Whooper Swan *Cygnus cygnus* January population censuses for Northwest Mainland Europe, 1995–2015

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Abstract

Internationally coordinated censuses of Whooper Swans *Cygnus cygnus* across continental northwest Europe were undertaken in mid-winter 1995, 2000, 2005, 2010 and 2015. The estimate of 138,500 birds in 2015, the highest to date, represented a more than doubling of the population size (at an annual increase of 4.1%) since the first census total of 59,000 swans in 1995. The largest increase was in Denmark, where numbers almost trebled from 21,740 in 1995 to 62,620 in 2015. More than 97% of all swans were counted in just six countries. The percentage of total numbers increased significantly between 1995 and 2015 in Denmark (from 36.5% to 45.2%) and Germany (26.0% to 34.7%), but declined significantly in Sweden (14.2% to 8.4%), Norway (13.1% to 3.6%), Poland (6.2% to 4.0%) and the Netherlands (2.4% to 1.7%). The counts show an increasing discrepancy between national trends in abundance for Whooper Swans in Sweden and especially in Denmark in comparison with results obtained only from mid-winter International Waterbird Count (IWC) site coverage. This demonstrates the increasing tendency for Whooper Swans to winter in areas away from traditionally counted IWC sites and confirms the continued need for a regular cycle of coordinated dedicated swan counts to anchor population trends generated from other data sources.

Key words: census, distribution, mainland Europe, population size, Whooper Swan.

The Eurasian (global) population of the Whooper Swan *Cygnus cygnus* breeds continuously across the boreal and sub-boreal region from Iceland (22°W) to Anadyr in Far Eastern Russia (179°W, BirdLife International 2018). From an expedient management point of view, historically the population has been divided into five flyway population units based on discrete geographical wintering ranges. These are defined as the (i) Icelandic breeding population, (ii) Northwest Mainland European population, (iii) North Europe and West Siberian population (wintering in the Black Sea and Eastern Mediterranean) (iv) Western and Central Siberian population Central Russian population (wintering in the Caspian), and (v) East Asian population (Brazil 2003; Rees 2005; Wetlands International 2018). Although not completely discrete, the Northwest Mainland Europe population (hereafter NWMEWS) breeds in Fennoscandia, western Russia and the southern Baltic and winters in Denmark,

Germany, Sweden, Norway, Poland and the Netherlands, with small (but unknown) numbers also regularly occurring in southeast England (Laubek *et al.* 1999; Hall *et al.* 2016).

A recent expansion in breeding range is likely to be a partial recovery into formerly occupied breeding areas, following a prolonged period of intense human persecution that continued into the early 20th century, which both reduced population abundance and restricted the swans' breeding range (Fjeldså 1972; Haapanen *et al.* 1973; Haapanen & Nilsson 1979; Nilsson 1979; Boiko *et al.* 2014). The Finnish breeding population was close to extinction in the 1950s, but between 1974–1989 and 2006–2010 expanded its range considerably (Finnish Breeding Bird Atlas 2019). Breeding abundance in Finland increased by *c.* 8.1% *per annum* during 1986–2018 (but by 4.1% *per annum* during 2007–2018; Laaksonen *et al.* 2019), while the Swedish population has also shown a 3.3% increase in abundance during 1998–2018 (Svensk Fågeltaxering 2019). Through the last century, the population's breeding range and abundance has expanded within Norway (Shimmings & Øien 2015), Sweden (Nilsson *et al.* 1998; Ottosson *et al.* 2012) Finland (Pöysä & Sorjonen 2000; Väisänen *et al.* 2011) and northwest Russia (at least since the 1980s; Hokhlova & Artemjev 2002).

In recent years, the species has also extended its breeding range to countries where it had been extirpated as a breeding species (Boiko *et al.* 2014). This occurred in Poland (where nesting was recorded in 1973; Tomiałoj 1990), Latvia (1973; Boiko & Kampe-Persson 2010), Lithuania (1973; Švažas *et al.* 1997, 2011), Estonia (since 1979; Luigujõe *et al.* 2002), Germany (where nesting was first recorded in 1982, but where it has become more established since the mid-1990s; Profus 1999; Gedeon *et al.* 2014) and the Netherlands (since 2005, currently two pairs, with a third territory occupied; van Dijk 2006, 2013). The Whooper Swan has also spread as far south as the Czech Republic as a breeding species, where a female wintering in the same site since 2007 started to breed successfully in 2017 (Šírek 2018) and Slovakia, where the species bred in 2019 (BirdLife Slovensko 2019). Whooper Swans colonised Denmark in 2002 (Nyegaard *et al.* 2014) and it seems that in the most biologically productive lakes (*e.g.* eutrophic lakes and artificial fishponds) in Latvia and Lithuania, increasing numbers of Whooper Swans (with a diverse genetic structure) are successfully displacing Mute Swans (with more restricted genetic variability; Butkauskas *et al.* 2012). However, the overall impact of such increases in breeding numbers and range can only be assessed at the population level on the winter quarters, where all breeding and non-breeding elements of the population aggregate and become easier to count.

