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RESEARCH PAPER

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Use of foster parents in species conservation may cause conflicting objectives:

Hybridization between Lesser White-fronted Goose *Anser erythropus* and Barnacle Goose *Branta leucopsis*

Fosterföräldrar i artbevarandeprojekt kan skapa motstridiga mål: Hybridisering mellan fjällgås Anser erythropus *och vitkindad gås* Branta leucopsis

Niklas Liljebäck[1], Kees Koffijberg[2], Christine Kowallik[3], Johan Månsson[1] & Åke Andersson[4]

[1] Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Grimsö 152, 730 91 Riddarhyttan, Sweden | niklas.liljeback@jagareforbundet.se, johan.mansson@slu.se [2] Sovon Vogelonderzoek Nederland, Toernooiveld 1, 6525 ED Nijmegen, the Netherlands | kees.koffijberg@sovon.nl [3] Friedhofstraße 66-b, 46562 Voerde, Niederrhein, Germany | c.kowallik@t-online.de [4] Ringgatan 39C, 752 17 Uppsala, Sweden | akearav@gmail.com

FOLLOWING THE USE of Barnacle Geese *Branta leucopsis* as foster parents in a conservation program for the endangered Lesser White-fronted Goose *Anser erythropus* in Sweden 1981–1999, mixed breeding pairs of the two species were established in the wild. We find indications that this was related to shared moulting habits of the two species in the Bothnian Sea during late 1990s. Starting in 2003, five mixed pairs produced at least 49 free-flying hybrid offspring until 2013, when the last breeding was confirmed. Reported numbers of hybrids did not increase in parallel to the production of young hybrids over time. After 2013, the number of hybrids started to decrease in Sweden and the Netherlands. Lower numbers of hybrids than expected can partly be explained by management actions taken, but may also be associated with low survival due to genetic outbreeding. Mixed pairs and their offspring entirely

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adopted the migratory habits of Barnacle Geese, overlapping very little with sites used by Lesser White-fronted Geese. We find no evidence that the hybrids ever posed a serious threat to Lesser White-fronted Geese breeding in Fennoscandia.

Keywords: translocation | intergeneric hybrid | distribution | wintering grounds | migration route | Anatidae

Introduction and background

Hybridization has been highlighted as a potential threat to endangered taxa (Allendorf *et al.* 2001, Jackiw *et al.* 2015). Under certain conditions, hybrids may constitute an issue for conservation of small populations and translocations of captive-bred individuals may be of special concern in this context (IUCN/SSC 2013). Even if hybridization is a natural and pronounced process in the genetic ancestry of goose species (Ottenburghs *et al.* 2016a), introgression of alien genes may alter species barriers or diminish population-specific adaptations (e.g. Muñoz-Fuentes *et al.* 2007, Todesco *et al.* 2016). One case where hybrids have gained special attention in relation to translocations concerns hybrids between Lesser White-fronted Goose *Anser erythropus* and Barnacle Goose *Branta leucopsis* (hereafter LWfG × BG). The existence of hybridizing pairs and their offspring have provoked disputes regarding the potential threat they may pose to the small, and highly endangered, populations of Lesser White-fronted Goose breeding in Fennoscandia (Jones *et al.* 2008).

Geese and ducks are among the bird taxa most likely to hybridize in nature (Randler 2008, Nijman *et al.* 2010, Ottenburghs *et al.* 2016a) and recurrent hybridizations may account for their low level of genetic differentiation (Ruokonen *et al.* 2000, Gonzalez *et al.* 2009). Contrary to hybridization among ducks, the extent of hybridization in geese is poorly understood (for review, see Ottenburghs *et al.* 2016b). Only recently, more insight has emerged, both from geese in the wild and in captivity (Kampe-Persson & Lerner 2007, Ottenburghs *et al.* 2016b, Ottenburghs 2017). The Lesser White-fronted Goose is one of the goose species that has been observed to hybridize with other goose species. Hybrids, either in the wild or in captivity (or presumably originating from captivity), have been reported with Greater White-Fronted Goose *Anser albifrons*, Greylag Goose *A. anser*, Snow Goose *A. caerulescens*, Bar-headed Goose *A. indicus*, Emperor Goose *A. canagicus*, Brent Goose *Branta bernicla*, Barnacle Goose, and Red-breasted Goose *B. ruficollis* (McCarthy 2006, Kampe-Persson & Lerner 2007, Nijman *et al.* 2010, Ottenburghs *et al.* 2016a, Ottenburghs 2017).

Being a threatened species, a conservation program for the Lesser White-fronted Goose breeding in Sweden (*Projekt Fjällgås*) was launched by the Swedish Association for Hunting and Wildlife Management in the late 1970s (von Essen 1991). Its main objective was to decrease mortality caused by observed severe

hunting pressure on stopover and wintering sites along known eastern migration routes (Jones *et al.* 2008). To meet this objective, the Swedish conservation program adopted a translocation approach, using semi-domestic Barnacle Goose pairs as foster parents, with known wintering areas in Western Europe (mainly the Netherlands; von Essen 1991). In 1981, the first captive-bred goslings were released together with their foster parents in Swedish Lapland, in an area that was still inhabited by breeding Lesser White-fronted Geese at that time (von Essen 1991, Andersson & Holmqvist 2010). The project was successful in the sense that released young Lesser White-fronted Geese adopted the migration route presented by their foster parents and subsequently established a wintering tradition in the Netherlands. Following this human-mediated migration route, the population avoided the previously observed high mortality during migration. Consequently, the population size slowly started to increase (von Essen 1991, Koffijberg *et al.* 2005, 2006). However, the use of foster parents also had the unfortunate effect that a small number of captive-bred male Lesser White-fronted Geese became erroneously imprinted on the foster parent species and later paired with female Barnacle Geese and successfully produced hybrid offspring.

Hybrid families were frequently reported from staging sites in Sweden and from wintering areas in the Netherlands. As a response, the Swedish conservation program decided at an early stage to remove Lesser White-fronted Goose males in mixed pairs, and their offspring, whenever possible.

Kampe-Persson & Lerner (2007) provide a general overview of goose hybrids recorded in Sweden, including LWfG × BG hybrids. So far, no attempt has been made to investigate numbers and dispersal of LWfG × BG hybrids in detail, nor to evaluate whether the culling of mixed pair males and their hybrid offspring were successful to reduce putative conservation problems.

