GENETIC EVALUATION OF NET FEED EFFICIENCY IN INDIGENOUS CHICKEN IN KENYA

Miyumo Sophie Atieno

A Thesis submitted to the Graduate School in Partial Fulfillment for the Requirements of the award of Master of Science Degree in Animal Breeding and Genetics of Egerton University

EGERTON UNIVERSITY

NOVEMBER, 2017

DECLARATION AND RECOMMENDATION

Declaration

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

Miyumo Sophie Atieno
KM11/3311/12

Signature: ________________ Date: 15/11/2017

Recommendation

This thesis is the candidate's original work and has been prepared with our guidance and assistance; it has been submitted with our approval as the official university supervisors.

Prof. Dr. Alexander K. Kahi
Department of Animal Sciences
Egerton University, Kenya

Signature: ________________ Date: 15/11/2017

Dr. Chrilukovian B. Wasike
Department of Animal Sciences,
Maseno University,

Signature: ________________ Date: 15/11/2017

COPYRIGHT

ACKNOWLEDGEMENTS

First and foremost, I give all the glory to the Almighty God for successful completion of this study. I would like to acknowledge several institutions and individuals whose help and support in one way or another culminated in successful completion of this study. With gratitude, I recognize the role played by Egerton University’s Graduate School and Department of Animal Sciences for offering me the opportunity to pursue postgraduate studies. I am deeply indebted to the Smallholder Indigenous Chicken Improvement Programme (InCIP) hosted by the Centre of Excellence for Livestock Innovation and Business (CoELIB) at Egerton University for the financial support through fee payment and research funds, and for allowing me to use facilities at the poultry unit for data collection.

I am grateful to my supervisors, Prof. Dr. Alexander K. Kahi and Dr. Chrilukovian B. Wasike for their technical advice, guidance, professional supervision, inspiration, mentorship and unlimited support during the entire study period. I also recognize the immense support I received from Dr. Thomas K. Muasya in terms of data analysis. The unwavering kind technical support and advice on presentation skills from Dr. Tobias O. Okeno and Dr. Anthony Kingori are highly appreciated. Thank you Mr. Joel O. Khobondo for the many discussions, insights and directions you provided during my research period. My sincere thanks to the CoELIB Director, Prof. Dr. Alexander K. Kahi, for the opportunity to work for the InCIP programme during my study period which has greatly contributed to my experience during the research work. I wish to appreciate my colleagues at InCIP poultry unit, Mr. Joseph Gachoki and Mr. Churchil Arogo, for their support during production of experimental flock and data collection. I highly appreciate Mr. Victor Onyango Otieno of CoELIB Media for his endless IT support. Finally, I also wish to thank my fellow colleagues the entire CoELIB staff team and fellow postgraduate students from the Department of Animal Science for the moral support and encouragement.

ABSTRACT

Indigenous chicken are a valuable asset and form an integral part of many households in Kenya in terms of food security, economic and social roles. Given their value to the agricultural sector, various interventions are being developed and implemented to realize their potential in the sector. Such interventions involve genetic improvement of production traits which directly translate to increased revenues. However, this is likely to be accompanied with increased inputs, especially feed resources, to complement the high performance. Feed costs account for a major portion of production costs. Therefore, considering feed efficiency in genetic improvement provides an avenue to reduce costs. The objective of this study was to assess the genetics of net feed efficiency (NFE) in indigenous chicken by identifying non-genetic and genetic sources of variation, estimating genetic and phenotypic parameters and determining the relationship between feed efficiency and production traits. Residual feed intake (RFI), residual gain (RG), and residual intake and gain (RIG) were used as measures of NFE, estimated from weekly body weight and feed intake records between 11 to 20 weeks of age. Non-genetic sources of variation were determined using a general linear model. Genetic and phenotypic parameters were estimated using random regression sire model while the relationship between efficiency and production traits (growth, feed intake and maintenance requirement) were determined by multivariate sire models. Sex, hatch group and interaction between sex and cluster significantly influenced ($P<0.05$) variation in growth and efficiency traits. The NFE traits had considerable genetic variation; the variance declined as age progressed in the case of RFI (112.55g to 6.75g) and RG (6.01g to 0.03g) while the estimates increased throughout the experiment in RIG (17.27g to 1950.11g). The heritability estimates ranged from 0.34 to 0.13 for RFI, 0.77 to 0.00 for RG and 0.67 to 0.98 for RIG, following similar trends as their respective genetic variances. The genetic relationship between feed efficiency and production traits varied with age with estimates being significant in some ages while others had no relationship. The moderate to high heritability estimates show that use of RFI at 98 days (0.34), RG at 91 days (0.30) and RIG at 98 days (0.52) and 119 days (0.48) in breeding programmes aimed at improving meat production would be the most effective. Considering correlated responses on production traits, selection for RG between 77 and 91 days of age would be the most suitable. This is because it was associated with higher growth rates (0.55 to 0.42) and equally improve RFI (-0.67 to -0.99) and RIG (0.46 to 0.73). Consequently, improved RG between 77 and 91 days of age will not have significant influence on feed intake (0.04 to 0.14) and maintenance requirement (0.05 to 0.19). The results from this study need to be applied with caution given the high standard errors for the genetic parameters resulting from the small sample size and single generation of birds. In conclusion, there is scope for genetic improvement of feed efficiency alongside production traits in indigenous chicken breeding programmes.

TABLE OF CONTENT

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE
GENERAL INTRODUCTION

1.1 Background

Indigenous chicken (IC) account for over 70% of the total poultry population in Kenya. These chicken significantly contribute to the socio-economic and nutritional needs of many households in both urban and rural areas (FAO, 2010). The IC industry has tremendously grown in terms of population of birds and quantity of meat and eggs produced in response to increased demand for their products (Magothe *et al*., 2012). This shows the potential of IC in generating higher income and transforming living standards of households. However, appropriate interventions along the IC product value chain have to be considered; from production to marketing of the products to ensure full potential is realised. Several studies have been carried out on genetic diversity, production systems, breeding goals and marketing systems to provide relevant information for developing efficient production and marketing strategies towards commercializing IC (Magothe *et al*., 2010; Magothe *et al*., 2011; Bett *et al*., 2012; Okeno *et al*., 2012; Ngeno *et al*., 2013; Okeno *et al*., 2013a, 2013b; Ngeno *et al*., 2015).

Evaluation of consumption patterns of IC products show that meat accounts for a higher proportion of products consumed than eggs (Pym *et al*., 2006). This is partly due to the widespread practice of allowing hens to incubate and hatch most of the eggs laid and hence the high economic value attached to growth and body weights traits of the birds (Okeno *et al*., 2011). Consequently, the focus of most improvement programmes is on these traits in order to increase the slaughter weight at maturity. Considering that IC are largely reared under extensive systems, nutrient concentrations of scavenge feed resources may not match the improvement in growth traits. This is because birds may not obtain nutrients sufficient to meet maintenance and growth requirements (Kingori *et al*., 2004).

In commercial poultry industry, feed supply to the fast growing birds is identified as a major constraint since it consitutes about 60% to 70% of the total cost of production (Aggrey and Rekaya, 2013). Boddicker *et al*. (2011) demonstrated that selection for improved performance led to both increased feed consumption and feed conversion, a reflection of the strong and antagonistic relationship between production and feed intake. In this case, genetic improvement on production with no regard to changes in feed intake is likely to increase input costs resulting to reduced production efficiency. In an attempt to enhance production efficiency in the livestock industry, feed efficiency is targeted as a means to optimize biological productivity and profitability.

Feed efficiency refers to the amount of saleable product produced for each unit of feed consumed and is expressed as either gross feed efficiency or net feed efficiency (Binda *et al*., 2012). Gross feed efficiency, mostly measured by feed conversion ratio (FCR), assumes that the total amount of feed consumed is directed to production with no regard to how feed is partitioned for various functions in the body (Varkoohi *et al*., 2011). This assumption and the statistical properties associated with FCR (a ratio trait) prevents gross feed efficiency from being an ideal measure of efficiency (Willems *et al*., 2013). Net feed efficiency (NFE) refers to the efficiency of feed utilization after accounting for the requirements for growth and maintenance of body tissues (Aggrey *et al*., 2010). It is measured by residual feed intake (RFI), residual body weight gain (RG) or residual intake and weight gain (RIG) (Crowley *et al*., 2010; Berry and Crowley, 2012). Residual feed intake is the difference between actual feed intake and that predicted on the basis of requirements for production and maintenance. Similarly, RG is the difference between actual body weight gain and that predicted on the basis of daily feed intake and maintenance requirement. Residual intake and gain combines the benefits of both RFI and RG in a linear function with the purpose to identify animals that are feed efficient and fast-growing while being independent of maintenance requirement. Net feed efficiency traits have been used in the beef and poultry industry to improve efficiency in feed utilization (Aggrey *et al*., 2010; Berry and Crowley, 2012; Case *et al*., 2012; Willems *et al*., 2013). In IC, NFE traits have not been measured largely because they are raised under free range systems. However with confinement, it is important that their feed use efficiency is determined for efficient production.

1.2 Statement of the problem

In developing breeding objectives, traits that influence revenue and costs in the production system have to be identified. In indigenous chicken, most of improvement programmes emphasize selection on traits that directly influence revenue such as weight gain and egg production with little attention paid to traits that influence costs of production. One of the traits not given attention is net feed use efficiency measured by RFI, RG and RIG. Consequently, performance, estimates of genetic parameters and relationships for net feed efficiency measures are lacking to facilitate selective breeding. Ignoring net feed efficiency in the breeding objective biases the breeding objective upwards by underestimating feed costs and thus overestimating profitability. This in turn undermines the realised response to selection.

1.3 Objectives

The overall objective of this study was to contribute to improved and efficient productivity of indigenous chicken in Kenya through the assessment of the genetic variability of net feed use efficiency. The specific objectives were:

1. To determine the non-genetic sources of variation and temporal variability in growth and net feed efficiency traits in indigenous chicken.
2. To estimate the genetic and phenotypic parameters for net feed efficiency traits in indigenous chicken.
3. To determine the genetic and phenotypic relationship between net feed efficiency traits and production traits.

1.4 Research questions

1. Does sex, cluster, genotype, hatch and age affect growth and net feed efficiency traits in indigenous chicken?
2. What are the estimates of the genetic and phenotypic parameters for net feed efficiency traits in indigenous chicken?
3. What is the magnitude of genetic and phenotypic relationship between net feed efficiency traits and production traits?

1.5 Justification

Feed intake is positively correlated with productive traits; this implies that genetic improvement in productivity will increase feed intake translating to higher production costs. Residual feed intake (RFI), residual body weight gain (RG) and, residual intake and weight gain (RIG) as measures of net feed efficiency provide avenues for genetic improvement of feed efficiency in IC. Quantifying genetic variation in net feed efficiency traits in IC flock helps to identify the most efficient birds since this reflects differences in efficiency with which birds use feed for production and maintenance requirement. In addition, feed efficient birds are valuable in environments vulnerable to climate change that result to fluctuations in quality and quantity of feed resources. An analysis of the genetics of feed intake establishes the scope of variation in this trait thus enabling selective breeding for this trait.

References

Aggrey, S. E., Karnuah, B. A., Sebastian, B., and Anthony, N. B. (2010). Genetic properties of feed efficiency parameters in meat-type chickens. *Genetics Selection Evolution, 42*, 25-30.

Aggrey, S. E., and Rekaya, R. (2013). Dissection of Koch's residual feed intake: Implications for selection. *Poultry Science, 92,* 2600-2605.

Berry, D. P., and Crowley, J. J. (2012). Residual intake and body weight gain: A new measure of efficiency in growing cattle. *Journal of Animal Science, 90*, 109-115.

Bett, H. K., Bett, R. C., Peters, K. J., Kahi, A. K., and Bokelmann, W. (2012). Linking utilisation and conservation of indigenous chicken genetic resources to value chains. *Journal of Animal Production Advances, 2* (1), 33-51.

Binda, B. D., Yousif, I. A., Elamin, K. M., and Eltayeb, H. E. (2012). A comparison of performance among exotic meat strains and local chicken ecotypes under Sudan conditions. *International Journal of Poultry Science, 11 (8),* 500-504.

Boddicker, N., Gabler, N. K., Spurlock, M. E., Nettleton, D., and Dekkers, J. C. M. (2011). Effects of ad libitum and restricted feed intake on growth performance and body composition of yorkshire pigs selected for residual feed intake. *Journal of Animal Science, 89,* 40–51.

Case, L. A., Wood, B. J., and Miller, S. P. (2012). The genetic parameters of feed efficiency and its component traits in turkey (*Meleagris gallopova*). *Genetics Evolution Science, 44*, 2-6.

Crowley, J. J., McGee, M., Kenny, D. A., Crews, D. H., Evans, R. D., and Berry, D. P. (2010). Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *Journal of Animal Science, 44*, 958-972.

FAO. (2010). *Smallholder Poultry Production: Chicken genetic rsources used in smallholder production systems and opportunities for their development.* Food and Agriculture Organization of the United Nations: Rome.

Kingori, A. M., Tuitoek, J. K., Muiruri, H. K., and Wachira, A. M. (2004). Protein requirements of growing indigenous chickens during the 14-21 weeks growing period. *South African Journal of Animal Science, 33* (2), 78-82.

Magothe, T. M., Muhuyi, B. W., and Kahi, A. K. (2010). Influence of major genes for crested-head, frizzled-feather and naked-neck on body weights and growth patterns of indigenous chicken reared intensively in Kenya. *Tropical Animal Health and Production, 42,* 173-183.

Magothe, T. M., Muhuyi, W. B., and Kahi, A. K. (2011). Genetic parameters for egg and body weights of indigenous chicken in Kenya. *Animal Production Society of Kenya, 36*.

Magothe, T. M., Okeno, T. O., Muhuyi, W. B., and Kahi, A. K. (2012). Indigenous chicken production in Kenya: Current status. *World's Poultry Science Association, 68,* 119-132.

Ngeno, K., Magothe, T. M., Okeno, T. O., Bebe, B. O., and Kahi, A. K. (2013). Heritabilities and correlations between body weights and growth curve parameters of indigenous chicken populations reared intensively in Kenya. *Research Journal of Poultry Sciences, 6* (3), 43-52.

Ngeno, K., van der Waaij, E. H., Megens, H. J., Kahi, A. K., van Arendonk, J. A., and Crooijmans, R. P. (2015). Genetic diversity of different indigenous chicken ecotypes using highly polymorphic MHC linked and non-MHC linked microsatellite markers. *Animal Genetic Resources, 56*, 1-3.

Okeno, T. O., Kahi, A. K., and Peters, K. J. (2011). Breed selection practices and traits of economic importance for indigenous chicken in Kenya. *Livestock Research for Rural Development, 23*.

Okeno, T. O., Kahi, A. K., and Peters , K. J. (2012). Characterization of indigenous chicken production systems in Kenya. *Tropical Animal Health and Production, 44*, 601 - 608.

Okeno, T. O., Magothe, T. M., Kahi, A. K., and Peters , K. J. (2013a). Breeding objectives for indigenous chicken: Model development and application to different production systems. *Tropical Animal Health and Production, 70*, 193-203.

Okeno, T. O., Kahi , A. K., and Peters, K. J. (2013b). Evaluation of breeding objectives for purebred and crossbred selection schemes for adoption in indigneous chicken breeding programme. *British Poultry Science, 54*, 62 - 75.

Pym, R. A., Guerne Bleich, E., and Hoffmann, I. (2006). The relative contribution of indigenous chicken breeds to poultry meat and egg consumption in the developing countries of Africa and Asia. *In Conference Proceedings of the XII European Poultry Conference, Italy* (Vol 1014).

Varkoohi, S., Pakdel, A., Moradi Shahr Babak, M., Nejati Javaremi, A., Kause, A., and Zaghari, M. (2011). Genetic parameters for feed utilization traits in Japanese quail. *Poultry Science 90*, 42-47.

Willems, O. W., Miller, S. P., and Wood, B. J. (2013). Assessment of residual body weight gain and residual intake and body weight gain as feed efficiency traits in the turkey (*Meleagris gallopova*). *Genetics Selection Evolution, 45*, 26-34.

CHAPTER TWO

GENERAL LITERATURE REVIEW

2.1. Indigenous chicken production in Kenya

Indigenous chicken (IC) are the most popular and dominant farm species in developing countries due to their capacity to survive and produce under relatively harsh scavenging conditions with very low inputs, and consumer preference for their products (Pym *et al*., 2006; Kingori *et al*., 2010). In Kenya, they represent over 77% of the total poultry population and are widely distributed depending on human population, environmental conditions and availability of feed resources (Thornton *et al*., 2002; Khobondo *et al*., 2014). Consequently, they contribute substantially to food security and socio-economic development to households both in the rural and urban areas (Muchadeyi *et al*., 2007a, 2007b).

Indigenous chicken contribute about 50% and 8% to the poultry meat and egg production and consumption, respectively in developing countries (Njue *et al*., 2002; NAFRI, 2005). The relatively low contribution to meat and egg production is attributed to seasonal effects, low nutrition levels and low genetic potential (Pym *et al*., 2006). However, irrespective of the production potential, the quantity of their products has greatly increased by more than 79% and 34% for meat and egg, respectively (Magothe *et al*., 2012). This is as a result of the increase in the human population with a consequent increase in demand for proteins as well as increase in health consciousness among the human population that favour presumed organic and lean characteristic (Kingori *et al*., 2010). Generally, the production and consumption of meat from IC is higher than eggs given that a large proportion of the laid eggs (over 80%) are set under the hen to produce chicks while hens are required to go broody and rear chicks before resuming production (Henning *et al*., 2005).

Indigenous chicken consists of a heterogenous population classified on the basis of feather morphology resulting from expression of major genes (Normal feather, naked neck, crested head, frizzle feather and feathered shank), body size (giant-type and dwarf-type) and according to region of placement (ecotype) (Magothe *et al*., 2010; Okeno *et al*., 2012; Mwacharo *et al*., 2013). Molecular characterization using non-MHC (major histocompatibility complex) linked microsatellite markers indicate that the degree of genetic variation within population in Kenya is moderate to low, with birds clustered into four genetic groups: Coastal-Lamu, Eastern, Northern and a combination of Western and Rift valley region (Mwacharo *et al*., 2007; Ngeno *et al*., 2015).

2.2. Comparative performance of growth and feed utilization in indigenous chicken

Indigenous chicken are mostly kept for meat. Over 80% of the eggs laid are used for hatching, purposely to maintain flock sizes. This justifies an emphasis on growth traits, in addition to the economic value attached to these traits by actors along the indigenous chicken value chain (Okeno *et al*., 2011). Most research has focused on growth to identify high performing genotypes and ecotypes to provide information required to develop genetic improvement programmes. Mean performance estimates for growth and body weight presented in Table 2.1 show that on average, indigenous chicken grow at a rate of 8.50g/day to attain a weight of 1.3kg by 20 weeks. However, when comparing their performance between production systems with different levels of inputs there was significant variation where birds under intensive systems have higher growth rates and body weights than in low input systems (Demeke, 2003; Gondwe and Wollny, 2005; Lwelamira *et al*., 2012).

Various groups of indigenous chicken classified by genotype and ecotype, exhibited significant variation in growth performance when exposed to similar environmental conditions (Table 2.1). This suggests that the differences could be due to genetic factors. However, the observed delay in manifestation of variation in body weight during the early period of growth after hatch, possibly due to the fact that significant growth is observed after age at point of inflection (Oke, 2011). Given that growth and body weight are time series traits, variation in their performance would be expected to vary with age across the different genetic groups since growth involves large number of genes being activated and deactivated at different stages of growth (Ngeno, 2012). The variation in performance across studies is an indication that different genotype/ecotype have different sensitivity to changes in the environment (Bourdon, 2000).

Table 2.1: Comparative performance of growth and feed utilization in indigenous chicken

Country	System	Type	Traits [4]					Source
			BW_0	BW_8	BW_{20}	ADG	FCR	
Ethiopia	Intensive	IC[1]		240.0^{a}	1300.0^{a}	9.28^{a}	11.1	Demeke (2003)
	Extensive	IC		197.0^{b}	985.0^{b}	7.03^{b}		
		Genotype[2]						
Kenya	Intensive	Nana	32.6^{a}	454.6^{a}	1356.8^{a}	9.69^{a}		Magothe *et al*. (2010)
		Nana	33.0^{a}	429.9^{b}	1235.0^{b}	8.82^{b}		
		Frfr	33.0^{a}	426.4^{b}	1289.1^{ab}	9.20^{ab}		
		Crcr	33.0^{a}	442.7^{ab}	1269.0^{b}	9.06^{b}		
Nigeria	Intensive	Nana	22.3^{c}	184.8^{b}	1210.0^{b}		19.3^{a}	Oke (2011)
		Nana	24.4^{bc}	216.0^{b}	1300.0^{b}		10.9^{b}	
		Frfr	30.9^{a}	260.2^{a}	1543.0^{a}		19.6^{a}	
		NaFr	27.2^{ab}	249.2^{a}	1460.0^{a}		6.35^{c}	
Ghana	Intensive	Nana	33.1^{a}	588.3^{b}	1581.0^{c}		3.3^{a}	Hagan and Adjei, (2012)
		Nana	32.2^{a}	603.8^{a}	1676.0^{b}		2.9^{b}	
		Frfr	32.5^{a}	600.3^{a}	1650.0^{b}		2.9^{b}	
		NaFr	33.5^{a}	598.8^{a}	1870.0^{a}		2.4^{c}	
		Ecotype[3]						
Kenya	Intensive	Bomet	32.8^{b}	488.8^{b}	1254.9^{a}			Ngeno (2012)
		Kakamega	33.7^{a}	591.1^{a}	1387.8^{a}			
		Bondo	33.2^{a}	523.9^{a}	1392.6^{a}			
		Narok	32.3^{b}	460.3^{c}	1226.5^{a}			
Tanzania	Intensive	Kuchi		541.0^{a}	1706.0^{a}	12.19^{a}		Lwelamira (2012)
	Extensive			375.0^{b}	1240.0^{b}	8.86^{b}		

[1] IC = Indigenous Chicken; [2] Genotype means genetic groups of indigenous chicken based on morphological differences: nana = normal feathered, Nana = naked neck, Frfr = frizzle feathered, Crcr = crested head, NaFr = cross between naked neck and frizzle feathered chicken; [3] Ecotype means groups of indigenous chicken originating from a particular ecological zone

[4] BW = body weight in grams at various weeks of age (week 0, 8 and 20), FCR = feed conversion ratio, ADG = average daily gain.

^{abc} Means in a column for each study with one or more letter superscripts in common are not significantly different ($p<0.05$)

Animals that have not been subjected to intensive artificial selection are expected to exhibit high genetic variance which provides scope for selection (Iraqi *et al*., 2002). Moderate to high heritability estimates for body weight between week 0 to week 26 have been reported in indigenous chicken implying that improvements could be made on these traits through genetic selection (Norris and Ngambi, 2006; Magothe *et al*., 2011; Ngeno *et al*., 2013). Comparing heritability across different stages of growth, these studies reported high estimates during the early period of development, followed by a decreasing trend as birds approach maturity. Given that body weight at hatch and at early ages (post-hatch) are determined by both an individual's own genetic potential and the maternal effects (pre-ovopositional and post-ovopositional maternal effects), the confounding effect of both factors may have contributed to the high heritability estimates at early ages (Norris and Ngambi, 2006). Therefore, if selection is to be carried out at younger ages, considering the relationship between direct and maternal effects would optimize genetic progress in a selection programme, especially if an antagonistic relationship between the effects exists. Selection for body weight between week 8 and week 12 is suggested as the most suitable point given the considerable heritability estimates (0.35 – 0.56), lack of maternal influence and high genetic correlation with both juvenile and mature body weights (Norris and Ngambi, 2006; Magothe *et al*., 2011; Ngeno *et al*., 2013).

Since breeding programmes are likely to centralize their activities in controlled and improved environmental conditions, the improvement obtained may be negatively affected under on-farm conditions due to varying levels of genotype by environment interactions (Lwelamira, 2012). As such, commercialization of the genetically improved indigenous chicken will require adoption of good management, at least semi-intensive management, to complement the improved performance and minimize environmental variation (Lwelamira, 2007). However, this is likely to be accompanied by increase in inputs especially feed intake to meet the high productivity and maintenance requirement. If feed resources are limited, improved performance may be a disadvantage because of the partition process where most of the nutrients are diverted to maintenance requirement with little left for production since about 70% to 75% of the total energy intake is directed to maintenance (Okine *et al*., 2004). Therefore, there is need to quantify the amount of feed required by indigenous chicken for production and maintenance as well as the economic contribution of feed supply as an input cost to the total cost of production under improved management.

