

Phenotypic and morphometric differentiation of indigenous chickens from Kenya and other tropical countries augments perspectives for genetic resource improvement and conservation

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ABSTRACT Indigenous chickens at the Swahili coast and other traditional migratory corridors in Kenya represent important populations that are inconclusively characterized. Using a comprehensive dataset of Kenyan indigenous chickens and additional mined data of chickens from 8 African and 5 Asian countries, we performed univariate and multivariate assessments to uncover the underlying phenotypic and morphometric variability. Kenyan indigenous chickens expressed differentiation of several qualitative and quantitative traits, both among different counties in the Swahili coast, and among coastal, western, and northern migratory corridors. There was a substantial population stratification of these chickens, particularly distinctive clustering of chickens from Marsabit, Lamu, and Kilifi

counties. The pooled dataset further clarified a closer phenotypic and morphometric proximity of chickens within different geographical regions. We additionally revealed a preponderance of bantam and rumpless traits to hot and humid locales, and feathered shanks to cooler regions. Currently, most chicken breeding programs in developing countries rely on phenotypic and morphometric properties. Hence, the high chicken diversity and population stratification observed in our study, possibly shaped by natural and artificial selective pressures, reveal opportunities for complementary phenotypic and genotypic assessments to identify resources for effective breed improvement and conservation strategies of indigenous chickens in the tropics.

Key words: phenotypic, morphometric, indigenous, chicken, Kenya

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INTRODUCTION

Domestic chickens (*Gallus gallus domesticus*) are among the most abundant and widely spread domestic animals (Lawler, 2014). Their uses have greatly

diversified, ranging from anthropometric purposes like entertainment and ornamentation to biomedical research and as an important source of protein (both meat and eggs) (Granevitze et al., 2007; Scanes, 2007; Wu and Kaiser, 2011). Indigenous domestic chickens are often reared under the traditional scavenging system by small-holder farmers in developing countries (Magothe et al., 2012; Desta et al., 2013). The indigenous chickens are popular in these regions because of their tolerance to common poultry diseases and fluctuations in both feed quality and quantity, hence requiring minimum or no input (Desta and Wakeyo, 2012). Because of the natural and artificial selection, indigenous chicken exhibit a wide spectrum of phenotypic and morphologic properties (Wragg et al., 2012). This denotes a rich genetic diversity that requires intensive characterization

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for breeding and conservation purposes (Dessie et al., 2011).

Points and patterns of introduction of domestic chickens into Africa and their subsequent radiation within and across different countries played important roles in constituting the genetic stock of African indigenous chickens (Mwacharo et al., 2013b; Osman et al., 2016). Importance of ancient maritime and terrestrial trade routes that interconnected Africa with other continents are well appreciated in previous chicken studies (Mwacharo et al., 2007; Mwacharo et al., 2013a; Osman et al., 2016). In Kenya, the Swahili coast was at the center of the Indian Ocean trade which facilitated the maritime introduction of domestic chickens into Africa (Prendergast et al., 2017). Additionally, traditional migratory corridors established during the peopling of Kenya, particularly the northern Kenya corridor (Lake Turkana basin) for the Nilotic ethnic groups and western corridor (Mount Elgon catchment) for the Bantu ethnic groups (Sayed et al., 2017), have an important implication with regards to the terrestrial spread of indigenous chickens from other African regions into Kenya, and their subsequent population differentiation (Ngeno et al., 2014a; Moraa et al., 2015).

Chicken breeding and conservation programs require extensive and continuous characterization of chickens. Phenotypic and morphometric approaches are fundamental in chicken breed management in resource poor settings because they are simple, fast, and cost-effective (Dorji and Sunar, 2014). In the present study, we accomplished a comparative phenotypic and morphometric analysis supported by a large-scale indigenous chicken dataset covering 12 counties located in the historical coastal, western, and northern migration corridors in Kenya. We further retrieved and incorporated published phenotypic data of indigenous chicken from other countries in and out of Africa to decipher the phenotypic relationships among indigenous chickens at a broader scope.

MATERIALS AND METHODS

Study Design and Data Collection

The study of indigenous chickens in Kenya was carried out according to the permission and guidelines provided by the Directorate of Veterinary Services at the State Department of Livestock, Ministry of Agriculture Livestock and Fisheries of Kenya (Permit number RES/POL/VOL.XXVII/162).

Indigenous chicken were sampled in Kenya from 2012 to 2015 through rural participatory approach. Sampling covered the Kenyan Swahili coast (Kilifi, Kwale, Lamu, and Mombasa counties), western Kenya (Bungoma, Busia, Kakamega, Homabay, West Pokot, and Trans-Nzoia counties), and northern Kenya (Marsabit and Turkana counties). These regions are renowned for indigenous chicken keeping, represent the traditional migratory corridors in Kenya, and have not

been affected by the cockerel and pullet exchange programs (Gifford-Gonzalez and Hanotte, 2011).

