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Goose hybrids, captive breeding and restocking of the Fennoscandian populations of the Lesser White-fronted goose (*Anser erythropus*)

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Abstract

The lesser white-fronted goose (*Anser erythropus*) is the most threatened of the Palearctic goose species with a declining population trend throughout its distributional range. The current estimate of the Fennoscandian subpopulation size is 30–50 breeding pairs, whereas it still numbered more than 10 000 individuals at the beginning of the last century. Reintroduction and restocking have been carried out in Sweden and Finland using captive lesser white-fronted goose stock with unknown origins. We have carried out a study of the genetic composition of captive-bred stock by sequencing a 221 bp hypervariable fragment of the mitochondrial DNA (mtDNA) control region from 15 individuals from the Hailuoto farm, Finland. Two out of the three maternal lineages detected in the captive stock are also present in wild populations. The third maternal lineage among the captive lesser white-fronted geese originates from the closely related greater white-fronted goose (*Anser albifrons*). None of the investigated wild lesser white-fronted goose individuals carried the mtDNA of the greater white-fronted goose. The presence of greater white-fronted goose mtDNA in the lesser white-fronted goose captive stock suggests that hybridization has occurred during captive propagation.

Introduction

At the beginning of the twentieth century, the Fennoscandian subpopulation of lesser white-fronted geese consisted of at least 10,000 individuals (Merikallio 1915; Nordenhaug and Nordenhaug 1984). The current breeding population consists of only 30–50 breeding pairs (Lorentsen et al. 1998). Maintenance of captive stocks of lesser white-fronted geese and the restocking of wild populations have been given a low priority as a conservation measure – as long as the wild populations are able to persist (Madsen 1996). However, in Finland attempts to supplement the wild population were made during the years 1989–1997 when 143 captive lesser white-fronted geese were released close to the breeding areas of the wild individuals (Lorentsen et al. 1999; Markkola et al. 1999). The survival of the released individuals was low and no breeding attempts were confirmed. In Sweden, a population of lesser white-fronted geese of captive origin has been reintroduced and maintained in the wild by using semi-captive barnacle geese (*Branta leucopsis*) as foster parents (von Essen 1996; Lorentsen et al. 1999; von Essen et al. 2000). The traditional migration routes of the wild lesser white-fronted geese through Russia and Kazakhstan are associated with high losses of geese due to hunting. Because the goslings follow their barnacle goose foster parents to safer wintering areas in Western Europe, the reintroduced Swedish individuals have a relatively high level of survival. From 1981 to 1999, a total of 348 birds has been released in Swedish Lapland. The size of the population in the release area in the spring of 1999 was approximately 50 individuals (von Essen et al. 2000) and, although the population is not self-sustaining, more than twenty successful breeding attempts have been observed.

