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GENETICS OF BODY WEIGHT OF
RING-NECKED PHEASANT (PHASIANUS COLCHICUS) POPULATION

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# GENETICS OF BODY WEIGHT OF RING-NECKED PHEASANT (PHASIANUS COLCHICUS) POPULATION

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# ABSTRACT

## GENETICS OF BODY WEIGHT OF RING-NECKED PHEASANT (PHASIANUS COLCHICUS) POPULATION

By John F. Kassid

In a population of Ring-Necked Pheasants (Phasianus colchicus) a divergent selection program was initiated for high and low twelve-week body weight. Data were collected from 8 sires, 59 dams, and 1197 offspring over a period of two generations.

Divergent selection for 12-weeks weight has resulted in mean body weight differences of about 2, 49, 168, 283 and 381 gm in the males and 2, 54, 156, 264 and 327 gm in the females at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age, respectively, between the two divergent selected lines.

The heavy selected line gained more weight by plus selection than was lost from the light selected line by minus selection. The males gained or lost more weight than females.

Experimental data transformation to logarithmic and percentage scale did not appear to give a noticeably better fit than the actual scale. Thus there was little evidence that size genes were acting multiplicatively.

Average heritability estimates for the first generation of selection calculated from parent-offspring regression techniques after omitting all values that fall outside the

possible biological range of heritability were found to be .47 ± .1, .44 ± .08, .66 ± .07, .50 ± .04 and .63 ± .03 for body weights at one-day, 4-weeks, 8-weeks, 12-weeks, and 18-weeks of age, respectively. Heritability estimates for the second generation heavy selected line at these time intervals would be .29 ± .18, .64 ± .21, .46 ± .24, .77 ± .26 and .33 ± .16, respectively, while for the second generation light selected line they were equal to .47 ± .42, .59 ± .24, .41 ± .23, .20 ± .42 and .59 ± .08, respectively.

Average realized heritability estimates for 12-weeks body weight after negative heritability estimates were omitted from the statistical analysis were found to be .50 and .33 in males and females of the light selected line, respectively, while they were equal to .71 and .38 in the heavy selected line for males and females, respectively.

These results suggest the existence of high additive genetic variance, which in turn indicate that mass selection would be the best single procedure to use to select for body weight.

Duration of fertility ranged from 10-21 days with an average of about 15 days.

An average of 0.82 for the degree of coefficient of correlation between egg weight and day-old chick weight was calculated. Chick weight at hatching time was found to represent 64-67 percent of the weight of the egg from which it hatched.

Hen-housed egg production for the heavy females selected as parental stock was 60.63 and 48.57 percent for base

and first generation, respectively. For the light selected females it was 48.83 and 34.19 percent for the same generations, respectively. Hen-day egg production for heavy females selected as parental stock was 61.87 and 51.61 percent for base and first generation, respectively. For the light selected females it was 56.70 and 39.66 percent for the same generations, respectively.

Percent mortality was 19.58, 31.93, 37.03 and 24.20 for the base, first, second generation and control population, respectively. Chi-square analyses indicate that mortality is not independent of selection. Highly significant differences ($p < .01$) in mortality were found between base generation and first generation, base generation and second generation and, finally, between control and second generation.

To my daughter

Rana

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# TABLE OF CONTENTS

Page

# LIST OF TABLES

LIST OF TABLES (Continued . . .)

# LIST OF FIGURES

## LIST OF APPENDICES

# INTRODUCTION

Selection is considered to be the best tool for genetic improvement in a given population. The basis for genetic improvement achieved by selection in any population will be due to the genetic variation within that population. If most of the gene action is of the additive type, individual phenotypic selection should be effective in changing the population means for this characteristic in either an upward or downward direction; on the other hand if dominance and epistasis constitute much of the genetic variation then aids to mass selection are recommended (i.e. progeny, sib test).

Heritability of a character is an important factor affecting genetic improvement. Accurate estimates of heritabilities of economic traits are needed in poultry breeding practices for the formulation of efficient selection schemes to ensure that the highest genetic gains are obtained.

Many estimates of heritability have been reported for body weight in poultry, a trait which is frequently considered as the most important one in breeding programs directed toward the improvement of meat type birds. From these estimates it would be logical to conclude that body weight has a moderate to high heritability.

In single trait selection experiments, simultaneous changes in unselected traits as a result of selection for one particular trait are termed correlated responses. The genetic cause of correlation is chiefly pleiotropy which results in more permanent genetic correlations, though linkage is a cause of transient correlation (Falconer, 1960a).

The primary objective of this study was to accumulate additional empirical knowledge on size inheritance in Ring-Necked pheasants.

# REVIEW OF LITERATURE

## Body weight

Body weight, which is considered as one of the typical multifactorial or polygenic traits and one of the most important inherited traits in the fowl, was studied by many investigators over the past 50 years in order to determine its genetic make-up and to establish certain genetical techniques to improve it.

Many reports have been published concerning the number of genes that control this trait. Asmundson and Lerner (1933), Knox and Marsden (1944) and Hurry and Nordskog (1953) demonstrated that inherited differences in body growth were affected by multiple genetic factors, the exact number of which has not yet been determined exactly. On the other hand, Festing and Nordskog (1967) reported that body weight is controlled by both independent and pleiotropic genes.

Goodale (1938) reported that at least 32 pairs of genes were responsible for the heaviest mice that he obtained in his experiment on the inheritance of body weight in the albino mouse.

Falconer (1953a) gave an approximate estimation of the minimum number of loci which affect weight in a random population of mice to be equal to at least nineteen loci on the assumption that

1) All genes concerned have equal effects.
2) All genes concerned act additively both within loci and between loci.
3) The alleles at all loci have frequencies of .5.

Data from MacArthur's experiments (1944a, b, 1949) were used by Falconer (1953a) who reported a much higher estimation of the minimum number of loci which affect weight, being equal to at least fifty-four loci. Godfrey (1953) reported that one sex-linked gene and at least fifteen pairs of autosomal genes affect growth rate prior to 9 weeks of age in domestic fowl and thereby influence mature body size.

MacArthur (1944a) elaborated on the geometric theory of size-gene interaction that size genes or modifiers act geometrically by multiplying rather than summing each other's effects. Falconer (1953a) stated from his selection experiment for large and small size in mice that size genes act multiplicatively on an arithmetic scale while they act on a logarithmic scale additively.

Body weight is also affected by environmental factors due to genetic-environmental interactions. The preponderance of the genetic part is due to the presence of polygenes where many genes are present which have minor effects (Hurry and Nordskog, 1953).

## Sexual dimorphism

Reports by Asmundson (1942); Knox and Marsden (1944); Asmundson (1948); Hutt (1949); Knox *et al*. (1952); Siegel (1962a);

Washburn and Siegel (1963); Marais and Joubert (1964); Kinney and Shoffner (1965); Nestor *et al*. (1967); Buvanendran (1969) and Sefton and Siegel (1974) on sexual dimorphism show that almost all domesticated avian species show sexual dimorphism for body size.

Marais and Joubert (1964) stated that in the Muscovy duck, the male is about twice the size of the female. On the other hand, Siegel (1962a) reported that in the fowl the male is about 10-15 percent heavier than the female. Asmundson (1942) and Knox and Marsden (1944) stated that turkey female's weight is 65 and 66 percent as much as the male's, respectively.

Sefton and Siegel (1974) reported from their study on inheritance of body weight in Japanese quail that sexual dimorphism became evident at the age of sexual maturity with females being heavier than males. This difference is due to the fact that increase in total body weight is associated with the reproductive maturation and the large female reproductive system. Hutt (1949) stated that "the differences in the size of male and female fowls are apparently determined by sex-linked genes, of which the males, with two sex chromosomes must have more than the females, which have only one sex chromosome."

Buvanendran (1969) reported from his work on the sexual dimorphism for 10-week body weight of White Leghorns that the genetic correlation between male and female weights was .586 ± .170. He stated that this figure is an indication of a considerable genotype-sex interaction. Similar results were obtained by Kinney and Shoffner (1965) who reported a value of .66 ± .08 for the genetic correlation between 8-week body weight of males and females. From these findings, Kinney and Shoffner (1965) stated that 8-week body weight of the males and the females should not be considered as the same trait.

## Phenotypic variation

The phenotypic variation observed in any trait (i.e. body weight) can be divided into hereditary and non-hereditary variation. The hereditary variation can be partitioned still further according to the nature of the genic effects, into the additive genetic variation, which is contributed by the average effects of genes in any combination with other genes (Lush, 1940), and the non-additive genetic variance which is contributed by interactions of genes. These interactions can be either from dominance (interaction between allelic genes) and/or epistasis (interaction of non-allelic genes). Development of this partitioning concept was largely due to Fisher (1918), Wright (1921), Fisher *et al*. (1932) and Wright (1935).

Several investigators have attempted to determine the relative importance of non-additive genetic effects on body weight. Among those who reported evidence of the non-additive variance contribution to the total variability of body weight are Moyer *et al*. (1962) and Mahmoud *et al*. (1965), while

Yao (1959, 1961) reported significant dominance effects in certain incrosses and incrossbreds.

On the other hand, many researchers failed to show the existence of non-additive genetic variation in body weight genetic architecture (Hazel and Lamoreux, 1947; Martin et al. 1953; Brunson et al. 1956; Chai, 1956; Goodman et al. 1957; Kan et al. 1959b; Goodman and Jaap, 1960; Comstock et al. 1963; Miller et al. 1963 and Silva et al. 1976).

Diallel mating as a method of studying non-additive genetic variance was used in excellent experiments that were carried on by Hayman (1954a, b); Jinks (1954); Dickinson and Jinks (1956); Griffing (1956); Kempthorne (1956). These experiments were confined mostly to plant material, and they will be of great benefit to refer to mainly in case of examining the effect of non-additive genetic variance.

Influence of sex-linked genes and maternal effect on the inheritance of body weight was examined in different published reports. The reports of Godfrey (1953); Brunson et al. (1956); Jaap and Grimes (1956); Jerome et al. (1956); Newcomer (1957); Thomas et al. (1958); Hutt (1959); Kan et al. (1959a,b); Merritt (1966) and Joubert et al. (1974) indicated that sex-linked genes may be of considerable importance in the inheritance of body weight, while reports of Hazel and Lamoreux (1947); Shaklee et al. (1952) and McCartney (1955) overlooked the effect of sex-linkage, by stating that sex-linked genes have no influence on body weight.

Maternal effects have been investigated by several workers (Hazel and Lamoreux, 1947; Bumgardner and Shaffner, 1954; Brunson *et al*. 1956; King, 1961; Yao, 1961; Friars *et al*. 1962; Moyer *et al*. 1962; Merritt, 1966; Shimizu *et al*. 1968; and Joubert *et al*. 1974) who demonstrated that maternal influence has an effect on body weight, and on heritability estimates. Contrary to that, Jerome *et al*. (1956) reported from their work with New Hampshires that for fall body weight the heritability calculated from the sire variance component exceeds that calculated from the dam component. These results suggest that maternal effects contribute little or no additive genetic variance.

## Selection experiments

Review of literature revealed a considerable amount of selection experiments which have been performed by numerous researchers over the past years to investigate the effect of selection and to estimate realized genetic parameters needed frequently in animal breeding research and practice. Fisher (1918); Wright (1921); Fisher (1930); Wright (1931); Haldane (1932) and Lush (1945) have developed the theory upon which much of these estimates were primarily based.

Many selection experiments have been conducted to study the inheritance of body weight. The results of these experiments have contributed significantly to our present knowledge and understanding of the genetic phenomena involved. It is impossible to list all the publications dealing with body weight selection experiments and their statistical analyses procedures, but a review of the most important papers that would be of primary interest will be given. Among papers that have been designed to discover the mode of body weight inheritance and those that have dealt with the statistical investigations of the subject are those of Goodale (1938, 1941); Hazel and Lush (1942); Hazel (1943); MacArthur (1944a,b); MacArthur and Chiasson (1945); MacArthur (1949); Mather and Harrison (1949); Lerner and Dempster (1951); Falconer and Latyszewski (1952); Falconer (1953a, b); Falconer and King (1953); Kyle and Chapman (1953); Martin *et al*. (1953); Clayton *et al*. (1957); Osborne (1957); Mode and Robinson (1959); Young (1961); Nordskog and Festing (1962); Robertson (1962); Siegel (1962a,b); Abplanalp *et al*. (1963); Maloney *et al*. (1963a, b); Rahnefeld *et al*. (1963); Siegel (1963a, b); Nordskog *et al*. (1964); Gill (1965a, b, c); Magee (1965); Searle (1965); Bohren *et al*. (1966); Gaffney (1966); Gill and Clemmer (1966); Ideta and Siegel (1966a, b); Maloney and Gilbreath (1966); Merritt *et al*. (1966); Roberts (1966a, b); Festing and Nordskog (1967); Kinney and Shoeffner (1967); Maloney *et al*. (1967); Roberts (1967a, b); Richardson *et al*. (1968); Shimizu *et al*. (1968); Parker *et al*. (1969); Hill (1970); Merat (1970); Mukherjee and Friars (1970); Parker *et al*. (1970a, b); Hill (1971); Burrows (1972); Hill (1972); Becker and Bearse (1973); Cheung and Parker (1974); Hill and Nicholas (1974); Nordskog *et al*. (1974); Berger and Harvey (1975); Bruns and Harvey (1976); Marks (1978) and Siegel (1978).

Collectively, these selection experiments have shown that

1) Selection is an effective force in changing the mean of the population over many generations, either upward or downward, until all desired genes are fixed.
2) Alternating periods of changes for several generations due to selection which have been followed by generations of little or no change, were observed in some of these experiments.
3) Selection is a slow process in changing the mean of the population.
4) Effect of selection is permanent.
5) Heritability estimate remains substantially unaltered by continued selection.
6) Environmental, epistatic and dominance effect will impede progress due to selection.

This discrepancy between expected and observed genetic changes led Wyatt (1954) to question the magnitude of the heritability estimate, since selection continues to be effective until all desired genes are fixed. Genetic slippage was the term used by Dickerson (1955) to describe the situation where the observed genetic gain falls below the expected genetic gain, where he attributed this genetic slippage to possible inter-environmental (i.e. adverse environmental time trends and genotype-environmental interaction) and intra-environmental (i.e. lower heritability, reverse mutation and inbreeding) factors.

Divergent selection experiments

In poultry, measurement of the direct and correlated responses to selection for body weight have been achieved either throuth two-way selection (that is, starting from the base population, selecting the high and low line to represent the right and left-hand tail of the phenotypic distribution respectively) or one-way selection, where the response will be measured as a deviation from a genetically controlled line.