In this study, we investigate the occurrence of free-flying hybrids of LWfG × BG in Western Europe. Based on datasets retrieved from citizen science portals and goose census schemes, we analyse numbers, dispersal/distribution, and trends in six different countries. Furthermore, archives of the Swedish conservation program were searched for additional information about the sites used by mixed pairs and annual production of hybrid offspring. We compare data on reproduction with the information gathered during staging and wintering along the migration route. Based on our findings we discuss whether the hybrids with Barnacle Geese pose a risk in the conservation of Lesser White-fronted Goose populations breeding in Fennoscandia.

Material and methods

DATA ON MIXED PAIRS ON BREEDING SITES

Between 1981 and 1999, a total of 301 young Lesser White-fronted Geese were released in Swedish Lapland. Of them, 257 were released accompanied by their Barnacle Goose foster parents. The remaining 44 young were released in the same area but without company of, or having been associated with, foster parents. All goslings carried individual combinations of colour rings. The 44 birds released without foster parents generated few resightings and are not treated further in this study.

Mainly volunteer ring readers along the flyway reported resightings of ringed Lesser White-fronted Goose individuals (including information on family status). Reports were filed and stored in a database by the conservation program. From this database we retrieved data on the number of ringed Lesser White-fronted Goose males in mixed pairs, including information about documented number of hybrid offspring produced on an annual basis. In addition, we found information about (1) site use by Lesser White-fronted Goose males, (2) when Lesser White-fronted Goose males in "mixed pairs" were culled, and (3) culling of hybrids, but also (4) supporting information, e.g., about local movements (see also Andersson 2019).

Culling of Lesser White-fronted Goose males in mixed pairs, and hybrids, was carried out under the legal framework of permissions granted by the Swedish Environmental Protection Agency (2006–2011; Dnr 412-1257-07, 412-3431-09, and 412-3412-10) and later (2011–2015) by County Administrative Boards of Jämtland, Gävleborg, Uppsala, Västra Götaland and Skåne.

CITIZEN SCIENCE DATA ON OBSERVED HYBRIDS FROM STAGING AND WINTERING SITES

From about 2000 onwards many European countries have launched web-based species gateways (data portals) where the public can report observed species with various additional information. Most reports are

submitted by enthusiastic volunteers but some also by professional conservation officials and researchers. Even though citizen science data are non-systematic, the large data volume provide useful information especially for rarer taxa, including hybrids (e.g. Snäll *et al.* 2011). We extracted data from such species gateways in Norway (https://www.artsobservasjoner.no), Sweden (https://www.artportalen.se), Finland (https://www.tiira.fi), Denmark (https://dofbasen.dk), Germany (https://www.ornitho.de) and the Netherlands (https://waarneming.nl) until spring 2017. Furthermore, a large number of ornithological reports (e.g., national, regional, or local annual bird reports) were screened for information. For the Netherlands, we also retrieved records from the national waterbird monthly census scheme, co-ordinated by Sovon Vogelonderzoek Nederland (e.g. Hornman *et al.* 2020). From these sources 1,303 reports were extracted (including obvious mis-identifications; see Table 1 for a complete overview of data sources and references used).

Since proper identification of hybrid geese may pose a significant challenge (McCarthy 2006), a verification was carried out for observations associated with photographic documentation. Moreover, specific remarks on observation details were checked, e.g., when administrators of the species gateways had approved, or added comments about, observations. From the 1,303 reports scrutinized for our analyses (Table 1), 37 reports (3%) undoubtedly referred to hybrids of other goose species. For Germany in the period 2011–2017 many reports included photos and 26% of all records submitted involved other goose species. Common mistakes were misidentification of Greylag Goose × Canada Goose *Branta canadensis* and Greylag Goose × Barnacle Goose, but also Barnacle Goose × Snow Goose or Ross's Goose *A. caerulescens/rossii*. Certainly, the most challenging hybrid type for identification in the context of this study relates to hybrids of Barnacle Goose × Greater White-fronted Goose. In Germany and the Netherlands, hybrid young of mixed pairs of these two species were indeed sometimes found in reports (documentation showing the adults as well), but hybrid offspring was none the less reported as Lesser White-fronted Goose hybrids, likely because observers were aware of this hybrid type and its conservation issues. In this study, we assume that all reports lacking documentation or additional remarks made by administrators, were correctly identified hybrids and hence included them in the

TABLE 1. Overview of data sources used in the study to describe distribution of hybrids between Lesser White-fronted Goose *Anser erythropus* and Barnacle Goose *Branta leucopsis*. We present the total number of reports (including multiple records of the same flock or individuals) for each region before examination are stated, followed by the number of rejected reports within brackets. Rejection of reports was based on verification of photos or through enquiries to observers. Note that data was downloaded in 2017–2018, consequently reports in later years are not covered.
— Översikt för datakällor för att beskriva utbredningen av hybrider mellan fjällgås Anser erythropus *och vitkindad gås* Branta leucopsis*. Det totala antalet rapporter (som kan inkludera flera rapporter gällande samma flock eller individ) för varje region anges, följt av antalet rapporter som uteslutits inom parentes. Uteslutning av rapporter baserades på granskning av fotografier eller på direktförfrågningar till observatörer. Notera att dessa data laddades ned 2017–2018 och att rapporter sålunda kan ha tillkommit efter vårt datauttag.*

Country *Land*	Period *Antal*	N reports (N rejected) *N rapporter (N uteslutna)*		Data sources *Datakällor*
Norway	2000–2017	0	(0)	artsobservasjoner.no
Finland	2006–2017	1	(0)	tiira.fi
Sweden	2000–2017	864	(18)	artportalen.se, Swedish conservation program database
Denmark	2008–2016	20	(3)	dofbasen.dk
Germany: Schleswig-Holstein	1998–2009	17	(0)	Bruns & Berndt (1999), Berndt *et al.* (2001), Bruns *et al.* (2002), Koop *et al.* (2007), Koop *et al.* (2009), Jeromin *et al.* (2014)
Germany: Niedersachsen	2000–2007	3	(0)	Krüger & Kruckenberg (2011)
Germany (all parts)	2011–2017	31	(11)	ornitho.de
The Netherlands	1999–2017	330	(5)	Koffijberg *et al.* (2005), waarneming.nl,

analysis. The identified errors show that we should be careful about the absolute numbers presented, especially as the majority of reports lacked any documentation to support identification.

