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Genetic response to short-term index selection in females and mass selection in males of the Nigerian heavy local chicken ecotype

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Abstract

The study aimed to determine genetic gain in growth and egg production in the Nigerian indigenous chicken (NIC) subjected to multiple trait index selection for females and mass selection for males. The experimental birds (G_0 generation) were generated from a reference population of NIC and reared according to sire families from hatch. At point of lay, females were housed individually in laying cages for egg production. Hens were selected based on index scores calculated using an index of weighted breeding values constructed from own performance in body weight at first egg (BWFE), egg weight (EW) and egg production (EN), trait heritabilities and relative economic weights while cocks were selected based on own performance in body weight at 39 weeks of age (BW_{39}). Selected parents were mated to generate the G_1 generation which in turn yielded the parents of the G_2 generation. A control population was used to measure environmental effects. Data were analyzed using the Restricted Maximum Likelihood (REML) computer programme. For hens, expected average direct genetic gain per generation was 12.58, 2.98g and 25.04g for EN, EW and BWFE, respectively while realized genetic gain was 2.19 and 1.59 for EN, 1.65 and 0.26g for EW, and -25.60 and 123.64g for BWFE for G_0 and G_1 generations, respectively. The corresponding values for ratio of realized to expected genetic gains were 2.27 and 1.22, 3.15 and 0.24, and 0.95 and 2.21, respectively. Heritability (h^2) ranged from 0.12 to 0.24 for EN, 0.34 to 0.43 for EW and 0.57 to 0.69 for BWFE, across the three generations. Similar improvements in BW_{39} were observed in males with an average expected gain of 508.50g per generation. In conclusion, growth and egg production in the NIC can be improved using mass selection for cocks and index of weighted breeding values for hens.

Keywords: Genetic gain, mass selection, selection index, body weight, egg production, indigenous chicken.

Introduction:

Selection within the local stock has been advocated as one of the ways to improve the performance of indigenous chickens (Kperegbeyi *et al.,* 2009; Pym, 2010). However, this scheme has not received the much needed attention over the years in Nigeria due to a number of factors which include high cost in finance, time and expertise. Studies on the genetic improvement of the Nigerian indigenous chicken (NIC) have been very few and far in-between (Oluyemi, 1979; Nwosu and Omeje, 1985; Udeh and Omeje, 2001; Oleforuh-Okoleh, 2011). Most of the studies have also concentrated on improvement of performance through modification in nutrition, husbandry practices and in crossing the local chicken with some exotic strains (Nwosu and Omeje, 1985; Udeh and Omeje, 2001; Ogbu *et al.,* 2015a; 2015b). A number of studies have demonstrated the existence of high within strain genetic variability in performance traits of the NIC that could be exploited for genetic improvement in these traits through selection and selective breeding (Ogbu and Omeje, 2011; Ogbu, 2012a).

When selection is directed at a single trait, performance in unselected but economically important traits could be lost reducing the overall economic merit of the selected population (Nath *et al.,* 2011). Improvement of the economic worth of the NIC by simultaneously improving the traits that contribute to net economic merit is therefore very crucial. The genetic gain attainable in a population by selection for several traits simultaneously is the product of the selection differential (determined by the selection intensity), the correlation between the index and true aggregate breeding value or aggregate genotype (a measure of accuracy of selection) and the genetic variability in the population for the traits to be improved (Kluyts *et al.,* 2007; Bahmanimehr, 2012). Progress is enhanced when the correlation between the aggregate genotype and the selection index is maximized. Schemes to achieve this were proposed by Smith (1936) and Hazel (1943) with modifications by other workers in response to a variety of challenges (Kluyts *et al.,* 2007). Multiple trait selection in the NIC is virtually non-existent with only one cited case of index selection in the light ecotype (Oleforuh-Okoleh, 2011). Wide spread application of multiple trait index selection in rural poultry and livestock development in Nigeria is hampered by (1) absence of large volume of performance data and pedigree information needed for reliable estimate of parameters for the construction of selection indexes, (2) the predominant small holder husbandry system, (3) the lack of standardized production and marketing systems which hamper reliable estimation of relative economic weights of traits included in the definition of breeding objectives, (4) the complexities associated with the construction of highly efficient selection indexes such as the Smith-Hazel index, and (5) the need of high technical knowhow and computational power. Cotterill (1985) had observed that the lack of reliable estimates (or indeed no estimates) of heritability and genetic correlations, together with lack of expertise and computing programmes required to construct Smith-Hazel indices are two major problems restricting widespread application of index selection in tree breeding. Kluyts *et al.* (2007) also observed that even though the theory of selection indices has been introduced into animal breeding more than 60 years and is highly developed in various forms, its application in practical breeding may not be very extensive due partly to difficulties in the derivation of relative economic values as well as the paucity of information on relationships among traits. A number of alternative selection indices have been constructed in a bid to circumvent the difficulties associated with the construction of the Smith-Hazel index. These include the base index (Williams 1962a, b), the weight-free index (Elston, 1963), and the heritability index (Heidhues and Henderson, 1962). Interest in the application of multiple trait index selection for rural poultry improvement in Nigeria can be enhanced by adopting the simplified selection indices. Such indices though less efficient under some circumstances, benefits from considerable simplicity (Cotterill, 1985) enabling easy understanding and application by rural farmers who control the production of indigenous chickens in Nigeria. The present study was therefore conceived to evaluate the performance, and the genetic response in egg production (egg number and egg weight) and body weight at first egg in indigenous chickens subjected to multiple trait selection using an index of weighted breeding values constructed from trait performance values, relative economic weights and heritabilities.

