



RESEARCH ARTICLE

Chicken Genetic Signatures Reveal a Long-Term Historical Relationship Between Zanzibar and Oman

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Abstract

Background and Objective: Understanding the historical dispersal of indigenous chickens offers valuable insights into past human mobility, trade networks and livestock adaptation. This study examined the maternal genetic relationships between indigenous chicken populations from Zanzibar (Unguja and Pemba) and Oman using mitochondrial DNA (mtDNA) D-loop sequence analysis.

Materials and Methods: mtDNA sequences were analyzed to assess genetic diversity, population structure, phylogenetic relationships and historical gene flow. Haplotype and nucleotide diversity indices, Analysis of Molecular Variance (AMOVA), pairwise F_{ST} values, phylogenetic networks and neutrality tests were employed to infer evolutionary and demographic patterns.

Results: High haplotype diversity and a predominance of within-population genetic variation (81.39%) were observed, indicating repeated introductions followed by local population expansion rather than long-term isolation. Extensive sharing of maternal haplotypes between Zanzibar and several Omani ecotypes, particularly Dhofar and Musandam, was detected. A dominant ancestral haplogroup accounted for nearly 79% of all haplotypes and exhibited a star-like topology, consistent with demographic expansion from a common maternal source. Gene flow estimates ($Nm > 1$) across most population pairs suggest sustained historical maternal exchange sufficient to counteract genetic drift. Notably, some Omani ecotypes showed greater genetic differentiation among themselves than relative to Zanzibar populations, reflecting localized divergence following dispersal.

Conclusion: These genetic patterns closely correspond with archaeological and historical evidence of Indian Ocean maritime trade linking East Africa and the Arabian Peninsula. The findings indicate that chickens were repeatedly transported as part of long-standing trade, settlement and provisioning systems. Overall, this study highlights the utility of mtDNA in reconstructing livestock dispersal histories and underscores the importance of conserving indigenous chicken populations as reservoirs of genetic, cultural and adaptive diversity.

INTRODUCTION

The long-standing relationship between Oman and Zanzibar likely facilitated the exchange of domestic animals. Zooarchaeological studies in Zanzibar trace early introductions of zebu cattle (*Bos indicus*) and domestic chickens (*Gallus gallus*) with Asian taxa¹⁻⁵. Several studies have shown that the global spread of chickens is closely linked to human movement, as chickens are non-migratory birds⁵⁻⁹. Notably, multiple genetic studies using mitochondrial DNA (mtDNA) to assess chicken dispersal from their centers of origin have provided insights into prehistoric human migration, trade routes and cross-cultural diffusion^{8,10-12}.

Early traders and explorers from Arabia, the Persian Gulf, western India and China likely visited Zanzibar as early as the first century AD. The Arabian Peninsula played a central role in the dispersal of commodities, plants, crops and animals between India and Africa^{13,14}. Utilizing monsoon winds, these traders sailed across the Indian Ocean and anchored at the sheltered harbors of Zanzibar. Several scholars have reported that domestic chickens in Zanzibar were introduced through maritime exchanges¹⁵. Furthermore, shared life histories are expected to influence gene flow (Nm) through their effects on dispersal¹⁶. These sustained maritime interactions not only promoted cultural and economic exchange but also enabled repeated movement of domestic animals, such as chickens, creating opportunities for long-distance dispersal and maternal gene flow that can now be traced using mitochondrial DNA evidence.

The aim of this study was to examine the maternal lineage relationships between chickens from Zanzibar and Oman in the context of the long-standing interactions between these two regions. Mitochondrial DNA sequences are widely used to estimate phylogenetic relationships among taxa and to conduct molecular evolutionary analyses¹⁷. Evolutionary relationships can be inferred from the mitochondrial control region (D-loop), which evolves more rapidly than nuclear genomic DNA. In particular, a highly variable segment of the control region, containing the highest proportion of variable sites of any mitochondrial region, has proven especially useful for defining closely related mitochondrial lineages within species¹⁸. The sequential accumulation of mutations along maternal lineages allows these lineages to be associated with populations from different geographical regions worldwide^{19,20}.

MATERIALS AND METHODS

A total of 138 mtDNA sequences representing eight chicken ecotypes from Zanzibar and Oman were analyzed. Two ecotypes from Zanzibar-Pemba (PEMB) and Unguja

(UNGJ)-were named after their respective main islands^{3,31}. Six ecotypes from Oman, namely Musandam (MU), Batinah (BT), North Hajar (NH), East Hajar (EH), East Coast (EC) and Dhofar (DF), were sampled and named according to the major agroecological zones of Oman²².

