

Research Article

Response to Selection of Indigenous Chicken in Rwanda Using Within-Breed Selection Strategy

Richard Habimana^{1,2,*} , Kiplangat Ngeno³ , Tobias Otieno Okeno⁴

¹Department of Animal Production, University of Rwanda, Nyagatare, Rwanda

²Department of Animal Science, Egerton University, Egerton, Kenya

³Department of Agriculture and Natural Resources, Moi University, Eldoret, Kenya

⁴Department of Agriculture, Murang'a University of Technology, Murang, Kenya

Abstract

The study evaluated response to selection from within-breed selection strategy for conventional (*CBS*) and genomic (*GBS*) breeding schemes. These breeding schemes were evaluated in both high-health environments (nucleus) and smallholder farms (commercial). Breeding goal was to develop a dual-purpose IC for both eggs and meat through selective breeding. Breeding objectives were body weight (BW), egg weight (EW), egg number (EN) and resistance to Newcastle disease (AbR). A deterministic simulation was performed to evaluate rates of genetic gain and inbreeding. Base population in the nucleus was made up of 40 cockerels and 200 pullets. Selection pressure was 4% and 20% in the males and the females, respectively. The impact of nucleus size and selection pressure on rates of genetic gain and inbreeding of the breeding program was investigated through sensitivity analysis. SelAction software was used to predict rates of genetic gain and inbreeding. Results showed that using *CBS* in the nucleus, the breeding goal was 340.41\$ and 1.13 times higher than that in the commercial flock. Inbreeding rate per generation of selected chicken in the nucleus was 1.45% and lower by 1.32 times compared to their offspring under smallholder farms. Genetic gains per generation in the nucleus for BW and EN traits were 141.10 g and 1.07 eggs and 1.12 and 1.10 times greater than those in smallholder farms, respectively. With *GBS*, the breeding goal was increased by 3.00 times whereas inbreeding rate was reduced by 3.15 times. Besides, using *GBS*, the selected birds in the nucleus were relatively similar to those in a commercial environment. Finally, the study revealed that the nucleus size and mating ratio influence the rates of genetic gain and inbreeding in both *GBS* and *CBS*. This study shows that IC in Rwanda have the potential to be improved through within-breed selection strategy using either *CBS* or *GBS*.

Keywords

Genetic Gain, Inbreeding, Indigenous Chicken, Selection, Rwanda

1. Introduction

Indigenous chickens (IC) are favourable breed to poor rural households despite their slow growth rate and low egg pro-

duction. This because they have a higher disease resistance and are productive under poor nutrition and high temperature

*Corresponding author: hrichard86@yahoo.fr (Richard Habimana)

Received: 15 December 2023; **Accepted:** 18 January 2024; **Published:** 25 June 2024



Copyright: © The Author(s), 2024. Published by Science Publishing Group. This is an **Open Access** article, distributed under the terms of the Creative Commons Attribution 4.0 License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution and reproduction in any medium, provided the original work is properly cited.

than exotic chickens [24]. In tropics, IC have high genetic variability within populations [60, 25, 53]. Thus, it is to genetically boost their productivity through selective breeding. Selective breeding involves convention and genomic breeding programs as short and long-term strategies.

Conventional breeding program utilises the phenotypic characteristic and pedigree information to estimate breeding values (EBV) and response to selection. The EBV from phenotypic data has been effective over the generations in implementing a selection program and realising genetic improvement [5]. Several limitations, however, are faced in the application of EBV [63], which include the aptitude to precisely and timely record the phenotypic data on candidates and/or their close relatives; the expense of data recording and the onset of a majority of the production traits are late in life thus hinders genetic gain per unit time [29]. All these limitations led to the development of a more accurate and better tool for selection such as the genomic approach [61].

Genomic selection (GS) has reshaped the way genetic evaluations and selection of elite populations are performed [34]. It increases the accuracy of EBV and by decreasing generation interval, it optimizes genetic gain in breeding programs [78]. With the highly advanced technological development and the decrease of the genotyping costs, GS is widely used in animal breeding in developed countries [19, 35]. The adoption of GS in the developing countries especially in IC breeding programs, however, is limited due to the perceived high cost without due considerations to returns.

In selection programs, the interaction between genotype and environment (G x E) has been rarely put into consideration because most experiments are done in a controlled nucleus breeding station [78]. This has been a matter of great concern in animal breeding much longer because G x E interaction reduces the response to selection in extensive management systems [52, 50]. To develop superior germplasm that performs optimally within specific climatic conditions, G x E should, therefore, be considered in-flock selection and planning of breeding strategy [63]. Furthermore, there is a need to evaluate improved genetic stock under specific climatic conditions before its release for commercial utilisation [73].

To improve IC genetic stock, crossbreeding using improved exotic breeds, within-local flocks selection, and their

combinations have been utilized in developing countries [37, 48, 2]. Crossbreeding using exotic breeds was the most preferred because there is a belief that crossing IC with the exotic chicken results in improved IC [1, 38, 55]. This method, however, has been unsuccessful due to several reasons, which include exorbitant costs of getting and sustaining exotic breeding cocks, lessened broodiness in the crossbreds, and unreliable stock [1, 38, 55]. An alternative breeding strategy that capitalises on specific-desired attributes such as within-breed selection has been recommended [59]. Within-breed selection strategy is appropriate for IC improvement because it preserves economically important traits needed for sustaining production. It also reduces genetic dilution and erosion during breeding [20].

Based on the above lines of reasoning, this study investigated the hypothesis that IC could be improved through within-breed selection strategy. This hypothesis was tested using a deterministic simulation of breeding schemes that resemble those used in IC breeding programs in developing countries.

2. Materials and Methods

2.1. Procedure

A deterministic simulation was conducted to simulate two different breeding approaches in a closed single-tier nucleus-breeding program. The considered breeding schemes were conventional and genomic. The conventional scheme represented the existing chicken breeding programs, while the genomic scheme was an alternative breeding program. The adoption of a single-tier nucleus breeding system aligns with the practice in many developing countries, where chickens not selected as replacement stock in breeding stations are sold to farmers for commercial production. This implies alignment between the breeding goals within the breeding stations and those of the farmers. The simulation focused on modeling the IC breeding program in Rwanda to test the hypothesis of the current study.

Table 1. Phenotypic variances (Var-P), economic values (EV – US\$), heritability (along the diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations of traits in the breeding objective

Traits	Correlations											
	BW	EN	EW	AbR	ENC	BWC	BWGS	ENGs	EWGS	AbRGS	BWCGS	ENCGS
Var (P)	139,929.56	130.69	18.80	5,677,315.41								
EV (US\$)	2.15	0.19	-0.001	-0.23								
BW	0.24	0.22	0.10	-0.07	0.17	0.75	0.34	0.06	0.04	-0.03	0.26	0.04

