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Evaluation of the genetic structure of the breeding Common Tern (*Sterna hirundo*) population by means of microsatellite markers

A. Sruoga[1,2], D. Butkauskas[1], P. Prakas[1], A. Paulauskas[2]

[1] *Laboratory of Population Genetics, Institute of Ecology of Vilnius University, Akademijos 2, LT-08412 Vilnius, Lithuania aniolas@ekoi.lt*

[2] *Department of Biology, Vytautas Magnus University, Vileikos 8, LT-44404, Kaunas, Lithuania*

Samples of tissues of the Common Tern (*Sterna hirundo*) breeding in Lithuania were collected in the colonies distributed in the basins of the River Nemunas and the River Dauguva located near Kalviai, Kietaviškės, the Nemunas delta, Lazdijai, Kretuonas, Zarasai and Ignalina. By means of 11 primer pairs designed for the analysis of microsatellite loci of taxonomically close bird species, allele frequencies at 11 polymorphic loci of the Common Tern were established. The heterozygosity ranged from 0.1809 to 0.4029 in separate colonies. No significant differences in the genetic variability of the colonies under study have been detected. However, a lower genetic variability was established for the Nemunas delta colony, which reflects a greater effect of natural selection. A high genetic differentiation was calculated for the entire population (R_{ST} = 0.1545). Deviation from the Hardy–Weinberg equilibrium as a deficit of heterozygosity was detected in six out of the seven colonies investigated. It might be caused by a high level of inbreeding and a genetic drift. The Common Tern subpopulations breeding in the basins of the River Nemunas and the River Dauguva are genetically differentiated and form separate clades in the dendrogram obtained using the UPGMA algorithm. The obtained data allow a conclusion that the differences in the genetic structure of the Common Tern colonies are influenced by the geographic distribution of large rivers.

Key words: Common Tern, microsatellite analysis, genetic differentiation

INTRODUCTION

The Common Tern is a colonial breeding species. Almost half of the Common Tern population (46%) breeding in Lithuania is concentrated in five largest (with more than 100 breeding pairs) colonies: the Nemunas delta (Šilutė district), Kalviai (Klaipėda district), Lazdijai (Lazdijai district), Kretuonas (Švenčionіai district) and Zarasai (Zarasai district). A significant decrease in the Common Tern population is currently observed in most of their habitats in Europe. A similar decrease in the population of this species has also been observed in Lithuania. In 2002, the Common Tern population was estimated to comprise 1500–2500 breeding pairs [1]. This is by 500 pairs less than the number given in the latest review of the populations of birds breeding in Lithuania [2]. It is important to find out whether the decrease in the Common Tern population has a negative influence on the genetic variability of the species. Assessment of the condition of the population of the Common Tern breeding in Lithuania could be of use in creating the species protection strategy. Investigations into the intraspecific genetic diversity are fragmentary in most bird species. This applies to Common Terns too, although their biology, ecology, behavior, taxonomy and morphology are described in several scientific publications [3, 4]. The entire population of Common Terns breeding in Lithuania was considered as an integral unit. However, the first investigations of the past years, carried out by means of protein and isoenzyme electrophoretic analysis, showed that separate colonies of Common Terns, particularly those located in different regions of the country, were genetically differentiated [5]. In order to evaluate the differentiation and genetic diversity of Common Terns, it is necessary to use markers suitable for reconstruction of phylogenetic relationships at the population level. Microsatellite markers are successfully applied in examining the genetic structure of bird populations [6]. A widespread use of the microsatellite loci in the population genetics, phylogenetics, conservation genetic researches is mainly determined by the microsatellite features: their

abundance in the genome, high degree of polymorphism, co-dominant inheritance [7]. The aim of our study was to evaluate, using microsatellite markers, the genetic structure and phylogenetic relationships of the population of Common Terns breeding in different districts of Lithuania.

