

2018

The genetic diversity of local african chickens: A potential for selection of chickens resistant to viral infections

Mpenda, Fulgence

Poultry Science Association Inc.

<http://dx.doi.org/10.3382/japr/pfy063>

Provided with love from The Nelson Mandela African Institution of Science and Technology

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/329794775>

The genetic diversity of local african chickens: A potential for selection of chickens resistant to viral infections

Article in *The Journal of Applied Poultry Research* · November 2018

DOI: 10.3382/japr/pfy063

CITATIONS

0

READS

253

5 authors, including:



Fulgence Ntangere Mpenda

The Nelson Mandela African Institute of Science and Technology

4 PUBLICATIONS 8 CITATIONS

SEE PROFILE



Megan Schilling

Pennsylvania State University

24 PUBLICATIONS 36 CITATIONS

SEE PROFILE



Zoe Campbell

Washington State University

16 PUBLICATIONS 8 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Bushmeat Project [View project](#)



Newcastle disease vaccine adoption [View project](#)

The genetic diversity of local african chickens: A potential for selection of chickens resistant to viral infections

F. N. Mpenda,^{*,1} M. A. Schilling,[†] Z. Campbell,[‡] E. B. Mngumi,^{*} and J. Buza^{*}

**Department of Global Health, School of Life Sciences and Bioengineering, The Nelson Mandela African Institution of Science and Technology, P.O. Box 447, Arusha, Tanzania;*

†Department of Animal Science, Pennsylvania State University, University Park, PA, USA; and ‡Paul G. Allen School for Global Animal Health, Washington State University, Pullman, WA, USA

Primary Audience: Researchers, Breeders, Extension services, Animal Genetic Resources

SUMMARY

Viral infections impose a great threat to backyard chicken production among poor rural households in developing countries. These infections limit the contribution of chicken production in improving the livelihoods of poor communities, particularly in Africa. Chicken viral infections lack treatment options; control and prevention depend primarily on adoption of vaccines and good farm management practice such as the institution of biosecurity measures. In backyard production systems, these control options are less practical and less feasible to implement. Research has demonstrated the role of genetic diversity of farmed animals and birds in explaining variation in resistance to infectious diseases and suggests that heterogeneous populations are less susceptible to disease than homogeneous populations. Local African chicken ecotypes have high genetic diversity and have demonstrated the ability to survive persistent exposure to pathogens and harsh environmental conditions. This suggests that local African chickens have the genetic potential to enhance breeding strategies for resistance to viral infections. Despite the ongoing threat of infectious disease and dynamic of diseases epidemiology attributed by climate change, little has been done to harness the genetic potential of local African chicken ecotypes to breed for resistant traits. To lay the foundation for future research, this review paper presents a summary of challenges facing current chicken viral infections control and prevention options in local African chickens, and gives an overview of documented information on the genetic diversity and population structure of local African chicken ecotypes.

Key words: backyard production systems, disease resistance, indigenous chickens, backyard poultry, genetic diversity, local African chicken, animal genetic resource, climate change

2019 J. Appl. Poult. Res. 28:1–12
<http://dx.doi.org/10.3382/japr/pfy063>

INTRODUCTION

Chickens are the most common species of poultry raised globally with the world population of chickens estimated at 18 billion [1].

¹Corresponding author: mpenda83@gmail.com

About 80% of chickens that are raised in Africa are local African chickens [1]. The majority (60%) of African households raise local African chickens under backyard systems [2, 3]. Local African chickens are well adapted to harsh and stressful environmental conditions and are good scavengers [1, 4]. Local African chickens serve as a chief source of high-quality meat protein and a source of income [3, 5, 6], and play significant role in sociocultural activities such as traditional ceremonies and rituals [1, 3].

The production of local African chickens is constrained by high mortality rates due to infectious diseases [7, 8]. Viral diseases such as Newcastle disease (ND), Marek's disease (MD), and infectious bursal disease (IBD, Gumboro) cause enormous losses in chicken productivity under backyard production [9–11]. More importantly, chicken viral infections do not have well-known treatment options; control and prevention depend on proper vaccine administration and appropriate implementation of biosecurity measures to halt spread and transmission of infections between chicken flocks [1, 12–14]. In backyard systems, the implementation of vaccination and biosecurity measures is a challenge due to farmers' lack of resources to buy vaccines and because local chickens are free ranging [1, 12, 13].

Selection for chickens resistant to viral infections is a promising approach for control and prevention of chicken viral infections [15]. Phenotypic and genotypic individual variations within and between chicken breeds or ecotypes have been documented [15–17]. For example, chicken lines, which are less susceptible to MD, have been under development for years [15]. This individual variation in resistance and susceptibility to infectious disease is attributed to genetic diversity within and among populations [18, 19].

Genetic diversity can buffer populations against infectious diseases, and populations with high genetic diversity are more resistant to infections than homogeneous populations [20–22]. Local African chicken populations are highly genetically diverse and are heterogeneous [24–26]. Most of the local African chickens have not been subjected to purposive artificial selection, but have instead subjected to natural selection through exposure to harsh and stressful environmental conditions and endemic infectious dis-

ease agents [27]. Local African chickens may harbor genes responsible for disease resistance, and may be appropriate in the changing environmental conditions caused by climate change [23–25]. However, despite the well-known genetic diversity of local African chickens, little has been done to investigate their genetic potential for disease resistance through artificial selection.

Most studies investigating genetic diversity and population structure of local African chicken ecotypes use microsatellite markers and mitochondrial DNA D-loop region, which yields limited information relative to variations in resistance and susceptibility to viral infections [24, 25, 28, 29]. There is a paucity of studies involving molecular tools with high genomic coverage which would perform genome-wide scan of genomic variations such as microsatellite markers, single nucleotide polymorphism (SNP), and genomic structural variations (such as copy number variants [CNV]), and decipher how these genomic variations may be associated with the variability in resistance and susceptibility of African local chickens to viral infections. The dearth of information may lead to underestimates of the genetic potential of local Africa chickens for selection of chickens resistant to viral infections. The present review paper is aimed at: (i) presenting a summary of information on challenges of control and prevention of chicken viral infections in African local chickens under backyard production systems and (ii) presenting a summary of documented information on the genetic diversity and population structure of locally adapted African chicken ecotypes and its implication for selection of chickens resistant to viral infections in the changing environment due to climate change.

LOCAL AFRICAN CHICKENS AND KUROIILERS

Local African chickens are chickens that are reared under backyard production systems [1, 10]. Various names are used depending on the country of origin to refer to local African chicken (Table 1). In this paper, the name 'local African chicken' will refer to African indigenous chicken

Table 1. Summary of Production Dynamic Studies for Local African Chickens.

Study	Country	Name*	Production system	Average flock size	Reason of keeping chickens	Constraints
[28]	Sudan	Native chicken	Extensive /backyard	25	Meat provision and cash generating	Infectious diseases and predation
[7]	Tanzania	Rural chicken	Extensive /backyard	5	Food and sale (source of income)	Poor nutrition, infectious diseases, and predation
[8]	Kenya	Indigenous chicken	Small-scale free range	22	Food and cash income	Infectious diseases and poor nutrition
[29]	Ethiopia	Indigenous chicken	Extensive	16	Food and source of income	Infectious diseases and predation
[23]	Malawi	Scavenging chicken	Scavenging	13	Food and sociocultural functions	

*Various names, which are synonymously, used referring to local African chickens.

genotypes adapted to harsh tropical environmental conditions.