Some reports have been published on divergent selection for body weight (Schnetzler, 1936; MacArthur, 1944a, b; MacArthur and Chiasson, 1945; MacArthur, 1949; Godfrey and Williams, 1952; Falconer, 1953a, b; Godfrey and Goodman, 1955; Falconer, 1954; Clayton *et al*. 1957; Schierman *et al*. 1959; Falconer, 1960b; Maloney and Gilbreath, 1962; Nordskog and Festing, 1962; Siegel, 1962a, b; Maloney *et al*. 1963a, b, c; Siegel, 1963a, b; Ideta and Siegel, 1966a, b; Maloney and Gilbreath, 1966; Festing and Nordskog, 1967; Maloney *et al*. 1967 and Carte and Siegel, 1968).

In general these experiments have indicated that:

1) Asymmetrical response was more commonly observed than uniform response in divergence between heavy and light lines, where heavy line gained more weight by plus selection than was lost from light line by minus selection.

2) Positive regression was obtained, where heavy parents produced heavy offspring and light parents produced light offspring.
3) Selection was effective in producing considerable change in two-way directions over many generations with and without inbreeding.
4) Overlapping between the heavy and light lines practically ceased after the sixth generation of practicing divergent selection (MacArthur, 1944a).
5) Crosses between heavy and light line individuals resulted in offspring that were intermediate between the parents.
6) Males gained or lost more weight than females where divergent selection was implemented.

## Selection limit

Selection has been known as a powerful force in changing the mean expression of the selected trait, but it has been universally accepted that this power is limited, where selection may fail to change the mean value of the population any further.

Various theories have been advanced to interpret the cessation of genetic changes observed by Mather and Harrison (1949); Lerner and Dempster (1951); Robertson and Reeve (1952); Falconer and King (1953) and Yamada *et al*. (1958) in their long term selection experiments. Briefly, these theories can be classified into three categories (Lush, 1945; Lerner 1950).

1) Exhaustion of genetic variance.
2) Counteracting of natural selection to artificial selection.
3) Preponderance of non-additive gene action (and perhaps genotype-environmental interaction).

Differences between a selection limit (ceiling) and plateau were discussed by Lawrence (1964) from his work with Drosophila melanogaster. In long term selection studies, failure of traits to respond to selection for several generations, followed by an immediate response (Roberts, 1966a) for no obvious reason, suggest that plateaus rather than selection limits might be the most common cause.

Roberts (1966b), working with two divergent lines (large and small) of mice to determine the limits to artificial selection for six-week body weight, estimated the heritabilities of these two divergent lines by reporting an estimate of .194 and .180 for large and small line, respectively. The heritability for large line was not significantly different from zero while that for the small line was on the border line of the 5% level of probability to be statistically significant. He explained these results by stating that the additive genetic variance in the large line had been exhausted through the fixation of all alleles affecting large size, while in the small line a substantial proportion of residual additive genetic variance was present. Roberts (1966b) also elaborated on these findings by saying that selection for small line will reach its limit despite the fact that the substantial proportion of the additive genetic variance is present and the loci affecting body weight in this line had not been fixed by selection.

Irradiating the large line after reaching its limits for body weight at 6 weeks of age gave a negative result of introducing new genetic variance while outcrossing to an unselected strain and then starting to select from the cross gave a positive result, but nine generations were sufficient to recover the original limit (Roberts, 1967b).

Roberts (1966a) reported that despite the fact that exhaustion of genetic variance and fixation of all alleles affecting the trait were not obtained, selection limit may be reached. He ascribed this contingency to opposition of natural selection to the direction of artificial selection and to selection favoring those individuals that are heterozygous at some loci.

Monte Carlo technique (simulation genetic systems by automatic digital computers, where sets of pseudo-random numbers are employed) was employed in quantitative genetics by many investigators who studied various genetical parameters that are involved in inheritance (Cockerham, 1954; Fraser, 1967a, b; Barker, 1958a, b; Fraser, 1960a, b, c; Lewontin and Dunn, 1960 and Gill, 1965a, b, c). Among the parameters that have been examined through the Monte Carlo technique by the above mentioned authors are additive genetic variance, epistatic effect, linkage, genetic drift, selection intensity, inbreeding, gene frequency and environmental variation).

Finite populations were used by Gill (1965a, b, c) when he examined the relationship of some of these parameters to genetic progress through selection. In addition to that, Robertson (1961) and Gill and Clemmer (1966) studied the effect of selection on estimation of the degree of inbreeding coefficient when populations of restricted size were used.

## Heritability

In poultry as in any other livestock animals, most of the economic traits are quantitative in nature, where multiple genetic factors are controlling them, which in turn accounts for their genetical and physiological complicity.

The total observed variation in these economic traits, as well as in the whole population, consists of genetic variance ($\sigma^2H$), environmental variance ($\sigma^2E$), and genetic environmental interactions ($\sigma^2HE$). Thus the total variance is $\sigma^2P = \sigma^2H + \sigma^2E + \sigma^2HE$. The fraction of the total actual observed variation associated with a characteristic which is accounted for by genetic variance is known as the heritability.

Abplanalp and Kosin (1952) pointed out that heritability may be defined in two ways: 1. In a broad sense, and

2. in a much narrower sense. The broader definition is, "heritability is that fraction of the observed phenotypic variance which can be ascribed to known genetic differences between individuals." The narrower definition indicates that "heritability can be limited to include only the average gene effects, such as would be expected to appear if the genes were acting additively." So this means that heritability in the narrower sense includes in the numerator variations due to additive gene effects; while in the broad sense heritability includes in the numerator variations due to dominance and epistasis besides the additive gene effects.

In terms of variances, Aplanalp and Kosin (1952) used a formula for heritability in the narrower sense:

$$h^2 = \frac{\sigma^2_g}{\sigma^2 g+\sigma^2 d+\sigma^2 i+\sigma^2 e+\sigma^2 j}$$

The corresponding formula for heritability in the broader sense is:

$$h^2 = \frac{\sigma^2 g+\sigma^2 d+\sigma^2 i}{\sigma^2 g+\sigma^2 d+\sigma^2 i+\sigma^2 e+\sigma^2 j}$$

In the formulas, the symbols represent the following:

$\sigma^2 g$ = additively genetic variance.

$\sigma^2 d$ = variance due to dominance.

$\sigma^2 i$ = variance due to non-linear genetic interactions (epistasis).

$\sigma^2 e$ = variance due to environmental effects

$\sigma^2 j$ = variance due to interaction between genotype and environment.

Theoretically, heritability can range between 0.0 and 1.0. These two extreme values are rarely encountered in practice, however. A figure referring to heritability is descriptive of a specific trait in a particular population at a given time. If we look at the equation for heritability in the narrower sense, which is quite useful since it leaves out genetic effects that probably won't be recovered in later generations, we see that the formula is in fractional form. Since it is a fraction, the value of the heritability can be changed by changes in the additively genetic variance represented in the numerator or by changes in any one or all of the components of variance represented in the denominator.

The additively genetic variance is closely associated with the gene frequency of the gene influencing the trait. For most situations it is largest when the gene frequency for the influencing gene is near .5, and this is true where the alleles at a locus show no dominance.

Knowing the degree of heritability of the traits that we are interested in is very helpful in achieving the following:

1) Devise a sound and efficient breeding program.
2) Predict and estimate the gain to be expected under mass selection.

3) Construct selection index (see for example, Hazel (1943)).
4) Determine the accuracy of selection.
5) Predict the expected breeding value.
6) Determine the type of selection to be practiced.
7) Determine type of mating system to be used.

Additive gene action for a trait is important when the heritability is high, while variations due to additive gene action are small when heritability is low.

If the heritability of the desired trait is high, then additive gene action will also be high and mass selection would be recommended with little real use of progeny test, pedigree or inbreeding. On the other hand, if the heritability of a trait is low then pedigree, family selection, or even the progeny test should be considered.

## Methods of estimating heritability

Different procedures for estimating heritability have been developed by numerous investigators. Their possible associated biases were given by Lerner (1950); Lerner (1958); Falconer (1960a) and Lush (1948). All methods of estimating heritability rest on the degree to which related animals resemble each other more than less closely related animals do (Lush, 1948 and Kempthorne and Tandon, 1953).

In general, there are two techniques that have been used to estimate heritability. These techniques are based on analysis of variance and regression coefficients, though in certain cases we can cast the analysis in either form.

The magnitude of an estimate is influenced by many factors which lead in some cases to a biased estimation of heritability, some of these factors are:

1) Absolute amount of genetic variation present (Moyer _et_ _al_. 1962).

2) Environmental differences (Lush, 1940, 1948).
3) Type of mating system rather than random (Lush, 1940, 1948).
4) Sampling errors (Lush, 1940, 1948).
5) Experimental design and method of statistical analysis (Moyer _et_ _al_. 1962).
6) Genetic-environmental interaction (Lush, 1948).
7) Dominance deviation (Lush, 1948).
8) Epistatic deviation (Lush, 1948).
9) Initial frequency of genes being selected (Friars _et_ _al_. 1962).

The methods that have been used to estimate the heritabilities of various traits observed in animals were given by Lush (1948). These methods are

1) Isogenic lines
2) Regression of offspring on mid-parent
3) Regression of $F_3$ progenies on $F_2$ individuals
4) Resemblance of parent and offspring
5) Intra sire regression of offspring on dam
6) Selection experiments method
7) Resemblance between full sibs

8) Resemblance between half sibs
9) Resemblance to grandparents
10) More remote relatives

Advantages and disadvantages of most of these methods were discussed briefly by Lush (1948); Dickerson (1959), Falconer (1960a) and Turner and Young (1969).

Suggested formulas to estimate the standard errors of the heritability coefficients were given by Osborne and Paterson (1952); Graybill *et al*. (1956); Dickerson (1959); Henderson (1959); Swiger *et al*. (1964); Nestor *et al*. (1967); Jensen and Barr (1971) and Becker (1975).

Klein *et al*. (1973) reported a tabulated standard errors of heritability as estimated by using the following four different procedures:

1) Regression of offspring on mid parent values
2) Regression of offspring on single parent values
3) Intraclass correlation of full sibs
4) Intraclass correlation of half sibs

These estimates were based on two assumptions:

1) Random mating
2) Constant number of offspring per family

In addition to the suggested formulas to estimate the standard errors of the heritability coefficients, confidence intervals for genetic heritability were also investigated. Graybill *et al*. (1956); Graybill and Robertson (1957); Bogyo and Becker (1963) and Broemeling (1969) reported on confidence limits of heritability where in some cases estimation formulae have also been suggested.

An excellent reference to many examples was presented by Becker (1975) in his manual of quantitative genetics in which estimation of variance components and heritabilities were given for one way layout, nested, factorial, diallel and optimal designs. In addition to that he also presented many examples where regression methods were employed to estimate heritabilities and their associated standard errors.

## Heritability estimates of body weight in chicken

Many investigators have estimated the heritability of body weight in the chicken. El-Ibiary and Shaffner (1951)reported a series of heritability estimates of New Hampshire's body weight at consecutive ages by using two methods which employed variance components analyses. Heritability estimates range from .00-.57, .05-.38, .03-.38, and .03-.54 for 2, 6, 8 and 10 weeks of age, respectively. Martin et al. (1953), with Rhode Island Reds, calculated the heritability estimates at 3, 6, 9 and 12 weeks of age. These estimates were .31, .29, .27 and .31, respectively.

Amer (1965) reported from his work on Fayoumi pullets that heritability estimates for body weight due to the dam's contributions were higher than due to the sire's contributions. On the basis of both the sire's and the dam's contribution, he reported that heritability estimates were .36, .54, and .76

at hatching, 4 and 8 weeks of age, respectively.

Gaffney (1966) gave an average estimate of the heritability of body weight at 4 and 8 weeks of age being equal to about .52 by using the variance components analyses and intra-sire regression of offspring on dam methods.

Merritt (1966) reported from his experiment with a random bred strain of meat type fowl many heritability estimates ranging from .17 - 1.37 and .24 - 1.14 for body weight at 7 and 9 weeks of age.

Godfrey and Williams (1952) stated from their selection experiment with two divergent lines of domestic fowl where one line was selected for rapid growth and the other line was selected for slow growth as measured by body weight at 6 and 12 weeks of age for 2 successive generations that heritability estimates were .19 and .30 for 6 week body weight at the first and the second generation, respectively, while heritability estimates were .31 and .32 for 12 week body weight for the first and the second generation, respectively.

Maloney *et al.* (1967) used the intra-sire regression technique to measure the heritability estimates for six week body weight which was found to respond to the divergent selection for 12 week body weight. Their estimates in the high line were 59 and 57 percent for males and females, respectively, while in the low line, these estimates were 42 and 58 percent for males and females, respectively.

Heritability of body weight at 8 weeks of age was also studied by Dillard _et_ _al_. (1953); Hurry and Nordskog (1953); Wyatt (1954); Goodman _et_ _al_. (1957); Friars _et_ _al_. (1962); Siegel (1962a, b); Rico (1964); Kinney and Shoffner (1965); Mahmoud _et_ _al_. (1965); and Carte and Siegel (1968).

Dillard _et_ _al_. (1953) reported a value of .32 for 8 week body weight in a population of New Hampshire pullets by using the method of intra-sire regression of daughters on dams. This result is in close agreement to that found by Hurry and Nordskog (1953) at the same age being equal to .33 and to Rico (1964) who reported a heritability estimate of .31 for White Plymouth Rock at the same age. The estimates of Dillard _et_ _al_. (1953); Hurry and Nordskog (1953) and Rico (1964) were also in close agreement with those of Carte and Siegel (1968) who reported an averaged realized heritability estimate at the same age being equal to .33 for males and .30 for females. Siegel (1962a) reported a similar result from his experiment, with White Plymouth Rocks, conducted to investigate the short term response of individual selection in two divergent lines for body weight at 8 weeks of age. His mean realized heritability estimates were .30 and .27 for males and females, respectively. Similar results were also obtained by Siegel (1962b) in another experiment, where he reported a heritability estimate of .31 and .28 for males and females, respectively.

Higher estimates of heritability were given by Wyatt (1954) who reported that heritability estimates for body weight at eight weeks of age were .4 and .46 estimated from regression of daughters on dam and from full sib correlation, respectively. Another higher estimate was given by Mahmoud et al. (1965) who calculated the heritability of eight week body weight of New Hampshires under two environments, as being .49 ± .13 when birds were fed diets with 18 percent protein and .36 ± .22 for those with similar genotypes fed a 24 percent protein ration.