Laubek *et al.* (1999) were already describing "a massive expansion of the breeding range towards the south…" when reporting on the first ever, coordinated international winter census of the Whooper Swans in continental Europe, undertaken in January 1995. A total of 52,000 birds was counted during that survey and the estimated population size was revised upwards to 59,000 based on expert opinion because of incomplete coverage. The main concentrations were found in Denmark

(36.5%) and adjacent parts of Germany (26.0%), with the remainder in Sweden (14.2%), Norway (13.1%), Poland (6.2%), and with smaller numbers in the Netherlands (Laubek *et al.* 1999). This was considered to represent an ongoing increase in population size from 14,000–15,000 birds in the 1970s (Ogilvie 1972; Atkinson-Willes 1981) to 25,000 in the 1980s (Monval & Pirot 1989) and 35,000–40,000 in the 1990s (Laubek 1995).

As Laubek *et al.* (1999) stressed at the time, counts and resightings of individually marked birds showed substantial movements of Whooper Swans from their traditional wintering areas in Denmark, Sweden and Norway to sites further south and west, particularly in colder winters. The NWMEWS population was also increasingly resorting to feeding on farmland, away from traditionally counted wetland habitats (*i.e.* those more likely to be covered under the International Waterbird Censuses (IWC) organised by Wetland International), to a greater extent than other waterbird species (Laubek *et al.* 1999). It was therefore already clear in the mid-1990s that, in order to maintain adequate surveillance of the NWMEWS population, a specially organised single-species survey was necessary, and at that time it was agreed that this survey would be carried out on a five-year cycle under the auspices of the Wetland International/IUCN-SSC Swan Specialist Group. This analysis presents the results of these surveys, reporting the numbers and distribution of the NWMEWS population from counts undertaken in January 1995, 2000, 2005, 2010 and 2015, with a view to describing changes in total population size and shifts in distribution for the NWMEWS over the past two decades.

Methods

The NWMEWS census in each year was organized by the first author in cooperation with the national waterbird count organisers in Norway, Finland, Denmark, Sweden, Estonia, Latvia, Lithuania, Poland, Germany, Switzerland, Austria, Czech Republic, the Netherlands, Belgium and France. National organisers were requested to extend the usual count coverage of the IWC site network to attempt to attain complete coverage, not only of Whooper Swans, but also of Bewick's Swans *Cygnus columbianus bewickii*. The individual observers were requested to carry out ground counts and also to record flock size, sample numbers of adults and first winter swans, family sizes and habitat use. The data for breeding success and habitat use are not presented here, but will form the basis of a future analysis.

In Sweden, appeals were made via the press and regional television to obtain knowledge of Whooper Swan numbers outside of conventional count networks, which generated a very few previously unknown resorts. In restricted coastal areas difficult to accurately count from the ground, data from aerial surveys were used from Fyn, Lolland and Falster (Denmark), Curonian Lagoon and Nemunas River Delta (Lithuania, only until 2010) and southwest Skåne (Sweden). National coordinators were also asked to attempt, in combination with local observer knowledge, to estimate the potential numbers of Whooper Swans which were likely present in each country at

sites, which were not counted, but where swans were likely to have been present. This difference was added to the total counts to derive the estimated national totals for each country in the following analysis.

Counts were coordinated around the middle weekend of January for each of the special survey years to coincide with the IWC for those years. However, counts were accepted from a period of 1–2 weeks before and after the nominated dates, and very occasionally were accepted from late December to early February in cases where counts were missing and location meant that the risk of double-counting was low. Detailed accounts of country-specific monitoring methods and protocols can be found where appropriate in the national reports cited in Table 1.

To consider the effects of weather on the swans' distribution, we extracted mean January temperatures for each of the census years for Schiphol Airport, the Netherlands (52.30ºN, 4.76ºE), Copenhagen Airport, Denmark (55.61ºN, 12.66ºE) and Gdansk Airport, Poland (54.38ºN, 18.46ºE) from https://www.tutiempo.net/clima/.

There is an argument that states that the annual change in the overall abundance of the NWMEWS could adequately be monitored using IWC data, avoiding the need for the major logistical challenge of mounting five year total population surveys. However, IWC sites tend to (i) be large and not representative of Whooper Swan wintering sites as whole, (ii) are increasingly night time roosts of swans feeding elsewhere on agricultural land, and/or (iii) for other reasons do not necessarily reflect sites used by the population overall. To test whether IWC Whooper Swan trends reflect those at a wider range of sites at the national level, we examined more detailed annual count data from Denmark and Sweden. In Denmark, comprehensive Whooper Swan counts are made annually, not just in census years. Mid-winter nationwide counts of all Danish wetlands of importance to all waterfowl species (including all SPAs) are undertaken in conjunction with counts of sites known to support Whooper Swans in the middle of January at the same time as the IWC. We therefore also compare the annual totals recorded for Denmark derived from these surveys during 1987–2017 with counts of Whooper Swans made at sites that contribute to the annual mid-winter IWC, to determine how adequately annual trends recorded from these sites reflect the changes in overall abundance recorded at the national level. We do the same for Sweden for the census years to make the same comparison there. Finally, we compare the trend generated for this population as a whole by Wetlands International from IWC counts with the estimated population sizes produced from the censuses undertaken in January 1995, 2000, 2005, 2010 and 2015 to assess whether the trends in annual population size sampled at IWC sites are representative enough to use as a proxy for changes in the population size as a whole. We generated population indices from an initial population of 15,000 birds from 1972 (Atkinson-Willes 1981) based on an index value of 100 for that year, and used the IWC census indices from 1972–2015, to compare this trend with those counts derived from the five dedicated surveys. The annual IWC indices are generated from national waterbird

