ESTIMATION OF GENETIC PARAMETERS USING DIFFERENT METHODS IN RHODE ISLAND CHICKENS SELECTED FOR PART- PERIOD EGG PRODUCTION

BY

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CERTIFICATION

THIS thesis titled **"ESTIMATION OF GENETIC PARAMETERS USING DIFFERENT METHODS IN RHODE ISLAND CHICKENS SELECTED FOR PART-PERIOD EGG PRODUCTION"** by Bartholomew Ifeanyi (Snr) NWAGU meets the regulations governing the award of the degree of doctor of Philosophy of Ahmadu Bello University, Zaria and is approved for its contribution to scientific knowledge and literary presentation.

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DECLARATION

I hereby declare that this thesis has been written by me and that it is a record of my own research work. It has not been presented in any previous application for higher degree. All quotations are indicated and the sources of information are specifically acknowledged by way of references.

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Bartholomew Ifeanyi (Snr) Nwagu

DEDICATION

This thesis is dedicated to my entire family and especially to my dearest wife, son and daughter, Mrs Flora O. Nwagu, Chukwuebuka Ifeanyi (Jr) and Chinwe for their undying love, patience, understanding and prayers throughout the period of study**.**

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ABSTRACT

Data from 4,336 pullets, progeny of 144 sires and 779 dams for strain A and 4,843 pullets, progeny of 158 sires and 1108 dams for strain B belonging to six generations under selection for part- period egg production to 280 days of age were used for this study. The data were used to compare heritability (h^2) estimates from **daughter-dam regression method**, with those estimated by variance component estimate method from five procedures **(Harvey method, TYPE 1, MIVQUE, ML and REML of SAS).** Response to selection, genetic and non-genetic correlations among egg production traits in the two strains were investigated. Effective number of parents and co-efficient of inbreeding were also calculated for both lines. The chickens were grouped into selected and control populations within the male and female lines.

The estimates of genetic parameters over the years were obtained after correcting the data for hatch and year effect. The traits considered in the computation of response to selection and genetic parameters were egg number (**EGG280D**), age at sexual maturity (**ASM)**, average egg weight (**EWTAV**) and body weight at 40 weeks of age (**BWT40**).

The heritability estimates from different variance component methods were close to one another in magnitude and in agreement with those found in literature. The heritability estimates obtained from variance components (half-sib) were 0.18, 0.15, 0.24 and 0.16 for age at sexual maturity (**ASM**), egg number (**EGG280D**), egg weight average (**EWTAV**) and body weight at 40weeks of age (**BWT40**), respectively, for the male line. The corresponding values for the female line were 0.20, 0.16, 0.29 and 0.21. The estimates obtained from daughter – dam regression for **ASM**, **EGG 280D**, **EWTAV** and **BWT40** were 0.19, 0.05, 0.28, and 0.27, respectively, for the male line and 0.19, 0.25, 0.27 and 0.20, respectively, for the female line. The standard errors associated with the parameter estimates were very low which is an indication of their reliability.

Direct genetic response to selection was higher in the female than male line (3.4 vs 0.42 eggs per generation). Selection is therefore much more effective in improving part year egg production in the female line as compared to the male line. The genetic correlation estimates between the different economic traits over five generations ranged from -0.70 ± 0.38 to 0.82 ± 0.42 vs -0.71 ± 0.47 to 0.76 ± 0.29 for the male and female lines respectively. The correlation between egg number and egg weight was small and not

significantly different. Age at sexual maturity was highly and negatively correlated with egg production to 280days in both lines, being higher than – 0.60 in most cases. However the genetic correlation between egg number and matured body weight (**BWT40)** showed no definite trend in the male and female lines.

In the female line, the correlated response in age at sexual maturity as a result of direct selection for egg production to 280days had negative value. This is also true for body weight due to selection for increased egg number to 280days. There was a reduction of 0.89g per year in egg weight due to selection for increased number. In the male line however except for body weight at 40 weeks, which showed a positive correlated response of 3.4g per year, all other traits considered showed negative correlated responses to selection for egg number to 280days of age.

The average inbreeding co-efficient due to finite population for both male and female populations were equal with a value of 0.005 while values for the control population were 0.008 vs 0.007 for the male and female line, respectively. The effective number of parents in each generation averaged 174 vs 187 for male and female lines, respectively.

It was observed that there was an increasing trend in the co-efficient of inbreeding per generation over the period of study. Although inbreeding could be adjudged mild in the study population, there is need to widen the genetic base of the population to avoid intense inbreeding that could result in selection plateau in due course.

The use of the various estimation procedures or options in this study revealed that generally the maximum likelihood estimators of **SAS** are more appropriate in dealing with Animal breeding data as they are capable of dealing with both random and fixed effects in a mixed model and are able to handle unbalanced data characteristics of Animal breeding data. However, if **Harvey's** method is to be used for analysis, data set with missing cells should be edited out before analysis to obtain meaningful estimates. Daughter – dam regression is recommended in the estimation of heritability due to the fact that random sampling errors associated with estimates are minimized. The offspring – parent method excludes the effects of environment more efficiently than those based on half or full – sibs.

TABLE OF CONTENTS

PAGE

TITLE PAGE:……..……..i

CERTIFICATION:……..……..ii

DECLARATION:…….iii

DEDICATION: …….iv

ACKNOWLEDGEMENT:……v

ABSTRACT:……..… vi

TABLE OF CONTENT:……viii

LIST OF TABLES:……xi

CHAPTER ONE:……1

INTRODUCTION:……1

CHAPTER TWO:……6

LITERATURE REVIEW:……...…6

2.1 Variance components estimation:…..…….6

2.2 Tools for the estimation of variance components:…….7

2.3 Some traditionally important methods of variance component estimation:…9

2.4 Analysis of variance based methods:……..... 9

2.5 Minimum Variance (or Norm) Quadratic unbiased Estimation:……..11

2.6 Maximum likelihood:…….12

2.7 Restricted Maximum Likelihood:…….13

2.8 Heritability from variance component:……15

2.9 Heritability from offspring- parent regression:……...17

2.10 Correlations:……..20

2.11 Primary and secondary traits of economic importance…….……24

2.12 Selection for traits of economic importance:…….……..26

2.13 Factors affecting Genetic progress:…….27

2.14 Population size and short term response to selection:……29

2.15 Prediction of effective population size:……31

2.16 Inbreeding and reproductive performance of laying hens:……33

CHAPTER THREE:……..……37

MATERIALS AND METHODS:……..37

3.1 The Location of Study:……37

3.2 Stock Composition:……37

3.3 Stock Management:……...38

3.4 Data:……40

3.5 Selection Procedure:……..40

3.6 Data Collection…….…..….42

3.7 Estimation of Genetic Parameters:…….…..42

3.7.1 Estimating Variance Component:……..…..44

3.7.2 Heritability:…….…..46

3.8 Parent Offspring Regression (intrasire regression of offspring on dam)…. 46

3.9 Estimation of Correlation:……..……...47

3.10 Estimation of Expected Genetic progress:…….…..49

3.11 Estimation of Expected and Realized response to selection for primary traits under selection:……..…49

3.12 Estimation of Realised responses (Phenotypic and Genetic):.…….....…50

3.13 Selection Differential:……51

3.14 Effective Population Size and Rate of Inbreeding: …….52

CHAPTER FOUR:……..……..55

4.0 RESULTS:……...……...……..55

4.1 Effective population size and inbreeding:……..…….55

4.2 Maternal effects:……..…….55

4.3 Heritability estimates:…..…….…….56

4.4 Genetic Correlation:……56

4.5 Genetic and non-genetic estimates using one way analysis of variance model:…….…..…….57

4.6 Selection differential:…….……..……57

4.7 Responses of egg number (primary trait) to selection:……..58

4.8 Correlated Responses:……..58

CHAPTER FIVE:……..…..……..78

5.0 DISCUSSION:……..78

5.1 Effective Population and inbreeding:…..……78

5.2 Selection response:……...79

5.3 Correlated responses:……..81

5.4 Genetic Correlation:……..……..82

5.5 Heritability estimates:…….……83

CHAPTER SIX:…….…87

6.0 CONCLUSION AND RECOMMENDATION……..…….87

6.1 CONCLUSION:……87

6.2 RECOMMENDATION:…….……..88

REFERENCES:……..89

LIST OF TABLES

TABLE

1. Effective number of sires, dams and parents and expected level of inbreeding in the selected population:..……..……..…….……..….59

2. Effective number of sires, dams and parents and expected level of inbreeding in the control population:…….…….…..60

3. Maternal effect and sex linkage in the male line:..……..……..61

4. Maternal effect and sex linkage in the female line:…….……62

5. Heritability estimates from various methods for male line:...……..63

6. Heritability estimates from various methods for female line:……..64

7. Genetic correlation (± SE) of egg number with other traits by year from sire components in the male line:…..…….……..…...65

8. Genetic correlation (± SE) of egg number with other traits by year from dam components in the male line:…….…….….66

9. Genetic correlation (± SE) of egg number with other traits by year from sire + dam component in the male line:……..…….……....67

10. Genetic correlation (± SE) of egg number with other traits by year from sire components in the female line:……68

11. Genetic correlation (± SE) of egg number with other traits by year from dam components in the female line:……..…….……69

12. Genetic correlation (±SE) of egg number with other traits by year in from sire + dam component in the female line:……...…70

13. Genetic, phenotypic and environmental correlations of egg no. with other traits by generation in the male line from one-way analysis:..…….….71

14. Genetic, phenotypic and environmental correlations of egg no. with other traits by generation in the female line from one way analysis:..……...72

15. Selection differential of egg number to 280 days of age:...……..…….….73

16. Average performance by generation, population, traits and phenotypic and genetic change of the male line:…..……..…….……74

17. Average performance by generation, population, traits and phenotypic and genetic change of the female line:…….……..75

18. Realised response and predicted gain for egg production up to 280 days:……..…….76

19. The expected correlated response per generation, E(CR),in secondary traits from selection on egg production to 280 days of age:……...77

CHAPTER ONE

INTRODUCTION

Breeding practices in poultry aim at genetic improvement of birds through successive generations. This requires intimate knowledge of the various characteristics of the breeds. Since the ultimate objective of poultry breeding is to improve those qualities, which have a definite market value such as increased egg production, improved quality of egg and improved quality and quantity of meat, the success of a breeder in evolving valuable strains would depend on how best he can combine the desirable qualities. In practical breeding, selection is used and it involves making decision based on available information. This information becomes even more relevant especially in those flocks under selection, in view of the fact that continued selection tends to bring about changes in the heritability and genetic correlations among traits (Sharma and Krishna, 1998).

Reliable estimates of genetic variances, covariances and heritabilities are needed to formulate breeding plans, predict response to selection and estimate genetic merit of animals. If the objective is solely to estimate genetic parameters such as heritability, simple methods of estimation, which involve only parent and offspring generations, based on parent- offspring regression or collateral relatives (full or half-sibs) can be used (Falconer and Mackey, 1998). With records on one or both parents and their offspring, the regression of offspring on one parent or both parents gives an unbiased estimate of heritability assuming no environmental covariance and no selection (other than on the parents only for that trait). If both parental records are available, heritability can also be estimated as the sum of the partial regressions of progeny on sire and dam in a multiple

regression analysis (Gimelfarb and Willis, 1994). In a short-term experiment, the estimated heritability (h^2) can be used in the classical equation of quantitative genetics,)G= $ih^2 \sigma_p$ to predict the response in offspring to selection, where ΔG is genetic change, i is the standardized selection differential and σ_p is the phenotypic standard deviation of the trait under selection (Falconer and Mackey, 1998). The prediction equation assumes that the regression of offspring on parent is linear, which would be so if the genotypes and the phenotypes have a multivariate normal distribution. The use of linear regression for estimating heritability or for the prediction of change from selection is justified only when such linear relationships can be reasonably explained on genetic grounds (Robertson, 1977). Thus an average estimate based on linearity either underestimates or overestimates the true heritability (Ibe and Hill, 1988). In this case the response by a character to selection predicted by non linear offspring-parent regression fitted to family data may be quite different from the response predicted by linear regression fitted to the same family data (Kempthorne, 1960; Gimelfarb and Willis, 1994).

Low genetic correlation could result from data not corrected for hatch effect as observed in the report of Oliver *et al.* (1957) who observed 0.22 genetic correlations between short-term egg numbers and percent production. When estimates were however made within hatches Bohren *et al.* (1966) observed a correlation of 0.79 while Morris (1964) obtained 0.74 from data corrected for hatch effect. Using four strains of White Leghorn, Srivastava *et al*. (1989) reported genetic response of 2.48 to 3.23 eggs per generation or per year after four generations of selection. They observed close agreement between predicted and realised responses for strain one while in the remaining three strains the realised response was approximately one and a half times that of the predicted

response. Such disparity in response could be caused, among other factors, by genetic drift, error of measurement, genotype - environmental interactions, time trend and natural selection (Hill, 1972,a, b)

Srivastava (1985) reported that the only possible reason for variable responses among the four strains could be either genotype - environment interaction or correlated responses. Kinney and Shoffner, (1967) suggested that the nature of genetic variance present in each strain might also contribute to the estimated response. Poggenpoel and Erasmus, (1978), Ayyagari *et al*. (1980) and Barua, (1983) reported variable results between realised and predicted response. Gowe *et al*., (1959a) reported significant regression of 3.71 eggs per generation without correction for environmental effects. After correction for environmental effects and using random bred control line, regression reduced to 1.26 eggs per generation, but was not significant. Poggenpoel and Erasmus (1978) reported control corrected regression coefficient of 3.04 eggs. Morris (1963), and Mohapatra and Srivastava, (1971) reported gains of 3.0 and 2.01 eggs per generation. Johari *et al*. (1989) reported positive and significant response to selection for part period egg production ranging from 1.44 to 2.21. The results of Gowe and Fairful, (1986), Poggenpoel (1987) and Lie (1988) supported these reports from their work on White Leghorn. Brah *et al*. (1986) reported gains ranging from 2.60 to 3.40 eggs per generation while Liljedahl *et al*. (1979) reported gains ranging from 4.4 to 6.2 eggs per generation over four years of selection. However Nordskorg *et al*. (1974) found no appreciable response in White Leghorn lines selected for part record rate of lay until the 8th of the 11 generations of selection for which the realised heritability was estimated to be 0.07.

Inbreeding, a system of mating where the mates are more closely related than the average members of the population being mated has been used for the production of genetically uniform strains for subsequent crossing to utilize heterosis. The higher the effective population size, the lower the expected inbreeding depression. Rates of in-breeding are largely inflated in selected populations because of the reduced effective population size. Inbreeding reduces genetic variability, vigor and reproductive performance and increases the probability of fixation of unfavorable genes. In recent years, various methods have been proposed to reduce the rate of inbreeding in selection programmes while keeping genetic gains at the same level (Nomura *et al*. 2002). These methods assume various selection and mating strategies. For example, a reduction in the weight of family mean in index selection (Toro and Perez-Enciso, 1990) for weighted ancestral Mendelian sampling estimates (Grundy *et al*. 1998). The limited use of selected parents (Toro and Nieto, 1984: Wei 1995) have been shown to be efficient methods. Other methods include non-random mating of selected parents, such as factorial mating designs (Woolliams 1989), minimum co - ancestry mating (Toro *et al*. 1988) and compensatory mating (Santiago and Caballero, 1995). Among these, minimum co - ancestry mating is a simple and intuitively appealing method, since it directly aims at minimizing the average inbreeding of progeny. Also there is some evidence that the depressive effects of inbreeding on certain traits can be dampened by rigid selection for that trait.

