GENETIC PARAMETERS OF LYSINE REQUIREMENT BY THE CHICK

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ABSTRACT

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By

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Among the common plant protein sources of the world, only soybean meal is rich in lysine. When soybean oil meal is unavailable or it is not economically feasible to include it in the growth diet of monogastrics such as chicks, rats and man, lysine is the first-limiting amino acid for growth. This experiment was designed in an attempt to improve the efficiency and growth rate of chicks on low lysine diets. A bi-directional selection experiment was conducted to evaluate the magnitude of genetic mechanisms regulating lysine requirement.

A heterogenic base population of egg-type chickens was randomly separated into four lines and each line was closed with regard to matings for each subsequent generation. Data from four generations plus the base population were evaluated for each line selected for either high or low growth rate in a lysine deficient dietary environment. A third line identified as a natural selection line was maintained by random matings among survivors of those fed the lysine deficient diet. The fourth line, a random control line, was

reproduced by random matings among individuals fed only the control diet.

The control diet utilized in this experiment was formulated to be adequately balanced with all known nutrients for optimum growth of chicks and it had a 1.0 percent lysine level. The deficient diet was identical in composition to the control except that it contained only 0.5 percent lysine.

Full sibs of the same sex were randomly divided with regard to opportunity to express their growth potential in each of the two nutritional environments. Juvenile growth rate (measured as the gain from one day to three weeks of age) was analyzed for diet, sex, generation and line differences. Realized heritability computed as deviations from the random control line as measured in the lysine deficient environment was 1.33 for the line under natural selection, .10 for the high growth rate selected line and -.19 for the low growth rate selected line.

The component of variance procedure for estimating heritability provided slightly higher estimates than those computed as realized heritability. In the 0.5 percent lysine deficient environment average heritability estimates were .23 from the sire source of variance, .26 from the dam and .25 from the combined sire plus dam component of variance. Contemporary full-sibs were fed the 1.0 percent lysine control diet and heritability estimates from the component of

variance method were .35, .39 and .37, respectively, for sire, dam and combined sire plus dam sources of variance.

Reciprocal cross line progeny were analyzed in comparison to pure line progeny from the second, third and fourth generations. A highly significant diet by line interaction effect was shown and the cross line progeny always grew best in the 1.0 percent lysine control environment. For two of the three generations, pure line progeny grew better than the cross line progeny in the 0.5 percent lysine environment. Cross line progeny showed a positive heterosis and it was calculated to average 17 percent in the nutritionally adequate environment with (1.0% lysine) and a negative heterosis averaging five percent for cross line progeny in the deficient environment with 0.5 percent lysine available from the ration.

Results of this short-range experiment to alter the lysine requirement of chicks for growth indicate that mass selection as a technique was relatively inefficient. However, heritability estimates and the expression of heterosis among cross line progeny indicate the need for further research using large numbers per line, applying greater selection pressure and the utilization of a more rapidly growing broiler type stock.

In each generation, mortality was higher for chicks fed the 0.5 percent lysine diet than for those fed the 1.0 percent lysine diet. Males exhibited a higher mortality rate on the 0.5 percent lysine diet

while females had the highest mortality rate when grown in the 1.0 percent lysine environment. From an analysis of differences in fertility, hatchability, egg production and adult livability rates, it was apparent that the 0.5 percent lysine diet fed during the early growth period, one day to three weeks of age, had no latent consequences or long-range manifestations.

GENETIC PARAMETERS OF LYSINE REQUIREMENT BY THE CHICK

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Howard Lee Enos

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CHAPTER I

INTRODUCTION

In the face of an increasing world population, poultry raising must meet several challenges, and among these, the greatest is that of competing with man for food. Unquestionably, poultry maintains high status by its efficiency in converting feedstuffs to high quality meat and eggs needed to feed the human population. However, poultry daily consume large quantities of cereal crops, thereby threatening their own existence as they compete directly with man for foodstuffs. This dictates the necessity of increasing the conversion efficiencies of poultry and is one challenge to the poultry scientist of today.

Differences in individual requirements based upon the physiological ability to utilize certain diets may be traced to the genetic constitution of an individual or a family. Many instances arise in nutritional studies where birds grow and lay at comparable rates under similar environments but react at varied rates to nutritional stresses. Why do certain birds show resistance to deficiencies in the ration, while others react quickly to them? Why do some birds perform well on a given nutrient level, while others show definite

lags in growth and production performance? It seems important, then, that geneticists study these differences to elicit more efficient utilization of nutrients.

A population of organisms with variable genetic backgrounds, as well as individuals within a species, have independent and distinctive nutritional requirements which must be met for optimum well being. The importance of these differences depends clearly upon the degree and cause of the variability among individuals.

Theoretically, additional knowledge of genetic variability for the utilization of specific amino acids would enhance breeding progress and the development of strains of birds which may more efficiently utilize feed for growth and other performance characteristics. The individual and family traits identified under dietary stressing conditions would establish selection criteria to assist in the development of genetically more uniform stock according to its inherent ability to utilize nutrients in the ration.

Lysine ($C_6H_{14}N_2O_2$), was selected as the amino acid for investigation because it is essential for growth of chicks (Almquist, 1957). The L-isomer is the only biologically active form utilized by the chick (N.R.C., 1960) and by man (Ryan & Wells, 1964), therefore, L-lysine is the nutrient being considered. L-lysine is unlike other amino acids and is a desirable nutrient for study because it is believed to exist biochemically as a single component required to

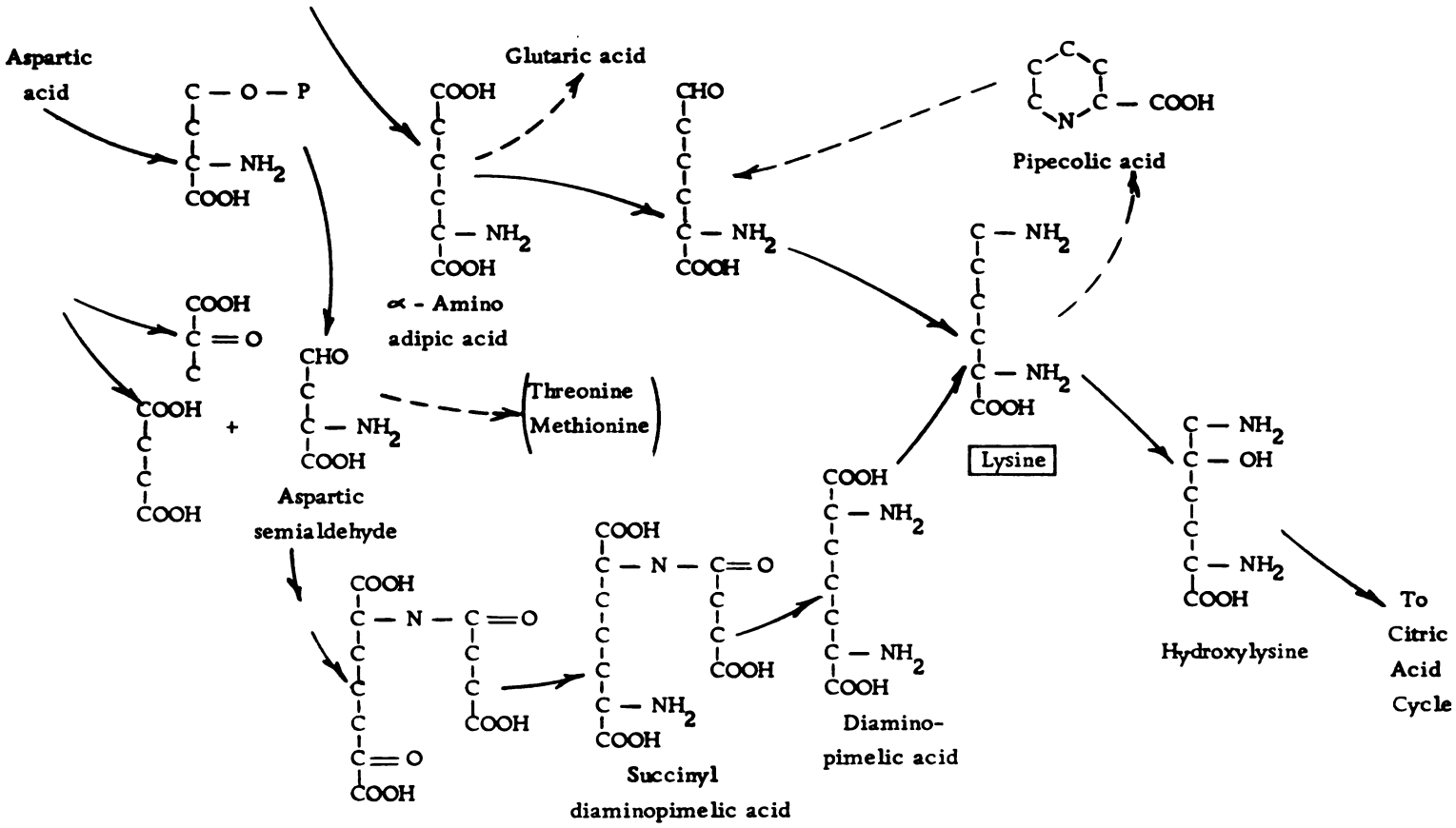
support metabolic activity, and this amino acid (L-lysine) is not known to be "spared" by other nutrients in the diet.

Among the common plant protein sources of the world, only soybean oil meal is rich in lysine (Almquist, 1957; Dean and Scott, 1965; Merck, 1961; Morton and Amoroso, 1967 and Nyhan, 1967). When soybean oil meal is unavailable or it is not economically feasible to include it in the growth diet of chicks, lysine is the first-limiting amino acid for growth. Lysine is also the first-limiting amino acid for growth of young children and some other monogasteric (single stomach) species when the daily protein intake is predominately of the following cereal grain or legume: corn, wheat, rice, peanut meal or zein.

A survey of physiology and biochemical texts as well as other sources of information failed to identify the biosynthesis of lysine with other nutrients, enzymes or hormonal systems. Recently, Nesheim (1969) said "It appears that the chick may have two pathways of lysine degradation." Fig. 1 is redrawn from Wagner and Mitchell (1964) for the reader's inspection; attention is called to the independent nature of lysine or the need of lysine before the metabolic process may continue into the citric acid cycle.

The impending consequence of the world's population and food supply situation requires scientific consideration of the genetic-nutrional interrelationship to avoid a crisis of disease and starvation. In addition, acknowledgment of the independent role of the

Fig. 1. Pathways for biosynthesis of lysine



Source: Wagner & Mitchell 1964

amino acid lysine as a component of protein metabolism motivated the author to develop experiments with the chick as a laboratory tool. Consequently the following objectives were designed into an experiment:

1. To demonstrate that lysine requirement is inherited by selecting divergent lines through mass selection for growth rate.
2. To evaluate the genetic parameters for lysine requirement as expressed through growth and to estimate heritability of the trait.
3. To investigate the latent effects of a low lysine diet consumed during early growth and the consequence of imbalanced dietary protein intake during early growth on reproductive performance.

CHAPTER II

REVIEW OF LITERATURE

As early as 1902 Sir Archibald Garrad recognized significant variability for metabolic function and he called these findings "inborn errors of metabolism". A few years later Mendel (1915) recognized lysine as the first-limiting amino acid of the diet for growth.

In Mendel's (1915) experiments, the rats being fed zein as the sole source of protein lost weight and died. With the addition of the amino acid tryptophan, life was sustained for experiments six months in duration and the rats showed essentially no change in body weight. Gordon (1963) using the chick in a 200 day feeding trial confirmed Mendel's work. When the zein-trypotophan diet was supplemented with lysine in subsequent experiments, growth and body weight change occurred. From this experiment it was concluded that lysine was the first-limiting amino acid for growth, a finding also in agreement with Almquist, (1957) Schwartz et al. (1958), Dean and Scott (1965), and others.

Numerous studies of genetic-nutritional interrelationships have been reported among a wide range of organisms. Beadle and Tatum (1941) found different nutritional requirements between strains, and within strains, of Neurospora. These researchers concluded that

different mutations block specific chemical steps in the biochemical reactions which make up the patterns of metabolism. Mitchell and Houlahan (1946) demonstrated that a "riboflavinless mutant" strain of Neurospora had different and variable quantities of a particular enzyme, and when deficient of the enzyme it did not synthesize adequate riboflavin. Because it was found that between and within strain variation existed these workers proposed the theory of "leaky genes", a concept also described as "partial genetic blocks".

The text Genetics and Metabolism by Wagner and Mitchell (1955) is recognized as the initial attempt to organize the literature on this subject. Cited in their book, and from their own scientific papers, Wagner and Mitchell (1955) reported that in one group of five closely related species of Drosophila, three of the species were different from one another in respect to their nutritional requirement.

In mammals, variations in nutrient requirement and utilization have also been demonstrated. Marked differences between strains of inbred rats have been shown for thiamine utilization, and a series of two-way selection experiments for body size in mice (Falconer and Latyszewski, 1952; and Falconer, 1960) showed significant variation for feed utilization on high and low planes of nutrition. Their studies showed the differences in growth and feed utilization to represent attainable genetic parameters.

In man, Williams (1951) identified a genetic weakness in the metabolic system which tended to enhance chronic alcoholism. Vitamin B deficiencies have been determined as one of the main causes of the alcoholic problem. Williams (1956) demonstrated that laboratory rats had a high degree of individuality for alcohol consumption. Inbred lines were uniform among individuals of the same line but the lines were distinctly different in their consumption patterns.

Phenylketonuria in man is genetically linked to a deficiency of the enzyme phenylalanine hydroxylase (Wallace et al., 1957). More recently, Colombo et al. (1964) and Ghadimi et al. (1965) described a condition called "hyperlysinemia" in children, and these researchers found similar biochemical abnormalities among clinical patients. The cases reported to date of hereditary hyperlysinemia (Nyhan, 1967) have a high incidence of consanquinity of the parents. Children showing a mild case of lysine intolerance are mentally retarded, while those with a severe lysine intolerance usually die. Ryan and Wells (1964) identified a hereditary block in a subsidiary pathway which inhibits lysine metabolism. These types of inherited metabolic variations are probably more prevalent in animals and man than has yet been reported.

Perhaps the classic example of genetic differences for metabolic functions within the classes of a species is found in the Dalmatian dog. High volumes of uric acid are excreted in the urine of higher

primates, such as man and chimpanzee, and also by the Dalmatian dog. The Dalmatian is unlike other carnivores which excrete low quantities of uric acid and a higher proportional volume of allantoin (Friedman and Byers, 1948). Among dogs, the difference was resolved by determining that uric acid is not efficiently reabsorbed in the kidneys of the Dalmatian as it is for other dogs. It appears that this intra-species difference is genetically based and may or may not be directly involved with some enzyme process which influences the transport of uric acid through the cell membranes.

