

Population structure among breeding and wintering Long-tailed Ducks *Clangula hyemalis* in the Western Palearctic

Populationstruktur hos häckande och övervintrande alfåglar Clangula hyemalis i Västpalearktis

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Abstract

We used gel electrophoresis of common proteins and alloenzymes to study genetic variability among Long-tailed Ducks breeding in the northeast European tundra and wintering in the Baltic Sea. The observed genetic variability in the studied breeding population was lower than in birds sampled on winter ground in the Baltic. We found a similar genetic structure among the breeding birds and certain samples from wintering grounds in the Baltic Sea. The wintering birds showed evidence of genetic structure between years, possibly resulting from winter movements of different subpopulations of Long-tailed Ducks in the Baltic Sea. These findings are consistent with results of field surveys of Long-tailed Ducks wintering in the Baltic Sea.

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Introduction

The Long-tailed Duck *Clangula hyemalis* has a Holarctic distribution with a wide breeding range at high latitudes in northern Eurasia and North America. The main breeding areas cover arctic regions of Russia, Canada and USA. Breeding populations are also found in Greenland, Iceland, Norway, Sweden and Finland (Cramp & Simmons 1977). The Long-tailed Duck breeds in various habitats characteristic of coastal arctic tundra, wooded tundra and arctic-alpine zone. The boundary separating two breeding populations from western and eastern arctic is probably extending through Taymyr peninsula (Isakov 1970). Population delineation is based on the geographic isolation of Atlantic and Pacific flyways. The total Western Palearctic population of the Long-tailed Duck is estimated at about 5 million individuals (Scott & Rose 1996). The great majority of Long-tailed Ducks breeding in European Russia, western Siberia and Fenno-Scandinavia winter in the Baltic Sea. The Baltic Sea annually holds more than 4 million wintering Long-tailed Ducks (Dur-

inck *et al.* 1994). In certain areas of the Baltic Sea these ducks occur in very large numbers, forming huge concentrations of up to 1 million birds (Nilsson 1980, Vaitkus 1999, Skov *et al.* 2000).

The migratory movements of the Western Palearctic population of the Long-tailed Duck are poorly understood from small-scale and fragmentary ringing data (Cramp & Simmons 1977). Little is known about the population-genetic structure of breeding and wintering Long-tailed Ducks and their site fidelity to certain wintering areas. Available data on genetic variability of blood serum antigens and proteins of the Long-tailed Duck (Slavenaite *et al.* 1998, Sruoga *et al.* 1999, Slavenaite & Sruoga 2003) are not sufficient for evaluation of the genetic structure and variability of different populations of Long-tailed Ducks. The breeding and wintering populations of the Long-tailed Duck are threatened by increasing gas, oil and other developments. For conservation and wise management of the species it is important to define the genetic variability and possible gene flow among different breeding and wintering populations.



Figure 1. Sites where breeding (1) and wintering (2) Long-tailed Ducks were sampled for genetic analysis. *Lokaler där häckande (1) och övervintrande (2) alfågglar insamlades för genetiska analyser.*

Genetic variability is an essential parameter for adaptation to changing environmental conditions (Soule 1986). It can be effectively used for evaluation of genetic structure of populations (Altukhov 2003). In this study we applied polyacrylamid gel electrophoresis of nonspecific proteins and alloenzymes to investigate genetic variability among breeding Long-tailed Ducks sampled in northeast European tundra and wintering birds sampled along the eastern Baltic coast.

Material and methods

Samples of breeding Long-tailed Ducks (10 males and 7 females) were collected in July 1985 in the Kara River estuary area (northeast European Russia, 70°40'N, 65°02'E). The study site, located in the coastal tundra between the Kara, Tabju and Sopchaju Rivers (Figure 1), is one of the key breeding areas of the Long-tailed Duck in the northeast European tundra of Russia. Breeding densities of up to 10 pairs/km² were recorded in this territory in 1982–1987 (Mineev 1994). This area is

distinguished by a mosaic of habitats formed by hummocks with numerous pools and small lakes in moist depressions.

Samples of 73 wintering Long-tailed Ducks were collected dead in fishing nets in January–March 1994, 1999–2001 (Table 1) in the Baltic coastal waters off the Curonian Spit, Lithuania (55°30'N, 20°55'E). This is an important wintering area of the Long-tailed Duck with up to 10,000 birds/km² counted in 1991–2001 and the key stop-over site of migratory Long-tailed Ducks wintering in high numbers in the southeast Baltic Sea (Vaitkus 1999, Svazas *et al.* 2001).

