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Genomics Tools for the Characterization of Genetic Adaptation of Low Input Extensively Raised Chickens

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Abstract

Evolutionary change emanating from differential contribution of genotypes to the next generation can determine success in survival and reproduction in chickens. For extensively raised chickens reared under low-input production systems in smallholder farming areas, conditions of resources deprivation and exposure to diverse and threatening natural selection pressures are common in many countries worldwide. Numerous studies have demonstrated that village chickens and other extensively raised chicken populations represent a valuable source of biodiversity adapted to the local production conditions and selection pressures. Manipulation of their acquired adaptive genetic diversity depends on unravelling the selection footprints in the genomes of these chickens that could point towards candidate genes for traits that enable the animals to survive under the harsh production environments. This chapter summarizes the evidence for chickens' adaptation to extreme environments and describes an inventory of modern tools that could be used in characterizing the production systems of chicken genetic resources. The role of natural selection in shaping the biodiversity of chicken genetic resources is discussed. The continued advancement of biotechnological tools to assess chicken populations has been beneficial to research in genetic adaptation. Genomics tools, as evidenced by assays of whole genome and transcriptome sequences, and single nucleotide polymorphism (SNP) genotypes of chickens, now allow analyses of functional genomic regions that are linked to adaptation. The use of these methods to characterize and investigate signatures of selection in the chicken genomes is highlighted. This chapter looks at how information on the selection hotspots in the chicken genomes can be manipulated to improve genetic adaptation in indigenous chicken populations with the desire to transfer the benefits to other chicken breeds raised under similar production systems.

Keywords: selection footprints, production system, landscape inventory, chicken genetic resources, genetic adaptation

1. Introduction

Chicken production in Africa and many developing countries plays an integral role in small-holder farming systems and relies upon rearing of scavenging indigenous chickens commonly referred to as village chickens [1]. Chickens fulfil several household needs that are cultural, economic and/or social. However, the contribution of indigenous chickens from rural localities to chicken biodiversity has assumed prominence [2]. Purpose-driven artificial selection and breeding for traits of economic importance are undocumented in village chicken populations. Instead, the chickens are regarded as subjects of natural selective pressures applied through factors such as endemic diseases, climate, nutrition and other variables. The result is a variety of plumage colours, productivity levels, body sizes and disease resistance phenotypes. The resultant biodiversity ensures that the chickens can survive in diverse ecological zones by natural selection of genotypes promoting survival fitness. It is therefore hypothesized that the village chicken populations could harbour genomic segments similar to those found in the ancestral chickens *Gallus gallus domesticus*. The gene pool has survived the historical selection pressures and allows village chickens to survive in the harsh and diverse environmental conditions.

In response to the global shift in environmental and market demands for chicken products, the diversity in village and other chicken populations could be needed in future for chickens' genetic advances and improvements. Evolution of chickens and programs for their artificial selection rely on the availability of sufficient levels of genetic variation. Village chickens are regarded as important genetic reservoirs that have evolved in harsh environments over many generations in the absence veterinary and intensive management [3]. Adoption of the free range organic farming systems could result in increased demand and dependency on village chicken genotypes that are already thriving in a very similar production system [4]. Marker-assisted selection and introgression are possible vehicles of harnessing the valuable genetic variation in village chickens for the benefit of high-performing commercial populations [5]. However, the success of genetic improvement strategies relies on a systems approach that ensures that other production constraints are met [5].

This chapter looks at village chicken populations, the characteristics of their production systems and how that shapes their genomic architecture. The chapter describes the production challenges and opportunities experienced in village chicken production systems and how they could be regarded as selection pressures for village chicken populations. The importance of identifying selection footprints in genomes of different village chicken population is highlighted. Lastly, this chapter examines the potential role of next generation sequencing and genotyping technologies aided by advances in statistical genomics in determining signatures of selection and explaining the adaptive genetic diversity found in extensively raised chicken populations.

