RATES OF GENETIC GAIN FOR ALTERNATIVE INDIGENOUS CHICKEN BREEDING PROGRAMMES IN THE TROPICS

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and has not, wholly or in part, been presented in this or any other University for an award of a degree.

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Recommendation

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ABSTRACT

In-silico predictions to project the response to selection in livestock breeding programmes are done to estimate the possible genetic and economic gains. In these predictions, genetic and phenotypic parameters from various studies are used as some of the input parameters. Since parameters are affected by various factors such as sample sizes and genetic gain is a function of these parameters, the sources from which these parameters are obtained should be accounted for. Reduction of genetic variance due to selection (Bulmer effect) should also be accounted for since it reduces long-term genetic gain. Genomic selection should also be considered as it can accelerate the rate of genetic gain. There is therefore a need to consider the effect of sources of information, Bulmer effect and potential benefits of genomic selection on response to selection in indigenous chicken (IC) breeding programmes. The objective of this study was to contribute to genetic improvement of IC through estimation of pooled parameter estimates, accounting for Bulmer effect in response to selection and integration of genomic selection in IC breeding programme. The study addressed three specific areas; 1) Estimation ofpooled parameter estimates for traits of economic importance in IC breeding programme2) Estimation of Bulmer equilibrium genetic gains for a closed nucleus IC breeding programme and 3) Comparison of genetic gains for an IC breeding programme utilising genomic and conventional selection.Meta-analysis was used to compute pooled parameter estimates while deterministic computer simulation approach was used to model, estimate and evaluate Bulmer effect and response to selection.Two conventional strategies utilising pooled (CSP) and non-pooled parameters (CSN) and one genomic selection (GSS) strategies were considered in the simulation. The results demonstrate that parameters obtained through meta-analysis deviated from the ones obtained from single studies. The deviation for heritability for body weight at twenty weeks was 0.23 from the pooled value. The response to selection for CSN was 1.5 times more than response realised in CSP. The loss in genetic variances in CSN was 38% lower than that obtained in CSP. The GSS realised additional 54.5% and 60% accuracy and response to selection, respectively compared to CSP. Genomic selection had a reduced rate of inbreeding by 67.6% compared to CSP. It is concluded that use of non-pooled parameter estimates leads to over-estimation of potential response to selection and therefore pooled parameters should be used in modelling animal breeding programmes. It is also concluded that genomic selection optimises genetic gains and reduce rates of inbreeding in IC breeding programmes.

TABLE OF CONTENTS

DECLARATION AND RECOMMENDATION ii
COPYRIGHT iii
ACKNOWLEDGMENTS iv
ABSTRACT v
LIST OF TABLES x
LIST OF FIGURES xii
LIST OF ABRREVIATIONS AND ACRONYMS xiii

CHAPTER ONE 1
INTRODUCTION 1
1.1 Background 1
1.2 Statement of the problem 3
1.3 Objectives 3
    1.3.1 Overall objective 3
    1.3.2 Specific objectives 3
1.4 Research questions 3
1.5 Justification 4

CHAPTER TWO 5
LITERATURE REVIEW 5
2.1 Introduction 5
2.2 Indigenous chicken production systems 5
    2.2.1 Free range system 6
    2.2.2 Semi-intensive system 6
    2.2.3 Intensive system 6
2.3 Indigenous chicken breeding goal in Kenya 7
2.4 Simulation studies for prediction of response to selection 7
2.5 Genetic and phenotypic parameters for traits of economic importance in indigenous chicken 8
2.6 Meta-analysis 10

2.7 Previous and current genetic improvement efforts 10
2.8 Genomic selection in indigenous chicken breeding programme 11
2.9 Bulmer effect and rate of inbreeding 12

CHAPTER THREE 15

POOLED PARAMETER ESTIMATES FOR TRAITS OF ECONOMIC IMPORTANCE IN INDIGENOUS CHICKEN IN THE TROPICS 15

3.1 Introduction 15
3.2 Materials and methods 17
  3.2.1 Data and traits 17
  3.2.2 Data analysis 18
3.3 Results 20
  3.3.1 Weighted heritabilities 20
  3.3.2 Weighted correlations 24
  3.3.3 Least square analysis 31
3.4 Discussion 31
  3.4.1 Weighted heritabilities 31
  3.4.2 Weighted correlations 32
  3.4.3 Least square analysis 34
3.5 Conclusion 34

CHAPTER FOUR 35

OPTIMISATION OF RESPONSE TO SELECTION USING POOLED PARAMETER ESTIMATES AND GENOMIC SELECTION IN INDIGENOUS CHICKEN BREEDING PROGRAMMES 35

4.1 Introduction 35
4.2 Methodology 37
  4.2.1 Procedure 37
  4.2.2 The indigenous chicken breeding goals 38
  4.2.3 Genetic and phenotypic parameters 38
  4.2.4 Breeding structure and schemes 39

4.2.5 Population structure and information sources 41
4.2.6 Prediction of response to selection 41
4.2.7 Prediction of genetic and economic gain and inbreeding 42
4.3 Results 43
4.3.1 Response to selection 43
4.3.2 Genetic gains for individual traits 44
4.3.3 Nucleus size and mating ratio of males to females 44
4.4 Discussion 46
4.5 Conclusion 49

CHAPTER FIVE 51
GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS 51
5.1 Introduction 51
5.2 Methodological approaches 52
5.2.1 Estimation of pooled genetic parameters 52
5.2.2 Evaluation of genetic response 52
5.3 Design of an alternative indigenous chicken breeding programme 53
5.4 Potential challenges and sustainability of the alternative IC breeding programme 56
5.5 General Conclusions 57
5.6 Recommendations for researchers 57
5.7 Research gaps 57

REFERENCES 58

APPENDICES 78
Appendix A: SAS Output for Weighted Heritability for Body Weight at Eight Weeks for Objective One 78
Appendix B: SAS Output for Weighted Heritability for Body Weight at Twelve Weeks for Objective One 79
Appendix C: SAS Output for Weighted Heritability for Egg number at Twelve Weeks for Objective One 80

Appendix D: SelAction Outputs for Objectives Two and Three 81
Appendix E: Abstract of Published Paper on Objective One 86
Appendix F: NACOSTI Permit 87

LIST OF TABLES

Table 2.1 Genetic and phenotypic parameters for production and reproduction traits in indigenous chicken 9

Table 3.1 Number of studies used for the estimation of pooled parameter estimates for IC in the tropics 17

Table 3.2 List of traits and their abbreviations considered for estimation of pooled parameter estimates for IC in the tropics 18

Table 3.3 Weighted heritabilities (h^2), standard error (SE) and number of studies (N), between study variance, and Q statistic for body weight, egg number, reproductive effcicency and antibody response traits 22

Table 3.4 Weighted heritabilities (h^2), standard error (SE) and number of studies (N), between study variance, and Q statistic for egg weight and feed efficiency traits 23

Table 3.5 Weighted genetic (above diagonal) and phenotypic (below diagonal) correlations among body weight traits 26

Table 3.6 Weighted genetic (above diagonal) and phenotypic (below diagonal) correlations between body weight and egg traits 27

Table 3.7 Weighted genetic (above diagonal) and phenotypic correlations (below diagonal) between body weight, antibody response, egg and reproductive traits 28

Table 3.8 Weighted genetic (above diagonal) and phenotypic (above diagonal) correlations between egg weight and number traits 29

Table 3.9 Weighted genetic (above diagonal) and phenotypic (below diagonal) correlations between body weight, daily gain and feed efficiency traits 30

Table 3.10 Significant factors in the analysis of heritabilities of some traits of IC in the tropics 31

Table 4.1 Economic values (EV in US$), phenotypic variances ($\boldsymbol{\sigma}\mathbf{P2}$), heritabilities (along diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations 40

Table 4.2 Genetic gain (1US$ = KES 100), rate of inbreeding and accuracy of selection in conventional selection schemes with non-pooled (CSN), with pooled parameter estimates (CSP) and genomic selection schemes (GSS) per generation 44

Table 4.3 Genetic gain for individual traits in conventional with non-pooled (CSN), with pooled (CSP) parameter estimates and genomic selection schemes (GSS) per generation.. 44

LIST OF FIGURES

Figure 4.1 The trends for rates of genetic gain and inbreeding with increase in nucleus size in conventional breeding scheme with pooled parameter estimates (CSP) and genomic selection scheme (GSS) 45

Figure 4.2 The trends for rates of genetic gain and inbreeding with increase in mating ratio in conventional breeding scheme with pooled parameter estimates (CSP) and genomic selection scheme (GSS). 46

Figure 5.1 The nucleus population and interaction with the commercial population 55

LIST OF ABRREVIATIONS AND ACRONYMS

CS	Conventional selection
GS	Genomic selection
IC	Indigenous chicken
InCIP	Indigenous Chicken Improvement Programme
KALRO	Kenya Agricultural and Livestock Research Organization
KAPP	Kenya Agricultural Productivity Programme
NPDP	National Poultry Development Programme
NRI	Non-ruminants Research Institute

CHAPTER ONE

INTRODUCTION

1.1 Background

Kenya has a population of thirty two million birds of which 75% are indigenous chicken (IC) (Kenya National Bureau of Statistics, 2009). The IC play multiple roles in most rural households such as supply of food, income and cultural and religious roles (Ochieng *et al*., 2012; Padhi, 2016).In Kenya and other developing countries, the demand for meat and eggs from indigenous chickens is increasingand these products are preferred by consumers as they are perceived to taste better and more nutritious (Bett *et al*., 2012).

The IC are hardy, and therefore able to survive in harsh environments (Ajayi, 2010; Conan *et al*., 2012; Gebremariam *et al*., 2017) and require low levels of inputs for production and mostly left to scavenge with minimal supplementation (Kingori *et al*., 2010). Their production level, however, is low due to their low genetic potential, poor nutrition and diseases (Magothe *et al.*, 2012b). Indigenous chicken lay approximately 40-100 eggs per year in 3-4 clutches (Addisu *et al*., 2013; Atela *et al*., 2016; Yadessa *et al*., 2017) and attain an average mature body weight between 1.5 to 2.3kg for males and 1.08 to 1.7kg for femalesat 24 weeks; (Magonka *et al*., 2016; Sarker *et al*., 2014; Shahjahan *et al*., 2011). Genetic improvement for traits of economic importance can be achieved through between and within populationas there exists a high genetic diversity within and between indigenous chickens (Magothe *et al*., 2012a; Ngeno *et al*., 2014).

In Kenya, traits of economic importance for IC have been identified and their economic values estimated (Bett *et al*., 2011; Okeno*et al*.,2012). Development of the breeding goal for IC in Kenya has also been done under different production systems (Okeno *et al*., 2013). The traits in the breeding goal include egg number, egg weight, broodiness, survival rate, average daily gain, live weight, mature weight, fertility and feed intake. Previous studies have shown that IC can be improved through selection based on market driven demands (Faruque *et al*., 2015; Muasya *et al*., 2015; Niknafs *et al*., 2013). Positive genetic and monetary gains for various IC production systems have been predicted in different studies (Faruque *et al*., 2015; Okeno *et al*., 2013). This shows that improvement of different economically important traits would be profitable. In these predictions genetic and phenotypic parameters are used as some of the input parameters. Estimation of these genetic and phenotypic parameters for a particular population is usually done before they are used in evaluation of breeding programmes. In the absence of parameters from a specific population, parameters from other locations can be used (Jembere *et al*., 2017). Parameters from different locations, however, have been found to vary due to method of estimation and time of data collection among other factors (Jembere *et al*., 2017). Due to these variations, use of parameters from different locations could lead to over/under estimation of response to selection (Akanno *et al*, 2013). This presents a need for pooling of parameters across similar locations to obtain pooled parameters for estimation of genetic gains. According to de Oliveira *et al*. (2018), combination of values to be used as input parameters from different studies can ensure that they are more accurate and reliable. The amount of genetic gain that can be achieved is a function of these input parameters and is affected by other factors which include loss in genetic variance due to selection, the Bulmer effect and inbreeding (Cervantes *et al*., 2016; Nietlisbach *et al*., 2016).

Inbreeding causes inbreeding depression which leads to a reduction in performance which includes reduced ability to survive and reproduce (Curik *et al*., 2017; da Silva *et al*., 2019). Reduction in genetic variance due to selection on the other hand affects the long-term response due to selection and reduces the profitability of breeding programmes by reducing genetic variance after each selection cycle (Seyedsharifi *et al*., 2018; van Grevenhof *et al*., 2012).Prediction of response to selection should therefore account for the Bulmer effect and inbreeding since they can influence the profitability of a breeding programme (Biscarini *et al*., 2015; Martikainen *et al*., 2020). Reduction in genetic variance due to selection, the Bulmer effectand inbreeding werehowever not accounted for in prediction of response to selection in IC in Kenya in Okeno *et al*. (2013).

Increase in rates of inbreeding could be reduced by adoption of genomic selection (GS) strategy (Chu, 2019). This is because GS has the ability to generate information on Mendelian sampling term (Bonk *et al*., 2016; Santos *et al*., 2019) which makes the breeding values between siblings to be less correlated (Wolc *et al*., 2015). This allows better differentiation within families and therefore less co-selection of sibs to be used as parents for the next generation (Daetwyler *et al*., 2007). In addition to its ability to reduce rate of inbreeding in long-term selection, GS accelerates the rate of genetic gain as it increases accuracy of selection and reduces generation intervals (Chu, 2019).

1.2 Statement of the problem

Previous studies, which have evaluated potential response to selection in IC breeding programmes in Kenya, have utilised non-pooled rather than pooled parameter estimates. Loss in genetic variance due to selection, the Bulmer effect, and inbreeding was moreover not accounted for in these studies. This could result in over or under-estimation of response to selection, and therefore choice of wrong breeding goals. These evaluations have also been based only on conventional selection. The bias that can result from utilisation of non-pooled rather than pooled parameters and ignorance of loss in genetic variance and inbreeding has not been investigated. The potential of genomic selection to accelerate the rate of genetic gains and reduce rates of inbreeding in IC breeding in Kenya has also not been evaluated.

1.3 Objectives

1.3.1 Overall objective

The overall objective of this study was to contribute to genetic improvement of IC through estimation of pooled parameter estimates, accounting for Bulmer effect in response to selection and integration of genomic selection in IC breeding programme.

1.3.2 Specific objectives

i. To estimate pooled parameter estimates for traits of economic importance in an IC breeding programme
ii. To estimate Bulmer equilibrium genetic gains for a closed nucleus IC breeding programme
iii. To compare genetic gains for an IC breeding programme utilizing genomic and conventional selection

1.4 Research questions

i. What are the pooled genetic parameter estimates for traits of economic importance for an IC breeding programme?
ii. What are the Bulmer equilibrium genetic gains for a closed IC breeding programme?
iii. What are the genetic gains for an IC breeding programme utilizing genomic or conventional selection?

1.5 Justification

Use of pooled parameter estimates and accounting for the reduction in genetic variances due to selection, the Bulmer effect, and inbreeding would ensure that the expected genetic gains of alternative breeding objectives are not over or under-estimated. This would help in avoiding wrong choice of a breeding goal since it affects the returns and therefore profitability of a given breeding programme. Adoption of genomic selection would help to increase the accuracy of identifying superior individuals and selection intensities, resulting in faster rates of genetic gain, reduction or maintenance of the rates of inbreeding as well as maintenance of genetic diversity. This knowledge is therefore useful in planning, implementation and evaluation of IC breeding programmes.

CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

Indigenous chickens have been found to play significant roles in the society which include nutritional, socio-cultural and economic empowerment (Mahoro *et al*., 2017; Okeno *et al*., 2013). Meat and eggs from chickens provide high quality protein which have been found to be important for growth and maintenance of human body (Melesse, 2014). Rearing of chickens provide economic empowerment as a source of income to rural youth and women hence plays a role in poverty reduction and provision of emergency cash needs (Moges *et al*., 2010; Reta, 2009). Indigenous chickens are preferred over exotic breeds because of their unique traits. These traits include natural immunity against common diseases and hardiness and are therefore able to tolerate harsh environmental conditions and poor husbandry practices (Padhi, 2016). The poultry subsector contributes 7.8% of national GDP and 24% of the agriculture GDP (Ipara *et al*., 2019). Agriculture sector moreover, accounts for 60% of employment in Kenya (Birch, 2018).

Due to significant roles of IC in rural household and national economy, several attempts have been made in Kenya to improve their productivity. The attempts include the cockerel-pullet exchange programme, which was implemented in 1976 through the National Poultry Development Programme (NPDP) (Magothe *et al*., 2012b). The programme was terminated in 1993 with little success due to lack of understanding of the production environment under which the IC are raised and operational breeding programmes to ensure continuous supply of breeding stock to the farmers (Magothe *et al*., 2012b).To address the challenges faced in this programme and others that followed, IC production systems were characterized, traits of economic importance were identified, breeding goals were formulated and a breeding programme for IC structured (Bett *et al*., 2011; Okeno *et al*., 2012). Potential genetic and monetary gains were estimated afterwards by Okeno *et al*. (2013) using conventional selection methods under different production systems.

2.2 Indigenous chicken production systems

Indigenous chickens are mainly kept under three production systems based on the levels of input and outputs and management levels (Magothe *et al*., 2012a; Mengesha, 2012). The production systems are free range, semi-intensive and intensive(Okeno *et al*., 2013).According to

Magothe *et al*. (2012a), the choice of the production system by a farmer depends on land availability and the purpose for which the chickens are reared.