Table 1. Counted and estimated national totals for the Northwest Mainland European Whooper Swan population, derived from the five-year internationally coordinated mid-winter counts in all of the countries. Superscripts give source publications for the census in each country as follows: [1]Nilsson (2016), [2]Holm *et al.* (2016), [3]Lehikoinen *et al.* (2013), [4]Stīpniece (2017), [5]Šniaukšta (2015), [6]Neubauer *et al.* (2015) and M. Wieloch (unpubl. data), [7]Wahl & Degan (2009), [8]Hornman *et al.* (2016), [9]Teufelbauer *et al.* (2015), [10]Keller & Burkhardt (2006, 2011), Strebel (2016), [11]Jacob & Alvares (2016) and Devos (2015). *Data from Germany for the census in 2000 and 2010 have not been carefully analysed and checked, so for the time being represent best estimates. **For convenience includes combined data for Lake Constance from Austrian, German and Swiss counts.

Country	1995 (counted)	1995 (estimated)	2000 (counted)	2000 (estimated)	2005 (counted)	2005 (estimated)	2010 (counted)	2010 (estimated)	2015 (counted)	2015 (estimated)
Norway	5,445	7,800	5,000	5,000	3,788	5,000	6,301	6,301	5,013	5,013
Sweden[1]	7,439	8,440	7,022	7,022	8,832	8,832	4,299	4,299	11,648	11,648
Denmark[2]	20,348	21,740	22,948	22,948	31,253	31,253	31,297	31,297	62,624	62,624
Finland[3]	250	300	302	350	481	550	473	510	1,261	1,300
Estonia	175	200	202	202	586	586	580	580	661	661
Latvia[4]	15	15	27	27	102	102	5	5	34	34
Lithuania[5]	92	92	377	377	270	270	190	190	171	171
Poland[6]	3,143	3,700	2,587	3,000	7,323	7,323	3,511	4,000	4,940	5,500
Germany[7]	13,868	15,500	(20,000)*	20,000	26,983	29,000	(30,000)*	30,000	44,465	48,000
Netherlands[8]	1,386	1,400	1,526	1,526	1,829	1,829	2,212	2,212	2,358	2,358
Czech Republic	2	2	2	2	2	2	15	15	1	1
Austria[9]	1	1	3	3	2	2	7	7	13	13
Switzerland[10]	25	25	3	3	27	27	26	26	49	49
Lake Constance**	273	273	218	218	608	608	569	569	763	763
Belgium[11]	7	7	23	23	23	23	36	36	77	77
France	10	20	15	15	16	16	96	96	236	236
TOTAL	**52,479**	**59,515**	**60,255**	**60,716**	**82,125**	**85,423**	**79,617**	**80,143**	**134,314**	**138,448**

count databases supplied to Wetlands International (for methods, see Wetlands International 2019a). For Whooper Swan, these were (in most recent years) based on 25,000–44,000 birds counted during 2011–2015 in 12 countries but dominated by counts from northern Germany and the reduced sites list in Denmark, with contributions from the Netherlands and Sweden (but see Wetlands International 2019b for national contributions of count data and the proportions of imputed counts from each country).

We tested for changes in the percentage of the population totals in each of the six most important countries using 2-sample tests for equality of proportions. Simple linear regression was used to test for changes in the proportions of annual national mid-winter counts in Denmark that came from the "reduced sites list" of sites counted under the IWC count scheme against year.

Results

Numbers and distribution

Total numbers counted in each annual census were 52,500 (in 1995), 60,300 (2000), 82,100 (2005), 79,600 (2010) and 134,300 (2015). However, on the basis of estimated numbers of missed birds, the total population size was estimated as 59,500, 60,700, 85,400, 80,100, and 138,500, respectively, in these five years (Table 1, Fig. 1).

Based on the combined estimated totals for each country in all five years, the majority of the NWMEWS population wintered in Denmark (40.0%) and Germany (33.5%), with lower numbers in Sweden (9.5%), Norway (6.8%), Poland (5.5%) and the Netherlands (2.2%; see Fig. 2) and with < 1% in all other countries. In the 2015 census, the majority was counted in Denmark (45.2%), Germany (34.7%), Sweden (8.4%), Poland (4.0%), Norway (3.6%) and the Netherlands (1.7%). Based on the results of 2-sample tests for equality of proportions, these represent statistically significant increases in the percentages wintering in Denmark and Germany (from 36.5% and 26.0% respectively, see Table 2), where most of the increase between 2010 and 2015 was accommodated, but significant declines in the proportions in mid-winter in Sweden (from 14.2%), Poland (6.2%), Netherland (from 2.4%) and Norway (from 13.1%; Table 2 and Fig. 1).