The chicken is a superior laboratory animal and has been studied extensively. Results of many investigations show that its ability to withstand certain types of dietary deficiencies is inherited. These differences have been demonstrated between (and within) strains, breeds, and strain crosses. A specific example from the area of vitamin nutrition is the report of Lamoreux and Hutt (1948). They demonstrated, with five generations of selection, differences for the utilization of riboflavin within the Single Comb White Leghorn breed. In considering further the inherited differences for vitamin, mineral, protein and amino acid requirements in poultry, the reader is referred to comprehensive reviews by Lerner (1958) and Nesheim (1966). The following citations deal with the variation of performance for the amino acids and are considered to have more than a casual relationship to lysine, the topic of this dissertation.

Griminger (1955) reported that the requirement for either DL-methionine, L-tryptophan, or L-lysine did not vary for rapid or slow-growing chicks. The study, however, did not compare the genetic influence on chicks for differences in their ability to utilize these nutrients. A later study (Griminger and Fisher, 1962) showed significant differences among dams in the growth potential of their offspring on arginine and lysine-deficient diets.

Nesheim and Hutt (1962) reported strain differences in the arginine requirement among Single Comb White Leghorn chickens. Subsequent selection and testing (Hutt and Nesheim, 1966) showed that the two lines were widely different in their arginine requirement but, when tested for biological efficiency, the lines were not significantly different. More recently, Hutt and Nesheim (1967) stated that, following four generations of selection for high and low arginine utilization, and by backcrossing to produce F_1 individuals, they acquired intermediates, "as in typical polygenic inheritance".

Hess et al. (1962) reported an experiment in which selection for growth rate differences on a methionine-deficient diet was considered. The experimental results indicated widespread differences between the F-line (fast-growing) and the S-line (slow-growing) as measured by body weight at three weeks of age. In a more recent report, Wilson and Hess (1968) confirmed that "selection was quite effective in separating high and low three-week body weight lines

on both normal and methionine deficient diets." However, genetic differences for methionine requirement were not conclusively shown following a series of three-week growth trials. In their studies four selected lines and a control were tested in a factorial design over three generations on both methionine deficient and adequately supplemented rations. The conclusion, following a series of growth trials on graded levels (0.19, .29, .39, .49, .59, and .69 percent) of methionine, was that differences in growth rate were linked with appetite and not due to a change in methionine requirement.

Williams and Grau (1956) reported better growth on any lysine level with a reduction of dietary energy simply through stimulation of feed intake. Lowering the energy concentration did not change the lysine requirement proportional to other nutrients but did influence the growth response on low level lysine diets. Although numerous workers have reported that dietary protein level influences the response of chicks at various ages to amino acid level, the requirement may vary in exact proportion of the amino acid content of the diet to the total protein available. Singsen et al. (1965) reported that a lysine deficient diet (0.59 percent lysine) fed to four weeks of age effectively retarded the onset of egg production among meat-type chickens. Mortality was not significantly affected by the lysine-deficient ration, while skeletal weight was slightly less but approached

"normal". Tissue weight was approximately one third that of (normal) control birds.

Evidence of an apparent inherited difference for lysine was provided by Enos and Moreng (1965). Individuals, representing different pedigreed sire families, exhibited significant differences in growth rate to four weeks of age when consuming a dietary lysine deficient ration. More recently, Godfrey (1968) reported low heritability for lysine utilization in Japanese quail (Coturnix coturnix japonica). At generations eight and ten in his experiment the D (deficient lysine) line consumed significantly more feed and grew significantly faster than either the F (full lysine) line or the C (control) line. Even though continued selection did not change the mean performance on the deficient diet, he concluded that the lysine requirement must have changed, but that it required the better environment for expression of the genetic change.

After the present experiment was designed and particularly during 1966-1968, a host of scientific papers appeared on the relationship between various amino acids and especially the antagonism between arginine and lysine. When the dietary imbalance among amino acids is great, or when the lysine level is excessive (more than 1.0 percent), chicks show marked increases in their arginine requirement.

Authors of the following citations have considered the problem of arginine-lysine antagonism: Jones (1961 and 1964), Boorman and

Fisher (1966), O'Dell and Savage (1966), Smith and Lewis (1966), Jones et al. (1967), Dean and Scott (1968), Hill and Shao (1968), Nesheim (1969), Smith (1968) and Squibb (1968); however, in these experiments, excess lysine was the problem. To this author's knowledge only Hill and Shao (1968) have considered the reverse situation of an antagonistic response when a lysine deficiency exists. Hill and Shao (1968) included in their study lysine as the first-limiting amino acid, and it resulted in a reduction of weight gain. They also reported that with high arginine levels in the diet and an existing lysine deficiency, the consequence of the imbalanced amino acids was augmented by further depressing growth rate.

CHAPTER III

MATERIALS AND METHODS

A. Experimental Design

Selection has been one of the most important tools of animal and plant breeders for many years. Centuries ago man realized that selection was a powerful tool for "improving" a species when "improvement" means change favoring the breeder's ideal.

Selection favoring the breeder's choice of a phenotype operates as a force to change the gene frequency, thus changing the genotypes within the offspring population. Consequently, the genotype is modified in varying degrees depending upon the selection intensity for a phenotype (trait observed) performing in a particular environmental situation.

This experiment was designed to examine the lysine requirement for optimum growth performance of the chick and to determine if the requirement is inherited (genetically controlled). If the assumption is made that the total variance among individuals for growth response in a poor nutritive environment is large, the individuals that deviate farthest in each direction from the mean could possibly have highly inherited different genetic make-ups and different nutritive requirements.

Since lysine is the first-limiting amino acid and biologically independent for growth of chicks and other species, it was theorized that a diet deficient in lysine would impose rigorous stress on a population. Thus it was hypothesized that two-way directional selection pressure for growth response under dietary stressing conditions (low level lysine, 0.5 percent) would separate genotypes due to inherited differences for lysine requirement. To test the hypothesis a bi-directional selection experiment was designed (Fig. 2). The performance of the selected lines was also compared with that of a random control population.

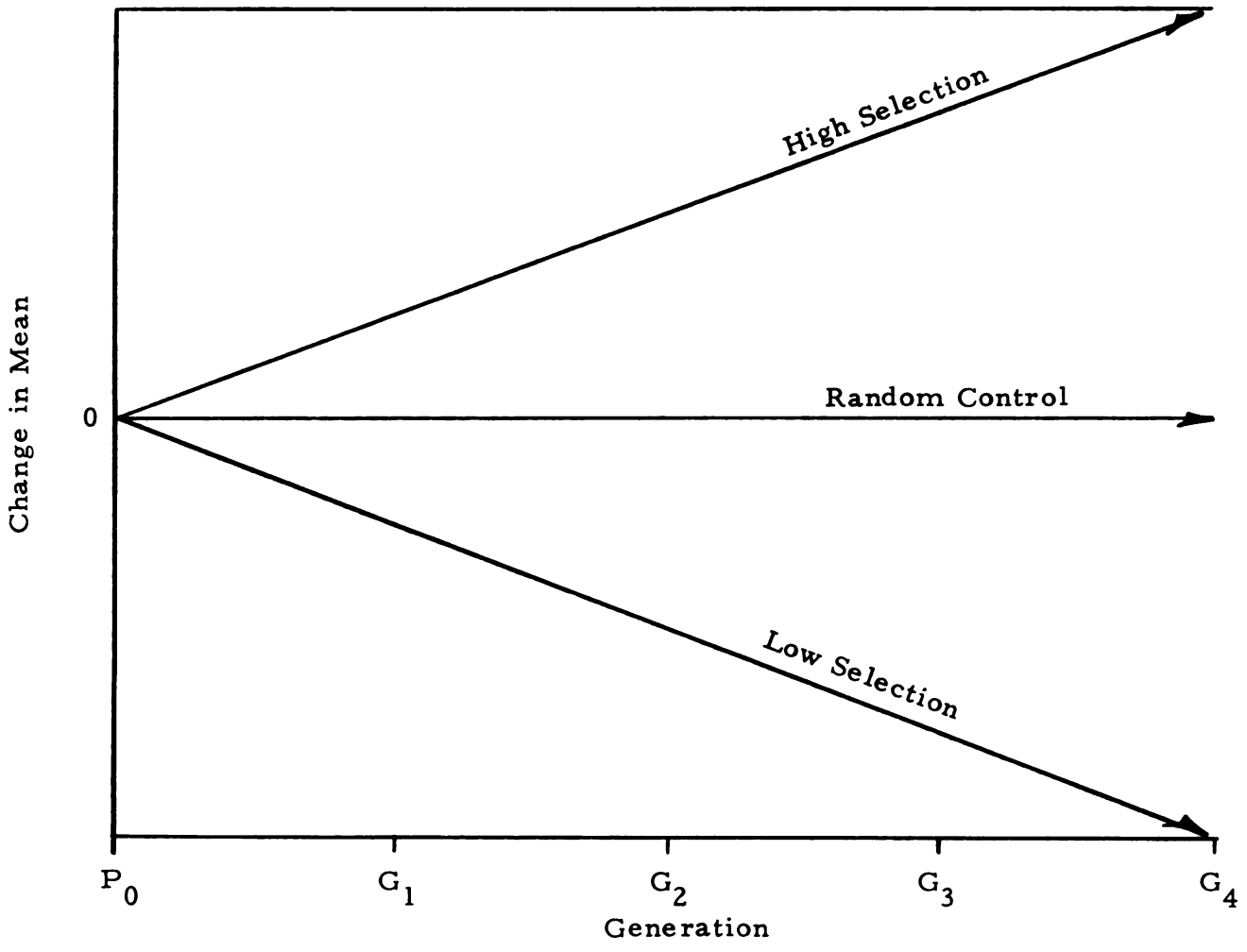
If the chick's genotype for lysine requirement as expressed by growth (phenotype) responds to directional selection in an additive genetic fashion, then two lines may be developed, one for high growth rate and another for low growth rate under conditions of low dietary lysine availability. Numerous experiments have been reported of divergent directional selection: Falconer, (1953), Martin and Bell, (1960), Siegel, (1962) and Maloney et al., (1963) to name a few. Two-way divergent selection was used as a method to eliminate environmental bias as related to selection response. To observe the bi-directional phenomenon the following conditions were assumed:

(a) The trait (gain in weight) has moderate to high heritability.

(b) Gene action is on an additive genetic scale.

(c) Individual phenotype selection should be effective in changing the mean of the population.

Fig. 2. Theoretical model of a two-way selection for growth and a random control line



(d) The effect of appetite was considered to be random among lines and no attempt was made to study quantitative dietary lysine consumption.

B. Nutrient Environment

It was hypothesized that differences of genetic potential for growth could be identified under poor environmental conditions, as opposed to otherwise adequate environments which tend to protect the less fit individuals of a population. A dietary stressing environment was considered suitable as an aid to selection; therefore, a dietary deficiency was designed into an experiment.

Growth rate was selected as the criterion since it is the first characteristic influenced by lysine level above maintainance requirement. Almquist (1957) states that about 30 percent of the optimal amount of lysine is maintenance value and all other available lysine is utilized for growth. It was concluded that a diet calculated to provide 50 percent of the L-lysine requirement would, in fact, make available only about 20 percent (50-30=20) to promote growth. In addition, L-lysine was selected as the nutrient for study because it is not synthesized by the body and cannot be spared by other nutrients, therefore exhibiting an independent role as an essential element in protein metabolism. As cited previously the L-isomer is the only active form of lysine used by the chick and L-lysine is believed to be biologically the first-limiting amino acid for growth. The experiment

was designed with two specific diets to be fed to sets of sexed progeny as contemporaries within generation. The diet was mixed as a complete twenty percent protein chick starter (Table 1) annually as one lot of feed. The first mixing of ingredients was complete except for L-lysine. After the first mixing, the batch of feed was divided in half by weight. One half was labeled "deficient" lysine as it contained only lysine from the raw feedstuffs at a formulated level of 0.5 percent lysine. To the second half of feed, 0.5 percent "L-lysine monohydrochloride" (N.B.C. 1964 - 68) was added, and the mixer was run briefly to blend the added 0.5 percent lysine throughout the supply of feed. This lot was labeled "control" lysine ration. Hereafter in the text the nutrient environments containing L-lysine will be referred to as 1.0 percent lysine or 0.5 percent lysine.

The chick starter diets for the growth trials were calculated to provide 2,020 productive energy (Calories) per kilogram of feed and 20 percent protein. Formulation work related to the growth diets (Table 1) was based on values in the NOPCO (1962) feed ingredient analysis chart. The two diets were:

(a) Control nutrient environment with 1.0 percent lysine and adequate in all other known nutrients (Almquist 1957, Klain et al., 1960, and N.R.C. 1960).

(b) Deficient nutrient environment with 0.5 percent lysine and adequate in all other known nutrients.

Table 1. Composition of 20 percent protein chick starter[1]

Ingredients	Percent
Ground Corn (yellow)	49.5
Corn Gluten (42.5%)	28.0
Soybean Oil Meal (50.0%)	3.5
Ground Oats	11.0
Dehydrated Alfalfa Meal (17.0%)	4.0
Limestone	1.0
Dicalcium Phosphate	2.0
Iodized Salt	0.5
Subtotal	99.5
Minerals added per kilogram of diet	
$MnSO_4$ (70%)	154.00 mg
Zn Oxide	96.80 mg
Vitamins added per kilogram of diet	
Vitamin A	5280.00 IU
Vitamin D_3	1100.00 IU
Folic Acid	0.66 mg
Pyridoxine (B_6)	3.30 mg
Vitamin B_{12}	11.00 mcg
Vitamin K	0.55 mg
Vitamin E	22.00 IU
Riboflavin	2.20 mg
Pantothenic Acid	2.20 mg
Choline	2635.00 mg
Niacin	56.00 mg
Amino Acids added per kilogram of diet	
L Arginine	0.41%
L Lysine[2]	0.50%
DL Methionine	0.10%
DL Tryptophan	0.10%

[1] 2,020 productive energy (Cal.) per kilogram; Cal./protein ratio = 101:1

[2] For the L-lysine deficient diet, omit 0.50 percent L-lysine

C. Genetic Material

Two cases of hatching eggs (720 eggs) representing a heterogenic germ plasma source of egg-type chickens, (Enos and Moreng, 1965) were obtained from a commercial poultry breeder in 1959 by the Colorado Agricultural Experiment Station. From 1959 to 1964 the Colorado State University Avian Science Research Center maintained the stock under a closed flock breeding program. The original egg supply produced 508 potential breeders at 21 weeks of age, and, until 1964, this flock of egg-type chickens was reproduced by random matings among 17.25 sires and 85.75 dams on the average, annually. The consequence of the relatively small population before the initiation of the selection experiment was considered. The two necessary assumptions concerning the base population were:

1. Randomness existed in the population structure and the effective population size was adequate to maintain heterogenic variance and approximately zero inbreeding.
2. Randomness did exist in the population structure, but the effective population size was inadequate, and while a heterogenic variance still existed, the inbreeding level was increasing.

The coefficient of inbreeding was estimated for the base population and calculated from the actual number of males and females for each generation using the following approximation formula (Lush, 1948):

$$F = F' + \left(\frac{1}{8N_m} + \frac{1}{8N_f} \right) (1 + F'' - 2F')$$

where:

F is the expected inbreeding in the present generation;

F' is the inbreeding of the previous generation;

F'' is the inbreeding of two generations ago;

N_m is the actual number of breeding males;

N_f is the actual number of breeding females.