2.2.1 Free range system

Under the free range system birds are left to scavenge for food like insects, green grass and scattered grains with occasional supplementation especially during cropping seasons (Mahoro *et al*., 2017). During the night, they are confined in the farmers' houses, simple constructed houses or hand woven baskets (Malatji *et al*., 2016). It is characterized by low input–low output production, whereby there is low egg and meat production (Kingori *et al*., 2010). In this system, there are usually high mortality rates because the birds are exposed to many diseases and predators and also due to poor biosecurity measures (Haoua *et al*., 2018; Reta, 2009).There is normally no selection or controlled breeding in this system leading to high rates of inbreeding (Getu, 2014; Muchadeyi *et al*., 2009)). Free range system is mostly found in the rural areas where land is available and has been found to be the most dominant in tropical areas (Abanigbe *et al*., 2013; Moges *et al*., 2010). Scavenging chickens are mostly kept under this system with the flock size being between 1-50 chickens(Dana *et al*., 2010; Mtileni *et al*., 2012).

2.2.2 Semi-intensive system

In this system, the chickens are reared in a fenced space or enclosed gardens and fed routinely but also allowed to scavenge for some of their feeds (Mengesha, 2012;Wantasen *et al*., 2014). The chickens are supplemented with grains and food wastes with provision of water and veterinary care (Barbosa *et al*., 2005; Mahoro *et al*., 2017). This is mostly found in urban and peri-urban areas where land is limited (Getu, 2014).Local and/or exotic breeds or hybrids are mostly kept in this type of production system (Barbosa *et al*., 2005; Burgos *et al*., 2007). According to Burgos *et al*. (2007)farmers who are involved in this type of system have some knowledge on farming and marketing.

2.2.3 Intensive system

In intensive system, the birds are fully confined in constructed structures which are well equipped and they are usually provided with homemade or commercial feeds (Okeno *et al*., 2012). This system is characterised by larger flock sizes as compared to the free range or semi-intensive systems (Burgos *et al*., 2007). Due to high costs of production, it is mostly practiced in urban areas by people who are able to provide the high costs of inputs (Burgos *et al*., 2007). This system involves high costs of feeds, veterinary and housing and is usually not affordable to poor farmers (Menge *et al*., 2005).Most of the birds raised under this system are either commercial chicken (layers and broilers) or crossbreds of IC with exotic breeds (Alemneh & Getabalew, 2019; Okeno *et al*., 2013). This production system has been observed to be the least practised by farmers in most tropical countries (Haoua *et al*., 2015; Mahoro *et al*., 2017; Yusuf *et al*., 2017). After characterisation of IC production systems in Kenya (Okeno *et al*., 2012), different breeding goals were developed based on the identified traits of economic importance (Okeno *et al*., 2013).

2.3 Indigenous chicken breeding goal in Kenya

The breeding goals for IC in Kenya have already been defined (Okeno *et al*. 2013). The breeding goals were developed after identification of traits of economic importance with consultation with producers, marketers and consumers (Bett *et al*., 2011; Okeno *et al*., 2011). Three breeding goals were developed; breeding for production of both eggs and meat (ICD), and breeding for either meat (ICB) or eggs (ICL). The traits considered in the ICD breeding goal were egg number, egg weight, average daily gain, live weight, age at first egg, feed intake, fertility, hatchability, faecal egg count, and antibody response. The traits in ICL were similar to the ones in ICD but without average daily gain and live weight traits. For the ICB, the traits were similar as in ICD but selection emphasis was put on growth traits. All the breeding goals exhibited positive genetic and monetary gains. Pure line and crossbreeding alternative selection strategies were considered. There was a positive genetic gain and high profit levels for pure and crossbred lines selection in all the breeding goals indicating that within and between breed selection would be possible and profitable. The predictions for the potential genetic and monetary gains for the different breeding goals were conducted through a simulation study.

2.4 Simulation studies for prediction of response to selection

Simulation studies are done to predict an outcome of a certain treatment and avoid certain risks that could result from actual implementation of a certain experiment (Kikolski, 2017). In animal breeding, conducting simulations before performing the actual experiment is preferred because less time is needed to perform the study, and also there is no cost incurred to purchase the animals (França & Travassos, 2013; Medrano, 2010). Losses that could be incurred due to making wrong decisions are also avoided or minimised (Kikolski, 2017; Medrano, 2010). Simulations have been done to predict response to selection in different livestock species such as dairy and poultry (Ebrahimtaher *et al*. 2018; Kariuki *et al*., 2014). To perform such as studies input parameters are required which include genetic variances, heritabilities, genetic and phenotypic correlations (Ebrahimtaher *et al*., 2018).

2.5 Genetic and phenotypic parameters for traits of economic importance in indigenous chicken

The estimation of genetic and phenotypic parameter for reproductive and productive traits in IC has been done in Kenya and other tropical countries. In Kenya, different studies have been done on genetic and phenotypic parameter estimates for egg and body weights for IC (Magothe *et al*., 2006). In this study, the heritabilities for egg weight and body weight at twelve weeks were 0.98 and 0.35, respectively. In another study by Ngeno *et al*. (2013), heritabilities, genetic and phenotypic correlations between body weights were estimated. A strong genetic correlation between body weight at 16 weeks and total number of eggs has been observed (Dana, 2011). In Nigeria, Rotimi *et al*.(2016) conducted a study for heritability estimates for body weight at different ages for different ecotypes and concluded that within breed selection can be used to genetically improve IC. Genetic and phenotypic parameters for some productive and reproductive traits are presented in Table 2.1.

Table 2.1 Genetic and phenotypic parameters for production and reproduction traits in indigenous chicken

Trait 1	**h^2**	**σ_p**	**Trait 2**	**h^2**	**σ_p**	**r_g**	**r_p**	**Source**
EW1	0.20	16.97	EW30	0.56	9.93	0.81	0.41	Bahmanimehr, (2012)
BW12	0.34	105.73	BW16	0.37	125.09	0.71	0.60	Lwelamira *et al*. (2012)
BW20	0.29	272.10	BW2	0.39	-	0.82	0.79	Cahyadi *et al*. (2015)
BW1	0.56	7.98	EW1	0.20	16.97	0.51	0.10	Bahmanimehr, (2012)
Ab	0.22	1.55	BW8	0.30	57.09	-0.09	-0.05	Lwelamira*et al*. (2012)
BWFE	0.31	94.65	EN	0.17	12.93	-0.74	-0.18	Oleforuh-okoleh,(2011)
BW4	0.32	22.10	BWG4	0.77	1.57	-	-	Ogbu *et al*. (2015)
EW	0.21	3.32	EN	0.17	12.93	-0.84	-0.25	Oleforuh-okoleh, (2011)
Fertility	0.21	-	BW12	0.67	-	-0.33	-0.45	Badwi &El-karim, (2015)

EN-egg number; Ab-antibody response; BW-body weight at given weeks; EW-egg weight at given weeks; h^2 –heritability; r_g-genetic correlation; r_p-phenotypic correlation; σ_p-phenotypic standard deviation.

Genetic and phenotypic parameters have been considered only applicable in the population in which they have been estimated (Koots and Gibson 1996; Miyumo *et al*., 2018). There are challenges, however, which limit the availability of population specific parameters. These challenges include lack of performance recording or absence of certain parameters for traits of interest (Akanno *et al*., 2013; Ilatsia *et al*., 2011). This brings the need for the use of parameters from other populations. The literature estimates are, however, obtained by use of varying methods, the sample sizes that are used differ, and this leads to varied estimates which are contradictory (Akanno *et al*., 2013; Giannotti *et al*., 2005).To account for the various factors that affect the results obtained in various studies, meta-analysis can be done (Akanno *et al*., 2013). Results obtained from a meta-analysis process can be taken to be generally acceptable for application in various animal populations (Lee, 2019).

2.6 Meta-analysis

Meta-analysis is a process that is carried out to provide a summary of information derived from different but related studies(Normand, 1999). It is also done to assess the variability between different studies and reach an overall understanding of a problem (Eisend, 2017; Gurevitch *et al*., 2018). Various meta-analysis studies have been done to obtain pooled genetic and phenotypic parameters in different species such as beef cattle (de Oliveira *et al*., 2018; Giannoti *et al*., 2005), small ruminants, (Jembere *et al*., 2017; Safari *et al*., 2005) and pigs (Akanno *et al*., 2013). These studies have been done due to unavailability of some parameters for some traits in some specific animal species and also due to variability of analysis methods and sample sizes used in various locations (de Oliveira *et al*., 2018). Through meta-analysis pooled parameters are obtained which can be considered to be applicable across similar populations for prediction of potential response to selection. There have been various attempts to improve IC productivity in Kenya with the most recent one being based on the already developed breeding goals and the projected genetic gains.

2.7 Previous and current genetic improvement efforts

Genetic improvement efforts have previously been attempted through importation of exotic breeds for meat and egg production through National Poultry Development Programme(NPDP), which was later considered as uneconomical (Magothe *et al*., 2012b). The other efforts to increase farmers' income were by importation of European breeds (Rhode Island Red) to crossbreed with the IC through cockerel and pullet exchange program but also failed because the crossbred progenies could not survive in the existing environmental and management conditions (Magothe *et al*., 2012b).

The second attempt was initiated through Indigenous Chicken Improvement Program (InCIP), which was initially funded by Government of Kenya and World Bank through Kenya Agricultural Productivity Project (KAPP) in 2003 and later by European Union (EU) through African Union (AU) in 2006. The program was undertaken by Egerton University in collaboration with State Department of Animal Production, Ministry of Livestock Development and Kenya Agricultural and Livestock Research Organization (KALRO) (Okeno *et al*., 2013). In InCIP, the challenges faced in NPDP attempts to improve IC were addressed through activities such as characterization of IC production systems, development of breeding goals in consultation with actors in IC value chain and design of IC breeding programme (Bett, 2012; Okeno *et al*., 2013). The most recent attempt to improve IC through crossbreeding based on the traits of economic importance and structure designed by Okeno *et al*. (2013) was initiated in Non-Ruminants Research Institute of Kenya Agricultural and Livestock Research Organization (KALRO) (Ilatsia *et al*., 2017). In this breeding programme, pure breeding is done after which the pure breeds are crossed with two imported breeds to obtain egg, meat or dual purpose breeds. Some level of genetic improvement has been achieved and dissemination is done to the farmers through sale of unselected animals (Ilatsia *et al*., 2017).Improvement of IC by crossbreeding through conventional selection could be limited because it may take a long time for the genetic improvement to be realized in terms of egg and growth performances (Ngeno *et al*., 2014). This challenge can be overcome through adoption of genomic selection.

2.8 Genomic selection in indigenous chicken breeding programme

Genomic selection (GS)involves simultaneous selection for many markers which are found across the whole genome so that all quantitative trait loci are in linkage disequilibrium with at least one marker (Meuwissen, 2007). The major benefit of this method of selection over pedigree based method is increase in the accuracy of estimated breeding values and response to selection and use in sex limited traits and the ones measured late in life (Avendaño *et al.*, 2010; Wolc *et al*., 2016).

According to Fulton. (2012), GS can be implemented in layer and broilers breeding programmes to reduce generation intervals and improve on traits like disease resistance. In layers, it can be used to reduce the generation interval from 1 year to 6 months and the number of animals that are to be maintained in a nucleus (Wolc*et al*., 2015). Genomic selection results in reduction in the rate of inbreeding between individuals because of the ability of markers to generate information on Mendelian sampling terms (Daetwyler *et al*., 2007). This reduces the emphasis placed on family information and therefore reduction of correlations of Estimated Breeding Values among family members and co-selection of relatives. Using pure line of brown egg laying population, it has been demonstrated that, individuals selected based on genomic information outperformed the ones selected on pedigree information for 12 out of 16 traits considered which included fertility and mortality (Wolc *et al*., 2015). Application of GS requires phenotypic information and is influenced by genetic and phenotypic parameter estimates(Wang, 2011).Phenotypic performance is to be recorded for a reference population, which is also genotyped (Meuwisen *et al*., 2015). A reference population is a group of animals with phenotypes and genotypes whose relationship with the selection candidates affects accuracy of the genomic predictions (Clark *et al*. 2012). For the selection candidates, only genotypic information is needed (Meuwissen *et al*., 2015). Using the genotypes and the marker effects which have been estimated within a reference population, genomic breeding values are estimated after which selection of animals to be used as parents for the next generation is done (Eynard *et al*., 2018; Wang, 2011). Genetic and phenotypic parameters influence application of GS. This is because accuracy of selection is one of the determinants of genetic gain that can be realised in a given period of time (Mathews *et al*., 2019). Accuracy of selection depends on accuracy of estimation of marker effect and the linkage disequilibrium between the marker and causal variants (Boichard *et al*., 2016). The accuracy of marker effect estimation depends on size of reference population and the heritability of a given trait (Boichard *et al*., 2016;Zhou *et al*., 2014). The genetic correlations determine whether two traits can be improved together or not with a positive correlation indicating that increase in one trait leads to increase in the other trait (Toghiani, 2012). The response to selection that can be achieved through conventional or genomic selection strategies is affected by reduction of genetic variance, Bulmer effect and inbreeding in animal populations (Bulmer, 1971; Holt *et al*. 2005; Nietlisbach *et al*., 2016).

2.9 Bulmer effect and rate of inbreeding

Reduction in genetic variance due to selection is referred to as the Bulmer effect (Rutten *at al*., 2002). Selection of sires and dams has the effect of reducing the genetic variance, but Mendelian sampling has the effect of restoring it (Wellmann & Bennewitz, 2019). The value where both effects balance each other is the Bulmer equilibrium genetic variance. Reduction in genetic variance due to long term selection causes a reduction in the response realised in livestock breeding programmes(Van Grevenhof *et al*., 2012). It reduces the response to selection in traditional and genomic selection strategies. According to Seyedsharifi *et al*. (2018), the bias of genetic progress per generation is four times more in dairy cattle progeny testing than in GS strategies. Ignoring the Bulmer effect leads to over-estimation of the possible response and the accuracy of selection (Rutten *et al*., 2002). In a study done byWei *et al*. (1996), the cumulative response predictions without Bulmer effect tend to be higher than the ones that account for it.

Different simulation studies have evaluated the effect of Bulmer effect on response to selection in different species including beef and dairy cattle (Rosa *et al*., 2007; Seyedsharifi *et al*., 2017; Van Grevenhof *et al*., 2012).

Selection results to reduced additive genetic variance of selected parents compared to unselected individuals as the parents are selected from a group with similar breeding values. A reduction in the variances of the parents causes a reduction in the variances of the offspring because the offspring inherits half of the breeding value of each parent. The variances of the breeding value of the offspring is given by the equation below (Rutten *et al*., 2002);

$$\pm_{A}^{2} = \frac{1}{4}\pm_{A,s}^{2} + \frac{1}{4}\pm_{A,d}^{2} + \pm_{MS}^{2} \tag{1}$$

where $\pm_{A,s}^{2}$, is the additive genetic variance of the selected sires, $\pm_{A,d}^{2}$,is the additive genetic variance of the selected dams and $\pm_{MS}^{2}$ is the additive genetic variance due to Mendelian sampling.

The Mendelian sampling term is equal to half of the base generation additive genetic variance. Selection of sires and dams has the effect of reducing the genetic variance, but the Mendelian sampling has the effect of restoring it (Wellmann & Bennewitz, 2019). The value where both effects balance each other is the equilibrium genetic variance reached within approximately three generations. Accounting for Bulmer effect is important when comparing costs of programmes with selection response (Janssen *et al*., 2018). Directional selection can cause the Bulmer effect (Bulmer, 1971) and inbreeding, due to selection of a few individuals (Wellmann & Bennewitz, 2019). This leads to unequal contribution of parents to the next and subsequent generations due to selection of superior sires and dams increased rates of inbreeding (Howard *et al*., 2017; Sell-Kubiak *et al*., 2018). The long-term contribution of each individual is the proportional contribution of the individual to the genes in the population. The rate of inbreeding is predicted as Bijma *et al*. (2001);

$$\Delta F = \frac{1}{2} N E(r)^{2} \tag{2}$$

where N is the number of parents and $E(r)^{2}$ is the square of the expected contributions. Inbreeding can be reduced through GS as compared to conventional selection (Liu *et al*., 2016; Wolc *et al*., 2015). This is because conventional selection relies on increasing accuracy of between family variance to increase genetic gain, and this leads to selection of related individuals with high breeding values through truncation selection which increases inbreeding levels (Daetwyler *et al*., 2007).On the other hand, genome wide predictions uses markers to explain the Mendelian sampling term of the breeding values which makes the breeding values between sibs to be less correlated (Doublet *et al*., 2019). This leads to differentiation within families and hence decreases co-selection of sibs which in turn decreases the rates of inbreeding (Bonk *et al*., 2016). Selection can lead to inbreeding which causes inbreeding depression in selected traits (Charlesworth & Willis, 2009; Curik *et al*., 2017; Fang *et al*., 2003). Inbreeding eventually leads to reduction of additive genetic variance due to fixation of alleles due to directional selection (Kristensen & Sørensen, 2005). Inbreeding depression has been found to have strong effects not only on fitness, reproductive and survival traits (Doekes *et al*., 2019; Filho *et al*., 2015)but also on production traits (Malhado *et al*., 2013; Pereira*et al*., 2016). This is due to expression of deleterious alleles or loss a favouring a heterozygote combinations (Bosse *et al*., 2019; Charlesworth & Willis, 2009). In a small population as in a closed nucleus, the chances of two related animals being selected together are high (Fernando *et al*., 2011; Mwangi *et al*., 2016) which leads to increased rates of inbreeding (Mwangi *et al*., 2016). The reduced variances due to inbreeding often lead to reduction in response to selection after a given number of generations, despite continuous selection for a certain trait as demonstrated by Holt *et al*. (2005), due to exhaustion of genetic variability (Osborne *et al*., 2016).