Observer bias is an underlying potential weakness in any analyses based on data from public gateways. The reporting rate of hybrids to the online platforms may have changed over time, e.g., as observers became more aware of the conservation issues with specific hybrids of Barnacle Goose and Lesser White-fronted Goose as described above. However, as the hybrid families were intensively monitored by the Swedish Lesser White-fronted Goose project and individual observers—and enquiries were made among observers reporting hybrids in Sweden and the Netherlands—we assume that the data presented here do give a good overview of the trends in numbers and dispersal of hybrids.

For annual estimates of hybrid numbers (Figure 1), we restricted data to reports from Sweden and the Netherlands, which constituted the most long-term and comprehensive datasets. Reports from Norway, Finland, Germany and Denmark were scattered, and in this study only used to describe the geographical distribution of hybrids. In Sweden, our estimated numbers of hybrids and their distribution were verified directly with local ornithologists at most sites, to avoid misinterpretations. Sightings in the Netherlands were screened for possible errors and, when necessary, enquiries with the observer were made to clarify details.

Results

MIXED PAIRS OF LESSER WHITE-FRONTED AND BARNACLE GEESE BREEDING IN SWEDEN

In total, six Lesser White-fronted Goose males (1.7% of all released young with foster parents) were observed to produce hybrid offspring with Barnacle Goose females (Table 2, Figure 2). All the males originated from releases in two consecutive years, 1996 (2) and 1997 (4). One male bred in 1999 at Öster Malma close to Stockholm (Figure 2). This male (ID 431; Table 2) and its two hybrid offspring were taken out immediately at the breeding site, hence these two hybrids were not included in estimated production of free-flying hybrids (Figure 1). From 2002 and onwards one or more of the

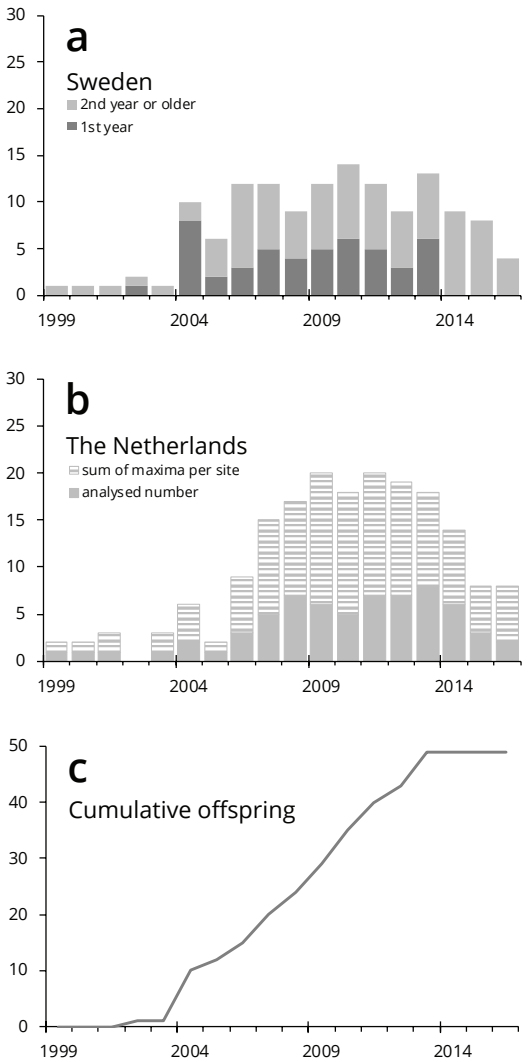

FIGURE 1. Number of hybrids of Lesser White-fronted Goose *Anser erythropus* × Barnacle Goose *Branta leucopsis* 1999–2016 in (**a**) Sweden during the post-breeding period, separated for adult (light grey) and first-year birds (dark grey), and (**b**) the Netherlands during wintering. The Dutch numbers are the estimates used in our analyses (solid grey), and additionally the highest possible number (hashed grey), based on maximum numbers at each site, a total which includes potential duplicate counts and likely is a biased overestimation. For comparison, we show (**c**) the cumulative number of hybrids produced in Sweden (cf. Table 2). — *Antal hybrider av fjällgås* Anser erythropus × *vitkindad gås* Branta leucopsis *1999–2016 (**a**) i Sverige under sommar och höst, fördelat på adulta (ljusgrå staplar) och årsungar (mörkgrå staplar), och (**b**) från övervintring i Nederländerna. Vintersiffrorna visar den uppskattning vi använt (fyllda ljusgrå staplar) samt det högsta möjliga antalet baserat på de högsta summorna från varje enskild lokal, vilket troligen inkluderar dubbelräknade individer och sålunda en överskattning. För jämförelse anges (**c**) det kumulativa antalet hybrider som blivit flygga i Sverige (jfr tabell 2).*

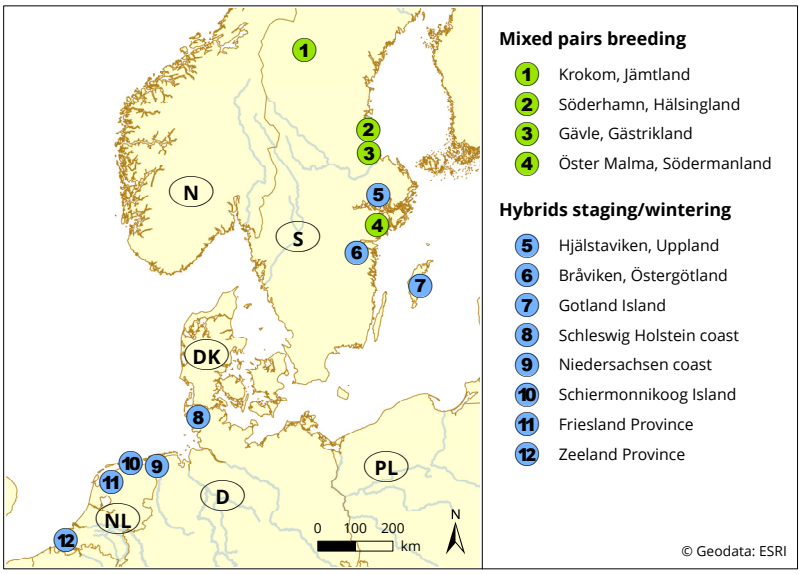

FIGURE 2. Map depicting sites mentioned in this paper, with regard to mixed pairs of Lesser White-fronted Goose *Anser erythropus* × Barnacle Goose *Branta leucopsis* and hybrids between the two species. — *Karta som visar lokaler nämnda i denna studie, med avseende på blandpar av fjällgås* Anser erythropus × *vitkindad gås* Branta leucopsis *och deras hybridavkomma.*