Traits	Correlations											
	BW	EN	EW	AbR	ENC	BWC	BWGS	ENGs	EWGS	AbRGS	BWCGS	ENCsGS
EN	0.23	0.24	-0.19	-0.04	0.76	0.17	0.08	0.25	-0.08	-0.01	0.06	0.19
EW	0.20	-0.13	0.44	-0.01	-0.14	0.15	0.03	-0.04	0.44	-0.00	0.05	-0.03
AbR	-0.07	-0.02	-0.00	0.27	-0.03	-0.05	-0.02	-0.01	0.00	0.36	0.02	-0.00
ENC	0.04	0.16	-0.02	-0.00	0.24	0.22	0.06	0.19	-0.06	-0.01	0.06	0.25
BWC	0.18	0.04	0.04	-0.01	0.23	0.24	0.26	0.04	0.07	-0.02	0.26	0.06
BWGS	0.17	0.07	0.03	-0.02	0.06	0.25	0.97	0.03	0.02	-0.01	0.14	0.02
ENGs	0.05	0.09	-0.04	-0.01	0.19	0.04	0.03	0.97	-0.03	-0.00	0.02	0.08
EWGS	0.04	-0.08	0.29	-0.00	-0.06	0.07	0.02	-0.03	0.97	-0.00	0.04	-0.02
AbRGS	-0.03	-0.01	-0.00	0.19	-0.01	-0.02	-0.01	-0.00	-0.00	0.97	-0.01	-0.00
BWCGS	0.25	0.06	0.05	-0.02	0.08	0.25	0.14	0.02	0.04	-0.01	0.97	0.03
ENCsGS	0.04	0.19	-0.02	-0.00	0.11	0.05	0.02	0.07	-0.02	-0.00	0.03	0.97

Var (P), phenotypic variance; EV: Economic value in US \$; BW, body weight at 16 weeks (g); EN, egg number (16 weeks); EW, Egg weight (30 weeks); AbR, antibody response at 35 days after the second immunisation. BWC: Bodyweight in production; ENC: Egg number production environment. Letters GS in front of the traits indicates genomic markers (genomic traits) associated with phenotypic traits.

2.2. Indigenous Chicken Breeding Goal and Traits in the Breeding Objective

Breeding goal was to develop a dual-purpose IC for both meat and eggs production through within-breed selection. Breeding objective traits were identified through a participatory approach and included body weight (BW), Egg weight (EW), egg number (EN) and resistance to Newcastle disease (AbR) [41]. Inclusion of the traits of economic importance in the breeding objective requires the estimation of their economic values [6]. Economic value of a trait is the change in profit attributed to change in a unit's genetic merit of a trait, holding other traits constant [26]. Economic values for the above-mentioned traits had been estimated [39] and are presented in Table 1. These values were adopted in the current study after adjustments using cumulative discounted values of each trait.

2.3. Genetic, Phenotypic Parameters and Genetic Correlations

Phenotypic and genetic parameters should be obtained from the same population when evaluating breeding programs. Due to several challenges such as poor data recording, small data size, and small populations in developing countries, however, it may be difficult to generate genetic and phenotypic parameters from the same population [77]. The current study, therefore, used the consensus genetic and phenotypic parameters for IC generated from Meta-Analysis [56]. Since the

correlation between the same trait may deviate from unity in different environments due to G x E [50], correlations between traits in the breeding objective in the current study were sourced from the literature [3, 36] and subjected to Meta-Analysis and are presented in Table 1.

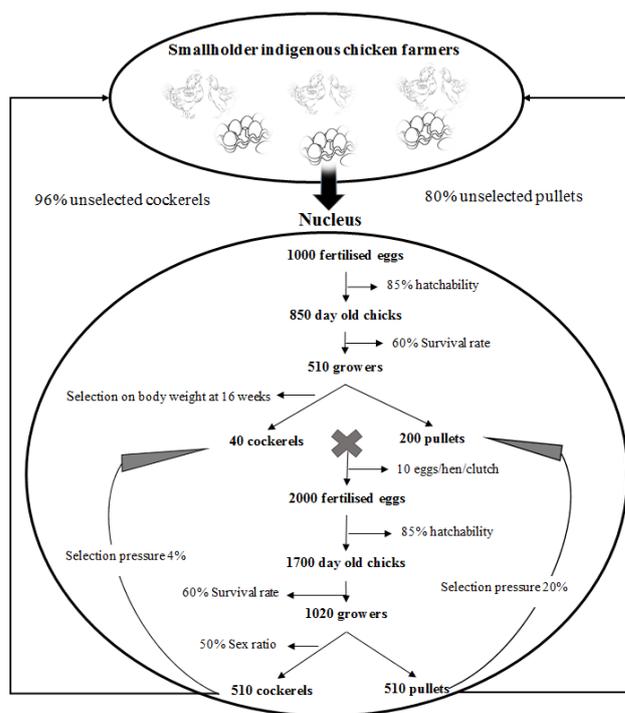


Figure 1. Breeding structure for the simulated indigenous chicken breeding program in Rwanda.

2.4. Breeding Program, Schemes and Population Structure

A single-tier nucleus breeding program was established within the research station by purchasing fertilized eggs from the smallholder farmers. Figure 1 shows the design of breeding program and selection schemes modelled. Two breeding approaches under consideration were conventional and genomic.

Conventional Breeding Schemes (CBS): This approach assumed that parents were chosen solely based on pedigree and phenotypic information. This mirrors the existing breeding program in many developing countries, where selection relies on performance records. In this scheme, it was assumed that selection is done within the breeding station (nucleus) and the unselected birds to replace parents are returned to smallholder farmers for raising (commercial) where recording is minimal. Response to selection was therefore monitored both within the nucleus and in the smallholder farms.

Genomic Breeding Scheme (GBS): This scheme was similar to CBS but assumed that the candidates in the nucleus were genotyped and therefore had genotypic information in addition to performance records on traits in the breeding objective. Candidates were, therefore, selected on genetic markers as an additional source of information.

The initial population structure was obtained by incubating and hatching one thousand fertile eggs purchased from smallholder farmers (Figure 1). Forty cockerels and 200 pullets were selected based on body weights at 16 weeks and used as the base population. Each hen was assumed to lay 10 fertilized eggs per clutch with a hatchability of 85%, the survival rate to weaning of 60%, and a sex ratio of 0.5 [40]. Selection was by truncation using Best Linear Unbiased Prediction Estimated Breeding Values (BLUP-EBV). For sex-limited traits and those phenotyped later in life such as EN and EW, the candidates were selected based on information from their female ancestors and sibs' performances. For BW and AbR, the candidates were selected based on their own performance before maturity and phenotypic data from their male and female ancestors and sibs' performance.

Common environmental effect within the nucleus was assumed constant since the animals were within the same station. The performance of the chicks hatched in the nucleus but raised in the smallholder farms was simulated by accounting for the genetic correlation between on-station and smallholder farms for different traits in breeding objective [17]. This is because, in Rwanda, the majority of IC farmers are smallholder rearing their chickens under extensive management with nutrient deficiency, disease prevalence and stress [44, 41]. The transfer of superior genes to smallholder farms from the nucleus was through both cockerels and pullets.

2.5. Prediction of Response to Selection

Conventional breeding scheme (CBS)

Genetic gain for each trait was calculated based on the method described by [75].

$$\Delta G = \frac{b'Gi}{\sigma_i} \quad (1)$$

where ΔG is a vector containing selection response for each trait; b is a vector of index weights and G , is a matrix of co-variances between information sources and true breeding values of selection candidates, i , selection intensity and σ_i , standard deviation of the index. Total gain in the breeding goal was calculated as [82]:

$$\Delta H = i\sigma_i \quad (2)$$

where ΔH is the breeding goal

The response to selection was calculated for all traits in the breeding objective (H), which represented the total of the true breeding values of traits, each weighted by its respective economic value. It was computed as [62]:

$$H = A_1V_1 + A_2V_2 + \dots \quad (3)$$

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

Genomic breeding scheme (GBS)

In this scheme, traits were incorporated into the selection index as additional correlated traits with a heritability close to unity. This is due to the fact that marker information is entirely heritable and lacks residual variance. [64, 14]. Consequently, the environmental correlation between the true and extra trait is insignificant and was set to null [15]. Phenotypic and genetic correlations between the true and additional trait were calculated as hr_{gg} and r_{gg} , where h is the square root of the heritability of the trait and r_{gg} , the accuracy of genomic estimated breeding values. The r_{gg} was determined by the size of the reference population (n_p), the effective number of loci in the base population (n_G), and the correlation of true breeding values of genotyped individuals and their phenotypes (r). They were computed based on the model below [15, 13].

$$r_{gg} = \sqrt{\frac{\lambda r^2}{\lambda r^2 + 1}} \quad (4)$$

where $\lambda = \frac{n_p}{n_G}$ and r^2 , heritability, $n_G = 2N_E L$, N_E is the effective size of the base population, and L is the size of the genome in Morgan units. The IC genome was presumed as 32 in Morgan units [23], the effective population size was 17.14 based on the formula of [76] as follows:

$$N_E = \frac{4N_f * N_m}{N_f + N_m} \quad (5)$$

where N_f : number of females; N_m : number of males

Phenotypic and genetic correlations between the genomic traits were computed as per the procedure of [14] and are presented in Table 1.

