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Genetic and phenotypic parameter estimates for selection within Ugandan indigenous chickens

Geoffrey Akiiki Beyihayo¹ · Donald Rugira Kugonza² · Elly K. Ndyomugyenyi¹ · Richard Echodu³ · Marion W. Okot¹ · Filomena Dos Anjos⁴

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Abstract

The high genetic variation within indigenous chickens (IC) which provides an opportunity to select superior stock for sustainable production and conservation is under-exploited. This study is aimed at estimating heritability and genetic and phenotypic correlation coefficients of productive and reproductive traits of Ugandan IC as a basis for selection. Data on traits were collected across two consecutive generations, weight (W) and shank length (SL) of chicks at hatching (HW) as well as at 2 (W2; SL2), 4 (W4; SL4), 6 (W6; SL6), 8 (W8; SL8), and 12 (W12; SL12) weeks of growth. Body weights at onset of lay (WFE) were also measured. In addition, egg number (EN-60), egg weight (EW), clutch number (CLN-60), and clutch size (CLS-60) over a period of 60 days were recorded. Genetic parameters were estimated using the univariate animal model analysis with restricted maximum likelihood procedure using the variability package of R, version 4.1.1. Heritability of traits ranged from 0.30 and 0.72 except SL4 (0.02), SL12 (0.14), and EN-60 (0.17). The traits EN-60 and W4 were negatively phenotypically correlated (- 0.49). Body weight at first egg was highly genetically correlated (0.99) with SL8. Egg number was significantly, negatively, and genetically correlated (- 0.96) with SL12. In conclusion, shank length is a potential phenotypic marker when selecting for live weight at onset of lay and egg yield. The shank length could, therefore, permit selection of superior chickens at an early age.

Keywords Variation · Selection · Trait · Indigenous chicken · Phenotypic marker

Introduction

Indigenous chickens (IC) continue to retain a wide range of desirable attributes and contribute to the nutritional and social-economic well-being of rural households in Asia and Africa (Mahendra 2016; Rajkumar 2021). However, the contribution of IC to the well-being of rural households is limited by their innate slow growth and low egg productivity (Wong et al. 2017). On average, the on-set of lay is

- ² Department of Agricultural Production, Makerere University, Kampala, Uganda
- ³ Department of Biology, Gulu University, Gulu, Uganda
- ⁴ Faculty of Veterinary, Eduardo Mondlane University, Maputo, Mozambique

delayed up to 7.2 months, and hens lay only 36 eggs per year. On the side of cockerels, sexual maturity is delayed up to 5.9 months (Nakkazi et al. 2014; Ssewannyana et al. 2008). The high genetic variation within IC, which provides an opportunity to identify replacement stock with desired productive and reproductive traits, remains under exploited (Adoligbe et al. 2020; Fleming et al. 2016; Lubandi et al. 2018; Magothe et al. 2010; Ssewannyana et al. 2008; Wong et al. 2017). The common practice of genetic improvement through cross breeding with highly specialized breeds has accelerated loss of important adaptation, broodiness, and reproductive traits critical for survival under harsh, rural resource-constrained farming systems (Tadelle et al. 2000; Dana et al. 2010; Semahoro et al. 2018). Unlike cross breeding, selecting within the surviving Ecotypes provides an opportunity to conserve the IC genetic resources and its associated multiple traits (Dana et al. 2010; Osei-Amponsah et al. 2013; Zonuz et al. 2013). In addition, the unique genomic and phenotypic selection signatures acquired by IC over generations for their adaptation to harsh environments

Geoffrey Akiiki Beyihayo beyigeo@gmail.com

¹ Department of Animal Production and Range Management, Gulu University, Gulu, Uganda

need to be conserved (Fleming et al. 2016; Elbeltagy et al. 2019).

Acquisition and expression of traits by the offspring depends on the degree of inheritance and association of responsible genes. Apart from varying across genotypes and environments, genetic parameters change with age and physiological status of chickens (Magothe et al. 2007; Dana et al. 2011; Gwaza et al. 2016; Singh et al. 2018; Chomchuen et al. 2022; Sanda et al. 2022). The variation in heritability of traits with age, therefore, requires timing of selection at a stage when heritability is at its peak (Adeyinka et al. 2006; Osei-Amponsah et al. 2013; Singh et al. 2018).