Mitochondrial DNA sequences: For the six Omani chicken populations, genomic DNA was extracted using a standard silica-column-based commercial kit (DNeasy Blood and Tissue Kit, Qiagen, UK). A 550 bp fragment of the mtDNA D-loop region was amplified by PCR using the primers L16750 (5'-AGGACTACGGCTTGAAAAGC-3') and H522 (5'-ATGTGCCTGACCGAGGAACCAG-3'). PCR amplification was performed in a 25 μ L reaction volume containing 1 \times reaction buffer, 75 mM MgCl₂, 5 mM of each dNTP, 10 pM of each primer and 1 U of Taq DNA polymerase (SABC Inc.), under the following cycling conditions: 35 cycles of 1 min at 94 °C, 1 min at 63 °C and 1 min at 72 °C. PCR products were purified and sequenced in both forward and reverse directions using the BigDye™ Terminator v3.1 Cycle Sequencing Ready Reaction Kit on an ABI PRISM 3100 sequencer (Applied Biosystems, Warrington, UK). Forward and reverse sequences were manually edited and aligned to generate consensus sequences using BioEdit version 7.0.9.0²³.

The raw sequences generated were further edited and aligned with additional sequences using DNASTAR version 7.1 (DNASTAR Inc., Madison, WI, USA) and aligned using MEGA software²⁴. In addition, 40 mtDNA sequences of chickens from Zanzibar were retrieved from GenBank (<http://www.ncbi.nlm.nih.gov/genbank>), comprising 20 sequences from the Unguja ecotype and 20 from the Pemba ecotype³. The corresponding GenBank accession numbers for the Unguja and Pemba ecotypes are provided in Appendix 1.

Data analyses: All Zanzibar and Oman chicken mtDNA sequences were aligned using AlignIR software (LI-COR Inc.). Extra nucleotide bases were trimmed to produce sequences of uniform length (350 bp) and any nucleotides outside the D-loop region were excluded from analysis. To assess genetic relationships within and among chicken populations from Zanzibar and Oman, analysis of molecular variance (AMOVA) and pairwise F_{ST} were conducted using Arlequin version 3.0²⁵. Genetic distances for each population were calculated at $p < 0.05$ following the algorithm of Excoffier and Lischer²⁵. Pairwise F_{ST} tests were performed using 10,000 permutations to evaluate genetic differentiation. The level of genetic differentiation was estimated using Weir and Cockerham's²⁶ estimator of Wright's²⁷ fixation index. The number of haplotypes among Zanzibar and Oman chickens was estimated using DnaSP version 6.12.03²⁸.

Isolation by distance among chicken populations from Zanzibar and Oman was assessed using regression of pairwise estimates of gene flow against geographic distance. The level of gene flow among populations (Nm), based on Hudson *et al.*²⁹, was also computed in DnaSP version 6.12.03. Median-joining networks were constructed to infer evolutionary relationships among mtDNA haplotypes following the algorithm of Bandelt *et al.*³⁰, using Network version 4.6.1.0 (<http://www.fluxus-engineering.com/sharenet.htm>). Phylogenetic networks based on the neighbour-joining (NJ) method were inferred among mitochondrial sequences of Zanzibar and Oman chickens using SPLITSTREE4 version 4.16.2³¹.

RESULTS

Genetic variation within and between chicken populations:

Analysis of molecular variance (AMOVA) based on mitochondrial DNA (mtDNA) haplotype frequencies revealed a strong partitioning of genetic variation within chicken populations from Zanzibar and Oman. The majority of the genetic variation (81.39%) was distributed within populations, whereas only 18.61% of the total variation was attributable to differences among populations (Table 1). This distribution was statistically significant ($p < 0.001$), indicating non-random genetic structuring across the studied populations.

The fixation index ($F_{ST} = 0.18611$) indicates moderate genetic differentiation between Zanzibar and Oman chicken populations. However, the predominance of within-population variation suggests substantial historical connectivity and shared ancestry rather than prolonged isolation. Such a pattern is characteristic of domestic species whose dispersal and population structure are strongly shaped by human-mediated movements rather than by natural geographic barriers.

Genetic differentiation and gene flow among ecotypes:

Pairwise genetic differentiation (F_{ST}) and gene flow (Nm) estimates among the eight chicken ecotypes further clarified the extent of connectivity between Zanzibar and Oman populations (Table 2). Overall, gene flow was high ($Nm > 1$) for most population pairs, indicating effective historical exchange of maternal lineages. This magnitude of gene flow is sufficient to counteract the effects of genetic drift, thereby maintaining genetic similarity among populations over time.

Chicken populations from Unguja and Pemba exhibited particularly strong genetic connectivity with several Omani ecotypes, notably Dhofar, Musadam, East Coast and North Hajar. These population pairs were characterized by low F_{ST} values and high Nm estimates, reflecting frequent or sustained maternal gene exchange. In contrast, higher F_{ST} values were observed among some Omani ecotypes, suggesting greater genetic differentiation within Oman than between certain Omani and Zanzibari populations.

Notably, the genetic distance between Unguja and Pemba ecotypes was smaller than the distances between Zanzibar chickens and some Omani populations, reflecting close genetic affinity between the two Zanzibar islands. This pattern supports the interpretation that Zanzibar chickens share a common maternal pool that has remained relatively cohesive despite external introductions.