other five males were observed to breed (Table 2) in colonies of Barnacle Geese in the archipelago near Söderhamn and Gävle, along the southwestern coast of the Bothnian Sea, or at one site close to Krokom in Jämtland County (Figure 2, Table 2). In total, 42 hybrid offspring could be assigned to the known mixed breeding pairs in the period 2002–2013. The number of young and the number of years with successful breeding varied among mixed pairs, with one pair raising in total 15 hybrids during six breeding seasons (male 841, Table 2). In addition, seven (5+2) hybrid offspring were reported but without the ID (colour ring code) of the male Lesser White-fronted Goose having been determined. Thus, our data indicate a total production of at least 49 fledged and free-flying LWfG × BG hybrids in Sweden between 2002 and 2013.

Besides the birds released within the Swedish conservation program, an early mixed breeding pair in Sweden was reported already in 1985. According to Kyrk (1987) and Kampe-Persson & Lerner (2007) this pair consisted of an escaped Lesser White-fronted Goose male (from a park) breeding with a female Barnacle Goose in a feral population of the latter species close to Stockholm, thus having no connection to the Swedish conservation program. The few and scattered reports (n = 14, 1985–2000) of single hybrids in Sweden in the years before 2000 likely refer to offspring from this pair, as do individuals observed in the Netherlands in 1999–2001 (see Figure 1).

NUMBERS AND PHENOLOGY AT STAGING AND WINTERING SITES

Reports of hybrids LWfG × BG were made annually from the winter 2004/2005 onwards (Figure 1). In Sweden, after the first known mixed breeding in the wild (in 2002, see Table 2), the number of hybrids jumped from zero in 2003/2004 to ten in 2004/2005 (including two older hybrids not reported earlier but probably from the breeding in 2002). Our data suggest that mixed pairs were successfully breeding annually from 2004 to 2013 (Figure 1). Numbers of recorded juvenile hybrids varied between 2 and 8 individuals per year during this period. The last Lesser White-fronted Goose male producing hybrid offspring likely died during the breeding season 2013, as juvenile hybrids were found with a solitary Barnacle Goose during autumn and no young were reported in 2014 or following years (cf. Table 2). The total estimated numbers (juveniles and older birds) in Sweden varied between 0 and 14 individuals during 2000/2001–2016/2017 with the peak number of 14 hybrids in 2010/2011 (Figure 1).

In the Netherlands, hybrids were reported annually from 2003/2004 onwards. The highest numbers were recorded between 2008/2009 and 2013/2014 (maximum of 8–15 birds per year, Figure 1) followed by a gradual decrease. The numbers in the Netherlands and Sweden correlated well (1999–2016, n = 18, $r = 0.78$, $p < 0.001$), but were significantly lower in the Netherlands (3–10, mean: 7.0) than in Sweden (2–14,

TABLE 2. Descriptive data on all six Lesser White-fronted Goose *Anser erythropus* males known to breed with Barnacle Goose *Branta leucopsis*. (BG). All males released as part of the Swedish conservation program carried individually coded colour rings. Brood size listed by size, and not chronological order. See Figure 2 for the location of breeding sites.
— Deskriptiva data för alla sex fjällgåshannar Anser erythropus *som bekräftats samhäcka med vitkindad gås* Branta leucopsis *(VG). Alla hannar som släppts ut som en del av det svenska artbevarandeprogrammet bär individuella färgringskombinationer. Kullstorlek listas i storleksfördelning, inte i kronologisk ordning. Se figur 2 för häckningsplatsernas belägenhet.*

Ring ID *Ring ID*	Release year (as 1CY bird) *Utsläppsår (som 1K)*	Year, first known pairing with BG (age, years) *År för första kända häckning med VG (ålder)*	N years with known hybrid offspring *Antal år med känd hybrid-avkomma*	Known N hybrid offspring *Antal kända hybrid-avkommor*	Known brood size *Känd kullstorlek*	Breeding site *Häckplats*	Known destiny *Känt öde*
405	1996	2004 (8)	2	4	2+2	Krokom	Culled 2007
431	1996	1999 (3)	1	(0[1])	2	Öster Malma	Culled 1999
838	1997	2004 (7)	3	6	2+2+2	unknown[2]	Culled 2007
840	1997	2005 (8)	3	9	2+2+5	Söderhamn	Culled 2007
841	1997	2004 (7)	6	15	1+1+2+3+3+5	Söderhamn	Last report December 2012
844	1997	2002 (5)	3	8	1+3+4	unknown[2]	Last report 2008[3]

[1] The two hybrids were trapped when hatched, kept in captivity, and later killed.
De två hybriderna infångades vid kläckning, hölls i fångenskap, och avlivades sedermera.
[2] Breeding sites not known but male 838 was observed with young offspring close to Gävle and male 844 close to Gävle and Söderhamn.
Häckplatserna är okända, men hanne 838 observerades med ung avkomma nära Gävle och hanne 844 nära Gävle och Söderhamn.
[3] Male 844 lost colour rings in summer 2008, whereafter it only carried a metal ring and was less likely to be identified in the field.
Hanne 844 förlorade färgringar sommaren 2008, varefter den endast hade en metallring och därför var svårare att identifiera i fält.

mean: 8.7). Four hybrids were culled in Sweden prior to 2015, and another eight during 2015–2017. The cumulative number of hybrids produced was not reflected by increasing numbers being observed, neither at staging sites in Sweden nor at wintering sites in the Netherlands. Instead, the numbers in both countries remained at fairly stable levels, but started to decrease immediately after the last known successful breeding in 2013 (Figure 1).

