Association of Haemoglobin Genotype with Residual Feed Intake in West African Dwarf Does

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Summary

The interaction effect of haemoglobin genotypes (Hb^{AA}, Hb^{AB}) and residual feed intake (RFI) classes (RFI^{LL}, RFI^{MM}, RFI^{HH}) on feed efficiency, haematological and serum parameters in on-farm West African Dwarf (WAD) does was studied for pre-selection of breeding animals. Ninety-six does were fed for 112 days. Feed intake was measured daily, body weight and other variables were measured at 28-day intervals. Dry matter intake (DMI); average daily gain (ADG) and feed conversion efficiency (FCE) were computed while body condition score (BCS) was estimated using the five-point scale for goats. Blood samples were collected after 112 days via jugular vein puncture and analyzed for insulin-like growth factor (IGF-I), insulin, leptin, urea and complete cell counts. Phenotypic RFI was calculated for each animal as the residual from a multiple regression model of DMI on ADG and mid-test metabolic bodyweight ($BW^{0.75}$). The WAD does with heterozygous Hb^{AB} genotype had higher serum insulin and IGF-1 concentrations than the homozygous Hb^{AA} genotype ($P < 0.019$). Does within the low RFI (RFI^{LL}) class recorded higher IGF-1 ($P < 0.050$), PCV ($P < 0.002$) and Hb concentration ($P < 0.038$) than does within the medium (RFI^{MM}) and high (RFI^{HH}) classes. The interaction of Hb genotype and RFI revealed significant differences ($P < 0.050$) on FCE, IGF-1 and monocytes values among does. The result of Hb genotype x RFI class interaction on RFI was not significant ($P = 0.077$), although values increased numerically in ascending order to rank does into pre-selection classes. WAD does of Hb^{AA} and Hb^{AB} genotypes with negative-RFI values (-0.004, -0.005) were deemed most efficient nutritionally and could be selected as parents.

Key words

feed conversion efficiency, insulin-like growth factor-1, haemoglobin genotypes, monocytes, residual feed intake

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Introduction

It has been suggested that to ensure economic and environmentally sustainable production, livestock breeders must utilise efficient animals in the production process (Bazerra et al., 2013). Animals with lower feed consumption per unit weight gain (feed efficiency) are preferred by farmers and are thus more feed efficient (Wang et al., 2012; Dige et al., 2021). Residual feed intake can be used to select for growth rate or daily weight gain, feed consumption and feed efficiency, it adjusts for metabolic weight and captures variation in activity, protein turn-over, digestibility and heat increment of fermentation in animals, independent of body size (Pryce et al., 2014; Zulkifli, 2016). Post weaning RFI is moderately heritable in ruminants (Snowder et al., 2003; Clemmons et al., 2017; Muncha et al. 2022) and enables selection of progeny that eat less without sacrificing growth performance (Del Claro et al. 2012).

Although RFI has been shown to be uncorrelated with live weight and rate of gain (Bazerra, 2013), it is related to weight gain composition (Kelly et al., 2012); with RFI-negative animals tending to have leaner carcasses with less finishing muscular fat, less back fat, less intermuscular fat, more lean meat, lower heat production, lower methane emission and less manure production (Richardson et al., 2001, Bazerra et al., 2013) than less-efficient steers. Apart from increased feed efficiency, RFI can be used to select animals that release lower amount of pollutants per unit of product into the environment (Bazerra et al. 2013). Nkrumah et al. (2006) identified significant differences in methane emissions from beef steers that differed in RFI and low-RFI steers produced 28% less methane than animals with high RFI, suggesting a potential for reducing the environmental impacts of cattle production. Also, CO_2 production was higher in pigs with positive RFI (Barea et al. 2010).

Haematological parameters enable quick evaluation of the general health, welfare and immunity status, which is important for breeding nutritionally efficient and sound animals. Richardson et al. (2001) identified a number of blood parameters correlating with expected progeny differences (EPDs) and RFI. For example, animals with high RFI showed higher insulin and cortisol levels and lower levels of triglycerides, which suggested their responses to changes in body composition and nutrient use efficiency. Negative correlations were found between RFI and percent body protein and, between RFI and protein gain (Richardson et al., 2001), thus implying that more efficient animals have a mechanism for more efficient protein deposition, a lower degradation rate, or a lower expenditure of energy compared to less-efficient animals. Haemoglobin (Hb) concentration plays diverse roles in oxygen transport, but haemoglobin genotype is a heritable genetic identity - independent of haemoglobin concentration level or haematological parameters which are highly influenced by the environment - transmitted from parent to offspring. There exists a wide diversity of haemoglobin genotypes among Nigerian goat population (Bindu and Raghavan, 2010; Agaviezor et al., 2013; Osaiyuwu et al., 2013; Yakubu et al., 2014; Aygun, 2016). Although the Hb polymorphism (Hb^{AA}, Hb^{AB}, Hb^{BB} and Hb^{AC}) in the Nigerian goat has been detailed (Salako et al. 2007; Agaviezor et al. 2013; Osaiyuwu et al. 2013; Yakubu et al. 2014), its association with RFI in West African Dwarf goats has not been investigated.