Materials and methods

The Study Site

This research was carried out at the local chicken research unit of the poultry farm of the Department of Animal Science, University of Nigeria, Nsukka, latitude 05^0 22^1 North and longitude $07^0 24^1$ East. Nsukka belongs to the humid rainforest zone of South – eastern Nigeria with annual rainfall range of 986 to 2098mm, natural day length of 12 – 13 hours, average minimum and maximum temperature of 21^0C and 29.7^0C, respectively and Relative humidity range of 34% to 78% (meteorological station, Department of Crop Science, University of Nigeria, Nsukka, 2016, unpublished).

Reference and base populations

The reference population is the population of heavy ecotype local chickens randomly assembled from rural areas in Obudu, Cross River State, a montane region of South – eastern Nigeria and its adjourning towns of Vandeikiya, Katsina – Ala and Wannune in Benue State and maintained in the Department of Animal Science Farm, University of Nigeria, Nsukka for Teaching and Research. The base population (G_0 generation) subjected to selection consisted of chicks generated from five sire families (1 cock: 10 hens) established from the reference population.

Management of the experimental birds

Chicks were identified and grouped according to sire (genetic) family and reared as such from hatch to 20 weeks of age (woa) on deep litter. The chicks were fed chicks starter (18% CP and 2800 Kcal ME/kg) from hatch to 8 woa and growers mash (15% Cp and 2670Kcal ME/kg) from 8 to 20 woa. Males and females were reared separately from 12 woa. Feed and water were provided *ad libitum* during the brooding and grower phases. At 20 woa, pullets were moved into individual laying cages for egg production and were fed layers mash (16.5% CP and 2,600Kcal ME/kg) at 100g/bird/day for G_0, and G_1 generations and 120g/bird/day for G_2 generation. Water was provided *ad libitum*. Table 1 (a, b, and c) contains the percentage composition of the experimental rations. As much as was possible, birds belonging to the G_0, G_1 and G_2 generations were subjected to similar management practices. Throughout the study routine vaccination and prophylactic medication against endemic diseases and parasites was dutifully carried out to ensure optimal health and performance by the birds.

Selection in the G_0 and subsequent generations

Selection of sires

Sires were selected using mass selection based on individual (own) body weight performance at 39 woa when dams were selected. The Selected sires were used in breeding to generate the subsequent generation.

Selection of dams

At the end of 16 weeks egg production, hens belonging to each generation were subjected to selection using a selection index constructed using individual performances in egg production (egg number, EN), egg weight (EW) and body weight at first egg (BWFE) in addition to the relative economic weights and heritabilities of the traits. Females were on the average 39 weeks old when they were subjected to selection and birds were ranked for selection based on their index score (I).

Effective population size (N_e) and inbreeding coefficient (ΔF)

For the purpose of the current study, the effective population size (N_e) is the size of an idealized population which would give rise to the rate of inbreeding observed in the populations for each generation. The effective population size was calculated for the case of unequal breeding sex ratio using the expression by Kliman *et al.* (2008).

$$N_e = \frac{4N_m N_f}{N_m + N_f}$$

Where, N_m and N_f are numbers of breeding males and females, respectively. The inbreeding coefficient (F) was then obtained using the expression:

$$Ft = \left(\frac{1}{2Ne}\right) + \left[1 - \left(\frac{1}{2Ne}\right)\right]F_{t-1} \text{ (Souza Jr. et al., 2000).}$$

Where, F_t is inbreeding coefficient in the t^th^ generation and F_{t-1} is the inbreeding coefficient in the (t-1)th generation.

Determination of the relative economic weights of index traits

Relative economic weight (REW) of a trait is the additional gain or loss (in monetary terms) derived from a unit change in the trait value irrespective of changes in other traits (Nordskog, 1981). The relative economic weights (REW) of the index traits (Table 2) had been determined previously (Ogbu *et al.,* 2014) for the population under study based on the bio-economic variables generated from the birds in each generation.