In quantitative genetics, animal breeding includes among other things the estimation of genetic parameters with which the genetic differences in the traits of animals are evaluated since selection is made based on genetic content rather than

phenotypic manifestation. The accuracy of these estimates depend on the method used and the data structure. Various methods have been used to estimate genetic parameters. However the accuracy of these methods are yet to be fully evaluated from available literature. This study attempts to provide such needed information.

The broad objective of this study is therefore to estimate genetic parameters using different methods while the specific objectives are: -

1. To estimate and compare heritability values from variance components obtained from various **SAS** subroutines **(TYPE1, MIVQUE, ML, AND REML), Harvey's and daughter – dam regression methods**
2. To estimate the genetic, phenotypic and environmental correlations between some economic traits.
3. To evaluate the response to selection in the primary trait.
4. To compute inbreeding co- efficient in the selected population

CHAPTER 2

2.0 LITERATURE REVIEW

2.1 VARIANCE COMPONENT ESTIMATION

Variance components are linear models that incorporate random terms which generate variance and covariance matrix with known structure but with unknown parametric values, the estimations of which are used in animal breeding. When data are obtained from samples or unbalanced designs, problems occur resulting in differences in estimation criteria and in the use of different algorithms when solution do not converge. Depending on the estimation criteria and the algorithm that is used, it is possible to obtain different solutions.

Using matrix algebra, the, mixed linear model (Cadena-Meneses and Castillo-Morales, 2000) is

$$Y = X\alpha + Z\beta + \varepsilon$$

where α is the vector (p x 1) of unknown parameters of fixed effects ; X is a known (N x p) matrix, with incidences of zero and ones, although it may include co-variables; β is a vector (q x 1) with effects of the form $\beta[b'_1, b'_2, \ldots\ldots b'_c]$ with bi; of other q_i and $q_1 + q_2 + \ldots\ldots + q_c$ with $E(b_i)=0$, $Var(b_i)= \sigma_i^2 Iq_i$ and cov $(b_i , b_i') = 0$ for $i \neq i'$; $[Z_1, Z_2, \ldots\ldots Z_c]$ is a known incidence matrix, with Z_i with N x q_i dimensions and vector (N x 1) having error terms with $E(\varepsilon) = 0$ and Var $(\varepsilon) = \sigma_e^2 I_N$. If D =diag $(\sigma_i^2 Iq_i)$,then Var (β) = D, V = Var (Y) = $ZDZ' + \sigma_e^2 I_N$, and therefore $Y = X\alpha + Z\beta + \varepsilon$ is such that E (Y) = $X\alpha$ and Var (Y) = V.

An animal population generally presents great variability among members, and this makes it possible to select the subjects, which would best improve the traits of interest to the researcher. The phenotypic variance (σ_p^2) is the sum of the variances attributable to genetic (G) and environmental (E) variation sources, as well as to the interactions that occur between them (Herrera, 1986). This can be represented by : $\sigma_p^2 = Var (G + E) = \sigma_g^2 + 2\,\sigma_{ge} + \sigma_e^2$, and if it is assumed that no correlation exists between genotype and environment , $\sigma_{ge} = 0$, the partition of the phenotypic variance is : $\sigma_p^2 = \sigma_g^2 + \sigma_e^2$, where σ_p^2 is the phenotypic variance or variance of the variable , σ_g^2 is the genetic variance or variance due to individual genetic content, and σ_e^2 is the variance of the environmental effects to which the individuals have been exposed. σ_g^2 and σ_e^2 are referred to as variance components and σ_p^2 is considered the total variance.

2.2 TOOLS FOR THE ESTIMATION OF VARIANCE COMPONENTS

In order to obtain estimation of variance components two computational packages have been used: SAS (1988,1996) and LSMLMW (Harvey, 1990).

SAS **- The SAS procedures of interest is the VARCOMP procedure. This calculates the variance components in a general linear model. It has four available methods for the estimation of variance components. There are the** Type1 **Method, that is equivalent to what is generated by GLM in its Type1 option of sums of squares; the** MIVQUE0 **method, based on the minimum norm or minimum variance technique (Hartley *et al*., 1978); the Maximum Likelihood Method (**ML**) that calculates the estimations of maximum likelihood of the variance components, utilizes the W transformation developed by Hemmerle and Hartley (1973) and employs the results of** MIVQUE0 **as values of the first iteration; the Restricted Maximum Likelihood Method, which first separates the likelihood in two parts, one containing the fixed effects and the other the random effects, utilizes algorithms similar to those of** ML**, and has the same initial values as** MIVQUE0**. It is necessary to specify the fixed effects, which must be written at the beginning of the model.**

HARVEY – **The Harvey's (1990) Mixed Model Least-Squares and Maximum Likelihood computational packages defines nine specific models: MODELS 1 to 9. MODEL 1 solves problems of fixed factors in a manner similar to SAS, and results are the same as the SAS GLM Type III. It utilizes Henderson's Method III (1953) to solve the specific mixed models, which are adjusted in MODELS 2 to 7. For each MODEL, there is a specific type of random effect (Harvey, 1990). The MODELS 8 and 9 are the same as MODELS 2 and 3, but are solved by means of Henderson' mixed model method (1984), making it possible to obtain** MINQUE **or iterative** MINQUE **variance component estimations.**

The estimates of maximum likelihood usually are more preferred for asymptotically stable properties. The estimates based on analysis of variance only have the property of being unbiased. Where there are a few observations, the best choice would be REML**. In real situations of animal breeding with many observations,** ML **is preferred. It is not recommendable to use the** MINQUE **(or** MIVQUE**) estimations due to the fact that they are the first step of the iterative process. There is no reason to stop at this first step, when the iteration can be continued and the** I-MINQUE **or** REML **obtained. The choice between** SAS **and** HARVEY **will depend on the computational and economic resources, available to the user. When they are available, then** SAS **is recommended (Cadena-Meneses and Castillo-Morales, 2000).**

2.3 SOME TRADITIONALLY IMPORTANT METHODS OF VARIANCE COMPONENT ESTIMATION

Mixed models have been extensively used in Animal Breeding Applications. In this class of models, the prediction of random effects that include breeding values assume known variances. However, we do not know the variances of field data and should normally estimate variance components. Therefore, accurate prediction of breeding values depends on accurate variance component estimation.

Many animal breeders have made efforts to develop a variety of statistical approaches and computing algorithms for variance component estimation. Essential landmark research papers have been published on variance component estimation in animal breeding (Lee 2000). In this manner analysis of variance (ANOVA**)-based methods, Minimum variance quadratic unbiased estimation** (MIVQUE) **and likelihood-based methods will be considered.**

2.4 ANALYSIS OF VARIANCE –BASED METHODS

Estimation of variance has been developed from Fisher's (1925) ANOVA **table, which summarizes a partitioning of observed variability. The principle of** ANOVA **method is to equate** ANOVA **sums of squares to their expected values, which are linear functions of the variance components. Those expected values must be such as not to include functions of fixed effects. Variance components are estimated by solving a system of equations. For balanced data, estimates from** ANOVA **are best-quadratic unbiased estimators and they are reduced to best-unbiased estimators under normality. For unbalanced data, uniformly best variance component estimators do not exist. Henderson (1953) developed three different sets of quadratic forms by adapting the** ANOVA **method for balanced data. (Later, Henderson developed method IV, which was more closely related to the quadratics used in** MIVQUE, **so often called Diagonal** MIVQUE**). Henderson's Method 1 uses quadratics that is analogous to the sums of squares from balanced data and is applicable to random models in which $\underline{X}\,\underline{\beta} = I\mu$. $\underline{\beta}$ is the vector of unknown fixed effect, and μ. is the vector of unknown random effect. $\underline{X}$ and $\underline{I}$ are the known design matrices for the fixed and random effects respectively. Henderson's Method II is a translation invariant procedure, which adjusts the data, for fixed effects and uses a variant of model I. Henderson's Method III is the fitting constants method, which uses the reductions in sums of squares due to fitting one model and its sub models. This method is not unique in specifying reduction in sums of squares. The Method III is applicable to mixed models. For sampling variances of the estimates from the three methods, closed form expression are possible, but they would be very complicated; no one has derived them.**

Variance components estimated by ANOVA **– based methods are not necessarily nonnegative, which is a fatal property for researchers to avoid. Solution to this problem is however overcome by equating negative estimates to zero. A great merit of the ANOVA – based methods is unbiasedness of their estimates. However, covariance structure created from genetic relationships in a population under selection make variance estimates to be biased (Sorenson and Kennedy, 1984).**

2.5 MINIMUM VARIANCE (OR NORM) QUADRATIC UNBIASED ESTIMATION

This estimates variance components with desirable properties of unbiasedness and minimum variance. It is called the minimum variance quadratic unbiased estimation

(MIVQUE). The **MIVQUE** assumes normality. On the other hand, in minimum norm quadratic unbiased estimation **(MINQUE),** a known Euclidean norm is minimized instead of a known variance. The **MINQUE** does not require the normality assumption and reduces to **MIVQUE** under normality. Details of both methods, have been discussed in articles by LaMotte (1970, 1973) and Rao (1970, 1971a, b, 1972). The articles may be elegant from theoretical point of view, but complicated in practical application to real data. Solving **MIVQUE/ MINQUE** equations requires no iteration. However, solution to the equations depend on the choice of the initial chosen estimates of the variance components, and furthermore needing the initial estimates makes **MINQUE** useless. The **MIVQUE/ MINQUE** equations are similar to those for restricted maximum likelihood **(REML**). Hocking and Kutner, (1975) observed that **MINQUE** equals to a first iterate of **REML**. In practice it is often suggested to solve the **MINQUE/MIVQUE** equations repeatedly up to convergence. Harville (1977) found that the estimates at convergence equal to **REML** solutions. Therefore, if the solutions are within the parameter spaces, they are equivalent to REML estimates. In animal breeding applications with a single trait model with only additive genetic effects, Sorenson and Kennedy, (1984) and Van Tassell *et al*. (1995) obtained **MIVQUE** of the genetic and residual variances. They as well as Lee (2000) however reported that the **MIVQUE** of variance components were biased and their mean squared errors large. This is because **MIVQUE** is the first step of the iterative process.

2.6 MAXIMUM LIKELIHOOD (ML**)**

Hartley and Rao, (1967) developed maximum likelihood (**ML**) procedure for the estimation of variance components. Assuming that y ~N(Xβ,V), log likelihood function of y is :

$$l_{\beta,\hat{\sigma}ly}a - 5\log|V| - 5(y - X\beta)'V^{-1}(y - X\beta),$$

Equating the derivates of this function with respect to variance components to zero gives ML estimates **of the variance components if the solutions from the equations are in the parameter space. This is because the likelihood function must be maximized within the parameter space. So, if the** ML **estimate is the boundary value of the parameter space, then the likelihood is likely to differ from zero at maximum. The estimation of ML demands attributing a distribution to the data, which in case of random and mixed models suggests doing just that for the random effects. This is, of course, not a requirement of ANOVA estimation, other than requiring finite variance components and contains no terms in the fixed effects. To date, nearly all closed form results for** ML **estimation of variance components are on the basis of normality assumption: e.g. for the 1-way classification the random effects have the first- and second- moment properties well defined, and are additionally taken as being normally distributed. It is under these conditions and their direct extension to multi-way classification, that the development of** ML **methodology has proceeded. Details of the procedure have been discussed by Henderson (1973), Laird (1982) and Searle *et al.* (1992). Laird (1982) and Searle *et al.* (1992) presented expectation –maximization (EM) algorithms. The** ML **estimates have attractive features of large sample properties (Hartley and Rao, 1967). First, the estimates are asymptotically unbiased. Second, the asymptotic dispersion matrix of the estimators is available. It is expressed as the inverse of Fishers information matrix. Third, the dispersion matrix of the estimators asymptotically achieves the Cramer-Rao lower bound for dispersion matrix of unbiased estimates. That is, the estimators have the property of asymptotic efficiency (Mood *et al.* 1975; Casella and Berger, 1990). In animal breeding applications, the empirical variance component estimates did not differ from their corresponding input values in the simulation study of Rothschild *et al.* (1979). The** ML **estimators have almost the same statistical properties as** REML **regardless of merit or demerit. However, ML does not take account of the degrees of freedom, which are involved in estimating fixed effects, while** REML **overcomes the problem. Only this difference has led researchers to prefer** REML **to** ML**, especially in animal breeding analyses where the number of levels for fixed effects is large.**

2.7 RESTRICTED MAXIMUM LIKELIHOOD (REML)

Patterson and Thompson, (1971) developed restricted maximum likelihood to estimate variance components. In order to account for the loss in degrees of freedom on estimating fixed effects, the method uses restricted likelihood where estimates of the fixed effect are adjusted, i.e. linearly independent error contrasts $K^1 y$, **where**

$K^1X = 0$ **and** K^1 **has full row rank, are used instead of** y**. This method led the variance component estimates to be invariant to constraints to get estimates of fixed effects. The likelihood of** K^1y **with** K^1**y~** $N(0, K^1VK)$ **is as follows:**

$$l_{\hat{\sigma}^2 ky}\left(= l_\beta\right)a - 5\log|K'VK| - 5y'K(K'VK)^{-1}K'y, \quad (1)$$

In fact, maximizing the restricted likelihood does not require knowing reference to the matrix of the error contrast (K)**, and the likelihood function is expressed as follows (Harville 1977) :**

$$l_\beta a - 5\left\{\log|V| + \log|X'V^{-1}X| + \left(y - X\hat{\beta}\right)V^{-1}\left(y - X\hat{\beta}\right)\right\}$$

(2)

Harville (1977) and Searle (1979) developed another equivalent form :

$$l_\beta a - 5\left\{\log|R| + \log|G| + \log|C| + y'Py\right\} \quad (3)$$

Where $P = V^{-1} - V^{-1}X\,(X'V^{-1}X)^{-1}X'V^{-1}$.

As in ML, REML **estimates must be in the parameter space. In addition to the attractive large sample properties shown in** ML, **the** REML **estimates are likely to have the property of unbiasedness if the values which maximize the likelihood are in the parameter space when considering that, for balanced data, the solutions to** REML **equations are equivalent to those from ANOVA (Patterson and Thompson, 1974; Corbeil and Searle, 1976; Searle** ***et al.*** **1992). In animal breeding, a number of simulation studies showed that input values of the variance components were obtained by** REML **regardless of selection (Jensen and Mao, 1991; Lee and Pollak, 1997a; Schenkel and Schaeffer, 1998). However, parent misidentification or splitting data cannot explain the selection. Random deletion or misidentification of parent identifications in selected populations results in significant differences between variance component estimates and their corresponding input values. Thus correct and complete pedigree information is important (Lee and Pollak, 1997b; Kennedy and Sorenson, 1988; Schaeffer** ***et al.*** **1998). Partitioning data by gender and analyzing only male or female data did not account for selection on females (males), and variance component estimates differed from their input values (Lee and Pollak, 1997a). Since the likelihood functions (1), (2) and (3) are highly nonlinear, there are no closed form solutions for variance components. Development of computing algorithms for** REML **estimation of variance components has been a nontrivial task and a great concern (Harville, 1977, Harville and Callanan, 1990; Searle** ***et al.*** **1992). Various maximization methods are available, and these methods are typically divided into the three parts:**

1) methods using first and second derivatives of the likelihood,
2) methods using only first derivative,
3) derivative free methods.