2.6. Prediction of Inbreeding Rate

Rate of inbreeding was computed based on [81]. In the first step, a regression model was used to predict long-term contributions.

$$E(r) = \alpha + \beta(BV - \overline{BV}) \quad (6)$$

where $E(r)$ is the expected contribution, α , the contribution of an individual with an average breeding value, β accounts for the increase of the contribution of parents with a higher breeding value implying that the parents with high breeding values will have more selected offspring. Secondly, the square of the expected contributions was computed. This results in the calculation of inbreeding as;

$$\Delta F = \frac{1}{2} NE(r)^2 \quad (7)$$

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

2.7. Optimum Nucleus Size

Optimal nucleus population size was investigated by simulating the effect of the nucleus size and different mating ratios on response to selection. This was considered by increasing the number of breeding parent flock in the base population from 240 to 24,000 hens and mating ratio from 1:5 to 1:100. The use of artificial insemination (AI) was adopted when the mating ratio was increased. With AI, it has been reported semen from one cock can be used to inseminate 100 hens by use of extenders [47].

SelAction software [62] was used to model and simulate different breeding systems and schemes in the current study. This software predicts rates of genetic gain and inbreeding for livestock breeding programs using deterministic simulation approaches. It presents the total response to selection, response for males and females separately. It also accounts for rate of inbreeding. Response to selection and rate of inbreeding are presented per generation [62].

3. Results

This study revealed that the within-breed selection strategy improves egg and meat production of IC in Rwanda. Furthermore, it revealed that *GBS* performed better than *CBS* based on rates of genetic gain and inbreeding.

3.1. Response to Selection in Breeding Program

Response to selection was presented as overall genetic gain, rate of inbreeding, accuracies of selection and genetic gains of individual traits realised in the two breeding schemes. Rates of genetic gain, inbreeding and accuracies of selection in the *CBS* and *GBS* are presented in Table 2. In *CBS*, the genetic gain was 1.13 times higher in the nucleus than in commercial. Rate of inbreeding per generation of selected chicken in the nucleus was 1.32 times less inbred than their offspring under field conditions. The accuracy of selection was 1.17 times higher in the nucleus than in smallholder farms. In *GBS* on the other hand, there was no difference in rates of genetic gain, inbreeding and accuracy of selection between the nucleus and smallholder farms. When *GBS* and *CBS* were compared, the *GBS* was 3.0 and 3.15 times superior to *CBS* in genetic gain and reduction in the rate of inbreeding, respectively. In addition, accuracy of selection was 1.8 times higher in *GBS* than in *CBS*.

Table 2. Rates of genetic gain (US\$), inbreeding (%) and accuracy of selection in the conventional (*CBS*) and genomic (*GBS*) breeding schemes.

Scheme		Response (US\$)	Rate of inbreeding (%)	Accuracy of index
<i>CBS</i>	Nucleus	340.41	1.45	0.55
	Commercial	301.17	1.91	0.47
<i>GBS</i>	Nucleus	1,024.45	0.46	0.97
	Commercial	1,024.44	0.46	0.97

CBS, Conventional breeding scheme; *GBS*, Genomic breeding scheme; US\$: United State dollars

Genetic gain for individual traits in *CBS* and *GBS* are displayed in Table 2. There were differences in genetic gain per trait in the *CBS* and *GBS* and also between nucleus and commercial. In *CBS*, the genetic gains for BW and EN traits

were 1.12 and 1.10 times greater in the nucleus than in smallholder farms, respectively. Contrarily, the correlated responses of EW and AbR to BW and EN traits were lower in the nucleus than in the commercial flock. In *GBS*, the genetic

gains for BW and EN traits were similar in the nucleus and commercial. Correlated responses of EW and AbR were, however, greater in commercial than in the nucleus. Genetic gains for BW and EN were 3 times more and 2 times less in

GBS than in CBS, respectively. The correlated response of AbR was also greater in GBS than in CBS, but that of EW was lower in GBS than in CBS.

Table 3. Genetic gains for individual traits realised in conventional (CBS) and genomic (GBS) breeding schemes.

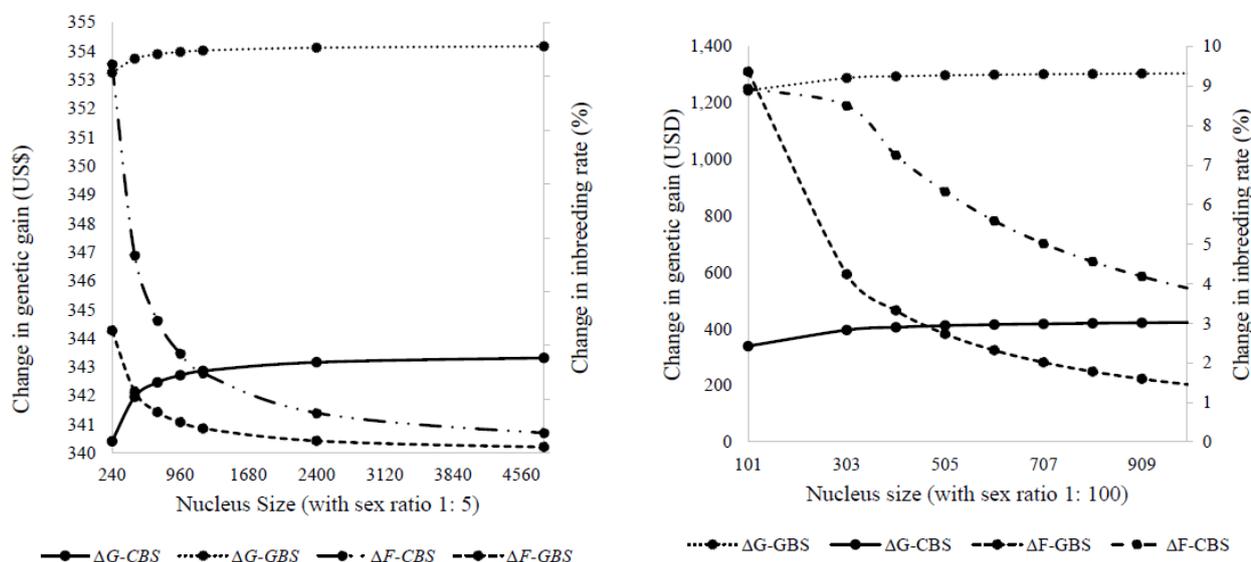
Trait	CBS		GBS	
	Nucleus	Commercial	Nucleus	Commercial
BW	158.24	141.39	476.44	476.44
EN	1.07	0.97	0.49	0.48
EW	0.24	0.43	0.13	0.20
AbR	-82.10	-72.17	-45.39	-30.37

