AGRICULTURAL BIOLOGY,
2017, V. 52, № 6, pp. 1166-1174
(SEL'SKOKHOZYAISTVENNAYA BIOLOGIYA)

ISSN 2412-0324 (English ed. Online)
ISSN 0131-6397 (Russian ed. Print)
ISSN 2313-4836 (Russian ed. Online)

UDC 636.52/.58:575.174.5

doi: 10.15389/agrobiology.2017.6.1166rus
doi: 10.15389/agrobiology.2017.6.1166eng

STUDYING THE STRUCTURE OF A GENE POOL POPULATION OF THE RUSSIAN WHITE CHICKEN BREED BY GENOME-WIDE SNP SCAN

N.V. DEMENTEVA[1], M.N. ROMANOV[1, 2], A.A. KUDINOV[1], O.V. MITROFANOVA[1], O.I. STANISHEVSKAYA[1], V.P. TERLETSKY[1], E.S. FEDOROVA[1], E.V. NIKITKINA[1], K.V. PLEMYASHOV[1]

[1]*All-Russian Research Institute for Farm Animal Genetics and Breeding — branch of L.K. Ernst Federal Science Center for Animal Husbandry,* Federal Agency of Scientific Organizations, 55A, Moskovskoe sh., pos. Tyarlevo, St. Petersburg—Pushkin, 196625 Russia, e-mail dementevan@mail.ru (corresponding author);
[2]*School of Biosciences, University of Kent,* Canterbury, Kent, UK, CT2 7NJ, e-mail m.romanov@kent.ac.uk
ORCID:
Dementeva N.V. orcid.org/0000-0003-0210-9344
Kudinov A.A. orcid.org/0000-0002-7811-576X
Stanishevskaya O.I. orcid.org/0000-0001-9504-3916
Fedorova E.S. orcid.org/0000-0002-1618-6271
Plemyashov K.V. orcid.org/000-0002-3658-5886
Romanov M.N. orcid.org/0000-0003-3584-4644
Mitrofanova O.V. orcid.org/000-0003-4702-2736
Terletsky V.P. orcid.org/0000-0003-4043-3823
Nikitkina E.V. orcid.org/0000-0002-8496-5277
The authors declare no conflict of interests
Acknowledgements:
Supported financially by Russian Science Foundation, project № 16-16-04060. Chicken blood samples were provided by Genetic collection of rare and endangered breeds of chickens (ARRIFAGB) under the program of Federal Agency of Scientific Organizations for support of bio resource collections
Received August 11, 2017

Abstract

A population of the Russian White chickens, bred at the gene pool farm of ARRIFAGB for 25 generations using individual selection, is characterized by resistance to a lowered temperature in the early postnatal period and white colour of the embryonic down. In 2002-2012, breeding was carried out by panmixia, and by now a new population of the Russian White chickens has been formed on the basis of the surviving stock. Comparison of the genetic variability of this population and the archival DNA of representatives of the 2001 population using microarray screening technology will help to assess the population structure and the preservation of the unique characteristics of its genome. The material for the study was DNA extracted from 162 chicken blood samples. Two groups of the Russian White breed were studied, the 2001 population and the current population. Genome-wide analysis using single nucleotide markers (SNP) included screening by means of the Illumina Chicken 60K SNP iSelect BeadChip microarray. Quality control of genotyping, determination of the population genetic structure by multidimensional scaling (MDS), calculation of linkage disequilibrium (LD) and allele frequency in the groups were carried out using PLINK 1.9 software program. The construction of a cluster delimitation model based on SNP genotypes was carried out using the ADMIXTURE program. According to the MDS analysis results, the current population can be divided into four MDS groups, which, when compared to the data of the pedigree, adequately reflect the origin of the studied individuals. The representatives of the ancestral population were genetically similar to the MDS3 group of the current population. Using the F-statistic of the two-way analysis of variance, a significant effect of the group, chromosome, chromosome in the group, and the distance between SNP markers on LD (r^2) values was observed. In the 2001 group, the maximum r^2 and the high incidence of LD equal to 1 were observed for all chromosomes, with a distance between SNP markers being 500-1000 Kb. There was also the greatest number of monomorphic alleles in this group. Based on the SNP analysis, we may conclude that the current Russian White chicken population is characterized by the disintegration of long LD regions of the ancestral population. Modelling clusters using the ADMIXTURE program revealed differences between the current population groups determined by MDS analysis. The groups composed of individuals included in MDS1 and MDS2 had a homogeneous structure and differed from each other at K = 4 and K = 5. The MDS4 group formed a genetically heterogeneous cluster different from the MDS1 and MDS2 groups at K of 2-5. The MDS3 group was phylogenetically close to the 2001 population (at K of 2-5). In general, the analysis of the current gene pool population of the Russian White chickens showed its heterogeneity while one of its groups (MDS3) was similar to the ancestral population of 2001, which in turn is characterized by a large number of monomorphic alleles and a high frequency of long LD regions. Thus, SNP scanning allowed evaluating the genetic similarity of individuals and the population structure of the Russian White chicken breed. Understanding the genetic structure is