Chicken were sampled as described in a subset of the data collected before 2015 (Moraa et al., 2015). Briefly, households willing to participate in the study were selected with the assistance of local veterinary officers. In each sampled household, farmers were interviewed on the family history of their chicken and only unrelated adult chicken (>6 mo old) were sampled. We sought to randomly sample 2 chickens, a male and a female, in each household, and about 20 chickens in every county. Sampling was also informed by chicken availability at the time of visit and flock history. Neighboring households (<0.5 km apart) were skipped to avoid sampling related chickens. Phenotypic and morphometric parameters were collected on-site following the standard chicken descriptor criteria of the Food and Agriculture Organization (FAO, 2012). These included forearm length of the ulna, shank length, shank thickness, keel length, and live body weight. Linear measurements were taken in millimeters (mm) to 2 decimal points using veneer calipers, whereas weight was measured with a digital weighing scale in kilograms (kg) to 2 decimal points. Phenotype data collected included feather morphology and coloration, comb type and color, presence or absence of toe-nails, as well as the colors of skin, shank, wattles, and earlobes. The gender of the chicken and unique attributes like bantams or kuchi was also recorded.

Additional data was obtained through literature search for peer-reviewed articles in PubMed, Google Scholar, and ResearchGate electronic databases using combinations of the following key words: “chicken”, “phenotype”, “morphological”, and “characterization”. We focused on primary research papers with original indigenous chicken phenotypic data published in English language. Reference lists of the selected papers were cross-checked for additional relevant studies. Authors were contacted for papers or data that were not publicly available. For each paper, we recorded the authors’ names, publication year, study-location, number of chicken studied, and all the traits reported plus their respective statistics.

Statistical Analysis

We first assessed the characteristics of chickens from the Kenyan Swahili coast, being the epicenter of the ancient Indian Ocean trade. We then compared the coastal chickens to those from the western and northern migratory corridors. The occurrence and distribution of qualitative traits were compared across different regions using Kruskal-Wallis test. PermutMatrix v.1.9.3 was used to construct a heat map illustrating the variability of color traits across the 12 counties. Overall variation in the frequencies of different comb types was assessed using Cochran Q test. Comparison of quantitative traits across regions was performed using ANOVA, and between regions using Tukey’s HSD test. The overall

correlation among these traits was tested using Pearson correlation.

We explored the differentiation of phenotypic and morphometric properties between indigenous chicken sexes. Using the observed gender as the grouping variable, we loaded all variables without cross-validation flags in a discriminant analysis model implemented in PAleontological STatistics (**PAST**) software v.3.16, with the final model retaining variables with the most favorable confusion matrix. The axis scores generated were plotted into a frequency polygon using the same software.

Finally, we assessed the structuring patterns of different chicken populations based on their phenotypic and morphometric traits using Canonical Variates Analysis (**CVA**) and hierarchical clustering analysis in the **PAST** software v.3.16. The CVA analysis followed the steps outlined in the discriminant analysis, but used the geographical regions as grouping variable. Scree plot of eigenvalues of all the axes was used to select a pair of the most suitable axes for plotting the CVA diagram. The variability scores of the selected axes were utilized to plot the CVA diagrams using R software v.3.4.2 (R Core Team, 2017). A hierarchical clustering tree was computed using the **UPGMA** (Unweighted Pair Group Method with Arithmetic Mean) algorithm with Euclidean indices. The tree was viewed using FigTree v.1.4.3.

We standardized the mined dataset by converting the total number of observations of each qualitative trait into ratios based on *N*-values of each study, making the units of the quantitative traits uniform across all studies. Our Kenyan chicken data was grouped per county before pooling it with the mined dataset. We then carried out the CVA procedures as outlined above. Kenyan counties were grouped according to the 3 migration corridors. The other chicken were grouped into eastern Africa (Tanzania and Ethiopia), western Africa (Nigeria and Ghana), southern Africa (Botswana and Zimbabwe), northern Africa (Algeria and Libya), and Asian (Bhutan, Sri-Lanka, Bangladesh, Philippines, and Oman). All analyses, unless specified, were conducted using IBM SPSS Statistics software v.20. *P* values < 0.05 were considered significant.

