Assessment of Population Differentiation Using DNA Fingerprinting and Modified Wright's F_{ST}-Statistics

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Abstract—Using our results and literature data on multilocus DNA fingerprinting, we propose a method of obtaining unbiased estimates of the between-population genetic similarity index and a measure of population subdivision based on modified Wright's F_{ST}-statistics. On the basis of multiple comparison T^2 Hotelling's test and Holmes' procedure, the F_{ST}-statistics was applied to assess differentiation of four (Pacific and Atlantic) subpopulations of humpback whale *Megaptera novaeangliae*, six populations of Californian island gray fox *Urocyon littoralis*, and geographically isolated Ob' and Yakutia populations of Siberian white crane *Crus leucogeranus*. It was shown that the regional humpback whale subpopulations do not constitute a single panmictic unit ($P < 10^{-4}$). The subdivision index of the Pacific and Atlantic populations expressed in terms of F-statistics varied from 0.101 to 0.157. The differentiation estimates for the island fox populations, which ranged from 0.2109 to 0.4027, indicate that subdivision of these populations is a function of the distance between the islands, island size, and population size. In particular, the smallest and the greatest differences were found respectively between the populations of the geographically closest northern islands ($F_{ST} = 0.2157$, $F_{ST} = 0.2109$) and between those of the most distant northern and southern islands ($F_{ST} = 0.4027$, $F_{ST} = 0.3869$). Subdivision of the island populations with minimum areas and low population number was intermediate ($F_{ST} = 0.3789$). Mean values of heterozygosity, within-population genetic similarity index, and the number of coinciding fragments for two random individuals of Siberian white crane from the Ob' and Yakutia population were not statistically significantly different ($P \geq 0.852$, $P \geq 0.491$, $P \geq 0.325$). However, pairwise comparisons of mean F_{ST} values indicated that the differentiation estimates for samples from these populations fall within the limits of population subdivision ($P = 0.01$). The subdivision estimate (0.108–0.133) of various groups of Siberian white cranes is comparable to interregional subdivision of humpback whale. Based on the results of this study, we recommend the approach based on modified Wright's F_{ST}-statistics for studying genetic population structure aimed at detecting population subdivision.

INTRODUCTION

Modern molecular–genetic methods of analysis of polymorphic DNA regions and mini- and microsatellite loci serve as efficient tools for identifying individuals and estimating relatedness, heterozygosity, and genetic diversity in populations [1–25]. The review [3] presents a comprehensive analysis of investigation of genetic biodiversity in populations, in particular, estimation of within- and between-population variability of outbred, inbred, and parthenogenetic populations using multilocus DNA fingerprinting in relation to ecological, etological, demographic and evolutionary problems.

Theoretical studies dealing with the use of multilocus DNA fingerprinting are focused on the issues of obtaining unbiased estimates of relatedness, heterozygosity, genetic similarity and their comparative analysis [26–29]. At the same time, the potential possibilities of using DNA fingerprinting data for assessing population subdivision in terms of Wright's F_{ST}-statistics are poorly studied [27].

The main aim of the present work is to test the principal possibility to employ mini- and microsatellite markers and multilocus DNA fingerprinting technique for assessing population subdivision. To this end, we use our published results and literature data for populations of humpback whale *Megaptera novaeangliae* [4], island grey fox *Urocyon littoralis* [9], and Siberian white crane *Grus leucogeranus* [14, 15].

MATERIALS AND METHODS

Primary data. Efficiency of using the measure of population subdivision was tested using three data sets presented in [4, 9, 14, 15]. The first set included data on 40 DNA fingerprinting loci (probe M13) [14, 15] for four populations of humpback whale *Megaptera novaeangliae* (populations 1–4). The first sample represents an Atlantic population (5 individuals, population 1) and three samples of five individuals each from the northern Pacific ocean (populations 2–4). The second set included binary data for 80 loci (probe 33.6) for