CHAPTER THREE

POOLED PARAMETER ESTIMATES FORTRAITS OF ECONOMIC IMPORTANCE IN INDIGENOUS CHICKEN IN THE TROPICS

Abstract

Genetic and phenotypic parameter estimates obtained in different studies, may be heterogeneous. This is because they are obtained in different locations, using different sample sizes and estimation methods. The choice of which parameter estimates to use, is in most cases subjective and this may lead to underestimation or overestimation of potential genetic gain. The objective of the current study was to use meta-analysis to estimate genetic and phenotypic parameters of traits of economic importance in indigenous chicken (IC) breeding program. Estimates from literature were included where it was clearly indicated that the study was conducted on indigenous chicken and in the tropics. Information captured included country of study, method of evaluation, sample size, mean and standard deviation or standard errors of the estimate, and for genetic correlations, number of sires. Seventy three (73) heritabilities and 38 genetic and phenotypic correlations traits were used. A random effect model was used so as to include the variances within and between studies. Weighted heritabilities for body weight at hatch (Bw0) and twelve weeks (Bw12), egg number at twelve weeks (EN12) and antibody response (Ab) were 0.46, 0.24, 0.12, and 0.27, respectively. Pooled and non-pooled heritability values were varied for body weight among other traits for instance the pooled genetic value for body weight at hatch was 0.46 as compared to 0.56 in one of the studies. Heritability estimates differed due to method of estimation, location and time at which the data was collected. The weighted genetic and phenotypic correlations were also varied from the ones from single studies. It is concluded that pooled parameter estimates differ from parameters from single studies.

3.1 Introduction

Indigenous chicken (IC) play multiple roles in rural households which include but not limited to provision of food, income and cultural and religious roles (Ochieng *et al*., 2012; Padhi, 2016). Due to their importance, there have been efforts to improve the IC in Kenya which included importation of exotic breeds (Magothe *et al*., 2012b) for crossbreeding. According to Okeno *et al*. (2013), there exists opportunities for pure breeding of IC for meat and/or eggs to meet the increased demand (Bett *et al*., 2012). Pure breeding would ensure production of chicken that are well adapted to the existing management and environmental conditions. In improvement of IC, a breeding plan needs to be developed. Development of a breeding plan requires estimation of genetic and phenotypic parameters (Dana *et al*., 2011).

Accurate estimation of these input parameters which include heritabilities, genetic and phenotypic correlations is required to ensure their reliability (de Oliveira *et al*., 2018). Presence of many parameter estimates in the literature poses a challenge to breeders on what values to choose. They may not also be available for all the traits to be included in the breeding goal or may not be present at all for a specific population. This brings the necessity to utilise parameter estimates from other populations that are also adapted to the harsh environmental conditions. According to Koots and Gibson. (1996), parameters estimated elsewhere can be used in a different population. This is because the use of population specific parameters may not be possible because most breeding programs especially in developing countries, are faced with a critical challenge of inconsistent and limited pedigree and performance recording (Mrode *et al*., 2020; Wasike *et al*., 2011). Parameters obtained in different locations may vary due to the use of different methods of estimation and sample sizes with different selection history.

Due to the differences in methods of estimation and sample sizes, the parameters in the literature could be heterogeneous (Hippel, 2015; Veroniki *et al*., 2016). This means that the variation between the studies is above that expected by chance (Veroniki *et al*., 2016). Due to heterogeneity, meta-analysis can be used to obtain a more precise estimate by combining estimates across studies (Kang, 2015).

Meta-analysis involves combination of data from different studies to obtain a single, more precise estimate and discover sources of variation (Eisend, 2017; Haidich, 2010). In meta-analysis, a random effect model is used to account for the within and between study sources of variation (Borenstein *et al*., 2010; Jackson & Bowden, 2016). Due to varied levels of accuracy as measured by the sampling variance, weighting of the estimates is required based on the accuracy of estimation (Marın-Martınez&Sánchez-Meca, 2010). According to Borenstein *et al*. (2009), the results from meta-analysis can be considered as robust across the kinds of populations that have been sampled.

Pooling of parameter estimates has been done in beef cattle and small ruminants (Diaz *et al*., 2014; Jembere *et al*., 2017; Safari *et al*., 2005). The objective of the current study was to pool genetic and phenotypic parameters for traits of economic importance for IC through meta-analysis.

3.2 Materials and methods

3.2.1 Data and traits

A literature search was done to obtain the relevant articles. The database was constructed from forty five (45) published articles which were published from 1987 to 2018 (Data references are provided in the appendices). The studies used the word native or indigenous to refer to various chickens which have adapted to the harsh environmental conditions in the tropics. Where there was more than one article from the same location on the same trait, the most recent one was used. The numbers of studies from different countries are presented in Table 3.1. The traits that were considered are the ones which have been identified as economically important in the breeding objectives for the IC in Kenya.

Table 3.1 Number of studies used for the estimation of pooled parameter estimates for IC in the tropics

No. of studies	Countries
1	Bangladesh, Cameroon, Mexico, Saudi Arabia, South Africa
2	Ethiopia, Sudan, Thailand, Tanzania, Ghana
3	Kenya, India
6	Egypt
7	Iran
11	Nigeria

A list of productive, reproductive, disease resistance and feed efficiency traits that were considered with their abbreviations are presented in Table 3.2. The recorded data included the heritabilities, genetic and phenotypic correlations, standard errors, standard deviations, and number of records used to obtain the results.

Table 3.2 List of traits and their abbreviations considered for estimation of pooled parameter estimates for IC in the tropics

Growth	Weight at hatch (Bw0), 1(Bw1), 2(Bw2), 3(Bw3),4(Bw4),5(Bw5), 6(Bw6), 7(Bw7),8(Bw8), 10(Bw10), 11(Bw11),12(Bw12), 14(Bw14), 16(Bw16), 18(Bw18), 20(Bw20), 21(Bw21), 22(Bw22), 24(Bw24), 26(Bw26), 28(Bw28), 32 (Bw32), 36(Bw36), 40(Bw40), 72(Bw72) weeks, weight at sexual maturity (WSM)
Feed efficiency	Average daily gain for 4(ADG4), 7(ADG7), 8(ADG8), 12(ADG12), 14(ADG14), 16(ADG16), 21(ADG21), 28(ADG28), 35(ADG35), Feed Intake at 37-40(FI 37-40), Residual Feed Intake at 11(RFI11), 12(RFI12), 37-40(RFI37-40), 57-60(RFI57-60), Residual Gain at 11(RG11), 12(RG12), 13(RG13), Residual Intake and Gain at 11(RIG11), Feed Conversion Ratio at 37-40(FCR 37-40) weeks
Egg number	Egg number at 90(EN90), 270 (EN270) days, 8(EN8), 12(EN12), 16(EN16), 28(EN28), 30(EN30), 39(EN39), 40(EN40), 52(EN52), 72(EN72), 22-23(EN22-23), 24-25(EN24-25), 26-27(EN26-27), 28-29(EN28-29), 21-30(EN21-30), 21-49(EN21-49), 31-40(EN31-40), 28-32(EN28-32), 21-49(EN29-49) weeks, 1(ENM1), 5(ENM5), 6(ENM6) months
Egg weight	Egg weight at 1(EW1), 16(EW16), 21(EW21), 28(EW28), 30(EW30), 32 (EW32), 35(EW35), 36(EW36), 39(EW39), 40(EW40),64(EW64), 72(EW72), and 28-32(EW28-32) weeks
Disease resistance	Antibody response (Ab)
Reproduction	Hatchability (HA), Fertility (FERT),and Age at first egg (AFE) in days

3.2.2 Data analysis

3.2.2.1 Heterogeneity test

This procedure was carried out to test whether all the estimations from the different studies were the same, with only random variations. An alternative hypothesis that at least one estimate differed from the others was tested. The test was based on Cochran. (1954), Q statistic (Giannotti *et al*., 2005);

$$Q = \sum_{i=1}^{k} w_i \left(\hat{h}_i^2 - \hat{h}_+^2\right)^2 \quad (3)$$

where $w_i = 1/s_i^2$ and $\hat{h}_+^2 = \sum_{i=1}^{k} w_i \hat{h}_i^2 / \sum_{i=1}^{k} w_i$ (Hedges and Olkin, 1985) and $\hat{h}_i^2$ and s_i^2 were the value of the i^{th} heritability of given trait and the sampling variance, respectively. The Q statistic was based on Chi-square distribution (Akanno *et al*., 2013).

3.2.2.2 Weighted heritability estimates

Weighted heritability parameter estimates were obtained using a random effect model. The random effect model was adopted because it accounts for both between and within studies variances. The random effect model used was;

$$\bar{\ }_{i} = \text{«} + s_{i} + e_{i} \tag{4}$$

where $\bar{\ }_{i}$ is the estimate of a parameter in the i^{th} study, μ is the population mean, s_i is the between study component of the deviation from the mean, e_i is the within study component due to sampling error in the i^{th} estimate.

The combined variance method was used to calculate the standard errors where they were not reported (Safari *et al*., 2005). A weighted mean standard deviation was calculated using the model as described by Safari *et al*. (2005);

$$SD_w = \left[\frac{\sum_{i=1}^{y} s_i^2 n_i^2}{\sum_{i=1}^{y} n_i} \right]^{0.5} \tag{5}$$

where s_{i} is the standard error and n_i is the number of records for the i^{th} estimate. The standard error was calculated by dividing the standard deviation by square root of the number of records for the estimate.

3.2.2.3 Genetic and phenotypic correlations

The genetic and phenotypic correlations were first transformed to Fishers normal scale using the following equation (Safari *et al*., 2005);

$$Z = 0.5 \log \left[\frac{1+r}{1-r} \right] \tag{6}$$

where r is the correlation value for a given trait. The standard errors were calculated using the following model (Jembere *et al*., 2017);

$$se_z = (n-3)^{-0.5} \qquad (7)$$

Where *n* is the number of records for phenotypic correlations and number of sires for the genetic correlations. The weighted means of the transformed correlations were calculated and transformed back to correlations as described by Safari *et al*.(2005);

$$r_w = \frac{e^{2z}-1}{e^{2z}+1} \qquad (8)$$

where r_w is the weighted mean correlation and *z* is the weighted mean for the *Z* transformed correlations.

3.2.2.4 Least square analysis

A least square analysis was done for the traits with sufficient data to identify factors that may affect the heritability estimates. The following model was used;

$$Y_{ijkl} = \text{«} + A_i + M_j + C_k + e_{ijkl} \qquad (9)$$

where Y_{ijk} is the heritability estimate, « the overall mean, A_i is the age of the data, M_j the method of estimation, C_k is the country of origin and e_{ijkl} is the error term.

3.3 Results

3.3.1 Weighted heritabilities

Weighted heritability estimates for growth, egg, disease resistance, feed and reproductive efficiency traits are presented in Table 3.3 and 3.4. A total of 72 traits were used. Heritability values for all traits ranged from low to high (0.02 to 0.91). The genetic and phenotypic parameters were classified as low (0.19 and below), moderate (0.20 to 0.39) and high (0.40 and above) according to Gagliardi *et al*. (2011). Weighted heritability estimates for body weight traits ranged between 0.02 and 0.67.Generally, body weight traits were moderately to highly heritable. Egg weight traits had higher heritabilities as compared to other traits (0.07 to 0.91), though most of the estimates were obtained from single studies. Among egg weight traits, EW72 had the highest heritability of 0.91. Egg weight had higher weighted heritability values than egg number traits. The standard errors associated with each trait did not follow a defined pattern. Most of the egg number trait estimates were obtained from single studies. The heritabilities ranged from low (0.09) to high (0.42). The EN72 had the highest value of 0.42 while EN22-23 had the lowest value of 0.05. Some of the studies did not include the number of records or standard errors, therefore the weighted estimates could not be obtained as the inverse of the variance was used as the weighting factor. There were variations between pooled values and values in the individual studies, for instance the pooled heritability value for Bw0 was 0.46 as compared to 0.22 as found in Iraqi *et al*. (2000).

Weighted heritabilities for reproductive efficiency and antibody response traits were moderate to high (0.21 to 0.42). Weight at sexual maturity (WSM) had the highest heritability of 0.42. The AFE had the highest number of studies showing that, it was most likely to be recorded. Weighted heritabilities for feed efficiency traits were low to high at 0.15 to 0.77. Residual Gain at11 weeks (RG11) had the highest heritability of 0.77. The numbers of estimates for calculating feed efficiency traits were few compared to the other traits, meaning that less emphasis may have been put on these traits, despite their importance in IC production.

Table 3.3 Weighted heritabilities (h^2), standard error (SE) and number of studies (N), between study variance, and Q statistic for body weight, egg number, reproductive efficiency and antibody response traits

Trait	N	h^2±SE	σ^2bs	Q	95% CI	Trait	N	h^2±SE	σ^2bs	Q	95%CI
Growth						**Egg number**					
Bw0	17	0.46±0.15	0.71	207.81***	0.17 to 0.75	EN12	7	0.12±0.01	1.93	90.41***	0.10 to 0.14
Bw1	1	0.14±0.05	-	-	0.04 to 0.24	EN16	1	0.24±0.16	-	-	-0.07 to 0.55
Bw2	7	0.21±0.07	-	20.28***	0.07 to 0.35	EN28	1	0.14±0.20	-	-	-0.25 to 0.53
Bw3	1	0.07±0.04	-	-	-0.01 to 0.15	EN40	1	0.10±0.19	-	-	-0.27 to 0.47
Bw4	18	0.26±0.06	0.12	32.88***	0.14 to 0.38	EN52	1	0.09±0.20	-	-	-0.30 to 0.48
Bw5	1	0.03±0.03	-	-	-0.03 to 0.09	EN72	1	0.42±0.44	-	-	-0.44 to 1.28
Bw6	8	0.30±0.06	-	15.15*	0.18 to 0.42	EN90	7	0.32±0.07	0.02	4.29^{ns}	-0.02 to 0.26
Bw7	1	0.02±0.03	-	-	-0.04 to 0.08	ENM1	2	0.21	-	0.70^{ns}	-
Bw8	17	0.21±0.03	0.01	238.09***	0.15 to 0.27	ENM2	2	0.12	-	0.06^{ns}	-
Bw10	5	0.28±0.14		-	-0.01 to 0.55	ENM4	2	0.14	-	0.60^{ns}	-
Bw11	1	0.29±0.13		-	0.04 to 0.54	ENM5	1	0.12	-	-	-
Bw12	21	0.24±0.04	0.06	62.03***	0.16 to 0.32	ENM6	1	0.11	-	-	-
Bw16	13	0.24±0.07	0.56	139.54***	0.10 to 0.38	EN22-23	1	0.05	-	-	-
Bw18	1	0.29	-	-	-	EN24-25	1	0.07	-	-	-
Bw20	9	0.22±0.05	0.03	106.81***	0.12 to 0.32	EN26-27	1	0.06	-	-	-
Bw21	1	0.20	-	-	-	EN28-29	1	0.11	-	-	-
Bw24	1	0.70±0.06	-	-	0.58 to 0.82	EN30-31	1	0.38	-	-	-
Bw26	1	0.11	-	-	-	EN21-30	1	0.20±0.20	-	-	-0.19 to 0.59
Bw28	1	0.55±0.05	-	-	-0.05 to 0.65	EN31-40	1	0.14±0.13	-	-	-0.11 to 0.39
Bw32	1	0.58	-	-	-	EN41-49	1	0.29±0.20	-	-	-0.10 to 0.68
Bw36	1	0.36±0.00	-	-	-	EN21-49	1	0.30±0.00	-	-	-
Bw72	1	0.67±0.45	-	-	-0.92 to 2.84	**Reproductive efficiency**					
-	-	-	-	-	-0.21 to 1.55	HA	3	0.40	0.50	10.30***	-
-	-	-	-	-	-	AFE	13	0.25±0.28	0.67	340.00***	-0.30 to 0.83
-	-	-	-	-	-	WSM	6	0.42±0.52	0.31	44.73***	-0.50 to 1.54
-	-	-	-	-	-	FERT	3	0.21±0.04	0.14	22.61***	0.13 to 0.29
-	-	-	-	-	-	**Antibody response**					
-	-	-	-	-	-	Ab	3	0.27	0.07	0.19^{ns}	-

$P<0.1$*, $P<0.05$**, $P<0.01$***ns – not significant

Table 3.4 Weighted heritabilities (h^2), standard error (SE) and number of studies (N), between study variance, and Q statistic for egg weight and feed efficiency traits

Trait	N	h^2±SE	σ^2bs	Q	95%CI	Trait	N	h^2±SE	σ^2bs	Q	95%CI
Egg weight						**Feed efficiency**					
EW1	1	0.10±0.01	-	-	0.08 to 0.12	ADG4	4	0.15±0.06	3.20	6.65*	0.03 to 0.27
EW16	1	0.34±0.24	-	-	-0.13 to 0.81	ADG8	4	0.64±0.23	3.42	7.80*	0.19 to 1.09
EW21	1	0.42±0.03	-	-	0.36 to 0.46	ADG12	4	0.46±0.21	1.02	2.64^{ns}	0.05 to 0.87
EW28	2	0.36±0.02	-	1.13^{ns}	0.32 to 0.40	ADG16	2	0.19±0.18	-	2.22^{ns}	-0.16 to 0.54
EW30	3	0.44±0.02	-	51.17***	0.40 to 0.48	ADG20	2	0.21±0.16	-	1.41^{ns}	-0.10 to 0.52
EW32	2	0.43±0.02	-	57.80***	0.39 to 0.47	RFI11	1	0.25±1.11	-	-	-1.93 to 2.43
EW35	1	0.07±0.26	-	-	-0.44 to 0.58	RFI12	1	0.29±0.43	-	-	-0.55 to 1.13
EW36	1	0.10±0.05	-	-	0.00 to 0.20	RFI37-40	1	0.21±0.05	-	-	0.11 to 0.31
EW40	1	0.43±0.20	-	-	0.04 to 0.80	RFI57-60	1	0.29±0.06	-	-	0.17 to 0.41
EW64	1	0.47±0.44	-	-	-0.39 to 1.33	RG11	1	0.77±4.67	-	-	-8.38 to 9.92
EW72	1	0.91±0.49	-	-	-0.05 to 1.87	RG12	1	0.71±4.59	-	-	-8.28 to 9.71
EW28-32	4	0.35±0.14	1.12	131.93***	0.08 to 0.62	RG13	1	0.30±2.17	-	-	-3.95 to 4.55
						RIG11	1	0.69	-	-	-

P<0.1*, P<0.05**, P<0.01*** ns - not significant

3.3.2 Weighted correlations

Weighted correlations for growth, reproduction, feed efficiency and antibody response traits are presented in Tables 3.5 to 3.9. The numbers of studies that contributed to each weighted correlation were less than the ones used for the heritabilities. The numbers of studies available for growth traits were more than for all the other traits. All the genetic and phenotypic correlations between body weight traits were positive. In general, the genetic correlations (0.17 to 0.98) were higher than the phenotypic correlations (0.03 to 0.75). The Bw4 and Bw6 had the highest genetic correlation of 0.98, for the phenotypic correlations, Bw8 and Bw10 had the highest at 0.75.