RESULTS

General Characteristics of Chickens in this Study

A total of 681 indigenous chickens from 12 counties in Kenya were sampled. Overall, 419 (61.5%), 168 (24.7%), and 94 (13.8%) chickens represented coastal, western, and northern Kenya respectively, with a general balance between females (54.5%) and males (45.5%) ($P = 0.346$) (Figure 1a and Table 1). We retrieved published phenotypic and morphometric data of a total of 21,361 indigenous chickens for the extended comparative analysis. This dataset was obtained from 28 stud-

Table 1. General demographic information of indigenous domestic chicken sampled from Kenya in the current study.

	Total n	Females n (%)	Males n (%)
Coastal Kenya ¹			
Kilifi	104	51 (49.0)	53 (51.0)
Kwale	82	40 (48.8)	42 (51.2)
Lamu	193	100 (51.8)	93 (48.2)
Mombasa	40	20 (50.0)	20 (50.0)
Western Kenya			
Bungoma	25	17 (68.0)	8 (32.0)
Busia	19	9 (47.4)	10 (52.6)
Kakamega	29	20 (69.0)	9 (31.0)
Homabay	64	41 (64.1)	23 (35.9)
West Pokot	18	9 (50.0)	9 (50.0)
Trans-Nzoia	13	9 (69.2)	4 (30.8)
Northern Kenya			
Marsabit	61	35 (57.4)	26 (42.6)
Turkana	33	20 (60.6)	13 (39.4)
Total	681	371 (54.5)	310 (45.5)

¹Sub-region names represent counties.

Chi-square $P = 0.346$ for the overall female and male frequency variation.

ies conducted in 13 countries (8 African and 5 Asian) (Figure 1b; Supplementary table S1).

Phenotypic Variations among Indigenous Chickens in Kenya

In the analysis of chickens in the coastal Kenya counties, barred ($P = 0.001$), crested ($P = 0.006$), kuchi ($P = 0.001$), toe-nailed ($P = 0.048$), and mottled ($P = 0.018$) showed disproportionate distribution across the 4 counties (Table 2). Mixed plumage pattern was the most common among coastal chickens, occurring in 282 (67.3%) chickens ($P > 0.05$), whereas the least was mottled, occurring in only 20 (4.8%). The other plumage patterns were barred and plain, observed in 159 (37.9%) and 37 (8.8%) chickens, respectively. Notably, kuchi chickens were not recorded in Kilifi county, constituted less than 10% of chickens in Kwale (3.7%) and Mombasa (7.5%), but were the majority in Lamu county (65.8%) (Table 2).

Significant differences were observed among chickens from the coastal, western, and northern Kenya migratory corridors. These differences were attributable to disproportionate occurrence of barred, mixed, bantam, kuchi, feathered shank, toe-nailed ($P = 0.001$), and crested and rumpless phenotypes ($P < 0.05$) across the 3 regions. Kuchi and bantam traits displayed the most restricted distribution, with kuchi chicken occurring only in the coastal region and bantam showing bias towards the northern Kenya region (Table 3).

A total of 7 comb types were observed in the Kenyan indigenous chickens (Figure 2). Apart from single comb type being the most common across the board, albeit with significant differences in frequency within the coastal region and other regions ($P = 0.001$), interesting comb type patterns were observed. Lamu and Mombasa counties had the highest comb type variability at