Using this formula the inbreeding was calculated to be about four percent at the time of initiation of this selection study. Selection experiments generally assume the inbreeding level to be zero in the base population. With an estimated four percent inbreeding level among individuals of the base population, inbreeding was considered to be of little consequence and will hereafter, as in most selection experiments, be considered zero.

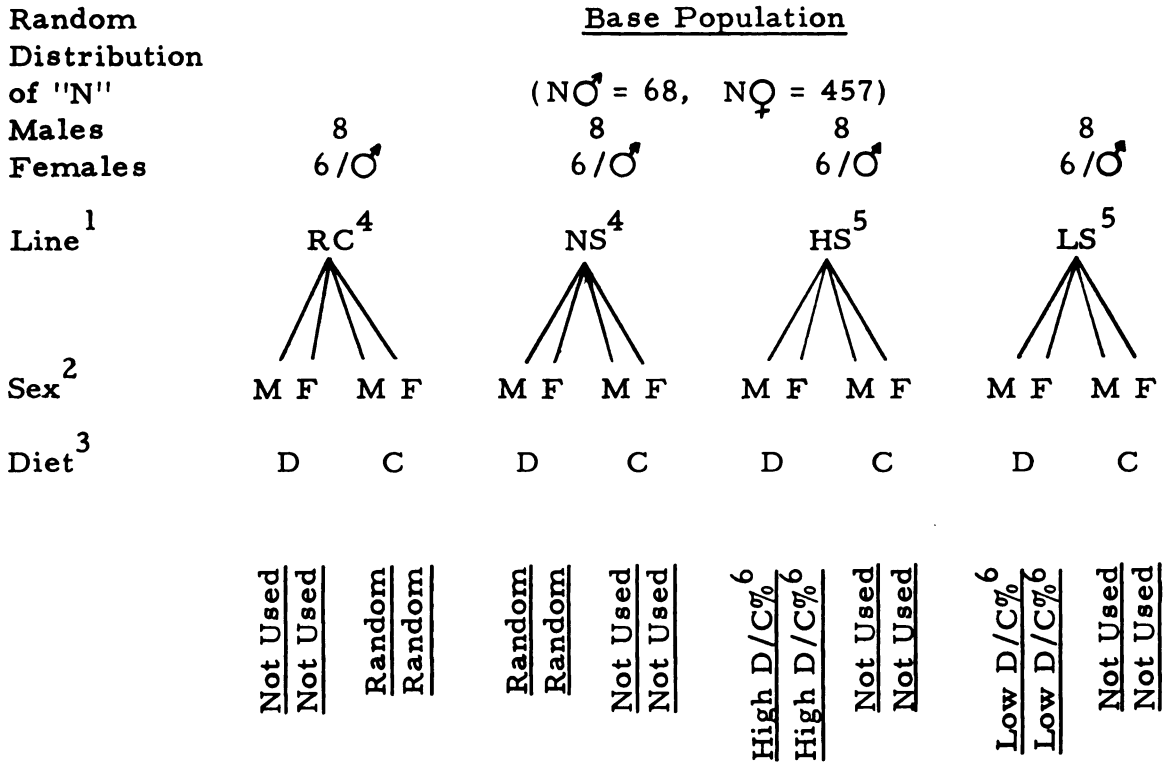
D. Selection Procedure

The base population after random selection from the initial population consisted of 32 males and 192 females. Each male was randomly assigned to one of four lines and then mated to a minimum of six females respectively. Because of increasing concern over low numbers per line the number of females selected for mating with each male was increased from six to nine females per sire in producing the fourth generation. The 32 sire-dam groups used to launch the

study were subdivided into four lines and is presented in diagramatic form in Table 2. One line was designated as the restricted random control (RC) line. Restricted random, meaning that one male offspring (son) each generation was retained at random from those available and this procedure was carried out respectively for each of the eight sires; thus, the sire pool was maintained as eight families, but each sire was mated to females on a random choice basis from within its own line. Throughout the experiment the restricted random mating line (RC) was tested in both nutritive environments. However, breeding stock for the restricted random control, hereafter to be identified as the RC, line was fed only the 1.0 percent lysine adequately balanced diet.

In addition to the RC line another type of control line was maintained, and it differed from the RC line only in that the breeding stock of the NS line had survived when fed the 0.5 percent lysine deficient diet from one day to three weeks of age. This line was influenced by lysine deficiency stress and will in the future be referred to as line NS (Table 2), meaning natural selection. Males of the natural selection (NS) line were selected on the basis of one son per sire family by random choice and mated at random to females within its own line. However, only birds that were fed the specific deficient 0.5 percent lysine diet could represent the closed line. The use of the notation "NS" in this paper should not be confused by the

Table 2. Procedures for creating and maintaining four independent lines.



[1] RC = Random Control; NS = Natural Selection; HS = High Selection; LS = Low Selection.

[2] M = Male, F = Female.

[3] D = Deficient (0.5% lysine), C = Control (1.0% lysine).

[4] Restricted random control (RC); one restriction was imposed on the line in that one son was selected at random from each sire's offspring and subsequently was mated to a random choice of females fed the control diet. The same restriction applied to the reproduction phase of the NS line except breeders came from only birds that were reared, one day to three weeks of age, on the deficient diet.

[5] Pedigreed lines (HS) and (LS) were restricted by the selection of the son for high or low growth performance of each sire's offspring and further restricted in that no close (full-sib) matings were permitted.

[6] D/C%; means that the merit of an individual was determined by a mathematical procedure of dividing its own three week gain (grams) in weight by the average gain of its contemporary full-sibs of the same sex on the control diet.

reader with another common definition of "natural selection" meaning a non-controlled environmental situation, but is in fact a selection of the more fit (survivors) among the total number of the species within the closed line being subjected to a poor nutritive regime of low level, 0.5 percent available, lysine.

Artificial selection was imposed by the investigator for highest growth rate (gain in grams) among pedigreed individuals of another line and this was termed the high selected line (HS) (Table 2). The low selected (LS) line (Table 2) was reproduced among pedigreed individuals with the poorest gain in weight on the experimental lysine deficient diet (0.5 percent lysine). The use of the restriction of no full-sibs in the mating system for both lines HS and LS was practiced in order to suppress, for the short term (four generation) experiment, the increasing rate of inbreeding common in small populations.

The unit of data for analysis was the gain in weight from one day to three weeks of age for chicks. This age period represented the accelerated portion of the growth curve (Almquist, 1957) and, in addition, the dietary requirement for lysine declines with age beyond four weeks. Gain data for progeny on the deficient diet, when compared with the average of their contemporary full-sibs of the same sex on the control diet were expressed as rations; deficient/control x 100 = percent (D/C%). This percentage was used as the criterion for selection. The following example should help clarify the procedure:

(a) Assume sire No. 410 from the HS line was mated to six dams and produced 60 progeny.

(b) Sexed by vent method and assume equality of sexes, thus 30 males and 30 females.

(c) Randomly assign individuals, within sexed groups, to control (1.0% lysine) or deficient (0.5% lysine) diet. For unequal "N" offspring, assign the extra chick to the deficient environmental regime.

(d) Assume two mortality per sex and one each per dietary treatment combination; thus, 14 male control, and 14 male deficient, 14 female control, and 14 female deficient chicks yield data.

(e) Average the weights of full-sibs of the same sex on the control diet, and assume they gained 120 grams.

(f) Divide each individual gain value for chicks on the deficient diet by the average of their full-sib controls of the same sex. Example: progeny No. 620, weighed 80 grams; therefore, 80/120 (100) = 66.67%, and No. 630 weighed 30 grams so, 30/120 (100) = 25.00%.

(g) Selected from this example among the HS line would be progeny No. 620, because it had the highest percent gain relative to his controls.

(h) Similar computations were made for each individual in both the HS and LS lines at every generation interval.

(i) If this example had assumed growth response of individuals among the LS line, then progeny No. 630 would be selected.

In reality the following question must be answered. Which individual, No. 620 or No. 630 from the previous example, is the better? Number 620 with a 66.67% value was selected for highest growth rate (grams gained from 1 day to 3 weeks of age) on the deficient diet and apparently has the lowest lysine requirement.

This concept of weighing individuals for merit or breeding value has been employed in this experiment since 1964. Wilson (1967) proposed a similar procedure for selecting desirable families in a discussion of alternative systems that may enhance selection efficiency. Individual selection was utilized in this experiment while Wilson's recommendation was a family selection scheme; however, both designs use the same method of estimating breeding values.

For each generation after the primary selection was made, in lines RC, NS, HS and LS, alternate males were chosen to replace any male lost because of an accident, normal mortality, infertility, or other cause. For the high and low growth rate lines, respectively, the first choice alternates were full-brothers, with half-brothers as further removed choices.

E. Other Measurements

Throughout the growth studies, individual mortality was recorded daily with regard to diet, sex and line. While the measurement for genetic change was restricted to gain in weight, several response characteristics were observed. Among them were the reproductive fitness traits, fertility and hatchability, which were measured as percent. Individual egg production was recorded daily for 280 days (ten, 28-day periods).

F. Physical Environment

Growth trials were conducted for sexes separately in groups of approximately 20 chicks. Chicks were assigned at random to growing battery locations. The electrically heated, wire floored batteries were thermostatically controlled for uniform brooding temperatures and adjusted to provide the following:

(a) 1 day to 1 week of age, approximately 55° Centigrade.

(b) 1 week to 2 weeks of age, approximately 52.5° Centigrade.

(c) 2 weeks to 3 weeks of age, approximately 50° Centigrade.

The battery room per se was artificially illuminated with fluorescent lighting fixtures to provide a constantly lighted environment. The room was equipped with ventilation fans adjusted to maintain the temperature range of 39° to 44° Centigrade. Feed and water were checked daily and provided on an ad libitum basis throughout the studies.

Following the experimental three week growth period, the chicks were provided a standard chick starter diet for one week in the battery room. During that week the electric heaters were shut off and the room temperature lowered to condition the chicks for cold room brooding on the research farm. At four weeks of age the chicks were moved to the farm where a floor rearing management program was utilized. The flock was vaccinated two days after delivery to the farm for Newcastle disease. During the rest of their lives, standard feeding programs, vaccination and management practices were followed for optimum growth, development and reproductive success.

Since the chicks were hatched in April, annually, there was no particular physiological advantage in utilizing a special lighting program. Therefore, the birds grew and developed under natural daylight conditions at 40° latitude until housing time. When the pullets were twenty weeks old they were housed in individual wire cages. Feed and water were available ad libitum throughout the 10 consecutive 28-day egg production periods. The environmental control features of the windowless poultry laying house had the following specifications:

(a) Fourteen hours of artificial light per 24 hour day.

(b) Four cfm (cubic feet per bird per minute) of outside fresh air supplied as forced air against 3/8 inch static pressure.

(c) Direct drive, blade type, thermostatically controlled fans.

(d) Winter conditions - If the environmental temperature dropped below 22° Centigrade the fans were regulated by time clock for minimum air movement (1 cfm for 2 consecutive minutes for every 10 minutes of total time).

(e) Summer conditions - Evaporative pads were placed around the fans and flushed with water so that all incoming air was pre-cooled. With this system 11° Centigrade temperature differential was realized, even at high environmental temperatures of about 56° Centigrade.

G. Statistical Procedure

In dealing with the data, the first question to be answered was the presence of, or lack of, significant differences between main factors of diet, sex, generation and line effects. In addition, the existence of, or lack of, interactions involving lines was considered critically important. Least squares analyses of variance with unequal numbers in computerized programs were used to statistically evaluate the data. Standard tests for homogeneity of variance were employed (Bartlett, 1937; and/or Pearson and Hartley, 1954). The Duncan's (1955) Multiple Range F test for comparison of means was used to statistically compare different groups.

The first statistical model employed in the general analysis was a four-way fixed factorial analysis of variance with unequal number of observations per treatment combination.

$$Y_{ijkln} = u + D_i + S_j + G_k + L_l + DS_{ij} + DG_{ik} + DL_{il} + SG_{jk} + SL_{jl} + GL_{kl} + DSG_{ijk} + DSL_{ijl} + DGL_{ikl} + SGL_{jkl} + DSGL_{ijkl} + e_{ijkln}$$

where:

Y_{ijkln} = the observation for the n^{th} chick in the l^{th} line of the k^{th} generation for the j^{th} sex on the i^{th} diet;

u = the overall common mean;

D_i = the effect of the i^{th} diet, $i = 1, 2$;

S_j = the effect of the j^{th} sex, $j = 1, 2$;

G_k = the effect of the k^{th} generation, $k = 1. . .5$;

L_l = the effect of the l^{th} line, $l = 1. . .4$;

DS_{ij}, DG_{ik}, DL_{il}, SG_{jk}, SL_{jl} and GL_{kl} = the two-way interactions associated with the designated subclasses;

DSG_{ijk}, DSL_{ijl}, DGL_{ikl} and SGL_{jkl} = the three-way interactions associated with the designated subclasses;

$DSGL_{ijkl}$ = the four-way interaction associated with the designated subclasses;

e_{ijkln} = the random error among observations.

In addition to the four-way analysis of variance, several three-way, two-way and one-way analysis of variance calculations were made. A special computerized program was written to perform the necessary calculations to obtain the appropriate deficient/control

(D/C) percent value. Each D/C percent was used as the best estimate of the individual merit or breeding value in the selection phase of the experiment.

These analyses were computed for three week gain in weight of all chicks (without regard to sex) in the control nutritive environment (1.0% lysine) and for growth of their contemporary full-sibs in the deficient nutritive environment (0.5% lysine). In addition, the D/C percent estimates of breeding value were analyzed in the same manner.

Least squares analysis of variance (Harvey, 1960) with unequal subclass frequencies of a hierarchial design for sires, dams within sires and offspring (progeny) nested within dam within sire was used for each set of data separated by diet, generation interval and by RC, NS, HS and LS line.

The statistical model for this hierarchial analysis of variance design was:

$$Y_{ijk} = u + S_i + D_{ij} + e_{ijk}$$

where:

Y_{ijk} is the record of the k^{th} individual chick from the j^{th} dam mated to the i^{th} sire;

u = the overall common mean;

S_i = additive effect of the i^{th} sire;

D_{ij} = additive effect of the j^{th} dam in the i^{th} sire group;

e_{ijk} = experimental random error among offspring.

The format for handling the data, identifying source of variation and the expected mean squares (EMS), appears in Table 3.

The coefficients k_1, k_2 and k_3 were calculated according to the method derived by Henderson (1953) and King and Henderson (1954) where:

k_1 and k_2 = effective number or coefficient of dams with unequal numbers per set;

k_3 = effective number or coefficient for sires with unequal numbers per set.

The general formula for computing the coefficient, k, is:

$$k = \frac{1}{df}\left(N - \frac{\Sigma n_i^2}{N}\right)$$

where:

k = coefficient being computed;

$\frac{1}{df}$ = one/degrees freedom for the specific k;

N = the total number of progeny;

Σn_i^2 = the sum of progeny for each i^{th} quantity squared.