an important point in the panmictic breeding and tracking of historical changes in the molecular organization of the genome of a gene pool population with a limited number of animals.

Keywords: population structure, genetic diversity, SNP genotyping, Russian White breed of chickens

Modern methods do not find noticeable application in in-depth studying domestic chicken native gene pool. At the same time, conservation and usage of beneficial qualities of their non-commercial breeds remains an important scientific and economic task. Gene pool poultry can be used in biotechnology and as a model for studying biological processes and identification of genes (genetic markers) associated with economically useful traits [1-4].

The white-feathered **Russian Whites,** a chicken breed with primary use for eggs, is being maintained in the Gene Pool Farm of the All-Russian Research Institute of Genetics and Breeding Farm Animals (ARRIGBFA) since 1953 and initially had a linear structure [1]. Two lines, No. 10 and No. 16, differed in adaptability to lower temperatures in the early postnatal period [1]. Another experimental group of this breed was characterized by the white color of neoptile, and entire population was kept at low temperatures for 25 generations [1]. Russian Whites breeding has been based on individual selection of parents. Until 2002, the population was reproduced within lines No. 10 and No. 16, and then, until 2012, the chickens were kept at a commonly accepted temperature and bred by panmixia method, as a result of which the linear breed structure was lost. Based on the surviving poultry, a new population of Russian Whites was formed, features of which were white down of one-day old chicks and ability of adaptation to lower temperatures (22-23 °C) compared to commonly accepted for this age (30-33 °C). At present, keeping at low temperatures is not applied [1].

Improvement of small population for desirable traits is impossible without an assessment of population genetic structure. Mini- and microsatellite molecular markers and other methods of DNA polymorphism study, widely used earlier [2-7], recently are given way to the numerous single nucleotide polymorphism (SNP). Thousands of SNPs allow genotyping of the whole genome and make it possible to associate the found marker variations with quantitative traits. SNP scanning is a highly effective genetic analysis tool that can identify structural features of the population, which can be used in breeding [8-11]. A combination of molecular genetic data with mathematical models enhances the accuracy of animal breeding value prediction for selection and management efficiency, which accelerates genetic progress in breeding populations [12, 13]. While breeding small populations, there is a prevalence increasing of extended haplotype areas, including regions of homozygosity (ROH), steadily passed on to the offspring over generations [14-16], which tends to reduce genetic diversity in a small population [17, 18].

Multidimensional scaling (MDS analysis) is a widely used tool to assess the differentiation of the studied groups (populations, breeds) [19]. Suggested methods are based on the predetermined structure of analyzed groups and calculation of genetic distance between individuals by using the algorithm for phylogenetic clustering [20]. Bayesian clustering models have been developed. They include genotyping in tens of thousands of loci and, as in STRUCTURE and ADMIXTURE software, can regard Hardy-Weinberg equilibrium and linkage disequilibrium (LD).