The association between traits indicates the underlying genetic interactions, and it is always important to know the effect of selecting one trait on others (Sanda et al. 2022). Genetic and phenotypic correlations determine a combination of traits that can be considered simultaneously in a multi-trait selection program (Magothe et al. 2007; Sanda et al. 2022). A moderate to high genetic correlation among traits is required to achieve a high breeding value (Magothe et al. 2007; Niknafs et al. 2012). Negative additive genetic correlations have been reported for egg production and live weight (Ghazikhani et al. 2007). Such negative genetic correlation of traits creates a puzzle for upgrading multipurpose IC reared mostly for both meat and eggs.

Genetic improvement through selection of superior replacement stock requires population-specific genetic parameter estimates of productive and reproductive traits. Genetic and phenotypic parameter estimates guide the setting of breeding objectives, stage of selection, and marker traits in a breeding program. In addition, previous genetic parameter estimation studies targeted a single Ecotype from a selected province (Dana et al. 2011; Norris and Ngambi 2006). Therefore, this study is aimed at estimating the genetic and phenotypic parameters of productive and reproductive traits of a mixed population of IC Ecotypes under a supplemented scavenging system.

Materials and methods

Acquisition of eggs and rearing of chickens

One thousand two hundred (1200) fresh fertile IC eggs (1–5 days) were purchased from selected rural households in six agro-ecological zones of Uganda as previously described (Beyihayo et al. 2022). Briefly, eggs from six IC Ecotypes (Madi, Acholi, Lango, Nteso, Nsoga, and Ngisu) were collected for the study. Rural households rearing IC with no access to exotic chicken or eggs were selected. In addition, egg-contributing rural households were selected on the basis of having kept IC for a minimum of 3 years. Ownership of an indigenous mature cock by the household was also

considered for higher egg fertility and hatchability. Eggs were packed in paper trays and delivered to Gulu University Poultry Unit for artificial incubation using a commercial incubator operated by an Automatic Computer Controller (Model: XM-18, India). Seven hundred thirteen (713) chicks were hatched, wing tagged, and brooded artificially for 4 weeks using a commercial chick starter (20.3% crude protein, 7.5% crude fiber, 0.5% phosphorus, and 1.1% calcium) purchased from Biyinzika Enterprises Limited. Heat for the brooder was provided by clay pots using charcoal as a source of fuel for a period of 2 weeks. After the brooding period, chickens were reared under a scavenging system and supplemented with 15% and 11% crude protein diets during their growth and laying phases, respectively. Chickens were vaccinated following a schedule recommended for commercial egg-type chickens.

Chickens were sexed at 8 weeks of age into 250 pullets and 241 cockerels. Using body weight at the onset of lay and the number of eggs laid in two consecutive clutches as criteria, 16 out of the 68 hens evaluated were selected to become parents for the second generation. Hens weighing at least 1213 g at the onset of lay, with the potential of laying 16 eggs and above in two consecutive clutches were selected (Figs. 1 and 2). Four cockerels were selected based on live body weight at 12 weeks of age for random mating with the selected hens at each generation (Fig. 3).



Fig. 1 Indigenous hens-generation one



Fig. 2 Indigenous hens—generation two



Fig. 3 Indigenous cocks

The selected cockerels weighed between 657 and 992 g at 12 weeks. The ratio of cocks to hens was maintained at 1:4 to increase the chances of fertility for each hen and variation within the population. Unselected chickens were then culled due to limited space. The collection of fertile eggs intended for hatching and raising the next generation was done at or above 32 weeks of age. Fresh fertile eggs collected within 10 days from different selected hens were pooled and incubated at once. The second generation consisted of 181 chicks at hatching. They comprised 55

cockerels and 85 hens at 8 weeks of age and were evaluated following the same protocol as in the first generation.

Data collection

Data were collected across two consecutive generations of indigenous chickens of both sexes raised at the Gulu University Poultry Unit. The live weight of chicks at hatching (HW) as well as at 2 (W2), 4 (W4), 6 (W6), 8 (W8), and 12 (W12) weeks of growth were measured using a portable electronic scale (Model: TS200, Canada). Shank lengths (SL) were also measured at 2 (SL2), 4 (SL4), 6 (SL6), 8 (SL8), and 12 (SL12) weeks of growth using a Tailor's measuring tape as described by the African Union Inter-African Bureau for Animal Resources (AU-IBAR 2015) field manual. Locally made trap nests were used to collect data on egg production traits. The reproductive traits, such as body weight of hens at on-set of lay (WFE), egg weight (EW), clutch number (CLN-60), clutch size (CLS-60), and number of eggs laid within 60 days (EN-60), were recorded.

