled within sex analysis of 232 males and 222 females.
[2] Values for 118 males slaughtered.
[3] $\sigma_1\sigma_2$ = Covariance between trait 1 and trait 2.

TABLE IV

COMPONENTS OF VARIANCE BY SOURCE FOR NINE TRAITS MEASURED FOR VARIANCE-COVARIANCE ANALYSIS[1] OF CONTROL LINE

Source	21-day weight	42-day weight	ADG 21-42	56-day weight	84-day weight	Hindleg weight	Bone weight	Muscle weight	Percent muscle
Total	2.482	8.592	0.020	4.890	5.785	0.071	0.002	0.060	0.00035
Sires	-0.007	0.624	0.002	0.507	1.033	0.007	0.0003	0.007	-0.000005
Dams in Sires	1.883	5.189	0.012	1.414	1.185	0.024	0.00004	0.020	0.000014
Progeny in Dams in Sires	0.600	2.779	0.006	2.970	3.567	0.040	0.002	0.033	0.000021

[1]Values for traits through 56-day weight calculated from the pooled analysis of 233 males and 222 females. Values for 84-day weight and carcass traits calculated from 118 males slaughtered.

the additive genetic variance, V_D is the variance due to dominance deviations and V_{EC} is the variance due to common environment (primarily maternal effects). The larger dam component, therefore, would suggest a substantial amount of non-additive genetic variance either as dominance, variation due to common environment or both. Thus, h^2 and r_g estimates were obtained from the sire components of variance and covariance.

Estimates of h^2 for the live performance traits were based on the pooled-within-sex analysis of variance and covariance whereas the estimates of h^2 for the "carcass" traits were based on the analysis of the 118 males slaughtered. The estimates of h^2 thus obtained and their standard errors are given on the diagonal in Table V. Reported estimates of h^2 range from 0.39 to 0.44 for 28-day weight (Gall et al., 1967; Hull 1960); and from 0.35 to 0.59 for 42-day weight (Gall et al., 1967; Hull 1960; Falconer, 1953 and 1960a). Gall, et al. (1967) reported a h^2 estimate of 0.52 for carcass weight. The low h^2 estimate of 0.10 for 56-day weight is lower than the 0.25 to 0.45 values generally reported. The low estimate obtained in this study was the result of a negative sire variance component in the females.

From this analysis it was apparent that genetic variation in the base population for muscle weight did exist. The h^2 estimate of 0.44 agrees with estimates of similar traits in the livestock species. Cundiff et al. (1969) reported estimates of h^2 for growth of retail product in cattle ranging from 0.44 to 0.68. Brackelsberg et al. (1971) reported a h^2 estimate of 0.70 for weight of round.

Table V gives the estimates of genetic correlation among the nine traits studied to the right of the diagonal and estimates of phenotypic correlation to the left of the diagonal. Estimates of r_g between

TABLE V

ESTIMATES OF HERITABILITY, GENETIC CORRELATION AND PHENOTYPIC CORRELATION FROM VARIANCE-COVARIANCE ANALYSIS OF CONTROL LINE[1]

	42-day weight[2]	ADG 21-42[2]	56-day weight[2]	84-day weight	Hindleg weight	Bone weight	Muscle weight
42-day weight	0.21 ± .09	1.19 ± .31	0.71 ± .20	1.01 ± .38	0.35 ± .28	1.02 ± .40	-.02 ± .42
ADG 21-42	0.82**	0.53 ± .12	1.29 ± .42	0.96 ± .08	0.13 ± .22	0.28 ± .19	-.14 ± .21
56-day weight	0.62**	0.38**	0.10 ± .08	0.92 ± .06	1.14 ± .62	0.96 ± .04	1.11 ± .57
84-day weight	0.55**	0.38**	0.87**	0.71 ± .24	1.25 ± .40	0.71 ± .12	1.32 ± .37
Hindleg weight	0.39**	0.16	0.76**	0.85**	0.38 ± .18	1.29 ± .42	1.00 ± .44
Bone weight	0.21*	-0.07	0.51**	0.54**	0.68**	0.61 ± .23	1.28 ± .39
Muscle weight	0.36**	0.15	0.62**	0.84**	0.98**	0.60**	0.44 ± .18

[1] Estimates of heritability are on the diagonal, estimates of genetic correlation are on the upper off diagonal and phenotypic correlations are on lower off diagonals. SE are given for h^2 and r_g.

[2] Estimates for traits through 56-day weight were obtained from the pooled within sex analysis of 233 males and 222 females. All others were obtained from the analyses of the 118 males slaughtered.

* ($P < .05$). ** ($P < .01$).

21-day weight or percent muscle and the other traits were not obtained because of negative sire components of variance for these two traits. From the r_g values in Table V it can be observed that "mature" weight, measured as either 56-day or 84-day weight, has a relatively high genetic relationship with muscle weight as would be expected. Furthermore, there was a high r_g between 84-day weight and the weights of the dissected parts of the hindleg which indicated that response to selection for muscle weight would probably be closely paralleled by correlated response in 84-day weight. This was borne out in the present selection study as will be shown later. Luff and Goldspink (1971) reported significant positive phenotypic correlations between muscle weight and body weight in four different strains of mice; but they did not report the magnitude of the coefficients.

Phenotypic correlations were, in general, significant ($P < .05$), positive and lower than the corresponding genetic correlations. As age increased, r_p between live weight and hindleg muscle weight tended to increase and all measures of r_p between live weights and "carcass" weights were significantly positive ($P < .05$). Values of r_p between average daily gain and the "carcass" weights were non-significant. This corresponded to the lower values of r_g between these traits.

The values of h^2, r_g and r_p obtained from the analyses of the sexes separately for 21, 42 and 56-day weight and ADG are presented in Appendix Table XXV.

Direct Response to Hindleg Muscle Weight Selection

Generation means for hindleg muscle weights in the selection and control lines are presented in Table VI and the means are plotted on

TABLE VI

MEAN HINDLEG MUSCLE WEIGHT
BY LINE AND GENERATION

Generation	Hindleg Muscle Weight (g)		
	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		2.49 ± 0.06	
1	2.64 ± 0.07^{a}	2.57 ± 0.06^{a}	2.38 ± 0.07^{b}
2	2.67 ± 0.06^{a}	2.55 ± 0.07^{a}	2.36 ± 0.06^{b}
3	2.59 ± 0.10^{a}	2.54 ± 0.06^{a}	2.27 ± 0.05^{b}
4	2.65 ± 0.06^{a}	2.47 ± 0.04^{b}	2.20 ± 0.06^{c}
5	2.82 ± 0.08^{a}	2.60 ± 0.04^{b}	2.15 ± 0.06^{c}
6	2.82 ± 0.07^{a}	2.66 ± 0.03^{b}	2.11 ± 0.06^{c}

[a] Means with different superscripts in same generation significantly different ($P < .01$)

generations in Figure 3. Each generation mean represents the average of from 21 to 24 males in each line (see Table I) except for generation zero which was based on 50 males and the means for generation six which were based on 35, 118 and 33 males in HML, control and LML, respectively.

From the base population mean of 2.49 g there was an immediate and significant ($P < .01$) divergence of the two selection lines. The lines continued to diverge throughout the duration of the study with the divergence in each generation highly significant ($P < .01$). In general the control line remained fairly stable although the mean did show a tendency to increase in generations five and six. Furthermore, it is apparent from Figure 3 that the control line means are closer to the means of HML indicating that selection was possibly more effective for light muscle weight than for heavy muscle weight. The values after six generations of selection were 2.82, 2.66 and 2.11 g for HML, control and LML, respectively. The upward response of 0.16 g in HML represented 6.4% of the generation zero mean whereas the downward response of 0.55 g in LML represented 22.0% of the initial mean.

Table VII gives for each selection line selection differentials (SD) and subsequent response expressed as deviations from the control line obtained in this study. When response to selection is calculated as deviations from control line mean and the deviations are plotted on cumulative selection differential, a more complete picture of the genetic response to selection is obtained (Figure 4). The plotted points on the graph represent the deviation of the respective selection line mean from the control line mean for each generation. It is obvious from Figure 4 that the response to selection for light muscle weight was of greater magnitude and was more consistent than was

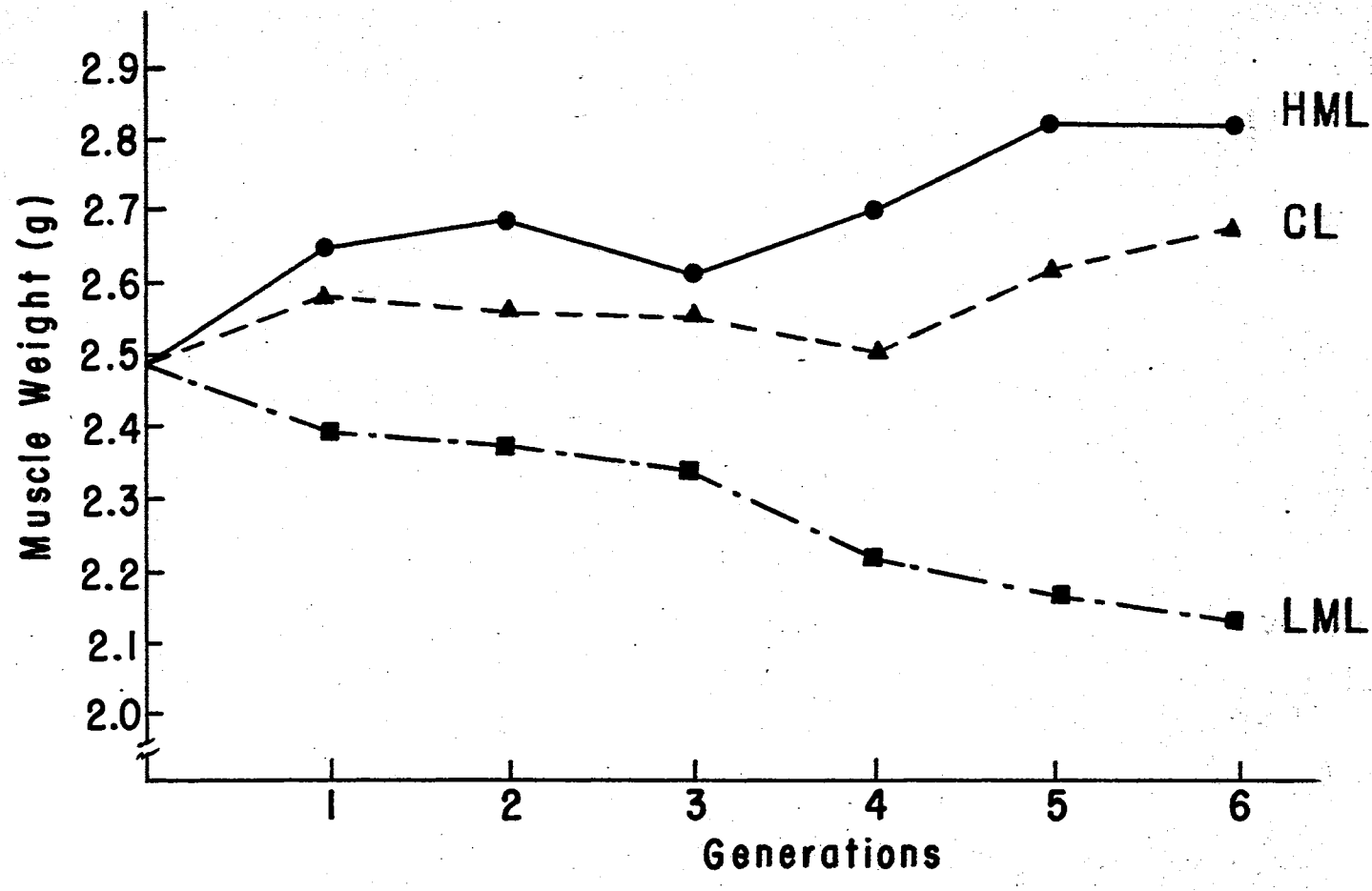

Figure 3. Responses to Selection for Total Hindleg Muscle Weight Plotted on Generations

TABLE VII

CUMULATIVE SELECTION DIFFERENTIALS FOR HINDLEG MUSCLE WEIGHT AND SUBSEQUENT RESPONSE AS DEVIATIONS FROM CONTROL LINE

Heavy-Muscle Line		Generation	Light-Muscle Line	
Cumulative SD (g)	Response (g)		Cumulative SD (g)	Response (g)
0.35	0.07 ± .09	1	-0.35	-0.19 ± .09*
0.63	0.12 ± .09	2	-0.57	-0.19 ± .09*
0.83	0.05 ± .12	3	-0.72	-0.27 ± .08**
1.19	0.18 ± .08*	4	-0.89	-0.27 ± .08**
1.43	0.22 ± .09*	5	-1.02	-0.45 ± .08**
1.73	0.16 ± .08*	6	-1.18	-0.55 ± .07**

*P < .05.
**P < .01.

