

"WATERFOWL POPULATION STRUCTURE: PHYLOGEOGRAPHIC INFERENCE" DR. COBETUA K.F.

ABSTRACT

Population genetics and also the phylogeographic structure of 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 because of the presence of huge, 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 these species' gene pools is in step with the occurrence of historical and contemporary hybridization and incomplete sorting of haplotype lineages in mallards and wigeons.

KEYWORDS

Birds Water ,fow population, Phylogenetics mtDNA,

In recent years, the study of the population structure and migration of assorted species of animals has widely utilized molecular genetic methods of study. By sequencing the varied parts of mitochondrial and nuclear DNA and comparing the sequences of demes, groups, populations, and species, conclusions will 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 can be the aim of phylogeography or phylogeographic analysis. This relatively new discipline on the geographic distribution of intraspecific gene flow was initiated by Avise (Avise 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 bi-



ology. Analysis of the genealogies of mitochondrial DNA was originally the first 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 kinds of DNA, in addition as genome-wide variability, because of advances in next-generation sequencing data.

Geographic variation of the subfamily Anatinae is way less evident than for several other orders or families of Aves (McCracken et al., 2001, Kulikova et al., 2005). this is often partly explained by the greater opportunities for the resettlement and migration of ducks, which results in intraspecific panmixia irrespective of the extent of the habitat. At the identical time, many species of ducks display natal philopatry to varying degrees. The degree of philopatry incorporates a great impact on the population structure. within the absence of an exchange of people between populations, significant genetic differentiation can occur (Chesser, 1991). Consequently, philopatry can promote the isolation of populations, their divergence, or extinction (Gadgil, 1971). for many birds, natal philopatry is inherent mainly in males (Greenwood, 1980, Greenwood and Harvey, 1982). However, for ducks, natal philopatry in females is taken into account to be more pronounced, while male ducks display a more typical natal dispersion (Rohwer and Anderson, 1988, Avise et al., 1992). The formation of pairs of ducks often occurs on wintering ground, when the birds from different populations meet. Couples typically return within the spring to the female's breeding areas (or birthplace) (Weller, 1965, Anderson et al., 1992). At the identical time, the spring flocks of migrant birds often incorporate singlesex birds; during this case, pairing occurs either during the migration or in breeding areas (Y.N. Zhuravlev, personal observation). As results of these differences within the degree of natal philopatry of females and males, there are also differences in 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 which will shape the genetic structure of a species is interspecific



hybridization. The order of Anseriformes, particularly, is understood for his or her propensity to hybridize (Panov, 1989). Thus, for Anseriformes, approximately 400 successful, interspecific crosses and 78 options that lead to fertile offspring are identified, including 11 intergeneric and eight intertribal (e.g., Mallard Anas platyrhynchos × Common eider Somateria mollissima) hybridization patterns. additionally to several episodes of so-called "random hybridization," interbreeding between sympatric species also regularly occurs. for instance, the Branta canadensis, honker hutchinsii, and also the White Goose, blue goose, 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, Johnsgard, 1967, Grant and Grant, 1992, Tubaro and Lijtmaer, 2002). There are quite 115 variants of crosses between species of this family, of which approximately one-third cause viable and fertile hybrids (Johnsgard, 1960, Greig, 1980). The frequent occurrence of interspecific hybridization in ducks is presumably because of the following:

1.A reduction within the likelihood of nondisjunction or unequal chromosome segregation during meiosis thanks to the nice similarity of karyotypes of various species (Shields, 1982).

2. Extensive sympatry of the many species (Carboneras, 1992).

3. Promiscuity, that is, the brevity of the wedding ties.

4.Strong selective pressures towards the first 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).

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Thus, many factors determine the population genetic structure of duck species. Additionally to mutation, natural process, 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 that the most famous and diverse species of duck and contains a Holarctic distribution. Every year, a major portion of this species makes seasonal migrations, the space of which may be a thousand kilometres or more. Although there are alittle number of settled populations, this can be an exception to the overall rule. As a results of long displacements and exchanges of people between remote territories, the Mallard is represented by one subspecies across a considerable area of Eurasia and therefore the northern a 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 within the former USSR (Shevareva, 1968). G.M. Kotyukov and Y. Rusanov distinguished five populations within the same territory, explaining this discrepancy as being because of the relatively even distribution of the species at breeding, blurred boundaries between neighbouring populations and therefore 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's a really orthodox view of the inappropriate use of the term "population" about this species and also the existence of one panmictic population of A. platyrhynchos in Eurasia (Cheltsov-Bebutov and Koshkin, 1968). Besides, the mallard is incredibly labile and responds quickly to changing conditions. Thus, in recent years, the "city group" has appeared in very different locations compared to birds living within the natural environment (Bird migrations..., 1997).