The main characteristic of local African chickens under backyard production settings is unlimited movement of birds, which allow birds to search for nutrition needs [3, 26, 27]. Rearing local African chickens require little or no feed supplementation, as they are scavengers. This makes production of local African chickens under backyard systems cost effective, and, therefore, appropriate for resource-poor households in rural communities of African. Further information on production systems of local African chickens is reviewed in detail elsewhere [2, 27].

A new hybrid chicken called the Kuroiler was introduced to Africa from India [30–32]. The Kuroiler is dual-purpose scavenger chicken raised for egg and meat production [33]. Like local African chickens, Kuroilers can thrive under harsh tropical environmental conditions, and they can scavenge for nutrition needs just like local African chickens [33–35]. The breed outperforms local chickens in terms of meat and egg production [32, 34, 35]. In a pilot study conducted in Uganda, Kuroilers and local Ugandan chickens were kept under the same scavenging settings, and the Kuroilers had higher production performance compared to local Ugandan chickens [30]. At 25 wk of age, the average body weight of the male Kuroiler chickens was 2.6 kg, compared to 1.6 kg for the male local Ugandan chicken [30]. Additionally, at 6-wk of age, Kuroilers had a higher average body weight than Sasso, a chicken originated from France, and Fulani, an indigenous chicken from Nigeria [32].

Furthermore, the Kuroiler chicken reported to lay 4–5 times more eggs compared to Desi, a local Indian chicken breed [35]. Although not supported by empirical studies, Kuroilers are said to be resistant to infectious diseases [30, 31]. Thus, increased production of Kuroiler chicken may have a significant impact on improving the quality of livelihood for resource-poor rural households.

THE GENETIC DIVERSITY OF LOCAL AFRICAN CHICKENS

Genetic diversity is derived from genes, segments of DNA that contain essential information for life on earth [21]. The concept of genetic variation derives from the possibility that individuals in a given population may carry polymorphic (different) DNA sequences of a given genomic region [21]. Therefore, genetic diversity can be defined as varieties of genes within a species [21]. The genetic diversity is at three levels: species, population, and individual [36]. Within a population of a given species, individuals may have unique genetic composition resulting in genetic variability among members of the same species leading to population substructuring [37]. Individual genomic differences in population are determinant of genetic diversity of a given population [21, 37, 38].

Local African chickens have high genetic diversity based on qualitative and quantitative traits [3, 16, 16, 39, 39]. The phenotypic diversity in terms of physical and morphological parameters such as plumage color and type, body shape

and size, and productivity performance is evident among local African chicken ecotypes [4, 16, 40, 41]. Variability in phenotypic parameters within and among local African chickens has been reported in most African countries, including Sudan [42], Ethiopia [43], Botswana [40], Nigeria [44], and Algeria [45].

The pattern of variations in phenotypic parameters is geographic and ecotype specific. Using morphological measurements, Lyimo et al. [41] were able to differentiate individuals of 5 Tanzania chicken ecotypes into 3 clusters, and ecotypes from the same geographical area tend to cluster together [16, 41, 46]. These findings are consistent with another report that involved 2 Benin chicken ecotypes from the Forest and Savanna ecological areas where the 2 ecotypes were different in terms of phenotypic parameters [47]. These observations are in agreement with Mahammi et al.'s [48], who postulated that the genetic diversity of Algerian chicken ecotypes are under 2 opposite evolutionary forces: the geographical location and climatic conditions, which induce differentiation and the high level of distribution and gene flow which homogenizes the population genetically [48]. The abundance of phenotypic variability within and between local African chickens may be an indication of their high genotypic variations. The phenotypic diversity of African chickens has been reviewed in detail elsewhere [49–51].

Genotypic diversity analysis of microsatellite markers has been extensively used to evaluate the genetic diversity and population structure in chickens [39, 52, 53]. Based on the mean number of alleles and heterozygosity values, reports indicate that local chickens from different parts of the world are highly genetically diverse as compared to pure commercial breeds (Table 2). When compared to local chickens from other parts of the world, local African chickens have demonstrated higher genetic diversity (Table 2).

Based on population structure indices, reports indicate that local chicken populations are genetically closely related [39, 53, 54]. The genetic variation of local African chickens is largely accounted for by the within ecotype variations. For example, 96.8% of the total variation among Zimbabwean chickens attributed to within ecotype variations [20]. Similar findings were observed among local chicken ecotypes of

Tanzania [41], Kenya [39], Egypt [55], Sudan [56], Ethiopia [57], South Africa [53], and Algeria [48]. The available information suggests little differentiation among African local chicken populations.

CHICKEN VIRAL INFECTIONS IN BACKYARD PRODUCTION SYSTEMS

Infectious diseases are the major constraint of local African chicken production in backyard systems (Table 1). Diseases caused by viruses are most important in backyard chicken production as they lack treatment options [64, 65]. Viral infection that rank as most important to small-holder farmers in Africa is ND [23, 26, 66], followed by IBD and MD [13]. Here, we summarize some of the most important viral diseases affecting chickens in backyard systems.

Newcastle disease is highly contagious, devastating, and endemic in many developing countries where backyard chickens are common [11]. The disease is caused by Newcastle disease virus (NDV), an avian paramyxovirus serotype 1 [11, 64]. The majority (80%) of losses in local African chicken production and about half of the early chick mortalities (chicks from hatch to 6 wk of age) were caused by ND [10].

Novel virulent NDV strains have been reported in chicken flocks in African continent [67, 68]. The evolution and emergence of new virulent NDV genotypes may explain the reported cases of vaccine failures [67–69]. Along with the effort to develop antigenic-matched ND vaccines to improve the efficacy of the current ND vaccines, selection of chicken resistant to the circulating virulent NDV strains is a promising alternative strategy.

Infectious bursal disease is a contagious viral disease that affects young chickens [70]. The disease compromises the immune system of infected birds and predisposes infected birds to opportunistic viral and bacterial infections [71]. High morbidities and mortalities due to IBD have been reported all over the world, and the disease is of economic importance as it affects the productivity and well-being of birds [71, 72]. The worldwide prevalence and distribution of IBD have been reviewed in detail [73, 74].

Table 2. Genetic Diversity and Population Structure Statistics Estimated in Local and Commercial Chickens.

Country	Chicken type	MNA ¹	Ho ²	Fst ³	Reference
Ethiopia	Local chicken	11	0.5	0.12	[58]
Tanzania	Local chicken	5.7	0.62	0.05	[41]
South Africa	Local chicken	6.6	0.6-	0.01	[53]
	Conserved local chicken*	4.7	0.5	0.16	
Algeria	Local chicken	7.1	0.5	–	[48]
	Commercial	3.9	0.2	–	
Sudan	Local chicken	5.3	0.5	0.03	[59]
	Commercial	3.2	0.4	0.32	
Ghana	Local chicken	6.6	0.6	0.01	[60]
	Commercial	6.0	0.5	0.29	
Egypt	Local chicken	6.9	0.6	0.08	[61]
Britain	British chicken	3.6	0.4	0.25	[62]
Sweden	Swedish chicken	4.7	0.3	0.44	[63]

¹Mean number of alleles per locus.