With the help of genome wide SNP genotyping, we first revealed a subpopulational structure of the modern Russian Whites chickens from the ARRIGBFA collection, possessing unique genetic material of domestic and foreign breeds, and found the differences of the studied poultry groups from the original population.

Our aim was to show the possibilities of whole genome SNP scanning for characterization of the genetic structure features in a small chicken population of domestic origin and the dynamic changes in its molecular architecture by a comparison of the current population of the Russian White breed with the population of 2001.

Techniques. DNA was extracted from blood samples collected from Russian White chickens (*Gallus gallus*) of ARRIGBFA bioresource collection (Genetic Collection of Rare and Endangered Chicken breeds, St. Petersburg-Pushkin). Two groups were analyzed: the population of 2001 (n = 6, unrelated individuals from two lines) and the modern population (n = 156). The SNP analyses included screening of 162 DNA samples with the Illumina Chicken 60K SNP iSelect BeadChip microchip (Illumina, USA). The quality of the genotyped SNP loci was monitored using PLINK 1.9 software [23]. In addition, DNA samples with a genotyping quality of SNP loci more than 90 % evaluated using GenomeStudio software (Illumina, USA) were selected for analysis. Hardy-Weinberg error (HWE) limits were set ($P \leq 0.0001$). SNPs, which were in linkage disequilibrium (--indep-pairwise 50 5 0.5) in the PLINK 1.9 software were deleted. To eliminate gender effects, SNP markers located on sex chromosomes were excluded. Population genetic structure was detected by MDS analysis with PLINK 1.9 software. Allele frequency and linkage disequilibrium in groups were also calculated using PLINK 1.9.

Multivariative analysis of variance (ANOVA) was carried out in the RStudio program [24]. The effects of group, chromosome, their interaction, and SNP interval on LD value were estimated by the linear model [10]:

$$r^2_{ij} = \mu + BL_i + Gga_j + (BL \times Gga)_{ij} + bSNP_{int} + e_{ik},$$

where r^2_{ij} is pair LD value, μ is the overall average LD, Bl_i is the effect of i group, Gga_j is the effect of the chicken chromosome j (chromosomes 1 to 28), SNP_{int} is the effect of interval between SNP markers, which was determined as the distance between markers (the number of nucleotides pairs), b is the regression constant.

Clustering based on SNP genotyping was carried out using ADMIXTURE software [25].

Results. Depending on SNP genotyping, the current population was conditionally divided into MDS groups and compared to the pedigree data and to genotyping of the ancestral population of 2001. Location of the points, as resulted from multidimensional scaling (Fig. 1), was influenced by low frequency monomorphic alleles and minor allele frequency (MAF). This complicated estimation of the variability of the remaining markers. Preliminarily, a restriction level of 0.1 has been chosen for MAF filtering to exclude all monomorphic alleles and minor alleles with a frequency under 10 %.

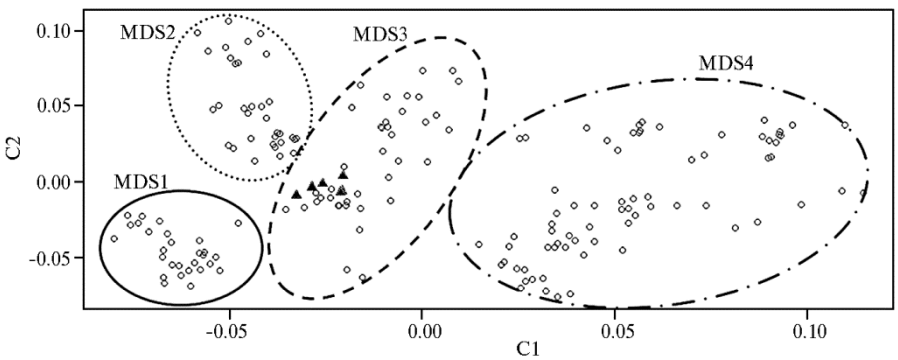

Fig. 1. Clustering (MDS1-MDS4) **of Russian White chickens based on SNP genotyping:** ○ — individuals of current population, ▲ — stored individual DNA samples of 2001; C1, C2 — coordinates (Genetic Collection of Rare and Endangered Chicken Breeds, ARRIGBFA, St. Petersburg-—Pushkin).