2.3. Feed efficiency in livestock

Feed efficiency is a functional trait that plays a major role in improving production efficiency by establishing benchmarks and goals for production and finance, which may result in decisions that increase productivity while reducing costs of production (Maddock and Lamb, 2009). It is a measure of how much saleable product is produced for each unit of feed consumed and describes the relationship between input of feed and output of product. In most livestock industries, feed efficiency has been targeted as a means of reducing the cost of production since 60 to 70% of the total costs associated with animal production are feed costs (Herd *et al*., 2003). This has been demonstrated by studies in beef cattle in feedlots where 10% improvement in average daily gain (ADG) improved profitability by 18%; whereas, a 10% improvement in feed efficiency returned a 43% increase in profits (Fox *et al*., 2001).

Efficiency of feed use is not a directly measurable trait, but must be computed as a function of feed consumed, gain in body weight and time (Exton *et al*., 2000). Feed efficiency can be expressed either as gross feed efficiency or net feed efficiency. Gross feed efficiency deals with total feed consumed with no regard to how feed is partitioned for various functions in the body and is commonly measured by feed conversion ratio (FCR). Net feed efficiency, on the other hand, deals with the efficiency of feed use after accounting for feed used for separate functions in the body and is measured by residual feed intake (RFI), residual body weight gain (RG), and residual intake and weight gain (RIG) (Berry and Crowley, 2013).

2.3.1. Gross feed efficiency

Gross feed efficiency measured by FCR is the ratio of feed intake to live-weight gain. It provides an indication of animals' ability to convert feed to body weight and forms a useful management tool when evaluating the economics of producing livestock. Efficient animals have low FCR values while inefficient animals have high FCR values (Exton *et al*., 2000). It has been used extensively to define feed efficiency due to its ease of computation and the direct association of costs and profits to quantities of feed (Aggrey *et al*., 2010).

On the downside of being a ratio trait, its statistical properties and difficulties in accurate predictions of correlated responses in feed intake and body weight gain in future generations prevent it from being an ideal measure (Aggrey *et al*., 2010). Attempts to improve the ratio trait have been made by using a linear index based on the component traits of FCR rather than direct selection on the ratio trait to increase selection responses (Famula, 1990). However, the studies reported that the advantage of the linear index decreases as the correlation between feed intake and body weight increases or as the heritability of both traits move towards equality. In addition, the unfavourable relationship that exists in FCR with growth and mature weight indicates that selection for improved FCR will indirectly increase, which is undesirable for an integrated production system (Mrode and Kennedy, 1993). Given that FCR is a gross efficiency measurement, it does not partition feed into portions needed to support maintenance and growth requirement (Koch *et al*., 1963).

2.3.2 Energy partition in poultry

The total amount of feed consumed by an animal goes through several processes to finally allow a proportion of energy contained in the feed to be used for production and maintenance requirements (Figure 2.1). The energy contribution from poultry diets is described in terms of metabolizable energy (ME) and is generally partitioned into energy retained (ER) in body tissues (as fat and protein) and heat production (HP) (Lawrence and Fowler, 2002). In thermo-neutral conditions, HP represents heat associated with the utilization of ME intake for maintenance and productive processes. Van Milgen *et al*. (2001) further subdivided heat production into fasting heat production (FHP), heat production due to physical activity (AHP) and thermic effect of feeding (TEF) in which FHP and AHP account for 36 to 37% of ME intake with physical activity being a major component of maintenance in poultry.

Maintenance energy is the amount of energy required by an animal to sustain their body tissues with no net change in body tissue. It is estimated using metabolic body weight, which is calculated as a fractional power of shrunk body weight commonly expressed as body weight adjusted to three quarter power ($BW^{0.75}$) (Sakomura, 2004). Metabolic body weight is proportional to an animal's fasting energy expenditure and hence, an individual's maintenance energy requirement will scale with weight (Evans *et al*., 2002).

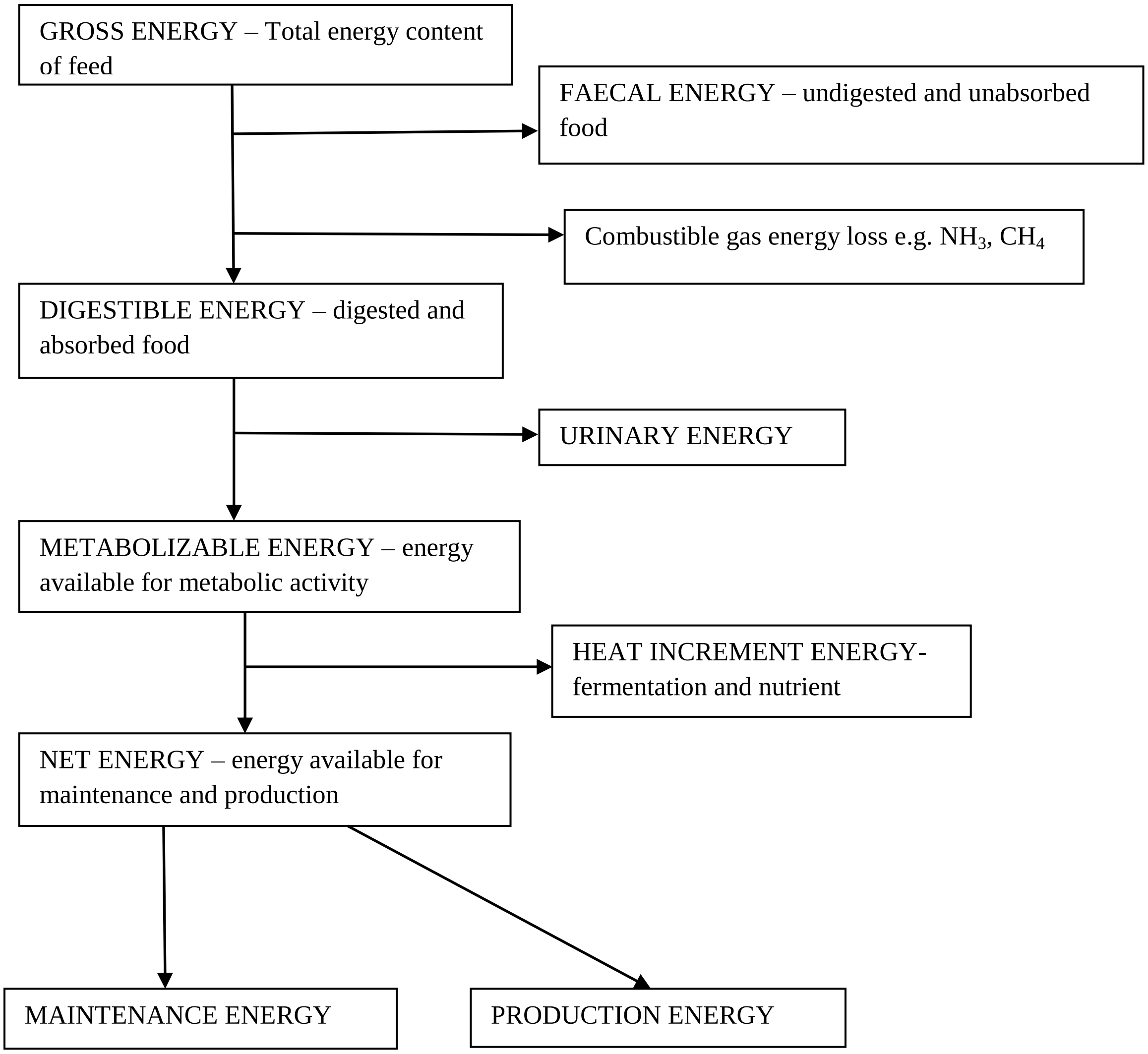


Figure 2.1: Energy partition in the body of domestic animals (Baldwin and Sainz, 1995)

2.3.3. Net feed efficiency

The concept of residual feed intake was introduced by Koch *et al*. (1963) in beef cattle, as the residual portion of feed intake that is not accounted for by body weight and weight gain. The study observed that differences in both weight maintained and weight gain affected feed requirements suggesting that feed intake could be partitioned into; the feed intake expected for the given level of production and a residual portion. The residual portion of feed intake, known as RFI, could be used to identify animals which deviate from their expected level of feed intake and is defined as the difference between actual feed intake and that predicted on the basis of requirements for production and maintenance of body weight.

An animal’s energy requirement is met when the energy intake equals the energy required (RFI = 0). For animals with positive RFI, their energy intake exceed their requirement for maintenance and growth while those with negative RFI require less energy to produce the same weight gain and maintain it. Residual feed intake is a linear function of feed intake, body weight and growth rate (Koch *et al*., 1963). Several attempts have been made to improve the model by adjusting for various factors that were thought to influence predicted feed intake such as body composition, physical activity, feeding patterns and digestibility (Bentsen, 1983; Luiting *et al*., 1991; Archer *et al*., 1998; Basarab *et al*., 2003). However, some of the variables did not offer additional information and were therefore not included in the model (Bentsen, 1983; Luiting *et al*., 1991). From these studies, between 38% and 58% of the variation in feed intake was explained by differences in growth rate and maintenance requirement in growing animals.

Residual body weight gain (RG) was also proposed by Koch *et al*. (1963) as an alternative measure for identifying between-animal variation in feed efficiency among growing animals. It is the difference between actual body weight gain and that predicted on the basis of actual feed intake and maintenance requirement (Crowley *et al*., 2010). Residual weight gain uses a similar principle to that of RFI where the predicted body weight gain is obtained by regressing actual body weight gain on observed feed intake and maintenance requirement. Crowley *et al*. (2010) observed that between 16% and 54% of the variation in growth rate of growing cattle was explained by differences in feed intake and maintenance requirement. Hence, improved RG is, on average, associated with faster growth rates but independent of feed intake. Unlike RFI where negative values are deemed more efficient, positive RG values are deemed efficient (Koch *et al*., 1963).

Recently, Berry and Crowley (2012) proposed an alternative net feed efficiency measure known as residual intake and body weight gain (RIG), which combines the benefits of both RFI and RG in a linear function. They suggested that the lack of correlation between RFI and ADG, and RG and feed intake could result in the likelihood of efficient animals having relatively slow growth rates and higher feed intake levels, respectively. Therefore, by combining RFI and RG into RIG, the trait can be used to identify animals that require a shorter duration in the feedlot (high growth rate) but also have a less than expected daily feed intake to support such growth while simultaneously accounting for differences in maintenance requirement. This is because RIG is positively correlated to ADG and negatively to feed intake but independent of maintenance requirement. Residual intake and gain is computed as the sum of RFI and RG, with RFI multiplied by negative one (-1) to account for a negative RFI being favourable and a positive RG being favourable hence putting both RFI and RG on a positive scale to allow for their combination into an RIG value (Willems *et al*., 2013).

2.4. Source of variation in feed use efficiency

Feed efficiency in chicken is influenced by both genetic and non-genetic factors. The genetic influence arises from the individuals' own genetic effect as well as depending on how the individuals are reared, the influence of the dam (Mrode and Kennedy, 1993). On the other hand, non genetic factors arising from production environment and the physiological differences and changes in the birds result in variation in feed efficiency measures of the birds (Tadelle *et al.*, 2003). Effective accounting for these sources of variation is important in ensuring accurate estimation of the variance components and genetic parameters, and breeding values for genetic improvement programmes (Mrode, 2005).

2.4.1. Non-genetic (Fixed effects) sources of variation

Sex

The difference in physiological nature between males and females requires that the sexes are treated differently when evaluating performance. This is due to the presence of different levels of endogenous hormones that influence performance between the sexes (Saadey *et al.*, 2008). Large differences between male and female animals with regard to feed intake and growth rate has been observed, indicating that sex has a significant influence on performance (Tadelle *et al.*, 2003; Saadey *et al.*, 2008). Therefore this shows the importance of including sex as a factor contributing to variation in feed efficiency.

Physiological stage of development

As an animal's age progresses, there are corresponding changes in the developmental process and physiological functions governing the utilization and deposition of nutrients (Aggrey *et al*., 2010). Feed intake and growth rate as components of feed efficiency vary with age, therefore, it is expected that observations on these factors as age progresses will contribute to the variation in feed efficiency. Berry and Crowley (2012) observed a decline in feed efficiency on beef cattle as their age increased, indicating that gradual change in body composition as age progress influences feed efficiency. In birds, feather development, skeletal growth, tissue accretion and fat deposition are different developmental process which influence feed efficiency (Aggrey *et al*., 2010).

Hatch group

In poultry species that are hatched artificially, hatch group is used to account for environmental effect that influences birds hatched on the same date and managed in the same group (Aggrey *et al*., 2010; Willems *et al*., 2013). Although birds within the same group may not have genetic relations, environmental effect is likely to influence resemblance in performance amongst them. The size of the effect depends on the trait in question and the time when the trait is measured (Mrode, 2005).

Genotype

Within the indigenous chicken population, distinct genotypes have been identified based on morphological differences, namely normal feathered, naked neck, frizzle feathered, dwarf size, crested head and feathered shanks (Khobondo *et al*., 2014). These genotypes identified by qualitative criteria may show association with quantitative traits, either because of pleiotropy or linkage with genes that influence traits of economic importance (Fayeye *et al*., 2006; Magothe *et al*., 2010). It would be therefore important to determine the effect of genotype on feed efficiency and the genotypes ranked accordingly for this trait.

Cluster group

The population of indigenous chicken in Kenya have been classified based on agro-ecological zone of placement (Ngeno, 2012). Molecular characterization using microsatellite markers show that several genetic groups exist within the population; Coastal, Central, Eastern, Northern and a combination of Western and Rift valley (Mwacharo *et al*., 2007; Ngeno *et al*., 2015). At phenotypic level the genetic groups have been found to have between and within group variation in growth performance and this is likely to influence feed efficiency traits (Ngeno *et al*., 2012).

2.4.2. Random effects

Additive genetic effects

This is the proportion of the genetic variance that is attributed to an individual's own genes and represents the breeding value of an animal for a particular trait (Falconer and Mackay, 1996). It is the component that is transmitted from parent to offspring, therefore making it important in selection. Significant genetic variation in net feed efficiency in poultry species has been reported in broilers, Japanese quails and turkeys (Aggrey *et al*., 2010; Varkoohi *et al*., 2011; Willems *et al*., 2013). These studies reflect the existence of a large difference between the true breeding value of the best individual and the worst individual for feed efficiency and hence through successful selection process, the response would be expected to be high. Given that these estimates are population-specific, there is need to estimate the genetic variation in net feed efficiency in indigenous chicken since this information is not available.

Permanent environmental effects

This is the environmental component that is common to all repeated observations on the same individual for the same trait over different time periods and represents the between-individuals variation for the same trait (Mrode, 2005). It is partly caused by the non-additive genetic component (dominance and epistasis) and partly due to environmental factors that affect an individual permanently (Falconer and Mackay, 1996). Phenotypic variation due to permanent environmental effect in net feed efficiency has not been largely estimated due to the type of model applied in most studies (Table 2.2). Therefore, it would be important to quantify this effect to determine whether birds selected for feed efficiency can perform in environments different from the selection environment.

Residual effects

All other factors whose contribution to the phenotypic variation cannot be accounted for in the analysis are summed up as residual error variance. It represents the within-individual variation which measures the differences between records of the same individual (Mrode, 2005). The component is due to temporary differences of environment between successive measurements caused by either nutritional factors, climatic factors or error in measurements

(Falconer and Mackay, 1996). The size of residual component dictates the accuracy and reliability of estimates (Mrode, 2005).

2.5. Genetic and phenotypic parameters for net feed efficiency traits in livestock

Genetic and phenotypic parameters are ratios of variance components and they include heritability, correlations and repeatability. They provide insight on the impact selection for a trait would have on the program and the correlated responses that might occur in other traits (Bourdon, 2000). Genetic and phenotypic parameters may vary between populations at a given period or over time within the same population as observed in Table 2.2 on the growth and feed efficiency traits. This variability in the estimates is mostly caused by differences in population history, environment, breed, sex, size of data and the type of model used for estimation (Falconer and Mackay, 1996).

Table 2.2: Genetic and phenotypic parameters of feed efficiency and growth traits

Species	**Type**[a]	**Country**	**Model**[b]	**Traits**[c]		**Parameter estimates**[d]				**Source**
				Trait 1	Trait 2	h^2_1	h^2_2	$r_{g(1,2)}$	$r_{p(1,2)}$	
Beef cattle	AA, HF, CL	Ireland	MAM	RFI	ADG	0.38	0.30	0.01	-0.06	Crowley *et al*. (2010)
				“	ADFI		0.49	0.59	0.81	
				“	MBW		0.69	-0.17	-0.11	
				RG	ADG	0.45		0.82	0.70	
				“	ADFI			-0.03	0.00	
				“	MBW			0.06	0.00	
				“	RFI			-0.46	-0.40	
				RIG	ADG	0.36		0.47	0.41	Berry and Crowley (2012)
				“	ADFI			-0.35	-0.34	
				“	MBW			0.11	0.00	
				“	RFI			-0.87	-0.85	
				“	RG			0.83	0.85	
Poultry	Turkey	Canada	MAM	RFI	ADG	0.21	0.18	-0.04	0.06	Case *et al*. (2012)
				“	ADFI		0.25	0.62	0.66	
				“	MBW		0.35	0.09	0.00	
				RG	ADG	0.19		-0.43	0.66	Willems *et al*. (2013)
				“	ADFI			-0.41	0.00	
				“	MBW			-0.28	0.00	
				“	RFI			-0.76	-0.58	
				RIG	ADG	0.23		0.29	0.42	
				“	ADFI			-0.57	-0.31	
				“	MBW			-0.22	0.00	
				“	RFI			-0.93	-0.86	
				“	RG			0.94	0.91	

[a] AA = Aberdeen Angus; HF = Hereford; CL = Charolais; IC = Indigenous chicken. [b] MAM = multivariate animal model; MSM = multivariate sire model; [c] ADG = average daily gain; ADFI = average daily feed intake; MBW = metabolic body weight; RFI = residual feed intake; RG = residual body weight gain; RIG = residual intake and weight gain; [d] h^2_1, h^2_2 = heritability for trait 1 and 2 respectively; $r_{g(1,2)}$ and $r_{p(1,2)}$ = genetic and phenotypic correlation respectively, between trait one and two

2.5.1. Heritability

Heritability measures the strength of relationship between the phenotypic values and genetic values (Bourdon, 2000). It is estimated from performance records on animals and pedigree information used to establish genetic relationships between those animals. Heritability helps explain the degree to which genes control the expression of a trait and is used to predict response to selection, and help producers decide if it is more efficient to improve traits through management or through selection (Falconer and Mackay, 1996).

A summary of estimates of heritability of net feed efficiency measures is presented in Table 2.2. The estimates ranged from 0.21 to 0.45 for RFI, 0.19 to 0.45 for RG and 0.23 to 0.36 for RIG, showing that net feed efficiency measures are moderately to highly heritable. These estimates vary widely across the studies due to species, breed and environment differences. The studies reported consistency in heritability estimates of RFI and RG with their component traits. The heritability estimates for RIG were also found to be between the estimates of its component traits of RFI and RG (Table 2.2). These estimates indicate that there is scope for genetic improvement of net feed efficiency. Currently, published estimates on heritability for net feed efficiency in indigenous chicken in Kenya are not available, therefore making it difficult to improve on feed efficiency.

2.5.2. Correlation

Genetic improvement on feed efficiency not only depends on heritability but also on the magnitude and direction of correlation between feed efficiency and traits that are essential to the production system. Correlation measures the strength of relationship between two variables and is classified based on strength (weak or strong), mathematical sign (positive or negative) and by being either favourable or unfavourable (Bourdon, 2000). Phenotypic correlation is concerned with performance between two traits and it gives a sense of the observable relationship between traits. Genetic correlation, on the other hand relates to breeding values between traits; it indicates the relative importance of pleiotropic effects on two traits.

Various studies have reported higher genetic correlations between feed efficiency traits and production traits than their respective phenotypic correlations (Table 2.2). Residual feed intake is genetically and phentoypically correlated with feed intake while having no correlation with its regressor traits, implying that feed efficient animals will consume less feed with little or no change in ADG and MBW. Similarly, residual gain is correlated to ADG with no association with its regressor traits indicating that improved RG will result to faster growth rates without greatly affecting feed intake and MBW. Studies have shown significant genetic and phenotypic correlations between RIG and both ADG and feed intake indicating the dual benefit of RIG in improving animal efficiency by reducing feed intake and also the time to reach a given body weight, while still being independent of MBW. Strong genetic correlations between the different measures of feed efficiency were observed, suggesting the feed efficiency measures are not under identical genetic influence but selection on any of the measures, will affect measures of feed efficiency. Given that genetic parameters are population specific, it is crucial that correlations are estimated in indigenous chicken to ensure there are no unfavourable correlated responses to genetic selection on feed use efficiency.

References

Aggrey, S. E., Karnuah, B. A., Sebastian, B., and Anthony, N. B. (2010). Genetic properties of feed efficiency parameters in meat-type chickens. *Genetics Selection Evolution, 42*, 25-30.

Archer, J. A., Arthur, P. F., Herd, R. M., Parnell, P. F., and Pitchfold, W. S. (1998). Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in British Breed cattle. *Journal of Animal Science, 75*, 2024-2032.

Baldwin, R. L., and Sainz, R. D. (1995). Energy partitioning and modeling in animal nutrition. *Animal Review of Nutrition, 15*, 191-211.

Basarab, J. A., Price, M. A., Aalhus, J. L., Okine, E. K., Snelling, W. M., and Lyle, K. L. (2003). Residual feed intake and body composition in young growing cattle. *Canadian Journal Animal of Science, 83*, 189-204.

Bentsen, H. B. (1983). Genetic variation in feed efficiency of laying hens at constant body weight and egg production: I. Efficiency measured as deviation between observed and expected feed consumption. *Acta Agriculturae Scandinavica, 1983*, 289-304.

Berry, D. P., and Crowley, J. J. (2012). Residual intake and body weight gain: A new measure of efficiency in growing cattle. *Journal of Animal Science, 90*, 109-115.

Berry, D. P., and Crowley, J. J. (2013). Cell biology symposium: genetics of feed efficiency in dairy and beef cattle. *Journal of Animal Science, 91 (4)*, 1594-1613.

Bourdon, R. M. (2000). *Understanding Animal Breeding* (2nd ed.). Prentice Hall, Upper Saddle River: Prentice Hall.

Case, L. A., Wood, B. J., and Miller, S. P. (2012). The genetic parameters of feed efficiency and its component traits in turkey (*Meleagris gallopova*). *Genetics Evolution Science, 44*, 2-6.

Crowley, J. J., McGee, M., Kenny, D. A., Crews, D. H., Evans, R. D., and Berry, D. P. (2010). Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *Journal of Animal Science, 44*, 958-972.

Demeke, S. (2003). Growth performance of local and exotic chicken under intensive and rural household condition in Ethiopia. *Livestock Research for Rural Development, 15*, 26-30.

Evans, J. L., Golden, L. B., and Hough, L. B. (2002). A new genetic prediction for cow maintenance energy requirements. *In Proceedings of the Beef Improvement Federation Symposium, Oklahoma* (pp. 79-88). Stillwater: Oklahoma State University.

Exton, S. C., Herd, R. M., and Davies, L. (2000). Commercial benefits to the beef industry from genetic improvement in net feed efficiency. *Asian-Australian Journal of Animal Science, 13*, 338-341.

Falconer, D. S., and Mackay, T. F. (1996). *Introduction to Quantitative Genetics* (4th ed.). London: Longman group.

Famula, T. R. (1990). The equivalence of two linear methods for the improvement of traits expressed as ratios. *Theoretical and Applied Genetics, 79*, 853-856.

Fayeye, T. R., Ayorinde, K. L., Ojo, V., and Adesina, D. M. (2006). Frequency and influence of show major genes on body weight and body size parameters of Nigerian local chicken. *Livestock Research and Rural Development, 18*, 1-9.

Fox, D. G., Tedeschi, L. O., and Guiroy, P. J. (2001). Determinig feed intake and feed efficiency of individual cattle fed in groups. *Journal of Animal Science, 33*, 80-98.

Gondwe, T. N., and Wollny, C. B. (2005). Evaluation of growth potential of local chicken in Malawi. *International Journal of Poultry Science, 4* (2), 64-70.

