

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

Sophie Miyumo¹ · Alexander K. Kahi² · Chrilukovian B. Wasike³

Received: 1 March 2016 / Accepted: 16 August 2016 / Published online: 25 August 2016
© Springer Science+Business Media Dordrecht 2016

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 were 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 to assess temporal variation across clusters. The overall mean performance for daily gain (ADG), daily feed intake (ADFI), weekly metabolic body weight (MBW), RFI, RG and RIG was 10.38 g/day, 133.01 g/day, 164.12 g/day, 0.00 (± 14.23), 0.00 (± 1.83) and 0.00 (± 14.64), 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. Interaction between sex and cluster significantly influenced ADFI, RFI and RIG. There was a significant temporal variation within and among clusters resulting in re-ranking of the phylogenetic groups in efficiency across the test period. Results indicate that growth and feed efficiency traits are influenced by non-genetic factors which should be accounted for, to reduce bias and improve accuracy of performance evaluations in the indigenous chicken.

Keywords Feed efficiency · Indigenous chicken · Non-genetic factors

Introduction

Indigenous chicken (IC) is a valuable asset and forms an integral part of many households in Kenya in terms of food security, economic and social roles (Magothe et al. 2012). Poultry industry in general and specifically IC are faced by various challenges which limit their production potential, with feed supply to the birds identified as a major constraint (Besbes 2009). The availability of feed resources in the region exhibit seasonal variation resulting in high costs of feeds. Feed represents about 60–70 % of the total production costs in poultry enterprises. Increased feed costs directly affect profitability hence the importance of feed efficiency in the industry (Aggrey et al. 2010). Feed conversion ratio (FCR) has conventionally been used to measure and improve efficiency in IC (Tadelle et al. 2003; Binda et al. 2012). However, the improvement of the ratio trait presents a challenge since selection pressure tends to be placed on the component traits in a non-linear manner resulting in unpredictable genetic response (Aggrey et al. 2010). Further, the confounding effects resulting from the relation 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) has been proposed as an alternative measure since it describes the efficiency with which animals partition feed with respect to production and maintenance requirements independent of production levels (Berry and Crowley 2013). It is measured by residual feed intake (RFI), residual body weight gain (RG) and residual intake and weight gain (RIG) estimated from linear combinations

✉ Chrilukovian B. Wasike
wasikebwire@yahoo.co.uk

¹ Smallholder IC Improvement Program, Department of Animal Sciences, Egerton University, PO Box 536, 20115 Egerton, Kenya

² Animal Breeding and Genomics Group, Department of Animal Sciences, Egerton University, PO Box 536, 20115 Egerton, Kenya

³ Department of Animal Sciences, Maseno University, PO private bag 40105, Maseno, Kenya

of growth, body weight and feed intake traits. Negative values of RFI and positive values of both RG and RIG indicate efficiency. The RFI and RG are independent of growth and feed intake, respectively. This presents the possibility of slow-growing animals with relatively low feed intake ranking as efficient animals in the case of RFI while animals with positive RG could have faster growth rates and high feed intake (Crowley et al. 2010). Consequently, Berry and Crowley (2012) proposed an amalgamation of both traits into RIG to minimize the likelihood of the uncertainties from RFI and RG while being independent of maintenance. The improvement of feed efficiency requires that non-genetic sources of variation in performance are identified since they influence the expression of genes and provide a better understanding of biological and/or environmental mechanisms on performance (Mrode 2005). Accounting for these factors also helps to unmask true differences between groups and reduce bias in performance evaluation. This study aimed at determining: (i) the environmental factors that influence efficiency of feed utilization and (ii) temporal variation in growth and feed efficiency traits among the phylogenetic IC clusters of Kenya.

Materials and methods

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. The climatic condition in the study site was considered moderate and optimal for IC performance (Ayuya et al. 2011). The unit has a population of IC collected from various agro-ecological zones (II–IV) in Kenya. The population has been clustered into three distinct phylogenetic groups based on major histocompatibility complex (MHC)-linked microsatellite markers (Ngeno et al. 2015). Cluster 1 constitutes birds from the Western, North-Rift and South-Rift regions, cluster 2 constitutes birds from the Eastern region and cluster 3 constitutes birds from the coastal region (*Kuchi*). The study used first generation birds from the three clusters 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. The truncation point for selection was set at 10 g/day for males and 6 g/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 1.

