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PHYLOGEOGRAPHY AND GENETIC DIVERSITY OF THE COMMON SNIPE *GALLINAGO GALLINAGO* LINNAEUS, 1758 IN THE PALEARCTIC ACCORDING TO THE DATA OF THE mtDNA

Abstract. There are practically no studies on the genetic diversity and phylogeography of the common snipe. At the same time, there is a lot of research in this field for a number of other species of waders. It is known that comparison of phylogeographic data on the widest possible range of species that have an assumed common evolutionary history due to the influence of similar biogeographic, geological and climatic factors is necessary to establish the factors of similarity or differences in the patterns of formation and dynamics of their ranges, the patterns (regularities) of the formation of the population genetic structure. Thereby the goal of this article is to get data on the phylogeography of the common snipe in the Palearctic. The mtDNA control region is used as a genetic marker. As the result of analyzing data on polymorphism of mtDNA control region of common snipe, we have found out that its population is characteristic of low genetic diversity and genetic homogeneity. Also it has been shown that there are some signs of distinct genetic line of common snipe present at the easternmost part of its range in the Palearctic.

Keywords: *Gallinago gallinago*, common snipe, genetic diversity, phylogeography, the mtDNA control region, the Palearcric

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ФИЛОГЕОГРАФИЯ И ГЕНЕТИЧЕСКОЕ РАЗНООБРАЗИЕ БЕКАСА (*GALLINAGO GALLINAGO* LINNAEUS, 1758) В ПАЛЕАРКТИКЕ ПО РЕЗУЛЬТАТАМ АНАЛИЗА мтДНК

Аннотация. Работы по исследованию генетического разнообразия и филогеографии бекаса практически отсутствуют. В то же время имеется много исследований в данном направлении для ряда других видов куликов. Как известно, сопоставление филогеографических данных по как можно большему спектру видов, имеющих предполагаемую общую эволюционную историю в силу влияния схожих биогеографических, геологических и климатических факторов, необходимо для установления факторов общности или различий паттернов становления и динамики их ареалов, закономерностей формирования популяционно-генетической структуры. В этой связи целью данной работы стало получение данных по филогеографии бекаса в Палеарктике. В качестве генетического маркера был выбран контрольный регион мтДНК. В результате было установлено, что популяция бекаса характеризуется низким уровнем генетического разнообразия и генетической гомогенностью. Однако были обнаружены признаки возможного формирования удаленной генетической линии в крайней восточной части ареала вида в Палеарктике.

Ключевые слова: *Gallinago gallinago*, бекас, генетическое разнообразие, филогеография, контрольный регион мтДНК, Палеарктика

Для цитирования: Филогеография и генетическое разнообразие бекаса (*Gallinago gallinago* Linnaeus, 1758) в Палеарктике по результатам анализа мтДНК / К. В. Гомель [и др.] // Вес. Нац. акад. навук Беларусі. Сер. біял. навук. – 2021. – Т. 66, № 1. – С. 17–25 (*на англ.*). https://doi.org/10.29235/1029-8940-2021-66-1-17-25

Introduction. Comparison of phylogeographic data on the widest possible range of species that have an assumed common evolutionary history due to the influence of similar biogeographic, geological and climatic factors is necessary to establish the factors of similarity or differences in the patterns of formation and dynamics of their ranges, the patterns (regularities) of the formation of the population genetic

structure. Such studies contribute to the advancement of the goals of comparative phylogeography – a direction the theoretical basis of which was determined by J. C. Avise et al. [1].

The main task of such study is to establish how similarities or differences in biogeographic history, in ecological plasticity and phenotypic flexibility can explain the differences or similarities observed in the genetic structure and diversity of genetic lines in different species with a similar range. Considering that the methodological basis of this direction is the comparison of information arrays by a large number of species, the lack of species-specific molecular genetic data with a view of their further joint analysis is still one of the main reasons impeding sweeping generalizations and conclusions. Therefore, the accumulation of information on intraspecific phylogeography for different animal species is an important source for the further study in this direction [2].