The variance components for sires (σ_S^2) and dams (σ_D^2) were computed by using the Henderson (1953) method. Formulas for these computations are in Table 4. Lush (1948), in his mimeographed notes, effectively described the use of the component of variance as a

Table 3. Hierarchial analysis of variance model and expected mean squares

Source of Variation	df	MS	EMS[1]
Sires	S-1	MS_S	$\sigma^2_W + k_2\sigma^2_D + k_3\sigma^2_S$
Dams/Sires	D-S	MS_D	$\sigma^2_W + k_1\sigma^2_D$
Offspring/Dams/Sires	n-D	MS_W	σ^2_W

[1] Coefficients k_1, k_2 and k_3 computed as per Henderson (1953) and King and Henderson (1954)

means of estimating heritability from data for sets of full-sibs and half-sibs, as well as a procedure to estimate heritability by combining the sire and dam components of variance. Also shown in Table 4 are the formulas for computing standard error of heritability estimates, Dickerson (1960) and Becker (1967).

Realized heritability, defined as the response to selection, was computed by using the following formula:

$$h^2 = \frac{R}{S}$$

where:

h^2 = realized heritability;

R = response (gain);

S = selection differential (intensity).

Falconer (1960) says of this method, "it provides the most useful empirical description of the effectiveness of selection." Magee (1965) proposed that the term selection differential be applied only in situations where mass selection is for only one trait; its computational formula is:

$$\Delta G = \breve{P} - \overline{P}$$

where:

ΔG = genetic change

$\breve{P}$ = phenotypic average of selected animals

Table 4. Computational formulas for variance components, heritability estimates and standard error of heritability

Variance Component[1]	Heritability[2] Estimate ($\hat{h}^2$)	Standard Error[3] ($\hat{h}^2$)
$\sigma^2_S = \frac{MS_S - (MS_W + k_2 \sigma^2_D)}{k_3}$	$\hat{h}^2_s = \frac{4\sigma^2_S}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$	$\frac{4\sqrt{\frac{2}{k_3^2}\left[\frac{MS_S^2}{df_S} + \frac{MS_D^2}{df_D}\right]}}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$
$\sigma^2_D = \frac{MS_D - MS_W}{k_1}$	$\hat{h}^2_d = \frac{4\sigma^2_D}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$	$\frac{4\sqrt{\frac{2}{k_1^2}\left[\frac{MS_D^2}{df_D} + \frac{MS_W^2}{df_W}\right]}}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$
$\sigma^2_W = MS_W$	$\hat{h}^2_{s+d} = \frac{2(\sigma^2_S + \sigma^2_D)}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$	$\frac{2\sqrt{\sigma^2_S + \sigma^2_D + 2\left[\frac{k_2}{k_3}\left(\sigma^2_D - \frac{2ME_W^2}{df_W k_1^2}\right)\right]}}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$

[1] Henderson (1953)

[2] Lush (1948)

[3] Dickerson (1960) and Becker (1967)

$\overline{P}$ = phenotypic average of all the population in which they were born.

With ΔG being equated to the response, meaning gain from the mean of one generation to the mean of the next generation, and $(\breve{P} - \overline{P})$ being equal to intensity or selection differential, then realized heritability could be calculated.

In another phase of the experiment, pure line and reciprocal cross line matings between the HS and LS selected lines were made. This was done to find the mean of the F_1 offspring populations. The mean of the cross line population was expected to lie at some midpoint between the selected lines.

The F_1 cross line progeny provided data for a measure of heterosis with respect to growth rate performance following selection in a low (0.5% lysine) nutritive environment. Mathematical procedures of Crow (1952) and Falconer (1960) were utilized in computing realized heterosis.

$$\text{Percent heterosis} = \frac{\text{Cross line mean} - \text{Pure line mean}}{\text{Pure line mean}} \times 100$$

Percent heterosis is the degree of response;

Pure line mean is the average of the parental types HS x HS plus LS x LS;

Cross line mean is the average of the F_1 progeny types HS x LS plus LS x HS.

CHAPTER IV

RESULTS AND DISCUSSION

Annually, feed samples of each diet, control (1.0% lysine) or deficient (0.5% lysine), were taken for chemical analysis. As presented in Table 5, one may observe that some variation existed among the feed supplies used during this experiment. Actual amino acid determinations were made from two random samples collected by the investigator and again randomly divided into three samples by the laboratory. This procedure was routinely followed except in 1967 when the samples were destroyed by weevil. The samples were processed in a commercial chemical laboratory on a "Spinco Amino Acid Analyzer", courtesy of the Ralston Purina Company. Each amino acid value shown in Table 5 represents the mean of six determinations while the D/C percent represents the ratio of available dietary lysine between the two diets calculated for the specific generation interval, along with the overall average for the duration of the experiment.

Sufficient variation was present between the diets annually so that the percentages (D/C) ranged from a low of 48.42 percent to a high of 64.37 percent. In theory, the actual difference annually in lysine should be .50 percent, however, the actual differences as determined by chemical analysis were .49, .31, .31, --, and .37

Table 5. Protein and amino acid analysis of the control diet formulated to contain 1.0% lysine and the deficient diet to have 0.5% lysine[1]

Control Diet (1.0% Lysine)						
Item	P_0	G_1	G_2	G_3	G_4	Avg.
Protein	21.1	23.4	25.4	--[2]	23.5	23.3
Lysine	.95	.83	.87	--	.87	.88
Arginine	1.25	1.22	0.91	--	1.01	1.10
Tryptophane	.18	.17	.23	--	.15	.18
Cystine	.50	.59	.64	--	.57	.57
Methionine	.49	.44	.42	--	.53	.47

Deficient Diet (0.5% Lysine)						
Item	P_0	G_1	G_2	G_3	G_4	Avg.
Protein	19.0	21.9	24.3	--[2]	22.3	21.9
Lysine	.46	.52	.56	--	.50	.51
Arginine	1.00	1.25	1.33	--	.86	1.11
Tryptophane	.17	.17	.23	--	.13	.18
Cystine	.49	.57	.64	--	.59	.57
Methionine	.36	.46	.47	--	.51	.45
D/C (Lysine)	48.42	62.65	64.37	--	57.47	57.95

[1] Amino acid assay values, Spinco process, courtesy of Ralston Purina Co., Checkerboard Square, St. Louis, Missouri. (1964-68)

[2] Samples were destroyed by weevil

percent, respectively, for generations designated as P_0 for the base generation and each subsequent generation denoted by the sub-generation number G_1, G_2, G_3 and G_4. The overall average difference in the two diets for level of lysine was .37 percent.

Growth rate, as measured by grams of weight gained during the juvenile period from initial hatch weight at one day of age to three weeks of age, was analyzed for main effects of diet, sex, generation and line, each being considered as a fixed factor in the design. Table 6 shows the numerical values for this computation for the main effects as well as all two-way and three-way interactions. All of the categories showed statistically significant variability at the five percent or higher level of probability.

By design it was intended that the 0.5 percent lysine diet would, on the average, severely depress growth as compared with the 1.0 percent lysine control diet; therefore, the data on punch cards were sorted and reanalyzed as though they represented two different and separate experiments. Displayed in Table 7 is the analysis of variance result for chicks being fed on the control diet (1.0% lysine). For the analysis with diet removed as a factor, the remaining main effects being analyzed in the three-way were sex, generation and line. For birds on the control diet (1.0% lysine), the effects of sex and generation were found to be statistically significant; however, no significant differences existed between the four experimental lines of birds (Table 7).

Table 6. Least squares analysis of variance, fixed factorial design, for three week gain (grams) in weight for all four lines of birds in the experiment

Source of Variation	df	MS	F	Sig.
Total	7362			
Diet	1	6573375.97	15671.86	<.005
Sex	1	6206.20	14.80	<.005
Gen.	4	74354.79	177.27	<.005
Line	3	1273.17	3.04	<.05
DxS	1	9366.22	22.33	<.005
DxG	4	45979.94	109.62	<.005
DxL	3	1671.58	3.99	<.01
SxG	4	12192.59	29.07	<.005
SxL	3	1675.06	3.99	<.01
GxL	12	2671.96	6.37	<.005
DxSxG	4	10595.17	25.26	<.005
DxSxL	3	3502.97	8.35	<.005
DxGxL	12	744.96	1.78	<.05
SxGxL	12	1853.17	4.12	<.005
Error*	7295	419.44		

*The 4-way interaction DxSxGxL ($F = 1.50$) was not significant ($P > .05$) and this source of variation was pooled in the overall error term

Table 7. Least squares analysis of variance, fixed factorial design, for three week gain (grams) for all four lines on the control diet (1.0% lysine).

Source of Variation	df	MS	F	Sig.
Total	3610			
Sex	1	14169.00	25.82	<.005
Gen.	4	103153.87	187.95	<.005
Line	3	200.83	0.37	N.S.*
SxG	4	21465.82	39.11	<.005
SxL	3	3444.98	6.28	<.005
GxL	12	2243.91	4.09	<.005
SxGxL	12	2883.79	5.25	<.005
Error	3571	548.84		

* N.S. means not significant here and throughout the text

Data for the birds being fed the 0.5 percent lysine deficient diet were also analyzed by the least squares analysis of variance for unequal numbers considering sex, generation and line as fixed factors. From this analysis, and as shown in Table 8, the effect of sex difference was no longer statistically significant while generation effects were significant as they were for the contemporary full-sibs on the control (1.0% lysine) diet (Table 7).

Referring again to Table 8, there was a statistically significant difference among the four lines when they were fed the deficient diet with 0.5 percent lysine. It is apparent that only one interaction was significant, that being the G x L (generation x line) effect. This interaction of generation x line was highly significant ($P < .005$). Theoretically, this interaction G x L (Table 8) should be significant if the selection experiment did indeed produce divergently separating lines as measured by the criterion, three week gain (grams) in weight. The importance of this interaction will be discussed later in a detailed study of means by line per generations of time.

As described earlier in the experimental design, Chapter III, Materials and Methods, Section A, a computed percentage value for each individual chick on the deficient (0.5% lysine) diet was used to select breeders in each the HS (high selection) and LS (low selection) lines for growth, from one day to three weeks of age, rather than selecting for each individual gain (grams) in weight.

Table 8. Least squares analysis of variance, fixed factorial design, for three week gain (grams) for all four lines on the deficient diet (0.5% lysine)

Source of Variation	df	MS	F	Sig.
Total	3751			
Sex	1	104.75	0.36	N.S.
Gen.	4	12770.03	43.65	<.005
Line	3	2694.62	9.21	<.005
SxG	4	493.94	1.69	N.S.
SxL	3	139.10	0.48	N.S.
GxL	12	1134.06	3.88	<.005
SxGxL	12	136.96	0.47	N.S.
Error	3712	292.53		

The preceding discussion in this chapter dealt with the actual gain (grams) in weight per bird from one day to three weeks of age. The next consideration was the statistical analysis for the deficient/control (D/C) percent values which were the actual criteria for selection among the HS and LS, divergently selected lines.

The least squares analysis of variance technique was used for the data with unequal numbers per subclass. A tabular display of results for the three factor analysis, including sex, generation and line as main effects, appears in Table 9. This analysis indicated that all main effects and each two-way interaction were highly significant ($P < .005$). Since all four lines of the experiment were included in the preceding analysis but only two of them, HS and LS, were artificially influenced by a high degree of selection pressure, the data were sorted to permit reanalyzation by analysis of variance for only the selected lines, HS and LS. The results of the analysis for those individuals within the selected lines fed the control (1.0% lysine) diet are presented in Table 10. The main effect of generation was highly significant ($P < .005$); however, the factors of sex and line were not significant ($P > .05$). In a similar manner, the data for the full-sibs on the deficient (0.5% lysine) diet were analyzed (Table 11). Of particular interest was the non-significant differences for sex and line. The comparison of the analysis for the 1.0 percent lysine and 0.5 percent lysine treatments is in exact agreement with the main

Table 9. Least squares analysis of variance, fixed factorial design, for three week deficient/control (D/C) percent and for all four lines in the experiment[1]

Source of Variation	df	MS	F	Sig.
Total	3751			
Sex	1	2436.39	8.61	<.005
Gen.	4	16379.70	57.85	<.005
Line	3	2981.41	10.53	<.005
SxG	4	4610.71	16.29	<.005
SxL	3	1680.23	5.94	<.005
GxL	12	683.96	2.42	<.005
SxGxL	12	403.90	1.43	N.S.
Error	3712	283.13		

[1]Each D/C percentage value was computed individually within dam of sire family and of the same sex

Table 10. Least squares analysis of variance, fixed factorial design, for three week gain (grams) for selected lines HS and LS on the control diet (1.0% lysine)

Source of Variation	df	MS	F	Sig.
Total	1750			
Sex	1	595.21	1.01	N.S.
Gen.	4	55912.37	94.71	<.005
Line	1	405.42	0.69	N.S.
SxG	4	14276.10	24.18	<.005
SxL	1	2376.26	4.03	<.05
GxL	4	947.49	1.60	N.S.
SxGxL	4	1304.02	2.21	N.S.
Error	1731	590.37		

Table 11. Least squares analysis of variance, fixed factorial design, for the three week gain (grams) for selected lines HS and LS on the deficient diet (0.5% lysine)

Source of Variation	df	MS	F	Sig.
Total	1824			
Sex	1	30.20	0.10	N.S.
Gen.	4	8036.25	26.61	<.005
Line	1	417.24	1.38	N.S.
SxG	4	599.55	1.98	N.S.
SxL	1	62.06	0.21	N.S.
GxL	4	278.76	0.92	N.S.
SxGxL	4	70.79	0.23	N.S.
Error	1805	302.05		

factors of sex, generation and line for the analysis of selected HS and LS lines (Tables 10 and 11 for 1.0% and 0.5% lysine dietary environments, respectively). When dietary groups were analyzed separately, it became clear that pooling of some two-way and the higher order interaction of SxGxL could be carried out. However, this was not done in order to look at the relative effects of the possible interactions from one dietary environment to the other (1.0% lysine vs. 0.5% lysine). A comparison of the various interactions points out that sex was involved in two of the two-way interaction levels for the 1.0 percent lysine environment but had no interaction effect relative to the analysis for the 0.5 percent lysine environment. Sex, as a main factor, was not itself a significant source of variation among main effects for either dietary regime.

The least squares analysis of variance result for deficient/control (D/C) percent (Table 12) also points out that sex differences were not of significant concern ($P > .05$). The analysis of D/C information, since it is based on full-sibs of the same sex, reduces the model from two nutritional dimensions (1.0% vs. 0.5% lysine) to one effect. The reduction of the model for analysis in this way can also be acceptable since sex differences were not significant in either dietary environment. Having compared the analysis for diets, separately, and from the D/C approach, one arrives at the same conclusion: sex as a main factor can be pooled for further analysis

Table 12. Least squares analysis of variance, fixed factorial design, for three week deficient/control (D/C) percent for selected HS and LS lines[1]

Source of Variation	df	MS	F	Sig.
Total	1824			
Sex	1	140.36	0.47	N.S.
Gen.	4	7047.96	23.85	<.005
Line	1	515.38	1.74	N.S.
SxG	4	3064.64	10.37	<.005
SxL	1	53.45	0.18	N.S.
GxL	4	408.35	1.38	N.S.
SxGxL	4	193.93	0.66	N.S.
Error	1805	295.53		

[1]Each D/C percentage value was computed individually within dam of sire family and of the same sex

and generations as an effect are highly significant ($P < .005$); thus, future evaluation should be considered for each generation interval (P_o, G_1, G_2, G_3, and G_4) separately. Although the least squares analysis of variance result indicated that sex as an effect could be pooled for both dietary regimes, the correlation of three week gain (grams) with D/C for male, female and pooled sexes, was considered. A stepwise linear computerized program was employed to measure the degree of correlation between three week gain in grams with the three week deficient/control values for males, females and sexes pooled within line HS and LS. Presented in Table 13 are the appropriate correlation "r" values each being highly significant ($P < .01$). These high correlations between the two measurements, the computed D/C value and the empirical grams of gain value, add support to the previously drawn conclusion that sexes could be pooled and that either one, male or female, is as good as the other in making predictions.