Phylogenetic relationships among Zanzibar and Oman chickens:

Neighbour-Joining (NJ) phylogenetic network analysis based on mtDNA D-loop sequences revealed three major clusters representing the evolutionary relationships among the studied chicken populations (Fig. 1). Two of these clusters comprised mixed ecotypes from both Zanzibar and Oman, whereas the third, more isolated cluster consisted exclusively of Omani chickens, primarily from the Musadam and North Hajar ecotypes.

Table 1: Molecular Variance (AMOVA) of the chicken populations from Zanzibar and Oman

| Source of variation | df | Sum of squares | Variance components | Variations (%) | F_{ST} | p-value |
|---------------------|-----|----------------|---------------------|----------------|----------|---------|
| Between Populations | 7 | 10.971 | 0.07259 Va | 18.61 | 0.18611 | 0.0001 |
| Within Populations | 130 | 41.268 | 0.31745 Vb | 81.39 | | |
| Total | 137 | 52.239 | 0.39004 | 100.00 | | |

Table 2: Gene flow (Nm, above the diagonal) and Pairwise differentiation coefficient (F_{ST} ; below the diagonal) of eight chicken ecotypes from Zanzibar and Oman

| | Zanzibar | | Oman | | | | | |
|-------------|----------|---------|---------|---------|-------------|------------|------------|--------|
| | Unguja | Pemba | Musadam | Batinah | North Hajar | East Hajar | East coast | Dhofar |
| Unguja | - | 6.17000 | 1.15000 | 0.76000 | 0.86000 | 0.66000 | 0.780000 | 1.67 |
| Pemba | 0.09425 | - | 1.43000 | 1.03000 | 1.16000 | 0.93000 | 1.090000 | 2.34 |
| Musadam | 0.20743 | 0.26168 | - | 4.02000 | 8.55000 | 3.04000 | 3.700000 | 8.19 |
| Batinah | 0.29199 | 0.35422 | 0.00075 | - | 6.64000 | 7.05000 | 9.780000 | 3.47 |
| North Hajar | 0.25439 | 0.29579 | 0.00618 | 0.02232 | - | 4.90000 | 8.250000 | 2.72 |
| East Hajar | 0.41428 | 0.46340 | 0.10701 | 0.00544 | 0.05843 | - | 4.710000 | 2.19 |
| East Coast | 0.21009 | 0.24194 | 0.00075 | 0.01946 | 0.03430 | 0.09615 | - | 2.46 |
| Dhofar | 0.10445 | 0.12416 | 0.05782 | 0.13324 | 0.12985 | 0.28331 | 0.09104 | - |

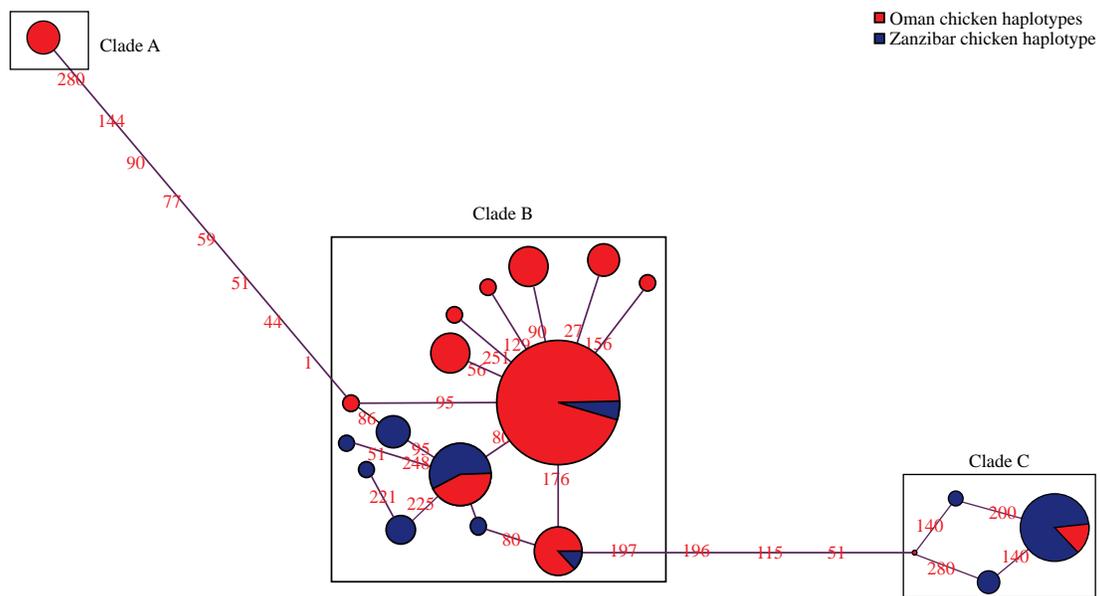


Fig. 2: Median-joining network profiles of 19 haplotypes observed in Zanzibar and Oman Chickens

Note that the circle size corresponds to haplotype frequency and the number between the haplotype nodes refers to the position of nucleotide mutations (Appendix 3)

strengthens confidence in the robustness of the inferred maternal relationships. Moreover, the results reveal a complex yet coherent genetic structure shaped by shared ancestry, substantial historical gene flow and limited regional differentiation. Collectively, these findings provide strong genetic evidence for long-standing connectivity between chicken populations of Zanzibar and Oman, consistent with historical maritime interactions across the western Indian Ocean.

