The Icelandic Whooper Swan *Cygnus cygnus* population: current status and long-term (1986–2020) trends in its numbers and distribution

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Abstract

The eighth international census of Whooper Swans *Cygnus cygnus* wintering in Britain, Ireland and Iceland (also including the Isle of Man and the Channel Islands) took place in January 2020, to update the estimates of the size, mid-winter distribution, habitat use and breeding success of the Icelandic Whooper Swan population. The total of 43,255 swans counted represented a 27.2% increase in numbers since the previous census in 2015. Overall, 36.8% of the population (15,927 birds) was recorded in England, 33.4% (14,467) in the Republic of Ireland, 11.7% (5,052) in Scotland, 10.7% (4,644) in Northern Ireland and 6.8% (2,923) in Iceland, with < 1% (242) in Wales, the Isle of Man and the Channel Islands combined. Despite numbers increasing in both the Republic of Ireland and Northern Ireland since 2015, the proportion of the total population in the Republic of Ireland was significantly lower in 2020 and no significant difference was detected for Northern Ireland, whereas proportions in England and Scotland were significantly higher in 2020 and lower in Iceland. Breeding success was not associated with temperatures on either the breeding or wintering grounds. It also showed no clear trend over time, suggesting that increased survival may be the demographic driver of the population growth.

Key words: census, distribution, habitat use, population size, productivity, Whooper Swan.

The Whooper Swan *Cygnus cygnus* breeds across the northern Palearctic, from Iceland and northern Scandinavia to the Pacific coast of Russia, with five flyway populations described on the basis of their geographical separation in the breeding or wintering ranges (Rees 2005; Wetlands International 2020; Rees *et al.* 2019). Those breeding and wintering in Europe have been assigned to the two westernmost populations – the Icelandic and the Northwest Mainland European (hereafter NWME) populations. Count and ringing programmes have shown that the majority of the Icelandic-breeding population migrates to Britain and Ireland, with small but increasing numbers remaining in Iceland to overwinter (Rees *et al.* 2002; Hall *et al.* 2016). Sightings of swans ringed in Iceland wintering on mainland Europe (Garðarsson 1991), and conversely of swans ringed in Finland reported in Britain (Laubek *et al.* 1998) indicate only limited movement between the two populations. Net levels of immigration/emigration and whether this varies between years remains unknown, but estimates are in the region of a few hundred birds each year (Rees *et al.* 2002; Newth *et al.* 2007).

Information on abundance and trends in numbers over time is critical for informing the long-term conservation and management of swan populations (Rees *et al.* 2019). Estimates of the size and trends of European Whooper Swan populations have recently been derived from counts made in mid-winter, when birds are more concentrated and therefore easier to census than at other times of the year. Whooper Swans of the Icelandic population have been monitored by national count schemes undertaken during mid-winter since the 1950s, currently through the Wetland Bird Survey (WeBS, in England, Scotland, Wales, Northern Ireland, the Isle of Man and the Channel Islands), the Irish Wetland Bird Survey (I-WeBS, in the Republic of Ireland) and the Icelandic annual winter bird census, with additional counts made by the Irish Whooper Swan Study Group (IWSSG). Whilst WeBS and I-WeBS cover many wetland sites in Britain and Ireland, the dispersal of Whooper Swans to non-wetland habitats (usually farmland) during the day to feed means these surveys miss a substantial part of the population. Similarly, in Iceland, overwintering swans can be rather scattered and accessing sites where the birds are located can be difficult, particularly in harsh weather conditions. Species-specific surveys therefore are required to achieve coverage of these additional areas, in order to provide accurate estimates of Icelandic Whooper Swan population size and to describe any changes in its winter distribution.

International censuses of the Icelandic Whooper Swan population have taken place at *c.* 5-year intervals since 1986. Since 1995, they have also been scheduled to coincide with censuses of the NWME population, which winters in mainland Europe (Laubek *et al.* 2019). Whilst early censuses of the Icelandic population showed numbers fluctuating at < 20,000 birds, more recent surveys indicate a steady growth in population size, with count totals of 20,856, 26,366, 29,232 and 34,004 recorded in 2000, 2005, 2010 and 2015, respectively (Hall *et al.* 2016). Causes of this increase however remain unclear, and there is a need for research into demographic rates and their environmental drivers to provide a better understanding of the reasons underlying the population changes observed in the 21st century. Studies of other *Cygnus* species have shown that breeding success in particular can be highly responsive to temperature (Wood *et al.* 2016), which in turn can have a strong effect on population growth rates (Nuijten *et al.* 2020a). Breeding success can be sensitive to temperatures in either the breeding area or the winter area (*i.e.* a carry-over effect from a winter to the subsequent breeding season, *sensu* Harrison *et al.* 2011), but no research to date has tested this for Icelandic-breeding Whooper Swans. There was also some indication of a south-easterly shift in the swans' mid-winter distribution over this period, with an increasing proportion seen in England. Although the number of swans remaining in Iceland for the winter has increased since the late 20th century, the corresponding increase in population size means that there have only been small variations between censuses in the proportion of the total population which does not migrate to Britain or Ireland (Hall *et al.* 2012).

This paper provides the most recent assessment of the Icelandic Whooper Swan population, following a coordinated international census in January 2020. In addition to updating information on the size, distribution, and habitat use of the wintering population, we consider the demographic drivers of population change by making a preliminary analysis of whether temperature during the breeding season (in Iceland) and in winter (in the UK) is affecting the swans' breeding success each year.

Methods

The 2020 census of the Icelandic Whooper Swan population was coordinated by the Wildfowl & Wetlands Trust (WWT) as part of the Goose & Swan Monitoring Programme (GSMP) undertaken for the UK's Joint Nature Conservation Committee (JNCC). It was organised in Britain, the Isle of Man and Channel Islands by WWT, in Ireland by Birdwatch Ireland and the Irish Whooper Swan Study Group (IWSSG), and in Iceland by Ólafur Einarsson. Counts were undertaken by a network of volunteers (including GSMP, WeBS and I-WeBS counters and IWSSG members) and professional staff of the partner organisations listed above. In addition to recording flock size, date and location, counters were asked to report on the number of young in each flock, either by counting a sample of young and recording brood sizes, or where possible to record all young and broods within the flocks. Counters were also asked to record the habitats where the birds were located (from a list of 10 habitat categories used from the 2000 census onwards; see Table 5 for habitat classifications) and whether the site was used for feeding and/or roosting. Full details of the methods used, which have been consistent over time to permit a direct comparison of counts made in different years, are described in Worden *et al.* (2009).

In Britain and Ireland, the census was scheduled to take place on the weekend of 11–12 January 2020 to coincide with the monthly WeBS and I-WeBS counts, which also include the Isle of Man and the Channel Islands. Counters were additionally asked to visit sites known to have held, to currently hold or considered potentially suitable for Whooper Swans, not regularly covered by these annual schemes. In Ireland, an aerial survey was carried out covering the Shannon and Fergus Estuary, Lough Derg, Lower River Shannon, the Shannon Callows, Little Brosna and River Suck. Data in Iceland were collected mainly through the annual winter bird census (the "Icelandic Christmas Bird Count"), organised by the Icelandic Institute of Natural History, which was undertaken during late December 2019 and early January 2020. An aerial survey of the southern lowlands of Iceland (not covered by the winter bird census) was carried out on 22 February 2020. Due to cloud cover during the aerial census and counter availability, areas around Landbrot and Meðalland, South Iceland and Fellströnd and Skarðsströnd, West Iceland, were not counted; numbers of birds present in these areas therefore were estimated by the Iceland national coordinator, based on information on swans in these areas in 2019/20 outside of the census period. The broad range of dates across which Iceland was surveyed is considered acceptable because the number of birds counted is comparatively small, there is thought to be little movement of swans between the Icelandic sites during mid-winter, and next to no migration from Iceland to Britain and Ireland during the midwinter period (Ó. Einarsson, pers. comm.).

Submitted data were assessed by the national organisers to identify any duplicate records where sites had been surveyed more than once or where birds were believed by counters to have moved between adjacent sites. Any counts deemed to be duplicates were omitted from the analysis (except when assessing site importance; see below). All aspects of this approach are consistent with previous censuses for this population. Criteria used to select data for inclusion in the analysis included the following: proximity to the census weekend, coordination with adjacent sites and whether the count was said by the observer to be most representative of the number of birds present at the site. For those sites not surveyed on the census weekend, counts up to a week either side were included if the national count coordinators considered, on the basis of previous counts and information provided, that a flock had been missed and that bird movement from nearby censused sites was unlikely. Counts made outside this time period were only included in exceptional circumstances and only if the risk of double-counting was thought to be minimal.