In Table 13 one can also see that the correlations within sex and for sexes pooled are comparable between lines HS and LS; thus, any error committed by pooling sex effects within line would be no greater in the HS line than in the LS line. Comparisons between lines can be made, having previously pooled the data for within line effects. The average of all data in Table 13 is .798 with a range no greater or less than the mean by .065.

Table 13. Correlation (r) between three week gain (grams) and deficient/control (D/C) percentage computed separately for sex of progeny of the HS and LS lines

Sex	HS		LS	
	N	r**	N	r**
Male	(424)	.733	(531)	.753
Female	(385)	.863	(485)	.838
Pooled	(809)	.798	(1016)	.795

**All computed r values are highly significant ($P < .01$), Snedecor and Cochran (1967)

The principal factors of this experiment were diet (two levels), two sexes, a base generation (P_0) and four subsequent generations (G_1, G_2, G_3 and G_4) for each of four separate lines. In the previous discussion, the effect of these main factors was considered for their probable effect on interpretations from the experiment as a whole. Both diet and generation effects were found to be highly significant ($P < .005$). Further, it was determined that sex as a main effect and as a factor of the overall experiment could be discounted; thus, the two sexes, male and female, could be pooled with regard to the parameter, grams gained from one day to three weeks of age, being investigated.

The mean three week gain (grams) and its standard error (S.E.) for the specific number of observations per diet, generation and line with sexes pooled, are presented in Table 14. The Multiple Range F test for differences in means (Duncan, 1955) was applied to the data and, where the means were found to be significantly different ($P < .05$) they have been identified (Table 14). At the base generation interval (P_0), there were no significant differences ($P > .05$) among lines within each nutritive environment. Consequently, one may conclude that the chance segregation of the base population, as genetic material, did fit the expectation of complete randomness of sampling as measured by mean three week gain (grams) of their progeny. There were approximately equal numbers of full-sibs of the same sex fed on each dietary regime (1.0% or 0.5% lysine).

Table 14. Mean three week gain (grams) by diet, generation and line with sexes pooled

Gen.	Line	1.0% Lysine N	$\bar{x}$ gms.	P<.05	S.E.	0.5% Lysine N	$\bar{x}$ gms.	P<.05	S.E.
P_0	RC	114	121	a[1]	1.91	133	55	a[1]	1.56
	NS	106	115	a	2.06	120	55	a	1.78
	HS	115	115	a	2.03	123	58	a	1.66
	LS	132	117	a	1.85	159	56	a	1.50
G_1	RC	241	130	a	1.60	229	45	b	1.22
	NS	253	129	a	1.40	286	47	a b	1.07
	HS	230	131	a	1.75	248	51	a	1.28
	LS	240	131	a	1.76	266	49	a b	1.22
G_2	RC	125	102	a	2.01	127	48	a b	1.39
	NS	108	100	a	2.40	139	49	a	1.30
	HS	107	97	a	2.10	107	43	b	1.46
	LS	129	96	a	2.45	147	45	a b	1.25
G_3	RC	109	95	b	3.13	114	38	b	1.46
	NS	124	106	a	2.21	145	48	a	1.34
	HS	109	109	a	2.58	116	47	a	1.30
	LS	130	103	a b	2.40	140	43	a b	1.26
G_4	RC	322	121	a b	1.27	289	47	b	0.99
	NS	358	117	b	1.20	345	55	a	0.78
	HS	234	121	a b	1.66	215	52	a	1.16
	LS	325	124	a	1.29	304	53	a	0.88

[1]Within each dietary and generation group of four lines, the means with the same subscript letter are not significantly different at the five percent level of probability (Duncan, 1955)

To illustrate the effect of change from generation to generation, the means in Table 14 for each line on the control (1.0% lysine) diet have been graphed in Fig. 3 as deviations from the control (RC, line) mean. In a similar graph (Fig. 4), the deviations from the control (RC, line) for the 0.5 percent lysine dietary treatment effect are shown. In addition to the change for selected lines NS, HS and LS from RC line means, the actual grams deviation for the RC line itself has been plotted as the broken line in Figures 3 and 4 to illustrate the generation to generation effect. These presentations make it very clear that there was some poorer growth performance for all four lines in the early generations but all lines showed considerable improvement in the later phase of the study.

Due to the extreme variation, with reference to change in means from generation to generation, another approach for presentation of the data was considered. Table 15 shows the percent change from the RC line for each selected line (NS, HS and LS) by generation interval, along with the calculated percent change in mean on a within line basis from generation to generation. Each calculation of percent change ($\%\Delta_{\bar{x}}$) from line RC or change from generation to generation within the same line was made for both the control (1.0% lysine) and deficient (0.5% lysine) nutrient environmental treatments.

The percent change ($\%\Delta_{\bar{x}}$) from previous generation and direction, either upward or downward, was extreme (Table 15); the most

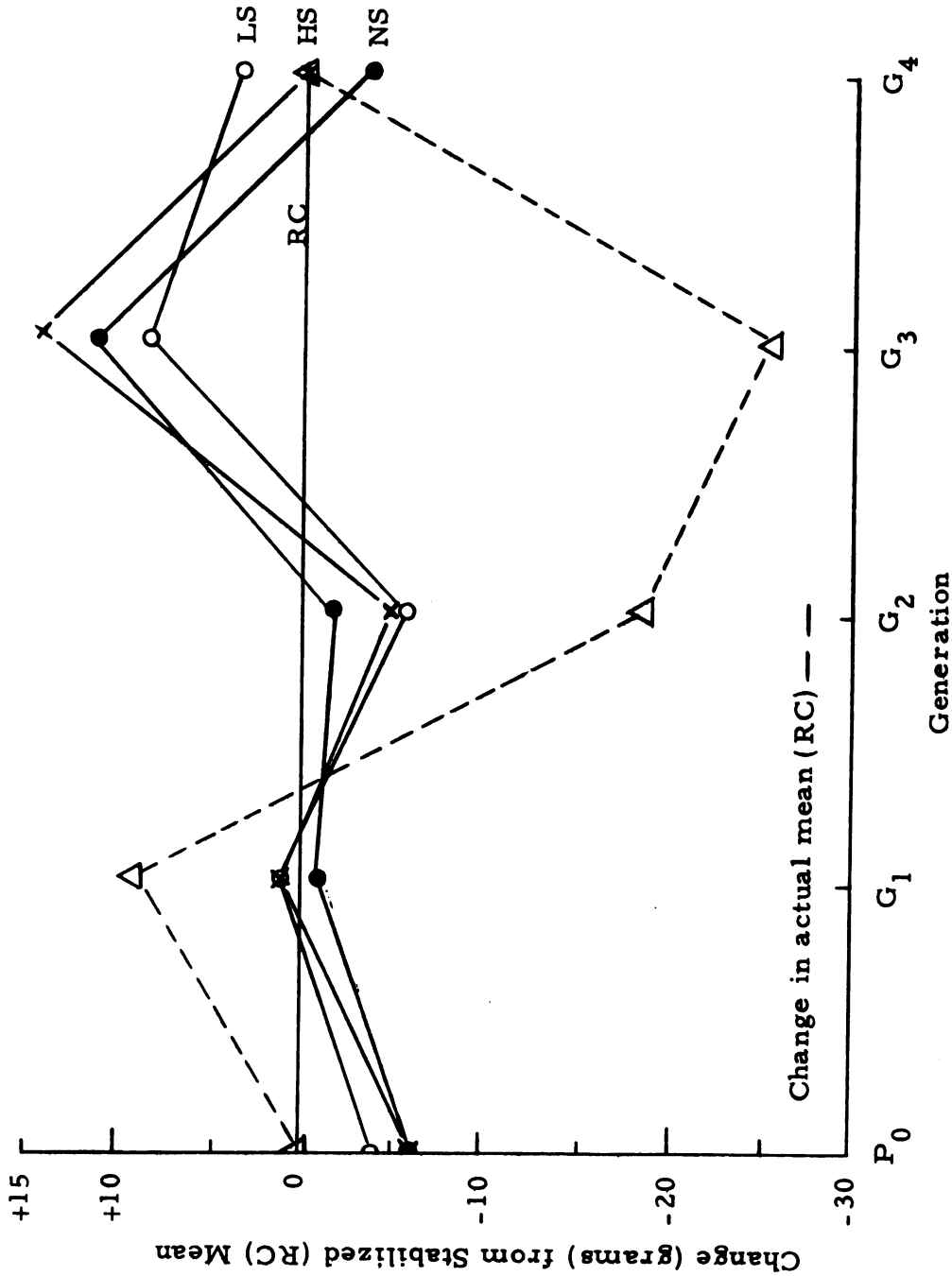


Fig. 3. Deviations by line (NS, HS and LS) in grams gained from mean of control (RC, line) on the 1.0% lysine diet

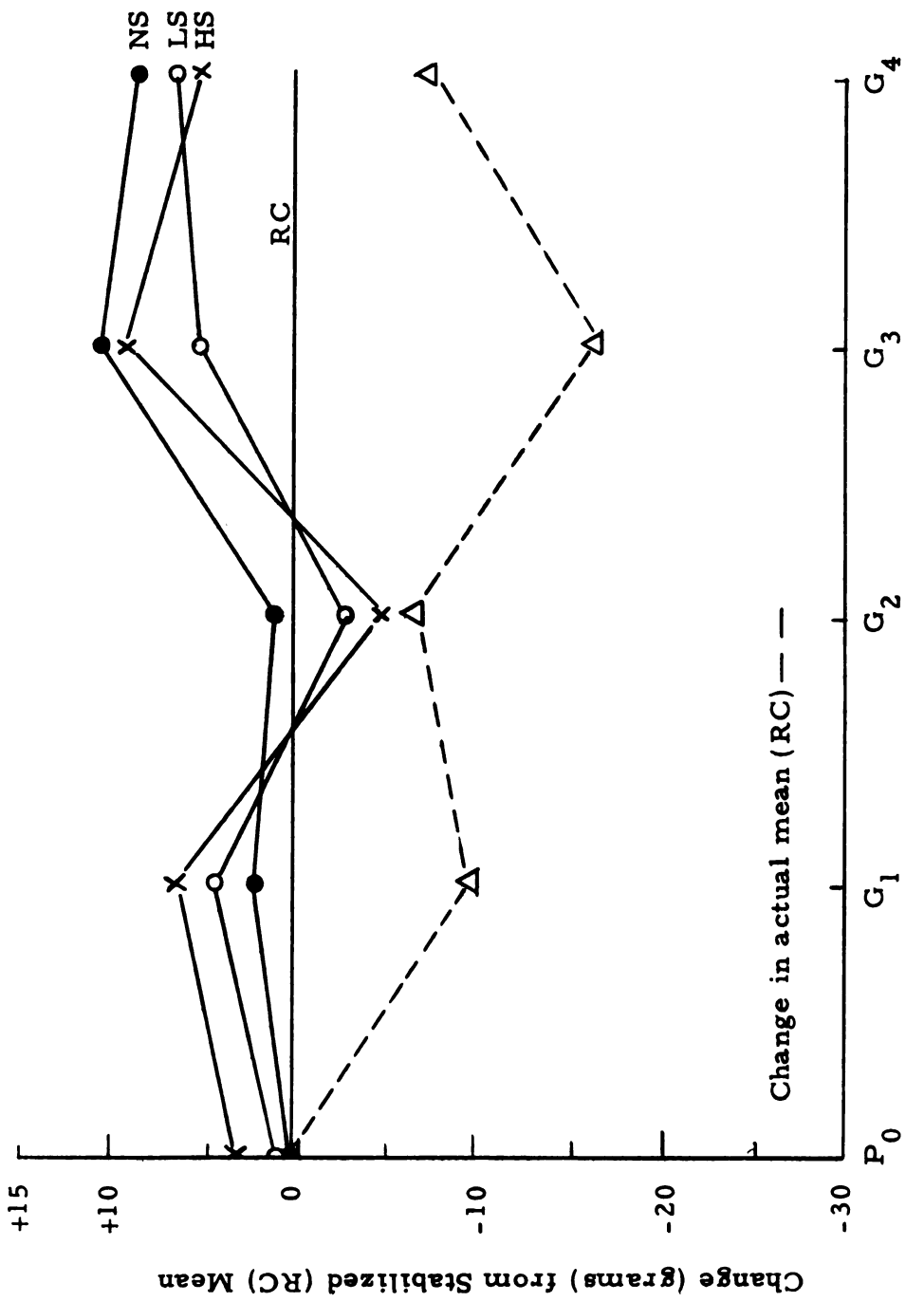


Fig. 4. Deviation by line (NS, HS and LS) in grams gained from mean of control (RC, line) on the 0.5% lysine diet

Table 15. Percent change in mean ($\%\Delta_{\bar{x}}$) for three week gain (grams) by diet, generation and line with sexes pooled

		1.0% Lysine		0.5% Lysine	
		$\%\Delta_{\bar{x}}$ from present	$\%\Delta_{\bar{x}}$ from previous	$\%\Delta_{\bar{x}}$ from present	$\%\Delta_{\bar{x}}$ from previous
Line	Gen.	Gen. $\bar{x}$ of line RC	Gen. $\bar{x}$ of same line	Gen. $\bar{x}$ of line RC	Gen. $\bar{x}$ of same line
RC	G_1	0.0	+ 7.4	0.0	-18.2
	G_2	0.0	-21.5	0.0	+ 6.7
	G_3	0.0	- 6.9	0.0	-20.8
	G_4	0.0	+27.4	0.0	+23.7
NS	G_1	- 0.8	+12.2	+ 4.4	-14.5
	G_2	- 2.0	-22.5	+ 2.1	+ 4.3
	G_3	+11.6	+ 6.0	+26.3	- 2.1
	G_4	- 3.3	+10.4	+17.0	+14.6
HS	G_1	+ 0.2	+13.9	+13.3	-12.1
	G_2	- 4.9	-26.0	-10.4	-15.7
	G_3	+14.7	+12.4	+23.7	+ 9.3
	G_4	- 0.0	-11.0	+10.6	+10.6
LS	G_1	+ 0.2	+12.0	+ 8.9	-12.5
	G_2	- 5.9	-26.7	- 6.2	- 8.2
	G_3	+ 8.4	+ 7.3	+13.2	- 4.4
	G_4	+ 2.5	+20.4	+12.8	+23.3

extreme being +27.4 percent for the RC line on the 1.0 percent lysine diet. The least extreme case occurred for the NS line on the 0.5 percent lysine diet with -2.1 percent. In view of the extreme generation to generation variation in growth performance, one becomes quite concerned with the probable causes and desires to learn if the source of variation is predominately genetic or environmental. Detailed analysis of the possibility of genetic change will be presented later after including data and information obtained for cross line progeny of the selected HS and LS lines and performance tested on each nutritional plane.