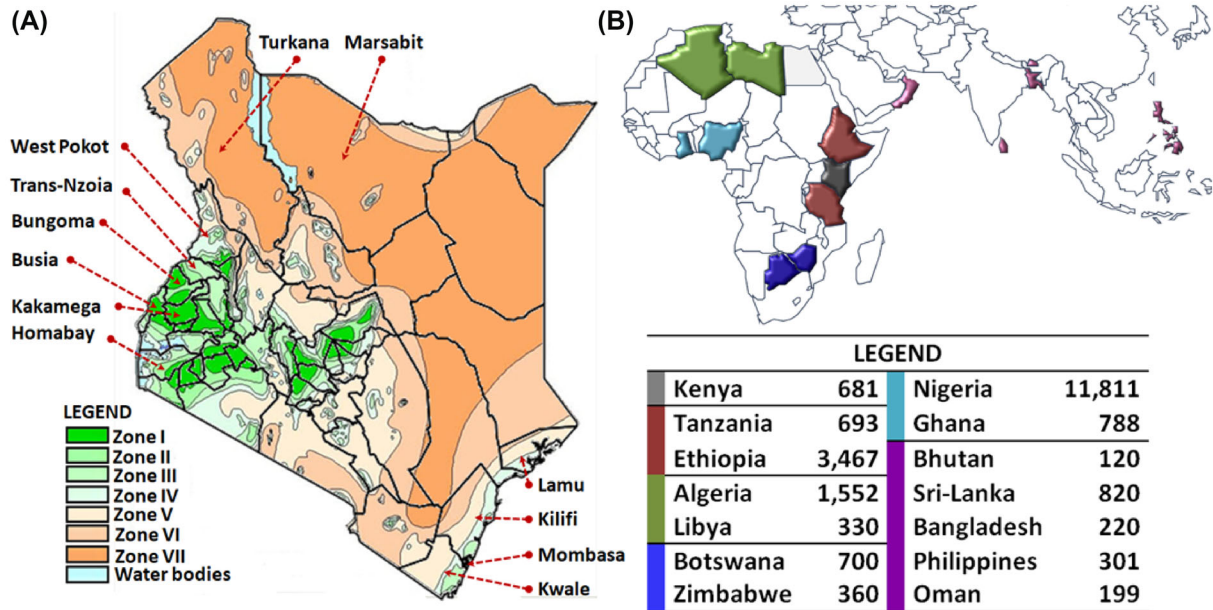


Figure 1. Maps showing sampling locations. (a) 12 counties sample in Kenya. (b) Countries represented in the pooled dataset of indigenous chickens. Number of samples is indicated per country with the color codes matched to the map. Maps adopted from www.infonet-biovision.org and SmartDraw 2017 (www.smartdraw.com).

the coast, with strawberry being the most common in Lamu (Figure 2a). This high comb diversity in Lamu and Mombasa evidently contributed to overall higher comb type diversity in the coast compared to the western and northern regions (Figure 2b).

A wide color spectrum was observed in the Kenyan chicken combs, skin, shanks, earlobes, and wattles (Figure 3), with several colors showing differential frequencies across the 4 coastal counties (Supplementary table S2) and the 3 migratory corridors (Supplementary table S3). The most common color phenotypes were: red and pale comb colors; cream, yellow, and white skin colors; yellow, cream, and white shank colors; white and

yellow earlobe colors; as well as red and pale wattle colors (Figure 3).

Regional Variation of Kenyan Chicken Body Weight and Linear Traits

Chicken live body weight as well as 3 linear traits (shank thickness, forearm length, and keel length) exhibited regional differentiation within coastal Kenya ($P = 0.001$, $P = 0.001$, $P = 0.016$, and $P = 0.001$, respectively) (Table 4). Notably, chicken from Lamu county expressed the highest values of all the quantitative traits, likely attributable to the kuchi chicken

Table 2. Distribution of different phenotypes among indigenous chickens in the coastal region of Kenya.

	Frequency, n (%) ¹				Total n = 419	P value ²
	Kilifi n = 104	Kwale n = 82	Lamu n = 193	Mombasa n = 40		
Plumage pattern						
Plain	7 (6.7)	9 (11.0)	16 (8.3)	5 (12.5)	37 (8.8)	0.621
Barred	52 (50.0)	45 (54.9)	52 (26.9)	10 (25.0)	159 (37.9)	0.001
Mottled	10 (6.6)	5 (6.1)	3 (1.6)	2 (5.0)	20 (4.8)	0.018
Mixed	71 (68.3)	60 (73.2)	131 (67.9)	20 (50.0)	282 (67.3)	0.079
Plumage structure						
Frizzled	5 (4.8)	4 (4.9)	2 (1.0)	3 (7.5)	14 (3.3)	0.086
Crested	10 (9.6)	10 (12.2)	5 (2.6)	1 (2.5)	26 (6.2)	0.006
Naked neck	3 (2.9)	3 (3.7)	8 (4.1)	1 (2.5)	15 (3.6)	0.928
Type						
Bantam	1 (1.0)	2 (2.4)	0	1 (2.5)	4 (1.0)	0.189
Kuchi	0	3 (3.7)	127 (65.8)	3 (7.5)	133 (31.7)	0.001
Others						
Rumples	8 (7.7)	4 (4.9)	5 (2.6)	2 (5.0)	19 (4.5)	0.250
Feathered shank	2 (1.9)	2 (2.4)	4 (2.1)	1 (2.5)	9 (2.1)	0.993
Toe-nailed	55 (52.9)	37 (45.1)	70 (36.3)	18 (45.0)	180 (43.0)	0.048

¹Percentages indicate the prevalence of each trait within each county.

²Variation of each trait across the 4 coastal counties was compared using Kruskal-Wallis test.

Table 3. Distribution of different phenotypes among indigenous chickens in different regions in Kenya.