MATERIALS AND METHODS

Erythrocytes and liver homogenates were taken from Common Terns belonging to seven different colonies located in Lithuania: Kalviai, Kietaviškės (Kaišiadorys district), Lazdijai, the Nemunas delta, Kretuonas, Ignalina (Ignalina district) and Zarasai, which are distributed in the basins of the River Nemunas and the River Dauguva (Fig. 1).

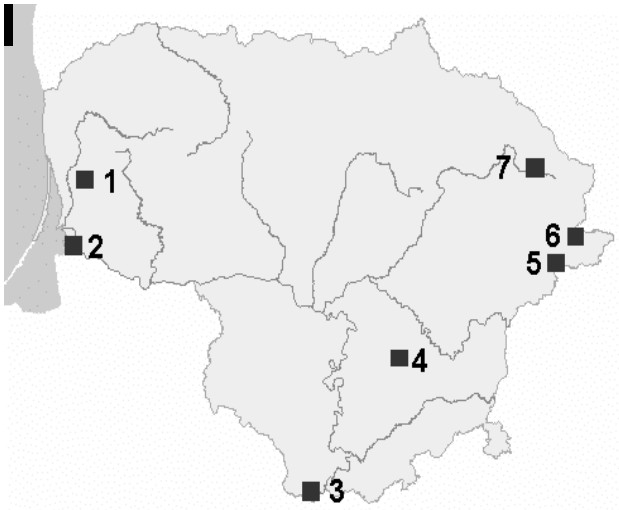

Fig. 1. Geographical distribution of Common Tern population colonies studied. 1 – Kalviai, 2 – Nemunas delta, 3 – Lazdijai, 4 – Kietaviškės, 5 – Kretuonas, 6 – Ignalina, 7 – Zarasai

Samples of liver tissues were taken from embryos after incubation of eggs in the laboratory. Additional blood samples were collected from two-three-week aged tern fledglings, from a wing vein into heparinized tubes. Approximately 100–150 µl of blood, which was centrifuged for 10 min at 3000 rpm was taken from each bird. Erythrocytes were separated from plasma and later were used for DNA extraction. Genomic DNA was extracted by means of the universal method of DNA extraction from different tissues [8]. Microsatellite primers were chosen using the data bank (http://tomato.bio.trinity.edu/home.html). The polymerase chain reaction was carried out in a 25 µl volume containing 2.5 µl 10 × PCR buffer, 2.5 µl, 2 mMdNTP, 0.1 µM of each primer, 0.5 µl of Taq polymerase, 2.5 µl $MgCl_2$, 0.2 µg of genomic DNA, and the remaining volume was water. Amplification was done by an Eppendorf Mastercycler gradient thermocycler: 3 min at 94 °C; 30 cycles of 1 min at 94 °C, then increasing the annealing temperature by one degree from 43 °C to 57 °C (from 2 to 15 cycles) and continuing amplification for the other 15 cycles at 57 °C for annealing, followed by 5 min of a final elongation step at 72 °C. PCR products were fractionated using 10% polyacrilamide gels and the Tris-EDTA-borat buffer electrophoresis analysis (200 V). After electrophoresis the gels were stained with ethidium bromide. The amplification products were evaluated in UV using an image multimedia detecting system. Relative sizes of alleles were determined with the help of TotalLab v1.10 software.

Statistical analysis was performed using GENEPOP (2003), TFPGA (1997), Fstat (2002), STATISTICA (1995) computer programs. The genetic diversity of the population was quantified by the frequency of alleles, the mean number of alleles per locus, the proportion of polymorphic loci ($P_{0.95}$; frequency of the most common alleles <0.95), the mean heterozygosity (H_o) observed and the expected Hardy–Weinberg heterozygosity (H_e) (TFPGA). The non-parametric Wilcoxon test was applied in testing differences in the variability among all pairs of the populations comparing the observed heterozygosity for each locus in all the populations (STATISTICA). Conformity to the Hardy–Weinberg equilibrium was analysed using a single locus test by the Marcov chain method (TFPGA). GENEPOP was used to calculate the number of immigrants per generation (N_m), and a multi-locus test for heterozygote deficit or excess was performed. Genetic distances among the populations according to Nei [9] (1972) were calculated using TFPGA. A dendrogram based on genetic distances was constructed using the unweighed pair-group arithmetic average (UPGMA) cluster analysis by TFPGA. Population genetic differentiation was investigated using the Raimond and Rousset [10] test. The values of the inbreeding coefficients F_{ST} and R_{ST} were calculated by Fstat. A correlation between genetic and geographic distances of the population was evaluated using the Mantel [11] test.