Hagan, J. K., and Adjei, A. I. (2012). Evaluation of the growth and carcass yield characteristics of crossbred naked-neck and frizzle cockerel phenotypes reared under hot and humid environments. *ARPN Journal of Agricultural and Biological Science, 7* (8), 576-582.

Henning, J., Meers, J., Pym, R., Morton, J., and Than, H. L. (2005). Village chicken production in Myanmar: Characteristics, constraints and methods for improving the health of village chickens. *In International Conference on The Opportunities for village chickens to assist with poverty alleviation with special emphasis on the sustainable control of Newcastle Disease.* ACIAR: AusAID Southern Africa Disease Control Project.

Herd, R. M., Archer, J. A., and Arthur, P. F. (2003). Reducing the cost of beef production through genetic improvemnt in residual feed intake: Opportunity and challenges to application. *Journal of Animal Science, 81*, 9-17.

Iraqi, M. M., Hanafi, M. S., Khalil, M. H., El-Labban, A. F., and Ell-Sisy, M. (2002). Genetic evaluation of growth traits in a crossbreeding experiment involving two local strains of chickens using multi-trait animal model. *Livestock Research for Rural Development, 14* (5), 1-9.

Kennedy, B. W., van der Werf, J. H., and Meuwissen, T. H. (1993). Genetic and statistical properties of residual feed intake. *Journal of Animal Science, 71*, 3239-3250.

Khobondo, J. O., Okeno, T. O., Lihare, G. O., Wasike, C. B., and Kahi, A. K. (2014). The past, present and future genetic improvement of indigenous chicken of Kenya. *Animal Genetic Resources*, *55*, 125-135.

Kingori, A. M., Wachira, A. M., and Tuitoek, J. K. (2010). Indigenous chicken production in Kenya: A review. *International Journal of Poultry Science, 9* (4), 309-316.

Koch, R. M., Swiger, L. A., Chambers, D., and Gregory, K. E. (1963). Efficiency of feed use in beef cattle. *Journal of Animal Science, 22*, 486-494.

Lawrence, T. L., and Fowler, V. R. (2002). *Efficiency and growth: Growth of farm animals*. New York: CABI Publishing.

Luiting, P., Schrama, J. W., Van der Hel, W., and Urff, E. M. (1991). Metabolic differences between white leghorns selected for high and low residual feed consumption. *British Poultry Science, 32*, 763-782.

Lwelamira, J. (2007). *Prospects for improving performance among two local chicken ecotypes of Tanzania through selection*. Unpublished PhD thesis, Sokoine University of Agriculture, Tanzania.

Lwelamira, J. (2012). Genotype-Environment (G X E) interaction for body weights for Kuchi chicken ecotype of Tanzania reared under intensive and extensive management. *Global Journal of Medical Research, 12*(5), 57-65.

Maddock, T. D., and Lamb, G. C. (2009). *The economic impact of feed efficiency in beef cattle.* Retrieved from http://edis.ifas.ufl.edu.

Magothe, T. M., Muhuyi, B. W., and Kahi, A. K. (2010). Influence of major genes for crested-head, frizzled-feather and naked-neck on body weights and growth patterns of indigenous chicken reared intensively in Kenya. *Tropical Animal Health and Production, 42*, 173-183.

Magothe, T. M., Muhuyi, W. B., and Kahi, A. K. (2011). Genetic parameters for egg and body weights of indigenous chicken in Kenya. *Animal Production Society of Kenya, 36*.

Magothe, T. M., Okeno, T. O., Muhuyi, W. B., and Kahi, A. K. (2012). Indigenous chicken production in Kenya: Current status. *World's Poultry Science Association, 68*, 119-132.

Mrode, R. A. (2005). *Linear models for the prediction of animal breeding values* (2nd ed.). Oxon, UK: CABI publishing.

Mrode, R. A., and Kennedy, B. W. (1993). Genetic variation in measures of food efficiency in pigs and their genetic relationships with growth rate and backfat. *Animal Production - Glasgow, 56*, 225.

Muchadeyi, F. C., Eding, H., Wollny, C. B., Groeneveld, E., Makuza, S. M., and Shamseldin, R. (2007a). Absence of population substructuring in Zimbambwe chicken ecotypes inferred using microsatellite analysis. *Animal Genetics, 38* (4), 332-339.

Muchadeyi, F. C., Wollny, C. B., Eding , H., Weigend, S., Makuza, S. M., and Simianer, H. (2007b). Variation in village chicken production systems among agro-ecological zones of Zimbabwe. *Tropical Animal Health and Production, 39* (6), 453-461.

Mwacharo, J. M., Nomura, K., Hanada, H., Jianlin, H., Hanotte, O., and Amano, T. (2007). Genetic relationships among Kenyan and other East African indigneous chickens. *Animal Genetics, 38* (5), 485-490.

Mwacharo, J. M., Nomura, K., Hanada, H., Han, J. L., Amano, T., and Hanotte, O. (2013). Reconstructing the origin and dispersal patterns of village chicken across East Africa: insights from autosomal markers. *Molecular ecology, 22* (10), 2683-2697.

NAFRI. (2005). Indigenous chicken and rural livelihoods in LAO PDR. NAFRI Report.

Ngeno, K., Bebe, O. B., and Kahi, A.K., (2012). Genetic evaluation of growth traits in ecotypes of Kenyan indigenous chicken. *Family Poultry Communications, 21,* 5-12.

Ngeno, K., Magothe, T. M., Okeno, T. O., Bebe, B. O., and Kahi, A. K. (2013). Heritabilities and correlations between body weights and growth curve parameters of indigenous chicken populations reared intensively in Kenya. *Research Journal of Poultry Sciences, 6* (3), 43-52.

Ngeno, K., van der Waaij, E. H., Megens, H. J., Kahi, A. K., van Arendonk, J. A., and Crooijmans, R. P. (2015). Genetic diversity of different indigenous chicken ecotypes using highly polymorphic MHC linked and non-MHC linked microsatellite markers. *Animal Genetic Resources, 56*, 1-3.

Njue, S. W., Kasiiti, J. L., Macharia, M. J., Gacheru, S. G., and Mbugua, H. C. (2002). Characteristics and parameters of family poultry production in Africa: Health and management improvements of family poultry productions in Africa. *IAEA-TECDOC, Vienna,* 39-46.

Norris, D., and Ngambi, J. W. (2006). Genetic parameter estimates for body weight in local Venda chickens. *Tropical Animal Health and Production, 38* (8), 605-609.

Oke, U. K. (2011). Influence of some major genes on growth traits of local pullets in humid tropical environment. *Agriculture and Biology Journal of North America, 2* (4), 570-576.

Okeno, T. O., Kahi, A. K., and Peters , K. J. (2012). Characterization of indigenous chicken production systems in Kenya. *Tropical Animal Health and Production, 44*, 601 - 608.

Okeno, T. O., Kahi, A. K., and Peters, K. J. (2011). Breed selection practices and traits of economic importance for indigenous chicken in Kenya. *Livestock Research for Rural Development, 23*.

Okine, E. K., Basarab, J. A., Goonewardene, L. A., and Mir, P. (2004). Residual feed intake and feed efficiency: Differences and Implicactions. *In Florida Ruminant Nutrition Symposium, Florida, USA* (dairy.ifas.ufl.edu/files/rns/2004/Okine.pdf [Verified August 2010]).

Pym, R. A., Guerne Bleich, E., and Hoffmann, I. (2006). The relative contribution of indigenous chicken breeds to poultry meat and egg consumption in the developing countries of Africa and Asia. *In Conference Proceedings of the XII European Poultry Conference, Italy* (Vol. 1014).

Saadey, S. M., Galal, A., Zaky, H. I., and El-Dein, A. Z. (2008). Diallel crossing analysis for body weight and egg production traits of two native egyptian and two exotic chicken breeds. *International Journal of Poultry Science, 7* (1), 64-71.

Sakomura, N. K. (2004). Modelling energy utilization in broiler breeders, laying hens and broilers. *Revista Brasileira de Ciencia Avicola, 6* (1), 1-11.

Schaeffer, L. R., and Dekkers, J. C. (1994). Random regression in animal models for test-day production in dairy cattle. *In Proceedings of the 5th World Congress Applied to Livestock Production, Guelph, Canada* (Vol. 18, pp. 443-446).

Tadelle, D., Alemu, Y., and Peters, K. J. (2000). Indigenous chickens in Ethiopia: genetic potential and attempts at improvement. *World's Poultry Science Journal, 56* (1), 45-54.

Thornton, P. K., Kruska, R. L., Henniger, N., Kristjanson, P. M., Atieno, F., and Odero, E. N. (2002). Mapping poverty and livestock in developing world. *International Livestock Research Institute, Nairobi, Kenya* (Vol. 1).

van der Werf, J. H. (2004). Is it useful to define residual feed intake in animal breeding programs? *Australian Journal of Experimental Agriculture, 44*, 405-409.

Van Milgen, J., Noblet, J., Dubois, S., Carre, S., and Juin, H. (2001). Utilization of metabolizable energy in broiler chickens. *Poultry Science, 80 (Suppl. 1),* 170 (Abstr.).

Varkoohi, S., Pakdel, A., Nejati Javaremi, A., Moradi Shahr Babak, M., Kause, A., and Zaghari, M. (2011). Genetic parameters for feed utilization traits in Japanese quails. *Poultry Science, 90*, 42-47.

Willems, O. W., Miller, S. P., and Wood, B. J. (2013). Assessment of residual body weight gain and residual intake and body weight gain as feed efficiency traits in the turkey (*Meleagris gallopova*). *Genetics Selection Evolution, 45*, 26-34.

CHAPTER THREE

NON GENETIC SOURCES OF VARIATION AND TEMPORAL VARIABILITY IN GROWTH AND NET FEED EFFICIENCY TRAITS AMONG PHYLOGENETICALLY DISTINCT CLUSTERS OF INDIGENOUS CHICKEN IN KENYA

3.1. Introduction

Considering feed efficiency alonside production traits in indigenous chicken (IC) improvement programmes is critical in minimising feed costs in IC systems. However, prior to inclusion of the trait in breeding programmes it is important to characterize performance by identifying the mean net feed use efficiency in IC. Previous study on efficiency using feed conversion ratio (FCR) reported that IC require an average of 4.95g to 5.20g of feed for every unit of gain per day from hatch to week 12 of age (Tadelle *et al*., 2003; Binda *et al*., 2012). Further, environmental effects such as sex, physiological age of development, hatch group, feather morphology (genotype) and agro-ecological origin (ecotype) have been reported to significantly influence mean phenotypic performance on growth and feed efficieny traits in IC (Aggrey et al., 2010; Magothe et al., 2010; Ngeno et al., 2012; Willems et al., 2013). With regards to ecotypes, IC originating from different agro-ecological zones in Kenya have undergone molecular characterization using non-MHC (Major Histocompatibility Complex) linked microsatelite markers (Mwacharo *et al*., 2007; Ngeno *et al*., 2015). These studies reported that IC ecotypes can be classified into four phylogenetically distinct clusters namely Western and Rift valley cluster, Eastern cluster, Coastal cluster and Northern cluster. At phenotypic level, these cluster groups have shown significant between and within group variation on growth patterns and body weight traits (Ngeno *et al*., 2012).

Prior to improvement of feed efficiency in IC, there is need to characterize net feed efficiency (NFE) traits by estimating the mean performances. In addition, identifying non-genetic sources of variation on mean performance is key since they influence the expression of genes and provide a better understanding of biological or environmental mechanisms on performance (Mrode, 2005). Accounting for such factors help to unmask true differences between groups as well as reduce bias in performance evaluation. This Chapter aimed at estimating the mean performances on feed intake, growth and net feed efficiency traits in IC and non-genetic factors that influence mean performances on these traits. Further, temporal variation in NFE traits among phylogenetic IC clusters of Kenya was determined.

3.2. Materials and methods

3.2.1. Study site, experimental flock design and management

The study was conducted at the Smallholder Indigenous Chicken Improvement Program Research Unit (INCIP-RU) at Egerton University, Njoro-Nakuru which falls under the agro-ecological zone I (Ayuya *et al*., 2011). The climatic condition in the study site was considered moderate and optimal for IC performance. The study used the first generation of birds from three clusters, Western and Rift valley (cluster 1), Eastern (cluster 2) and (Coastal cluster 3), as parents to produce the experimental flock. Fifty four parents, consisting of three males and 15 females from each cluster to adopt a mating ratio of 1:5, were selected based on growth performance from hatch to 20 weeks in which the truncation point for selection of parents was set at 10g/day for males and 6g/day for females. The selected parent flock consisted of 36 birds of normal feathered genotype from the three clusters and 18 birds of naked neck genotype from only cluster one.

Eggs were collected daily, identified by their sire-family and stored at room temperature for not more than four days prior to artificial incubation. At hatch, each chick was weighed, wing-tagged and allocated a number identifying the cluster, genotype and the sire family. Throughout the experimental period, the birds were fed rations with nutrient composition recommended for IC in confinement (King'ori *et al*., 2004). Starter ration was given from day 0 to 7th week of age, growers ration from 8th to 20th week of age and the parent population were fed layers ration. Clean water was provided *ad libitum*. Health management practices such as vaccination, deworming and disinfection were carried out procedurally.

3.2.2. Data collection

Birds were individually weighed at hatch (BW_0) and thereafter on a weekly basis up to 20 weeks of age (BW_{20}), using a digital weighing scale calibrated to the nearest 1 gram. Feed efficiency is effectively assessed during the linear or rapid growth phase of the birds (Case *et al*., 2012). Growth inflection in indigenous chicken has been observed at the age of 10 weeks therefore, body weight data from 10 weeks was used in this study (Tadelle *et al*., 2003; Magothe *et al*., 2010). Feed intake was considered on an individual basis to account for inherent differences between individuals. However, the cost of collecting feed intake data on individual animals is a key determinant of the length of feed intake recording. Varied lengths of feed intake recording have been suggested in poultry species, with no standard test length. To select the most optimal length of test period for this study, an average test period of 42 days was used considering past studies on feed efficiency in poultry species (Tadelle *et al*., 2003; Binda *et al*., 2012; Aggrey *et al*., 2010; Varkoohi *et al*., 2010; Case *et al*., 2012; Belgi *et al*., 2016).

Feed intake data collection commenced when birds were transferred to individual battery cages and allowed one week acclimatization. Birds were given measured *ad libitum* potions of growers ration throughout the feeding trial. Individual daily feed intake was measured as the difference between the supplied feed and left over feed (the amount of feed left remaining in the trough at the time of introducing new feed) 24 hours later. Each bird in the experimental flock of 107 birds had 42 daily feed intake and 10 weekly body weight records. The structure of the data and summary statistics for growth and feed efficiency traits are presented in Table 3.1.

3.2.3. Statistical analysis

Estimation of net feed efficiency traits

To estimate NFE traits, average daily feed intake per week (ADFI), average daily gain per week (ADG) and weekly metabolic body weight (MBW) were considered. Average daily gain per week was obtained as the difference between consecutive weekly body weight measurements divided by seven days. Average daily feed intake per week was calculated as the sum of total feed consumed in a week divided by seven days. Weekly MBW was obtained as final weekly body weight raised to the power of 0.75 ($BW^{0.75}$). Residual feed intake was computed as the difference between measured average daily feed intake ($ADFI_O$) and expected average daily feed intake ($ADFI_E$) while RG was computed as the difference between measured average daily gain (ADG_O) and expected average daily gain (ADG_E). Expected feed intake ($ADFI_E$) is feed intake predicted on basis of measured ADG and estimated MBW, while expected daily gain (ADG_E) is daily gain predicted on basis of measured ADFI and estimated MBW.

A random effect model as presented in equation 1 and 2 was fitted on the data to estimate $ADFI_E$ and ADG_E for RFI and RG, respectively by considering age as a continuous predictor and bird as a random regressor. The model allows parameters to vary between- and within-individuals hence improve accuracy of prediction of the response variable and also aids in selection when confronted with birds with similar NFE values (Karaman *et al.*, 2013; Aggrey and Rekaya, 2013). The PROC MIXED of SAS 9.1 (SAS, 2002) was used for the random effects regression models.

Table 3.1: Distribution and summary statistics for growth and feed intake data across ages 11 to 20 weeks

Age (Weeks)	Body weight (g)			Feed intake (g)		
	No. records	μ	±SD	No. records	μ	± SD
11	48	534.45	173.30	336	125.26	23.38
12	63	620.82	180.43	441	114.36	28.19
13	76	709.91	191.52	532	121.70	25.36
14	82	795.77	213.80	574	127.54	32.62
15	107	906.62	252.97	749	134.66	35.09
16	107	995.06	270.68	749	134.61	33.21
17	59	1130.22	304.55	413	145.26	34.11
18	44	1234.31	342.16	308	146.72	37.86
19	31	1334.57	393.76	217	150.50	37.60
20	25	1445.11	394.89	175	153.17	36.22

μ = mean; ±SD = standard deviation

$$RFI_{ij} = ADFIo_{ij} - \left(b_0 + \left(b_1 + \alpha_{1i}\right)ADG_{ij} + (b_2 + \alpha_{2i})MBW_{ij} + (b_3 + \alpha_{3i})AGE_i + e_{ij}\right) \qquad \text{(equ 1)}$$

Where: RFI_{ij} is j^{th} observation of residual feed intake of i^{th} bird; $ADFIo_{ij}$, ADG_{ij}, MBW_{ij} and AGE_{ji} are measured weekly average daily feed intake, gain, metabolic body weight and age of i^{th} bird, respectively; b_k are fixed regression coefficients (k = 0, 1, 2, 3); $\alpha_{ki\ (k\ =\ 1,\ 2,3)}$ is random regression coefficient specific to i^{th} bird for the traits; and e_i is error term ~ N (0, σ^2_e).

$$RG_{ij} = ADGo_{ij} - \left(b_0 + \left(b_1 + \alpha_{1i}\right)ADFI_{ij} + (b_2 + \alpha_{2i})MBW_{ij} + (b_3 + \alpha_{3i})AGE_i + e_{ij}\right) \qquad \text{(equ 2)}$$

Where: RG_{ij} is j^{th} observation of residual gain of i^{th} bird; $ADGo_{ij}$, $ADFI_{ij}$, are measured weekly average daily gain and feed intake respectively, while MBW_{ij}, AGE_{ji}, b_k, $\alpha_{ki\ (k\ =\ 1,\ 2,3)}$ and e_i are as described in equ 1.

Residual intake and gain (RIG) was computed as the sum of RFI and RG. Residual feed intake was multiplied by negative one to put both RFI and RG on a positive scale since a negative RFI and a positive RG are favourable. The linear combination of RFI and RG into RIG was as presented in equ 3:

$$RIG_{ij} = \left(-1 \times RFI_{ij}\right) + RG_{ij} \qquad \text{(equ 3)}$$

Where: RIG_{ij}, RFI_{ij} and RG_{ij} is j^{th} observation of residual intake and weight gain, residual feed intake and residual gain of i^{th} bird, respectively.

Factors influencing mean growth and net feed efficiency traits

A fixed effect analysis of variance on growth and net feed efficiency traits was carried out to determine the factors that influence growth and feed efficiency using the GLM procedure of SAS 9.1 (SAS, 2002). The independent variables fitted included sex, cluster, genotype, hatch group and first order interaction between cluster and sex. Birds entered the experiment with different body weights ranging between 310g and 680g, and as such preliminary analyses of initial weight as a covariate for the efficiency traits and their component traits were carried. Based on the level of significance (α = 0.05), initial weight was fitted as a linear covariate for ADFI, ADG, MBW and RG, and as a quadratic covariate for RFI and RIG in the fixed effect analysis. The general fixed effect model used for the analyses is presented in equation 4:

$$Y_{ijklm} = \mu + S_i + G_j + C_k + H_l + (CS)_{ki} + e_{ijlkm} \qquad \text{(equ 4)}$$

where: Y_{ijklm} is the performance trait of the m^{th} bird; μ the overall mean; S_i is the effect of i^{th} sex (i = male, female); G_j is the effect of j^{th} genotype (j = normal feather, naked-neck); C_k is the effect of k^{th} cluster group ($k = C_1, C_2, C_3$); H_l is the effect of l^{th} hatch group ($l = 1, 2, ...8$); $(CS)_{ki}$ is the effect of interaction between cluster and sex; and e_{ijklm} is the random error term. Further, an analysis was done to determine the temporal variability in RFI, RG and RIG between clusters across various age points. Equ 4 taking into account repeated records of the NFE traits was used.

3.3. Results

The overall mean, mean square values and levels of significance of fixed effects included in the analysis of variance for the growth and feed efficiency traits are presented in Table 3.2. Least square means for the factors that significantly influenced growth and NFE traits are presented in Table 3.3 and Table 3.4. Sex significantly influenced ($P<0.05$) variation in ADG and RG while cluster and genotype did not have significant effects ($P>0.05$) on any of the traits. However, an interaction between cluster and sex had a significant effect ($P<0.05$) on ADFI, RFI and RIG. Apart from ADFI, hatch group had a significant effect ($P<0.05$) on all traits with different hatch groups showing superiority and inferiority for the traits evaluated.

Least square means for RFI, RG and RIG for the clusters across ages are presented in Figure 3.1, 3.2 and 3.3 respectively. At the onset of the experiment, cluster 2 had the lowest RFI value while cluster 1 had the highest RFI estimate. Thereafter, RFI values in cluster 2 and 3 increased at the rate of 0.99g/d and 1.02g/d, respectively while in cluster 1 the estimates decreased at the rate of -0.81g/d. Generally, more differences were observed in RFI between clusters in later experimental periods from week 17 than in earlier periods. Residual gain varied significantly between cluster 3, having the highest RG estimates, and clusters 1 and 2 from the onset of the experiment to week 17 thereafter, no significant difference was observed to the end of the experiment. For RIG, at the onset of the test cluster 2 had the highest estimates while cluster 1 had the least with estimates decreasing at the rate of -1.04g/d and -0.91g/d for cluster 2 and 3, respectively and in cluster 1 the estimates increased at the rate of 0.82. Similar to RFI, RIG had more differences between clusters in the later stages of the experiment from week 16.