2. Chicken populations and genotypes

Despite their socio-economic importance and some efforts to characterize them, insufficient knowledge exists about the genetic composition and potential of village chickens in Africa and

most developing countries. Their hypothesized value as a genetic reservoir remains uncharacterized [2, 3]. Local chickens across the African continent are commonly referred to as either 'village' or 'indigenous' chickens regardless of their population boundaries. However, the chicken populations consist of phenotypically distinct variants reared by rural farmers in different agro-ecological zones (eco-zones) or farming regions in different parts of Africa. Most countries use the term 'eco-types' to describe chickens from various farming systems characterized by different environmental conditions [6, 7]. A number of molecular studies using autosomal and mitochondrial markers have been conducted with the objective of investigating genetic diversity and structures of village chickens of a number of African countries that include Zimbabwe [8, 9], South Africa [10–12], Tanzania [7], Sudan [13], Kenya and other East African countries [14] and Ethiopia [15].

Recently genome-wide SNP data have been used to further characterize village chicken populations [16–18]. These studies confirmed the notion that local chicken populations of Africa are diverse and could be a genetic reservoir of genes not found in other chicken populations. The previous studies failed to comprehensively characterize the chicken genetic resources in terms of their unique genetic features and adaptation to local conditions. Chicken populations with genetically distinct genotypes often possess rare and peculiar genetic features due to unique alleles and allelic combinations. There should be differentiation of the overall genetic diversity of a population to its adaptive genetic diversity described by the genetic attributes of host chicken populations. This would enable their survival in a certain environments where other populations would fail to thrive. There are challenges in deciphering the genetic causes enabling village chicken populations' survival in extremes of environments. However, identifying the dimension in which chickens have adapted to their local environments could enhance our understanding of, and ability to genetically manipulate, the village chicken genotypes.

3. Characteristics of extensive and smallholder chicken production systems

Village chicken production systems typically have households that keep different poultry species and farm other livestock and crop species under the extensive system of production [1, 19]. Chickens have been found to dominate in number and economic contribution in most village livestock production systems [8, 19, 20]. Flock sizes predominantly range from 4 to 50 birds per household [4, 19, 21–23]. The chickens are mostly non-descript breeds utilized for both meat and egg production [23]. Molecular genetic studies have reported high within-population diversity and a deficiency of population substructures across the chicken populations.

Smallholder farmers have limited resources that are allocated to many enterprises contributing to their livelihoods. As a result, inputs towards chicken production in the form of housing, nutrition and veterinary intervention are minimal and, in many households, are non-existent [19, 24, 25]. The chickens scavenge for their feed [26] and are exposed to the full variability of environmental conditions. Little is understood of how disease epidemiology coupled with

poor infrastructure and inadequate diagnostic facilities makes health control challenging [4, 24]. The chickens are raised as mixed flocks combining different age groups. In addition, contacts with wild birds and other livestock species aids in transmission of diseases and jeopardizes biosecurity [1, 27].

Characterization studies of village chicken production systems aim to identify their production challenges and potential. Various studies surveyed and reported the health and disease challenges facing the village chickens from various production systems in Africa and other developing countries [28–32]. Nutrition has been reported as a major challenge due to either insufficient or poor-quality feed [33–35]. Other challenges reported include predation and uncharacterized or unimproved gene pool [36]. Regardless of its shortcomings, the extensive or scavenging method is considered the most important in smallholder chicken production [1, 4]. It is a low-input production system that allows farmers to produce eggs and meat without resorting to expensive poultry feeds, often unaffordable to the rural farmers.

4. Natural selection pressures as forces of genetic adaptation in village chickens

It is evident that the prevalent chicken production constraints present selection pressures on village chicken production systems resulting in certain genes being favored or eliminated from a population. Mortality in village chicken populations is high particularly in young chicks resulting in their failure to reach reproductive maturity and breed, passing their genes to the next generation. Local chickens are raised under harsh, extensive and heterogeneous environments of Southern Africa characterized by inadequate water supply, low quantities of feed which is often of poor quality, and a host of many parasites and disease-causing pathogens [8, 37]. The chickens scavenge for food and water in an environment infested by a number of gastrointestinal parasites and other disease-causing pathogens such that they are continuously re-infected by parasites on different infective stages [38]. The local chickens are regarded as adapted to, or at least tolerant of, the parasite-infested feed resources [39]. The adaptation is considered a valuable attribute that could find application even in the commercial sector under free-range production systems. The mortality due to diseases, parasites, climatic and nutritional stress represents selection pressures whereby the chicken genotypes able to survive the harsh production conditions are able to survive whilst the rest are selected out. Reproductive wastage due to poor hatchability and predation are other selection pressures resulting in fewer breeders contributing to the next generation. To survive this selection pressure, adaptation traits such as plumage colour, good mothering ability and the ability to sense danger and respond promptly become important. Dark plumage colour is considered as a camouflage against predators particularly in mature birds [40].