six geographically isolated populations of island grey fox *Urocyon littoralis* inhabiting six Californian islands [9]. For convenience, the samples are designated as follows: population 1 (San Miguel), population 2 (Santa Rosa), population 3 (Santa Cruz), population 4 (San Clemente), population 5 (San Nicolas), population 6 (Santa Catalina) [9]. The third set consists of the binary data for 67 DNA fingerprinting loci (probe M13) of 21 individuals of Siberian white crane *Grus leucogeranus* from the breeding facilities of the Oka State Nature Reserve. The birds originate from geographically isolated populations of West (Ob' population, 3 individuals) and East (Yakutia population, 18 individuals) Siberia [14, 15]. Previous studies have shown that the sample of 18 birds from the Yakutia population is heterogeneous and divided into two homogeneous clusters at the threshold value of genetic similarity indices 0.74 [14, 15]. Because of this, for further analysis we used two groups of birds from the Yakutia population: group 1 (individuals 1–9) and group 2 (individuals 10–18). The group represented by three individuals from the Ob' population [14, 15] is denoted as group 3.

Estimation of within-population index of genetic similarity. A common measure of within-population genetic variation in outbred, inbred, and parthenogenetic populations based on DNA fingerprinting data is genetic similarity index estimated as [25]

$$S_{xy} = \frac{2n_{xy}}{n}, \quad n = n_x + n_y,$$

where S_{xy} is the index of genetic similarity of individuals x and y; n_x and n_y are the numbers of fragments detected by fingerprinting in individuals x and y, respectively; and n_{xy} is the numbers of fragments shared by individuals x and y.

Based on the second-order Taylor series, it can be shown that the unbiased estimate of the mean between-population similarity index $\hat{S}_{xy}$ is obtained as

$$\bar{S}_{xy} = \frac{2\bar{n}_{xy}}{\bar{n}} + \frac{2\bar{n}_{xy}\mathrm{Var}(\bar{n})}{\bar{n}^3} - \frac{2}{\bar{n}^2}\mathrm{Cov}(\bar{n}_{xy}, \bar{n}),$$

where $\bar{n}_{xy}$ is the mean number of coinciding fragments for two random individuals x and y and $\bar{n}$ is the mean total number of fragments in two individuals. The expression for $\bar{S}_{xy}$ shows that, in contrast to the known formula [27], the unbiased estimate is determined by the first- and second-order moments of $\bar{n}_{xy}$ and $\bar{n}$.

Mean values of $\bar{n}_{xy}$ and $\bar{n}$ are estimated from fingerprinting data based on a set of pairs lacking identical individuals (i.e., if the values n_{xy} and n_{wz} for pairs x–y and w–z are included in the computation, the n_{xw} value for pair x–w should not be included in the admissible set). For n individuals, the pair number is estimated as $[n/2]$, where $[]$ is an integer.

The sample variance estimate $\mathrm{Var}(\bar{n})$ is computed as

$$\mathrm{Var}(\bar{n}) = \frac{\sum_{i=1}^{N^*}(n_i - \bar{n})^2}{N^*(N^* - 1)},$$

where n_i is estimated on the basis of a set of pairs lacking identical individuals.

Covariance $\mathrm{Cov}(\bar{n}_{xy}, \bar{n})$ is estimated from the data on the number of DNA restriction fragments for each pair of individuals upon the estimation of $\bar{n}_{xy}$ and $\bar{n}$. The sample estimate of $\mathrm{Cov}(\bar{n}_{xy}, \bar{n})$ is calculated from the initial data as

$$\mathrm{Cov}(\bar{n}_{xy}, \bar{n}) = \mathrm{E}(n_{xy}n) - \mathrm{E}(n_{xy})\mathrm{E}(n).$$

It is readily shown that the unbiased variance estimate based on the second-order Taylor series

$$\mathrm{Var}(\bar{S}_{xy}) = \frac{4\bar{n}_{xy}\mathrm{Var}(\bar{n})}{\bar{n}^3} - \frac{4}{\bar{n}^2}\mathrm{Cov}(\bar{n}_{xy}, \bar{n}).$$