Previous studies indicated that no single mechanism was responsible for determining animal feed efficiency (Herd et al., 2003; Cantalapiedra-Hijar, 2018). One major limitation to application of RFI as a feed efficiency trait is that its measurement is time-bound, laborious and expensive. Nevertheless, serum metabolites such as insulin, leptin, insulin-like growth factor-1 (IGF-1), and urea concentrations or haematological parameters have been evaluated for variation among individuals for feed efficiency, and as possible biomarkers of feed efficiency in farm animals (Hoque et al., 2009; Lawrence et al., 2012). The effect of Hb genotypes and its interaction with RFI on the performance and health of WAD goats could open up a new window for selective breeding and improvement. Furthermore, important serum and haematological parameters could be used as possible biomarkers for predicting RFI and other performance indexes. The objective was to determine the associative effects of Hb-genotype and RFI on the performance and health of WAD does.

Materials and Methods

Ethical Approval

The experimental procedures for the study were approved by the TETFund committee of the Federal University Oye-Ekiti, Nigeria; and were also in line with ARRIVE 2.0 (Percie du Sert, et al., 2020) and PREPARE guidelines for planning animal research and testing (Smith et al., 2018).

Location of Research

The study was conducted at the Goat Unit of the Teaching and Research Farm of the Federal University Oye-Ekiti, Nigeria with GPS coordinates: latitude 07°48.338´ N, longitude 05°29.922´ E; Global Positioning System, GARMIN GPS 72H, with mean daily temperature, humidity ranges, rainfall and altitude of 21.7–31.1 °C, 72–78%, 177.8 cm/annum and 460 MSL.

Experimental Materials and Procedures

Ninety-six WAD does (initial BW = 12.9±3.72 kg, average age = 10-12 months) were acquired locally for breeding, tagged, quarantined, and administered with prophylactic treatments (oral multivitamins for three days; subcutaneous injection of ivermectin at 1 mL per 50 kg BW and vaccinated against *Pestes des petits* ruminants (PPR) intramuscularly). Animals were housed individually in concrete-floor pens (1.0 × 2.2 m^2) equipped with feeding and watering troughs. The experiment was preceded by an adjustment period of 21 days, followed by a 112-day study period during which animals consumed Guinea grass forage ad-libitum and were supplemented with African yam beans-based concentrate ration (Forage-concentrate ratio, 60:40). The nutritional composition of the diet was DM: 563.63 g kg^{-1}, and 106.25, 566.63, 385.50, 5.65 and 15.26g kg^{-1} DM for crude protein, NDF, ADF, calcium and phosphorus respectively.

Measurement of Production Variables and Performance Traits

Daily feed intake was estimated as feed offered minus feed refused, from which daily dry matter intake (DMI) was estimated and averaged for each 28-day period. Fasting body weights (BW)

were taken at the beginning, at 28-day intervals and at the end of the trial with portable, digital, electronic scale (model: WH-A08, made in China, Patent No:201030634194.3) of 50 kg capacity, mounted on a tripod stand. Body condition scores (BCS) were recorded at 28-day intervals based on the 5-point scoring scale for goats: too thin/very thin = 1, thin = 2, satisfactory/good = 3, satisfactory but tending towards fat = 4 and too fat/obese = 5 (Ockert, 2015).

From body weight changes and feed intake record, average daily gain (ADG) and feed conversion efficiency (FCE) were estimated. Expected daily DMI of each doe was obtained from the linear regression of DMI on ADG and mid-test average metabolic weight (AMW). This procedure of Sainz and Paulino (2004) provided average estimates of coefficients β_0, β_1, β_2 and the residual (ε) for each doe (equation 1), and thus allowed the estimation of expected DMI. This indicates the amount of feed needed to maintain the metabolic weight and average daily gain for each individual and the expected value for animals of similar weights and rates of gain.

$$DMI_{expected} = \beta_0 + \beta_1 \text{ x } ADG + \beta_2 \text{ x } AMW + \varepsilon_{ijk} \quad (1)$$

where: DMI = expected daily dry matter intake (kg d^{-1}), β_0 = equation intercept, β_1 and β_2 = coefficients of the equation, ADG = average daily gain (kg d^{-1}), AMW = average metabolic bodyweight ($kgBW^{0.75}$), ε_{ijk} = uncontrolled/residual error component due to average daily gain and average metabolic bodyweight in kth replicate.