BW, body weight at 16 weeks (g); EN, egg number (16 weeks); EW, Egg weight (30 weeks); AbR, antibody response at 35 days after the second immunisation

3.2. Optimum Nucleus Size

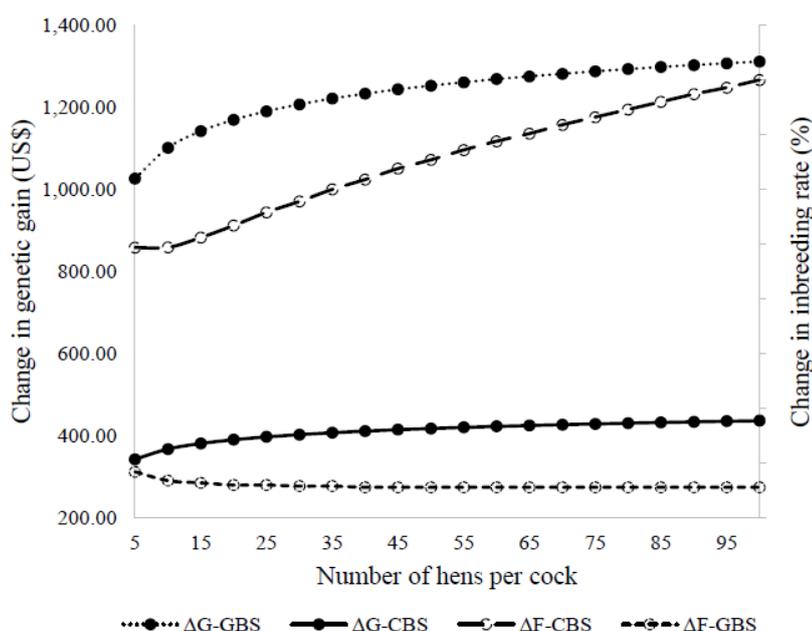
Figure 2 demonstrates the effect of the increase in the nucleus size on the rate of change in genetic gain and inbreeding in CBS and GBS. Nucleus size did not affect considerably the

genetic gain. There was a sharp increase of genetic gain up to a nucleus size of 960 and 303 hens, with sex ratios of 1:5 and 1:100, respectively and then, increased at a diminishing rate in both CBS and GBS. Rate of inbreeding declined at a diminishing rate with a gradual increase in nucleus size in both CBS and GBS.



$\Delta G-CBS$, change in genetic gain in the conventional breeding scheme; $\Delta G-GBS$, change in the genetic gain in the genomic breeding scheme (with a sex ratio of 1:5, $\Delta G-GBS$ was divided by 2.9 to be plotted together with $\Delta G-CBS$); $\Delta F-CBS$, change in the rate of inbreeding in the conventional breeding scheme; $\Delta F-GBS$, change in the rate of inbreeding in a genomic breeding scheme

Figure 2. Trends for the rate of genetic gain and inbreeding attributed to the increase in nucleus size.



ΔG -CBS, change in genetic gain in the conventional breeding scheme; ΔG -GBS, change in the genetic gain in the genomic breeding scheme (with a sex ratio of 1:5, ΔG -GBS was divided by 2.9 to be plotted together with ΔG -CBS); ΔF -CBS, change in the rate of inbreeding in the conventional breeding scheme; ΔF -GBS, change in the rate of inbreeding in a genomic breeding scheme

Figure 3. Trends for change in the rate of genetic gain and inbreeding due to the increase in the mating ratio.

4. Discussion

Findings of the present study confirm our hypothesis that the use of within-breed selection strategy improves egg and meat production of IC in Rwanda. Furthermore, this study revealed that based on rates of genetic gain and inbreeding, GBS outperformed CBS. This was confirmed by a low and high response to selection for overall breeding goal and individual traits realised in CBS and GBS, respectively.

4.1. Rates of Genetic Gain and Inbreeding of Indigenous Chicken in CBS and GBS

Generally, the rate of genetic gain for the breeding goal of IC in CBS in this study was adequate, but inferior to that realised in GBS (Table 2), confirming the findings from the previous studies [72, 51, 18]. This could be attributed to an increased accuracy of index realised in GBS (Table 2). High accuracy has been associated with high selection response [18]. It indicates, therefore, that GBS would increase the values of genetic improvement. The GBS is associated with higher accuracy than CBS because genomic relationships are more accurate than pedigree-based relationships [45]. Accuracy is positively correlated with heritability [78] and in GBS, the marker information is entirely heritable [64, 15]. This is

because markers are linked to a gene affecting the trait [45]. Besides, the increase in accuracy is attributed to the upgraded measurement of the relationships between animals and better prediction of the Mendelian sampling terms [11, 28]. With GBS, Mendelian sampling terms are better exploited than with CBS [10], and thus accuracy from GBS increases compared to those realised in CBS. This is because GBS captures not only the additive genetic relationship between individuals but also the information about linkage disequilibrium between markers and traits [35]. This study suggests GBS be a breeding scheme that results in more rapid genetic progress compared to CBS.

The simulated performance of the chickens selected in the nucleus using CBS was less than the performance of their descendants raised in the smallholder farms (Table 2), confirming $G \times E$ [52, 50]. Since, in practice, environments in which chickens are kept and selection is done, are often different, the breeding goal should, however, reflect the economic and production environment in which the animals are reared [59, 43]. This is done by involving genetic correlations caused by $G \times E$ [74], which is generally lower than unity [17]. A loss in genetic gain should be expected when $G \times E$ is less than 0.8 [52, 21]. This is because, $G \times E$ reduces the accuracy of selection and, hence, effective heritability of EBV for commercial population performance [16]. The $G \times E$ is a cause of genetic variation with regards to the environment [50]

as genes are affected by environmental change [69]. The effect of selection is to change gene abundance [27] and adaptation of animals in a new environment can, therefore, happen through the modification of their chromatin structure, especially change in the gene sequence through recombination, genetic drift and mutation, [69]. Improvement obtained in the nucleus by using *CBS* would not, therefore, be fully realised in the production environment where G x E interaction is significant. These findings are supported by [14, 21, 51] who demonstrated that using *CBS*, the performance of selected animals in the nucleus could be a poor predictor of performance of their offspring under field conditions due to G x E. This study advises that by using *CBS*, G x E should, therefore, be considered to develop superior germplasm among IC that performs optimally under specific management practices.

This study revealed, however, that by using *GBS*, the performance of chickens in the nucleus was not different from that of their descendants in smallholder farms (Table 2). This indicates that *GBS* had better opportunities to exploit G x E than *CBS*. This could be explained by the fact that in *GBS*, there is either less or no emphasis on own performance under ideal nucleus environments and high selection accuracy in a harsh environment for both sexes [50]. The *GBS* possesses the ability to move the emphasis to performance in field conditions [50], confirming the use of *GBS* to select chicken in the nucleus for the improvement of their offspring performance under the field conditions [14, 21]. This shows that *GBS* is much better in increasing resilience and reducing the environmental sensitivity of animals [50]. Being a good predictor of performance of IC in smallholder farms, *GBS* would thereby be a beneficial breeding scheme to adopt in Rwanda. This is because so far there is no information about G X E and the majority of IC farmers are smallholder rearing their chickens under extensive management [44, 41].