Construction of selection indices

In each generation a selection index was constructed using performance values in each trait, trait relative economic weight and heritability. This is the index of weighted breeding values - an extension of the heritability index by Heidhues and Henderson (1962). The relative economic weights and the heritabilities of the traits were therefore used as weighting factors for own performances in the traits. The index has the general form:

$$I = \Sigma a_i h_i^2 \chi_i$$

Where, I is index score, a_i is relative economic weight, h_i^2 is heritability, and χ_i is the standardized phenotypic value of the i^th^ trait. The standardized phenotypic value of a trait was obtained using the expression:

$$\chi_i = \frac{X_i - \mu_i}{\sigma_i} \text{ (Stanfield, 1969)}$$

where, X_i is phenotypic value for i^th^ trait for an individual, μ_i is population mean and σ_i is population phenotypic standard deviation. A constant, K was added to each calculated index score so that the value of index scores (I) was always positive.

Data collection and analysis

Performance traits

Data collected included egg production (total egg number, EN) from point of lay to 16 weeks of lay, average egg weight (EW), and body weight from hatch to 20 woa and at first egg (BWFE) for hens and body weight at 39 woa for cocks. Data collected were subjected to analysis of variance to test for effect of generation. An index score was calculated for each selection candidate and used to rank individuals for purposes of selection. The index scores in each generation were subjected to analysis of variance to determine variance components. Only individuals with complete data were included in each analysis.

Estimation of heritability

A sire model (half-sib analysis) was used to estimate heritability (Souz Jr. *et al.,* 2000). The model is:

$$\gamma_{ij} = \mu + s_i + \ell_{ij}$$

Where, γ_{ij} = performance in index trait or index score of the j^{th} progeny of the i^{th} sire, = population mean for index trait or index score, S_i = the random effect of sire, 1_{ij} = residual. All effects were assumed to be random, normally and independently distributed with expectation zero and common variance. From sire component of variance, additive genetic heritability for index traits and index score for each generation were calculated using the expression:

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_w^2} \quad \text{(Souz Jr. } et\ al., \text{ 2000)}$$

Where, σ_s^2 is sire variance, and σ_w^2 is residual variance. The denominator represents total (phenotypic) variance.

Determination of selection parameters

Selection intensity (i)

The selection intensity (i) or standardized selection differential was calculated using the following expression.

$$i = \frac{\Delta S}{\sigma_P} \quad \text{(Becker, 1992).}$$

Where, ΔS is selection differential (difference between means of selected population and population before selection) and σ_P is phenotypic standard deviation.

Cumulative selection differential

This is the sum of the expected selection differential in the current generation and the expected selection differential in the previous generation(s).

$$\text{Cum}\Delta s_i = \sum_{i=1}^{n} \Delta s_i \quad \text{(Ibe, 1998).}$$

Where, $\text{Cum}\Delta s_i$ is cumulative selection differential up to (and including) the i^{th} generation (i = 0, ---, n) and Δs_i is expected selection differential in the i^{th} generation

Expected direct genetic response (R) to selection

The expected direct response to selection (R) was calculated as the difference between the means of selected and control populations in the trait concerned. That is,

$$R_i = \overline{X}_{iS} - \overline{X}_{iC} \quad \text{(Cheng } et\ al., \text{ 1996)}$$

Where, R_i is expected direct genetic response in the i^{th} trait, $\overline{X}_{iS}$ is mean of the selected population in the i^{th} trait and $\overline{X}_{iC}$ is mean of control population in the i^{th} trait.

Cumulative direct genetic response (CumR)

This was calculated as the sum of the expected direct genetic response in the current generation and the cumulated response in the previous generation(s) thus,

$$\text{CumR}_i = R_i + \text{CumR}_i - 1$$

(Oluyemi, 1979b; Marks, 1983)

Where, CumR_i is cumulative direct genetic response up to the i^{th} (current) generation, R_i is expected direct genetic response in the i^{th} generation, and $\text{CumR}_i - 1$ is cumulative direct genetic response in the $(i -1)^{th}$ generation.

Expected average direct genetic response per generation

The expected average direct response per generation for each trait

$$\overline{R}_i = b_{\mathbf{cumR,N}}$$

Where, $\overline{R}_i$ is average direct genetic response per generation for i^{th} trait and $b_{cumR,N}$ is regression of cumulative responses (cumR) on generation number (N).

Expected direct genetic gain per year

The expected annual direct genetic gain (R/yr) was calculated using the following expression

$$\text{R/yr} = \frac{R_i}{t.} \quad \text{(Ibe, 1998)}$$

Where, R_i is expected direct genetic gain for the i^{th} generation, and t is generation interval. Thus for a generation interval of one (1) year and no overlap of generations, the annual genetic gain becomes:

$$\text{R/yr} = \frac{R_i}{1} = R_i$$

Realized (observed) genetic response (ΔG_R)

The observed (realized) genetic response (ΔG_R) which is the response realized in the progeny as a result of selection in the parental generation was calculated as the difference between the mean of the progeny of the selected parents and the mean of the parental population before selection. That is,

$$\Delta G_R = \overline{Xip} - \overline{Xiw}$$

Where $\overline{Xip}$ is mean of i^{th} trait for progeny population, and $\overline{Xiw}$ is mean of i^{th} trait for parental population before selection.

