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Waterfowl Population Structure: Phylogeographic Inference

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ABSTRACT

Population genetics and the phylogeographic structure of dabbling duck species were investigated using 5'-end sequencing of the mtDNA control region and ODC-6 of nuclear DNA. Overall, a weak phylogeographic structure and low genetic differentiation in mallards (*Anas platyrhynchos*) and European wigeons (*Anas penelope*) were discovered, which was likely due to the presence of large, long-term population sizes and significant intracontinental dispersal. Haplotypes of the mtDNA of spot-billed ducks (*Anas zonorhyncha*) and American wigeons (*Anas americana*) were found in Mallard and European wigeon samples, respectively. This presence of closely related species haplotypes in the gene pools of these species is consistent with the occurrence of historical and contemporary hybridization and incomplete sorting of haplotype lineages in mallards and wigeons.

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In recent years, the study of the population structure and migration of various species of animals has widely utilized molecular genetic methods of analysis. By sequencing the various parts of mitochondrial and nuclear DNA and comparing the sequences of demes, groups, populations and species, conclusions can be reached not only about the genetic diversity, differentiation of the study groups and gene flow between groups but also about their past and possible future. This is the purpose of phylogeography or phylogeographic analysis. This relatively new discipline on the geographic distribution of intraspecific gene flow was initiated by *Avice* (*Avice et al., 1987*), author of the book “Phylogeography” (2000). Phylogeographic approaches examine historical, non-equilibrium aspects of microevolution, and reveal the links between population demography and genealogy and associates formerly separated population genetics and phylogenetic biology. Analysis of the genealogies of mitochondrial DNA was originally the primary tool in phylogeography. However, phylogeographic studies now use data on the variability of individual genes and/or of noncoding regions of nuclear, ribosomal, plastid and other forms of DNA, as well as genome-wide variability, due to advances in next generation sequencing data.

Geographic variation of the subfamily Anatinae is much less evident than for many other orders or families of Aves (*McCracken et al., 2001*; *Kulikova et al., 2005*). This is partly explained by the greater opportunities for the resettlement and migration of ducks, which leads to intraspecific panmixia regardless of the extent of the habitat. At the same time, many species of ducks display natal philopatry to varying degrees. The degree of philopatry has a great impact on the population structure. In the absence of an exchange of individuals between populations, significant genetic differentiation can occur (*Chesser, 1991*). Consequently, philopatry can promote the isolation of populations, their divergence or extinction (*Gadgil, 1971*). For most birds, natal philopatry is inherent mainly in males (*Greenwood, 1980*; *Greenwood and Harvey, 1982*). However, for ducks, natal philopatry in females is considered to be more pronounced, while male ducks display a more typical natal dispersion (*Rohwer and Anderson, 1988*; *Avice et al., 1992*). The formation

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of pairs of ducks often occurs on wintering ground, when the birds from different populations meet. Couples typically return in the spring to the breeding areas (or birthplace) of the female (Weller, 1965; Anderson et al., 1992). At the same time, the spring flocks of migrant birds often consist of single-sex birds; in this case, pairing occurs either during migration or in breeding areas (Y.N. Zhuravlev, personal observation). As a result of these differences in the degree of natal philopatry of females and males, there may be differences in the phylogeography. These variations in geographical distribution are detectable by the analysis of mitochondrial DNA, which is inherited through the maternal line, and nuclear DNA, which is inherited from both parents.

An important factor that can shape the genetic structure of a species is interspecific hybridization. The order Anseriformes, in particular, is known for its propensity to hybridize (Panov, 1989). Thus, for Anseriformes, approximately 400 successful, interspecific crosses and 78 options that result in fertile offspring have been identified, including 11 intergeneric and 8 intertribal (e.g., Mallard *Anas platyrhynchos* × Common eider *Somateria mollissima*) hybridization patterns. In addition to many episodes of so-called “random hybridization,” interbreeding between sympatric species also regularly occurs. For example, the Canadian Goose, *Branta canadensis hutchinsii*, and the White Goose, *Chen caerulescens*, belong to different genera enter in hybridization. Particularly among the members of the family Anatinae, hybridization occurs frequently both in captivity and in nature (Johnsgard, 1960, 1967; Grant and Grant, 1992; Tubaro and Lijtmaer, 2002). There are more than 115 variants of crosses between species of this family, of which approximately one-third lead to viable and fertile hybrids (Johnsgard, 1960; Greig, 1980). The frequent occurrence of interspecific hybridization in ducks is presumably due to the following:

