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Genetic diversity in pigeon (*Columba livia domestica*) from three agro-ecological zones in Nigeria

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A R T I C L E I N F O

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A B S T R A C T

Background: The domesticated pigeon (*Columba livia domestica*) possesses many valuable traits including high nutritional value and fast growth. However, there is a paucity of information on the genetic diversity and population structure of Nigerian domestic pigeon populations.
Methods and results: We examined the pattern of the genetic variability using three concatenated sequences from cytochrome oxidase subunit I (*COI*), cytochrome B (*CYTB*), and D-loop. We studied 150 captured pigeons from three agro-ecological zones in Nigeria. The result showed 52 haplotypes (HT1-HT52) occurred only in Nigerian populations based on the three concatenated sequences. The overall haplotype diversity was 0.876 ± 0.019, and nucleotide diversity 0.055 ± 0.027. The phylogenetic tree showed significant clustering and genetic relationship of Nigerian domestic pigeons. The median-joining network showed two groups (A and B) in the Nigerian pigeon population. The group A exhibits historical population expansion which are supported by neutrality test results and Bayesian skyline plot (BSP) for the 146 Nigerian pigeon populations.
Conclusions: This study revealed unique haplotypes, low genetic diversity, and population differentiation of Nigerian domestic pigeons.

1. Introduction

The domestication of pigeons is believed to occur as early as 3000 B·C from the rock dove (Glover, 1999). Today, over 300 breeds of domestic pigeons have been reported by breeders and scientists worldwide (Biała et al., 2015). One of the unique attributes of wild rock pigeons is their innate homing ability (i.e. ability to return to their nest using magnetoreception) (Blechman, 2007). The homing pigeon is a variety of domesticated pigeons (*Columba livia domestica*) selectively bred for its ability to find its way home over extremely long distances. Pigeons were previously used as a means of communication before the invention of the telephone (Podbielska and Radko, 2022). Moreover, it was proven that human population density might affect the genetic diversity of pigeons in the eastern United States (Carlen and Munshi-South, 2021) and natural selection might influence the population of pigeons (Murray et al., 2017).

Generally, domestic pigeons are valued for high nutritional value, fast growth rate, extraordinary phenotype, sporting activities, and food. In Nigeria, the homing pigeon is one of the important animal genetic resources and is valued for its meat, eggs, aesthetic, recreational, spiritual, and ritual purposes (Sola-Ojo and Atteh, 2017). Despite these innate potentials of domestic pigeons, there is a dearth of information on their genetic studies across various agroecological zones of Nigeria. Our recent study investigated the effect of locations on the phenotypes of domestic pigeons in Nigeria at the morphological level (Abubakar et al., 2021). This method is less accurate for selective breeding and commercial selection.

The utilization of molecular genetics most especially the mitochondrial genome has enhanced the understanding on characterization,

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Abbreviations

COI	Cytochrome C Oxidase I
CYTB	Cytochrome b
PCR	Polymerase Chain Reaction
FTA	Flinders Technology Associates
DNA	Deoxyribonucleic acid
nHT	Number of haplotypes
HTdiv	Haplotype diversity
ndiv	Nucleotide diversity
ML	Maximum Likelihood
F_{ST}	Fixation index

phylogenetic and identification of different species. For instance, the D-loop is a potential marker for maternal identification of relationships, genetic linkage and forensic science investigations of pigeons (Tsai et al., 2009; Lee et al., 2010; Stefaniuk-Szmukier et al., 2021). Moreover, Cytochrome B (*CYTB*) is useful as a barcoding tool for genetic studies among chicken strains (Yacoub et al., 2015). This marker classified and revealed *C. livia* as the ancestor of the Pakistani domestic pigeon (Firyal et al., 2014). Other gene in mitochondrial genome including Cytochrome C oxidase subunit 1 (*COI*) has been used for the identification system of animals (Alajmi et al., 2021; Hebert et al., 2003). Previous study examined the usage of *COI* sequences and microsatellite as an intraspecific genetic marker among the population of some Egyptian pigeon breeds (Ramadan et al., 2011, 2018). This gene was used to examine the mtDNA genetic diversity and phylogenetic analyses in giant domestic pigeon breeds and revealed high genetic diversity and significant interbreeding (Balog et al., 2024).

Recent study on genetic diversity of Nigerian laughing doves (*Streptopelia senegalensis*) using *COI* and *CYTB* (Sola-Ojo et al., 2024), common carp black strain population using D-loop and *CYTB* (Sumana et al., 2024), and mitochondrial DNA (mtDNA) *CYTB* gene in native Egyptian rabbits (Darwish and Emam, 2024). Additionally, analysis of different mitochondrial (mtDNA) regions including *COI*, *CYTB*, 12S RNA, 16S RNA, and D-loop revealed the genetic diversity and population structure of Nigerian greater cane rats (*Thryonomys swinderianus*) (Babarinde et al., 2023), and mtDNA *CYTB* and nuclear DNA *CYP2U1* in Nigerian Muscovy ducks (*Cairina moschata*) (Adeola et al., 2022, 2020). Other fragments of the genome such melanocortin 1 receptor (MC1R), unveiled the association between the variants of this *MC1R* gene and plumage coloration in Nigerian domestic pigeons (Jiang et al., 2022).

Microsatellite markers has also been used to examine the genetic structure of racing pigeons in Poland (Podbielska and Radko, 2022) and eight diverse domestic pigeon breeds (Biała et al., 2015). In another study, it unveil the hybridization of domestic pigeons between hills in South Korea (Kim et al., 2022). Whole genome data have also revealed the evolutionary history of rock doves from different environments and its domestication event (Hernández-Alonso et al., 2023).