Factors affecting count coverage

There was relatively little variation between the five winters in weather conditions that would affect the distribution of Whooper Swans during the surveys, with the notable exception of 2010 when January temperatures were ≥ 4°C below those recorded in other years (Fig. 2). In 2010, unusually high pressure over Greenland and Iceland resulted in more easterly winds bringing cold air into northern Europe from Siberia and the Arctic from mid-December 2009, which brought snow to much of northern and western Europe. Further snowfalls in the first half of January 2010, especially in Scandinavia, Poland, Germany and the Netherlands thus likely had a major effect on Whooper Swan distributions and our ability to count them. It is not clear whether this was the case across the entire range, nor how great a difference there was between inland and coastal sites. However,

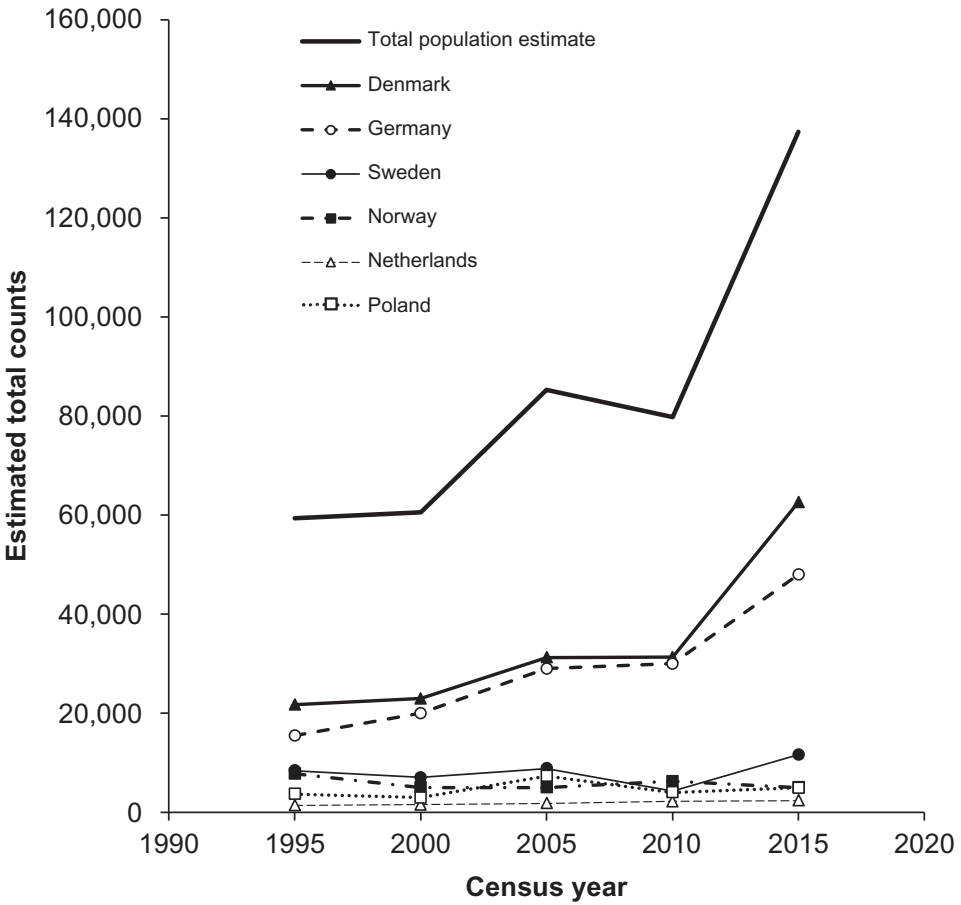

Figure 1. Estimated numbers of Northwest Mainland European Whooper Swans in the six most important countries for the population, based on counts recorded during the five-yearly internationally-coordinated mid-winter censuses 1995–2015. These countries accounted for an average of 98.1% (± 0.2 se range 97.6–98.7%) of the flyway population in the years considered here.

as a result, counts from that year are thought to under-represent the true numbers present, not only because observers were unable to access some sites, but displacement of swans from regularly-counted sites (following the freezing of open waters at these sites) would lead to unrepresentative mid-winter distributions, as the swans moved to areas outside their usual mid-winter locations.

National counts *versus* IWC site counts from Denmark and Sweden

Annual national count totals of Whooper Swans in Denmark in mid-winter show that the proportion wintering at IWC sites has fallen significantly ($r^2 = 0.59$, $P < 0.001$) from 65% in 1987 to 10–15% in January of 2014–2017 (Fig. 3a). Data from Sweden show less dramatic changes, but outside of

