Wild hybrids of Lesser White-fronted Goose (*Anser erythropus*) x Greater White-fronted Goose (*A. albifrons*) (Aves: Anseriformes) from the European migratory flyway

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Abstract

The Lesser White-fronted Goose (*Anser erythropus* (Linnaeus, 1758)) is one of the most threatened Palearctic goose species, with the Fennoscandinavian subpopulation in particular having seen a drastic decline over the last century. In the 1990s, captive-bred Lesser White-fronted Geese were used successfully for reintroduction and restocking in Sweden and Finland. The discovery of Greater White-fronted Goose (*Anser albifrons* (Scopoli, 1769)) mtDNA haplotypes in some of these captive-bred birds (Ruokonen et al. 2000) suggested that hybridisation had occurred during captive propagation and led to the discontinuation of the release of captive goslings. Here we report two hybrids of Lesser x Greater White-fronted Geese that were collected on their wintering grounds in England in 1936 and Holland in 1966. Birds from western Russia normally do not migrate south to Western Europe. Hence, these birds most likely originated from the Fennoscandinavian subpopulation and were collected prior to the commencement of the captive-breeding programmes. Both specimens show a heterogeneous set of morphological characters, some of which shared with the putative parent species and others being intermediate between the two White-fronted Goose species. A Canonical Discriminant Function analysis positions both specimens between the two putative parent species, making their hybrid status likely. We show, thus, that hybridisation between Greater and Lesser White-fronted Geese does occur naturally, albeit perhaps infrequently, and argue that the presence of Greater White-fronted Goose mtDNA haplotypes in Lesser White-fronted Goose may be the result of this naturally occurring hybridisation. Our data provide additional information on the debate whether the restocking programmes were halted for the right reasons and whether it is desirable to re-commence with the reintroduction programme.

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1. Introduction

The Lesser White-fronted Goose (*Anser erythropus* (Linnaeus, 1758)) breeds in the Arctic tundras of the
Palearctic from northern Scandinavia to the Chukotka Mountains in East Siberia (Øien and Aarvak 2003; Stepanyan 2003). It has seen a drastic decline throughout most of its range over the course of the 20th century, and the species is currently classified as Vulnerable (IUCN 2004). The Fennoscandinavian subpopulation of A. erythropus is the most threatened subpopulation, having seen a decline from more than 10,000 individuals at the beginning of the last century to some 45–55 breeding pairs (or fewer than 200 individuals) at present (IUCN 2004). Attempts at supplementing the wild population were made in Finland during 1989–1997 when 143 captive-bred A. erythropus were released close to the breeding areas of their wild congeners (Lorentsen et al. 1998), but this release did not lead to successful reproduction (Ruokonen et al. 2000). In Swedish Lapland, from 1991–2000, captive A. erythropus have been reintroduced in the wild using semi-captive Barnacle Geese [Branta leucopsis (Bechstein, 1803)] as foster parents (Von Essen 1991), and these birds have successfully reproduced (for a more detailed overview, see Anderson 2003).

Most individuals of the Fennoscandinavian population migrate south following a south-eastern route to the Volga Basin in Russia and western Kazakhstan (Aarvak and Øien 2003). Many geese are lost along this route due to hunting. The reintroduced Swedish A. erythropus goslings follow their B. leucopsis foster parents along a safer, more south-westerly route to safer wintering areas in the Low Countries (Netherlands, Belgium, Germany), and, subsequently, the reintroduced Swedish population had relatively higher survival rates (Koffijberg et al. 2006).

Ruokonen et al. (2000) sequenced parts of the mtDNA of 15 captive-bred A. erythropus from Finland and discovered that two of the maternal lineages were also found in the wild populations, but that a third lineage must have originated from a Greater White-fronted Goose [A. albifrons (Scopoli, 1769)]. No haplotypes of A. albifrons were detected in a sample of 81 wild A. erythropus (Ruokonen et al. 2004), which suggested that hybridisation had occurred at some point in time during the captive breeding of Lesser White-fronted Geese. Ruokonen et al. (2000) suggested that, since the Finnish captive-bred A. erythropus were originally obtained from Sweden, it was probable that the Swedish captive stock was also contaminated with A. albifrons genes and, as such, were not representative of the original wild Fennoscandinavian subpopulation of A. erythropus (see also Tegelstrom and von Essen 1996). Given that the Swedish reintroduced population reproduces successfully, and that these reintroduced geese are occasionally observed in Finland and Norway, there was a clear risk that individuals of captive origin would mix with the supposedly pure wild breeding populations (Ruokonen et al. 2000). As a consequence of this discovery, the Swedish captive-breeding project discontinued the release of goslings in 2000 (Anderson 2003).