RESULTS

By means of 11 microsatellite primer pairs designed for *Larus novaehollandiae scopulinus* (RBG-13, RBG-18, RBG-29, RBG-39) [12] and *Rissa tridactyla* (K-16, K-31, K-56) [13] 14 loci were amplified, 11 whereof were polymorphic. Thereinafter, genotypes and allele frequencies were determined (on average 15.4 individuals per sample) for a total of 108 individuals (Table 1).

Five polyallelic loci were detected, in which the number of alleles varied from 3 to 7. Furthermore, two alleles at the locus were detected for the remaining six loci (Table 1). The mean number of the alleles per polymorphic locus was 3.5. Two loci with the primers K-31, RBG-18, RBG-27 were amplified

Table 1. **Allele frequencies and deviation from Hardy–Weinberg equilibrium in different Common Tern colonies**

Loci	Alleles	Colonies						
		Kalviai n(23)	Kietaviškės n(15)	Nemunas delta n(19)	Lazdijai n(22)	Kretuonas n(7)	Zarasai n(9)	Ignalina n(13)
K-16	138	0.9348	0.9333	1.0000	0.9545	1.0000	1.0000	1.0000
	142	0.0652	0.0667	–	0.0455	–	–	–
K-31(1)	150	0.7174	0.5357	0.7105	0.7000	1.0000	1.0000	1.0000
	154	0.2826	0.4643	0.2895	0.3000	–	–	–
	186	0.0250	–	–	0.0357	0.6667	0.5833	0.5833
K-31(2)	192	0.6000	0.6538	0.6111	0.5357	–	–	–
	200	0.3750	0.3462	0.3889	0.4286	0.3333	0.4167	0.4167
	268	–	–	–	–	0.5000	0.5000	0.4091
K-56	280	–	0.1333*	0.2105*	0.0909*	–	–	–
	282	1.0000	0.8667	0.7895	0.9091	0.5000	0.5000	0.5909
	200*	–	–	0.0526	0.1000	–	–	–
	208	–	–	0.3421	0.7500	–	0.1667	0.1154
	216	0.2000*	–	0.1579	–	0.5833	0.3333	0.3846
RBG-13	220	0.3000	0.5385*	0.2895	0.0500	0.0833	0.2500	0.2692
	224	0.1500	0.2308	0.0263	–	0.0833	–	0.0385
	232	0.2500	0.0385	0.1053	0.1000	0.1667	0.0833	0.0385
	244	0.1000	0.1923	0.0263	–	0.0833	0.1667	0.1538
RBG-18(1)	174	0.6957*	0.8462	0.6333*	0.8684	0.9286	1.0000	1.0000
	178	0.3043	0.1538	0.3667	0.1316	0.0714	–	–
RBG-18(2)	216	1.0000	1.0000	1.0000	0.9773	0.8571	0.5625	0.9615
	230	–	–	–	0.0227	0.1429	0.4375	0.0385
	188	–	–	0.0667*	0.1053*	–	0.2143	0.7500*
	191	0.1154	0.2000	0.1333	0.0789	0.1667	0.2857	0.1000
	195	0.3077	0.7000	0.1667	0.3158	0.3333	0.4286	0.0500
RBG-27(1)	200	0.3077	–	0.4667	0.0526	0.3333	–	0.0500
	203	–	–	–	0.0263	–	–	–
	208	0.1538	0.1000	0.1000	0.3421	–	0.0714	0.0500
	214	0.1154	–	0.0667	0.0789	0.1667	–	–
RBG-27(2)	233	0.8846	0.6667	0.8333	0.6538	–	0.1667	0.3333
	247	0.1154	0.3333	0.1667	0.3462	–	0.8333	0.6667
	139	0.2727*	0.2222*	0.4167*	0.1111	–	–	0.0417
	141	0.3636	0.2778	0.1667	0.5000	–	0.1875*	0.2917
	145	–	–	–	–	0.7500	0.3750	0.1250
RBG-29	147	0.1364	0.1667	0.1667	–	–	0.0625	0.2917
	150	0.1364	0.2778	0.1667	0.1667	–	0.1875	0.0833
	158	0.0455	0.0556	–	–	0.2500	0.1250	0.1250
	163	0.0455	–	0.0833	0.2222	–	0.0625	0.0417
RBG-39	75	1.0000	1.0000	1.0000	1.0000	0.3000	1.0000	1.0000
	81	–	–	–	–	0.7000	–	–