Data analysis

Descriptive statistics of productive and reproductive traits were carried out using R software package, version 4.1.1 (R Core Team 2021). Heritability of traits was estimated using equation.

$$h^2 = \frac{\sigma_g^2}{\sigma_p^2}$$

where h^2 is the broad sense heritability, σ_g^2 is the genotypic variance, and σ_p^2 is the phenotypic variance.

Genetic analysis was performed using univariate animal model with the restricted maximum likelihood program (Dana et al. 2011).

$$\mathbf{y}_i = \mathbf{X}\mathbf{b}_i + \mathbf{Z}\mathbf{a}_i + \mathbf{e}_i$$

Correlations among traits were estimated by the animal model for traits i (i = 1 and i = 2) using the variability package of R, version 4.1.1 (R Core Team 2021).

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_i is the vector of observations; b_i is the vector of fixed effects of generation; a_i is the vector of random direct genetic effects; e_i is the vector of random residual effects; and X_i and Z_i are the incidence matrices relating the observations to the respective fixed and direct genetic effects for trait *i*.

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 Table 1
 Averages, variance components, and heritability of productive and reproductive traits of indigenous hens under a supplemented scavenging system

Trait	Mean ± SE	CV (%)	σ_g^2	σ_p^2	h^2
HW (g)	25.35 ± 0.72	9.10	1.66	5.35	0.31
W2 (g)	80.12 ± 3.15	19.57	176.17	245.74	0.72
W4 (g)	178.32 ± 5.70	14.73	462.07	689.96	0.67
W6 (g)	281.46 ± 10.16	11.39	304.26	1027.35	0.30
W8 (g)	409.89 ± 13.85	12.81	1412.83	2756.01	0.51
W12 (g)	623.10 ± 27.59	18.10	7388.59	12715.39	0.58
WFE (g)	1498.57 ± 60.64	16.96	38852.51	64597.21	0.60
SL2 (cm)	3.38 ± 0.06	7.23	0.03	0.06	0.57
SL4 (cm)	4.70 ± 0.11	6.44	0.00	0.09	0.02
SL6 (cm)	5.617 ± 0.09	4.93	0.02	0.08	0.30
SL8 (cm)	6.52 ± 0.08	5.22	0.07	0.12	0.64
SL12 (cm)	7.98 ± 0.12	4.28	0.02	0.12	0.14
EW (g)	37.34 ± 1.02	9.95	6.44	13.82	0.47
EN-60	19.29 ± 1.10	20.60	3.24	19.07	0.17
CLN-60	1.94 ± 0.25	1.06			
CLS-60	8.70 ± 0.53	4.73			

HW, *W2*, *W4*, *W6*, *W8*, and *W12*, weights at hatching, 2, 4, 5, 8, and 12 weeks of age respectively; *SL2*, *SL4*, *SL6*, *SL8*, and *SL12*, shank length at 2, 4, 6, 8, and 12 weeks of age respectively; *WFE*, body weight at onset of lay; *EW*, egg weight; *EN-60*, *CLN-60*, and *CLS-60*, egg number, clutch number, and clutch size over a period of 60 days, respectively; σ_g^2 , genotypic variance; σ_p^2 , phenotypic variance; h^2 , broad sense heritability

Results

Averages, variance components, and heritability of traits

The averages, genetic variance, phenotypic variance, and heritability of productive and reproductive traits of indigenous hens under a supplemented scavenging system are summarized in Table 1. Starting with a hatching weight (HW) of 25.35 g, chicken gained up to 1498.57 g of body weight at on-set of lay (WFE). Shank length (SL) increased from 3.38 cm at 2 weeks to 7.98 cm at 12 weeks of growth. On average, hens laid 19.29 eggs within a period of 60 days, spread across 1.90 clutches of 8.70 eggs each. Heritability ranged from 0.02 to 0.72. Majority of the traits had values above 0.3 which is moderate and adequate for targeted increased genetic improvement. Low heritability values were estimated for trait SL4 (0.02), SL12 (0.14), and EN-60 (0.17). Body weight at 2 weeks of growth (W2) was highly heritable (0.72) compared to other traits in the study.