Expected genetic gain (response) in index score (aggregate economic breeding value)

This was calculated using the expression:

$$\Delta G_I = i_I . \sigma_{GI} . h_I . \sqrt{K} \quad \text{(Pirchner, 1983)}$$

Where, ΔG_I is expected genetic gain in index score (aggregate economic breeding value), i_I is selection intensity factor for index score, σ_{GI} is additive genetic standard deviation of index score, $h_I = \sqrt{h_I^2}$ is square root of heritability of index score, and K = number of traits included in the index.

Expected genetic gain in the component traits of the index due to selection on the index score (I)

This was calculated using the expression,

$$\Delta gi = \frac{\Delta S_I}{\sigma_I^2} \sigma_{G(xi,I)} \quad \text{(Yamada, 1977)}$$

Where, Δg_i is expected genetic gain, ΔS_I is selection differential for index σ_I^2 is variance of index, $\sigma_{Gxi,I}$ = $\text{Cov}_{G(xi,I)}$ is covariance between genotypic value of i^{th} trait and index score.

Effectiveness of Selection

The effectiveness of selection was tested by the ratio of observed (realized) to expected genetic response for each trait. That is,

Effectiveness of selection =

$$\frac{\text{Realise genetic gain}}{\text{Expected genetic gain}} = \frac{\Delta G_R}{\Delta gi} \text{ or } \frac{\Delta G_R}{R} \quad \text{(Fairfull and Gowe, 1990).}$$

Results and Discussion

The percentage and proximate composition of the diets fed to the experimental birds over the generations of selection are presented in Table 1 while Table 2 contains the population size at selection, the effective population size and the inbreeding level of the populations in each generation. Selected males were 8 (8.50%), 5 (8.30%), and 8 (22.20%) in G_0, G_1, and G_2 generations, respectively (Table 2). The corresponding numbers of selected dams were 47 (55.95%), 50 (35.20%), and 60 (33.30%), respectively. Thus sires were more intensely selected (range of selection intensity: 1.620 to 1.804) than dams (range: 0.709 to 1.076) across generations. The effective population size (N_e) varied across generations for the population under selection due to the changing numbers of breeders being 27.4, 18.8, and 22.9 for G_0 (base), G_1, and G_2 generations, respectively. The corresponding values for the control populations were 30, 40, and 40, respectively. In the populations subjected to selection, the inbreeding coefficient (F) increased from 0.0285 (2.85%) in G_0 generation to 0.0759 (7.59%) in G_2 generation or an increase of 0.0474 (4.74%) relative to the base population (G_0 generation) while in the control populations inbreeding coefficient was 0.0269, 0.0391, and 0.0511 in G_0, G_1, and G_2 generations respectively showing that accumulation of inbreeding was slower in these populations probably on account of random mating system, no selection and higher effective population size (Arriel iet al., 1993; Souza Jr. *et al.,* 2000; Kliman *et al.,* 2008).

Table 1: Percentage and proximate composition of experimental diets

	Chick Mash	**Growers mash**	**Layers mash**
Feed ingredients (DM Basis)	Percentage composition	Percentage composition	Percentage composition
Maize	53.0	43.5	43.0
Wheat offal	13.0	30.0	18.0
Soya bean cake	18.0	10.0	17.5
Palm kernel cake	9.0	10.0	9.0
Fish meal	3.0	2.5	2.5
Bone meal	3.0	0.25	3.0
Lysine	0.25	0.25	0.25
Methionine	0.25	0.25	0.25
Vitamin premix	0.25	0.25	0.25
Salt	0.25	3.0	0.25
Oyster shell	-	-	6.0
Total	100	100	100
Calculated:			
Crude protein (%)	18%	15%	16.5%
Energy (Kcal ME/kg)	2,800	2,670	2,600
Proximate composition	**Crude protein**	**Energy (Kcal ME/kg)**	
Maize	9.0	3430	
Wheat offal	17.0	1870	
Soya bean cake	44.0	2400	
Palm kernel cake	18.0	2800	
Fish waste	50.0	2700	

Parameters used in the construction of selection indices

The trait parameters (economic values in naira/unit (a), heritabilities (h^2) and phenotypic standard deviation (σ_p)) used in the construction of selection indices across generations is presented in Table 3. Economic weight was 3.15, 3.82, and 2.89 for EN; 5.77, 6.93, and 5.28 for EW, and -1.00 for BWFE for G_0, G_1, and G_2 generations, respectively. Heritability was low to moderate for EN (range, 0.12 ± 0.08 to 0.24 ± 0.16), moderate to high for EW (0.34 ± 0.21 to 0.43 ± 0.21), and high for BWFE (0.57 ± 0.26 to 0.69 ± 0.48). The heritability estimates for the traits were within the ranges generally reported in chickens (Oleforuh-Okoleh, 2011; Bahmanimehr, 2012). The phenotypic standard deviation remained relatively stable and positive for each trait across the three generations. The positive phenotypic standard deviation (σ_P) r all traits indicates persistent variation among individuals of each generation in these traits.