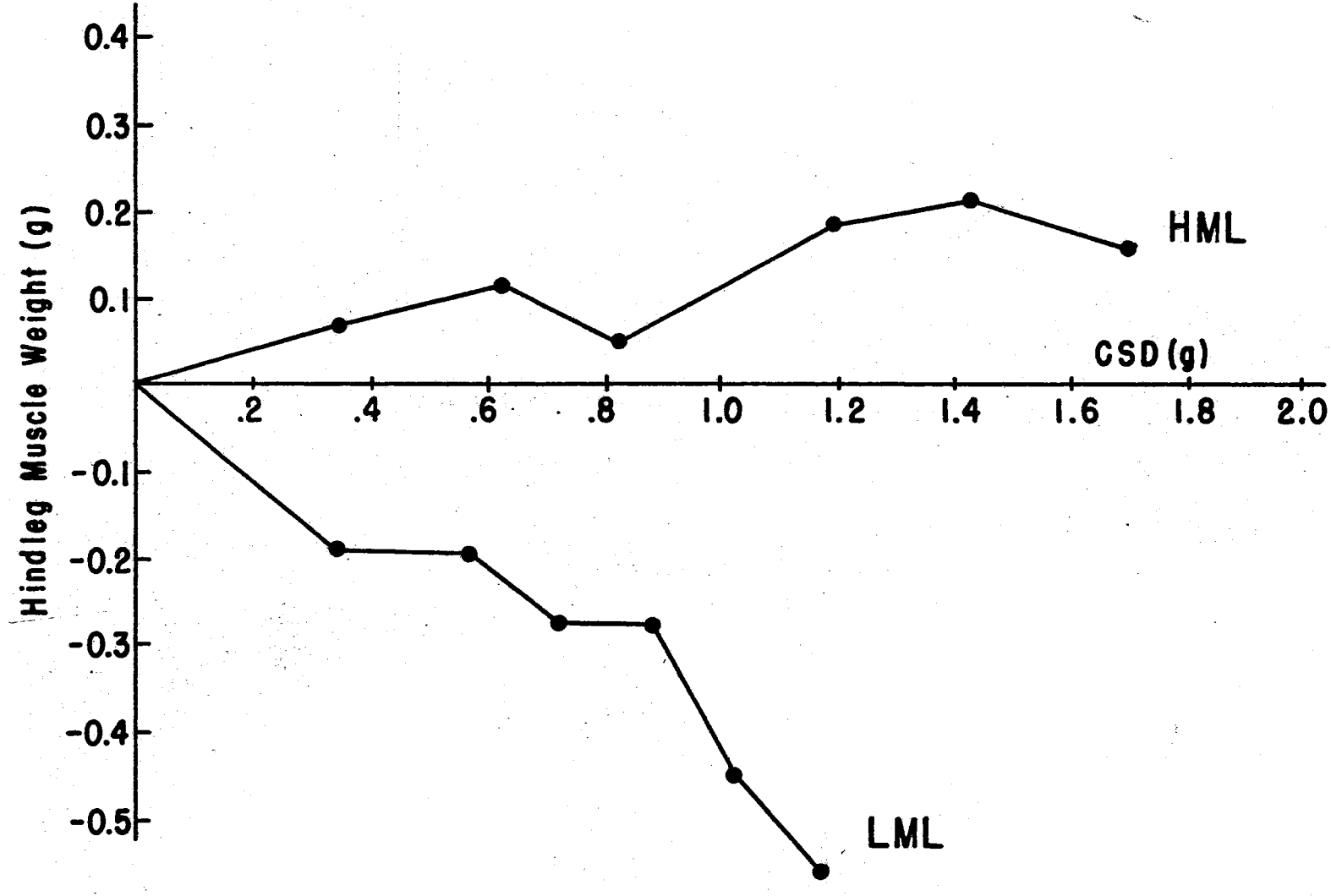

Figure 4. Responses to Selection as Deviations from the Control Line Plotted on Cumulative Selection Differential (CSD)

response to selection for heavy muscle weight. Furthermore, this greater response was obtained in spite of a smaller realized selection differential in LML.

The major factors contributing to the magnitude of the selection differential are phenotypic variation and proportion of the population saved. The proportion saved was designed to be the same in this study. Although the actual range was from 0.25 to 0.28 in the selection lines, differences in the proportion saved each generation were small ($\leq .02$) and, therefore, could not be considered as a major factor contributing to the differences in SD observed. The pooled estimates of the phenotypic variance of muscle weight were 0.0702 and 0.0445 for HML and LML, respectively. The corresponding F value for testing the equality of the variances was 1.58, which for 144 and 140 degrees of freedom was highly significant ($P < .01$). As a result of this larger variation, the selected individuals in HML would be expected to deviate further from the respective generation mean than the selected individuals of LML from their respective mean. The values in Table VII verify this expected trend.

Selection response (R) may be predicted by the equation: R = (heritability) x (selection differential). For a given generation the ratio of total response to cumulative SD provides an estimate of realized h^2. The best linear unbiased estimate of realized h^2 for the duration of the study is given by the regression of selection response on cumulative SD. In this study selection was practiced only in males with the dams being a non-selected random sample which, therefore, had an expected selection differential of zero. As a result, the regression of selection response on cumulative selection differential was an

estimate of $\frac{1}{2}h^2$. Consequently, h^2 was estimated as twice the regression coefficient.

The estimates of h^2 and standard errors were 0.18 ± 0.08 and 0.88 ± 0.20 for HML and LML, respectively. The difference between the estimates of h^2 was 0.70 ± 0.22 which was significant ($P < .01$) thus verifying that the response to selection was greater in LML. The possible causes of this asymmetry will be discussed later.

To estimate h^2 for divergence between HML and LML, total divergence was regressed on cumulative selection differential for divergence (Figure 5). The estimate of h^2 for divergence was 0.45 ± 0.07. According to Falconer (1953), h^2 estimated by resemblance between relatives approximated the average result of divergent selection which is given by the estimate of h^2 for divergence. From the variance-covariance analysis previously discussed, it was estimated that the h^2 of muscle weight was approximately 0.44 in the base population (Table V). From the selection study the estimated h^2 of divergence was 0.45 which indicated that continued two-way selection for hindleg muscle weight for six generations did not niticeably alter the average h^2 of hindleg muscle weight. However, the results from divergent selection indicated that predicted response based on the average estimate of h^2 would overestimate the upward response which would actually be obtained and underestimate the downward selection response.

Correlated Selection Responses

Correlated responses were studied for reproductive performance as measured by percent of total matings producing litters and litter size; litter weights at 12 days; individual weights at 21, 42, 56 and 84 days;

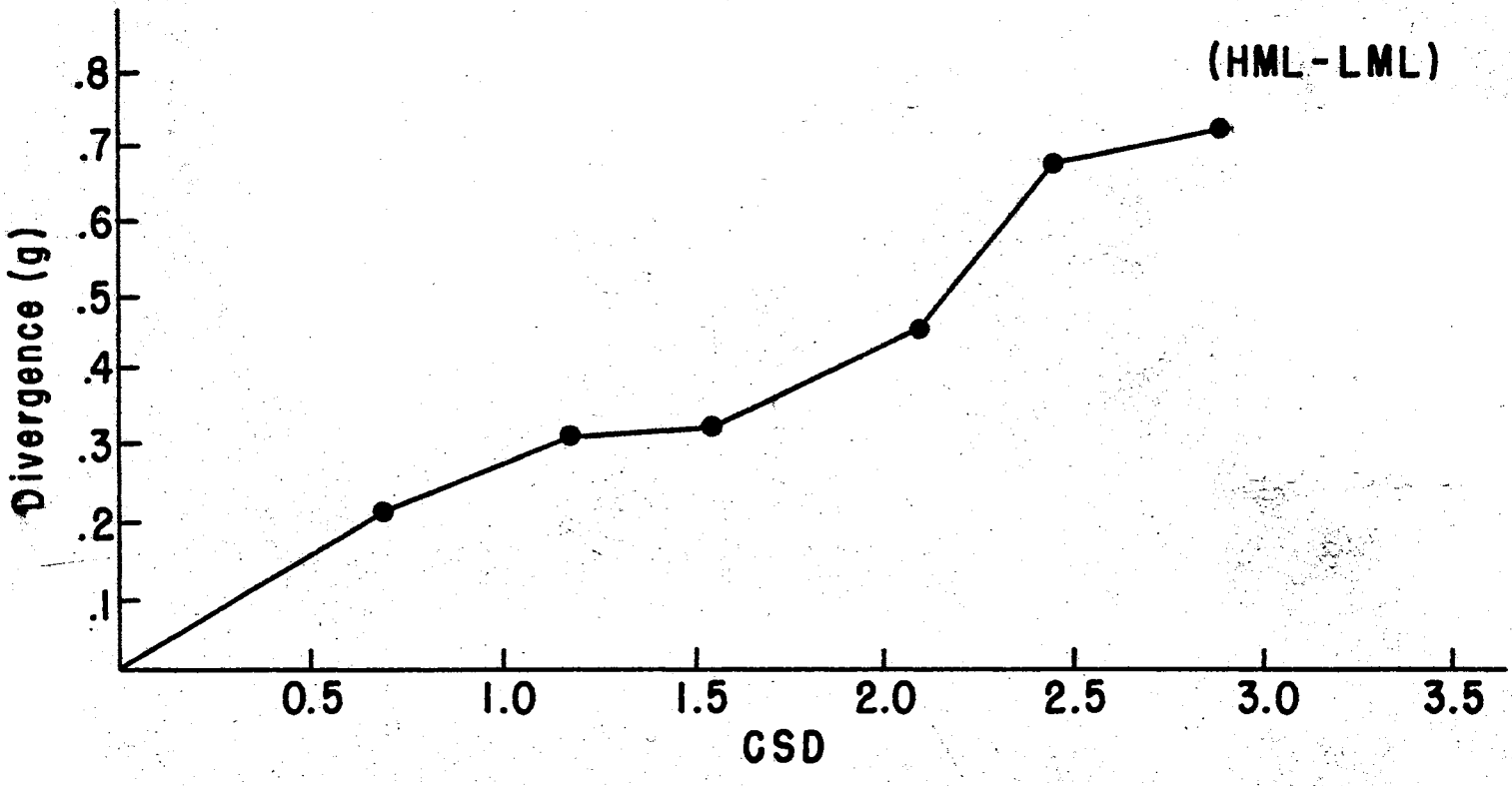

Figure 5. Total Divergence in Hindleg Muscle Weight Between Heavy and Light Muscle Lines Plotted on Cumulative Selection Differential (CSD) for Divergence

average daily gain from 21 to 42 days of age and for the ratio of hindleg muscle weight to 84-day weight.

Weight at 84 Days

All males slaughtered each generation were weighed at 84 days immediately prior to being sacrificed. Since the selection criteria was muscle weight at 84 days, the correlated response in 84-day weight would be of primary concern. Figure 6 gives the generation means by line for 84-day weight.

From a consideration of Figure 6 it is obvious that the correlated response in 84-day weight exhibited asymmetry similar to the asymmetry observed in the direct response of muscle weight (Figures 3 and 4). After six generations of divergent selection for hindleg muscle weight, HML exceeded LML by 7.5 g in 84-day weight. This divergence between the two selection lines represented 25.3% of the initial mean as compared to the 28.4% divergence observed in the primary selection response. The correlated response upward of 2.19 g represented 7.1% of the initial mean whereas direct response downward represented 22.9% of the initial muscle weight mean.

These values are in line with what would be expected based on the high positive genetic correlation as estimated from the variance-covariance analysis of the base population. Using the correlated response technique demonstrated by Falconer (1954), the estimate of r_g between muscle weight and 84-day weight was 0.74 ± 0.12.