Village chickens face a number of nutritional constraints that include (i) low quality and fluctuating scavenging feed resource base [33, 37, 41]; (ii) inadequate and erratic supplementary feeding that in most cases depends on the availability of crop and household residues at the different households and not so much on the nutritional requirements of the birds; and (iii)

presence of anti-nutritional factors in the unprocessed feeds [26]. Chickens are known to compete with humans for grain and other nutritional sources. As a result of human food insecurity in most smallholder farming systems, chickens are often found feeding on residues. In most instances, the composition of such residues as feed does not meet the nutritional requirements of the chickens. Examples of such feeds are maize hauls from mealie-meal processing as well as low quality beans and other legumes residues [26, 33]. Chickens surviving under village chicken production systems should therefore be able to tolerate and adapt to the high roughage diets and anti-nutritional factors found in most of the feeds that the chickens scavenge on. Although protein is not a limiting factor, the worms and insects that the chickens feed on could be vectors of parasites and diseases. It is imperative for the chickens to develop a defense mechanism that prevents or fights infections from the different nutritional sources.

Breeding and selection in village chickens has been largely a natural selection feature and as such the chickens are generally described as non-descript birds not specialized for any particular production traits [9]. However, of concern is that absence of cock-sharing among villages, a lack of pedigree records and disorganized mating structures present problems with inbreeding resulting from breeding too few cocks in flocks where the hens are their close relatives [9, 29]. Although hen to cock ratios of 5:1 has been reported, most farmers in these village chicken production systems have been found to choose a few cocks that they use to propagate into the next generation based on preferred phenotype and morphological features [39]. Farmers have been observed to select based on features such as body size, plumage colour, among other attributes [9]. In many cases, there are no organized breeding programs and these unconventional selection practices could result in inheritance of only a few genes from the few breeding stock of the next generation.

5. Rationale for studying genetic adaptation in local chicken populations

Genetic adaptation is key to survival in harsh production environments where management interventions are limited [4]. Adaptation will enable animals to survive and produce optimally in the face of extreme environmental conditions, limited and poor quality feed and diseases and parasite infections which are characteristics of most village chicken and other livestock production systems. The change in consumer demands resulting in changes in production methods has shifted poultry breeding goals from merely meat and egg production oriented to incorporation of such traits as welfare and disease resistance and other adaptive traits particularly in poultry. It is on this basis that local chickens that have been raised and have adapted to the extensive systems of production are important. With the advent of genomic (GAS) and marker (MAS) assisted selection and marker assisted introgression (MAI) techniques, genes conferring adaptation can be selected to improve resistance or tolerance to selection pressure in a population or can be introgressed into other populations.

Adaptation to local environments is a phenomenon associated with village chickens and other indigenous livestock genetic resources. Village chicken populations could be sources of alleles and allelic combinations developed over long periods of time and conferring adaptive

advantages to the chickens carrying them [3]. The drivers for selection in the farming systems of African livestock include socio-cultural factors and potential for livestock survival in wide-ranging environments [42]. To survive, African livestock need to adapt to the varying virulence of communicable diseases, climatic challenges and nutritional constraints [42]. Adaptive and survival traits requisite to chickens raised under typical village chicken production systems for example include the ability to escape predators by running or flying, hens going broody in order to naturally hatch chicks without artificial incubation and birds learning how to scavenge for feed and water resources [33].

Although hypothesized to have developed adaptive mechanisms to survive the harsh environments they are raised in [4, 8], the genetic mechanisms involved in adaptation of village chickens largely remains unclear. The environmental factors which trigger the chickens' adaptation are not known and efforts are still underway to investigate whether that adaptation is genetic and heritable. Questions such as how many genes are involved in adaptation, the nature of the genetic variation conferring the adaptation and whether adaptation utilizes pre-existing genetic variation or new mutations after an environmental challenge remain unanswered.

Knowledge of the adaptive traits developed by local chicken populations is important as part of an inventory of the genetic resources that are present and the useful genes that they might be carrying [42]. Adaptive genetic diversity enables populations' flexibility and survival in changing production environments, consumer demands and environmental and climate changes [4, 43]. A diverse array of genes found in indigenous livestock populations allows populations to survive in diverse and changing environments and should be the target for conservation [43]. It is therefore important that the genetic adaptation is characterized to enable accurate conservation measures.