²Average observed heterozygosity.

³Population differentiation index.

*The local chicken under conservation program characterized by limited movement leading to inbreeding.

In an outbreak of IBD among broiler and layer chickens of Ethiopia, mortality was estimated to be 50% [71]. Mazengia et al. [75] reported morbidity of 38% and case mortality of 99% among Ethiopian locally adapted chickens. In a serosurvey conducted among local Tanzanian chickens, 59% of the chickens were seropositive, and more importantly, 83% of flocks were seropositive [76]. This information indicates that IBD is widespread amongst exotic and local chickens in the African continent.

Another important chicken viral infection is MD, a lymphotropic and highly contagious disease, that affect mostly immature birds [77]. The disease is caused by the herpes virus, Marek's disease virus (MDV) [77]. The disease spreads easily through contact with infected birds, bird droppings, and fomites, and can spread through aerosol and dandruff [78, 79]. The morbidity of MD is about 50%, and mortality can reach up to 100% if occurs in susceptible flocks [79].

CHICKEN VIRAL INFECTION CONTROL STRATEGIES IN BACKYARD PRODUCTION SYSTEMS

Under backyard production settings, the prevention and control of chicken viral infections are a challenge. The control and prevention of chicken viral infections solely depend on vacci-

nation and institution of appropriate biosecurity measures [64, 65]. Like other viral infections in animals, chicken viral infection lacks treatment options.

Vaccination adoption significantly decreases chicken mortalities from viral infections [65, 80]. For example, in a community-based ND vaccination program conducted in Tanzania, ND vaccination effectiveness was almost 70% [81]. Under experimental settings, ND vaccination can result in 100% of flock protection to the disease [82]. However, control of chicken viral infections by vaccination remains a challenge, particularly under backyard systems due to lack of vaccination programs and improper vaccination attributed to limited veterinary extension services in rural areas [83]. Limited financial resources among poor rural households to purchase vaccines and lack of storage facilities, like unavailability of the cold chain for ND vaccines, are significant constraints facing vaccination adoption in backyard production systems [64, 84]. Furthermore, chicken viral infection control by vaccination has limited ability to prevent the spread and transmission of viruses to uninfected chickens [84]. The vaccination aims to prevent clinical disease [84], and vaccinated birds can shed viruses in their secretions such as in feces, tears, and mucosal, thereby spreading infections in the surrounding area [85].

Another strategy is biosecurity, which is designed to prevent the spread of infectious

agents within and between flocks. Biosecurity has three main components: isolation, traffic control, and sanitation [1]. The main characteristic of isolation is the confinement of birds within a controlled environment [1, 86]. Traffic control is designed to limit movement within and between flocks. Sanitation deals with disinfection of materials, people, and equipment entering and leaving the farm, and cleanliness of farm caretakers [86]. Biosecurity is an essential means of preventing infections; however, not much information is available to support its feasibility in backyard production systems [87]. A systematic literature review by Conan et al. [1] found that most of the biosecurity measures devised under intensive production systems are not feasible or effective under backyard chicken production systems. Given the challenges of implementing vaccination and biosecurity measures in backyard systems, genetic selection of chickens resistant to viral infections could be a more robust and cost-effective solution to preventing and controlling infectious diseases.

CLIMATE CHANGE AND CHICKEN INFECTIOUS DISEASES

Climate change is an average change in weather pattern: temperatures, humidity, wind, and rainfall [88]. The change in weather patterns caused by climate change is linked with the dynamic of diseases epidemiology [89, 90]. The change in average temperatures, rainfall, and climate extremes impacts the distribution of pathogens and host–pathogen interaction due to disruption of ecosystem structure [90]. Environmental stressors like weather extremes, infectious agents, and dwindling of feeds influence chicken production [89–91]. More importantly, these environmental stressors are increased by direct and indirect impact of global climate change.

Extreme temperatures and relative humidity compromise the ability of birds to resist infections [92]. The extreme weather like high ambient temperatures is associated with chicken's oxidative stress due to lipid peroxidation and disruption of energy balance, which may lead to immunosuppression [24]. On the other hand, in cold conditions, some pathogens like NDV sur-

vive for longer time increasing the chance of diseases occurrence [25]. The change in the pattern of pathogens distribution and host–pathogen interaction poses an unprecedented risk of new disease occurrence in susceptible chicken populations.

Environment is a main driver of selection pressure of a given population to adapt for survival and reproduction [92, 93]. For example, difference in chicken genomic regions is demonstrated to be linked with the environmental conditions of chicken population [91]. It is likely that chicken populations adapted to harsh environmental conditions like local African chickens may have selection signatures for adaptation to extreme environmental conditions attributed to climate change. The understanding of genetic mechanisms responsible for chicken adaptation to harsh environmental conditions is critically important for breeding chickens resistant to infectious diseases [92]. Likewise, along with the effort to mitigate effect of climate change, it is prudent to breed and conserve chicken genetic resources adapted to survive extreme weather conditions caused by global climate change.

GENETIC DIVERSITY AND DISEASE RESISTANCE VARIABILITY

Genetic diversity contributes to population fitness in response to a changing environment [20, 22, 94]. Population genetic variations allow individual adaptation to the changing environment like adaptations to endemic infectious diseases and climate change [95, 96]. The correlation between genetic diversity and population fitness is demonstrated using molecular quantitative genetics data [20]. Springbett et al. [97] demonstrated that a heterogeneous population is less likely to suffer from catastrophic disease epidemics as compared to homogeneous population using stochastic models [97]. In contrast, the loss of genetic diversity has been associated with species extinction [20, 22, 94].

Disease resistance is defined as the ability of the host to resist infections [36]. For the host to resist infection, the infectious agent should be cleared before getting into the host cell. The resistant host should prevent pathogen attachment and entry into the host cell [36]. Alternatively,

genetic resistance to disease refers to the ability of the host to suffer minimal adverse effects following infection, also, is known as tolerance [36, 98].

At the molecular level, mechanisms of disease resistance are complex and not fully understood. Genetic resistance to infectious agents is polygenic and influenced by the interaction of biological and environmental factors [71, 99]. The mechanisms of disease resistance are mainly controlled by immune responses, which are comprised of both innate and adaptive immunity [100, 101]. The innate immune response is the first line of defense, which clears pathogens in the very early stages of infection and initiates adaptive immune responses [101, 102]. Most of the studies on the mechanisms of disease resistance investigate the role of innate immune responses with the assumption that the innate immune responses determine an individual resistance or susceptible to infectious agents [100–102].

The major histocompatibility complex (MHC) haplotypes are associated with variation in disease susceptibility and resistance [101, 103–105]. The MHC molecules play a significant role in antigen processing and presentation [106]. The MHC can process and present all possible antigens due to the presence of multiple variants of each gene within the population [106]. The MHC genotype restricts the antigen recognition by T-cells. The defect in the MHC molecule may prevent the antigen recognition by specific T-cells. Therefore, the antigen specificity of T-cell is controlled by the MHC molecules [106].