However, there are no or few molecular study to understand the genetic diversity and population structure of Nigerian domestic pigeon population in West Africa. Hence, this study investigate the genetic diversity and population structure of the domestic pigeon population in Nigeria using the *COI, CYTB*, and *D-loop*. In addition, data from wild and domestic pigeon populations from other parts of the world were retrieved from public databases to unravel the genetic relationship with the Nigerian pigeon population.

2. Materials and methods

2.1. Compliance with ethical standards

The University Ethical Review Committee, University of Ilorin, Nigeria (UERC/ASN/2021/2278) approved the procedures for animal sampling procedures. In the current study, all experimental procedures were performed adhering to the Research Guidelines for the Institutional Review Board of Kunming Institute of Zoology, Chinese Academy of Sciences (SMKY-20160105-11).

2.2. Study animals

A total of 150 adult homing pigeons were sampled from four locations in North Central, South West, and North West of Nigeria as follows: OKO - Oke Suna Prayer Centre, Kwara State from North Central ($n = 24$); ILR - Oja Tuntun, Ipata and Oloje, Kwara State from North Central ($n = 36$); OSG - Oja Aba and Oluode, Osun State from South West ($n = 39$); and KBB - Birnin kebbi Sabon/Sofon Kasua, Kebbi State from North West ($n = 51$) (Fig. 1 and Table S1). Blood samples were carefully collected through wing venipuncture of each captured bird with no cross-contamination and carefully stamped on FTA cards.

2.3. DNA extraction, PCR amplification, and sequencing

We extracted Genomic DNA from the whole blood of 150 sampled adult Nigerian homing pigeons preserved on the FTA cards using Qiagen DNeasy Blood and Tissue Kit (Qiagen, Inc., Germantown, MD) following the user-developed protocol (Qiagen Inc., 2006). We amplified the fragments of the *COI*, *CYTB* and *D-loop* using different set of primers (Supplementary Table S2). Further, PCR was performed using different conditions for molecular markers (Supplementary Table S2). The amplified PCR products were sequenced using the Big Dye Terminator Cycle sequencing kit (Applied Biosystems, Foster City, CA) on ABI 3500 Genetic Analyzer by State Key Laboratory of Genetic Resources & Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences.

2.4. Data analysis

2.4.1. Alignment of sequences

150 *COI*, *CYTB*, and *D-loop* sequences of the Nigerian domestic pigeon were mapped to the reference sequence of Pigeon *COI*, *CYTB*, and *D-loop*, respectively using SeqMan Pro of Lasergene 7.1.0 (DNAStar Inc., Madison, USA). Additionally, we retrieved *COI*, *CYTB*, and *D-loop* sequences of wild and domestic pigeons from Asia, America, and Europe were downloaded from the public databases for further analyses. 162 concatenated sequences comprising of 150 de novo and 12 mitogenome sequences from public databases were aligned (Supplementary Table S3), using ClustalX 2.1 (Larkin et al., 2007) in MEGA version 6.06 (Tamura et al., 2013).

2.5. Population analyses

2.5.1. Mitochondrial genetic diversity

Haplotypes were identified using DnaSP 5.10.1 (Librado and Rozas, 2009). Furthermore, the genetic diversity was estimated by calculating the number of haplotypes (nHT), Haplotype diversity (HTdiv), and Nucleotide diversity (πdiv) with standard deviations (SD) using Arlequin version 3.5.2.2 (Excoffier and Lischer, 2010).

2.5.2. Phylogenetic analyses

We constructed a rooted neighbor-joining (NJ) tree (Saitou and Nei, 1987) with the Maximum Composite Likelihood evolutionary distance approach (Tamura et al., 2004) using MEGA version 6.06 software (Tamura et al., 2013). We employed bootstrap test at 1000 replications that assessed the confidence of each node (Felsenstein, 1985). Moreover, the relationships between haplotypes by constructing median-joining networks from 162 *Columba* spp. (comprising domestic pigeons from Nigeria (*Columba livia domestica*) ($n = 150$, de novo) and 12 mitogenome sequences was visualized (Supplementary Table S3). We constructed a network using the median-joining (MJ) algorithm (Bandelt et al., 1999)