Comparatively, Friars et al. (1962) reported higher heritability estimates computed from the dam component of variance, which averaged about .87 for both the males and the females at 8 weeks of age, than what previous investigators have reported. On the other hand, they also reported lower heritability estimates computed from the sire component of variance, which averaged about .13 for both the males and the females at 8 weeks of age, than what had been previously known. The differences have been attributed to maternal effect and heavier selection pressure that had been practiced on the males which lessened the variance between sire families and caused the sire components of variance to be less than the dam components of variance.

Goodman et al. (1957) reported various heritability estimates from their work on the growth rate to eight weeks of age in two closed flock strains. The heritability estimates for the male progeny ranged from .13 to .68 and .17 to .69 from sire and dam variance components, respectively, while for the female progeny the heritability estimates ranged from .00 to .25 and .56 to .81 from sire and dam variance components, respectively. Heritability estimates of body weight at 9 weeks of age were investigated by Merritt et al. (1966) who reported realized heritability estimate for body weight of the chicken at 63 day of age being equal to .49, while Goodman and Godfrey (1956) reported an estimate of .43 which then was confirmed from another experiment to be equal to about .5 (Godfrey and Goodman, 1956).

Kruger et al. (1952) gave a range for heritability estimates of 10 week body weight in the domestic fowl being equal to .33 - .46 calculated from doubling the full sib correlation and doubling the regression of progeny on dam, respectively.

Different estimates of heritability of body weight at 12 weeks of age were given by numerous investigators. In New Hampshire fryers, Lerner et al. (1947) estimated the heritability of body weights by using the analysis of variance technique. They stated that heritability of body weight at twelve weeks of age was about .48, .6, and .50 on the basis of the contribution of sire, dam and both, respectively. These estimates were higher than the Godfrey and Williams (1952) and Martin et al. (1953) estimates which range between .31 - .32.

Realized heritability estimates for body weight at 12 weeks of age were obtained through the use of the divergent selection program in domestic fowls. Maloney _et_ _al_. (1963b) estimated the realized heritabilities of body weight at 12 weeks of age as being .34, .07 and .22 for the high line, low line and the two way selection, respectively. Maloney and Gilbreath (1966) used a population of Silver Oklabar chickens for fifteen generations and estimated higher realized heritability estimates than that which was reported by Maloney _et_ _al_. (1963b). Their reported realized heritability estimates, based on combined means of both sexes, were .45, .17 and .23 for high, low and differences obtained between lines, respectively. In another divergent selection experiment, Maloney _et_ _al_. (1967) gave an estimate for the realized heritabilities for these divergent lines as being equal to 47.2 and 35.1 percent for the males and females in the high line, respectively, while they were equal to 12.3 and 12.7 percent for males and females in the low selected line for 12 week body weight. Realized heritability estimates for the difference between the high and low line were equal to 35.6 and 27.8 percent for males and females, respectively.

Pirchner and Krosigk (1973) used White Leghorns to estimate heritability of body weight at 18 weeks of age by employing dam and sire components of variance techniques. The average heritability estimates were about .55 and .70 from sire and dam components, respectively.

Hazel and Lamoreux (1947) reported the heritability of body weight at twenty-two weeks of age as being 31.6 percent.

In another series of experiments, body weight heritabilities at different ages were determined. Siegel (1963b) reported mean heritability estimates for body weight at 4, 24 and 38 weeks of age as being equal to .53, .46 and .38 for females, while for males at 4 weeks of age it was .53. These estimates are in agreement with those estimates reported by Siegel (1963a) of .47, .44 and .43 for 4, 24 and 38 week body weights, respectively.

King (1961) estimated the heritability of body weight at 32 weeks of age as being .62. Festing and Nordskog (1967) reported from their 2-way selection experiment for body weight at 32 weeks of age in chickens asymmetrical heritability estimates where the heritability for upward and downward selection was .34 and .52, respectively.

Ideta and Siegel (1966a) reported from their study on the realized heritabilities of unselected traits (24 and 38 week body weights) when 2-way selection (one upward and one downward) was employed for body weight at eight weeks of age, that realized heritabilities based on the regression of divergence on the expected secondary selection differential for unselected traits was .44 and .54 for body weight at 24 and 38 weeks of age, respectively.

Estimate for mature pullet body weight heritability was given by Goodman and Godfrey (1956) as .57, while Yamada (1958), using closed flocks of Single Comb White Leghorns, Barred Plymouth Rocks and Rhode Island Reds for a period of about four years, gave a lower estimate of heritability, being .46 for body weight at 300 days based on combined sire and dam components. Shoffner and Sloan (1948) reported much higher heritability estimate of adult body weight taken at approximately 300 days of age, being .75 calculated by the method of intra-class correlation.

Many investigators have reported on the heritability of broiler's body weight at different ages. Peeler _et_ _al_. (1955) found that heritability estimates for broiler weight range from .15 to .38 by employing the analysis of variance and intra-sire regression of offspring on dam techniques. Moyer _et_ _al_. (1962) estimated heritability of body weight at 4, 6 and 8 weeks of age in cross-bred broiler chickens by using components of variance model. Sire component heritability estimates averaged for the males at 4 and 8 weeks of age .20 and .24, respectively, while for the females they averaged .26 and .35, respectively. Using dam variance components led to higher estimates in comparison to those from the sire components. On the other hand, heritability estimates calculated by Godfrey and Goodman (1955) on their selection experiment for small and large body size in broiler chickens averaged about 26 percent for six and twelve week body weights.

Dev et al. (1969) reported from their work on the genetics of eight week body weight in three broiler populations of chickens an averaged estimate of .25 for the realized heritability of eight week body weight. Higher heritability estimates of 59 day live weight in broilers were given by Siegel and Essary (1952) who reported a range of .26 - .76 with an average of .49 by employing half sib and full sib correlation techniques.

Heritability estimates of 10 week body weight in broilers were studied by Lankford and McClung (1952) who reported a range of .2 to .63 by using analysis of variance technique, while Brunson et al. (1955) reported that heritability of 10 week body weight in broilers was equal to .45 which falls in Lankford and McClung's (1952) range.

Glazener et al. (1951) reported from their work on the effect of inbreeding on broiler weights and feathering in the fowl a range of 51-79 percent as an estimate for twelve week body weight heritability in the fowl.

A range of .71 to .85 was reported by Peeler et al. (1955) for the heritability of body weight at sexual maturity in broilers which was derived from the analysis of variance and intra-sire regression of offspring on dam techniques.

A compiled estimate of heritabilities from many previous experiments for a number of traits in domestic fowl which was given by Kinney (1969) will be of great help for those seeking information about the genetic architecture of body weight at different ages and other reproductive traits in poultry. Also another excellent review which will be of great help to many people was given by Siegel (1962a) where a summary of 176 published heritability estimates of body weights obtained at ages ranging from 6 to 12 weeks was shown in a histogram.

### Heritability estimates of body weight in turkey

During recent years a considerable amount of investigational research has been carried on to study the criteria of genetic parameters of body weight in turkeys. Abplanalp and Kosin (1952); Bumgardner and Shaffner (1954); Goodman *et al*. (1954); Kondora and Shoffner (1955); McCartney (1955); Johnson and Asmundson (1957a, b); McCartney (1961) and Krueger *et al*. (1972) reported that body weight is a highly heritable trait in the turkey.

Jaap (1938); Asmundson and Lerner (1940); Asmundson (1944, 1945, 1948) and Asmundson and Pun (1954a, b) reported from their investigational works with turkeys that body size, growth rate and conformation traits are influenced by genetic variation.

Heritability of body weight at different time intervals was examined by numerous scientists. Bumgardner and Shaffner (1954) reported on the heritability of body weight of medium-sized white turkeys at 2, 4, 8, 16 and 24 weeks of age by employing the analysis of variance technique. Their estimates varied from 2 percent at 4 weeks of age to 46 percent at 16 weeks of age for males. For the females, these values ranged from 3 percent at 4 weeks of age to 32 percent at eight weeks of age.

Abplanalp and Kosin (1952) used intra class correlation and offspring dam regression methods to estimate the heritability of body weight at 4, 8, 14 and 26 weeks of age for Broad Breasted Bronze and Beltsville small white turkeys. The highest estimates at 14 weeks of age for Bronze males was 71 percent and 39 percent for Bronze females. The highest estimate at 8 weeks of age for Beltsville small white male turkeys was 33 percent, for the females it was 24 percent at 26 weeks of age. Krueger _et_ _al_.(1972) studied the heritability of body weight and conformation traits and their genetic association in turkeys. They used Broad Breasted Bronze turkeys and estimated the heritability of body weight at 8 and 14 weeks of age by using full sib correlations method. They found that the heritability of body weight varied from .31 to .41 using male progeny and .20 to .39 using female progeny.

Heritability of body weight at 8, 16 and 24 weeks of age was studied by Johnson and Asmundson (1957a) who gave a range of .5 to .6 for the heritabilities at these three ages, while a wider range of .28 to .65 was reported by Nestor _et_ _al_. (1967) for the heritabilities at the above mentioned three ages. McCartney (1961) calculated heritability estimates on random bred control population of turkeys at 8, 16 and 24 weeks of age. The heritability estimate based on full sib correlation averaged approximately .6 for body weight at these three ages.

In another study, McCartney _et_ _al_. (1968) reported that realized heritability estimates for 8 and 24 week body weights averaged .44 and .39, respectively.

Heritabilities of body weight at 12 weeks of age were calculated by Mukherjee and Friars (1970) who reported that they range from medium to high while Johnson and Gowe (1962) estimated them to be .35 and .36 for males and females, respectively.

From the same experiment, Johnson and Gowe (1962) reported that heritability of 24 week body weight was .4 and .48 for males and females, respectively. These results were confirmed by Cook _et_ _al_. (1962) who gave an average estimate of the heritability at 24 weeks of age after employing sire and dam variance component methods as being .45. Kondra and Shoffner (1955) estimated the heritability of body weight at 24 weeks of age using the method of intra-sire regression of offspring on dam. Their heritability estimates ranged from .24 to 1.12. McCartney (1955) used White Holland turkeys in order to study the heritability and genetic, phenotypic and environmental correlations of body weight at 16 and 24 weeks of age. The estimates of the heritability based on half sib correlations were .23 and .33 for males at 16 and 24 weeks of age, respectively. Heritability estimates for the females were .59 and .61 at 16 and 24 weeks of age, respectively.

Analysis of variance technique was employed by Goodman *et al*. (1954) for the purpose of estimating the heritability of 25-week body weights of Broad Breasted Bronze and White Holland turkeys, which was found to average about .30. Based on that, they recommended a combination of mass and family selection for the most efficient improvement in body weight.

A lower estimate than what was reported by Goodman *et al*. (1954) was obtained by Kentucky workers (1950) who got an estimate of 23 percent for 26-week old small type white male turkeys where intra-sire regression method was employed.

### Heritability estimates of body weight in other species of poultry

Research dealing with the area of estimating the heritability of body weight in other species is meager, and to the author's knowledge, heritability estimates for body weight in Ring-Necked pheasants has not ever been reported.

A review of the literature revealed a limited amount of work that has been done to estimate the heritability of body weight in Japanese Quail. Sefton and Siegel (1974) gave many heritability estimate ranges for body weights at different ages. These ranges were .03 to 1.42, .12 to .37, .11 to .68, -.03 to 1.18, .28 to .79, .49 to .65, .51 to .72, .39 to

.65 and .49 to .76 for males at 1, 7, 14, 21, 28, 35, 42, 49 and 56 days, respectively. For the females the ranges were -.05 to 1.82, .25 to .56, .25 to .48, .12 to .70, .17 to .65, -.43 to .68, -.21 to 1.48, .25 to .46 and .34 to .46 for the above same ages, respectively. Marks and Lepore (1968) reported that the average heritability estimates at 14 days of age were .12 - .60 and .21 - .56 for males and females, respectively.

Estimates of the heritability of body weight at four weeks of age in Coturnix by Yoshida and Collins (1967); Marks and Lepore (1968) and Marks (1971) ranged from .22 to .76 in males and .27 to .76 in females, which are in close agreement with Sefton and Siegel's (1974) estimates.

Parshotam and Johnson (1974) reported on their study of the intra-sire regression of offspring on dam as a measure of the additive genetic variance for five week body weight in Coturnix coturnix Japonica. Heritability estimate was .43 based on the regression of daughter's weight on dam's weight. They also stated that heritability estimate was .24 based on regression of son's weight on dam's weight, where the ratio of the standard deviation of female weight on the standard deviation of male weight served as a correction factor to adjust for sex differences.

Sittman _et_ _al_. (1966) and Collins _et_ _al_. (1970) reported estimates of the heritability of body weight at six weeks of age (near sexual maturity), ranging from .38 - .72

and from .06 to .25, respectively, while Collins and Abplanalp (1965) gave an estimate for the realized heritability for 6 week body weight in Japanese quail of .14.

Strong _et al_. (1978) reported from their study on the inheritance of body weight at sexual maturity in Coturnix by using paternal half-sister correlation and maternal half sister correlation that heritability estimate was found to be less than .2 and greater than 1.0, while Kawahara and Inoue (1966) and Kawahara and Kusaka (1970) found it to be .42 and .31, respectively.

Estimated heritabilities of body weight at ages further removed from sexual maturity were given by Rodero and Martinez de Minguel (1963); Marks and Kinney (1964) and Kawahara and Saito (1976), who reported medium to high estimates.

### Genetic and phenotypic correlation

The concept of correlation, which is widely used by researchers, resulted primarily from the works of Galton and Pearson near the turn of the century. Gill (1974) stated that "correlation is a measure of the degree of association or interdependence of two variables". Correlation estimates range from .00 to 1.00. .00 means that there is no correlation, while 1.00 means there is perfect correlation. Perfect correlation is not found in many biological systems. By using correlation we can tell how accurate our predictions are.

Genetic correlation, which should not be confused with phenotypic correlation, is a correlation that exists between breeding values of two traits in the same individual, while the phenotypic correlation is a combination outcome of genetic and environmental correlations. Since the relationship between the additive effects of two traits is measured by the genetic correlation, then covariance between these additive effects will be used to estimate the genetic correlation (Peeler _et_ _al_. 1955).

The genetic correlation can be caused either by linkage or pleiotropy where linkage effect is transient, while pleiotropic effect is more permanent (Falconer and King, 1953; Bohren _et_ _al_. 1966 and Cheung and Parker, 1974).

Standard errors of genetic correlation have been investigated by Robertson (1959) and Tallis (1959), who suggested statistical formulae to estimate standard errors of genetic correlation, while many tabulated standard errors for genetic correlation were given by Klein _et_ _al_. (1973).