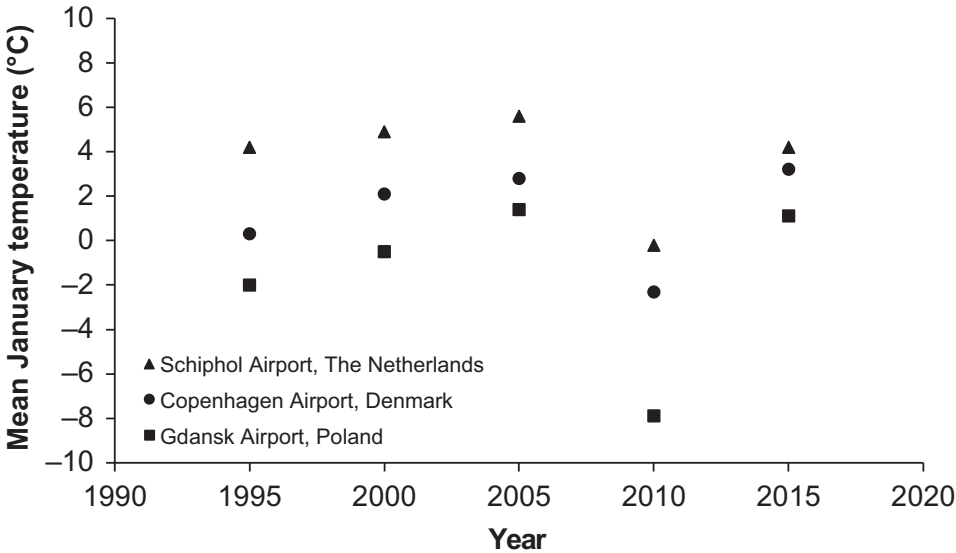

Figure 2. Mean monthly average January temperature for Schiphol Airport, the Netherlands (52.30°N, 4.76°E), Copenhagen Airport, Denmark (55.61°N, 12.66°E) and Gdansk Airport, Poland (54.38°N, 18.46°E) in the international Whooper Swan census years. Data extracted from https://www.tutiempo.net/clima/ for the relevant sites.

the severe winter of 2010, counts from IWC sites comprised only 18–28% of the national totals, so may not be representative of numbers wintering elsewhere in Sweden (Fig. 3b).

Comparisons between the NWMEWS totals and the IWC trend indices

Using the IWC index with the 1972 count of 15,000 swan as an anchor, and an IWC index of 100 for that year, estimated totals for each of the 1995–2015 censuses fell outside of the 95% confidence intervals around the generated IWC index predictions for NWMEWS population size (Fig. 4). It was evident that the 2010 total count was a substantial underestimate of numbers likely to be present in that year, and in the final year (2015) the value generated by the IWC index equated to 41% of the census total (Fig. 4).

Discussion

Population size and changes in distribution

Focused coordinated censuses of NWMEWS, made every five years since the initial survey in 1995, showed that the population increased from 59,500 swans in 1995 to 138,500 in 2015, a 133% increase in overall abundance at an annual rate of increase of 4.1% over the period. This exceeds the 3.3% *per annum* rate of increase during 1972–2015 and the short-term (but classified "uncertain") trend of 1.6% for 2006–2015

Table 2. Percentage of the total numbers of Northwest Mainland European Whooper Swans counted in the six most important countries for the population in winter (accounting for > 97.5% of the total population) in 1995 and 2015. Results of 2-sample tests for equality of proportions to test between the two years are presented as *Z* values with associated *P* values.

	Percentage of total annual count			
Country	**1995**	**2015**	***Z***	***P***
Denmark	36.5	45.2	35.9	< 0.001
Germany	26.0	34.7	37.7	< 0.001
Sweden	14.2	8.4	–39.0	< 0.001
Poland	6.2	4.0	–21.8	< 0.001
Netherlands	2.4	1.7	–9.7	< 0.001
Norway	13.1	3.6	–78.7	< 0.001

generated by TRIM indexing of mid-January International Waterbird Count (IWC) data from 12 countries (reported in Wetlands International 2019b). The recent estimate of 120,000 Whooper Swans for this population made by Wetlands International (2018) was based on the preliminary estimate of 120,000 individuals recorded during the 2015 survey. The results presented here show that the preliminary figure was an underestimate and we therefore recommend a revision of this estimate to reconcile with the finalised census result of 138,500 birds.

The greatest increase in winter numbers occurred in Denmark and Germany, where numbers have increased almost threefold since 1995, while numbers in Sweden and Poland increased by a more moderate 38.0% and 48.7% respectively. The comparatively modest numbers wintering further south in the Netherlands increased by 68.4%, with the overall result being that there has been a shift in the centre of gravity of the winter distribution of Whooper Swans in this flyway towards Denmark away from all other important countries except Germany since 1995. Elsewhere, the relatively small numbers wintering in Norway and the Baltic States have changed little, although the small numbers in Estonia and Finland have increased 3- and 4-fold respectively. The increase in numbers wintering at the southern edge of the wintering range is probably linked to a southward expansion of the breeding range, as ringing recoveries have shown that Whooper Swans wintering on Lake Constance originate from breeding populations in Brandenburg (Germany) and Latvia (Werner *et al.* 2018). Relatively modest changes in numbers in Sweden and Poland, however, suggest that climate change is not necessarily a major driver of Whooper Swan winter distributional changes. This is especially the case in comparison with much stronger responses amongst duck species (and to a lesser extent goose species) with similar ranges which show increases in these countries with increasingly mild winters (Nilsson 2013; Pavón-Jordán *et al.* 2019). The increasing frequency of mild winters may also have reduced winter mortality for Whooper Swans, as well as contributed to improved body condition among breeding