DISCUSSION

Mitochondrial DNA as a robust tracer of historical dispersal:

Mitochondrial DNA (mtDNA), particularly the hypervariable D-loop region, has long been recognized as one of the most informative molecular markers for reconstructing maternal genealogies and historical dispersal patterns in domesticated species, owing to its high mutation rate, lack of recombination and strict maternal inheritance^{18,19,32}. These characteristics enable the preservation of evolutionary signals across extended temporal scales and make mtDNA especially suitable for tracing population movements associated with human migration and trade^{8,33,34}.

In the present study, mtDNA analysis revealed a strong signature of historical connectivity between chicken populations from Zanzibar and Oman, providing molecular evidence that complements archaeological, historical and

ethnographic records of long-standing maritime interactions in the western Indian Ocean^{13,14,35}. This concordance between genetic and historical data reinforces the robustness of mtDNA-based inferences for reconstructing livestock dispersal trajectories.

The predominance of genetic variation within populations (81.39%), as revealed by AMOVA, is characteristic of indigenous livestock populations shaped by repeated introductions followed by local population expansion rather than long-term isolation^{10,36}. Similar patterns have been reported in indigenous chickens across East Africa, southern Africa and Asia, where human-mediated movement has played a dominant role in shaping population structure^{11,33}. The moderate yet significant F_{ST} value observed between Zanzibar and Oman chickens indicates some degree of regional differentiation but not sufficient to obscure their shared ancestry, supporting a scenario of historical gene exchange followed by localized adaptation^{27,29}.

Shared maternal lineages and ancestral haplogroups: One of the most compelling findings of this study is the extensive sharing of maternal haplotypes between Zanzibar and Oman chicken ecotypes. Both phylogenetic network and median-joining analyses consistently grouped chickens from Unguja and Pemba with multiple Omani ecotypes, particularly Dhofar, Musadam, East Coast and North Hajar. The dominance of Clade B, which accounted for nearly 79% of all haplotypes and

included individuals from all sampled regions, indicates the presence of a widespread ancestral maternal lineage that predates regional differentiation.

The star-like topology observed within this dominant clade is characteristic of demographic expansion from a common ancestral haplotype, a pattern widely documented in domesticated chickens and other livestock species^{8,10,30}. Such configurations are commonly interpreted as signatures of early dispersal events associated with human migration, trade and settlement^{9,37}. The presence of identical or closely related haplotypes in geographically distant populations provides strong evidence that these chickens did not originate independently but instead descend from a shared maternal pool shaped by sustained historical connectivity across regions.

Gene flow dynamics and historical connectivity: Estimates of gene flow ($Nm > 1$) across most population pairs indicate that historical maternal exchange between Zanzibar and Oman chickens was sufficiently high to counteract the effects of genetic drift^{27,29}. This level of connectivity implies repeated or sustained movement of chickens rather than a single introduction event. Notably, the strongest gene flow signals were detected between Zanzibar chickens and the Dhofar and Musadam ecotypes from Oman.

This observation is particularly meaningful given the historical importance of Dhofar as a maritime node linking the Arabian Peninsula with East Africa and the Indian subcontinent^{13,38}. Interestingly, some Omani ecotypes exhibited greater genetic differentiation among themselves than with Zanzibar chickens, suggesting that internal ecological, cultural, or management differences within Oman may have driven localized divergence after initial dispersal³⁹. Such asymmetric patterns of differentiation are consistent with targeted livestock introductions shaped by trade routes, political influence and selective breeding rather than uniform dispersal¹⁶.

Maritime trade as a driver of livestock dispersal: The genetic patterns observed in this study align closely with historical accounts of Indian Ocean maritime trade. For centuries, Omani and other Arabian seafarers exploited predictable monsoon wind systems to establish trade networks linking Arabia, East Africa, India and Southeast Asia^{4,14}. Zanzibar's strategic location, sheltered harbor and fertile environment made it a central hub in this network, a role further intensified after the relocation of the Omani capital to Zanzibar in the mid-nineteenth century⁴⁰.

Chickens, owing to their small size, hardiness and versatility, were particularly well suited for transport during maritime voyages. They served as reliable sources of food, trade goods and breeding stock and were easily integrated into local production systems upon arrival¹⁵. Repeated transport of chickens by traders, settlers and administrators would have facilitated the sustained gene flow detected in this study, rendering the observed genetic connectivity a biological reflection of broader socio-economic integration within the western Indian Ocean world.