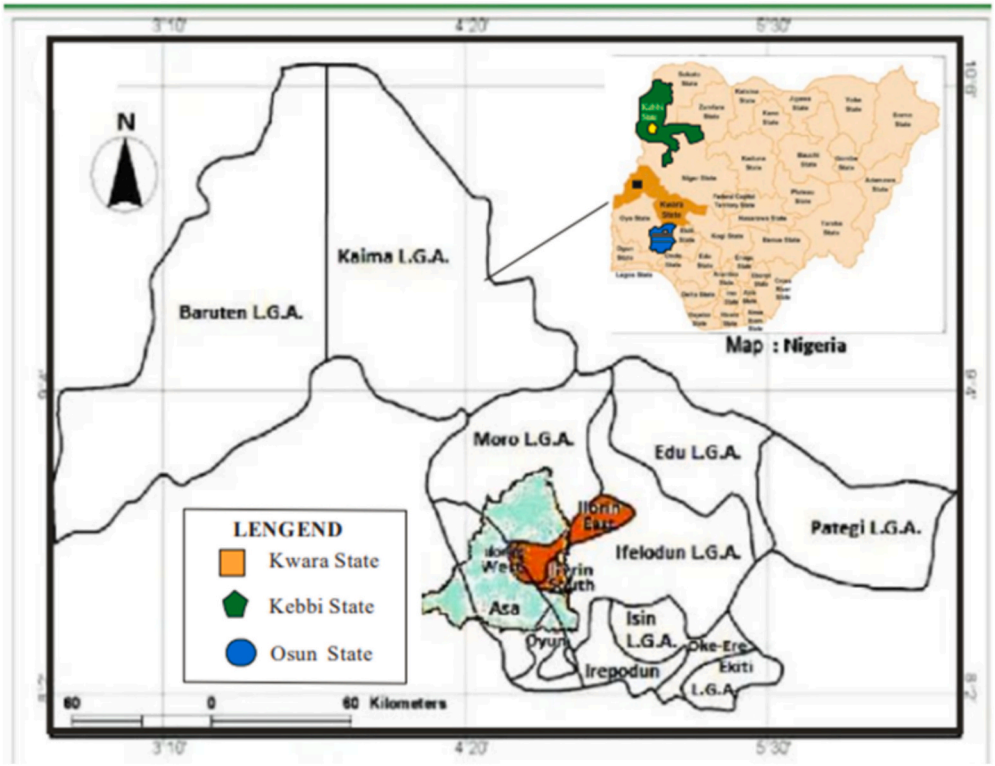


Fig. 1. Sampling localities and geographical positions of 150 Nigerian domestic pigeons (*Columba livia domestica*).

implemented in Network 5.0.1.1 (www.fluxus-engineering.com).

2.5.3. Population genetic structure and historical demographics

We adopted similar methods reported in our recent study (Sola-Ojo et al., 2024). Briefly, population dynamics and demographic patterns, demographic statistical parameters for Tajima's *D* (Tajima, 1989), Fu's *Fs* (Fu, 1997) tests, and population F_{ST} of Nigerian pigeon populations were calculated using Arlequin version 3.5.2.2 (Excoffier and Lischer, 2010). The mismatch distribution patterns were estimated (Fu, 1997) with their various geographical regions. The genetic variation within populations was inferred among populations, and groups of populations, analysis of molecular variance (AMOVA) with 50,000 permutations was done using Arlequin version 3.5.2.2 software. Further, we conducted Bayesian Skyline Plot (BSP) analysis in BEAST (v2.0) (Drummond and Rambaut, 2007), employing a random starting tree model. Since the mutation rate for pigeons is unknown, we used the commonly applied mitochondrial genome mutation rate of 2 % per million years (Myr) (Nabholz et al., 2016) to calibrate the BSP. Each analysis was run three times, starting from a random tree, using Markov Chain Monte Carlo (MCMC) simulations for 100 million generations, with sampling every 100,000 generations and discarding the first 10 % as burn-in. The HKY substitution model, without site invariants, was selected as the best-fit model via the IQ-TREE web server (Minh et al., 2020), and we applied a strict molecular clock model, the coalescent Bayesian skyline tree prior with 10 groups, and a piecewise-constant skyline model. Tracer (v1.7.1) (Rambaut et al., 2018) was used to assess convergence across all runs.

3. Results

3.1. Variation and genetic diversity based on the three concatenated sequences

162 concatenated sequences comprising 150 de novo and 12 mitogenome sequences were classified into 61 haplotypes (Supplementary Table S4). The 150 Nigerian individuals (GenBank: OK255742–OK255891) constitute 52 haplotypes. The most frequent haplotypes (HT3 and HT8) occurred only in Nigerian individuals (Supplementary Table S4). The remaining nine haplotypes, HT53-61 and HT3, occurred only in the 12 mitogenome sequences. We recorded an estimated haplotype diversity (HTdiv) value of 0.876 ± 0.019 across all Nigerian individuals (Table 1). Within the Nigerian pigeon population, nine haplotypes were observed in the OKO (Oke Suna Prayer Centre, Kwara State) population with a diversity value of 0.779 ± 0.068 (Table 1). The nucleotide diversity (πdiv) values were also very low, with the Nigerian pigeon population having a value of 0.055 ± 0.027 and a range of 0.187 ± 0.124 in OKO to 0.080 ± 0.040 in OSG. The mean number of pairwise differences in the Nigerian pigeon population was 17.464 ± 7.803, with the least value within OKO pigeon populations (1.873 ± 1.110) and the highest in KBB (24.515 ± 10.947) pigeon population, as shown in Table 1. The Nigerian pigeon populations were grouped into two groups (A and B). The Tajima's D (−1.539*) and Fu's Fs (−26.821*) test of selective neutrality were both significant in Group A of Nigerian pigeon population samples that showed population expansion (Table 1).

3.2. Genetic similarity and haplotype network analyses with three concatenated sequences

The phylogenetic tree was constructed using 61 haplotypes consisting of domestic pigeon (*Columba livia domestica*) from Nigeria (n = 150 de novo), wild, mitogenome *C. livia* (*n* = 12), *Streptopelia decaocto* (*n* = 1), and *Cairina moschata* (n = 1). The phylogenetic tree showed clustering of the Nigerian domestic pigeon (*Columba livia domestica*) haplotypes (Fig. 2A). Out of the 150 Nigerian pigeon considered, 146 individuals clustered together. More so, these individuals are about 30 mutation steps. The median-joining network of 162 *Columba* spp. based on concatenated sequences revealed 61 haplotypes (Fig. 2B). We found 61 haplotypes with HT3 and HT8 showed the highest frequency, which was present in Nigerian populations. In addition, 52 haplotypes (HT1-HT52) occurred only in Nigerian populations. HT3 and HT8 exhibit star-

Table 1
Genetic diversity of Nigerian pigeon populations based on three concatenated mitochondrial regions.