* A significant deviation from the Hardy–Weinberg equilibrium ($p < 0.05$).

simultaneously. Some loci (K-56, RBG-18(2)) were polymorphic in several but not all colonies. For RBG-39 locus, a unique allele whose relative size was 81 bp was detected only in the Kretuonas colony. A significant deviation from the Hardy–Weinberg equilibrium was found in all colonies except Kretuonas. In five loci – K-56, RBG-13, RBG-18(1), RBG-27(1), RBG-29(1) (Table 1) – the most significant deviation from the Hardy–Weinberg equilibrium was observed in the Nemunas delta colony which is subjected to the highest pressure of natural selection.

The proportion of the polymorphic loci in different colonies ranged from 55% in Ignalina to 82% in Kietaviškės (Table 2). The same degree of polymorphism (73%) in Kalviai, the Nemunas delta and Lazdijai shows a similar level of genetic variability in three colonies belonging to the Nemunas River basin. The mean number of alleles per locus ranged from 2.3 in Kretuonas to 2.8 in the Nemunas delta. The observed heterozygosity in all colonies varied from 0.1809 to 0.4029, the expected heterozygosity ranging from 0.3121 to 0.3795. The value of H_o in Kretuonas was higher than

Table 2. **The rate of genetic variability in different Common Tern colonies**

Colonies	Mean number of alleles per locus	Polymorphism (%)	The mean of heterozygosity	
			Observed (H_o)	Expected (H_e)
Kalviai	2.7272	72.7273	0.2948	0.3557
Kietaviškės	2.3636	81.8182	0.3120	0.3504
Nemunas delta	2.8181	72.7273	0.1809	0.3795
Lazdijai	2.7272	72.7273	0.2831	0.3679
Kretuonas	2.3000	80.0000	0.4029	0.3450
Zarasai	2.4545	63.6364	0.2943	0.3608
Ignalina	2.7272	54.5455	0.2843	0.3123

Table 3. **Differentiation and genetic distances among Common Tern colonies (above the diagonal: p-values for test of genetic differentiation (Raymond and Rousset, 1995); below the diagonal: Nei's genetic distance (Nei, 1972) between all pairs of colonies)**

	Kalviai	Kietaviškės	Nemunas delta	Lazdijai	Kretuonas	Zarasai	Ignalina
Kalviai	***	0.1455	0.0290	0.0016	0.0000	0.0000	0.0000
Kietaviškės	0.0412	***	0.0036	0.0592	0.0000	0.0000	0.0000
Nemunas delta	0.0246	0.0712	***	0.0453	0.0000	0.0000	0.0000
Lazdijai	0.0486	0.0598	0.0515	***	0.0000	0.0000	0.0000
Kretuonas	0.2887	0.3492	0.3067	0.3151	***	0.0905	0.0017
Zarasai	0.2460	0.2186	0.2547	0.1863	0.1263	***	0.2095
Ignalina	0.1921	0.2069	0.1941	0.1532	0.1746	0.0620	***

that of H_e, but in the other colonies a significant deficit of heterozygosity was detected. The non-parametric Wilcoxon test yielded *P* values ranging from 0.1891–0.3579 when the colony of the Nemunas delta was compared to all other colonies and 0.8182–1.0000 when all other colonies were compared to each other. These results suggest that only slight differences in the amount of genetic variability exist between seven tern colonies.