Referring to the environmental source of variation, there are two possibilities that must be considered: first, an actual change in the nutritional environment or the diets fed annually; second, the possibility of differences of the physical environment, including daily care and management during the growth trials.

When considering nutritional change from one generation (annually) to the next, it is important to recognize the possibility that, although the formulation procedure was not changed, the feedstuff ingredients and the micro nutrient supplies, including vitamins, minerals and amino acids (such as the "L-lysine monohydrochloride"), were acquired annually without specific quality control measures being employed. Some variation might arise at this level. The method used in this experiment to identify the possibility of meaningful

variation due to the diets, annually, was presented in Table 5. These results were from chemical laboratory analysis of the diets fed, analyzed especially for protein and amino acid levels. Some variation was noted and, in light of the numerous papers recently published concerning the problem of an arginine-lysine antagonism, the ratio of these two amino acids was considered within each diet fed at each generation interval (Table 5). The ratio of the amino acids, arginine: lysine, has been computed from the data in Table 5 and is presented in Table 16. To the author's knowledge, only Hill et al. (1961) Hill et al. (1966), and Hill and Shao (1968) have considered the effect of arginine to lysine where lysine was deficient. All other references cited in the review of literature dealt with the arginine-lysine antagonistic response where lysine was considered to be in excess of the requirement for the chick. A visual comparison of the growth performance graphs, Fig. 3 and Fig. 4, with the computed arginine: lysine ratios, Table 16, is interesting. In general, as the direction of the annual deviation for the A : L ratio (Table 16) shifted away from the base generation (P_0), a shift to the opposite direction occurred for the mean three week gain of offspring on the 1.0 percent lysine diet (Fig. 3). A similar comparison for the full-sibs on the 0.5 percent lysine diet does not appear nearly as obvious with regard to the magnitude of directional change; however, the A : L ratios were only slightly variable (Table 16) for the deficient dietary treatment as compared to the control nutritive supply.

Table 16. Arginine: lysine ratio computed for each diet and generation

Diet	Gen.	% Arginine in diet	% Lysine in diet	A:L ratio
Control	P_0	1.25	0.95	1:0.76
(1.0% lysine)	G_1	1.22	0.83	1:0.68
	G_2	0.91	0.87	1:0.96
	G_3	--	--	--
	G_4	1.01	0.87	1:0.86
Deficient	P_0	1.00	0.46	1:0.46
(0.5% lysine)	G_1	1.25	0.52	1:0.42
	G_2	1.33	0.56	1:0.42
	G_3	--	--	--
	G_4	0.86	0.50	1:0.58

Annually, the wire floored brooding batteries were located in the same fan ventilated, light controlled facility; however, the animal caretaker was not the same from year to year. Responsibility and management instructions for the caretaker were identical, but the performance in relation to the execution of work assignments introduces a potential for variation. For example, change from generation to generation could be attributable to a lack of precision in the adjustment of heating elements, for optimum brooding temperature relative to age of chicks, or perhaps to the maintenance of feed and water level in the troughs throughout the experiment.

Since there was a high degree of correlation (Table 13) between the actual empirical three week gain in grams with the individuals' computed D/C percent, it appears unnecessary to evaluate realized heritability on but one of these measurements. Magee (1965) has described the effective relationship of heritability to genetic change ($G\Delta$) and concluded that genetic change should be estimated only for the trait under direct influence through selection intensity.

In this two-way directional selection experiment, the D/C percent value was the criteria for choosing breeding stock. Consequently, realized heritability estimates, as shown in Table 17, were calculated for each selected line as a deviation from the control (RC) line for the D/C parameter. The ratio for each deviation response (gain) from one generation to the next was divided by the selection

Table 17. Computed realized heritability using deviations from the mean of the random control (RC) line by response/selection differential for trait one (t_1) three week deficient/control (D/C) percent with sexes pooled

Gen.	Line	Parental Gen. Mean	Deviation from RC	Deviation Response	Selection Differential	Offspring Mean	Deviation from RC	Realized Heritability
G_1	RC	42.8	--	--	--	29.5	--	--
	NS	44.0	+1.2	+2.9	+ 3.2	33.6	+4.1	+0.91
	HS	40.2	-2.6	+5.6	+18.2	32.5	+3.0	+0.31
	LS	43.4	+0.6	+1.9	- 1.5	32.0	+2.5	-1.27
G_2	RC	29.5	--	--	--	35.1	--	--
	NS	33.6	+4.1	+5.6	+ 5.1	44.8	+9.7	+1.10
	HS	32.5	+3.0	-0.6	+12.4	37.5	+2.4	-4.00
	LS	32.0	+2.5	+6.1	- 0.5	43.7	+8.6	+1.41
G_3	RC	35.1	--	--	--	39.9	--	--
	NS	44.8	+9.7	-6.5	+12.3	43.1	+3.2	+0.53
	HS	37.5	+2.4	-2.1	+20.1	40.2	+0.3	-0.10
	LS	43.7	+8.6	-7.9	- 8.2	40.6	+0.7	-0.96
G_4	RC	39.9	--	--	--	30.7	--	--
	NS	43.1	+3.2	+5.9	+ 9.8	39.8	+9.1	+0.60
	HS	40.2	+0.3	+5.9	+33.2	36.9	+6.2	+0.15
	LS	40.6	+0.7	+5.6	- 6.0	37.0	+6.3	-0.93
Accumulative Response	NS			+7.9	+30.4			+0.26
	HS			+8.8	+83.9			+0.10
	LS			+5.7	-16.2			-0.35

differential (intensity) for the particular line and generation. These estimates (Table 17) were quite variable from generation to generation and many calculated estimates of realized heritability go beyond one, and, these values cannot be accepted as valid since unity is the theoretical maximum of heritability. For the duration of the experiment (P_0 to G_4), the accumulative deviation response divided by the accumulative selection differentials for the D/C percent parameter, as shown in Table 17, provided realized heritability estimates of +0.26, +0.10 and -0.35 for lines NS, HS and LS, respectively. Accumulative selection differentials, as shown in Table 17, were +30.4 for the NS line, +83.9 for the high growth rate selected (HS) line and -16.2 for the low selected (LS) growth rate line.

In view of the fact that the empirical data for this experiment were obtained as grams of weight gained (three weeks minus one day weight), it was considered essential to estimate realized heritability for the gain in weight measurement. Since the trait (weight gain) was not the criteria for selection of individuals for breeding, estimations of realized heritability computed in the usual way [response (gain) divided by selection differential (intensity)] could not be made with validity because gain in weight does not meet the restrictions as described by Lush (1945) and redefined by Magee (1965).

These authors point out that frequently the concept and use of selection differential is in error and that the term, properly used,

applies only when there is mass selection for one trait (t_1) and when the response or change from generation to generation is for that same trait (t_1) being selected. Magee (1965) identifies "secondary selection differential" as an appropriate term for the situation where one looks at a second trait for differences between means of the breeders and the population as a whole of (t_2) which is different than the one used as selection criteria (t_1) where "t_1" represents the trait being selected and "t_2" identifies a second trait observed. In the cases for proper use of "t_2" the breeder must not have considered the second trait in the selection process.

Computed estimates of realized heritability were made for a second trait (t_2), three week gain in weight, using the secondary selection differential. The secondary selection differential was computed directly using the mean of the breeders ($\breve{P}$) minus the mean of the population ($\overline{P}$) in which they were born. These estimates were made from the deviation of the HS (high) and LS (low) line from the control (RC) line as observed on the 0.5 percent lysine diet. Realized heritability estimates were made using the secondary selection differential for the NS line which was reproduced by random matings among survivors in the low (0.5% lysine) dietary stress nutritive environment.

Shown in Table 18 on a generation by generation basis are the realized heritability estimates for the second trait (t_2), three week

Table 18. Computed realized heritability using deviations from the mean of the random control (RC) line by response/secondary selection differential for trait two (t_2) of gain (grams) with sexes pooled and fed the 0.5% lysine diet

Gen.	Line	Parental Gen. Mean	Deviation from RC	Deviation Response	Secondary Sel. Diff.	Offspring Pop. Mean	Deviation from RC	Realized Heritability
G_1	RC	55	--	--	--	45	--	--
	NS	55	0	+ 2	- 1	47	+ 2	-2.00
	HS	58	+ 3	+ 3	+ 5	51	+ 6	+0.60
	LS	56	+ 1	+ 3	- 5	49	+ 4	-0.60
G_2	RC	45	--	--	--	48	--	--
	NS	47	+ 2	- 1	+ 1	49	+ 1	+1.00
	HS	51	+ 6	-11	+ 2	43	- 5	-5.50
	LS	49	+ 4	- 7	-10	45	- 3	+7.00
G_3	RC	48	--	--	--	38	--	--
	NS	49	+ 1	+ 9	+ 3	48	+10	+3.00
	HS	43	- 5	+14	+10	47	+ 9	+1.40
	LS	45	- 3	+ 8	- 9	43	+ 5	-0.89
G_4	RC	38	--	--	--	47	--	--
	NS	48	+10	- 2	+ 3	55	+ 8	-0.67
	HS	47	+ 9	- 4	+ 4	52	+ 5	-1.00
	LS	43	+ 5	+ 1	- 3	53	+ 6	-0.33
Accumulative Response	NS			+ 8	+ 6			+1.33
	HS			+ 2	+21			+0.10
	LS			+ 5	-27			-0.19

gain (grams) in weight. These estimates were as variable and unrealistic as those computed for the first trait (t_1) the D/C percent parameter. The accumulative response in comparison to the accumulative secondary selection differential used to estimate realized heritability for the second trait (t_2) was in partial agreement with the estimates from the D/C parameter. For a total time span of five generations from P_0 to G_4, both the high and low growth rate selected lines declined with regard to their mean three week gain performance while the NS line changed very slightly.

An accumulative secondary selection differential of six grams was realized for the NS line but the mean gain for P_0 and G_4 offspring were identical (55 grams) on the 0.5 percent lysine diet. For the high selected (HS) line, the accumulative selection intensity accounted for +21 grams while mean performance declined six grams (Table 18). With reference to the low selected (LS) line, the accumulative secondary selection differential was -27 grams with a very slight change in mean growth of minus three grams per chick on the average.

If a difference in genetic ability exists, a specific expression in the low 0.5 percent lysine nutritive environment was not detectable with reference to a change in mean performance (Table 14). Further, there was no indication of genetic involvement from the numerous estimates of realized heritability (Tables 17 and 18). Since

contemporary full-sib groups were fed a control diet with 1.0 percent lysine, growth rate data for these individuals, as well as the full-sibs on the 0.5 percent lysine diet, were available for further analysis.

The component of variance procedure, Henderson (1953), King and Henderson (1954) and Harvey (1960), was employed for estimating heritability for gain in weight (grams), from one day to three weeks of age, from inter-related sets of sibs. A numeric example of the analysis of variance and expected mean squares (EMS) is presented in Table 19. Additional calculations from these values allow one to obtain variance component estimates for the effect due to sire (σ^2_S), dam (σ^2_D), and for the variance of all offspring (σ^2_W).

A numeric example has been worked through to show the procedure for computing variance component for sires, (σ^2_S) heritability estimate ($\hat{h}^2_s$) for sires and the standard error of the estimate of heritability [S.E. ($\hat{h}^2_s$)] for sires (Table 20). This example represents the actual data for the sire variance component of the low selected line (LS) in the fourth generation on the 0.5 percent lysine diet, and it reveals a value of 0.24 as the estimate for heritability of three week gain in weight due to sire effect with 0.20 for the standard error of the heritability estimate.

Heritability estimates computed by the component of variance method for progeny fed the control (1.0% lysine) diet appear in Table 21. Some deviation exists from one estimate to another;

Table 19. Numeric example of analysis of variance table for the hierarchal analysis design with its appropriate expected mean squares for generation four (G_4) of the low selected line (LS) provided the 0.5% lysine diet

Source of Variation	df	SS	MS	EMS*
Total	303	71075.47		
Sires	6	5281.25	880.21	$\sigma^2_W + 6.11\sigma^2_D + 42.65\sigma^2_S$
Dams/Sires	49	12891.50	263.09	$\sigma^2_W + 5.32\sigma^2_D$
Offspring/Dams/Sires	248	52902.73	213.32	σ^2_W

*Methods for computing coefficients $k_1 = 5.32$, $k_2 = 6.11$ and $k_3 = 42.65$ were presented in the Materials and Methods, Chapter III.

Table 20. Numeric example showing computations for component of variance, heritability and standard error of heritability from the sire variance component for the low selected line (LS) at the fourth generation interval (G_4) on the 0.5% lysine diet *

Parameter	Formula	Computation
Variance Component (σ^2_S)	$\frac{MS_S - (MS_W + k_2\sigma^2_D)}{k_3}$	$\frac{880.21 - (213.32 + 6.11 \times 9.36)}{42.65} = 14.30$
Heritability Estimate ($\hat{h}^2_s$)	$\frac{4\sigma^2_S}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$	$\frac{4\ (14.30)}{236.98} = 0.24$
Standard Error of Heritability $\left[S.E.(\hat{h}^2_s)\right]$	$\frac{4\sqrt{\frac{2}{k_3^2}\left[\frac{MS_S^2}{df_S} + \frac{MS_D^2}{df_D}\right]}}{\sigma^2_S + \sigma^2_D + \sigma^2_W}$	$\frac{4\sqrt{\frac{2}{(42.65)^2}\ \frac{(880.21)^2}{6} + \frac{(263.98)^2}{49}}}{236.98} = 0.20$

*Given to complete these computations are the EMS values in Table 19

The variance component for dam is: $\sigma^2_D = 9.36$

The total phenotypic variation is: $\sigma^2_S + \sigma^2_D + \sigma^2_W = 236.98$

Table 21. Heritability estimates from component of variance for three week weight gain (grams), with sexes pooled on the 1.0% lysine diet

Gen.	Line	$\hat{h}^2_s$	S.E.	$\hat{h}^2_d$	S.E.	$\hat{h}^2_{s+d}$	S.E.
P_0	RC	-.166	.204	1.030	.562	.432	.405
	NS	.537	.480	.393	.420	.465	.356
	HS	-.113	.227	1.173	.574	.530	.412
	LS	-.009	.111	-.234	.313	-.122	.157
G_1	RC	.612	.406	.219	.201	.416	.145
	NS	.493	.359	.397	.233	.445	.240
	HS	.365	.311	.475	.267	.420	.239
	LS	.642	.437	.295	.217	.468	.263
G_2	RC	.664	.448	-.188	.291	.238	.265
	NS	.667	.496	.238	.422	.453	.354
	HS	.043	.274	.835	.557	.439	.396
	LS	.963	.642	.238	.305	.600	.373
G_3	RC	-.162	.198	.265	.450	.018	.296
	NS	.685	.578	.734	.433	.710	.424
	HS	.004	.262	.559	.496	.281	.345
	LS	.126	.223	.153	.376	.139	.246
G_4	RC	.357	.264	.454	.216	.405	.197
	NS	.614	.369	.067	.133	.340	.200
	HS	.142	.201	.501	.274	.322	.210
	LS	.590	.379	.101	.148	.345	.209
Mean		.353	.344	.385	.344	.369	.287

however, 85 percent of the 60 estimates representing 3612 progeny are within the mathematical limit of unity. From the component of variation analysis, estimates of heritability for three week gain in weight on the average were as follows: sires, $(\hat{h}^2_s) = .35 \pm 34$; dams, $(\hat{h}^2_d) = .39 \pm .34$; and combined sires plus dams, $(\hat{h}^2_{s+d}) = .37 \pm .29$. These estimates are in relatively good agreement with other published heritability estimates (Godfrey, 1968, and Kinney, 1969).