Table 3.2: Overall mean, mean square values and level of significance of fixed factors that influence growth and net feed efficiency traits in indigenous chicken

Traits	**ADFI (g/d)**	**ADG (g/d)**	**MBW (g)**	**RFI (g/d)**	**RG (g/d)**	**RIG (g/d)**
Overall means (n=107)	133.01±18.52	10.38±2.67	164.12±43.62	0.00±10.23	0.00±1.83	0.0 ±14.64
Fixed effects						
Sex	23.18^{ns}	38.90**	63.99^{ns}	2.08^{ns}	33.97**	0.57^{ns}
Genotype	310.17^{ns}	0.01^{ns}	10.16^{ns}	347.26^{ns}	0.02^{ns}	0.16^{ns}
Cluster	199.77^{ns}	1.65^{ns}	73.41^{ns}	201.15^{ns}	0.76^{ns}	0.35^{ns}
Hatch	279.04^{ns}	8.93*	166.20**	354.55*	6.88*	0.02*
Sex*Cluster	1462.74**	0.19^{ns}	101.31^{ns}	1225.90***	1.72^{ns}	0.01***
Initial weight	^{a}3663.09***	^{a}214.59***	^{a}101768.55***	^{b}1010.21**	^{a}1.15***	^{b}0.02**

(±) standard deviation;ADFI = average daily feed intake; ADG = average daily gain; MBW = metabolic body weight; RFI = residual feed intake; RG = residual gain; RIG = residual intake and gain

***P<0.001, **P<0.01, *P<0.05, ns= not significant within rows

^{a}covariate fitted as a linear effect

^{b}covariate fitted as a quadratic effect

Table 3.3: Least square means^{a} (±s.e.) of growth and net feed efficiency traits across sex and hatch groups

Trait	ADFI (g/d)	ADG (g/d)	MBW (g)	RFI (g/d)	RG (g/d)	RIG (g/d)
Sex						
Male	137.03±2.71^{a}	11.40±0.37^{a}	220.67±3.77^{a}	2.91 ± 2.53^{a}	0.89 ± 0.32^{a}	-2.01 ± 2.59^{a}
Female	135.88±2.76^{a}	9.91±0.38^{b}	221.80±3.53^{a}	3.26 ± 2.57^{a}	-0.50 ± 0.32^{b}	-3.81 ± 2.63^{a}
Hatch groups						
Hatch$_1$	136.52±3.83^{a}	8.70±0.52^{a}	166.17±1.83^{a}	8.43 ± 3.61^{a}	-1.28 ± 0.46^{a}	-9.71 ± 3.69^{a}
Hatch$_2$	135.47±5.91^{a}	9.72±0.80^{ab}	161.36±2.83^{a}	4.00 ± 5.49^{a}	-0.55 ± 0.69^{a}	-4.55 ± 5.62^{a}
Hatch$_3$	136.56±4.24^{a}	10.85±0.58^{b}	166.46±2.03^{b}	1.87 ± 3.93^{a}	0.34 ± 0.50^{b}	-1.53 ± 4.02^{a}
Hatch$_4$	130.57±4.32^{a}	11.11±0.59^{b}	165.66±2.07^{b}	-3.95 ± 4.02^{b}	0.67 ± 0.51^{b}	4.62 ± 4.11^{b}
Hatch$_5$	137.59±4.17^{a}	10.75±0.57^{b}	166.17±2.00^{b}	-3.62 ± 3.81^{a}	0.09 ± 0.48^{a}	3.53 ± 3.90^{a}
Hatch$_6$	144.17±8.33^{a}	11.87±1.13^{b}	166.59±3.99^{b}	-2.96 ± 7.70^{a}	1.06 ± 0.97^{b}	4.02 ± 7.87^{a}
Hatch$_7$	128.49±3.87^{a}	11.20±0.53^{b}	164.75±1.86^{b}	-5.66 ± 3.52^{b}	0.77 ± 0.44^{b}	6.44 ± 3.60^{b}
Hatch$_8$	142.29 ±4.19^{a}	11.02±0.57^{b}	167.57 ± 2.01^{b}	-2.39 ± 3.91^{a}	0.27 ± 0.49^{b}	2.66 ± 4.00^{a}

[a] Least square means within a column with different superscript differ ($p<0.05$)

±s.e. = standard error; ADFI = average daily feed intake; ADG = average daily gain; MBW = metabolic body weight; RFI = residual feed intake; RG = residual gain; RIG = residual intake and gain

Table 3.4: Estimates of least square means[a] (±s.e.) for traits significantly influenced by the interaction between sex and cluster

Traits	Sex	Cluster		
		CL 1	CL2	CL3
ADFI (g/d)	Male	141.82 ± 2.93^{a}	138.51 ± 4.03^{ab}	130.76 ± 5.42^{b}
	Female	125.18 ± 2.65^{a}	138.61 ± 4.84^{ab}	143.87 ± 5.33^{b}
RFI (g/d)	Male	6.63 ± 2.71^{a}	4.34 ± 3.77^{a}	-2.24 ± 5.02^{b}
	Female	-6.79 ± 2.43^{a}	4.35 ± 4.53^{ab}	12.20 ± 4.95^{b}
RIG (g/d)	Male	-6.10 ± 2.78^{a}	-3.24 ± 3.87^{a}	3.31 ± 5.14^{b}
	Female	6.34 ± 2.49^{a}	-4.66 ± 4.64^{ab}	-13.10 ± 5.07^{b}

[a] Least square means within a row with different superscript differ ($p<0.05$)

±s.e. = standard error; ADFI = average daily feed intake; RFI = residual feed intake; RIG = residual intake and gain

CL1 = cluster 1; CL2 = cluster 2; CL3 = cluster 3

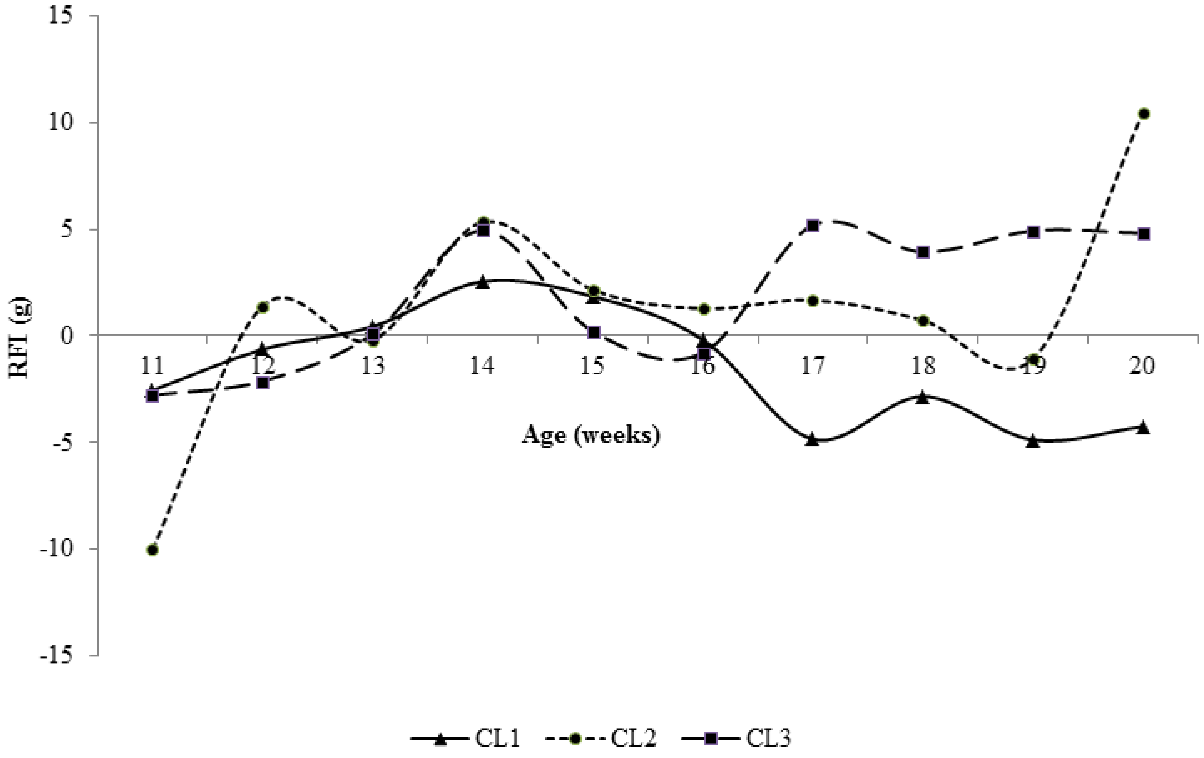


Figure 3.1: Estimates of least square means for residual feed intake (RFI g/day) among cluster 1 (CL1), cluster 2 (CL2) and cluster 3 (CL3) across 11 weeks to 20 weeks of ages

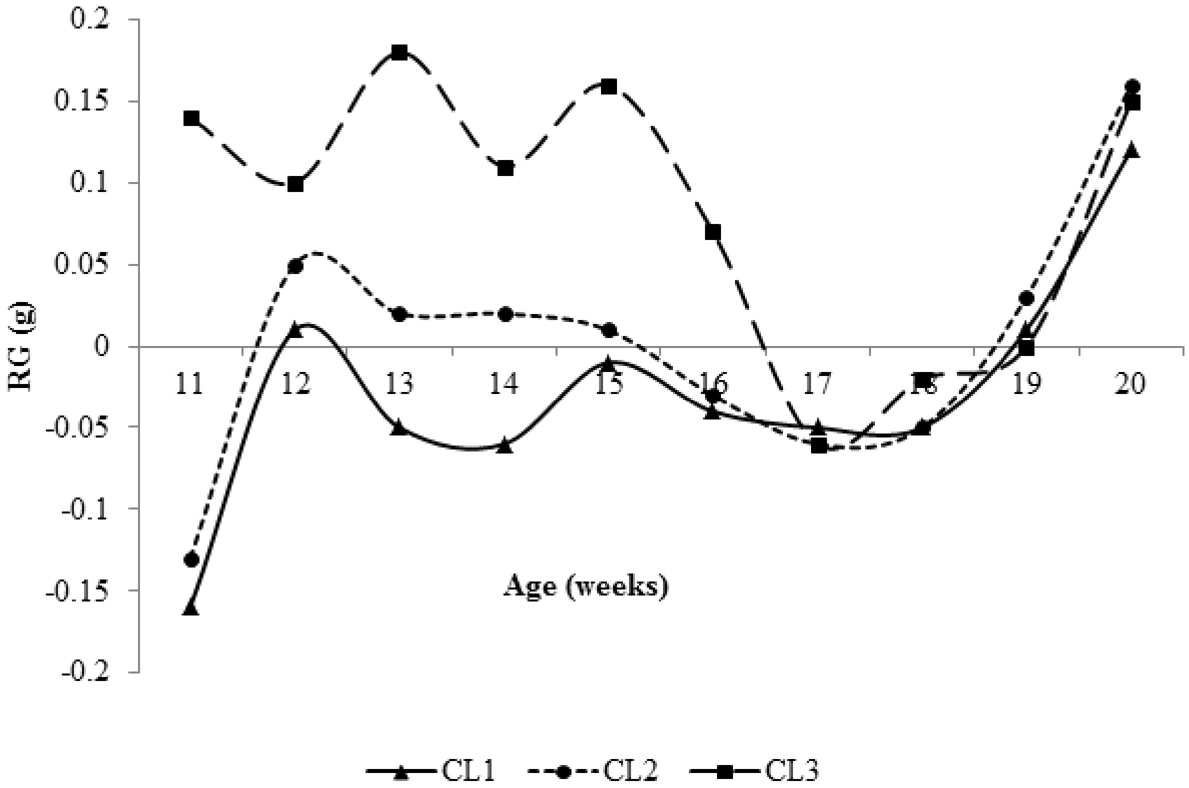


Figure 3.2: Estimates of least square means for residual gain (RG g/day) among cluster 1 (CL1), cluster 2 (CL2) and cluster 3 (CL3) across 11 weeks to 20 weeks of ages

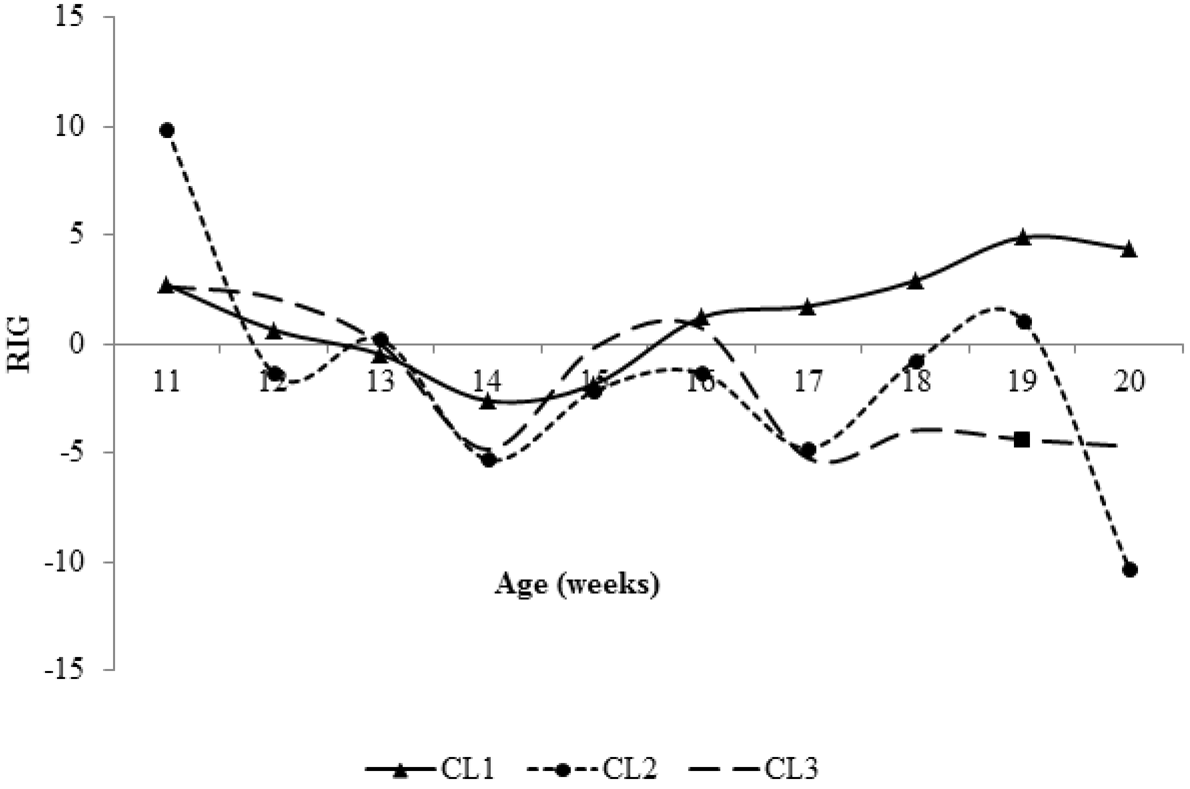


Figure 3.3: Estimates of least square means for residual intake and gain (RIG) among cluster 1 (CL1), cluster 2 (CL2) and cluster 3 (CL3) across 11 weeks to 20 weeks of ages

3.4. Discussion

Significant variation between the sexes showed that male birds were superior for ADG and RG compared to female birds. Such variation between the sexes has been associated with differences in physiological nature between males and females upon onset of the endocrinology functions which coincides with the period of test in this study (Leeson and Summers, 2010). Recent advancement in characterisation of IC in Kenya identified three distinct genetic groups/clusters using non-MHC linked microsatellite markers (Ngeno *et al*., 2015). This distinction was however non-existent with regard to growth and net feed efficiency. Similarly, irrespective of the birds genotype there was resemblance in their efficiency, however previous studies on IC genotypes reported significant influence of major genes on growth performance (Magothe *et al*., 2010). The interaction between sex and cluster indicated that there was sexual dimorphism between clusters for ADFI, RFI and RIG in which males from cluster three and females from cluster one were the most efficient for RFI and RIG and had the lowest ADFI. At phenotypic level, cluster three could be considered a suitable male line and cluster one a female line for selection to improve growth and feed efficiency in IC birds which will perform within a similar production environment as used in this study. The significant variation in growth and NFE traits between hatch groups may have resulted from differences in initial age at entry into the experiment between the hatch groups (Aggrey *et al*., 2010; Case *et al*., 2012). Hatch groups with older birds at entry into the experiment were approaching the growth decline phase and as such may have contributed to inefficiency for the NFE traits. On the other hand, hatch groups with younger birds at entry into the experiment were more efficient for the NFE traits which may be due to accelerated growth rates approaching maximum at the onset of the experiment.

Efficiency performance across age among the clusters show that in using RFI and RIG to define feed efficiency, cluster 1 began the test as the least efficient but tended to improve on efficiency as they approached maturity while cluster 2 was the most efficient during the early stages of the experiment but the efficiency decreased as the test period progressed. The re-ranking of clusters in RFI and RIG across test periods is an indication of age being a significant contributor to possible variation in feed efficiency over time (Durunna *et al*., 2012). In addition, the change in efficiency over time is considered to have implications on body composition (Aggrey *et al*., 2010). Cluster 2 is likely to shift from protein accretion to fat deposition earlier resulting in increased percentage of fat deposition as the birds approach maturity. Cluster 1, on the other hand, is likely to have a higher percentage of leanness towards maturity as result of delayed shift in protein to fat deposition. Such implications indicate the need to further consider body composition in efficiency evaluation in IC.

In the case of RG, cluster 3 was the most efficient throughout the test period while cluster one was the least efficient. Birds from cluster 3 (*Kuchi* ecotype) have been considered ideal for meat production given their potential to attain 1700g by the age of 20 weeks under improved management conditions (Lwelamira, 2012). Consequently, this may have influenced the observed superiority in RG given the positive relationship between RG and growth (Crowley *et al*., 2010). The NFE traits greatly fluctuated across the different age points within the clusters which may have resulted to lack of significant influence of cluster on mean performances for the NFE traits. Indigenous chicken in Kenya have not undergone intensive selection for particular traits contributing to birds with different phenotypic background. In addition, clustering of the birds on the basis of non-MHC linked markers was more of a phylogeny classification and not trait distinct grouping which could also explain the large differences in the NFE traits within and among the clusters across age during the test. This has further been demonstrated by previous studies on growth patterns of the cluster constituents indicating that IC ecotypes significantly differed in body weight from hatch to 8 weeks of age (Ngeno *et al*., 2012). Despite birds used in this experiment have only been selected once for growth traits, this is not sufficient to identify particular IC lines and associate them with high growth performance and as such distinct variation among the clusters is not expected with regards to efficiency.

3.5. Conclusion

The mean performance of growth and NFE traits in IC is influenced by sex, hatch group and an interaction between sex and cluster while cluster and genotype have no effect on these traits. There is significant variation within and among clusters across ages resulting to re-ranking of the phylogenetic groups for the NFE traits across the test period. Large differences were observed during the later period of the experiment in RFI and RIG, and during the earlier period of the experiment in RG. For improvement of growth and efficiency traits in IC, the non-genetic sources of variation identified in this study need to be adjusted for in genetic evaluations. This will allow for unbiased and accurate estimation of genetic parameters.

References

Aggrey, S. E., Karnuah, B. A., Sebastian, B., and Anthony, N. B. (2010). Genetic properties of feed efficiency parameters in meat-type chickens. *Genetics Selection Evolution*, *42*, 25-30.

Aggrey, S. E., and Rekaya, R. (2013). Dissection of Koch's residual feed intake: Implications for selection. *Poultry Science, 92*, 2600-2605.

Ayuya, O. I., Lagat, J. K., and Mironga, J. M. (2011). Factors influencing potential acceptance and adoption of clean development mechanism projects: Case of carbon trade tree project among smale-scale farmers in Njoro district, Kenya. *Research Journal of Environmental and Earth Sciences, 3* (3), 275-285.

Begli, H. E., Torshizi, R. V., Masoudi, A. A., Ehsani, A., and Jensen, J. (2016). Longitudinal analysis of body weight, feed intake and residual feed intake in F2 chickens. *Livestock Sciences, 184,* 28-34.

Binda, B. D., Yousif, I. A., Elamin, K. M., and Eltayeb, H. E. (2012). A comparison of performance among exotic meat strains and local chicken ecotypes under Sudan conditions. *International Journal of Poultry Science, 11* (8), 500-504.

Case, L. A., Wood, B. J., and Miller, S. P. (2012). The genetic parameters of feed efficiency and its component traits in turkey (*Meleagris gallopova*). *Genetics Evolution Science, 44,* 2-6.

Crowley, J. J., McGee, M., Kenny, D. A., Crews, D. H., Evans, R. D., and Berry, D. P. (2010). Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *Journal of Animal Science, 44,* 958-972.

Durunna, O. N., Colazo, M. G., Ambrose, D. J., McCartney, D., Baron, V. S., and Basarab, J. A. (2012). Evidence of residual feed intake reranking in crossbred replacement heifers. *Journal of Animal Science, 90,* 734-741.

Karaman, E., Narinc, D., Firat, M. Z., and Aksoy, T. (2013). Nonlinear mixed effects modeling of growth of Japanese quail. *Poultry Science, 92,* 1942-1948.

King'ori, A. M., Tuitoek, J. K., Muiruri, H. K., and Wachira, A. M. (2004). Protein requirements of growing indigenous chickens during the 14-21 weeks growing period. *South African Journal of Animal Science*, *33* (2), 78-82.

Leeson, S., and Summers, J. (2010). Broiler breeder production. *Nottingham University Press.*

Lwelamira, J. (2012). Genotype-Environment (G X E) interaction for body weights for Kuchi chicken ecotype of Tanzania reared under intensive and extensive management. *Global Journal of Medical Research, 12* (5), 57-65.

Magothe, T. M., Muhuyi, B. W., and Kahi, A. K. (2010). Influence of major genes for crested-head, frizzled-feather and naked-neck on body weights and growth patterns of IC reared intensively in Kenya. *Tropical Animal Health and Production, 42,* 173-183.

Mrode, R. A. (2005). *Linear Models for the Prediction of Animal Breeding Values*. Trowbridge, UK: Cromwell Press.

Mwacharo, J. M., Nomura, K., Hanada, H., Jianlin, H., Hanotte, O., and Amano, T. (2007). Genetic relationships among Kenyan and other East African indigneous chickens. *Animal Genetics, 38* (5), 485-490.

Ngeno, K., van der Waaij, E. H., Megens, H. J., Kahi, A. K., van Arendonk, J. A., and Crooijmans, R. P. (2015). Genetic diversity of different indigenous chicken ecotypes using highly polymorphic MHC linked and non-MHC linked microsatellite markers. *Animal Genetic Resources, 56,* 1-7.

Ngeno, K., Bebe, B. O., and Kahi, A. K. (2012). Genetic evaluation of growth traits in ecotypes of Kenyan indigenous chicken. *Family Poultry Communications (FAO), 21* (2), 4-12.

SAS. (2002). SAS User's Guide (Version 9.1.3). *Statistical Analysis System Institute, SAS Inc.* Cary: NC.

Tadelle, D., Kijora, C., and Peters, K. J. (2003). Indigenous chicken ecotypes in Ethiopia: Growth and feed utilization potentials. *International Journal of Poultry Science, 2* (2), 144-152.

Varkoohi, S., Pakdel, A., Nejati Javaremi, A., Moradi Shahr Babak, M., Kause, A., and Zaghari, M. (2010). Genetic parameters for feed utilization traits in Japanese quails. *Poultry Science, 90,* 42-47.

Willems, O. W., Miller, S. P., and Wood, B. J. (2013). Assessment of residual body weight gain and residual intake and body weight gain as feed efficiency traits in the turkey (*Meleagris gallopova*). *Genetics Selection Evolution, 45,* 26-34.

CHAPTER FOUR

GENETIC AND PHENOTYPIC PARAMETERS FOR NET FEED EFFICIENCY IN INDIGENOUS CHICKEN IN KENYA

4.1. Introduction

Majority of the indigenous chicken (IC) population are reared under the extensive system where the production output is low despite the increasing demand for their products, especially meat (Magothe *et al*., 2012). Currently, adoption of the semi-intensive and intensive systems is gradually increasing in response to the increasing demand for the IC products (King'ori *et al*., 2010). However, producing IC under high input systems is not economically viable given that the birds will take up to six to eight months taken to reach the required market weight (1.8kg to 2.0kg) (Okeno *et al*., 2013). The prolonged time to attain market weight indicates low growth rates in IC, a reflection of low genetic potential. Given that growth is a function of efficiency with which birds convert feed consumed into production, there is need to consider feed efficiency alongside growth traits in IC breeding programmes (Aggrey *et al*., 2010).

Genetic improvement of net feed efficiency (NFE), as described in Chapter 1, provides an avenue for selecting IC that can maintain the same performance or perform better on less feed resource. Prior to selection, quatifying the level of variation in NFE traits caused by genetic effects and the level of inheritance provides basis for improvement. Component traits of NFE measures, feed intake and body weight traits, change over time due to activation of genes at different periods along the growth pattern (Belgi *et al*., 2016). As such, modelling variation in NFE traits on a longitudinal scale would be appropriate to reflect genetic factors that describe the change in efficiency over time. Previous studies have reported moderate to high heritability estimates for the NFE traits in poultry suggesting possibilities of genetic improvement of efficiency (Aggrey *et al*., 2010; Case *et al*., 2012; Willems *et al*., 2013; Belgi *et al*., 2016). However, heritability estimates are population specific therefore, the need to estimate parameters for IC. This Chapter aims to estimate genetic and phenotypic parameters of net feed efficiency in IC during the growers' period on a longitudinal scale.

4.2. Materials and methods

4.2.1. Data on body weight and feed intake

The study used data on body weight and feed intake between ages 11 weeks and 20 weeks resulting in each bird in the experimental flock of 107 birds having 42 daily feed intake and 10 weekly body weight records. Description of the study, experimental flock and mating design, and management practices is presented in Chapter 3. A total of 4494 daily feed intake and 642 weekly body weight records were available for analysis.

4.2.2. Statistical analysis

Net feed efficiency traits namely residual feed intake (RFI), residual gain (RG) and residual intake and gain (RIG) were computed using equations 1, 2 and 3 as described in Chapter 3. The distribution of records for the respective NFE traits across ages at seven days interval and the corresponding mean performances are presented in Figure 4.1. The number records for NFE traits increased with age from the beginning of the experiment to between 105 (15 weeks) and 112 days (16 weeks) after which they gradually decreased to the end of the experiment. The observed distribution of records across the test period was due to differences in initial age at entry into the feeding experimental cages across the hatch groups. The initial age ranged from week 10 to week 14, and thereafter data collection on feed intake lasted for six weeks for each bird.