On the basis of allele frequencies the genetic distance estimates among the colonies were calculated. The lowest values of the genetic distances (Nei, 1972) were found among the colonies belonging to the basin of the River Nemunas (0.0246–0.0712) (Table 3). Low values of genetic distances (0.0620–0.1746) among the northeast Lithuanian colonies belonging to the basin of the River Dauguva were identified too. The highest values of genetic distances were observed between Kretuonas and all other colonies. The values of the Raymond and Rousset test of comparing the colony pairs showed that Common Tern colonies of the Nemunas delta and northeast Lithuania were significantly differentiated. A significant differentiation was not found between the following colony pairs: Kalviai–Kietaviškės, Kietaviškės–Lazdijai, Zarasai–Kretuonas, Zarasai–Ignalina. The investigation revealed a distinet genetic structuring of the Common Tern population breeding in Lithuania. The F_{ST} (0.1463) and R_{ST} (0.1545) values show a the general scope of genetic differentiation of the population. When comparing the colonies of the River Nemunas basin (Kalviai, Kietaviškės, the Nemunas delta, Lazdijai) and those of northeast Lithuania of the River Dauguva basin (Kretuonas, Zarasai, Ignalina), lower R_{ST} values were obtained (0.0361 and 0.0958, respectively). The number of immigrants per generation (N_m) was 1.3681 and indicated a significant, though low, gene flow among the Common Tern colonies.

The UPGMA cluster analysis divides four colonies of the River Nemunas basin and three colonies of northeast Lithuania into two clades (Fig. 2). The bunching of the colonies belonging to the River Nemunas basin in the dendrogram reflects their close geographical distances. Zarasai and Ignalina form a separate clade, and Kretuonas is situated close to this clade but is farther from the other colonies.

The coefficient of correlation between the genetic and geographic distances of the Common Terns, estimated by the Mantel test, was significant and equal to 0.4628 for overall dataset. The correlation coefficients between the genetic and geographic distances were 0.7252 and 0.1899, respectively, when colonies of the River Nemunas basin and the northeast Lithuania colonies of the River Dauguva basin were pooled separately. These results show the importance of geographical differences in the formation of the population structure of the Common Tern, but this is not the only factor responsible for the determination of genetic distances among different tern colonies. Nevertheless, a segregation of the Common Tern population into two subpopulations in the breeding area, which is distributed in the basins of two biggest rivers, could be suggested by the results of genetic analysis.

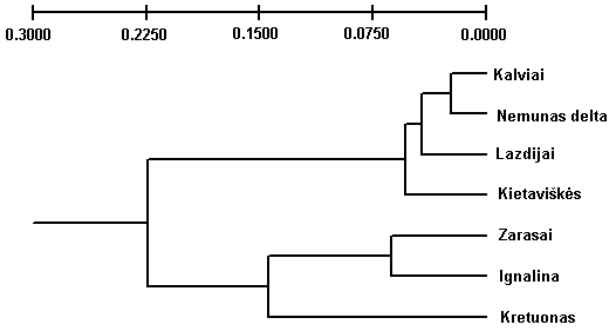

Fig. 2. Cluster analysis of Common Tern population breeding in different colonies in Lithuania, performed by the UPGMA method based on Nei's (1972) genetic distances