1. A reduction in the likelihood of nondisjunction or unequal chromosome segregation during meiosis due to the great similarity of karyotypes of different species (Shields, 1982).
2. Extensive sympatry of many species (Carboneras, 1992).
3. Promiscuity, that is, the brevity of the marriage ties.
4. Strong selective pressures towards the early reproduction of species at higher latitudes (Rohwer and Anderson, 1988).
5. Ethological similarity (Johnson, 2000).
6. The numerical dominance of males over females in populations of ducks (Baldassarre and Bolen, 1994).

Thus, there are many factors that determine the population genetic structure of duck species. In addition to mutation, natural selection and genetic drift, other important factors include migrations that support gene flow between populations and natal and interspecific hybridization philopatry.

The Mallard *A. platyrhynchos* is the most famous and numerous species of duck and has a Holarctic distribution. Every year, a significant portion of this species makes seasonal migrations, the distance of which is a thousand kilometres or more. Although there are a small number of settled populations, this is an exception to the general rule. As a result of long displacements and exchanges of individuals between remote territories, the Mallard is represented by a single subspecies across a substantial area of Eurasia and the northern part of North America. Regarding the population structure of this species, there are quite contradictory opinions. T.P. Shevareva analysed 3014 meetings of ringed birds and justified the presence of 9 populations of this species in the former USSR (Shevareva, 1968). G.M. Kotyukov and Y. Rusanov distinguished five populations in the same territory, explaining this discrepancy as being due to the relatively even distribution of the species at breeding, blurred boundaries between neighbouring populations and the formation of pairs of males to females with strangers in places of wintering that are more limited compared to the nesting areas (Bird migration..., 1997). There is a very orthodox view of the inappropriate use of the term “population” in relation to this species and the existence of a single panmictic population of *A. platyrhynchos* in Eurasia (Cheltsov-Bebutov and Koshkin, 1968). In addition, the mallard is very labile and responds quickly to changing conditions. Thus, in recent years, the “city group” has appeared in very different locations compared to birds living in the natural environment (Bird migrations..., 1997).

In the present study, a phylogeographic analysis of mallards was conducted based on the sequencing data of the mtDNA control region (Kulikova et al., 2012; Kulikova et al., 2005). One-hundred eighty-three birds from 5 populations were studied: Far Eastern ($n = 73$), North European ($n = 33$), Alaskan ($n = 31$), Aleutian ($n = 17$) and Indian ($n = 29$). High genetic diversity (average values $\pi = 0.012 \pm 0.0062$ and $H = 0.9847 \pm 0.005$) was found in each of the investigated populations. The results of demographic tests suggest that the mallard, during its historical development, underwent exponential growth in the recent past. This was evidenced by a “radial” type of haplotype distribution in the TCS network of haplotypes, with statistically significant values for tests of selective neutrality ($D_A = 2.4$; $p < 0.005$) and for the most plausible estimates of the growth of populations in the recent past ($g = 701.15$, with a 95% confidence interval 666.03–736.27). The genetic differentiation of populations of mallards was extremely low, with values ranging from $F_{ST} = 0.0015$ (Alaska/ Europe) to $F_{ST} = 0.1461$ (Aleutian Islands/Alaska). The genetic variability was concentrated mainly within populations (95.47%). In pairwise comparisons of the populations, the most differentiated were the Indian ($\Phi_{st} = 0.076$) and Aleutian populations ($\Phi_{st} = 0.109$), while the rest of the populations did not differ from one another ($\Phi_{st} = 0.0029$). Because the Aleutian bird population is mostly sedentary (Rower, unpublished data), they are partially genetically isolated from the Eurasian and North American populations. A similar situation exists for the Indian mallards, as most of the Indian population does not migrate to nesting areas outside of India, especially in the southern and eastern coast of the Indian subcontinent. Only a small number of mallards fly for wintering in north India from Northern Kazakhstan, the Baraba steppe and the Southern Urals (Bird migration..., 1997).