One challenge in the study and characterization of village chicken populations has been finding appropriate tools and frameworks to characterize adaptive genetic diversity. In the tropics, indigenous chickens genetic resources are plenty and could provide a foundation for adapted breed development through genetic improvement and diversification [44]. Nine major genes of indigenous chickens that could become useful in genetic improvement initiatives have been identified [44]. However, knowledge is still sparse on the genetic constituents of the indigenous chickens of Africa. Efforts to collate information by FAO Domestic Animal Diversity Information System (DAD-IS) points to some unique genetic variants found in the local chicken populations across the African continent. Recent developments in genomics and bioinformatics have opened up platforms to study genetic mechanisms of adaptation as well as ways to manipulate the advantageous alleles and genotypes.

6. Previous attempts to characterize and manipulate adaptive genetic diversity in village chicken populations

Utilization of the vast amounts of genetic variability within village chickens could be useful to their adaptation to local environments through promotion of favourable genetic variants

associated with traits such as disease resistance. The unravelling of the genomic architecture for fitness and robustness of the individual chickens is the missing link to the direct application of modern molecular techniques to improve adaptation through breeding programs. Positive selection towards enhanced robustness could advance adaptation of indigenous chickens to harsh and extreme environmental conditions. This would result in chickens that carry alleles necessary for adaptability to the local conditions. The genetic link between the environment and adaptation has not been fully explained but studies abound demonstrating the association between genotypes and the environment for possible inference on genetic adaptation. More data and cases are required to draw clearer conclusions.

Conventional approaches to study adaptive traits in chickens have involved controlled experiments whereby particular environmental challenges are simulated and the response of chickens is monitored [39]. These methods have the limitation that the actual environment where these chicken populations are raised is too heterogeneous in nature and complex to be fully simulated under restricted experimental designs. Resistance to diseases and parasites, for example, are complex traits influenced by both the genes of the animal and the environment under which these animals are living. Under varying environmental conditions, the enteric bacterial pathogens have shown different effects on the intestinal epithelium. Understanding the avian immune system and the response of the chicken as a host is vital in designing prevention strategies for intestinal diseases in poultry. Host response after interactions with pathogens has not yet been fully unravelled.

There has been some work reported using morphological marker genes for genetic improvement in livestock. Crossbreeding experiments of the Fayoumi breed showed an increase in egg production when breeds carrying the naked neck (*Na*) genes were used [45]. Similarly, economically important traits of feed efficiency of chickens under heat stress through use of dwarf gene (*dw*) carrying breeds and egg production and egg weight enhancement by crossing with naked neck (*Na*) and frizzle (*F*) genes-harbouring breeds have been demonstrated [46].

Autosomal microsatellites and mitochondrial DNA sequences have been used to infer on the genetic structures and maternal origins of most village chicken populations of Africa revealing lack of population sub structuring within village chicken populations of a number of countries such as Kenya and other east African countries [14], Zimbabwe [8], Ethiopia [15] and South Africa [12]. The studies have also shown a considerable level of sub structuring between countries. mtDNA studies have shown multiple maternal lineage and high level of genetic diversity in the studied African populations. Core set analysis of the South African chicken populations has shown that they are a reservoir of genetic diversity that could make a significant contribution to the global diversity found in chicken genetic resources ([12]. Other studies have used single nucleotide polymorphism (SNPs) within candidate genes associated with traits of economic importance to study genetic variability and infer on traits such as immune response and growth. Elucidating the genetic variability in indigenous chicken at gene loci important for the immune system e.g. Toll like receptor 7 (*TLR7*) nowadays relies on molecular genetic tools. A study used a total of 24 SNPs and 35 haplotypes within the family of Toll Like Receptors genes to investigate genetic variability in immune response traits of Sri Lankan Indigenous chickens [47]. An investigation of the polymorphism at a single *Mx* locus

inferred on resistance of populations to Avian Influenza [48]. The genetic diversity of two important immunity candidate genes, the inducible nitric oxide synthase (*INOS*) and natural resistance-associated macrophage protein 1 (*NRAMP1*) in indigenous Malaysian chickens, was carried out using the polymerase chain reaction-restriction fragment polymorphism (PCR-RFLP) [49].