Artificial selection experiments for the improvement of a particular trait have frequently resulted in associated changes of other unselected characteristics. These associated changes are termed correlated responses. Theoretical aspects of correlated responses and estimation procedures of genetic, phenotypic and environmental correlations have been reviewed by Lerner (1958) and Falconer (1960a).

A considerable number of selection experiments have been conducted in order to study direct and correlated responses to selection. Among the publications are those of Hazel (1943); Hazel et al. (1943); Lerner (1950); Reeve and Robertson (1953); Falconer (1954); Clayton et al. (1957); Robertson (1959); Martin and Bell (1960); VanVleck and Henderson (1961); Maloney and Gilbreath (1962); Nordskog and Festing (1962); Siegel (1962a, b); Maloney et al. (1963b); Siegel (1963b); and Bohren et al. (1966).

Correlated responses have also been investigated by Falconer (1960b), Bell and McNary (1963) and Yamada and Bell (1963) under two different environments, where asymmetrical correlated responses have been observed.

There are three types of correlated responses which occur between a selected trait and un unselected trait. Falconer (1954) discussed these three types of correlated responses. These three types are:

1) If two traits are genetically correlated, then selection for the primary trait will cause direct change in the secondary trait. For example, see Lerner (1946) and Falconer (1954).
2) If two traits are genetically uncorrelated, then no correlated response would be expected, but the secondary trait may nevertheless show an undirected departure from the original population, following selection for the primary trait. For example, see

Mather and Harrison (1949).

3) If the secondary trait forms an important part of the total fitness, then selection for the primary trait in either direction might result in secondary trait decline. This type of response has been termed "genetic homostasis" by Lerner (1950, 1954). For example, see Nordskog and Festing (1962).

Hutt (1949) indicated that body weight at hatching depends more upon the weight of the egg from which that chick hatches than upon anything else. Upp (1928), Halbersleben and Mussehl (1922) and Wiley (1950) found that egg weight and day old chick weight are highly correlated. Upp (1928) estimated the positive coefficient of correlation between egg weight and chick weight at hatching time to be equal to .68 - .84. Hutt (1949) reported that under normal conditions chick weight at hatching time represents 61-68 percent of the egg from which it hatched, while Halbersleben and Mussehl (1922) observed that chick weight at hatching recovers sixty-four percent of the egg weight.

Gaffney (1966) found that four week body weight is affected by egg size, especially in the female progeny, while at eight weeks of age, male's weight was negligibly affected, and the magnitude of effect in females weight was almost half that at four weeks. On the other hand, Halbersleben and Mussehl (1922) reported that at thirty-five days of age all chicks hatched from small and large eggs will average approximately the same weight.

These results were not in agreement with those reported by Wiley (1950) who reported further that any disadvantages newly hatched chicks acquired from the small eggs were overcome by the twelfth week of age. In addition to the findings of Halbersleben and Mussehl (1922) and Wiley (1950), Upp (1928) examined the relationship of chick weight at hatching and the subsequent growth rate at various ages and found that chick weight at hatching is not a reliable index for two, four and twelve week weights. Upp's results were confirmed by Funk (1930) who observed no significant correlation between day old weight and weight at 4, 8, 12, 16, 20 and 24 weeks of age.

Since Hazel (1943) reported a method for estimating the genetic correlations, numerous reports have been published concerning the genetic relationship between various economic traits in poultry. Estimate of the degree of genetic relationship is subjected to biases in the same manner as heritability estimates. The biases reflect large sampling error, which results in a wide range of estimates.

McCartney (1955) observed a positive genetic correlation of about .92 between body weight at 16 and 24 weeks of age of White Holland turkeys. Johnson and Asmundson (1957a), in a strain of Bronze turkeys, observed that genetic correlations between body weights at 8 and 16, 8 and 24 and 16 and

24 weeks of age averaged .86, .83 and .99, respectively. McCartney (1961) obtained corresponding estimates of .49, .71 and .90. In another study, McCartney _et al_. (1968) estimated an average realized genetic correlation in White turkeys between body weights at 8 and 16, 8 and 24 and 16 and 24 weeks of age as being 1.08, .73 and .98, respectively. Nestor _et al_. (1967) reported from their work with random bred control turkeys that genetic correlation estimates among body weights at 8, 16 and 24 weeks of age were large (above .55) and positive. Johnson and Gowe (1962) estimated the mean genetic and phenotypic correlations between 12 week and 24 week body weights of domestic turkey males as being equal to .64 and .61, respectively, while for the females they were equal to about .8 and .67, respectively. Funk (1930) reported from his work on the rate of growth in Bronze and White Holland turkeys a similar result to that reported by Bumgardner and Shaffner (1954) by showing that as age increased, the correlations of weights at younger ages with 24 week body weight will increase. Bumgardner and Shaffner (1954) have shown that these correlation coefficient values reached .71 for males and .52 for females between 16 and 24 week weights.

Genetic correlation of .75 in some broiler type populations of chicken were reported for eight week body weight between the two sexes by Comstock (1956).

In two divergent growth selected lines, Maloney *et al.* (1963c) reported highly significant correlations between 6 and 12 week body weights. These correlations were equal to .25 and .53 in the high and low lines, respectively. On the other hand, Ideta and Siegel (1966b) reported from their study on White Plymouth Rocks, where two divergent growth selected lines had also been established, that mean realized genetic correlations between 8 week body weight and post juvenile (24 and 38 weeks) weights were equal to .62 and .52 for 24 and 38 weeks of age, respectively.

An excellent review with numerous reported estimates of genetic and phenotypic correlation was given by Kinney (1969). This information will be of great help to those seeking information regarding the subject of genetic, phenotypic and environmental correlation.

A clear understanding of the heritability and the genetic correlation of the trait we are studying is vitally important to the effectiveness of selective breeding programs. We need reliable and accurate estimates of heritability and genetic, environmental and phenotypic correlations so that we have efficient selection which will result in achieving maximum improvement in total productivity.

# MATERIAL AND METHODS

A three year experiment (1974-1977) to study the genetic parameters of body weight in Ring-Necked pheasants was conducted at the Department of Poultry Science Research and Teaching Center, Michigan State University.

The base population was obtained on October 1, 1974 from the Michigan Department of Natural Resources Game Farm, Mason, Michigan. It was composed of four hundred and eighty one-day old chicks.

All pheasant chicks were wing banded, individually weighed at one day old, and then housed in brooding facilities at the Michigan State University Poultry Science Research and Teaching Center (P.S.R.T.C.).

The brooding facilities consisted of twelve floor pens (3.05 x 4.88 m), which had been thoroughly cleaned and disinfected.

The pens were separated from each other by wire netting partitions. Each pen housed forty straight-run chicks.

Heat was provided by infra-red heat bulb lamps, and gas heated hover type brooders. For the first week, corrugated chick guards were used to form a circle (about 120 cm in diameter) around the heat source; the purpose of the circle was to confine the chicks to this area. Heat lamps and gas heated brooders were added or removed as necessary in order to regulate the temperature inside the house.

Attempts were also made to provide the maximum amount of ventilation in keeping with the comfort of the chicks and the weather conditions. When the pheasant chicks were four weeks of age all heat lamps were removed, and all birds were individually weighed.

A pheasant starter ration (Appendix Table 1) and water were provided _ad libitum_. For the first two weeks of the experimental period flat type feeders and jar-waterers were employed, and these were then replaced by hanging feeders and automatic waterers. Water in the water founts was kept at a certain level to prevent dampness of the shavings litter beneath the founts.

At six weeks of age, pheasant chicks were switched from pheasant starter to pheasant grower ration (Appendix Table 3).

At eight weeks of age, pheasant chicks were individually weighed and specked through the use of specks in order to control the cannibalism problem. Specks were fitted over the beak with plastic pin attached through the nostril, so the bird could see to both sides, up and down but not straight ahead.

At twelve weeks of age, all birds were individually weighed and sex was determined by the use of the plumage color.

Mass selection (which is a method of selection that is based on individual body weights) was employed at 12-weeks of age in a divergent selection program where two lines were separated from the base population, one selected for heavier body weights and the other for light body weights, the criterion of selection being weight at 12 weeks of age. The line selected for heavier body weights consisted of all the selected males that had body weights of 1150 grams or above and the selected females that had body weights of 825 grams and above. The line selected for light body weights consisted of all the selected males that had body weights of 800 grams or below and the selected females that had body weights of 700 grams or below.

Forty-five females (25 light and 20 heavy) and nineteen males (9 light and 11 heavy) were saved to produce next generation progenies. The ranges of 12-week body weight of these birds were 510-700, 675-800, 825-940 and 1150-1210 grams for light females, light males, heavy females and heavy males, respectively, while their 12-week body weight means were 656, 764, 863 and 1163 grams, respectively.

The selected birds were then transferred to different pens, while the culled birds were saved for an additional weighing which was scheduled to be taken on February 4, 1975, when all birds were eighteen weeks old. When the birds were thirteen weeks of age, the ration was switched from pheasant grower to pheasant flight (Appendix Table 5), and the birds were then raised in complete darkness to minimize cannibalism. All birds were raised on pheasant flight until time of lighting.

At eighteen weeks of age, all birds were again individually weighed, then all the culled birds which had been saved for eighteen week weighings were sent back to Mason, Michigan to be used in the put-take program which was initiated in Michigan in 1972 to provide pheasant hunting recreation on state-owned lands.

On June 16, 1975, all the selected birds, which were about 37 weeks of age, were removed from darkened pens and housed in individual cages, mounted in battery frames.

The birds at the time of caging received 14 hours of light (6 a.m. to 8 p.m.) per day as provided by 60 watt frosted incandescent light bulbs. At the same time all birds were switched from pheasant flight to pheasant breeder ration (Appendix Table 7).

At the conclusion of a two week pre-lighting period, the birds were moved from the battery and housed in individual wire cages which measured 7x14x12 inches (.18 x .36 x .31 m) and were mounted on the wall within four single male mating pens, each of which measured 10 x 16 feet (3.05 x 4.88 m). Sixteen hours of light per day (6 a.m. to 10 p.m.) was provided by one 60 watt frosted incandescent light bulb per breeding pen .

Twenty-eight females (17 light + 11 heavy) and four breeding males (2 light + 2 heavy) were used to produce next generation progenies. Heavy males were mated to heavy females and light males were mated to light females in order to develop two divergent lines of Ring-Necked pheasant, where one line was selected for heavier body weight and the other line was selected for lighter body weight.

The ranges of 12-week body weight of these birds were 510-685, 675-750, 850-940 and 1170-1210 grams for light females, light males, heavy females and heavy males, respectively, while their 12-week body weight means were 639, 713, 886 and 1190 grams, respectively.

Eight light females were mated with one light male in the first pen, while nine light females were mated with the second light male in the second pen. In the third pen five heavy females were mated with one heavy male, while six heavy females were mated with the second heavy male in the fourth pen. Stud mating system was employed where two pullets were dropped in a 10 x 16 foot (3.05 x 4.88 m) single male mating pen in the morning and returned to their cages in the afternoon. Stud mating system allows all females to be rotated so that each pullet will be available for natural mating at least once each week. After the matings were made, seven days were allowed to assure good fertility before pedigreed egg production was recorded.

Individual egg production records were maintained on all females selected as parental stock, where daily individual egg production was recorded between July 5, 1975 and October 31, 1975 and then hen housed and hen day egg productions were calculated. All pedigreed eggs, which were collected daily, were held at 60 degrees Fahrenheit in order to cut down on the embryonic development during the holding stage. During the breeding season, pedigreed eggs were set at 14-day intervals in Jamesway 252 incubators to allow for the maximum number of chicks per hatch and a good hatchability. All eggs were brought to room temperature before being placed in the incubator.

The eggs were incubated for three weeks at 99.5°F (37.3°C) and 60% relative humidity. After twenty-one days of incubation, the eggs were transferred to hatching units operated at 98.5°F (36.1°C) and 70% relative humidity for three days. At time of transfer to the hatcher, eggs were placed in wire pedigree baskets according to dam number to make it possible to pedigree the chicks.

On the day of hatching, percent hatchability was calculated, and all birds were individually weighed, wing banded and pedigreed by sires and dams. Chicks were then transferred to the P.S.R.T.C. for brooding. A total of five hundred and seventy-three birds were hatched in the first generation.

Gathering eggs from the previous pullet breeders was continued for six weeks after the removal of the males from the mating pens. These eggs were also set in the incubator in order to study the duration of fertility.

Mortality was recorded as it occurred and dead birds were removed from the pens and sent to the veterinary diagnostic laboratories, Department of Pathology, M.S.U. to determine the cause of death. Mortality calculation was expressed as a percent of the total birds died to the total chicks housed for each generation separately.

The first generation chicks were exposed to the same breeding and management procedures which were practiced in the base population. Attempts were also made to give the same environmental conditions in order to minimize any effect that could result from any fluctuating in these environmental factors. All chicks which were hatched in the first generation came from eight different hatches, where eight breeding pens were used in 1975 to accommodate them. Both of the growth-selected lines from each hatch were brooded together in the same pen in order to minimize the environmental effect. All birds within each hatch were individually weighed at 4, 8, 12 and 18 weeks of age.

The same feeding program as for the base population, where pheasant starter (Appendix Table 1), pheasant grower (Appendix Table 3), pheasant flight (Appendix Table 5) and pheasant breeder (Appendix Table 7) were used from 0-6 weeks of age, 6-13 weeks of age, 13 weeks of age until time of lighting, and after time of lighting, respectively, was used for the first generation birds. Pheasant starter, grower, flight and breeder rations were adequate in all known nutrients based on calculated analysis (Appendices Tables 2, 4, 6, 8).

At twelve weeks of age, mass selection was used and the same specific standards that were used on the base population were employed. None of the heavy males or the heavy females that were saved to produce the selected heavy line for the next generation came from light male and light female crossing. The same thing stands true for light males and light females, where none of them came from heavy male and heavy female crossing.

Fifty-seven females (27 light and 30 heavy) and twenty-three males (6 light and 17 heavy) were saved to produce next generation progenies. The ranges of 12-week body weight of these birds were 516-700, 591-791, 825-978 and 1186-1387 grams for light females, light males, heavy females and heavy males, respectively, while their 12-week body weight means were 646, 746, 879 and 1246 grams, respectively.

All the selected birds were again raised in complete darkness until time of lighting. On June 4, 1976 all the selected birds were removed from darkened pens and housed in the same individual cages mounted in battery frames which were used the previous year. At time of caging all birds received 16 hours of light (6 a.m. to 10 p.m.) per day as provided by 60 watt frosted incandescent light bulbs. The same individual wire cages that are mounted on the wall within four single male mating pens that were used the previous year, were used again in the second year. Thirty-one females (15 light + 16 heavy) and four breeding males (2 light + 2 heavy) were used in the breeding system.