In this work, we demonstrate the results of a study on the phylogeography of a widespread (in terms of its range) Palearctic species – the common snipe (*Gallinago gallinago* (Linnaeus, 1758)). The mtDNA control region is used as a genetic marker.

According to the BirdLife International, the common snipe has an extremely wide range that does not give grounds to consider it as an endangered or vulnerable species [3]. The common snipe's range covers the entire Palearctic biogeographic region, with the exception of some southern and northern regions. The species, mainly migratory, winters in Europe and Africa (Fig. 1) and is characterized by a high degree of fidelity to wintering sites [3, 4]. The common snipe is mostly found in areas where there is a combination of grass cover and moist soils. The species includes two subspecies: *G. g. faeroeensis* (C. L. Brehm, 1831) – Iceland, the Faroe Islands, the Orkney Islands and the Shetland Islands; it winters in the British Isles [4]. *G. g. gallinago* (Linnaeus, 1758) is spread nearly across the entire range of this species. The subspecies winters from Western Europe, the Mediterranean, and Equatorial Africa through the Middle East, Arabia and the Indian subcontinent to Eastern China, South Korea, South Japan, the Philippines, and Borneo [4].

In zoogeographic terms, the nature of the range and peculiarities of the intraspecies and ecological structure of common snipe populations are fundamentally very similar to those of many other species of waders previously related to a separate suborder and recently to several suborders of the order

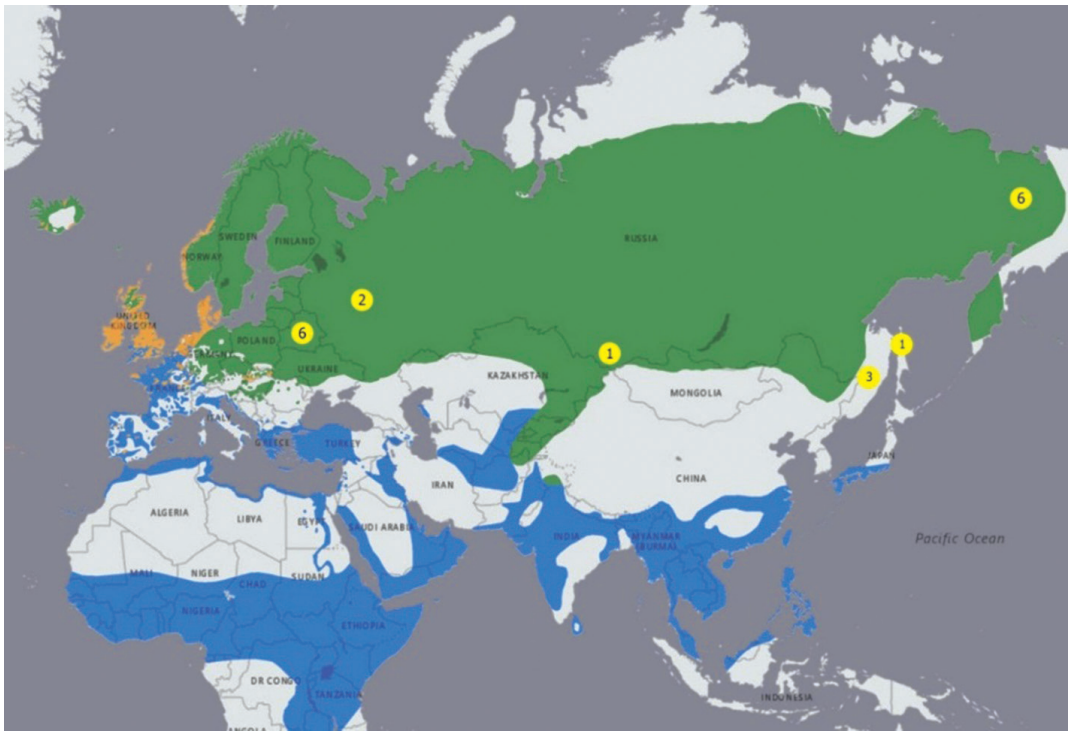

Fig. 1. Distribution of the common snipe in the Palearctic and distribution of samples to study the species phylogeography (orange color – the sedentary habitat zone, green – the nesting range, blue – wintering sites, numbers in yellow circles – the number of samples from this location)