If a site was counted twice within the census period, the count made on the date closest to those made at other sites in the vicinity was used for determining the total population size, to reduce the possibility of duplicate records. On considering the importance of sites for the species, however, the highest count recorded at each site was used and compared to the current 1% thresholds for describing sites of international and national importance for the Icelandic population. For the purpose of analyses presented here, a site was taken as being a single count area (such as a large lake), or as a complex of sub-sites (*e.g.* fields or small waterbodies used by the same flock) that fall within the catchment area of a larger roost site.

We determined the proportion of young among wintering flocks, as a measure of breeding success and survival of cygnets to midwinter, for comparison with historical data on considering annual variation and trends in Whooper Swan productivity over time, and for determining whether such changes were related to environmental variables such as temperature. Because International Swan Censuses (ISCs) take place at *c.* five-year intervals, total annual productivity data are too few (n = 8) to provide sufficient statistical power. Mean annual estimates of the percentage of cygnets recorded in age assessments of Whooper Swans made at three UK sites each year therefore were used in the analysis, at: (i) Martin Mere and the Ribble Estuary in northwest England, (ii) Caerlaverock in southwest Scotland, and (iii) Welney and the Ouse Washes in southeast England. These data were available for 33 winters between 1986/87–2019/20 (with the exception of 1989/90). Data were also collated on two environmental variables: temperature in Iceland during the Whooper Swans' breeding season (April–August; Brazil 2003) and (to allow assessment of carry-over effects of temperature on breeding success) temperatures during the previous winter (October–March). For the former, monthly air temperature measurements recorded at four weather stations across Iceland (in Akureyri, Stykkisholmur, Seydisfjodur and Storhofdi) for April–August inclusive were obtained from the Icelandic Meteorological Office (https://www.vedur.is/vedur/vedurfar/medaltalstoflur/#30ara) and the mean value was calculated for each year. For the latter, Central England Temperature (CET; Parker *et al.* 1992) data were obtained for the previous winter (October–March; Brazil 2003). CET shows strong correlations with temperatures recorded at local weather stations across Britain and therefore represents a valuable measure of temperature at both local and national scales (Croxton *et al.* 2006).

Statistical analyses

All statistical analyses were carried out using R version 3.6.3 (R Core Team 2020), with statistically significant results inferred where $P < 0.05$. To quantify the uncertainty associated with the estimates of population size and breeding success, 95% confidence intervals (CIs) were calculated. CIs indicate the likely range in which the mean estimate would be found if the sampling exercise was repeated. More specifically, if the same population was surveyed on multiple occasions and the 95% CIs were estimated for each occasion, the resulting CIs would contain the true population parameter in approximately 95% of the cases (Crawley 2013). The 95% CI values were calculated for three key population-level measures: (i) total population size, (ii) percentage of cygnets within the population, and (iii) mean brood size. CIs were calculated not only for the 2020 data, but also for the estimates reported in each of the previous censuses between 1986 and 2015, to facilitate historical comparisons. The only exceptions were for the 1986 census, for which brood size data were lacking, and for which the total number of individuals included in the age assessment was not reported.

Historically, ornithologists have not given CI values for counts based on individual total censuses, because these were considered to lack an estimate of the variance required to calculate a confidence interval. However, as each count recorded the number of individuals encountered within a defined area in a given time, they were likely governed by a Poisson process, for which the variance is equal to the mean (Garwood 1936; Crawley 2013). A count of *n* individuals therefore would come from a Poisson distribution with a mean of *n* and a variance of *n*. This Poisson distribution approach has been used to estimate CIs associated with individual counts in many fields outside of ornithology, including limnology and parasitology (*e.g.* Lund *et al.* 1958; Edgar & Laird 1993; Torgerson *et al.* 2012). To derive CI values for total Whooper Swan population size in each census year, CIs were first estimated for each county that reported data in the census. Counties were selected as these represented the smallest spatial units for which data have been reported consistently across the eight censuses from 1986 onwards (*e.g.* Table 1). CI values for the total count (*N*) reported for each county were calculated using the *poisson.test*(*N*) function in R, which uses the methodology described by Clopper & Pearson (1934). The CIs for each county could then be summed to give the 95% CI for the total population size (Greenwood & Robinson 2006). The 95% CI values for population size were rounded to the nearest integer to allow the CIs to be interpreted in terms of numbers of individual swans. The 95% CI for the percentage of cygnets within a sample was estimated using the methodology for binomial samples reported by Clopper & Pearson (1934), implemented using the *binom.test*(N_c,N_t) function in R where N_c and N_t were the number of cygnets and the total number of aged individuals, respectively. The 95% CI for mean brood size was estimated after Crawley (2013) as:

$$CI = \bar{x} \pm z * S / \sqrt{n}$$

where $\bar{x}$ was the mean brood size, z was the value of the Gaussian (*i.e.* normal) distribution associated with the alpha (*i.e.* the likelihood that the true parameter value lies outside of the CI, also known as the Type I error rate, which is 0.05 for a 95% CI) required for a 95% CI (–1.96 and +1.96 for the lower and upper limits of the 95% CI, respectively), *S* was the standard deviation of the brood size samples, and *n* was the total number of brood size estimates within the sample.

Two-sample binomial tests for equality for proportions (Crawley 2013) were used to compare the differences in the proportion of swans recorded: (i) in each country, and (ii) on each habitat type (permanent waterbodies, pasture, arable, and "other"), between the 2015 and 2020 censuses; these tests allowed temporal changes in distribution and habitat use, respectively, to be assessed. Country comparisons were carried out for Iceland, Northern Ireland, the Republic of Ireland, England, Scotland, Wales, and the Isle of Man, but not for the Channel Islands, as the latter held only a single individual in 2020 and none in 2015. Similarly, to assess changes in breeding success relative to the last census in 2015, the proportions of cygnets recorded in each country (and for the total population) in the 2015 and 2020 censuses were compared using a two-sample binomial test for equality for proportions. Finally, the recorded brood sizes in 2015 and 2020 were compared using Mann-Whitney U (*i.e.* Wilcoxon rank sum) tests; these were used because Shapiro-Wilk tests indicated that the normality assumption of a parametric *t*-test was not met for either the 2015 ($W = 0.86$; $P < 0.001$) or 2020 ($W = 0.83$; $P < 0.001$) census data, and thus non-parametric alternatives were required.

Inter-annual variation in the percentage of cygnets recorded at the three sites where age checks are made each year, from 1986/87–2019/20 inclusive, was assessed in a two-stage modelling process (following Wood *et al.* 2016), using linear models with Gaussian error structures in all cases. First, to assess the extent of between-year variation in the recorded percentage of cygnets, three models of temporal variation were run: (i) a linear trend over time, (ii) a quadratic trend over time, and (iii) no trend over time (*i.e.* the null model). Second, to attempt to explain the observed between-year variation in the percentage of cygnets recorded, four models of environmentally-linked variation were run: (i) an effect of the temperature during the breeding season in Iceland, (ii) an effect of the temperature during the previous winter in the UK, (iii) additive effects of the Icelandic and UK temperature variables, and (iv) the null model. A further model containing a two-way interaction between the Icelandic and UK temperature variables was not included due to high collinearity (Variance Inflation Factor > 10; Dormann *et al.* 2013). Model assumptions and collinearity were checked using the *performance* package (Lüdecke *et al.* 2020). The relative support of each model was evaluated using second-order Akaike's Information Criterion (AICc) values, whereby the temporal and environmental models with the lowest AICc values were considered to be the best-supported models of temporal and environmentally-linked variation in the percentage of cygnets, respectively (Burnham *et al.* 2011). Finally, linear models were also used to test for consistent linear temporal trends in: (i) the temperature during the breeding season in Iceland, and (ii) the temperature during the previous winter in the UK.

Results

Coverage

Coverage of sites known to be used by swans during the 2020 census was thought to have been good, with weather during the census period mainly settled and mild (Met Office 2020; Met Éireann 2020). Overall, 96.2% of 884 counts where swans were recorded in Britain and Ireland were made during or up to three days before/after the census weekend. The remainder were visited either in the week of the census or the week after the census, during which time it is possible that bird movements occurred. However, attempts were made to minimise the possibility of duplicate counts being included in the census total.

In Britain, 51.8% of the counts (where swans were recorded, $n = 226$) were undertaken on the scheduled census dates, a further 44.7% were conducted within three days either side and all counts were carried out between 5–19 January 2020. Counts in Northern Ireland were carried out between 9–19 January 2020; 31.8% ($n = 136$) on the census weekend and 56.5% within three days either side. In the Republic of Ireland, counts were undertaken between 8–29 January; 54.8% (n = 549) on the scheduled census dates and 44.7% within three days either side.