The current study revealed that the rate of inbreeding was lower in *GBS* than *CBS* (Table 2). The reason for this lower rate of inbreeding is that, by offering information on Mendelian sampling terms, genomic markers distinguish relatives, comprising full sibs, which decreases the likelihood of co-selection of relatives [12, 15]. Marker information is entirely heritable and has no residual variance since it is supposed that genotypes can be observed without error [64], thus, as heritability increases, accuracy of selection increases thereby rate of inbreeding decreases [15]. This infers that *GBS* should be adopted by breeding programs at the earliest possible time to improve genetic gain over the shortest period and to restrain the inbreeding rate as per the recommendation by [59, 18]. The challenge of implementing *GBS*, however, was the exorbitant cost of genotyping [67]. Fortunately, the cost of genotyping is, however, becoming low [66] and it is therefore supposed that genomic selection would be largely applied in poultry breeding programs even in Rwanda.

Genetic gain realised for individual traits differed between

CBS and *GBS* (Table 3), and also between nucleus and commercial. Genetic gain per generation for BW observed in this study was positive and higher than 69.92g of IC in Tanzania [37], 38.72g of IC from Kenya [59] and 72.00g of Ethiopian chicken [80]. Genetic gain for EN obtained in this study was lower than 1.36 IC eggs from Kenya [59], 2.45 eggs for Tanzanian medium IC [37], 2.6 eggs for the Indian chicken ecotype [74] and 3.10 eggs for chicken in Nigeria [58]. These dissimilarities could be attributed to either population size considered, selection procedure used, or selection intensities employed [70]. This is because the most important factors which affect genetic gain include effective population size, accuracy of selection, and selection intensity [58]. Optimal genetic gain could be realised by maximising these aforementioned factors [9]. Regrettably, with restricted resources, all these factors cannot be maximised concurrently [58]. For instance, increasing the intensity of selection lowers an effective population size and leads to a reduced genetic gain [49]. Correlated genetic gain achieved for EW was lower in the nucleus than in commercial in the two breeding schemes, contrarily to BW and EN. This difference could be caused by the negative phenotypic and genetic correlation between EW and EN [56]. This suggests that selection of IC for EN would compromise egg size. However, eggs from IC can be marketed with their present low weight with no problem [37]. Furthermore, egg consumers are currently not ready to pay much more for bigger eggs [4, 54]. The negative genetic gain for AbR realised in the two breeding schemes was a sign of decreased AbR combating Newcastle disease and thereby low immunity. Observed decline in correlated response for AbR in the two breeding schemes suggests that intense selection for BW and EN would compromise the immune system of fowls. In poultry as in other livestock species, the antagonistic relationship between functional and production traits has been demonstrated [32, 42, 31]. The current study suggests that selecting IC for BW together with EN and selection of IC for EW alongside AbR and crossing them would, therefore, assist in the utilisation of hybrid vigour and complementarities.

4.2. Optimum Nucleus Size

Increase in nucleus size resulted in an upturn in genetic gain and a decrease in the rate of inbreeding in both *CBS* and *GBS* (Figure 2). The cause for this trend was that the increase in nucleus size would increase the number of selected unrelated parents and hence reduce the rate of inbreeding [30]. In *GBS*, by increasing the amount of genomic information and the size of the reference population improves the genetic gains [18]. Rates of inbreeding may be reduced by increasing the flock size and the numbers of sires and dams selected [77]. Increasing flock size, however, could increase the cost of a nucleus flock program [33]. Researches have, therefore, recommended to focus on ways to obtain a maximum genetic response in nucleus herds/flocks of small size and to limit

inbreeding at the same time [7]. Through this study, there was, therefore, a sharp increase of genetic gain up to a nucleus size of 960 and 303 hens with sex ratios of 1:5 and 1:100, respectively and then, a diminishing increase as the nucleus size gets much larger. Since this study also revealed an effect of sex ratio on nucleus size, the optimal nucleus size in Rwanda, therefore, could be considered as one ranging between 303 and 960 hens with sex ratios varying between 1:100 and 1:5, respectively.

In addition, the current study showed that the increase in mating ratio resulted in a great genetic response in both *CBS* and *GBS* (Figure 3). This trend may be because, by increasing the mating ratio, the selection intensity of males increased, leading to the improvement of response to selection due to a positive correlation between selection intensity and genetic response [8]. This result could justify the use of semen from one cock to inseminate one hundred (100) hens using artificial insemination reproductive technology [47]. This later approach allowed the quick dissemination of genetic material from a small number of superior males to a high population of females [47]. Besides, a higher mating ratio yielded a greater rate of inbreeding in *CBS*. This could be because, once the number of parents is small, the rate of inbreeding is expected to be higher [72]. Inbreeding leads to increased homozygosity within the population, resulting in reduced genetic variance [82]. Increase in inbreeding is of great burden in livestock breeding programs because it decreases the long-term response to selection due to reduced genetic variance in a population [14]. Even if inbreeding cannot be avoided [22], the mating ratio would, therefore, depend on an optimal rate of inbreeding not more than 1% per year recommended by FAO [68] to void the loss of merit and genetic variance. This study revealed that an increase in the mating ratio led to a reduction in the rate of inbreeding in *GBS*. This is because using genomic information reduces the probability of co-selection of relatives in the parents [12, 15]. As recommended by [46], the nucleus size and mating ratio that capitalize on genetic gain while limiting the rate of inbreeding in IC would further result in an optimal genetic contribution of the current generation to next generations.

4.3. Practical Implications

In general, the two breeding schemes for IC improvement simulated in this study had a positive response to selection, but with a considerable difference between them. This implies that the adoption of any of them would lead to the genetic improvement of IC. This study, however, proved that *GBS* was highly efficient in terms of rates of genetic gain and inbreeding. High genetic gain and low inbreeding rate both in the nucleus and under smallholder farmers' conditions obtained with *GBS* indicates that within-breed selection of IC would be worthfully considered. In Rwanda, due to the growing demand for chicken products due to the increasing human population, limited land resources, economic growth

and urbanisation [65], there would be a need to adopt *GBS*, a breeding scheme that would lead to faster genetic progress [59]. Implementation of *GBS* in Rwanda, however, may remain a challenge due to inadequate well-established infrastructure and trained personnel [57] for its smooth operation. This implies that Rwanda could at the moment start with *CBS* while developing infrastructure for implementation of *GBS*.

5. Conclusion

This study has established that it is promising to improve IC in Rwanda for dual-purpose for both meat and egg through within-breed selection strategy using either *CBS* or *GBS*. Both *CBS* and *GBS* simulated in this study had a considerable positive response to selection. The *GBS* with the higher selection response and lower inbreeding rate, however, appears to be a favourable breeding program scheme. Besides, the *GBS* being a good predictor of the IC performance under field conditions should, therefore, be adopted to greatly improve IC genetic progress, both in speed and accuracy. Lastly, *CBS* and *GBS* schemes would rely on an optimal nucleus size and appropriate mating ratio for optimising selection response at the same time constraining the rate of inbreeding in IC in Rwanda.

Acknowledgments

This content is derived from activities funded by the United States Agency for International Development (USAID) under the CGIAR Fund, grant number BFS-G-11-00002, as part of the Feed the Future initiative. It also received support from the predecessor fund, the Food Security and Crisis Mitigation II grant, award number EEM-G-00-04-00013.

Conflicts of Interest

The authors declare no conflicts of interest.