The genetic origin of captive stock reared for restocking purposes should be compatible with that of the wild populations (Avise and Nelson 1989; Wayne et al. 1992; Roy et al. 1996; Hedrick et al. 1997; Glenn et al. 1999). The released individuals should be genetically similar to the original wild population in order to preserve local adaptation and to avoid outbreeding depression that may result from the mixing of differentially adapted stocks (Templeton 1986). If the captive stock is founded with individuals collected from the target population to which the captive-reared individuals will be released later, the captive material is supposedly representative of the original population. However, the origin and the pedigrees of the captive individuals are not always known. The levels of genetic diversity among the individuals used to establish captive stocks and the relatedness of the captive individuals need to be assessed with the help of genetic markers (Brock and White 1992; Longmire et al. 1992; Rave et al. 1994; Signer et al. 1994; Tegelström and Sjöberg 1995; Tegelström and von Essen 1996). Moreover, information on levels of diversity and the relatedness of the individuals can be used to avoid the potentially harmful effects of inbreeding. In practice, inbreeding is usually minimized and effective population size maximized by mixing different captive breeding groups and manipulating the reproductive output of the individuals. The natural origins of the captive lesser white-fronted geese maintained in several farms in Finland and in Sweden are largely unknown, but individuals can be traced to wildfowl farms in Britain, Germany and The Netherlands (Delacour 1954; von Essen 1996). The species has long been a favourite in captivity, raised both by private farmers and in zoos for decades. In order to maintain levels of genetic diversity and to avoid inbreeding, individuals have been exchanged between the farms. The genetic similarity between the individuals in one of the captive breeding groups has been studied (Tegelström and von Essen 1996). The average DNA fingerprinting similarity of 0.39 among the breeding pairs was higher than in natural goose populations in general (Larsson et al. 1995) but lower than in goose populations that have experienced population bottlenecks (Rave 1995; Tegelström and Sjöberg 1995). We have previously studied the genetic structure of wild lesser white-fronted goose populations by investigating variation in mtDNA (Ruokonen et al. 2001). We found 14 mitochondrial haplotypes among lesser white-fronted geese sampled from the whole distributional area of the species. The haplotypes grouped into two diverged mitochondrial lineages: 'W' (prevalent in the western distributional area) and 'E' (prevalent in the eastern distributional area). Three out of the 14 haplotypes were detected in the Fennoscandian wild subpopulation. One of the haplotypes (W1) is clearly prevalent (found in 81% of the individuals). The second haplotype (E1) was found in two individuals. The third haplotype (W4) was found in only one individual and it was unique to the Fennoscandian subpopulation. Haplotype and nucleotide diversities (0.342 and 0.007, respectively) in the Fennoscandian subpopulation were also low compared to the average for other breeding areas (0.669 and 0.012). The low level of variation may reflect a recent population decline, but our analysis of five museum individuals from the years 1925–1937 suggests that Fennoscandian Lapland was colonized by a few individuals: all the museum specimens studied belong to haplotype W1 (Ruokonen et al. 2001). The haplotype frequencies detected in Fennoscandia differ significantly from those among individuals from Bolshezemelskaya Tundra, Russia, the closest sampled breeding area, suggesting that there is a restricted amount of female gene flow between these two breeding areas.

In the present study we investigate variation in mtDNA lineages in individuals from one of the Finnish captive breeding stocks of the lesser white-fronted goose. The results are interpreted in the context of the available information on genetic variation in the wild populations of the lesser white-fronted goose and the closely related greater white-fronted goose.

Material and methods

Altogether 15 captive lesser white-fronted geese from Hailuoto farm, Finland, were sampled in 1993 for the study. Because there were no pedigree data available, 8 females and 7 males out of 28 individuals were chosen randomly for the study. Three of the captive individuals studied (C25, C27 and C28) originated from the Swedish farm in Öster-Malma, all the others have hatched in the Hailuoto farm. For the purpose of comparison, 6 greater white-fronted geese (*Anser albifrons albifrons*) from Kazakhstan (ALB 2–4, 6–8) were included in the study. Additional lesser white-fronted geese sampled in Fennoscandia, Yamal, Kazakhstan and China (accession numbers AF159955, AF159956, AF234602-AF234609) and

greater white-fronted geese sampled in Bulgaria and Russia (accession numbers AF159957, AF159958) previously sequenced by us (Ruokonen et al. 2000, 2001) were used for the alignment.