Reports indicate that chicken variations in susceptibility to infectious diseases are linked with the MHC haplotypes [107, 108]. For instance, antibody responses to NDV are significantly associated with 2 MHC LEI0258 microsatellite alleles, 205 and 307 bp, in Tanzanian chicken ecotypes [109]. The allelic variant 205 bp was positively associated with the elevated level of antibody responses to NDV vaccine, whereas allelic variant 307 bp was negatively associated with the same trait [109]. Also, chicken with the same genetic composition may respond differently when exposed to different infectious agents. Chicken populations with similar MHC haplotype (B1B1) vary on antibody responses to *Salmonella pullorum* and susceptibility to MDV

infection [110]. Interestingly, chickens with high antibody responses to *S. pullorum* antigen had high mortality rate to MDV challenge, whereas chickens with low antibody responses to *S. pullorum* antigen had low mortality rates in response to MDV challenge [110]. The association of the MHC variants with chicken variations in susceptibility to disease was reviewed elsewhere [111].

The toll-like receptor (TLR) genes signaling and interferon (IFN) signaling feature explain a significant role played by non-MHC genes for chicken's variation in susceptibility to diseases [112, 113]. Toll-like receptors constitute a group of pathogen-associated molecular patterns that play a crucial role in infectious agent's recognition and induction of innate immune response [114]. Although the role of TLR in chicken variations in susceptibility to diseases is not fully understood, reports indicate that TLR allelic variants are associated with variability in chicken resistance to diseases (Table 3). Specifically, 2 non-conservative mutations within the leucine-rich region domain (Tyr383His and Gln611Arg) of TLR4 are associated with susceptibility to *Salmonella* infection in two lines of chickens (line C and 72, Table 3).

The Mx protein, an IFN-induced dynamin-like GTPase, is among non-MHC genes that play significant antiviral activities [115]. The Mx allelic variants have been associated with chicken variability in susceptibility to viral infections [115, 116]. The Mx gene genotypes (genotype AA and GG) among Indonesian chicken, Tolaki, had significant differences in antiviral activities. Genotype AA had a higher antiviral activity of 50% compared to genotype GG, which had the antiviral activity of 10% [117].

Taken together, the literature in the present review suggests that local African chickens may have higher resistance to infectious disease compared to exotic breeds and commercial. Local African chicken are genetically diverse and have not been subjected to purposive artificial selection, and subjected to natural selection due to persistent exposure to harsh tropical environmental conditions and endemic infectious diseases. Additional evidence is provided by Jovanović et al. [36], who argued that local breeds adapted to endemic infectious diseases have an evolutionary advantage over exotic breeds. Considerable studies have been conducted among African chicken ecotypes to support this

Table 3. Genes/Variants Associated with Disease Resistance/Susceptibility in Chickens.

Disease	Gene/variant	Role	Reference
Salmonellosis	TLR4	Two non-conservative changes in leucine-rich region domain associated to chicken susceptibility to salmonellosis	[104]
	NRPMP1	Single SNP A101991G associated with chicken resistance to salmonellosis	[118]
Marek's disease (MD)	GH1	Conferred chicken resistance to MD	[119]
	CHTF18	Indel mutation with an additional of 7 nucleotides associated with chicken resistance to MD	[120]
Lymphoid leukosis	LDLR	Cysteine-to-tryptophan change in low density lipoprotein receptor (LDLR) for Avian leukosis viruses reduces binding affinity of the virus	[121]
Influenza	Mx gene	Amino acid substitution of Mx protein at position 631 (Ser to Asn) enhance antiviral activities in chicken	[122]
Coccidiosis	LEI 0071	The LEI 0071 is associated with reduction of parasite growth (<i>Eimeria maxima</i>) in chicken.	[123]

assumption [16, 109, 124]; however, few studies have been conducted to associate the observed variation in disease phenotypic parameters among individuals in the chicken populations with genomic structural variation such as SNP and CNV using a whole genome scan approach.

CONCLUSIONS AND APPLICATIONS

1. Chicken is the dominant poultry species raised by the majority of poor rural households in Africa as a chief source of high-quality meat and egg protein and for income generation. However, local African chicken productivity is primarily compromised by diseases, particularly diseases due to chicken viral infections. Chicken viral infections control and prevention by vaccination and institution of biosecurity measures are less effective and plausible in backyard production systems.
2. The genetic selection of resistant chicken to viral infections is a promising strategy. African local chickens have demonstrated to be highly genetically diverse and adapted to harsh tropical environmental conditions. Therefore, local African chicken is a potential candidate chicken population for selection of resistant chicken to viral infections in changing environment attributed by climate changes. However, there is a

paucity of information on the possible linkage between the genetic diversity of local African chickens and their variability in resistance and susceptibility to chicken viral infections. Here, we call on concerted effort to identify and breed chickens that are resistant to viral infections and adapted to extreme environmental conditions. The endeavor should consider the untapped potential of the genetic diversity of local African chickens by performing genetic association studies to identify allelic variants associated with chicken variation in resistance and susceptibility to chicken viral infections.

3. The conservation of genetic diversity potential of local African chickens is highly recommended considering unprecedented effect of climate change on global chicken production. We call on the establishment of institutions within respective ministries in African countries responsible for coordination of animal genetic resource conservation activities and mobilization of resources for the same.

REFERENCES AND NOTES

1. Conan, A. F. L., G. S. Sorn, and S. Vong. 2012. Biosecurity measures for backyard poultry in developing countries: a systematic review. *BMC Vet. Res.* 8:240–250.
2. Mapiye, C. M. M., J. F. Mupangwa, M. Chimonyo, R. Foti, and M. J. Mutenje. 2008. A research review of village