In Iceland, counts were undertaken between 25 December 2019 and 22 February 2020. Coverage was good for all regions, except for areas around Landbrot and Meðalland in southern Iceland, where low cloud hampered the aerial survey, and Fellströnd and Skarðsströnd in west Iceland which were not covered by a counter (Ó. Einarsson, pers. comm.).

Numbers and distribution

A total of 43,255 (95% CI = 40,554–46,201) Whooper Swans was recorded during the January 2020 census (Table 1; Fig. 1a,b), representing a 27.2% increase on the 34,004 birds recorded in 2015. Lower and upper 95% CI limits represented –6.2 and +6.8% of the estimated total population size, respectively, which were lower than in any of the previous seven censuses (Fig. 1c), indicating greater precision of the 2020 census total.

During the 2020 census, Britain held the highest percentage of the overall population (49.1%), with Ireland holding 44.2%, whilst Iceland held 6.8%, and all countries except for the Isle of Man recorded an increase in the number of wintering Whooper Swans compared to the previous census (Table 1, Fig. 1a). The increasing percentage of swans occurring in England, evident for each census since 1986 (Fig. 2), continued in 2020, with 36.8% of the population recorded compared with 35.5% in 2015 (χ^2_1 = 13.59, P < 0.001 on comparing the 2015 and 2020 count data). Scotland held 11.7% of the population in 2020, which was significantly higher than the 11.1% recorded in 2015 (χ^2_1 = 5.66, P = 0.017), following a decline in the percentage of Whooper Swans recorded in the country in mid-winter up to the 2010 census (Fig. 2). In Ireland, the majority of birds were in the Republic of Ireland (33.4% of the total population), compared with 10.7% in Northern Ireland (Table 1; Fig. 2). Both countries saw an increase in numbers counted compared with the 2015 census (Fig. 1), but the decline in the percentage of the total population in the Republic of Ireland continued in 2020 (Fig. 2) and was significantly lower in 2020 than 2015 (0.334 *vs.* 0.349; χ^2_1 = 16.76, P < 0.001). The proportion of the population in Northern Ireland did not differ significantly between 2015 and 2020 (0.103 *vs.* 0.107; χ^2_1 = 3.03, P = 0.082, n.s.), suggesting that a decreasing trend from 1991–2015 may have stabilised (Fig. 2). Numbers of Whooper Swans over-wintering in Iceland were similar in 2015 and 2020 (Table 1; Fig. 2), but given the increase in total population size this resulted in a significantly lower proportion of birds in Iceland in 2020 (0.074 *vs.* 0.068; χ^2_1 = 12.31, P < 0.001). Counts amounting to < 1% of the total population were recorded in Wales, the Isle of Man and the Channel Islands (Table 1; Fig. 1a).

Whooper Swans were recorded at 211 sub-sites within 71 sites across England during the 2020 census, extending from Northumberland to Cornwall (Fig. 3a). None were reported for three counties which held birds in 2015 (1.2 % of the total

Table 1. Numbers of Whooper Swans recorded in Iceland, Ireland and Britain during the international census in January 2020, and the percentage change compared with the January 2015 census.

	No. of swans	% change (2015)
England		
Cambridgeshire	7,751	19.0
Norfolk	3,962	83.9
Lancashire	2,194	1.0
Lincolnshire	658	166.4
Cumbria	423	–10.2
Nottinghamshire	405	994.6
North Yorkshire	197	89.4
Northumberland	142	–16.5
Suffolk	96	+
Shropshire	34	183.3
Cheshire	19	20.8
Humberside	17	88.9
County Durham	8	+
Gloucestershire	5	25.0
Oxfordshire	4	+
Herefordshire	2	+
Greater Manchester	2	+
Somerset	2	–33.3
Derbyshire	1	–93.3
Leicestershire	1	+
Warwickshire	1	+
Essex	1	+
Dorset	1	+
Cornwall	1	0
Total	**15,927**	**31.8**
Isle of Man	**27**	**–35.7**
Channel Islands	**1**	**+**
Scotland		
Grampian	1,036	116.3
Highland	934	10.4
Dumfries & Galloway	687	23.1
Strathclyde	586	19.3
Borders	329	27.0
Orkney	322	114.7
Lothians	291	15.0
Tayside	261	–24.6
Western Isles	237	53.9
Fife	208	70.5
Shetland	146	62.2
Central	15	–58.3
Total	**5,052**	**33.5**
Wales		
Gwynedd	103	–8.8
Dyfed	80	77.8
Clwyd	19	–17.4
Powys	11	–45.0
South Glamorgan	1	+
Total	**214**	**6.5**
Northern Ireland		
Londonderry	1,478	128.1
Antrim	1,146	49.0
Down	788	53.0
Fermanagh	492	–37.2
Armagh	490	–5.4
Tyrone	250	–25.8
Total	**4,644**	**32.0**
Republic of Ireland		
Offaly	1,506	208.0
Galway	1,485	–17.2
Roscommon	1,322	–3.3
Donegal	1,159	122.0
Westmeath	982	152.4
Mayo	973	–22.7
Wexford	928	18.2
Clare	875	38.4
Cavan	813	–22.8
Limerick	493	175.4
Cork	488	100.0
Tipperary	441	45.1
Waterford	432	–0.7
Kerry	419	–10.9
Longford	394	85.0
Letrim	386	27.8
Sligo	273	37.9
Louth	208	123.7
Laois	197	64.2
Kildare	175	8.0
Monaghan	172	–65.3
Meath	119	–43.1
Kilkenny	81	268.2
Wicklow	79	31.9
Dublin	40	+
Carlow	27	+
Total	**14,467**	**22.1**
Iceland		
South	1,477	0.2
Southwest	589	–0.1
West	550	10.0
North	294	–0.1
Southeast	13	–0.5
Total	**2,923**	**28.3**
Overall total	**43,255**	**27.2**

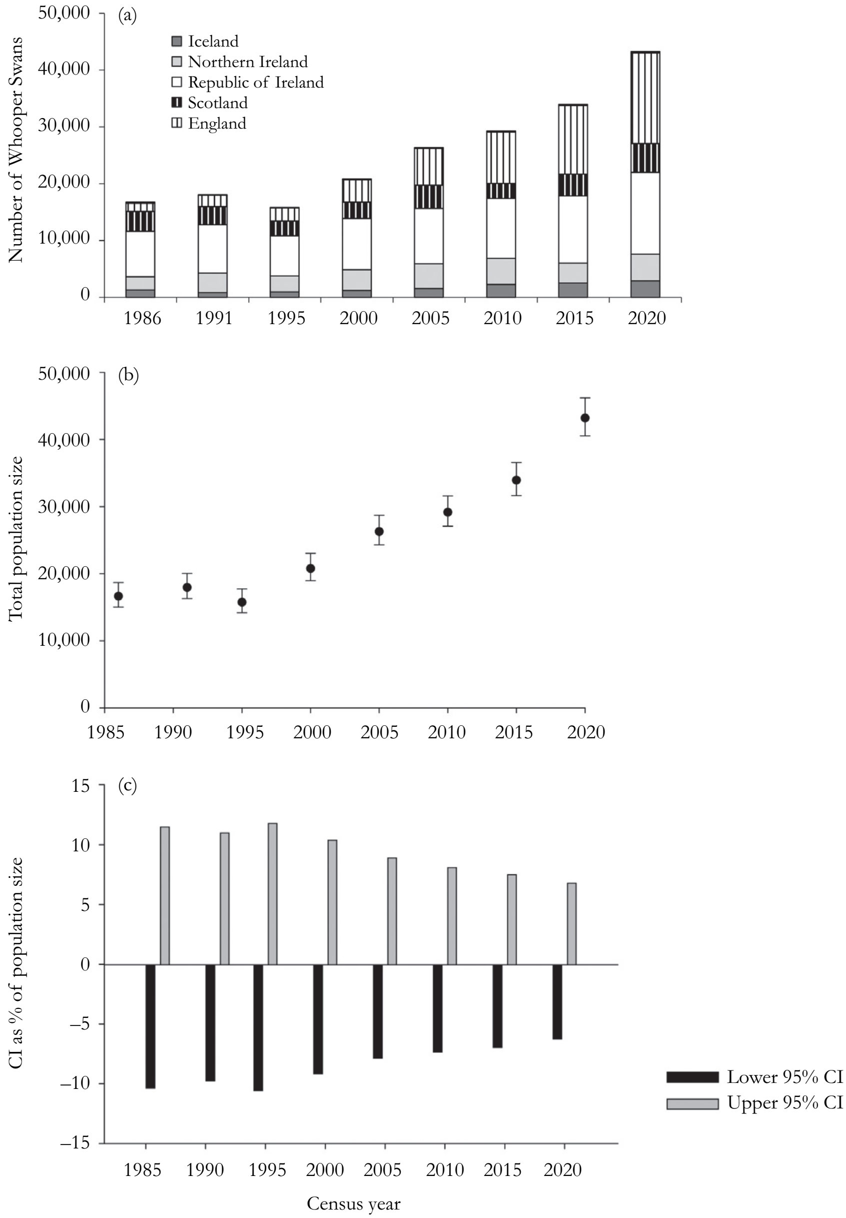

Figure 1. Icelandic Whooper Swan census results. (a) Numbers recorded in Iceland, Ireland and Britain during the international censuses from 1986–2020. Note: Wales, the Isle of Man and the Channel Islands have been combined because each held < 1% of population during each census. (b) The total population size with the 95% confidence intervals (CI) shown for each census. (c) The size of the 95% CIs as a percentage of the total population estimate, indicating the relative precision of each census.