Evolutionary interpretation of haplogroup structure: The identification of three major haplogroups provides further insight into the temporal layering of chicken dispersal events. Clades B and C, which include chickens from both Zanzibar and Oman, likely represent older lineages associated with early maritime exchanges. Their broad geographic distribution and high frequencies suggest early introduction followed by population expansion as chickens became integrated into local farming systems^{11,36}.

In contrast, Clade A, which is restricted to the Musadam and North Hajar ecotypes, appears to represent a more recent or localized lineage. This pattern may reflect later introductions into Oman or region-specific breeding practices that limited subsequent dispersal³⁷. The coexistence of ancient shared haplogroups alongside localized lineages underscores the complex demographic history of chickens in the region, shaped by multiple waves of introduction, expansion and regional differentiation.

Concordance with archaeological and nuclear genetic evidence: The mtDNA patterns reported here are consistent with archaeological evidence documenting the introduction of Asian domesticates, including chickens, to the Swahili Coast through maritime trade^{1,2}. Zooarchaeological records from Zanzibar indicate the presence of domestic chickens alongside other Asian taxa, supporting early transoceanic animal movement.

Moreover, previous nuclear genetic studies using microsatellite markers have revealed comparable levels of genetic diversity and heterozygosity between Zanzibar chickens and major Omani ecotypes, particularly Dhofar and Musadam^{7,41}. The concordance between mitochondrial and nuclear datasets strengthens the robustness of these conclusions and suggests that the observed maternal connections reflect genome-wide historical processes rather than marker-specific artifacts.

Implications for conservation and indigenous livestock management:

Beyond historical reconstruction, these findings have important implications for the conservation of indigenous chicken genetic resources. The persistence of ancient maternal lineages in both Zanzibar and Oman chickens highlights their genetic and cultural value as living repositories of historical connectivity and local adaptation^{12,35,36}. Recognition of these linkages can inform conservation strategies aimed at preserving indigenous ecotypes while avoiding indiscriminate crossbreeding that could erode historically significant lineages.

Understanding historical gene flow also provides a framework for designing sustainable breeding programs that balance productivity enhancement with the preservation of genetic heritage and resilience⁴². Collectively, the genetic evidence demonstrates that the long-standing relationship between Zanzibar and Oman is deeply embedded in the maternal genetic structure of contemporary chicken populations. Shared haplotypes, high gene flow and congruent phylogenetic patterns confirm that maritime trade and political integration played central roles in shaping chicken dispersal across the western Indian Ocean, illustrating how livestock genetics can serve as a powerful proxy for reconstructing past human connectivity.

CONCLUSION

This study demonstrates that mitochondrial DNA D-loop analysis provides robust evidence of long-standing maternal genetic connectivity between indigenous chicken populations of Zanzibar and Oman. The extensive sharing of haplotypes, predominance of a widespread ancestral haplogroup and high gene flow estimates indicate repeated historical introductions rather than isolated dispersal events. These genetic patterns closely reflect documented Indian Ocean maritime trade networks, underscoring the influence of sustained human movement, commerce and political integration in shaping livestock genetic structure across the western Indian Ocean. The coexistence of ancient shared lineages alongside localized haplogroups further highlights multiple waves of chicken introduction followed by regional adaptation. Concordance between mitochondrial DNA patterns, archaeological records and previous nuclear genetic evidence strengthens the reliability of these conclusions. Beyond reconstructing historical connectivity, the findings emphasize the conservation significance of Zanzibar and Omani chickens as reservoirs of unique genetic heritage. Preserving these indigenous populations is critical for maintaining adaptive diversity, safeguarding cultural legacy and supporting resilience in future sustainable poultry breeding programs.