The standard method to maximize the likelihood is to use its first and second derivatives with respect to variance components (Patterson and Thompson, 1971, Thompson 1973, Meyer 1983 and Searle ***et al.*** **1992). The representative gradient**

methods may be Newton-Raphson method and Fisher scoring (Press *et al*. 1992, Searle *et al*. 1992). Searle *et al*. (1992) described a general form of the various gradient methods to determine the search direction for the next step of iteration.

2.8 HERITABILITY ESTIMATED FROM VARIANCE COMPONENT

The heritability of a trait is one of its most important properties. It expresses the proportion of the total variance that is due to the average gene effect. It has a predictory role expressing the reliability of the phenotypic value as a guide to the breeding value. It tells something about the amount of progress that might be made in selection for a particular trait. Heritabilities differ greatly according to the trait. On the whole the traits with the lowest heritabilities are those closely connected with reproductive fitness while traits with the highest heritabilities are those that might be judged on biological grounds to be least important as determinants of natural fitness.

Theoretically, heritability can range from 0 to 1.0, but these extreme values are rarely encountered in practice. A particular heritability value is descriptive of a trait in a particular population. Since it is a fraction, its value can be varied by changes in the additive genetic variance of the numerator or by any changes in any one or all of the components of variance in the denominator. The additive genetic variance is closely associated with the number of the genes influencing the trait. Heritability expresses the reliability of the phenotypic value as a guide to the breeding value or the degree of correspondence between phenotypic value and breeding value. Hence h^2 enters into almost every formula connected with breeding methods and many practical decisions about procedure depend on its magnitude. Heritabilities cannot easily be estimated with any great precision and most estimates have rather large standard errors. Low heritability

estimates indicate that there is a low correlation between phenotype and genotype or that the variations due to additive gene action are probably small.

A number of methods have been described to estimate heritabilities (Lush, 1949; Lerner 1950; Falconer and Mackay, 1998). The choice of the method often depends on the circumstances and the type of data available for analysis. Commonly used methods are full - and half - sib correlations, intrasire regression of offspring on dam, and realized heritabilities. Heritabilities based on sib correlations are normally calculated from variance component analysis. The covariance components that can be obtained from this analysis are those among sires, dams and full - sibs. The heritability from variance components may be subject to large sampling errors and can be overestimated due to inclusion of sex - linked and non - additive genetic effects (Kinney, 1969).

The validity of the h^2 estimate based on an intrasire regression of offspring on dam, is dependent on the absence of maternal effects contributing to the resemblance between daughters and dams (Kinney, 1969). It is expressed as $h^2 = b_{op}$. Heritability estimates may be obtained by calculating correlation co - efficient for a trait (the correlation between different records by the same *individuals*). It gives an estimate of the upper limit of h^2 and may be higher than the true h^2, if permanent environmental effects on the individual are important (Lush 1949).

2.9 HERITABILITY ESTIMATE FROM OFFSPRING - PARENT REGRESSION

The heritability of a quantitative trait may be estimated by the regression of progeny on parental performance. Since the sampling variance of the estimate of any linear regression coefficient is inversely proportional to the sum of squares for the

independent variate, we might improve our heritability estimate by rearing and measuring a relatively large number of potential parents but selecting only the best and the poorest for mating. However since a cost is incurred in measuring the discarded parents, we might expect that an optimum intensity of selection should be practiced, such that the sampling variance of the regression estimate is minimized for a given total expenditure in rearing and measuring parents and progeny. Latter and Robertson, (1960) derived expressions for optimum progeny family size for offspring - parent regression when no selection is practiced. Soller and Genzi, (1967) and Hill (1970) have discussed the optimum selection intensity in selection experiments in which family structure is ignored. Reeve (1961) also showed that selection or assortative mating should cause only a negligible bias to estimates of heritability from regression, so long as gene effects on the quantitative trait are small relative to its phenotypic standard deviation.

Reliable estimates of genetic variance, covariances and heritabilities are needed to formulate breeding plans, predict response to selection and estimate the genetic merit of animals. If the objective is solely to estimate genetic parameters such as heritability, simple methods of estimation which involve only parent and offspring generation and are based on parent - offspring regression or collateral relatives (full or half - sibs) can be used (Falconer and Mackay, 1998). With records on one or both parents and their offspring, the regression of offspring on one parent or both parents gives an unbiased estimate of heritability assuming no environmental covariance and no selection (other than the parents only for that trait). Correction for differences in variance of the trait between the sexes should be made and the genetic correlations between the traits in males and females equals to one. If both parental records are available, heritability can also be

estimated as sum of the partial regressions of progeny on sire and dam in a multiple regression analysis (Gimelfarb and Willis, 1994).

In a short - term experiment, the estimated heritability (h^2) can be used in the classical equation of quantitative genetics, $\Delta G = ih^2\sigma_p$ to predict the response in the offspring to selection, where i is standardized selection differential and σ_p is the phenotypic standard deviation (Falconer and Mackay, 1998). The prediction equation assumes that the regression of offspring on parent is linear, which would be so if the genotypes and phenotypes have a multivariate normal distribution. The use of linear regression for estimating heritability or for the prediction of change from selection is justified only when such linear relationships can be reasonably explained on genetic grounds (Robertson 1977). On the average, estimate based on linearity either underestimates or overestimates the true heritability (Ibe and Hill, 1988). In this case the response by a character to selection predicted by nonlinear offspring - parent regression fitted to family data may be quite different from the response predicted by linear regression fitted to the same family data (Kempthorne 1960; Gimelfarb and Willis, 1994).

Nonlinear offspring - parent regressions have been found for various traits (Nishida, 1972; Nishida and Abe, 1974; Maki – Tanila, 1982; Ibe and Hill, 1988, Gimelfarb and Willis, 1994 and Koerhuis 1996). Equivalently, different estimates of realized heritability have been obtained for different selection intensities using either actual or hypothetical (simulated) selection (Clayton *et al*. 1957; Meyer and Enfield, 1975; Sumpf *et al*. 1978). The results have been discussed by the above authors and by Kempthorn (1960) and Bulmer (1980). Various factors were considered as possible causes of nonlinearity, notably skewness of genotypic and / or environmental components

and genes of large effect, particularly with directional dominance, as in traits of reproduction (Frankham 1990). Some recent studies, particularly that of Gimelfarb and Wills, (1994), have again focused attention on what is an old, and generally ignored problem. Linearity is a fundamental assumption of many modern likelihood or variance component-based methods. In their work Mbaga and Hill, (1997) observed that the estimates of heritability from mid - parent regression using standardized but not unstandardized data, were similar to those obtained from multiple regression on the two parents indicating that there is no added advantage in considering the two parents separately over regression on mid - parent provided the data are standardized. However there was a small negative correlation of performance of the mates, and the estimate of heritability obtained from the sum of the two ordinary regressions of progeny on sire and progeny on dam was slightly biased downward. Significantly, nonlinearity in the relationship between offspring and sires as well as between daughters and mid - parent was found, but the contributions of nonlinear terms were rather small except for very extreme parents. None of the offspring - dam relations displayed nonlinearity. This could be due to the large maternal contributions to the offspring's phenotype. Maternal effects often mask genetic effects if maternal effect acts linearly or had the opposite nonlinear structure so as to cancel the genetic nonlinearity. Nonlinear heritability may be due to directional dominance and symmetrical gene frequencies (Robertson 1977; Bulmer 1980; Maki – Tanila, 1982; Gimelfarb 1986 and Frankham 1990), particularly when dominance is incomplete and the recessive genes are at low or moderate frequencies. Mbanga and Hill, (1997) concluded that if however there is substantial non-normality, transformation

to improve normality and linearity may be employed before subjecting the data to analyses. This agrees with the suggestions of Ibe and Hill, (1988) and Koerhuis (1996).

2.10 CORRELATIONS

Correlation can be phenotypic (r_p), genotypic (r_g) or environmental (r_e). Phenotypic correlation among traits can be defined as the gross correlation that includes both the environmental and genetic portions of the covariance. Phenotypic correlation is the observed association between two traits, which also includes genetic and environmental factors. Phenotypic correlations are important because they directly affect size of selection differentials. This is especially true when the correlations are high, whether negative or positive. Oluyemi and Roberts (1979) defined genetic correlations among traits as the genetic associations of one trait with others, which are to be improved. Genetic correlation is therefore the correlations between the additive breeding values of two traits.

Genetic correlation among traits means that the same genes or closely linked genes affect two or more traits. The measure of correlation is correlation coefficient, r. This is the degree of association between two traits. Theoretically, r ranges from -1 to +1. Bohren *et al*. (1966) observed that correlation coefficients are affected by sampling errors and therefore the value obtained will be limited in its representations of the association between the two traits in question. Correlation coefficient also varies with the population used in its estimation.

The chief cause of genetic correlation is pleiotropy, though linkage is a cause of transient correlation, particularly in populations derived from crosses between divergent

strains. Pleiotropy is a situation whereby one gene may affect two or more traits. Linkage means that the genes are carried on the same chromosomes. Falconer and Mackay, (1998) observed that closely linked genes would tend to stay together over several generations. However when the genes are farther apart, their associations will readily be broken by crossing over during synapses in meiosis. This will lead to a progressive reduction in the magnitude of the correlation coefficient between traits determined by such genes over several generations of selection. Since Hazel (1943) developed a method of calculating the genetic correlations among traits, many estimates among various traits of poultry have been reported. Genetic correlation is calculated from covariance and variances of the two traits. The estimates so obtained from such variances and covariance components are subject to the same sources of bias with regard to variance component.

Low genetic correlation is an indication that probably very few of the same genes affect the two traits. Genetic correlations may be positive or negative. Positive estimates mean that selection for improvement of one trait will result in the improvement of the other even though direct selection for its improvement has not been practiced. Positive genetic correlation between two traits may or may not be desirable depending on the traits in question. Negative genetic correlation is also a possibility. When this is the case, selection for the improvement of one trait, if successful, results in a decline in the other trait to which it is genetically correlated. A classic case is the genetic correlation between egg number and egg weight.

Kinney (1969) in his review presented several correlation estimates among production traits such as correlations of egg number, egg weight and age at sexual

maturity and body weight. Nordskog *et al*. (1975) reported negative phenotypic correlations of egg number and egg weight of close to zero for White Leghorn and Fayoumi populations, which had undergone selection for six generations. The corresponding genetic correlations were - 0.15± 0.20 and - 0.31 ± 0.06. Kinney *et al*. (1967) reported r_g of - 0.07, - 0.55, - 0.22 for egg number and 32-week body weight, egg number and 32-week egg weight and egg number and age at sexual maturity, respectively. Atkare and Khan, (1988) reported negative genetic correlation between egg production to 280 days of age and body weight at 40 weeks as well as egg weight at 40 weeks to be - 0.61 and - 1.03, respectively. The phenotypic correlations were - 0.004 and - 0.09 respectively. These estimates are similar to those reported by Craig *et al.* (1969) but different from the estimates of Poggenpoel and Erasmus, (1978) and Srivastava (1985). They reported that egg production to 280 days of age was to a large extent independent of 40-week body weight. Atkare and Khan, (1988) reported moderate to high genetic correlation between body weight at 40 weeks and egg weight at 40 weeks which agrees with the result of Friars *et al*. (1962).

King *et al*. (1963) demonstrated that when there is large maternal effect, the genetic correlations between two traits might carry opposite signs. For example, they reported that the genetic correlation between egg production and 32-week egg weight were - 0.28 and 0.01 from sire and dam components respectively. The opposite signs exhibited by the sire and dam component estimates for the correlation between egg production and 32 week egg weight are an indication that maternal effect need to be reckoned with when designing a selection programme for such population. The report of King *et al*. (1963) also showed that phenotypic correlations were generally of lesser

magnitude than corresponding genetic correlation regardless of signs. The denominator in the formula for the estimation is higher than that in r_g estimate. Therefore if only phenotypic correlation is considered in a selection programme, one could be tempted into a false security and thereby give less weight to correlated responses. They also reported correlations of 0.32 and 0.18 between 32 - week body weight and egg weight at 32 weeks as well as between sexual maturity and egg weight respectively. These estimates agreed with earlier estimates of King (1961). Hogset and Nordskog, (1958) reported phenotypic correlations of +0.37, -0.06 and -0.04 between egg weight and body weight, egg weight and egg production and body weight and egg production, respectively.

Negative genetic correlation between body weight and egg production could arise through the positive association of body weight with egg size. Liljedahl *et al*. (1979) reported that egg number and age at sexual maturity were strongly negatively correlated. They reported -0.18 and 0.05 for genetic and phenotypic correlations respectively between egg number and egg weight. Higher genetic correlations are often obtained for populations that have been selected over a number of generations due to the concentration of favourable genes.

2.11 PRIMARY AND SECONDARY TRAITS OF ECONOMIC IMPORTANCE

Since the principal objective of a poultry breeder is to produce a strain of poultry that will lay maximum number of egg within one year from sexual maturity, the primary trait normally selected for is egg number. In order to reduce the generation interval from two to one year, egg production to a certain fixed age has been taken as the norm in poultry breeding and selection work (Bohren 1970). Secondary traits include age at

sexual maturity, egg weight and body weight. Egg production is the major index of performance of layer productivity.

A chicken will lay for close to 365days (about one year) and this can be divided into three phases (Oluyemi and Roberts, 1979). Phase one is the first three months of laying. It starts from about the point of lay to about the peak at 2 - 3 months. During this period egg size and body weight increases. The first phase ends at about the forty - second week of age in some strains. This is followed by phase II that is characterized by gradual decline in egg production but not in egg and body size. This phase lasts till about the sixty- second week from point of lay. Phase III is made up of the remaining pullet year and terminates in moulting.

In order to reduce generation interval by half, when selecting for egg production, record of egg production to about 40 - 42 weeks of age of birds are normally used (Bohren, 1970). Correlations for egg to 40 - 42 weeks of age referred to as partial egg production with residual and egg production to full year have been exhaustively reviewed by Bohren (1970).

Bohren *et al*. (1966) and Bohren (1970) have indeed shown that theoretically, genetic correlation between partial and residual egg record could change from positive to negative in the course of selection. However, there is no evidence that such change has taken place in practice. Hale and Clayton, (1965) reported an average of 0.45 as genetic correlation between partial and residual egg number from Light Sussex and Brown Leghorn populations. Abplanalp (1957) reported a genetic correlation 0.55 from a commercial White Leghorn population. Andrews (1966) reported positive genetic correlation between part and full period percentages of production. Morris (1964) and

Bohren (1970) reported genetic correlations of 0.92 and 0.58, respectively, while Bohren *et al*. (1966) reported 0.38 between number of eggs in two periods.