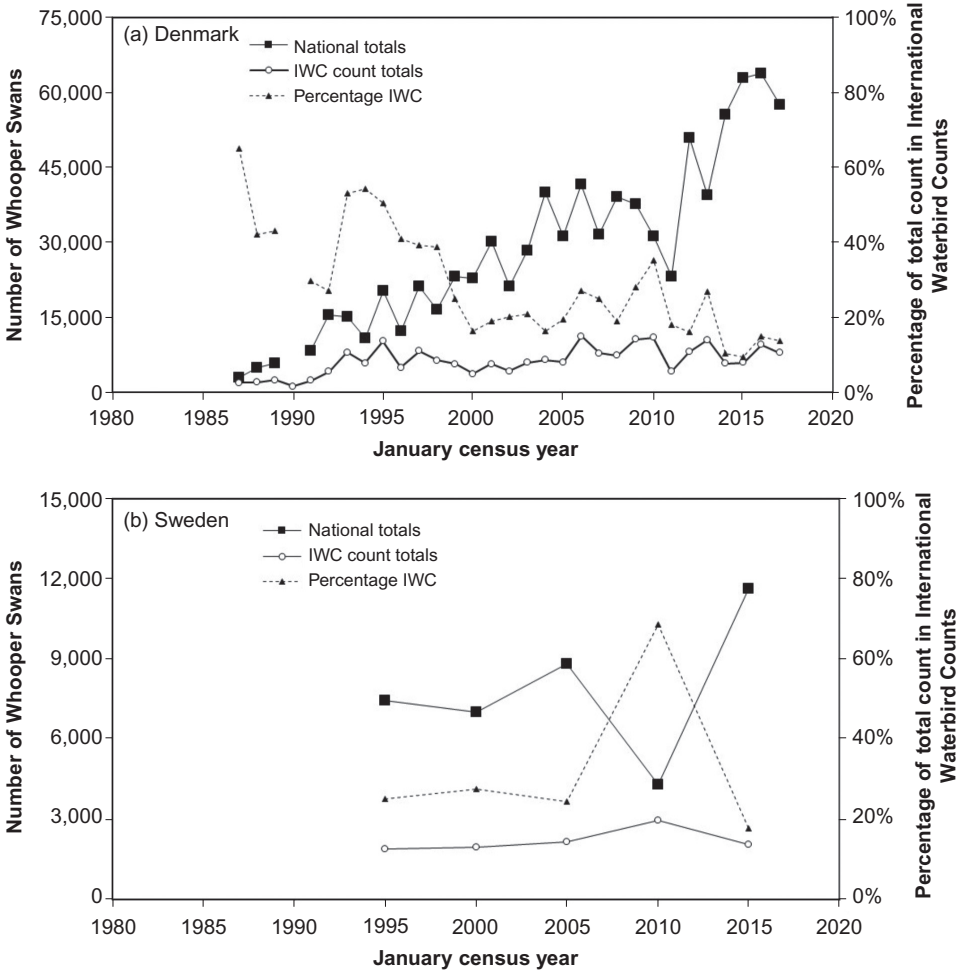

Figure 3. Changes in annual national counts of Whooper Swans *Cygnus cygnus* compared to those from IWC sites (and changes in this percentage) for (a) Denmark (1987–2017) and (b) Sweden (1995–2015).

individuals in spring, which could potentially also contribute to the increases in wintering numbers in some areas (Švažas 2001). The factors supporting the uneven rate of expansion in numbers in host wintering countries over the last 25 years remain obscure. We could speculate that this could be linked to the increasing use of farmland habitats for winter survival in this population, which has been especially apparent in Denmark. This has similarly been evident in the Icelandic Whooper Swan population, which winters primarily in Britain and Ireland (Hall *et al.* 2016). Another potential contributory explanation for increased numbers of wintering swans in Denmark is the restoration of many lakes and wetlands in the Danish countryside in

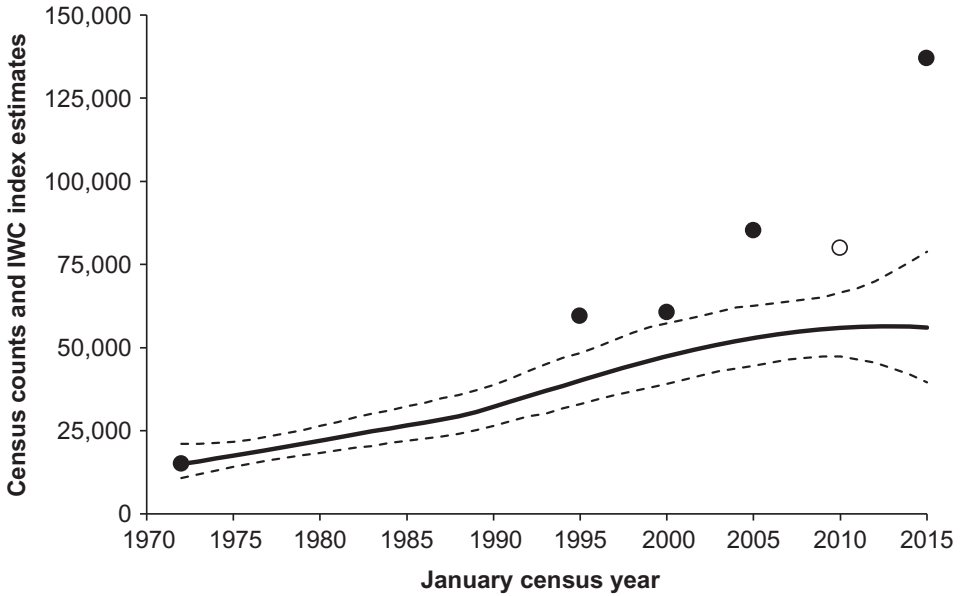

Figure 4. Northwest Mainland European Whooper Swan population counts (1972 and results of the 5–yearly international Whooper Swan censuses made between 1995 and 2015, shown as solid dots) and annual population size estimates from the IWC indices (solid line, with dashed lines indicating 95% confidence limits). The index uses an initial population of 15,000 birds (Atkinson-Willes 1981) and an index value of 100 from 1972 (Wetlands International 2019a). Note that the 2010 population census (unfilled circle) is considered to be an underestimate, affected by bad weather conditions in that year (see text).