In Sweden, observations of hybrids were mainly done during the post-breeding period in August, lasting until onset of autumn migration in September–October, and during April–June. In the Netherlands, most arrivals were recorded in October, likely to directly follow departures from Sweden, where number of reports decreased simultaneously (Figure 3). Monthly number of reports in the Netherlands showed a typical pattern for wintering birds, with birds leaving the country again mainly in April and May, associated with departure of Barnacle Goose flocks. Concurrently, numbers in Sweden increased again, especially in April (Figure 3).

DISPERSAL AND DISTRIBUTION

The majority of reports on LWfG × BG hybrids originated from Sweden (68%, N = 1,266) and the Netherlands (26%; Table 1, Figure 4b). Scattered observations were also reported from Germany (4%) and Denmark (2%). Only one observation was reported from Finland and none from Norway. The distribution of hybrids (Figure 4b) shows large similarities with the resighting data of the ringed male Lesser White-fronted Geese of the mixed pairs (Figure 4a) with absolute majority of reports in Sweden and the Netherlands. Apart from that, we find higher numbers of reports and a more scattered distribution for hybrids compared to their parents (Figure 4). In Sweden, clusters of reports and/or high number of hybrids were mainly found along the Bothnian Sea coast, close to the cities of Gävle and Söderhamn and an area near Krokom in the province of Jämtland, reflecting the known breeding sites of mixed pairs (Figures 2, 4). Swedish clusters also include three stopover sites: Lake Hjälstaviken in the province of Uppland, the coastal bay Bråviken in the province of Östergötland and the island Gotland

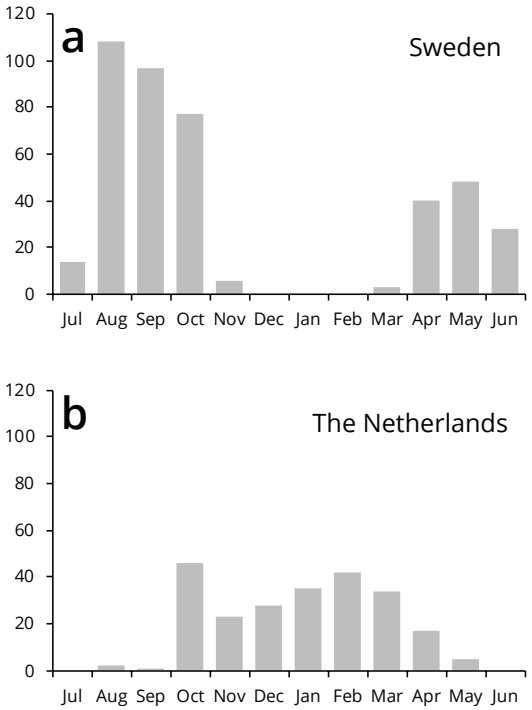

FIGURE 3. Monthly number of reports (sum of all records per month) of hybrid Lesser White-fronted Goose *Anser erythropus* × Barnacle Goose *Branta leucopsis* in (**a**) Sweden and (**b**) the Netherlands, 1999/2000–2016/2017.
— Antal rapporter per månad (summerat över år) av hybrider fjällgås Anser erythropus × *vitkindad gås* Branta leucopsis *i (**a**) Sverige och (**b**) Nederländerna 1999/2000–2016/2017.*

in the Baltic Sea (cf. Figure 2). Further south, clusters of reports are found along the Wadden Sea coast in southern Denmark and the coasts of Schleswig-Holstein and Niedersachsen in Germany (during spring migration, cf. Figure 2) and in the Wadden Sea area and Delta area of the Netherlands (autumn and winter). Lake Hjälstaviken was the single most important site in Sweden, with 554 (64%) of 864 reports, and confirmed records of all but one of the five known mixed breeding pairs. In the Netherlands, most sightings of hybrids were made at the West Frisian island of Schiermonnikoog in Wadden Sea (106 of 330 reports, 32%, cf. Figure 2). At Lake Hjälstaviken, the maximum count was eight hybrids at a single occasion, at Schiermonnikoog Island the corresponding number was six individuals.

Discussion

ESTABLISHMENT OF LESSER WHITE-FRONTED × BARNACLE GOOSE PAIRS AND HYBRID DISPERSAL

Our analyses indicate increasing numbers of hybrid LWfG × BG from 2004/05 until 2013/2014, especially in Sweden (breeding, post-breeding, and staging) and in the Netherlands (wintering). These two countries supported the most important staging and wintering sites for both Barnacle Goose and Lesser White-fronted Goose from the Swedish breeding population during this period (Ganter *et al.* 1999, Koffijberg *et al.* 2006). Even if we need to be careful about the precision in our annual estimate of numbers of hybrids, as our data mainly rely on non-systematic observations, we find that the increase of hybrids coincided with the establishment of six mixed breeding pairs in Sweden, all consisting of Lesser White-fronted Goose males and Barnacle Goose females (Table 2). Our finding that only males raised by foster parents established mixed breeding confirms earlier studies (see ten Cate (1985) for review). Fabricius (1991) studied partner preference in geese using an experimental set-up where Greylag Goose goslings were imprinted on Canada Goose parents. In this experiment, 14% of the Greylag goslings—all males—later paired with Canada Geese. Hence, we assume that imprinting of the released Lesser White-fronted Goose males, raised by foster parents, have played a key role to explain the establishment of mixed pairs in Sweden. Notwithstanding these assumptions, we find that additional circumstances may have further enhanced the establishment of mixed pairs between the two species.

The observation that all males involved in mixed pairs originated from two specific years calls for an explanation. Conditions in Swedish Lapland and methods used by the project during the release in 1996 and 1997 were similar to other years (Andersson 2019). Hence, we cannot find any details in the performance of the release projects per se that may have induced a change of behaviour of the released birds.