Three isoenzyme systems (malate dehydrogenase (Mdh, E.C.1.1.1.37), malic-enzyme (Me, E.C.1.1.1.40), esterase (Est, E.C.3.1.3) and non-enzymatic proteins were examined and 22 polymorphic loci were detected. Preparation of liver samples, conventional polyacrylamide electrophoresis and staining procedures followed standard laboratory techniques (Harris & Hopkinson 1976, Korochkin 1977, Sruoga *et al.* 1999). The arrangement of protein fractions in electrophoregrams was esti-

mated according to relative electrophoretic mobility (R_m).

The population genetic structure and genetic variability of Long-tailed Ducks were evaluated by means of allele and genotype frequencies, expected (\bar{H}_e) and observed (\bar{H}_o) heterozygosity, and polymorphism level (the locus was regarded as polymorphic if the frequency of the predominating allele did not exceed 0.95). Genetic distance (D) and genetic identity (I) between populations were calculated according to Nei (1972) and Rogers (1972). The BIOSYS-2 package release 1.7 software (Swofford & Selander 1997) was used for calculation of analyzed parameters.

The data of genetic analysis were compared with results of direct field surveys of breeding and wintering populations of the Long-tailed Duck. The results of the long-term study of a breeding population of the Long-tailed Duck in northeast European tundra of Russia including the Kara River estuary area (Mineev 1994, 2003) were used for evaluation of certain population parameters (trends of the population size, population substructure and spatial heterogeneity, etc.) affecting the extent of genetic variation.

The data on numbers, distribution, habitat selection, dispersal behaviour and large-scale movements of Long-tailed Ducks wintering in the Baltic Sea, and particularly along the Lithuanian coast (Svazas 1993, Svazas *et al.* 2001, Durinck *et al.*

1994, Vaitkus 1999, Zydalis 2002) enabled to connect the results of direct observations of wintering birds with specific patterns in population structure as revealed by genetic methods.

Results

The observed genetic variability of breeding Long-tailed Ducks in the coastal tundra in the Kara River estuary area was lower than in most wintering birds sampled in the Baltic Sea. In ducks of the investigated breeding population the percentage of polymorphic loci (36.4%) was significantly lower than in wintering individuals (62–81%) (Table 1). The mean allele number per locus varied between 2.1–2.4 in wintering birds sampled in 1999–2001. A lower number of alleles per locus (1.5) was observed in the breeding population.

The mean observed and expected heterozygosity among investigated breeding and wintering ducks was also different (Table 1). The observed heterozygosity in the breeding population was lower than in investigated wintering populations. Almost equal values of expected heterozygosity were determined for breeding Long-tailed Ducks sampled in 1985 and for wintering birds sampled in 1994 (0.192 and 0.191, respectively). Expected and observed heterozygosity of ducks sampled in the breeding area in the Kara River estuary in 1985 and of wintering ducks sampled in the Bal-

Table 1. Genetic variability among breeding and wintering Long-tailed Ducks *Clangula hyemalis* (samples of wintering ducks were collected in the Baltic Sea in 1994 and in 1999–2001; breeding birds were sampled in the Kara River estuary area in 1985).

Genetisk variation inom häckande och övervintrande populationer av alfågel (övervintrande fåglar provtagna i Östersjön 1994 och 1999–2001, häckande fåglar vid mynningen av Kara floden 1985).

| Sample | No. individuals | Mean number of alleles/locus | Polymorphic loci (%) | Mean heterozygosity (H) | |
|------------------|------------------------|----------------------------------|--------------------------|-----------------------------|--------------------------|
| | | | | Observed (\bar{H}_o) | Expected (\bar{H}_e) |
| <i>Stickprov</i> | <i>Antal individer</i> | <i>Medel antal Alleler/locus</i> | <i>Variabla loci (%)</i> | <i>Medelheterozygositet</i> | |
| Breeding, 1985 | 17 | 1.5 (0.2) | 36.4 | 0.156 (0.063) | 0.192 (0.057) |
| Wintering, 1994 | 12 | 1.5 (0.2) | 36.4 | 0.195 (0.077) | 0.191 (0.056) |
| Wintering, 1999 | 20 | 2.1 (0.3) | 61.9 | 0.260 (0.064) | 0.348 (0.064) |
| Wintering, 2000 | 23 | 2.3 (0.2) | 81.0 | 0.273 (0.069) | 0.456 (0.054) |
| Wintering, 2001 | 18 | 2.4 (0.3) | 76.2 | 0.315 (0.073) | 0.410 (0.060) |