The genetic correlations between body weight and egg weight were mainly moderate to high and positive (0.37 to 0.57) while the phenotypic correlations ranged from very low to high (0.05 to 0.60). The phenotypic correlations were mainly obtained from single studies. The genetic correlations between body weight and egg number were mainly low and negative (-0.07 to -0.13) for the early stages. The genetic and phenotypic correlations between Bw16 and EN8 were high and moderate at 0.51 and 0.36, respectively. The genetic and phenotypic correlations between Bw16 and EN16 were low at 0.22 and 0.23. Phenotypic correlations between body and egg weight were mainly moderate and positive. The phenotypic correlations between body weight and egg number were mainly low and negative. The Bw16 and EN8, however, had a moderate and positive phenotypic correlation at 0.36 although this value was obtained from a single study.

There were very few studies for correlations between reproductive efficiency traits and growth traits. The genetic correlations between Bw0 and Bw12 and AFE were positive although they were low. The genetic correlation between Bw8 and AFE was negative (-0.04). The genetic correlation between EN12 and AFE was moderate at -0.30. The genetic correlations between Bw12 and FERT and HA were negative at -0.33 and -0.03, respectively. As for the phenotypic correlations, the one for Bw12 and AFE was low at 0.05. The correlation between AFE and EW 28-32, however was moderate at 0.34. The correlation between Bw12 and FERT was high at 0.80. Antibody response had negative genetic and phenotypic correlations with all the production and reproduction traits. The genetic correlations between egg weights at different levels were high and positive ranging from 0.43 to 0.98. The genetic correlation between EW1 and EN12 was low and negative at -0.05. The phenotypic correlation between EW1 and EN12 was moderate and negative with a value of -0.39.

The genetic correlations between Bw4 and ADG8 to ADG20 were high and positive (0.44 to 0.97) except for ADG4 which was negative at -0.66. The genetic correlation between Bw8 and ADG16 was moderate at 0.23. The value between Bw8 and ADG20 was, however, low and negative at -0.14. Both genetic and phenotypic correlations between FI and RFI were high at 0.72 and 0.83, respectively. The phenotypic correlations between Bw8 and ADG8 to ADG20 ranged from low (0.15) to high (0.42). All these values were obtained from single studies. Antibody response had low negative genetic and phenotypic correlations with all the production and reproduction traits.

Table 3.5 Weighted genetic (above diagonal) and phenotypic (below diagonal) correlations among body weight traits, with number of studies in the parenthesis ().

	Bw0	Bw2	Bw4	Bw5	Bw6	Bw7	Bw8	Bw10	Bw12	Bw16	Bw20
Bw0		0.70(4)	0.56(4)	0.31(1)	0.37(1)	0.17(1)	0.60(6)	0.34(1)	0.26(4)	0.30(1)	0.93(1)
Bw2	0.23(4)		0.81(2)	0.62(1)	0.60(2)	0.39(1)	0.56(3)	0.93(1)	0.87(2)	0.71(2)	0.76(1)
Bw4	0.14(3)	0.47(3)		0.89(1)	0.98(4)	-	0.94(5)	0.90(1)	0.61(2)	-	0.83(1)
Bw5	0.08(1)	0.21(1)	0.48(1)		0.83(1)	0.52(1)	-	-	-	-	-
Bw6	0.17(3)	0.30(3)	0.49(3)	0.45(1)		-	0.98(1)	0.99(1)	0.84(2)	-	-
Bw7	0.04(1)	0.05(1)	-	0.26(1)	-		-	-	-	-	-
Bw8	0.17(6)	0.31(3)	0.39(6)	-	0.38(3)	-		0.96(2)	0.54(8)	0.54(5)	0.47(6)
Bw10	0.11(1)	0.40(1)	0.50(1)	-	0.57(1)	-	0.75(1)		-	-	-
Bw12	0.18(4)	0.53(2)	0.27(3)	-	0.60(2)	-	0.61(9)	-		0.68(5)	0.51(3)
Bw16	0.03(1)	0.27(1)	-	-	-	-	0.38(7)	-	0.43(6)		0.76(4)
Bw20	0.41(1)	0.60(1)	0.38(3)	-	-	-	0.45(7)	-	0.29(5)	0.35(6)	

Table 3.6 Weighted genetic (above diagonal) and phenotypic (below diagonal) correlations between body weight and egg traits with number of studies in the parenthesis ().

	Bw0	3w8	Bw12	Bw16	FEW	EW30	EW28-32	EN8	EN12	EN16
Bw0		-	-	-	0.51(1)	0.57(1)	0.38(2)	-	-0.13(2)	-
Bw8	-		-	-	0.40(1)	0.45(1)	0.37(2)	-	-0.07(2)	-
Bw12	-	-		-	0.40(1)	0.45(1)	0.41(2)	-	-0.12(2)	-
Bw16	-	-	-		-	-	-	0.51(1)	-	0.22(1)
FEW	0.09(1)	0.60(1)	0.19(1)	-		-	-	-	-	-
EW30	0.25(1)	0.28(1)	0.31(1)	-	-		-	-	-	-
EW28-32	0.07(1)	0.05(1)	0.27(3)	-	-	-		-	-	-
EN8	-	-	-	0.36(1)	-	-	-		-	-
EN12	-0.04(1)	0.07(1)	0.08(3)	-	-	-	-	-		-
EN16	-	-	-	0.23(1)	-	-	-	-	-	

Table 3.7 Weighted genetic (above diagonal) and phenotypic correlations (below diagonal) between body weight, antibody response, egg and reproductive traits with number of studies in the parenthesis ().

	Bw0	Bw8	Bw12	EW12	EW40	EW28-32	EN12	AFE	FERT	HA	Ab	WSM
Bw0		-	-	-	-	-	-	0.08(2)	-	-	-	-
Bw8	-		-	-	-	-	-	-0.16(2)	-	-	-0.08(2)	-
Bw12	-	-		-	-	-	-	0.05(3)	-0.33(1)	-0.03(1)	-0.07(2)	-
EW12	-	-	-		-	-	-	0.46(3)	-	-	-	-
EW40	-	-	-	-		-	-	0.64(1)	-	-	-	-
EW28-32	-	-	-	-	-		-	0.35(2)	-	-	-	-
EN12	-	-	-	-	-	-		-0.30(4)	-	-	-	-
AFE	0.01(1)	-0.04(1)	-0.10(1)	0.08(1)	0.09(1)	0.34(3)	-0.36(3)		-	-	-0.04(2)	0.31(1)
FERT	-	-	0.80(1)	-	-	-	-	-		-	-	-
HA	-	-	-0.72(1)	-	-	-	-	-	-		-	-
Ab	-	-0.05(2)	-0.02(2)	-	-	-	-	-0.03(1)	-	-	-	-0.04(1)
WSM	-	-	-	-	-	-	-	-0.03(1)	-	-	-0.04(2)	-

Table 3.8 Weighted genetic (above diagonal) and phenotypic (above diagonal) correlations between egg weight and number traits with number of studies in the parenthesis ().

	EW1	EW12	EW21	EW28	EW30	EW32	EW28-32	EW39	EN12	EN39
EW1		-	-	-	-	-	-	-	-0.05(1)	-
EW12	-		-	-	-	-	-	-	-0.24(3)	-
EW21	-	-		0.49(1)	0.43(1)	0.44(1)	-	-	-	-
EW28	-	-	0.10(1)		0.98(1)	0.98(1)	-	-	-	-
EW30	-	-	0.10(1)	0.56(1)		0.97(1)	-	-	-	-
EW32	-	-	0.10(1)	0.55(1)	0.58(1)		-	-	-	-
EW28-32	-	-	-	-	-	-		-	-	-
EW39	-	-	-	-	-	-	-		-	-0.21(3)
EN12	-0.39(1)	0.03(1)	-	-	-	-	0.14(3)	-		-
EN39	-	-	-	-	-	-	-	-0.16(3)	-	

Table 3.9 Weighted genetic (above diagonal) and phenotypic (below diagonal) correlations between body weight, dailygain and feed efficiency traits with number of studies in the parenthesis ().

	Bw4	Bw8	ADG4	ADG8	ADG12	ADG16	ADG20	FI	RFI	FCR
Bw4		-	-0.66(1)	0.44(1)	0.49(1)	0.97(1)	0.63(1)	-	-	-
Bw8	-		-	0.06(1)	0.22(1)	0.23(1)	-0.14(1)	-	-	-
ADG4	0.07(1)	-		-	-	-	-	-	-	-
ADG8	0.12(1)	0.20(1)	-		-	-	-	-	-	-
ADG12	0.20(1)	0.23(1)	-	-		-	-	-	-	-
ADG16	-0.12(1)	0.42(1)	-	-	-		-	-	-	-
ADG20	0.23(1)	0.15(1)	-	-	-	-		-	-	-
FI	-	-	-	-	-	-	-		0.72(1)	-0.09(1)
RFI	-	-	-	-	-	-	-	0.83(1)		0.51(1)
FCR	-	-	-	-	-	-	-	0.07(1)	0.47(1)	

3.3.3 Least square analysis

The significant factors in the analysis of heritabilities of some traits of IC in the tropics are presented in Table 3.10. The R^2 for the least square analysis ranged from 0.81 to 0.99 for some of the mostly studied traits. Method of estimation, country and age of the data affected heritability estimates for Bw8 significantly ($P<0.05$). The year in which the estimates were obtained, which was included as a covariate, was significant for Bw8 EW30 and EW28-32 ($P<0.05$). This was in reference to the year 2018.

Table 3.10 Significant factors in the analysis of heritabilities of some traits of IC in the tropics

Trait	N	R^2	Method	Country	Data age
Bw8	17	0.99	***	***	***
EW30	3	0.99			**
EW28-32	4	0.99			*
AFE	13	0.81		*	

P<0.1*, P<0.05**, P<0.01***

3.4 Discussion

3.4.1 Weighted heritabilities

The moderate to high heritabilities for growth traits showed that this trait can be genetically improved through selection (Ngeno *et al.*, 2013; Rotimi *et al.*, 2016). These findings are similar to the results found in Nellore cattle and goats by de Oliveira *et al*. (2018) and Jembere *et al*. (2017), respectively. Different studies have recommended improvement of body weight of IC at 8 and 12 weeks (Badwi & El-karim, 2015; Faruque *et al.*, 2017; Muasya *et al.*, 2015; Ngeno *et al.*, 2013). This may explain why the two body weights had the highest number of published studies beside Bw0. Lwelamira *et al*. (2009), indicated a high heritability of 0.45 for Bw20 whereas this study obtained a pooled value of 0.22 for the same trait. This shows the importance of meta-analysis of parameter estimtes to obtain an average value from a number of studies (Deeks *et al.*, 2001). According to Møller &Myles. (2016), pooling of parameter estimaters increases the relability of the estimates. This could show the reliability of the values in this study rather than the values found in single studies.

The majorly low heritability estimates for egg number at early stages showed that it can be improved through selection of Bw16, due to their positive genetic relationship. This would reduce the amount of time needed to acquire egg production performance at EN72 which has a high heritability. The moderate to high heritabilities for egg weight especially for EW16 and EW21 showed that this trait can be improved by individual selection (Singh *et al*., 2018).

The moderate to high heritabilities for all the reproductive traits show that they can be improved for the enhancement and profitability of chicken breeding programmes. In a study done by Sapkota *et al*. (2020) in indigenous chicken in Iran, it was shown that fertility can be improved through selection. Selection for AFE could result in its marked improvement (Faruque *et al*., 2017) and this would benefit farmers as hens that mature early produce more eggs (Sapkota *et al*., 2020). Consequently, more eggs would be available for sale leading to increased income to farmers. The moderate heritability for Ab of 0.27 coupled with vaccination shows that selection for this trait can be successful (Agbenyegah, 2017), and therefore resistance to diseases in chickens would be enhanced (Mpenda*et al*., 2018). The Ab may be improved through improvement of Bw, AFE and EN90 traits without a notable reduction in genetic gain (Lwelamira, 2012).

The moderate to high heritability values for the feed efficiency traits indicates that it is possible to genetically improve animals for efficient feed utilization (Miyumo *et al*., 2018; Ogbu *et al*., 2015).Despite the feeding constituting 60-70% of total cost of production (Thirumalaisamy *et al*., 2016), studies related to feed efficiency are few. This is because they are mostly reared under extensive production systems (Miyumo *et al*., 2018) and therefore it becomes difficult to record their performances. This calls for more studies on feed efficiency traits in IC as it determines the profitability of such an enterprise. This would also improve the reliability of the pooled estimates as more values would be available for analysis. The differences between the heritability values for the traits in economic importance in IC in the single studies and the values in this study shows the need to merge the results from different studies to get an overall estimate (Shorten &Shorten, 2013).

3.4.2 Weighted correlations

The positive genetic and phenotypic correlations for body weights at different ages shows that there is a favourable relationship that exists between them (Ige, 2013). This means that growth rate can be improved at one level, due to selection at a different level. This was similar to results found in a similar study in Nellore cattle by de Oliveira *et al*. (2018). The deviation for some of the studies from the pooled values especially for genetic correlation between Bw12 and Bw8, which were among the most studied growth traits, show the importance of pooling the estimates. For instance, the correlation between these two traits was 0.86 in Dana *et al*. (2011), whereas the pooled value is 0.54. This value could be regarded to as more precise because according to Diaz *et al*. (2014) meta-analysis can increase the precision of estimates. The high and positive genetic correlations between body weight and egg weight indicate that selection of either of the traits would result in a joint genetic progress of the two traits (Rincón *et al*., 2015;Rosa *et al*., 2018). This implies that one of the traits can be included in a breeding goal, instead of both.

Negative genetic and phenotypic correlations between early body weight and most of the egg number traits shows that these traits are dominated by disparate and non-linked loci (Shann-Ren *et al*., 2018). This means that selection for high body weight could decrease the number of eggs laid (Tongsiri*et al*., 2019). Nevertheless, the positive genetic correlation between Bw16 and EN8 and EN16 implies that they could be improved together (Okeno *et al*., 2013).Selection for EW 28-32 would improve the AFE due to their positive genetic correlation; therefore the hens will lay more eggs as the time needed to start laying would be shortened. Improvement of egg production would increase the AFE due to the negative association between the traits. Okeno *et al*. (2013) showed that increased EN would reduce AFE by 2.46 days. The negative genetic relationship between Bw12 and FERT shows that improvement of Bw12 would reduce fertility.

The negative correlations between Bw and HA indicates that improvement of body weight would lead to a reduction of hatchability of eggs though to a very small extent. This could imply that females should be improved for a reduction in body weight. FERT and HA have high genetic and phenotypic association therefore both traits can be improved together. The antibody response had negative genetic and phenotypic correlations with all the production and reproduction traits. However, such low values do not result in significant effect in primary humoral immune response following selection for the production traits (Lwelamira *et al*., 2009).The majorly moderate to high and positive genetic correlations between Bw4 and Bw8 with ADG8, ADG12, ADG16 and ADG20 imply that selection for either of the traits would improve the others (Ohagenyi *et al*., 2013). Improvement of RFI would also improve the FCR due to their high positive genetic and phenotypic correlations. Miyumo *et al*. (2018) recommended selection for improvement of RFI and hence feed efficiency in IC at 98 days.

3.4.3 Least square analysis

The significant effect of method of estimation on the parameter estimates could be because an animal model method yields better results than paternal half-sib method (Villemereuil*et al*., 2013). This is because it utilizes information from the full pedigree and allows accurate consideration of environment within which the animals are found (Villemereuil *et al*., 2013). This was similar to the results found by Akanno *et al*. (2013). The location defined by country, from which the data was obtained was significant for Bw8 and AFE. This was similar to what was found by Giannotti *et al*. (2005) in beef cattle. This could be explained by differences in factors like temperature and humidity that can affect the chicken production and reproduction levels as demonstrated in broilers and local chicken by Nayak *et al*. (2015) and Uzokwe & Bakare. (2013). In a study done in Rhode Island Red and white chicken by Kabir *et al*. (2006), it was indicated that heritability can be decreased by increased temperatures and humidity.