Until the end of 2004, when the legal courts decided otherwise (Raad van State 2004), the possible genetic impurity of overwintering A. erythropus in the Netherlands was the rationale for the Dutch authorities to exclude A. erythropus from the list of species for which the EU Habitat and Bird Directive (Anonymous 2007) was applicable. As a consequence, important wintering areas were no longer protected, and the overwintering geese were allowed to be disturbed (Raad van State 2004).

There is clearly cause for concern if hybridisation between Lesser and Greater White-fronted Geese was an artefact of captive breeding and if the subsequent release of these hybrid individuals were to contaminate wild populations. However, there have been several reports of apparently natural hybrids of these two species in the wild (Panov 1989), including birds from the Fennoscandinavian subpopulation (Shackleton 1956; Voous and Wattel 1967), suggesting that hybridisation between these two species occurs also naturally in the wild.

Our study evaluates the status of two apparent hybrids between Lesser and Greater White-fronted Geese that were collected on their wintering grounds in the Netherlands and in England prior to the commencement of the reintroduction programmes in Sweden and Finland and that, in all likelihood, originated from the Fennoscandinavian subpopulation. The aim is to test whether hybridisation between the two species might already have occurred naturally prior to the captive-breeding programme of the Lesser White-fronted Goose.

2. Materials and methods

2.1. Materials

We traced and located two specimens of apparent hybrids of A. erythropus × A. albifrons in the collections of the Zoological Museum Amsterdam (ZMA 19267: Fig. 1) and the Natural History Museum, Tring (BMNH 1936.2.18.1). The former was mentioned in a report by Voous and Wattel (1967), whereas the existence of a possible hybrid in the collections of the BMNH was mentioned in an editorial footnote to a paper by Shackleton (1956). The specimen ZMA 19267 is an adult male collected by C.J. Coldewey in the Biesbosch, South Holland, The Netherlands, on 28 December 1966. The specimen BMNH 1936.2.18.1 is an adult male collected by R.G. Berkeley near Berkeley Castle, Gloucestershire, England, UK, on 12 February
Both specimens had been identified by the respective collectors as possible hybrids.

2.2. Morphometrics

To test the hypothesis that these specimens were hybrids, the diagnostic characters of the two purported parental species had to be established. We selected the following characters for this purpose:

1. extent of yellow eye ring (either clearly swollen or vestigial)
2. wing length (fully stretched and flattened)
3. tail length
4. tarsus length
5. mid-toe length
6. culmen length from feathering at forehead to the tip of the beak
7. bill depth of both mandibles, at level of the feathering at the forehead
8. ratio of wing versus tail length
9. ratio of tarsus versus mid-toe length
10. ratio of culmen length versus bill depth

Following the methods described in Roselaar (1988), the first 7 characters were measured by Kees Roselaar on 24 skins of *A. albifrons* and 26 *A. erythropus* (all adult males) deposited in the ZMA, the BMNH, and the National Natural History Museum Naturalis (Leiden, The Netherlands), and on ZMA 19267. Data from BMNH 1936.2.18.1 were kindly provided by Mark Adams. The measured *A. albifrons* specimens originated from Western Europe (Netherlands, Germany), whereas the measured *A. erythropus* specimens originated from Europe and Asia (Norway, Netherlands, Hungary, Russia, Kazakhstan, Azerbaijan, India, Myanmar, Japan).