	Frequency, n (%) ¹				P value ²
	Coast n = 419	Western n = 168	Northern n = 94	Total n = 681	
Barred	159 (37.9)	49 (29.2)	3 (3.2)	211 (31.0)	0.001
Frizzled	14 (3.3)	6 (3.6)	0	20 (2.9)	0.190
Mixed	282 (67.3)	115 (68.5)	83 (88.3)	480 (70.5)	0.001
Plain	37 (8.8)	18 (10.7)	9 (9.6)	64 (9.4)	0.778
Crested	26 (6.2)	20 (11.9)	5 (5.3)	51 (7.5)	0.042
Rumpless	19 (4.5)	3 (1.8)	0	22 (3.2)	0.038
Naked neck	15 (3.6)	14 (8.3)	5 (5.3)	34 (5.0)	0.057
Bantam	4 (1.0)	0	39 (41.5)	43 (6.3)	0.001
Kuchi	133 (31.7)	0	0	133 (19.5)	0.001
Feathered shank	9 (2.1)	23 (13.7)	1 (1.1)	33 (4.8)	0.001
Toe-nailed	180 (43.0)	54 (32.1)	11 (11.7)	245 (36.0)	0.001
Mottled	20 (4.8)	16 (9.5)	7 (7.4)	43 (6.3)	0.091

¹Percentages indicate the prevalence of each trait within each county.

²Variation of each trait across the 3 regions was compared using Kruskal-Wallis test.

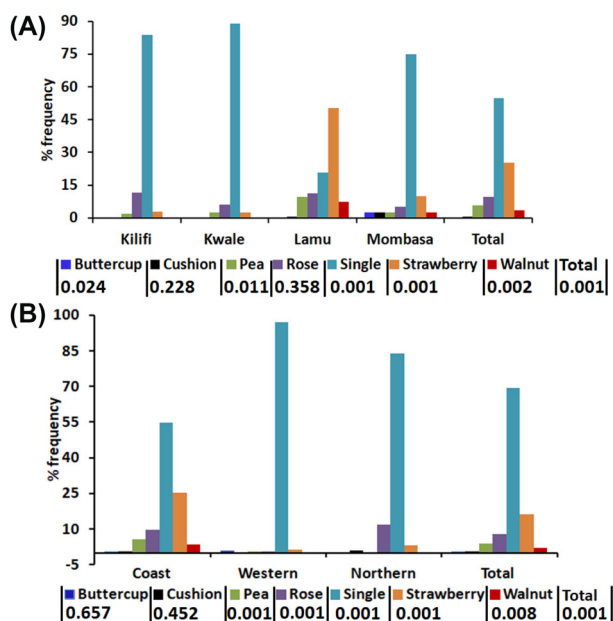


Figure 2. Diversity of comb type trait. (a) Comparisons among indigenous chickens from coastal and (b) 3 regional divisions in Kenya. Vertical axes represent percent frequencies whereas x axes represent different geographical regions. Captions below each graph show P values for Kruskal-Wallis and Cochran Q P values for comparison of each comb type across different regions and the overall difference in occurrence of the comb types, respectively.

in the county. Live weight further showed differences across the coastal, western, and northern Kenya regions as well as in all pair-wise comparisons between the regions (Table 5). Coastal chickens were the heaviest, whereas their counterparts from northern Kenya were the lightest, mirroring the biased occurrence of kuchi and bantams in coastal and northern regions, respectively. The coastal chickens also had superior ($P < 0.05$) shank lengths and thickness, as well as keel lengths (Table 5). In addition, the 5 quantitative chicken traits showed positive pair-wise correlation ($P = 0.001$) (Table 6).

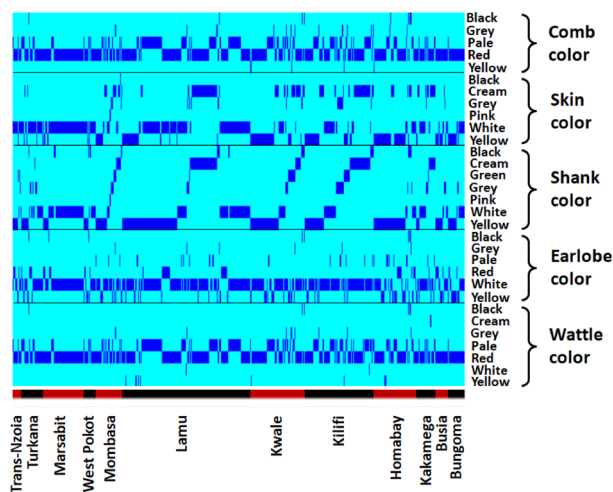


Figure 3. Heat map representing the color profiles of different body parts of indigenous chickens from Kenya. Cyan represents absence whereas dark blue represents presence of the color traits. Red and black colors in the bar at the bottom of the heat map demarcate portions of the map representing various counties. Statistics of the diversity of each trait is presented in Supplementary table S1 and S2.