REFERENCES

1. Wilson, T.H, 1999. Book review Shanga: The archaeology of a Muslim trading community on the coast of East Africa. By Mark Horton. British institute in Eastern Africa Memoir 14, London, 1996, xvi + 458 pp. ISBN 1-872566-09-x. Afr. Archaeol. Rev., 16: 191-195.
2. Chami, F.A, 2019. Chicken bones from a Neolithic limestone cave site, Zanzibar: Contact between East Africa and Asia. Stud. Afr. Past, Vol. 1.
3. Lyimo, C.M., A. Weigend, U. Janßen-Tapken, P.L. Msoffe, H. Simianer and S. Weigend, 2014. Assessing the genetic diversity of five Tanzanian chicken ecotypes using molecular tools. South Afr. J. Anim. Sci., 43: 499-510.
4. Boivin, N., A. Crowther, R. Helm and D.Q. Fuller, 2013. East Africa and Madagascar in the Indian Ocean world. J. World Prehist., 26: 213-281.
5. Lyimo, C.M, 2015. Genetic characterization of Tanzanian indigenous chickens in relation to the worldwide spectrum of chicken diversity. 1st ed., Cuvillier Verlag, Göttingen, Germany, ISBN: 978-3-95404-964-6. Pages:172.
6. West, B. and B.-X. Zhou, 1988. Did chickens go North? New evidence for domestication. J. Archaeol. Sci., 15: 515-533.
7. Tixier-Boichard, M., B. Bed'hom and X. Rognon, 2011. Chicken domestication: From archeology to genomics. C. R. Biol., 334: 197-204.
8. Storey, A.A., J.S. Athens, D. Bryant, M. Carson, K. Emery and E. Matisoo-Smith *et al*, 2012. Investigating the global dispersal of chickens in prehistory using ancient mitochondrial DNA signatures. PLoS ONE., Vol. 7. 10.1371/journal.pone.0039171
9. Thomson, V.A., O. Lebrasseur, J.J. Austin, T.L. Hunt, D.A. Burney and A. Cooper *et al*, 2014. Using ancient DNA to study the origins and dispersal of ancestral polynesian chickens across the pacific. Proc. Natl. Acad. Sci., 111: 4826-4831.
10. Muchadeyi, F.C., H. Eding, H. Simianer, C.B.A. Wollny, E. Groeneveld and S. Weigend, 2008. Mitochondrial DNA D loop sequences suggest a Southeast Asian and Indian origin of Zimbabwean village chickens. Anim. Genet., 39: 615-622.
11. Razafindraibe, H., V.A. Mobegi, S.C. Ommeh, Rakotondravao, G. Bjørnstad and H. Jianlin *et al*, 2008. Mitochondrial DNA origin of indigenous Malagasy chicken. Ann. N. Y. Acad. Sci., 1149: 77-79.
12. Dana, N., L.H.V.D. Waaij, T. Dessie and J.A.M.V. Arendonk, 2010. Production objectives and trait preferences of village poultry producers of Ethiopia: Implications for designing breeding schemes utilizing indigenous chicken genetic resources. Trop. Anim. Health Prod., 42: 1519-1529.
13. Boivin, N., R. Blench and D.Q. Fuller, 2009. Archaeological, linguistic and historical sources on ancient seafaring: A multidisciplinary approach to the study of early maritime contact and exchange in the Arabian peninsula. In: The Evolution of Human Populations in Arabia, Petraglia, M.D. and J.I. Rose, (Eds.). Springer Netherlands, Dordrecht, pp: 251-278.