There is currently an increased focus on genetic characterization and conservation of biodiversity globally. Whilst these previous studies have provided the much-needed information on the genetic diversity of chicken genetic resources, there has not been much success in terms of characterizing the adaptive chicken diversity. This has mainly been due to the neutral nature and sparse genome distribution of markers used in earlier studies. Although recent genomic studies using either genomewide SNP or sequence data have highlighted the utility of such genomic tools in characterizing adaptive genetic diversity [16–18] very few studies have actually used the data to infer adaptive genetic diversity in chicken populations [18].

7. Genomics tools for characterization of signatures of selection and genetic adaptation

There have been significant developments in our understanding of the genome of chickens and the statistical applications that can be used in elucidation of genetic adaptation and robustness of local livestock populations including chickens. The chicken genome was sequenced in 2004, which opened new avenues for the exploration the genomic architecture and advance genomic studies. Alternative genomic variants such as Linkage disequilibrium (LD) blocks, Copy Number variations (CNVs) and Runs of Homozygosity (ROH) have increasingly found use in studying genetic diversity and drawing of inferences on genetic adaptation in chicken populations. Contrary to prior markers that were either found in non-coding regions of the genome or sparsely distributed, genomics tools present the required genomic coverage to investigate regions associated with traits of economic importance.

7.1. Copy number variations

Copy number variations (CNVs) have gained enormous research recognition in recent times as genomic structural variants of interest in chicken biodiversity studies [50, 51]. Copy number variations (CNVs) are defined as deletions, duplications or insertions, which change the genomic diploid state of an individual [52–54]. The last few years have seen major advances in genomics demonstrating that the alterations in the DNA could have no effect phenotypically, or account for traits for adaptation and even underlie disease etiology and susceptibility [55, 56] thereby providing increasing evidence of their contribution to breed diversity. Prevalence of CNVs have been reported in chickens and associations suggested with traits of economic importance [50, 57]. Bioinformatics and statistical pipelines have been developed to screen for CNVs and infer on biological functions [56, 57] and associated CVNs to resistance to Marek disease in divergent chicken lines. CNVs that have potential roles in economically important traits in chickens have been suggested [58]. Other studies also associated CNVs to diseases [59].

Numerous reports produced from CNV studies were mostly restricted to commercial or experimental chicken lines and, thus far to the best of our knowledge, none were used in village or extensively raised chicken populations. However, there is scope to use CNVs in these nondescript and uncharacterized chicken populations that have been exposed to natural selection pressures.

7.2. Runs of homozygosity

Runs of homozygosity (ROH) are lengthy continuous regions of the genome where, in the diploid state, the copies inherited from the parents are identical. These stretches have been found to estimate inbreeding coefficients that are much better at detecting the overall burden of rare and recessive mutations based on high-throughput, beadchip single nucleotide polymorphism (SNP) genotypes [60]. Associations have been made between ROH and genetic defects arising from intensive selection and inbreeding in other species [61]. There have been very few studies using runs of homozygosity in village chickens. Previous studies have suggested inbreeding to be a problem in village chickens that are raised as small fragmented flocks with a lot of cock sharing of few male animals within villages [16]. Runs of homozygosity have potential as estimators of inbreeding through identification of genomic regions they affect [62].

7.3. Linkage disequilibrium and haplotype blocks

Linkage disequilibrium (LD) is defined as non-random association of alleles more than one loci [63, 64]. In genetics, LD is a useful tool increasingly finding application in the genomic era with the availability of data from high-density SNP panels. The decay and extent of LD at a pair-wise distance can be used to estimate trends in effective population size [17, 65, 66]. LD will therefore be useful in extensively raised chicken populations in smallholder farming systems where, due to non-collection of pedigree information, calculation of population genetic parameters could be possible. LD estimates have been used to determine trends in effective population size in egg and meat producing chicken lines [64]. A study used the chicken 60K panel to determine LD and estimate effective population sizes in extensively raised chicken populations of southern Africa [16]. Estimates of inbreeding and trends in effective population sizes provide information required to monitor and conserve village chicken populations in the absence of pedigree data. Such information also sheds light on demographic forces that influence genetic diversity of village chicken populations.