- chicken production constraints and opportunities in Zimbabwe. *Asian-Australas. J. Anim. Sci.* 21:1680–1688.
3. Mtileni, B. J., F. C. Muchadeyi, A. Maiwashe, P. Phitsane, T. Halimani, M. Chimonyo, and K. Dzama. 2009. Characterisation of production systems for indigenous chicken genetic resources of South Africa. *Appl. Anim. Husb. Rural Dev.* 2: 18–22.
 4. Msoffe, P., M. Mtambo, U. Minga, P. Gwakisa, R. Mdegela, and J. Olsen. 2002. Productivity and natural disease resistance potential of free ranging local chicken ecotypes in Tanzania. *Livest. Res. Rural Dev.* 14. <https://www.lrrd.cipav.org.co/lrrd14/3/msof143.htm>.
 5. Ahlers, C., R. Alders, B. Bagnol, A. B. Cambaza, M. Harun, R. Mgomozulu, H. Msami, B. Pym, P. Wegener, E. Wethli, and M. Young. 2009. Improving village chicken production: a manual for field workers and trainers. Series No. 139. ACIAR, Canberra, Australia.
 6. Martin, L., A. Jeremiah, D. Michael, and P. Janet. 2015. Management, feeding and breeding practices of local chickens in the remote areas of Morobe province, Papua New Guinea. *J. South Pacific Agric.* 18: 1–52.
 7. Marwa, L., B. Lukuyu, S. Mbagu, S. Mutayoba, and M. Bekunda. 2016. Characterization of local chicken production and management systems in Babati, Tanzania. Pages 19–21 in *Proc. Tropentag 2016 Conf. Solidarity Competing World—Fair Use Resour.* ILRI, Nairobi, Kenya.
 8. Okeno, T. O., A. K. Kahi, and K. J. Peters. 2012. Characterization of indigenous chicken production systems in Kenya. *Trop. Anim. Health Prod.* 44:601–608.
 9. Alexander, D. 2000. Newcastle disease and other avian paramyxovirus. *Rev. Sci. Tech.* 19:443–462.
 10. Sonaiya, F. 2008. Smallholder family poultry as a tool to initiate rural development. Pages 5–7 in *Proc. FAO Int. Conf. Poultry. Twenty-First Century: Avian Influenza and Beyond.* Bangkok, Thailand.
 11. Permin, A., and M. Bisgaard. 2013. A general review on some important diseases in free-range chickens. Pages 181–187 in *Proc. Poultry as a tool in poverty eradication and promotion of gender equality.* Tune Landboskole, Denmark.
 12. Cristalli, A., and I. Capua. 2007. Practical problems in controlling H5N1 high pathogenicity avian influenza at village level in Vietnam and introduction of biosecurity measures. *Avian Dis.* 51:461–462.
 13. Mazengia, H. 2012. Review on major viral diseases of chickens reported in Ethiopia. *J. Infect. Dis. Immun.* 4:1–9.
 14. Alders, R. G. 2014. Making Newcastle disease vaccines available at village level. *Vet. Rec.* 174:502–503.
 15. Bacon, L. D., H. D. Hunt, and H. H. Cheng. 2000. A review of the development of chicken lines to resolve genes determining resistance to diseases. *Poult. Sci.* 79:1082–1093.
 16. Msoffe, P., U. Minga, J. Olsen, M. Yongolo, H. R. Juul-Madsen, P. Gwakisa, and M. Mtambo. 2001. Phenotypes including immunocompetence in scavenging local chicken ecotypes in Tanzania. *Trop. Anim. Health Prod.* 33:341–354.
 17. Miller, M. M., and R. L. Taylor. 2016. Brief review of the chicken Major Histocompatibility Complex: the genes, their distribution on chromosome 16, and their contributions to disease resistance. *Poult. Sci.* 95:375–392.
 18. Spielman, D., B. W. Brook, D. A. Briscoe, and R. Frankham. 2004. Does Inbreeding and loss of genetic diversity decrease disease resistance? *Conserv. Genet.* 5:439–448.
 19. Emam, M., H. Mehrabani-Yeganeh, N. Barjesteh, G. Nikbakht, K. Thompson-Crispi, S. Charkhkar, and B. Mallard. 2014. The influence of genetic background versus commercial breeding programs on chicken immunocompetence. *Poult. Sci.* 93:77–84.
 20. Reed, D. H., and R. Frankham. 2003. Correlation between fitness and genetic diversity. *Conserv. Biol.* 17:230–237.
 21. Springbett, A., K. MacKenzie, J. Woolliams, and S. Bishop. 2003. The contribution of genetic diversity to the spread of infectious diseases in livestock populations. *Genetics* 165:1465–1474.
 22. Shapiro, B. 2017. Pathways to de-extinction: how close can we get to resurrection of an extinct species? *Funct. Ecol.* 31:996–1002.
 23. Gondwe, T. N., and C. B. A. Wollny. 2007. Local chicken production system in Malawi: household flock structure, dynamics, management and health. *Trop. Anim. Health Prod.* 39:103–113.
 24. Akbarian, A., J. Michiels, J. Degroote, M. Majdeddin, A. Golian, and S. De Smet. 2016. Association between heat stress and oxidative stress in poultry; mitochondrial dysfunction and dietary interventions with phytochemicals. *J. Anim. Sci. Biotechnol.* 7:37–50.
 25. Memarzadeh, F. 2012. Literature review of the effect of temperature and humidity on viruses. *ASHRAE Trans.* 118:1049–1060.
 26. Kitalyi, A. J. 1998. Village Chicken Production Systems in Rural Africa: Household Food Security and Gender Issues. FAO, Rome, Italy.
 27. Guèye, E. 2000. The role of family poultry in poverty alleviation, food security and the promotion of gender equality in rural Africa. *Outlook Agric.* 29:129–136.
 28. Yousif, I. A., M. A. Berima, and I. A. Ishag. 2015. Evaluation of the Sudanese native chicken production system and major constraints. *U. of K. J. Vet. Med. Anim. Prod.* 6:127–135.
 29. Getu, A., and M. Birhan. 2014. Chicken production systems, performance and associated constraints in North Gondar Zone, Ethiopia. *J. Fish. Livest. Prod.* 2:1–5.
 30. Sharma, J., J. Xie, M. Boggess, E. Galukande, D. Semambo, and S. Sharma. 2015. Higher weight gain by Kuroiler chickens than indigenous chickens raised under scavenging conditions by rural households in Uganda. *Livest. Res. Rural Dev.* 27. <http://www.lrrd.org/lrrd27/9/shar27178.html>.
 31. Fleming, D., J. Koltjes, A. Markey, C. Schmidt, C. Ashwell, M. Rothschild, M. Persia, J. Reecy, and S. Lamont. 2016. Genomic analysis of Ugandan and Rwandan chicken ecotypes using a 600 k genotyping array. *BMC Genomics* 17:407–423.
 32. Yakubu, A., and M. Ari, 2018. Principal component and discriminant analyses of body weight and conformation traits of Sasso, Kuroiler and indigenous Fulani chickens in Nigeria. *J. Anim. Plant Sci.* 28:46–55.
 33. Dessie, T., and F. Getachew. 2016. The Kuroiler Breed. African chicken genetic gains Fact Sheet 2. ILRI, Nairobi, Kenya. Accessed Jul. 2018.
 34. Ahuja, V., M. Dhawan, M. Punjabi, and L. Maarse. 2008. Chicken out of poverty? Story of ‘kuroiler’ from India. Accessed Jul. 2018. <http://www.keggfarms.com/pdf/Vinod%20Ahuja%20Report%20for%20World%20Poultry%20Science%20Congress.pdf>.
 35. Isenberg, D. 2007. Keggfarms (India)-Which Came First, the Kuroiler or the Kegg. Harvard Business School Case Study No. 9-807-089. Harvard Business School, Boston.