14. Groucutt, H.S. and M.D. Petraglia, 2012. The prehistory of the Arabian peninsula: Deserts, dispersals and demography. *Evol. Anthropol.: Issues, News, Rev. s*, 21: 113-125.
15. Prendergast, M.E., E.M.Q. Morales, A. Crowther, M.C. Horton and N.L. Boivin, 2017. Dietary diversity on the Swahili coast: The fauna from two Zanzibar trading locales. *Int. J. Osteoarchaeol.*, 27: 621-637.
16. Turner, T.F. and J.C. Trexler, 1998. Ecological and historical associations of gene flow in darters (Teleostei: Percidae). *Evolution*, 52: 1781-1801.
17. Zhang, W.Q. and M.H. Zhang, 2013. Complete mitochondrial genomes reveal phylogeny relationship and evolutionary history of the family Felidae. *Genet. Mol. Res.*, 12: 3256-3262.
18. Edwards, S.V., 1993. Mitochondrial gene genealogy and gene flow among island and mainland populations of a sedentary songbird, the grey crowned babbler (*Pomatostomus temporalis*). *Evolution*, 47: 1118-1137.
19. Ingman, M., H. Kaessmann, S. Pääbo and U. Gyllensten, 2000. Mitochondrial genome variation and the origin of modern humans. *Nature*, 408: 708-713.
20. Herrnstadt, C., J.L. Elson, E. Fahy, G. Preston, D.M. Turnbull and N. Howell *et al*, 2002. Reduced-median-network analysis of complete mitochondrial DNA coding-region sequences for the major African, Asian and European haplogroups. *Am. J. Hum. Genet.*, 70: 1152-1171.
21. Msoffe, P.L.M., M.M.A. Mtambo, U.M. .Minga, J.E. Olsen, H.R. Juul-Madsen and A.M. Katule *et al*, 2004. Productivity and reproductive performance of the free-range local domestic fowl ecotypes in Tanzania. *Livest. Res. Rural Dev.*, Vol. 14.
22. Al-Qamashoui, B., O. Mahgoub, I. Kadim and E. Schlecht, 2014. Towards conservation of omani local chicken: Phenotypic characteristics, management practices and performance traits. *Asian-Australas. J. Anim. Sci.*, 27: 767-777.
23. Hall, T., 2011. BioEdit: An important software for molecular biology. *GERF Bull. Biosci.*, 2: 60-61.
24. Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei and S. Kumar, 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance and maximum parsimony methods. *Mol. Biol. Evol.*, 28: 2731-2739.
25. Excoffier, L. and H.E.L. Lischer, 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.*, 10: 564-567.
26. Weir, B.S. and C.C. Cockerham, 1984. Estimating F-statistics for the analysis of population structure. *Evolution*, 38: 1358-1370.
27. Wright, S., 1949. The genetical structure of populations. *Ann. Eugenics*, 15: 323-354.
28. Rozas, J., A. Ferrer-Mata, J.C. Sánchez-DelBarrio, S. Guirao-Rico, P. Librado and A. Sánchez-Gracia *et al*, 2017. DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Mol. Biol. Evol.*, 34: 3299-3302.
29. Hudson, R.R., M. Slatkin and W.P. Maddison, 1992. Estimation of levels of gene flow from DNA sequence data. *Genetics*, 132: 583-589.
30. Bandelt, H.J., P. Forster, B.C. Sykes and M.B. Richards, 1995. Mitochondrial portraits of human populations using median networks. *Genetics*, 141: 743-753.
31. Huson, D.H. and D. Bryant, 2005. Application of phylogenetic networks in evolutionary studies. *Mol. Biol. Evol.*, 23: 254-267.
32. Bandelt, H.J., P. Forster and A. Rohl, 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.*, 16: 37-48.
33. Mwacharo, J.M., G. Bjørnstad, V. Mobegi, K. Nomura, H. Hanada and O. Hanotte *et al*, 2011. Mitochondrial DNA reveals multiple introductions of domestic chicken in East Africa. *Mol. Phylogenet. Evol.*, 58: 374-382.
34. Lyimo, C.M., A. Weigend, P.L. Msoffe, P.M. Hocking, H. Simianer and S. Weigend, 2015. Maternal genealogical patterns of chicken breeds sampled in Europe. *Anim. Genet.*, 46: 447-451.
35. Lyimo, C., 2025. The origins and spread of domestic chickens in Africa: A synthesis of archaeological, ethnographic and genetic perspectives. *Int. J. Anim. Sci. Technol.*, 9: 123-139.
36. Mtileni, B.J., F.C. Muchadeyi, A. Maiwashe, E. Groeneveld, L.F. Groeneveld and S. Weigend *et al*, 2011. Genetic diversity and conservation of South African indigenous chicken populations. *J. Anim. Breed. Genet.*, 128: 209-218.
37. Peters, J., O. Lebrasseur, H. Deng and G. Larson, 2016. Holocene cultural history of Red jungle fowl (*Gallus gallus*) and its domestic descendant in East Asia. *Quat. Sci. Rev.*, 142: 102-119.
38. Prendergast, M.E., M. Buckley, A. Crowther, L. Frantz, H. Eager and N.L. Boivin *et al*, 2017. Reconstructing Asian faunal introductions to Eastern Africa from multi-proxy biomolecular and archaeological datasets. *PLoS ONE*, Vol. 12. 10.1371/journal.pone.0182565
39. Dutech, C., H.I. Joly and P. Jarne, 2003. Gene flow, historical population dynamics and genetic diversity within French Guianan populations of a rainforest tree species, *Vouacapoua americana*. *Heredity*, 92: 69-77.
40. Sheriff, A., 1987. *Slaves, Spices and Ivory in Zanzibar: Integration of an East African Commercial Empire into the World Economy, 1770–1873*. 1st ed., Boydell & Brewer Ltd, Oxford, United Kingdom, ISBN: 9781782049784, 1782049789, 9780852550151. Pages:320.
41. Al-Qamashoui, B., H. Simianer, I. Kadim and S. Weigend, 2014. Assessment of genetic diversity and conservation priority of omani local chickens using microsatellite markers. *Trop. Anim. Health Prod.*, 46: 747-752.

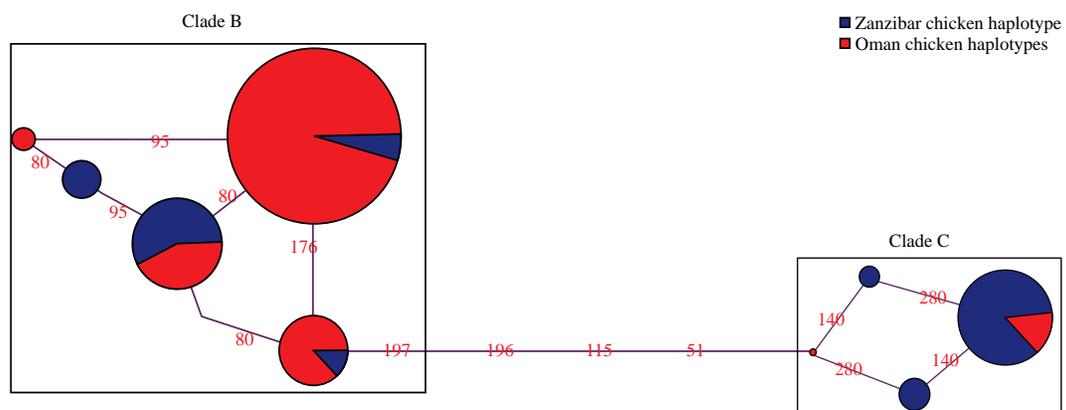
APPENDIX

Appendix 1: Mitochondrial DNA Sequence accession number of Zanzibar chickens from National Centre for Biotechnology Information (NCBI) Gene Bank