Population	Size[a]	nHT[b]	HTdiv (SD)[c]	πdiv (SD)[d]	*D*[e]	*Fs*[f]	MNPD (SD)[g]
OKO[h]	24	9	0.779 (0.068)	0.187 (0.124)	−1.003	−3.021*	1.873 (1.110)
ILR[i]	36	15	0.875 (0.039)	0.060 (0.030)	−2.838*	3.839	17.965 (8.163)
OSG[j]	39	19	0.884 (0.040)	0.058 (0.029)	−2.826*	1.335	17.462 (7.928)
KBB[k]	51	22	0.886 (0.033)	0.080 (0.040)	−2.316*	3.643	24.515 (10.947)
Nigeria	150	52	0.876 (0.019)	0.055 (0.027)	−2.255*	−4.571	17.464 (7.803)
Nigeria[l]	146	48	0.869 (0.020)	0.085 (0.051)	−1.539*	−26.821*	2.457 (1.337)
Nigeria[m]	4	4	1.000 (0.176)	0.556 (0.407)	0.184	−0.523	5.000 (3.068)

Asterisks indicate statistical significance at 5 % level.
[a] Total number of samples in each region.
[b] Number of haplotypes.
[c] Haplotype diversity (standard deviation).
[d] Nucleotide diversity (standard deviation).
[e] Tajima's *D* test of selective neutrality.
[f] Fu's *Fs* test of selective neutrality.
[g] Mean number of pairwise differences (standard deviation).
[h] OKO (Oke Suna Prayer Centre), Kwara State.
[i] ILR (Oja Tuntun, Ipata and Oloje), Kwara State.
[j] OSG (Oja Aba and Oluode), Osun State.
[k] KBB (Birnin kebbi Sabon/Sofon Kasua), Kebbi State.
[l] Group A of Nigerian pigeon population samples that showed population expansion.
[m] Group B of Nigerian pigeon population samples.

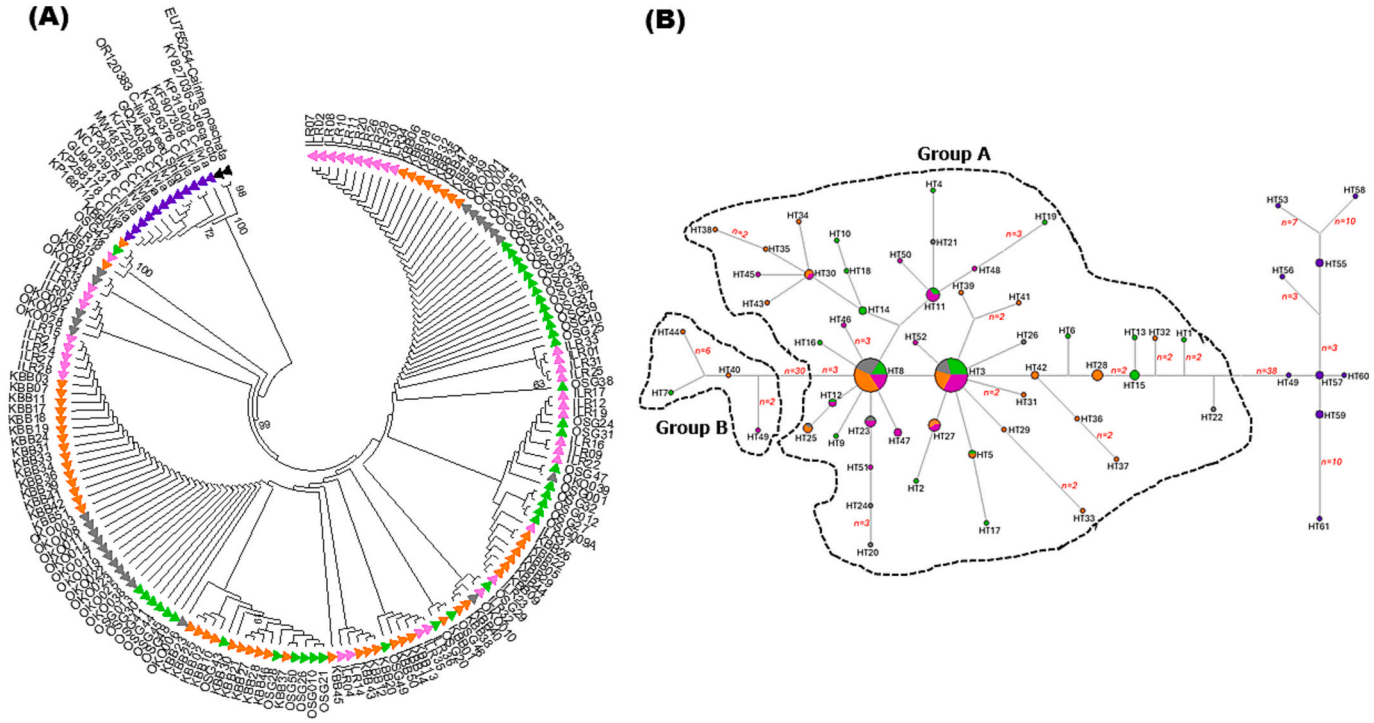


Fig. 2. Phylogenetic tree and network of three concatenated mitochondrial regions of Nigerian laughing doves. (A) Maximum Likelihood tree of three concatenated mitochondrial regions of Nigerian *Columba* spp. Reference sequences used for ML tree analysis included: 162 domestic pigeons (*Columba livia domestica*) from Nigeria, m = 150 (de novo) and those retrieved from NCBI. Outgroup taxa (*Cairina moschata*, EU755254) is black. (B) Median-joining network of three concatenated mitochondrial regions of *Columba* spp. constructed using NETWORK version 4.6. Reference sequences used for haplotype network analysis included: 161 domestic pigeons (*Columba livia domestica*) from Nigeria, m = 150 (de novo) and those retrieved from NCBI. Sizes of the circles are proportional to haplotype frequencies.

like patterns indicating rapid population expansion (Fig. 2B).