Caceres (1967) reported that there was consistent gain in part period residual and annual number of eggs in a population where selection was strictly for number of eggs in part period and in research both age at sexual maturity and egg weight declined. The estimate of the genetic correlation between partial and residual records over eighteen generations was 0.57 while that between partial and residual egg records were 0.85. Bohren (1970) therefore concluded that the selection based on partial egg records to improve the annual egg record would be valid for some populations when selection is only on number of eggs in the part period, while response may be erratic when selection for other traits is included.

2.12 SELECTION FOR TRAITS OF ECONOMIC IMPORTANCE

When selection is applied to the improvement of the economic traits, it is generally applied to several characters simultaneously and not just to one, because economic value depends on more than one character. This is usually referred to as multiple trait selection. For example, the profit made from a herd of pigs depends on their fertility, mothering ability, growth rate, efficiency of food utilization and carcass qualities. How then, should selection be applied to the component characters in order to achieve the maximum improvement of economic value? There are several possible procedures (Liu *et al*. 1995). One might select in turn for each character singly in successive generations (tandem selection); or one might select for all the characters at the same time but independently, rejecting all individuals that fail to come up to a certain standard for each character regardless of their values for any other characters (independent culling levels). The method that is expected to give the most rapid improvement of economic value, however, is to apply the selection simultaneously to all the component characters together, appropriate weight being given to each character according to its relative economic importance, its heritability, and the genetic and

phenotypic correlations between the different characters. The practice of selection for economic value is thus a matter of some complexity. The component characters have to be combined together into a score, or index, in such a way that selection applied to the index, as if the index were a single character, will yield the most rapid possible improvement of economic value.

For traits of low heritability, selection of complete families of full or halfsibs without regards to individual performance is more efficient than selection on individual phenotypes. However for traits with higher values of heritability, the situation may be reversed but in all cases maximum efficiency can be obtained by selecting on basis of combination of family average and individual record.

Lush (1949) described the relative merits of individual selection and family selection in breeding for traits of low heritability while Lerner (1950) did the same with particular reference to poultry breeding. Based on these works, for traits of low heritability, selection of complete families of full or half - sibs without regard to individual is more efficient than selection on the basis of individual phenotypes.

Maximum efficiency can be obtained by selecting on the basis of a combination of family average and individual record. This is because of fine distinction between when to apply individual or family selection. The prediction of the female breeding value is obtained from her own performance and the means of her full and half sisters. However, in egg production studies, virtually all the traits are manifested in the females only. Therefore, prediction of the male breeding values is obtained from the means of his full and half sisters (Liljedahl *et al*. 1979).

2.13 FACTORS AFFECTING RATE OF GENETIC PROGRESS

The success of any breeding work and indeed its efficiency is dependent upon three factors. These include the intensity of selection, the accuracy of selection and the generation interval (Dickerson and Hazel, 1944). Intensity of selection is that proportion of the population that is allowed to be parents of the following generation. It may also be measured as the average superiority of the selected individuals above the average of the whole group. This is also referred to as selection differential. The second factor, the accuracy of selection, depends on some factors. It should be noted that the characters being selected could only be measured on the phenotype since there is no possibility of measuring such a character on the genotype. The phenotypic value of any trait is made up of portion due to genetic constitution and the environmental factor. Only part of the total variation between animals in a given character is directly due to genetic differences. Therefore the phenotypic identification of genetic superiority of an individual with respect to a given character is subject to errors proportional in magnitude to the degree to which non- genetic sources of variation affect it. In other words the accuracy of selection of genotypes by phenotypic measurement of individuals is proportional to the degree of heritability of a character. Since only the fraction of the variation determined by heritability of a character would contribute to improvement then the rate of genetic change of a population will be dependent on that fraction as well as on the selection intensity. Better estimate of the genotype of an animal can be obtained if information about the phenotype of animals related to it is available. Such information is obtainable from full and half - sibs of a given animal or from its offspring. This will enable the breeder increase the accuracy of selection.

The last factor, which affects the efficiency of selection, is the interval between generations. When the average age of the parents of a given generation is lower, less information about the animal is available to the breeder consequent upon which the accuracy of selection decreases. For larger animals, Dickerson and Hazel, (1944) showed that the reduction in the age of parents would more than compensate for the advantage of the increase in the accuracy of selection by progeny testing, when the progeny tested information is not available early in the life of an animal even when reproductive rates are relatively high and individual heritability is low. Dempster and Lerner, (1947) showed that greater efficiency is obtained by more widespread use of younger birds. They suggested that the use of pullets not only leads to more rapid improvement but also results in a considerable saving in the cost of breeding operations. Lerner and Cruden, (1948) suggested that selection might be done based on a part record thereby reducing considerably the interval between generations. Their estimate of genetic correlation between part period production and total production on a survivor basis was 0.74.

2.14 POPULATION SIZE AND SHORT-TERM RESPONSE TO SELECTION

Rate of response after one generation of selection depends on three factors: selection intensity, the additive genetic standard deviation and the accuracy of genetic evaluation. In addition, the response to selection in subsequent generations is highly dependent on population size. Two modifications are necessary, especially if the population size is limited (Verrier *et al*. 1991). The first modification is due to the effect of population size and structure on selection intensity. The second modification is due to the genetic drift acting on decrease in genetic variance; drift is the sum of inbreeding and sampling effects. The effect of drift on genetic variance is not independent of the effect of

selection, since selection acts directly, by inducing linkage disequilibrium (Bulmer, 1971), and indirectly through inbreeding. The main influence of population size in a short - term response is through selection intensity. Inbreeding depression will cause a further reduction in response rate, for traits connected with reproductive efficiency (Campo and Turrado, 1997).

There has been little experimental information published on the effects of population size and selection intensity on the short - term selection response. Frankham *et al*. (1968) studied the response to mass selection for increased number of bristles in *Drosophila* over 12 generations, using a factorial design of three population sizes (10, 20 and 40 pairs of parents) and four selection intensities (10, 20, 40 and 80%). Jones *et al*. (1968) reported the long - term response of these lines after 50 generations of selection. Hanrahan *et al*. (1973) examined the mean response after 14 generations of within full - sib family selection for postweaning gain in mice; population sizes of 1, 2, 4, 8, and 16 pairs were each evaluated at selection intensities of 50 and 25%. Eisen (1975) studied the long - term selection response in the same lines. Silvela *et al*. (1989) analysed the effect of selection intensity and population size on percent oil in maize over 10 generations, using 6, 10, or 50 plants and the selection intensity was 17 or 5%. In general, the selection response tended to increase with increasing population size, and there was no consistent effect of selection intensity.

The effect of population size keeping the selection intensity constant has been studied by Vasquez and Bohren, (1982), who selected for 8 week body weight in chickens over three generations, by considering three population sizes (44, 22, or11) with 10 females mated to each male. They observed a significant decrease in the mean

response as the population size decreased. The same effect has been reported in larger populations of *Drosophila* by Weber (1990) for wing height and Weber and Diggins, (1990) for ethanol resistance with lines of 40, 200, or 1000 and 160 or 1600 selected parents, respectively. The difference between lines seemed to have emerged rapidly. Hospital and Chevalet, (1993) investigated the effect of population size on optimal selection intensity by computer simulation. Although it is generally considered that for mass selection the selected proportion that maximizes ultimate cumulative response is 0.5 (Robertson, 1961), and response is 2N times that in the first generation, they showed that optimum selection intensity might be much lower unless population size is small. Experimental studies have been reported to analyse the effect of selection intensity on the selection response. Clayton *et al*. (1957) and Frankham (1977) considered individual selection abdominal bristle score in *Drosophila*. The first experiment studied three different intensities (20, 27, or 80%) with the same number of parents (20) whereas the second experiment compared three selection intensities (10, 20, or 40%). Ruano *et al*. (1975) analysed the effect of five different intensities (5, 10, 20, 33, or 50%) on selection response in egg laying in *Tribolium*. In general, the lines selected at the lowest proportions led to the largest initial responses.

2.15 PREDICTION OF EFFECTIVE POPULATION SIZE

Prediction of the effective populations under selection was first considered by Robertson (1961), who derived a formula to predict the effective size of populations consisting of full - sib families, when selection is practiced on a phenotypic value or an index including family information. Robertson (1961) introduced the idea of the

accumulation of selective advantages of individuals over generations. Santiago and Caballero, (1995) derived a formula more applicable to more general situations such as different number of males and females and non- random mating. Wray and Thompson, (1990) developed a method to approximate the effective size of selected populations, as a function of the mean and variance of the contributions of ancestors in the first generation, to descendants in the limit. Their method however requires complex recurrence computations. In order to overcome this problem, Woolliams *et al*. (1993) derived equations to predict the mean and variance of the contributions of ancestors to descendants. However, in all of the above studies, discrete generations have been assumed.

In the absence of selection, many authors (Crow and Denniston, 1988; Caballero 1994) have addressed the problem of overlapping generations in the prediction of effective population size. HiIl (1972) derived a prediction equation that made individuals born in a year responsible for the amount of random drift in the limit. His equation shows that the effective size of populations with overlapping generations is the same as that for discrete - generation populations, with the same variance in lifetime family size and the same number of individuals entering the population each generation. Based on the rate of inbreeding, Johnson (1977) obtained the same result.

In an open nucleus breeding system, the nucleus is open to some gene flow, usually through females from the base. The gene flow into the nucleus is expected to reduce the rate of inbreeding below the value it would have if the nucleus were closed. Especially in small - scale systems, this reduction in the rate of inbreeding may be of considerable importance. The rate of inbreeding in open nucleus breeding was studied by

James (1977) who gave a method for predicting the asymptotic rate of inbreeding. However, this method requires finding of the numerically largest eigen value of the complex transition probability matrix. To overcome this, James (1994) developed a simple approximation. The method enables the breeder to predict rates of inbreeding (Bondoc and Smith, 1993), but ignores the important fact that selection itself reduces the effective population (then inflates the rate of inbreeding) because selected animals are more likely related than random chosen animals. A theoretical framework for the effective size of selected populations was established by Robertson (1961) and has been improved by several authors (Caballero 1994). For an undivided population with overlapping generations it was shown by Nomura (1996) that the effective size of a selected population with overlapping generations is the same as that of for a discrete - generation population having the same non - selective and selective components of variance in lifetime progeny number and the same number of individuals entering the population at each generation.

2.16 INBREEDING AND REPRODUCTIVE PERFORMANCE OF LAYING HENS

Inbreeding has been used for the production of genetically uniform strains of chickens and for the development of lines for subsequent crossing to utilize heterosis. Important factors hindering the development and maintenance of inbred lines are the decline in performance and loss of vigor. In spite of past successes, the question of selection plateau is still with us. Realized gains from selection for egg rate almost invariably has been less than predicted. Yet, there seems no evident decline in the level of genetic variance of experimental flocks.

Perhaps a distinction should be made between natural and artificial selection. For the latter, animal breeders reach for maximum gain in the direction selection is applied. This is commonly referred to as directional selection. Natural selection may reverse the direction of artificial selection by lowering the reproductive fitness of the more extreme deviants. Thus, for a given trait, artificial selection favors the extreme deviants as opposed to natural selection, which favours those deviants closest to the population mean. In general, there seems to be agreement on how artificial selection should be measured, but this evidently is not the case with natural selection, although Haldane (1954) has provided an answer to this problem. He proposed that only those with desirable characters survive in nature to be parents of the next or subsequent generation.

Latter and Robertson, (1962) hypothesized that the decline in reproductive fitness is the result of gene frequency changes of two kinds: one from directional selection, and the other from random fixation due to limited population size. Thus, fitness changes can be explained in terms of phenotypic deviation and/or heterozygosis (Robertson 1956). In a recent study on chickens using serum protein and enzyme marker genes (Mina 1978), it was observed that heterozygosity greatly exceeded theoretical levels as estimated from pedigree information. This is in accord with earlier studies reported on the B blood group system in chickens (Schultz and Briles, 1953).

Quantitative traits, such as body size and egg size, as well as reproductive traits, such as egg production, hatchability and fertility (including viability), are usually assumed to be determined by many genes, each with small effects (polygenes). Therefore, we feel safe to apply the usual methods of quantitative genetics to measure genetic variance and to predict improvement by selection. In addition, for fitness traits,

one can argue with some logic, as Lerner (1950) and others have, that non-additive gene action may be important. That is, for single traits, or components of single metric traits, gene action is additive, but the totality of the components determining reproductive capacity, when expressed as a single value (i.e., fitness, over dominance and/or epistasis), is important. Hence, heterozygotes are most fit.

The usual method used to measure the degree of heterozygosity is Wright's coefficient of inbreeding (F_X). The regression of a trait on F_X is a measure of inbreeding depression. On the other hand, non-reproductive traits, such as body size and egg size, are thought to be essentially additive and, therefore, are not subject to inbreeding depression. A perusal of current literature on the subject leads to the conclusion that, the so-called metric traits are less subject to inbreeding depression than reproductive traits. Several workers have given experimental results of the effects of inbreeding on economic traits in chickens. Such effects include decline in egg production traits (Hays and Talmadge, 1949 and Goher 1974), although no significant detrimental effects of inbreeding on egg production could be established (Lerner and Hazel, 1947, Morris 1962). However, inbreeding has been shown to retard sexual maturity (Morris 1962, 1963 and Goher 1974). Inbreeding effects on egg quality traits have not been consistent. Grundy *et al*. (1998) studied the effect of inbreeding on production and reproduction traits and observed a decline in egg weight and shell thickness. Goher (1974) also reported decline in egg weight and shell thickness. However, Wei 1995 reported that inbreeding did not affect fertility but hatchability decreased. Toro and Nieto, (1984) reported no change in average egg weight as a result of inbreeding. John *et al*. (2000) in their work obtained no body weight decline following inbreeding. A possible explanation for the increase in

body weight with inbreeding could be that those genes with depressive effects on egg production and which were presumably made homozygous by inbreeding were favorable to body growth and fat anabolism. The well-known relationship between body size and egg production fits into this model. It is possible that the accumulation of those genes causing body size increases was done in the first few generations. Then as a result of increased body size, egg production dropped because in addition to other reasons, more nutrients would be diverted to maintenance than to production. The observed decrease in mortality is more difficult to explain. However, it could be that the influence of good management in decreasing mortality was more important than the influence of deleterious genes accumulated by inbreeding in increasing it. It appears that there is no general agreement in literature on the effect of inbreeding on body weight.

There is some evidence that the depressive effects of inbreeding on certain traits can be removed by rigid selection for these traits. At least theoretically, the role of selection in this is to accumulate favorable alleles that will subsequently be made homozygous by inbreeding. Experimental support for this has come from Knox (1946), Duzgunes (1950) and Shultz (1953). Stepheson *et al.* (1953) observed that inbreeding is a much stronger force than selection in influencing egg production. They contended that it would not be practical to establish an inbreed line with increments of inbreeding per generation so small that selection could overcome the injurious effects.