Eggs were collected daily, identified by their sire family and stored at room temperature for not more than

4 days prior to artificial incubation. At hatch, each chick was identified using a wing tag with a code identifying the cluster, genotype and the sire family, and then weighed. Throughout the experimental period, 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.

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 g. Feed efficiency is effectively assessed during the linear or rapid growth phase of the birds (Case et al. 2012). Growth inflection in IC has been observed at the age of 10 weeks; therefore, body weight data was collected from 10 weeks of age (Tadelle et al. 2003; Magothe et al. 2010). Feed intake was considered on an individual basis. This was to account for inherent differences between birds. The length of feed intake recording is determined majorly by the cost of collecting feed intake data on individual birds. Varied lengths of feed intake recording have been suggested in poultry species, with no standard test length. A test period of 42 days was used in this study, being an average test length derived from previous feed efficiency studies 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 1-week acclimatization. Birds were given measured ad libitum portions of growers ration throughout the feeding trial. Individual daily feed intake was measured as the difference between the weight of supplied feed and left over feed (the amount of feed left remaining in the trough at the time of introducing new feed) 24 h 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 the growth and feed efficiency traits are presented in Table 1.

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

Table 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	\pm SD	No. records	μ	\pm 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

consecutive weekly body weight measurements divided by 7 days. Average daily feed intake per week was calculated as the sum of total feed consumed in a week divided by 7 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 observed average daily feed intake ($ADFI_O$) and expected average daily feed intake ($ADFI_E$) while RG was computed as the difference between observed average daily gain (ADG_O) and expected average daily gain (ADG_E).

A random effect model was fitted on the data using PROC MIXED of SAS 9.1 (SAS 2002) to estimate $ADFI_E$ and ADG_E and eventually RFI and RG, respectively. Age was fitted as a continuous predictor and bird as a random regressor. The model allows parameters to vary between and within individuals, thus improving 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 model used is presented in Eqs. 1 and 2.

$$RFI_{ij} = ADFI_{Oij} - \left(b_0 + (b_1 + \alpha_{1i})ADG_{ij} + (b_2 + \alpha_{2i})MBW_{ij} + (b_3 + \alpha_{3i})AGE_i + e_{ij} \right) \quad (1)$$

where RFI_{ij} is j^{th} observation of residual feed intake of i^{th} bird; $ADFI_{Oij}$, ADG_{ij} , MBW_{ij} and AGE_{ji} are observed weekly average daily feed intake, gain, metabolic body weight and age

of i^{th} bird, respectively; b_k are fixed regression coefficients ($k=0, 1, 2, 3$); α_{ki} ($k=1, 2, 3$) is random regression coefficient specific to i^{th} bird for the traits; and e_i is error term $\sim N(0, \sigma^2_e)$.

$$RG_{ij} = ADG_{Oij} - \left(b_0 + (b_1 + \alpha_{1i})ADFI_{ij} + (b_2 + \alpha_{2i})MBW_{ij} + (b_3 + \alpha_{3i})AGE_i + e_{ij} \right) \quad (2)$$

where RG_{ij} is j^{th} observation of residual gain of i^{th} bird; ADG_{Oij} and $ADFI_{ij}$ are observed weekly average daily gain and feed intake, respectively, while MBW_{ij} , AGE_{ji} , b_k , α_{ki} ($k=1, 2, 3$) and e_i are as described in Eq. 1.

Residual intake and gain (RIG) was computed as the sum of RFI and RG. Residual feed intake was multiplied by -1 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 Eq. 3

$$RIG_{ij} = (-1 \times RFI_{ij}) + RG_{ij} \quad (3)$$

where RIG_{ij} , RFI_{ij} , and RG_{ij} are j^{th} observation of residual

intake and weight gain, residual feed intake and residual gain of i^{th} bird, respectively.