3.3. Population genetic structure and historical demographics based on the three concatenated sequences

The pairwise F_{ST} was calculated to infer the population dynamics and maternal genetic structure of the Nigerian domestic pigeon. Least-square procedure to fit the expected and observed mismatch distribution did not converge after 2000 steps. The F_{ST} distance between Nigerian domestic pigeon sampling localities was low (Table 2). Among the four populations, the highest genetic distance (F_{ST}) was observed between OKO and KBB populations. Contrarily, the lowest (negative F_{ST}) was observed between OSG and the remaining three populations (Table 2). The genetic distance between OKO and ILR populations was zero. In the analysis of molecular variance (AMOVA) among different populations within Nigeria, F_{ST} was not significant ($P > 0.05$; Table 3).

Table 2
Pairwise F_{ST} of Nigerian domestic pigeon populations based three concatenated mitochondrial regions.

	OSG	OKO	KBB	ILR
OSG	–			
OKO	0.0013	–		
KBB	−0.0037	−0.0166	–	
ILR	0.0149	0.0000	−0.0071	–

OSG (Oja Aba and Oluode) is Osun State; OKO (Oke Suna Prayer Centre) is Kwara State; KBB (Birnin kebbi Sabon/Sofon Kasua) is Kebbi State; ILR (Oja Tuntun, Ipata and Oloje) is Kwara State. F_{ST} values of *COI*. *- F_{ST} *P* values significance level 0.05.

3.4. Genetic structure and diversity of Nigerian pigeon populations with specific mitochondrial regions

The genetic structure and diversity of the Nigerian wild and domestic pigeon populations from Europe, America, and Asia downloaded from the public databases using *COI*, *CYTB*, and *D-loop* regions were examined separately (Supplementary File S3). Using *COI* sequences only, the 150 Nigerian individuals constitute three haplotypes resulting from two polymorphic sites (Supplementary File S5). The most frequent haplotype (HT1) was shared between 204 Nigerian and other populations from Europe, America, and Asia while the remaining two haplotypes, HT2 and HT3, occurred only in Nigerian samples (Supplementary Table S5). The haplotype diversity (HTdiv) across all Nigerian individuals was estimated and a value of 0.052 ± 0.025 was obtained (Supplementary File S6). The nucleotide diversity (πdiv) values were also very low, with the Nigerian pigeon population having a value of 0.026 ± 0.068 and a range of 0.039 ± 0.188 in KBB (Birnin kebbi Sabon/Sofon Kasua, Kebbi State) to 0.076 ± 0.076 in OSG. The mean number of pairwise differences in the Nigerian pigeon population was 0.053 ± 0.123, with the least value within KBB pigeon populations (0.039 ± 0.106) and the highest in OSG (0.151 ± 0.217) pigeon population (Supplementary Table S6).

Further, 201 Nigerian pigeon populations were analyzed with the retrieved sequences using *CYTB* only and detected 21 haplotypes (Supplementary Table S7). Moreover, a similar pattern recorded in the *COI* was unveiled, with the most frequent haplotype (HT1) shared between the Nigerian and other populations from Europe, America, and Asia while the remaining two haplotypes (HT2 and HT3) occurred only in Nigerian samples (Supplementary Table S7). Based on the *CYTB* sequences, the HTdiv of 0.247 ± 0.047 was estimated for the Nigerian pigeon population with KBB and OKO having the highest (0.322 ± 0.082) and lowest (0.163 ± 0.099) values, respectively. Moreover, the πdiv in Nigerian pigeon population was low (0.0028 ± 0.028) with OSG and KBB recorded the same value (0.067) but different standard deviations (0.0076 and 0.060, respectively). The mean number of pairwise differences in the Nigerian pigeon population was 0.416 ± 0.383, with the lowest value within KBB pigeon populations (0.039 ± 0.106) (Supplementary Table S8). Contrarily, 14 haplotypes were revealed across 209 Nigerian pigeons and Global *Columba livia* using D-loop (Supplementary Table S9). Interestingly, the most frequent haplotype (HT13) occurred only in the Nigerian pigeon population. We recorded HTdiv of 0.411 ± 0.047 for the Nigerian population ranging from 0.535 ± 0.080 to 0.286 ± 0.081 in OSG and KBB populations, respectively (Supplementary Table S10). However, the OKO population had the highest nucleotide diversity of 0.344 ± 0.392 and the KBB population recorded the lowest nucleotide diversity of 0.064 ± 0.068. Additionally, the mean number of pairwise differences in the Nigerian pigeon population was 0.485 ± 0.42 based on D-loop (Supplementary Table S10).

3.5. Genetic similarity and haplotype network analyses using three specific mitochondrial regions

The phylogenetic tree was constructed using 25 haplotypes from 229 *Columba* spp. (comprising domestic pigeons from Nigeria (*Columba livia domestica*) ($n = 150$) de novo; wild and domestic pigeons (*Columba livia domestica*) from Europe, America, and Asia ($n = 54$); *Columba* spp. ($n = 25$) outgroup taxa retrieved from the GenBank) based on 618 bp of the *COI* gene (Supplementary File S3). The phylogenetic tree showed clustering of the three Nigerian domestic pigeon haplotypes together with European, American, and Asian wild and domestic pigeon (*Columba livia domestica*) haplotypes (Fig. 3A). It was in the same monophyletic clade as the global *Columbia livia*. Further, median-joining network of *COI* gene revealed 25 haplotypes (Fig. 3B). Of the 25 haplotypes observed, HT1 showed the highest frequency, which was present in Nigerian populations and others from Europe, America, and Asia. The two other haplotypes, HT2 and HT3, occurred only in Nigerian populations. HT1 exhibits a star-like pattern indicating rapid population expansion (Fig. 3B).