36. Jovanović, S., M. Savić, and D. Živković. 2009. Genetic variation in disease resistance among farm animals. *Biotechnol. Anim. Husbandry* 25:339–347.
37. Rao, V. R., and T. Hodgkin. 2002. Genetic diversity and conservation and utilization of plant genetic resources. *Plant Cell. Tissue and Organ Culture*. 68:1–19.
38. Keambou, T., B. Hako, S. Ommeh, C. Bembide, E. Ngono, Y. Manjeli, F. Wamonje, B. Wanjala, M. Wamalwa, and C. Cho. 2014. Genetic diversity of the Cameroon indigenous chicken ecotypes. *Int. J. Poult. Sci.* 13:279–291.
39. Mwacharo, J., K. Nomura, H. Hanada, H. Jianlin, O. Hanotte, and T. Amano. 2007. Genetic relationships among Kenyan and other East African indigenous chickens. *Anim. Genet.* 38:485–490.
40. Badubi, S., M. Rakereng, and M. Marumo. 2006. Morphological characteristics and feed resources available for indigenous chickens in Botswana. *Livest. Res. Rural Dev.* 18:205–211.
41. Lyimo, C. M., A. Weigend, U. Janßen-Tapken, P. L. Msoffe, H. Simianer, and S. Weigend. 2013. Assessing the genetic diversity of five Tanzanian chicken ecotypes using molecular tools. *S. Afr. J. Anim. Sci.* 43:499–510.
42. Mohammed, M. D., Y. I. Abdalsalam, and A. M. Kheir. 2015. Comparison of the egg characteristics of different Sudanese indigenous chicken types. *Int. J. Poult. Sci.* 4:455–457.
43. Duguma, R. 2006. Phenotypic characterization of some indigenous chicken ecotypes of Ethiopia. *Livest. Res. Rural Dev.* 18:21–25.
44. Adekoya, K. 2013. Morphological characterization of five Nigerian indigenous chicken types. *J. Sci. Res. Dev.* 14:55–56.
45. Dahloum, L., N. Moula, M. Halbouche, and S. Mignon-Grasteau. 2016. Phenotypic characterization of the indigenous chickens (*Gallus gallus*) in the northwest of Algeria. *Arch. Anim. Breed.* 59:79–90.
46. Msoffe, P., M. Mtambo, U. Minga, J. Olsen, H. R. Juul-Madsen, P. Gwakisa, S. Mutayoba, and A. Katule. 2004. Productivity and reproductive performance of the free-range local domestic fowl ecotypes in Tanzania. *Livest. Res. Rural Dev.* 16:1–12.
47. Youssao, I., P. Tobada, B. Koutinhouin, M. Dahouda, N. Idrissou, G. Bonou, U. Tougan, S. Ahounou, V. Yapi-Gnaoré, and B. Kayang. 2010. Phenotypic characterisation and molecular polymorphism of indigenous poultry populations of the species *Gallus gallus* of Savannah and forest ecotypes of Benin. *Afr. J. Biotechnol.* 9:369–381.
48. Mahammi, F., S. Gaouar, D. Laloë, R. Faugeras, N. Tabet-Aoul, X. Rognon, M. Tixier-Boichard, and N. Saidi-Mehtar. 2016. A molecular analysis of the patterns of genetic diversity in local chickens from western Algeria in comparison with commercial lines and wild jungle fowls. *J. Anim. Breed. Genet.* 133:59–70.
49. Ajayi, F. 2010. Nigerian indigenous chicken: a valuable genetic resource for meat and egg production. *Asian J. Poultry Sci.* 4:164–172.
50. Dana, N., T. Dessie, L. H. van der Waaij, and J. A. van Arendonk. 2010. Morphological features of indigenous chicken populations of Ethiopia. *Anim. Genet. Resour.* 46:11–23.
51. Khobondo, J., T. Muasya, S. Miyumo, T. Okeno, C. Wasike, R. Mwakubambanya, A. Kingori, and A. Kahi. 2015. Genetic and nutrition development of indigenous chicken in Africa. *Livest. Res. Rural Dev.* 27:122–129.
52. Muchadeyi, F., H. Eding, C. Wollny, E. Groeneveld, S. Makuza, R. Shamseldin, H. Simianer, and S. Weigend. 2007. Absence of population substructuring in Zimbabwe chicken ecotypes inferred using microsatellite analysis. *Anim. Genet.* 38:332–339.
53. Mtileni, B., F. Muchadeyi, A. Maiwashe, E. Groeneveld, L. Groeneveld, K. Dzama, and S. Weigend. 2011. Genetic diversity and conservation of South African indigenous chicken populations. *J. Anim. Breed. Genet.* 128:209–218.
54. Chen, G., W. Bao, J. Shu, C. Ji, M. Wang, H. Eding, F. Muchadeyi, and S. Weigend. 2008. Assessment of population structure and genetic diversity of 15 Chinese indigenous chicken breeds using microsatellite markers. *Asian-Australas. J. Anim. Sci.* 21:331–330.
55. Eltanany, M., U. Philipp, S. Weigend, and O. Distl. 2011. Genetic diversity of ten Egyptian chicken strains using 29 microsatellite markers. *Anim. Genet.* 42:666–669.
56. Hasballa, M. A. B. 2008. Assessment of population structure and genetic diversity of Sudanese native chickens using microsatellite markers. MSc Diss. Univ. Khartoum, Khartoum, Sudan.
57. Goraga, Z., S. Weigend, and G. Brockmann. 2012. Genetic diversity and population structure of five Ethiopian chicken ecotypes. *Anim. Genet.* 43:454–457.
58. Bekerie, E. M., Z. S. Goraga, A. M. Johansson, and H. Singh. 2015. Genetic diversity and population structure of four indigenous chicken ecotypes representing South and South Western Ethiopia. *Int. J. Genet.* 5:18–24.
59. Yousif, I. A., H. Eding, S. Weigend, and H. H. Musa. 2013. Population structure and genetic diversity of Sudanese native chickens. *Afr. J. Biotechnol.* 12:6424–6431.
60. Osei-amponsah, R., B. B. Kayang, A. Naazie, Y. D. Osei, I. A. Youssao, V. C. Yapi-Gnaore, M. Tixier-Boichard, and X. Rognon. 2010. Genetic diversity of Forest and Savannah chicken populations of Ghana as estimated by microsatellite markers. *Anim. Sci. J.* 81:297–303.
61. Ramadan, S., B. B. Kayang, E. Inoue, K. Nirasawa, H. Hayakawa, S. Ito, and M. Inoue-Murayama. 2012. Evaluation of genetic diversity and conservation priorities for Egyptian chickens. *OJAS* 2:183–190.
62. Wilkinson, S., P. Wiener, D. Teverson, C. Haley, and P. Hocking. 2012. Characterization of the genetic diversity, structure and admixture of British chicken breeds. *Anim. Genet.* 43:552–563.
63. Abebe, A. S., S. Mikko, and A. M. Johansson. 2015. Genetic diversity of five local Swedish chicken breeds detected by microsatellite markers. *PLoS One* 10:e0120580.
64. Alexander, D. J. 2001. Newcastle disease. *Br. Poultry Sci.* 42:5–22.
65. Sharif, A., T. Ahmad, M. Umer, A. Rehman, and Z. Hussain. 2014. Prevention and control of Newcastle disease. *Int. J. Agric. Innov. Res.* 3:454–460.
66. Awuni, J. 2002. Strategies for the improvement of rural chicken production in Ghana. Pages 33–37 in *Proc. Characteristics Parameters Family Poultry. Prod. Africa*. IAEA, Vienna, Austria.
67. Kim, S. H., S. Nayak, A. Paldurai, B. Nayak, A. Samuel, G. L. Aplogan, K. A. Awoume, R. J. Webby, M. F. Ducatez, P. L. Collins, and S. K. Samal. 2012. Complete genome sequence of a novel Newcastle disease virus strain isolated from a chicken in West Africa. *J. Virol.* 86:11394–11395.
68. Samuel, A., B. Nayak, A. Paldurai, S. Xiao, G. L. Aplogan, K. A. Awoume, R. J. Webby, M. F. Ducatez, P. L.