We speculate that contemporary use of sites by non-breeding birds of the two species during summer likely initiated social bonding for Lesser White-fronted Geese males to Barnacle Goose flocks. During late 1990s, when mixed pairs were established, the Barnacle Goose population was expanding its breeding

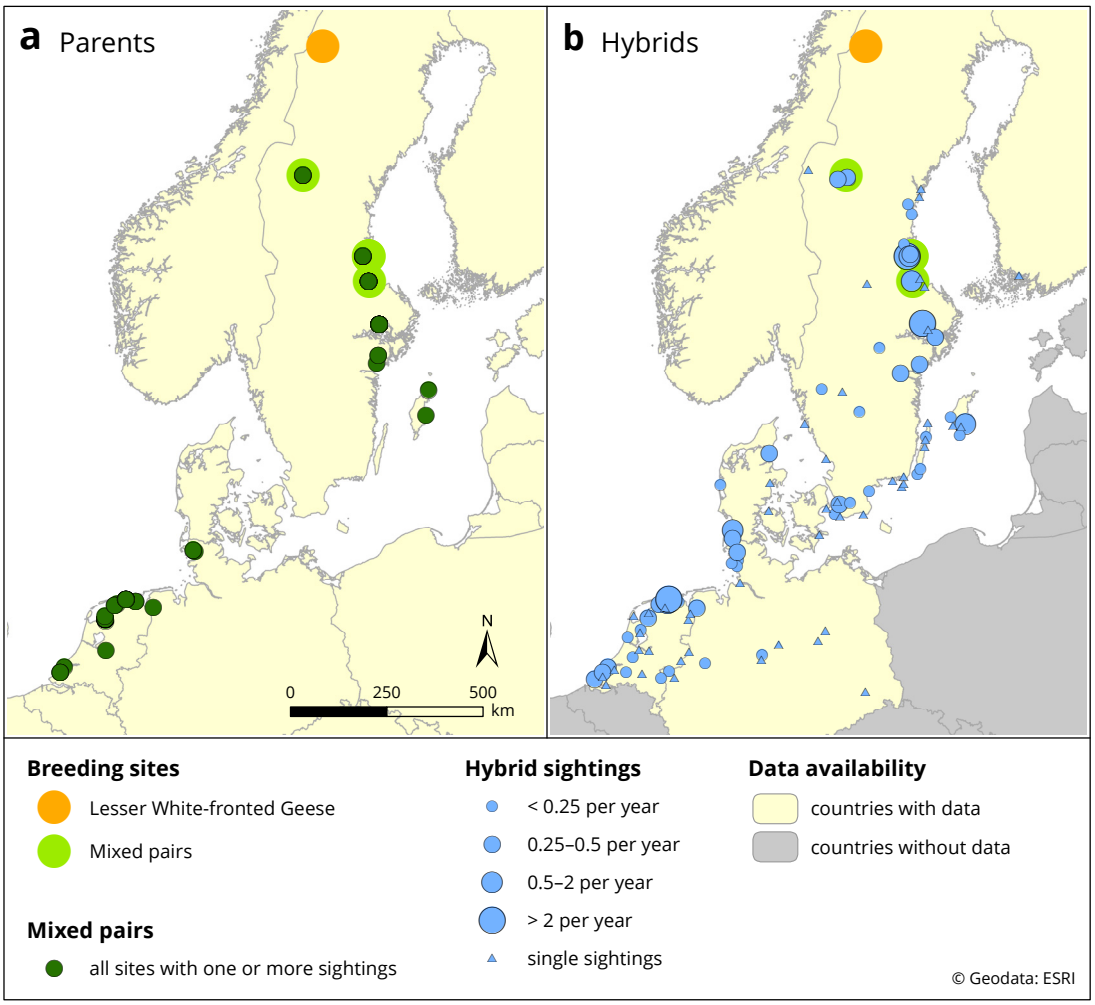

FIGURE 4. (**a**) Known breeding sites of mixed pairs of Lesser White-fronted Goose *Anser erythropus* and Barnacle Goose *Branta leucopsis* (light green circles, see also Figure 2), with the breeding area for Lesser White-fronted Goose in Arjeplog Mountains in Lapland (orange circle) shown for comparison. Dark green circles indicate reports of ringed Lesser White-fronted Goose males producing hybrid offspring. (**b**) All records of Lesser White-fronted Goose × Barnacle Goose hybrids in our study, i.e. until 2016/2017, with the size of blue circles indicating the number of sightings per year.

*— (**a**) Kända häckplatser för blandpar av fjällgås* Anser erythropus *och vitkindad gås* Branta leucopsis *(ljusgröna cirklar, se även figur 2), med fjällgässens häckningsområde i Arjeplogsfjällen i Lappland (orange cirkel) markerat för jämförelse. Mörkgröna cirklar indikerar rapporter av ringmärkta fjällgåshannar som producerat hybridavkomma. (**b**) Alla rapporter av hybrider fjällgås × vitkindad gås i vår studie, dvs. till 2016/2017, med antal rapporter per år representerade som olikstora blå cirklar.*

distribution in Sweden (Bengtsson 2007), at least partly due to naturalized populations of the species (Kampe-Person 2021). Breeding pairs settled along the southwest coast of the Bothnian Sea (e.g., around Gävle and Söderhamn), but also at inland sites (BirdLife Sweden 1998–2005). As a result, there were several new and small, but growing, populations of Barnacle Geese in these regions. At the same time, an increasing numbers of non-breeding Lesser White-fronted Geese (including previously released birds) were found to use the same region in the Bothnian Sea during summer. Because of these parallel changes in spatial distribution of the two species, the likelihood for initiation of pair bonding across the species barriers increased. Even if

the pairs were not established during their first summer, the Lesser White-fronted Goose males may have established social bonds to the Barnacle Goose flocks, followed by true pair bonds forming in later years. At least for Barnacle Geese, it is known that more than half of the pair bonds are established during summer (Black *et al.* 2014). In addition, the period of primary moult is known to facilitate exchange of geese from different flyways, probably due to males being attached to females and thereby also adopting their migration traditions (Koelzsch *et al.* 2019). As female site fidelity is high in goose species and typically determine the future breeding site (Black *et al.* 2014), pair bonds established during moulting may explain the breeding distribution of mixed pairs as found in this study.