Residual feed intake (RFI) was estimated using the regression model (equation 2) by Koch et al. (1963) as the difference between actual intake and expected intake:

$$RFI_{Phe} = DMI_{(actual)} - (\beta_0 + (\beta_{1(phe)} \text{ x } DWD)) - (\beta_{2(phe)} \text{ x } AMW) \quad (2)$$

where RFI_{Phe} = phenotypic residual feed intake, DMI = actual daily dry matter intake, ADG = average daily gain, AMW = metabolic body weight at mid test (56^{th} day), β_0 = general mean, $\beta_{1(phe)}$ and $\beta_{2(phe)}$ = partial regression coefficients of animal's DMI on ADG and AMW respectively, and ε = uncontrolled error of the jth animal.

At the end of the trial, average values of RFI±SD were calculated for individual does, ranked and classified into three: low-RFI (RFI^{LL}, -0.004 ± 0.001; n = 48); medium-RFI (RFI^{MM}, 0.000 ± 0.00; n = 17) and high-RFI (RFI^{HH}, 0.017 ± 0.005; n = 31) classes at frequencies 0.50, 0.18 and 0.32 respectively.

Blood Sampling and Collection

Fasting blood samples of 10 mL were collected from each doe by the jugular vein-puncture method. Five millilitres (5mL) was dispensed into sample bottles containing ethylene-diamine-tetra-acetic acid (EDTA) and remaining 5 mL was dispensed into sterile sample bottles for serum analysis. These samples were stored under ice-pack in separate cooler boxes and transported to the laboratory.

Determination of Haemoglobin Genotype and Haematological Parameters

Blood samples in EDTA bottles were examined for haemoglobin genotypes using the horizontal starch gel electrophoresis in tris-boric acid buffer system following the procedure reported by Aygün, (2016). Haematological indices were determined on hemolysates collected at 28^{th} and 84^{th} day for packed cell volume (PCV, %); haemoglobin concentration (Hb, g dL^{-1}); red blood cells (RBC, x 10^{12} L^{-1}); mean corpuscular volume (MCV, fL); mean corpuscular haemoglobin (MCH, pg); mean corpuscular haemoglobin concentration (MCHC, g L^{-1}); white blood cells, WBC, (x10^9 L^{-1}); neutrophils (%); lymphocytes (%); neutrophils-lymphocyte ratio (NLR), monocytes (%); eosinophils (%); and basophils (%) as described by Jain (1986).

Serum Samples Collection and Analyses

Blood samples for serum analyses were obtained as described above at 28-day intervals. Upon withdrawal, samples were allowed to clot for 20 minutes at room temperature and clots were subsequently removed. All samples were then centrifuged at 3500 RPM for 20 minutes (Generic 3500 RPM centrifuge machine handi shape-8 Tube with Timer), returned into fresh sterile tubes and stored at -25 °C until assay was performed.

Stored serum was analyzed for insulin-like growth factor-1 (IGF-1), leptin and insulin levels using the enzyme-linked immunosorbent assay (ELISA) technology kits (Bioassay Technology Laboratory, Shangai, China) following the procedures of Engvall (2010); Gan and Patel (2013) and Alhaji and Farhana (2021). The results were interpreted according to kit reference values. Blood urea nitrogen (BUN) concentration was determined in the Cobas C-311 automated analyzer developed by Roche. All sample determinations were conducted at the Public-Private-Partnership (PPP) laboratory of the University College Hospital (UCH) Ibadan, Nigeria.

Experimental Design and Statistical Analysis

The experimental design was completely randomized design (CRD) in factorial arrangement. The repeated measures analytical procedure of SAS/STAT 8.1 (1999) was used to analyze generated data, while the model equation was of the form:

$$Y_{ijkl} = \mu + Hb_i + R_j + HbxR_{ij} + M_k + HbxM_{ik} + RxM_{jk} + HbxRxM_{ijk} + \varepsilon_{ijk}$$

where, Y_{ijkl} = Observation in ith haemoglobin genotype, in jth residual intake, in kth month, on lth replicate, μ = General mean, Hb_i = Haemoglobin genotype (i: 1 = Hb^{AA}, 2 = Hb^{AB}), R_j = Residual feed intake value (j:1 = low, 2 = medium, 3 = high), $HbxR_{ij}$ = Interaction of ith haemoglobin genotype and jth residual feed intake value, M_k = Effect of month kth within subject (individual animal's) data (j = 1, 2, 3, 4), $HbxM_{ik}$ = Interaction effect of haemoglobin genotype ith and kth month, RxM_{jk} = Interaction effect of residual feed intake value jth and kth month, $HbxRxM_{ijk}$ = Interaction of haemoglobin genotype ith, residual feed intake jth, and month kth, ε_{ijklm} = Random error containing all uncontrollable sources of variation ~ NID (0, δ^2).