- Collins, and S. K. Samal. 2013. Phylogenetic and pathotypic characterization of Newcastle disease viruses circulating in West Africa and efficacy of a current vaccine. *J. Clin. Microbiol.* 51:771–781.
69. Snoeck, C. J., M. F. Ducatez, A. A. Owoade, O. O. Faleke, B. R. Alkali, M. C. Tahita, Z. Tarnagda, J. B. Ouedraogo, I. Maikano, P. O. Mbah, J. R. Kremer, and C. P. Muller. 2009. Newcastle disease virus in West Africa: new virulent strains identified in non-commercial farms. *Arch. Virol.* 154:47–54.
70. Mohamed, M. A., K. E. Elzanaty, B. M. Bakhit, and M. M. Safwat. 2014. Genetic characterization of infectious bursal disease viruses associated with Gumboro outbreaks in commercial broilers from Asyut Province, Egypt. *ISRN Vet. Sci.* 2014:1–9.
71. Zeleke, A., E. Gelaye, T. Sori, G. Ayelet, A. Sirak, and B. Zekarias. 2005. Investigation on infectious bursal disease outbreak in Debre Zeit, Ethiopia. *Int. J. Poult. Sci.* 4:504–506.
72. Kelly, P. J., D. Chitauro, C. Rohde, J. Rukwava, A. Majok, F. Davelaar, and P. R. Mason. 1994. Diseases and management of backyard chicken flocks in Chitungwiza, Zimbabwe. *Avian Dis.* 38:626–629.
73. Khataby, K., S. Fellahi, C. Loutfi, and E. M. Mustapha. 2016. Avian infectious bronchitis virus in Africa: a review. *Vet. Q.* 36:71–75.
74. Bande, F., S. S. Arshad, A. R. Omar, M. Hair-Bejo, A. Mahmuda, and V. Nair. 2017. Global distributions and strain diversity of avian infectious bronchitis virus: a review. *Anim. Health Res. Rev.* 18:70–83.
75. Mazengia, H. 2012. Review on major viral diseases of chickens reported in Ethiopia. *J. Infect. Dis. Immun.* 4:1–9.
76. Swai, E., M. Kessy, P. Sanka, and P. Mtui. 2011. A serological survey for infectious bursal disease virus antibodies in free-range village chickens in northern Tanzania. *J. S. Afr. Vet. Assoc.* 82:32–35.
77. Balachandran, C., N. Pazhanivel, S. Vairamuthu, and B. Murali Manohar. 2009. Marek's disease and lymphoid leucosis in chicken—a histopathological survey. *Tamilnadu J. Vet. Anim. Sci.* 5:167–170.
78. Demeke, B., S. Jenberie, B. Tesfaye, G. Ayelet, M. Yami, C. E. Lamien, and E. Gelaye. 2017. Investigation of Marek's disease virus from chickens in central Ethiopia. *Trop. Anim. Health Prod.* 49:403–408.
79. Kennedy, D. A., P. A. Dunn, and A. F. Read. 2018. Modeling Marek's disease virus transmission: a framework for evaluating the impact of farming practices and evolution. *Epidemics* 23:85–95.
80. Van der Goot, J., G. Koch, M. De Jong, and M. Van Boven. 2005. Quantification of the effect of vaccination on transmission of avian influenza (H7N7) in chickens. *Proc. Natl. Acad. Sci. U. S. A.* 102:18141–18146.
81. Msoffe, P. L., D. Bunn, A. Muhairwa, M. Mtambo, H. Mwamhehe, A. Msago, M. Mlozi, and C. J. Cardona. 2010. Implementing poultry vaccination and biosecurity at the village level in Tanzania: a social strategy to promote health in free-range poultry populations. *Trop. Anim. Health Prod.* 42:253–263.
82. Ali, M., B. Muneer, Z. Hussain, S. Rehmani, T. Yaqub, and Naem M. 2014. Evaluation of efficacy of killed and commercially available live Newcastle disease vaccine in broiler chickens in Pakistan. *J. Anim. Plant Sci.* 24:1663–1667.
83. Blackie, S. 2014. Village chicken production system in the greater Accra region Ghana. *J. Biol. Agric. Healthc.* 4:89–94.
84. Marangon, S., and L. Busani. 2007. Vacunación en establecimientos avícolas. *Rev. Sci. Tech.* 26:265–274.
85. Davison, F., and V. Nair. 2005. Use of Marek's disease vaccines: could they be driving the virus to increasing virulence? *Expert Rev. Vaccines* 4:77–88.
86. Pollock, S. L., C. Stephen, N. Skuridina, and T. Kosatsky. 2012. Raising chickens in city backyards: the public health role. *J. Community Health* 37:734–742.
87. Fasina, F. O., A. Ali, J. Yilma, O. Thieme, and P. Ankers. 2012. The cost-benefit of biosecurity measures on infectious diseases in the Egyptian household poultry. *Prev. Vet. Med.* 103:178–191.
88. Houghton, J. T., L. G. Meiro Filho, B. A. Callander, N. Harris, A. Kattenburg, and K. Maskell. 1996. *Climate Change 1995: The Science of Climate Change*. 1st ed. Cambridge Univ. Press, New York, USA.
89. Parham, P. E., and E. Michael. 2010. Modeling the effects of weather and climate change on malaria transmission. *Environ. Health Perspect.* 118:620–626.
90. Wu, X., Y. Lu, S. Zhou, L. Chen, and B. Xu. 2016. Impact of climate change on human infectious diseases: empirical evidence and human adaptation. *Environ. Int.* 86:14–23.
91. Fleming, D. S., S. Weigend, H. Simianer, A. Weigend, M. Rothschild, C. Schmidt, C. Ashwell, M. Persia, J. Reecy, and S. J. Lamont. 2017. Genomic comparison of indigenous African and Northern European chickens reveals putative mechanisms of stress tolerance related to environmental selection pressure. *G3 (Bethesda)* 7:1525–1537.
92. Naskar, S., G. R. Gowane, A. Chopra, C. Paswan, and L. L. Prince. 2012. Genetic adaptability of livestock to environmental stresses. Pages 317–378 in Sejian, V., S. M. K. Naqvi, T. Ezeji, J. Lakritz, and R. Lal (eds.) *Environmental Stress and Amelioration in Livestock Production*. Springer, Berlin Heidelberg, Germany.
93. Sorensen, J. G., M. F. Schou, and V. Loeschcke. 2017. Evolutionary adaptation to environmental stressors: a common response at the proteomic level. *Evolution* 71:1627–1642.
94. Zhu, Y., H. Chen, J. Fan, Y. Wang, Y. Li, J. Chen, J. Fan, S. Yang, L. Hu, and H. Leung. 2000. Genetic diversity and disease control in rice. *Nature* 406:718–722.
95. Rääkkönen, J., A. Bignert, P. Mortensen, and B. Fernholm. 2006. Congenital defects in a highly inbred wild wolf population (*Canis lupus*). *Mamm. Biol.* 71:65–73.
96. Allentoft, M. E., and J. O'Brien. 2010. Global amphibian declines, loss of genetic diversity and fitness: a review. *Diversity* 2:47–71.
97. Springbett, A., K. MacKenzie, J. Woolliams, and S. Bishop. 2003. The contribution of genetic diversity to the spread of infectious diseases in livestock populations. *Genetics* 165:1465–1474.
98. Råberg, L., D. Sim, and A. F. Read. 2007. Disentangling genetic variation for resistance and tolerance to infectious diseases in animals. *Science* 318:812–814.
99. Zekarias, B., A. A. Ter Huurne, W. J. Landman, J. M. Rebel, J. M. Pol, and E. Gruys. 2002. Immunological basis of differences in disease resistance in the chicken. *Vet. Res.* 33:109–125.