7.4. Landscape genomics

Landscape genomics combines genome-wide information with geo-environmental resources analysis to identify potentially valuable genetic material [67, 68]. With regards to village chickens, the aim for landscape genomics is to learn from their co-evolution and production systems and use the knowledge gained to better match different genotypes with production circumstances. Regions where chicken genomes face selection pressure from environmental conditions such as high temperatures, lack of water in drought *etc.* are expected to show higher genomic divergence across habitats compared to the neutral genome background. By per-

forming genomewide-scans on chickens from populations living in different habitats or across agro-ecological cline, from dry to wet areas, for example, landscape genomics offers the opportunity of analyzing the immune response of chickens across a naturally occurring environmental gradient [67]). By collecting samples from chickens from different environmental conditions and assessing their phenotypic performance and genotypes at certain loci, one can have an idea of how the environment has influenced the immune system of the chickens to infection by pathogens. In previous chicken studies, it has been shown that agro-ecological zones or climatic regions have an important role in defining free ranging chicken production systems [8]. The eco-zones influence the type of feed animals has as well as disease and parasite pathogen profiles. Agro-ecological zone also influences the physiological function and response of chickens to disease-causing pathogens thereby determining immune response status. As in most species, chickens raised within a certain locality tend to develop adaptive traits that help them survive in the given environmental challenges. By applying landscape genomic techniques, one will be able to overlay the genetic profiles of chickens over the environmental coordinates, identify and characterize genes conferring adaptive features to the different environmental conditions. As a new tool, reports of case studies on the application of landscape genomics are sparse for village chickens. The Mediterranean goat breeds have been characterized using landscape genomic approaches and results in one study showed regions of genomes being under different selection pressures in different environments [67]. One of the major requirements for landscape genomics is a dense set of molecular markers both neutral and those under selection to be able to make inferences on the role of selection versus neutral evolutionary forces on shaping genetic diversity. Both next generation sequencing and high-density SNP panels have provided such platforms.

7.5. Signatures of selection

An alternative approach to ascertain regions of genome with relevant genes for genetic adaptation and robustness in chickens could be the detection of selection signatures using genomewide SNP data or sequences [69, 70]. The principle that loci across the genome are influenced by genome-wide evolutionary forces like migration, random genetic drift, mutation etc is the basis for population genomics. Locus-specific forces *e.g.* selection help create particular patterns of variability in the regions of associated genes And loci [70]. Comparison of the genetic diversity of across numerous loci on the genome, it is possible to uncover loci exhibiting an atypical variation pattern which are could be linked to areas in the genome affected by selection [69]. Signatures of selection have been investigated in a number of chicken populations [17, 18]. Signature of selection analysis does not necessarily require conventionally-measured performance as in GWAS analysis. This makes it a suitable tool to screen for advantageous loci in extensively raised village chicken populations.

7.6. Comparative genomics

With plummeting costs of whole genome sequencing, more and more sequence data are being generated across different species. Comparative genomics involves sequencing and comparing genomes of different species in search of genomic regions differentiating species. In several

avian species including chickens, use of comparative analysis of genome sequences has emerged as a powerful tool for understanding metabolic processes and gene functions influenced by selection [71]. Inter-species comparison of selection signatures can play a role in detecting relevant functional polymorphisms in experiments using populations collected from a variety of environmental conditions. An analysis comparing the evolution of chicken (*Gallus gallus*) and zebra finch (*Taeniopygia guttata*) genomes [71] showed that an important cytokine receptor, the interleukin 4 receptor alpha-chain (*IL-4R α*), has significantly an abundance of substitutions at nonsynonymous sites which could be a crucial mechanism in its adaptive evolution.

7.7. Transcriptomic analysis

Complete sequencing of the chicken genome and the availability of data on various transcriptomes of specific tissues ushered in another field of functional genomic analyses of chickens. A complete set of transcribed mRNA and the related amounts for specific stages of development or physiology is known as a transcriptome [51]. Studying transcriptomes is now considered essential for unravelling the functional elements of the genome and understanding the molecular and physiological processes in cells and tissues in chickens. Transcriptome analysis identifies genes expressed and gene pathways affected in chickens raised under the heterogenous village chicken production systems, giving an indication of potential candidate genes for adaptation and robustness. Transcriptome sequencing and gene expression analysis were used to investigate genes conferring resistance to colonization of chicken intestines by *Campylobacter jejuni* [72]. A study of gene expression profiles reported differentially expressed genes in chicken intestines infected with *Ascaridia galli* [73]. With the chicken genome and other functional genomic tools available, generated transcripts can easily be aligned to the chicken genome and other transcripts of reference chickens to assess the gene expression profile under different conditions.