The estimates of heritability from 3753 offspring fed the 0.5 percent lysine diet were somewhat lower than those computed for growth performance on the 1.0 percent lysine diet. From among the 60 estimates of heritability for three week gain in the low (0.5% lysine) dietary nutrient environment, 88 percent appeared to be realistic heritability estimates and none of the estimates approached 1.0, the upper limit of heritability. Estimates made within the 0.5 percent lysine dietary group (Table 22) were less variable than those from the 1.0 percent lysine dietary treatment environment (Table 21).

The paternal half-sib component of four times the sire component of variance $(4\sigma^2_S)$ divided by the total phenotypic variance $[(\sigma^2_P) = \sigma^2_S + \sigma^2_D + \sigma^2_W]$ estimated heritability for sires $(\hat{h}^2_s) = .23 \pm .26$, the maternal half-sib component $(4\sigma^2_D/\sigma^2_P)$ estimated heritability $(\hat{h}^2_d) = .26 \pm .31$, and from the full-sib analysis of two times the joint effects of sires plus dams $[2(\sigma^2_S + \sigma^2_D)/\sigma^2_P]$ the heritability estimate $(\hat{h}^2_{s+d}) = .25 \pm .24$ (Table 22).

Table 22. Heritability estimates from component of variance for three week weight gain (grams), with sexes pooled on the 0.5% lysine diet

Gen.	Line	$\hat{h}^2_s$	S.E.	$\hat{h}^2_d$	S.E.	$\hat{h}^2_{s+d}$	S.E.
P_0	RC	-.116	.128	.318	.398	.101	.262
	NS	-.218	.100	.164	.386	-.027	.235
	HS	.535	.390	-.159	.290	.188	.242
	LS	.343	.295	.111	.282	.227	.221
G_1	RC	.310	.215	-.136	.153	.087	.128
	NS	.020	.119	.432	.242	.226	.177
	HS	.183	.177	.102	.193	.143	.147
	LS	-.050	.101	.476	.264	.213	.191
G_2	RC	.443	.363	.035	.342	.239	.268
	NS	.214	.231	-.064	.298	.075	.195
	HS	.144	.317	.723	.524	.433	.382
	LS	.680	.484	.198	.287	.439	.300
G_3	RC	.524	.517	.720	.461	.622	.410
	NS	.298	.374	.647	.418	.473	.359
	HS	.204	.331	.443	.438	.323	.331
	LS	.354	.352	.351	.359	.352	.288
G_4	RC	.131	.156	.345	.228	.238	.168
	NS	.258	.190	.063	.150	.160	.127
	HS	.189	.204	.181	.232	.185	.176
	LS	.241	.201	.158	.179	.200	.147
Mean		.234	.262	.256	.306	.245	.238

The data in Tables 21 and 22 were reorganized and presented in Table 23 for greater ease in comparing heritability among the lines. It may be observed that the heritability estimates were quite similar from each level of the variance component analysis and agreed very well between lines. For the 1.0 percent lysine dietary control fed situation, the best estimates of heritability with generations pooled, were .31, .48, .40 and .29 for lines RC, NS, HS and LS respectively. In the 0.5 percent lysine environment, the combined sire + dam estimates of heritability were .26, .18, .26 and .29 for lines RC, NS, HS and LS respectively.

One essential consideration of all selection work, whether experimental or commercial in nature and of particular importance in small populations, is the consequence of inbreeding. Inbreeding in general terms is the degree of relationship among individuals. More specifically, the coefficient of inbreeding refers to the homozygous condition or the probability that two genes at any particular locus in an individual are identical by descent. Wright (1934) described the path coefficients method of calculating the degree of inbreeding by saying that the level of inbreeding is equal to one half the coefficient of relationship of its common ancestors. Wright's path coefficient procedure was used to estimate the coefficient of inbreeding for the males in each of the selected lines (HS and LS) in this experiment,

$$F_x = \tfrac{1}{2} \Sigma \left[(\tfrac{1}{2})^n (1 + F_{CA}) \right]$$

Table 23. Summary of calculated heritability estimates by line for diets separately and generations pooled for each level of the component of variance

Source	Line			
	RC	NS	HS	LS
Control 1.0% lysine diet				
Sire ($\hat{h}^2_s$)	.261	.599	.088	.462
Dam ($\hat{h}^2_d$)	.356	.366	.709	.111
Combined ($\hat{h}^2_{s+d}$)	.309	.483	.398	.286
Deficient 0.5% lysine diet				
Sire ($\hat{h}^2_s$)	.258	.114	.251	.314
Dam ($\hat{h}^2_d$)	.256	.248	.258	.259
Combined ($\hat{h}^2_{s+d}$)	.257	.181	.255	.287

where:

F_x is percent inbreeding of individual "x";

n is the number of paths;

F_{CA} is the inbreeding of the common ancestor.

A brief review of the design of this experiment as it influences the breeding relationships within each line is important. First, each sire was to be represented in the next generation by a son, either by random choice for lines RC and NS or by selection as determined by the criteria for the HS and LS line respectively. Second, for lines RC and NS, each of eight sires was mated at random to females from within the closed line. For the high selection (HS) and low selection (LS) lines, a pedigree mating plan was used as a means of avoiding close matings. Neither full nor half-sib matings were allowed. All matings were completed by artificial insemination for individually caged females. The number of males and females used during this experiment are present by line in Table 24 and by generation in Table 25. Because of the potential consequence of low numbers in the effective breeding population which could contribute to an inbreeding depression, the number of dams mated to each sire was increased in the fourth generation. The increase in the number of dams had the effect of slowing down the rate of increase of "F", the coefficient of inbreeding. The actual number of males and females that contributed offspring to the breeding population of the next generation are

Table 24. Average male:female ratio by line during the experiment

Line	Ratio of Selected Breeder Pop.	Ratio of Br. Prod. Offspring	Ratio of Effective Breeder Pop.*	Sum of Effective Pop.
RC	1:6.6	1:5.8	1:5.2	40:209
NS	1:6.6	1:5.8	1:5.2	40:206
HS	1:6.4	1:5.3	1:4.9	39:188
LS	1:6.6	1:6.0	1:5.6	38:214
Total				157:817

*Effective being defined as having produced members of the next generation selected breeding population

Table 25. Average male:female ratio by generation during the experiment

Gen.	Ratio of Selected Breeder Pop.	Ratio of Br. Prod. Offspring	Ratio of Effective Breeder Pop.*	Sum of Effective Pop.
P_0	1:6.0	1:5.2	1:4.5	32:145
G_1	1:6.0	1:5.2	1:5.1	32:165
G_2	1:6.0	1:5.3	1:4.7	32:151
G_3	1:6.0	1:5.3	1:4.4	31:136
G_4	1:8.8	1:7.7	1:7.3	30:220
Total				157:817

*Effective being defined as having produced members of the next generation selected breeding population

tabulated in Table 26, along with the coefficient of "F" or the estimate of the percent of inbreeding at each generation interval and by line. With no more than eight percent for the highest degree of inbreeding for any line, it is concluded that an inbreeding depression is unlikely as a major factor influencing the course of this experiment. Further, there must be reasons other than "inbred" for lack of progress in the direction of selection, whether it be for the high or for the low gain (grams) in weight.

In theory, the bi-directional selection scheme will separate two lines from each other with regard to the parameter under selection, and the amount of dispersion is influenced by two factors. The first of these factors is the intensity (i) or selection differential (S) applied for the trait. The second factor is the heritability (h^2) of the trait being selected. Application of this concept allows the researcher to predict genetic change or progress from one generation to another due to selection. The formula used for this prediction was:

$$G\Delta = i\, h^2$$

where:

$G\Delta$ = the amount of genetic change;

i = intensity or selection differential;

h^2 = heritability of the trait selected.

Table 26. Coefficient of inbreeding "F" by line and generation interval

Gen.	Line	Mating system	Actual No. Males	Actual No. Females	Coefficient of "F"
P_0	RC	Restricted Random	8	36	.000
G_1			8	40	.015
G_2			8	40	.030
G_3			8	30	.046
G_4			8	63	.059
P_0	NS	Restricted Random	8	32	.000
G_1			8	43	.015
G_2			8	38	.030
G_3			8	34	.045
G_4			8	59	.059
P_0	HS	Pedigree Selection	8	37	.000
G_1			8	40	.000
G_2			8	37	.000
G_3			8	32	.068
G_4			7	42	.078
P_0	LS	Pedigree Selection	8	40	.000
G_1			8	42	.000
G_2			8	36	.000
G_3			7	40	.049
G_4			7	56	.066
Total N			157	817	

Predictions for direction and progress using this model for this experiment did not provide any estimates of genetic change (GΔ) similar to the behavior observed for either measurement, D/C percent or three week gain (grams) as parameters.

From the lack of divergence in the mean performance (after four generations of selection) of the high (HS) and low (LS) selected lines, and in view of the relatively large selection differential which was calculated, one may say that generally the trait being selected did not exhibit additive gene action. To further test for genetic change (GΔ) among the selected lines (also called pure lines), a series of reciprocal line crosses were made and their cross line F_1 progeny were measured for growth rate on both diets; these diets being the control with 1.0 percent lysine and the deficient with 0.5 percent lysine by formulation.

The diets fed to the pure lines and the F_1 cross lines progeny were the same diets from the same batch of feed mixed on an annual basis. Least squares analysis of variance computations were made on data representing the second, third and fourth generations to test for diet, line, and diet by line interaction effects. The statistical model for this analysis was:

$$Y_{ijk} = \mu + D_i + L_j + DL_{ij} + e_{ijk}$$

where:

Y_{ijk} = the mean observed for the k^{th} individual in the j^{th} line on the i^{th} diet;

μ = the overall common mean;

D_i = the effect of the i^{th} diet, i = 1, 2;

L_j = the effect of the j^{th} line, j = 1...4;

DL_{ij} = the two-way interaction associated with the designated subclasses;

e_{ijk} = the random error among observation.

The analysis of variance for these data pooled for generations (Table 27) show highly significant differences for diet line and diet by line (D xL) interation effects. Included as lines for this analysis were the high (HS) and low (LS) selected lines and F_1 cross line progeny from HS♂ x LS♀ and LS♂ x HS♀. The diet by line interaction was also highly significant ($P < .005$), a result not previously observed among the pure line alone.

An examination of the means by diet and line, whether pure line HS and LS or cross line progeny from HS x LS and LS x HS (Table 28), show that the cross line progeny on the control 1.0 percent lysine diet were always superior in three week gain in weight as compared to the pure line progeny. For growth response observed under dietary deficient 0.5 percent lysine fed conditions, generally, the pure line progeny grew more rapidly than the cross line progeny. The lack of a uniform response characteristic for full-sibs tested on two

Table 27. Least squares analysis of variance for three week gain (grams) for pure line HS and LS progeny and for F_1 cross line progeny with generations G_2, G_3 and G_4 pooled

Source of Variation	df	MS	F	Sig.
Total	3883			
Diet	1	5302628.96	11249.40	<.005
Line	3	9412.69	19.97	<.005
DxL	3	36270.01	76.95	<.005
Error	3876	471.37		

Table 28. Mean three week gain (grams) for pure line and cross line progeny by diet and generation interval with sexes pooled

Gen.	Line	1.0% lysine				0.5% lysine			
		N	$\bar{x}$ gms.	P < .05	S.E.	N	$\bar{x}$ gms.	P < .05	S.E.
G_2	HSxHS	107	97	b[1]	2.10	107	43	b[1]	1.46
	LSxLS	129	96	b	2.45	147	45	b	1.25
$G_2(F_1)$	HSxLS	101	113	a	1.80	95	52	a	1.74
	LSxHS	80	117	a	2.48	63	48	a b	1.86
G_3	HSxHS	109	109	b	2.58	116	47	a	1.30
	LSxLS	130	103	c	2.40	140	43	a	1.26
$G_3(F_1)$	HSxLS	155	137	a	1.86	179	45	a	1.09
	LSxHS	151	132	a	1.81	126	41	a	1.24
G_4	HSxHS	234	121	b	1.66	215	52	a	1.16
	LSxLS	325	124	b	1.29	304	53	a	0.88
$G_4(F_1)$	HSxLS	277	133	a	1.69	229	40	b	1.12
	LSxHS	142	125	b	1.95	112	40	b	1.23

[1]Within each dietary and generation group of four lines, the means with the same subscript letter are not significantly different at the five percent level of probability (Duncan, 1955)

dietary levels of lysine shown in Table 28 indicate the existence of the diet by line interaction which was verified by the analysis of variance (Table 27). To more easily visualize the interaction effect, a series of two-way contingency tables (appearing in Table 29) were assembled to show the diet by generation by line of sire and line of dam effects.

Heterosis as a behavioral phenomenon has been reported for many different traits in animals and plants. The expression of hybrid vigor results from recombinations of many hereditary factors. Gowen (1964), with the help of many colleagues, published an entire book summarizing the information available at that time on heterosis. One type of heterosis (Gowen, 1964) which may be identified by crossing inbred lines is an expression of interaction between allelic genes. Another kind is hybrid vigor resulting from interaction effects at the chromosomal and/or cytoplasmic sites.

Of specific concern in this experiment was a test for hybrid vigor, "heterosis", through F_1 cross line progeny from the high (HS) and low (LS) selected lines and, further, to measure the relative advantage of selecting in a poor nutritional environment for optimum performance of F_1 cross line progeny in different nutritional regimes.

A study and analysis of the performance data for the pure line vs. cross line progeny was made by estimating the percent heterosis

Table 29. Two-way contingency tables for cell means showing diet by line interaction effect for line of sire and line of dam by diet and generation[1,2]

Gen.		1.0% lysine		0.5% lysine	
		Dam		Dam	
$G_2(F_1)$	Sire	HS	LS	HS	LS
	HS	HSHS 97	HSLS 113	HSHS 43	HSLS 52
	LS	LSHS 117	LSLS 96	LSHS 48	LSLS 45
$G_3(F_1)$					
	HS	HSHS 109	HSLS 137	HSHS 47	HSLS 45
	LS	LSHS 132	LSLS 103	LSHS 41	LSLS 43
$G_4(F_1)$					
	HS	HSHS 121	HSLS 133	HSHS 52	HSLS 40
	LS	LSHS 125	LSLS 124	LSHS 40	LSLS 53

[1] Pure line genotype sources are shown as HSHS and LSLS

[2] Cross line genotype sources are shown as HSLS and LSHS

for the cross line progeny. Estimates of percent heterosis were calculated by generation according to the following formula:

$$\text{Percent heterosis} = \frac{\text{Cross line mean} - \text{Pure line mean}}{\text{Pure line mean}} \times 100$$

where:

Percent heterosis is the degree of response;

Pure line mean is the average of the parental types HS x HS plus LS x LS;

Cross line mean is the average of F_1 progeny types HS x LS plus LS x HS.