Modern population of Russian Whites could be conditionally divided into four clusters (MDS1-MDS4). Clusters MDS1 and MDS2 were separated along the C2 axis, MDS1, MDS2, MDS3 were separated from MDS4 along the C1 axis. The MDS1 cluster included mainly individuals descending from rooster No. 99. The MDS2 cluster grouped the offsprings of roosters No. 98 and No. 99 (Table 1). The MDS4 cluster predominantly comprised birds the ancestor of which was rooster No. 97. The MDS3 cluster consolidated the descendant of rooster No. 58 and the intermediates close in origin to the other clusters.

1. Distribution of Russian White chickens of current population for MDS clusters depending on ancestor roosters (Genetic Collection of Rare and Endangered Chicken Breeds, ARRIGBFA, St. Petersburg—Pushkin)

Father rooster, No.	Ancestor rooster, No.	Cluster				Total
		MDS1	MDS2	MDS3	MDS4	
981206	98	0	10	3	0	13
981205	98	0	16	0	1	17
981501	98	0	0	5	0	5
991803	99	0	14	0	0	14
991203	99	16	0	1	0	17
970905	97	0	0	0	12	12
971103	97	0	0	0	16	16
970907	97	0	0	0	15	15
971601	97	0	0	0	13	13
581706	58	0	0	9	0	9
481701	58	1	0	8	7	16
639		0	0	9	0	9
Total		17	40	35	64	156

Individuals from the selected clusters were grouped to study their genetic features (Table 2). Structure of the groups was estimated based on the presence and extension of genomic regions with linkage disequilibrium detected with SNP markers. The maximum average LD value was found in the 2001 population. The number of monomorphic alleles in this group also appeared to be the highest. The MDS3 group held a central position together with the 2001 population, but unlike it, had a minimal number of monomorphic SNPs and a significant number of minor alleles with a frequency of less than 10 %. In the 2001 group, the maximum values of r^2 and the high frequency (0.24) of linkage disequilibrium equal to 1 were found for all chromosomes with a significant distance between SNP markers (500-1000 kb). The overall calculated LD value per chromosome was high both in the current and in the ancestral population and varied from 0.150±0.006 to 0.587±0.006.

2. Characterization of ancestral population 2001 and current gene pool population of Russian Whites on the base of MDS clustering with SNP marker loci (Genetic Collection of Rare and Endangered Chicken Breeds, ARRIGBFA, St. Petersburg—Pushkin)

Indicator	Group				
	MDS1	MDS2	MDS3	MDS4	2001
Total genotyped SNP	57636	57636	57636	57636	57636
Including:					
loci with high genotyping quality (> 0.90)	43224	43224	43224	43224	43224
loci with monomorphic alleles	9176	8157	1507	5393	19833
loci with minor alleles (MAF ≤ 0.1)	5943	7800	10443	8200	3827
HWE (P ≤ 0.0001)	949	1021	1244	1543	0
LD (*M*±SEM)	0.272±0.001	0.241±0.001	0.193±0.001	0.197±0.001	0.506±0.001
LD frequency = 1 at distance between SNP 500-1000 кbp	0.07	0.03	0.02	0.02	0.24

N o t e. MAF — minor allele frequency, HWE — the number of SNPs not satisfying the Hardy-Weinberg equilibrium test (at P ≤ 0.0001), LD — linkage disequilibrium, *M* — average mean LD, ±SEM — standard mean error.