DISCUSSION

The levels of genetic variability expressed as the number of polymorphic loci, the mean number of alleles per loci and heterozygosity were determined in the Common Terns. The highest genetic diversity was assessed in Kretuonas colony. The reconstruction of favorable breeding conditions after the scrubs on the island of Lake Kretuonas had been cut might have led to resettlement of the breeding colony which possesses a high genetic diversity. Apparently, the restored colony was formed of the individuals of a different origin, therefore, the total genotype of the colony is characterized as more heterogeneous as compared to stable colonies that have been in existence for a long time. A relatively small amount of heterozygosity as compared to that of all other populations was observed in the Nemunas delta colony. This can be explained by the fact that this colony is young and unstable. Several factors determine the annual fluctuations of the colony size of the Nemunas delta: breeding nests are sometimes destroyed in sandy islands as a result of water rise in the Curonian Lagoon, short floods in spring, especially rainy weather and disturbance by holiday-makers. As a result, the number of breeding pairs ranged from 10–20 to 150.

In six from seven colonies, a deficit of heterozygosity as compared to the expected Hardy–Weinberg values was observed. The largest deviation from the Hardy–Weinberg equilibrium was found in the Nemunas delta. In our opinion, this is so because the highest pressure of natural selection falls on this colony due to especially difficult breeding conditions. The deviation from the Hardy–Weinberg equilibrium in the colonies of the Common Terns might be caused by a high inbreeding level, the genetic drift and a relatively small number of the sample studied.

The level of inbreeding was assessed in the Common Terns population by estimating the F_{ST} and R_{ST} coefficients. Recent theoretical analyses have not recommended to apply classical F-statistics to the microsatellite data but to use H_{ST}, R_{ST}, G_{ST} coefficients instead [14, 15]. The calculated R_{ST} value exceeds 0.15 and shows an intensive differentiation of the Common Tern population. These data are controversial in comparison to observations of Van Treuren et al. [16] when genetic analysis of the population structure of socially organized oystercatchers (*Haiatopus ostralegus*) by microsatellites revealed a nonsignificant genetic differentiation among colonies of oystercatchers breeding in different parts of the same island. Absence of evidence of genetic differentiation might be caused by relatively small distances (20–50 km) between the colonies, breeding biology of this marine bird species, the specificity of the loci or by other multiple reasons. In our case, a high amount of inbreeding is caused by phylopatry of the Common Terns (after migrating in autumn the terns return to their native breeding places). When colonies of the River Nemunas basin and those of northeast Lithuania belonging to the River Dauguva basin were pooled separately, the lower values of R_{ST} were obtained and showed a lower genetic differentiation within these groups. Consequently, it can be stated that geographic differences are the main factor determining the genetic differentiation of Common Tern populations.

In our opinion, individuals of the Zarasai, Kietaviškės, the Nemunas delta colonies are mostly involved in an inter-population genetic interchange. Seasonal fluctuations in the abundance of the individuals depending on various environmental factors were observed in these colonies. When the environmental conditions are unfavorable in the native colonies, some part of individuals from Zarasai and Kietavikės join geographically close colonies. A sudden increase in the colonies of Kietaviškės and Zarasai could be most probably determined only by immigration of the birds ready for breeding. Buddle [17] reported a case when 50% of fledglings of the Common Terns were pecked to death by the nesting adults when the distance between the nearest nests was less than 0.5–1.2 m. According to ornithological observations in Lithuania, the minimal distances between the nests were 0.34 m and 0.44 m in the thickest colonies of Kalviai and Lazdijai, respectively. Despite this high density in the colonies, no increased aggression of the adult birds against the fledglings was observed. Thus, a sudden increase in the number of breeding individuals in the Kietaviškės colony was most likely determined by the immigration from dense and numerous colonies of Lazdijai. In a similar way the unstable colony of Zarasai could be joined by the immigrants from Ignalina and Kretuonas. When the conditions are favorable, the population of the Nemunas delta most probably is increased by the immigrants from small and sporadic colonies located between Smalininkai and Kulautuva near the Nemunas River. The breeding conditions are similar in these colonies – unstable sandy islands of the river. Hence, five largest colonies of the Common Terns constituting nearly

half of the national population are genetically differentiated, therefore it is important to ensure a conservation of all five basic colonies thus preserving the intra-specific variability in Lithuania. Taking into consideration the results of this investigation, the strategy of protecting the species should be created, focusing attention on all largest differentiated colonies rather than preserving separate most successful ones.