Table 2: Population size at selection, effective population size, and inbreeding coefficient

Gen/pop.	Pop. Size (no./sex)	Selected breeders	% selection	Selection intensity (i)	Effective pop. Size (N_e)	ΔF
Reference pop.	M = 15	M = 5*	33.33	1.032	48.0	0.0104
	F = 60	F = 50*	83.33	0.295		
G_0	M = 94	M = 8	8.50	1.804	27.35	0.0285
	F = 84	F = 47	55.95	0.709		
Control**	30	M = 15*	-	-	30.00	0.0269
		F = 15*	-	-		
G_1	M = 60	M = 5	8.30	1.792	18.81	0.0552
	F = 142	F = 50	35.20	1.027		
Control	M = 35	M = 20*	-	-	40.00	0.0391
	F = 48	F = 20*	-	-		
G_2	M = 36	M = 8	22.20	1.620	22.86	0.0759
	F = 60	F = 20	33.30	1.076		
Control	M = 40	M = 20*	-	-	40.00	0.0511
	F = 52	F = 20*	-	-		

*: random selection , **: random breeding population, ΔF: inbreeding coefficient, M: males, F: females.

Table 3: Economic values (a in naira/unit), heritabilities (h^2) and phenotypic standard deviations used in the construction of selection indices across generations

Trait	Symbol	Unit	a*	h^2	σ_p
G_0					
Egg number	EN	no.	3.15	0.12 ± 0.08	13.82
Egg weight	EW	Kg	5.77	0.34 ± 0.21	4.49
Body weight at first egg	BWFE	Kg	-1.00	0.64 ± 0.38	167.01
G_1					
Egg number	EN	no.	3.82	0.14 ± 0.06	14.01
Egg weight	EW	Kg	6.93	0.43 ± 0.21	5.50
Body weight at first egg	BWFE	Kg	-1.00	0.57 ± 0.26	162.41
G_2					
Egg number	EN	no.	2.89	0.24 ± 0.16	11.82
Egg weight	EW	Kg	5.28	0.34 ± 0.24	4.25
Body weight at first egg	BWFE	Kg	-1.00	0.69 ± 0.48	185.80

*source: Ogbu *et al.,* 2014.

Population trait values and selection parameters for index traits

The selection parameters for traits included in the selection index are summarized in Table 4 for G_0, G_1, and G_2 generations. There were positive selection differentials for EN and EW across the generations leading to progressive increases in cumulative selection differentials in these traits. The selection differential for BWFE was negative for G_0 and G_1 but positive for G_2 generation while cumulative selection differentials were negative for the three generations. Selection intensity for EN increased from 0.530 in G_0 to 0.806 in G_2 generation averaging 0.729 for the three generations. For EW the selection intensity was 0.149 in G_0, 0.167 in G_1 but very low (0.002) in G_2 generation. For body weight at first egg, there were negative selection intensities in G_0 and G_1 generations while it was positive but very low (0.031) in G_2 generation. The positive selection differentials (Δs) obtained for EN and EW across generations followed from the superior mean values of these traits in the selected populations compared to their mean values before selection as against the results observed for BWFE. Regression of cumulative selection differential on generation number (the per generation selection differential) for EN and EW was 10.74 egg and 0.47g, respectively and these were higher than the values of 1.67 eggs and -1.21g for egg number and egg weight to 40 weeks, respectively, reported by Nwagu *et al.* (2007) in a population of Rhode Island chickens selected for 5 generations. Our range of 7.32 to 11.94 eggs for selection differential was also higher than the values of 1.12 to 9.45% hen day egg production (HDP%) or 1.53 to 7.18 eggs reported by Faruque *et al.* (2010) while the values for EW were generally lower than the range of 0.19 to 1.87g reported by the same workers.