100. Glass, E. J., R. Baxter, R. J. Leach, and O. C. Jann. 2012. Genes controlling vaccine responses and disease resistance to respiratory viral pathogens in cattle. *Vet. Immunol. Immunopathol.* 148:90–99.
101. Kapczynski, D. R., C. L. Afonso, and P. J. Miller. 2013. Immune responses of poultry to Newcastle disease virus. *Dev. Comp. Immunol.* 41:447–453.
102. Iwasaki, A., and R. Medzhitov. 2015. Control of adaptive immunity by the innate immune system. *Nat. Immunol.* 16:343–353.
103. Janeway, C. A., P. Travers, M. Wal-port, and M. J. Shlomchik. 2001. *Immunobiology—the immune system in health and disease*. 5th ed. Garland Science, New York, NY. <https://www.ncbi.nlm.nih.gov/books/NBK10757/>.
104. Leveque, G., V. Forgetta, S. Morroll, A. L. Smith, N. Bumstead, P. Barrow, J. Loredo-Osti, K. Morgan, and D. Malo. 2003. Allelic variation in *TLR4* is linked to susceptibility to *Salmonella enterica* serovar Typhimurium infection in chickens. *Infect. Immun.* 71:1116–1124.
105. Hunt, H. D., S. Jadhao, and D. E. Swayne. 2010. Major histocompatibility complex and background genes in chickens influence susceptibility to high pathogenicity avian influenza virus. *Avian Dis.* 54:572–575.
106. Janeway, C. A., P. Travers, M. Wal-port, and M. J. Shlomchik. 2001. *Immunobiology—the major histocompatibility complex and its functions*. 5th ed. Garland Science, New York, NY. <https://www.ncbi.nlm.nih.gov/books/NBK10757/>.
107. Schat, K., R. Taylor, and W. Briles. 1994. Resistance to Marek's disease in chickens with recombinant haplotypes of the major histocompatibility (B) complex. *Poult. Sci.* 73:502–508.
108. Goto, R. M., Y. Wang, R. L. Taylor, P. S. Wakenell, K. Hosomichi, T. Shiina, C. S. Blackmore, W. E. Briles, and M. M. Miller. 2009. BG1 has a major role in MHC-linked resistance to malignant lymphoma in the chicken. *Proc. Natl. Acad. Sci. U. S. A.* 106:16740–16745.
109. Lwelamira, J., G. Kifaro, P. Gwakisa, and P. Msoffe. 2008. Association of LEI0258 microsatellite alleles with antibody response against Newcastle disease virus vaccine and body weight in two Tanzania chicken ecotypes. *Afr. J. Biotechnol.* 7:714–720.
110. Pevzner, I., I. Kujdych, and A. Nordskog. 1981. Immune response and disease resistance in chickens. II. Marek's disease and immune response to GAT. *Poult. Sci.* 60:927–932.
111. Miller, M. M., and R. L. Taylor. 2016. Brief review of the chicken Major Histocompatibility Complex: the genes, their distribution on chromosome 16, and their contributions to disease resistance. *Poult. Sci.* 95:375–392.
112. Haunshi, S., and H. H. Cheng. 2014. Differential expression of Toll-like receptor pathway genes in chicken embryo fibroblasts from chickens resistant and susceptible to Marek's disease. *Poult. Sci.* 93:550–555.
113. Ruan, W. K., and S. J. Zheng. 2011. Polymorphisms of chicken toll-like receptor 1 type 1 and type 2 in different breeds. *Poult. Sci.* 90:1941–1947.
114. Majewska, M., and M. Szczepanik. 2006. The role of toll-like receptors (TLR) in innate and adaptive immune responses and their function in immune response regulation. *Postepy Hig. Med. Dosw. (Online)* 60:52–63.
115. Verhelst, J., P. Hulpiau, and X. Saelens. 2013. Mx proteins: antiviral gatekeepers that restrain the uninvited. *Microbiol. Mol. Biol. Rev.* 77:551–566.
116. Fulton, J. E., J. Arango, R. A. Ali, E. B. Bohorquez, A. R. Lund, C. M. Ashwell, P. Settar, N. P. O'Sullivan, and M. D. Koci. 2014. Genetic variation within the Mx gene of commercially selected chicken lines reveals multiple haplotypes, recombination and a protein under selection pressure. *PLoS One* 9:e108054.
117. Pagala, M. A., C. S. Muladno, and S. Murtini. 2013. Association of Mx gene genotype with antiviral and production traits in Tolaki chicken. *Int. J. Poult. Sci.* 12:735–739.
118. He, X., M. Fang, Z. Zhang, Y. Hu, X. Jia, D. He, S. Liang, Q. Nie, and X. Zhang. 2013. Characterization of chicken natural resistance-associated macrophage protein encoding genes (*Nramp1* and *Nramp2*) and association with salmonellosis resistance. *Genet. Mol. Res.* 12:618–630.
119. Liu, G. E., T. Brown, D. A. Hebert, M. F. Cardone, Y. Hou, R. K. Choudhary, J. Shaffer, C. Amazu, E. E. Connor, and M. Ventura. 2011. Initial analysis of copy number variations in cattle selected for resistance or susceptibility to intestinal nematodes. *Mamm. Genome* 22:111–121.
120. Kaya, M., L. Preeyanon, J. B. Dodgson, and H. H. Cheng. 2016. Validation of alternative transcript splicing in chicken lines that differ in genetic resistance to Marek's disease. *Anim. Biotechnol.* 27:238–244.
121. Elleder, D., D. C. Melder, K. Trejbalova, J. Svoboda, and M. J. Federspiel. 2004. Two different molecular defects in the Tva receptor gene explain the resistance of two *tva'* lines of chickens to infection by subgroup A avian sarcoma and leukosis viruses. *J. Virol.* 78:13489–13500.
122. Ko, J. H., H. K. Jin, A. Asano, A. Takada, A. Ninomiya, H. Kida, H. Hokiyama, M. Ohara, M. Tsuzuki, and M. Nishibori. 2002. Polymorphisms and the differential antiviral activity of the chicken Mx gene. *Genome Res.* 12:595–601.
123. Lillehoj, H., Y. Hong, and C. Kim. 2008. Quantitative genetic and functional genomics approaches to investigating parasite disease resistance and protective immune mechanisms in avian coccidiosis. *Dev. Biol.* 132:67–75.
124. Hassan, M., M. Afify, and M. Aly. 2004. Genetic resistance of Egyptian chickens to infectious bursal disease and Newcastle disease. *Trop. Anim. Health Prod.* 36:1–9.

Acknowledgments

Authors would like to thank the Program for Enhancing Health and Productivity in Livestock (PEHPL) for the financial support. The PEHPL is funded by the Bill & Melinda Gates Foundation.