Univariate random regression (RR) sire model (equ 5) was fitted on the RFI, RG and RIG data to estimate genetic and phenotypic parameters by restricted maximum likelihood (REML) using the WOMBAT software (Meyer, 2007).

$$Y_{ijtk} = F_i + \sum_{k=0}^{M_{A-1}} \emptyset_{jtk}\beta_k + \sum_{k=0}^{M_{B-1}} \emptyset_{jtk}S_{jk} + \sum_{k=0}^{M_{C-1}} \emptyset_{jtk}P_{jk} + e_{ijtk} \qquad \text{(equ 5)}$$

Where: Y_{ijtk} is the record of j^{th} bird taken at t^{th} age within i^{th} fixed effect group; F_i is a set of fixed effects; β_k is the fixed regression coefficients; S_{jk}, and Pe_{jk} are the vectors of the k^{th} random regression for sire and permanent environmental effects for bird j, respectively; $\emptyset_{jtk}$ is the vector of the k^{th} Legendre polynomials for record of j^{th} bird taken at t^{th}age (for which age is standardized to $-1<t<1$); M_{A-1}, M_{B-1}, and M_{C-1} are the corresponding order of polynomials fitted for fixed, sire, and permanent environmental effects, respectively; and e_{ijtk} is the residual effect. The model was based on the assumptions that:

$$E\begin{pmatrix} a \\ pe \\ e \end{pmatrix} = \begin{bmatrix} K_a \otimes A & 0 & 0 \\ 0 & K_{pe} \otimes I & 0 \\ 0 & 0 & R \end{bmatrix} \qquad \text{(equ 6)}$$

Where: K_a and K_{pe} are the (co) variance matrices between random regression coefficients for genetic and permanent environmental effects, respectively; A is the relationship matrix; I is the identity matrix, ⊗ is the kronecker product between matrices and R is a block diagonal matrix containing residual variances. Correlations between random regression coefficients for different fixed and random effects were set to zero.

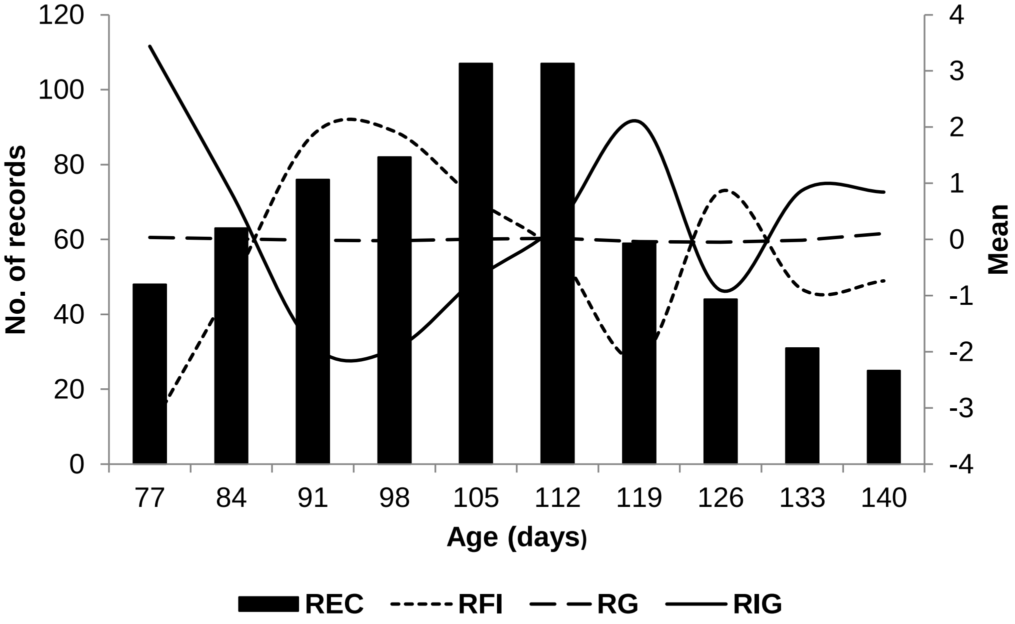


Figure 4.1: Number of records (REC) and means of residual feed intake (RFI), residual gain (RG) and residual intake and gain (RIG) between ages 77 days (11 weeks) to 140 days (5 months) in a seven-day interval

Fixed effects that were used in the univariate analyses above were included on the basis of their significant influence on NFE traits determined using equ 4 in Chapter 3. These included hatch group and an interaction between sex and cluster for RFI and RIG; and sex and hatch group for RG. Since birds entered the experiment with different body weights, initial weight was fitted as a linear covariate ($\alpha = 0.05$) for RG, and as a quadratic covariate ($\alpha = 0.05$) for RFI and RIG in the analyses to correct for these differences (Chapter 3).

The Legendre polynomials (LP) fitted for additive genetic and permanent environmental (PE) effects in each of the NFE trait were limited to order five given the small age range between records (Liu *et al*., 2006). Heteroscedastic residual variance was modelled by fitting nine classes between ages 77 days (11 weeks) and 140 days (5 months) at an interval of seven days. Therefore, seven models were fitted for each of the NFE traits and designated as *L(m,n)* where *m* and *n* were the orders polynomial fit for the additive genetic and PE effects respectively. The RR models were compared using the Bayesian Information Criterion (*BIC*) due to the penalty term and the stringency it places on complex models (Liu *et al*., 2006). Models *L(4,5)* with 34 parameters, *L(3,4)* with 25 parameters and *L(5,5)* with 39 parameters had the lowest criteria values hence most parsimonious for RFI, RG and RIG, respectively (Table 4.1). During the analysis there was need to use the Parameter Expanded-Expectation Maximization (PX-EM) algorithm for the initial iteration runs to get variance estimates closer to the true values, and then switching to Average Information (AI) algorithm in order to achieve convergence. Such convergence problems have been reported to result from some eigenvalues of the estimated covariance matrix being zero or near zero due to fitting orders beyond cubic, especially for the additive genetic effect (Boligon *et al*., 2010).

Table 4.1: Order of fit, number of parameters (np) and fit statistics for additive genetic and permanent environment effects for residual feed intake (RFI), residual gain (RG) and residual intake and gain (RIG)

Model	(np)	RFI			RG			RIG		
		log ML	-1/2 AIC	-1/2BIC	log ML	-1/2AIC	-1/2BIC	log ML	-1/2AIC	-1/2BIC
L22_9	15	-1806.59	-1821.59	-1854.86	675.63	660.63	627.30	-1807.08	-1822.08	-1855.35
L23_9	18	-1773.17	-1791.17	-1831.09	1275.68	1257.68	1217.68	-1774.13	-1792.13	-1832.05
L33_9	21	-1773.38	-1794.38	-1840.96	1275.74	1254.74	1208.07	-1774.16	-1795.16	-1841.74
L34_9	25	-1878.19	-1903.19	-1958.64	**236.56**	**211.56**	**156.01**	-1750.24	-1775.24	-1830.70
L44_9	29	-1826.52	-1855.52	-1919.84	1033.33	1004.33	939.89	-1876.26	-1905.26	-1969.58
L45_9	34	**-1490.30**	**-1524.30**	**-1599.71**	804.44	770.44	694.89	-1831.42	-1865.42	-1940.84
L55_9	39	-1529.54	-1568.54	-1655.04	727.47	688.47	601.81	**-1485.41**	**-1524.41**	**-1610.91**

Log ML = Log maximum likelihood; AIC = Aikake Information Criterion; BIC = Bayesian Information Criterion

4.3. Results

Variance component estimates in RFI, RG and RIG from 77 days to 140 days of age are presented in Figure 4.2. Additive genetic variance for RFI decreased from 112g at the start of the test period to near zero at 126 days of age then gradually increased to the end of the test period. Phenotypic and permanent environment (PE) variances showed a similar declining trend from 456g and 240g, respectively, at the beginning of the test to 121g and 32g, respectively at 133 days of age before sharply increasing to 780g and 696g at the end of the test, respectively.Variation in RG due to additive genetic effect decreased throughout the study period with highest estimate of 6.01g observed at age 77 days. Permanent environment and phenotypic variances, on the other hand, increased throughout the test period with highest estimates of 24.09g and 26.67g, respectively, at the end of the test. Genetic and phenotypic variances for RIG were high in early and late ages of test period. The PE variance for RIG on the other hand showed a declining trend throughout the test period from 591.91g to 46g.

Estimates of heritability and permanent environmental variance as a proportion of phenotypic variance for RFI, RG and RIG are as presented in Table 4.2. Residual feed intake had low to moderate heritability across the test period with estimates increasing gradually from 77 to 98 days, sharply dropping to low estimates at day 126 and fluctuating thereafter to the end of the test period. Permanent environmental variance as a proportion of phenotypic variance was higher than heritability estimates, but a mirror image of the estimates. Residual gain had relatively high heritability estimates at the beginning of the test which gradually decreased to low estimates at mid test period age (105 days) and thereafter remained low to the end of the experimental period. Permanent environmental variance as proportion of phenotypic variance highly fluctuated within the experimental period with high estimates between ages 77 to 98 days and plateaued from 119 to 140 days. Contrary to its component traits, RIG had high heritability estimates at the start and end of test period with low estimates between 105 and 112 days. The permanent environmental variance as a proportion of phenotypic variance was a mirror image of the heritability estimates where low estimates observed at the beginning and end of the test period with high estimates in between. Generally, the ratio of PE to phenotypic variance was higher the heritability estimates in RFI and RG, while in RIG the heritability estimates weres higher throughout the test.

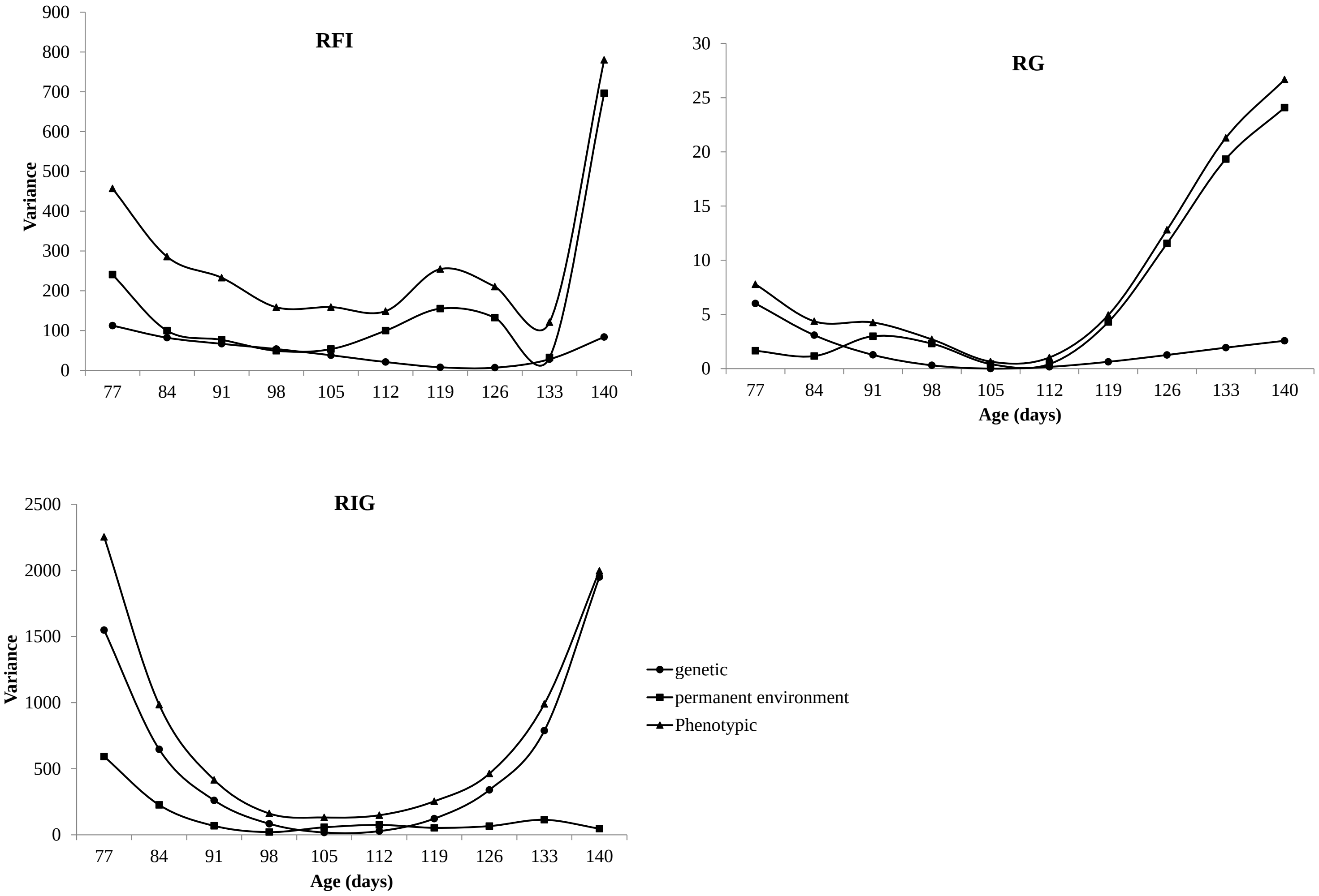


Figure 4.2: Estimates of genetic (σ^2s), permanent environmental (σ^2pe), residual (σ^2re) and phenotypic (σ^2p) variances for residual feed intake (RFI), residual gain (RG), and residual intake and gain (RIG)

Table 4.2. Genetic (h^2) and permanent environmental (c^2) variances as proportions of phenotypic variance for residual feed intake (RFI), residual gain (RG), and residual intake and gain (RIG)

Age	**RFI**		**RG**		**RIG**	
	h^2± se	**c^2±se**	**h^2±se**	**c^2±se**	**h^2±se**	**c^2±se**
77	0.25±0.11	0.53±0.12	0.77±0.67	0.21±0.65	0.69±0.36	0.26±0.39
84	0.29±0.13	0.35±0.15	0.71±0.59	0.27±0.59	0.66±0.45	0.23±0.46
91	0.29±0.16	0.33±0.18	0.30±0.17	0.70±0.17	0.63±0.38	0.16±0.27
98	0.34±0.12	0.31±0.15	0.11±0.11	0.86±0.12	0.52±0.32	0.13±0.24
105	0.24±0.10	0.34±0.13	0.01±0.11	0.65±0.17	0.13±0.10	0.43±0.20
112	0.14±0.11	0.67±0.16	0.16±0.14	0.41±0.30	0.19±0.10	0.51±0.19
119	0.03±0.21	0.61±0.20	0.13±0.19	0.87±0.19	0.48±0.15	0.21±0.24
126	0.03±0.13	0.63±0.12	0.10±0.13	0.90±0.18	0.73±0.13	0.14±0.13
133	0.23±0.12	0.27±0.10	0.09±0.07	0.91±0.09	0.80±0.18	0.11±0.18
140	0.11±0.25	0.89±0.79	0.10±0.16	0.90±0.19	0.98±0.56	0.02±0.58

h^2; heritability, genetic variance as proportion of phenotypic variance, c^2; permanent environmental variance as proportion of phenotypic variance, ±se; standard error for the parameters

Estimates of the genetic and phenotypic correlation estimates for RFI, RG and RIG from ages 77 to 140 days are presented in Table 4.3, 4.4 and 4.5. The genetic correlation between RFI records at adjacent ages (77 to 105 days) had unity to moderate positive estimates, but gradually declined to moderate to high negative estimates as the interval between records increased (between 77 days and 112 to 140 days). Contrary to the genetic correlation, positive phenotypic correlations were observed between RFI records at day 77 and from day 133 to 140. In the case of RG, the genetic correlation between records at consecutive ages (77 to 105 days) was high and positive, however, as the interval between records increased (between 77 days and 112 days to 140 days) high and negative estimates were observed. However, the phenotypic correlations between records at 77 and 91 days had high to moderate positive estimates, thereafter between 77 and 98 to 140 days the estimates ranged from moderate to low. Similar genetic correlation pattern in RFI was observed in RIG where unity to moderate and positive estimates were observed at adjacent ages (77 to 105 days) while with increase in age interval (between 77 days and 112 to 140 days) the estimates were high and negative. With regards to phenotypic correlation, the estimates followed a similar trend as the genetic correlations. Generally, for all the NFE traits, the estimates of genetic correlations were higher than those of phenotypic correlations and decreased as the interval of ages between records increased.

Table 4.3. Genetic (lower diagonal) and phenotypic (upper diagonal) correlations for residual feed intake (RFI) from ages 77 to 140 days

Age	**77**	**84**	**91**	**98**	**105**	**112**	**119**	**126**	**133**	**140**
77	1	0.46±0.34	0.18±0.16	-0.06±0.38	-0.24±0.18	-0.35±0.36	-0.29±0.25	-0.21±0.35	0.11±0.33	0.35±0.32
84	0.96±0.28	1	0.53±0.21	0.29±0.19	-0.09±0.05	-0.41±0.91	-0.43±0.08	-0.39±0.28	-0.04±0.26	0.34±0.30
91	0.79±0.36	0.94±0.33	1	0.71±0.18	-0.17±0.14	-0.73±0.39	-0.38±0.26	-0.81±0.15	-0.06±0.21	0.24±0.24
98	0.56±0.37	0.80±0.09	0.96±0.26	1	0.46±0.29	-0.08±0.16	-0.16±0.23	-0.71±0.23	-0.74±0.31	0.03±0.22
105	0.32±0.24	0.62±0.32	0.85±0.38	0.96±0.15	1	0.53±0.24	0.23±0.18	-0.05±0.27	-0.51±0.39	-0.34±0.30
112	-0.02±0.19	0.35±0.26	0.64±0.24	0.84±0.22	0.95±0.23	1	0.62±0.39	0.62±0.39	-0.55±0.36	-0.74±0.06
119	-0.49±0.25	-0.21±0.25	0.14±0.39	0.41±0.26	0.64±0.38	0.84±0.35	1	0.57±0.35	-0.08±0.31	-0.74±0.28
126	-0.91±0.12	-0.99±0.04	-0.90±0.41	-0.74±0.38	-0.54±0.35	-0.26±0.36	0.30±0.32	1	0.29±0.39	-0.66±0.35
133	-0.51±0.38	-0.79±0.04	-0.95±0.49	-0.99±0.46	-0.96±0.29	-0.84±0.34	-0.41±0.38	0.75±0.33	1	0.17±0.35
140	-0.25±0.31	-0.58±0.36	-0.82±0.38	-0.95±0.37	-0.99±0.32	-0.96±0.05	-0.66±0.31	0.52±0.34	0.96±0.32	1

(±) standard error for the estimates

Table 4.4. Genetic (lower diagonal) and phenotypic (upper diagonal) correlations for residual gain (RG) from ages 77 to 140 days

Age	**77**	**84**	**91**	**98**	**105**	**112**	**119**	**126**	**133**	**140**
77	1	0.64±0.52	0.22±0.33	-0.01±0.44	-0.24±0.15	-0.18±0.06	-0.04±0.41	-0.01±0.43	-0.03±0.43	-0.10±0.40
84	0.99±0.01	1	0.87±0.34	0.72±0.63	0.42±0.33	-0.65±0.59	-0.76±0.55	-0.74±0.59	-0.74±0.61	-0.75±0.61
91	0.99±0.06	0.99±0.01	1	0.99±0.68	0.70±0.47	-0.68±0.40	-0.97±0.07	-0.79±0.22	-0.78±0.26	-0.92±0.19
98	0.99±0.24	0.99±0.16	0.99±0.52	1	0.76±0.35	-0.67±0.31	-0.97±0.07	-0.79±0.54	-0.79±0.16	-0.91±0.19
105	0.69±0.61	0.71±0.66	0.73±0.31	0.76±0.20	1	-0.51±0.41	-0.75±0.40	-0.76±0.38	-0.74±0.41	-0.70±0.48
112	-0.99±0.73	-0.99±0.72	-0.99±0.73	-0.99±0.19	-0.66±0.55	1	0.73±0.42	0.99±0.75	0.99±0.22	0.71±0.47
119	-0.99±0.60	-0.99±0.52	-0.99±0.50	-0.99±0.70	-0.71±0.49	0.99±0.13	1	0.99±0.41	0.99±0.04	0.96±0.06
126	-0.99±0.83	-0.99±0.71	-0.99±0.45	-0.99±0.33	-0.74±0.37	0.99±0.60	0.99±0.05	1	0.99±0.34	0.97±0.07
133	-0.99±0.35	-0.99±0.47	-0.99±0.66	-0.99±0.36	-0.76±0.53	0.99±0.57	0.99±0.21	0.99±0.68	1	0.99±0.09
140	-0.99±0.88	-0.99±0.64	-0.99±0.42	-0.99±0.32	-0.79±0.38	0.98±0.56	0.99±0.52	0.99±0.25	1.00±0.07	1

(±) standard error for the estimates

Table 4.5. Genetic (lower diagonal) and phenotypic (upper diagonal) correlations for residual intake and gain (RIG) from ages 77 to 140 days

Age	77	84	91	98	105	112	119	126	133	140
77	1	0.85±0.08	0.70±0.13	0.48±0.17	0.06±0.19	-0.25±0.22	-0.40±0.24	-0.45±0.45	-0.43±0.91	-0.40±0.62
84	0.97±0.14	1	0.80±0.05	0.53±0.10	0.03±0.15	-0.43±0.17	-0.53±0.18	-0.52±0.28	-0.49±0.56	-0.52±0.13
91	0.92±0.37	0.98±0.07	1	0.40±0.34	0.05±0.15	-0.46±0.18	-0.56±0.14	-0.59±0.13	0.84±0.18	-0.59±0.74
98	0.84±0.51	0.92±0.27	0.97±0.54	1	0.35±0.12	-0.64±0.20	-0.40±0.13	-0.66±0.14	-0.02±0.16	-0.56±0.49
105	0.39±0.11	0.45±0.05	0.55±0.56	0.75±0.43	1	-0.77±0.22	0.10±0.12	0.41±0.28	0.34±0.15	-0.19±0.25
112	-0.82±0.71	-0.84±0.18	-0.78±0.06	-0.59±0.42	0.09±0.79	1	0.54±0.06	0.79±0.56	0.49±0.11	0.25±0.21
119	-0.94±0.16	-0.99±0.69	-0.98±0.75	-0.90±0.69	-0.38±0.28	0.88±0.35	1	0.82±0.39	0.60±0.18	0.57±0.35
126	-0.90±0.17	-0.97±0.06	-0.99±0.54	-0.96±0.53	-0.52±0.39	0.80±0.58	0.98±0.16	1	0.89±0.46	0.78±0.24
133	-0.78±0.39	-0.90±0.34	-0.95±0.69	-0.93±0.45	-0.53±0.38	0.74±0.57	0.93±0.56	0.98±0.76	1	0.89±0.22
140	-0.56±0.62	-0.74±0.54	-0.82±0.56	-0.80±0.47	-0.42±0.39	0.66±0.58	0.80±0.47	0.87±0.57	0.95±0.17	1

(±) standard error for the estimates

4.4. Discussion

High genetic variation observed in RFI and RG during the early stages of the experiment (Figure 4.2) indicate that selection for efficiency at the onset of the linear growth phase, between ages 77 days and 84 days, would yield higher genetic response. Meyer (2005) however, postulated Legendre Polynomials being prone to end range problems and may have influenced the high genetic variance estimates observed especially at 77 and 140 days. Therefore these values should be treated with caution to avoid upward bias in estimates of genetic gain in selection programs. During the test period, the genetic variance of RFI, RG and RIG was lowest between ages 105 and 126 days, a period coinciding with point at which indigenous chicken attain maximum growth as they approach asymptote growth and other physiological changes that may have resulted to low genetic influence on efficiency traits at these ages (Magothe *et al*., 2010; Tholon and Queiroz, 2011). The permanent environmental variance of RFI and RG was higher than the genetic influence throughout the test suggesting that birds in this study need to be selected to perform in an environment similar to the experimental conditions i.e. an intensive or at least semi-intensive environment to reduce the effects of genotype by environment interaction on performance (Mrode, 2005).