Population Stratification of Indigenous Chicken Based on Phenotypic Traits

We explored the overall differentiation of indigenous chickens based on their phenotypic and morphometric properties. We first assessed the level of sexual dimorphism in the Kenyan chicken dataset using the observed gender as the standard. Loading a total of 49 variables (Supplementary table S4) into the discriminant analysis model, the gender of 84.9% of the chickens were correctly assigned (Figure 4). A greater proportion of males (90.3%) than of females (78.4%) were accurately predicted. This analysis demonstrated that the female and male indigenous chickens are distinguishable by their phenotypic and morphometric traits.

We then computed CVA and a hierarchical tree to assess the overall relationship among indigenous chickens from different migratory corridors in Kenya based on 54

Table 4. Comparison of quantitative traits of indigenous chickens from Kenyan coast.

	Kilifi Mean (SE) ¹	Kwale Mean (SE)	Lamu Mean (SE)	Mombasa Mean (SE)	<i>P</i> value ³
Live weight ²	1.94 (0.05) ^{c4}	1.55 (0.06) ^b	2.21 (0.05) ^a	1.93 (0.11) ^c	0.001
Shank length ²	109.35 (1.85)	105.15 (1.84)	113.96 (2.45)	112.34 (3.21)	0.082
Shank thickness	14.49 (0.25) ^c	13.34 (0.26) ^b	15.53 (0.29) ^a	14.53 (0.46) ^{a,b,c}	0.001
Forearm length	146.49 (2.34) ^b	147.83 (1.87) ^{a,b}	155.08 (2.38) ^a	144.01 (3.03) ^b	0.016
Keel length	128.76 (1.76) ^b	126.76 (1.98) ^b	139.23 (2.25) ^a	126.14 (3.61) ^b	0.001

¹SE = standard error of mean.

²Weight and lengths are in kilograms (**kg**) and millimeters (**mm**), respectively.

³*P* values indicate the variation in each trait across the 4 counties compared by ANOVA.

⁴Different superscript letters within the same row indicate different pairs of means (Tukey's HSD test, *P* < 0.05).

Table 5. Comparison of quantitative traits of indigenous chicken from Kenyan coast against other regions in the country.

	Coast Mean (SE) ¹	Western Mean (SE)	Northern Mean (SE)	<i>P</i> value ³
Live weight ²	1.99 (0.03) ^{a4}	1.81 (0.05) ^b	1.19 (0.04) ^c	0.001*
Shank length ²	110.94 (1.31) ^a	104.88 (4.49) ^b	54.15 (2.55) ^c	0.001*
Shank thickness	14.51 (0.15)	12.66 (0.23)		0.001 [¥]
Forearm length	148.66 (1.21)	147.37 (1.76)		0.543 [¥]
Keel length	130.94 (1.14)	126.40 (1.77)		0.033 [¥]

¹SE = standard error of mean.

²Weight and lengths are in kilograms (**kg**) and millimeters (**mm**), respectively.

³*P* values indicate the variation in each trait across the 3 regions compared by ANOVA (*) or two-sample *t* test ([¥]).

⁴Different superscript letters within the same row indicate different pairs of means (Tukey's HSD test, *P* < 0.05).

Table 6. The correlation between different quantitative traits of indigenous chickens in Kenya.

	Live weight	Shank length	Shank thickness	Forearm length	Keel length
Live weight	1				
Shank length	0.466*	1			
Shank thickness	0.832*	0.73*	1		
Forearm length	0.532*	0.576*	0.559*	1	
Keel length	0.712*	0.636*	0.668*	0.495*	1

*(Asterisks) on the Pearson correlation coefficients indicate *P* = 0.001 for correlation between the traits compared.

phenotypic and morphometric variables (Supplementary table S5). Interestingly, chicken from Marsabit, Lamu, and Kilifi formed substantially distinctive clustering (Figure 5a and Supplementary figure S1). The fourth cluster comprised of mixed populations with overlapping sub-clusters, also including a few individual offshoots from the former 3 clusters (Figure 5a). When we pooled the Kenyan chicken data with other chickens from other countries, we observed very distinctive population stratification (Figure 5b) in a CVA analysis based on 31 variables listed in Supplementary table S6. This analysis separated chicken from coastal Kenya from those from the inland regions, with western and northern Kenya chickens showing a closer proximity. Overall, this analysis demonstrated a closer intra- than inter-population phenotypic and morpho-

logical proximity of chickens from the 3 migratory corridors in Kenya and other regions in Africa and Asia (Figure 5b).

DISCUSSION

This study employed a comprehensive dataset to decipher phenotypic and morphometric variability of indigenous domestic chickens. We present a large-scale characterization of indigenous chickens from the Kenyan Swahili coast, an important gateway into Kenya and the rest of Africa (Prendergast et al., 2017), in comparison to chickens from other traditional migratory corridors in the western and northern Kenya (Sayed et al., 2017). We further show the interactions among Kenyan chicken populations and how they relate to chickens from other African countries and Asia.