According to Akanno *et al*. (2013),variations between time, which was indicated by the year of study, in which heritability estimates are taken, affects the values that are obtained as observed for some traits in this study. All the factors however, were not significant in Bw0, Bw4, Bw12, Bw16, EN12 and ADG8 traits. The non-significance of these factors on some of the heritabilities estimates justifies the use parameters obtained in different locations in addition to weighting of those estimates.

3.5 Conclusion

The differences between pooled estimates and ones obtained from single studies show that the poled parameters could be more precise as they have been calculated from a larger amount of data based on the accuracies of their estimation. Live weight traits at different ages were mostly studied than all the other traits.

CHAPTER FOUR

OPTIMISATION OF RESPONSE TO SELECTION USING POOLED PARAMETER ESTIMATES AND GENOMIC SELECTION IN INDIGENOUS CHICKEN BREEDING PROGRAMMES

Abstract

This study tested the hypothesis that utilisation of pooled genetic and phenotypic parameters, genomic selection and accounting for Bulmer effect would optimize response to selection in indigenous chicken breeding programme. This premise was tested using deterministic simulation in a three breeding schemes defined based on the sources of information used in estimation of breeding values. The three schemes used either conventional breeding scheme with non-pooled parameter (CSN), or pooled parameter estimated (CSP) and genomic information in genomic selection scheme (GSS). A one tier closed nucleus-breeding programme was considered with a mating ratio of 1:5 for males to females, respectively. Four traits used in the breeding goal were live weight at twelve weeks (LW), egg number at twelve weeks (EN), age at first egg (AFE), and antibody response (Ab). The response to selection for CSN 1.5 times larger, with a 38% lower rate of inbreeding and 10% higher accuracy as compared to CSP. The GSS realized additional 60% genetic gain, 67.6% less inbreeding and additional 54.5% accuracy to selection as compared to CSP. When compared to CSN, GSS had 63.33% more genetic gain, 55.1% lower rate of inbreeding and 31.34 % higher accuracy of selection. The GSS scheme had the lowest rate of inbreeding at 0.22% compared to 0.49% and 0.68% for CSN and CSP, respectively. Live weight contributed to the highest genetic and economic gain in all the schemes. The results indicate that the use of pooled parameter estimates, genomic information and accounting for Bulmer effect, optimises response to selection while non-pooled inputs over and under estimate rates of genetic gain and inbreeding, respectively.

4.1 Introduction

Most developing countries have recognized the social, economic and nutritional roles played by indigenous chicken (IC) to improve livelihoods of the resource poor rural households (Kattel, 2016; Moussa *et al*., 2019). This could be confirmed by attempts made by different countries to improve productivity of IC in terms of growth and egg production. The improvement attempts have focused on genetics, nutrition, health, housing and capacity building of farmers on general management and marketing (Ayieko *et al*., 2015; Mpenda *et al*., 2018; Wondmeneh *et al*., 2014). Genetic improvements have been initiated through different experiments modelled to provide information for informed decision-making before actual investments in breeding programmes. Modelling of breeding programmes, however, require population specific input parameter estimates, constant monitoring of loss in genetic variance due to intense selection and adoption new technologies such as genomic selection for sustainable long-term genetic gains (Lillehamer *et al*., 2016; Miyumo *et al*., 2018; Rutten *et al*., 2002).

Estimation of population specific parameter estimates require pedigree and performance recording which is the biggest challenge in developing countries due to small flock sizes and lack of commitment by smallholder farmers (Mrode *et al*., 2020; Wasike *et al*., 2011; Wondmeneh *et al*., 2014). The IC breeding programmes therefore have been modelled using input parameters sourced from different studies as recommended by Koots & Gibson. (1994). Such input parameters, however, should be used with caution as they could lead to biasness in predictions due to two reasons. Firstly, they are generated from different studies carried out in different geographical zones and with different data sizes and structures (Dana *et al*., 2011; Haunshi & Shanmugam, 2012; Ngeno *et al*., 2013). Secondly, the data analysis were performed using different methods (Haunshi & Shanmugam, 2012; Niknafs *et al*., 2013). To overcome these challenges, the use of pooled parameters was proposed as they account for variations related to geographical differences in data source, size, structure and analytical procedures (de Oliveira *et al*., 2018). The use of pooled input parameters and accounting for loss in genetic variance in modelling IC breeding programmes in developing countries, however, has been assumed.

Genetic variance has been demonstrated to decrease over time due to selection (Khaw *et al*., 2014; Seyedsharifi *et al*., 2018; Willoughby *et al*., 2015). Selection can lead to increased rates of inbreeding because the chances of two related animals being selected together are high especially is in small populations like IC ((Mwangi *et al*., 2016; Okeno *et al*., 2012). According to Esfandyari *et al*. (2017), inbreeding eventually leads to reduction in additive genetic variance due to fixation of alleles. High rate of inbreeding has been demonstrated to negatively affect response to selection for individual traits and levels beyond 0.1% would not be optimal for evolution (Franklin & Frankham, 1998; Tongsiri *et al*., 2019). Ignoring loss in genetic variance or not accounting for mitigation strategies such as genomic selection against it could be detrimental to long term genetic gain in a breeding programme.

Genomic selection (GS) has been demonstrated to be more efficient in making selection decisions hence reducing inbreeding levels in animal populations (Kasinathan *et al*., 2015; Liu *et al*., 2018; Thomasen *et al*., 2020). It has been extensively used in developed countries to optimize response to selection in breeding programmes for two main reasons. First, it generates information on Mendelian sampling term more accurately leading to less co-selection of sibs as estimated breeding values between individuals within families can be differentiated better hence reduced rates of inbreeding (Daetwyler *et al*., 2007; Júnior *et al.*, 2016;Tsai *et al*., 2016). Second, it accelerates the rate of genetic gain, as it increases the accuracy of selection and reduces the generation interval (Miller, 2010). Its adoption in the developing countries especially in IC breeding programmes, however, is limited due to assumed high genotyping costs without considering the returns. Based on the above lines of arguments, this study investigated the premise that, use of pooled input parameter estimates, accounting for loss in genetic variance and adopting genomic selection in IC breeding programmes in the developing countries would accelerate genetic gains. This hypothesis was tested using deterministic simulation of breeding schemes that resemble those used in IC breeding programmes in the developing countries.

4.2 Methodology

4.2.1 Procedure

Deterministic simulation was used to model different breeding schemes in a closed single tier nucleus-breeding programme. The breeding schemes were conventional and genomic. Conventional schemes mimicked the current chicken breeding programmes while the genomic scheme represented an alternative. A single tier was considered since in most developing countries chickens produced from the breeding stations and not selected as replacement stock are sold to farmers for production. This implies that, the breeding goal within the stations and that of the farmers are in tandem. The IC breeding programme in Kenya was modelled to investigate the hypothesis of the current study.

4.2.2 The indigenous chicken breeding goals

Three breeding goals for IC in Kenya were developed in consultation with farmers, traders and consumers. They included IC-Broiler, IC-Layer and IC-Dual Purpose (Okeno*et al.*, 2012). They targeted improvement of IC for meat, eggs and both, respectively. The breeding goal targeting improvement of IC as dual purpose was adopted in the current study. This is because majority of farmers raise IC for multiple roles which include provision of both meat and eggs (Mutua, 2018). The traits considered in the breeding goal in the current study were live weight at twelve weeks (LW), egg number for twelve weeks (EN), age at first egg (AFE) and tolerance to disease (Ab) (Bett *et al*., 2011; Okeno *et al*., 2012). Antibody response (ab) was used as indicator trait for disease tolerance. Since most farmers in the tropics raise their chicken under semi- intensive or extensive production systems (Okeno *et al*, 2012), it is important to breed for disease tolerance as this exposes the birds to numerous disease causing pathogens.

Inclusion of traits of economic importance in the breeding goal requires estimation of their economic values (Amer2001; Bytyqi*et al*., 2015). The economic value of a trait is the change in profit attributed to change in a unit genetic merit of a trait, holding other traits constant(Hazel, 1943). Okeno *et al.* (2012) had estimated the economic values for traits in the breeding goal of IC in Kenya and are presented in Table 4.1. These economic values were adjusted for inflation rates by multiplying each trait by its cumulated discounted expressions (Kearney *et al*., 2005).

4.2.3 Genetic and phenotypic parameters

Genetic and phenotypic parameter estimates are some of the input parameters needed when modelling breeding programmes. They should be population specific to minimise biasness. In cases where such estimates are not available like in most developing countries, parameter estimates from other areas in the tropics have been recommended (Jembere *et al*., 2017; Koots &Gibson, 1996). Such parameters, however, could lead to biasness and therefore use of pooled parameters has been proposed (Akanno *et al*., 2013). The genetic and phenotypic parameters used in this study therefore were sourced from various studies in the tropics, but subjected to meta-analysis to obtain pooled values as found in Ndung'u *et al*. (2020). The non-pooled and pooled parameters used are presented in Table 4.1. The phenotypic variances and non-pooled parameters were sourced from Okeno *et al*. (2013).

4.2.4 Breeding structure and schemes

A single tier closed nucleus breeding structure resembling that used in IC breeding programmes in developing countries was considered. The activities within the nucleus included chicken identification using wing tags, phenotyping, genotyping, breeding values prediction, selection and mating. The best candidates were selected by truncation based on Best Linear Unbiased Prediction-Estimated Breeding Values (BLUP-EBVs) and used as replacement stock while the rest of the flock was culled. Three breeding schemes were considered.

Conventional Selection Schemes with non-pooled input parameter estimates (CSN): This schemes assumed that the parents were selected based on the pedigree and phenotypic information only. This represents the current breeding programmes in most developing countries where selection is based on performance records. The input parameter estimates used to model this scheme were sourced from different studies in the tropics. This mimics most of breeding models, which have been used to develop livestock breeding programmes in developing counties like Kenya.

Conventional Selection Schemes with pooled input parameter estimates (CSP): This scheme is similar to *CSN* but the input parameter estimates used in the model were subjected to meta-analysis. The aim was to obtain pooled parameters estimates that account for variances in data sizes, geographical conditions and statistical evaluation models. The scheme aims at reducing the biasness that could be attributed to use of no-pooled parameter estimates.

Genomic Selection Scheme (GSS): This scheme was similar to *CSP* but with selection of candidates based on genetic markers as additional source of information to phenotypes. It represents the selection technologies used in the developed countries to optimise response to selection but its adoption in the developing countries has been slow.

Table 4.1 Economic values (EV in US$), phenotypic variances (σ_P^2), heritabilities (along diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations

Traits	**EV***	σ_P^2 *	**Pooled parameters****				**Non-pooled parameters***			
			EN	LW	AFE	Ab	EN	LW	AFE	Ab
EN	0.0887	130.64	**0.12**	-0.12	-0.30	-0.04	**0.35**	-0.06	-0.19	-0.04
LW	0.7346	15627.50	0.08	**0.24**	0.05	-0.07	-0.02	**0.43**	-0.15	-0.07
AFE	-0.1394	144.24	-0.36	-0.10	**0.25**	-0.04	-0.16	-0.04	**0.47**	-0.03
Ab	-0.1831	39.44	-0.02	-0.05	0.00	**0.27**	-0.02	-0.07	0.00	**0.28**

Source: *Non-pooled parameters; Okeno *et al.* (2013), ** Pooled parameters; Ndung'u *et al*. (2020)

4.2.5 Population structure and information sources

A base population of 4800 indigenous chicken (IC) with sex ratio of 0.5 was assumed. Ninety-six males were selected from a population of 2400 males while 480 hens were selected as parents of the future generation from a population of 2400 females. The difference in proportion of cocks and hens selected was because few males are required for breeding compared to females. The mating ratio assumed one cock to five hens. Each hen was assumed to lay 15 eggs per clutch with hatchability of 95% and survival rate to sexual maturity of 70% (Yitbarek & Atalel, 2013). Selection was by truncation using BLUP-EBVs. For the sex-limited traits and those phenotyped later in life such as EN, AFE and Ab, the candidates were selected based on phenotypic data from their female ancestors and sibs' performances. On the other hand, the candidate were selected for LW based on own performance before maturity and phenotypic data from their male and female ancestors and sibs' performance. Since all the birds were raised within the same environment, common environmental effect was assumed constant. The effect of the nucleus size and different mating ratios on response to selection was considered by increasing the number of breeding females in the population from 480 to 2880. The mating ratio of males to females ranged from 1:5 with 480 to 1:30 with 2880 females. Use of artificial insemination was assumed since the semen from one cock inseminates 100 hens by use of extenders (Mohan *et al.*, 2018).

4.2.6 Prediction of response to selection

The rates on generic gain and inbreeding per generation were computed and compared under conventional and genomic breeding schemes.

Conventional selection schemes

The response to selection was computed for all the traits in the breeding goal (H) which was the sum of the true breeding values (TBV) of traits a weighted by their economic weights. A selection index, which was the sum of the TBVs for the traits in the breeding goal and their economic weights, was computed as (Rutten *et al.*, 2002):

$$H = A_1V_1 + A_2V_2 + \cdots \tag{10}$$

where A are true breeding values, and V are weighting factors for each trait.

Genomic selection scheme

In this scheme, genomic traits were included in the selection index as extra correlated traits with heritability equal to one (Dekkers, 2007). The genetic and phenotypic correlations between the true and the extra trait were calculated ashr_{gg} and r_{gg}, where h is the square root of the heritability of the trait and r_{gg} the accuracy of the genomic estimated breeding values. Ther_{gg} was determined by the size of the reference population (n_p), the effective number of loci in the base population (n_G), and the correlation of the true breeding values of the genotyped individuals and their phenotypes (r), and were computed based on the model below (Van Grevenhof *et al*., 2012).

$$r_{gg} = \sqrt{\frac{\lambda r^2}{\lambda r^2}} \tag{11}$$

where, $a = \frac{n_p}{n_G}$ and r^2 is the heritability, $n_G = 2N_E L$,where N_E is the historic effective size of the base population and L is the size of the genome in Morgan. The IC genome was assumed to be 32 in Morgan units (Groenen *et al*., 2009), the effective population size was 16.02 (Okeno *et al*., 2012). The genetic and phenotypic correlations between the genomic traits were calculated following the procedure of Dekkers.(2007).

4.2.7 Prediction of genetic and economic gain and inbreeding

The response to selection for each trait was calculated as;

$$\Delta \boldsymbol{G} = \boldsymbol{b}'\boldsymbol{G}\boldsymbol{i}/\boldsymbol{\sigma}_{\boldsymbol{I}} \tag{12}$$

where $\Delta\boldsymbol{G}$is a vector containing selection response for each trait; $\boldsymbol{b}$ is a vector of index weights and $\boldsymbol{G}$, is a matrix of co-variances between information sources and true breeding values of selection candidates, i, the selection intensity and σ_I, the standard deviation of the index. The total gain in the breeding goal in economic units was calculated as;

$$\Delta H = i\sigma_I \tag{13}$$

where ΔH is the breeding go[illegible]. The rate of inbreeding was computed in three steps. In the first step, a regression model was [illegible]ed to predict the long-term contributions

$$E(r) = \alpha + \beta(BV - \text{[illegible]}\bar{V}) \tag{14}$$

where *E(r)* is the expected contribution, α, the contribution of an individual with an average breeding value, β accounts for the increase of the contribution of parents with higher breeding value implying that the parents with high breeding values have more selected offsprings (Ruttenet al. 2002). Secondly, the square of the expected contributions was calculated. This results to the calculation of inbreeding as;

$$\Delta F = {}^{1}/_{2} NE(r)^2 \tag{15}$$

where N is the number of parents, and $E(r)^2$, the square of the expected contributions.

The SelAction software (Rutten *et al.*, 2002) was used to model and simulate different breeding programmes and schemes in the current study. The software predicts rates of genetic gain inbreeding for livestock breeding programmes using deterministic simulation approach. The response to selection and the rate of inbreeding are presented per generation (Rutten *et al*., 2002).

4.3 Results

The findings of the current study confirm our premise that use of pooled input parameter estimates, accounting for loss in genetic variance and adoption of genomic selection optimizes response to selection (Table 4.2). The rates of genetic gain and inbreeding were lower and higher, respectively, in breeding schemes that used pooled(CSP) compared to one that adopted non-pooled parameters (CSN). The genomic scheme (GSS) on the other hand out performed the conventional scheme in response to selection.

4.3.1 Response to selection

The genetic gain, loss of genetic variance and accuracy of selection per generation in the three breeding schemes are presented in Table 4.2. The genetic gain for CSN was 1.5 times higher than that realised by CSP. The corresponding rate of inbreeding on the other hand was 38% lower than that realised in CSP. The accuracy of selection followed the same trend with CSN realising 13% higher accuracy of selection than CSP. The GSS scheme realised additional 54.5 and 60% accuracy and genetic gain, respectively compared to CSP. It also had a reduced rate of inbreeding by 67.6% compared to CSP. When compared to CSN, GSS had 63.33% more genetic gain, 55.1% lower rate of inbreeding and 31.34 % higher accuracy of selection. The GSS scheme had the lowest rate of inbreeding at 0.22% compared to 0.49% and 0.68% for CSN and CSP schemes, respectively.

Table 4.2 Equilibrium genetic gain (1US$ = KES 100), rate of inbreeding and accuracy of selection in conventional selection schemes with non-pooled (CSN), with pooled parameter estimates (CSP) and genomic selection schemes (GSS) per generation

Strategy	Response (US$)	Rate of inbreeding (%)	Selection Accuracy
CSN	61.13	0.49	0.67
CSP	40.58	0.68	0.58
GSS	99.83	0.22	0.88

4.3.2 Genetic gains for individual traits

The genetic gains for individual traits in the breeding goal in the three breeding schemes are presented in Table 4.3. The genetic gain for individual traits followed the same trend as observed in the overall genetic gains for each scheme in Table 4.2. For instance the genetic gain for EN was -0.39 in CSN as compared to -0.49 in CSP. The live weight in CSN was 27.64g higher than that of CSP, AFE reduced by 1.40 days in CSN but increased by 0.34 days in CSP and immune antibody system changed by -0.24 in CSN and -0.27 in CSP. In all the traits except for EN and Ab, the GSS realized higher genetic gain compared to CSP. The genetic gain for LW was at least doubled in GSS compared CSP. The highest genetic gain was obtained from the live weight trait in all the schemes.