The ranges of 12-week body weight of these birds were 516-678, 591-735, 847-978 and 1265-1387 grams for light females, light males, heavy females and heavy males, respectively, while their 12-week body weight means were 627, 663, 910 and 1326 grams, respectively.

Divergent mating, where heavy males were mated to heavy females and light males were mated to light females, was again employed.

Nine light females were mated with one light male in the first pen, while six light females were mated with the second light male in the second pen. In the third pen ten heavy females were mated with one heavy male, while six heavy females were mated to the second heavy male in the last pen. Stud mating system was also employed so that each pullet was rotated for natural mating at least once each week. The rate of inbreeding in the population was kept to a minimum by deliberately avoiding matings of close relatives.

Daily individual egg production was recorded between June 26, 1976, and September 3, 1976, and hen housed and hen day egg productions were calculated.

The same system of holding and incubation conditions that was used the previous year was again used. A total of 6 hatches (four hundred and five baby chicks) were made in the second generation.

In addition to that, a total of three hundred and ninety eggs from the Michigan Department of Natural Resources

Game Farm, Mason, Michigan were set in the incubator to secure chicks to be used as a control.

At hatching time, percent hatchability was calculated, and all birds that were hatched were wing banded and individually weighed at one day of age. The chicks were then transferred to the P.S.R.T.C. for brooding.

Two hundred and nineteen baby chicks were hatched from two different control hatches. These chicks represent a control group that came from a random population, where no selection and/or preferred mating system had been applied for many generations.

This control group was to be used to make a comparison between the two divergent lines that were subjected to upward and downward type of selection, and to determine how well these two lines were responding to these kinds of selection.

The two control hatches were hatched at the same time as the second and third selected hatches were hatched, so chicks that came from the first control group were raised in the same pen with the chicks that came from the second selected hatch. The second control hatch of chicks were raised in the same pen with the third selected hatch chicks.

Eight brooding pens were used in 1976 to accommodate the six selected hatches and the two control hatches. Chicks from each hatch were again put in the same pen, no matter what type of selection was practiced on them.

The second generation chicks were also exposed to the same brooding and management practices that were used in the base and the first generation. All possible attempts were made to furnish the same environmental conditions that the chicks had been exposed to in the previous two generations.

The same feeding program used in the previous two generations was used up to eighteen weeks of age. All birds within each hatch were individually weighed at 4, 8, 12 and 18 weeks of age.

All birds, after twelve week weighings, were raised in darkness until eighteen weeks old, at which time they were released.

On March 2, 1977, the experiment was terminated and all data were subjected to statistical analysis.

# RESULTS AND DISCUSSION

The analysis of the data was confined to the birds which lived until the end of 18 weeks weighing period from each generation and gave a complete record with respect to the required data.

The application of the regression techniques was considered in part of the statistical analysis, where parent's record was repeated for each progeny. Repeating parent's records was found to be more efficient than taking progeny means (Bohren _et_ _al_. 1961). Regression computations in this study were done on CYBER 170 Computer at Michigan State University.

## Effect of selection

Individual selection for heavy and light body weight at 12-weeks of age has been practiced for two generations in Ring-Necked Pheasant population.

The mean body weights for each sex at the five successive ages for all generations are given in Tables 1 and 2. These tables show that selection has resulted in mean body weight differences of about 2, 49, 168, 283 and 381 gm in the males and 2, 54, 156, 264 and 327 gm in the females at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age,

TABLE 1. Mean body weights (gm) at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age for base, first and second generation and the control population of the light selected line of Ring-Necked pheasants.

| Age | Base generation 1975 | | First generation 1976 | | Second generation 1977 | | Control 1977 | |
|---|---|---|---|---|---|---|---|---|
| | Males n=182 | Females n=204 | Males n=108 | Females n=108 | Males n=49 | Females n=43 | Males n=80 | Females n=86 |
| one-day old | 20.96 | 20.01 | 19.72 | 19.18 | 19.12 | 18.72 | 21.07 | 21.47 |
| 4-weeks | 222.31 | 197.77 | 172.68 | 146.34 | 181.42 | 157.51 | 235.06 | 212.02 |
| 8-weeks | 575.91 | 489.41 | 542.71 | 433.20 | 494.53 | 411.69 | 589.86 | 496.57 |
| 12-weeks | 932.82 | 743.87 | 970.83 | 729.65 | 826.81 | 616.76 | 916.02 | 724.37 |
| 18-weeks | 1341.73 | 981.69 | 1179.62 | 906.00 | 1159.91 | 824.97 | 1335.82 | 991.76 |

TABLE 2. Mean body weights (gm) at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age for base, first and second generation and the control population of the heavy selected line of Ring-Necked pheasants.

| Age | Base generation 1975 | | First generation 1976 | | Second generation 1977 | | Control 1977 | |
|---|---|---|---|---|---|---|---|---|
| | Males n=182 | Females n=204 | Males n=92 | Females n=82 | Males n=93 | Females n=70 | Males n=80 | Females n=86 |
| one-day old | 20.96 | 20.01 | 21.12 | 20.81 | 20.94 | 20.37 | 21.07 | 21.47 |
| 4-weeks | 222.31 | 197.77 | 194.95 | 170.94 | 230.81 | 211.88 | 235.06 | 212.02 |
| 8-weeks | 575.91 | 489.41 | 630.89 | 509.42 | 663.02 | 567.47 | 589.86 | 496.57 |
| 12-weeks | 932.82 | 743.87 | 1110.68 | 846.51 | 1109.33 | 880.57 | 916.02 | 724.37 |
| 18-weeks | 1341.73 | 981.69 | 1440.91 | 1073.17 | 1541.38 | 1151.61 | 1335.82 | 991.76 |

respectively, between the two diverse selected lines. In addition to that the effectiveness of the two-way selection was so pronounced that second generation females in the heavy body weight selected line were about 1, 30, 73 and 54 gm heavier than males in the light body weight selected line at one-day, 4-weeks, 8-weeks, and 12-weeks of age, respectively, while they were about even in weight at 18-weeks of age.

The response in one-day, 4-weeks, 8-weeks, 12-weeks, and 18-weeks old body weights to the divergent selection program where the criterion of selection being weight at 12-weeks of age over a period of 2 generations are shown in Figures 1, 2, 3, 4 and 5. The points utilized in these figures are the generation's body weight means at the above specific ages as exhibited by respective sexes. The results show the effectiveness of the divergent selection program in increasing and decreasing body weight at these ages in both sexes.

The following conclusions can be drawn from an inspection of Tables 1 and 2 and Figures 1, 2, 3, 4 and 5.

1) There is no doubt about the efficacy of selection both in increasing and decreasing weight.
2) Selection response as exhibited by the divergence between the two selected lines shows a considerable amount of change in two-way directions.
3) In general the heavy selected line gained more weight by plus selection than was lost from the light selected line by minus selection.

4) In general males gained or lost more weight than females.
5) Progress in both selected lines appears erratic. This irregularity is similar to that reported in other selection experiments.

Falconer (1953a) suggested possible causes of an asymmetrical response to two-way selection. These causes are:

1) Unequal gene frequencies: where the frequency of genes acting in one direction being higher than those acting in the other direction. Bohren _et_ _al_. (1966) stated that "probably the most frequent contribution to asymmetry in practice will be from loci contributing negatively to the covariance and having frequencies other than .5."

2) Directional dominance: where more numerous loci having the dominant allele act in one direction than those that have the dominant allele and act in other direction. In addition to that, directional dominance causes inbreeding depression which in turn results in an asymmetrical response to selection.

3) Unsuitable metric: when scale of measurement used makes the genes action multiplicative instead of additive.

Falconer (1953a) referred to Mather (1949) by saying that removing directional dominance due to unsuitable scale can be obtained by transforming weight measurement to a suitable scale. It should be noted that MacArthur (1944a) and Falconer (1953a) agree that logarithmic scale meets the conditions of being a suitable scale.