Quantitative estimation of population differentiation based on the modified Wright's F_{ST}-statistics. The generally accepted, widely known, and efficient measure of population subdivision is Wright's F-statistics F_{ST} [30]:

$$F_{ST} = \frac{\bar{H}_M}{\bar{H}_B + \bar{H}_M},$$

where $\bar{H}_M$ is the estimate of between-population heterozygosity and $\bar{H}_B$ is the mean within-population heterozygosity. Because of the estimation of values of $\mathrm{Cov}(\bar{H}_M, \bar{H}_B)$, $\mathrm{Var}(\bar{H}_B)$, and $\mathrm{Var}(\bar{H}_M)$ directly from the fingerprinting data without computer simulation presents difficulties [28], we used the modified Wright's F_{ST}-statistics based on D_M and D_B or S_M and S_B (D_M/S_M and D_B/S_B are mean between-population and within-population indices of genetic dissimilarity/similarity) [27]:

$$F_{ST} = \frac{\bar{D}_M}{\bar{D}_B + \bar{D}_M}, \quad F_{ST} = \frac{1 - \bar{S}_M}{2 - \bar{S}_B - \bar{S}_M}.$$

As in the present study we obtain the subdivision measure for different pairs of local populations, F_{ST} is employed in the form of $F_{ST_{kj}}$ (where k and j are the population numbers). The mathematical expectation of the between-population genetic similarity was estimated as [27]

$$\bar{S}_{M_{ij}} = 1 + \bar{S}'_{ij} - \frac{\bar{S}_i + \bar{S}_j}{2},$$

where $\bar{S}_i$, and $\bar{S}_j$ are the within-population means of similarity indices i and j respectively; $\bar{S}'_{ij}$ is the mean similarity index for a pair of individuals randomly taken from populations i and j. This expression can be used in the case when the condition $\bar{S}'_{ij} \leq 0.5(\bar{S}_i + \bar{S}_j)$ is fulfilled. The necessary fulfillment of this condition is related to the following: (1) between-population genetic similarity $\bar{S}_{M_{ij}}$ for $\forall i, j$ must vary in the [0, 1] range; (2) if $\bar{S}'_{ij} > 0.5(\bar{S}_i + \bar{S}_j)$, then either $\bar{S}'_{ij} > \bar{S}_i$ or $\bar{S}'_{ij} > \bar{S}_j$ must be true. In view of these restrictions, the between-population genetic similarity is estimated as

$$\bar{S}_{M_{ij}} = 1 + \bar{S}'_{ij} - \frac{\bar{S}_i + \bar{S}_j}{2}, \quad \text{if} \quad \bar{S}'_{ij} \leq 0.5(\bar{S}_i + \bar{S}_j),$$

$$\text{and} \quad \bar{S}_{ij} = 1, \quad \text{if} \quad \bar{S}'_{ij} > 0.5(\bar{S}_i + \bar{S}_j).$$

Sample variance of similarity indices is calculated as

$$\text{Var}(\bar{S}_{M_{ij}}) = \text{Var}(\bar{S}'_{ij}) + 1/4[\text{Var}(\bar{S}_i) + \text{Var}(\bar{S}_j)]$$
$$- \text{Cov}(\bar{S}'_{ij}, \bar{S}_i) - \text{Cov}(\bar{S}'_{ij}, \bar{S}_j).$$

Mean within-population genetic similarity indices $\bar{S}_i$, and $\bar{S}_j$ are estimated as shown above. Sample variance $\text{Var}(\bar{S}'_{ij})$ can be determined using analogous formulas under condition of selection of individuals x and y from populations i and j, respectively. The estimation of covariances $\text{Cov}(\bar{S}'_{ij}, \bar{S}_i)$ and $\text{Cov}(\bar{S}'_{ij}, \bar{S}_j)$ is related to obtaining these values for the same individuals based on the DNA fingerprinting data. For this, we used the following expression [27]:

$$\text{Cov}(\bar{S}'_{ij}, \bar{S}_i) = \frac{N^* \text{Cov}(S_{xi, yi}, S_{xi, zi})}{N_{ij} N_i},$$

where N_i is the number of similarity indices for the ith population, N_{ij} is the number of similarity indices between different pairs taken from populations i and j, respectively, and N^* is the number of different combinations of within and between-population comparisons that include common individuals from the ith population.