Table VIII presents the estimates of r_g between hindleg muscle weight and six of the traits studied as calculated from the correlated response in the respective trait. The estimates of r_g for 84-day weight, hindleg weight, 56-day weight and 21-day weight agree

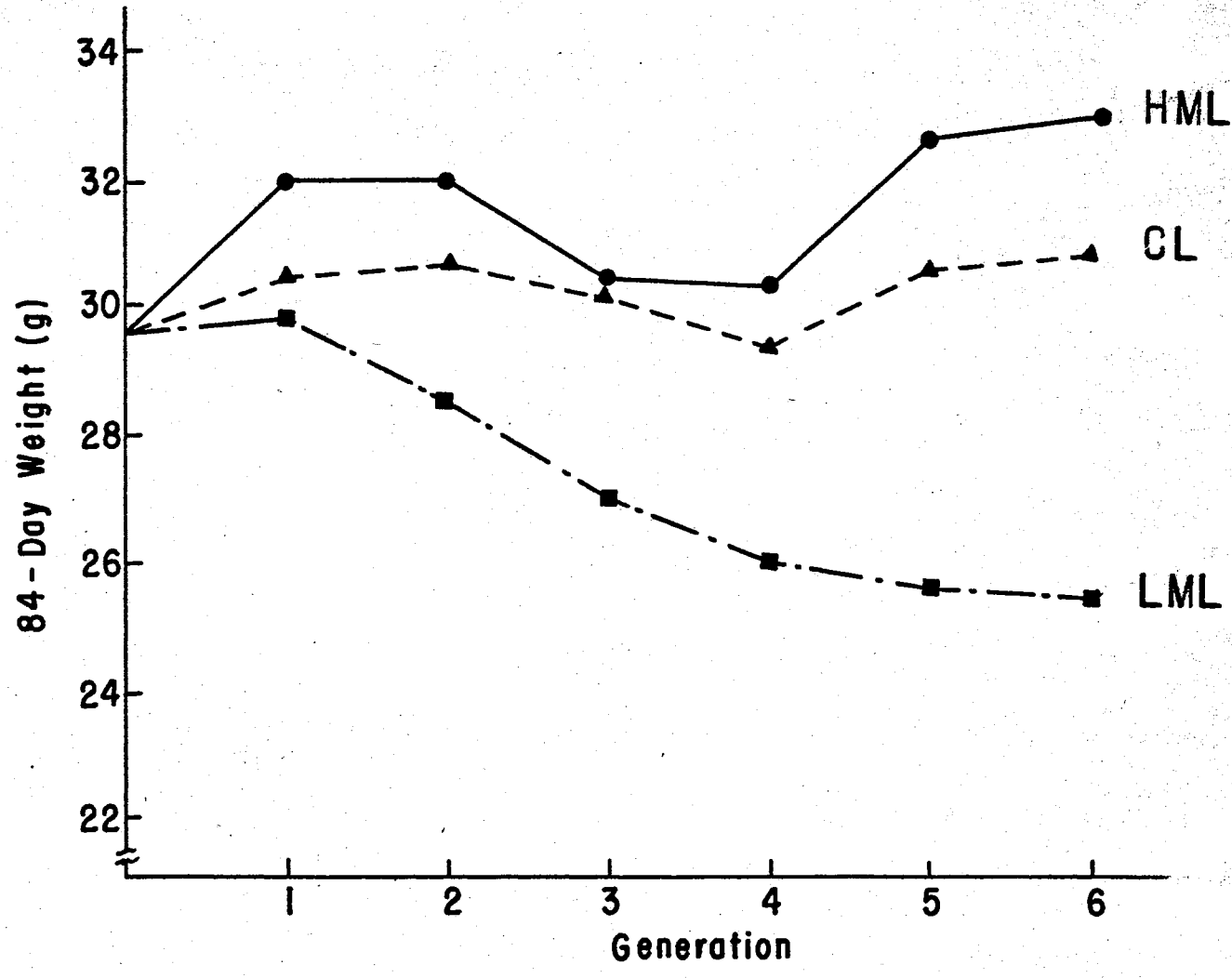

Figure 6. Correlated Responses in 84-Day Weight Plotted on Generations

TABLE VIII

ESTIMATES OF GENETIC CORRELATION BETWEEN HINDLEG MUSCLE WEIGHT AND SELECTED PERFORMANCE TRAITS FROM SELECTION RESPONSES AND VARIANCE-COVARIANCE ANALYSIS

Correlated response measured in:	Direct response measured in muscle weight	Variance-Covariance analysis
21-day weight	0.20 ± *	*
42-day weight	1.03 ± .42	-0.02 ± .42
ADG (21 to 42 days of age)	0.96 ± .30	-0.14 ± .21
56-day weight	0.80 ± .20	1.11 ± .57
84-day weight	0.74 ± .12	1.32 ± .37
Hindleg weight	1.07 ± .33	1.00 ± .44

*. Unavailable due to negative sire component.

generally with the estimates of r_g obtained from the variance-covariance analysis. The high values for ADG and 42-day weight are larger than the corresponding estimates from the variance-covariance analysis. The relatively small variances for ADG and muscle weight indicated that the estimate of r_g between these two traits from variance-covariance analysis would be highly subject to sampling errors, and, consequently, can not be considered very reliable. The low estimate of 0.20 for r_g between muscle weight and 21-day weight suggested that correlated response in 21-day weight would not exhibit as marked a divergence as did hindleg muscle weight. This was the case in this selection study as will be shown in the section on 21-day weights.

The asymmetrical nature of the correlated response was examined by plotting the correlated response on cumulative "consequential" selection differential. Consequential selection differential (CSD) was used to define the selection differential realized in the correlated character (84-day weight) as a consequence of selection for the primary character (muscle weight). Table IX shows the cumulative CSD and subsequent response for 84-day weight by generations for the selection lines. Correlated selection response in 84-day weight is plotted on cumulative CSD in Figure 7. The estimates of h^2 obtained from the regression were 0.20 ± 0.20, 1.32 ± 0.16 and 0.62 ± 0.10 for upward, downward and divergent selection, respectively. These values exhibited the same trend as the estimates of h^2 for muscle weight and verified the suspected asymmetry of response in 84-day weight.

To test whether selection for 84-day weight would have been as effective as direct selection for muscle weight, two procedures were used. Spearman's rank correlation coefficient (Conover, 1971) was

TABLE IX

CUMULATIVE CONSEQUENTIAL SELECTION DIFFERENTIALS (CSD) AND SUBSEQUENT RESPONSE IN 84-DAY LIVE WEIGHT

Heavy-Muscle Line		Generation	Light-Muscle Line	
Cumulative CSD (g)	Response (g)		Cumulative CSD (g)	Response (g)
1.96	1.50 ± 1.0	1	-2.19	-0.60 ± 1.3
4.16	1.30 ± 0.7*	2	-3.79	-2.10 ± 0.8**
4.86	0.30 ± 0.8	3	-5.89	-3.10 ± 0.7**
7.36	1.00 ± 0.9	4	-7.19	-3.30 ± 0.9**
9.76	2.10 ± 0.9**	5	-7.99	-4.90 ± 0.8**
13.26	2.10 ± 0.6**	6	-9.09	-5.40 ± 0.5**

*$P < .05$.
**$P < .01$.

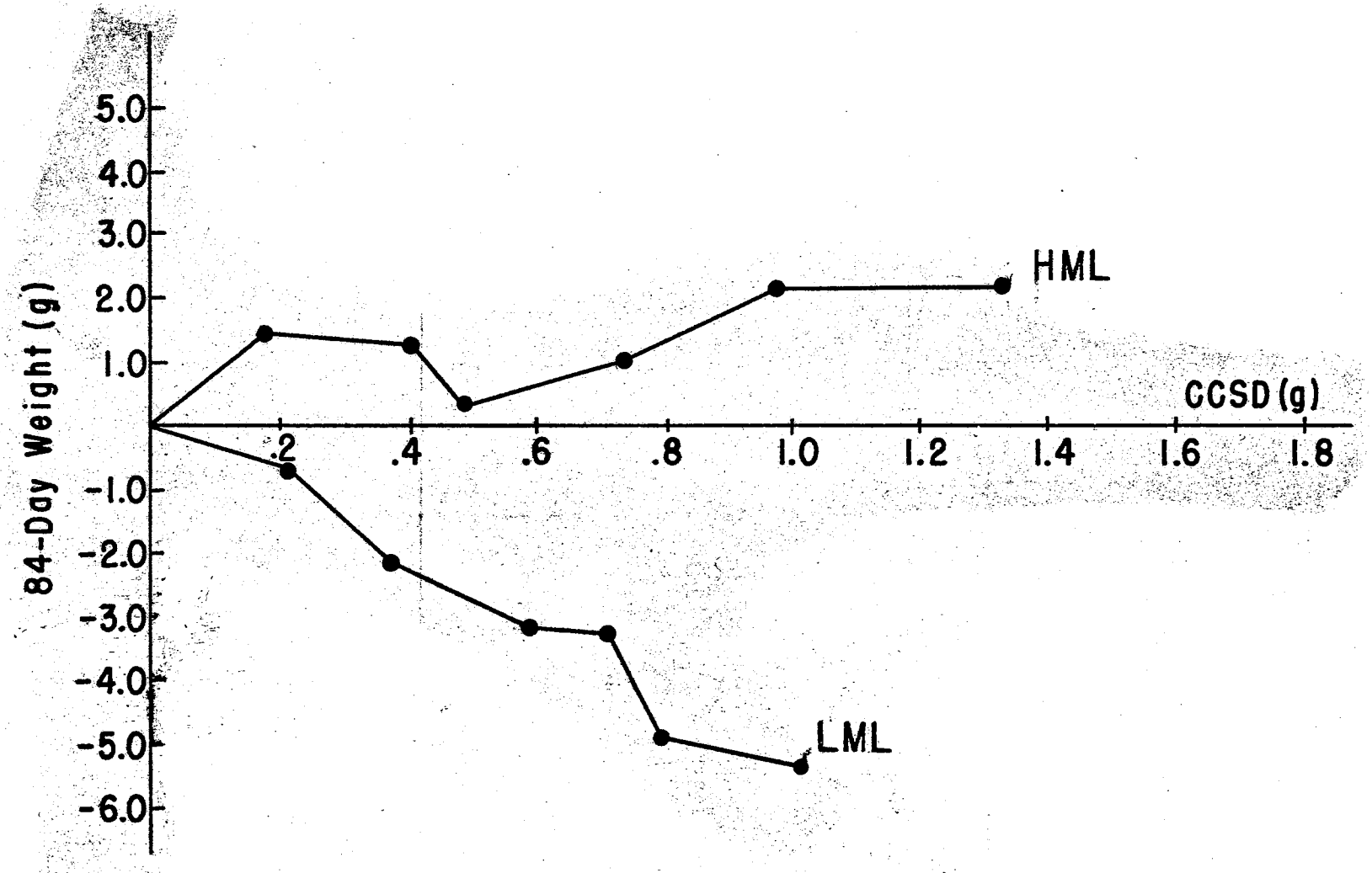

Figure 7. Correlated Responses in 84-Day Weight as Deviations from the Control Line Plotted on Consequential Cumulative Selection Differential (CCSD)

calculated to indicate the degree to which ranking of sires based on muscle weight agreed with the ranking based on 84-day weight. Table X gives the rank correlation coefficients for the selection lines by generation. The significant positive coefficients indicated that, on the average, a sire tended to rank high (or low) on 84-day weight if he ranked high (or low) based on muscle weight. Although tests for significant differences between Spearman's correlation coefficients are not available, it can be observed from Table X that except for generation two, the correlation coefficients tended to be larger in HML. This indicated that there was closer agreement between the two ranking procedures in HML than in LML.

A second approach was to consider the consequential SD for hindleg muscle weight which would have resulted if the sires had been selected based on 84-day weight. The ratio of consequential SD to actual SD would then be an approximation of the relative effectiveness of selection based on 84-day weight as compared to selection based on hindleg muscle weight. Table XI gives the comparison by line and generation of the CSD's obtained when 84-day weight was the ranking criteria and the actual SD's obtained in this study. Selection differentials obtained from selection based on 84-day weight would have been, on the average, 83 and 72% as large as the selection differentials obtained from direct selection for muscle weight for HML and LML, respectively.

TABLE X

SPEARMAN'S RANK CORRELATION COEFFICIENTS BETWEEN RANKING OF SLAUGHTERED MALES BASED ON MUSCLE WEIGHT AND RANKING BASED ON 84-DAY WEIGHT

Generation	Heavy-Muscle Line	Light-Muscle Line
1	0.88**	0.70**
2	0.50*	0.90**
3	0.87**	0.66**
4	0.84**	0.71**
5	0.86**	0.73**
6	0.98**	0.71**

*P < .05.
**P < .01.