We observed an interesting bias of some adaptive traits like rumpless and bantam to hot and humid regions (coast and northern Kenya, respectively), and feathered shanks to cooler and wet regions (western Kenya). These traits are important for thermoregulation (Magothe et al., 2012). Such adaptive traits and desirable properties like those embodied by the kuchi avail important considerations for national chicken breed improvement and conservation programs.

Based on a comprehensive list of phenotypic and morphometric variables, we revealed local differences in indigenous chickens from 4 coastal counties in Kenya despite their geographical proximities. A similar observation was made when we compared coastal chickens with those from western and northern inland regions of the country. These findings were further clarified in multivariate assessments which isolated majority of chickens from Marsabit, Lamu, and Kilifi. Generally, these findings corroborate previous studies that have reported dissimilarities among chicken populations from different geographical locations (Mwacharo et al., 2007; Ngeno et al., 2014b; Moraa et al., 2015). Geographical isolation could explain this differentiation. For instance, Lamu county is characterized by islands and vast forests which tend to modulate contacts with other regions. As observed by previous studies (Magothe et al., 2012; Moraa et al., 2015), we report an exclusive presence of kuchi

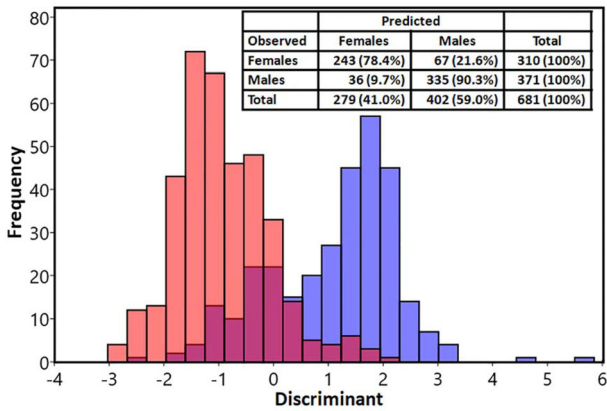


Figure 4. Analysis of sexual dimorphism in Kenyan indigenous chickens based on phenotypes. (a) Histograms depicting the degree of separation of the chicken. Females are represented by red bars, males by blue, whereas misclassification is indicated by purple. The caption indicates the overall classification with an 84.9% correct prediction rate.

chicken at the coastal corridor, particularly in Lamu. Kuchi are heavy bodied chickens tolerant to adverse environmental conditions and diseases (Lwelamira et al., 2009). Their predominance and restriction within Lamu possibly enhance the separation of Lamu chickens from other coastal Kenya chickens. On the other hand, extreme aridity has traditionally isolated northern Kenya regions like Marsabit, limiting their contact with other Kenyan communities (Mwacharo et al., 2007). Northern Kenya corridor, particularly Marsabit county, exhibited the highest presence of bantam chickens. Due to their small size, bantam chickens have a better capacity for heat dissipation (Islam, 2005), a property that

gives them a survival edge in hot and arid regions like Marsabit. Like the kuchi in Lamu, bantams possibly swayed the out-clustering of Marsabit chicken population.

Despite the geographical isolation, likely presence of directional movements of chickens can be inferred. For instance, as argued by other researchers (Mwacharo et al., 2007; Magothe et al., 2012), there is likely an active local chicken trade and transfer of germplasm among communities in western Kenya, resulting into a complex stratification pattern as seen in our analysis. Additionally, CVA results suggest that the movement of chicken from Lamu and Kilifi into other coastal regions, and from Marsabit into the rest of northern and western regions seems more plausible than in the reverse direction. This could be paralleling human migration along urbanization clines.

The comparison of chickens from different countries covering sparse geographical scope underscored our speculation, suggesting a generally increased population differentiation with an increase in geographical distance and isolation. This is a well-documented concept in chicken population genomic studies (Mwacharo et al., 2007; Lyimo et al., 2014). It can be attributed to heterogeneity in natural and artificial selective pressures affecting chickens in different locations, coupled with human and geographical delimitations which segregate various indigenous chicken populations (Desta et al., 2013; Bettridge et al., 2018). This analysis further indicates the potential effect of the introduction of chickens into Kenya, and Africa at large, over different periods through multiple entry points (Lyimo et al., 2014; Prendergast et al., 2017).