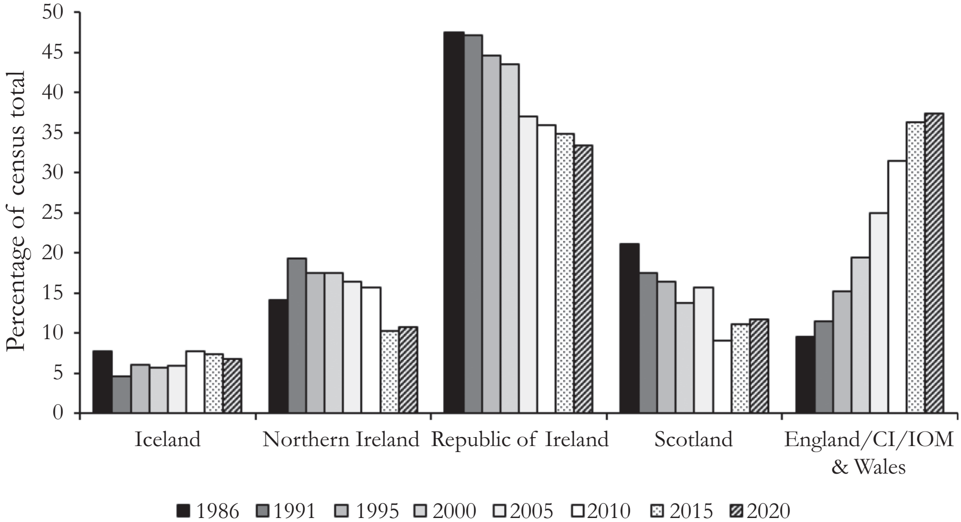

Figure 2. Changes in the distribution of Whooper Swans across Iceland, Ireland and Britain during the international censuses of 1986–2020. Note: counts from Wales, the Channel Islands (CI) and the Isle of Man (IOM), which each contributed < 1% of the census totals each year, have been combined with those from England.

for England in 2015), but nine counties held birds in 2020 where none was seen in 2015 (< 1% of the 2020 English total; Table 1). The main concentration was at the Ouse Washes, Cambridgeshire/Norfolk (9,122 birds) with large numbers also recorded on the Nene Washes, Cambridgeshire (Fig. 3a) (2,618; Supporting Materials Table S1); these two sites accounted for 73.7% of the swans recorded in England with both sites seeing increases in numbers compared to the 2015 census. Elsewhere, Martin Mere, Lancashire, saw a decrease in the number of birds with 879 birds recorded in 2020 compared to 1,462 in 2015, while the nearby Ribble Estuary recorded 867 birds compared with 380 in 2015. Of the other English sites with Whooper Swans, five held 196–448 birds, and the remainder held < 100 swans. The species was also widespread in Scotland, occurring at 230 sub-sites within 216 sites across the country from the Shetland Islands to Dumfries & Galloway (Fig. 3a), most notably at Loch of Strathbeg (681 birds), Petley, Portmahomack (near Loch Eye; 241 birds) and on the River Earn (between Forteviot Bridge and Kinkell Bridge, Tayside; 202 birds). A further seven sites held 118–186 birds and the remainder had < 100 swans.

Swans were recorded at 550 sub-sites within 271 sites across counties in Ireland in 2020 and, as with previous censuses, there was great variation both between censuses and between counties in the numbers recorded. Nonetheless, highest counts in Ireland continued to be from Loughs Neagh & Beg (2,288), with numbers increasing at Shannon Callows (942), Shannon & Fergus Estuary (899) and Lough Foyle (890); at the

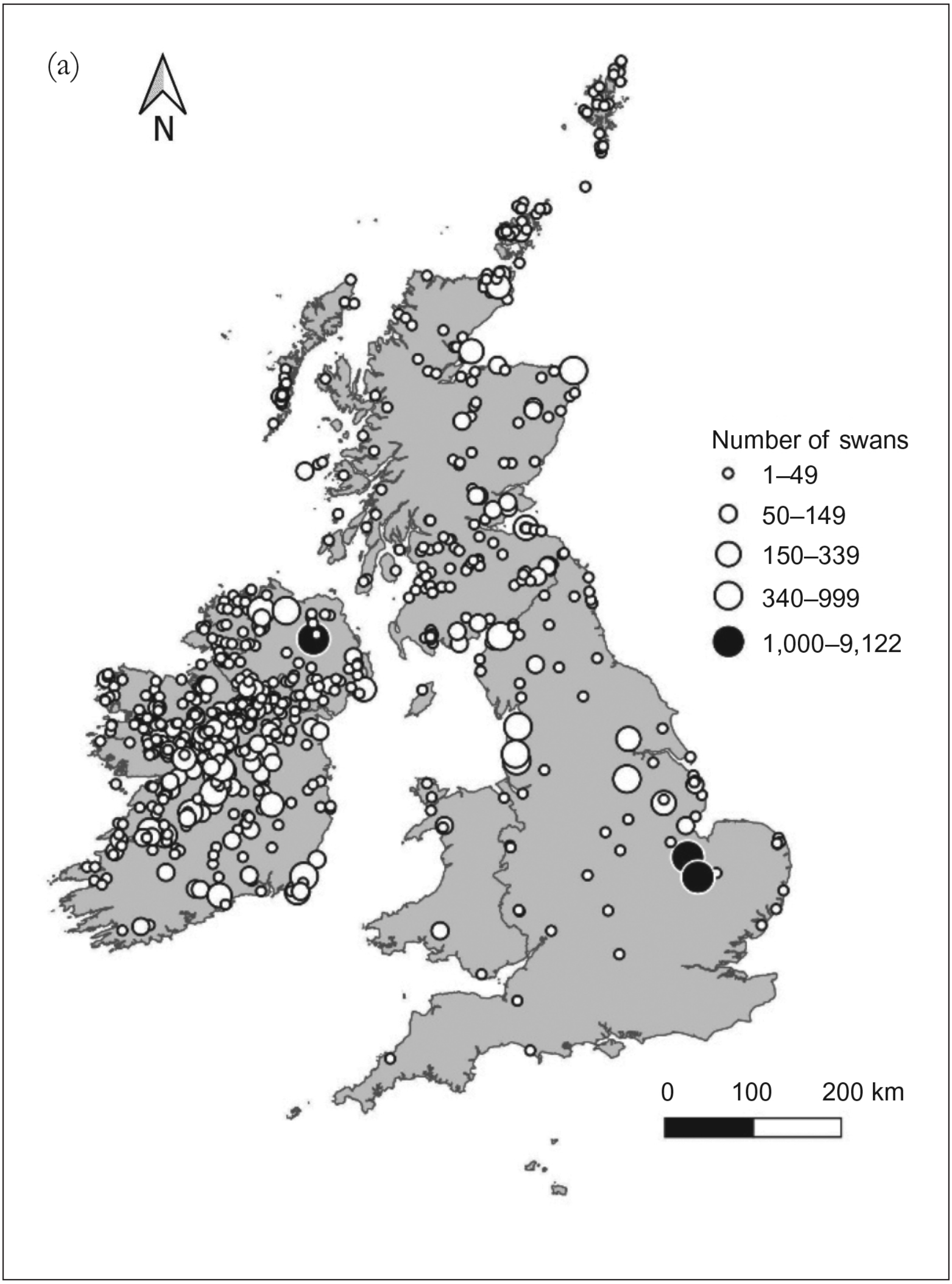

Figure 3. Distribution of Whooper Swans recorded during the January 2020 international census in: (a) Britain and Ireland, and (b) Iceland. Symbols represent total numbers at a site.