In general, it is assumed that if similarity indices $\bar{S}_i$, $\bar{S}_j$, and $\bar{S}'_{ij}$ are similarly biased, their bias in the $\bar{S}_{M_{ij}}$ linear combination is insignificant. In view of the above restrictions, the expression for $F_{ST_{ij}}$ in terms of between-population and within-population similarity indices is

$$F_{ST_{ij}} = \frac{\bar{S}_i + \bar{S}_j - 2\bar{S}'_{ij}}{2(1 - \bar{S}'_{ij})}.$$

It can be shown that the unbiased estimate of modified Wright's F_{ST}-statistics is determined as

$$\bar{F}_{ST_{ij}} = \frac{\bar{S}_i + \bar{S}_j - 2\bar{S}'_{ij}}{2(1 - \bar{S}'_{ij})} + \frac{(\bar{S}_i + \bar{S}_j - 2)}{2(1 - \bar{S}'_{ij})^3}\text{Var}(\bar{S}'_{ij})$$

$$+ \frac{\text{Cov}(\bar{S}_i, \hat{S}'_{ij})}{2(1 - \bar{S}'_{ij})^2} + \frac{\text{Cov}(\bar{S}_j, \hat{S}'_{ij})}{2(1 - \bar{S}'_{ij})^2}.$$

The unbiased estimate of sample variance $\text{Var}(\bar{F}_{ST_{ij}})$ is

$$\text{Var}(\bar{F}_{ST_{ij}}) = \frac{\text{Var}(\bar{S}_i) + \text{Var}(\bar{S}_j)}{4(1 - \bar{S}'_{ij})^2}$$

$$+ \frac{(\bar{S}_i - \bar{S}_j - 2)^2}{4(1 - \bar{S}'_{ij})^4}\text{Var}(\bar{S}_{ij})$$

$$+ \frac{(\bar{S}_i - \bar{S}_j - 2)}{2(1 - \bar{S}'_{ij})^3}(\text{Cov}(\bar{S}_i, \bar{S}'_{ij}) + \text{Cov}(\bar{S}_j, \bar{S}'_{ij})).$$

Since we wish to extend the obtained estimates to the total set of the samples, the estimates must account for genetic sampling. In this case, resampling of the fingerprint loci using the jackknife procedure provides a good approximation [33].

All computations and estimations of population subdivision using the modified Wright's F_{ST}-statistics based on the t and Hotelling's T^2 tests, and Holmes' procedure for the Bonferroni correction were conducted using special software programs [31]. The algorithms and comparison procedures are presented in [32].

RESULTS AND DISCUSSION

The results of analysis of F_{ST} values as a subdivision measure of populations of Atlantic (1) and Pacific (2–4) humpback whale using Hotelling's T^2 test are presented in Tables 1 and 2, respectively. A multiple comparison of the F_{ST} values for the Pacific populations showed the absence of statistically significant differences in the modified Wright's F-statistics values between any population pairs ($P = 0.97$, Table 1). A multiple comparison of the F_{ST} values for populations 2–3 and 3–4, 2–4 and 3–4, and 2–3 and 2–4 showed that their subdivision is the same regardless of the pair (Table 2, $P = 0.844$). Based on these estimates and Hotelling's T^2 and Holmes' tests, we can accept the null hypothesis on random mating in the three Pacific populations of humpback whale. However, similar results obtained using another procedure (nonparametric Mantel's multiple comparison) warrants caution in drawing an ultimate conclusion using canonical multiple tests [4].

Table 1. Estimation of mean values of modified Wright's F-statistics in populations of Atlantic (1) and Pacific (2–4) humpback whales by means of Hotelling's T^2 test ($\alpha = 0.05$)

Population no.			F	DF	P
Within-region subdivision (Pacific ocean)					
2–3	2–4	3–4			
0.003	0.008	0.023	0.0961	3,37	0.97
Between-region subdivision					
1–2	1–3	1–4			
0.101	0.157	0.144	13.31	3,37	$<10^{-4}$

Analysis of interregional subdivision parameters revealed the reverse trend. The regional populations obviously cannot be regarded as a single panmictic unit ($P < 10^{-4}$, Table 1). The estimates of subdivision for populations 1–2 ($F_{1-2} = 0.101$), 1–3 ($F_{1-3} = 0.157$), and 1–4 ($F_{1-4} = 0.144$) are statistically identical ($P > 0.379$). The same conclusion obtained by a different method was earlier presented in [4].