CHAPTER THREE
MATERIALS AND METHODS

3.1 LOCATION OF STUDY

The experiment was carried out at the National Animal Production Research Institute (NAPRI), Shika, about 22 km North West of Zaria, Kaduna State, Nigeria. The Station is located on Latitude 11^{o} 12'N, Longitude 7^{o} 33'E, and an altitude of 610m above sea level, in the subhumid zone of the country. The mean annual temperature is 24.4^{o} C while the mean annual rainfall of 1107mm is seasonally distributed as follows: 0.1% in the late dry season (January – March), 25.8% in the early wet season (April – June), 69.6% in the late wet season (July – September), 4.5% in the early dry season (October to December) (Osinowo *et al*. 1993). Mean relative humidity is 21% during the harmattan and 72% during the rainy season. The experimental site was the poultry breeding unit of the Poultry Research Programme.

3.2 STOCK COMPOSITION

The chickens for this study were obtained from a random-bred population of breeder hens, which form part of the poultry breeding flocks maintained at the Institute.

The initial stocks (Grandparents) comprised of two strains (A and B) of egg-type chickens each with 2 lines (male and female). These birds, even though from different sources, segregated for same type of colour genes i.e. gold/silver. The males and females of the sire line were gold, while those of the dam line were silver. These initial stocks were mated to produce F_1 using a checker board arrangement. They were mated in all possible combinations, but keeping the sire and dam sides as discrete populations. This gave rise to 4 F_1 progeny genotypes for each line. The matings for the formation of the F_2 were set up using a 4 X 4 diallel crossing technique, to produce 16 different

combinations in the F_2. After the formation of the F_2 generation, the genotypes were randomly mated for more than one generation to produce the F_3, which formed the base generation. The selection programme commenced with chicks of the F_3 generation. The base population was divided into six populations (i.e. 3 each for male and female line) with about 500 birds per generation. The populations are the control, single trait (egg number) and multiple traits (egg number and egg weight). In this base generation, due to lack of pedigree information, rate of lay (120 days egg production) was used as basis for the first generation of selection. The males were selected on body conformation using phenotypic appearance. From generation two, the selection programme was adjusted so as to concentrate on egg number with independent culling level set on egg and body weights at housing and maturity. 1000 hens were used for the selection populations out of which 250 are selected. For the control population 108 hens were randomly picked as parents for the next generation from 250 hens. Pen mating was done by trap nesting at mating ratio of 1 male: 9 females. Selection was based on a single trait i.e. egg number to 280 days of age as opposed to 120 days used during the 1st generation (Oni 1996, Adeyinka 1998).

3.3 STOCK MANAGEMENT

Chicks were hatched at the Institute's hatchery using the Western 19,000 egg capacity incubator over 3 – 8 hatches at one weekly interval. Fertile eggs marked with sire and dam identifications were collected over seven days and on the eight-day the eggs were set in the incubator. After hatching, the chicks were identified using wing bands and vaccinated against New Castle disease intra-ocularly using New Castle Disease Vaccine. The birds were brooded and reared to 18 weeks of age in deep litter floor pens. Sexing was done at about 8 –12 weeks. Floor space allowed per bird varied from 0.15 to 0.50 m^2 depending on age of bird. Feed was provided based on body requirement from hatching until 18 weeks of age on standard diets formulated at the Institute, containing a minimum of 20 and 15 - 16% crude protein for chicks and growers diets, respectively. At 18 weeks of age,

five hundred pullets of each strain were randomly placed in individual cages. At laying, birds were fed *ad-libitum* on layer ration containing 16 - 17% crude protein and drinking water was available at all times. Birds were reared from day old to point of lay when they were transferred to individual laying cages. The brooder house was made of sidewalls raised to the roof to enable the pens retain heat during the cold and wet season. The house was partitioned into brooding pens each of 2.3m x 3.1m and surrounded by wire netting. The growing and mating houses measured 65.5m x 7.6m. Each house was made of two wings each measuring 30.48m^2. A holding room measuring 4.6m x 7.6m separated the two wings. The houses, except the cage house, were partitioned into smaller pens. The mating house was partitioned into 40 pens per wing, each pen measuring 1.50m x 3.05m. All buildings have low sidewalls that were finished to the roof with wire meshing. The end walls to each house were to the roof (Adeyinka 1998).

3.4 DATA

Data on 4336 pullets, progeny of 144 sires and 779 dams for strain A and 4843 pullets, progeny of 158 sires and 1108 dams for strain B for six generations (1991-1995 and 2001) under selection for part-period egg production to 280 days of age were used.

The number of individuals monitored to 280 days were 1000 and 250 hens for the selection and control lines respectively. The number of hens monitored however varied from year to year and ranged from 326 – 1000 and 71 to 299 for selection and control lines, respectively, depending on factors such as hatchability and infrastructural facilities.

3.5 SELECTION PROCEDURE

Selection was based on an index, which combines information on individual production, the sire and family averages. The selection indexes were based on the method developed by Hazel (1943), Osborne (1957a,b) and Henderson (1963). The female's breeding value was predicted from her own phenotype (performance) and the average of

full and half-sisters. However, since virtually all of the traits studied are manifested in the females only, the male's breeding value was predicted from the means of his half and full sisters.

$$I_{\&} = \left(P - \overline{X}\right) + b_1\left(D - \overline{X}\right) + b_2\left(S - \overline{X}\right)$$

$$I_{\%} = b_3\left(D' - \overline{X}\right) + b_4\left(S' - \overline{X}\right)$$

Where $\overline{X}$ = Population mean for the trait

P = a candidate's female breeding phenotypic value for the trait.

D and D' = average phenotypic values for the trait of full sisters of a female and male breeding candidate, respectively.

S and S' = average phenotypic values for the trait of half sisters of a female and male breeding candidate, respectively.

b_1 , b_2 , b_3 and b_4 = regression coefficients of the trait on the index for females and males

$$b_1 = \frac{2n(1 - h^2)}{4 + (n - 2)h^2} \quad \text{and} \quad b_2 = \frac{4nd(1 - h^2)(2 - h^2)}{(4 + (n - 2)h^2)\left(4 + \left[n(d + 1) - 2\right]h^2\right)}$$

$$b_3 = \frac{nh^2}{4 + (n - 2)h^2} \quad \text{and} \quad b_4 = \frac{2ndh^2(2 - h^2)}{(4 + (n - 2)h^2)(4 + [n(d + 1) - 2]h^2)}$$

Where: d is the number of dams

n is the number of offspring per dam

h^2 is the heritability estimate

Birds within generations were hatched over 3 or more hatches. Data were corrected for hatch effect using Least Square procedures (Harvey, 1987) when hatch to which a bird belongs has significant effect on the trait being evaluated. The hatch – corrected data were then used for subsequent genetic analysis. Heritability estimate obtained was used to obtain weights b_1, b_2, b_3 and b_4 in the selection index. This procedure gave an unbiased prediction of selection response, as the index values were unbiased estimates of the animal's additive genetic values.

3.6 Data Collection

The following traits were measured:

1. Age at sexual maturity (days) (**ASM**): This was obtained by recording the age to first egg for each pullet.
2. Egg number (**EGG280 D**): Eggs laid from first egg were recorded and collected on daily basis up to 280 days of age.
3. Egg weight (gm) (**EWTAV**): This was obtained by taking the average weight of eggs at 35, 36, 37 and 38 weeks of age.
4. Body weight at maturity (gm) (**BWT40**): This was obtained by weighing the surviving hens at 40 weeks of age.

Data from hens with all the parameters measured were used in the data analysis. Likewise data from hens that produced less than ten eggs to 280days were excluded. For genetic and performance analysis, the data were edited to exclude records of dams with two offsprings per sire and sires with less than nine offsprings. This is to minimize the prediction error variance associated with the estimates. Estimates were obtained using SAS (1996) after correcting for hatch and generation/year effect.

3.7 Estimation of genetic parameters

In estimating genetic parameters (i.e. heritabilities and correlations), full model was used in computing the variance component and this was partitioned into those due to sire, dam or environment. The model fitted was of the nested or hierarchical design (Henderson 1953). In this design, each sire was mated to several dams and each mating produced several progenies.

Statistical model:

$$Y_{ijkl} = \mu + h_i + s_j + d_{(jk)i} + e_{ijkl}$$

Where Y_{ijkl} is the record of the l^{th} progeny of k^{th} dam mated to the j^{th} sire within the i^{th} hatch.

μ = the common mean.

h_i = the effect of the i^{th} hatch

s_j = the effect of the j^{th} sire

$d_{(jk)i}$ = the effect of the k^{th} dam mated to j^{th} sire within the i^{th} hatch

e_{ijkl} = the uncontrolled environmental and genetic deviations attributable to the individuals.

$$e_{ijk} = NID(0\ \sigma_e^2)$$

$$\Sigma a_i = \Sigma b_j = \Sigma s_{jk} = 0$$

The analysis of variance table is given below:

Analysis of variance

Source of Variation	Df	Sum of Squares	Means Squares	Expected Mean Squares
Between Sires	S-1	SS_S	MS_S	$\sigma_W^2 + K_2\ \sigma_D^2 + K_3\ \sigma_s^2$
Between dams within sires	D-S	SS_D	MS_D	$\sigma_W^2 + K_1\ \sigma_D^2$

Progeny within sires	N..-D	SS_W	MS_W	σ_W^2

S = Number of sires

D = Number of dams

n_i = Number of individuals within i^{th} sire

n. = Total number of individuals

K_1 = Number of dam per sire

K_2 = Number of offspring per dam

K_3 = Number of offspring per sire

3.7.1 Variance components estimation.

The variance components were estimated using **Harvey's 1990, Mixed Model Least-Squares and Maximum Likelihood (LSMLMW) method**, and **(TYPE1, Minimum variance quadratic unbiased estimation (MIVQUE), Maximum Likelihood (ML), AND Restricted Maximum Likelihood (REML) of SAS 1996** computer programme. Two algorithms were utilized for all estimation techniques sequentially adjusted sums of squares (Milliken and Johnson, 1984) for HM3 and Giesbrecht's algorithm (Giesbrecht 1983) for **ML** and **REML and MIVQUE.** The basic equations for **MIVQUE** and **REML** were:

$$\underset{(r \times r)}{\{tr(QV_1QV_1)\}} \underset{(r \times 1)}{\hat{\sigma}^2} = \underset{(r \times 1)}{[y'QV_1Qy]}$$

then $\hat{\sigma}^2 = [tr\,(QV_1QV_1)]^{-1}\ [y'QV_1Qy]$:

and for ML $\underset{(r \times r)}{[tr\,(V^{-1}V_1V^{-1}V_1)]} \underset{(r \times 1)}{\hat{\sigma}^2} = \underset{(r \times 1)}{[y'QV_1Qy]}$;

where tr is the trace operator, the sum of the diagonal elements of a matrix;

$Q = V^{-1} - V^{-1} X (X'V^{-1}X) X'V^{-1}$ for V as the dispersion matrix of y and X as the design for fixed effects; is the vector of variance component estimates and r is the number of random variables in the model.

Variance components were estimated computationally as indicated below:

$$\sigma^2_w = MS_W$$

$$\sigma^2_s = \frac{MS_S - (MS_W + k_2 * MS_D)}{k_3}$$

Where k_2 = Average number of progeny per dam

and k_3 = Average number of progeny per sire

$$k_1 = k_2 = \left(n.. - \frac{\sum_j n_{ij}^2}{n_{i.}} \right) \Big/ df(dams)$$

$$K_3 = \left(n.. - \frac{\sum_i n_{i.}^2}{n..} \right) \Big/ df(sires)$$

where : n.. = total number of progeny

n_{ij} = number of offspring of the j^{th} dam within the i^{th} sire

$n_{i.}$ = number of offspring of the i^{th} sire

$$\sigma^2_T = \sigma^2_S + \sigma^2_D + \sigma^2_w$$

Where: σ^2_T = Total variance

σ^2_S = Variance due to sire

σ^2_D = Variance due to dam

$\sigma^2_w = \sigma^2_e$ = Error variance

Variance components thus obtained were used to calculate heritabilities. The data used to estimate heritabilities were pooled after correcting for year and hatch effects so as to remove negative variances obtained when data was analyzed by year/generations. How ever other genetic estimates were obtained by year/generations.

3.7.2 Heritability Estimation

Heretability estimates were obtained using the formulae outlined below:

$h_s^2 = \frac{4 * \sigma_s^2}{\sigma_T^2}$ where h_s^2 = heritability from sire component

$h_D^2 = \frac{4 * \sigma_D^2}{\sigma_T^2}$ where h_D^2 = heritability from dam component

$h^2_{S+D} = \frac{4 * \sigma^2_{S+D}}{\sigma_T^2}$ where h^2_{S+D} = heritability from sire + dam component

3.8 PARENT - OFFSPRING REGRESSION: (Intrasire regression of offspring on dam for the estimation of heritability)

The regression of offspring on dam was done using the model below. The symbol Z was used to designate the offspring mean while the symbol Y is the record on the individual offspring and X is the dam's record.

Statistical model:

$Z_{ij} - \alpha_i = \mu + \beta(x_{ij} - \bar{x}\,..) + e_{ij}$

Z_{ij} = mean of the records of the offspring from a mating of the i^{th} sire mated to the j^{th} dam.

μ = common mean

α_i = effect of the i^{th} sire

β = regression co-efficient of Z on X

x_{ij} = record on the j^{th} dam mated to i^{th} sire.

$\bar{x}$ .. = phenotypic mean

e_{ij} = the deviation of the means of the progeny.

The regression from the sire families is pooled to obtain the common regression coefficient, β.

$$\hat{\beta} = \frac{Cov_D(X,Z)}{Var_D(X_{ij})}$$

$Var_D(X_{ij})$ = the variance of dams within sire

$h^2 = 2\beta$

3.9 ESTIMATION OF CORRELATION

The genetic, environmental and phenotypic correlation between two traits was obtained by using variance component analysis (Becker, 1975).

1. Single parent design, one way layout.

The models and procedure for analysis are the same as for estimation of heritabilities. Each trait X or Y was analysed as given for heritability estimate. In addition the analysis of covariance between X and Y was also carried out. The covariance between X and Y are given below.

Analysis of covariance between X and Y

Source of Variation	Df	Sum of Cross Products	Mean Sum of Cross Products	Expected Sum of Cross Products
Between Sires	S-1	SCP_S	MCP_S	$Cov_W + kCov_s$
Progeny within sires	n.-S	SCP_W	MCP_W	Cov_W

S = number of sires

n_i = number of individuals within the i^{th} sire.

n.. = total number of individuals.

Estimating cov_W and cov_S

$cov_W = MCP_W$

$cov_S = (MCP_S - MCP_W)/k$

k = m= number of measurements per individual

$$K = \frac{1}{N-1}\left(m. - \frac{\sum m_k^2}{m.}\right)$$

Estimating correlation.