2.3. Analysis

The analysis of how the characters in the apparent hybrids differed from the parent species were conducted for each character separately and with a Canonical Discriminant Function (CDF) analysis (Quinn and Keough 2002) for a set of continuous characters (characters 2–10). The distribution of the measurements of characters 2–10 appeared not to differ significantly from a normal distribution. Following Roselaar et al. (2006), for hybrid divers, in which the observed value of the purported hybrids for characters 2–10 was not within Mean ± 1.96 SD or Mean ± 2.56 SD for those found in *A. erythropus* and/or *A. albifrons*, we considered the difference to be significant at *P* = 0.05 or *P* = 0.01 level, respectively (see Quinn and Keough 2002). Significance of the difference was assumed if *P* ≤ 0.05 was in a two-tailed test.

3. Results

Both ZMA 19267 and BMNH 1936.2.18.1 were originally sent to zoological museums because the collectors (i.e., Coldewey and Berkeley) noticed that they had obvious, swollen orange-yellow or yellow eye rings, similar to those in *A. erythropus*, but that in other respects the birds were more like *A. albifrons*. Berkeley stated that among the hundreds of *A. albifrons* he had shot at Berkeley Castle, many had some yellow colouring around the eye, but none “quite so pronounced as this one”. Our study of the museum skins concurs with this conclusion as all *A. erythropus* had clear yellow or orange-yellow eye rings (although often shrivelled and faded), but at most a vestigial narrow flattened ring in *A. albifrons*.

ZMA 19267 is significantly larger than *A. erythropus* in characters 5 (*P* < 0.05) and 2, 3, 6, 7 (all *P* < 0.01), whereas character 8 is significantly smaller than that observed in *A. erythropus* (*P* < 0.05). It is also significantly smaller than *A. albifrons* in character 6 and 8 (*P* < 0.05). One specimen of *A. albifrons* (ZMA 22358) has a large bill, although not significantly larger than that of the other *A. albifrons* specimens combined; if this specimen is excluded from the dataset, ZMA 19267 still
has a significantly smaller bill than \textit{A. albifrons}. BMNH 1936.2.18.1 is significantly larger than \textit{A. erythropus} in characters 2, 5, 7 (\(P < 0.05\)) and 3, 6 (all \(P < 0.01\)). It is significantly smaller than \textit{A. albifrons} in character 6 and 7 (\(P < 0.01\)). Both ZMA 19267 and BMNH 1936.2.18.1 show similar differences from their putative parent species, and characters that differ significantly from those in the putative parent species differ always in the same direction in the two apparent hybrids, i.e., they are either larger or smaller than in the putative parent species (Table 1). When one apparent hybrid differs significantly in any particular character from one parent species, the other hybrid is significantly more likely to show the same pattern of difference in this character (Fisher’s Exact Probability Test, \(P = 0.01\)). The same relationship holds for characters that do not differ between the hybrids and the putative parent species.

For males of the two putative parent species, the overall assignment of individuals to their original sample by the CDF analysis was 100%, thus showing a clear-cut separation between the two species (Fig. 2). Both ZMA 19267 and BMNH 1936.2.18.1 are positioned between these two species, with ZMA 19267 being relatively more similar to \textit{A. albifrons} and BMNH 1936.2.18.1 being relatively more similar to \textit{A. erythropus}.

4. Discussion

4.1. Hybridisation in \textit{A. erythropus} and \textit{A. albifrons}

The order Anseriformes (geese, swans, and ducks) is one of the avian orders most prone to hybridisation,
with the incidence of hybridisation (i.e., the number of species within an order that have hybridised in nature divided by the total number of species in that order (sensu Grant and Grant 1992) as high as more than 70% (Gray 1958). The occurrence of natural hybridisation between *A. erythropus* and *A. albifrons* as largely inferred on the basis of field observations of aberrant individuals (Nagy 1950; Shackelton 1956; Gray 1958; Lerner 2005) is supported by our analysis of measurements of two apparent hybrids, both of which show a heterogeneous set of characters and are positioned intermediate in our Discriminant Function analysis (Fig. 2).