Total DNA was isolated from either blood or other tissue with phenol-chloroform extractions according to the standard procedure. DNA from feathers was isolated according to Walsh et al. (1991) with minor modifications. For total DNA isolated from blood and muscle, primers L16642 and H411-AL (Ruokonen et al. 2000) were used for amplification of an approximately 470 bp fragment of the mitochondrial DNA containing the domain I of the control region. For total DNA isolated from feathers, a shorter fragment (approximately 280 bp) was amplified with primers L180 5'TGGTTATGCATA-TTCGTGCATAGA'3 and H466 5'TTTCACGTGAG-GAGTACGACTAAT'3. Standard PCR amplifications were performed in a reaction volume of 100 μl containing total DNA, 1 μM of each primer, 10 mM Tris-HCl pH 8.8, 1.5 mM $MgCl_2$, 50 mM KCl, 0.1% Triton X-100, 200 μM of each dNTP and 2U of Dynazyme (Finnzymes). Amplification profiles were: 30 cycles of denaturation at 94 °C for 1 min, annealing at 55 or 60 °C (depending on the primers used) for 1 min and synthesis at 72 °C for 2 min. Double-stranded DNA sequencing of the PCR products was performed by using dye terminator automatic sequencing with ABI PRISM 377 according to ABI PRISM User's manual. A 221 bp fragment of the domain I of the control region (nucleotides 189–410 in Ruokonen et al. 2000) containing approximately half of the variable sites in the whole control region in geese was aligned and edited manually. Pairwise genetic distances for the haplotypes were estimated using Kimura's 2-parameter method (Kimura 1980) and were used for constructing a Neighbor-joining tree with 500 bootstrap replicates in the MEGA program (Kumar et al. 1993). Nucleotide positions containing gaps were omitted from the analysis.

The possibility that PCR amplification of mitochondrial-like nuclear copies could explain the presence of similar sequences in the two species has been excluded in an earlier study (Ruokonen et al. 2000). MtDNA enriched isolates, long PCR, PCR amplification of the control region from multiple tissues with different ratios of mtDNA and nuclear DNA, and comparison of the sequences obtained from amplification with multiple PCR primer pairs have been used to ensure that amplified sequences are of mitochondrial origin.

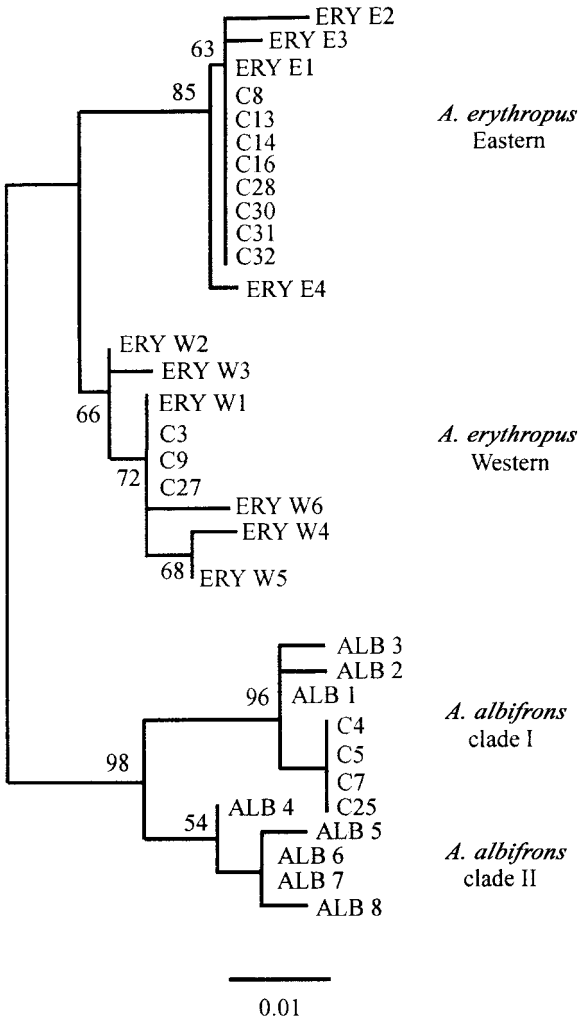

Figure 1. Neighbor-joining tree based on Kimura's 2-parameter distances among mtDNA control region haplotypes of the wild and captive lesser white-fronted geese and greater white-fronted geese. Bootstrap values at the nodes are based on 500 replicates, only values above 50% are shown. ERY = lesser white-fronted goose, ALB = greater white-fronted goose, C = captive lesser white-fronted goose.

The sequences have been deposited in GenBank (accession numbers AF234610-AF234616).