The low to moderate heritability estimates for RFI (Table 4.2) would infer to low accuracy of selection especially if mass selection is used. However, the 0.34 estimate at 98 days of age presents a suitable age for selection to obtain better response. Given the magnitude of the estimate, using family information as a selection criterion would improve on accuracy of selection. Contrary to these results, higher heritability estimates (0.42 to 0.45) were reported in broiler chicken and could be due to the intensive selection the birds had undergone for growth traits (Aggrey *et al*., 2010). The heritability for RG during the early ages and for RIG at both extremes of the trajectory was highly overestimated and unrealistic which could be due to numerical instability and artefacts of Legendre Polynomials at extreme ages (Nobre *et al*., 2003). Besides, extreme heritability estimates has been attributed to the influence of biological factors (Meyer, 2005; Faro *et al*., 2008; Aggrey *et al*., 2010). In this study, activation of different genes associated with physiological development during the rapid growth phase (at ages 77 and 84 days) and onset of sexual maturity (at ages 126 to 140 days) may have contributed to the high heritability in RG and RIG, respectively. To avoid selecting for RG based on artificial estimates, age 91 days would be the most appropriate age for selection given the moderate heritability of 0.30 and age at which heritability was highest with the lowest environmental influence on RG, an indication of high genetic influence as opposed to environmental effect. Similar to RFI, using family information as a selection criterion would help to improve on accuracy. For RIG, the variance ratio curves converged at 98 and 119 days that also had high heritability estimates implying that these are potential selection points for RIG. In addition, given the high estimates of heritability at the two points, mass selection would be an appropriate basis of selection.

In all the NFE traits, the genetic correlations between adjacent observations were high and positive but decreased in magnitude as the interval between ages increased (Table 4.3, 4.4 and 4.5). Favourable genetic correlations were observed among records in the early phase of the experiment, between ages 77 days to 105 days indicating that similar set of genes encode for efficiency during this period. However, the negative correlation between records at early phase and late phase (126 - 140 days) of the experiment suggest that improvement in efficiency during the linear growth phase could be associated with inefficiencies as the birds attain asymptote growth as they approach sexual maturity (Tholon and Queiroz, 2011). The unfavourable correlations indicate that feed efficiency has a different genetic background at different stages of growth. The body composition of birds during the early phase of growth is different from that of the late phase; therefore it is possible that the internal allocation of resources above maintenance into protein and fat deposition could contribute towards the negative correlation between the early and late ages. Based on the heritability estimates, genetic correlations favour selection for RFI and RIG at ages 98 days and RG at 91 days. This is however limited to the early phase of rapid growth given the inefficiencies expected at later ages due to the negative correlations.

4.5. Conclusion

The NFE traits in indigenous chicken have a large scope of variation to enable their improvement through selective breeding. Selection for RFI at 98 days, RG at 91 days and RIG at 98 and 119 days would improve on feed use efficiency in IC. The test period (77 to 140 days) can be partitioned into three phases; linear growth phase, growth rate transition phase and sexual maturity phase in relation to biological processes that influence nutrient partitioning. It may be difficult to improve efficiency as birds attain asymptote growth while approaching sexual maturity using efficiency records during the linear growth phase owing to the negative relationship between records in these phases. However, given the high standard errors estimates resulting from use of small data set from a single generation, these results need to be applied with caution. The NFE traits are phenotypically independent of their regressor traits; however selection for their improvement at the identified ages would require determination of their genetic influence on production traits.

References

Aggrey, S. E., Karnuah, B. A., Sebastian, B., and Anthony, N. B. (2010). Genetic properties of feed efficiency parameters in meat-type chickens. *Genetics Evolution Science, 42,* 25-30.

Begli, H. E., Torshizi, R. V., Masoudi, A. A., Ehsani, A., and Jensen, J. (2016). Longitudinal analysis of body weight, feed intake and residual feed intake in F2 chickens. *Livestock Science, 184,* 28-34.

Boligon, A. A., Mercadante, M. E., Forni, S., Lobo, R. B., and Albuquerque, L. G. (2010). Covariance functions for weights from birth to maturity in Nellore cows. *Journal of Animal Science,* 1151-1154.

Case, L. A., Wood, B. J., and Miller, S. P. (2012). The genetic parameters of feed efficiency and its component traits in turkey (*Meleagris gallopova*). *Genetics Evolution Science, 44,* 2-6.

Faro, L., Cardoso, V. L., and de Albuquerque, L. G. (2008). Variance component estimates applying random regression models for test-day milk yield in Caracu heifers. *Genetics and Molecular Biology, 31* (3), 665-673.

Kingori, A. M., Wachira, A. M., and Tuitoek, J. K. (2010). Indigenous chicken production in Kenya: a review. *International Journal of Poultry Science, 9* (4), 309-316.

Liu, Y. X., Zhang, J., and Schaeffer, L. R. (2006). Optimal random regression models for milk production in dairy cattle. *Journal of Dairy Science, 89,* 2233-2235.

Magothe, T. M., Muhuyi, B. W., and Kahi, A. K. (2010). Influence of major genes for crested-head, frizzled-feather and naked-neck on body weights and growth patterns of indigenous chicken reared intensively in Kenya. *Tropical Animal Health and Production, 42,* 173-183.

Magothe, T. M., Okeno, T. O., Muhuyi, W. B., and Kahi, A. K. (2012). Indigenous chicken production in Kenya: I. Current status. *World's Poultry Science Journal, 68* (1), 119-132.

Meyer, K. (2005). Random regression analyses using B-splines to model growth of Australian Angus cattle. *Genetics Evolution Science, 37,* 473-500.

Meyer, K. (2007). WOMBAT - A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *Journal of Zheijang University SCIENCE B, 8* (11), 815-821.

Mrode, R. A. (2005). *Linear models for the prediction of animal breeding values* (2nd ed.). Oxon, UK: CABI publishing.

Nobre, P. R., Misztal, I., Tsuruta, S., Bertrand, J. R., Silva, L. O., and Lopez, P. S. (2003). Analysis of growth curves in Nellore cattle by multiple-trait and random regression models . *Journal of Animal Science, 81,* 918- 926.

Okeno, T. O., Magothe, T. M., Kahi, A. K., and Peters , K. J. (2013). Breeding objectives for indigenous chicken: Model development and application to different production systems. *Tropical Animal Health and Production, 70,* 193-203.

Tholon, P., and Queiroz, S. A. (2011). Estimation of (co)variance componenets and genetic parameters for weights of red-winged tinamou using random regression models. *Revista Brasileira de Zootecnia, 40* (4), 781-787.

Willems, O. W., Miller, S. P., and Wood, B. J. (2013). Assessment of residual body weight gain and residual intake and body weight gain as feed efficiency traits in the turkey (*Meleagris gallopova*). *Genetics Evolution Science, 45,* 26-34.

CHAPTER FIVE

GENETIC AND PHENOTYPIC CORRELATION BETWEEN NET FEED EFFICIENCY AND PRODUCTION TRAITS IN INDIGENOUS CHICKEN

5.1. Introduction

The pleiotropic and linkage nature of genes influence how the expression of polygenic traits vary jointly making it important to study correlation parameters between traits. This is because depending on the magnitude and mathematical sign of the correlation estimate, improvement in one trait may have either favourable or unfavourable effect on other traits (Bourdon, 2000). Functional traits are known to have an antagonistic relationship with production traits (Falconer and Mackay, 1996). As such, genetic improvement of feed efficiency requires understanding of the relationship between net feed efficiency and production traits such as average daily feed intake (ADFI), average daily gain (ADG) and metabolic body weight (MBW). By quatifying these relationships, this ensures that upon selection for net feed efficiency there are no unfavourable correlated responses on meat producion traits.

Feed conversion ratio has been previously used to improve efficiency in IC (Binda *et al*., 2012; Sola-Ojo *et al*., 2012). However, improvement of the ratio trait presents a challenge due to the confounding effects resulting from the relationship between FCR and its component traits, and the relation between its components traits prevent FCR from being an ideal measure of efficiency (Willems *et al*., 2013). Net feed efficiency (NFE) traits are cited to be phenotypically independent of their component production traits as result of the distributing properties of the regression procedure used for its estimation (Netter *et al*., 2004; Crowley *et al*., 2010). However, there is no guarantee that the phenotypic or genetic correlation between the NFE traits and their component traits will be zero (Kennedy *et al*., 1993). This is especially the case if the traits are estimated using phenotypic regressions.

Previous studies on body weight traits characterized the different phases of growth in IC indicating that growth inflection was observed at 77 days of age, maximum growth at 105 days of age and asymptotic body weight as maturity is approached at 140 days of age (Tadelle *et al*., 2003; Magothe *et al*., 2010). Knowledge on these parameters provide basis for improving efficiency and developing feeding strategies to maximize on growth potential. Considering the growth parameters, the objective of this Chapter was to estimate the phenotypic and genetic correlations among the different measures of NFE and production traits (ADFI, ADG and MBW) at 77 days, 105 days and 140 days of age.

5.2. Materials and methods

5.2.1. Data collection and statistical analysis

Description of the study site, experimental flock and mating design, management practices and data collection has been presented in Chapter 3. Net feed efficiency traits namely residual feed intake (RFI), residual gain (RG) and residual intake and gain (RIG) were computed using equ 1, 2 and 3 as described in Chapter 3. Records on production (ADFI, ADG and MBW) and NFE (RFI, RG and RIG) traits at 77, 105 and 140 days of age were selected for analysis given their biological significance in indigenous chicken production. This resulted in each bird having three records on ADFI, ADG, MBW, RFI, RG and RIG corresponding to 77, 105 and 140 days.

A multivariate sire model was used to obtain genetic and phenotypic correlation between traits at 77, 105 and 140 days of age. A series of multivariate models with four response variables were fitted to estimate the correlation between the NFE traits at 77 days (NFE_{77}) and production traits at 77, 105 and 140 days, NFE traits at 105 days (NFE_{105}) and production traits at 105 and 140 days and NFE traits at 140 days (NFE_{140}) and production traits at 140 days. In addition, tri-variate models were fitted for the correlation among the NFE traits at 77, 105 and 140 days of age. The estimates were obtained by restricted maximum likelihood (REML) using the WOMBAT software (Meyer, 2007). The multivariate model written in matrix notation is presented in equ 7:

$$\begin{bmatrix} y_1 \\ \vdots \\ y_i \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & X_i \end{bmatrix} \begin{bmatrix} b_1 \\ \vdots \\ b_i \end{bmatrix} + \begin{bmatrix} Q_1 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & Q_i \end{bmatrix} \begin{bmatrix} s_1 \\ \vdots \\ s_i \end{bmatrix} + \begin{bmatrix} e_1 \\ \vdots \\ e_i \end{bmatrix} \qquad \text{(equ 7)}$$

Where: Y_i is the vector of observations for the i^{th} trait; b_i is the vector of fixed effects for the i^{th} trait; S_i is the vector of random sire additive genetic effects for the i^{th} trait; e_i is the vector of random residual effect for the i^{th} trait; and X_i, and Q_i are the incidence matrices relating records of the i^{th} trait to fixed and random sire effects, respectively.

Fixed effects that were used in the multivariate analyses above were included on the basis of their significant influence on growth and NFE traits determined in Chapter 3. These included sex for ADG and RG, hatch group for all traits except ADFI and an interaction between sex and cluster for ADFI, RFI and RIG. Since birds entered the experiment with different body weights, initial weight was fitted as a linear covariate ($\alpha = 0.05$) for ADG, MBW, ADFI and RG, and as a quadratic covariate ($\alpha = 0.05$) for RFI and RIG to correct for these differences (Chapter 3). The multivariate analysis involved a cholesky transformation given the unequal design matrix as result of the traits being affected by different fixed effects. Due to the various combinations of the multivariate models, several local variance components and variance ratios were obtained. Consequently, the resulting variance components and variance ratios were pooled by weighting each estimate by the inverse of its sampling variance to obtain global estimates as presented in equ 8:

$$\bar{E} = \frac{\sum(w \ x \ E)}{\sum w} \qquad \text{(equ 8)}$$

Where: $\bar{E}$ is the weighted mean; w is the reciprocal of the sampling variance (weight); and E is the variance component and ratio to be pooled.

5.3. Results

Estimates of genetic variance for NFE and productive traits between ages 77 days to 140 days are presented in Figure 5.1. Variation due to genetic effect in ADFI, MBW and RIG increased during the test period with the highest estimate of 96g, 38g and 103g at 140 days, respectively. On the other hand, the genetic variance in ADG, RFI and RG declined with highest estimates of 3.09g, 216g and 0.05g at 77 days, respectively.

Estimates of genetic and phenotypic correlations between NFE traits and productive traits at 77, 105 and 140 days of age are presented in Table 5.1, 5.2 and 5.3. Genetic correlation between RFI_{77} and $ADFI_{77, 105, 140}$ and RFI_{77} and $ADG_{77, 105, 140}$ were high and positive but decreased as age progressed in the production traits. Conversely, correlation between RFI_{77} and $MBW_{77, 105, 140}$ increased from -0.35 to 0.70. The correlation between RG_{77} and $ADFI_{77, 105, 140}$ was low but positive. In the case of ADG, the correlation between RG_{77} and $ADG_{77,105,140}$ was between 0.12 and 0.55 while its correlation with $MBW_{77, 105, 140}$ ranged from 0.05 to 0.19. The correlation between RIG_{77} and $ADFI_{77, 105, 140}$ increased from -0.69 to -0.35 while its correlation with $ADG_{77,}$ was -0.77 which increased to -0.17 at $ADG_{105,}$ and later declined to -0.56 at ADG_{140} and the correlation with $MBW_{77, 105, 140}$ decreased from 0.39 to -0.54.

The phenotypic correlation between RFI_{77} and $ADFI_{77}$ was 0.86, which declined to -0.26 at $ADFI_{105}$ and increased to 0.43 at $ADFI_{140}$. On the other hand, the correlation between RFI_{77} with $ADG_{77, 105, 140}$ and $MBW_{77, 105, 140}$ increased from -0.10 to 0.29. Residual gain at 77 days (RG_{77}) had low correlations with $ADFI_{77, 105, 140}$ and $MBW_{77, 105, 140}$ ranging from -0.19 to 0.19. However, RG_{77} had a correlation of 0.44 with ADG_{77}, decreasing to -0.40 at ADG_{105} and later slightly increased to 0.12 at ADG_{140}. Residual intake and gain at 77 days (RIG_{77}) had a phenotypic correlation of -0.86 with $ADFI_{77}$, which increased to 0.25 at

$ADFI_{105}$ and then declined to -0.27 at $ADFI_{140.}$ The correlation between RIG_{77} with $ADG_{77, 105, 140}$ and $MBW_{77, 105, 140}$ gradually decreased from 0.16 to -0.26.

Genetic correlation between RFI_{105} and $ADFI_{105}$ was 0.33, decreasing to -0.43 at $ADFI_{140}$. Correlation with $ADG_{105, 140}$ and $MBW_{105, 140}$ increased from -0.88 to -0.03. In the case of residual gain, RG_{105} had negative correlations of -0.40 and 0.50 with $ADFI_{105, 140}$, respectively and of -0.02 and -0.46 with $MBW_{105, 140}$, respectively. On the other hand, RG_{105} had correlations of 0.57 with ADG_{105}, which decreased to -0.30 at ADG_{140}. For RIG_{105}, the trait had negative correlation of -0.33 with $ADFI_{105}$, which increased to 0.35 at $ADFI_{140}$. However, RIG_{105} had positive correlation of 0.88 and 0.82 with ADG_{105} and MBW_{105}, respectively but this declined to -0.06 and -0.25 at ADG_{140} and MBW_{140}, respectively.

The phenotypic correlation between RFI_{105} and $ADFI_{105}$ was 0.64 decreasing to -0.14 at $ADFI_{140}$ while its correlation with $ADG_{105, 140}$ and $MBW_{105, 140}$ increased from -0.05 to 0.08 and 0.12 to 0.13, respectively. The correlation between RG_{105} and $ADFI_{105, 140}$, $ADG_{105, 140}$ and $MBW_{105, 140}$ declined from -0.22 to -0.33, 0.18 to -0.66 and -0.37 to -0.70, respectively. In the case of RIG_{105}, the phenotypic correlation with $ADFI_{105, 140}$ and $MBW_{105, 140}$ increased from -0.64 to 0.14 and -0.13 to -0.11, respectively, while the correlation with $ADG_{105, 140}$ declined from 0.05 to -0.08.

Positive genetic correlations of 0.67, 0.36 and 0.17 were observed between RFI_{140} and $ADFI_{140}$, ADG_{140} and MBW_{140}, respectively. However, the genetic correlation between RG_{140} and the production traits at day 140, and between RIG_{140} and production traits at day 140 had negative estimates ranging from -0.69 to -0.12. The phenotypic correlation between RFI_{140} and the production traits at 140 days had low to high positive estimates while RG_{140} and RIG_{140} had negative correlations with the production traits at 140 days.

Estimates of genetic and phenotypic among the net feed efficiency traits at ages 77 days, 105 days and 140 days are presented in Table 5.1, 5.2 amd 5.3. Residual feed intake at 77, 105 and 140 days had high and negative genetic correlations with $RG_{77, 105, 140}$ and $RIG_{77, 105,140}$. On the other hand, the correlation between $RG_{77, 105}$ and $RIG_{77, 105}$ had positive and high estimates while RIG at 140 days had high and negative correlations with $RG_{77, 105, 140}$. The phenotypic correlation among the efficiency traits had no specific pattern but fluctuated from positive to negative estimates between ages 77 days, 105 days and 140 days. Generally, the genetic correlation had higher estimates than the phenotype correlations.

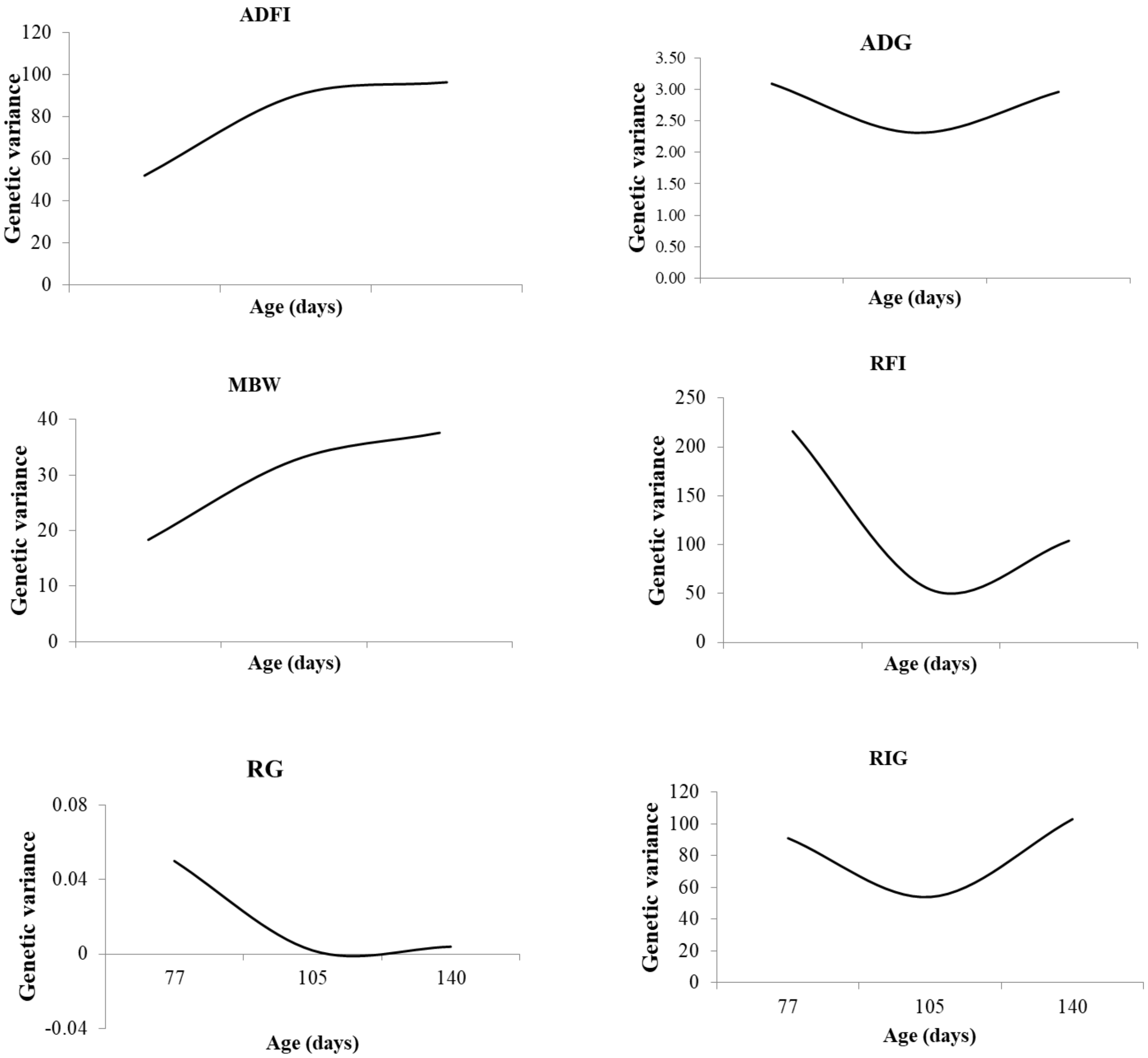


Figure 5.1: Estimates of genetic variance for net feed efficiency and production traits at ages 77 days, 105 days and 140 days

Table 5.1: Heritability (bold), genetic (above diagonal) and phenotypic (below diagonal) correlations between different net feed efficiency traits at 77 days of age and production traits at 77 days, 105 days and 140 days of age

Trait	**ADFI$_{77}$**	**ADG$_{77}$**	**MBW$_{77}$**	**RFI$_{77}$**	**RG$_{77}$**	**RIG$_{77}$**
ADFI$_{77}$	**0.13±0.45**	0.99±0.82	0.39±0.47	0.73±0.86	0.04±0.37	0.19±0.70
ADG$_{77}$	-0.04±0.40	**0.58±0.41**	0.31±0.77	0.82±0.90	0.55±0.68	-0.17±0.62
MBW$_{77}$	-0.01±0.21	0.39±0.63	**0.91±0.18**	-0.35±0.72	0.05±0.53	0.41±0.47
RFI$_{77}$	0.86±0.40	-0.14±0.65	-0.13±0.91	**0.88±0.63**	-0.67±0.49	0.99±0.57
RG$_{77}$	-0.19±0.64	0.44±0.52	0.18±0.63	-0.24±0.42	**0.38±0.36**	0.68±0.52
RIG$_{77}$	-0.86±0.91	0.16±0.49	0.15±0.62	-0.99±0.69	0.26±0.48	**0.38±0.63**
ADFI$_{105}$	0.65±0.31	0.95±0.43	-0.02±0.72	-0.26±0.62	0.14±0.60	0.25±0.43
ADG$_{105}$	-0.03±0.42	0.85±0.69	0.48±0.61	0.12±0.49	-0.40±0.41	-0.10±0.67
MBW$_{105}$	0.04±0.44	0.46±0.60	0.88±0.81	-0.15±0.78	0.16±0.51	0.08±0.65
RFI$_{105}$	0.75±0.64	-0.16±0.72	-0.15±0.72	-0.72±0.61	-0.33±0.72	0.72±0.48
RG$_{105}$	-0.11±0.67	0.56±0.51	0.17±0.80	0.04±0.75	-0.76±0.69	-0.18±0.65
RIG$_{105}$	-0.78±0.33	0.08±0.41	0.13±0.85	0.69±0.54	0.44±0.43	-0.16±0.78
ADFI$_{140}$	0.49±0.61	0.82±0.62	-0.05±0.52	0.43±0.57	0.12±0.49	-0.27±0.63
ADG$_{140}$	0.32±0.40	0.79±0.79	0.52±0.83	0.29±0.40	0.12±0.58	-0.26±0.51
MBW$_{140}$	0.19±0.41	0.94±0.42	0.75±0.68	0.25±0.30	0.19±0.61	-0.23±0.31
RFI$_{140}$	0.72±0.62	-0.06±0.53	-0.17±0.86	0.56±0.56	-0.46±0.44	0.19±0.47
RG$_{140}$	0.09±0.67	0.68±0.68	0.12±0.41	-0.63±0.86	0.40±0.41	0.77±0.50
RIG$_{140}$	-0.68±0.55	0.02±0.73	0.07±0.71	0.28±0.68	-0.12±0.46	0.74±0.36

ADFI = Average daily feed intake; ADG = Average daily gain; MBW = Metabolic body weight; RFI = Residual feed intake; RG = Residual gain; RIG = Residual intake and gain; (±) standard error

Table 5.2: Heritability (bold), genetic (above diagonal) and phenotypic (below diagonal) correlations between different net feed efficiency traits at 105 days of age and production traits at 77 days, 105 days and 140 days of age