the last two decades (*e.g.* Hoffman & Baatrup-Pedersen 2007) that have recreated roosting habitats for swans. The provision of safe, open water night-time roosting habitats in extensive agricultural areas where such roost sites formerly did not exist has rendered new feeding opportunities for swans in areas well away from the coast. It may also be the case that Whooper Swans wintering on agricultural *vs.* more natural habitats derive fitness benefits, as has been shown for some goose populations (Fox *et al.* 2005) such that changes in habitat use has contributed to demographic changes in the population. An analysis of changes in habitat use, and any associated potential linkages to reproductive success in the NWMEWS, therefore remains a priority for future analyses.

Changes in distribution and potential effects of weather

Laubek *et al.* (1999) showed that the distribution of Whooper Swans in 1995 was related to the 0°C isotherm in January of that year and reviewed the literature related to the effects of hard winters on the winter distribution of the population. Numbers in Denmark were highest in cold winters in the 1960s and 1970s (Joensen 1974), but data

from the 1990s found no evidence for this (Laubek 1995; Pihl *et al.* 1996, 1997; Pihl & Laubek 1998) because there were no severe winters with prolonged snow cover in those years. In 2010, temperatures were substantially lower in the Baltic than in all other years: the mean January temperatures at Copenhagen Airport, Denmark (55.61°N, 12.66°E, altitude 5 m a.s.l.) were 0.3°C, 2.1°C, 2.8°C and 3.2°C in 1995, 2000, 2005 and 2015, but –2.3°C in 2010 (Fig. 2). In that year, compared to counts in 2005, numbers were lower in Sweden, but relatively unchanged in Denmark (see Fig. 1). Heavy snow hampered access to many sites in 2010, for instance many sites in northeast Germany were impossible to reach because of drifting snow, so we should be extremely cautious about reported numbers and distributions from many parts of the winter range in that season as being truly reflective of other years of milder or indeed more severe conditions.

Count quality, error and problems with estimation

We acknowledge that there could be problems with the misidentification of Bewick's and Whooper Swans, especially associated with areas covered by aerial survey, but we concur with Laubek *et al.* (1999) that this likely contributes very little to errors in the overall totals generated at the regional level, especially in most recent years where the majority of swans are counted inland. Misidentification is most likely to occur during aerial census, which only contributed to a very limited degree to totals from Lithuania, Sweden and Denmark (Nilsson & Haas 2016; Nielsen *et al.* 2019).

We cannot know about the numbers of birds occurring at hitherto unknown sites, which can potentially be a problem in a population showing increases in abundance, "colonising" wintering areas not formerly occupied and consolidating within (especially farmland) feeding areas not traditionally occupied in winter.

Milder winters also keep areas of open water ice-free in winter in the northern parts of the wintering ranges as never before, especially in Fennoscandia. However, with the advent of national online bird reporting portals (such as www.DOFbasen.dk in Denmark, www.ornitho.de in Germany, www.telmee.nl and www.waarneming.nl in the Netherlands, www.dabasdati.lv in Latvia) we know much more about the general mid-winter distribution and aggregation of swans, which helps to extend coverage to new areas during the survey years. Particularly important sites not counted in specific years have been taken into account by country coordinators with access to within- and between-winter numbers to provide the informed estimates that contribute to the totals in Table 1. Hence, while we cannot eliminate the contribution from missed birds in uncounted areas, with the exception of 2010, we are confident that these do not drastically affect the annual totals presented here. Although 11.8% of the final total was estimated during the first 1995 survey, this had fallen to 0.8% in 2000, 3.9% in 2005, 0.7% in 2010 and 3.0% in 2015 (Table 1). Hence, across most years, the proportion contributed to the total made by estimating numbers of missed swans in areas not subject to counts is relatively small, but naturally the true number present (but not counted) remains unknown.