Factors influencing 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 310 and

680 g. As a result, preliminary analyses were performed to determine the order of fit of initial weight as a covariate for the efficiency traits and their component traits. Initial weight thus 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 at $\alpha = 0.05$. The general fixed effect model used for the analyses is presented in Eq. 4:

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

where: Y_{ijklm} is the performance trait of the m^{th} bird; μ is the overall mean; S_i is the effect of i^{th} sex ($i = \text{male, female}$); G_j is the effect of j^{th} genotype ($j = \text{normal feather, naked neck}$); 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 ($l = 1, 2, \dots, 8$); $(CS)_{ki}$ 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. Equation 4 taking into account repeated records of the NFE traits was used.

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 2. 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.

Least square means for the levels of factors that significantly influenced growth and NFE traits are presented in Table 3. Cocks had significantly higher ADG and RG than hens. ADG, MBW, both RFI and RIG, and RG of birds born of hatch

groups 1, 1 and 2, 4 and 7, and 1, 2 and 5 differed significantly from other hatch groups.

The interaction between cluster and sex had a significant effect ($P < 0.05$) on ADFI, RFI and RIG (Table 4). The differences between males and females in different clusters were significant. The observed differences were not linear.

Least square means for RFI are presented in Fig. 1. 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 0.99 and 1.02 g/day, respectively, while in cluster 1, the estimates decreased at the rate of -0.81 g/day. Generally, more differences were observed between clusters in later experimental periods from week 17 than in earlier periods.

Temporal variability of RG is presented in Fig. 2. The highest RG variability was observed in 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 -1.04 and -0.91 for cluster 2 and 3, respectively, and in cluster 1, the estimates increased at the rate of 0.82 (Fig. 3). Similar to RFI, RIG had more differences between clusters in the later stages of the experiment from week 16.

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

Table 2 Overall mean, mean square values and level of significance of fixed factors that influence mean performance in growth and feed efficiency traits in indigenous chicken

Traits	ADFI (g/day)	ADG (g/day)	MBW (g)	RFI (g/day)	RG (g/day)	RIG
Overall means ($n = 107$)	133.01 \pm 18.52	10.38 \pm 2.67	164.12 \pm 43.62	0.00 \pm 10.23	0.00 \pm 1.83	0.00 \pm 14.64
Fixed effects						
Sex	23.18 ^{ns}	38.90 ^{**}	63.99 ^{ns}	2.08 ^{ns}	33.97 ^{**}	0.5731 ^{ns}
Genotype	310.17 ^{ns}	0.01 ^{ns}	10.16 ^{ns}	347.26 ^{ns}	0.02 ^{ns}	0.1568 ^{ns}
Cluster	199.77 ^{ns}	1.65 ^{ns}	73.41 ^{ns}	201.15 ^{ns}	0.76 ^{ns}	0.3507 ^{ns}
Hatch	279.04 ^{ns}	8.93 ^{ns}	166.20 ^{**}	354.55 [*]	6.88 ^{ns}	0.0249 ^{ns}
Sex*cluster	1462.74 ^{**}	0.19 ^{ns}	101.31 ^{ns}	1225.9 ^{***}	1.72 ^{ns}	0.0009 ^{***}
Initial weight	3663.09 ^{a,***}	214.59 ^{a,***}	101768.55 ^{a,***}	1010.21 ^{b,**}	1.15 ^{a,***}	0.0182 ^{b,**}

ns not significant

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

^a Covariate fitted as a linear effect

^b Covariate fitted as a quadratic effect

Table 3 Least square means (\pm s.e.) of growth and net feed efficiency traits across sex and hatch groups