TABLE XI

COMPARISON OF ACTUAL SELECTION DIFFERENTIALS (SD) FOR HINDLEG MUSCLE WEIGHT WITH CONSEQUENTIAL SELECTION DIFFERENTIALS (CSD) FOR HINDLEG MUSCLE WEIGHT OBTAINED FROM SELECTION BASED ON 84-DAY WEIGHT

	Heavy-Muscle Line			Light-Muscle Line		
Generation	84-day wt CSD (g)	Muscle wt SD (g)	Ratio CSD/SD	84-day wt CSD (g)	Muscle wt SD (g)	Ratio CSD/SD
1	0.24	0.27	0.78	-0.07	-0.16	0.44
2	0.07	0.20	0.33	-0.15	-0.15	1.00
3	0.32	0.36	0.78	-0.14	-0.17	0.82
4	0.24	0.25	0.96	-0.10	-0.16	0.62
5	0.23	0.30	0.77	-0.11	-0.16	0.69
6	0.25	0.25	1.00	-0.14	-0.18	0.78
AVERAGE	0.225	0.271	0.83	-0.118	-0.163	0.72

Ratio of Hindleg Muscle Weight to 84-Day Weight

The ratio of muscle weight to 84-day weight was used to study any changes which may have occurred in relative proportion of hindleg muscle weight as a result of selection. Table XII presents the mean values by line and generation for ratio of muscle to 84-day live weight and the means are plotted in Figure 8. There was a tendency for proportion of muscle to increase in both selection lines from generation one to four. The proportion of muscle in HML consistently exceeded that in LML throughout the experiment with the differences in generations four, five and six significant ($P < .01$).

From these results it would appear that upward selection for muscle weight has not resulted in a significant increase in proportion of hindleg muscle. LML, on the other hand, had a significantly ($P < .05$) lower proportion of hindleg muscle weight than HML and the control line. These results agree with the conclusion of Cundiff et al. (1969) that selection for growth of retail product in cattle would be effective but that proportion would be altered very little. Robinson and Bradford (1969) reported that the weight of the gastrocnemius muscle, a muscle of the hindleg system, increased with size in 84-day old mice which had been selected for rapid growth between 21 and 42 days. These researchers did not, however, present results of muscle as a percent of body size which could be used for direct comparison with the results of the present study.

Correlated Response in Reproductive Performance

Table XIII gives the total number of matings and the proportion of litters born by line in each generation. Total number of matings was

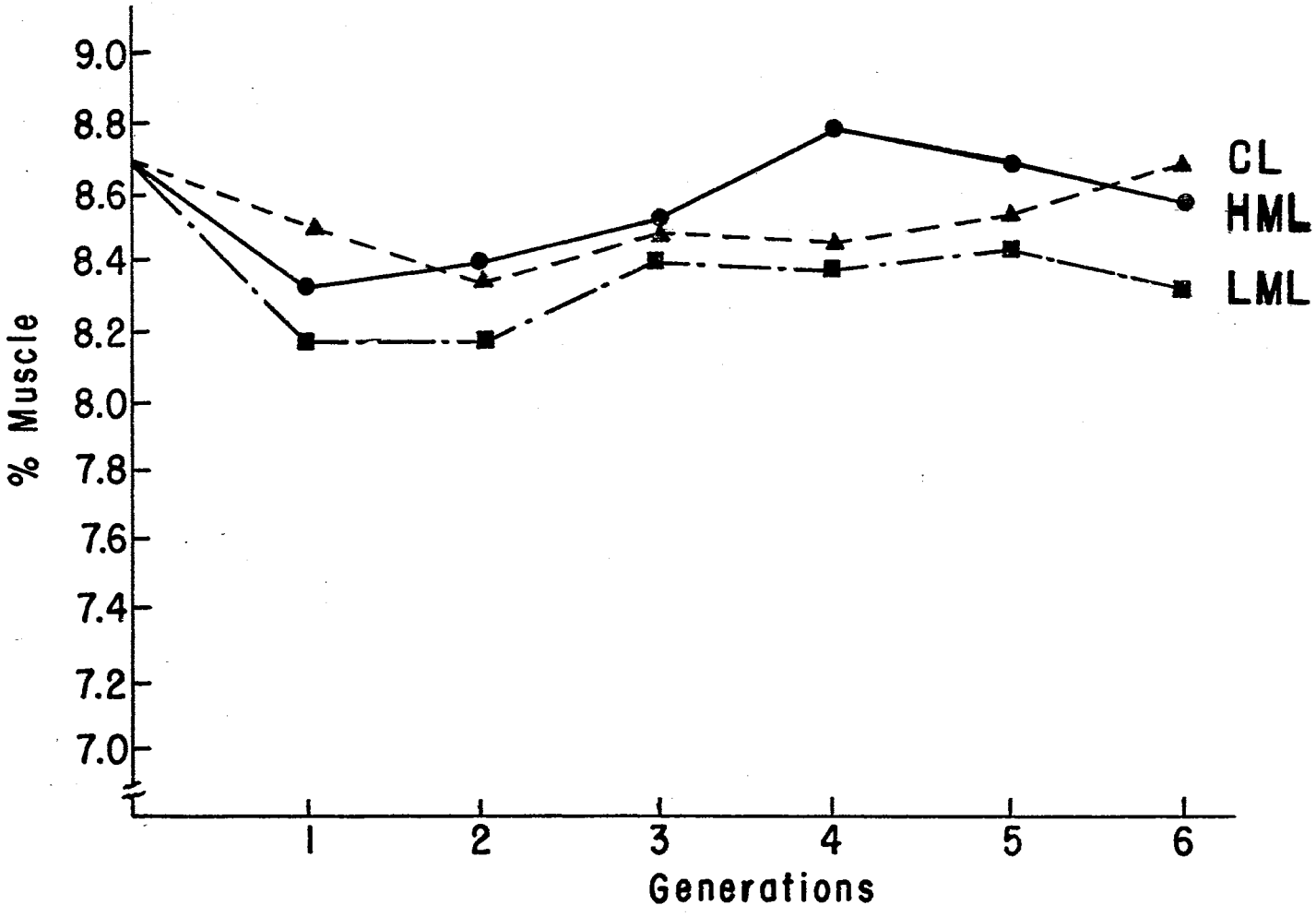

Figure 8. Correlated Responses in Ratio of Hindleg Muscle Weight to 84-Day Weight (Percent Muscle)

TABLE XII

HINDLEG MUSCLE WEIGHT AS PERCENT OF 84-DAY WEIGHT
BY LINE AND GENERATION

Generation	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		8.64 ± .04	
1	8.26 ± .09	8.45 ± .11	8.17 ± .16
2	8.40 ± .13	8.33 ± .10	8.18 ± .07
3	8.51 ± .12	8.44 ± .11	8.40 ± .09
4	8.78 ± .08[a]	8.43 ± .09[b]	8.39 ± .09[b]
5	8.68 ± .08[a]	8.52 ± .12[a]	8.44 ± .11[b]
6	8.57 ± .07[a]	8.64 ± .02[a]	8.31 ± .11[b]

[a] Means in the same generation with different superscripts significantly different ($P < .05$).

TABLE XIII

TOTAL NUMBER OF MATINGS AND PERCENT LITTERS BORN IN EACH LINE AND GENERATION

	Heavy-Muscle Line		Control Line		Light-Muscle Line	
Generation	Total Matings	% Born	Total Matings	% Born	Total Matings	% Born
0			44	91		
1	16	94	44	91	16	94
2	16	88	44	89	16	94
3	18	94	48	85	18	89
4	14	93	48	88	18	83
5	16	88	48	85	18	83
6	14	93	96	85	14	93

the number of females placed in mating cages with the males which were selected to contribute progeny to the next generation. From these data it can be observed that conception rate has apparently been altered very little by selection for hindleg muscle weight.

The average number of live young at three days by line and generation is presented in Table XIV. It is apparent that there has been a significant decrease in the number of live mice per litter at three days in LML. Significant differences ($P < .05$) were obtained between HML and LML and between the control line and LML in generations four, five and six. Elliott, Legates and Ulberg (1968) reported lower fertility in a line of mice selected for small body size at 42 days and attributed this lower fertility to fewer matings, more ovulation failures, a lower ovulation rate and lower fertilization rate than that observed in their unselected control line. MacArthur (1949) found that litter size was positively correlated with body size.

The average number of live young at three days from crosses between generation five males from each selection line and control line females was 9.92 ± 0.43 for 12 litters sired by HML sires and 9.50 ± 0.68 for 14 litters sired by LML males. This non-significant difference in litter size between these crosses suggested that the smaller litter size in LML was due primarily to differences in the ovulation capabilities between females of LML and females of the other two lines.

Twelve Day Litter Weights

Correlated response in 12-day litter weight was measured in each line each generation on litters which had been standardized to eight mice each at three days. Table XV presents the generation means by

TABLE XIV

AVERAGE NUMBER OF LIVE MICE PER LITTER AT THREE DAYS BY LINE AND GENERATION

	Number of Litters and Live Mice per Litter					
	Heavy-Muscle Line		Control Line		Light-Muscle Line	
Generation	No. of litters	No. of mice	No. of litters	No. of mice	No. of litters	No. of mice
0			40	9.50		
1	7	9.43	38	9.74	6	9.00
2	11	10.64	NA		11	10.91
3	22	9.09	40	8.90	22	9.05
4	21	9.57[a]	39	9.13[a]	20	8.00[b]
5	29	9.28[a]	20	9.65[a]	25	7.40[b]
6	22	9.68[a]	81	9.73[a]	19	8.05[b]

[a] Means in same generation with different superscripts are significantly different ($P < .05$).

NA = Not available.

TABLE XV

MEAN TWELVE-DAY LITTER WEIGHTS BY LINE AND GENERATION[1]

	Twelve-day litter weights (g)					
	Heavy-Muscle Line		Control Line		Light-Muscle Line	
Generation	No. of litters	Litter weight	No. of litters	Litter weight	No. of litters	Litter weight
0			40	52.0		
1	15	53.2	40	53.9	15	53.8
2	14	52.7	39	51.4	15	50.9
3	17	51.9[a]	40	50.8[a]	16	48.4[b]
4	13	48.4[a]	39	48.4[a]	15	43.8[b]
5	14	51.1[a]	40	47.2[b]	15	47.2[b]
6	13	47.0[a]	79	49.5[b]	13	45.9[a]
Overall Mean	86	50.8[a]	318	50.5[a]	89	48.4[b]

[1] Litters standardized to 8 mice per litter at three days of age.

[a] Means in same row with different superscripts significantly different ($P < .05$).

line for 12-day litter weight and the number of litters contributing to each generation mean. By generation two the selection lines had diverged and the difference of 1.8 g approached significance ($P \doteq .10$). Twelve-day litter weights in HML were significantly ($P < .05$) heavier than those of LML in generations three through five. In generation six HML exceeded LML by 1.1 g although the difference was not statistically significant.

Twelve-day litter weight has been considered a good measure of lactation performance (Falconer, 1953; Eisen, Legates and Robison, 1970; Lang and Legates, 1969; and White, Legates and Eisen, 1968) and it would appear from the data in Table XV that lactation performance from birth to 12 days was altered very little in HML but tended to be depressed in LML. Differences between HML and the control line were not significant until generation five in which average 12-day litter weight was significantly ($P < .05$) larger in HML than in the control line. However, the control line significantly ($P < .05$) exceeded the HML in generation six. LML was significantly ($P < .05$) lower than the control line after generation two with the exception of generation five. The average for the three lines over all six generations also pointed out that there was little change in HML as compared to the controls but that LML was significantly ($P < .05$) lower than both HML and the control line. These results are in general agreement with work reported on correlated response in 12-day litter weight when selection was based on 42-day weight in mice (Falconer, 1953 and 1955; Lang and Legates, 1969).

White, Legates and Eisen (1968) measured the maternal effects among lines of mice after 40 generations of selection for 42-day

weight. Dams from lines selected for increased weight, decreased weight and a non-selected control line nursed litters composed of one male and one female from each of the three lines. These researchers found that mean 12-day litter weight of their control line was significantly ($P < .01$) heavier than either of their selection lines and that their high line was significantly ($P < .01$) heavier than their low line.

Weight at 21 Days

All mice were weaned and individually weighed at 21 days of age. Mean 21-day weights by line and generation are given in Table XVI. The means are plotted on generations in Figure 9.