Results and discussion

The phylogenetic relationships of the mitochondrial haplotypes of captive lesser white-fronted geese and wild lesser and greater white-fronted geese are shown in Figure 1. Three out of the 15 captive lesser white-fronted geese (C3, C9, C27) are identical to the W1

haplotype, which is the most common Western haplotype in the wild lesser white-fronted goose (see Introduction). Eight captive individuals (C8, C13, C14, C16, C28, C30-32) possess the Eastern haplotype E1 that is most common in the Eastern distributional area of the species. However, the mtDNA sequence from four of the captive individuals (C4, C5, C7, C25) groups together with the greater white-fronted geese haplotypes, differing by one nucleotide substitution (C↔G, nucleotide 164) from haplotype ALB1 (Figure 1).

There are several possible explanations for the occurrence of greater white-fronted goose type mitochondrial DNA in the captive stock of lesser white-fronted goose. The simplest explanation is that greater white-fronted goose type mtDNA is also present in wild lesser white-fronted goose populations. The lack of monophyly could then be due either to recent divergence of the species or a consequence of hybridization of female greater white-fronted and male lesser white-fronted geese under natural conditions. Although the speciation of the lesser and greater white-fronted geese probably occurred as late as during the Pleistocene (Ruokonen et al. 2000), there is no support for poly- or paraphyletic status in mtDNA among these species (Figure 1, Ruokonen et al. 2000, 2001). While hybridization between the two species is believed to be occasional in natural populations (Nagy 1950; Shackleton 1956; Panov 1989), it is difficult to reliably detect and identify hybrids because of the morphological similarity between the two species. Some hybrids of lesser white-fronted and greater white-fronted goose from a German farm were described in the paper by Nagy (1950). The morphological features of the male parental species dominated among the characters of hybrids. Hybrid offspring from a mating between a male lesser white-fronted goose and a female greater white-fronted goose had the lesser white-fronted goose's yellow eye-ring and white forehead plumage that extends up between the eyes. Traits such as body size, shape and size of the white frontal patch show phenotypic variation in both species (Øien et al. 1999). Identification of hybrids is thus difficult and hybrids will, in most cases, go undetected. However, no haplotypes of greater white-fronted goose were detected among the mitochondrial haplotypes of 81 wild lesser white-fronted goose individuals sampled from the species' whole distributional area. All the analysed wild lesser white-fronted geese carry either one of the two most common haplotypes (W1 or E1) or one of their close derivatives (Ruokonen et al. 2001). The absence of haplotypes of greater white-fronted goose in the wild lesser white-fronted geese indicates that hybridization between female greater white-fronted geese and male lesser white-fronted geese is not common in the wild and that introgression, if it occurs, is a rare phenomenon that is unlikely to explain the presence of greater white-fronted goose mtDNA among the captive lesser white-fronted geese.

Although the integrity of lesser white-fronted and greater white-fronted geese is maintained in the wild, behavioural and morphological constraints to mate-choice may be relaxed under captive conditions. Hybridization in captivity between the lesser white-fronted goose and two *Anser* and three *Branta* goose species was reported by Gray (1958) and hybrids between lesser white-fronted and greater white-fronted geese are reported to be fairly frequent (Nagy 1950). Although the fertility of the greater white-fronted and lesser white-fronted goose hybrids is unknown, intrageneric goose hybrids are usually fertile (Delacour 1954; Gray 1958). We conclude that the most probable explanation for the occurrence of the greater white-fronted goose mtDNA among the captive lesser white-fronted geese is that hybridization between the two species has taken place at some point in the history of captive breeding of lesser white-fronted geese.

The presence of heterospecific mtDNA in the captive stock of lesser white-fronted geese indicates that there may be introgression of nuclear alleles as well. The number of hybridization events and numbers of hybrid offspring, the size of the captive population and the degree of the subsequent mixing of the different captive stocks are unknown. Therefore, the proportion and possible effects of heterospecific nuclear alleles in the captive population are impossible to evaluate on the basis of the present data. The fact that some of the captive lesser white-fronted geese have unusually pale eye-rings or long and heavy bills, may indicate the presence of greater white-fronted goose nuclear alleles in the captive stock of lesser white-fronted goose. MtDNA is maternally inherited and the female is the heterogametic sex in avian species. Consequently the W sex chromosome is inherited together with mtDNA to the female offspring and all the captive females carrying the greater white-fronted goose mtDNA will also have the W sex chromosome of greater white-fronted goose.