Trait	**ADFI$_{105}$**	**ADG$_{105}$**	**MBW$_{105}$**	**RFI$_{105}$**	**RG$_{105}$**	**RIG$_{105}$**
ADFI$_{77}$	0.10±0.43	0.99±0.52	0.47±0.78	0.61±0.60	-0.28±0.27	-0.59±0.60
ADG$_{77}$	-0.01±0.34	0.51±0.64	0.59±0.88	0.31±0.79	-0.27±0.20	-0.17±0.78
MBW$_{77}$	0.04±0.57	0.54±0.33	0.38±0.70	0.42±0.20	-0.15±0.36	-0.45±0.62
RFI$_{77}$	-0.26±0.61	0.11±0.32	-0.14±0.71	0.96±0.59	-0.19±0.43	0.78±0.59
RG$_{77}$	0.14±0.80	-0.42±0.58	0.16±0.64	0.04±0.89	0.22±0.72	0.46±0.48
RIG$_{77}$	0.15±0.41	-0.13±0.64	-0.08±0.39	0.69±0.57	0.12±0.63	0.65±0.57
ADFI$_{105}$	**0.32±0.24**	-0.65±0.39	-0.66±0.34	0.33±0.50	-0.40±0.64	-0.33±0.50
ADG$_{105}$	0.14±0.57	**0.56±0.24**	0.67±0.71	-0.88±0.81	0.72±0.33	0.88±0.58
MBW$_{105}$	0.34±0.63	0.54±0.38	**0.42±0.23**	-0.82±0.50	-0.02±0.46	0.82±0.50
RFI$_{105}$	0.64±0.79	-0.05±0.28	0.12±0.20	**0.57±0.38**	-0.71±0.43	-0.99±0.54
RG$_{105}$	-0.22±0.82	0.18±0.34	-0.37±0.27	0.08±0.45	**0.34±0.34**	0.73±0.65
RIG$_{105}$	-0.64±0.78	0.05±0.68	-0.13±0.40	-0.99±0.56	0.43±0.41	**0.57±0.38**
ADFI$_{140}$	0.46±0.73	0.75±0.55	-0.09±0.21	-0.14±0.31	-0.33±0.62	0.14±0.41
ADG$_{140}$	0.27±0.65	0.98±0.33	0.62±0.39	0.08±0.24	-0.66±0.32	-0.08±0.31
MBW$_{140}$	0.34±0.64	0.95±0.40	0.84±0.67	0.13±0.11	-0.71±0.57	-0.11±0.42
RFI$_{140}$	0.63±0.87	-0.02±0.69	-0.15±0.51	-0.33±0.45	0.07±0.43	0.47±0.54
RG$_{140}$	0.02±0.54	0.79±0.24	0.16±0.72	-0.46±0.15	-0.88±0.59	0.43±0.43
RIG$_{140}$	-0.72±0.71	0.06±0.61	0.09±0.82	-0.25±0.25	-0.11±0.64	-0.34±0.47

ADFI = Average daily feed intake; ADG = Average daily gain; MBW = Metabolic body weight; RFI = Residual feed intake; RG = Residual gain; RIG = Residual intake and gain; (±) standard error

Table 5.3: Heritability (bold), genetic (above diagonal) and phenotypic (below diagonal) correlations between different net feed efficiency traits at 140 days of age and production traits at 77 days, 105 days and 140 days of age

Trait	**ADFI$_{140}$**	**ADG$_{140}$**	**MBW$_{140}$**	**RFI$_{140}$**	**RG$_{140}$**	**RIG$_{140}$**
ADFI$_{77}$	0.33±0.53	0.99±0.46	0.99±0.77	0.57±0.70	0.15±0.46	-0.35±0.
ADG$_{77}$	0.32±0.73	0.21±0.52	0.99±0.73	0.71±0.53	0.26±0.	-0.56±0.
MBW$_{77}$	0.21±1.25	0.94±0.46	0.16±0.52	0.71±0.60	0.13±0.	-0.54±0.
RFI$_{77}$	0.43±1.21	0.29±0.54	0.25±0.62	0.36±0.72	-0.99±0.	0.29±0.
RG$_{77}$	0.12±1.29	0.12±0.84	0.19±0.71	-0.63±0.99	0.21±0.	-0.29±0.
RIG$_{77}$	0.17±1.42	-0.16±0.73	-0.13±0.92	0.28±0.81	-0.19±0.	0.89±0.
ADFI$_{105}$	0.76±0.68	0.99±0.41	0.99±0.90	-0.43±0.70	-0.51±0.	0.35±0.
ADG$_{105}$	0.27±0.64	0.13±0.33	0.99±0.42	-0.03±0.63	-0.31±0.	-0.06±0.
MBW$_{105}$	0.34±0.31	0.95±0.34	0.05±0.68	0.16±0.75	-0.46±0.	-0.25±0.
RFI$_{105}$	-0.43±0.51	0.08±0.43	0.13±0.71	0.97±0.52	-0.89±0.	0.99±0.
RG$_{105}$	-0.33±0.91	-0.66±0.72	-0.70±0.64	-0.24±0.68	0.42±0.	-0.89±0.
RIG$_{105}$	0.14±0.21	-0.08±0.67	-0.11±0.59	0.48±0.64	-0.09±0.	0.99±0.
ADFI$_{140}$	**0.91±0.37**	0.99±0.71	0.99±0.31	0.67±0.92	-0.29±0.	-0.69±0.
ADG$_{140}$	0.48±0.99	**0.35±0.14**	0.99±0.47	0.36±0.52	-0.21±0.	-0.42±0.
MBW$_{140}$	0.45±0.31	0.95±0.21	**0.27±0.17**	0.17±0.59	-0.52±0.	-0.24±0.
RFI$_{140}$	0.64±0.62	0.12±0.34	0.06±0.31	**0.84±0.16**	0.37±0.	-0.99±0.
RG$_{140}$	-0.25±0.51	-0.42±0.21	-0.53±0.62	-0.44±0.61	**0.43±0.25**	-0.36±0.
RIG$_{140}$	-0.64±0.58	-0.12±0.33	-0.07±0.51	-0.99±0.43	-0.11±0.	**0.82±0.17**

ADFI = Average daily feed intake; ADG = Average daily gain; MBW = Metabolic body weight; RFI = Residual feed intake; RG = Residual gain; RIG = Residual intake and gain; (±) standard error

5.4. Discussion

The high and positive genetic correlations between RFI_{77} with $ADFI_{77,\ 105,\ 140}$ and $ADG_{77,\ 140}$ in Table 5.1 indicate that selecting for low RFI_{77} will improve feed efficiency with an expected correlated response of reduced feed intake. However, this would be associated with fast growing birds consuming more feed than needed for growth. On the other hand, RG_{77} was under similar genetic influence as ADG_{77} implying that selection for this efficiency trait would result in increased growth while having low effect on feed intake and maintenance requirement (Crowley *et al*., 2010; Willems *et al*., 2013). In the case of RIG_{77}, the trait had unfavourable correlations with $ADG_{77,105,140}$ and MBW_{77} but favourale correlations with $ADFI_{77,105,140}$ and $MBW_{105,140}$. These relationships suggest that selection for high RIG_{77} for efficiency would result in lower feed intake and growth rates, while the maintenance requirement would increase at 77 days but later decrease as age progressed. Contrary to this, other studies have reported that improved RIG would result in animals with high growth rates while having no effect on maintenance requirement (Berry and Crowley, 2012). At phenotypic level, RFI_{77} and RG_{77} were positively correlated with feed intake and growth, respectively while having low association with their respective regressor traits. Statistically, this could partly be due to the properties of least square regressions used to estimate the efficiency traits (Case *et al*., 2012; Herd and Bishop, 2000). On the other hand, efficiency in RIG has been associated with reduced feed intake, increased growth and no influence on maintenance requirement (Berry and Crowley 2012; Willems *et al*., 2013). However, in this study growth had low associations with RIG_{77} given the low estimates.

The genetic correlation between RFI_{105} and $ADFI_{105}$ was moderate and positive while with ADG_{105} and MBW_{105} the correlation was high and negative (Table 5.2). These suggest that improved efficiency at 105 days will result in reduced feed intake and increased growth rate but will be associated with increased maintenance requirement. On the other hand, RFI_{105} had low to moderate genetic association with the production traits at 140 days. Based on the correlation between RG_{105} and the production traits at 105 and 140 days (Table 5.2), selection for high RG_{105} will result in reduced feed intake levels and increased growth rates with no influence on maintenance requirements. In the case of RIG_{105}, its correlation with the production traits at 105 days indicate that high RIG_{105} will reduce feed intake and increase growth rate but result in increased maintenance requirement which was similar to results reported in turkey at 105 days (Willems *et al*., 2013). Phenotypically, RFI_{105} and RIG_{105} were associated to only $ADFI_{105}$ in which birds that were efficient in either of the traits had reduced feed intakes. The correlations between RG_{105} and the production traits observed in this study differ from those reported in turkey at similar ages where RG had significant phenotypic correlation with growth and zero influence on feed intake and maintenance requirement (Willems *et al.*, 2013).

Genetic correlations between efficiency and production traits at 140 days (Table 5.3) show that improvement in RFI_{140} and RIG_{140} will favour feed intake by reducing intake levels with no effect on growth and maintenance. Efficiency in RG_{140} however, would result in reduced maintenance requirement without influence on ADFI and ADG. The phenotypic correlations showed that RFI_{140} and RIG_{140} had favourable relationship with $ADFI_{140}$ given the positive and negative estimates in RFI and RIG, respectively. On the other hand, RG_{140} was negatively associated with ADG_{140} and MBW_{140}, an indication of reduced growth and maintenance requirement.

The genetic correlations among the NFE traits suggest that selection for efficiency using $RFI_{77,105,140}$ would equally result in improved RG and RIG at all ages understudy. The correlation between RG and RIG however, was only favourable at ages 77 and 105 days while at 140 days improvement in either of the traits would result in reduced efficiency in the other trait as indicated by the negative correlations between them. Net feed efficiency has been suggested as an alternative measure for efficiency given the favourable relationship it has with production traits (Berry and Crowley, 2013). In the current study, $RG_{77,\ 105}$ had favourable correlations with production traits across all ages suggesting their suitability for selection to improve efficiency in indigenous chicken. In addition, RG_{77} would be the most appropriate given the high genetic variance (Figure 5.1) and the need to carry out selection at an early age. The high genetic correlations between the NFE traits is an indication that the efficiency traits are under similar genetic influence, this implies that by just including RG_{77} in breeding programmes this will equally improve RFI and RIG.

5.5. Conclusion

The correlations between net feed efficiency and production traits vary across the ages studied, as the birds progress from growth inflection period to asymptote growth period. This indicates that the genetic relationships at different ages are under different genetic influence. The selected age points (77, 105 and 140 days of age) are associated with different biological processes on the basis of indigenous chicken growth pattern and could have resulted in the observed variations in the correlation estimates. Similarly, the difference in body composition of the birds between 77 and 105 days (high protein accretion) and between 105 and 140 days (shift to fat deposition) may have also contributed towards the different inter-relationships between the efficiency and production traits at these time periods. For selection purposes, residual gain at 77 days would be the most appropriate given that it is associated with higher growth rates and is independent of feed intake and maintenance requirement from ages 77 days to 140 days. In addition, selection for residual gain will also improve RFI and RIG given the significant and favourable correlations.

References

Berry, D. P., and Crowley, J. J. (2012). Residual intake and body weight gain: A new measure of efficiency in growing cattle. *Journal of Animal Science, 90*, 109-115.

Berry, D. P., and Crowley, J. J. (2013). Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. *Journal of Animal Science, 91*, 1594 - 1613.

Binda, B. D., Yousif, I. A., Elamin, K. M., and Eltayeb, H. E. (2012). A comparison of performance among exotic meat strains and local chicken ecotypes under Sudan conditions. *International Journal of Poultry Science, 11* (8), 500-504.

Bourdon, R. M. (2000). *Understanding Animal Breeding* (2nd ed.). Upper Saddle, New Jersey: Prentice Hall.

Case, L. A., Wood, B. J., and Miller, S. P. (2012). The genetic parameters of feed efficiency and its component traits in turkey (*Meleagris gallopova*). *Genetics Evolution Science, 44,* 2-6.

Crowley, J. J., McGee, M., Kenny, D. A., Crews, D. H., Evans, R. D., and Berry, D. P. (2010). Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *Journal of Animal Science, 44*, 958-972.

Falconer, D. S., and Mackay, T. F. (1996). *Introduction to Quantitative Genetics* (4th ed.). London: Longman.

Herd, R. M., and Bishop, S. C. (2000). Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livestock Production Science, 63,* 111 - 119.

Kennedy, B. W., van de Werf, J. H., and Meuwissen, T. H. (1993). Genetics and statistical propeties of residual feed intake. *Journal of Animal Science, 71*, 3239 - 3250.

Magothe, T. M., Muhuyi, B. W., and Kahi, A. K. (2010). Influence of major genes for crested-head, frizzled-feather and naked-neck on body weights and growth patterns of indigenous chicken reared intensively in Kenya. *Tropical Animal Health and Production, 42,* 173-183.

Meyer, K. (2007). WOMBAT - A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *Journal of Zheijang University SCIENCE B, 8* (11), 815-821.

Netter, J., Wasserman, W., and Kutner, M. H. (2004). *Applied linear statistical models* (5th ed.). New York: McGraw-Hill.

Sola-Ojo, F. E., Ayorinde, K. L., Fayeye, T. R., and Toye, A. A. (2012). Effects of Heterosis and Direction of Crossing on Production Performance of F1 Offspring of Dominant Black Strain and Fulani Ecotype Chickens. *Agrosearch, 12* (1), 95-105.

Tadelle, D., Kijora, C., and Peters, K. J. (2003). Indigenous chicken ecotypes in Ethiopia: Growth and feed utilization potentials. *International Journal of Poultry Science, 2* (2), 144-152.

Willems, O. W., Miller, S. P., and Wood, B. J. (2013). Assessment of residual body weight gain and residual intake and body weight gain as feed efficiency traits in the turkey (*Meleagris gallopova*). *Genetics Evolution Science, 45,* 26-34.

CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSION

6.1. Aim of the study

Improvement of indigenous chicken (IC) has been focused on meat production given the economic value attached to growth and body weight at slaughter (FAO, 2010; Okeno *et al*., 2011). However, the antagonistic relationship between production traits and feed intake pose a major constraint to production since improvement of production performance results in an increase in feed requirements and consequently increased cost of production. It is therefore important to consider feed efficiency as an avenue for selecting IC that have the ability to maintain the same performance rate on less feed resource to reduce on costs of production. The aim of the study was to assess the efficiency of feed use in IC during the linear growth period for efficient production of meat.The objectives of the study were to; i) determine the non-genetic sources of variation and temporal variability in growth and net feed efficiency traits, ii) estimate variance components, genetic and phenotypic parameters for the net feed efficiency traits on a longitudinal scale, and iii) determine the genetic and phenotypic correlation between net feed efficiency traits and production traits.

6.2. Methodology

Efficiency of feed use in indigenous chicken was described as net feed efficiency (NFE) measured by residual feed intake (RFI), residual gain (RG) and residual intake and gain (RIG) traits. The traits were computed from longitudinal body weight and feed intake data of intensively raised birds from 77 to 140 days of age using least square regressions of PROC MIXED of SAS 9.1 (SAS, 2002). During the analysis, the regressor traits were allowed to vary between and within birds as described by Aggrey and Rekaya (2013). Thereafter, a general linear model was used to determine the influence of non-genetic sources of variation on feed intake, growth and efficiency traits by fitting sex, cluster, genotype and hatch as fixed effect and initial body weight as a covariate using the PROC GLM of SAS 9.1 (SAS, 2002).

Genetic evaluation of the feed use efficiency along the growth trajectory (ages 77 days to 140 days) was carried out using random regression sire model by fitting Legendre polynomials of age as basis function. Fixed effects and covariates that were significant in Chapter 3 were adjusted for in the analyses.The genetic parameters were estimated by restricted maximum likelihood (REML) in WOMBAT software (Meyer, 2007). Using model fit statistics the most optimal models that best described RFI and RG had higher orders for the permanent environmental (PE) effects than the additive genetic effect while in RIG fitting equal orders for both genetic and PE effects was most optimal (Table 4.1).

The genetic and phenotypic relationships between the efficiency and production traits at 77 days, 105 days and 140 days of ages were estimated using multivariate sire models by restricted maximum likelihood (REML) in WOMBAT software (Meyer, 2007). The ages were selected for the analysis given their biological significance with regards to production in indigenous chicken (Magothe *et al*., 2010). The models fitted the NFE traits at; 77 days (NFE_{77}), 105 days (NFE_{105}) and 140 days (NFE_{140}) against production traits at 77, 105 and 140 days. In addition, the relationship among the NFE traits at 77, 105 and 140 days of age was determined.

6.3. Basis for assessing feed efficiency in indigenous chicken

Majority of the indigenous chicken in developing countries are under small-scale production reared in low input systems with preference for well adapted birds that are dual purpose and are able to reproduce to maintain flock sizes (Besbes, 2009; Okeno *et al*., 2012). Low input systems are considered complex and due to the negative relationship between production and functional traits, emphasis on one component could have negative repercussions on another (Tadelle *et al*., 2003). Therefore, breeding programmes should focus improvement on the objectives for which birds are being produced based on the market requirements. Meat is a preferred product of IC to eggs. Consequently, growth traits are of more relative economic importance in the indigenous chicken value chain and form the basic objective in breeding programmes (FAO, 2010; Okeno *et al*., 2011).

Performance evaluation of growth traits in indigenous chicken under different management levels indicates that the birds have potential for improved performance under intensive system (Magothe *et al*., 2010; Lwelamira, 2012; Okeno *et al*., 2012). However, there is need to improve their genetic profile to make their production economically viable in this system (Okeno *et al*., 2013). This could be achieved through use of pure line selection strategies on growth rate and live weight as it results in higher response to selection and economic gains per year (Okeno *et al*., 2013; Wondmeneh *et al*., 2014).

Improvement in growth should be balanced against available feed resources. If the latter are limited, improved growth may be a disadvantage as nutrient intake will not be enough to meet maintenance and growth requirement. This is explained by the linear relationship between growth and feed intake indicating that improvement in growth will be accompanied by increased feed intake due to (Exton *et al*., 2000). Consequently evaluation of production or feed intake independently provides little or no indication of the efficiency of production (Herd *et al*., 2003). Considering feed efficiency as a trait alongside production traits provides an avenue for maximizing on outputs at the least cost possible.

6.4. Sources of variation in growth and efficiency traits in indigenous chicken

Designing effective breeding programmes require quantification of genetic and environmental sources of variation for the traits of interest (Falconer and Mackay, 1996). Environmental sources of variation play a major role in the expression of growth and feed related traits and should therefore be adjusted for to enable effective performance evaluation (Durunna *et al*., 2011). Physiological differences between male and female birds influenced variation in ADG and RG with males showing superiority in growth and efficiency (Chapter 3). These results were synonymous to those reported in literature (Saadey *et al*., 2008). This influence is so pronounced that genetic influence on growth and efficiency diminished between ages 105 days to 126 days, time when birds approach sexual maturity (Chapter 4). At phenotypic level, significant interaction between sex and cluster in Chapter 3 indicate that cluster three could be a suitable male line and cluster one a female line for selection to improve growth performance and feed efficiency in indigenous chicken between ages 77 and 140 days (Chapter 3). Pre-test factors such as birds' initial performance have a direct influence on performance in subsequent period as a result of management factors during the pre-growers period (Mendes *et al*., 2011). In this study, differences in body weight at entry into the experiment had significant contributions on variation in production and efficiency traits with results indicating a linear covariance with growth, feed intake, maintenance and RG, and a quadratic covariance with RFI and RIG. Contrary to these results, studies in beef cattle have reported that the NFE traits are less influenced by pretest environmental effects compared to their component traits (growth, feed intake and body weight) (Herd and Bishop, 2000; Arthur *et al*., 2001). Results from Figures 3.1, 3.2 and 3.3 shows the presence of re-ranking of indigenous chicken clusters for efficiency across test periods, an implication that irrespective of the genetic origin of the birds there is divergent performance potentials.

Considerable variation in net feed efficiency due to additive genetic effects has been reported in various species indicating the suitability of including efficiency in selection index alongside production traits (Mrode and Kennedy, 1993; Herd and Bishop, 2000; Aggrey *et al*., 2010). Similarly, substantial genetic variation in feed efficiency was observed in indigenous chicken (Chapter 4) although this study considered efficiency on a longitudinal scale. Most genetic studies on feed efficiency often work on summarized phenotypes or assume a uniform correlation between repeated records that can induce bias in the parameter estimations (Arthur *et al*., 2001). Feed efficiency is a compound trait affected by both feed intake and growth factors that vary with age. Therefore, flexible approaches that allow appropriate modeling of variances along a trajectory should be considered (Mrode, 2005). This is underscored by the genetic variation in RFI and RG that decreased as the test period progressed and increasing variance in RIG throughout the experiment (Figure 4.2). The high estimates of permanent environmental variance (Figure 4.2) suggest that if efficiency is defined using RG, the selected birds would have to perform in an environment similar to the experimental conditions or at least semi-intensive environment to reduce the effects of genotype by environment interaction on performance (Mrode, 2005; Durunna *et al*., 2011). The drastic drop in genetic variance between ages 105 and 112 days in all the NFE traits could be a result of high variation in permanent environmental effect associated with changes in physiological development (Tholon and Queiroz, 2011).

6.5. Genetic and phenotypic parameters for net feed efficiency and production traits

Estimates of genetic parameters for net feed efficiency traits indicate that these traits are heritable. As a result a considerable proportion of the observed genetic variance can be passed on to the next generation and hence the possibility of improving efficiency through selection (Herd *et al*., 2003; Berry and Crowley, 2013). This has further been demonstrated by evaluating progeny from a single generation resulting from divergent selection of efficient and inefficient sires and dams (Richardson *et al*., 2001). By allowing heritability to vary with age, the estimates had similar trends (Table 4.2) as the genetic variance suggesting that selection at 91 days for RG and 98 days for RFI and RIG would be the most appropriate and precautionary points. This is due to the high estimates and end-range problems encountered when using Legendre polynomials as basis function of age (Meyer, 2005; Baldi *et al*., 2010). On the basis of the magnitude of heritability estimates, using family information as a selection criterion for RFI (98 days) and RG (91 days) would improve on accuracy while using mass selection for RIG (98 days and 119 days) would be the most convenient (Bourdon, 2000).

Since perfromance on the efficiency traits vary with age (Chapter 3) the traits cannot be assumed to be under similar genetic influence along a trajectory. Therefore, the need to predict the response on efficiency at maturity when birds are selected at an earlier age during the growing phase. Using information from Table 4.3, 4.4 and 4.5, selection on the efficiency during the early stages of the linear growth phase (between ages 77 days and 98 days) would positively influence efficiency at consecutive ages while this advantage would decrease as the birds approach sexual maturity. Similarly, in Chapter 5 when a multivariate sire model was used, high genetic variation was observed at 77 days in the RFI and RIG, while RG was highly influenced at 105 days. Genetic studies on growth in indigenous chicken have identified body weight at 12 weeks as a suitable selection point to improve on body weight given that it is the most heritable and has a favourable genetic correlation with juvenile weight and maturity weight (Magothe *et al*., 2011). However, improvement of this body weight trait is likely to have an effect on feed efficiency given the relationship that exists between feed intake and body weight traits. Therefore, in such a case there would be a need to determine the correlation between efficiency and production traits.

The opportunity to improve flock efficiency through exploitation of genetic variation is also dependent on the magnitude of correlations with other key production traits. This is because selection for high growth rates lead to increased feed and maintenance requirements, and expression of these production traits in the breeding flock presents an antagonistic relationship (Okine *et al*., 2004). Net feed efficiency traits have been widely applied in efficiency studies because they are phenotypically independent of production traits which allow for comparisons between individuals of different levels of production (Herd and Bishop, 2000; Herd *et al*., 2003). The independence is based on the theoretical assumptions of properties of residuals from least square regressions (Crews, 2005). However, from a biological perspective Table 5.2 shows that RG at 105 days had significant phenotypic correlations with feed intake and maintenance requirement at 140 days (Chapter 5). A similar study on laying hens reported significant correlation between RFI and maintenance, suggesting that the independence of RFI from growth represented inherent variation in basic metabolic process between hens with similar egg mass production and body weight (Luiting *et al*., 1991).