In the present study, phylogeographic analysis of mallards was conducted supported 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 π = 0.012 ± 0.0062 and H = 0.9847 ± 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 within the recent past. This was evidenced by a "radial" kind of haplotype distribution within the TCS network of haplotypes, with statistically significant values for tests of selective neutrality (DA = 2.4; p < 0.005) and for the foremost plausible estimates of the expansion of populations within 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 FST = 0.0015(Alaska/ Europe) to FST = 0.1461 (Aleutian Islands/Alaska). The genetic variability was concentrated mainly within populations (95.47%). In pairwise comparisons of the populations, the foremost differentiated was the Indian (Φ st = 0.076) and Aleutian populations (Φ st = 0.109), while the remainder of the populations failed to differ from each other (Φ st = 0.0029). Because the Aleutian bird population is generally sedentary (Rower, unpublished data), they're partially genetically isolated from the Eurasian and North American populations, an identical situation exists for the Indian mallards, as most of the Indian population doesn't migrate to nesting areas outside of India, especially on the southern and eastern coast of the Indian subcontinent. Only alittle number of mallards fly for wintering in north India from Northern Kazakhstan, the Baraba steppe and therefore the Southern Urals (Bird migration..., 1997).

Thus, supported the mtDNA sequence data, the genetic differentiation of populations of mallards was low. Ornithological studies and ringing data may support the purpose of Cheltsov-Bebutov and Koshkin (1968), who argued that the concept of the population "is hardly applicable about occupation time and space groups of dabbling ducks." Nevertheless, there are sedentary populations of mallards (e.g., within the southern and eastern coasts of India, the Himalayas, Iceland, England, Japan, and also 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 therefore the closely related Spot-billed duck, Anas zonorhyncha, which are sympatric within the south of Far East Russia, mallards and spot-billed ducks clad to be very similar genetically (Kulikova et al., 2004). the speed of genetic differentiation was low for mitochondrial and nuclear markers (mtDNA control region FST = 0.19; ODC-6 FST = 0.0), and phylogenetic reconstructions combined mtDNA haplotypes and ODC-6 alleles of mallard and spot-billed duck in common clusters irrespective 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 within 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 kinds 1 and a pair of of Johnson and Sorenson (1998). The matching of the haplotypes found in coastal mallards with the previously known A and B haplogroups was supported the analysis of a pooled sample of North American species: Mallard, Mottled duck, American Anas rubripes 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 within 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 haven't 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 ± 1.1%. If used as a calibrated molecular clock, the 5'-area of mtDNA of ducks would be adequate 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 = 180-680thousand years ago).

The presence of divergent groups of mtDNA haplotypes within the genomes of mallards and spot-billed ducks is explained in light of two hypotheses: 1) incomplete sorting of haplotype lines or 2) interspecific hybridization. the possibility of discrepancies existing



between gene trees and species because of the unfinished sorting of lines and preservation of the ancestral haplotype polymorphism is great when 2Ne > T, where Ne = population effective size and T = time between coalescence of a standard ancestral haplotype variant and species divergence (Nei, 1987, Avise, 2000). The Mallard includes a very large effective population size, and so, incomplete sorting of haplo-type lines and alleles could be 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 within the genomes of the species. However, these sorts of mtDNA haplotypes were identical or differed by only 1 or two positions, which is according to the recent divergence of the mallards and spot-billed ducks. On the opposite hand, paraphilia could result from hybridization. during this case, within the groups of identical mtDNA haplotypes and DNA alleles, a sufficient number of species-specific differences should have accumulated in addition.

About the distribution of the A and B groups of mtDNA haplotypes and also the two varieties of ODC-6 alleles in gene pools of mallards and spot-billed ducks, the subsequent five facts support the hypothesis of contemporary hybridization:

1.Hybridization between mallards and spot-billed ducks within the wild is commonly mentioned within 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 an analogous hybridization of ordinary mallards with other species closely associated with it are widely known (Johnsgard, 1967, Braithwaite and Miller, 1975, Rhymer et al., 1994, Rhymer, 2001).

2.Two divergent styles of alleles were found not just for the sixth intron of ODC-6 but also for the seventh intron of beta fibrinogen (BF-7) additionally as several other nuclear



loci (MD Sorenson, RJ Harrigan, unpublished data). The consistency of information on different nuclear loci reflects a general history of allopatry and divergence instead of stochastic processes, like 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 within 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 1 A mtDNA (Kulikova et al., 2005).

4.Haplotypes of group B found in mallards from Primary were typical for spot-billed ducks of the SB type. This finding is more in step 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 numerous parts of the range of a species.

5.Mallards and spot-billed ducks have increased heterozygosity at the ODC-6 locus. Notably, spot-billed duck heterozygosity was significantly more than expected under Hardy–Weinberg equilibrium. the surplus of heterozygotes may be a common and expected results 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 meant to be reached within the next generation, irrespective of the frequency of alleles within the first generation.