Genetic and phenotypic correlation of traits

Genetic and phenotypic correlation coefficients of productive and reproductive traits of IC are summarized in Table 2. Most of the phenotypic correlation coefficients were positive, significant, and ranging from moderate to high. The highest significant (P < 0.001) phenotypic correlation coefficient (0.83) was between SL2 and W2. The lowest (P < 0.001) and only negative phenotypic correlation coefficient

 Table 2
 Genetic correlation (lower triangle) and phenotypic correlation (upper triangle) of productive and reproductive traits of IC hens under a supplementary scavenging system

	HW	W2	SL2	W4	SL4	W6	SL6	W8	SL8	W12	SL12	WFE	EW	EN-60
HW	1**	0.53**	0.66**	- 0.07	0.28	0.11	0.24	0.18	0.25	0.12	0.23	0.35	0.05	0.29
W2	0.86	1**	0.83**	- 0.02	0.28	0.14	0.36	0.21	0.37	- 0.22	0.05	0.56**	0.45*	0.12
SL2	1.04*	0.92	1**	- 0.17	0.16	-0.05	0.25	0.07	0.25	- 0.18	0.06	0.36	0.25	0.18
W4	- 0.38	- 0.13	-0.50	1**	0.33	0.49**	0.48**	0.70**	0.64**	0.33	0.03	0.37	0.12	- 0.49**
SL4	0.02	1.37	0.36	2.02	1**	0.57**	0.72**	0.65**	0.56**	0.36	0.35	0.40*	0.21	0.25
W6	0.09	0.07	- 0.15	1.09	1.63	1**	0.47*	0.78**	0.54**	0.56**	0.29	0.45*	- 0.03	- 0.22
SL6	-0.24	0.50	-0.05	0.85	1.99	0.72	1**	0.60**	0.79**	0.11	0.19	0.70**	0.51**	-0.08
W8	0.07	0.19	- 0.11	0.99*	1.85	1.09	0.81	1**	0.73**	0.66**	0.37	0.52**	0.15	- 0.11
SL8	0.34	0.50	0.19	0.84	2.25	1.08	0.83	1.03*	1**	0.37	0.40*	0.81**	0.54**	- 0.29
W12	0.12	- 0.38	-0.28	0.60	- 0.10	0.80	- 0.15	0.59	0.46	1**	0.61**	0.18	- 0.26	- 0.17
SL12	0.95*	0.30	0.45	0.62	0.38	1.10	- 0.05	0.88	0.83	1.06	1**	0.38*	- 0.03	- 0.16
WFE	0.51	0.76	0.47	0.67	2.52	0.87	0.91	0.91	0.99*	0.17	0.64	1**	0.65**	- 0.25
EW	0.27	0.84	0.44	0.51	2.61	0.56	1.10	0.64	0.74	- 0.37	-0.04	0.91	1**	0.10
EN-60	0.36	0.70	0.87	- 1.10	- 2.14	- 1.29	- 0.44	- 1.16	-0.71	- 1.26	- 0.96*	- 0.26	0.11	1**

HW, *W2*, *W4*, *W6*, *W8*, and *W12*, weight at hatching, 2, 4, 6, 8, and 12 weeks of age, respectively; *SL2*, *SL4*, *SL6*, *SL8*, and *SL12*, shank length at 2, 4, 6, 8, and 12 weeks of age, respectively; *WFE*, body weight at onset of lay; *EN-60 and EW*, egg number and weight over a period of 60 days, respectively; **P < 0.001; *P < 0.01

(- 0.49) was between EN-60 and W4. Weight at first egg (WFE) was highly correlated with W2 (0.56), SL4 (0.40), W6 (0.45), SL6 (0.70), W8 (0.52), SL8 (0.81), and SL12 (0.38). Egg weight (EW) was highly correlated with W2 (0.45), SL6 (0.51), SL8 (0.54), and WFE (0.65). Significant genetic correlation coefficients ranged from – 0.96 (SL12-EN-60) to 1.04 (HW-SL2). Weight at first egg (WFE) was highly (P < 0.01) and positively genetically correlated (0.99) with SL8. Egg number (EN-60) was significantly (P < 0.01) negatively genetically correlated with shank length (SL12).