Additional multivariate dispersion analysis using the F-test (Table 3) showed significant (P < 0.0001) effect of groups, chromosomes, distances between SNP markers and the chromosome in the group on LD (r^2). The group and the distance between SNP markers exerted the greatest influence.

One of the effective methods for detecting differences between groups and

breeds of animals is cluster analysis of the admix models [25, 26]. While clustering in the ADMIXTURE program, the cross-validation coefficient (CV) was estimated to determine the optimal K value. The minimal error was observed at K = 12 (Fig. 2). The MDS1 and MDS2 groups had a homogeneous structure and did not differ at K = 2, partially differed at K = 3 and showed a significant difference at K = 4 and K = 5. The MDS4 group formed a genetically heterogeneous cluster which differed from MDS1 and MDS2 at K from 2 up to 5. The MDS3 group was more homogeneous and close to the 2001 population with a K value of 2 to 5.

3. Influence of MDS group, chromosome and interval between SNP markers on linkage disequilibrium (r^2) **in the population of Russian White chickens** (Genetic Collection of Rare and Endangered Chicken Breeds, ARRIGBFA, St. Petersburg—Pushkin)

Factor	DF	SS	MS	F	P
Group	4	3244	811.0	11947.40	P < 0.001
Chromosome	27	178	6.6	96.93	P < 0.001
SNP distance	1	244	243.8	3592.35	P < 0.001
Group × chromosome	105	289	2.8	40.61	P < 0.001

N o t e. DF — the number of degrees of freedom SS — sum of squares, MS — mean squares, F — Fisher distribution.

As is known, the traditional poultry breeding with individual records includes selection of parents for productivity, selection for own productivity, and selection of unrelated pairs. A panmictic breeding, as it was in current population of Russian Whites, it is difficult to determine the origin and genetic variability of the resulting offspring. The characterization of genetic variability solves the problem of determining the structure of population and makes it possible to estimate the dynamic changes in its molecular architecture.

In modern Russian White chickens, as descendants of 2001 population, a specific drift of genes could occur. Note, that the members of the population 2001 (2 individuals of line No. 16 and 4 individuals of line No. 10) took a position in the central part of distribution area of the same modern cluster MDS3 (see Fig. 1). Although the number of the ancestral individuals was small, their genotyping can be considered in data processing, since, due to a significant number of SNP markers used in population analysis, an increase in the number of analyzed individuals is not required for reliable estimates [27-29]. Unrelated individuals of different lines were very close to one another, because both lines descended from one rooster.

However, the genotypes of unrelated individuals which were involved in the analysis do not fully reflect the genetic breed diversity in 2001. Not all minor alleles of the population 2001 were accounted because of limited biomaterial available (6 individuals). Perhaps, some monomorphic alleles in the population were minor. At the same time, a part of minor alleles and all the monomorphic alleles were eliminated during MAF filtration in MDS analysis and could not affect the pattern of distribution and, consequently, the conclusions about the genetic proximity or remoteness of individuals and populations. In the preliminary analysis, the complete exclusion of minor alleles did not affect MDS clustering of the population. Removing SNPs that were in linkage disequilibrium (--indep-pairwise 50 5 0.5) did not change the cluster locations while varying criteria for filtering SNPs. Our findings have shown that the common origin has the most impact on the relative MDS distribution.

The presence of unique haplotypes is the essential characteristic of a population [19, 29]. Extension of genomic regions with linkage disequilibrium detected with SNP markers is considered the main structural feature of the studied groups [8]. A large number of markers in linkage disequilibrium was a distinctive feature of Russian Whites ancestral population, which influenced the LD

value. Long-distant linkage disequilibrium for significant number of SNPs found in unrelated animals indicates rather a limited number of ancestors involved in breeding. This is confirmed by other studies of commercial poultry lines [8, 17]. The modern population of Russian Whites is characterized by breakdown of long-range LD areas and a reduced frequency of the ancestral population haplotypes.