Table 4.3 Equilibrium genetic gain for individual traits in conventional with non-pooled (CSN), with pooled (CSP) parameter estimates and genomic selection schemes (GSS) per generation

Trait	CSN	CSP	GSS
Egg number	-0.39	-0.49	-3.24
Live weight	82.93	55.29	136.26
Age at first egg	-1.40	0.34	0.64
Antibody response	-0.24	-0.27	-0.60

4.3.3 Nucleus size and mating ratio of males to females

The effect of nucleus size and mating ratio of males to females on rates of genetic gain and inbreeding were investigated by changing nucleus size and mating ratios. Since the trends for CSN and CSP were identical, only CSP and GSS are presented. The rate of change in genetic gain and inbreeding when the nucleus size was increased is presented in Figure 4.1. Although, genetic gain realized in GSS ranked above the CSP, the rate of gain in both schemes increased at diminishing rate with increase in nucleus size. Similar, trend was also observed in the rate of inbreeding, but with GSS ranking below the CSP.

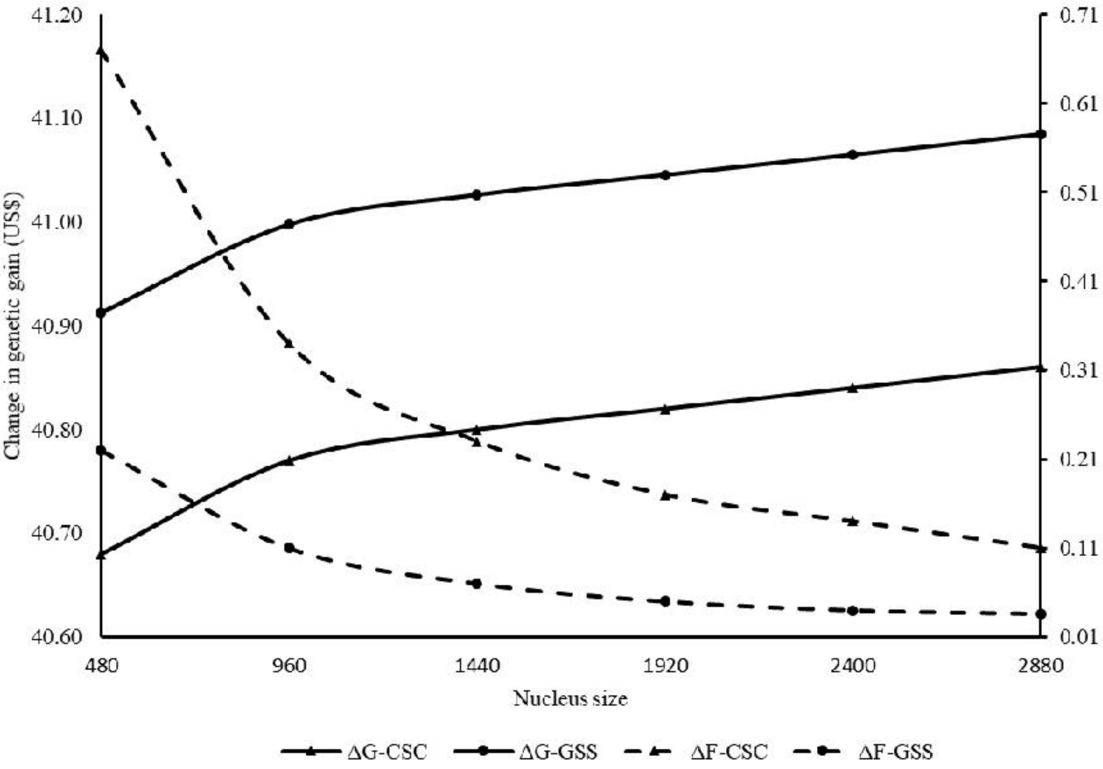

Figure 4. 1 The trends for rates of genetic gain and inbreeding with increase in nucleus size in conventional breeding scheme with pooled parameter estimates (CSP) and genomic selection scheme (GSS)

The change rates of genetic gain and inbreeding with increased mating ratio is presented in Figure 4.2. The genetic gain increased with increase in the mating ratio for both CSP and GSS schemes. It increased with increase in the number of hens per cock from 5 to 30 although at a diminishing rate in both schemes. The rate of increase, however, was higher for GSS than for the CSP scheme. The rate of inbreeding increased with increase in the mating ratio for the CSP scheme while it decreased with the increase in the mating ratio for the GSS.

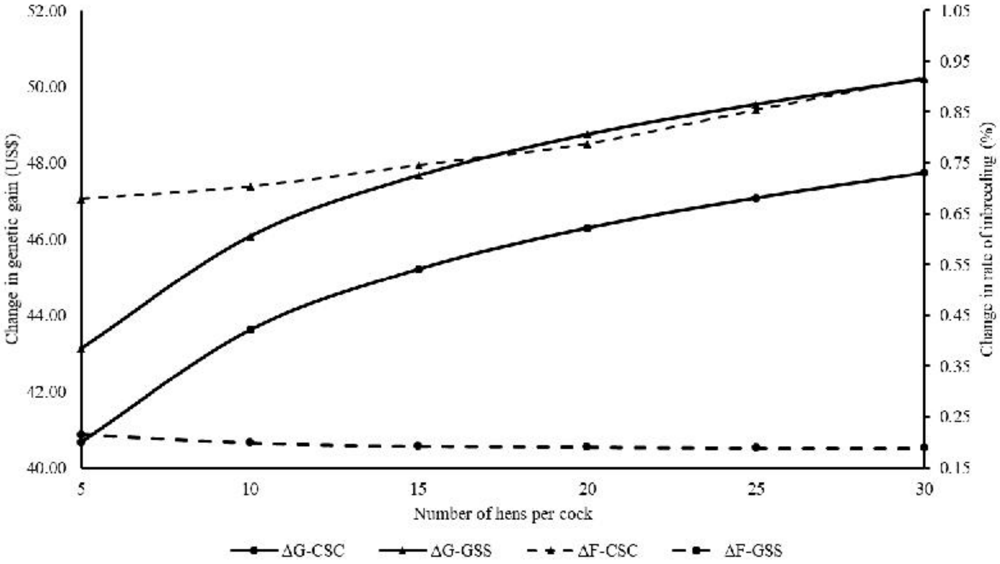

Figure 4. 2 The trends for rates of genetic gain and inbreeding with increase in mating ratio in conventional breeding scheme with pooled parameter estimates (CSP) and genomic selection scheme (GSS).

4.4 Discussion

The findings of the current study support the hypothesis that, not accounting for variations in sources of input parameter estimates and ignoring loss in genetic variance overtime overestimate response to selection. It also confirms that adoption of genomic selection in IC breeding programme would optimize response to selection. These findings are supported by Akanno *et al*. (2013), who demonstrated that, utilisation of input parameters from a single study could lead to biasness. This implies that in the event that primary data is not available to estimate the genetic parameters, there is need to subject parameters sourced from different studies to meta-analysis to obtain pooled parameters. As demonstrated in the findings (Table 4.2), the genetic gain realised in CSN was higher than those obtained in CSP. This could be attributed to differences in input parameters used in the two breeding schemes. The input parameters for CSN were obtained from different literature sources, which had higher heritability values, compared to those adopted in CSP where pooled parameters were used after meta-analysis (Table 4.1). The difference in heritability values obtained in CSN could be due to different data sizes, evaluation models, and the year in which the data was collected (Akanno *et al*., 2013). These values have direct impact on accuracy of selection and therefore true breeding values (Toghiani, 2012; Zhang *et al*., 2019).When comparing the impact of different levels of heritability on accuracy of selection, Toghiani. (2012) and Zhang *et al*. (2019) and found that, heritability had significant effect on both conventional and genomic breeding programmes. These studies found that higher heritability values resulted to higher accuracies. This could explain the higher accuracy of selection realized in CSN as compared to CSP (Table 4.2) in the current study. Since all other input parameters were constant in the two schemes considered, the economic and individual trait responses realized in Tables 4.2 and 4.3, respectively, could be attributed to differences in selection accuracies. This implies that it would be highly recommendable for each breeding programme to be evaluated based on primary data generated from the breeding programme to obtain a more precise estimation of response to selection. In a scenario where that is not feasible, meta-analysis of sampled input parameters should be carried out. Meta-analysis was conducted to obtain the input parameters in this study where lower heritability estimates were obtained for CSP as compared to CSN scheme. The parameters in CSN had been obtained directly from the literature (Okeno *et al*. 2013).

The lower heritability values could be given as the reason for the higher rate of inbreeding in the CSP scheme as compared to CSN (Table 4.2). According to Woolliams and Bijma. (2000) and Khaw *et al*. (2014), when heritability estimates are low and BLUP is used, the information from relatives is given more weight, which increases the possibility of relatedness and therefore high rates of inbreeding. This is consistent with the findings of the current study where low heritabilities obtained in CSP resulted to higher rates of inbreeding (Table 4.2). The high rate of inbreeding has been demonstrated to negatively affect response to selection for individual traits in the breeding goal in poultry (Tongsiri *et al*., 2019). This could explain the low genetic gain for individual traits and subsequent economic response realized under CSP in the current study. Generally, all the three breeding schemes modelled had higher rates of inbreeding than the recommended levels of 0.1% for evolutionary potential (Franklin & Frankham, 1998). This could be explained by low effective population size of 320 (Okeno *et al*., 2012) used in the current study compared to the recommended 500-1000 for conservation purposes (Frankham &Franklin, 1998). The highest genetic gains and lowest rates of inbreeding for GSS as compared to the CSN and CSP, implies that this scheme has the potential to yield more response to selection in IC breeding.

Genomic selection has been found to be superior to conventional breeding programmes in terms of response to selection and reduction in rates of inbreeding (Ebrahimpourtaher *et al*., 2018; Wolc *et al*., 2015). The high response to selection in the GSS compared to CSP scheme (Table 4.2) was attributed to high accuracy of selection and lower rates of inbreeding realized in the GSS scheme. The high accuracy realized could be attributed to the power of GSS to trace the inheritance of chromosomal segments and estimate relationships between selection candidates (Stock&Reents, 2013). Genomic information-based relationship matrix has been demonstrated to provide accurate relationship coefficients among individuals (VanRaden *et al*., 2009). Establishment of close relationships optimizes utilization of information from different related candidates and therefore increases accuracy of selection, which has direct impact on EBV and genetic gain (Meuwissen *et al*., 2013). The impact of increased accuracy on individual traits is evident in Table 4.2 in this study where all the traits in the breeding goal had high responses in GSS than those in CSP scheme. On the other hand, the independent management of ancestral contributions due to the use of genomic selection unlock the association between the genetic gain and relationships (Henryon *et al*., 2014). This is due to the establishment of more accurate relationships, which increases the accuracy of Mendelian sampling terms. This constrains identity-by-descent among the parents leading to low rate of inbreeding. This could explain the lower rates of inbreeding realized in the GSS compared to CSP in the current study. This study therefore shows that adoption of GSS in IC breeding programmes would optimize response to selection even with small nucleus sizes.

The effect of increasing the nucleus size was also investigated under the current conventional (CSP) and alternative GSS breeding programme. In the two schemes, the response to selection increased with increased population size but at diminishing returns (Figure 4.1). These findings are supported by Henryon *et al*. (2012) and Lillehammer *et al*. (2011), who demonstrated marginal diminishing returns in a pig genomic selection strategy. In these two studies, there were diminishing returns as more candidates were genotyped based on truncation selection. The diminishing returns observed in the current study could be attributed to truncation selection method adopted. This implies the best ranking animals would have high breeding values than low-ranking selection candidates. Therefore, as more candidates were added to the nucleus population after truncation selection, the contribution of the low ranking candidates could not outperform the high-ranking candidates. This means the benefits from the genetic gains derived from the low ranking candidates were not as much as those obtained from the high-ranking candidates. This leads to diminishing return to selection as more candidates were being recruited in to the nucleus. There was also an increase in the genetic gain with increase in mating ratio (Figure 4.2) although at diminishing return. This could be attributed to the increase in the selection intensity of the males. Previous studies have demonstrated that increasing selection intensity especially that of males has a huge positive impact on genetic gain (Abdel-Salam *et al*., 2010; Battagin *et al*., 2016; Granleese *et al*., 2017). The diminishing return in response to selection could be attributed to the increase in relatedness and reduction of genetic variability due to selection of more related animals for breeding(Doublet *et al*., 2019).

The decreasing rate of inbreeding with increased number of candidates in the nucleus population in the GSS scheme could be explained by capability of GSS scheme to rank full sibs. The GSS scheme uses genomic rather than numerator relationship matrix leading to generation of different breeding values for the full-sibs (Chu *et al*., 2019; Su *et al*., 2018). Such breeding values can be used to rank full-sibs, hence minimize chances of mating related individuals leading to low rate of inbreeding as observed in the current study. On the other hand, the decreasing rate of inbreeding in CSP could be attributed to the increase in the breeding population for both males and females. This is because the increase in the mating population increases the effective population size, which is indirectly proportional to the rates of inbreeding (Biscarini *et al*., 2015). This could explain the increasing trend of rate of inbreeding realized in Figure 4.2 as the number of males was kept constant while the female population was increased. This implies each male was mated to more females and hence close relationships in the future generations. Although, this study demonstrates that adoption of GSS would optimize response to selection, conventional breeding schemes would still play significant role in establishment of breeding programmes for IC in developing countries. This is because, the GSS scheme require reference population with both phenotyped and genotyped candidates (Lee *et al*.,2017). The level of recording for traits of economic importance for IC in particular in the developing countries is rudimentary. This is because resource poor rural households who do not see the value or have no capacity of recording mostly raise the indigenous chickens.

4.5 Conclusion

The findings of this study demonstrates that, in the absence of population specific input parameter estimates, information sampled from different studies should be subjected to meta-analysis to obtain pooled estimates to avoid overestimation of the expected genetic response when modelling breeding programmes. Adoption of genomic selection would optimise response to selection in IC breeding programmes.

CHAPTER FIVE

GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

5.1 Introduction

Poultry production and indigenous chickens (IC) in particular, has been recognized as an important avenue to ensure food security, wealth creation and poverty reduction among the resource limited rural households in developing countries (Dolberg, 2007). Because of the significant social and economic contribution of IC, Bett *et al*. (2012) and Okeno *et al*. (2013) structured a breeding programme in Kenya in consultation with actors in the value chain. In the process of designing the breeding programme, however, several assumptions were made. These included adoption of genetic and phenotypic input parameters from different individual studies in the tropics due to lack of such parameters in the local population and constant genetic variance throughout the evaluation period (Okeno *et al*., 2013). Such assumptions can affect the long-term sustainability of a breeding programme as they could lead to biasness hence over-or under estimation of response to selection. Over-or underestimation of response to selection could lead to wrong decision-making due to two reasons. Firstly, genetic parameters are affected by different factors such as data size, genetic models adopted, selection history of a population and geographical conditions under which the data has been collected (Akanno *et al*., 2013; Giannoti *et al*., 2005). Secondly, genetic variance which is one of the factors that affect genetic gain is always affected by selection intensity and selection methods adopted among others (Careau *et al*., 2015). The IC breeding programme design by Okeno *et al*. (2013), also did not account for new technologies such as genomic selection which have been recommended for optimization of response to selection. The current research therefore, focused on generating information on utilization of pooled genetic parameters in evaluation of the current IC breeding programme in Kenya, estimation of loss in genetic variance and feasibility of adopting alternative breeding programme using genomic selection.

This thesis addressed three major scientific questions in IC breeding programme in Kenya. They include: 1) What are the pooled genetic parameter estimates for traits of economic importance in IC breeding programme? (2) What are the Bulmer equilibrium genetic gains for a closed IC breeding programme? and (3) What are the genetic gains realised in IC breeding programme utilizing genomic selection compared to conventional breeding programme? In this section, therefore the methodological approaches used to answer the above questions, discussion of the major findings (Chapters 3 and 4) and their implication on IC improvement, conservation and utilization will be highlighted.

5.2 Methodological approaches

5.2.1 Estimation of pooled genetic parameters

The pooled genetic and phenotypic parameters for IC in the tropics were determined in the first objective. This was done by first collecting the parameters of interest, which included heritabilities, genetic and phenotypic correlations from published articles. These were collected for traits that have been identified as economically important for the IC in various tropical locations. The pooling of the parameters was done in two steps. After collection of the parameters, they were first tested whether they were homogenous according to Q statistic, which is based on Chi-Square test. In the second step, meta-analysis was done by weighting the heritabilities and the correlations using the inverse of the variance as the weighting factor. There are benefits that result from conducting a meta-analysis study. They include increase in precision of estimates because a large amount of data used to obtain the results (Israel & Ritcher, 2011). The sources of variations in results from different studies can also be identified (Stone & Rosopa, 2016).The generalisability of obtained results is also increased as well as determination of whether new studies are needed in a particular area (Lee, 2019). Meta-analysis, however, is associated with shortcomings, which include presence of biasness due to some factors. Biasness could be as a result of publication bias whereby unfavourable results could take more time to be published or non-significant results are not published at all (Ahmed and Sutton, 2012; Mikolajewicz & Komarova, 2019). Unsystematic original review of the studies to be included in the analysis or dissimilarity of the results from the different studies being too much could also lead to biasness (Esterhuizen & Thabane, 2016; Khan *et al.*, 2019). Since the validity of results from a meta-analysis study is based on the original articles used, bias can be minimised by carrying out a comprehensive literature search, to identify all the available published articles (Axel, 2008).