The formulae used for estimating general, genetic, environmental and phenotypic correlations are given below:

$$r_{g_{xy}} = \frac{\text{cov}_{xy}}{\sqrt{\sigma_{s_{(x)}}^2 \sigma_{s_{(y)}}^2}}$$

where $r_{g_{xy}}$ = genetic correlation of x and y

cov_{xy} = covariance between x and y

$\sigma^2_{s(x)}$ = variance component from sire for x

$\sigma^2_{s(y)}$ = variance component from sire for y

genetic correlation from sire component of variance was obtained using the formula given below :

$$r_g = \frac{4cov_{sxy}}{2Var_{sx} * 2Var_{Sy}}$$

$$S.E \quad of \quad r_g = \frac{1 - r^2_g}{\sqrt{2}} \sqrt{\frac{S.E \quad h^2_{(x)} \quad X \quad S.E \quad h^2_{(y)}}{h^2_{(x)} \quad h^2_{(y)}}}$$

environmental correlation from sire component of variance was estimated by the formula given below :

$$r_e = \frac{cov_{wxy} + 3cov_{sxy}}{Var_{wx} - 3(Var_{Sx})(Var_{Sy}) - Var_{Sy}}$$

where Var_{wx} = variance within the character x

phenotypic correlation from sire component of variance was computed using the formula given below :

$$r_p = \frac{cov_{wxy} + cov_{sxy}}{Var_{wx} + (Var_{Sx})(Var_{Sy}) + Var_{Sy}}$$

3.10 Estimation of expected genetic progress

Expected genetic progress in one generation of selection was estimated by:
)$G = h^2 \times SD$

Where h^2 is the heritability estimate calculated using variance component analysis.

SD is the selection differential, which refers to the superiority, or inferiority of those selected for parent, (P_s), as compared to the average of the population, (P) from which the breeding animals were selected.

$$SD = \left(\overline{P}_S - \overline{P}\right)$$

Where $\overline{P}_S$ is the average of the selected individuals

$\overline{P}$ is the average of the population before selection

3.11 Estimation of expected and realized response to selection for primary trait under selection

Expected response to selection for egg production to 280 days was calculated as per Falconer and Mackay (1998) using the formula

Response (R) = $ih^2 \sigma_p$

Where

i = intensity of selection

h^2 = heritability

σ_p = phenotypic standard deviation of the trait under selection

Realised phenotypic response per generation was calculated for the selected trait by the regression of generation means on generation number.

Genetic response (G) was estimated in a manner similar to phenotypic response after correction of selected line means for control deviation, using the following formula:

$G = (S_n - C_n) - (S_0 - C_o)$

Where S and C represent selected and control lines, respectively and the subscripts represent the generations. In this manner, environmental effects between generations were corrected for since it was assumed that environment had similar effects on selected and control lines within generation.

3.12 Estimation of Realized responses:

For phenotypic response, the formula as per Falconer and Mackay (1998) was used for the estimation.

$R_p = S_t - S_0$

Where R_p is phenotypic response

S_0 is the mean of the base generation

S_t is the mean of the t^{th} generation of selection

For genetic response, the estimation was obtained using the formula according to Falconer and Mackay (1998)

$R_g = (S_t - S_0) - (C_t - C_0)$

Where R_g is the genetic response of selected lines

C_0 is the mean of base generation of control

C_t is the mean of the t^{th} generation of control

S_0 is the mean of base generation of selected line

S_t is the mean of the t^{th} generation of selected line

The genetic response per generation was estimated by regression of annual response to selection on generation number.

Regression (b) of Y and X is

$$b_{XY} = \frac{\Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n}}{\Sigma X^2 - \frac{(\Sigma X)^2}{n}} = b_{XY} = \frac{n\Sigma XY - (\Sigma X)(\Sigma Y)}{n\Sigma X^2 - (\Sigma X)^2}$$

Where :

Y = generation means either corrected or uncorrected to control deviation

X = generation number

n = number of generation

The standard error of the regression coefficient was calculated as given below

$$S.E. = \left[\Sigma Y^2 - \frac{(\Sigma Y)^2}{n}\right] - b\left[\frac{\Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n}}{(n-2)\left[\Sigma X^2 - \frac{(\Sigma X)^2}{n}\right]}\right]$$

Regression coefficient was tested for statistical significance using t-test i.e

$t=\frac{\hat{b}}{SE(\hat{b})}$ with n-2 degree of freedom where there are n pairs of observation

3.13 Selection Differential

Selection differential was calculated as the difference between the mean performance of selected individual ($\overline{P}_{XS}$) and the mean of the population before selection from which the individuals were selected ($\overline{P}_{X}$). When selection differential is divided by phenotypic standard deviation (σ_p) of the trait under selection, the standardized selection differential or selection intensity (i) is obtained.

Thus

$$i = \frac{P_{\bar{x}_s} - P_{\bar{x}}}{\sigma_P} = \frac{S}{\sigma_P}$$

The effective selection differentials were calculated by weighting each parent according to the number of offsprings they produced, that survived and contributed to the sampling variance of the next generation.

3.14 Effective population size and rate of inbreeding

Effective population size, N_e, in each parental generation for the selected group was computed as per the formula described by Wright (1931).

$$N_e = \frac{4 N_m N_f}{N_m + N_f}$$

Where

N_m = number of male parents and N_f = number of female parents

However, because of the possibility of each parent contributing unequal number of progeny, Gowe *et. al.* (1959) suggested a modified formula which included a term for variance of family size. This was achieved by weighting the number of male and female parents with their respective variance in family size. By this formula, the effective number of individuals in each parental generation was calculated for the selected group as: -

$$\frac{1}{M_e} = \frac{1}{M_e}\left(1+\frac{{\sigma_M}^2-\bar{n}_M}{{\bar{n}_M}^2}\right)$$

and

$$\frac{1}{F_e} = \frac{1}{F_e}\left(1+\frac{{\sigma_F}^2-\bar{n}_F}{{\bar{n}_F}^2}\right)$$

Where

$\bar{n}_M$ = mean number of progeny per sire

$\bar{n}_F$ = mean number of progeny per dam

σ^2_M = the variance in number of progeny per sire

σ^2_F = the variance in number of progeny per dam

For the control line N_e was estimated as

$$N_e = \frac{16N_mN_f}{3N_m+N_f}$$

Where N_m and N_F are the numbers of male and female breeders respectively.

The increase in coefficient of inbreeding per generation due to finite population size was calculated as per Wright (1931) using the following formula.

$$\Delta F = \frac{1}{8N_M}+\frac{1}{8N_F} = \frac{N_M+N_F}{8N_MN_F}$$

For the control line, inbreeding coefficient per generation was computed as suggested by Gowe *et al*. (1959) as:

CHAPTER FOUR

4.0 RESULTS

4.1 EFFECTIVE POPULATION SIZE AND INBREEDING

Tables 1 and 2 show the effective population sizes and inbreeding coefficients in the male and female lines. At 18 weeks of age, the number of pullets housed ranged between 326 and 1000 per generation for each of the population (Table 1). The average number of parents in each generation was 174 vs 187 for male and female line populations, respectively. The coefficient of inbreeding per generation was 0.005 vs 0.005 for male and female line, respectively (Table 1). For the control population (Table 2) the values of inbreeding coefficient were 0.008 vs 0.007 for the male and female lines, respectively.

4.2 MATERNAL EFFECTS

Maternal effect is assumed when the variance component from dam group is higher than that of sire component. However, when the sire component of variance is higher than dam component, then the major genes contributing to the expression of such traits are assumed to be sex linked.

Tables 3 and 4 show the extent of maternal or sex linkage effect as computed from various variance component options. In the male line, egg weight and age at sexual maturity (**ASM**) were affected by sex linkage while egg number (**EGG280D**) and body weight at 40 weeks **(BWT40)** were affected by maternal environment in the **TYPE 1** methods. It is interesting to observe the values for **ML** and **REML** were similar. However, in the female line the various estimate options gave a variety of responses. Thus, it was only egg weight average (**EWTAV**) that was influenced by maternal environment from the four methods while egg number (**EGG280D**), body weight at 40 weeks and age at sexual maturity were influenced by sex linkage across the various estimate options.

4.3 HERITABILITY ESTIMATES

Tables 5 and 6 show the heritability estimates obtained from various variance component estimation methods and daughter - dam regression for male and female lines respectively. The results show that the standard error associated with the parameter (heritability) estimates was considerably lower than the heritability obtained, indicating the reliability of the estimates.

The results obtained from various SAS methods (**TYPE1, MIVQUE, ML, REML)** were also presented (Tables 5 and 6). It was observed that the heritability values obtained from the various methods employed were close to one another. Where the variance components were calculated to be negative, the component was set at zero and so no heritability estimate was obtained. It is important to note that when estimates were made per generation, predominantly negative estimates were obtained but this situation was reversed when estimates were based on pooled data after correcting for year and hatch effect. Almost in all cases estimates from sire component were lower than those obtained from the dam component.

4 .4 GENETIC CORRELATION

Tables 7- 14 show the genetic correlation of egg number with other traits for male and female lines, respectively. Egg number was consistently highly negatively correlated with age at sexual maturity, being higher than -0.60 in most cases.

Egg number was also highly negatively correlated with mature egg weight when r_g was obtained using sire component of variance in the earlier generations for both male and female lines. In the female line, genetic correlation values could not be given for two generations 4 and 5, as they were not estimated from dam component of variance. However, the standard errors associated with some of the estimates were higher than the actual parameter estimates.

4.5 GENETIC AND NON - GENETIC ESTIMATES USING ONE WAY ANALYSIS OF VARIANCE MODELS

Tables 13 and 14 showed genetic, phenotypic and environmental correlations of various traits with egg number using sire components of variance. The r_g, r_p and r_e between egg number and **ASM** were negative and generally high throughout the period under study for both male and female lines.

The r_g and r_e of egg number with egg weight were negative during the first two-generations. Phenotypic correlations were consistently negative and low throughout for **ASM** and **EWTAV** in the male and female lines. The r_e was negative for **ASM** and **EWTAV** and positive for **BWT40** in the male line and female line, respectively.

4.6 SELECTION DIFFERENTIAL

Table 15 shows the selection differential, standard deviation and selection intensity for egg number to 280 days. Selection differential of 6.80 vs 5.67 for male and female lines, respectively were obtained in the 5^{th} generation. The average of the selection differential over the five generations was 11.44 vs 11.63 eggs for male and female lines respectively.

The standard deviations for egg production in both male and female lines were 12.65 vs 16.72 while the average over the five-year period was 14.73 vs 14.53 for male and female lines respectively. The values of selection intensity were low for generation 5 in both male and female lines (0.46 vs 0.42) respectively. On the whole, the average standardised selection differential (selection intensity) was 0.78 vs 0.80 for male and female lines, respectively.

4.7 RESPONSES OF EGG NUMBER (PRIMARY TRAIT) TO SELECTION

Tables 16 and 17 show the average performance by generation, population, traits, genetic and phenotypic change in the male and female lines while table 18 shows realised response and predicted gain for egg production to 280 days of age. There was improvement in all traits measured in both the male and female lines in relation to the appropriate controls.

However there was little or no response to selection for egg number in the male line when compared to the female line. The phenotypic response was only 0.19 per generation while the genotypic response was 0.42. The female line population showed a much higher positive response to selection for egg number than the male line. The phenotypic and genotypic responses were 1. 67 and 3.1 for eggs per generation respectively. (Table17). Variable responses were obtained for **ASM, EWTAV** and **BWT40** in both the male and female lines.

4.8 CORRELATED RESPONSES

Table 19 shows the expected response to selection in age at sexual maturity as a result of direct selection on increase in egg production to 280 days of age. There was a decrease of about 2 days per generation in age at sexual maturity. The expected improvement in egg weight was slightly higher than zero in both lines. The expected gains per generation for **BWT40** were 8.23 and 16.61gms for the male and female lines, respectively.

Table 1: Effective number of sires, dams and parents and expected level of inbreeding in the selected population

Line	Gen	No. of females tested	Nm	N_f	Effective parents		Inbreeding)F
					Ne Wright	Ne (Gowe)	
Male	1	696	34	148	110.6	185.0	0.0045
	2	979	27	180	92.9	192.0	0.0053
	3	917	28	188	97.5	194.9	0.0051
	4	803	27	142	90.7	161.6	0.0055
	5	941	28	121	91.0	137.6	0.0055
	6	326	28	192	97.7	-	0.0051
	Average	775.5	28.7	161.8	96.7	174.2	0.0052
	Cumulative)F						0.0259
Female	1	845	35	234	121.8	243.0	0.0041
	2	1000	31	235	109.5	256.9	0.0046
	3	1000	31	224	108.9	202.9	0.0046
	4	998	28	206	98.6	82.3	0.0051
	5	1000	33	209	114.0	150.2	0.0044
	6	341	28	198	98.1	-	0.0051
	Average	864	31	217.7	110.6	187.9	0.0046
	Cumulative) F						0.0228

Table 2: Effective No of sires, dams, parents and expected level of inbreeding in the Control population

Line	Gen	Pop Size	Nm	N_f	Effective Parents (Wright)	)F
Male	1	170	13	130	160.0	0.0079
	2	110	11	115	136.7	0.0088
	3	289	14	94	154.8	0.0070
	4	207	14	95	155.3	0.0070
	5	105	12	61	120.7	0.0083
	6	167	12	80	132.4	0.0082
Average		174.6	12.6	95.8	143.3	0.0079
Cumulative)F						0.0472
Female	1	141	17	146	201.6	0.0057
	2	256	13	80	139.8	0.0076
	3	256	15	96	163.4	0.0067
	4	299	14	130	169.3	0.0074
	5	71	13	37	101.3	0.0080
	6	198	12	85	134.9	0.0082
Average		203.5	14	95.7	151.7	0.0073
Cumulative)F						0.0436

Table 3: Maternal Effect or Sex Linkage in the Male Line

	VARIANCE	COMPONENTS		
OPTION	EGG280D	BWT40	ASM	EWTAV
TYPE1				
VAR_S	3.29	1438.37	56.33	0.39
VAR_D	15.23	2472.75	0	0.03
VAR_E	54.49	17294.14	284.5	5.96
VAR_T	73.49	21205.26	340.83	6.38
MIVQUE				
VAR_S	3.25	1896.22	21.40	0.25
VAR_D	5.73	0	0	0
VAR_E	50.66	17434.09	289.6	5.49
VAR_T	59.64	19330.31	311.0	5.74
ML				
VAR_S	2.74	1460.8	49.72	0.29
VAR_D	5.47	0	0	0
VAR_E	51.82	17702.8	262.19	5.62
VAR_T	60.03	19163.6	311.91	5.91
REML				
VAR_S	2.83	1460.8	51.20	0.30
VAR_D	5.47	0	0	0
VAR_E	51.82	17704.9	261.95	5.62
VAR_T	60.03	19163.6	313.15	5.92

VAR_S = variance component due to sire

VAR_D = variance component due to dam

VAR_E = variance component due to error

VAR_T = Total variance component

Table 4: Maternal Effect or sex linkage in the Female Line

	VARIANCE	COMPONENTS		
OPTION	EGG280D	BWT40	ASM	EWTAV
TYPE1				
VAR_S	3.54	2516.24	9.88	0.25
VAR_D	16.54	7798.78	0	1.72
VAR_E	51.03	34013.39	220.49	5.89
VAR_T	73.11	44328.41	230.37	7.86
MIVQUE				
VAR_S	3.62	2003.82	10.12	0.15
VAR_D	6.07	0	3.24	0.23
VAR_E	46.78	27994.44	196.16	5.27
VAR_T	56.47	29998.26	209.52	5.69
ML				
VAR_S	3.15	1655.7	8.24	0.15
VAR_D	3.05	0	0.53	0.18
VAR_E	48.40	27435.7	197.5	5.48
VAR_T	54.60	29091.4	206.27	5.81
REML				
VAR_S	3.22	1693.9	8.47	0.16
VAR_D	3.05	0	0.53	0.19
VAR_E	48.41	29443.2	197.52	5.48
VAR_T	54.68	31137.1	206.52	5.83