Table 4: Population averages, and selection parameters of index traits across generations

		Population average				
Trait	**Generation**	**Before selection**	**After selection**	Δs	**i**	**CumΔs**
EN	G_0	75.60 ± 0.18	82.92 ± 0.15	7.32	0.53	7.32
	G_1	77.79 ± 0.14	89.73 ± 0.09	11.94	0.85	19.26
	G_2	79.38 ± 0.19	88.91 ± 0.11	9.53	0.81	28.79
Δs/gen				10.74		
EW	G_0	41.27 ± 0.06	41.94 ± 0.07	0.67	0.15	0.67
	G_1	42.92 ± 0.05	43.84 ± 0.08	0.92	0.17	1.59
	G_2	43.18 ± 0.07	43.19 ± 0.12	0.01	0.002	1.60
Δs/gen				0.47		
BWFE	G_0	1330.44 ± 2.14	1301.18 ± 2.47	-29.26	-0.21	-29.26
	G_1	1304.84 ± 1.58	1288.30 ± 2.08	-16.540	-0.10	-45.80
	G_2	1428.48 ± 3.05	1434.20 ± 5.52	5.72	0.03	-40.08
Δs/gen				-5.41		

EN: egg number, EW: egg weight, BWFE: body weight at first egg, Δs: selection differential, σ_P: phenotypic standard deviation, i: selection intensity, respectively.

The selection differential for BWFE were generally lower than that reported by Faruque *et al.* (2010) for body weight at 40 weeks of age (BW-40) (range: 21.26 – 95.21g) but higher than that by Nwagu *et al.* (2007) (-5.41g/generation vs -28.60g/generation). The observed higher selection intensity for EN compared to the values for EW and BWFE in each generation shows that the selection index employed in the present study applied greater selection pressure on egg production, than egg weight and BWFE probably in accordance with the traits relative economic weights. Faruque *et al.* (2010) reported a range of 4.91 – 12.22 and 0.19 – 0.77 for phenotypic standard deviation and selection intensity, respectively for HDP%, 2.76 – 3.53 and 0.058 - 0.597, respectively for egg weight, and 154.87 – 304.49 and 0.09 – 0.464, respectively for BW-40.

Direct and realized genetic responses in index traits

There were increasing trends in trait performance across generations with direct response to selection being positive for EN and EW over the three generations and in generations 1 and 2 for BWFE (Table 5).

Table 5: Generation wise performance and selection response for index traits

	EN	**EW**	**BWFE**
Performance in index traits			
G_0	75.60 ± 0.18^c	41.27 ± 0.06^c	1330.44 ± 2.14^b
G_1	77.79 ± 0.14^b	42.92 ± 0.05^b	1304.84 ± 1.58^c
G_2	79.38 ± 0.19^a	43.18 ± 0.07^a	1428.48 ± 3.05^a
Direct response in index traits			
G_0			
R	4.26	1.83	-0.71
CumR	4.26	1.83	-0.71
R/yr	4.26	1.83	-0.71
ΔG_R	2.19	1.65	-25.60
G_1			
R	11.79	2.83	5.15
CumR	16.05	4.66	4.44
R/yr	11.79	2.83	5.15
ΔG_R	1.59	0.26	123.64
G_2			
R	13.37	3.12	44.93
CumR	29.42	7.78	49.37
R/yr	13.37	3.12	44.93
ΔG_R	ND	ND	ND
$\bar{R}$	12.58	2.98	25.04

R: direct response, CumR: cumulative response, ΔG_R: realized response; a, b, c: in each column, means with different superscripts are significantly different ($p<0.05$).

Direct genetic response to selection was 4.26 eggs, 1.83g and -0.71g for EN, EW and BWFE, respectively in G_0 generation; 11.79 eggs, 2.83g, and 5.15g, respectively in G_1 generation, and 13.37 eggs, 3.12g, and 44.93g, respectively in G_2 generation. Cumulative selection gain increased from 4.26 to 29.42 eggs, 1.83 to 7.78g, and -0.71 to 49.37g for EN, EW, and BWFE, respectively from G_0 to G_2 generations. Realized genetic gain was lower than expected genetic gain for all traits in G_0 and G_1 generations except for BWFE in G_1 generation. Expected genetic response per generation was positive for all traits (12.58 eggs, 2.98g and 25.04g for EN, EW, and BWFE, respectively). The increasing trends observed in trait performance and the positive selection responses across generations indicate improvement in the traits subjected to index selection. Faruque *et al.* (2010) reported expected selection response of 0.084 – 0.709% for egg production, 0.048 – 0.468g for egg weight, and 5.32 – 23.80g for BW-40 in local chickens of Bangladesh. The discrepancies observed between expected and realized (observed) responses are common in intrapopulation selection (Souza *et al.,* 2000) and has been attributed to a number of factors which include sampling error, and genotype x environment interaction (Arriel *et al.,* 1993; Falconer and Mackay, 1996; Souza *et al.,* 2000). Sampling error could occur during the recombination of selected progenies while genotype x environment interaction may affect the response to selection in atypical years. Mackay and Gibson (1993) also suggested that variation between expected and realized genetic responses could arise from the effect of gametic-phase (linkage) disequilibrium.