Trait	ADFI (g/day)	ADG (g/day)	MBW (g)	RFI (g/day)	RG (g/d)	RIG
Sex						
Male	137.03 \pm 2.71 ^a	11.40 \pm 0.37 ^a	220.67 \pm 3.77 ^a	2.91 \pm 2.53 ^a	0.89 \pm 0.32 ^a	-2.01 \pm 2.59 ^a
Female	135.88 \pm 2.76 ^a	9.91 \pm 0.38 ^b	221.80 \pm 3.53 ^a	3.26 \pm 2.57 ^a	-0.50 \pm 0.32 ^b	-3.81 \pm 2.63 ^a
Hatch groups						
Hatch ₁	136.52 \pm 3.83 ^a	8.70 \pm 0.52 ^a	166.17 \pm 1.83 ^a	8.43 \pm 3.61 ^a	-1.28 \pm 0.46 ^a	-9.71 \pm 3.69 ^a
Hatch ₂	135.47 \pm 5.91 ^a	9.72 \pm 0.80 ^{ab}	161.36 \pm 2.83 ^a	4.00 \pm 5.49 ^a	-0.55 \pm 0.69 ^a	-4.55 \pm 5.62 ^a
Hatch ₃	136.56 \pm 4.24 ^a	10.85 \pm 0.58 ^b	166.46 \pm 2.03 ^b	1.87 \pm 3.93 ^a	0.34 \pm 0.50 ^b	-1.53 \pm 4.02 ^a
Hatch ₄	130.57 \pm 4.32 ^a	11.11 \pm 0.59 ^b	165.66 \pm 2.07 ^b	-3.95 \pm 4.02 ^b	0.67 \pm 0.51 ^b	4.62 \pm 4.11 ^b
Hatch ₅	137.59 \pm 4.17 ^a	10.75 \pm 0.57 ^b	166.17 \pm 2.00 ^b	-3.62 \pm 3.81 ^a	0.09 \pm 0.48 ^a	3.53 \pm 3.90 ^a
Hatch ₆	144.17 \pm 8.33 ^a	11.87 \pm 1.13 ^b	166.59 \pm 3.99 ^b	-2.96 \pm 7.70 ^a	1.06 \pm 0.97 ^b	4.02 \pm 7.87 ^a
Hatch ₇	128.49 \pm 3.87 ^a	11.20 \pm 0.53 ^b	164.75 \pm 1.86 ^b	-5.66 \pm 3.52 ^b	0.77 \pm 0.44 ^b	6.44 \pm 3.60 ^b
Hatch ₈	142.29 \pm 4.19 ^a	11.02 \pm 0.57 ^b	167.57 \pm 2.01 ^b	-2.39 \pm 3.91 ^a	0.27 \pm 0.49 ^b	2.66 \pm 4.00 ^a

^aLeast square means within a column with different superscript differ ($P < 0.05$)

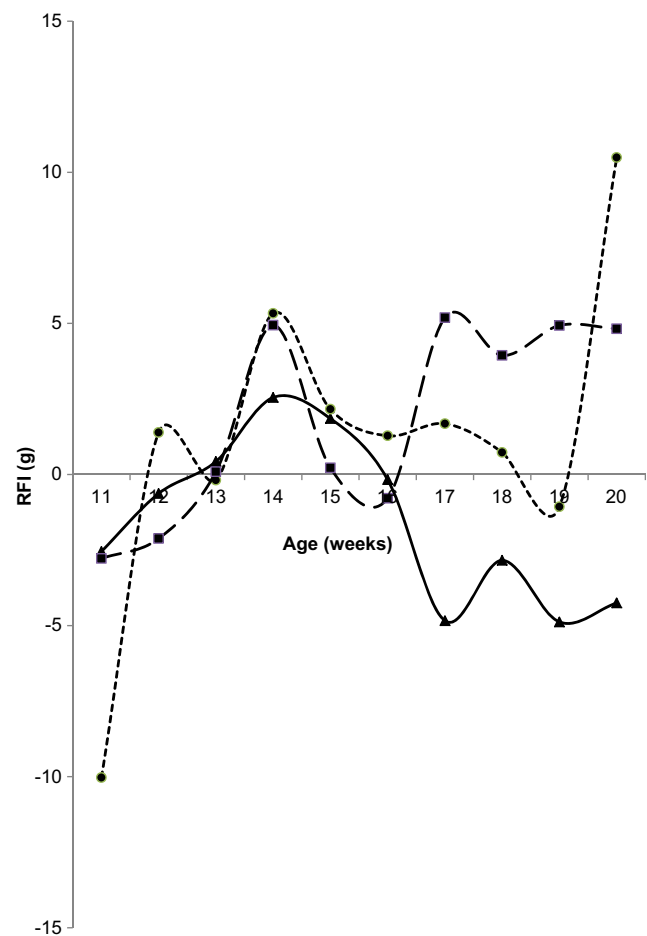
females upon onset of the endocrinology functions which coincides with the period of test in this study (Leeson and Summers 2010). Recent advancement in characterisation of IC in Kenya identified three distinct genetic groups/clusters using MHC microsatellite markers (Ngeno et al. 2015). This distinction was however non-existent with regard to growth and net feed efficiency. Similarly, irrespective of the bird 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 3 and females from cluster 1 were the most efficient for RFI and RIG and had the lowest ADFI. At phenotypic level, cluster 3 could be considered a suitable male line and cluster 1, 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