All five Lesser White-fronted Goose males (all with individual codes of coloured leg rings) that later paired with Barnacle Goose females, and produced free-flying hybrids, were observed at sites in the northern part of the Netherlands during their first winter after being released. Even if our data do not allow a precise determination of when the winter distribution of these males changed, we still find that mixed families with young concentrated in the province of Friesland whereas sites earlier used by the males were abandoned. The regular wintering flock of Lesser White-fronted Geese, on the other hand, continued to use their own network of wintering sites (Koffijberg *et al.* 2006, Koffijberg & van Winden 2013). Especially the Wadden Sea island of Schiermonnikoog (Friesland) stands out in numbers of reported hybrids (32% of all observations in the Netherlands, Figure 4). On this island, the proportion of Barnacle Geese originating from the Baltic (Swedish) breeding sites was larger than birds of Russian origin, as demonstrated by colour ring sightings (van der Jeugd *et al.* 2001). Thus, when paired with female Barnacle Geese, the male Lesser White-fronted Geese merely became a functional part of the Barnacle Goose flocks and adopted their network of stopover and wintering sites as well as breeding area.

This quick change in site use may explain the low degree of overlap of mixed pairs (and later hybrids) in relation to sites used by Swedish Lesser White-fronted Geese. In Sweden, hybrids have only been reported in three out of nine stopover sites regularly used by Lesser White-fronted Geese (Lake Hjälstaviken, Alnön near Sundsvall, and the Bråviken area, cf. Figure 2). Of these sites, both Lesser White-fronted Geese and hybrids (perhaps even all mixed pairs and hybrid offspring) frequently used only Lake Hjälstaviken. In the breeding area (and release site) of Lesser White-fronted Goose in the mountains of Arjeplog at 66°N, no hybrids or mixed pairs have been found despite high observer effort in the field during all years. The same applies to known Lesser White-fronted Goose pre-breeding areas like Ammarnäs and the important moulting site in Hudiksvall (cf. Figure 2). The northernmost site where LWfG × BG hybrids occurred was Krokom in Jämtland, at 63.2°N (cf. Figures 2, 4). Shared stopover sites were also found in the German Wadden Sea (important for Barnacle Geese as well; Ganter *et al.* 1999), but not at the important spring staging site for Lesser White-fronted Goose at Lolland/Falster (Roden Fed) in Denmark. From the seven regular wintering sites of Lesser White-fronted Goose in the Netherlands (see Koffijberg *et al.* 2006), mixed pairs or hybrids were only reported from Anjumerkolken and Ferwoude in Friesland and from Korendijksche Slikken in Zuid-Holland. Hybrids were never observed in Oudeland van Strijen in Zuid-Holland or Petten in Noord-Holland, which represent the core wintering sites in the Netherlands for Lesser White-fronted Geese (Koffijberg & van Winden 2013).

We found surprisingly few reports of LWfG × BG hybrids in Norway (0) and Finland (1), which suggest a high fidelity to migration routes and staging sites and hence a low degree of natal dispersal. In this context it is also important to note that Norway is within the Svalbard flyway of Barnacle Geese, which shows little overlap with the Russian–Baltic–North Sea flyway of the species (Black *et al.* 2014). Occasional sightings of Anser hybrids (likely LWfG × BG) are also known from the Russian breeding areas of Barnacle Geese (H. van der Jeugd, *pers. comm.*), but it is unknown whether these hybrids stem from mixed breeding pairs in Russia, Sweden, or elsewhere. Scattered reports in the more interior parts of Germany (Figure 4), where Barnacle Geese were rare in the past decades, may originate from captive populations. Both Lesser White-fronted Goose and Barnacle Goose are known to hybridize with other species in the wild and in captivity (McCarthy 2006, Kampe-Persson & Lerner 2007, Ottenburghs *et al.* 2016b). Hence, observations of hybrids are not necessarily linked to the Swedish conservation program for

Lesser White-fronted Goose but may originate from captive or naturalized populations.

PRODUCTION AND DEPLETION OF HYBRIDS

Our data indicate that from 1999 to 2013, at least 49 LWfG × BG hybrids were produced in Sweden (Figure 1). Even if a relatively high number of hybrids were produced over the years, this was not followed by a subsequent increase in the number of birds reported in the field. Instead, numbers remained at a rather stable level, followed by a decline after the last confirmed breeding in 2013 (Table 2, Figure 1). This can, at least partly, be attributed to management actions, as three of the five Lesser White-fronted Goose males in mixed breeding pairs were culled in 2007 (Table 2). however, our data suggest that this only had minor effect since a single male (ID 841; Table 2) was the father of most hybrids both before and after 2007. Furthermore, culling of 12 hybrids probably accelerated the depletion of hybrids, but the active removal of hybrids alone cannot explain the lack of coherence between the cumulative and reported numbers of hybrids (cf. Figure 2).

The observation effort and coverage by ornithologists in the Netherlands and Sweden are high, as well as the readiness to report rare taxa as hybrids (Snäll *et al.* 2011). Therefore we assume that the presented data mirror a representative development over time. We find only weak evidence for dispersal of hybrids outside the main migration route (see above). The annual survival in migratory Barnacle Geese is estimated to about 0.90 (Ebbinge *et al.* 1991). For Lesser White-fronted Geese, annual survival estimates in the 1990s and early 2000s ranged from 0.62 (first-year birds) to 0.89 (2nd year; Schekkerman & Koffijberg 2019). If survival rates of any of the parent species would apply to the hybrids, the annual number of observed birds would have kept more in pace with the cumulative number of offspring produced. Consequently, this suggests that survival of hybrids may have been low.

Hybrids of species with high genetic distances may show low survival and fitness due to outbreeding depression (Allendorf *et al.* 2001). Outbreeding depression occurs when breakdown of co-adapted gene complexes, often related to immune system, or loss of species- or population-specific adaptations, put negative pressure on the individual (Todesco *et al.* 2016). Since *Branta* and *Anser* species show relatively high genetic distances (e.g. Ottenburghs *et al.* 2016b), the LWfG × BG hybrids may show lower survival rates compared to birds of the parent species.

CONCERNS FOR CONSERVATION

Observations in Sweden 2017–2019 suggest that 1–3 hybrids may still be alive, being recorded in Barnacle Goose flocks. In the Netherlands, at least one well-documented report from a single hybrid was made in autumn and winter 2017/2018. It is not known if these birds are linked to the former mixed breeding pairs in Sweden or are of other origin. Mixed breedings in Sweden have not been reported since 2013 and the method of using foster parents was abandoned in 2000. Hence, the risk of establishment of new mixed breeding pairs in the wild is very low.