References

- [1] Adeleke, M. A., Peters, S. O., Ozoje, M. O., Ikeobi, C. O. N., Bangbose, A. M., Adebambo, O. A., 2011. Growth performance of Nigerian local chickens in crosses involving an exotic broiler breeder. *Trop. Anim. Health Prod.* 43, 643–650. <https://doi.org/10.1007/s11250-010-9747-3>
- [2] Assan, N., 2015. Prospects for indigenous chickens genetic improvement and conservation in Zimbabwe. *Agric. Adv.* 4, 49–56. <https://doi.org/10.14196/aa.v4i5.1876>
- [3] Besbes, B., Gibson, J. P., 1999. Genetic variation of egg production traits in purebred and crossbred laying hens. *Anim. Sci.* 68, 433–439. <https://doi.org/10.1017/S135772980005044X>
- [4] Bett, H. K., Peters, K. J., Bokelmann, W., 2011. Hedonic price analysis to guide in breeding and production of indigenous chicken in Kenya. *Livest. Res. Rural Dev.* 23, 142.

- [5] Bijma, P., 2000. Long-term Genetic Contributions - Prediction of Rates of Inbreeding and Genetic Gain in Selected Populations, Animal Breeding and Genetic Group, Department of Animal Sciences.
- [6] Bytyqi, H., Fuerst-Waltl, B., Mehmeti, H., Baumung, R., 2015. Economic values for production traits for different sheep breeds in Kosovo. *Ital. J. Anim. Sci.* 14, 603–609. <https://doi.org/10.4081/ijas.2015.3808>
- [7] Cervantes, I., Gutiérrez, J. P., Meuwissen, T. H. E., 2016. Response to selection while maximizing genetic variance in small populations. *Genet. Sel. Evol.* 48, 69. <https://doi.org/10.1186/s12711-016-0248-3>
- [8] Chen, J., Wang, Y. chun, Zhang, Yi, Sun, D. xiao, Zhang, S. li, Zhang, Yuan, 2011. Evaluation of breeding programs combining genomic information in chinese holstein. *Agric. Sci. China* 10, 1949–1957. [https://doi.org/10.1016/S1671-2927\(11\)60196-X](https://doi.org/10.1016/S1671-2927(11)60196-X)
- [9] Christensen, O. F., Legarra, A., Lund, M. S., Su, G., 2015. Genetic evaluation for three-way crossbreeding. *Genet. Sel. Evol.* 47, 1–13. <https://doi.org/10.1186/s12711-015-0177-6>
- [10] Chu, T. T., Bastiaansen, J. W. M., Berg, P., Romé H., Marois, D., Henshall, J., 2019. Use of genomic information to exploit genotype - by - environment interactions for body weight of broiler chicken in bio - secure and production environments. *Genet. Sel. Evol.* 1–13. <https://doi.org/10.1186/s12711-019-0493-3>
- [11] Daetwyler, H. D., Calus, M. P. L., Pong-Wong, R., de los Campos, G., Hickey, J. M., 2013. Genomic prediction in animals and plants: Simulation of data, validation, reporting, and benchmarking. *Genetics* 193, 347–365. <https://doi.org/10.1534/genetics.112.147983>
- [12] Daetwyler, H. D., Villanueva, B., Bijma, P., Woolliams, J. A., 2007. Inbreeding in genome-wide selection. *J. Anim. Breed. Genet* 124, 369–376.
- [13] Daetwyler, H. D., Villanueva, B., Woolliams, J. A., 2008. Accuracy of predicting the genetic risk of disease using a genome-wide approach. *PLoS One* 3. <https://doi.org/10.1371/journal.pone.0003395>
- [14] Dekkers, J. C. M., 2007a. Prediction of response to marker-assisted and genomic selection using selection index theory. *J. Anim. Breed. Genet.* 124, 331–341. <https://doi.org/10.1111/j.1439-0388.2007.00701.x>
- [15] Dekkers, J. C. M., 2007b. Marker-assisted selection for commercial crossbred performance. *J. Anim. Sci.* 85, 2104–2114. <https://doi.org/10.2527/jas.2006-683>
- [16] Dekkers, J. C. M., Chakraborty, R., 2004. Optimizing purebred selection for crossbred performance using QTL with different degrees of dominance. *Genet. Sel. Evol.* 36, 297–324. <https://doi.org/10.1051/gse:2004003>
- [17] Duenk, P., Calus, M. P. L., Wientjes, Y. C. J., Breen, V. P., Henshall, J. M., Hawken, R., Bijma, P., 2019. Estimating the purebred-crossbred genetic correlation of body weight in broiler chickens with pedigree or genomic relationships. *Genet. Sel. Evol.* 51, 1–11. <https://doi.org/10.1186/s12711-019-0447-9>
- [18] Ebrahimpourtaher, S., Alijani, S., Rafat, S. A., Sharifi, A. R., 2018. Potential of Genomic Breeding Program in Iranian Native Chickens. *Iran. J. Appl. Anim. Sci.* 8, 305–315.
- [19] Eggen, A., 2012. The development and application of genomic selection as a new breeding paradigm. *Anim. Front.* 2, 10–15. <https://doi.org/10.2527/af.2011-0027>
- [20] Esfandyari, H., Berg, P., Sørensen, A. C., 2018. Balanced selection on purebred and crossbred performance increases gain in crossbreds. *Genet. Sel. Evol.* 50, 1–14. <https://doi.org/10.1186/s12711-018-0379-9>
- [21] Esfandyari, H., Sørensen, A. C., Bijma, P., 2015. Maximizing crossbred performance through purebred genomic selection. *Genet. Sel. Evol.* 47, 1–16. <https://doi.org/10.1186/s12711-015-0099-3>
- [22] Falconer, D. S. (Douglas S., Mackay, T. F. C., 1996. Introduction to quantitative genetics. Longman.
- [23] Groenen, M. A. M., Wahlberg, P., Foglio, M., Cheng, H. H., Megens, H. J., Crooijmans, R. P. M. A., Besnier, F., Lathrop, M., Muir, W. M., Wong, G. K. S., Gut, I., Andersson, L., 2009. A high-density SNP-based linkage map of the chicken genome reveals sequence features correlated with recombination rate. *Genome Res.* 19, 510–519. <https://doi.org/10.1101/gr.086538.108>
- [24] Gwaza, D. S., Dim, N. I., Momoh, O. M., 2016. Genetic improvement of egg production traits by direct and indirect selection of egg traits in Nigerian local chickens. *Adv. Genet. Eng.* 05. <https://doi.org/10.4172/2169-0111.1000148>
- [25] Habimana, R., Okeno, T. O., Ngeno, K., Mboumba, S., Assami, P., Keambou, C. T., Breeding, A., Group, G., Eastern, B., 2018. Four gene pools of Rwandese indigenous chicken based on microsatellite markers, in: Proceedings of the World Congress on Genetics Applied to Livestock Production, 11.874. pp. 1–4.
- [26] Hazel, L. N., 1943. The genetic basis for constructing selection indexes. *Genetics* 28, 476–90.
- [27] Hennnatabadi, R. N., Seidavi, A., Gharahveysi, S., 2011. Estimation response to selection in three commercial lines of silkworm (*Bombyx mori* L.) having peanut cocoon. *J. Anim. Vet. Adv.* 10, 2208–2214. <https://doi.org/10.3923/javaa.2011.2208.2214>
- [28] Henryon, M., Berg, P., Sørensen, A. C., 2014. Invited review: Animal-breeding schemes using genomic information need breeding plans designed to maximise long-term genetic gains. *Livest. Sci.* 166, 38–47. <https://doi.org/10.1016/j.livsci.2014.06.016>
- [29] Janssen, K., Saatkamp, H. W., Calus, M. P. L., Komen, H., 2019. Economic optimization of full-sib test group size and genotyping effort in a breeding program for Atlantic salmon. *Genet. Sel. Evol.* 51, 1–14. <https://doi.org/10.1186/s12711-019-0491-5>
- [30] Kariuki, C. M., Komen, H., Kahi, A. K., van Arendonk, J. A. M., 2014. Optimizing the design of small-sized nucleus breeding programs for dairy cattle with minimal performance recording. *J. Dairy Sci.* 97, 7963–7974. <https://doi.org/10.3168/jds.2014-8545>