Selection index parameters and expected gain in index score (aggregate genotype)

Mean index score (aggregate genotype), selection differential for index score, phenotypic standard deviation of index score, heritability of index score, and expected genetic response in index score increased progressively across generations (Table 6).

Table 6: Generation wise selection index parameters and gain in index score

Parameter	G_0	G_1	G_2
I_s	11.07	12.18	12.37
I_μ	9.93	9.89	9.98
ΔS_I	1.14	2.28	2.39
σ_I	1.62	2.31	2.69
i_I	0.70	0.99	0.89
h_I^2	0.08 ± 0.23	0.09 ± 0.16	0.13 ± 0.38
ΔG_I	0.16	0.36	0.55
ΔG_{RI}	-0.04	0.09	ND

I_s: index score of population after selection, I_μ: index score of population before selection, Δs_I: selection differential for index score, i_I: selection intensity for index score, h_I^2: heritability of index score, ΔG_I: genetic gain in index score.

For instance, selection differential and expected gain in index score increased from 1.14 and 0.16, respectively in G_0 generation to 2.39 and 0.55, respectively in G_2 generation. Realized gain in index score was however negative (-0.04) in G_0 generation but positive (0.09) in G_1 generation. The phenotypic standard deviation and heritability of index score increased from 1.62 and 0.08, respectively in G_0 generation to 2.69 and 0.13, respectively in G_2 generation. The selection intensity for index remained relatively stable with a value of 0.703, 0.989, and 0.890 in G_0, G_1, and G_2 generations, respectively. The increasing values observed for selection differential and expected genetic gain in index score indicate that selection was effective in improving the aggregate genotype of the population and this was reflected in the higher value observed for mean aggregate genotype (mean index score) before selection (I_μ) in G_2 generation leading to a positive realized gain in index score in G_1 generation. There were however discrepancies between expected and realized gain in index score which could be attributed to the different methods of determination, effect of genotype x environment interaction, and low precision in estimation of genetic and phenotypic variances used in the calculation of expected responses (Arriel *et al.,* 1993). Progressive increases in values of phenotypic standard deviation and heritability of index score point to persistent availability of phenotypic and genetic variation in aggregate genotype within each generation.

Gain in index traits due to selection on index score (aggregate genotype)

Selection on index score (aggregate genotype) brought about genetic improvement in the index traits (Table 7).

Table 7: Expected and realized genetic gain in index traits based on selection on index score

	Trait		
	EN	**EW**	**BWFE**
G_0			
Δg_i	0.96	0.52	26.85
CumΔg_i	0.96	0.52	26.85
Δg_R	2.19	1.65	-25.60
$\Delta g_R/\Delta g_i$	2.27	3.15	-0.95
G_1			
Δg_i	1.53	1.08	36.63
CumΔg_i	2.50	1.60	63.48
Δg_R	1.59	0.26	123.64
$\Delta g_R/\Delta g_i$	1.22	0.24	2.21
G_2			
Δg_i	1.88	0.82	51.22
CumΔg_i	4.37	2.42	114.70
Δg_R	ND	ND	ND
$\Delta g_R/\Delta g_i$	ND	ND	ND
Δg_i/gen	1.71	0.95	43.93

Δg_i: expected genetic gain; Δg_R: realized genetic gain, ND: not determined.

Expected genetic gain in EN and EW was 0.96 eggs and 0.52g, 1.53 eggs and 1.08g, and 1.88 eggs and 0.82g, respectively in G_0, G_1, and G_2 generations while realized genetic gain in these traits were 2.19 eggs and 1.65g, respectively in G_0 generation and 1.59 eggs and 0.26g, respectively in G_1 generation. For BWFE, expected genetic gain was 26.85, 36.63 and 51.22g in G_0, G_1, and G_2 generations while realized genetic gain was -25.60 and 123.64g in G_0 and G_1 generations, respectively. Except for BWFE in G_0 generation, realized genetic gain (Δg_R) was positive and in most cases higher than expected genetic gain for the traits indicating that selection based on aggregate genotype (index score) actually improved the values of the component traits. The ratio of realized (observed) to expected genetic gain (which indicates effectiveness of selection) was thus positive (except for BWFE in G_0 generation) and mostly above unity. The ratios observed for EN were higher than the values reported by

Fairfull and Gowe, (1990) which gave a range of 0.77 to 1.47 (mean, 1.12) and that of Nwagu *et al*. (2007) which gave a range of 0.38 to 1.46 (mean, 1.08) for the same trait in Rhode Island Red chickens. The higher ratios indicate higher realized genetic gain in the Nigerian heavy local chicken ecotype probably due to favourable genotype by environment interaction as well as a surge in response to this initial selection stimulus.