The result of these estimations have been tabulated in Table 30 according to the response in each nutritive environment. Measurements for growth were recorded in either the control 1.0 percent lysine or the deficient 0.5 percent lysine nutritive environment. The average percent heterosis favored the cross line progeny in the control nutritive environment by 17 percent (Table 30); however, in the case of the deficient nutritional plane, there was no consistent response as generation G_2 showed a positive 14 percent heterosis while G_3 and G_4 were each negative, -4 and -25 percent respectively.

One aspect of the nutritional environment not yet considered is the overall effect of the low level 0.5 percent lysine (an imbalanced protein diet) on livability of experimental chicks. A specific line (NS) was incorporated in this study to observe the effect of the 0.5 percent

Table 30. The influence of nutritional environment on heterosis for three week gain (grams) of chicks from the high (HS) and low (LS) lines selected for growth on a 0.5 percent lysine diet

Gen.	Cross line mean	Pure line mean	Percent heterosis
	1.0% lysine diet		
G_2	115	97	+19
G_3	135	106	+27
G_4	129	123	+ 5
Mean			+17
	0.5% lysine diet		
G_2	50	44	+14
G_3	43	45	- 4
G_4	40	53	-25
Mean			- 5

lysine dietary environment as a force of natural selection. This treatment effect was called "natural selection" since reproduction from one generation to the next was by random choice of the breeders; however, random selection of breeders was permitted only among survivors on the poor nutritional environment. Presented in Table 31 are percent mortality data by diet, sex, generation and line. Considerable variation was evident with no consistent trend.

The diet by sex interaction is believed to exist because the 0.5 percent lysine diet contributed to a higher mortality rate among the males averaging 17.12 percent on the deficient diet, but only 8.12 percent on the control diet. For the females on the deficient diet the mortality rate was 15.15 percent and 10.14 percent on the control diet (Table 31). The higher mortaltiy rate of males in the deficient lysine environment is considered to be due to an inherent growth rate differential favoring the males, thus, they were stressed much more, resulting in the higher death rate, than the females when fed the lysine deficient diet. Also there was a marked difference in mortality rates as influenced by the dietary environment. Throughout the five generations involved, the average mortality rate was excessively high with 9.28 percent for progeny on the control diet (1.0% lysine) and 16.14 percent for those fed the deficient diet (0.5% lysine) during the critical three week growth period for this study.

The question as to how well a population of laying hens produce eggs is always of interest to investigators; consequently, the average

Table 31. Percent mortality from one day to three weeks of age by diet, sex, generation and line

Gen.	Line	Number offspring	1.0% lysine*		0.5% lysine*	
			Male	Female	Male	Female
P_0	RC	281	2.90	5.71	18.57	7.89
	NS	258	1.85	5.26	10.45	10.45
	HS	330	8.77	15.79	14.71	18.89
	LS	335	8.33	8.22	15.07	8.79
G_1	RC	536	4.80	8.96	12.67	15.25
	NS	603	7.53	6.20	9.26	11.39
	HS	561	9.49	13.11	14.74	14.89
	LS	607	12.03	13.11	14.20	14.58
G_2	RC	335	13.11	9.59	18.56	19.78
	NS	315	1.92	8.20	15.22	8.42
	HS	306	5.36	11.67	26.97	18.68
	LS	343	14.47	8.70	9.80	15.22
G_3	RC	271	8.57	5.88	30.00	15.00
	NS	305	0.00	9.09	21.05	20.00
	HS	265	6.90	14.29	35.29	17.14
	LS	325	15.28	17.65	25.00	27.50
G_4	RC	753	16.85	12.44	18.04	16.17
	NS	823	10.70	13.27	12.76	12.84
	HS	508	7.97	10.74	6.47	18.02
	LS	710	8.56	10.86	13.53	12.15
Means sex/diet			8.12	10.14	17.12	15.15
Diet			9.28		16.14	

*Percent lysine in starter diet; all birds were fed the same rations throughout the remainder of the study.

number of eggs produced by survivors of 280 days (ten, 28 day periods) was summarized (Table 32). Statistical evaluation for differences was completed and a ranking of means is denoted at the five percent level of probability (Duncan, 1955).

The data, average number of eggs per hen (Table 32), have been converted to percent production for diet, generation and line variables of the experiment and these percents are recorded in Table 33. Some variation exists from one generation interval to another but the direction of change and deviations within and between diets are nearly identical. From one generation to the next, the percent change was -4, -4, and +1 for the birds grown on the 1.0 percent lysine diet and -7, -2 and +2 for those fed the 0.5 percent lysine diet. An examination of the overall mean (Table 33) for each diet reveals no significant differences ($P > .05$).

From a commercial and economic point of view, mortality rate during the laying period is tremendously important. The mortality records for birds housed in this experiment have been summarized in Table 34 according to diet as a factor during the early growth period and for generation and line sources of variation. From these data, one may conclude that, in the adult population as a whole, livability of survivors of the dietary stress situation during growth was no different than that of the non-stressed (RC) line. The mortality rates were quite variable and no particular pattern was

Table 32. Average number of eggs produced for survivors during 40 weeks (280 days) on test

Gen.	Line	1.0% lysine* No. birds	No. eggs	Sig. P<.05	S.E.	0.5% lysine* No. birds	No. eggs	Sig. P<.05	S.E.
P_0	RC	41	174.51	a[1]	5.19	59	177.41	b[1]	6.22
	NS	39	168.59	a	6.53	55	173.98	b	5.42
	HS	42	175.81	a	5.38	50	189.22	a	4.86
	LS	49	167.00	a	6.12	71	175.41	b	4.91
G_1	RC	73	171.45	a	3.78	50	166.14	a	4.66
	NS	64	150.01	b	5.56	83	150.39	b	3.75
	HS	55	173.93	a	5.95	54	164.43	a b	6.05
	LS	59	150.39	b	5.17	59	156.80	a b	5.33
G_2	RC	46	160.85	a	7.17	46	160.26	a	5.43
	NS	27	134.11	b	8.84	45	153.31	a b	5.78
	HS	25	144.84	a b	8.64	41	135.02	b	8.67
	LS	33	154.85	a b	6.57	50	157.94	a b	5.35
G_3	RC	28	171.25	a	7.29	44	156.18	a	7.07
	NS	43	151.91	a b	6.68	49	155.22	a	5.57
	HS	31	146.65	b	9.08	34	147.38	a	6.89
	LS	43	147.74	b	6.06	52	166.13	a	6.01

*Percent lysine in starter diet; all birds were fed the same rations throughout the remainder of the study.

[1]Means with the same letter for a particular generation within dietary treatment are not significantly different at the five percent level of probability (Duncan, 1955).

Table 33. Percent egg production for survivors during 40 weeks (280 days) on test

Gen.	Line	1.0% lysine* No. birds	1.0% lysine* % prod.	0.5% lysine* No. birds	0.5% lysine* % prod.
P_0	RC	41	62.33	59	63.36
	NS	39	60.21	55	62.14
	HS	42	62.79	50	67.58
	LS	49	59.64	71	62.65
		171	61.19	235	63.76
G_1	RC	73	61.23	50	59.34
	NS	64	53.58	83	53.71
	HS	55	61.12	54	58.73
	LS	59	53.71	59	56.00
		261	57.55	246	56.50
G_2	RC	46	57.45	46	57.24
	NS	27	47.90	45	54.75
	HS	25	51.73	41	48.22
	LS	33	55.30	50	56.41
		131	53.85	182	54.36
G_3	RC	28	61.16	44	56.49
	NS	43	54.25	49	55.44
	HS	31	52.38	34	52.64
	LS	43	52.76	52	59.33
		145	54.74	179	56.12
Overall totals and mean		708	57.17	842	57.98

*Percent lysine in starter diet; all birds were fed the same rations throughout the remainder of the study.

Table 34. Laying house mortality during 40 weeks (280 days) on tests

Gen.	Line	1.0% lysine* No. housed	No. dead	% mort.	0.5% lysine* No. housed	No. dead	% mort.
P_0	RC	47	6	12.8	65	6	9.2
	NS	46	7	15.2	60	5	8.3
	HS	49	7	14.3	57	7	12.3
	LS	56	7	12.5	77	6	7.8
		198	27	13.6	259	24	9.3
G_1	RC	80	7	8.6	55	5	9.1
	NS	82	8	9.8	99	16	16.2
	HS	67	12	17.9	64	10	15.6
	LS	67	8	11.9	67	8	11.9
		296	35	11.8	285	39	13.7
G_2	RC	52	6	11.5	51	5	9.8
	NS	33	6	18.2	57	12	21.1
	HS	30	5	16.7	50	9	18.0
	LS	38	5	13.2	56	6	10.7
		153	22	14.4	214	32	15.0
G_3	RC	35	7	20.0	50	6	12.0
	NS	51	8	15.7	58	9	15.5
	HS	36	5	13.9	46	12	26.1
	LS	46	3	6.5	59	7	11.9
		168	23	13.7	213	34	16.0
Overall totals and means		815	107	13.1	971	129	13.3

*Percent lysine in the starter diet; all birds were fed the same rations throughout the remainder of the study.

evident. The rates were apparently not influenced by line and the mean adult mortality was 13.1 percent for birds started on the control 1.0 percent lysine diet while the chicks started on the deficient 0.5 percent lysine diet had an overall mortality rate of 13.3 percent (Table 34).

Fertility rate by generation and line as well as the percent hatchability was computed for the pure lines RC, NS, HS and LS and the results appear in Table 35. Artificial insemination was practiced for all matings during the tenure of this experiment. Fertility rate, while having some variation from line to line within generation interval, did not establish a consistent trend; therefore, this trait was not considered to have an influence on the overall experiment. The percent of fertile eggs hatched was very erratic from generation to generation but quite uniform among lines per generation. The overall weighted mean percent hatch (Table 35) shows generation three to be depressed as compared with all other generations among which there was little variation.

An examination of the data for fertility and hatchability among reciprocal line crosses (Table 36), compared with the pure lines (Table 35) shows the HS line of sire as having contributed to a higher percent fertility than line LS. The effect of line of dam was inconsistent and assumed to be random. The overall mean for percent hatched at the third generation interval for F_1 cross line progeny was

Table 35. Percent fertility and hatchability by generation for pure lines

Gen.	Line	No. eggs	% fertile	% hatched	Mean % hatched
P_0	RC	501	80.64	69.55	
	NS	474	74.26	73.30	
	HS	532	87.59	70.82	
	LS	533	79.92	78.64	73.13[1]
G_1	RC	988	83.91	64.66	
	NS	1045	79.81	72.30	
	HS	929	84.39	71.56	
	LS	1039	77.96	74.94	70.93
G_2	RC	534	88.76	70.68	
	NS	526	78.90	75.90	
	HS	546	89.38	62.70	
	LS	471	90.45	80.52	72.14
G_3	RC	799	78.60	43.15	
	NS	658	86.47	53.60	
	HS	801	81.40	40.64	
	LS	952	69.64	40.02	46.41
G_4	RC	1235	84.53	72.13	
	NS	1208	89.57	76.52	
	HS	814	82.92	75.26	
	LS	1005	86.17	81.99	76.30

[1]Weighted mean

Table 36. Percent fertility and hatchability by generation for reciprocal line crosses

Gen.	Line	No. eggs	% fertile	% hatched
$G_2(F_1)$	HS X LS	275	92.73	81.96
	LS X HS	319	86.21	72.00
$G_3(F_1)$	HS X LS	710	67.18	76.10
	LS X HS	662	76.59	72.78
$G_4(F_1)$	HS X LS	383	85.64	80.79
	LS X HS	278	70.14	63.59

approximately 74 percent, a value in good agreement with those of other generations for both pure line and cross line breeding. This indicates that there was nothing particular for that year which contributed to the low rate for hatchability among the pure lines of generation three. The low hatchability of 46.41 percent for the pure lines at generation three (Table 35) is accountable only to a variable introduced by man causing the high degree of error or due to equipment in the hatchery.

CHAPTER V

CONCLUSIONS

Mass selection pressure was applied to a population of egg-type chickens to evaluate the genetic parameters of the lysine requirement, estimate heritability and to evaluate the latent consequences of the early growth diet (one day to three weeks of age) upon subsequent reproductive performance. The rearing environment was deficient in lysine with 0.5 percent available.

This bi-directional selection experiment for pedigreed high and low growth rate lines indicated that the two-way selection was relatively inefficient in separating the lines when they were fed the lysine deficient diet; however, each selected line exhibited growth rate improvement as compared to the unselected RC (random control) line. Line NS (meaning natural selection) was maintained as survivors only of the deficient dietary environment, and no selection pressure other than dietary stress was applied. The high growth rate line designated as HS was intensely selected for gain in weight from one day to three weeks of age. The LS line represented the influence of maximum selection pressure for low (gain in weight) growth in the dietary lysine deficient environment.

Realized heritability estimates computed on deviations from the random bred control line were quite variable, 0.26, 0.10 and -0.35 for the lines NS, HS and LS, respectively. Estimates of heritability from the component of variance method were more consistent for each line. These estimates were to 0.23, 0.26 and 0.25 for the sire, dam and combined sire plus dam sources of variance with lines NS, HS and LS pooled. Considering the combined sire plus dam estimate of heritability as the best estimate, a comparison of the high (HS) and the low (LS) selected lines in the bi-directional selection experiment showed heritability for growth in the lysine deficient environment to be 0.26 and 0.29 for lines HS and LS, respectively.

Coefficients of inbreeding were estimated for each line in the study and the level of inbreeding was not found to be high enough to contribute significantly to an inbreeding depression.

Cross line breeding was practiced among the HS and LS selected line producing F_1 progeny during the second, third and fourth generations. These progeny were also tested in the two nutritional environments and they exhibited a high degree of positive heterosis when grown in the control dietary environment with 1.0 percent available lysine and a negative heterosis for the contemporary full-sibs grown in the 0.5 percent lysine dietary environment. The expression of differential heterosis by cross line progeny in the two different nutritional environments needs further study and may have commercial applicability.

The associated traits of egg production, adult livability and reproductive capacity as measured by fertility and hatchability were not influenced by nutritional background common to the individual or selected line.

This experiment has demonstrated a need for further research as to the genetic parameters for appetite control, patterns of feed consumption and feed efficiency among lines for various levels of lysine in the diet. It is probable that larger populations of a more rapidly growing stock would be more productive in studies of growth rate and adaptability of genetic stock to malnutrition type environments. Since heritability was found to be low, 0.26, a more intense selection design, as opposed to mass selection, should be employed for more rapid progress.

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