The F_{ST} estimates for all island fox sample pairs showed that they are subdivided into six populations in accordance with the number of isolated localities (Table 3). The subdivision index was lowest for the populations of the geographically closest islands ($F_{1-2} = 0.216$) and highest for population of the distant islands ($F_{1-4} = 0.387$; $F_{3-4} = 0.403$). A multiple comparison demonstrated that the differentiation of the populations of the three northern islands depends of geographic distance between them. For instance, the three northern island populations are ranged in the following order according to their subdivision: 1–3 ≫ 2–3 = 1–2 (where ≫ and = indicate statistical significance and nonsignificance, respectively; Table 4). For the populations of southern islands, the lowest subdivision value were recorded between populations 4–6 ($F_{4-6} = 0.2503$), and the highest, between populations 4–5 and 5–6 ($F_{4-5} = 0.3739$, $F_{5-6} = 0.3201$). Thus, the extent of subdivision of the island populations was shown to depend on the geographic distance between them and on the island size. For example, a multiple comparison (105 pairs compared using F-statistics) revealed statistically significant difference between three island pairs (Table 4). Significant differences in F_{ST} were detected between both the close (1–2, 3–4) and distant (2–3; 3–4; $P = 0.079$, $P = 0.104$; Table 4) populations including those of the island that are characterized by close location, minimal area, and small size (1–2; 1–5, $F_{1-2} = 0.2157$, $F_{1-5} = 0.3789$, $P = 0.101$; Table 5). These islands have the following areas (S, km^2) and size (N): 1-$S = 37$, $N = 310$; 2-$S = 217$, $N = 1850$; 3-$S = 249$, $N = 2120$; 4-$S = 145$, $N = 1230$; 5-$S = 58$, $N = 490$; 6-$S = 194$, $N = 1650$ [9]. The results obtained indicate that the modified Wright's F_{ST} adequately and effectively measures the level of differentiation in island fox populations depending on the

geographic distance between them, island size and population number.

Multiple analysis of heterozygosity, within-population genetic similarity index, and total number of frag-

Table 2. Multiple comparison of mean values of modified Wright's F-statistics for populations of Atlantic (1) and Pacific (2–4) humpback whales by means of Holmes' procedure for Bonferroni test ($\alpha = 0.10$)

Parameter	Mean 1	Mean 2	T^*	P_k
Within-region subdivision				
F_{2-3}–F_{3-4}	0.003	0.023	0.463	0.844
F_{2-4}–F_{3-4}	0.008	0.023	0.324	0.844
F_{2-3}–F_{2-4}	0.003	0.008	0.198	0.844
Between-region subdivision				
F_{1-2}–F_{1-4}	0.101	0.144	1.563	0.379
F_{1-2}–F_{1-3}	0.101	0.157	1.491	0.379
F_{1-3}–F_{1-4}	0.157	0.144	0.461	0.648

Note: T^*, t-statistics; P_k, P corrected by means of Holmes' procedure.

Table 3. Mean values of modified Wright's F_{ST}-statistics for six populations of island foxes ($\alpha = 0.10$)

Parameter	Mean $F_{ST} \pm SE$
F_{1-2}	0.2157 ± 0.0018
F_{1-3}	0.3510 ± 0.0014
F_{1-4}	0.3869 ± 0.0009
F_{1-5}	0.3789 ± 0.0011
F_{1-6}	0.3077 ± 0.0018
F_{2-3}	0.2109 ± 0.0024
F_{2-4}	0.3506 ± 0.0007
F_{2-5}	0.3307 ± 0.0010
F_{2-6}	0.2556 ± 0.0019
F_{3-4}	0.4027 ± 0.0009
F_{3-5}	0.3671 ± 0.0013
F_{3-6}	0.3126 ± 0.0025
F_{4-5}	0.3739 ± 0.0010
F_{4-6}	0.2503 ± 0.0027
F_{5-6}	0.3201 ± 0.0024

Table 4. Multiple comparison of mean values of modified Wright's F_{ST}-statistics for the island fox populations by means of Holmes' procedure for Bonferroni test ($\alpha = 0.10$)