Charadriiformes. Phylogeographic data are already available for a number of wader's species [5]. But even though the common snipe is a very widespread and numerous hunting species, we have to state that there is a complete absence of works devoted to the study of the phylogeography of this particular species.

Works on the study of phylogeography and evolutionary history, taking into account the breeding system and biotopic preferences, were carried out for the Ruff (*Calidris pugnax*), the Dunlin (*Calidris alpina*), the Temminck's Stint (*Calidris temminckii*), the Common Redshank (*Tringa totanus*), the Black-tailed Godwit (*Limosa limosa)*, the Kentish Plover (*Charadrius alexandrinus*), the Terek Sandpiper (*Xenus cinereus*), the Common Sandpiper (*Actitis hypoleucos*) [5 and inside references]. All of the listed species have a range similar to the common snipe's. The mtDNA control region, ND2 NADH dehydrogenase subunit 2 (the Common Sandpiper), cytochrome b (cyt b) and microsatellites (the Dunlin) were used as genetic markers [6]. With regard to the above-listed species, genetic structuring in the Palearctic region was established only for the dunlin [5–7] and the Black-tailed Godwit. Among the main reasons that led to the formation of genetic differentiation, long-term isolation during climatic changes within the last 250,000 years is indicated for the Dunlin [5, 7]. For the Black-tailed Godwit, the main factors that influenced the formation of genetic structuring are a strong division of the ancestral population, sufficient time for lineage sorting, and pronounced philopatry [5]. The absence of intraspecies genetic differentiation for other species of waders is explained by the use of different habitats during the period of breeding, migration and wintering (the Ruff), the use of ephemeral habitats (the Ruff, the Terek Sandpiper, the Kentish Plover), the polygamous breeding system (the Temminck's Stint, the Kentish Plover), incomplete lineage sorting (the Temminck's Stint), a wide and connected nesting range (the Terek Sandpiper, the Common Sandpiper), the absence of an affinity for specific wintering sites (the Terek Sandpiper), as well as incomplete habitat coverage in the framework of species research (the Redshank) [5].

When studying the genetic differentiation of Sanderling (*Calidris alba*) subpopulations from Greenland and Siberia [8], the mtDNA control region and microsatellites were used as genetic markers. Subpopulations of this species are separated by more than 2000 km. However, they mix in Europe during the migration period. The authors found only weak mtDNA differentiation between nesting sanderling populations and did not find any differentiation by microsatellite loci. Taking into account the geographic isolation of two nesting ranges, a low level of established differentiation may result from either historical isolation followed by significant gene flow, or recent isolation with no or weak subsequent gene flow. An interesting point is that for the Red Knot (*Calidris canutus)* (for the subspecies *C. canutus islandica* and *C. c. canutus*) with a similar distribution and ecology, a genetic differentiation was found dating back to the time of the Last Glacial Maximum based on the data of mtDNA control region's polymorphism [8].

Taking into account the work carried out on the phylogeography of waders in the Palearctic, it can be expected that genetic structuring of the common snipe throughout the entire range will be poorly expressed. The latter is due to pronounced migratory behaviour, a wide and connected nesting range and a wide wintering area.

Materials and research methods. In order to study the phylogeography and genetic structuring of the common snipe in the Palearctic, 19 samples were used: 6 from Belarus and 13 from Russia (Tab. 1).