In addition, the maximum likelihood (ML) tree of 20HT of 210 Nigerian and Global *Columbia* spp. was constructed based on 322 bp of *CYTB*. The ML revealed that the Nigerian individuals were in the same

Table 3
Geographical structure assessed using analysis of molecular variance (AMOVA).

Hierarchical clusters	Hierarchy	Variance components	% of variation	F	*P*-value
1. Nigerian populations (overall)[a]	1	Within populations	100.61	−0.00608	−0.5582
		Among populations	−0.61		
2. Among regions[b] (OSG vs OKO + ILR vs KBB)	3	Within populations	100.55	−0.00548	0.54350
		Within populations within regions	−1.12	−0.01122	0.01760
		Among regions	0.57	0.00567	0.49365
3. North Central (OKO + ILR) vs. remaining populations	2	Within populations	100.56	−0.00562	0.55132
		Within populations within regions	−0.69	−0.00694	0.62268
		Among regions	0.13	0.00131	0.65787
4. OSG vs. remaining populations[c]	2	Within populations	101.15	−0.01151	0.54448
		Within populations within groups	−0.02	−0.00015	0.32356
		Among groups	−1.14	−0.01135	1.00000
5. KBB vs. remaining populations[c]	2	Within populations	99.99	0.00014	0.56598
		Within populations within groups	−1.58	−0.01603	0.31085
		Among groups	1.59	0.01592	0.23851

AMOVA subdivides genetic diversity into hierarchical components and estimates the parameter F_{ST}, which assesses the relative divergence between populations. The statistical significance of variance components and F_{ST} indices were assessed by bootstrapping using 1000 replicates. Analyses were carried out sequentially for all samples based on three concatenated mitochondrial regions.

[a] Overall is Nigerian domesticated pigeon populations which were as follows (number of samples in parentheses): OKO (Oke Suna Prayer Centre) – Kwara ($n = 24$), ILR (Oja Tuntun, Ipata and Oloje) – Kwara; ($n = 36$), OSG (Oja Aba and Oluode) – Osun ($n = 39$) and KBB (Birnin kebbi Sabon/Sofon Kasua) – Kebbi ($n = 51$).

[b] Northwest (Kebbi State); North Central (Oke Suna Prayer Centre and Oja Tuntun, Ipata and Oloje, Kwara State); Southwest (Osun State).

[c] Remaining populations include all the populations listed above except the mentioned population.