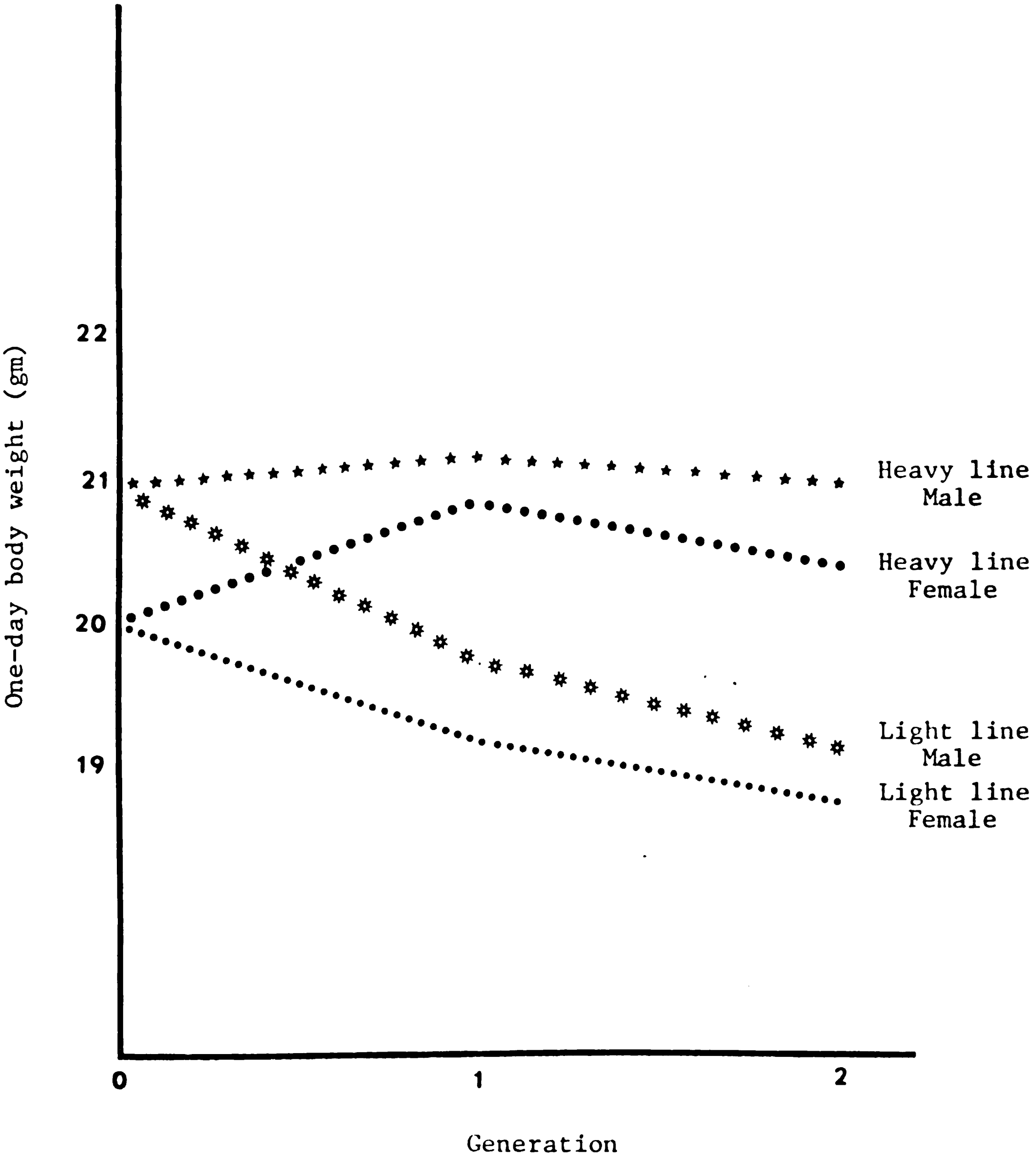

Figure 1. The effect of selection for 12-week body weight on one day body weight

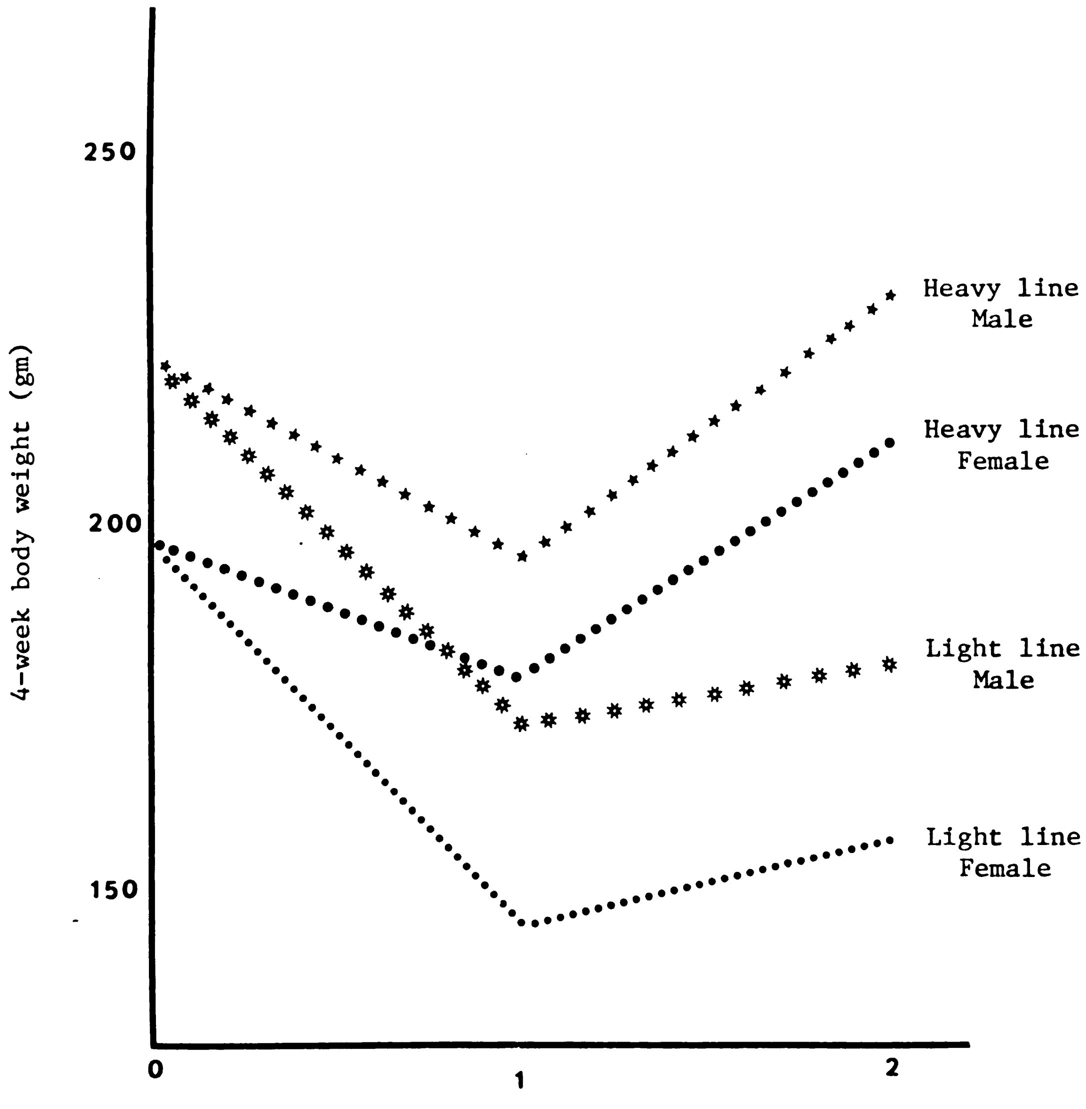

Figure 2. The effect of selection for 12-week body weight on 4-week body weight

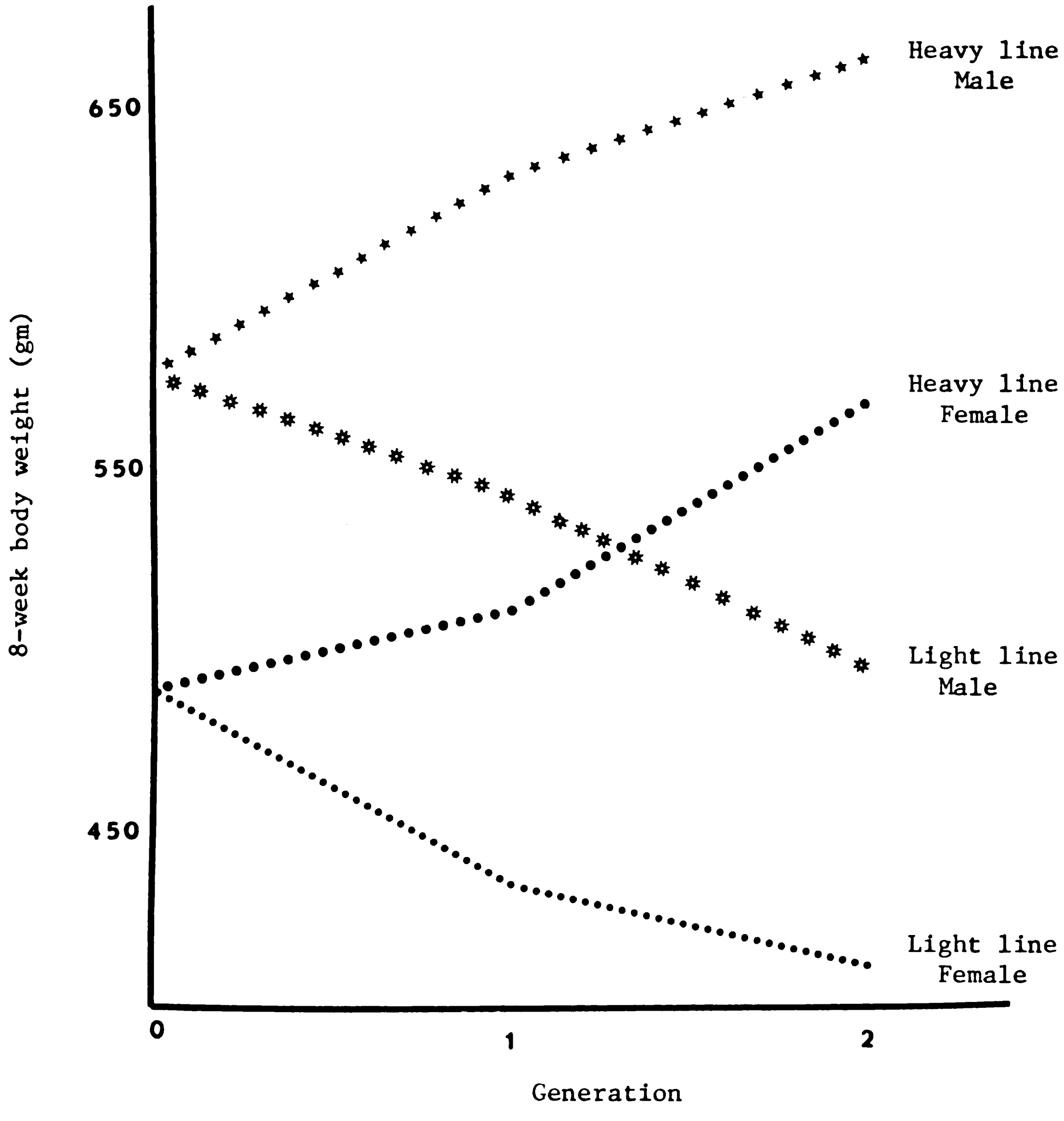

Figure 3. The effect of selection for 12-week body weight on 8-week body weight

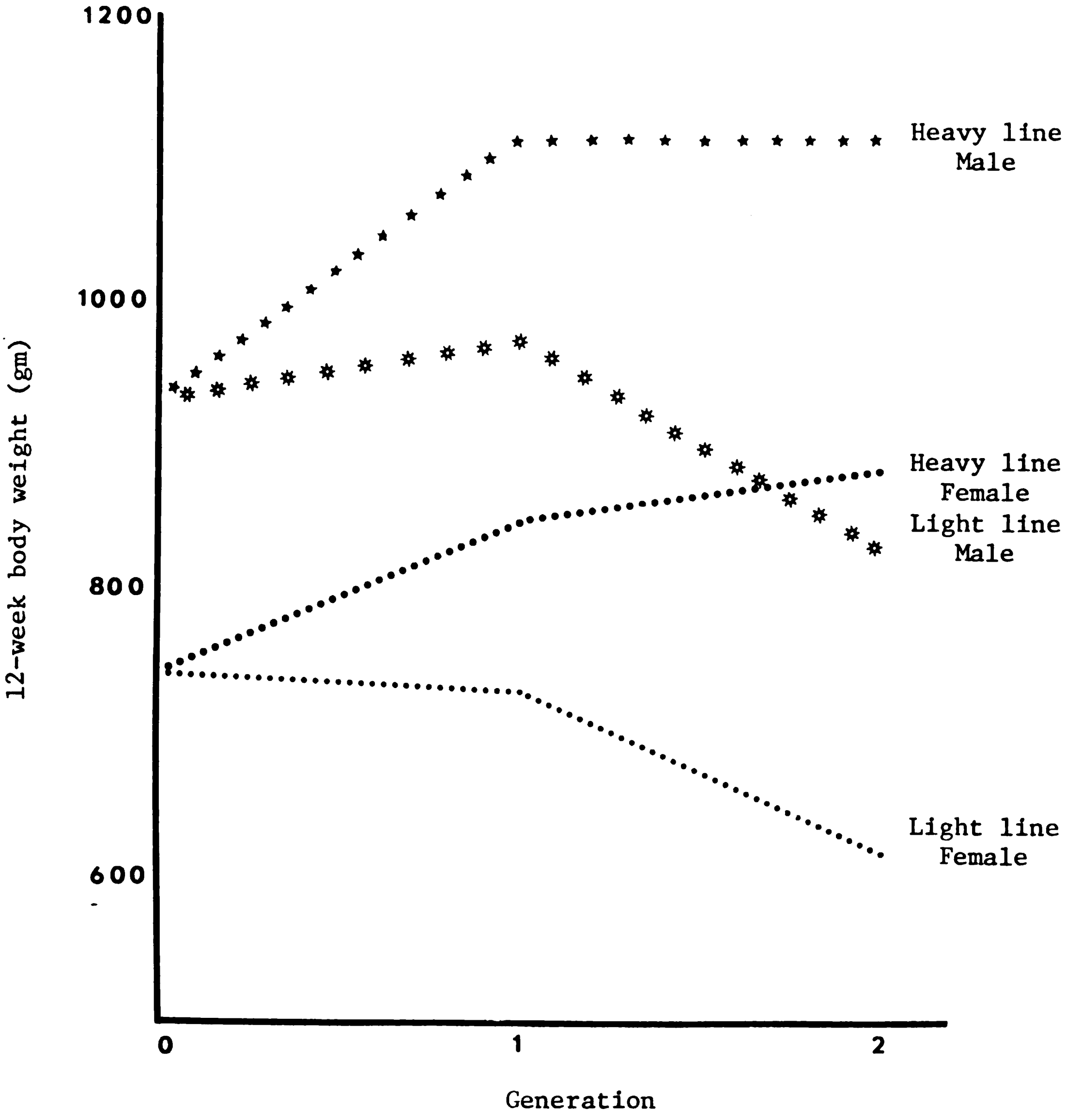

Figure 4. The effect of selection for 12-week body weight on 12-week body weight

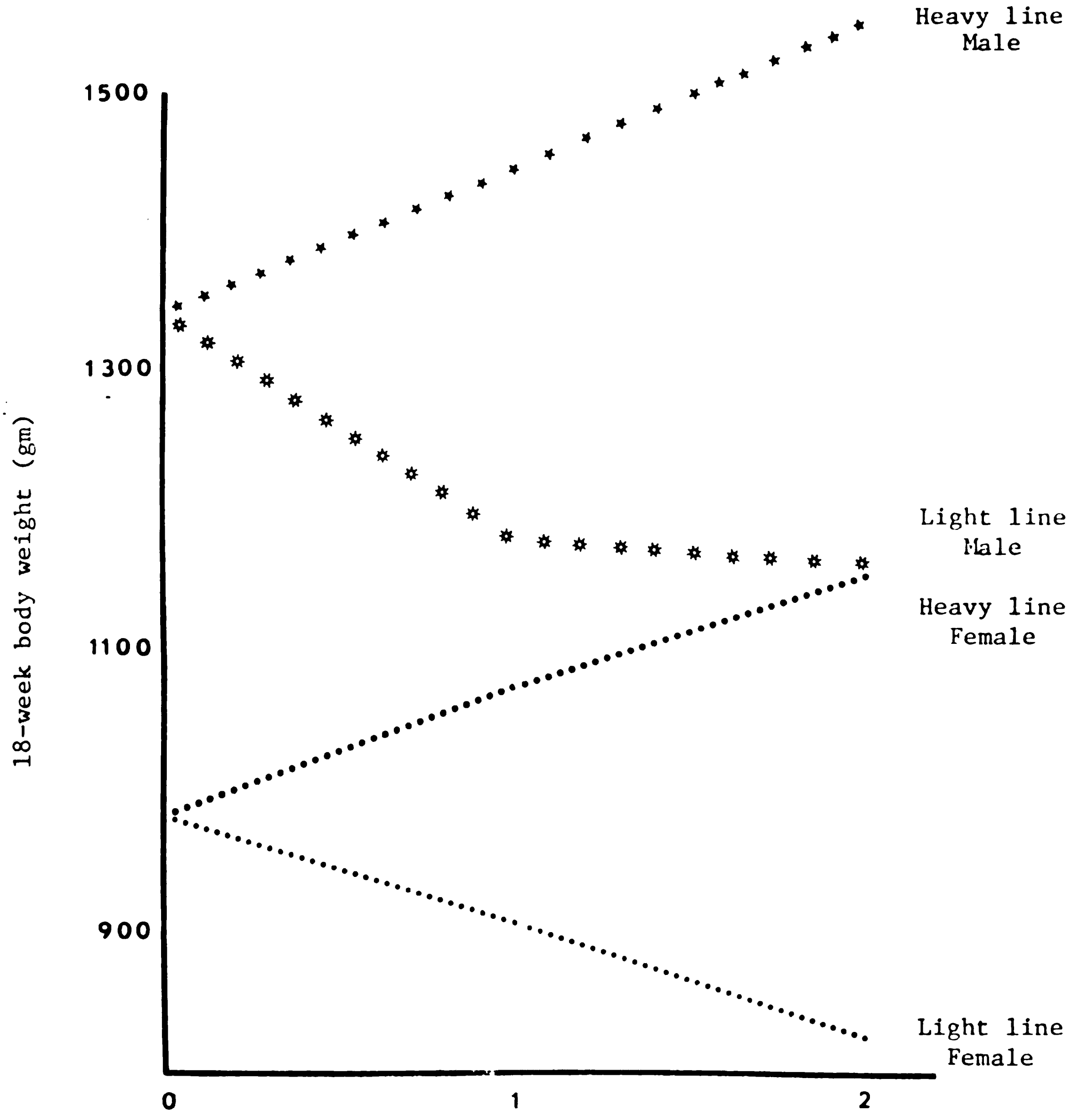

Figure 5. The effect of selection for 12-week body weight on 18-week body weight

Experimental data transformation to logarithmic and percentage scale are shown in Tables 3, 4, 5, 6 and 7.

The final conclusionsto be drawn from examining these tables are:

1. Transformed measurement to logarithmic or percentage scale did not appear to give a noticeably better fit than the actual scale.

2. There was little evidence that size genes were acting multiplicatively.

## Heritability estimates

The heritability estimates obtained herein were calculated from parent-offspring regression and from cumulative effects of selection (realized heritability) techniques.

The general model for the regression of offspring on one parent or mid-parent was considered in this study as

$$Y_{ijk} = \mu + S_j + b\,(X_i - \bar{X}) + e_{ijk}$$

where:

$Y_{ijk}$ = the phenotypic value of the k$^{th}$ offspring of the i$^{th}$ parent.

$\mu$= overall mean of the offspring population

$S_j$=Sex effect, j = 1 for males, 2 for females

b= regression coefficient

$X_i$=observed parent value (sire, dam or mid-parent)

$\bar{X}$= average phenotypic value of the parent population

$e_{ijk}$=the deviation peculiar to the k$^{th}$ progeny of parent i and sex j.