The random factors included month and all interactions, while the fixed factors were haemoglobin genotype and residual feed intake class. The covariance structure of the repeated data was modelled with compound symmetry procedure. Least square means (LSM) of the fixed effects were compared and separated using Tukey's test ($P < 0.05$) while the Pearson's phenotypic correlation procedure ($\alpha=_{0.010 - 0.050}$) was used to analyze linear association between RFI and feed efficiency traits, RFI and serum metabolites, monocytes, and NLR.

Results

The haemoglobin genotype assay revealed seventy does of Hb^{AA}, twenty-six does of Hb^{AB} and none of Hb^{BB} genotype, with genotypic frequencies of 0.712, 0.288 and 0.000, respectively (Table 1). Table 1 shows the effect of residual feed intake (RFI) class, haemoglobin genotype (Hb^{++}) and their interaction on feed efficiency traits and serum metabolites of test does. Significant differences ($P < 0.004$) were obtained between RFI classes for RFI value; also the leptin and IGF-1 values differed between RFI (RFI^{LL}, RFI^{MM}, RFI^{HH}) classes.

There was a significant interaction of Hb x RFI on FCE ($P < 0.021$) and IGF-1 ($P < 0.031$), while the same interaction effect on RFI of animals was marginal ($P = 0.077$). In Table 2, RFI classes exert influence on PCV ($P < 0.002$) and Hb ($P < 0.038$) values, and the same effect is marginal ($P = 0.096$) on RBC; but there is a significant effect ($P < 0.045$) of Hb x RFI interaction on monocytes percentage. Table 3 reveals that Hb^{AA} and Hb^{AB} individuals with low-RFI values, had similar BCS and monocytes percentages, but Hb^{AB} individuals posted the lowest FCE ($P < 0.021$) and higher IGF-1 ($P < 0.031$) values than Hb^{AA}. The Hb^{AA} and Hb^{AB} individuals in the high-RFI class had similar BCS and monocytes percentages but were differentiated by FCE and IGF-1 concentration ($P < 0.045$). The Hb^{AA} x RFI^{MM} individuals recorded the highest monocytes values ($P < 0.045$) and the lowest IGF-1 ($P < 0.031$) values.

Table 4 excludes the bivariate Pearson's correlation results on RFI versus feed efficiency traits, RFI versus serum metabolites, and RFI versus monocytes and NLR. There were significant negative and positive correlations ($P < 0.001$) of RFI x monocytes in Hb^{AA} x RFI^{LL} and Hb^{AB} x RFI^{LL} individuals respectively. A significant and positive correlation of RFI with each of ADG ($P < 0.01$), FCE ($P < 0.01$) and BCS ($P < 0.05$) was obtained in Hb^{AA} x RFI^{HH} individuals, while Hb^{AB} x RFI^{HH} individuals exposed significant correlations ($P < 0.050$) of RFI x insulin, and RFI x urea.

Table 1. Feed efficiency and serum metabolic traits of West African dwarf Does as influenced by haemoglobin genotype

	Residual Feed Intake class				Hb genotype			*P*-value		
Traits	RFI^{LL}	RFI^{MM}	RFI^{HH}	SEM	Hb^{AA}	Hb^{AB}	SEM	RFI	Hb	RFIxHb
n	48	17	31		70	26				
Residual feed intake (kg d^{-1})	0.0002^{b}	0.0045^{b}	0.0173^{a}	0.002	0.005	-0.001	0.002	0.004	0.216	0.077
Dry matter intake (kg d^{-1})	0.588	0.575	0.528	0.055	0.580	0.492	0.045	0.807	0.652	0.700
Average daily gain (kg d^{-1})	0.048	0.052	0.047	0.007	0.051	0.035	0.010	0.957	0.230	0.803
Feed conversion efficiency (%)	11.51	8.240	10.99	1.918	10.51	12.85	2.55	0.507	0.610	0.021
Body condition score	3.194	2.500	3.000	0.227	2.980	3.375	0.418	0.526	0.441	0.701
Insulin (ng mL^{-1})	9.711	11.733	9.070	2.136	8.580^{b}	14.47^{a}	1.700	0.930	0.019	0.209
Leptin (ng mL^{-1})	29.37^{a}	15.36^{b}	34.11^{a}	5.45	27.18	39.81	4.79	0.048	0.249	0.921
IGF-1 (ng mL^{-1})	187.7^{a}	93.73^{b}	161.9^{a}	45.77	129.2^{b}	319.0^{a}	39.6	0.050	0.010	0.031
Urea (mg dL^{-1})	40.53	46.78	44.33	3.071	42.06	45.33	2.46	0.930	0.298	0.352