Two important trends are evident from these data. In generation two the selection lines diverged significantly ($P < .05$) by 0.4 g. The difference between the selection lines consistently favored HML and were significant ($P < .05$) after generation two. Although differences between the control line and HML were not significant in generations three and five, the mean of the control line exceeded the means of both selection lines in generation three and this superiority remained through generation six. Lang and Legates (1969) reported a significant ($P < .05$) difference of 1.9 g in the 21-day weights of mice between lines selected for high and low 42-day weight with the difference favoring the high line. These workers, however, found that the line selected for heavy 42-day weight also exceeded the control line by 0.35 g although the difference was not significant statistically. Falconer (1955) also found that a line selected 21 generations for increased 42-day weight exceeded a non-selected line by 0.75 g while a line

TABLE XVI

MEAN 21-DAY WEIGHTS BY LINE AND GENERATION

Generation	21-day weight (g)		
	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		9.7 ± .12	
1	10.6 ± .14	10.9 ± .10	10.7 ± .14
2	10.6 ± .14[a]	10.1 ± .12[b]	10.2 ± .17[b]
3	9.3 ± .18[a]	9.5 ± .11[a]	8.9 ± .17[b]
4	8.3 ± .19[a]	8.7 ± .11[b]	7.5 ± .16[a]
5	9.0 ± .21[a]	9.3 ± .10[a]	8.7 ± .16[c]
6	8.7 ± .34[a]	9.4 ± .10[b]	8.1 ± .18[c]

[a] Means in same generation with different superscripts are significantly different ($P < .05$).

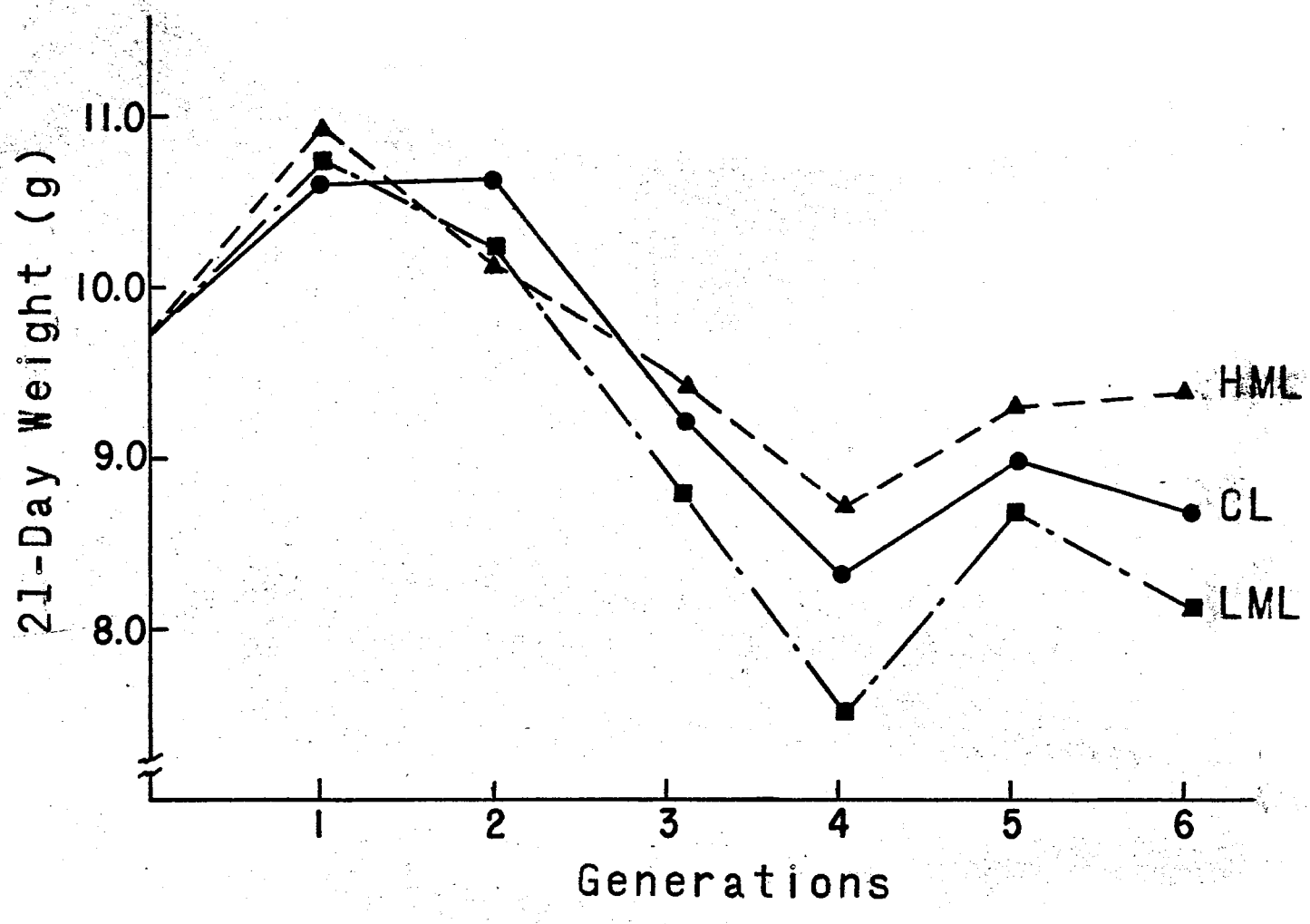

Figure 9. Correlated Responses in 21-Day Weight Plotted on Generations

selected 19 generations for decreased 42-day weight averaged 3.0 g lighter than the unselected line. White, Legates and Eisen (1968) reported that upward selection (H_6) for 42-day weight resulted in heavier mice at 21 days than no selection (C_2) or downward selection (L_6) and that downward selection resulted in mice significantly ($P< .01$) lighter at 21 days than the unselected control line. However, these workers reported no significant differences at 21 days between mice which had nursed H_6 and C_2 dams. The 21-day weights of young that had nursed L_6 dams were 1.31 g lighter than those raised by H_6 or C_2 dams; a significant ($P< .05$) decrease of approximately 13%.

From a comparison of the data in Tables XV and XVI, it can be observed that HML tended to exceed LML at both 12 and 21 days in generations two through six. Based on 12-day litter weights the control line was slightly lower than HML until generation six when it exceeded both selection lines and was equal to or higher than LML in all generations. After generation three the control line weaned heavier mice than both HML and LML. In this study, selection for hindleg muscle weight has apparently resulted in a decrease in total maternal performance from birth to 21 days in both selection lines with the more pronounced decrease observed in LML.

Average Daily Gain from 21 to 42 Days of Age and 42-Day Weight

Average daily gain (ADG) in grams per day was computed for the postweaning growth period from 21 to 42 days of age. The generation means by line for ADG are shown in Table XVII and the means are plotted in Figure 10.

In generation two ADG increased to 0.69 g/day in HML and decreased

TABLE XVII

AVERAGE DAILY GAIN FROM 21 TO 42 DAYS OF AGE BY LINE AND GENERATION

Generation	Average daily gain (g/day)		
	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		0.66 ± .01	
1	0.63 ± .01	0.64 ± .01	0.63 ± .01
2	0.69 ± .01[a]	0.65 ± .01[b]	0.60 ± .01[c]
3	0.68 ± .01[a]	0.64 ± .01[b]	0.60 ± .01[c]
4	0.68 ± .01[a]	0.65 ± .01[b]	0.58 ± .01[c]
5	0.69 ± .01[a]	0.66 ± .01[b]	0.58 ± .01[c]
6	0.79 ± .02[a]	0.70 ± .01[b]	0.57 ± .02[c]

[a] Means in the same generation with different superscripts are significantly different ($P < .05$).

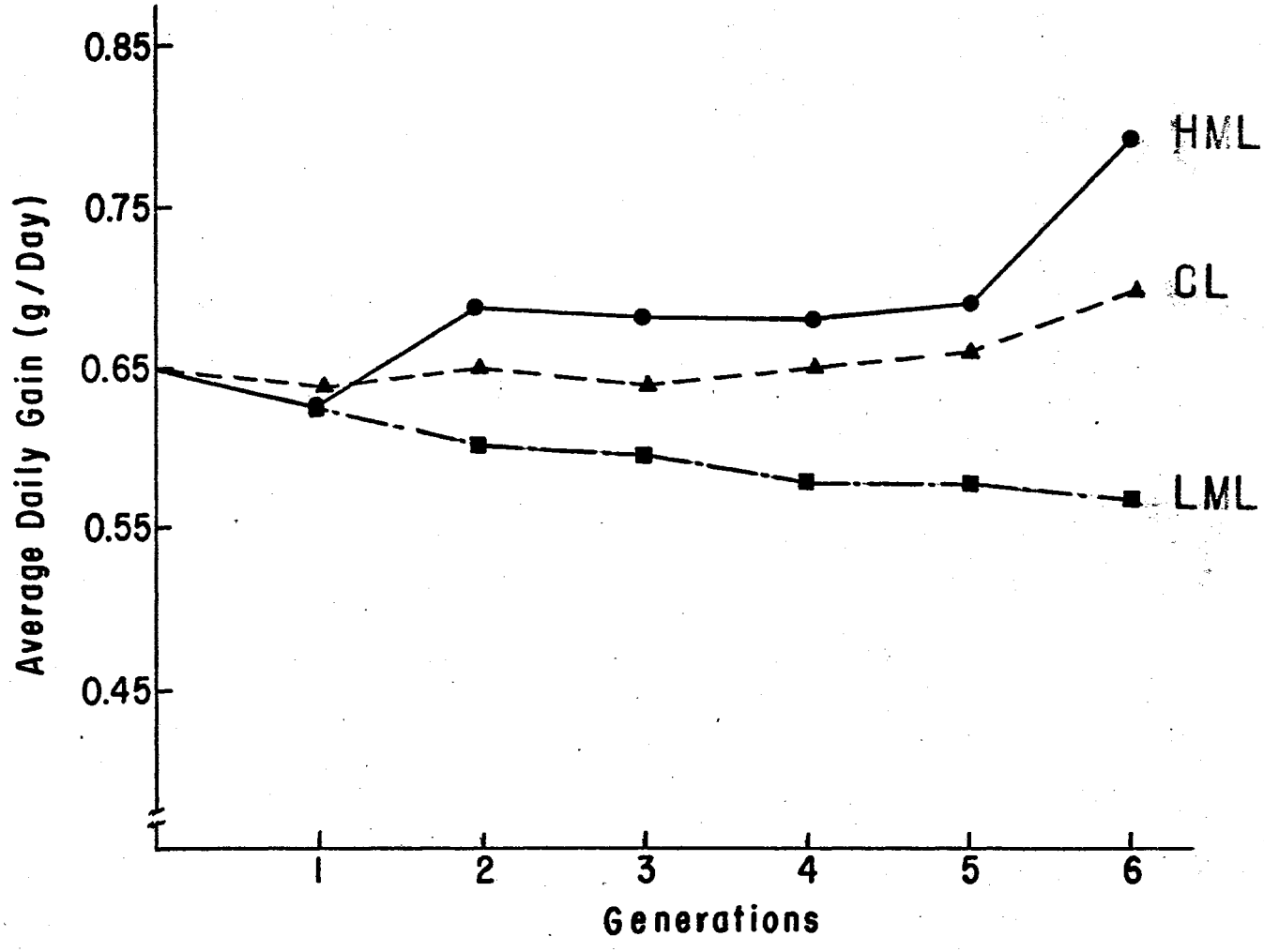

Figure 10. Correlated Responses in Average Daily Gain from 21 to 42 Days of Age Plotted on Generations

to 0.60 g/day in LML. Through generation five HML and the control line showed little change, and LML exhibited a slight decrease to 0.58 g/day. In HML a 0.10 g/day increase was noted in generation 6 while only a slight decrease was observed in LML. Several factors could explain this sudden jump in the mean of HML. An environmental factor may have accounted for a portion of this increase as suggested by the 0.04 g/day increase in the control line mean. Fewer half-sib families, and as a result fewer individuals, were measured in both selection lines in generation six (see Table II), so sampling error could have had a larger proportionate effect; and, of course, part of the increase could be attributed to correlated response to selection.