The ratio of A to B groups of mtDNA haplotypes within 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 type B is typical for spot-billed ducks, the unequal ratio of haplo-types may well be explained by asymmetric hybridization, leading to the spot-billed duck



receiving significantly greater mtDNA of mallards than contrariwise. mtDNA represents maternal inheritance; therefore, spot-billed duck males crossed with females of mallards (Nem = 12.89; 95% CI = 7.43–17.98) way more than mallard males crossed with spot-billed duck females. Unfortunately, there was little opportunity to estimate the gene flow, which might be expected to accompany the females of spot-billed ducks mating with mallard males because of limitations within the use of the most likelihood estimation algorithm (Beerli and Felsenstein, 2001). However, the low frequency (5%) of blood type haplotypes in populations of the Mallard with estimates of the quantity of migrants per generation 4Nem 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 a couple of were initially typical for the mallards and spot-billed ducks, respectively (as it's assumed), the 2:1 ratio may reflect differences within the effective population size of those species and therefore the asymmetry of gene flow. The observed heterozygosity of spot-billed ducks was significantly on top of expected per Hardy–Weinberg equilibrium, which could 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 are often explained by differences within the distribution of males and females. The recent resettlement of spot-billed ducks during a northwestern direction has increased the intersection area of the nesting habitats of mallards and spot-billed ducks. At the identical time, philopatry 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,

Thus, two divergent groups of mtDNA haplotypes and nDNA alleles in mallards and spot-billed ducks in Eurasia are identified. These findings are often interpreted as evidence of hybridization between the Mallard and Spot-billed Duck within the south of the



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Russian Far East. Nevertheless, the choice hypothesis of the preservation of ancestral polymorphisms and incomplete lineage sorting of haplotypes and alleles needs additional testing. However, the surplus of heterozygotes, the apparent uneven ratio of A and B groups of mtDNA haplotypes, the effective population size, and also the migration rate of mtDNA and ODC-6 are per the hypothesis of asymmetric hybridization. This asymmetry, in turn, implies that the predominant kind of breeding is spot-billed duck males with mallard females, not contrariwise.

The wigeon, wigeon, is one amongst the foremost widespread and various species of geese of the Anatidae family. Its breeding range covers the northern a part of the Palearctic from land Isles and Iceland within the west to the Anadyr geographic region and Kamchatka within the east and from the northern limits of the continent to the 50th parallel within 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 much Eastern (Bird migrations..., 1997), but there are not any clear boundaries between populations. Thus, in step with the ringing results, there's an exchange of genetic material between different populations (between 5 and 30%). Exchanges of people occur more often within the overlapping, peripheral areas of the population ranges likewise as within the common wintering areas (Bird migrations..., 1997).

The analysis of the genetic structure of the Far Eastern wigeon population was supported the variability of the nucleotide sequences of a part of the mtDNA control region (Kulikova and Zhuravlev, 2010). during 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; π = 0.0032) of wigeon were equivalent to those of other duck species. Anadyr and Primorye samples clad to be poorly differentiated (Fst = 0.096), and variability was concentrated mainly within populations (82.75%). Those findings may well be explained by the blending of birds from different parts of the range of the Far Eastern populations wintering in Japan, Ko-



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rea, Vietnam, and southern China (Bird migrations..., 1997) in addition because the natal dispersal of male ducks (Avise et al., 1992). The phylogeographic structure of wigeons within the Russian region territory wasn't pronounced, that is, the clustering of sampling within the phylogenetic reconstructions following the geographical area was missing, and 4 of the eleven identified haplotypes (including the central haplotype from which the TCS network radiated) were common for Primorye and Anadyr populations. supported the literature, the Anadyr and Primorye populations are known to belong to different corridors of spring and autumn migrations and should have different wintering areas (Birds migrations..., 1997). Ringing data has not been able to clarify whether the population of the Far Eastern wigeon may be 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 powerful, genetic subdivision within the Far Eastern population.

A haplotype of the American wigeon, wigeon, was found within the Anadyr wigeons. The encountered mtDNA haplotype of A. Americana supports the hypothesis of hybridization between these species within the Russian region. Phenotypic hybrids Americana × Penelope within the region are repeatedly observed, mainly within the area of Anadyr. Some male wigeons of the Anadyr population have a visible, greyish patina within the head coloration that's typical for hybrids of A. Penelope x A. Americana (Krechmar and Kondratyev, 2006). Only once, during the spring migration of ducks, includes 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 very fact that atiny low number of yankee wigeons not only flies within the Anadyr basin but also nests there (Krechmar and Kondratyev, 2006). Breeding American wigeons haven't been identified in the other area of the Russian region. Only occasional flights of A. Americana in Eastern Siberia and also the Far East are noted (Anon, 1997). The presumed hybrid had mtDNA haplotypes of the American wigeon and was captured within the vicinity of Anadyr. However, its hybrid nature couldn't be identified, as this individual was before its first (juvenile) molting.



During juvenile molting, primary (juvenile) feathers are replaced by secondary (definitive) feathers, which give the bird a definite, species-specific plumage. Genetic hybrids are previously captured in North America (e.g., California and Idaho). Two individuals of the Eurasian wigeon phenotype had mtDNA haplotypes that were typical of yankee wigeons (Peters et al., 2005). Thus, hybridization between Eurasian and American wigeons within the Anadyr geographical region is probable and may maybe even be expected given the close relationship between the 2 species (Peters et al., 2005), their presence within the same area (Krechmar and Kondratyev, 2006) and also the widespread success of interspecific hybridization within the family Anatinae (Kulikova and Zhuravlev, 2009, Johnsgard, 1960, Greig, 1980).

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