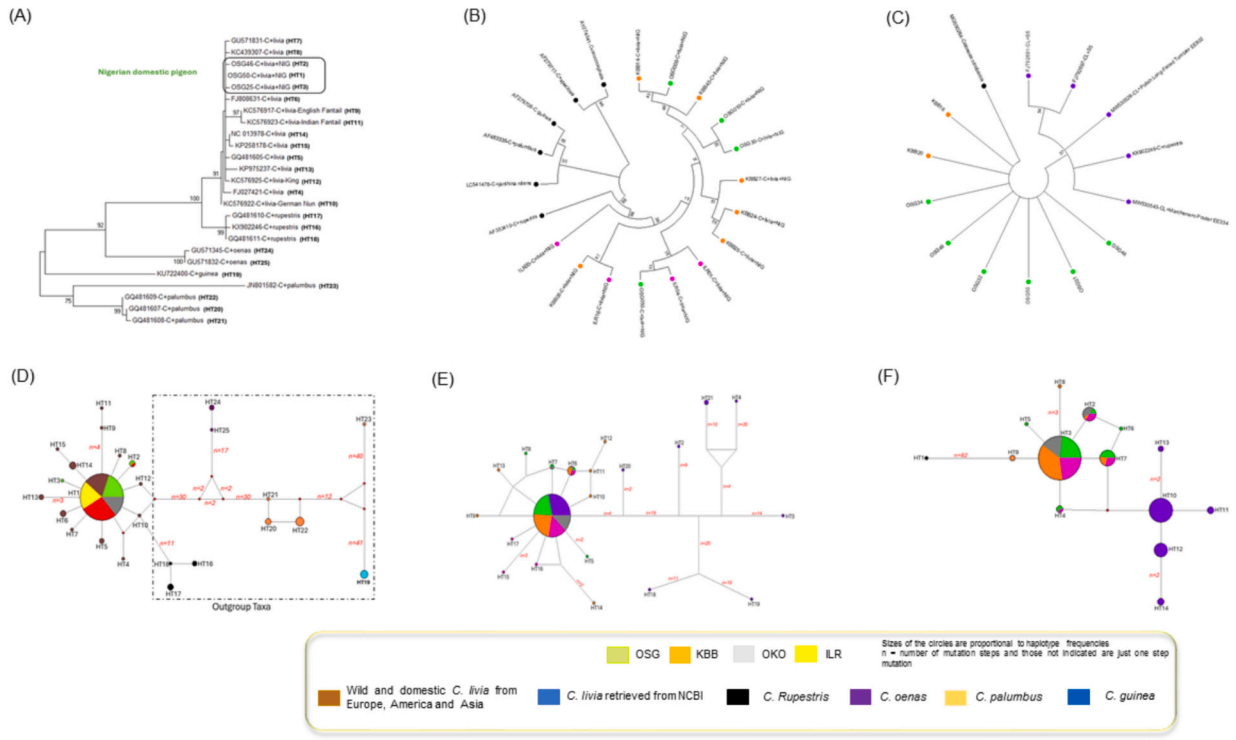


Fig. 3. Phylogenetic tree and network of cytochrome oxidase subunit I (*COI*), cytochrome *b* (*CYTB*) and D-Loop of Nigerian laughing doves. (A) Neighbor-joining (NJ) tree of 25 haplotypes from 229 *COI* sequences consisting of pigeon (*Columba livia domestica*) from Nigeria (Please check Table S3), (B) Median-joining network of *Columba* spp. *COI* constructed using NETWORK version 4.6 (Bandelt et al., 1999). Reference sequences used for haplotype network analysis. Sizes of the circles are proportional to haplotype frequencies. *m*, refers to number of mutation steps and those not indicated are just one step mutation. (C) Maximum likelihood (ML) tree of 20 haplotypes from 210 Nigerian and global *Columba* spp. based on 322 bp of *CYTB*. (D) Median-joining network of 210 Nigerian and global *Columba* spp. based on 322 bp of *CYTB* (Please check Table S7). (E) Maximum likelihood (ML) tree of 14 haplotypes from 209 Nigerian and global *Columba* spp. based on 542 bp of D-Loop (Please check Table S9). (F) Median-joining network of *Columba* spp. constructed based on D-Loop using NETWORK version 4.6. Reference sequences used for haplotype network (Please check Table S9).

monophyletic clade as the global *Columbia livia* (Fig. 3C). Based on the haplotype network, the Nigerian individuals and other Global *Columbia* spp. had the highest haplotype and exhibited a star-like pattern showing a rapid population expansion (Fig. 3D).

The haplotype network analysis was performed using 208 Nigerian and Global *Columbia* spp. based on 547 bp of D-loop. Based on the network, it was unveiled that most of the Nigerian pigeon population clustered together (Fig. 3E). This result is contrary to the findings of *COI* and *CYTB* where the Nigerian populations are in the same clade with the Global *Columbia* spp. Moreover, the 14 haplotypes of the D-loop showed

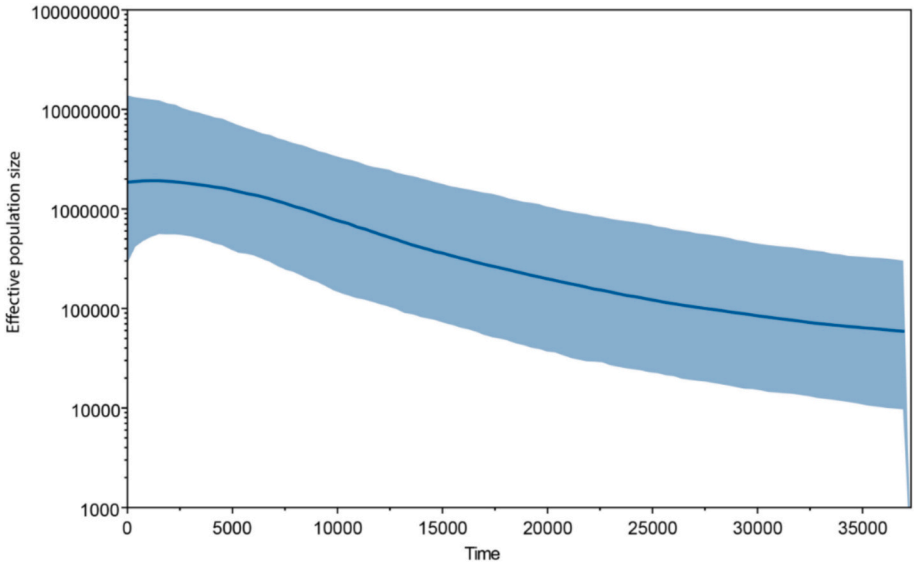


Fig. 4. Bayesian skyline plots of Nigeria Group A. The 95 % highest posterior density (HPD) is highlighted by a blue-shaded area. The X-axes represent thousands of years before present, while the Y-axes represent the mean effective population sizes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that the Nigerian pigeons together (Fig. 3F).

3.6. Population genetic structure and historical demographics based on three specific mitochondrial regions

We calculated the pairwise F_{ST} to infer the population dynamics and maternal genetic structure of the Nigerian pigeon for the three specific mitochondrial regions. Based on the *COI* gene, OSG and ILR populations had the highest genetic distance (F_{ST}) (Supplementary Table S11). A similar trend using the *CYTB* gene with the highest F_{ST} between KBB and OSG populations was observed (Supplementary Table S14).

Contrarily, three significant genetic distances between Nigerian pigeon populations including OKO vs OSG, KBB vs OSG, and KBB vs OKO individuals based on D-loop were recorded (Supplementary Table S13).

The BSP in Group A Nigerian pigeon population showed some gradual increase in effective population size (Fig. 4). Contrarily, we detected a stable thread in effective population size in Nigerian Group B pigeon population (Fig. S1).

4. Discussion

This study investigated the genetic diversity and population structure of domestic pigeon populations in Nigeria using the concatenated sequences from D-loop, *CYTB*, and *COI*. Low genetic diversity was revealed among Nigerian pigeon populations with nine haplotypes (Table 1 and Fig. 2A, B). This indicates that the populations of pigeons in Nigeria are subjected to interbreeding. Our findings are in accordance with previous studies that reported low genetic diversity in Egyptian pigeon breeds (Ramadan et al., 2011) and a high degree of similarity in the breed of pigeons studied (Biała et al., 2015). In addition, Lu et al. (2020) reported low genetic diversity in Chinese breeds of pigeons. In a previous study, it was found that genetic structure is mixed irrespective of their original locations (Podbielska and Radko, 2022). Contrarily to our findings, a recent study revealed higher haplotype diversity value (0.576±0.078) in Mediterranean pigeon group suggesting a long breeding history for giant pigeon breeds (Balog et al., 2024). Moreover, 52 haplotypes were revealed in Nigerian pigeon populations. The haplotypes with the highest frequency (HT3 and HT8) were present in the Nigerian populations only. The Group A Nigerian pigeon population showed a historical population expansion.