T a b l e 1. **Common snipe samples used to study species phylogeography in the Palearctic**

Sample code	Collection date	Place of collection
Samples from Belarus		
AV00181	04.04.2009	Gomel Oblast
AV02926	16.08.2005	
AV02928	02.08.2009	
AV02929	24.07.2009	
AV02934	11.08.2007	
AV03157	21.05.2017	Minsk Oblast

End of Tab. 1

Samples from Russia		
RYA350	11.05.2002	Primorsky Krai
AV02925	?	
AV02924	12.05.2004	
NNY005	26.05.2006	Chukotka Autonomous Okrug
RYA2318	03.08.2006	
#176	27.06.2009	
#171	18.06.2009	
#209	28.05.2010	
AV02933	15.07.2002	
AV02931	25.07.2009	Moscow Oblast
AV02930	11.10.2008	Moscow, zoo
CBH2315	05.07.2008	Sakhalin
1175	19.05.2011	Altai

For analysis, we used the common snipe samples from the Genetic Bank of Wild Fauna of the State Scientific and Production Association "Scientific and Practical Center of the National Academy of Sciences of Belarus for Bioresources". The distribution of common snipe samples is demonstrated in Fig. 1. The used common snipe samples belong to the range of the *G. g. gallinago* subspecies. DNA was isolated from muscle tissue and blood using the Blood-Plant-Animal DNA Preparation Kit (Jena Bioscience, Germany). The isolated DNA quality was assessed using the NanoPhotometer P 330UV/Vis (IMPLEN, Germany).

The following primers were used for the second/third domain of the common snipe control region: L438 (5′-TCACGTGAAATCAGCAACCC-3′) [7] and H1247 (5′-AACTTCAGTGCCATGCTTTG-3′) [9].

PCR amplification was performed in 25 µl of the reaction mixture containing 2.5 µl of 10× buffer with $(NH_4)_2SO_4$ (Thermo Scientific), 2.5 µl of the dNTPs mixture (2 mM of each nucleotide, Thermo Scientific), 3 µl $MgCl_2$ (25 mM, Thermo Scientific), 2 µl of the primers (5 pmol/µl) (manufactured by Primetech ODO), 0.1 µl of Taq-polymerase (Thermo Scientific 500U), 2 µl of test sample DNA, and 10.9 µl of ddH_2O.

Temperature and time PCR regimes for the D-loop mtDNA of the common snipe: initial DNA denaturation at 95 °C for 2 min, then 35 cycles – DNA denaturation at 95 °C for 30 sec, primer annealing at 58 °C for 30 sec, elongation at 72 °C 90 sec, final elongation at 72 °C for 5 min. The CFX96 Touch amplifier (Bio-Rad Laboratories, Inc. USA) was used for PCR.

PCR products were sequenced using the GenomeLab GeXP Genetic Analysis System (Beckman Coulter, Germany). For this, commercial reagents Dye Terminator Cycle Sequencing with Quick Start Kit (Beckman Coulter, Germany) and commercial protocols (Beckman Coulter) were used. Samples were sequenced using forward and reverse primers.

The sequences were checked and aligned (Muscle method) in MEGA version 6 [10]. To estimate the number of polymorphic sites, MEGA 6 and DnaSP version 6.10.04 were used [11]. Calculation of genetic diversity indicators: nucleotide diversity (π; Nei, 1987), the number of haplotypes (h), the average number of nucleotide differences (k), haplotype diversity (Hd, Nei 1987), the number of segregation sites (S), θ_s (theta per site (from S) Watterson 1975, Nei 1987) – the θ measure based on the number of segregating sites; was carried out in DnaSP. Haplotype network construction was carried out in the POPART program using the Median Joining Network algorithm [12].