Note: IGF-1 = Insulin-like growth factor-1, RFI^{LL} = low residual feed intake; RFI^{MM} = medium residual feed intake, RFI^{HH} = high residual feed intake, Hb^{AA} = haemoglobin genotype AA, Hb^{AB} = haemoglobin genotype AB, SEM = standard error of the means, Hb = heamoglobin, RFIxHb = interaction of RFI class and Haemoglobin genotypes, $^{a, b}$ indicate significantly different means according to Tukey's test ($P < 0.05$)

Table 2. Haematological traits of West African dwarf Does as influenced by residual feed intake and haemoglobin genotype

	Residual Feed Intake class				Hb genotype			*P*-value		
Traits	RFI^{LL}	RFI^{MM}	RFI^{HH}	SEM	Hb^{AA}	Hb^{AB}	SEM	RFI	Hb	RFIxHb
Packed cell volume (%)	24.90[a]	19.60[b]	25.47[a]	0.860	24.52	24.14	0.726	0.002	0.363	0.724
Haemoglobin concentration (g dL^{-1})	7.79[a]	6.12[b]	7.63[a]	0.323	7.47	7.73	0.248	0.038	0.946	0.890
Red blood cell count ($\times 10^{12}$ L^{-1})	4.16	3.27	4.23	0.215	4.01	4.35	0.181	0.096	0.524	0.804
Mean corpuscular volume (fl)	6.42	6.34	6.21	0.537	6.47	5.70	0.398	0.949	0.355	0.976
Mean corpuscular haemoglobin (pg)	1.98	1.99	1.85	0.163	1.96	1.84	0.121	0.821	0.565	0.924
MCHC (g dL^{-1})	314.1	314.0	300.2	10.21	305.9	322.6	8.310	0.686	0.313	0.501
White blood cells ($\times 10^{9}$ L^{-1})	15.54	11.92	13.37	1.005	13.72	16.89	3.321	0.218	0.113	0.685
Neutrophils (%)	42.90	38.00	35.47	2.626	39.09	41.43	2.226	0.814	0.286	0.157
Lymphocytes (%)	40.50	49.02	49.01	2.790	44.76	44.71	2.498	0.510	0.785	0.299
Neutrophil-lymphocyte ratio	1.06	0.78	0.72	0.272	0.87	0.93	0.259	0.725	0.915	0.440
Monocytes (%)	10.70	20.00	9.47	8.168	11.94	8.86	1.597	0.266	0.660	0.045
Eosinophils (%)	4.90	2.80	5.01	0.798	4.70	4.57	0.687	0.270	0.563	0.135
Basophils (%)	1.67	1.67	1.78	0.168	1.98	1.46	0.131	0.252	0.177	0.165

Note: RFI^{LL} = low residual feed intake; RFI^{MM} = medium residual feed intake, RFI^{HH} = high residual feed intake, HB^{AA} = haemoglobin genotype AA, Hb^{AB} = haemoglobin genotype AB, MCHC = mean corpuscular haemoglobin concentration. SEM = standard error of the means, Superscripts [a, b] indicate significantly different means according to Tukey's test ($P < 0.05$)

Table 3. Interaction effect of residual feed intake and haemoglobin genotype in West African Dwarf Does

Traits/Genotypic classes	Hb^{AA} x RFI^{LL}	Hb^{AB} x RFI^{LL}	Hb^{AA} x RFI^{MM}	Hb^{AB} x RFI^{MM}	Hb^{AA} x RFI^{HH}	Hb^{AB} x RFI^{HH}	SEM	*P*-value
Residual feed intake (kg d^{-1})	-0.005	-0.004	0.000	-	0.022	0.002	0.026	0.0767
Feed conversion efficiency (%)	12.601[ab]	6.986[b]	8.240[b]	-	8.486[b]	19.559[a]	2.224	0.0214
Body condition score	3.160	3.333	2.500	-	2.944	3.500	0.271	0.7008
IGF-1 (ng mL^{-1})	170.332[c]	254.888[b]	93.733[d]	-	81.290[d]	392.271[a]	58.947	0.0313
Monocytes (%)	11.250[b]	8.500[b]	20.000[a]	-	9.500[b]	9.333[b]	2.285	0.0451