- [31] Kaufmann, F., Das, G., Preisinger, R., Schmutz, M., König, S., Gauly, M., 2011. Veterinary Parasitology Genetic resistance to natural helminth infections in two chicken layer lines 176, 250–257. <https://doi.org/10.1016/j.vetpar.2010.11.007>
- [32] Lamont, S. J., Pinard-van der Laan, M. H., Cahaner, A., Poel, J. J. van der, Parmentier, H. K., 2009. Selection for disease resistance: direct selection on the immune response., in: Poultry Genetics, Breeding and Biotechnology. pp. 399–418. <https://doi.org/10.1079/9780851996608.0399>
- [33] Leitch, H. W., Smith, C., Burnside, E. B., Quinton, M., 1994. Genetic Response and Inbreeding with Different Selection Methods and Mating Designs for Nucleus Breeding Programs of Dairy Cattle. *J. Dairy Sci.* 77, 1702–1718. [https://doi.org/10.3168/jds.S0022-0302\(94\)77112-5](https://doi.org/10.3168/jds.S0022-0302(94)77112-5)
- [34] Liu, H., Henryon, M., Sørensen, A. C., 2017. Mating strategies with genomic information reduce rates of inbreeding in animal breeding schemes without compromising genetic gain. *Animal* 11, 547–555. <https://doi.org/10.1017/S1751731116001786>
- [35] Liu, T., Qu, H., Luo, C., Li, X., Shu, D., Lund, M. S., Su, G., 2014. Genomic selection for the improvement of antibody response to newcastle disease and avian influenza virus in chickens. *PLoS One* 9, 1–6. <https://doi.org/10.1371/journal.pone.0112685>
- [36] Lwelamira, J., 2012. Genotype-environmental (GxE) interaction for body weight for kuchi chicken ecotype of tanzania reared on-station and on-farm. *Int. J. Poult. Sci.* 11, 96–102.
- [37] Lwelamira, J., Kifaro, G. C., 2010. Desired-gain selection indices for improving performance of two Tanzania local chicken ecotypes under intensive management. *African J. Agric. Res.* <https://doi.org/10.5897/AJAR09.103>
- [38] Magothe, T. M., Okeno, T. O., Muhuyi, W. B., Kahi, A. K., 2012. Indigenous chicken production in Kenya: I. Current status. *Worlds. Poult. Sci. J.* 68, 119–132. <https://doi.org/10.1017/S0043933912000128>
- [39] Mahoro, J., 2017. Characterisation of production systems and development of breeding objectives for indigenous chicken in Rwanda. MSc. Thesis, Egerton University.
- [40] Mahoro, J., Muasya, T. K., Mbuza, F., Habimana, R., Kahi, A. K., 2017. Characterization of indigenous chicken production systems in Rwanda. *Poult. Sci.* 96, 4245–4252. <https://doi.org/10.3382/ps/pez240>
- [41] Mahoro, J., Muasya, T. K., Mbuza, F., Mbutia, J., Kahi, A. K., 2017b. Farmers' breeding practices and traits of economic importance for indigenous chicken in RWANDA. *Trop. Anim. Health Prod.* 50, 121–128. <https://doi.org/10.1007/s11250-017-1411-8>
- [42] Marcos-atxutegi, C., Gandolfi, B., Arangu, T., 2009. Veterinary Parasitology Antibody and inflammatory responses in laying hens with experimental primary infections of *Ascaridia galli* 161, 69–75. <https://doi.org/10.1016/j.vetpar.2008.12.011>
- [43] Mbutia, J. M., Rewe, T. O., Kahi, A. K., 2015. Analysis of pig breeding management and trait preferences in smallholder production systems in Kenya. *Anim. Genet. Resour. génétiques Anim. généticos Anim.* 56, 111–117. <https://doi.org/10.1017/s207863361400054x>
- [44] Mbuza, F., Denis, M., Janvier, M., Xavier, R., 2016. Characterization of low cost village Poultry production in Rwanda. *Int. J. Livest. Prod.* 7, 76–82. <https://doi.org/10.5897/IJLP2016.0300>
- [45] Meuwissen, T., Hayes, B., Goddard, M., 2016. Genomic selection: A paradigm shift in animal breeding. *Anim. Front.* 6, 6–14. <https://doi.org/10.2527/af.2016-0002>
- [46] Meuwissen, T. H. E., 1997. Managing inbreeding in selection and genetic conservation schemes of livestock.
- [47] Mohan, J., Sharma, S. K., Kolluri, G., Dhama, K., 2018. History of artificial insemination in poultry, its components and significance. *Worlds. Poult. Sci. J.* 74, 475–488. <https://doi.org/10.1017/S0043933918000430>
- [48] Mtileni, B. J., Muchadeyi, F. C., Maiwashe, A., Chimonyo, M., Dzama, K., 2012. Conservation and utilisation of indigenous chicken genetic resources in Southern Africa. *Worlds. Poult. Sci. J.* 68, 727–748. <https://doi.org/10.1017/S0043933912000852>
- [49] Muir, W. M., Cheng, H., Croney, C., 2014. Methods to address poultry robustness and welfare issues through breeding and associated ethical considerations 5, 1–11. <https://doi.org/10.3389/fgene.2014.00407>
- [50] Mulder, H. A., 2016. Genomic selection improves response to selection in resilience by exploiting genotype by environment interactions. *Front. Genet.* 7, 1–11. <https://doi.org/10.3389/fgene.2016.00178>
- [51] Mulder, H. A., Bijma, P., 2006. Benefits of cooperation between breeding programs in the presence of genotype by environment interaction. *J. Dairy Sci.* 89, 1727–1739. [https://doi.org/10.3168/jds.S0022-0302\(06\)72241-X](https://doi.org/10.3168/jds.S0022-0302(06)72241-X)
- [52] Mulder, H. A., Bijma, P., 2005. Effects of genotype x environment interaction on genetic gain in breeding programs. *J. Anim. Sci.* 83, 49–61. <https://doi.org/10.2527/2005.83149x>
- [53] Mwambene, P. L., Kyallo, M., Machuka, E., Githae, D., Pelle, R., 2019. Genetic diversity of 10 indigenous chicken ecotypes from Southern Highlands of Tanzania based on Major Histocompatibility Complex-linked microsatellite LEI0258 marker typing. *Poult. Sci.* 98, 2734–2746. <https://doi.org/10.3382/ps/pez076>
- [54] Natukunda, K., Kugonza, D. R., Kyarisiima, C. C., 2011. Indigenous chickens of the Kamuli plains in Uganda: II. Factors affecting their marketing and profitability. *Livest. Res. Rural Dev.* 23.
- [55] Ndegwa, J. M., R. Mead, R., Norrish, P., Shephered, D. D., Kimani, C. W., Wachira, A. M., 2012. Growth Characteristics of Six Reciprocal Crosses of Kenyan Indigenous Chicken. *J. Agric. Sci.* 4. <https://doi.org/10.5539/jas.v4n6p160>
- [56] Ndung'u, C. W., Okeno, T. O., Muasya, T. K., 2020. Pooled parameter estimates for traits of economic importance in indigenous chicken in the tropics. *Livest. Sci.* 1–34.