In retrospect, even when hybrids were most numerous, we find no evidence that they ever posed a serious risk to the small breeding populations of Lesser White-fronted Geese in Fennoscandia, as suggested by Jones *et al.* (2008). This conclusion finds support in a recent genetic study where no signs of introgression, from any goose species, were detected in Lesser White-fronted Geese breeding in Sweden and Norway (nor Russia; Díez-del-Molino *et al.* 2020). Consequently, the hybrids in this case never influenced the genetics of the endangered taxon in focus of conservation efforts. Nonetheless, in theory, the outcome and scenario may have been different should no actions have been taken, and/or if survival and fitness of the hybrids had been higher. Our study shows that any translocation program using foster parents should seriously take into account the risk that hybrids between the target and foster species may be produced and pose a problem for conservation.

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Svensk sammanfattning

Under perioden 1981–1999 användes adoptivföräldrar av vitkindad gås *Branta leucopsis* till fjällgåsungar *Anser erythropus* som sattes ut i ett svenskt artbevarandeprojekt kallat *Projekt Fjällgås*. Tanken med denna oortodoxa bevarandeåtgärd var att utsättningarna inte bara demografiskt skulle förstärka det vilda beståndet av fjällgås utan också ändra flyttvanorna i den svenska populationen. Metodvalet innebar att fjällgäss började övervintra i Nederländerna och den höga dödlighet som belastat fennoskandiska fjällgäss under flyttning utmed mer östligare flyttvägar minskade. Den svenska fjällgåspopulationen började långsamt öka i antal.

Användandet av adoptivföräldrar fick dock en oönskad sidoeffekt då några fjällgåsindivider sedan bildade par med vitkindade gäss. I det internationella åtgärdsprogrammet för fjällgås beskrivs hybrider som ett potentiellt hot i bevarandearbetet för fjällgås.

Data från internetbaserade rapporteringsportaler har laddats ner och fågelrapporter har genomsökts för att hitta rapporter av hybrider. *Projekt Fjällgås* databaser och arkiv har genomsökts för att hitta all information kring den hybridbildning som skedde.

I samtliga fall när en lyckad häckning mellan fjällgås och vitkindad gås har rapporterats har hanen i paret varit en utsättningsfågel från *Projekt Fjällgås* och burit en individuell kombination av färgringar. Att det bara är hanar som bildar par med sin adoptivart är i linje med tidigare studier av gäss. Vår sammanställning visar att totalt sex fjällgåshanar (1,7 % av det totala antalet utsatta fjällgäss 1981–1999) bildade par som producerade hybridungar. I ett av fallen kunde hela familjen direkt avlivas (detta skedde 1999 och dessa hybridavkommor kan inte tillräknas som friflygande). Av de resterande fem fjällgåshanarna kunde tre avlivas 2007. De sista rapporterna av samhäckning återfinns 2013, då en ensam vitkindad gås sågs med ung hybridavkomma.

Vi uppskattar att totalt minst 49 friflygande hybridungar blev flygga i Sverige under perioden 2000–2013. För 42 av dessa hybrider kan vi spåra vilken av fjällgåshanarna som är fader och för de resterande sju (två olika kullar med fem och respektive två ungar) kunde inte hanens identitet avgöras säkert. Den första häckningen i det vilda skedde 2002 och från 2004 rapporterades hybrider årligen med största antalet, 14 hybrider, 2010. Antalet hybrider rapporterade i Nederländerna korrelerar väl med antalen i Sverige över tid, men medelvärdet för perioden var lägre i Nederländerna (7,0) jämfört med Sverige (8,7). Efter den sista kända häckningen 2013 minskar antalet hybrider relativt snabbt.

Troligen är den enskilt viktigaste förklaringen till varför dessa fjällgåshanar bildade par över artbarriärer deras livshistoria med adoptivföräldrar. En bidragande förklaring kan vara att ungefär samtidigt som dessa hybridpar etablerades, expanderade häckningsområdet för vitkindade gäss, inte minst via spridning utmed kusterna i södra Norrland. Parallellt med detta började en del fjällgäss, även utsättningsfåglar, rugga i samma områden där kolonier av vitkindade gäss bildades. Dessa två utbredningsökningar skedde i slutet av 1990-talet. Det är troligt att fjällgäss då tillbringade somrarna sida vid sida med vitkindade gäss och parbildning skedde. Hos gäss är det honorna som bestämmer häckningsplats, flyttväg och övervintringsplats, och de uppvisar ofta stor ortstrohet. Sannolikt är det vitkindade gåshonors ortstrohet som sedan bestämde hybridavkommornas utbredning, vilket förklarar den låga graden av överlapp med fjällgåspopulationens val av lokaler. Hybriderna har i princip bara setts på platser viktiga för vitkindade gäss och aldrig i fjällgåsens häckningsområde eller på någon av de viktigaste övervintringsplatserna i Nederländerna.

Projekt Fjällgås har på olika sätt försökt minska antalet hybrider. Dels avlivades fyra av fjällgåshanarna som producerade hybridavkommor, men även minst 12 hybrider togs av daga. Likväl verkar hybriderna inte ha ökat i antal enligt vad man kan förvänta utifrån överlevnadsanalyser utförda på föräldraarterna. Hybrider mellan arter med stort genetiska avstånd kan förväntas få problem med s.k. utavelseffekter, t. ex. ett sämre immunförsvar. Möjligen kan detta ha bidragit till att antalen inte ökade i paritet med produktionen av unga hybrider. Under de senaste åren, 2018–2020, sågs några få hybrider i vitkindadgåsflockar i Sverige och Nederländerna. Hybrider mellan dessa arter rapporteras ibland på udda platser i västra Europa och dessa kan i många fall härledas till felbestämningar eller till avkommor från hybridpar i frilevande bestånd såsom parkfåglar.

Våra analyser visar att hybriderna troligen aldrig utgjorde ett reellt hot mot fjällgäss som häckar i Fennoskandien. Denna slutsats stöds också av sentida genetiska studier som visar att fjällgäss som häckar i Sverige och Norge inte bär på inslag av hybridgener. Men om inga insatser hade gjorts, och om hybriderna hade haft hög fitness, kunde situationen ha utvecklats annorlunda. Det är därför av största vikt för framtida bevarandeprojekt som tänker använda adoptivföräldrar till utsättningsfåglar att först utföra en riskanalys och förbereda sig för att kunna lösa problem som kan uppstå om hybrider bildas.

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