Compared parameters	Mean 1	Mean 2	T^*	P_k
$F_{1-3}-F_{2-3}$ (A)	0.3510	0.2109	3.01	0.011
$F_{1-2}-F_{1-3}$ (A)	0.2157	0.3510	2.99	0.011
$F_{1-2}-F_{2-3}$ (A)	0.2157	0.2109	0.073	0.942
$F_{4-5}-F_{4-6}$ (B)	0.3739	0.2503	2.355	0.063
$F_{4-5}-F_{5-6}$ (B)	0.3739	0.3201	1.084	0.564
$F_{4-6}-F_{5-6}$ (B)	0.2503	0.3201	0.902	0.564
$F_{1-2}-F_{3-4}$ (C)	0.2157	0.4027	3.506	0.079
$F_{1-2}-F_{1-5}$ (C)	0.2157	0.3789	3.429	0.101
$F_{2-3}-F_{3-4}$ (C)	0.2109	0.4027	3.407	0.104

Note: A, multiple comparison of three populations (populations 1–3); B, multiple comparison of three populations (populations 4–6); C, discriminating pairs detected in comparison of six populations (populations 1–6). T^*, *t*-statistics.

Table 5. Multiple comparison of mean heterozygosities, mean genetic similarity indices, and mean fragment number for two random individuals from the Siberian white crane populations by means of Holmes' procedure for Bonferroni test ($\alpha = 0.10$)

Compared groups	Mean 1	Mean 2	T^*	P_k
Heterozygosity				
2–3	0.765	0.719	0.940	0.852
1–3	0.753	0.719	0.669	0.852
1–2	0.753	0.765	0.188	0.852
Genetic similarity index				
2–3	0.234	0.207	1.408	0.491
1–3	0.312	0.207	1.029	0.614
1–2	0.312	0.234	0.967	0.614
Mean fragment number for two individuals				
1–2	21.843	18.533	1.628	0.325
2–3	18.533	21.843	1.408	0.327
1–3	21.843	21.843	0.000	1.000

Note: T^*, *t*-statistics; P_k, P corrected by means of Holmes' procedure.

Table 6. Comparative analysis of means of modified Wright's F_{ST}-statistics for the populations of Siberian white crane based on Hotelling's T^2 test ($\alpha = 0.05$)

Group no.			F	DF	P
1–2	1–3	2–3			
0.116	0.133	0.108	3.868	3,67	0.01

Table 7. Multiple comparison of mean values of modified Wright's F_{ST}-statistics for the populations of Siberian white crane by means of Holmes' procedure for Bonferroni test ($\alpha = 0.10$)

Compared parameters	Mean 1	Mean 2	T^*	P_k
$F_{1-3}-F_{2-3}$	0.133	0.108	0.514	0.894
$F_{1-2}-F_{1-3}$	0.116	0.133	0.468	0.894
$F_{1-2}-F_{2-3}$	0.116	0.108	0.133	0.894

ments for two random individuals from the Ob' and Yakutia populations of Siberian white crane showed that the difference these parameters did not statistically significantly differ between the populations ($P \geq 0.852$, $P \geq 0.491$, $P \geq 0.325$; Table 5). Nevertheless, pairwise comparisons of mean F_{ST} values for the Siberian white crane populations by Hotelling's T^2 test indicate population subdivision ($P = 0.01$; Table 6). The absence of differences of F_{1-2}, F_{1-3}, and F_{2-3} ($P \geq 0.894$; Table 7) revealed by Holmes' procedure suggest that the Ob' and Yakutia populations exhibit heterogeneous population structure characteristic of subdivided populations. Apparently, the subdivision level in populations 1–2 and 1–3 correctly reflects the potential power of F_{ST}-statistics to reveal isolation of the western and eastern white crane populations, whereas the statistically significant difference between F_{ST} and zero seems to indicate that 18 birds of the Yakutia population represent two groups that differentiate by M13 loci as subdivided populations. The diagnostic restriction fragments detected by us earlier and present in the fingerprinting profiles in six out of nine birds of the first group additionally confirm the correct assessment of significant differentiation of individuals of the Yakutian origin [15]. The presented estimates are of interest for studying genetic structure of natural populations of white crane, in particular, the presence of subpopulations in the Yakutian part of the nesting area of the species.

The analysis of the results conducted in the present work demonstrates high efficiency of multilocus fingerprinting for studying population genetic structure in order to reveal their subdivision on the basis of modified Wright's F_{ST}-statistics.

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