| SN | Abbreviation | Ecotype | Accession No. |
|----|--------------|---------|---------------|
| 1 | UNGJ1 | Unguja | KP067513 |
| 2 | UNGJ11 | Unguja | KP067514 |
| 3 | UNGJ12 | Unguja | KP067515 |
| 4 | UNGJ21 | Unguja | KP067516 |
| 5 | UNGJ22 | Unguja | KP067517 |
| 6 | UNGJ24 | Unguja | KP067518 |
| 7 | UNGJ25 | Unguja | KP067519 |
| 8 | UNGJ28 | Unguja | KP067520 |
| 9 | UNGJ31 | Unguja | KP067521 |
| 10 | UNGJ32 | Unguja | KP067522 |
| 11 | UNGJ35 | Unguja | KP067523 |
| 12 | UNGJ36 | Unguja | KP067524 |
| 13 | UNGJ37 | Unguja | KP067525 |
| 14 | UNGJ38 | Unguja | KP067526 |
| 15 | UNGJ8 | Unguja | KP067527 |
| 16 | UNGJ16 | Unguja | KP067535 |
| 17 | UNGJ5 | Unguja | KP067536 |
| 18 | UNGJ3 | Unguja | KP067542 |
| 19 | UNGJ20 | Unguja | KP067543 |
| 20 | UNGJ40 | Unguja | KP067544 |
| 21 | PEMB1 | Pemba | KP067497 |
| 22 | PEMB11 | Pemba | KP067498 |
| 23 | PEMB15 | Pemba | KP067499 |
| 24 | PEMB16 | Pemba | KP067500 |
| 25 | PEMB2 | Pemba | KP067501 |
| 26 | PEMB22 | Pemba | KP067502 |
| 27 | PEMB27 | Pemba | KP067503 |
| 28 | PEMB28 | Pemba | KP067504 |
| 29 | PEMB30 | Pemba | KP067505 |
| 30 | PEMB31 | Pemba | KP067506 |
| 31 | PEMB32 | Pemba | KP067507 |
| 32 | PEMB36 | Pemba | KP067508 |
| 33 | PEMB38 | Pemba | KP067509 |
| 34 | PEMB4 | Pemba | KP067510 |
| 35 | PEMB5 | Pemba | KP067511 |
| 36 | PEMB8 | Pemba | KP067512 |
| 37 | PEMB12 | Pemba | KP067531 |
| 38 | PEMB3 | Pemba | KP067532 |
| 39 | PEMB33 | Pemba | KP067533 |
| 40 | PEMB7 | Pemba | KP067534 |

Source: Lyimo *et al.*³

Appendix 2: Median-joining network of Zanzibar and Oman Chickens display the ancestry mtDNA haplotypes



Appendix 3: Haplotype frequency in each of the chicken ecotype from Zanzibar and Oman

| Haplotype | Zanzibar Chickens | | Oman Chickens | | | | | | Total |
|-----------|-------------------|------|---------------|----|----|----|----|----|-------|
| | UNGJ | PEMB | MU | BT | NH | EH | EC | DF | |
| 1 | 3 | 1 | 10 | 11 | 11 | 15 | 8 | 5 | 64 |
| 2 | 9 | 5 | | | | | | 2 | 16 |
| 3 | 4 | | | | | | | | 4 |
| 4 | 1 | 1 | | | | | | | 2 |
| 5 | 1 | 8 | | | 1 | 1 | 1 | 2 | 14 |
| 6 | 1 | 1 | | | | | | | 2 |
| 7 | 1 | | 2 | 1 | | | | 4 | 8 |
| 8 | | 1 | | | | | | | 1 |
| 9 | | 1 | | | | | | | 1 |
| 10 | | 1 | | | | | | | 1 |
| 11 | | 1 | | | | | | | 1 |
| 12 | | | 2 | 1 | 3 | | | | 6 |
| 13 | | | | | | | 1 | | 1 |
| 14 | | | 1 | 1 | | | 2 | | 4 |
| 15 | | | 1 | 1 | | | | 4 | 6 |
| 16 | | | 3 | | 1 | | | | 4 |
| 17 | | | | | 1 | | | | 1 |
| 18 | | | | | | 1 | | | 1 |
| 19 | | | 1 | | | | | | 1 |
| | 20 | 20 | 20 | 15 | 17 | 17 | 12 | 17 | 138 |

NB: In the bracket below, define the abbreviations of the relevant chicken ecotypes: UNGJ (Unguja), PEMB (Pemba), MU (Musadam), BT (Batinah), NH (North Hajar), EH (East Hajar), EC (East Coast) and DF (Dhofar)