The colonies of Kretuonas, Ignalina and Zarasai, attributed to the subpopulation of the Common Terns breeding in the Dauguva basin, form a single cluster in the dendrogram. Another big cluster is composed of the Nemunas basin subpopulation including the Kalviai, Kietaviškės, Nemunas delta and Lazdijai colonies. The Mantel test shows a fairly high correlation between genetic and geographic distances of the tern subpopulation belonging to the basin of the Nemunas River. Zarasai and Ignalina form one cluster in the dendrogram, though the colonies of Ignalina and Kretuonas are geographically closer. The results of the investigations allow to conclude that differences in the genetic structure of the Common Tern colonies are influenced by the geographical distribution of large rivers, the origin and life span of a colony. Stable and earlier established colonies are more original from the genetic point of view. Young and unstable colonies are influenced by immigrations which increase the genetic variability of the breeding population. In order to investigate the various mechanisms of natural selection and evaluate fluctuations in the size of the breeding Common Tern population it is necessary to analyze data of genetic studies, field observations and ringing. The stability of population structure is possibly based on the returning of mature birds to native breeding colonies; thus, maintenance of areas suitable for breeding is one of the keystones ensuring the stability of the Common Tern population and preserving it from a critical decrease.

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A. Sruoga, D. Butkauskas, P. Prakas, A. Paulauskas

UPINIŲ ŽUVĖDRŲ (*STERNA HIRUNDO*) PERINČIOS POPULIACIJOS GENETINĖS STRUKTŪROS ĮVERTINIMAS PANAUDOJANT MIKROSATELITINIUS ŽYMENIS

Santrauka

Upinių žuvėdrų (*Sterna hirundo*) populiacijos genetinės įvairovės tyrimams audinių pavyzdžiai surinkti iš Lietuvos teritorijoje (Nemuno ir Dauguvos upių baseinuose ties Kalviais, Kietaviškėmis, Nemuno delta, Lazdijais, Kretuono ežero saloje, ties Zarasais bei Ignalina) įsikūrusiose kolonijose perinčių paukščių. Panaudojus 11 pradmenų porų, sukurtų mikrosatelitinių sekų analizei taksonomiškai artimose rūšyse, nustatyti upinių žuvėdrų alelių dažniai 11 polimorfinių lokusų. Heterozigotiškumas atskirose kolonijose įvairavo 0,1809–0,4029 ribose. Ryškių genetinio variabilumo skirtumų tarp tirtų upinių žuvėdrų kolonijų nenustatyta. Tačiau Nemuno deltos kolonijoje nustatytas mažesnis alelių skaičius lokusui, žemesnės polimorfiškumo bei vidutinio heterozigotiškumo reikšmės, atspindinčios didesnę natūraliosios atrankos įtaką šiai kolonijai. Visos populiacijos mastu nustatytas aukštas vidupopuliacinės genetinės diferenciacijos lygis (R_{ST} = 0,1545). Nuokrypis nuo Hardžio-Vainbergo pusiausvyros, pasireiškęs heterozigotų deficitu, nustatytas šešiose iš septynių upinių žuvėdrų kolonijų, kurį sąlygoja imbrydingas bei genų dreifas. Tirtosios upinių žuvėdrų kolonijos UPGMA dendrogramoje formuoja atskiras sugrupuotų kolonijų atšakas sudarydamos dvi subpopuliacijas, priskiriamas Nemuno bei Dauguvos upių baseinams, ir tai atspindi populiacijos genetinės struktūros formavimąsi priklausomai nuo didžiųjų upių baseinų.