VAR_S = variance component due to sire

VAR_D = variance component due to dam

VAR_E = variance component due to error

VAR_T = Total variance component

Table 5: Heritability estimates from various methods the for male Line

		VARIABLES			
METHOD		Egg280d±S.E	Bwt40±S.E	ASM±S.E	Ewtav±S.E
TYPE1	h^2_S	0.180±0.07	0.270±0.13	0.660±0.08	0.250±0.02
	h^2_d	0.830±0.07	0.470±0.13	NA	0.019±0.02
	h^2_{S+D}	0.850± 0.07	0.490±0.13	NA	0.300±0.02
MIVQUE	h^2_S	0.220±0.06	0.390±0.14	0.280±0.02	0.170±0.01
	h^2_d	0.380±0.06	NA	NA	NA
	h^2_{S+D}	0.480+0.06	NA	NA	NA
ML	h^2_S	0.180±0.04	0.310±0.13	0.640±0.02	0.200±0.02
	h^2_d	0.360±0.04	NA	NA	NA
	h^2_{S+D}	0.450±0.06	NA	NA	NA
REML	h^2_S	0.190±0.04	0.310±0.13	0.650±0.02	0.200±0.02
	h^2_d	0.360±0.04	NA	NA	NA
	h^2_{S+D}	0.490+0.04	NA	NA	NA
HARVEY	h^2_S	0.130+0.05	0.070±0.04	0.150±0.05	0.240±0.06
	h^2_d	0.160±0.07	0.180±0.07	0.200±0.07	0.200±0.07
	h^2_{S+D}	0.150±0.03	0.160±0.03	0.180±0.04	0.240±0.04
DAUGTHER/DAM REGRESSION	h^2	0.050±0.03	0.270±0.05	0.190±0.04	0.280±0.06

Table 6: Heritability estimates from various methods for the female Line

		VARIABLES			
METHOD		Egg280d ±S.E	Bwt40 ±S.E	ASM±S.E	Ewtav±S.E
TYPE1	h^2_S	0.190±0.06	0.230±0.16	0.170±0.01	0.170±0.02
	h^2_d	0.910±0.06	0.700±0.16	NA	0.880±0.02
	h^2_{S+D}	0.980±0.06	0.680±0.16	NA	0.720±0.02
MIVQUE	h^2_S	0.260±0.06	0.270±0.14	0.190±0.03	0.110±0.01
	h^2_d	0.430±0.06	NA	0.060±0.03	0.160±0.01
	h^2_{S+D}	0.400±06	NA	0.200±0.03	0.180±0.01
ML	h^2_S	0.230±0.01	0.230±0.15	0.160±0.01	0.100±0.02
	h^2_d	0.220±0.01	NA	0.010±0.01	0.120±0.02
	h^2_{S+D}	0.280+0.01	NA	0.150±0.01	0.130±0.02
REML	h^2_S	0.240±0.01	0.220±0.15	0.160±0.01	0.110±0.02
	h^2_d	0.220±0.01	NA	0.010±0.01	0.120±0.02
	h^2_{S+D}	0.250±0.01	NA	0.140±0.01	0.160±0.02
HARVEY	h^2_S	0.230±0.04	0.270±0.04	0.020±0.04	0.340±0.05
	h^2_d	0.180±0.08	0.250±0.07	0.230±0.07	0.250±0.05
	h^2_{S+D}	0.160±0.03	0.210±0,03	0.200±0.04	0.290±0.04
DAUGTHER/DAM REGRESSION	h^2	0.250±0.04	0.200±0.05	0.190±0.07	0.270+0.05

Table 7: Genetic Correlation (± SE) of egg number with other traits by year from sire component in the Male Line

Generation	BWT40	ASM	EWTAV
1	0.64±0.31	-0.88±0.58	-0.42±0.36
2	-0.01±0.22	-0.70±0.38	-0.46±0.21
3	0.08±0.47	-0.96±0.55	- 0.56±0.37
4	0.77±0.22	0.07±0.42	-0.58±0.37
5	0.32±0.95	NA	0.10±0.43

Table 8: Genetic Correlation (± SE) of egg number with other traits by year from dam component in the male Line

Generation	BWT40	ASM	EWTAV
1	0.18±0.46	-0.66±0.79	NA
2	0.82±0.63	-0.34± 1.00	-0.32±0.86
3	-0.39±0.58	-0.59±0.96	-0.30±0.49
4	0.77±0.22	-0.77±1.1	-0.42±0.48
5	0.42±0.48	NA	-0.20±0.54

NA = Not Available

Table 9: Genetic Correlation (± SE) of egg number with other traits by year in the male Line from Sire + Dam components of variance

Generation	BWT40	ASM	EWTAV
1	0.35±0.23	-0.73±0.34	-0.67±0.39
2	0.24±0.16	-0.51±0.33	-0.43±0.20
3	0 .27±0.29	-0.72±0.40	-0.40±0.24
4	-0.25±0.21	NA	-0.58±0.37
5	0.35± 0.27	NA	-0.09±0.27

NA = Not Available

Table 10: Genetic Correlation (± SE) of egg number with other traits by year from sire component in the female Line

Generation	BWT40	ASM	EWTAV
1	0.12±0.40	-0.71±0.47	-0.55±0.38
2	0.20±0.28	NA	-0.58±0.26
3	0.77±0.28	0.76±0.29	-0.06±0.30
4	0.07±0.33	-0.99±0.25	-0.58±0.25
5	0.01+0.60	NA	-0.69±0.78

NA = Not Available

Table 11: Genetic Correlation (± SE) of egg number with other traits by year from dam component in the female Line

Generation	BWT40	ASM	EWTAV
1	0.86±0.40	-0.85±0.33	-0.45±0.38
2	-0.74±0.46	-0.47±1.1	-0.42±0.47
3	0.18±0.40	-0.37±0.81	-0.98±0.67
4	0.07±0.28	NA	NA
5	NA	NA	NA

NA = not available

Table 12: Genetic Correlation (± SE) of egg number with other traits by year in the female Line from Sire + Dam component of variance

Generation	BWT40	ASM	EWTAV
1	0.34+0.34	-0.77±0.44	-0.52+0.47
2	-0.41+0.17	-0.75±0.40	-0.68± 0.54
3	0.38±0.20	-0.64±0.35	-0.58±0.34
4	0.41+0.32	-0.55±0.37	NA
5	0.24+0.50	NA	NA

NA = not available

Table 13: Genetic, Phenotypic and Environmental correlation of egg number with other traits by generation in the male line from one way analysis

TRAIT	SOURCE	Generation				
		1	2	3	4	5
ASM	r_g	-0.73	-0.51	-0.72	-0.63	-0.56
	r_p	-0.67	-0.58	-0.68	-0.65	NA
	r_e	-0.66	-0.61	-0.68	-0.56	-0.30
EWTAV	r_g	-0.67	-0.43	-0.40	-0.58	-0.09
	r_p	-0.14	-0.13	-0.17	-0.03	-0.05
	r_e	-0.01	-0.02	-0.43	-0.08	-0.04
BWT40	r_g	0.35	0.24	0.27	-0.25	0.35
	r_p	0.20	0.17	0.15	0.04	0.10
	r_e	0.14	0.15	0.12	0.06	-0.02

r_g = genetic correlation

r_p = phenotypic correlation

r_e= environmental correlation

Table 14: Genetic, Phenotypic and Environmental correlation of egg number with other traits by generation in the female line from one way analysis

TRAIT	SOURCE	Generation 1	2	3	4	5
ASM	r_g	-0.77	-0.75	-0.64	-0.55	-0.55
	r_p	-0.67	-0.63	-0.63	-0.64	-0.64
	r_e	-0.63	-0.62	-0.63	-0.67	-0.67
EWTAV	r_g	-0.12	-0.44	-0.37	-0.06	-0.11
	r_p	-0.08	-0.63	-0.05	-0.03	-0.01
	r_e	-0.07	-0.62	-0.08	-0.07	-0.12
BWT40	r_g	0.34	-0.41	0.38	0.41	0.24
	r_p	0.20	0.15	0.24	0.12	0.19
	r_e	0.16	0.41	0.19	0.07	0.18

r_g = genetic correlation

r_p = phenotypic correlation

r_e= environmental correlation

Table 15: Selection Differential of egg number to 280 days of age

GEN	MALE LINE					FEMALE LINE				
	Whole Population	Selected Population	♠	σ	♠/σ	Whole Population	Selected Population	♠	Φ	♠/σ
1	35.34	48.06	12.72	15.43	0.824368	30.79	44.31	13.52	14.96	0.903748
2	35.25	50.74	15.49	16.72	0.926435	30.74	47.41	16.67	16.31	0.022072
3	27.99	38.38	10.39	12.65	0.821344	25.24	37.03	11.79	13.12	0.898628
4	39.15	50.94	11.79	14.11	0.835578	40.74	51.25	10.51	14.73	0.71351
5	34.67	41.47	6.80	14.74	0.46133	31.70	37.37	5.67	13.51	0.419689
Average			11.44	14.73				11.63	14.53	
♠/σ			0.778						0.80	

♠ = Selection differential

σ = Standard deviation

♠/σ = Selection intensity

Table 16: Average performance by generation, population, traits, and phenotypic and genetic change of the male line

		Generation						
Traits	Pop	1	2	3	4	5	b_p	b_g
Egg280D[a]	Whole[1]	35.34±15.43	35.25±16.72	27.99±12.65	39.15±14.11	34.67±14.74	0.19	
	Selected[2]	48.06±10.87	50.74±11.50	38.38±10.16	50.94±8.53	41.47±11.78		0.42
	Control[3]	34.18±14.36	35.56±16.63	25.38±13.37	39.49±15.83	35.63±13.50	-10.8	
ASM[b]	Whole[1]	203.13±18.55	207.73±22.09	222.34±18.57	214.08±17.29	212.33±22.58	2.95	
	Selected[2]	194.42±12.97	195.44±16.62	212.33±15.55	207.72±10.92	207.21±14.12		-0.21
	Control[3]	200.55±15.60	205.77±20.06	221.31±20.60	212.54±14.39	210.61±13.74	7.65	
Egg wt[c]	Whole[1]	55.99±4.24	54.88±3.65	55.97±4.08	55.92±4.62	48.29±3.69	-1.13	
	Selected[2]	55.61±4.09	54.39±3.25	55.93±3.92	55.66±4.20	48.16±3.64		-0.43
	Control[3]	55.61±4.43	54.65±3.82	54.45±4.76	56.25±0.94	50.6±3.13	0.55	
BWT40[d]	Whole[1]	1559.6±183.01	1726±213.30	1659.2±229.64	1708.4±223.29	1466±200.00	-12.18	
	Selected[2]	1601.5±188.32	1754.8±216.65	1687.5±229.87	1723.8±221.99	1600±228.00		34.45
	Control[3]	1685.7±223.86	1687.6±189.55	1704.9±177.14	1659.8±252.56	1430±192.63	-0.54	

[1]Whole = population before outstanding producers were selected
[2]Selected = Population of the selected group
[3]Control = Population of the control group
a Egg number to 280days
b Age at sexual maturity
c Matured egg weight
d Body weight at 40 weeks of age
Pop = population
b_p = phenotypic change
b_g = genetic change

Table 17: Average performance by generation, population, traits, and phenotypic and genetic change of the female line

Traits	Pop	Generation 1	2	3	4	5	b_p	b_g
Egg280D[a]	Whole[1]	30.79±14.96	30.74±16.31	25.34±13.12	40.74±14.73	31.70±13.51	1.67	
	Selected[2]	44.31±9.77	47.41±10.19	37.03±9.68	51.25±10.37	37.37±10.20		3.14
	Control[3]	38.31±13.33	28.37±17.02	19.94±11.13	34.39±14.87	25.52±11.20	0.68	
ASM[b]	Whole[1]	208.49±28.64	218.26±21.01	224.14±16.8	212.23±10.78	217.41±19.93	1.01	
	Selected[2]	197.56±12.91	203.58±12.78	214.52±17.24	206.98±8.862	207.22±9.12		-3.92
	Control[3]	201.48±1474	202.84±19.25	237.35±20.23	215.4±13.15	220.74±10.64	7.71	
Egg wt[c]	Whole[1]	43.35±17.27	55.73±3.71	55.64±4.26	54.85±4.36	48.86±3.46	-1.21	
	Selected[2]	54.17±9.77	55.11±3.57	54.87±3.84	54.63±4.8	48.91±3.19		-0.89
	Control[3]	48.72±13.77	54.83±5.66	54.8±5.92	55.03±3.73	49.24±3.42	0.03	
BWT40[d]	Whole[1]	1603.5±192.66	1777.2±218.81	1834.3±300.39	1703.2±288.48	1414.73±248.63	-28.6	
	Selected[2]	1607.7±182.72	1808.6±209.87	1908.8±282.08	1722.8±266.14	1440.00±228.00		6.12
	Control[3]	1615.5±198.91	1667.9±209.63	1687±194.56	1614.7±256.37	1446.00±180.00	-0.52	

[1]Whole = population before outstanding producers were selected
[2]Selected = Population of the selected group
[3]Control = Population of the control group
a Egg number to 280days
b Age at sexual maturity
c Matured egg weight
d Body weight at 40 weeks of age
Pop = population
b_p = phenotypic change
b_g = genetic change

Table 18: Realised Response and Predicted Gain for egg production up to 280 days

LINE	GEN	GENETIC RESPONSE	PREDICTED GAIN	REALISED/ PREDICTED RATIO
Male Line	1	1.16	3.05	0.38
	2	0.31	3.71	0.08
	3	2.61	1.45	1.79
	4	0.00	2.36	0.00
	5	0.96	2.45	0.39
Female line	1	0.00	5.14	0.00
	2	2.37	6.17	0.38
	3	5.30	3.77	1.40
	4	6.35	2.00	3.18
	5	6.18	0.85	7.27

Table 19: The expected correlated response E(CR) in trait from selection for egg production to 280 days

Correlated response i	LINE	h^2_x	h^2_i	r_g	*	σ	$E(CR)_I$
ASM d	Sire	0.15	0.27	-0.75	0.78	19.82	-2.33
	Dam	0.16	0.17	-0.85	0.80	19.43	-2.17
Egg wt.g	Sire	0.15	0.29	-0.04	0.78	4.06	0.22
	Dam	0.16	0.28	0.33	0.80	6.61	0.01
Body wt.g	Sire	0.15	0.25	0.23	0.78	269.85	8.23
	Dam	0.16	0.25	0.02	0.80	298.07	16.61

x = primary trait
* = Intensity of selection
σ = Standard deviation
i = correlated trait
r_g = genetic correlation

CHAPTER FIVE

5.0 DISCUSSION

5.1 EFFECTIVE POPULATION AND INBREEDING

The small number of effective parents in each generation averaging about 175 probably caused the average of 0.5% inbreeding per generation in each population. Nordskorg *et al.* (1974) reported an average inbreeding coefficient of 0.13 over seven generations of selection, which is higher than the value of 0.005 obtained in the present study. The effective number (160) reported by Nordskorg *et al.,* (1974) however, was considerably lower than the 174 and 188 obtained in the population being considered in this study. Although, it is generally recommended that, the rate of inbreeding in chickens be kept at a level lower than 1% (Morris and Pollot, 1997), Nomura *et al*. (2001 and 2002) obtained values higher than this critical level without blunting genetic gains over 15 generations. Burrow (1993) stated that in the absence of inbreeding, selection is an effective tool in the improvement of most economic traits of importance to the livestock breeder. It is however possible that, in closed populations, inbreeding depression may overwhelm the positive responses from selection resulting in zero gain in performance. This is due largely to limited population size and reduction in genetic variability. The higher the effective population size, the lower the expected inbreeding depression. Rates of inbreeding are largely inflated in selected populations of the reduced, effective population size. Inbreeding reduces genetic variability, vigour and reproductive performance and increases the probability of fixation of unfavourable genes. In recent years, various methods have been proposed to reduce the rate of inbreeding in selection programmes while keeping genetic gains at the same level (Nomura *et al*. 2002). These methods assume various selection and mating strategies. For example, a reduction in the weight on family mean in index selection (Toro and Perez-Enciso, 1990), for weighted ancestral Mendelian sampling estimates (Grundy *et al*. 1998) and limited use of selected parents (Toro and Nieto, 1984: Wei 1995) have been shown to be efficient methods. Other

methods include non – random mating of selected parents, such as factorial mating designs (Woolliams 1989), minimum co- ancestry mating (Toro *et al*. 1988) and compensatory mating (Santiago and Caballero, 1995). Among these, minimum co ancestry mating is a simple and intuitively appealing method, since it directly aims at minimizing the average inbreeding of progeny. All the methods for reducing inbreeding in selection programmes have been tested in simulated populations but in most of the studies, selection on single traits has been assumed. In studies conducted in beef cattle (McNeil et *al*. 1992), dairy cattle (Ahmad *et al*. 1974) and sheep (Erasmus *et al*. 1991) it was concluded that inbreeding had no appreciable influence on selection response. Burrow (1993) however categorically maintained that under mild levels of inbreeding, selection is an effective tool in improving performance in heritable traits.