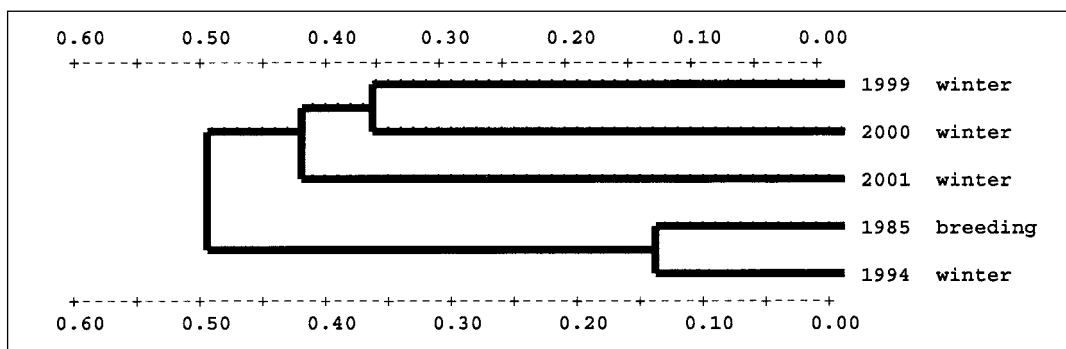


Figure 2. UPGMA cluster analysis of one breeding and four wintering samples of Long-tailed Ducks based on genetic distances (scale axis) calculated according to Rogers (1972). *UPGMA cluster analys av stickprover från alfåglar från en häckande och fyra vinterpopulationer baserade på genetisk distans enligt Rogers (1972).*

tic Sea in 1994 was lower than in wintering ducks sampled in 1999–2001. The highest expected heterozygosity was found among the wintering birds in 2000 ($\bar{H}_e = 0.456$). The highest observed heterozygosity was calculated for wintering ducks sampled in 2001 ($\bar{H}_o = 0.315$).

Genetic identity and genetic distances according to Nei (1972) of Long-tailed Ducks breeding in the Kara River estuary area were very similar to those of wintering birds sampled in the eastern Baltic along the Lithuanian coast in 1994 ($I = 0.938$, $D = 0.062$). A different population genetic structure was characteristic of wintering Long-tailed Ducks sampled in the same study area in winters 1999–2001. Genetic identity and genetic distances of Long-tailed Ducks sampled in Lithuanian marine waters in winters 1999–2000 were of the similar range ($I = 0.737$, $D = 0.263$), while different genetic distances were characteristic of birds sampled in winter 2001.

The UPGMA analysis using parameters of genetic distances according to Rogers (1972) revealed a clustering of the wintering populations from 1999–2001, while a separate cluster included the breeding birds and the winter sample from 1994 (Figure 2).

Discussion

The genotypic uniformity of Long-tailed Ducks breeding in the Kara River estuary can be explained by a relatively small sampling area and by high philopatry of breeding ducks (Anderson *et al.* 1992). A specific population genetic structure was characteristic of this subpopulation.

Genetic variability of Long-tailed Ducks sampled in the Baltic Sea during different years could be primarily caused by the different origin of wintering subpopulations. The population genetic structure of birds breeding in the Kara River estuary area was similar to that of ducks sampled in winter 1994 along the Curonian Spit. About 70,000 wintering Long-tailed Ducks were counted in Lithuanian marine waters off the Curonian Spit in January 1994. Similarity of genetic variability between breeding and wintering ducks indicate a common origin of these birds, though it may also represent a coincidence due to small sample size of breeding ducks.

Long-tailed Ducks sampled in the same wintering site in February–March 1999–2001 were genetically different from ducks sampled in winter 1994. Genetically similar were Long-tailed Ducks sampled off the Curonian Spit in February–March 1999 and 2000. In February and March, Lithuanian coastal marine habitats are used as stop-over sites of Long-tailed Ducks wintering in high numbers in the Pomeranian Bay and in other sites of the southeast Baltic Sea. Up to 1 million Long-tailed Ducks were recently recorded wintering in the Pomeranian Bay and in adjacent areas (Durinck *et al.* 1994, Skov *et al.* 2000). In late winter through early spring, these abundant wintering populations gradually migrate towards east with high numbers recorded off the Lithuanian coast (Svazas *et al.* 2001, Zydalis 2002). Up to 100,000 Long-tailed Ducks were counted along the Curonian Spit in late February – mid March 1999 and 2000. It is likely that the population genetic structure of Long-tailed Ducks sampled in 1999–2000

is representing the large population wintering in southeast Baltic.