Note: IGF-1 = insulin-like growth factor-1, Hb^{AA}*RFI^{LL}, Hb^{AB}*RFI^{LL}, Hb^{AA}*RFI^{MM}, Hb^{AB}*RFI^{MM}, Hb^{AA}*RFI^{HH}, Hb^{AB}*RFI^{HH} = WAD doe genotypic classes evaluated, SEM = standard error of the means, Superscripts [a, b, c, d] indicate significantly different means according to Tukey's test ($P < 0.05$)

Table 4. Comparative Pearson's phenotypic correlation coefficients of residual feed intake with feed efficiency traits in West African Dwarf Does in Ikole Nigeria

	WAD Hb genotypes x RFI				
Correlated Traits	Hb^{AA} x RFI^{LL}	Hb^{AB} x RFI^{LL}	Hb^{AA} x RFI^{MM}	Hb^{AA} x RFI^{HH}	Hb^{AB} x RFI^{HH}
RFIxDMI	0.213^{NS}	0.588^{NS}	-0.425^{NS}	0.252^{NS}	0.317^{NS}
RFIxADG	0.235^{NS}	-0.090^{NS}	-0.143^{NS}	0.381**	0.512^{NS}
RFIxFCE	-0.072^{NS}	-0.360^{NS}	0.145^{NS}	0.386**	0.172^{NS}
RFIxBCS	0.186^{NS}	0.447^{NS}	0.159^{NS}	0.529*	-0.500^{NS}
RFIxInsulin	0.209^{NS}	-0.075^{NS}	-0.321^{NS}	0.005^{NS}	0.702*
RFIxleptin	0.263^{NS}	-0.253^{NS}	-0.029^{NS}	-0.010^{NS}	0.503^{NS}
RFIxIGF-1	-0.064^{NS}	-0.256^{NS}	-0.461^{NS}	0.269^{NS}	0.508^{NS}
FRIxUrea	-0.008^{NS}	-0.012^{NS}	-0.300^{NS}	0.134^{NS}	-0.724*
RFIxMonocytes	-0.456**	0.905**	-0.554^{NS}	0.099^{NS}	-0.577^{NS}
RFIxNLR	-0.399^{NS}	-0.732^{NS}	0.029^{NS}	-0.358^{NS}	0.810^{NS}

Note: RFI = Residual feed intake, DMI = Dry matter intake, ADG = Average daily gain, FCE = Feed conversion efficiency, BCS = Body condition score, IGF-1 = Insulin-like growth factor - 1, NLR = Neutrophil-lymphocyte ratio. WAD = West African dwarf, Hb^{AA} x RFI^{LL}; Hb^{AB} x RFI^{LL}; Hb^{AA} x RFI^{MM}; Hb^{AA} x RFI^{HH}; Hb^{AB} x RFI^{HH} = WAD haemoglobin genotypes interacting with RFI class, Significance differences: $P < 0.01$ = **; $P < 0.05$ = *; $P > 0.05$ = NS

Discussion

The genotypic frequencies obtained confirm report on the prevalence of Hb^{AA} genotype (Bindu and Raghavan, 2010; Agaviezoor et al., 2013), and contradicts report of prevalence of heterozygous Hb^{AB} genotype (64.15%) by Osaiyuwu et al. (2013) in WAD goat populations in the humid tropical Nigeria. Yakubu et al. (2014) characterized the genetic pool of the WAD goat using Hb polymorphism and observed that genotype frequencies of Hb^{AA}, Hb^{AB} and Hb^{AC} (37.0, 61.0 and 2.0 %) violated the Hardy-Weinberg equilibrium. The Hb^{AB} individuals showed superiority in feed efficiency over Hb^{AA} individuals with higher serum insulin and IGF-1 metabolism ($P = 0.018, 0.010$). This was corroborated by the negative-RFI value and the numerically higher FCE of the Hb^{AB} individuals over Hb^{AA} individuals. These findings support the theory of superiority and better adaptability of heterozygous individuals. The Hb^{AB} individuals synthesizing higher hormone insulin would better regulate carbohydrate metabolism, decrease blood glucose concentration, increase cell permeability to monosaccharides, amino acids and fatty acids and also, better regulate leptin activity (Gentry, 2001).