Calculation of demographic data (presence/absence of population expansion in the past) was carried out in DnaSP and Arlequin 3.5.1.2 [13]. For that, such indicators as Fu's Fs, Tajima's D and raggedness index (r) were calculated. Negative values in case of Fs and D indicate the processes of population expansion in the past [14]. To estimate the confidence level (p) of these indicators, coalescent simulation was used using both theta and the number of segregating sites in DnaSP. In addition, a mismatch distribution graph between the pairs of sequences was constructed in DnaSP. Where there is a unimodal graph, this test indicates the fact of population expansion in the past. In this situation, low values of the

raggedness index (quantitative assessment of the smoothness of the mismatch distribution for the demographic scenarios of population expansion and stability in the past) and low values of the sum of squared deviations (SSD) from the sudden expansion model under testing correspond to it [15, 16].

In order to establish if there is differentiation between the genetic lines of the common snipe within the Palearctic range, the Fst indicator (distance method: pairwise difference, 1000 permutation) was calculated and an exact test on the presence of differentiation based on haplotype frequencies (an exact test of sample differentiation based on haplotype frequencies, default settings) was carried out in Arlequin.

Results and its discussion. As a result of the alignment, a sequence of 548 bp was obtained. Taking into account available ambiguous nucleotides, as well as insertions/deletions, the length of the analyzed sequence was 545 bp. The investigated sequence is characterized by the predominance of pyrimidine transitions. The number of variable sites equaled 5 (MEGA 6 data) or 4 (DnaSP, one site with the presence of an ambiguous nucleotide was not taken into account), and out of them, 2 sites were parsimony-informative (MEGA 6) or 1 (DnaSP, one site with the presence of an ambiguous nucleotide was not taken into account). Among the 19 investigated sequences, 4 haplotypes were found (Tab. 2).

T a b l e 2. **Common snipe haplotypes based on mtDNA control region polymorphism**

Haplotype	Haplotype according to PopART	Number of samples	Samples included in the haplotype
Hap_1	GG_1	13	181_Gomel_obl_Belarus, RYA350_Primorsky_Krai_Russia, 1175_Altai_Russia, RYA2318_Chukotka_Russia, 2928_Gomel_obl_Belarus, 2929_Gomel_obl_Belarus, 2930_Moscow_zoo_Russia, 2933_Chukotka_Russia, 209_Chukotka_Russia, 3157_Minsk_obl_Belarus, 2934_Gomel_obl_Belarus, CBH2315_Sakhalin_Russia, NNY005_Chukotka_Russia
Hap_2	GG_2	4	176_Chukotka_Russia, 2924_Primorsky_Krai_Russia, 2931_Moscow_obl_Russia, 171_Chukotka_Russia
Hap_3	GG_7	1	2925_Primorsky_Krai_Russia
Hap_4	GG_8	1	2926_Gomel_obl_Belarus

Fig. 2. Distribution of the common snipe haplotypes within the Palearctic range

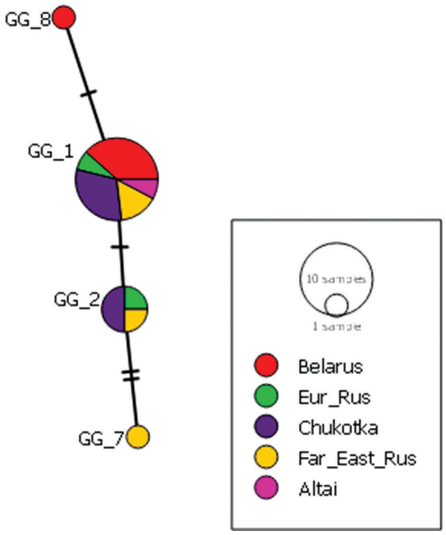

Fig. 3. Haplotype network (median-joining) for the common snipe based on mtDNA control region's polymorphism