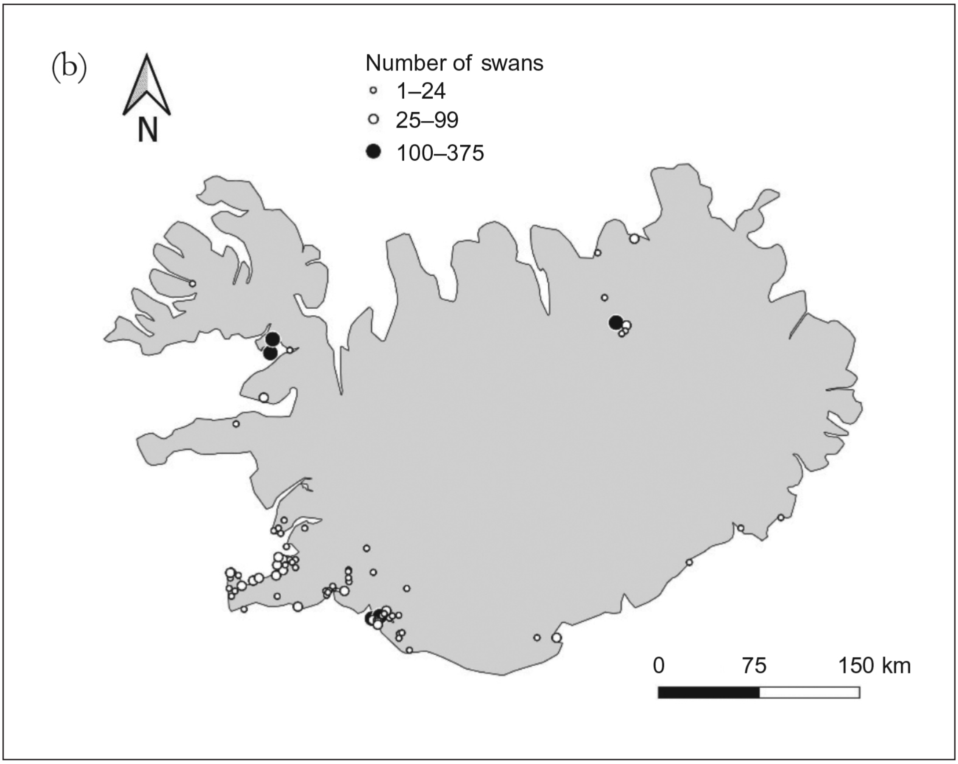

Figure 3 (*continued*).

latter two sites, numbers increased notably. Elsewhere in Ireland, 102–557 birds were recorded at 36 sites, whilst the rest held < 100 Whooper Swans. Birds were recorded at nine sites in Wales, one in the Isle of Man and one on Guernsey, Channel Islands, where all counts were of ≤ 80 individuals (Fig. 3a). In Iceland, birds were recorded at 88 sites in 2020, mostly in the south, southwest and west of the country (Table 1, Fig. 3b). Numbers recorded in most regions were similar to those counted during the 2015 census; however, greater numbers were counted in the west compared to the previous census (50 in 2015, *cf.* 550 in 2020). The largest concentrations were found at Þykkvibær (Southern Iceland; 804) and Berufjörður (West Iceland; 312). Counts at all other sites ranged from 1–280 birds.

Sites of conservation importance

Nine sites in Britain and 13 in Ireland were recorded with ≥ 340 Whooper Swans during the 2020 census (*i.e.* the published threshold for classifying sites of international importance, based on 1% of the population size recorded in the January 2015 census; Wetlands International 2020), and 16 of these sites also held ≥ 1% of the total number of Whooper Swans counted in

2020 (*i.e.* 432 swans; Supporting Materials Table S1). A further six sites in Britain and 17 sites in Ireland supported nationally important numbers (150 and 160, respectively; Burke *et al.* 2018; Frost *et al.* 2019), although only two of the six British sites would be of national importance on the basis of numbers counted in 2020 (*i.e.* a 1% threshold for Britain of 212; Table 1, Table S1). It should be noted however, that the assessment of site importance was based on counts from January 2020 only, and does not reflect the importance of sites during other months or over several years.

There was a notable change to the sites holding internationally important numbers compared with 2015 (Table S1). One site moved down to being of national importance in Ireland, whilst one site no longer held numbers above either the national or international thresholds. However, six sites (five in Ireland and one in Britain) moved up from being of national to international importance, while four sites that had not previously qualified entered the table in 2020. Most sites of international importance for Whooper Swans in Iceland are used by the birds during the breeding season, or as staging sites during spring and/or autumn migration (Einarsson 2000; Hall *et al.* 2016), and none of the Icelandic wintering sites held ≥ 1% of the total population during the 2020 census.

Age and brood size data

A total of 31,570 Whooper Swans (73.0% of the population) was aged during the 2020 census, with most birds aged in England (40.9%) and the Republic of Ireland (32.8%) (Supporting Materials Table S2). Overall, the percentage of cygnets was 17.3% (95% CI = 16.9–17.7%; Fig. 4a), ranging from 14.1% in England to 21.2% in Scotland. This equates to a population containing 35,778 adults and 7,477 cygnets. Lower and upper 95% CI limits represented ± 2.3% of the estimated percentage of cygnets, which was lower than in any of the previous censuses, indicating greater precision of the 2020 census total (Supporting Materials Fig. S1a). Overall, the percentage of cygnets in 2020 was lower than the 19.9% (95% CI = 19.4–20.4%) recorded during the 2015 census.

Mean brood size in 2020 was of 2.02 cygnets (95% CI = 1.97–2.07) per successful pair for the 1,996 families assessed (Supporting Materials Table S2; Fig. 4b), ranging from 1.95 in Northern Ireland to 2.81 in Iceland. The lower and upper 95% CI limits represented ± 2.3% of the estimated mean brood size, which was lower than in any of the previous censuses, again indicating greater precision of the 2020 estimate (Supporting Materials Fig. S1b).

This reduction in breeding success resulted from significantly lower percentages of cygnets recorded in the southern part of the range, in both England and the Republic of Ireland (Table 2). No other countries showed statistically significant differences between 2015 and 2020 (Table 2). Similarly, when the brood sizes in 2020 (2.02 cygnets per brood; 95% CI = 1.97–2.07) were compared with those recorded in 2015 (2.18; 95% CI = 2.12–2.23) for the population overall, the 2020 estimate was found to be significantly lower ($W = 1,841,752$, $P < 0.001$; Table 3). In particular, mean brood size in Northern Ireland declined from 2.23

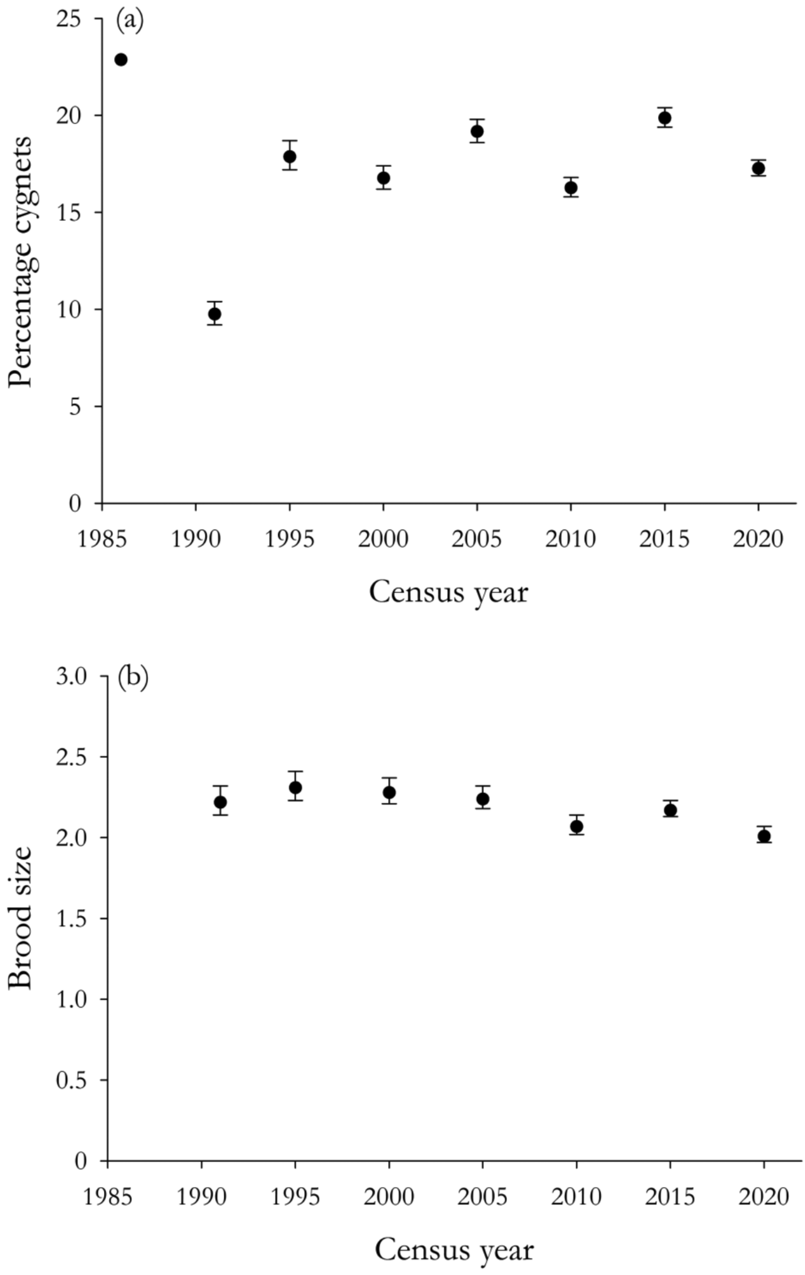

Figure 4. The estimate (± 95% CI) of (a) the percentage of cygnets, and (b) mean brood size, within the Whooper Swan population in each census year. Note: the 95% CI could not be calculated for the 1986 census because the number of age-assessed individuals was not reported.