TABLE 3. Average one-day old weights (gm) of male and female Ring-Necked pheasants of the base generation and after two generations of plus selection in the heavy line and minus selection in the light line. Gains and losses expressed in absolute grams, in differences of logarithms of weights, and in percentages.*

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | | Difference in | | | | Difference in | | |
| | Weight | Grams | Logs | % | Weight | Grams | Logs | % |
| Heavy Selected Line | 20.94 | | | | 20.37 | | | |
| | | -0.02 | -0.0004 | -.0954 | | +0.36 | +0.0077 | 1.799 |
| Base | 20.96 | | | | 20.01 | | | |
| | | -1.84 | -0.0399 | -8.778 | | -1.29 | -1.0657 | -6.447 |
| Light Selected Line | 19.12 | | | | 18.72 | | | |

*Table form was adapted from MacArthur (1944a)

TABLE 4. Average 4-week weights (gm) of male and female Ring-Necked pheasants of the base generation and after two generations of plus selection in the heavy line and minus selection in the light line. Gains and losses expressed in absolute grams, in differences of logarithms of weights, and in percentages.*

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | | Differences in | | | | Differences in | | |
| | Weight | Grams | Logs | % | Weight | Grams | Logs | % |
| Heavy Selected Line | 230.81 | | | | 211.88 | | | |
| | | +8.5 | +0.0163 | 3.82 | | +14.11 | +0.0299 | 7.13 |
| Base | 222.31 | | | | 197.77 | | | |
| | | -40.89 | -0.0883 | -18.39 | | -40.26 | -0.0989 | -20.36 |
| Light Selected Line | 181.42 | | | | 157.51 | | | |

*Table form was adapted from MacArthur (1944a).

TABLE 5. Average 8-week weights (gm) of male and female Ring-Necked pheasants of the base generation and after two generations of plus selection in the heavy line and minus selection in the light line. Gains and losses expressed in absolute grams, in differences of logarithms of weights, and in percentages.*

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | | Difference in | | | | Difference in | | |
| | Weight | Grams | Logs | % | Weight | Grams | Logs | % |
| Heavy Selected Line | 663.02 | | | | 567.47 | | | |
| | | +87.11 | +0.0612 | 15.13 | | +78.06 | +0.0643 | 15.95 |
| Base | 575.91 | | | | 489.41 | | | |
| | | -81.38 | -0.0662 | -14.13 | | -77.72 | -0.0751 | -15.88 |
| Light Selected Line | 494.53 | | | | 411.69 | | | |

*Table form was adapted from MacArthur (1944a).

TABLE 6. Average 12-week weights (gm) of male and female Ring-Necked pheasants of the base generation and after two generations of plus selection in the heavy line and minus selection in the light line. Gains and losses expressed in absolute grams, in differences of logarithms of weights, and in percentages.*

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | | Difference in | | | | Difference in | | |
| | Weight | Grams | Logs | % | Weight | Grams | Logs | % |
| Heavy Selected Line | 1109.33 | +176.51 | +0.0753 | 18.92 | 880.57 | +136.70 | +0.0733 | 18.38 |
| Base | 932.82 | | | | 743.87 | | | |
| Light Selected Line | 826.81 | -106.01 | -0.0524 | -11.36 | 616.76 | -127.11 | -0.0814 | -17.09 |

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*Table form was adapted from MacArthur (1944a).

TABLE 7. Average 18-week weights (gm) of male and female Ring-Necked pheasants of the base generation and after two generations of plus selection in the heavy line and minus selection in the light line. Gains and losses expressed in absolute grams, in differences of logarithms of weights, and in percentages.*

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | | Difference in | | | | Difference in | | |
| | Weight | Grams | Logs | % | Weight | Grams | Logs | % |
| Heavy Selected Line | 1541.38 | | | | 1151.61 | | | |
| – | | +199.65 | +0.0602 | 14.88 | | +169.92 | +0.0693 | 17.31 |
| Base | 1341.79 | | | | 981.69 | | | |
| | | -181.82 | -0.0632 | -13.55 | | -156.72 | -0.0755 | -15.96 |
| Light Selected Line | 1159.91 | | | | 824.97 | | | |

*Table form was adapted from MacArthur (1944a).

Estimates of the realized heritability in this study were calculated as outlined by Falconer (1960). Realized heritabilities were determined by the following formulae:

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

where:

$h^2$ = realized heritability

R = response (gain)

S = Selection differential (intensity)

Falconer (1960) stated that "the ratio of response to selection differential, however, has an intrinsic interest of its own, quite apart from whether it provides a valid estimate of the heritability. It provides the most useful empirical description of the effectiveness of selection, which allows comparison of different experiments to be made, even when the intensity of selection is not the same." Lush (1945) has defined selection differential as the difference between the mean of the selected animals and the mean of the population in which they were born. The cumulative selection differential at any one generation is the selection differential for the generation added to the sum of the differential for all previous generations.

Heritability estimates calculated by parent-offspring regression techniques for body weights at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age for the first generation (where heavy and light selected lines were considered as one group), second generation heavy and light selected lines, where sex differences between males and females were adjusted are shown in Table 8.

Average heritabilities and standard errors for the first generation of selection were .66 ± .11, .44 ± .08, .66 ± .07, .50 ± .04 and .88 ± .04 for body weights at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age, respectively (Table 8). For the second generation heavy selected line they were equal to -.07 ± .11, 1.74 ± .46, .79 ± .27, .31 ± .31 and .33 ± .16 for body weights at the same ages as stated before, respectively, while for the second generation light selected line they were equal to 1.05 ± .29, .36 ± .24, .41 ± .23, .20 ± .42 and .09 ± .34 at the above mentioned time intervals, respectively (Table 8).

If estimates of heritability that fall outside the possible biological range of heritability are omitted from the average calculations then the average heritability estimates and their associated standard errors for the first generation of selection would be .47 ± .1, .44 ± .08, .66 ± .07, .50 ± .04 and .63 ± .03 for body weights at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age, respectively. Heritability estimates for the second generation heavy selected line at these time intervals would be .29 ± .18, .64 ± .21, .46 ± .24, .77 ± .26 and .33 ± .16, respectively, while for the second generation light selected line they were

TABLE 8. Heritability ± standard error as estimated by regression of offspring weight on dam, sire and mid-parent's weight at one day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age, respectively, for the first generation, second generation heavy selected line and second generation light selected line, respectively.

| Regression of offspring weight | Heritability ± standard error for first generation of selection (heavy and light selected line considered as one group) | Heritability ± standard error for second generation heavy selected line | Heritability ± standard error for second-generation light selected line |
|---|---|---|---|
| One day old on dam's one day weight | 0.48 ± 0.12 | 0.29 ± 0.18 | 0.23 ± 0.44 |
| One day old on sire's one day weight | 1.06 ± 0.13 | -0.23 ± 0.07 | 2.23 ± 0.02 |
| One day old on mid-parent's one day weight | 0.45 ± 0.07 | -0.27 ± 0.08 | 0.70 ± 0.40 |
| Average | 0.66 ± 0.11 | -0.07 ± 0.11 | 1.05 ± 0.29 |
| 4-weeks old on dam's 4-week weight | 0.29 ± 0.09 | 0.60 ± 0.22 | -0.10 ± 0.25 |
| 4-weeks old on sire's 4-week weight | 0.73 ± 0.10 | 3.96 ± 0.96 | 0.88 ± 0.29 |
| 4-weeks old on mid-parent's 4-week weight | 0.31 ± 0.05 | 0.67 ± 0.20 | 0.30 ± 0.19 |
| Average | 0.44 ± 0.08 | 1.74 ± 0.46 | 0.36 ± 0.24 |
| 8-weeks old on dam's 8-week weight | 0.73 ± 0.09 | 0.24 ± 0.28 | 0.10 ± 0.26 |
| 8-weeks old on sire's 8-week weight | 0.83 ± 0.07 | 1.47 ± 0.32 | 0.60 ± 0.24 |
| 8-weeks old on mid-parent's 8-week weight | 0.43 ± 0.04 | 0.67 ± 0.20 | 0.52 ± 0.20 |
| Average | 0.66 ± 0.07 | 0.79 ± 0.27 | 0.41 ± 0.23 |
| 12-weeks old on dam's 12-week weight | 0.74 ± 0.07 | -0.62 ± 0.42 | 0.09 ± 0.69 |
| 12-weeks old on sire's 12-week weight | 0.46 ± 0.04 | 1.00 ± 0.27 | 0.28 ± 0.31 |
| 12-weeks old on mid-parent's 12-week weight | 0.29 ± 0.02 | 0.54 ± 0.24 | 0.22 ± 0.27 |
| Average | 0.50 ± 0.04 | 0.31 ± 0.31 | 0.20 ± 0.42 |
| 18-weeks old on dam's 18-week weight | 1.40 ± 0.07 | 0.22 ± 0.27 | -0.89 ± 0.47 |
| 18-weeks old on sire's 18-week weight | 0.74 ± 0.04 | 0.39 ± 0.11 | 0.63 ± 0.29 |
| 18-weeks old on mid-parent's 18-week weight | 0.51 ± 0.02 | 0.39 ± 0.11 | 0.54 ± 0.27 |
| Average | 0.88 ± 0.04 | 0.33 ± 0.16 | 0.09 ± 0.34 |
| Overall Average | 0.63 ± 0.07 | 0.62 ± 0.26 | 0.42 ± 0.30 |

equal to .47 ± .42, .59 ± .24, .41 ± .23, .20 ± .42 and .59 ± .28, respectively.

These results seem to indicate that heritability estimates vary between rather wide limits, where many estimates fall beyond the possible biological range of heritability. Under the conditions of our study the best explanation of the fluctuations of these heritability estimates would be large sampling errors due to small number of dams, sires and progeny.

At the time regression of offspring on mean of parents was considered "the most nearly unbiased estimate (short of selection experiments) of effective heritability" by Dickerson (1959) because it is an excellent technique in reducing sampling errors much more consistent and reliable estimates of heritability were obtained from regression of offspring on mid-parents in comparison to double regression of offspring on dam and double regression of offspring on sire.

Examining heritability estimates obtained from regression of offspring on mid-parents would reveal that most of them fall within the possible biological range of heritability except for the case of offspring's one-day weight which could be due to a combination of genetic and environmental factors.

Realized heritability estimates of 12-week old body weights for males and females of the light and heavy selected lines for the first, second and both generations of selection obtained in this study are given in Table 9. The results

TABLE 9. Selection responses, selection differentials and realized heritability estimates of body weights for 12-week old males and females of the light and heavy selected lines for the first, second and both generations of selection, respectively.

| | First generation | | Second generation | | Both generations | |
|---|---|---|---|---|---|---|
| | Light Selected line | Heavy Selected line | Light Selected line | Heavy Selected line | Light Selected line | Heavy Selected line |
| | Males | Males | Males | Males | Males | Males |
| Response (gm) | +38.01 | +177.86 | -144.02 | -1.35 | -106.01[1] | +176.51 |
| Selection differential (gm) | -162.83 | +199.83 | -205.38 | +139.28 | -368.21[2] | +339.12 |
| Realized heritability | -0.23 | 0.89 | 0.70 | -.01 | 0.29 | 0.52 |
| | Females | Females | Females | Females | Females | Females |
| Response (gm) | -14.22 | +102.64 | -112.89 | +34.06 | -127.11[1] | +136.7 |
| Selection differential (gm) | -162.84 | +199.83 | -205.38 | +139.28 | -368.21[2] | +339.12 |
| Realized heritability | 0.09 | 0.51 | 0.55 | 0.24 | 0.35 | 0.40 |
| Average | -0.07 | 0.70 | 0.63 | 0.12 | 0.32 | 0.46 |

[1] Accumulative selection responses from the first and second generation of selection.

[2] Accumulative selection differentials from the first and second generation of selection.

indicated that average realized heritabilities were .25 and .33 in the light selected line for males and females, respectively, while in the heavy selected line they were .47 and .38, respectively. If negative values of heritability estimates are omitted from statistical analysis, then average realized heritabilities would be .50 and .33 in males and females of the light selected line, respectively, while these estimates would be equal to .71 and .38 in the heavy selected line for males and females, respectively. In general these estimates are not in agreement with findings reported by Maloney (1963b), Maloney and Gilbreath (1966) and Maloney et al. (1967) who reported much lower values for heritability estimates at 12-weeks of age.

Data reported in Table 9 have shown that a single generation of two-way selection provides a very unreliable estimate of heritability in a population of this size. As the generations proceed the estimate from the total response becomes more and more reliable.

Heritability estimates obtained herein from the cumulative effects of selection and parent-offspring regression techniques were quite high which suggests the existence of high additive genetic variance. This will indicate that mass selection would be the best single procedure to use to select for body weight to ensure that highest genetic gains for body weight are obtained.

## Duration of Fertility

Fertility problems in chickens and turkeys have been examined by numerous investigators, while they have received very little attention in other species of poultry.

Several researchers have shown that spermatozoa can live in the hen oviduct and remain active for several weeks. Curtis and Lambert (1929) quoted Chappelier (1914) who stated that duration of fertility in chickens ranges from 10-18 days and in ducks from 7-11 days. Curtis and Lambert (1929) summarized the work of other authors by stating "Some variation is noted in the duration of fertility reported. Crew (1926) reports 23 days in one case and 20 in another as mentioned in the 1926 report. He had, however, noted a duration of 32 days in an earlier investigation. Dunn (1927) reports a maximum of about one month with two weeks as the average. Moore (1916) gives 15 days as a limit, and Kaupp (1919) and Gilbert (1904) 12 days. Gray (1916) suggests 15-18 days. Laurie (1919) finds 17 days and Lienhardt (1923) says that it is not over 30. Payne (1914) reports 16 days, Philips (1918) 15 days, Rolf (1916) 14 days, and Waite (1911) 15 and 20 days after the removal of the male from a flock. These findings all fall within a range of 12-30 days with the greater number of cases between 15 and 20."

Curtis and Lambert (1929) reported from their study of fertility in poultry that mean duration of fertility was about 11 days with 21 days as the extreme duration, while 15 days as an average duration of fertility from single mating with 29 days as the maximum duration of fertility was reported by Nicolaides (1934).

As was stated in the procedure section, gathering eggs from previous pullet breeders in the base generation continued for 6 weeks (from November 1 until December 14, 1975) after removal of males from the mating pens. Regarding the duration of fertility, data from 16 pullet breeders which continued to lay eggs after the removal of the males show that laying of the last fertile egg from a single mating varied from 10-21 days with an average of about 15 days (Table 10). In general these results are in close agreement with most of the published results that have been reported by previous investigators.

## Relationship of egg weight to chick weight at hatching

Data from one hundred and eighty-six one day old control pheasant chicks (80 males + 86 females) and one hundred forty-seven one-day old second generation chicks (19 males and 25 females from the light selected line + 59 males and 44 females from the heavy selected line) were used to determine the relationship of egg weight to chick weight at hatching.

From the results that were summarized in Table 11, it seems that the body weight of the chick at hatching time depends upon the weight of the egg from which that chick hatches.