Restocking with geese from captive stocks has been stopped in Finland, but it continues in Sweden.

Originally, all the founders of the Hailuoto stock, the stock investigated here, were obtained from two Swedish farms (four individuals from Öster-Malma and 11 from Eriksberg). Three of the original four founding individuals from Öster-Malma were included in our study: C25 (a female with Greater White-fronted goose mtDNA), C27 (a female with haplotype W1) and C28 (a male with haplotype E1). Therefore it is probable that the Swedish captive stocks also are contaminated with alien genes and are not representative of the original wild Fennoscandian subpopulation of lesser white-fronted geese.

According to the international action plan for the lesser white-fronted goose (Madsen 1996), reintroduction and restocking may be accepted as a way of minimizing the risk of extinction of the species if other efforts to conserve the wild population appear to have failed and if the IUCN criteria (Kleiman et al. 1994) for reintroductions are met. The main threat to both the wild and the released Lesser White-fronted geese of captive origin is over-hunting, despite the fact that the species has a protected status in most of the relevant countries (Lorentsen et al. 1999). In the Swedish restocking project, changing the migration route to safer wintering areas has diminished the hunting pressure for the reintroduced population. However, the project has been criticised for introducing the lesser white-fronted goose to wintering areas in the Western Europe where the species has earlier been only an accidental visitor (Delacour 1954; Cramp and Simmons 1977). There have also been cases of hybridization between the reintroduced birds and barnacle geese (P. Tolvanen, personal communication).

The original wild lesser white-fronted goose population in the reintroduction area in the Swedish Lapland is probably extinct, but reintroduced individuals have occasionally been observed in Finland and Norway (P. Tolvanen and I. J. Øien, personal communication). Thus, there is a clear risk that individuals of captive origin will mix with the wild breeding populations.

One of the preconditions for restocking is that there is a need to increase the size or genetic diversity of the wild population (Kleiman et al. 1994). Despite the small size of the Fennoscandian subpopulation, there are no indications of deleterious inbreeding effects. Offspring production in Fennoscandia is comparable to that in other breeding areas (Aarvak et al. 1997), suggesting that the recent population decline is not driven by the negative effects of low genetic variability. It is known that goose species in general have a high potential for population recovery and expansion from initially low numbers. The red-breasted goose (*Branta ruficollis*) population declined to less than 30,000 individuals during 1970–1990, but as a consequence of protective legislation and a shift in wintering areas the population had increased to more than 75,000 individuals by 1993 (Hunter et al. 1999). The low levels of genetic variability detected in the reintroduced Canada geese (*Branta canadensis*, Tegelström and Sjöberg 1995) have not reduced population viability or prevented the species colonizing new areas in Fennoscandia (Heggberget 1991).

Hybridization of endangered species or subspecies may occur in nature and may be regarded as beneficial if it counteracts the harmful effects of inbreeding in small populations (O'Brien et al. 1996). However, in some cases, a reduction in fitness resulting from the disruption of adaptive gene complexes has been observed in hybrid offspring. Although it has been shown experimentally that the effects of outbreeding depression can be reduced in successive generations and that the fitness of the population can be restored in the long term (Templeton 1986), a short-term reduction in fitness may involve a pronounced risk of extinction for a small population. To be able to evaluate the risks to the existing wild Fennoscandian subpopulation of the lesser white-fronted goose and to establish guidelines for future reintroductions, the extent of contamination with genetic material from greater white-fronted goose in the captive stock must be determined with the help of species-specific nuclear markers as well as mtDNA. If it is necessary to carry out reintroductions in order to enhance the survival of the Fennoscandian subpopulation, and if the present captive stock is not appropriate, individuals from other breeding areas should be preferred instead of captive hybrid stocks.

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