Table 2. A comparison of the proportions of cygnets reported in each country in the 2015 and 2020 censuses. No age assessment data were available from the Isle of Man.

Country	2015 census			2020 census			Comparison	
	No. aged	No. cygnets	P. cygnets (95% CI)	No. aged	No. cygnets	P. cygnets (95% CI)	χ^2_1	*P* value
Iceland	1,707	353	0.207 (0.188–0.227)	787	159	0.202 (0.175–0.232)	0.1	0.826
Northern Ireland	3,158	688	0.218 (0.204–0.233)	4,125	825	0.200 (0.188–0.213)	3.4	0.067
Republic of Ireland	9,099	2,047	0.225 (0.216–0.234)	10,360	1,930	0.186 (0.179–0.194)	44.3	< 0.001
England	9,725	1,556	0.160 (0.153–0.167)	12,927	1,827	0.141 (0.135–0.147)	15.1	< 0.001
Scotland	2,793	620	0.222 (0.207–0.238)	3,161	670	0.212 (0.198–0.227)	0.8	0.365
Wales	94	13	0.138 (0.076–0.225)	210	44	0.210 (0.157–0.271)	1.7	0.190
Total	26,576	5,278	0.199 (0.194–0.204)	31,570	5,457	0.173 (0.169–0.177)	63.4	< 0.001

(95% CI = 2.10–2.37) in 2015 to 1.95 (95% CI = 1.84–2.06) in 2020 (W = 48,346, $P = 0.009$), whilst in the Republic of Ireland mean brood size decreased from 2.49 (95% CI = 2.37–2.60) in 2015 to 1.98 (95% CI = 1.91–2.06) in 2020 (W = 178,458, $P < 0.001$). No other statistically significant differences in brood sizes between 2015 and 2020 were detected, for Iceland, England, Scotland or Wales (Table 3).

A comparison of the three temporal models of breeding success showed that inter-annual variation in the percentage of cygnets recorded at the three UK sites was not well-described by either a linear or quadratic trend, with the null model (*i.e.* no consistent trend over time) performing best (Table 4). Similarly, a comparison of the four models of the effects of environmental variables on breeding success indicated that the null model was the best-supported model (Table 4). Neither the temperatures in Iceland during the breeding period, nor in the UK during the previous winter, either independently or additively, performed better than the null model, and no model had an $R^2 > 3.6\%$, indicating that the temperature variables explained little of the inter-annual variation in the percentage of cygnets recorded. In addition, a highly significant linear increase in the temperature during the breeding season in Iceland between 1986/87 and 2019/20 was detected ($F_{1,31} = 12.57$, $R^2 = 28.9\%$, $P = 0.001$); the increase in temperature was described by the equation $y = -61.087 (\pm 19.456) + 0.034 (\pm 0.010) * \text{year}$. In contrast, no linear trend over time was found for the winter temperatures in the UK ($F_{1,31} = 2.50$, $R^2 = 7.5\%$, $P = 0.128$, n.s.).

Habitat use

Data on habitat use during the census were collected for 37,310 (86.3%) of the swans counted. When comparing overall habitat use between 2015 and 2020, a greater percentage of the total population was recorded on arable land in 2020 (0.308 *vs.* 0.412; $\chi^2_1 = 749.95$, $P < 0.001$), a lower percentage was recorded on permanent waterbodies (0.262 *vs.* 0.176; $\chi^2_1 = 709.77$, $P < 0.001$) and "other" habitats (0.040 *vs.* 0.022; $\chi^2_1 = 175.89$, $P < 0.001$, n.s.) in 2020, whilst no difference was detected for pasture (0.390 *vs.* 0.390; $\chi^2_1 < 0.01$, $P = 0.940$, n.s.).

As with previous censuses, there was a notable difference in the habitats used between countries, with a higher proportion (17.6%) of swans found on permanent waters in Iceland than in Britain and Ireland and a greater number of birds being found on arable land in Britain (70.7%) than elsewhere (Table 5). Pasture and arable land remained the most frequent habitat type used by Whooper Swans in Britain and Ireland during the 2020 census (Fig. 5), with an increase in numbers using these habitats compared to the 2015 census.

In Ireland, pasture was found to be the favoured habitat used by Whooper Swans (73.0%) particularly dry improved pasture (70.7% in Northern Ireland; 53.3% in the Republic of Ireland; Table 5). In Britain, most birds were recorded on arable land such as growing winter cereals or harvested waste such as cereal stubbles and sugar beet; however, the large concentration of birds at the Ouse Washes accounted for a high percentage (63.6%) of those birds found on this habitat type. Away from the Ouse

Table 3. A comparison (two-sample binomial test) of the brood sizes for Whooper Swan family groups recorded in each country in the 2015 and 2020 censuses. *n* refers to the number of family groups observed. No brood size data were available from the Isle of Man.

Country	2015 census			2020 census			Comparison	
	n	Mean	95% CI	*n*	Mean	95% CI	*W*	*P* value
Iceland	132	2.39	2.19–2.60	32	2.81	2.30–3.32	1,787	0.164
Northern Ireland	286	2.23	2.10–2.37	302	1.95	1.84–2.06	48,346	0.009
Republic of Ireland	395	2.49	2.37–2.60	728	1.98	1.91–2.06	178,458	< 0.001
England	714	1.95	1.88–2.02	750	2.01	1.93–2.08	266,393	0.859
Scotland	180	2.15	1.98–2.32	178	2.20	2.02–2.37	15,677	0.715
Wales	3	1.33	0.68–1.99	6	2.33	1.51–3.16	4	0.170
Total	1,710	2.18	2.12–2.23	1,996	2.02	1.97–2.07	1,841,752	< 0.001

Table 4. A comparison of the support (AICc) and explanatory power (R^2) of the models of the intra-annual variation in the percentage of cygnets recorded at three sites where Whooper Swan flocks have been age-checked annually since winter 1986/87, at: the Ouse Washes, southeast England, Martin Mere/Ribble Estuary, northwest England, and Caerlaverock, southwest Scotland. The best-supported models of the temporal and environmental variables are given in bold. *k* refers to the number of fitted parameters in the model.

Assessment	Model	*k*	AICc	ΔAICc	R^2 (%)
Temporal variables	**Null**	**1**	**170.33**	**0.00**	**0.0**
	Linear	2	171.67	1.34	0.1
	Quadratic	3	172.12	1.79	3.3
Environmental variables	**Null**	**1**	**170.33**	**0.00**	**0.0**
	Iceland	2	171.70	1.38	3.1
	UK	2	172.34	2.01	1.3
	UK + Iceland	3	174.14	3.81	3.6

Washes, 48% of swans recorded were found on arable land, with 27.1% recorded using pasture and 19.9% on permanent standing water.

In Iceland, the majority of birds were recorded using coastal and arable sites (35.6% and 33.5%, respectively; Table 5) and there was a notably smaller proportion of birds using riverine habitats compared with the 2015 census (51.5% in 2015, *cf.* 2.8% in 2020) (Fig. 5).