Table 4 Estimates of least square means (\pm s.e.) for traits significantly influenced by the interaction between sex and cluster

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

^aLeast square means within a row with different superscript differ ($P < 0.05$)

**Fig. 1** Estimates of least square means for residual feed intake (RFI g/day) among cluster 1 (heavy line), cluster 2 (dotted lines) and cluster 3 (dashed lines) across ages 11 to 20 weeks

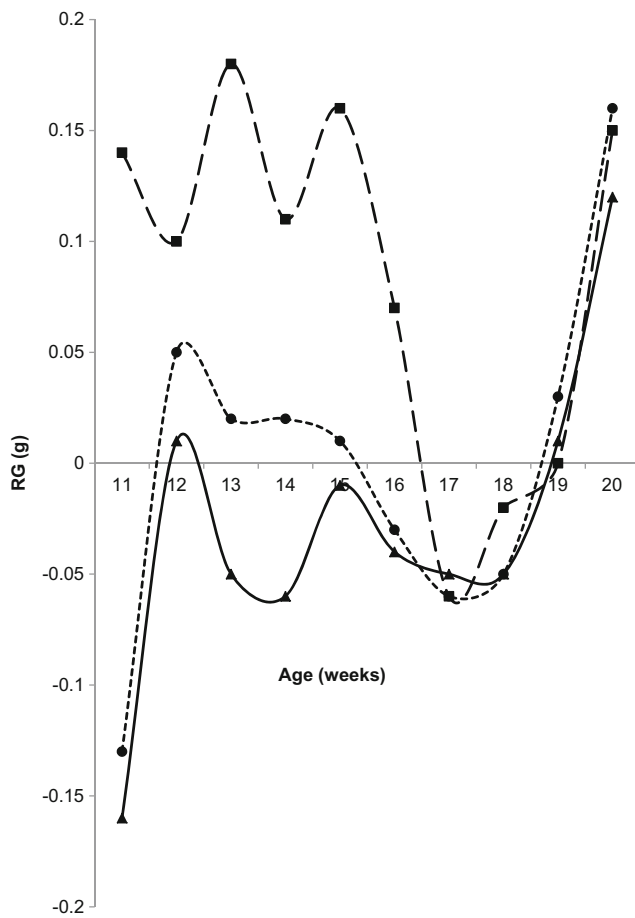


Fig. 2 Estimates of least square means for residual gain (RG g/day) among cluster 1 (heavy line), cluster 2 (dotted lines) and cluster 3 (dashed lines) across ages 11 to 20 weeks