Table XVIII and Figure 11 reflect the differences in 42-day weights of the three lines. These differences show the combined effects of 21-day weight (Table XVI and Figure 9) and ADG from 21 to 42 days (Table XVII and Figure 10). The increased rate of gain in HML over the control line counterbalanced the heavier 21-day weights of the control line resulting in heavier 42-day weights for HML after generation one. The combination of lighter 21-day weights and slower rates of gain in LML resulted in a steady decrease in 42-day weight. After six generations of divergent selection for muscle weight, HML exceeded the control line by 1.2 g and LML by 5.2 g. The divergence between the selection lines represented 22.1% of the initial mean and was statistically significant ($P < .05$).

Reports of experiments in which direct selection was applied on 42-day weight have shown divergence representing approximately 33% (White, Legates and Eisen, 1968), 68% (Falconer, 1955) and 39% (Lang and Legates, 1969) after 40, 20 and 32 generations of selection, respectively.

TABLE XVIII

MEAN 42-DAY WEIGHTS BY LINE AND GENERATION

Generation	42-day weights (g)		
	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		23.5 ± .17	
1	23.8 ± .25	24.3 ± .15	23.9 ± .24
2	25.1 ± .23[a]	23.7 ± .16[b]	22.8 ± .26[b]
3	23.6 ± .27[a]	22.9 ± .14[a]	21.5 ± .26[b]
4	22.6 ± .26[a]	22.4 ± .15[a]	19.7 ± .21[b]
5	23.5 ± .26[a]	23.2 ± .15[a]	20.9 ± .23[b]
6	25.3 ± .44[a]	24.1 ± .16[b]	20.1 ± .38[c]

[a] Means in same generation with different superscripts are significantly different ($P < .05$).

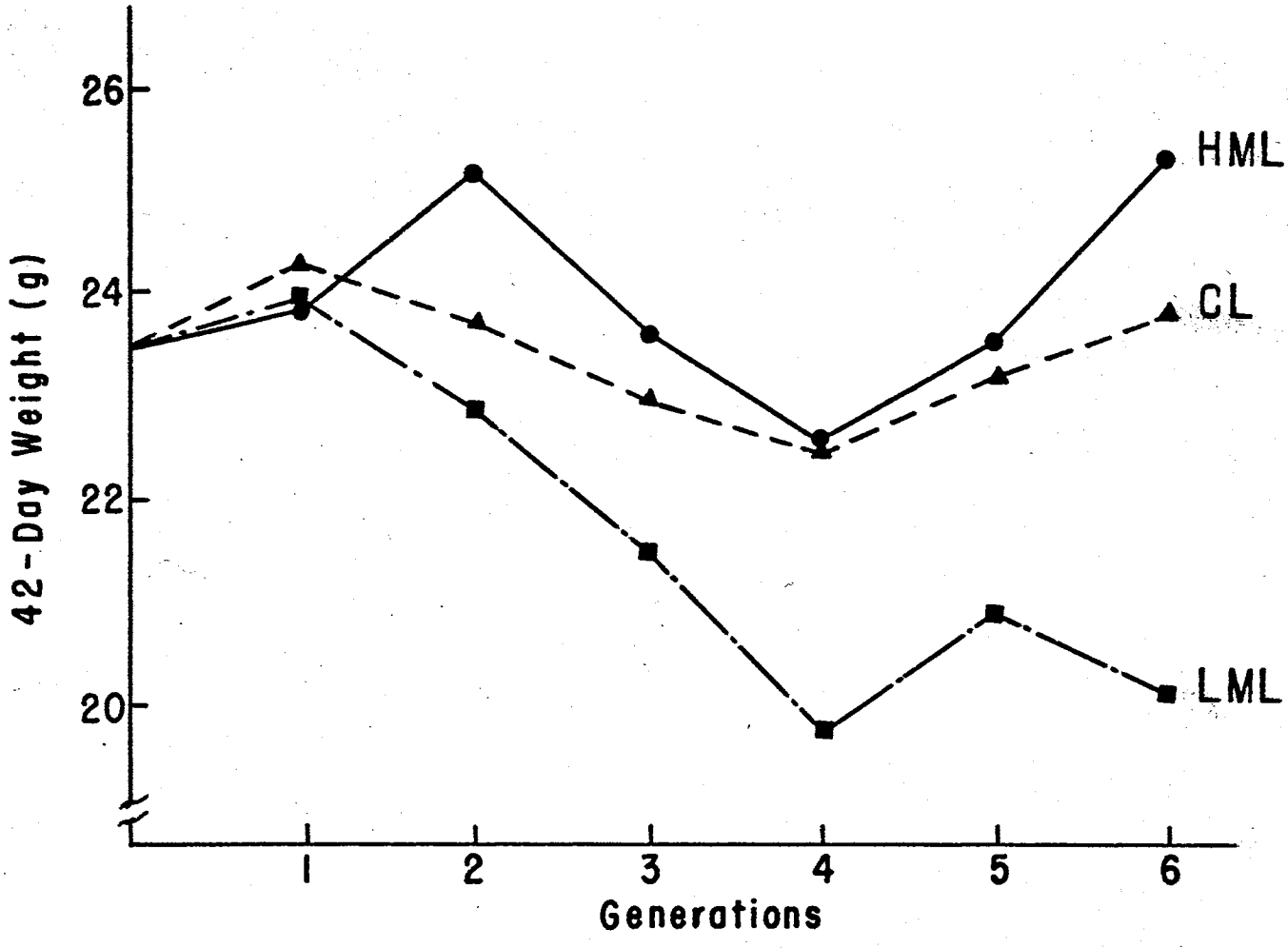

Figure 11. Correlated Responses in 42-Day Weight Plotted on Generations

Asymmetry of Direct and Correlated Selection Responses

A larger response to selection for hindleg muscle weight was obtained in LML than in HML. Correlated selection responses also exhibited asymmetry with the greater responses observed in LML. Falconer (1953, 1955 and 1960a) observed this phenomena in mice selected for 42-day weight and discussed some possible causes (see page 7). These will be examined here in an attempt to ascertain their contributions to the asymmetrical direct and correlated responses observed in this study.

Unsuitable Scale of Measurement

One possible cause of asymmetrical response is a scale of measurement such that the variance is not independent of the mean. If the variance increases as the mean increases, the expected response should be greater in the upward direction since progress expected from selection is proportional to the phenotypic standard deviation.

Phenotypic variances and coefficients of variation for hindleg muscle weight by line and generation and the respective F values for testing the equality of the variances are given in Table XIX. Although the variance in HML exceeded the variance of LML in every generation, the difference was significant only in generation three and approached significance in generations five and sic. However, unsuitable scale could not be considered as a factor contributing to the asymmetry observed in this study since the differences in variance favored HML, and the expected asymmetry would have been in the opposite direction from that actually observed.

TABLE XIX

PHENOTYPIC VARIANCES AND COEFFICIENTS OF VARIATION (CV) OF HINDLEG MUSCLE WEIGHT BY LINE AND GENERATION

	Heavy-Muscle Line		Light-Muscle Line		
Generation	Variance	CV (%)	Variance	CV (%)	F^1 Value
1	.0698	10.0	.0600	10.0	1.16
2	.0427	7.7	.0367	8.1	1.16
3	.1090	12.7	.0282	7.4	3.86*
4	.0440	7.9	.0367	8.9	1.17
5	.0765	9.8	.0462	10.0	1.65
6	.0762	9.8	.0527	10.9	1.44

[1] F test statistic for testing equality of variances.
* ($P<.05$).

Genetic Asymmetry

Two types of genetic situations which could be responsible for part of the asymmetry observed are directional gene frequencies and directional dominance. If no-dominance is assumed and the alleles that affect a trait in a positive direction are more frequent than the alleles affecting the trait in a negative direction, response to selection would be faster in the negative direction. Similarly, if a majority of the alleles affecting the trait exhibit dominance in the positive direction, response in the negative direction would be expected to be faster.

In this study the base population from which selection was initiated was formed by crossing three inbred strains and one non-inbred strain. The non-inbred strain had not been subjected to direct selection for size but had been mildly selected for reproductive performance. The base population, therefore, should have been intermediate relative to gene frequencies for body size. Under this assumption, genetic asymmetry would not be expected to be of major importance in early generations of selection. Directional dominance or over-dominance in one direction would be expected to favor response in the opposite direction since proportion of heterozygotes cannot be permanently increased but can be decreased. However this would also not be expected to be a major factor contributing to asymmetry in early generations.

Maternal Influence

White, Legates and Eisen (1968) suggested that favorable response to selection for increased body weight might be partly nullified if the

maternal effects were negatively correlated genetically with body weight. Falconer (1955) reported that asymmetry of response to selection for 42-day weight in mice was due almost entirely to maternal influence.

From the data presented in Table XV (Page 56) for 12-day litter weights it can be concluded that maternal ability when measured as 12-day litter weight was reduced in LML but showed little change in HML. From the graphs in Figure 9 (page 60), it was apparent that maternal ability as measured by 21-day weight was reduced in both selection lines and, furthermore, that the response was not noticeably asymmetrical. This is in contrast to the results reported by Falconer (1955) and White, Legates and Eisen (1968). In their studies selection was based on 42-day weight which would tend to favor individuals lighter at 21-days which made more rapid gains from 21 to 42 days. This would explain in part the noticeable asymmetry in 21-day weight in studies in which selection was based on 42-day weight.

In the present study the selection criteria, hindleg muscle weight at 84 days, would not be expected to be influenced to a large degree by maternal environment. Since there is a decrease in 12-day litter weight in LML, maternal influence could contribute to a small degree to the asymmetry observed in this study but this contribution would not be expected to be very large. Furthermore, since there was a tendency for both selection lines to be lighter than the control line at 21 days, it would be possible that response to upward selection would be retarded whereas response to downward selection would be accelerated by maternal influence from birth to 21 days. These conclusions are in agreement with those made by White et al. (1968) who reported a small but significant decrease in maternal performance of a line selected for

increased 42-day weight.

Inbreeding Depression

According to Falconer (1953), "If the character selected is subject to inbreeding depression and the degree of inbreeding increases during the course of selection, an asymmetrical response will result because the inbreeding depression will reduce the change in the upward direction and increase the change in the downward." Body weight in mice is known to be subject to inbreeding depression. The average 56-day weights of the three inbred strains ($F_x \doteq 1.0$) in the original cross was approximately 23 g while the average 56-day weight of the non-inbred strain was 30.2 g indicating a depression of about 7 g.

The average inbreeding coefficients for each line in this study are given in Table XX. Inbreeding increased in all lines throughout the experiment, but it occurred at a faster rate in the selection lines than in the control line after generation three. Inbreeding depression could, therefore, account for some of the asymmetry observed in this study. The proportion of the asymmetry accounted for would depend on the degree to which the direct response of muscle weight and the correlated responses of the other traits were influenced by the rate of inbreeding.

Reproductive traits and maternal performance are known to be of low h^2 and subject to large inbreeding depression. Inbreeding, therefore, could account for much of the asymmetry observed in the reproductive traits and weights at 12 and 21 days. Measures of mature weight and carcass components are moderately to highly heritable and therefore would not be expected to exhibit large depressions due to an increase

TABLE XX

AVERAGE INBREEDING BY LINE AND GENERATION

Generation	Average Inbreeding Coefficient		
	Heavy-Muscle Line	Control Line	Light-Muscle Line
0		.125	
1	.188	.188	.188
2	.194 ± .01	.200 ± .01	.194 ± .01
3	.212 ± .020	.214 ± .017	.220 ± .020
4	.243 ± .043	.224 ± .026	.247 ± .044
5	.256 ± .043	.230 ± .012	.282 ± .055
6	.297 ± .038	.235 ± .020	.325 ± .074

in inbreeding under the assumptions of additive gene action and equal gene frequencies.

Wright (1951) proposed that if a character showed a change on inbreeding without selection, directional dominance must be present. Although muscle weight measures were not obtained on the original inbred lines, the large size differences between the inbred and non-inbred lines indicated that there was also a large difference in muscle weight even though no selection had been brought to bear on it directly. This would suggest that directional dominance was operating at some of the loci influencing the inheritance of muscle weight.

From the limited data in this study, statements relative to the actual genetic basis of the asymmetry cannot be conclusive. However, from a consideration of these five possible causes, it may be concluded that the asymmetry of both the direct and correlated responses was not due to only one of the causes but was possible due to an interaction of directional gene frequencies, directional dominance, inbreeding and subsequent maternal performances, and perhaps other factors yet unknown.

Crosses Between Selection and Control Lines

In generation five, matings were made in the selection lines as usual. In addition, a random control-line female was placed in each mating cage to obtain selection-line by control-line crossbred progeny. Table XXI compares the performances of the crossbred progeny with mid-parent values.