Discussion

Population size and changes in distribution

The January 2020 Whooper Swan census found that the Icelandic Whooper Swan population had increased to 43,255 (95% CI = 40,554–46,201) birds, 27.2% more than the previous estimate of 34,004 (95% CI = 31,653–36,566) in 2015, and is the highest population estimate recorded to date (Fig. 1). The steady population growth since 2000 concurs with trends in Whooper Swan numbers elsewhere in Eurasia, such as for the NWME population which increased by 133% between 1995 and 2015 (Laubek *et al.* 2019; Lehikoinen 2020). Numbers wintering in Britain have increased 3.1 fold since 2000 (an increase of 14,295 birds), compared with 2.4 (1,723) and 1.5 (6,381) fold increases in Iceland and Ireland, respectively, over the same period, with the highest proportion of the population occurring in Britain for the first time in 2015 (Hall *et al.* 2016) and similarly in 2020. Numbers in Ireland have continued to increase, however, and the 19,111 swans recorded in January 2020 was the highest total to date.

Table 5. Percentage of Whooper Swans recorded on different habitat types in January 2020. Definitions of habitat classifications: 1) Permanent standing water = natural permanent lake, artificial lake/reservoir, gravel pit; 2) River = non-tidal river, freshwater marsh; 3) Coastal = tidal river/estuary, saltmarsh, brackish lake, mudflats, open coast; 4) Improved pasture (dry) = dry pasture managed to improve sward including reseeded pasture; 5) Rough/unimproved pasture (dry) = dry, unmanaged sward; 6) Improved pasture (wet) = improved pasture (flooded), reseeded pasture (flooded), turlough – improved, callow – improved; 7) Rough/unimproved pasture (wet) = rough/unimproved pasture (flooded), turlough – rough/unimproved, callow – rough/unimproved; 8) Arable (waste) = including stubble, potatoes, carrots, sugar beet; 9) Arable (growing) = winter cereal, oil seed rape; and 10) Other = all other habitat types (*e.g.* hot/cold water springs, seen in flight) not specified in one of the other categories. The data for Britain are further broken down into the constituent countries and Crown Dependencies (given in parentheses).

	Iceland	Northern Ireland	Republic of Ireland	Britain	(England)	(Scotland)	(Wales)	(Isle of Man)	(Channel Islands)
Number of swans (*n*)	**2,558**	**4,597**	**11,662**	**18,493**	**15,103**	**3,177**	**193**	**19**	**1**
Permanent waterbodies (%)	**56.9**	**7.4**	**20.4**	**12.8**	**7.0**	**40.4**	**13.0**	**0.0**	**0.0**
Permanent standing water	17.6	7.0	14.2	11.3	6.9	32.8	0.0	0.0	0.0
River	2.9	0.4	6.2	1	0.1	5.1	3.1	0.0	0.0
Coastal	36.5			< 1	0.0	2.5	9.8	0.0	0.0
All pasture (%)	**0.0**	**76.5**	**71.6**	**14.5**	**10.7**	**27.8**	**87.0**	**100.0**	**100.0**
Improved pasture (dry)	0.0	70.7	53.3	7.2	6.0	9.8	45.6	100.0	0.0
Improved pasture (wet)	0.0	1.4	12	5	3.1	12.2	41.5	0.0	0.0
Rough/unimproved pasture (dry)	0.0	0.2	1.3	< 1	0.0	3.1	0.0	0.0	100.0
Rough/unimproved pasture (wet)	0.0	4.2	5	1.8	1.6	2.7	0.0	0.0	0.0
All arable (%)	**33.5**	**16.1**	**6.1**	**70.7**	**80.7**	**27.9**	**0.0**	**0.0**	**0.0**
Arable growing			1.4	30.2	36.4	2.6	0.0	0.0	0.0
Arable waste	33.5	16.1	4.6	40.5	44.3	25.3	0.0	0.0	0.0
Other (%)	**9.6**		**1.9**	**1.9**	**1.6**	**3.9**	**0.0**	**0.0**	**0.0**

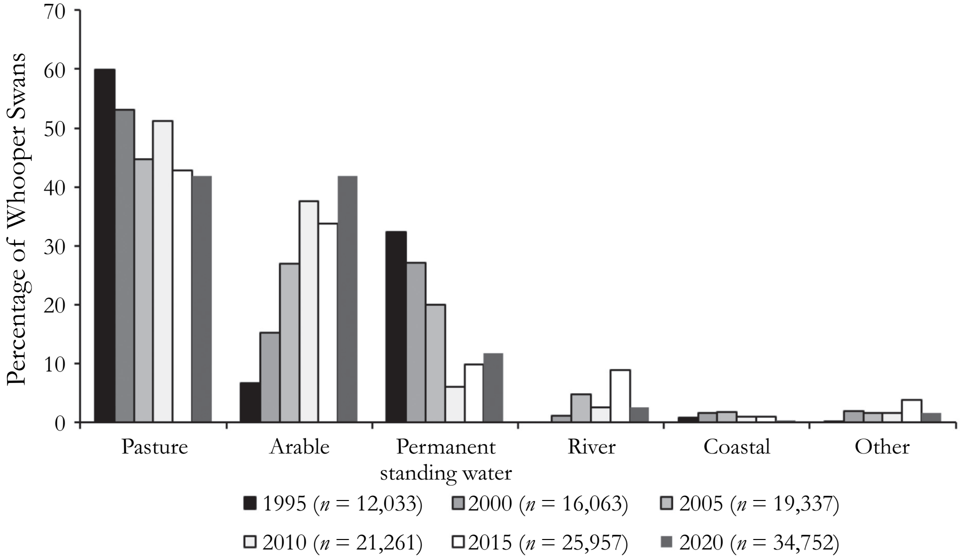

Figure 5. Distribution of Whooper Swans recorded on different habitat types in Britain and Ireland during the January 1995, 2000, 2005, 2010, 2015 and 2020 censuses.

Previous censuses have indicated a south-easterly shift in the swans' mid-winter distribution with an increasing proportion seen in England (Hall *et al.* 2016). This shift has continued, with an increase of 36.8% (15,927 birds) in England. Although all countries (except the Isle of Man) saw an increase in wintering numbers, the greatest increase occurred in Scotland, with the 2020 total count being 33.5% higher than in 2015. Despite this recent increase, numbers have fluctuated in Scotland in recent years; it is possible that snowfall and cold weather conditions in January 2015 could have seen some re-distribution of birds at that time, with fewer birds found in Scotland during the 2015 census as a result. The ongoing increase in England is mainly due to the continued increase in numbers at the Ouse Washes, with the census results being supported by annual counts (L. Marshall, pers. comm.).

The most recent census results show that Whooper Swan numbers in Ireland had increased by 24.3% between 2015 and 2020, representing a departure from the trend of recent census results (Burke *et al.* 2021) when numbers in previous censuses showed the all-Ireland population to be stabilising (Crowe *et al.* 2015). However, whilst the percentage of the total flyway population in Northern Ireland showed a small increase, the proportion in the Republic of Ireland fell slightly due to the larger rises in numbers in the other countries. With Britain, and England in particular, holding the highest percentages of the overall population, and despite numbers rising quicker in the Republic of Ireland, this also supports the theory of the continued shift in distribution.

Numbers over-wintering in Iceland continue to grow, although not at the rate observed between earlier census years (23.6% between 1995–2000, 29.7% from 2000–2005, 46.4% from 2005–2010 and 16% from 2015 and 2020). Numbers wintering in Iceland during the 2020 census were similar to those recorded in 2015, with a difference of 403 birds, a 16% increase. This smaller rate of increase at a time of a large increase in total numbers meant that the proportion of swans in Iceland fell slightly but significantly, from 7.4% in 2015 to 6.8% in 2020. Recent relatively mild winter conditions in Iceland have seen other Icelandic species choose not to migrate, such as the Icelandic Greylag Goose *Anser anser*, with several thousand birds short-stopping in Iceland and no longer migrating to Britain each winter (Mitchell & Brides 2020). Future monitoring of these populations needs to take into account the role that climate change plays on the distribution and timing of migration of swan and goose populations.

Distribution across sites

In England, censuses have shown Whooper Swan flocks to be more concentrated in certain areas and in large numbers at just a few sites. The continued increase in the number of birds using the Ouse Washes (by nine-fold since the 1995 census) and the neighbouring Nene Washes, where no birds were recorded during the 1995 census, means that these sites continue to hold the majority of Whooper Swans in England during the censuses. However, Whooper Swans were found at 20 more sites in England during 2020 compared to the 2015 census. In Lancashire, Martin Mere saw a decline of 40% compared to the numbers recorded in 2015; however, other sites in the area saw an increase in numbers, suggesting some local re-distribution taking place in Lancashire. Of particular note were the large numbers of birds found away from the more traditional areas frequented by Whooper Swans in England, *e.g.* in Nottinghamshire where numbers rose by 994.6% on the 2015 census, although this increase was from very low numbers recorded in Nottinghamshire in 2015. The consequences of rapid rises in swan numbers at key sites certainly warrants investigation, as there may be conservation implications in terms of disease transmission and food resources. One recent modelling study by Wood *et al.* (2021) found that swans using the Ouse Washes showed little sensitivity to increased competition for arable food resources (predominantly post-harvest remains of sugar beet, potatoes, and maize in early winter, together with early growth of wheat and oilseed rape in late winter). This indicates that the superabundance of these arable crops in the landscape surrounding the Ouse Washes mitigates the effects of competition, even at high swan densities. Continued increases in swan numbers at this site therefore are not expected to lead to food shortages for swans, although greater impacts on agricultural yields of wheat and oilseed rape were predicted (Wood *et al.* 2021), which could lead to conflicts between agriculture and conservation as observed for other swan populations (*e.g.* Laubek 1995). However, other sites with more limited food supplies, such as aquatic habitat, may show greater sensitivity to rising swan numbers.