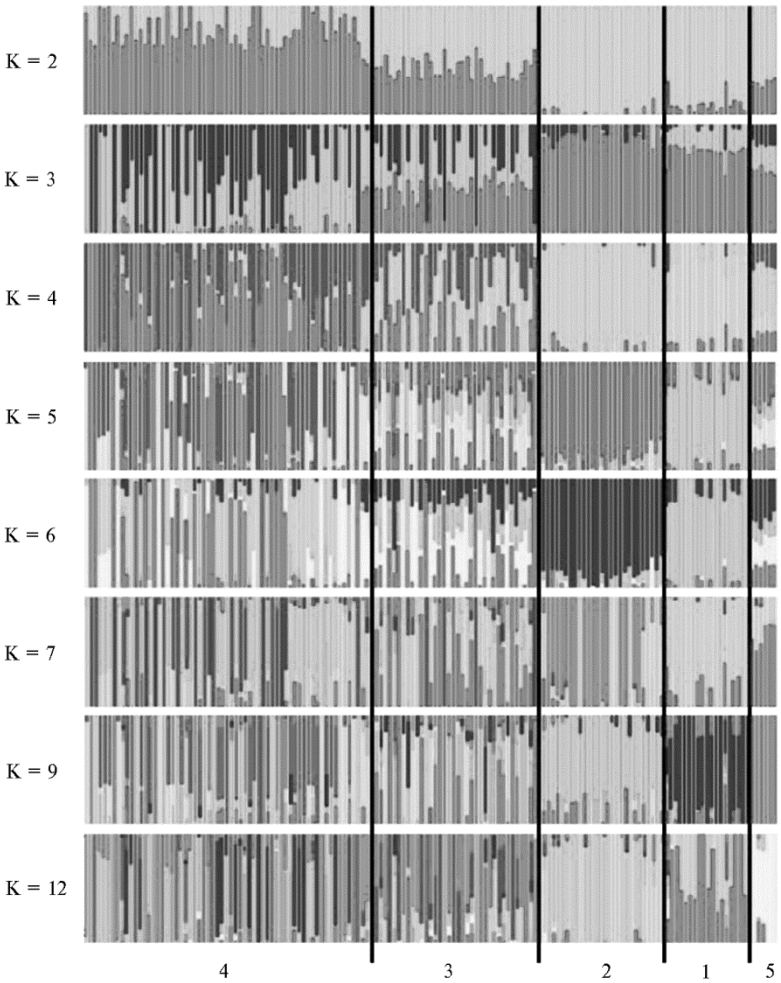

Fig. 2. Population variability on SNP markers in Russian White chicken breed as calculated using ADMIXTURE software: 1, 2, 3, 4 — MDS1, MDS2, MDS3 and MDS4 clusters of modern population, 5 — members of population 2001. K is the number of ancestral populations (Genetic Collection of Rare and Endangered Chicken Breeds, ARRIGBFA, St. Petersburg—Pushkin).

Thus, the heterogeneity of the modern gene pool population of Russian White chickens is based on their origin due to different ancestor roosters. A group (MDS3) was found which has the greatest similarity to the ancestral population of 2001. A distinguishing feature of the latter is a significant number of monomorphic alleles and a high frequency of long-range LD areas. In the modern population, the minor allele frequency increased and the LD values decreased. In general, SNP scanning makes it possible to identify the structural ties in breed based on the genetic similarity between individuals, which is especially important in panmictic breeding of small breeds when the number of animals is limited. The comparison of modern population and its ancestral population makes it possible to trace historical changes in the molecular organization of the Russian White breed

genome. Gene pool populations, the genetic variability of which has been formed for a long time, are a valuable source of biodiversity. Characterization of their genetic features is relevant as allows us to use the best animal qualities in breeding. In this paper, we report on important genetic characteristics of a small breed of domestic chickens. This information can be farther used for managing, conserving and using valuable genetic resources, and also for monitoring the dynamic changes in the molecular organization of genome for the limited gene pool population.