Although the residual traits are expected to be phenotypically independent of their regressor traits, they are not necessarily genetically independent (Crews, 2005). The sign and magnitude of the genetic correlations are influenced by the genetic and environmental correlations between the components in the regression models (Kennedy *et al*., 1993). Indigenous chicken tend to attain the desired market weight as they approach maturity and to be able to produce the birds efficiently there is need to ensure that selection for improved feed efficiency has no unfavourable genetic effects on production traits during the rearing period. The genetic correlations between the NFE traits and production traits at ages 77, 105 and 140 days varied across the ages (Table 5.1, 5.2, 5.3). From the results in Chapter 5, selection for efficiency using RG at 77 days would be the most effective given the favourable influence it had on growth at 77, 105 and 140 days with no effect on feed intake and maintenance requirement. The lack of genetic correlation between the efficiency and the production traits is mostly preferred since it provides an opportunity to improve on flock efficiency without influencing production levels and it is attributed to equal heritability, genetic and environmental correlations between the production traits (Herd *et al.*, 2003; Crowley *et al.*, 2010). The unfavourable genetic correlations between the NFE and production traits at certain ages (Table 5.1, 5.2 and 5.3) is a resultant of high genetic correlation and low environmental correlation between feed intake and the growth traits (Berry and Crowley, 2012; Willems *et al.*, 2013). From Table 5.1, 5.2 and 5.3, the correlation estimates between the NFE traits show that using RG at 77 days as a selection criterion will on average improve all measures of feed efficiency given their significant and favourable genetic correlations.

6.6. Conclusion

1. Sex significantly influence mean performance of ADG and RG while a significant interaction between sex and cluster affect ADFI, RFI and RIG. Apart from ADFI, hatch group has a significant effect on mean performance of ADG, MBW, RFI, RG and RIG. Statistically, cluster and genotype does not have significant effect on mean performance of growth and efficiency traits. There is re-ranking of IC phylogenetic groups in the efficiency traits across the ages studied indicating temporal variability in the NFE traits across the clusters.
2. Genetic effect and heritability of efficiency traits are moderate to high in the early phase of test (77 to 105 days) indicating that selection for RFI and RIG at 98 days of age and RG at 91 days of age would increase genetic gain. However, improvement in efficiency in early phase of the test would result in inefficiencies at later period of the experiment (126 to 140 days) based on genetic correlations
3. The nature of pleiotropic relationship between growth and efficiency traits indicate that improvement of RG at 77 days of age would positively influence growth, RFI and RG at 77, 105 and 140 days of age. Consequently, RG at 77 days of age will have no significant effect on feed intake and maitenance requirement

6.7. Recommendations

1. Upon evaluation of mean performance for growth and efficiency in indigenous chicken, known non-genetic sources of variation need to be adjusted for to unmask true differences between groups
2. For improvement of meat production in indigenous chicken, residual gain between 77 and 91 days of age should be considered for inclusion in the selection criteria alongside body weight traits to improve growth and efficiency concurrently
3. Due to high standard errors (genetic parameters) associated with the small sample size and single generation of birds in this study, there is need for further genetic evaluation for net feed efficiency using multi-generational and large data size to improve accuracy
4. Further studies on carcass quality to determine meat:bone for efficient birds and cost:benefit analysis to quantify the cost reduced per unit improvement on net efficiency should be carried out

References

Aggrey, S. E., and Rekaya, R. (2013). Dissection of Koch's residual feed intake: Implications for selection. *Poultry Science, 92,* 2600 - 2605.

Aggrey, S. E., Karnuah, B. A., Sebastian, B., and Anthony, N. B. (2010). Genetic properties of feed efficiency parameters in meat-type chickens. *Genetics Selection Evolution, 42,* 25-30.

Arthur, P. F., Archer, J. A., Johnston, D. J., Herd, R. M., Richardson, E. C., and Parnell, P. F. (2001). Genetic and phenotypic variance and covariance components for feed intake, feed efficiency and other postweaning traits in Angus cattle. *Journal of Animal Science, 79,* 2805 - 2811.

Berry, D. P., and Crowley, J. J. (2012). Residual intake and body weight gain: A new measure of efficiency in growing cattle. *Journal of Animal Science, 90,* 109-115.

Berry, D. P., and Crowley, J. J. (2013). Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. *Journal of Animal Science, 91,* 1594 - 1613.

Besbes, B. (2009). Genotype evaluation and breeding of poultry for performance under sub-optimal village conditions. *World's Poultry Science Journal, 65* (2), 260-271.

Bourdon, R. M. (2000). *Understanding Animal Breeding* (2nd ed.). Upper Saddle River, New Jersey: Prentice Hall.

Crews, D. H. (2005). Genetics of efficient feed utilization and national cattle evaluation: a review. *Genetics and Molecular Research, 4* (2), 152-165.

Crowley, J. J., McGee, M., Kenny, D. A., Crews, D. H., Evans, R. D., and Berry, D. P. (2010). Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. *Journal of Animal Science, 44,* 958-972.

Durunna, O. N., Plastow, G., Mujibi, F. D., Grant, J., Mah, J., and Basarab, J. A. (2011). Genetic parameters and genotype x environment interaction for feed efficiency traits in steers fed grwer and finisher diets. *Journal of Animal Science, 89,* 3394 - 3400.

Falconer, D. S., and Mackay, T. F. (1996). *Introduction to Quantitative Genetics* (4th ed.). London: Longman.

FAO. (2010). *Smallholder Poultry Production: Chicken genetic rsources used in smallholder production systems and opportunities for their development.* Food and Agriculture Organization of the United Nations: Rome.

Herd, R. M., and Bishop, S. C. (2000). Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livestock Production Science, 63,* 111 - 119.

Herd, R. M., Archer, J. A., and Arthur, P. F. (2003). Reducing the cost of beef production through genetic improvemnt in residual feed intake: Opportunity and challenges to application. *Journal of Animal Science, 81,* 9-17.

Kennedy, B. W., van der Werf, J. H., and Meuwissen, T. H. (1993). Genetic and statistical properties of residual feed intake. *Journal of Animal Science, 71,* 3239-3250.

Luiting, P., Schrama, J. W., Van der Hel, W., and Urff, E. M. (1991). Metabolic differences between white leghorns selected for high and low residual feed consumption. *British Poultry Science, 32*, 763-782.

Lwelamira, J. (2012). Genotype-Environment (G X E) interaction for body weights for Kuchi chicken ecotype of Tanzania reared under intensive and extensive management. *Global Journal of Medical Research, 12* (5), 57-65.

Magothe, T. M., Muhuyi, B. W., and Kahi, A. K. (2010). Influence of major genes for crested-head, frizzled-feather and naked-neck on body weights and growth patterns of indigenous chicken reared intensively in Kenya. *Tropical Animal Health and Production, 42,* 173-183.

Magothe, T. M., Muhuyi, W. B., and Kahi, A. K. (2011). Genetic parameters for egg and body weights of indigenous chicken in Kenya. *Animal Production Society of Kenya, 36*.

Magothe, T. M., Okeno, T. O., Muhuyi, W. B., and Kahi, A. K. (2012). Indigenous chicken production in Kenya: Current status. *World's Poultry Science Association, 68*, 119-132.

Mendes, A. S., Paixao, S. J., Restelatto, R., Reffatti, R., Possenti, J. C., and Moura, D. J. (2011). Effects of initial body weight and litter material on broiler production. *Brasileira de Ciencia Avicola, 13*(3), 165-170.

Meyer, K. (2005). Random regression analyses using B-splines to model growth of Australian Angus cattle. *Genetic Science Evolution, 37*, 473-500.

Meyer, K. (2007). WOMBAT - A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *Journal of Zheijang University SCIENCE B, 8* (11), 815-821.

Mrode, R. A. (2005). *Linear models for the prediction of animal breeding values* (2nd ed.). Oxon, UK: CABI publishing.

Mrode, R. A., and Kennedy, B. W. (1993). Genetic variation in measures of food efficiency in pigs and their genetic relationships with growth rate and backfat. *Animal Production - Glasgow, 56,* 225.

Okeno, T. O., Kahi, A. K., and Peters, K. J. (2011). Breed selection practices and traits of economic importance for indigenous chicken in Kenya. *Livestock Research for Rural Development, 23*.

Okeno, T. O., Kahi, A. K., and Peters , K. J. (2012). Characterization of indigenous chicken production systems in Kenya. *Tropical Animal Health and Production, 44,* 601 - 608.

Okeno, T. O., Magothe, T. M., Kahi, A. K., and Peters , K. J. (2013). Breeding objectives for indigenous chicken: Model development and application to different production systems. *Tropical Animal Health and Production, 70,* 193-203.

Okine, E. K., Basarab, J. A., Goonewardene, L. A., and Mir, P. (2004). Residual feed intake and feed efficiency: Differences and Implicactions. *In Florida Ruminant Nutrition Symposium, Florida, USA* (dairy.ifas.ufl.edu/files/rns/2004/Okine.pdf [Verified August 2010]).

Richardson, E. C., Herd, R. M., Oddy, V. H., Thompson, J. M., Archer, J. A., and Arthur, P. F. (2001). Body composition and implications for heat production of Angus steer progeny of parents selected for and against residual feed intake. *Animal Production Science, 41* (7), 1065 - 1072.

Saadey, S. M., Galal, A., Zaky, H. I., and El-Dein, A. Z. (2008). Diallel crossing analysis for body weight and egg production traits of two native egyptian and two exotic chicken breeds. *International Journal of Poultry Science, 7* (1), 64-71.

SAS. (2002). SAS User's Guide (Version 9.1.3). *Statistical Analysis System Institute, SAS Inc.* Cary: NC.

Tadelle, D., Kijora, C., and Peters, K. J. (2003). Indigenous chicken ecotypes in Ethiopia: Growth and feed utilization potentials. *International Journal of Poultry Science, 2* (2), 144-152.

Tholon, P., and Queiroz, S. A. (2011). Estimation of (co) variance componenets and genetic parameters for weights of red-winged tinamou using random regression models. *Revista Brasileira de Zootecnia, 40* (4), 781-787.

Willems, O. W., Miller, S. P., and Wood, B. J. (2013). Assessment of residual body weight gain and residual intake and body weight gain as feed efficiency traits in the turkey (*Meleagris gallopova*). *Genetics Selection Evolution, 45,* 26-34.

Wondmeneh, E., van der Waaij, E. H., Tadelle, D., Okeyo, M., and van Arendonk, J. A. (2014). A running breeding program for indigneous chicken in Ethiopia: evaluation of success. *In Conference Proceedings of the 10th World Congress on Genetics Applied to Livestock Production, Vancouver, Canada.*

APPENDICES

Appendix 1: Supplementary tables

ST 1: Nutrient composition of diets supplied to experimental birds and parents flock

Diets	**Nutrient composition**[1]							
	Age	CP (%)	ME (MJ/kg)	CF (%)	Ca (%)	P (%)	Lys (%)	Meth (%)
Starter ration	0 – 8	18	12.56	4	1	0.45	0.85	0.35
Growers ration	9 - 20	16	10.89	6	2.5	0.45	0.65	0.35
Layers ration	Parents	14	10.05	8	3	0.45	0.65	0.35

[1] CP = crude protein, ME = metabolizable energy, CF = crude fibre, Ca= calcium, P = phosphorus, Lys = lysine, Meth = methionine

ST 2: Least square means[1] (±s.e.) of growth and net feed efficiency traits across cluster, sex and genotype

Trait	**Clusters[2]**			**Genotype[3]**	
	CL1 (n = 64)	CL2 (n = 27)	CL3 (n = 16)	NM (n = 80)	NN (n = 27)
ADFI (g/d)	133.50 ± 2.02 ^{a}	138.56 ± 3.42 ^{a}	137.31 ± 4.03 ^{a}	134.15 ± 1.98^a	138.77 ± 3.50^a
ADG (g/d)	10.49 ± 0.28 ^{a}	10.95 ± 0.47 ^{a}	10.52 ± 0.55 ^{a}	10.64 ± 0.27 ^{a}	10.67 ± 0.48 ^{a}
MBW (g)	165.09 ± 0.97 ^{a}	165.93 ± 1.64 ^{a}	162.01 ± 1.93 ^{a}	216.00 ± 1.69 ^{a}	215.33 ± 2.88 ^{a}
RFI (g/d)	-0.08 ± 1.89 ^{a}	4.34 ± 3.18 ^{a}	4.98 ± 3.73 ^{a}	5.64 ± 1.83 ^{a}	5.52 ± 3.24 ^{b}
RG (g/d)	0.06 ± 0.24 ^{a}	0.39 ± 0.40 ^{a}	0.29 ± 0.47 ^{a}	0.21 ± 0.23 ^{a}	0.18 ± 0.41 ^{a}
RIG	0.12 ± 1.93 ^{a}	-3.95 ± 3.26 ^{a}	-4.89 ± 3.82 ^{a}	-5.45 ± 1.88 ^{a}	-5.37 ± 3.32 ^{b}

[1] Least square means within a row with similar superscript do not differ (p>0.05) ; (±s.e.) standard error

[2] CL1 = cluster 1; CL2 = cluster 3; CL3 = cluster 3

[3] NM = normal feathered genotype; NN= naked neck genotype

ST 3: Overall means (±s.d.) and least square means[1] (±s.e.) for residual feed intake (RFI g/d) at different age points across clusters

Age$_{(weeks)}$	Overall means	Cluster[2]		
		CL1	**CL2**	**CL3**
11	-3.40 ± 15.80	-2.55 ±3.57^{a}	-10.03 ± 6.36^{b}	-2.78 ±5.60^{a}
12	-0.82 ± 12.01	-0.63 ±2.32^{a}	1.39 ± 4.41^{a}	-2.12 ±4.36^{a}
13	1.86 ± 11.80	0.43 ±2.04^{a}	-0.19 ± 4.47^{a}	0.09 ±3.73^{a}
14	1.92 ± 8.73	2.55 ± 1.44^{a}	5.33 ± 2.73^{b}	4.94 ±2.73^{b}
15	0.71 ± 9.86	1.85 ± 1.38^{a}	2.16 ± 2.37^{a}	0.22 ±2.75^{b}
16	-0.24 ± 9.88	-1.17 ± 1.49^{a}	1.28 ± 2.55^{a}	-0.79 ±2.96^{a}
17	-2.13 ± 9.71	-4.84 ± 2.73^{b}	1.68 ± 1.71^{a}	5.19 ±4.43^{a}
18	0.85 ± 8.72	-2.84 ± 2.21^{a}	0.73 ± 3.22^{b}	3.94 ±5.88^{a}
19	-0.89 ± 8.78	-4.88 ± 2.50^{a}	-1.07 ± 3.23^{a}	4.93 ±6.00^{b}
20	-0.74 ± 14.27	-4.25 ± 4.40^{a}	10.49 ±8.41^{b}	4.82 ±10.93^{b}

[1] Least square means within a row with different superscript differ ($p<0.05$) ; (±s.d.) standard deviation ; (±s.e.) standard error

[2] CL1 = cluster 1; CL2 = cluster 3; CL3 = cluster 3

ST 4: Overall means (±s.d.) and least square means[1] (±s.e.) for residual weight gain (RG g/d) at different age points across clusters

Age$_{\text{(weeks)}}$	**Overall means**	**Cluster[2]**		
		CL1	**CL2**	**CL3**
11	0.04 ± 0.31	-0.16 ±0.07^{a}	-0.13 ±0.12^{ab}	0.14 ±0.10^{b}
12	0.01 ± 0.08	0.01 ±0.01^{a}	0.05 ±0.03^{a}	0.10 ±0.03^{b}
13	-0.03 ± 0.15	-0.05 ±0.02^{a}	0.02 ±0.05^{a}	0.18 ±0.05^{b}
14	-0.02 ± 0.18	-0.06 ±0.03^{a}	0.02 ±0.05^{a}	0.11 ±0.05^{b}
15	0.01 ± 0.13	-0.01 ±0.02^{a}	0.01 ±0.03^{a}	0.16 ±0.03^{b}
16	0.02 ± 0.16	-0.04 ±0.02^{a}	-0.03 ±0.04^{b}	0.07 ±0.04^{b}
17	-0.04 ± 0.11	-0.05 ±0.01^{a}	-0.06 ±0.02^{a}	-0.06 ±0.04^{a}
18	-0.05 ± 0.12	-0.05 ±0.02^{a}	-0.05 ±0.03^{a}	-0.02 ±0.05^{a}
19	-0.02 ± 0.08	0.01 ±0.02^{a}	0.03 ±0.03^{a}	0.00 ±0.06^{a}
20	0.11 ± 0.14	0.12 ±0.02^{a}	0.16 ±0.04^{a}	0.15 ±0.06^{a}

[1] Least square means within a row with different superscript differ ($p<0.05$) ; (±s.d.) standard deviation ; (±s.e.) standard error

[2] CL1 = cluster 1; CL2 = cluster 3; CL3 = cluster 3

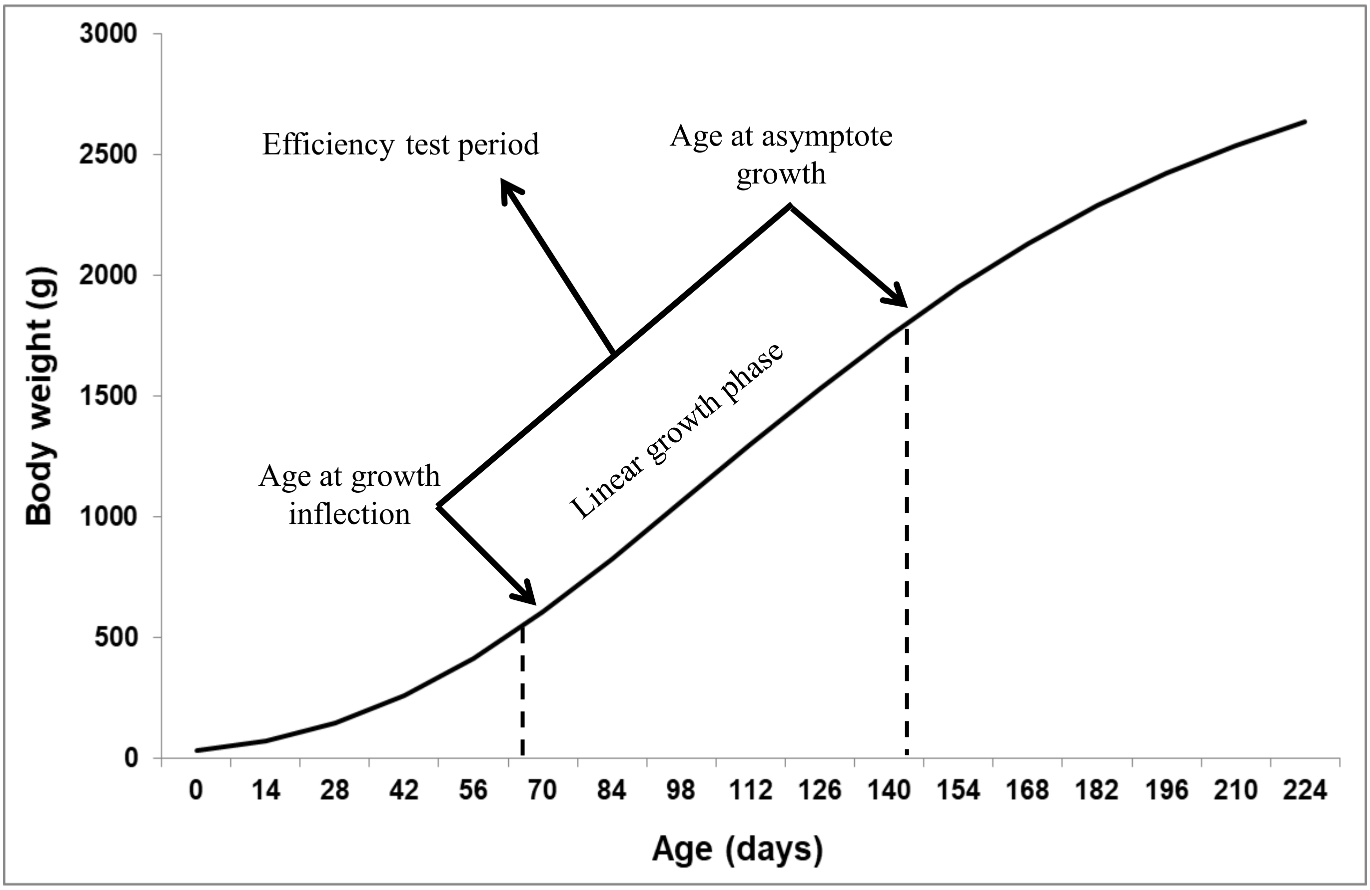
ST 5: Overall means (±s.d.) and least square means[1] (±s.e.) for residual intake and gain (RIG g/d) at different age points across clusters

Age$_{\text{(weeks)}}$	**Overall means**	**Cluster[2]**		
		CL1	CL2	CL3
11	3.44 ± 15.82	2.72 ±3.58^{a}	9.91 ±6.39^{b}	2.63 ±5.62^{a}
12	0.83 ± 12.02	0.64 ±2.33^{a}	-1.34 ±4.41^{a}	2.11 ±4.37^{a}
13	-1.88 ± 11.79	-0.48 ±2.03^{a}	0.21 ±4.46^{a}	-0.01 ±3.73^{a}
14	-1.95 ± 8.74	-2.61 ±1.44^{a}	-5.31 ±2.73^{a}	-4.84 ±2.74^{a}
15	-0.71 ± 9.87	-1.85 ±1.39^{a}	-2.15 ±2.37^{a}	-0.17 ±2.75^{a}
16	0.27 ± 9.89	1.21 ±1.49^{a}	-1.32 ±2.55^{a}	0.73 ±2.96^{a}
17	2.10 ± 9.71	1.73 ±1.71^{a}	-4.79 ±2.72^{b}	-5.25 ±4.43^{b}
18	-0.91 ± 8.71	2.90 ±2.21^{a}	-0.78 ±3.22^{b}	-3.96 ±5.89^{a}
19	0.87 ± 8.78	4.88 ±2.50^{a}	1.10 ±3.23^{a}	-4.93 ±6.00^{b}
20	0.84 ± 14.31	4.37 ±4.40^{a}	-10.32 ±8.40^{b}	-4.70 ±10.92^{b}

[1] Least square means within a row with different superscript differ ($p<0.05$) ; (±s.d.) standard deviation ; (±s.e.) standard error

[2] CL1 = cluster 1; CL2 = cluster 3; CL3 = cluster 3

Appendix 2: Supplementary figure



Indigenous chicken growth pattern based on predicted body weight using the Gompertz-Laird growth model

Appendix 3: Publication abstract

Non genetic sources of variation and temporal variability in growth and feed efficiency traits among phylogenetically distinct clusters of indigenous chicken in Kenya.

(Tropical Animal Health and Production 48, 1569 – 1575)

Abstract

This study aims to investigate the influence of non-genetic factors on feed efficiency in indigenous chicken. Residual feed intake (RFI), residual gain (RG), and residual intake and gain (RIG) were used as measures of feed efficiency. Feed intake and body weight data was collected on 107 experimental birds on a daily and weekly basis, respectively from ages 11 to 20 weeks. A general linear model was fitted to determine the effect of sex, cluster, genotype and hatch group on mean performance and temporal variation across clusters. The overall mean performance was 10.38g/d, 133.01g/d, 164.12g/d, 0.00 (±14.23), 0.00 (±1.83) and 0.00 (±14.64) for daily gain (ADG), daily feed intake (ADFI), weekly metabolic body weight (MBW), RFI, RG and RIG, respectively. Sex significantly influenced variation in ADG and RG while hatch group influenced all traits except ADFI. Cluster and genotype had no effect on the traits however, an interaction between sex and cluster significantly influenced ADFI, RFI and RIG. There was significant temporal variation within and among clusters resulting in re-ranking of the phylogenetic groups in efficiency across the test period. Results from this study indicate that growth and efficiency traits are influenced by non-genetic factors which should be adjusted for in evaluations to reduce bias when improving performance in indigenous chicken.

Appendix 4: List of publications and conference presentation

Miyumo, S., Kahi, A. K. and Wasike, C. B. (2016). Non genetic sources of variation and temporal variability in growth and feed efficiency traits among phylogenetically distinct clusters of indigenous chicken in Kenya. *Tropical Animal Health and Production* 48, 1569 – 1575.

Miyumo, S., Kahi, A. K. and Wasike, C. B. (2017). Genetic and Phenotypic Parameters for Feed Efficiency in Indigenous Chicken. *Livestock Sciences* (in-press: https://doi.org/10.1016/j.livsci.2017.11.011).

Miyumo, S., Kahi, A. K. and Wasike, C. B. (2015). Environmental Factors that Influence Growth and Feed Efficiency in Indigenous Chicken. In Conference Proceedings: *9th Egerton University International Conference, 25th – 27th March 2015, Egerton University, Njoro, Kenya*.