Scotland saw an increase in the number of sites where Whooper Swans were recorded, from 185 (in 2015) to 216 (in 2020), with birds more widely distributed than in England (Fig. 3a). The increase in total swan numbers and distribution across counties in Scotland during the 2020 census is likely due to the mild weather conditions that winter, in comparison with the much colder conditions in January 2015, which may have restricted the habitat and food resources available particularly in northern areas, and encouraged some birds to relocate out of Scotland for part of the 2014/15 winter. The notable decrease in the number of birds wintering on the Solway Estuary detected during 2020 (down by 28% compared to 2015), together with the large increase at Loch of Strathbeg (up by 126%), perhaps also suggests that the swans' distribution further north was not hampered given the relatively mild weather conditions experienced during the 2020 census.

Distribution across habitats

There has been a general increase in the percentage of birds using arable habitats in recent censuses, though a decrease was noted in 2015, and seems likely that this is linked to the ongoing growth in the number of Whooper Swans wintering at the Ouse Washes (an increase of 1,951 birds since 2015, equating to 4.5% of the flyway population) where they feed primarily on arable crops. In comparison, the percentage of swans using pasture across all countries was estimated at 39.0% in both the 2015 and 2020 censuses, with no significant difference detected between these two surveys, though the percentage of birds using pasture has declined over time (since 2000). It is worth highlighting that much of the survey effort for the census is carried out during the day when swans are feeding, but that permanent standing water habitats in close proximity to those feeding areas are still vital as roosting habitat, and likely as feeding habitat too in different areas or at different stages of the winter (Rees *et al.* 1997; Bowler 2021).

Confidence intervals

In this census 95% CI values were calculated to quantify the precision of the estimates of total population size, percentage cygnets and brood sizes. This included back-calculation of 95% CIs for all of the previous Whooper Swan censuses for which relevant data were available. A comparison of the relative size of the 95% CIs associated with each census indicated that the 2020 census achieved the greatest precision to date. This likely reflects the greater sampling effort in 2020; for example, the samples associated with the age assessment and brood size calculations were higher than had been achieved previously. As these methods have not been used more widely, it is difficult to compare the precision of the estimates reported here with those of other similar surveys, such as censuses of other swan populations. However, co-ordinated censuses of Trumpeter Swans *Cygnus buccinator* and Tundra Swans *Cygnus columbianus columbianus* in North America, using a stratified sampling design, aimed to achieve 95% CIs of ± 10% of the total population size; in practice, CI values of ± 7% were achieved by the complete censuses that were undertaken (Conant *et al.* 1991). The calculation of CI values in future censuses and other monitoring programmes will facilitate greater assessment of the precision of population size and breeding success estimates, both within and between programmes.

Comparison with WeBS counts

Whilst total census schemes such as the ISC cannot be undertaken for all species, where they can be practically carried out they provide valuable information for informing waterbird conservation. The WeBS count of Whooper Swans in Britain and Northern Ireland in January 2020 was 10,057 (Frost *et al.* 2021), which represents 39% of the combined census total for those countries, indicating that WeBS misses a notable proportion of the population. I-WeBS data for January 2020 has not yet been fully compiled, but January counts of Whooper Swans from previous years represent a similar percentage of the 2020 census total (30–35%). Whilst, WeBS and I-WeBS provide valuable information on population trends for some of the countries within the flyway, they do not provide comprehensive estimates of total population size for the total flyway. Such estimates of total population size help to inform the designation of sites of international and national importance, which represent a key part of the conservation strategy for species such as Whooper Swans (Table S1). The frequent itinerant movements of Icelandic Whooper Swans within their flyway, which cross international geopolitical borders, together with the tendency to frequent habitats away from wetlands to feed, highlight not only the importance but also the need for coordinated species-specific surveys, where possible, to derive new and updated population estimates. Information at such scale and detail cannot be brought about by more general national waterbird monitoring schemes alone but rely on well-coordinated surveys across a variety of habitats in different countries along the flyway.

Demographic drivers of the population change

The sustained increase in Whooper Swan population size requires explanation, especially as it contrasts with the population trends of the other swan species that share its winter grounds. The Bewick's Swan *Cygnus columbianus bewickii* increased in numbers across northwest Europe up to 1995, then underwent a *c.* 40% decline until 2010, after which it showed a slight recovery (Beekman *et al.* 2019). The Mute Swan *Cygnus olor*, which breeds in the UK, showed an increase in population size between the late 1980s and *c.* 2000, after which the population has remained stable (Wood *et al.* 2019). Given that there is limited interchange with other Whooper Swan populations (K. Brides, unpubl. data), the observed increase in the Icelandic-breeding Whooper Swan must be due to increased survival rates of one or more age classes, increased breeding success, or both. The analyses reported here showed no consistent trend in the percentage of cygnets recorded among the Whooper Swan population, and certainly no evidence of any increase over time. Furthermore, despite evidence that the mean temperature in Iceland in the breeding season has increased since the 1980s, there was no evidence that temperature affected Whooper Swan breeding success. This finding is in contrast to previous research on Bewick's Swans, as temperatures on the breeding grounds were shown to have a major, positive effect on the swans' productivity (Wood *et al.* 2016). The arctic breeding grounds of the northwest European Bewick's Swan population did, however, show a greater range of mean temperatures (4.0–8.7°C; Wood *et al.* 2016) than the sub-arctic breeding grounds of the Icelandic Whooper Swan population (6.7–9.1°C; this study), which may at least in part account for the different results. The poor explanatory power of the two environmental variables tested here highlights the need for further research to understand the environmental causes of the inter-annual variation in breeding success.

Given the evidence that there has been no increase in breeding success (this study), and that emigration and immigration are considered negligible (Rees *et al.* 2002; Hall *et al.* 2016; K. Brides, unpubl. data), the observed increase in Whooper Swan numbers must be due to increased survival rates of one or more age classes. A number of factors are likely to be contributing to the increase in Icelandic Whooper Swan numbers; mild winters experienced in wintering areas could have decreased Whooper Swan mortality over-time. Plentiful feeding opportunities, especially on the wintering grounds, is likely to result in breeding birds migrating back to Iceland in good body condition, potentially increasing breeding success; however, we have detected no such increase in breeding success in the available data. Furthermore, recent research has shown high availability of the arable food resources used by Whooper Swans in Northwest Europe (Wood *et al.* 2021). It may also be the case that Whooper Swans wintering on agricultural *versus* more natural habitats derive fitness benefits, as has been shown for some goose populations (Fox *et al.* 2005), such that changes in habitat use could have contributed to demographic changes in the population (Laubek *et al.* 2019). However, further research on Whooper Swan demography and habitat use would be needed to test for a causal link. From the census results it is clear that there has been no appreciable increase over time in either the percentage of cygnets in the population (Fig. 4a) or the mean brood size (Fig. 4b), despite a trend towards greater use of arable habitat.

Since the mid-20th century, migratory Whooper Swans have been protected by national and international legislation throughout their migratory ranges, meaning that it is illegal to take or harvest birds. Yet illegal shooting does occur, with 13.6% of live Whooper Swans x-rayed in the UK between 1980–2009 shown to have shot in embedded pellets in their body (Newth *et al.* 2011). Given the steady increase in population size and the large numbers feeding on arable type habitats, there is the potential for the population to come into greater conflict with humans and agriculture in the future (Laubek 1995).

Although the level of exchange between the Icelandic and NWME populations is considered to be limited, the absence of detailed analysis of the swans' movements, survival and mortality hinders our understanding of the extent to which the main demographic and environmental drivers are influencing the observed increase in population size. To gain a better insight into the ongoing re-distribution of the population, with the apparent shift to southeast England still occurring, it would be advantageous to use already collated colour-marking datasets to determine whether individual birds are changing their wintering areas over time, as recently undertaken for the Northwest European Bewick's Swan population (Nuijten *et al*. 2020b).

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