REFERENCES

1. Sokolova A.N. *Genetiko-selektsionnye metody sozdaniya populyatsii kur s povyshennoi ustoichivost'yu k neoplazmam. Avtoreferat doktorskoi dissertatsii* [Genetic and selection in chicken breeding for resystance to neoplastic growth]. St. Petersburg—Pushkin, 1999 (in Russ.).
2. Weigend S., Romanov M.N. Current strategies for the assessment and evaluation of genetic diversity in chicken resources. *World Poultry Sci. J.*, 2001, 57(3): 275-288 (doi: 10.1079/WPS20010020).
3. Soller M., Weigend S., Romanov M.N., Dekkers J.C.M., Lamont S.J. Strategies to assess structural variation in the chicken genome and its associations with biodiversity and biological performance. *Poultry Sci.*, 2006, 85(12): 2061-2078 (doi: 10.1093/ps/85.12.2061).
4. Romanov M.N., Weigend S. Analysis of genetic relationships between various populations of domestic and jungle fowl using microsatellite markers. *Poultry Sci.*, 2001, 80(8): 1057-1063 (doi: 10.1093/ps/80.8.1057).
5. Dunn I.C., Miao Y.-W., Morris A., Romanov M.N., Wilson P.W., Waddington D. A study of association between genetic markers in candidate genes and reproductive traits in one generation of a commercial broiler breeder hen population. *Heredity*, 2004, 92(2): 128-134 (doi: 10.1038/sj.hdy.6800396).
6. Tyshchenko V.I., Mitrofanova O.V., Dement'eva N.V., Terletskii V.P. Estimation of genetic variability in the breeds and hen experimental populations by DNA-fingerprinting. *Sel'skokhozyaistvennaya Biologiya* [*Agricultural Biology*], 2007, 4: 29-33 (in Russ.).
7. Mekchay S., Supakankul P., Assawamakin A., Wilantho A., Chareanchim W., Tongsima S. Population structure of four Thai indigenous chicken breeds. *BMC Genet.*, 2014, 15: 40 (doi: 10.1186/1471-2156-15-40).
8. Qanbari S., Hansen M., Weigend S., Preisinger R., Simianer H. Linkage disequilibrium reveals different demographic history in egg laying chickens. *BMC Genet.*, 2010, 11: 103 (doi 10.1186/1471-2156-11-103).
9. Yakovlev A.F., Smaragdov M.G. *Zootekhniya*, 2011, 5: 2-4 (in Russ.).
10. Khanyile K.S., Dzomba E.F, Muchadeyi F.C. Population genetic structure, linkage disequilibrium and effective population size of conserved and extensively raised village chicken populations of Southern Africa. *Front. Genet.*, 2015, 6: 13 (doi: 10.3389/fgene.2015.00013).
11. Smaragdov M.G., Saksa E.I., Kudinov A.A., Dementeva N.V., Mitrofanova O.V., Plemyashov K.V. Genome-wide analysis of across herd F_{st} heterogeneity in holsteinized cattle. *Russ. J. Genet.*, 2016, 52(2): 173-179 (doi: 10.1134/S1022795416020150).
12. Habier D., Fernando R.L., Dekkers J.C.M. The impact of genetic relationship information on genome-assisted breeding values. *Genetics*, 2007, 177(4): 2389-2397 (doi: 10.1534/genetics.107.081190).
13. Weng Z., Wolc A., Shen X., Fernando R.L., Dekkers J.C., Arango J., Settar P., Fulton J.E., O'Sullivan N.P., Garrick D.J. Effects of number of training generations on genomic prediction for various traits in a layer chicken population. *Genet. Sel. Evol.*, 2016, 48: 22 (doi: 10.1186/s12711-016-0198-9).
14. Meuwissen T.H., Hayes B.J., Goddard M.E. Prediction of total genetic value using genome-wide dense marker maps. *Genetics*, 2001, 157(4): 1819-1829.
15. Solberg T.R., Sonesson A.K., Woolliams J.A., Odegard J., Meuwissen T.H. Persistence of accuracy of genome-wide breeding values over generations when including a polygenic effect. *Genet. Sel. Evol.*, 2009, 41: 53 (doi: 10.1186/1297-9686-41-53).
16. Fariello M.I., Boitard S., Naya H., SanCristobal M., Servin B. Detecting signatures of selection through haplotype differentiation among hierarchically structured populations. *Genetics*, 2013, 193(3): 929-941 (doi: 10.1534/genetics.112.147231).
17. Muir W.M., Wong G.K.-S., Zhang Y., Wang J., Groenen M.A.M., Crooijmans R.P.M.A., Megens H.-J., Zhang H., Okimoto R., Vereijken A., Jungerius A., Albers G.A.A., Lawley C.T., Delany M.E., MacEachern S., Cheng H.H. Genome-wide assessment of worldwide chicken SNP genetic diversity indicates significant absence of rare alleles in commercial breeds. *PNAS*, 2008, 105(45): 17312-17317 (doi: 10.1073/pnas.0806569105).