For the investigated sample of sequences, the GG_1 haplotype was established, including the predominant (68 %) number of analyzed sequences of the mtDNA control region of the common snipe. The haplotype included the samples from the Far East of Russia, from Altai and Eastern Europe – Belarus, Russia (Moscow), i. e. the haplotype combines samples both from the edges and central part of the common snipe range. Since the common snipe is a migratory species, the probability of the presence of samples not only from local birds, but also from migrants must be considered. In this regard, representative samples that allow concluding that birds from different parts of the range belong to the same haplotype are as follows: from the western part of the range – AV00181, AV03157 (Belarus), from the eastern part of the range – RYA350 (Primorsky Krai), NNY005, #209 (Chukotka AO), CBH2315 (Sakhalin), from the central part of the range – 1175 (Altai). The second largest haplotype, GG_2, combined 4 samples of the common snipe from the Far East of Russia (3 samples) and European Russia (1 sample). In the latter haplotype, it is likely that the sample from European Russia (AV02931) belonged to a migratory bird, while all other samples most likely belonged to local birds. The remaining two haplotypes are unique – one of them is from the eastern part of the range (GG_7) and the other one is from the most extreme western part of the range (GG_8). The latter haplotype is unlikely to belong to the place of collection (Belarus) due to the late dates of bird catching.

Distribution of haplotypes within the range is shown in Fig. 2.

Genetic structure of the common snipe population in the form of a haplotype network is shown in Fig. 3.

Relying on the obtained haplotype network, it is possible to speak about the absence of certain genetic structuring. The presented haplotypes are equidistant from the haplotype with the highest frequency (GG_1). At the greatest distance from GG_1, there is a haplotype from the Far East of Russia (GG_7, Primorsky Krai). Such location of the latter haplotype is possibly associated with the formation of a genetic line for birds, which are at an extreme distance and winter in the nearby wintering range in the east. However, this requires verification due to the small sample size. Regarding the distant GG_8 haplotype noted in Belarus, we can most likely say that this is a migrant.

Haplotype structure of the common snipe population is consistent with the phylogenetic tree topology (Fig. 4).

As well as the above haplotype network, the structure of the common snipe phylogenetic tree confirms, despite low bootstrap values, the genetic similarity of birds from distant parts of the range (clade with bootstrap value = 28). Based on the tree structure, it is possible to assume that the ancestral haplotype was GG_8 (sample AV02926), since it is the most ancient in relation to the rest. The subsequently separated haplotype GG_1 (clade with bootstrap value = 28) spread widely due to the long-distance migrations of the species. The GG_2 haplotype along with GG_7 haplotype diverged from the latter is possibly a genetic line of birds adhering to remote wintering sites in the east, and this determines their isolation from the birds of the GG_1 haplotype line. The established differentiation of lines is supported by a high level of the Fst = 0.84 ($p < 0.001$) index and the data from an exact test of differentiation ($p < 0.001$). Given the small sample, the result obtained requires further verification.

Genetic diversity and demographic history data in relation to the common snipe is presented in Tab. 3.

Genetic diversity data on the common snipe population indicates its low level. Nevertheless, there are no signs that the population was exposed to sharp decreases in its size in the past (negative and statistically not significant values of Tajima's D index). There was weak evidence of a rapid increase in the common snipe's population in the past – Fs = –2.962 ($p = 0.015$). The latter is supported by the

Fig. 4. Phylogenetic relationship tree of the common snipe within the habitat range according to the data on mtDNA control region's polymorphism (HKY + G, excluding insertions/deletions and ambiguous nucleotides, 1000 replications)

mismatch distributions graph in relation to the frequencies of nucleotide differences among the analyzed sequences of the mtDNA control region and accompanying statistics (SSD, Raggedness index (r)) (Fig. 5).

Taking into account the data obtained on the genetic diversity and structure of the common snipe's population in the Palearctic, it is possible to speak about the gene flow between remote populations in the past and present time. Considering phylogenetic reconstruction and genetic subdivision data, it is possible to assume that the formation of distant genetic lines at the edge of the range (the Far East of Russia) is a possible consequence of their belonging to different wintering regions and general remoteness from other more western populations.