5.2.2 Evaluation of genetic response

The breeding programme for both conventional and genomic schemes was modelled in Selaction which uses deterministic simulation approach to estimate response to selection.

Deterministic modelling as opposed to stochastic modelling assumes constant input parameters and therefore generate similar output seven with repeated cycles of selection for a given set of parameters (Renard *et al*., 2013). The outputs from deterministic simulation are presented in terms of response realised for the whole population in consideration in a nucleus. On the other hand, stochastic modelling allows many rounds of selection which can result in estimation of a more accurate variance and response (Pryce *et al*., 2010). The economic gain moreover is presented as profit per individual animal in the breeding programme in stochastic modelling(Pedersen *et al*., 2009) as compared to the whole nucleus population in deterministic models. Since response to selection is only presented for the nucleus tier in Selaction software, it may not be possible to demonstrate the dissemination of genetic gains from a nucleus to the multiplier and commercial populations. Due to these limitations, a stochastic modelling procedure could also be considered. Deterministic models, however, take short-run time to obtain outputs and provide clear direction of selection.

5.3 Design of an alternative indigenous chicken breeding programme

A breeding programme for IC has been initiated in Kenya at Kenya Agricultural and Livestock Research Organization (KALRO), with selection based on conventional scheme (Ilatsia *et al*., 2017). In the nucleus, specific lines are being developed for production of egg and meat through pure breeding after which they are crossed with two imported breeds to obtain crossbreeds for production of meat, eggs or dual purposes (Ilatsia *et al.*, 2017). The realised genetic gains are disseminated through sale of the unselected cockerels and pullets from the research institution to the farmers. Kenya can therefore be considered to have a two tier breeding structure with a nucleus and a commercial population. The research institutions are the nucleus while the farmers who purchase the unselected pullets and cockerels are the commercial tier. Currently, truncation selection is practised in IC breeding in Kenya in the nucleus. With this strategy, much time is taken before animals are selected since their performances have to be recorded first before the breeding values are estimated. The rates of inbreeding could also be increased since truncation selection is done to select superior performers that could be related. Genomic selection therefore could be used to reduce time taken before selection, reduce rates of inbreeding and increase accuracy of selection. The cost of keeping animals not selected for breeding would also be reduced since selection can be done at hatch (Wolc, 2014). Due to these benefits, this strategy can be used to optimize response to selection in IC breeding programme as demonstrated in Chapter 4.

Utilisation of genomic selection, however, is limited for application in individual farms, which are the commercial population due to some reasons. First, the cost of genotyping is usually high (Pértille *et al*., 2016) and hence most farmers cannot afford since they are small scale in their operations. Secondly, technical knowledge is needed for estimation of breeding values from markers. Thirdly, phenotypic data is usually required for selection to be done after breeding values are estimated for the progenies but the data is not normally kept by individual farmers (Wasike*et al*., 2011). This implies that genomic selection would only be applicable in the nucleus.

A nucleus size consisting of 576 cocks and 2880 hens gave the highest genetic gain with the lowest rate of inbreeding for both conventional and genomic strategies. At this flock size the genetic gain increased at a constant rate. This population size would be appropriate for maintenance of genetic diversity based on results in Chapter 4. The 576 cocks and 2880 hens could be used as the initial parental population, which would produce 28,800male and female chicks for the base generation in the nucleus. The 28800 chicks would be the selection candidates. Genotyping of these selection candidates would be required to determine their genotypes. The initial population would be used to create a reference population in which all the animals would be genotyped (Wolc, 2014). These genotypes would assist in determination of markers effects for the obtained markers (Eggen, 2012). Estimation of the genomic breeding values of the produced chicks would be done by use of these marker effects and the chicks' own genotypes. Based on the breeding values, animals to be used as parents for the subsequent generation would be selected at the chick stage. The unselected chicks would be sold to the commercial population and the farmers would raise them to maturity for sale. After obtaining their performance records for the animals retained in the nucleus at maturity, they would be added to the reference population database while their offsprings are selected based on their genomic breeding values. The nucleus population and interaction with the commercial population is presented in Figure 5.1. A parental nucleus population of 576 cocks and 2880 hens would be genotyped to estimate their marker effects after recording their performances. A total of 28800 male and female chicks would be hatched from this parental flock. After hatching, all the chicks would be genotyped to estimate their genomic breeding values based on their own genotypes and the parents' genotypes and phenotypes. Selection of the chicks to be retained in the nucleus would be done based on the estimated breeding values while the remaining chicks that are expected to have improved performance as compared to the farmers flocks are disseminated to the commercial population. A total of 720 male and 3600 female chicks would be retained in the nucleus when 5% of the total male hatched chicks are selected for retention.

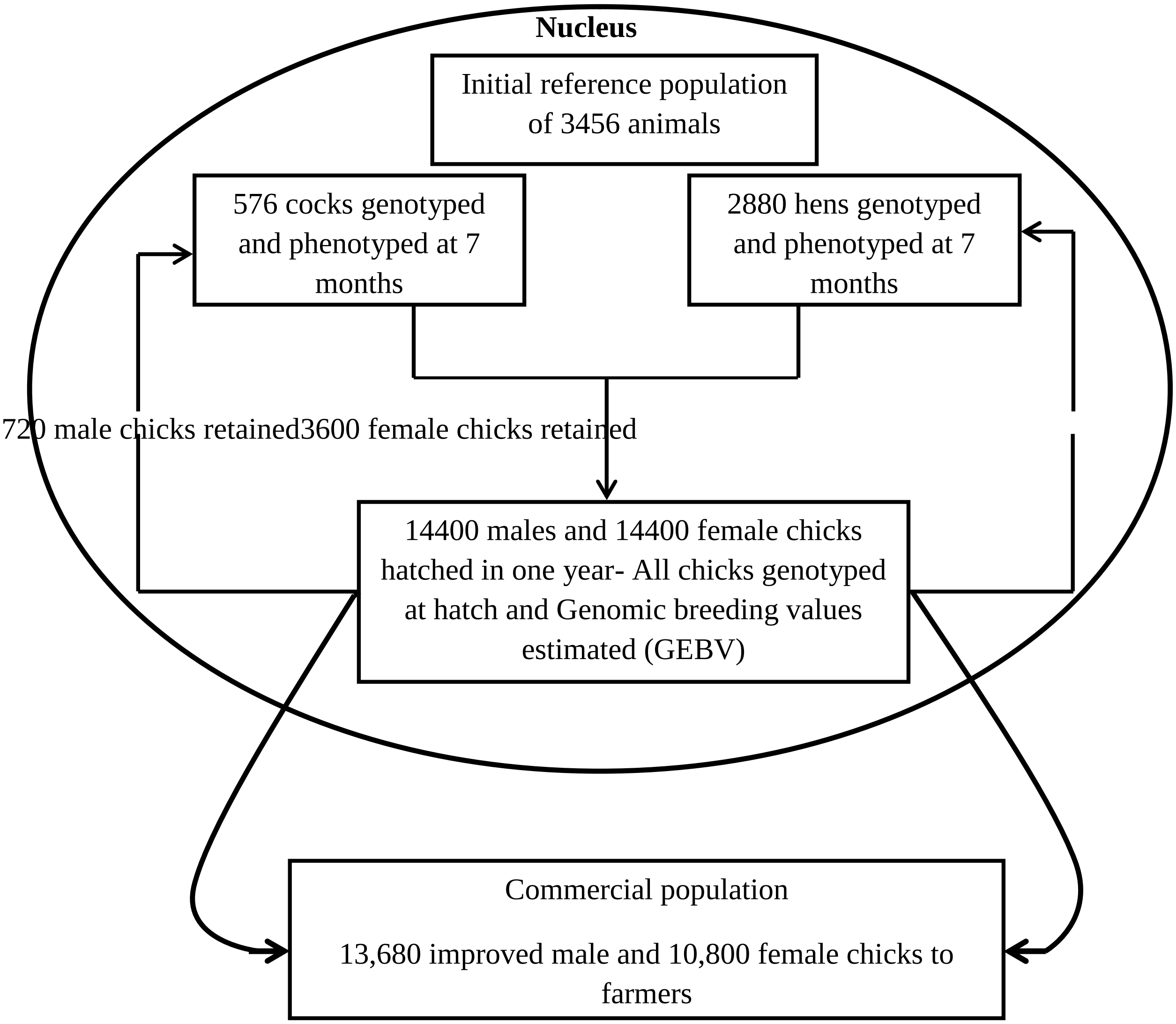

Figure 5. 1 The nucleus population and interaction with the commercial population

5.4 Potential challenges and sustainability of the alternative IC breeding programme

Establishment of sustainable breeding programmes has been a challenge in the developing countries. This has been attributed to small flock sizes, lack of pedigree and performance recording, poor infrastructure, political instabilities and lack of funds (Ampaire & Rothschild, 2010; Kimenyi *et al*., 2014; Wurzinger *et al*., 2011). In addition to these factors, breeding programmes face additional challenge as most IC are owned by smallholder farmers who do not only have capacity but also do not see the value of recording (Ampaire & Rothschild, 2010). Sustainability of a breeding programme requires mass phenotyping and pedigree recording and genotyping if genomic selection is to be adopted. The small flock size could be overcome by sampling the IC genotypes and raising them under the same environment or in different satellite nucleus breeding stations in different counties. In Kenya, this has been achieved to some extent and currently, the ICs are being selected for in government on-stations. The implementation of GS in the current breeding scheme, however, could be a challenge due to high cost of genotyping the initial and additional reference populations and the offsprings produced in the nucleus in each generation (Wolc *et al*., 2016). This challenge, however, could be mitigated by use of medium or low-density markers. The use of such markers has been demonstrated to significantly reduce the cost of genotyping as they are cheaper than high-density marker(Meuwissen *et al*. 2015).Adoption of such strategies would go a long way in reducing the cost of chicks to the farmers and for maintenance of the operational activities in the nucleus.

The lethargy of farmers to recording could be overcome by forming farmer group organizations where each member subscribes to own shares in the organisation. The share capital is used by the organization to build infrastructure to raise chicken. Such farmer organizations would be linked to the breeding programme. Such linkages would be beneficial for three reasons: First, the farmer organization would be able to sponsor their member for capacity building on chicken production management. This will improve efficiency of production since genetic improvement alone would not enable the improved chicken to realise their genetic potential without improved management. Secondly, the farmers can be involved in all in- all out, programme as they can have contract with the nucleus for a reliable supply of replacement stock and they can be able to procure inputs such as feeds at reduced prices because of purchasing in bulks. Thirdly, the nucleus could benefit, by recruiting best performing candidates from the farmer’s organization flocks to open up the nucleus. This would increase genetic diversity within the nucleus leading to a sustainable breeding programme.

5.5 General Conclusions

The general objective of this study was to contribute to genetic improvement of IC through estimation of pooled parameter estimates, accounting for Bulmer effect in response to selection and integration of genomic selection in IC breeding programme. From the findings, it can be concluded that:

i. Pooled genetic and phenotypic parameters differ from parameters obtained from single studies and can be considered as more precise as they have been obtained from a large data set
ii. Non-consideration of the reduction of genetic variance due to selection leads to over-estimation of genetic gains in IC breeding programmes
iii. Genomic selection optimises response to selection and control rates of inbreeding in IC breeding

5.6 Recommendations for researchers

i. Pooled parameters should be utilised in modelling IC breeding programmes
ii. Reduction in genetic variance due to selection should be accounted for in predictions of response to selection in IC breeding programmes
iii. Genomic selection should be used as a strategy for optimisation of genetic gain and reduction or maintenance of rates of inbreeding in IC populations

5.7 Research gaps

i. More studies should be done to obtain feed efficiency, immunity and egg production genetic and phenotypic parameters for indigenous chicken
ii. Stochastic modelling can be done for both conventional and genomic selection strategies to estimate the genetic gain and profitability since response to selection is estimated per individual animal in a breeding programme.
iii. A modelling approach that not only estimate rates of genetic gain and inbreeding but also compute both the cost and profit in a breeding programme should be considered.

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APPENDICES

Appendix A: SAS Output for Weighted Heritability for Body Weight at Eight Weeks for Objective One

```
 The SAS System 14:34 Thursday, May 26, 2020   1

                          The GLM Procedure

                        Class Level Information

                 Class Levels  Values

study   16  ampnsa asuquo bahman cahyadi dana firozja iraqi2 iraqi22 lwrmira lwrmra

             manjeli padhi prado rahman reddy zonuz

                   Number of Observations Read          17

                   Number of Observations Used          17

The SAS System        14:34 Thursday, May 26, 2020   2

                          The GLM Procedure

Dependent Variable: h2bw8

Weight: w

Sum of

    Source                  DF        Squares     Mean Square    F Value    Pr > F

    Model                   15     238.0857022      15.8723801    2301.46    0.0164

    Error                    1       0.0068967       0.0068967

    Corrected Total             16     238.0925989

              R-Square     Coeff Var      Root MSE    h2bw8 Mean

              0.999971      38.31680      0.083046      0.216735

    Source                  DF       Type I SS     Mean Square    F Value    Pr > F

    study                   15     238.0857022      15.8723801    2301.46    0.0164

    Source                  DF     Type III SS     Mean Square    F Value    Pr > F

    study                   15     238.0857022      15.8723801    2301.46    0.0164

The SAS System        14:34 Thursday, May 26, 2020   3

                          The GLM Procedure

       Source               Type III Expected Mean Square

       study               Var(Error) + 758.56 Var(study)
```

Appendix B: SAS Output for Weighted Heritability for Body Weight at Twelve Weeks for Objective One

```
The SAS System         14:52 Thursday, May 26, 2020   5

                                 The GLM Procedure

Dependent Variable: h2bw12

Weight: w

Sum of

     Source                  DF        Squares     Mean Square    F Value    Pr > F

     Model                    16     61.77521141      3.86095071      59.89    0.0006

     Error                   4      0.25786803      0.06446701

     Corrected Total            20     62.03307944

                  R-Square     Coeff Var      Root MSE    h2bw12 Mean

                  0.995843      109.2707      0.253904       0.232362

     Source                  DF       Type I SS     Mean Square    F Value    Pr > F

     study                  16     61.77521141      3.86095071      59.89    0.0006

     Source                  DF     Type III SS     Mean Square    F Value    Pr > F

     study                  16     61.77521141      3.86095071      59.89    0.0006

     The SAS System         14:52 Thursday, May 26, 2020   6

The GLM Procedure

        Source                Type III Expected Mean Square

        study                Var(Error) + 214.54 Var(study)
```

Appendix C: SAS Output for Weighted Heritability for Egg number at Twelve Weeks for Objective One

```
The SAS System        14:52 Thursday, May 26, 2020  11

                          The GLM Procedure

Dependent Variable: h2en12

Weight: w

Sum of

    Source                 DF        Squares     Mean Square    F Value    Pr > F

    Model                   5     88.44926460     17.68985292       9.04    0.2471

    Error                  1      1.95686901      1.95686901

    Corrected Total           6     90.40613361

              R-Square     Coeff Var      Root MSE    h2en12 Mean

              0.978355      1158.721      1.398881       0.120726

    Source                 DF       Type I SS     Mean Square    F Value    Pr > F

    study                  5     88.44926460     17.68985292       9.04    0.2471

    Source                 DF     Type III SS     Mean Square    F Value    Pr > F

    study                  5     88.44926460     17.68985292       9.04    0.2471

The SAS System        14:52 Thursday, May 26, 2020  12

The GLM Procedure

       Source                Type III Expected Mean Square

       study                Var(Error) + 4630.7 Var(study)
```

Appendix D: SelAction Outputs for Objectives Two and Three

```
SelAction Version 2.1, licensed to Test licence, Marc Rutten and Piter Bijma
 These results were generated 5/26/2020, 3:15:09 PM
 Using input from  File: C:\Users\laptop\Desktop\LS submitted to on 20-11-2019 wensday\cs
480 input FRIDAY
13th.d1s
  TRAITS USED
EN
             BW
             Ab
    AFE
  TRAIT PARAMETERS
 phenotypic variance  heritability
             EN       130.6400        0.1200
             BW    15,627.5000         0.2400
             Ab        39.4400         0.2700
            AFE       144.2400         0.2500
PHENOTYPIC CORRELATIONS
BW    Ab    AFE
 EN     0.08 -0.02 -0.36
 BW          -0.05 -0.10
 Ab                0.00
GENETIC CORRELATIONS
BW    Ab    AFE
 EN    -0.12 -0.04 -0.30
 BW          -0.07 0.05
 Ab               -0.04
BREEDING GOAL INFORMATION
        -0.0887 * EN
         0.7346 * BW
        -0.1394 * Ab
```

```
         0.0905 * AFE
  POPULATION SIZE
 number of selected male parents : 96
 number of selected female parents : 480
    number of male selection candidates per dam : 5.0
  number of female selection candidates per dam : 5.0
  total selected proportion male parents : 0.040
  total selected proportion female parents : 0.200
  CHARACTERISTICS OF THE USED GROUPS
  full-sib group 1 with        4.0 animals
  full-sib group 2 with        5.0 animals
  half-sib group 1 with        2.0 dams, producing       20.0 animals
  half-sib group 2 with        2.0 dams, producing       20.0 animals
  INDEX INFORMATION FOR MALE CANDIDATES:
 Own performance on EN
 Dam BLUP breeding value on EN
 Sire BLUP breeding value on EN
 Observations on full-Sib group 2 on EN
 Observations on half-sib group 2 on EN
 Mean EBV of the dams of hs-group 2 on EN
 Own performance on BW
  Dam BLUP breeding value on BW
  Sire BLUP breeding value on BW
 Observations on full-Sib group 1 on BW
 Observations on full-Sib group 2 on BW
 Observations on half-sib group 1 on BW
 Observations on half-sib group 2 on BW
 Mean EBV of the dams of hs-group 1 on BW
 Mean EBV of the dams of hs-group 2 on BW
 Own performance on Ab
  Dam BLUP breeding value on Ab
```