TABLE 10. Duration of fertility

| Female number | Total eggs laid after removal of the male (Nov.1-Dec.12, 1975) | Time last fertile egg was laid after removal of the male (Day) |
|---|---|---|
| 11057 | 21 | 17 |
| 11302 | 27 | 18 |
| 11189 | 24 | 17 |
| 11255 | 21 | 14 |
| 10945 | 22 | 16 |
| 11004 | 12 | 10 |
| 10931 | 18 | 15 |
| 11342 | 21 | 15 |
| 11299 | 23 | 17 |
| 11137 | 8 | 13 |
| 11264 | 17 | 15 |
| 11030 | 21 | 14 |
| 10968 | 24 | 21 |
| 11272 | 21 | 18 |
| 11284 | 19 | 14 |
| 11139 | 14 | 12 |
| Average | | 15 |

An intimate degree of association between egg weight and day-old chick weight was observed, where positive coefficient of correlation was .91, .86, .83, .76, .81 and .78 for control males, control females, second generation light selected line males, second generation light selected line females, second generation heavy selected line males and second generation heavy selected line females, respectively. These results confirmed findings reported previously by Halbersleben and Mussehl (1922), Upp (1928) and Wiley (1950).

In Table 11 is given the mean weight of the chicks hatched from the control group and the second generation which were used in this study and the mean weight of eggs used. From these results it was concluded that chick weight at hatching time represents 64-67 percent of the egg from which it hatched and that heavier eggs produced heavier chicks. It may be noted that these results confirmed Halbersleben and Mussehl (1922) and Hutt (1949) reports.

The slope and the Y-intercept for the regression of chick weight on egg weight that were characterized in Table 11 were calculated by using HP. 32E calculator. These statistical parameters were calculated by using the following equations which were already programmed into the calculator.

$$\text{Slope of the least square line} = \frac{n\Sigma XY - \Sigma X\Sigma Y}{n\Sigma X^2 - (\Sigma X)^2}$$

$$\text{Y-intercept of the least square line} = \frac{\Sigma Y\Sigma X^2 - \Sigma X\Sigma XY}{n\Sigma X^2 - (\Sigma X)^2}$$

TABLE 11. Summary of egg weight to day-old chick weight relationships

| | No. of individuals | Mean weight of eggs used (gm) | Average 1-day old weight (gm) | Percent chick weight of egg weight | Correlation of egg weight to day-old chick weight | Y-intercept | Slope of the line |
|---|---|---|---|---|---|---|---|
| Control males | 80 | 32.13 | 21.07 | 67.38 | .907 | -1.05 | .688 |
| Control females | 86 | 32.53 | 21.47 | 67.93 | .864 | 0.55 | .640 |
| Second generation light selected line males | 19 | 29.73 | 19.34 | 64.96 | .828 | -4.31 | .790 |
| Second generation light selected line females | 25 | 29.06 | 18.68 | 64.33 | .763 | 2.22 | .566 |
| Second generation heavy selected line males | 59 | 30.85 | 20.95 | 66.56 | .805 | -3.25 | .769 |
| Second generation heavy selected line females | 44 | 31.13 | 20.54 | 66.04 | .781 | 2.03 | .594 |

Egg production

Daily individual egg production was recorded for all females selected as parental stock in base and first generation only.

Mortality that occurred among the selected female parental stock at time where egg production was recorded resulted in a loss of 10 females in the base generation, where 7 females were lost from the light selected line and 3 females from the heavy selected line, while in the first generation 7 females were lost, where 5 and 2 females were lost from the light and heavy selected line, respectively.

From the individual egg production records, hen-housed and hen-day egg production were calculated by using the following formulae:

$$\text{H.H.} = \frac{\text{Total egg production}}{\text{Number of hen housed}} \times 100$$

$$\text{H.D.} = \frac{\text{Total egg production}}{\text{Number of hen days}} \times 100$$

Table 12 shows that hen-housed egg production for the heavy females selected as parental stock was 60.63 and 48.57 percent for base and first generation, respectively. For the light selected females it was 48.83 and 34.19 percent for the same generations, respectively. Hen-day egg production for heavy females selected as parental stock was 61.87 and 51.61 percent for base and first generation, respectively. For the light selected females it was 56.70 and 39.66 percent for the same generations, respectively.

Although hen-day and hen-housed egg production was lower for the first generation than for the base generation for both heavy and light selected lines, no conclusion can be drawn that this difference was due to genetics because egg production records for the control groups were not available for statistical comparisons.

## Mortality and Cause of Death

Mortality calculation was expressed as a percent of the total birds that died to the total chicks housed for each generation separately. Data from Table 13 show that percent mortality was 19.58, 31.93, 37.03 and 24.20 for the base, first, second generation and control population, respectively. Both heavy and light selected lines were grouped together in the first generation and in the second generation when percent mortality was calculated.

Chi-square analyses have shown that one may have 99.9 percent confidence that mortality is not independent of selection. Bonferroni chi-square analysis was performed to check which populations differ from the others ($p < .01$), where the following comparisons were investigated:

1) Control vs. base generation
2) Control vs. first generation
3) Control vs. second generation
4) Base generation vs. first generation
5) Base generation vs. second generation
6) First generation vs. second generation

TABLE 12. Hen-housed and hen-day egg production for base and first generation females selected as parental stock.

| Egg production | Base generation production (%) | First generation production (%) |
|---|---|---|
| Hen-housed (for heavy selected females) | 60.63 | 48.57 |
| Hen-housed (for light selected females) | 48.83 | 34.19 |
| Hen-day (for heavy selected (females) | 61.87 | 51.61 |
| Hen-day (for light selected females) | 56.70 | 39.66 |

TABLE 13. Number of birds hatched, survived, died and percent mortality for the total period of the experiment (October 1,1974-March 2, 1977)

| Generation | Number Hatched | Number Alive | Number Dead | Percent of Mortality |
|---|---|---|---|---|
| Base generation (1975) | 480 | 386 | 94 | $19.58^{a}$ |
| First generation (1976) | 573 | 390 | 183 | $31.93^{bc}$ |
| Second generation (1977) | 405 | 255 | 150 | $37.03^{c}$ |
| Control (1977) | 219 | 166 | 53 | $24.20^{ab}$ |

NOTE: 1) Values with different superscript differ significantly, $p < 0.01$).
2) Mortality was recorded up to 18 weeks of age.

Highly statistical differences ($p < 0.01$) were found between base generation and first generation, base generation and second generation and, finally, between control and second generation (Table 13).

The evidence so far suggests that two-way response to artificial selection for body weight in Ring-Necked pheasant depresses livability. This is in accord with Falconer (1953a, 1960) and Nordskog *et al*. (1964, 1974), who stated that total reproductive fitness is expected to decline when artificial selection for any character upsets equilibrium gene frequencies. Since livability is a component of the total reproductive fitness, it is not surprising that this character may decline when artificial selection changes the population mean in either direction.

Reports of laboratory examinations received from veterinary diagnostic laboratories, Department of Pathology, M.S.U. have indicated that according to the history, gross lesions and laboratory findings, diagnosis was characterized into air sacculitis, cecal coccidiosis, emaciation, necrotic core in cecum, pericarditis, peritonitis, pneumonia, post-mortem decomposition and pulmonary hemorrhage. These diagnoses were characterized about evenly among all generations.

# SUMMARY AND CONCLUSIONS

Individual selection for heavy and light selected lines at 12-weeks of age which was practiced for two generations in Ring-Necked pheasant populations have resulted in mean body weight differences of about 2, 49, 168, 283 and 381 gm in the males and 2, 54, 156, 264 and 327 gm in the females at one-day, 4-weeks, 8-weeks, 12-weeks and 18-weeks of age, respectively, between the two diverse selected lines.

The heavy selected line gained more weight by plus selection than was lost from the light selected line by minus selection. In addition to that males gained or lost more weight than females.

Progress due to selection for body weight in the light and heavy selected lines appears to be erratic. This irregularity is similar to that reported in other selection experiments.

Experimental data transformation to logarithmic and percentage scale did not appear to give a noticeably better fit than the actual scale. In addition to that there was little evidence that size genes were acting multiplicatively.

Heritability estimates obtained in this study were calculated from parent-offspring regression and from cumulative effects of selection (realized heritability) techniques.

After omitting all values that fall outside the possible biological range of heritability, then average heritability estimates calculated from parent-offspring regression techniques for the first generation of selection would be equal to .47 ± .1, .44 ± .08, .66 ± .07, .50 ± .04 and .63 ± .03 for body weights at one-day, 4-weeks, 8-weeks, 12-weeks, and 18-weeks of age, respectively. Heritability estimates for the second generation heavy selected line at these time intervals would be .29 ± .18, .64 ± .21, .46 ± .24, .77 ± .26 and .33 ± .16, respectively, while for the second generation light selected line they were equal to .47 ± .42, .59 ± .24, .41 ± .23, .20 ± .42 and .59 ± .08, respectively.

The best explanation of fluctuations of these values would be large sampling errors due to small number of dams, sires, and progeny.

Much more consistent and reliable estimates of heritability were obtained from regression of offspring on mid-parents in comparison to double regression of offspring on dam and double regression of offspring on sire.

Average realized heritability estimates after negative heritability estimates were omitted from the statistical analysis were found to be .50 and .33 in males and females of the light selected line,respectively, while they were equal to .71 and .38 in the heavy selected line for males and females, respectively.

These results suggest the existence of high additive genetic variance, which in turn indicates that mass selection would be the best method to ensure that highest genetic gains for body weight are obtained.

Duration of fertility ranged from 10-21 days with an average of about 15 days.

An intimate degree of association between egg weight and day-old chick weight was observed, where positive coefficient of correlation was .91, .86, .83, .76, .81 and .78 for control males, control females, second generation light selected line males, second generation light selected line females, second generation heavy selected line males and second generation heavy selected line females, respectively. It was also noted that chick weight at hatching time represents 64-67 percent of the weight of the egg from which it hatched and that heavier eggs produced heavier chicks.

Hen-housed egg production for the heavy females selected as parental stock was 60.63 and 48.57 percent for base and first generation, respectively. For the light selected females it was 48.83 and 34.19 percent for the same generations, respectively. Hen-day egg production for heavy females selected as parental stock was 61.87 and 51.61 percent for base and first generation, respectively. For the light selected females it was 56.70 and 39.66 percent for the same generations, respectively.

Percent mortality was 19.58, 31.93, 37.03 and 24.20 for the base, first, second generation and control population, respectively. Chi-square analyses have shown that one may have 99.9 percent confidence that mortality is not independent of selection.

Highly statistical differences ($p < 0.01$) in mortality were found between base generation and first generation, base generation and second generation and, finally, between control and second generation.

Since livability is a component of the total reproductive fitness, it is not surprising that this character may decline when artificial selection for any trait upsets equilibrium gene frequencies and results in decline of total reproductive fitness.

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# APPENDICES

## APPENDIX TABLE 1

Composition of the pheasant starter ration (fed 0-6 weeks of age) in percentage

| Ingredient | Percent |
|---|---|
| Corn | 46.35 |
| Soybean meal, 49% | 39.40 |
| Alfalfa, 17% | 3.0 |
| Fish meal, 60% | 2.5 |
| Meat and bone meal, 50% | 3.0 |
| Whey, dried | 2.0 |
| Salt | .25 |
| Dicalcium phosphate | 1.5 |
| Limestone | 1.25 |
| Premix (5004)[a] | .75 |

[a] Premix (5004), available from Dawes.

## APPENDIX TABLE 2

Nutrient composition of the pheasant starter ration on calculated analysis

| Nutrient | Percent |
|---|---|
| Crude protein | 28.00 |
| Fat | 2.61 |
| Fiber | 3.32 |
| Calcium | 1.47 |
| Phosphorus (available) | .70 |
| M.E., Cal/kg | 2730 |

## APPENDIX TABLE 3

### Composition of the pheasant grower ration (fed 6-13 weeks of age) in percentage

| Ingredient | Percent |
|---|---|
| Corn | 54.5 |
| Soybean meal, 49% | 25.5 |
| Wheat middlings | 7.5 |
| Alfalfa, 17% | 3.0 |
| Fishmeal, 60% | 2.5 |
| Meat and bone meal, 50% | 3.0 |
| Salt | .25 |
| Dicalcium phosphate | 1.5 |
| Limestone | 1.5 |
| Premix (5004)[a] | .75 |

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[a] Premix (5004), available from Dawes.

## APPENDIX TABLE 4

Nutrient composition of the pheasant grower ration based on calculated analysis

| Nutrient | Percent |
|---|---|
| Crude protein | 22.00 |
| Fat | 3.15 |
| Fiber | 3.64 |
| Calcium | 1.43 |
| Phosphorus (available) | .63 |
| M.E., Cal/Kg. | 2792 |

## APPENDIX TABLE 5

Composition of the pheasant flight ration (fed 13 weeks of age until time of lighting) in percentage

| Ingredient | Percent |
|---|---|
| Corn | 55.4 |
| Soybean meal, 44% | 14.1 |
| Oats | 10 |
| Wheat middlings | 10 |
| Alfalfa, 14% | 3.75 |
| Meat and bone meal, 50% | 3.0 |
| Salt | .25 |
| Dicalcium phosphate | 1.5 |
| Limestone | 1.5 |
| Premix (5004)[a] | .5 |

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[a] Premix (5004), available from Dawes.

## APPENDIX TABLE 6

### Nutrient composition of the pheasant flight ration based on calculated analysis

| Nutrient | Percent |
|---|---|
| Crude protein | 16.00 |
| Fat | 3.51 |
| Fiber | 5.30 |
| Calcium | 1.30 |
| Phosphorus (available) | .55 |
| M.E., Cal/Kg. | 2770 |

## APPENDIX TABLE 7

Composition of the pheasant breeder ration (fed after time of lighting) in percentage

| Ingredient | Percent |
|---|---|
| Corn | 53.25 |
| Soybean meal, 44% | 15 |
| Oats | 7.5 |
| Wheat middlings | 7.5 |
| Alfalfa, 17% | 3.0 |
| Fishmeal, 60% | 2.5 |
| Meat and bone meal, 50% | 3.0 |
| Whey, dried | 2.0 |
| Salt | .25 |
| Dicalcium phosphate | 1.5 |
| Limestone | 3.75 |
| Premix (5004)[a] | .75 |

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[a] Premix (5004), available from Dawes.

## APPENDIX TABLE 8

Nutrient composition of the pheasant breeder ration based on calculated analysis

| Nutrient | Percent |
|---|---|
| Crude protein | 18.00 |
| Fat | 3.44 |
| Fiber | 4.65 |
| Calcium | 2.40 |
| Phosphorus (available) | .68 |
| M.E., Cal/Kg | 2695 |