T a b l e 3. **Genetic diversity and demographic history estimates of the common snipe according to the polymorphism of mtDNA control region**

Estimate	Value
N	19
h	4
Hd ± SD	0,509 ± 0,117
π ± SD	0,00133 ± 0,00046
k	0,72515
Theta per site (from S) (Theta-W)	0,00210
Fu's Fs (DnaSP)	–0,787 NS
Tajima's D (DnaSP)	–1,07883 NS
Fu's Fs (Arlequin)	–2,96231*
Tajima's D (Arlequin)	–0,70719 NS
SSD (Arlequin)	0,0116 NS
Raggedness index (r) (Arlequin)	0,05 NS

N o t e. N – sample, SD – standard deviation, NS – statistically not significant, * – $p < 0.05$.

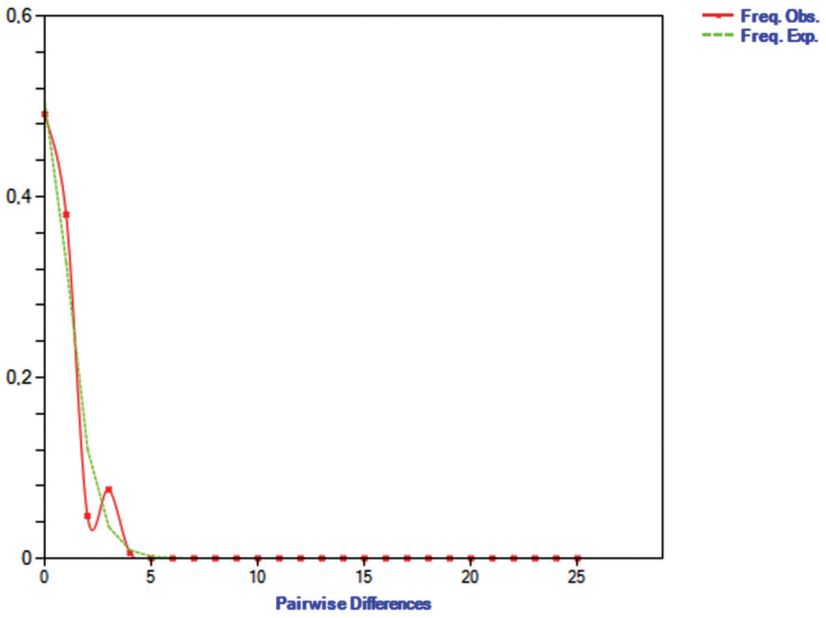

Fig. 5. Mismatch distributions graph in relation to the frequencies of nucleotide differences in a pairwise sequence comparison of the mtDNA control region of the common snipe for testing a model of a sudden population expansion in the past. Freq. Exp. – the expected frequency of differences, Freq. Obs. – the observed frequency of differences, X axis reflects pairwise difference, Y axis reflects frequency of the difference across sequences

The presence of a common haplotype (GG_1) for birds from geographically distant parts of the range may serve as evidence of populations' mix in wintering ranges. In addition, based on the results of our earlier study, the common snipe was attributed to the Northern Palearctic Group of the Transpalearctic Ornithofaunal Holocene Complex the representatives of which manifest zonal distribution dependences in a lesser degree [17]. At the end of the Pleistocene, the extended ranges of such species were formed in the periglacial and peripheral territories of glaciation regardless of individual refugia and refugial zones and then developed with a gradual expansion of northern boundaries as the glacier was retreating. Thus, the absence of long-term isolation during glaciation, wide topical plasticity, and consequently the extended nature of the range, as well as their potential to mix in the wintering range, could contribute to the formation of such a common haplotype.

Conclusion. In general, the results obtained are consistent with the conclusion [5] with respect to other species of waders with the similar (in terms of latitude and form) distribution as of the common snipe's that the nature of the formation of genetic structuring in them does not demonstrate a certain tendency, but is most likely determined by the characteristics of the species-specific breeding system, biotopic preferences and historical demography during the periods of climatic oscillations.

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