The high leptin concentration of the Hb^{AB} individuals was directly manifested by the high BCS of does. Similarly, the higher hormone IGF-1 level would stimulate increased anabolic processes in Hb^{AB} does than in Hb^{AA} does (Zhang et al., 2008). Thus, insulin and IGF-1 could be useful biomarkers of RFI in haemoglobin genotyped individuals because IGF-1 stimulates protein synthesis (Davis et al., 2012) since protein turnover is a main determinant of feed efficiency (Cantalapiedra-Hijar, et al., 2018). The ratio of Hb^{AB} to Hb^{AA} individuals (1:3) obtained in study revealed less dominant, virile and highly-adapted Hb^{AB} does on-farm. The higher feed efficiency demonstrated by Hb^{AB} individuals could be linked to their possible higher physiological affinity for oxygen transport than Hb^{AA}. This could be due to the possession of both alleles A and B, better respiration capacity, better environmental adaptability and serum metabolism than Hb^{AA} individuals.

The significant values of RFI^{LL}, RFI^{MM} and RFI^{HH} classes were related to corresponding levels of leptin, IGF-1, PCV and Hb content from low- to high-RFI animals. These levels conferred higher feed efficiency on low-RFI than medium- and high-RFI animals. The result from low-RFI individuals supports Johnston et al. (2002) who suggested the possibility for increasing growth rate, feed efficiency and percent lean meat through animal selection. This could be based on the complex interaction of observed serum metabolites and PCV/Hb complex. Kohn et al. (2005) reported that high serum urea concentration, as observed among present RFI classes, is an indication of high nitrogen metabolism in association with IGF-1 synthesis, which could result in lower protein utilization and efficiency. The high PCV was deemed adequate and represented no loss of blood or dehydration. The iron-containing, oxygen-transporting, metalloprotein Hb concentration was responsible for sufficient transport of oxygen to permit aerobic respiration within tissues, and results are similar to normal ranges of 21-25 %, and 7-15 g/dL for the Nigerian WAD goats (Daramola et al., 2005, Ogunbosoye et al., 2018). The PCV and Hb concentration levels within the normal ranges for WAD goats indicated healthy and good immunity status for RFI^{LL} and RFI^{HH} animal-classes. Furthermore, the similarity of DMI, ADG, FCE, BCS, insulin, urea, and blood parametric results among RFI classes signified their limitation for use as biomarkers of feed efficiency in WAD does. The present finding is similar to the observation of Clemmons et al. (2017) in steers where circulating serum urea nitrogen concentrations did not differ significantly between RFI^{LL} and RFI^{HH} animals. Similarly, Lawrence et al.

(2012) found no detectable differences between RFI groups for live weight, ADG and FCR on animals fed with ensiled or grazed grass herbage.

The interaction of Hb genotypes with RFI classes exposed FCE, IGF-1 and monocytes as potential traits (P = 0.021, 0.031, 0.045) for classifying research does. Although the effect was not significant (P = 0.077), RFI values were higher in individuals of Hb^{AA} and Hb^{AB} in the medium- and high-RFI classes than individuals of Hb^{AA} and Hb^{AB} in the low-RFI class. The negative values obtained by the low-RFI (nutrient-efficient) individuals support the work of Pryce et al. (2014) on the effectiveness of residual feed intake as a feed efficiency tool. Individuals with low-RFI impact positively on the environment through low-level greenhouse gas emission (enteric methane, nitrous oxide and carbon dioxide) and other waste products associated with urine and excreta (Muro-Reyes et al., 2011, Velazco et al., 2016). Residual feed intake thus represents genetic variation in basic metabolic processes for feed conversion efficiency (Arthur and Herd, 2008) in experimental does. Present results also indicate that low-RFI was phenotypically independent of ADG and FCE (Gilbert et al., 2017), and was also weakly correlated with BCS (Kushwaha et al., 2016) in the low-RFI individuals of Hb^{AA} and Hb^{AB}. Low RFI was moderately to strongly correlated with monocytes (rp = -0.456, 0.905, P = 0.010) and NLR in individuals with negative-RFI. The NLR in the peripheral blood reflects the balance between systemic inflammation and immunity and it is an important prognostic biomarker for diseases. The reverse association of RFI with NLR suggested moderate to high increases in NLR values as RFI value decrease.