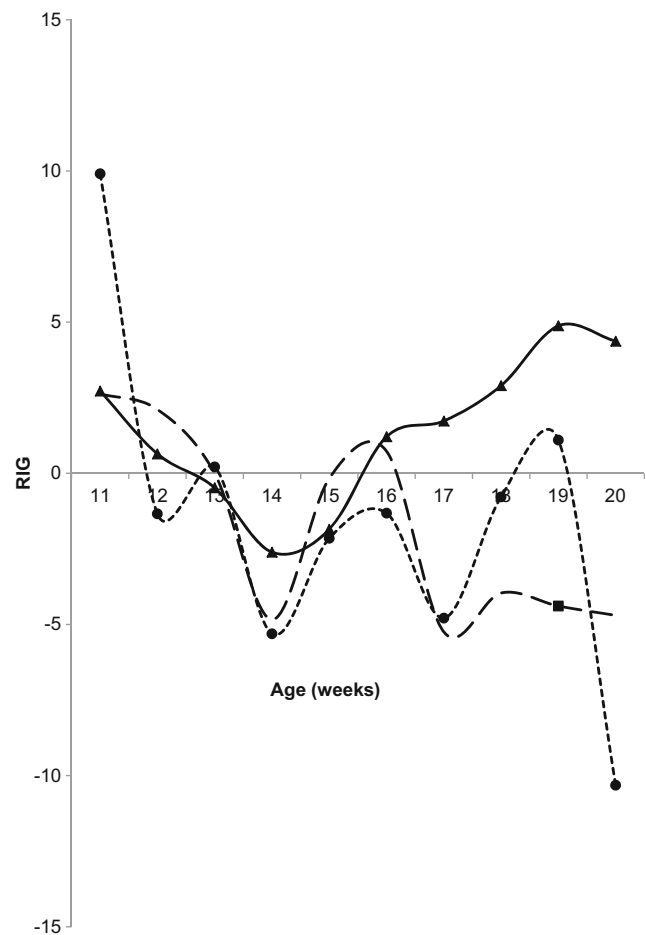


Fig. 3 Estimates of least square means for residual intake and gain (RIG) among cluster 1 (heavy line), cluster 2 (dotted lines) and cluster 3 (dashed lines) across ages 11 to 20 weeks

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 shows 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 such that 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 while cluster 1 is likely to have a higher percentage of leanness towards maturity as result

of delayed shift in protein to fat deposition (Aggrey et al. 2010). Such implications indicate the need to further consider body composition in efficiency evaluation in IC. On the other hand, when RG was used, cluster 3 was the most efficient throughout the test period while cluster 1 was the least efficient. Birds from cluster 3 (*Kuchi* ecotype) have been considered ideal for meat production given their potential to attain 1700 g 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 a 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 MHC 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 regard to efficiency.

In conclusion, the mean performance of growth and net feed efficiency 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 a significant variation within and among clusters across ages resulting to re-ranking of the phylogenetic groups for the NFE traits across the test period, with large differences being observed during the early period of the experiment in RFI and RIG, and during the later period of the experiment in RG. For improvement of growth and efficiency traits in indigenous chicken during the growers phase, the non-genetic sources of variation identified in this study need to be adjusted for genetic evaluations to allow for unbiased and accurate estimation of genetic parameters.

Acknowledgments The study was supported by the Smallholder Indigenous Chicken Improvement Programme (InCIP). The programme is funded by the European Union (EU) through the African Union (AU).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for care and use of animals were followed.

References

- Aggrey, S. E., & Rekaya, R. (2013). Dissection of Koch's residual feed intake: Implications for selection. *Poultry Science*, *92*, 2600–2605.
- Aggrey, S. E., Kamuah, 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
- Ayuya, O. I., Lagat, J. K., & Mirona, J. M. (2011). Factors influencing potential acceptance and adoption of clean development mechanism projects: Case of carbon trade tree project among small-scale farmers in Njoro District, Kenya. *Research Journal of Environmental and Earth Sciences*, *3* (3), 275–285.
- Berry, D. P., & 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., & Crowley, J. J. (2013). Cell biology symposium: genetics of feed efficiency in dairy and beef cattle. *Journal of Animal Science*, *91* (4), 1594–1613
- Besbes, B. (2009). Breeding village poultry for performance. *World's Poultry Science Journal*, *65*.
- Binda, B. D., Yousif, I. A., Elamin, K. M., & 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.
- Belgi, H. E., Torshizi, R. V., Masoudi, A. A., Ehsani, A., & Jensen, J. (2016). Longitudinal analysis of body weight, feed intake and residual feed intake in F2 chickens. *Livestock Sciences*, *184*, 28–34.
- Case, L. A., Wood, B. J., & 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., & 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., & 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., & 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., & 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., & Summers, J. (2010). *Broiler breeder production*. Nottingham, England: 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., & 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., & 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* (2 ed.). Oxon, UK: CAB International publishing.
- Ngeno, K., Bebe, B. O., & Kahi, A. K., (2012). Genetic evaluation of growth traits in ecotypes of Kenyan indigenous chicken. *Family Poultry Communications* (FAO), *21* (2), 4–12.
- Ngeno, K., van der Waaij, E. H., Megens, H. J., Kahi, A. K., van Arendonk, J. A., & 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
- SAS-Institute. (2002). *The SAS system for Windows. Release 9.1*. SAS Inst. Inc.: Cary, NC.
- Tadelle, D., Kijora, C., & 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., & Zaghari, M. (2010). Genetic parameters for feed utilization traits in Japanese quails. *Poultry Science*, *90*, 42–47.
- Willems, O. W., Miller, S. P., & 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.