The presumed hybrid ZMA 19267 differs significantly from *A. erythropus* in six of the ten characters, and the presumed hybrid BMNH 1936.2.18.1 shows the same significant difference in five of these six characters. In all of these five characters, both specimens differ in the same direction from *A. erythropus*, i.e., smaller or larger, and never one smaller and the other larger. The number of significant differences between the two hybrid specimens and *A. albifrons* is smaller but shows the same consistent pattern. In character 6, both ZMA 19267 and BMNH 1936.2.18.1 differ from both putative parent species in exactly the same manner, and in two other characters (7, 8), either ZMA 19267 or BMNH 1936.2.18.1 differs from both putative parent species. Also the CDF analysis revealed a clear-cut separation between *A. erythropus* and *A. albifrons*, with both ZMA 19267 and BMNH 1936.2.18.1 being positioned between these two species. On the basis of this set of characters, we postulate that both specimens most likely represent hybrids between the two species.

We hypothesise further that our hybrid specimens are the result of mixed pairing between a male *A. erythropus* and female *A. albifrons*, because experiments with captive *A. erythropus* and *A. albifrons* have shown that certain morphological features of the male parental species dominates among the characters of the hybrids (Nagy 1950). Crosses between male *A. erythropus* and female *A. albifrons* resulted in hybrids having *A. erythropus*’ eye ring, as indeed observed in our hybrids. The relative contribution of the different species and the different sexes in hybridisation between the two species can be solved when in addition to mtDNA – which are inherited only maternally – paternal-specific DNA, or nuclear DNA sequences, are isolated. In addition to individuals from wild populations, these sequences could be obtained from the reintroduced stock to assess the incidence of hybridisation more accurately.

4.2. Hybridisation and re-introductions

*Anser erythropus* and *A. albifrons* geese breed in the Arctic tundras, the former breeds well south of the Arctic Ocean, whereas the latter breeds throughout the Arctic, including on islands in the Arctic Ocean (Cramp and Simmons 1977). In northern Russia, at the southern edge of the breeding range of *A. albifrons* and the northern edge of *A. erythropus*, both species overlap in their breeding grounds (Cramp and Simmons 1977).

![Breeding ranges of Anser albifrons and A. erythropus](image-url)
Both presumed hybrid specimens included in our study were collected on their wintering grounds in 1936 and 1966, well before the commencement of any captive breeding and restocking programmes. Most likely, they are offspring of mixed pairs of the two species in the westernmost part of the breeding range of an *A. albifrons*, i.e., in north European Russia. Alternatively, since geese can form pairs during winter (Ganter et al. 2005), an *A. albifrons* paired with an *A. erythropus* on their breeding grounds in Fennoscandia.

We conclude that hybridisation between the two species occurs naturally regardless of stocking programmes. This perhaps happens infrequently, because 4% (2/47) of *A. erythropus* and less than 1% (2/273) of *A. albifrons* in the collections of the ZMA, BMNH, and Naturals are hybrids. The vast majority of these specimens was collected prior to the commencement of the captive breeding and restocking programmes and, thus, most likely represent natural hybrids. As such, the hypothesis that the most probable explanation for the occurrence of *A. albifrons* mtDNA among the Fennoscandian captive population of *A. erythropus* is due to hybridisation at some point of the captive breeding of *A. erythropus* (Ruokonen et al. 2004, p. 280) is not incontrovertible. Although we cannot exclude this possibility, our study demonstrates that natural hybridisation between the two species does occur, or at least has occurred in the past, even though Ruokonen et al. (2004) did not find any haplotypes of *A. albifrons* in the wild *A. erythropus* and suggested that hybridisation between male *A. erythropus* and female *A. albifrons* is not common in the wild.

The occurrence of hybridisation between *A. albifrons* and *A. erythropus* during captive propagation was the main reason for discontinuing the release of *A. erythropus* goslings in Sweden (Anderson 2003), and the possibility of the presence of alien DNA in overwintering *A. erythropus* led the Dutch authorities to consider them not to represent a natural population and, therefore, removing legal protection from them. We duly note, however, that natural hybridisation between bird species is a frequent and natural phenomenon, with on average at least one in ten bird species known to have bred in nature with another species and to have produced hybrid offspring (Randler 2002; Aliabadian and Nijman 2007). Our data provide additional information on the debate whether the restocking programmes were halted for the right reasons and whether it is desirable to re-commence with the reintroduction programme. We recommend that the reality of natural hybridisation is taken into account in evaluating the viability and success of not only the Lesser White-fronted Goose reintroduction programme, but also other reintroduction and restocking programmes.

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**References**