Thus, based on the mtDNA sequence data, the genetic differentiation of populations of mallards was low. Ornithological studies and ringing data may support the point of Cheltsov-Bebutov and Koshkin (1968), who argued that the concept of population “is hardly applicable in relation to moving in time and space groups of dabbling ducks.” Nevertheless, there are sedentary populations of mallards (e.g., in the southern and eastern coasts of India, the Himalayas, Iceland, England, Japan, and the Aleutian Islands), and our data show that the Aleutian and Indian Mallard populations are genetically isolated from the Eurasian and North American populations.

In a previously published study on Mallard and the closely related Spot-billed duck, *Anas zonorhyncha*, which are sympatric in the south of Far East Russia, mallards and spot-billed ducks turned out to be very similar genetically (Kulikova et al., 2004). The rate of genetic differentiation was low for mitochondrial and nuclear markers (mtDNA control region $F_{ST} = 0.19$; ODC-6 $F_{ST} = 0.0$), and phylogenetic reconstructions combined mtDNA haplotypes and ODC-6 alleles of mallard and spot-billed duck in common clusters regardless of the species. Thus, no species-specific alleles or haplotypes were found. However, two divergent groups or lines of mtDNA haplotypes and ODC-6 alleles were identified in the gene pools of both species. The identified groups of mtDNA haplotypes matched the A and B groups previously identified by Avise et al. (1990) and types 1 and 2 of Johnson and Sorenson (1998). The matching of the haplotypes found in coastal mallards with the previously known A and B haplogroups was based on the analysis of a pooled sample of North American species: Mallard, Mottled duck, American Black Duck and Mexican duck (McCracken et al., 2001). However, the haplotypes found in mallards and spot-billed ducks (marked as SB haplotypes) differed by 3–11 nucleotide substitutions from B-haplotypes in North American mallards. The MP tree united SB haplotypes in the monophyly cluster. Thus, the group of B haplotypes that appeared in Asia displayed divergence from B haplotypes found in North America. Haplotypes of the SB type have not been found in North America. The nucleotide divergence of A and B groups of mtDNA haplotypes of the pooled sample, including North American mallards, totalled $3.8 \pm 1.1\%$. If used as a calibrated molecular clock, the 5'-area of mtDNA of ducks would be equal to 8.8% nucleotide substitutions/million years (Sorenson and Fleischer, 1996), with the A and B groups of haplotypes having diverged approximately 430 thousand years ago (95% CI = 180–680 thousand years ago).

The presence of divergent groups of mtDNA haplotypes in the genomes of mallards and spot-billed ducks can be explained in light of two hypotheses: 1) incomplete sorting of haplotype lines or 2) interspecific hybridization. The chance of discrepancies existing between gene trees and species due to the incomplete sorting of lines and preservation of the ancestral haplotype polymorphism is great when $2N_e > T$, where N_e = population effective size and T = time between coalescence of a common ancestral haplotype variant and species divergence (Nei, 1987; Avise, 2000). The Mallard has a very large effective population size, and therefore, incomplete sorting of haplotype lines and alleles is a probable explanation for the observed paraphilias. During the time since the divergence of mallards and spot-billed ducks, diagnostic differences between identical groups of haplotypes should have accumulated in the genomes of the species. However, these types of mtDNA haplotypes were identical or differed by only one or two positions, which is consistent with the recent divergence of the mallards and spot-billed ducks. On the other hand, paraphilia could result from hybridization. In this case, within the groups of identical mtDNA haplotypes and nDNA alleles, a sufficient number of species-specific differences should have accumulated as well.

With regard to the distribution of the A and B groups of mtDNA haplotypes and the two types of ODC-6 alleles in gene pools of mallards and spot-billed ducks, the following five facts support the hypothesis of modern hybridization:

1. Hybridization between mallards and spot-billed ducks in the wild is often mentioned in the literature (Gluschenko and Shibnev, 1993; Shibnev and Gluschenko, 2001; Brazil, 1991; Kanouchi et al., 1998; Melvill, 1999; Zhuravlev et al., 2002). The experiments on the crossing of mallards and spot-billed ducks in captivity proved that hybrids are viable and fertile (Gillham and Gillham, 1996). Cases of a similar hybridization of ordinary mallards with other species closely related to it are widely known (Johnsgard, 1967; Braithwaite and Miller, 1975; Rhymer et al., 1994; Rhymer, 2001).
2. Two divergent types of alleles were found not only for the sixth intron of ODC-6 but also for the seventh intron of beta-fibrinogen (BF-7) as well as a number of other nuclear loci (MD Sorenson, RJ Harrigan, unpublished data). The consistency of data on different nuclear loci reflects a general history of allopatry and divergence rather than stochastic processes, such as the preservation of ancestral polymorphisms and incomplete sorting of haplotype and allele lines.
3. Data on sequencing the mtDNA control region of 39 mallards living in the zone of allopatry towards spot-billed ducks, i.e. in Europe and Western Russia, outside of the Russian Far East, shows that mallards in these regions have only one type A mtDNA (Kulikova et al., 2005).
4. Haplotypes of group B found in mallards from Primory were typical for spot-billed ducks of the SB type. This finding is more consistent with the hypothesis of allopatric speciation and subsequent hybridization than with the hypothesis of the conservation of ancestral polymorphisms and incomplete sorting of haplotype and allele lines because the latter implies a random distribution of alleles and haplotype types in different parts of the range of a species.
5. Mallards and spot-billed ducks have increased heterozygosity at ODC-6 locus. Notably, spot-billed duck heterozygosity was significantly higher than expected under Hardy–Weinberg equilibrium. The excess of heterozygotes is a common and expected result of hybridization between populations or species. On the contrary, under the conditions of maintaining an ancestral polymorphism, random mating, and incomplete lineage sorting of haplotypes and alleles, Hardy–Weinberg equilibrium is supposed to be reached in the next generation, regardless of the frequency of alleles in the first generation.

The ratio of A to B groups of mtDNA haplotypes in the mallards and spot-billed ducks is unequal, at 19:1 and 1.6:1, respectively. Assuming that haplotype group A is typical for mallards and group B is typical for spot-billed ducks, the unequal ratio of haplotypes could be explained by asymmetric hybridization, resulting in the spot-billed duck receiving significantly greater mtDNA of mallards than vice versa. mtDNA represents maternal inheritance; therefore, spot-billed duck males crossed with females of mallards ($N_e m = 12.89$; 95% CI = 7.43–17.98) much more than mallard males crossed with spot-billed duck females. Unfortunately, there was little opportunity to estimate the gene flow, which would be expected to accompany the females of spot-billed ducks mating with mallard males due to limitations in the use of the maximum likelihood estimation algorithm (Beerli and Felsenstein, 2001). However, the low frequency (5%) of group B haplotypes in populations of the Mallard with estimates of the number of migrants

per generation $4N_e m$ for locus ODC-6 obtained using the two-island model of population subdivision confirmed the asymmetry of gene flow in mtDNA.

The ratio of type 1 to type 2 ODC-6 alleles in Mallard and Spot-billed Duck was approximately equal, at 2:1. If ODC-6 allele types 1 and 2 were initially typical for the mallards and spot-billed ducks, respectively (as it is assumed), the 2:1 ratio may reflect differences in the effective population size of these species and the asymmetry of gene flow. The observed heterozygosity of spot-billed ducks was significantly higher than expected according to Hardy–Weinberg equilibrium, which might be stipulated by the introgression of the genes of Mallard into the gene pool of Spot-billed duck.

Asymmetric hybridization between mallards and spot-billed ducks can be explained by differences in the distribution of males and females. The recent resettlement of spot-billed ducks in a northwestern direction has increased the intersection area of the nesting habitats of mallards and spot-billed ducks. At the same time, phylopatry is typical for female ducks (Rohwer and Anderson, 1988). Males follow the females to breeding spots, where females often return year after year (Coulson, 1984; Kehoe et al., 1989). Because male spot-billed ducks demonstrate a greater predisposition for expansion than females, it is the males that form the northern edge of the species resettlement. As a result of this expansion of the spot-billed duck's range in a northern and northeastern direction, the breeding types in the intersection zone of the two species' ranges are more likely to be male spot-billed ducks \times female mallards than male mallards \times female spot-billed ducks.

Thus, two divergent groups of mtDNA haplotypes and nDNA alleles in mallards and spot-billed ducks in Eurasia have been identified. These findings can be interpreted as evidence of hybridization between the Mallard and Spot-billed Duck in the south of the Russian Far East. Nevertheless, the alternative hypothesis of the preservation of ancestral polymorphisms and incomplete lineage sorting of haplotypes and alleles needs additional testing. However, the excess of heterozygotes, the apparent uneven ratio of A and B groups of mtDNA haplotypes, the effective population size, and the migration rate of mtDNA and ODC-6 are consistent with the hypothesis of asymmetric hybridization. This asymmetry, in turn, implies that the predominant type of breeding is spot-billed duck males with mallard females, not vice versa.