8. Genomic tools in village chicken breed improvement programs

Selection and breeding are among the key forces moulding village chickens' genomic architecture and regulating their genetic diversity. Although a majority of chickens found in most smallholder production systems are uncharacterized and regarded as unimproved, farmers have indicated preferences for certain phenotypes that they select for in hens and cocks for breeding [9, 74]. However, these traditional breeding activities are conducted in the absence of pedigree records, without collecting performance data and lacking institutional support thereby creating a false impression that no selection and breeding programs for village chicken populations are available. Before the advent of genomics, it has thus been difficult to assess the impact of any selection and breeding in village chickens.

The nature of village chicken production makes selection and breeding challenging. The chickens are raised communally with a lot of sharing of breeding stock between households within communities. Mating is indiscriminate and left to chances of breeding stock mixing

during scavenging in the communal spaces. Due to limited resources and extension support, farmers tend to keep breeding stock for longer periods resulting in overlapping generations. In other systems, farmers have access to exotic breeds adding another dimension to genetic improvement through crossbreeding. However, all these factors present challenges for having organized breeding strategies for village chickens of setting up breed improvement programs for village chickens.

Genomics can provide valuable information to facilitate selection of animals in breeding programs. Genomics can be used to reconcile pedigree and define breeding population boundaries. Genomics, bioinformatics and statistics are also finding application in identifying loci and regions in the genome that are adapted to specific environments. When breed improvement programs are implemented, genomics can be used to monitor genetic progress and the direction thereof.

Community based breeding programs (CBBPs) refer to approaches of improving livestock genetics through incorporating farmer participation into selection and breeding processes, from inception through to implementation. Under circumstances where livestock keepers already rear mixed flocks of livestock together such as in communal grazing systems, the implementation of community-based breeding programs is appropriate [75, 76]. This would be beneficial through shared production capital (animal genotypes, grazing land etc.) and pooling of resources and services (veterinary, feeding and marketing) thereby enabling joint processes of making decisions. Key to community based breeding strategies is the consideration of farmers' views, needs and decisions, and to encourage active participation throughout the life-cycle of the program.

Genomics plays a crucial role in complementing CBBPs through provision of information that would otherwise be out of reach in the marginalized and low-input production systems. Genomics also provides information on the genetic architecture of populations, which is a requisite step in setting up selection programs. Genomics overcomes the challenge of missing pedigree and breed relations information which is a characteristic of most communal production systems where records are not kept as is seen in smallholder village chicken production systems. Numerous case studies exist of CBBPs combining with genomics technologies successfully. CBBPs have proven to be highly successful in Kenya, Bolivia, Ethiopia, Mexico and Peru. In these case studies, the productivity and profitability of indigenous breeds increased in the CBBPs without undermining the resilience and genetic integrity of the populations and potentially reducing genetic diversity. Although no reports of CBBPs are available for chickens to our knowledge, there is potential for combining genomics and CBBPs for the improvement of village chicken populations predominantly raised extensively as large interbreeding flocks in shared environments.

9. Conclusion

Village chicken populations are a source of unique and adapted genotypes that are robust enough to survive in harsh environmental conditions with minimum human interventions.

High throughput next generation sequencing and genotyping tools coupled with advances in statistical genomics are now allowing a comprehensive assessment of the adaptive genetic diversity in livestock species. Analyses of transcriptomes and whole genome sequences and SNP genotypes are tools that can be used to reveal the genetic composition of village chicken populations. Studies have opened doors to analyses of CNVs, ROH and use other bioinformatics and statistical tools such as linkage disequilibrium, comparative genomic analysis and transcriptome profiling to get a deeper insight on evolution of village chicken genomes to adapt to their environments.

Selection and breeding of village chickens is challenged by absence of pedigree and performance data to identify superior animals for use in the next generation. Genomic tools could be the panacea allowing selecting and breeding of chickens outside conventional breed improvement frameworks. In combination with strategies such as CBBPs, there are potential benefits of integrating genomics in the characterization and utilization of the genetic diversity the village chicken populations embody.

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