The phylogenetic tree showed significant clustering of the Nigerian pigeon with other populations from Europe, the USA, and Asia showing their genetic relationship. In a recent study, the signature of genetic divergence among different populations Bolle's Laurel Pigeon (*Columba bollii*) was detected (Marrero et al., 2024). These haplotypes (HT3 and HT8) with the highest frequency, comprises the majority, which are individuals across all the four different sampling sites in Nigeria together with others from Europe, America, and Asia. This suggested that most pigeons present in Nigeria descended from a common origin. Moreover, these haplotypes (HT3 and HT8) exhibited a star-like pattern (Fig. 2B). The observed pattern is often related to a rapid demographic expansion, possibly from a small founder population (Norwick et al., 2007). The signature of expansion observed in our study is consistent with the significant negative values of Tajima's *D* and Fu's *Fs* tests ($P < 0.05$; Table 1) as well as the star-like pattern in the network (Fig. 2B). Thus, the observed pattern in Nigerian Group A pigeon populations is probably due to a historical demographic expansion. In a previous study, it was reported that European doves are prone to exhibit demographic fluctuations and possess a lack of genetic structure (Calderón et al., 2016).

The extent of haplotype-sharing in the network indicates the absence of a definite population structure in the Nigerian pigeons. This finding was supported by the low F_{ST} (−0.0037 to 0.0149) distance between Nigerian pigeon populations being studied. These negative F_{ST} values obtained may be due to sampling size and low haplotype diversity (Lu et al., 2020). These values were lower than the 0.154 to 0.313 reported by (Ramadan et al., 2011), which is an indication that there were lower genetic differentiation and greater deficiency of heterozygosity among the population of pigeons studied. In a similar study, pairwise Fst showed that the South Korean populations were not genetically different from the Mongolian and Russian populations and the Fst value of the Korean populations exhibited low genetic differentiation (Kim et al., 2022). Contrarily, high genetic diversity was revealed between the Turtle doves from Morocco and Ukraine populations (Prakas et al., 2021). The genetic distance between OKO and ILR populations was zero. This is because the two locations are closer, and OKO is in the same geographical region as ILR.

A close relationship within the Nigerian pigeon population shows that the long-term breeding of domestic lineages of pigeons has not caused a significant depletion in their genetic variation and genetic diversity within the location of the pigeon studied and in accordance with the assertion of (Tajima, 1989). These findings were also in line with (Biała et al., 2015), which stated that all breeds and diverse morphological forms of *Columba livia* should be considered in genetic diversity studies based on their phenotypic characteristics within the population rather than based on subpopulation. Moreover, it was reported that significant interbreeding among pigeon breeds inferred a complex history of genetic mixing (Balog et al., 2024). The mismatch distribution did not converge after 2000 steps, possibly because *COI* sequences were conserved.

The AMOVA tests among populations to assess differentiation within Nigeria were not significant ($P > 0.05$; Table 3). This supported the general absence of genetic structure in Nigerian sampling sites. The absence of geographic signal and lack of genetic structure likely indicates the extensive genetic intermixing among pigeons in Nigeria. Previous studies for instance Muscovy duck (Adeola et al., 2022) have revealed a similar pattern due to intensive genetic intermixing resulting from human migrations and trading among other poultry species in Nigeria.

BSP showed a historical population expansion in the Nigeria Group A pigeon population (Fig. 4). Previous study utilized BSP to confirm widespread population expansion in North American boreal birds (Kimmitt et al., 2023). Also, increases in migration might result in an increasing BSP without any change in census population sizes (Miller et al., 2021).

5. Conclusion

This study investigated the genetic diversity and population structure of four pigeon populations from three different states of Nigeria using three concatenated sequences from *COI*, *CYTB*, and D-loop. Three haplotypes were revealed in Nigerian populations; two of them with the highest frequency showed a star-like pattern indicating historical population expansion and occurred only in Group A of Nigerian pigeon populations. Neutrality test results showed that 146 Nigerian pigeon populations experienced historical population expansion while four individuals in Group B do not. Our result suggested that the genetic structure could be due to the founders' effect. The absence of geographic signal in the studied pigeons from Nigeria indicates extensive genetic intermixing consistent with earlier findings of other poultry species in Nigeria. Finally, D-loop revealed small genetic differences between populations of Nigerian pigeons and can be used to investigate genetic diversity and origin of pigeons in studies designed for the improvement and development of pigeons. Future studies to further confirm the results should be based on complete mitochondrial genome sampled from sufficiently large number of individuals from across the locations.

CRediT authorship contribution statement

Foluke E. Sola-Ojo: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Ibraheem A. Abubakar:** Methodology. **Semiu F. Bello:** Writing – original draft, Visualization, Validation, Software, Resources, Investigation, Formal analysis, Data

curation, Conceptualization. **Isiaka H. Fatima:** Methodology. **Sule Bisola:** Methodology. **Adesina M. Olusegun:** Methodology. **Lameck A. Odongo:** Writing – review & editing, Formal analysis. **Ting-Ting Yin:** Writing – review & editing, Methodology, Funding acquisition. **Adeniyi C. Adeola:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Consent to participate

This declaration is not applicable.

Consent to publish

This declaration is not applicable.

Ethical approval

The University Ethical Review Committee, University of Ilorin, Nigeria (UERC/ASN/2021/2278) approved the procedures for animal sampling procedures. In the current study, all experimental procedures were performed adhering to the Research Guidelines for the Institutional Review Board of Kunming Institute of Zoology, Chinese Academy of Sciences (SMKY-20160105-11).

Declaration of competing interest

The authors have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.genrep.2025.102154.

Data availability

Data will be made available on request.

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