The wigeon, *Anas penelope*, is one of the most widespread and numerous species of game birds of the Anatidae family. Its breeding range covers the northern part of the Palearctic from the British Isles and Iceland in the west to the Anadyr river basin and Kamchatka in the east and from the northern limits of the continent to the 50th parallel in the south (Isakov, 1952). Their approximate number is variously estimated to be between 4 and 5 million individuals. There are five geographical populations of this species: Icelandic, European, West Siberian, East Siberian and Far Eastern (Bird migrations..., 1997), but there are no clear boundaries between populations. Thus, according to the ringing results, there is an exchange of genetic material between different populations (between 5 and 30%). Exchanges of individuals occur more often in the overlapping, peripheral areas of the population ranges as well as in the common wintering areas (Bird migrations..., 1997).

The analysis of the genetic structure of the Far Eastern wigeon population was based on the variability of the nucleotide sequences of part of the mtDNA control region (Kulikova and Zhuravlev, 2010). In this study, the Far Eastern population was represented by two samples: Primorye ($n = 43$) and Anadyr ($n = 8$). Indicators of genetic diversity of the Far Eastern population ($H = 0.6635$; $\pi = 0.0032$) of wigeon were comparable to those of other duck species. Anadyr and Primorye samples turned out to be poorly differentiated ($F_{st} = 0.096$), and variability was concentrated mainly within populations (82.75%). Those findings could be explained by mixing of birds from different parts of the range of the Far Eastern populations wintering in Japan, Korea, Vietnam and southern China (Bird migrations..., 1997) as well as the natal dispersal of male ducks (Avisé et al., 1992). The phylogeographic structure of wigeons within the Russian Far East territory was not pronounced, that is, the clustering of sampling in the phylogenetic reconstructions in accordance with the geographic area was missing, and four of the eleven identified haplotypes (including the central haplotype from which the TCS network radiated) were common for Primorye and Anadyr populations. Based on the literature, the Anadyr and Primorye populations are known to belong to different corridors of spring and autumn migrations and may have different wintering areas (Birds migrations..., 1997). Ringing data has not been able to clarify whether the population of the Far Eastern wigeon is a single, geographical population or whether it consists of several (probably three) populations with different wintering sites, migration routes and breeding areas. Our data indicates the absence of a strong, genetic subdivision in the Far Eastern population.

A haplotype of the American wigeon, *Anas americana*, was found in the Anadyr wigeons. The encountered mtDNA haplotype of *A. americana* supports the hypothesis of hybridization between these species in the Russian Far East. Phenotypic hybrids *americana* \times *penelope* in the region have been repeatedly observed, mainly in the area of Anadyr. Some male wigeons of the Anadyr population have a noticeable, greyish patina in the head coloration that is typical for hybrids of *A. penelope* \times *A. americana* (Krechmar and Kondratyev, 2006). Only once, during the spring migration of ducks, has a hybrid of Eurasian and American wigeons been observed in Southern Primorye (Nechaev and Gorchakov, 1995). Frequent meetings of hybrid individuals within the Anadyr population are explained by the fact that a small number of American wigeons not only flies in the Anadyr River basin but also nests there (Krechmar and Kondratyev, 2006). Breeding American wigeons have not been identified in any other area of the Russian Far East. Only occasional flights of *A. americana* in Eastern Siberia and the Far East have been noted (Anon, 1997). The presumed hybrid had mtDNA haplotypes of the American wigeon and was captured in the vicinity of Anadyr. However, its hybrid nature could not be identified, as this individual was before its first (juvenile) moulting. During the juvenile moulting, primary (juvenile) feathers are replaced by secondary (definitive) feathers, which give the bird a distinct, species-specific plumage. Genetic hybrids have been previously captured in North America (e.g., California and Idaho). Two individuals of the Eurasian wigeon phenotype had mtDNA haplotypes that were typical of American wigeons (Peters et al., 2005). Thus, hybridization between Eurasian and American wigeons in the Anadyr River basin is probable and should perhaps even be expected given the close relationship between the two species (Peters et al., 2005), their presence in the same area (Krechmar and Kondratyev, 2006) and the widespread success of interspecific hybridization in the family Anatinae (Kulikova and Zhuravlev, 2009; Johnsgard, 1960; Greig, 1980).

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