Discussion

Averages of phenotypic traits

The average body weight at 0, 2, 4, 8, and 12 weeks of age in the present study were higher than that of indigenous chicken Ecotypes in Eastern Uganda (Semahoro et al. 2018). In the current study, chicken were raised under a supplementary scavenging system different from the intensive system used by Semahoro et al. (2018). Probably, the disparity in body weight could be attributed to the management system and nutritional profile of feeds used in the two studies. In the current study, the mean shank length of hens at 8 to 12 weeks of age was higher than the values estimated for Nganda chickens within the same age range in Central Uganda (Semakula et al. 2011). The variation in shank length across different studies is a result of the differences in field guidelines used in collecting data on morphometric measurements (Beyihayo et al. 2022). The body weight of hens at onset of lay was within the range of 1200 and 1500 g reported for adult hens in Eastern and Western ecological zones of Uganda (Ssewannyana et al. 2008). The mean weight of eggs (37.34 g) was, however, lower than the value of 41.13 g recorded for eggs laid by scavenging hens in rural households (Beyihayo et al. 2022). In the current study, eggs were weighed at the on-set of lay, a period characterized by small and lightweight eggs (Anene et al. 2020; Udeh 2009). The average clutch size of 8.70 eggs per clutch in the present study was outside the range of 13 to 15 eggs reported for hens in Northern (Nakkazi et al. 2014), Western, and Eastern (Ssewannyana et al. 2008) ecological zones of Uganda. The small clutch size in the present study could be attributed to the short resting period between clutches as hens were not allowed to incubate and brood chicks. In addition, phenotypic differences in traits could be attributed to variations in feeding regimes and chicken Ecotypes used in various performance studies.

Heritability of traits

Heritability values of 0.72, 0.67, 0.30, and 0.51 in the current study were close to the values of 0.66, 0.55, 0.52, and 0.63 for body weight at 2, 4, 6, and 8 weeks, respectively

estimated for local chickens in Ghana (Osei-Amponsah et al. 2013). The heritability of body weight at 4 and 8 weeks of age in the current study is similar to the values estimated for Indian Ghagus chicken (Haunshi et al. 2022). Like in the current study, a similar body weight heritability value of 0.55 was estimated for Fars chickens at 12 weeks of age but lower values of 0.25 and 0.23 were reported for Iranian Azarbaijan and Esfahan Ecotypes (Ghazikhani et al. 2007). Likewise, body weight heritability of 0.72 and 0.67 in the current study differed from the estimates of 0.45 and 0.38 at 2 and 4 weeks of age, respectively (Chomchuen et al. 2022). However, a similar heritability of 0.3 at week 6 of growth was recently reported (Chomchuen et al. 2022). In related studies, Adeyinka et al. (2006) and Norris and Ngambi (2006) reported similar heritability values at hatching and a low value at the fourth week of growth. The decline in body weight heritability with increasing age was attributed to the corresponding reduction in maternal effect (Tongsiri et al. 2019). Heritability estimates for shank length in the present study ranged from 0.02 and 0.58 and are in agreement with the values of 0.57, 0.3, and 0.58 at 2, 6, and 8 weeks of age, respectively estimated for local chickens in Ghana (Osei-Amponsah et al. 2013).

The heritability value of 0.47 for egg weight in the current study was similar to 0.46 estimated for Mazandaran chicken but varied from 0.64, 0.22, and 0.25 associated with Far, Azarbaijan, and Esfahan chicken Ecotypes, respectively (Ghazikhani et al. 2007). The estimated heritability of egg number (0.17) was close to 0.15 reported by Tongsiri et al. (2019) and within a range of 0.16 to 0.18 for Mazandaran and Esfahan chickens in Iran (Ghazikhani et al. 2007). The heritability value of 0.17 for egg number highly varied from the average of 0.36 and 0.32 estimated for Ethiopian Horro chickens (Dana et al. 2011) and Iranian Fars chickens (Ghazikhani et al. 2007). The variation in heritability estimates of traits reported in different studies is attributed to the method of estimation (Ndung et al. 2020) and number of generations considered (Haunshi et al. 2022). The trait of body weight could be adequately improved by direct selection except for egg number which is associated with low heritability. Tongsiri et al. (2019) suggested the use of a multiple trait selection index method for improved egg number.