Genetic gain in body weight of males subjected to mass selection

There were positive genetic responses in BW_{39} of cocks subjected to mass selection (Table 8).

Table 8: Predicted, expected, and realized genetic response in BW_{39} in cocks following mass selection

	Generation			
Parameter	**G_0**	**G_1**	**G_2**	**Per gen**
R_P	79.30	80.22	30.53	-
R	297.06	437.00	580.00	508.50
CumR	297.06	734.06	1314.06	
ΔG_R	284.22	111.87	ND	
$\Delta G_R/R$	0.96	0.26	ND	
$\Delta G_R/R_P$	3.58	1.39	ND	

R_P, R, CumR, ΔG_R: predicted, expected, cumulative, and realized response, respectively. ND: not determined.

Progenies of selected cocks were on the average heavier at 39 weeks of age in G_0, G_1, and G_2 generations compared to the population from which their sires were selected (expected gain: 297.06, 437.00, and 508.50g, respectively; realized genetic gain: 284.22, and 111.87g, for G_0, and G_1 generations, respectively). The predicted responses were, however, very low compared to the expected responses probably due to low additive genetic variance in body weight at this age (Ogbu, 2012b). Ogbu (2012b) had reported low to moderate heritability values for body weight at 39 weeks of age in the same population. Predicted response is proportional to selection differential and additive genetic heritability. The ratio of realized to expected genetic gain was 0.96 for G_0, and 0.28 for G_1 generations (mean 0.61). Lower realized selection responses compared to expected responses were reported by Fairfull and Gowe (1990). Reasons adduced for the variable responses include genotype by environment interaction or correlated responses among traits (Fairfull and Gowe, 1990). Sampling error and variation in environmental effects across generations, account for variations in generational mean values of traits. The increasing trends in expected genetic response and the mean ratio of 0.61 or 61% obtained for realized to expected responses in this study shows that selection was effective to improve the 39 week body weight of males of the heavy local chicken ecotype. The ratio of realized to predicted responses were generally very high (3.58 and 1.39 in G_0, and G_1, generations, respectively). The values were therefore, higher than those by Oluyemi (1979b) who reported a range of 0.57 to 1.08 (57% to 108%) as ratio of realized to predicted responses for 12 week body weight in the Nigerian indigenous chicken.

Response in body weight of chicks and pullets following mass and index selection

Table 9 presents the body weight of chicks (0 – 8 woa, sexes combined) and pullets (12 – 20 woa) for G_0, G_1 and G_2 generations following mass selection in cocks and index selection in hens.

Table 9: Body weight from hatch to 8 weeks of age (sexes combined) and from 12 to 20 weeks of age (females) following mass selection in cocks and index selection in hens

	Generation					
Trait	G_0	G_1	$G_1 - G_0$	G_2	$G_2 - G_1$	$G_2 - G_0$
BW_0	30.30 ± 0.17^c	31.65 ± 0.15^b	0.70	33.48 ± 0.17^a	1.83	3.18
BW_4	151.41 ± 1.74^c	160.78 ± 1.16^b	9.37	166.86 ± 1.66^a	6.16	15.45
BW_8	344.19 ± 4.14^b	391.72 ± 3.09^a	47.53	399.63 ± 4.88^a	7.91	55.44
BW_{12}	667.98 ± 6.30	650.19 ± 5.41	-17.79	673.98 ± 6.48	23.79	6.00
BW_{16}	791.52 ± 6.24	779.97 ± 5.27	-11.55	812.54 ± 7.72	32.57	21.02
BW_{20}	911.59 ± 6.33	926.89 ± 5.01	15.30	939.64 ± 7.28	12.75	28.05

a, b, c: means on the same row with different superscripts are significantly different ($p<0.05$).

There were significant differences in hatch weight and body weight at 4 and 8 weeks of age. Hatch, 4 and 8 weeks body weights were highest in G_2 progenies followed by G_1 and least in G_0 progenies. For pullets, body weight from 12 to 20 weeks of age did not differ significantly between generations. However, birds belonging to G_2 generation were marginally heavier than those of G_1 and G_0 generations across the ages. The significant differences in juvenile body weight across generations could result from correlated responses from improve body weight following mass selection for adult body weight in males and slightly improved egg size and body weight (G_2 generation) in females. The marginal improvement in age wise body weight from 12 to 20 weeks of age also represents correlated responses in growth performance of females following index selection. The low response observed for body weight from 12 to 20 weeks of age was probably sequel to the negative weighting of body weight at first egg in the index and the very low selection intensity (mean, -0.277) for this trait across generations.

Conclusion

Egg production (total egg number and egg weight), growth performance and aggregate economic value of the heavy local chicken ecotype can be improved by multiple trait selection using a simplified selection index constructed from trait values, relative economic weights and heritabilities. The combination of only positively correlated traits in such an index could enhance selection response and genetic progress in the traits.

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