Sire BLUP breeding value on Ab

Observations on full-Sib group 1 on Ab

Observations on full-Sib group 2 on Ab

Observations on half-sib group 1 on Ab

Observations on half-sib group 2 on Ab

Mean EBV of the dams of hs-group 1 on Ab

Mean EBV of the dams of hs-group 2 on Ab

Dam BLUP breeding value on AFE

Sire BLUP breeding value on AFE

Observations on full-Sib group 2 on AFE

Observations on half-sib group 2 on AFE

Mean EBV of the dams of hs-group 2 on AFE

INDEX INFORMATION FOR FEMALE CANDIDATES:

Own performance on EN

Dam BLUP breeding value on EN

Sire BLUP breeding value on EN

Observations on full-Sib group 1 on EN

Observations on half-sib group 2 on EN

Mean EBV of the dams of hs-group 2 on EN

Own performance on BW

Dam BLUP breeding value on BW

Sire BLUP breeding value on BW

Observations on full-Sib group 1 on BW

Observations on full-Sib group 2 on BW

Observations on half-sib group 1 on BW

Observations on half-sib group 2 on BW

Mean EBV of the dams of hs-group 1 on BW

Mean EBV of the dams of hs-group 2 on BW

Own performance on Ab

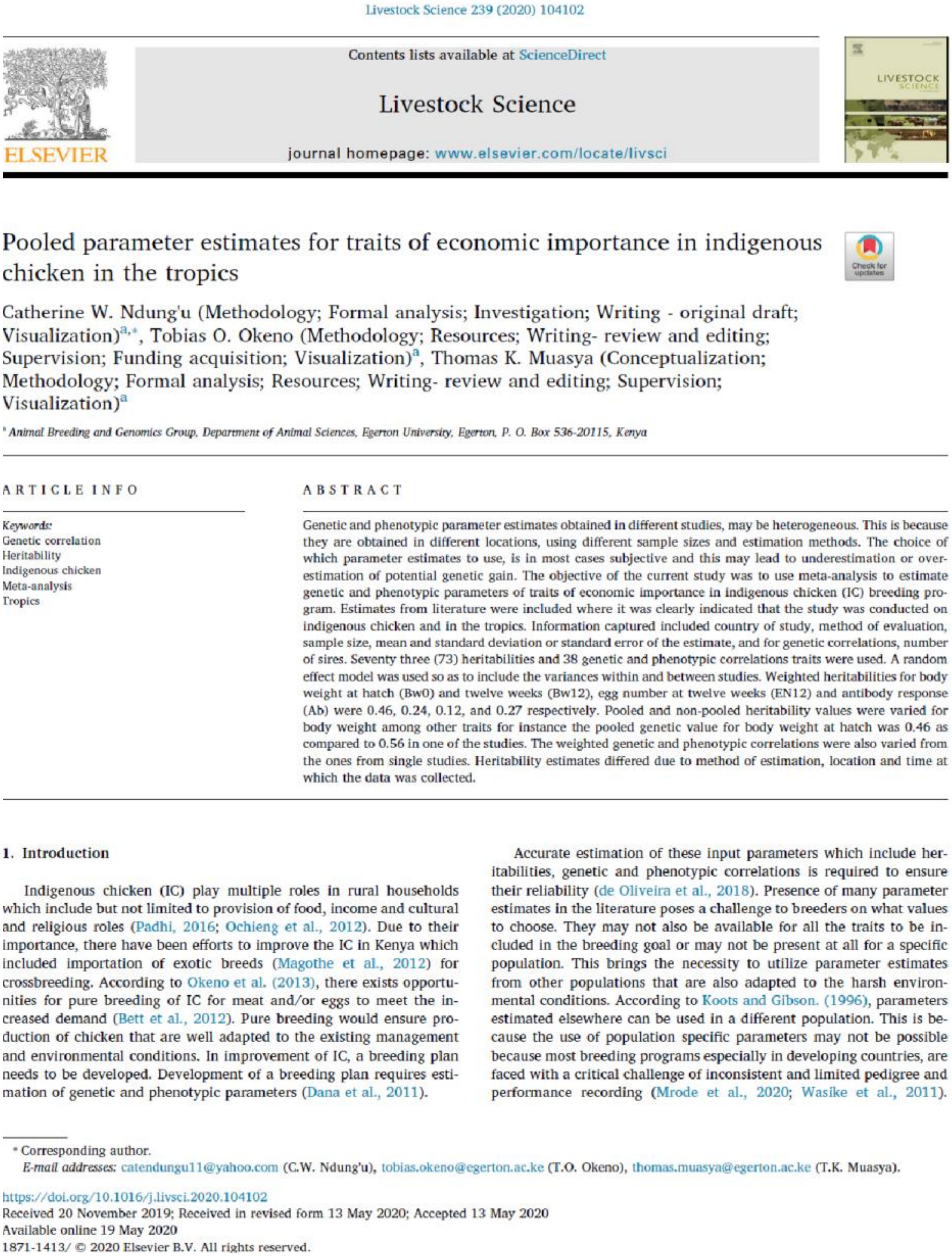
Dam BLUP breeding value on Ab

Sire BLUP breeding value on Ab

```
Observations on full-Sib group 1 on Ab
Observations on full-Sib group 2 on Ab
Observations on half-sib group 1 on Ab
Observations on half-sib group 2 on Ab
Mean EBV of the dams of hs-group 1 on Ab
Mean EBV of the dams of hs-group 2 on Ab
Own performance on AFE
Dam BLUP breeding value on AFE
Sire BLUP breeding value on AFE
Observations on half-sib group 1 on AFE
Mean EBV of the dams of hs-group 1 on AFE
          ******************   RESULTS   ********************
 EQUILIBRIUM PARAMETERS
            phenotypic variance  heritability
          EN       130.5335         0.1193
          BW    14,819.3409         0.1986
          Ab        39.4216         0.2697
         AFE       144.1608         0.2496
  PHENOTYPIC CORRELATIONS
BW    Ab    AFE
 EN     0.09 -0.02 -0.36
 BW          -0.05 -0.11
 Ab                 0.00
  GENETIC CORRELATIONS
BW    Ab    AFE
 EN    -0.09 -0.04 -0.30
 BW          -0.06  0.03
 Ab                -0.04
  RESPONSE
 males        females        total
          EN
```

```
 trait units:          -0.384         -0.252         -0.636
           economic units:           0.034          0.022          0.056
       % of total response:           0.083          0.055          0.138
             BW
             trait units:          33.554         21.874         55.427
           economic units:          24.648         16.068         40.717
       % of total response:          60.329         39.329         99.658
             Ab
             trait units:          -0.158         -0.105         -0.264
           economic units:           0.022          0.015          0.037
       % of total response:           0.054          0.036          0.090
            AFE
             trait units:           0.253          0.262          0.515
             economic units:           0.023          0.024          0.047
       % of total response:           0.056          0.058          0.114
TOTALRESPONSE
males         females         total
            economic units:          24.728         16.129         40.857
         variance of index:        532.044        534.655
        variance of breeding goal:       1,594.660
        accuracy of index:          0.578          0.579
increase of inbreeding:            0.668 % per generation
    ****** end of output  **
```

Appendix E: Abstract of Published Paper on ObjectiveOne



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Pooled parameter estimates for traits of economic importance in indigenous chicken in the tropics

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ABSTRACT

Genetic and phenotypic parameter estimates obtained in different studies, may be heterogeneous. This is because they are obtained in different locations, using different sample sizes and estimation methods. The choice of which parameter estimates to use, is in most cases subjective and this may lead to underestimation or overestimation of potential genetic gain. The objective of the current study was to use meta-analysis to estimate genetic and phenotypic parameters of traits of economic importance in indigenous chicken (IC) breeding program. Estimates from literature were included where it was clearly indicated that the study was conducted on indigenous chicken and in the tropics. Information captured included country of study, method of evaluation, sample size, mean and standard deviation or standard error of the estimate, and for genetic correlations, number of sires. Seventy three (73) heritabilities and 38 genetic and phenotypic correlations traits were used. A random effect model was used so as to include the variances within and between studies. Weighted heritabilities for body weight at hatch (Bw0) and twelve weeks (Bw12), egg number at twelve weeks (EN12) and antibody response (Ab) were 0.46, 0.24, 0.12, and 0.27 respectively. Pooled and non-pooled heritability values were varied for body weight among other traits for instance the pooled genetic value for body weight at hatch was 0.46 as compared to 0.56 in one of the studies. The weighted genetic and phenotypic correlations were also varied from the ones from single studies. Heritability estimates differed due to method of estimation, location and time at which the data was collected.

1. Introduction

Indigenous chicken (IC) play multiple roles in rural households which include but not limited to provision of food, income and cultural and religious roles (Padhi, 2016; Ochieng et al., 2012). Due to their importance, there have been efforts to improve the IC in Kenya which included importation of exotic breeds (Magothe et al., 2012) for crossbreeding. According to Okeno et al. (2013), there exists opportunities for pure breeding of IC for meat and/or eggs to meet the increased demand (Bett et al., 2012). Pure breeding would ensure production of chicken that are well adapted to the existing management and environmental conditions. In improvement of IC, a breeding plan needs to be developed. Development of a breeding plan requires estimation of genetic and phenotypic parameters (Dana et al., 2011).

Accurate estimation of these input parameters which include heritabilities, genetic and phenotypic correlations is required to ensure their reliability (de Oliveira et al., 2018). Presence of many parameter estimates in the literature poses a challenge to breeders on what values to choose. They may not also be available for all the traits to be included in the breeding goal or may not be present at all for a specific population. This brings the necessity to utilize parameter estimates from other populations that are also adapted to the harsh environmental conditions. According to Koots and Gibson. (1996), parameters estimated elsewhere can be used in a different population. This is because the use of population specific parameters may not be possible because most breeding programs especially in developing countries, are faced with a critical challenge of inconsistent and limited pedigree and performance recording (Mrode et al., 2020; Wasike et al., 2011).

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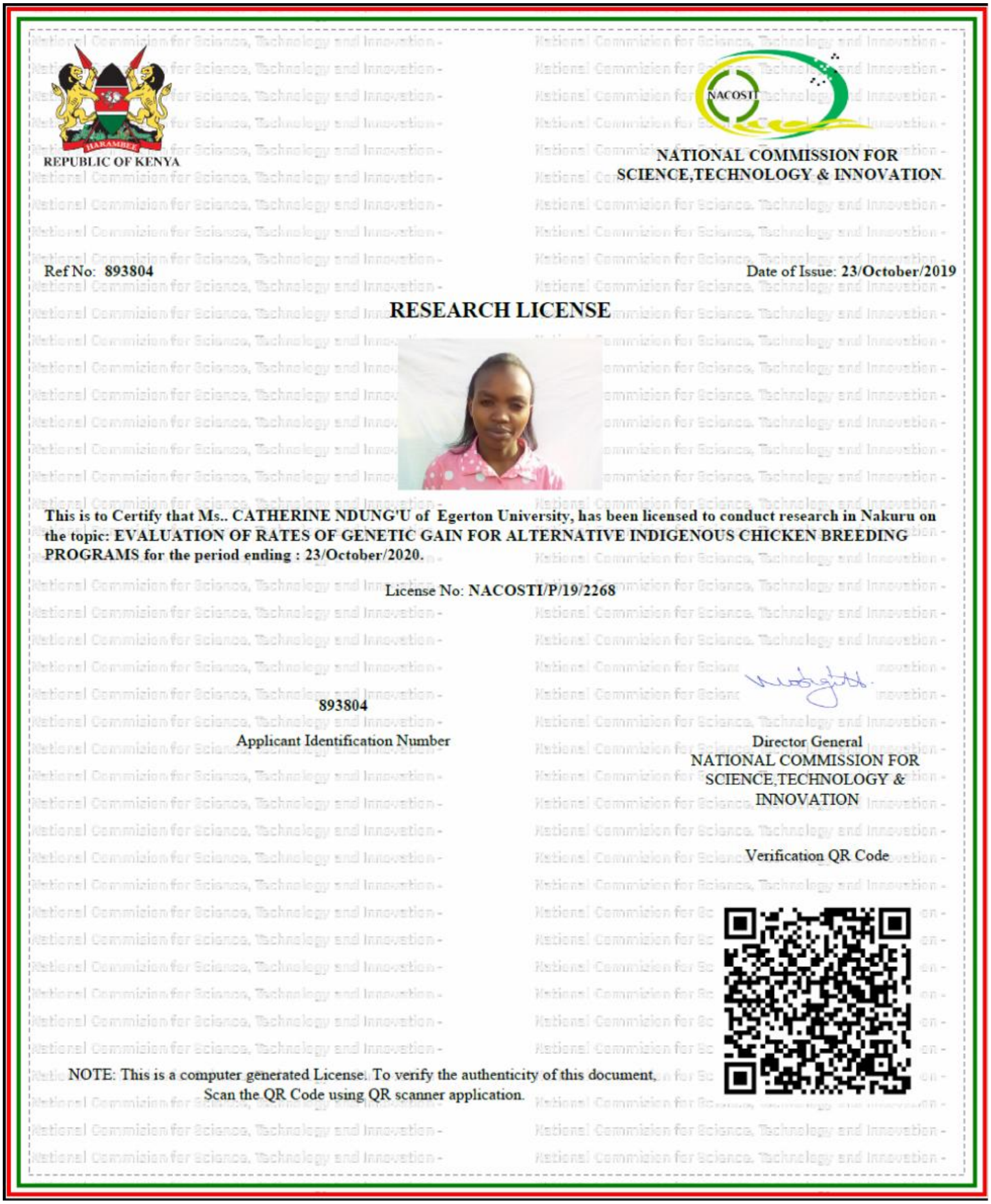

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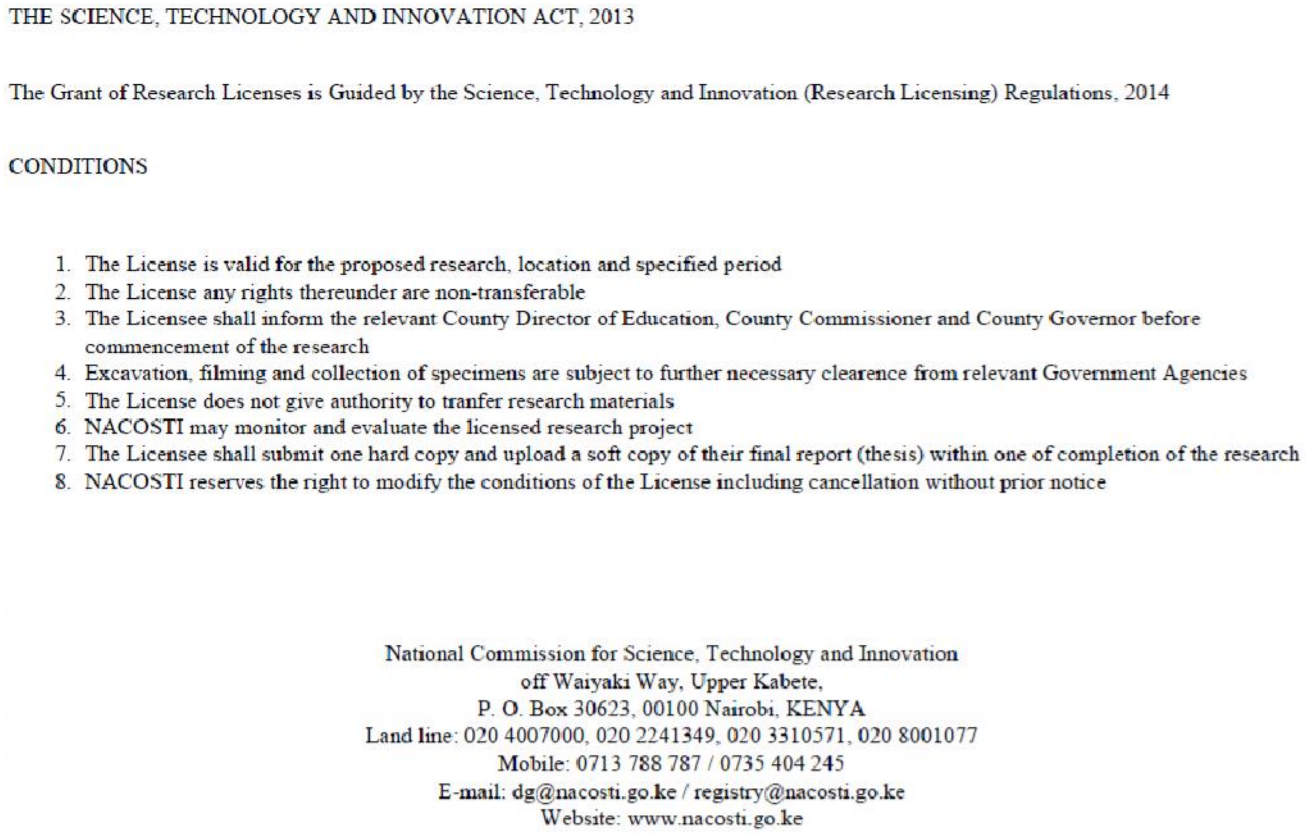

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