These findings tend to agree with the situation in this study where though there is an average inbreeding co-efficient of 0.005 (0.5%) over a period of six generations it has not diminished the gains of selection. It is however pertinent to note that there is an increasing trend in the inbreeding co-efficient per generation in this study population. This calls for a measure to widen the genetic base of the population to avoid selection plateau in due course. This could be achieved by introducing additional egg line to the breeding population.

5.2 SELECTION RESPONSE

The increases of 1.67 and 0.19 eggs per year in both female and male lines, respectively are similar to those reported by Gowe *et al*. (1959), Johari, *et al*. (1989), Gowe and Fairful, (1986), Poggenpoel (1987) and Lie (1988). However, when the mean of the selected line was adjusted by subtracting the mean of the appropriate control within a generation, the resulting genetic response was high in the female line but not in the male line. The responses observed were variable from generation to generation. Dickerson (1955, 1961, 1963) discussed the issues of variable response to continued selection for egg

production and concluded that they could be due to genetic 'slippage' which was due to fluctuating yearly environmental trend, negative genetic correlations between components of performance and random loss of useful genes by inbreeding.

Genetic slippage, he remarked was as a result of selection being mainly directed towards non-additive genetic effects of over dominance, which dissipates in the next generation. However slippage was not a problem in this work as selection was directed towards a single trait of egg number to 280 days. Inbreeding could possibly have reduced the actual genetic gains but it is expected that this would be offset by increase in selection efficiency from Osborne's index selection over mass selection used in this study.

The lack of response observed in the male line population selected over the generations is not unusual. Nordskog *et al.* (1974) reported a non-statistically detectable response in egg production in two breeds of chicken selected for increase in rate of egg production in the male line. They found no appreciable response in their White Leghorn selected for part year rate of lay until the 8th generation.

In both male and female line populations in this study, there was positive response in egg number over six generations. These values represented the phenotypic response of egg number to five generations of selection. After correction for environmental effect using the random bred control population, the response became reduced for the male line while the magnitude of the response was increased in the female line. The value of 3.1 eggs reported for the female line population in this study was higher than those reported by Johari *et al.* (1989) and Lie (1988) for the White Leghorn population. Liljedahl *et al.* (1979) however reported higher response of 4.4 - 6.2 eggs per generation in a selection experiment covering a similar period.

The magnitude of response in the female line population can probably be attributed to reduced age at sexual maturity. This is supported by the findings of Lijedahl and Weyde, (1980) who reported that over four generations of selection, age at sexual maturity contributed 50 and 80% response to selection.

5.3 CORRELATED RESPONSES

The actual responses in age at first egg in the male and female lines were -0.21 and -3.92 days respectively. These values are expected because as age at first egg is reducing, egg numbers to 280 days of age is increased. The genes that are responsible for increase in egg production are likely to cause a reduction in age at first egg. Therefore as the frequency of genes responsible for improved egg production increased, there was corresponding increase in those that cause reduction in age at first egg. The value of -3.92 days per generation obtained in this study is similar to that reported by Brah and Dev, (1987) in four populations of chickens. It can be concluded that the reduction in the age at sexual maturity per generation improved the number of eggs.

Egg weight was negatively correlated with egg number to 280 days of age in both male and female lines with the magnitude of these values being higher in the female line than in the male line (- 0.89 vs -0.43 per generation). These values are higher than those reported by Kolstad (1980). The reduction in egg weight as the egg number increased per generation was expected in view of the negative genetic correlation between egg number and weight. The explanation for this could be that the same genes responsible for improving egg number caused reduction in egg weight.

There was an increase in body weight of 34g per generation in the male and 6.12g in the female line. Kolstad (1980) reported gains of 11.8g per year in body weight similar to what was obtained in this study. The seemingly better response in the female line in terms of egg number could perhaps be due to the fact that originally, the line was selected for high egg number while the male line was for increased body weight and egg weight. Consequently egg production and of course, selection response to high egg number would naturally not be as high in the male line as compared to the female line.

In general, selection seems to be more effective in improving egg production of the female line population as compared to the male line The overall selection response of 3.14

eggs per generation in female line was similar in magnitude to 1.4-1.8 egg per generation (year) over 17-18 years of selection reported by Gowe (1977). The result of the male line population in this study is similar to those reported by Nordskog *et al*. (1974), in the White Leghorn line selected for part record rate of lay that no appreciable response occurs after the 8th of 11 generations of selection. Poggenpoel and Erasmus, (1978) reported a response of 3.3 eggs per generation over 17 generations.

In the female line, the gain in egg number is a joint effect of a reduction in age at first egg and increase in laying persistency. In the present study, one could conclude that the gain in egg number up to a certain age was determined mainly by age at first egg. Bohren (1970) however suggested that selection pressure should be placed on percent egg production measured from first egg to a certain date rather than on egg number to a certain date. This is because the hens that started laying late but with high persistency of egg production would have a better chance of being selected as parents of the next generation.

5.4 GENETIC CORRELATION

The estimates over five generations ranged from -0.70±0.38 to 0.82±0.42 vs -0.71±0.47 to 0.76± 0.29 for male and female lines, respectively. The correlation between egg number and egg weight was small and not significantly different. This is an indication that in the two populations under selection, an increase in the number of eggs does not have any appreciable depression on egg weight. The independent culling level applied against egg weight could have been responsible for the non-significant correlation between egg number and egg weight. The value of more than 80% of total variance in all traits across methods that could not be attributable to either sire or dam effects in this study was similar to that reported by Van Vleck *et al.* (1963).

The pooled estimates of genetic correlation over five years of body weight with egg number range from - 0.25 to 0.35 vs - 0.41 to 0.41 in the male and female line respectively when estimates were obtained from sire + dam component of variance. However the

estimates varied from generation to generation and depended on whether dam or sire components of variances were used.

Sires of hens were more accurately identified than the dam as chicks can cross from one compartment to another within a pedigree-hatching tray belonging to one sire. The effect of such crossing is that a number of chicks could be wrongly ascribed to a dam different from her true mother. It is almost impossible however for a chick to cross from one hatching tray to another as the hatching trays were covered and stacked one upon the other. Hence sires of chicks were more accurately identified. This probably is responsible for an improvement in the correlation estimates using sire information.

5.5 HERITABILITY ESTIMATE

The results obtained from different SAS methods (**TYPE1, MIVQUE, ML** and **REML**), Harvey's method and Daughter – Dam regression method showed that the estimates were close to one another. There appear therefore to be little differences in the efficiencies of the methods used in the estimation of variance components and hence the heritability. The very low values obtained both for the metric and reproductive parameters measured could be due to environmental variance. Where variance components were calculated to be negative, the component was set at zero and hence heritability estimates were not obtained. The heritability estimates from the dam component were in most cases, higher than those from the sire component for most traits, which is an indication of the existence of dominance deviations (non – additive genetic effects) and or maternal effects. This agrees with the observation of Jerome *et al*. (1956) but at variance with those by Barua (1983) and Mohapatra *et al.* (1971) who obtained lower heritabilities from dam components of variance than sire components. Osborne (1953) was of the view that when the heritability from the dam component of variance is lower than sire component, then sex linkage effect can be assumed.

Heritability estimates obtained in this study for egg number is high enough to justify putting considerably more emphasis on individual record. An increase in genetic progress could be expected from the greatest selection intensity possible. The h^2 for Egg280 D in the female line population was similar in magnitude to that obtained by Sorensen *et al.* (1980) and Kinney (1969). The h^2 estimates for age at sexual maturity, body weight at 40 weeks of age and egg weight at maturity were lower than those of Kolstad (1980) Kinney (1969), Sorensen *et al.* (1980), Atkare and Khan, (1988) and Krishna and Chaudhary, (1986). The lower value of h^2 estimates obtained in this study was probably due to large environmental component of variance, which increased the denominator, thereby reducing the resulting h^2 estimates.

Heritability estimates from regression of offspring on parent are usually more reliable than those based on half–sib data (Mbaga and Hill, 1997). In both methods, the observed covariance between the phenotypes of the relatives is divided by known correlation between their genotypes, i.e., the genetic relationship. Under random mating this relationship is one – half between parent and offspring and one-fourth among half – sibs. Thus the regression of offspring on parent is doubled to obtain the heritability estimate but the correlation among half – sibs is multiplied by 4. Sampling and non-random errors are thus inflated by only a factor of 2 in case of offspring – parent comparison, but by 4 with half – sib estimates. The offspring - parent method excludes the effects of environment more effectively than those based on full or half – sibs. The parents and offspring are not contemporary and are thus not subject to the same environment as may be the case with half – sibs. The regression method is not biased by selection among the parents, as is the case with the half – sib correlation method. A primary advantage of the offspring on parent regression technique is that unbiased estimates of h^2 may be obtained when the parents are selected for the trait under consideration.

It was observed that the heritabilities obtained from different variance component methods obtained through **SAS** and **Harvey's** were similar and compared favourably with

those in literature using similar methodologies (Huber *et al.* 1994; Cadena-Meneses and Castillo-Morales, 2000; Lee 2000). They were low for most of the traits and the main cause being increase in environmental variation. It is important to observe that the **Type1** method gave a very high heritability estimate from the dam component relative to other methods. This means that this option places more emphasis on the dam as a source of variation while in the other methods these variation is corrected for before estimate is made. The **Type1** method therefore tends to over estimate heritability from dam component of variance.

From the theoretical viewpoint, the maximum likelihood estimators are those which posses the best property of being Best Asymptotically Normal (BAN) (Mood *et al*. 1975). This means that maximum likelihood based estimators have a better convergence rate and attains minimum error faster. Two of the methods, which have been described, **ML** and **REML**, are forms of maximum likelihood estimations and therefore possess the same asymptotic properties for the estimation as produced by each one. It is not easy to decide between **ML** and **REML,** as there are advantages associated to both. When **REML** is applied to balanced data, it produces results, which are identical to the Analysis of Variance estimations, but it does not provide estimations of the fixed factor (Littell *et al*. 1996). It is also used where there are few observations. On the other hand, when **ML** estimations are applied to balanced data, the results obtained are not identical to those of the Variance Analysis; but **ML** provides estimates of the fixed factor, which are obviously BAN. In problems of animal breeding, the data tends to be unbalanced, with many observations, often thousands, and with many levels of factors, sometimes hundreds, with which the asymptotic properties of **ML** are strengthened, for the estimations of fixed as well as random effects. It is not advisable to use **MIVQUE** estimation due to the fact that they are the first step of the iterative process. There is no reason to stop at this first step, when the iterations can continue and **ML** or **REML** obtained. As to the choice of package to be used, **SAS** or **Harvey**, the advantages of either must be considered. The

major advantage of **SAS** is its ability to handle large unbalanced data. Its main disadvantage is that the most recent versions, which are those that include, **PROC MIXED** (Littel *et al*. 1996) require a lot of space on hard disc and in Ram memory. On the other hand, **HARVEY** does not solve some statistical problems such as inability to handle unbalanced data (data with missing values) and data must be prepared in standard (SDF) format, but it is more efficient than **SAS** for the estimation of variance components in the use of computational resources.

CHAPTER SIX

6.0 CONCLUSIONS AND RECOMMENDATIONS

6.1 CONCLUSION

From the results obtained from this study, the following conclusions are drawn:

1. Heritability estimates obtained from different procedures (**TYPE1, MIVQUE, ML** and **REML**), **Harvey's method** and **Daughter – Dam regression method** were close to one another. There appear therefore to be little differences in the efficiencies of these methods.
2. Maximum likelihood estimators were found to be more appropriate in dealing with animal breeding data as they take care of both random and fixed effects.
3. Environmental variations as measured by the random bred control population varied from year to year and affected the magnitude of the genetic parameter estimates in both strains of chickens.
4. Response to selection was improved by accuracy of selection.
5. There was a better response in the female line than in the male line for egg production to 280 days of age. In the production of commercial day old chicks, the strain that is used for the production of fertile eggs is the female line while the cocks of the male line are kept to mate with them. It is desirable that faster response be made within the female line population.
6. The genotypic response in the age at sexual maturity was highly and negatively correlated with egg production to a fixed age (i.e. 280 days of age).
7. The inbreeding level is low with efficient selection programme in place. It is however pertinent to observe that there is an increasing trend in the inbreeding co-efficient per generation.

6.2 RECOMMENDATIONS

Arising from the results obtained in this study, the following recommendations can be made:

1. Maximum likelihood approach is more appropriate in analyzing animal breeding data as they are capable of dealing with both random and fixed effects in a mixed model and are also able to handle unbalanced data.
2. Where Harvey's method is to be used in estimation, the data should be edited to remove missing points.
3. Daughter – Dam regression analysis is preferred in the estimation of heritability because sampling and non – random errors are minimized with estimates from daughter – dam regression than with half – sib estimates. Also the method excludes the effects of environment more efficiently than those based on half or full – sib methods.
4. As a result of the observed increasing trend in the inbreeding co-efficient per generation, it is recommended that the genetic base of the population be widened to avoid selection depression in due course.

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