The progeny of 12 litters from HML x C exceeded the mid-parent value for all traits except 21-day weight indicating a possible

TABLE XXI

MIDPARENT AND PROGENY MEANS FOR CROSSES BETWEEN SELECTION LINE MALES AND CONTROL LINE FEMALES

Trait	Mid-parent Averages	HML x C	Mid-parent Averages	LML x C
21-day weight (g)	9.2 ± .15	9.1 ± .28	9.0 ± .14	8.6 ± .30
42-day weight (g)	23.3 ± .20	24.8 ± .30	22.0 ± .19	22.1 ± .35
ADG 21 to 42 days (g/d)	0.67 ± .01	0.73 ± .01	0.62 ± .01	0.63 ± .01
56-day weight (g)	26.0 ± .23	27.1 ± .30	24.1 ± .20	23.6 ± .38
84-day weight (g)	31.5 ± .76	32.2 ± .52	28.0 ± .61	27.4 ± .51
Muscle weight (g)	2.71 ± .09	2.82 ± .04	2.38 ± .07	2.42 ± .04
Percent Muscle	8.58 ± .14	8.75 ± .14	8.46 ± .16	8.83 ± .10

heterotic effect. The progeny of 14 litters from LML x C exceeded the mid-parent values for ADG, muscle weight and percent muscle but not for the other traits measured. Both crosses resulted in progeny that were superior to the high parent for percent muscle. Heterosis for proportion would be expected since traits with low h^2 tend to exhibit the most heterosis. However, the limited numbers in this analysis prevented conclusive statements as to whether this was an actual genetic effect or the result of sampling error.

Since all dams were from the control lines, an examination of litter size and 12-day litter weights could indicate the degree to which the line of sire made a significant genetic contribution to these components. Average litter size at three days was 9.92 ± 0.43 and 9.50 ± 0.68 for HML x C and LML x C, respectively. The difference of 0.42 mice per litter favored the HML x C but was not statistically significant. Twelve-day litter weights showed a similar trend with an average weight per litter of 50.4 g in HML x C and 48.5 in LML x C. These results suggested that the differences between the selection lines in average litter size and 12-day litter weights were primarily due to differences in maternal performance.

Body Composition Analysis

The 24 males sacrificed and dissected in each line in generation five were ground and sampled for body composition analysis to examine the extent to which selection had altered the relationship of moisture, protein, ether extract and ash. Total body composition for each line is presented in Table XXII.

As reflected by the data in Table XXII, body composition has not

TABLE XXII

BODY COMPOSITION ANALYSIS FOR EACH LINE
AFTER FIVE GENERATIONS OF SELECTION

Component	Average body composition (%)[a]			
	Heavy-Muscle Line	Control Line	Light-Muscle Line	Pooled SE
Protein	19.8	19.7	19.7	0.20
Ether Extract	5.5	5.6	5.2	0.30
Moisture	69.0	69.1	69.3	0.30
Ash	5.8	6.0	5.8	0.14
Number of Mice	24	24	24	

[a] None of the differences in composition among lines were significant.

been altered to a significant degree by selection for hindleg muscle weight. These values for protein and ash agree in general with many published reports which give a range of 18 to 21% for protein and 3 to 6% for ash (Fowler, 1958; Hull, 1960; Biondini, Sutherland and Haverland, 1968; Robinson and Bradford, 1969; and Timon, Eisen and Leatherwood, 1969). A majority of these reports, however, reported proportion of ether extract as high as 15 to 18% and moisture as low as 55 to 60% for lines of mice selected for increased weight or grain. Timon, Eisen and Leatherwood (1970) reported percent ether extract in 57-day-old mice of 6.59% for unselected controls and 8.98% for mice selected for fast gain.

Although these data (based on only one generation out of six) are inconclusive, it may be hypothesized that selection based directly on muscle weight has effectively increased the size of the muscle and mature weight without increasing the rate of fat deposition. This hypothesis would be in line with conclusions made by Hull (1960) on data from three lines of mice selected for body weight at 21, 32 and 42 days, respectively. The three different programs of selection produced highly significant differences in the proportion of abdominal fat. Percent fat decreased as age at selection increased.

The value of studies with laboratory organisms lies in the more rapid and efficient accumulation of information relative to the basis of inheritance of a quantitative trait. From this selection study of the response to divergent selection for hindleg muscle system weight in mice, some answers have been obtained, yet other questions have been asked.

Direct selection for muscle weight in livestock species would be

expected to result in an increase in total muscle weight. This increase in muscle weight would, in all likelihood, be accompanied by a corresponding change in the live weight of the species. However, the asymmetry of response observed in this study suggested that response to selection for increased muscle weight would be lower than what would be expected if expected response was based on h^2 estimates of muscle weight obtained from the resemblances between relatives.

One question posed by this study was whether or not selection for proportion of muscle would be effective. From the data obtained in this study, the low variance of percent muscle (ratio of hindleg muscle weight to 84-day weight) would render such selection subject to large sampling errors. However, selection for increased and decreased muscle weight resulted in a significant divergence in the selection lines for percent muscle. It appeared, therefore, that some progress could be expected from direct selection pressure applied to proportion of a particular muscle or group of muscles. Furthermore, crosses between selection line males and control line females suggested a possible heterotic effect for proportion of hindleg muscle weight.

The large dam component of variance observed for the traits measured in this study poses another problem on which future studies could provide answers. Adequate estimation of the causal components of this source of variation could increase the effectiveness of breeding programs designed to produce meat animals that would be more efficient producers of retail product.

CHAPTER V

SUMMARY

From a base population of albino mice derived from a four-way cross of three inbred and one non inbred strain, two divergent selection lines in which selection was based on heavy and light hindleg muscle weights and two random mating control lines were initiated for a selection study of the inheritance of hindleg muscle weight in mice. In each selection line 24 males (which had previously been mated to two females) were slaughtered at 84 days of age and the hindlegs were dissected from the body. The muscle systems of the hindlegs were then separated from the bone and weighed. The half-sib families produced by these males were ranked from one to 24 based on the weight of the hindleg muscle systems of the sire and the respective selection criteria in each line. Four males (two from each litter when possible) were selected at random from each of the six highest ranking half-sib families in each line to obtain the 24 males for the next generation. All females were saved from these same half-sib families with additional females (as needed to obtain the necessary 48,) coming from the next ranking half-sib families (usually the next two). From the 20 control-line males randomly selected to perpetuate each control line, 24 (12 from each line) were selected at random for muscle weight determinations. In addition, a hierarchal design involving the full- and half-sib progeny of 31 generation five control-line sires was used to estimate the genetic parameters in the base population.

From the variance-covariance analysis of the base population, the estimate of the h^2 of hindleg muscle weight was 0.44 $\pm$ 0.18 indicating that genetic variation existed in the base population for hindleg muscle weight. Furthermore, the estimate of the genetic correlation (r_g) between muscle weight and 84-day weight was large and positive (1.32). The genetic correlation between hindleg muscle weight and weight at 56 days of age was also large and positive. Estimates of r_g between hindleg muscle weight and weight at 42 days of age and between hindleg muscle weight and average daily gain from 21 to 42 days of age were essentially zero.

Divergent selection for muscle weight resulted in significant ($P < .01$) response in both directions. After six generations of selection, muscle weight means were 2.82, 2.66 and 2.11 g for the heavy-muscle line (HML), control line, and light-muscle line (LML), respectively. The divergence of 0.71 between the selection lines represented 28.4% of the initial muscle weight mean. As deviations from the control line, the response in HML was 0.16 g while the response realized in LML was -0.55 g. Cumulative selection differentials were 1.73 and -1.18 for HML and LML, respectively. When selection response as deviations from the control line was regressed on cumulative selection differential, the estimates of realized h^2 were 0.18 $\pm$ .08, 0.88 $\pm$ .20 and 0.45 $\pm$ .07 for upward, downward and divergent selection, respectively.

Correlated response in 84-day weight exhibited a parallel asymmetry in that HML exceeded the control line by 2.10 g and LML was lighter than the control line by 5.40 g. When calculated from the correlated response in 84-day weight, the genetic correlation between hindleg muscle weight and 84-day weight was 0.74 $\pm$ .12.

Correlated responses were also measured in live weights at 21, 42 and 56 days of age as well as average daily gain (ADG) from 21 to 42 days of age. The correlated responses in these traits were, in general, in the same direction and followed the same trend as the direct response of hindleg muscle weight. Mice from HML were heavier at all three periods and tended to gain faster than LML. The differences between the mean weights of the selection lines increased as age increased within each generation. Asymmetry in favor of selection for light hindleg muscle system weight was noted in all of the correlated responses measured with the exception of 21-day weight. At 21 days HML exceeded LML, but both lines tended to be lower than the control line. After 21 days, HML exceeded the control line although in most cases the differences were not significant. LML was significantly ($P < .05$) lighter than both HML and the control line for 21, 42 and 56-day weights. LML also gained slower than the other two lines. Throughout the experiment, LML continued to decrease in all correlated traits whereas HML showed little increase over the control line mean.

Reproductive performance was significantly reduced in LML but was not noticeably altered in HML. Average number of live born per litter after six generations of selection were 9.68, 9.73 and 8.95 for HML, control and LML, respectively. Average 12-day litter weights for litters of eight mice each were 50.8, 50.5 and 48.4 g for HML, control and LML, respectively, indicating a significant ($P < .01$) depression of maternal performance to 12 days in LML but little change in HML.

The asymmetrical nature of both the direct and correlated responses suggested that an interaction of directional gene frequencies, directional dominance, inbreeding depression and maternal influences

inhibits progress to selection for increased muscle weight and produces a more rapid response to selection for decreased muscle weight.

The 24 mice sacrificed and dissected in each line in generation five were frozen, ground and sampled for body composition analysis to determine if any changes had occurred in the relative proportions of protein, ether extract, moisture and ash. Results indicated that no noticeable changes had occurred in either of the selection lines after five generations of divergent selection for hindleg muscle weight.

LITERATURE CITED

Bailey, C. B., W. D. Kitts and A. J. Wood. 1960. Changes in the gross chemical composition of the mouse during growth in relation to the assessment of physiological age. Can. J. Anim. Sci. 40:143.

Bell, A. E., C. H. Moore and D. C. Warren. 1955. The evaluation of new methods for the improvement of quantitative characteristics. Cold Spring Harbor Symp. on Quant. Bio. 20:197.

Biondini, P. E., T. M. Sutherland and L. H. Haverland. 1968. Body composition of mice selected for rapid growth rate. J. Anim. Sci. 27:5.

Blunn, Cecil T. and Marvel L. Baker. 1947. The relation between average daily gain and some carcass measurements. J. Anim. Sci. 6:424.

Brackelsberg, P. O., E. A. Kline, R. L. Willham and L. N. Hazel. 1971. Genetic parameters for selected beef carcass traits. J. Anim. Sci. 33:13.

Butterfield, R. M. 1965. Relationship of carcass measurements and dissection data to beef carcass composition. Res. Vet. Sci. 6:24.

Chapman, A. B. 1951. Effectiveness of selection in laboratory animals. J. Anim. Sci. 10:3.

Clayton, G. A., G. R. Knight, J. A. Morris and Alan Robertson. 1956. An experimental check on quantitative genetical theory. III. Correlated responses. J. Genet. 55:171.

Conover, W. J. 1971. Practical Nonparametric Statistics. John Wiley and Sons, Inc. New York. pp. 245-249.

Cundiff, L. V., K. E. Gregory, R. M. Koch and G. E. Dickerson. 1969. Genetic variation in total differential growth of carcass components in beef cattle. J. Anim. Sci. 29:233.

Dickerson, G. E. 1955. Genetic slippage in response to selection for multiple objectives. Cold Spring Harbor Symp. on Quant. Bio. 20:213.

Eisen, E. J., J. E. Legates and O. W. Robison. 1970. Selection for 12-day litter weight in mice. Genetics 64:511.

Elliott, D. S., J. E. Legates and L. C. Ulberg. 1968. Changes in the reproductive processes of mice selected for large and small body size. J. Reprod. Fert. 17:9.

Englert, DuWayne C. and A. E. Bell. 1969. Components of growth in genetically diverse populations of Tribolium castaneum. Can. J. Genet. Cytol. 11:896.

Falconer, D. S. 1953. Selection for large and small size in mice. J. Genet. 51:470.