A higher IGF-1 concentration synthesized by Hb^{AB} over Hb^{AA} individuals within the low-RFI class and lower association of IGF-1 with RFI (rp = -0.256, -0.064) seem to indicate higher physiological and cell accretion processes in Hb^{AB} than Hb^{AA} individuals. Cantalapiedra-Hijar, et al. (2018) report that efficient (low-RFI) animals have significantly lower energy metabolic rate regardless of the associated intake reduction. They suggest that lower heat production (from maintenance and production) could have originated from decreased protein turnover and higher efficiency of ATP production in mitochondria and conclude that energy metabolism could be a true determinant of animal-to-animal variation in feed efficiency. Monocytes are involved in the processes of the innate immune response and regulation of cellular homeostasis during infection and inflammation (Espinoza and Emmady, 2022). In present study, Hb^{AB} by low-RFI animals revealed low-level monocytes' percentage and highly positive association of monocytes with low RFI (P = 0.010), which probably indicated low-level activity in phagocytizing infectious organisms, particulates and cell debris (Jones, 2011). The low monocytes percent (8.50%) obtained from Hb^{AB} x RFI^{LL} does is consistent with report in literature (Jones, 2011; Njidda et al., 2014). Also, these individuals revealed an antagonism between RFI and each of ADG, FCE, insulin, leptin, IGF-1, urea, NLR; and low association of RFI with BCS and DMI. These associations may mark efficient metabolism and physiological processes in low-RFI animals. Findings in this study support Cantalapiedra-Hijar, et al. (2018) that association of leptin and feed efficiency is inconsistent, and that association of leptin and RFI or FCR depends on the physiological stage of an animal.

The Hb^{AA} individuals in the medium-RFI were next on RFI scale (RFI = 0.00), with higher monocytes percent than other individuals, but with moderately negative association with RFI (rp = -0.554). This might be an indication of high synthesis of monocytes to fight diseases, infections and stress due to low immunity status. These individuals (neutral RFI value) showed similar FCE values with Hb^{AA} individuals in high-RFI class, but lower than Hb^{AB} individuals in the same class. The linear association of RFI with all other traits examined was weak to moderate. The low BCS observed was possibly due to decreased levels of body fat reserve due to its mobilization (Castagnino et al, 2015) for growth, lactation and maintenance of pregnancy by does; and ultimately this condition assessed the impact of negative energy balance in individuals. The low IGF-1 synthesis might have resulted in the moderately negative association with RFI (rp = -0.461).

In individuals with positive-RFI values (RFI > 0.00), RFI increased positively with ADG, FCE and BCS in the Hb^{AA} individuals (P = 0.010 – 0.050), the same trait increased linearly with insulin concentration (P = 0.050) and decreased with serum urea nitrogen (P = 0.050) in Hb^{AB} individuals. This is similar to the report on differences for urea, IGF-1 and insulin among RFI classes of Nellore cattle (Nascimento et al, 2015). BCS value below 2.0 indicates low-level production of insulin, IGF-1 and urea, and may mark under-nutrition and low-level carbohydrate storage in farm animals (Caldeira et al. 2005), but the higher values (> 2.50) in present study signified adequate physical body condition and capacity for moderate fat accretion in body tissues by experimental animals. The Hb^{AB} individuals in high-RFI class demonstrated higher FCE and IGF-1 metabolism. Howbeit, it seemed the IGF-1 was not efficiently utilized, as evidenced by the weak association of RFI with urea and insulin (P < 0.050) respectively, thus revealing a complex interrelationship among IGF-1, insulin and Urea. Furthermore, as RFI increased, monocytes concentration reduced (rp = 0.099, -0.577) in heterozygous Hb^{AB}*RFI^{HH} genotype. The higher IGF-1 concentration of Hb^{AB} individuals in the high-RFI class foreclosed detrimental metabolic abnormality and diabetes (Li et al., 2004). Cantalapiedra-Hijar, et al. (2018) concluded that hormones and body composition could not be conclusively related to animal-to-animal variation in feed efficiency, and that analysis of potential biological networks underlying RFI variations in their study highlighted other pathways such as lipid metabolism, immunity and stress response. This study on interaction of haemoglobin genotypes with RFI classes has differentiated experimental WAD does based on FCE, serum IGF-1 concentration and monocytes percent.

Conclusion

Individuals of haemoglobin genotypes were differentiated by serum insulin and insulin-like growth factor-1 concentrations. Residual feed intake differentiated does on serum leptin, IGF-1, PCV and Hb concentrations. Interaction of Hb-genotype with residual feed intake produced significant differences among individuals on FCE, IGF-1 and monocytes percent. The Hb^{AB} individuals in low-RFI class were more feed-efficient and could be selected for breeding feed-efficient animals. Therefore, Hb genotype and RFI could be jointly incorporated in WAD selection programs in the humid tropics.

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Animal welfare statement

The authors confirm that the experimental procedures of this work complied with the ARRIVE guidelines 2019: for reporting animal research. The EU standards for the protection of animals used for scientific purposes were duly followed. The ethical policies of the journal, as noted to, and the journal's author guidelines have been adhered to the research policy of the Federal University Oye-Ekiti.

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