There also remains the question of how many Whooper Swans from the flyway considered here overwinter "undetected" in Britain among the large numbers from the Icelandic breeding population, which winter there and to what degree this may be affected by winter severity, as in 2010. Only 31 sightings and recoveries of Whooper Swans ringed on mainland Europe were reported to the British Trust for Ornithology (BTO) up to December 2015 (Hall *et al.* 2016), and > 90,000 resightings during 1993–2005 of > 1,000 NWMEWS fitted with neck-collars since the early 1990s produced only a single resighting of a continental swan in Ireland (G. McElwaine, pers. comm. and B. Laubek, unpubl. data), so it is unlikely many move as far west as Ireland even in hard weather. Nonetheless, counts of the NWMEWS population suggested that a significant number of Whooper Swans redistributed in 2010 to sites not covered in previous swan censuses. Moreover, ring recoveries and resightings of marked Whooper Swans from this population in the 1990s have shown that they do move from Germany and the Netherlands to the UK (mainly to Norfolk) during cold spells in continental Europe (*e.g.* Cranswick *et al.* 1996; Laubek *et al.* 1998). It is therefore possible that this was the destination for substantial numbers in mid-winter 2010, which would have escaped inclusion in the counts presented here. However, mid-winter counts in Norfolk from years before and after 2010 suggest that this was not the case, since numbers were not abnormally high in winter 2010 (British Trust for Ornithology WeBS data). More importantly, concurrent international censuses undertaken for the Icelandic Whooper Swan population found that numbers recorded across Britain, Ireland and Iceland in January 2010 were just 2,886 more than in 2005, in a population also thought to be increasing (Hall *et al.* 2012), with a long-term increase of 155% between 1995 and 2015 (Hall *et al.* 2016). Reports of Icelandic-marked Whooper Swans from traditional NWMEWS wintering areas suggest 1–2% of that population occurs in winter outside of what is considered their core range in Britain (primarily northernmost Denmark and Norway; Newth *et al.* 2007). However, further ringing and analysis of ring resightings data is required to determine whether the number of swans involved has changed over the years and the extent to which weather conditions influence movements between the populations.

Future perspectives

This paper was prepared in order to report on the results of the international Whooper Swan census for the Northwest Mainland European population ahead of the next census, scheduled for January 2020, so presents the total numbers counted rather than a more detailed analysis of changes in distribution within each of the countries in the swans' wintering range. For this reason, we lacked information on swan counts at the site level and so were unable to fit boot-strapped confidence intervals to the annual counts (boot-strapping country totals with replacement generates unrealistically large intervals). This ought to be a goal for future analyses and surveys as a basis for testing for significant changes in estimated population size between censuses. Time constraints

similarly precluded the analysis of data on habitat use, age ratios and brood size, which were also gathered in all countries simultaneously during the five censuses reported here. These data are highly relevant to understanding changes in the overall habitat use of the population and shifts in geographical distribution of the population as well as the demographic changes occurring over the time period. Analyses of these data therefore are an urgent priority, especially for setting the results of the coming 2020 census in perspective and providing effective feedback to the count network contributing such detailed data.

The discrepancy between the rate of population increase based on trends generated from IWC counts and that based on the results of five-year international swan censuses suggests that using IWC data to track the overall trends in the NWMEWS population increasingly underestimates the increase in its genuine size. This is to be expected, since it is our impression that increasing numbers occur on farmland, especially in Denmark and Sweden (where 31% of swans were recorded on farmland in the first survey compared to 83% in 2015, Nilsson 2016). Swans are therefore less likely to be detected whilst feeding in fields by day when wetlands are counted by the IWC, even if they overnight on waterbodies that are subject to count coverage. Comparing the annual national count totals from Denmark with numbers counted on IWC count sites in that country showed that the latter contributed 10–15% of national totals in 2014–2017 compared to 65% in 1987. This especially reflects the movement of increasing numbers of swans to overwinter inland, on agricultural land in areas not covered by the Danish IWC count network. This is evident if one compares the coastal distribution of Whooper Swans in Denmark in 1995 in Laubek (1999) with the more dispersed and inland mid-winter 2017 distribution in Nielsen *et al.* (2019). In Germany too, 62% of the counted total came from the IWC network in the 2005 census (Wahl & Degen 2009), but this had fallen to 51% in 2015; the Whooper Swan IWC index for Germany increased by 2.2% *per annum* between 1995 and 2015, compared to an increase of 6.0% in the national census totals (Wetlands International and J. Wahl, unpubl. data). As a result, Whooper Swans are becoming less well represented in these systematic monitoring data, which are so important for our international monitoring of other mid-winter waterbird populations, but are less well-designed for tracking annual Whooper Swan abundance. In Sweden, although the proportion of swans counted on IWC sites has shown no major changes over the last 25 years (except during hard weather), the relatively low (< 30%) proportion present on IWC count sites suggest changes in swan abundance at these sites may also not necessarily be representative of those at the national level.

Whooper Swans seem increasingly to be wintering in areas away from traditionally counted IWC sites throughout their range, as shown here especially for Denmark. This likely contributes to the increasing discrepancy between the IWC trend index and the trend revealed by the five-year census totals, confirming the continued need for the regular coordinated swan counts to anchor population trends

generated from other data sources. The five-year cycle has proved effective and feasible as a mean of delivering such regular census totals to anchor trends generated from IWC counts which are less and less able to reflect the true increase in the population overall.

Dedicated, intense survey at regular intervals also gathers important data on habitat use and reproductive success, not currently gathered and centrally analysed by IWC, which can help to interpret some of the factors that may influence the rate of increase in the population as a whole and the changes in distribution, which we have witnessed. We therefore contend that there is a continuing need to expend the considerable effort necessary to coordinate such concentrated endeavour in censusing the NWMEWS population at regular intervals, to determine the discrepancy between the IWC indices and the evolution of this important wintering population in time and space. For this reason, we are all keen to launch and contribute to the next complete census of Whooper Swans in this flyway in January 2020.

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