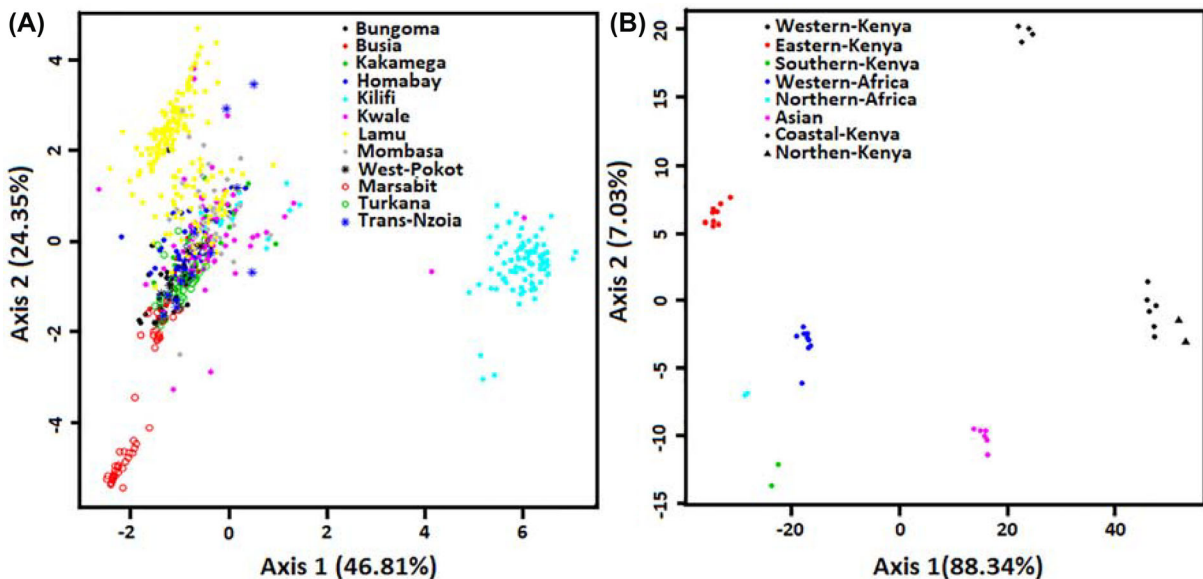


Figure 5. Multivariate projections of indigenous chicken population differences based on phenotypic and morphological relationships traits. (a) Canonical Variates Analysis (CVA) of 681 indigenous chickens from 12 counties in Kenya. (b) CVA of a pooled dataset representing 22,042 chickens. Data from our study was grouped per county whereas the rest were grouped per source study. Coastal, western, and northern Kenya represent regional grouping of counties as stated in Table 1. Chickens from other countries are represented as eastern Africa (Tanzania and Ethiopia), western Africa (Nigeria and Ghana), southern Africa (Botswana and Zimbabwe), northern Africa (Algeria and Libya), and Asian (Bhutan, Sri-Lanka, Bangladesh, Philippines, and Oman). In both figures, the first and second axes are shown, with the percentages indicating the proportions of the total variance explained by each axis.

Color profiles of chicken comb, skin, shank, earlobes, and wattles in Kenya were generally synonymous with earlier findings on Kenyan indigenous chicken (Ngeno et al., 2014a). Chicken weight and linear traits also unsurprisingly showed positive correlations, whereas male and female chickens displayed differential traits, both corroborating the findings of several previous studies (Dorji and Sunar, 2014).

In conclusion, we show a high diversity and important geographical differentiation in the phenotypic and morphometric properties of indigenous chickens drawn from 3 historical migratory corridors in Kenya. These findings highlight opportunities for selecting appropriate genetic resources for chicken breeding and conservation programs in Kenya and other tropical countries. To facilitate this, and to expand the platform for future phenomic studies (Houle et al., 2010) in chicken, standardization of approaches for identification, characterization, and reporting of chicken phenotypic and morphometric traits is required.

SUPPLEMENTARY DATA

Supplementary data are available at *Poultry Science* online.

Supplementary figure S1. Hierarchical tree showing the clustering pattern of indigenous chickens from 12 counties in Kenya based on phylogenetic and morphometric traits. Red, green, and blue colors indicated counties with distinct clustering patterns.

Supplementary table S1. Description of indigenous chicken data mined from published studies.

Supplementary table S2. Companion table for figure 3 showing comparison of color profiles of different chicken body parts across 4 counties in Kenyan coast.

Supplementary table S3. Companion table for figure 3 showing comparison of color profiles of different chicken body parts across the coastal, western, and northern Kenya regions.

Supplementary table S4. Discriminant analysis loading values for sexual dimorphism assessment among indigenous chickens from Kenya.

Supplementary table S5. Canonical Variates Analysis loading values for population stratification assessment of indigenous chickens from Kenya.

Supplementary table S6. Canonical Variates Analysis loading values (first five axes) for population stratification assessment of indigenous chicken in the pooled database.

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