- [57] NISR, 2019. Rwanda Statistical YearBook.
- [58] Nwagu, B. I., Olorunju, S. A. S., Oni, O. O., Eduvie, L. O., Adeyinka, I. A., Sekoni, A. A., Abeke, F. O., 2007. Response of Egg Number to Selection in Rhode Island Chickens Selected for Part Period Egg Production. *Int. J. Poult. Sci.* 6, 18–22.
- [59] Okeno, T. O., Kahi, A. K., Peters, K. J., 2013. Evaluation of breeding objectives for purebred and crossbred selection schemes for adoption in indigenous chicken breeding programmes. *Br. Poult. Sci.* 54, 62–75.
<https://doi.org/10.1080/00071668.2013.764492>
- [60] Okumu, O. N., Ngeranwa, J. J. N., Binopal, Y. S., Kahi, A. K., Bramwel, W. W., Ateya, L. O., Wekesa, F. C., 2016. Genetic diversity of indigenous chickens from selected areas in Kenya using microsatellite markers. *J. Genet. Eng. Biotechnol.*
<https://doi.org/10.1016/j.jgeb.2017.04.007>
- [61] Padhi, M. K., 2016. Importance of Indigenous Breeds of Chicken for Rural Economy and Their Improvements for Higher Production Performance. *Scientifica (Cairo)*.
<https://doi.org/10.1155/2016/2604685>
- [62] Rutten, M. J. M., Bijma, P., Woolliams, J. A., Van Arendonk, J. A. M., 2002. SelAction: Software to predict selection response and rate of inbreeding in livestock breeding programs. *J. Hered.* 93, 456–458. <https://doi.org/10.1093/jhered/93.6.456>
- [63] Saxena, V. K., Kolluri, G., 2018. Selection Methods in Poultry Breeding: From Genetics to Genomics, in: *Application of Genetics and Genomics in Poultry Science*. InTech.
<https://doi.org/10.5772/intechopen.77966>
- [64] Schrooten, C., Bovenhuis, H., Van Arendonk, J. A. M., Bijma, P., 2005. Genetic progress in multistage dairy cattle breeding schemes using genetic markers. *J. Dairy Sci.* 88, 1569–1581.
[https://doi.org/10.3168/jds.S0022-0302\(05\)72826-5](https://doi.org/10.3168/jds.S0022-0302(05)72826-5)
- [65] Shapiro, B. I., Gebru, G., Desta, S., Nigussie, K., 2017. Rwanda Livestock Master Plan Developed by the International Livestock Research Institute (ILRI) Livestock Master Plan (LMP) team. Kigali_Rwanda.
- [66] Sharma, A., Lee, J. S., Dang, C. G., Sudrajad, P., Kim, H. C., Yeon, S. H., Kang, H. S., Lee, S. H., 2015. Stories and challenges of genome wide association studies in livestock - a review. *Asian-Australasian J. Anim. Sci.*
<https://doi.org/10.5713/ajas.14.0715>
- [67] Sitzenstock, F., Ytournal, F., Sharifi, A. R., Caverio, D., Täubert, H., Preisinger, R., Simianer, H., 2013. Efficiency of genomic selection in an established commercial layer breeding program. *Genet. Sel. Evol.* 45. <https://doi.org/10.1186/1297-9686-45-29>
- [68] Smith, C., 1983. Estimated costs of genetic conservation in farm animals, in: *Animal Genetic Resources Conservation by Management, Data Banks and Training*. Proceedings of the Joint FAO-UNEP Expert Panel Meeting, pp. 21–30.
- [69] Soller, M., Weigend, S., Romanov, M. N., Dekkers, J. C. M., Lamont, S. J., 2006. Strategies to assess structural variation in the chicken genome and its associations with biodiversity and biological performance. *Poult. Sci.* 85, 2061–2078.
<https://doi.org/10.1093/ps/85.12.2061>
- [70] Takele taye Desta, Dana, N., Ayalew, W., Hanotte, O., 2011. Current state of knowledge on phenotypic characteristics of indigenous chickens in the tropics. *Worlds. Poult. Sci. J.* 67, 507–516. <https://doi.org/10.1017/S0043933911000559>
- [71] Täubert, H., Rensing, S., Reinhardt, F., 2011. Comparing conventional and genomic breeding programs with ZPLAN+. *Interbull Bull.* 0.
- [72] Thomasen, J. R., Liu, H., Sørensen, A. C., 2020. Genotyping more cows increases genetic gain and reduces rate of true inbreeding in a dairy cattle breeding scheme using female reproductive technologies. *J. Dairy Sci.* 103, 597–606.
<https://doi.org/10.3168/jds.2019-16974>
- [73] Venkatas, J., Adeleke, M. A., Peters, S. O., Adebambo, O. A., 2019. Phenotypic Differentiation of Purebred and Crossbred Indigenous Chicken Genotypes Using Multivariate Analysis. *Int. J. Poult. Sci.* 18, 301–308.
<https://doi.org/10.3923/ijps.2019.301.308>
- [74] Venkatramaiah, A., Mohapatra, S. C., Sinha, R., Ayyagari, V., Choudhuri, D., 1986. Selection response for part period egg number and egg mass in chickens - a comparison. *Theor. Appl. Genet.* 72, 129–134. <https://doi.org/10.1007/BF00261468>
- [75] Villanueva B., Wrayh N.R., Thompson R. Prediction of asymptotic rates of response from selection on multiple traits using univariate and multivariate best linear unbiased predictors. *Anim. Prod.* 1993; 57: 1–13.
- [76] Wang, M. S., Zhang, R. W., Su, L. Y., Li, Y., Peng, M. S., Liu, H. Q., Zeng, L., Irwin, D. M., Du, J. L., Yao, Y. G., Wu, D. D., Zhang, Y. P., 2016. Positive selection rather than relaxation of functional constraint drives the evolution of vision during chicken domestication. *Cell Res.* 26, 556–573.
<https://doi.org/10.1038/cr.2016.44>
- [77] Weigel, K. A., 2001. Controlling Inbreeding in Modern Breeding Programs. *J. Dairy Sci.* 84, E177–E184.
[https://doi.org/10.3168/jds.s0022-0302\(01\)70213-5](https://doi.org/10.3168/jds.s0022-0302(01)70213-5)
- [78] Wellmann, R., Bennewitz, J., 2019. Key genetic parameters for population management. *Front. Genet.* 10, 1–20.
<https://doi.org/10.3389/fgene.2019.00667>
- [79] Wolc, A., Kranis, A., Arango, J., Settar, P., Fulton, J. E., O’Sullivan, N. P., Avendano, A., Watson, K. A., Hickey, J. M., de los Campos, G., Fernando, R. L., Garrick, D. J., Dekkers, J. C. M., 2016. Implementation of genomic selection in the poultry industry. *Anim. Front.* 6, 23–31.
<https://doi.org/10.2527/af.2016-0004>
- [80] Wondmeneh, E. H., Van der Waaij, D. T., Okeyo, M., van Arendonk, J. A. M., 2014. A running breeding program for indigenous chickens in Ethiopia: evaluation of success, in: *Proceedings, 10th World Congress of Genetics Applied to Livestock Production*. pp. 10–12.
- [81] Woolliams, J. A., Bijma, P., 2000. Predicting rates of inbreeding in populations undergoing selection. *Genetics* 154, 1851–64.
- [82] Woolliams, J. A., Bijma, P., Villanueva, B., 1999. Expected genetic contributions and their impact on gene flow and genetic gain. *Genetics* 153, 1009–1020.