Genetic correlation of traits

Egg number and shank length at 12 weeks of age are negatively genetically correlated. The negative genetic correlation implies that hens with short shanks at 12 weeks are more likely to lay more eggs, and the reverse is true. On the other hand, shank length at 12 weeks of age is positively genetically correlated with hatching weight, implying that light chicks at the time of hatching are expected to have short shanks at 12 weeks of age and more likely to lay more eggs compared to heavy chicks. This implies that hens can probably be indirectly selected for large clutch size using shank length at 12 weeks as a phenotypic marker trait.

In the current study, egg number and weight at onset of lay were negatively genetically correlated with a coefficient of -0.26. Likewise, Ghazikhani et al. (2007) and Tongsiri et al. (2019) reported a similar negative value of genetic correlation between egg number and weight at onset of lay. Additionally, Zonuz et al. (2013) reported negative genetic correlations of egg number and body weight at 0 (-0.04), 8 (-0.09), and 12 (-0.14) weeks of growth. The antagonistic pleiotropic relationship involving three candidate genes, namely, CPEB3, MAST2, and CACNA1H, is responsible for the negative cross-phenotypic association between body weight and egg production traits (Tarsani et al. 2021). Probably, a gene controlled biological mechanism in light hens directs abundant nutrients for egg production as compared to body maintenance. Unlike most studies, Dana et al. (2011) reported positive genetic correlation between egg number and body weight excluding a negative correlation (-0.16)and -0.54) at 2 and 6 weeks of age. The positive genetic correlation could be due to errors introduced by the high mortality of 13 to 29% reported during the laying period. The genetic correlation coefficient between weight at onset of lay and egg weight was 0.908 and was higher than 0.6 reported by (Tongsiri et al. 2019). However, negative genotypic correlation coefficients were reported for egg number against egg weight (-0.39) and weight at onset of lay (-0.28) among local chickens in Nigeria (Oleforuh-okoleh 2011).

Phenotypic correlation of traits

Weight at onset of lay and shank length at 8 weeks of age in the current study were moderate, positively correlated, and in agreement with estimates reported for Ghagus chicken in India (Haunshi et al. 2022). Therefore, heavier hens at onset of lay can be indirectly selected using shank length at 8 weeks as a marker trait. The phenotypic and genotypic correlation coefficients between shank length and live weight were positive, significant, and similar to the values of 0.86 and 0.94, respectively, reported for local chickens in Ghana (Osei-Amponsah et al. 2013). The same study (Osei-Amponsah et al. 2013) reported high phenotypic correlation coefficients between body weight and shank length at 6 (0.93) and 12 (0.87) weeks of age. In a recent study involving Alpha and Noiler chicken genotypes, relatively lower genetic correlations of 0.59 and 0.71 were reported for body weight and shank length at 8 and 12 weeks of age, respectively (Sanda et al. 2022). Genetic correlations are indicators of pleiotropic association and chromosomal linkage of genes affecting a pair of traits (Sanda et al. 2022). The disparities in phenotypic and genotypic correlation coefficients reported from different studies are due to the influence of the chicken breeds, rearing environment (Chomchuen et al. 2022; Sanda et al. 2022).

Conclusions

Genetic improvement of IC with respect to shank length and body weight at onset of lay as well as egg weight but not egg number can be achieved through direct selection of superior chickens. Shank lengths at 8 and 12 weeks of age are potential phenotypic markers when selecting for both high body weight at onset of lay and egg yield. Breeders could, for instance, undertake selection of hens for higher body weight at onset of lay based on shank length. Light hens with short shanks are more likely to lay more eggs per clutch. Trait pairs including SL8-WFE, EW-WFE, SL2-W2, and SL8-W8 are, therefore, positively correlated and can be considered together in a breeding program. The significant positive phenotypic correlation between shank length and body weight permits indirect selection and improvement of the later. Further studies are required to estimate the genetic parameters of other reproductive traits such as broodiness, hatchability, and mothering ability in indigenous hens.

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Author contribution GAB and DRK conceptualized the study and methodology. MWO, FDA, and DRK mobilized resources. GAB collected and analyzed data and prepared initial draft of manuscript. EKN, DRK, and RO reviewed and edited the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated are available from the corresponding author on request.

Declarations

Ethics approval The animal study protocol was approved by the Research Ethics Committee of Gulu University (GUREC-2020-18; dated: 03/12/2020). The research protocol was registered with the Uganda National Council for Science and Technology (UNCST) for final clearance (NO. A154ES; dated: 15/11/2021).

Competing interests The authors declare no competing interests.

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