Long-tailed Ducks sampled along the Lithuanian coast in February 2001 were genetically different both from birds sampled in the Kara River estuary area and from wintering ducks sampled in Lithuanian marine waters in 1994 and 1999–2000. In February 2001 Long-tailed Ducks were sampled during a cold winter period when the major part of the Gulf of Riga and of other coastal marine waters of the northeast Baltic Sea was temporarily ice-covered. The Gulf of Riga with Irbe Strait is the most important wintering site of Long-tailed Ducks in the Baltic Sea, annually holding more than 1 million birds (Durinck *et al.* 1994, Skov *et al.* 2000). During the cold February 2001 more than 90,000 Long-tailed Ducks were counted along the edge of ice fields off the Curonian Spit. They largely included ducks normally wintering in more northern Baltic sites. Radar and direct observations conducted along the eastern Baltic coast revealed large-scale winter movements of Long-tailed Ducks between different sites within wintering seasons, caused by ice formation during cold weather periods (Vaitkus 1999, Svazas *et al.* 2001, Zydellis 2002).

The results of this study suggest a genetic variability and differences in population genetic structure among Long-tailed Ducks wintering in different areas of the Baltic Sea, even if different subpopulations may share the same wintering and stop-over sites. The pair formation in the wintering areas can cause gene flow and genotypic linkage between subpopulations of different origin, temporarily sharing the same wintering sites in the Baltic Sea. Intensive courtship and pair formation of Long-tailed Ducks starts in the eastern Baltic in January, and in March–April many Long-tailed Ducks leave their wintering areas in pairs (Svazas *et al.* 2001).

The suggested genetic variability and different population structure of subpopulations of Long-tailed Ducks wintering in the Baltic Sea highlights the need of appropriate conservation and wise management of their wintering sites of international importance. The whole Western Palearctic population of the Long-tailed Duck is largely dependent on key wintering sites located in certain shallow areas of the Baltic Sea. Potential large-scale oil spills can affect genetically unique groups of Long-tailed Ducks. Long-tailed Ducks clearly dominated among thousands of waterbirds killed during large-scale oil spills in the eastern Baltic in winters 1995 and 1997 (Zalakevicius *et*

al. 1995, Zydellis & Dagys 1997). The increasing anthropogenic pressure on the environment of the Baltic Sea (oil pollution, near-shore fisheries, offshore wind mill parks, etc.) results in a cumulative negative effect on the wintering population of the Long-tailed Duck. Basic biological information including data on population-genetic structure of populations and their genetic variability is essential for conservation and sustainable management of breeding and wintering populations of Long-tailed Ducks and their habitats.

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Sammanfattning

Alfågeln har ett vidsträckt utbredningsområde i norra Eurasien och Nordamerika. Den västpalearktiska populationen övervintrar huvudsakligen i Östersjön och inkluderar cirka 4 miljoner fåglar. Koncentrationer upp till en miljon individer har inräknats på vissa platser och tider, framförallt i Östersjöns östra och södra regioner.

I denna studie undersöktes alfåglar från ett häckningsområde vid Karaflodens mynning i Ryssland och övervintrande fåglar från kusten utanför Curonian Spit, Litauen, med hjälp av proteinelektrofores för att utröna kopplingar mellan den häckande populationen och övervintrare under olika år. Leverprover insamlades från 17 häckande fåglar under juli 1985, och sammanlagt från 73 fåglar som fastnat i fiskenät under januari–mars 1994 och 1999–2001 (Tabell 1). Totalt undersöktes genetisk variation på 22 loci.

Den genetiska variationen bland provet från häckningsområdet var lägre än för de övervintrande fåglarna. Detta tolkas som att de övervintrande fåglarna utgörs av blandningar från olika häckningsområden. Störst genetisk likhet påträffades mellan den häckande populationen och de övervintrande fåglarna som insamlats under 1994 (Figur 2). Betydligt större skillnader fanns mellan häckningspopulationen och de olika vintrarna 1999–2001, vilka också sinsemellan visade stora skillnader. Detta antyder att ursprungsområdet varierar för de alfåglar som övervintrar utanför Litauens kust under olika år. Om alfåglar från samma häckningsområde vanligen uppehåller sig i samma del av övervintringsområdet, vilket antyds av denna studie, blir konsekvensen att enskilda häckpopulationer kan drabbas väldigt hårt av lokala oljeutsläpp.