18. Fragomeni B.D.O., Misztal I., Lourenco D.L., Aguilar I., Okimoto R., Muir W.M. Changes in variance explained by top SNP windows over generations for three traits in broiler chicken. *Front. Genet.*, 2014, 5: 332 (doi: 10.3389/fgene.2014.00332).
19. Beynon S.E., Slavov G.T., Farré M., Sunduimijid B., Waddams K., Davies B., Haresign W., Kijas J., MacLeod I.M., Newbold C.J., Davies L., Larkin D.M. Population structure and history of the Welsh sheep breeds determined by whole genome genotyping. *BMC Genet.*, 2015, 16: 65 (doi: 10.1186/s12863-015-0216-x).
20. Saitou N., Nei M. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.*, 1987, 4(4): 406-425.
21. Pritchard J.K., Stephens P., Donnelly P. Inference of population structure using multilocus genotype data. *Genetics*, 2000, 155(2): 945-959.
22. Evanno G., Regnaut S., Goudet J. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol. Ecol.*, 2005, 14(8): 2611-2620 (doi: 10.1111/j.1365-294X.2005.02553.x).
23. Chang C.C., Chow C.C., Tellier L.C., Vattikuti S.S., Purcell S.M., Lee J.J. Second-generation PLINK: rising to the challenge of larger and richer datasets. *GigaScience*, 2015, 4: 7 (doi: 10.1186/s13742-015-0047-8).
24. *RStudio*. Available http://www.rstudio.com. No date.
25. Alexander D.H., Novembre J., Lange K. Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.*, 2009, 19(9): 1655-1664 (doi: 10.1101/gr.094052.109).
26. Deniskova T.E., Dotsev A.V., Bagirov V.A., Vimmers K., Reier Kh., Brem G., Zinov'eva N.A. Biodiversity assessment in interspecies hybrids of the genus ovis using STR and SNP markers. *Agricultural Biology*, 2017, 52(2): 251-260 (doi: 10.15389/agrobiology.2017.2.251eng).
27. Wragg D., Mwacharo J., Alcalde J., Hocking P.M., Hanotte O. Analysis of genome-wide structure, diversity and fine mapping of Mendelian traits in traditional and village chickens. *Heredity*, 2012, 109(1): 6-18 (doi: 10.1038/hdy.2012.9).
28. Ardlie K.G., Kruglyak L., Seielstad M. Patterns of linkage disequilibrium in the human genome. *Nat. Rev. Genet.*, 2002, 3(4): 299-309 (doi: 10.1038/nrg777).
29. Andreescu C., Avendano S., Brown S. R., Hassen A., Lamont S.J., Dekkers J.C. Linkage disequilibrium in related breeding lines of chickens. *Genetics*, 2007, 177(4): 2161-2169 (doi: 10.1534/genetics.107.082206).