Falconer, D. S. 1954. Validity of the theory of genetic correlation. J. Heredity. 45:42. Reprint.

Falconer, D. S. 1955. Patterns of response in selection experiments with mice. Cold Spring Harbor Symp. on Quant. Bio. 20:178.

Falconer, D. S. 1960a. Introduction to Quantitative Genetics. Ronald Press Co., New York.

Falconer, D. S. 1960b. Selection of mice for growth on high and low planes of nutrition. Genet. Res. 1:91.

Festing, Michael F. and A. W. Nordskog. 1967. Response to selection for body weight and egg weight in chickens. Genetics 55:219.

Fowler, Ruth E. 1958. The growth and carcass composition of strains of mice selected for large and small body size. J. Agr. Sci. 51:137.

Frahm, Richard R. and Ken-Ichi Kojima. 1966. Comparison of selection responses on body weight under divergent larval density conditions in Drosophila pseudoobscura. Genet. 54:625.

Gall, G. A. E., W. H. Kyle, J. C. Rogler and V. L. Anderson. 1967. Genetic parameters of protein metabolism and growth in mice. Genetics 56:215.

Hazel, L. N., Marvel L. Baker and C. F. Reinmiller. 1943. Genetic and environmental correlations between the growth rate of pigs at different ages. J. Anim. Aci. 2:118.

Hetzer, H. O. and W. R. Harvey. 1967. Selection for high and low fatness in swine. J. Anim. Sci. 26:1244.

Hull, P. 1960. Genetic relations between carcass fat and body weight in mice. J. Agr. Sci. 55:317.

James, J. W. 1965. Response curves in selection experiments. Hered. 20:57.

Joubert, D. M. 1956. An analysis of factors influencing postnatal growth and development of the muscle fiber. J. Agr. Sci. 47:59.

Krider, J. L., B. W. Fairbanks, W. E. Carroll and E. Roberts. 1946. Effectiveness of selecting for rapid and slow growth rate in swine. J. Anim. Sci. 5:1.

Lang, B. J. and J. E. Legates. 1969. Rate, composition and efficiency of growth in mice selected for large and small body weight. Theor. App. Genet. 39:306.

Lassiter, J. W., A. E. Cullison and J. L. Carmon. 1960. Variations in body composition of mice having the same average gain. J. Anim. Sci. 19:769.

Luff, A. R. and G. Goldspink. 1971. Total number of fibers in muscles of several strains of mice. J. Anim. Sci. 30:891.

MacArthur, John W. 1944. Genetics of body size and related characters. Am. Natur. 78:142.

MacArthur, John W. 1949. Selections for small and large body size in the house mouse. Genetics 34:194.

Masters, C. J. 1963. Nucleic acids and protein stores in Merino sheep. Aust. J. Biol. Sci. 16:192.

Mather, Kenneth. 1955. Response to selection. Cold Spring Harbor Symp. on Quant. Bio. 20:158.

Moore, R. W., E. J. Eisen and L. C. Ulberg. 1970. Prenatal and postnatal maternal influences on growth in mice selected for body weight. Genetics 64:59.

Orme, L. E., J. W. Cole, C. M. Kincaid and R. J. Cooper. 1960. Predicting total carcass lean in mature beef from weights of certain entire muscles. J. Anim. Sci. 19:726.

Palsson, Halldor. 1955. Conformation and body composition. In Progress in the Phisiology of Farm Animals, J. Hammond, ed. Butterworths Scientific Publications, London. pp. 521-529.

Robertson, Alan. 1959. The sampling variance of the genetic correlation coefficient. Biometrics 15:469.

Robertson, Forbes W. 1955. Selection response and the properties of genetic variation. Cold Spring Harbor Symp. on Quant. Bio. 20:166.

Robinson, D. W. and G. E. Bradford. 1969. Cellular response to selection for rapid growth in mice. Growth 33:221.

Robinson, D. W. and L. J. Lambourne. 1970. The influence of growth rate and retardation on the nucleic acid and nitrogen concentration in skeletal muscles and whole body composition of the mouse. Growth 34:235.

Staats, Joan. 1966. The laboratory mouse. In Biology of the Laboratory Mouse, 2ed., Earl L. Green, ed. McGraw-Hill Book Company, New York. pp. 1-10.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., New York.

Timon, V. M., E. J. Eisen and J. M. Leatherwood. 1970. Comparisons of ad libitum and restricted feeding of mice selected and unselected for postweaning gain. II. Carcass composition and energetic efficiency. Genetics 65:145.

White, J. M., J. E. Legates and E. J. Eisen. 1968. Maternal effects among lines of mice selected for body weight. Genetics 60:395.

Wright, S. 1951. The genetic structure of populations. Ann. Eugenics 15:323.

APPENDIX

TABLE XXIII

GENERATION MEANS BY LINE AND SEX FOR PERFORMANCE TO 56 DAYS

Gen.	Trait[1]	Heavy-Muscle Line		Control Line		Light-Muscle Line	
		Males	Females	Males	Females	Males	Females
1	Number	65	55	169	141	64	56
	21-day wt.	10.7 ± .15	10.4 ± .13	11.0 ± .10	10.9 ± .11	10.7 ± .12	10.7 ± .17
	42-day wt.	26.9 ± .27	22.8 ± .21	26.5 ± .15	22.4 ± .15	26.2 ± .26	22.1 ± .23
	ADG (21-42)	0.71 ± .01	0.84 ± .01	0.73 ± .01	0.54 ± .01	0.72 ± .01	0.53 ± .01
	56-day wt.	28.1 ± .76	23.7 ± .61	29.4 ± .19	24.0 ± .18	29.2 ± .29	24.0 ± .27
2	Number	50	52	146	124	59	44
	21-day wt.	10.8 ± .12	10.4 ± .17	10.3 ± .12	10.5 ± .12	10.3 ± .20	10.1 ± .12
	42-day wt.	27.4 ± .22	22.8 ± .24	22.5 ± .16	22.5 ± .12	24.8 ± .29	21.0 ± .22
	ADG (21-42)	0.79 ± .01	0.58 ± .01	0.57 ± .01	0.68 ± .01	0.50 ± .01	0.50 ± .01
	56-day wt.	29.9 ± .34	24.5 ± .26	24.9 ± .16	24.6 ± .16	27.4 ± .31	22.5 ± .23
3	Number	77	60	157	153	57	69
	21-day wt.	9.3 ± .15	9.2 ± .20	9.4 ± .11	9.6 ± .11	9.3 ± .17	8.6 ± .18
	42-day wt.	25.3 ± .27	21.7 ± .28	24.8 ± .18	21.4 ± .14	23.2 ± .22	19.6 ± .34
	ADG (21-42)	0.75 ± .01	0.58 ± .01	0.72 ± .01	0.56 ± .01	0.70 ± .01	0.52 ± .01
	56-day wt.	28.5 ± .28	23.5 ± .35	27.2 ± .18	22.8 ± .19	25.7 ± .27	21.2 ± .36

[1] weights in grams, ADG in grams per day.

TABLE XXIII

(CONTINUED)

Gen.	Trait[1]	Heavy-Muscle Line		Control Line		Light-Muscle Line	
		Males	Females	Males	Females	Males	Females
4	Number	50	53	146	146	53	52
	21-day wt.	8.6 ± .20	8.1 ± .18	8.6 ± .16	8.7 + .11	7.6 ± .16	7.4 ± .17
	42-day wt.	24.6 ± .29	20.8 ± .22	23.7 ± .17	21.1 ± .13	21.5 ± .20	19.2 ± .23
	ADG (21-42)	0.76 ± .01	0.60 ± .01	0.72 ± .01	0.58 ± .01	0.66 ± .01	0.50 ± .01
	56-day wt.	27.8 ± .35	22.9 ± .25	26.7 ± .20	22.6 ± .16	23.9 ± .21	19.6 ± .27
5	Number	31	48	152	160	70	52
	21-day wt.	9.5 ± .24	8.7 ± .20	9.6 ± .10	9.2 ± .10	8.9 ± .16	8.3 ± .17
	42-day wt.	25.8 ± .34	22.0 ± .21	24.9 ± .15	21.6 ± .14	22.3 ± .22	18.6 ± .24
	ADG (21-42)	0.77 ± .01	0.63 ± .01	0.74 ± .01	0.58 ± .01	0.64 ± .01	0.49 ± .01
	56-day wt.	24.7 ± .38	24.5 ± .24	27.7 ± .17	23.2 ± .14	24.6 ± .26	20.5 ± .23
6	Number	31	35	294	311	28	26
	21-day wt.	8.6 ± .35	8.7 ± .34	9.5 ± .10	9.3 ± .10	8.3 ± .19	7.9 ± .18
	42-day wt.	27.3 ± .59	23.5 ± .29	25.1 ± .20	22.6 ± .12	22.1 ± .42	17.8 ± .34
	ADG (21-42)	0.89 ± .02	0.70 ± .02	0.74 ± .01	0.66 ± .01	0.65 ± .02	0.47 ± .02
	56-day wt.	31.0 ± .70	24.8 ± .40	28.8 ± .14	24.2 ± .12	23.9 ± .52	18.9 ± .43

1 Weights are in grams, ADG is in grams per day.

TABLE XIV

MEANS, STANDARD DEVIATIONS (SD) AND COEFFICIENTS OF VARIATION (CV) FOR NINE TRAITS STUDIED IN VARIANCE-COVARIANCE ANALYSIS OF CONTROL LINE

	21-day weight (g)	42-day weight (g)	ADG 21-42 (g/day)	56-day weight (g)	84-day weight (g)	Hindleg weight (g)	Bone weight (g)	Muscle weight (g)	Percent muscle
POOLED[1]									
Mean	9.33	23.83	0.69	26.42					
SD	0.79	1.50	0.07	1.60					
CV (%)	8.57	6.31	9.58	6.04					
118 MALES[2]									
Mean	9.38	25.19	0.76	28.54	30.75	3.09	0.37	2.66	8.65
SD	0.77	1.67	0.08	1.72	1.89	0.20	0.04	0.18	0.45
CV (%)	8.25	6.62	9.92	6.04	6.14	6.51	11.46	6.88	5.25

[1] Values for 232 males and 222 females used in pooled within sex analysis.
[2] Values for 118 males slaughtered.

TABLE XXV

ESTIMATES OF HERITABILITY, GENETIC CORRELATION AND PHENOTYPIC CORRELATION FOR VARIANCE-COVARIANCE ANALYSIS OF MALES AND FEMALES SEPARATELY

	MALES			
	21-day weight	42-day weight	ADG 21-42	56-day weight
21-day weight	0.09 ± .08	-1.74 ± .59	-1.45 ± .63	0.49 ± .16
42-day weight	0.35**	0.23 ± .09	1.02 ± .42	1.34 ± .26
ADG 21-42	-.16*	0.86**	0.56 ± .10	0.78 ± .03
56-day weight	0.46**	0.53**	0.32**	0.27 ± .12

	FEMALES			
	21-day weight	42-day weight	ADG 21-42	56-day weight
21-day weight	x	x	x	x
42-day weight	0.53 **	0.06 ± .08	2.93 ± .67	x
ADG 21-42	-.35**	0.61**	0.33 ± .11	x
56-day weight	0.45**	0.81**	0.47**	x

x Unavailable due to a negative sire component for 21 and 56-day weights.

* ($P < .05$). ** ($P < .01$).

VITA

C. Reid McLellan, Jr.

Candidate for the Degree of

Doctor of Philosophy

Thesis: RESPONSE TO DIVERGENT SELECTION FOR HINDLEG MUSCLE SYSTEM WEIGHT IN MICE

Major Field: Animal Breeding

Biographical:

Personal Data: Born in Shreveport, Louisiana, November 12, 1945, the son of Dr. and Mrs. C. R. McLellan, Sr.; married Mary Lana Bernard, May 28, 1967; the father of one daughter, Loveda Noelle, and one son, Reid Bernard (Bucky) McLellan.

Education: Received the Bachelor of Science Degree from Louisiana State University in May, 1967, with a major in Animal Science. Received the Master of Science Degree from Oklahoma State University in May, 1970, with a major in Animal Science.

Experience: Reared on a farm in South Louisiana; served as part-time pastor of the Christian and Missionary Alliance Church, Stillwater, August 1969 to September 1971; Graduate Assistant, Oklahoma State University, 1967-1971.

Professional Organizations: American Society of Animal Science, The Biometric Society (ENAR) and The Society of Sigma Xi.

Date of Degree: May, 1972