

Population size and breeding success of the Icelandic Whooper Swan *Cygnus cygnus*: results of the 2015 international census

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Abstract

The seventh international census of Whooper Swans in Britain, Ireland, Iceland and the Isle of Man took place in January 2015, to update estimates of the size and mid-winter distribution of the Icelandic Whooper Swan population. The 34,004 swans recorded represented a 16% increase in numbers compared to the previous census in 2010, a 155% increase on counts made in 1995, and was the highest census total to date. The drivers behind this increase have yet to be determined, but it seems that it is not solely attributable to an improvement in breeding success in recent years and that changes in survival rates and perhaps interchange with the Northwest Mainland Europe population may also be accountable for the trend. Overall, 35.5% of the population (12,083 birds) was recorded in England, 34.9% (11,852) in the Republic of Ireland, 11.1% (3,784) in Scotland, 10.4% (3,518) in Northern Ireland, 7.4% (2,520) in Iceland and < 1% (247) in Wales and the Isle of Man. There was a significant decline in the proportion of birds wintering in Northern Ireland and the Republic of Ireland in comparison with the 2010 census, whilst conversely England saw a notable increase. Although a higher proportion of the population was recorded in Scotland in 2015 than in 2010, the results indicate a continuation of the overall shift to the southeast in the swans' winter distribution, recorded since the first international census in 1986. As in previous censuses, the majority of birds in Britain and Ireland were on pasture and arable land, whereas in Iceland the birds were found mainly on riverine and coastal habitats.

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

The Whooper Swan *Cygnus cygnus* has a widespread breeding distribution, extending from Iceland across northern Europe to eastern Siberia (Brazil 2003; Rees *et al.* 2002). The Icelandic-breeding population is one of five currently recognised for this species (Brazil 2003; Wetlands International 2016). Count and ringing programmes have shown that the majority of the Icelandic population winters in Britain and Ireland, with small but increasing numbers remaining in Iceland to overwinter (Rees *et al.* 2002; Hall *et al.* 2012). 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 some 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).

Whooper Swans have been monitored in Britain, Ireland and Iceland through national monitoring schemes since the 1950s, currently through the Wetland Bird Survey (WeBS), the Irish Wetland Bird Survey (I-WeBS), the Irish Whooper Swan Study Group (IWSSG) and the Icelandic annual winter bird census. 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 which include coverage of these additional areas are, therefore, required in order to provide accurate estimates of population size and changes in distribution.

International censuses of the Icelandic Whooper Swan population have taken place approximately every five years since 1986. Since 1995 they have also been scheduled to coincide with censuses of the Northwest European Whooper Swan population which winters on mainland Europe (Laubek *et al.* 1999). Whilst early censuses of the Icelandic population showed a fluctuation in numbers at < 20,000 birds, more recent censuses indicate a steady growth in population size, with count totals of 20,856, 26,366 and 29,232 recorded in 2000, 2005 and 2010, respectively (Hall *et al.* 2012). There was also some indication of a south-easterly shift in the swans' mid-winter distribution of swans 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 wintering in Iceland (Hall *et al.* 2012).

The seventh international census of Whooper Swans in Britain, Ireland and Iceland took place in January 2015. This paper presents the results of this census, including an update on the size and distribution of the wintering population and the breeding success recorded at the time of the census.

Methods

The 2015 census of the Icelandic Whooper Swan population was coordinated by the Wildfowl & Wetlands Trust (WWT) and was organised in Britain by WWT, in Ireland by BirdWatch Ireland and the IWSSG, and in Iceland by Ólafur Einarsson. Counts were undertaken by a network of volunteers (including WeBS and I-WeBS counters and IWSSG members) and professional staff of the partner organisations. In addition to recording flock size, date and location, counters were asked to report on the number of young in each flock, brood size, habitat type (from the list of 10 main habitat categories used during the 2000, 2005 and 2010 censuses; see Table 3 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, have been published previously in Worden *et al.* (2009).

In Britain and Ireland, the census was scheduled to take place on the weekend of 17–18 January 2015 to coincide with the monthly WeBS and I-WeBS counts. Counters were asked to also visit sites known to have held, to currently hold or may potentially be suitable for Whooper Swans but which are not regularly covered by these annual schemes.

Data in Iceland were collected mainly through the annual winter bird census, organised by the Icelandic Institute of Natural History, which was undertaken during December 2014 and January 2015. Supplementary counts were also carried out

in north and west Iceland in late January/early February. An aerial survey of the southern lowlands, which are not covered by the winter bird census, was carried out on 31 January. The broad range of dates across which Iceland was surveyed is considered acceptable because the number of birds counted is comparatively small and there is thought to be little movement of swans between the Icelandic sites during mid-winter (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 to have moved between adjacent sites, determined by information provided by counters. Any counts deemed to be duplicates were omitted from the analysis (except when assessing site importance; see below). 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 by counters 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 counts. 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 international and national importance. For the purpose of the analyses presented in this paper, 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 sequentially by a flock) that fall within the catchment area of a larger roost site.

Chi-squared tests in Minitab were used to assess changes in distribution and habitat use between the 2010 and the 2015 censuses, and also differences between countries in the proportion of juveniles recorded. Distribution was analysed as the proportion of the population recorded within each of the countries, because the national boundaries provided a rough overview of whether the swans were in the far north (Iceland), northeast (Scotland), northwest (Northern Ireland), southeast (England) or southwest (Republic of Ireland) parts of their wintering range.

Results

Coverage

In the weeks prior to the census weekend, the weather in Britain and Ireland was largely mild and wet, with windy and stormy conditions experienced across all countries, particularly Scotland (Met Office 2016; Met Éireann 2016). The weather became colder and more settled during the second half of the month,

including the census weekend, with some snowfall at times particularly over high ground in Scotland and northern England.

Coverage of sites known to be used by swans was thought to be good during the 2015 census period. Overall, 95.1% of the 804 counts (where swans were recorded) from Britain and Ireland included in the study were made during or up to three days before/after the census weekend. The remainder were visited in 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, 66% of the counts (where swans were recorded, $n = 311$) were undertaken on the scheduled census dates and a further 30% were conducted within three days either side. All the counts were carried out between 12–25 January 2015.

Counts in Northern Ireland were carried out between 16–25 January 2015, with 46% ($n = 114$) carried out on the census weekend and 51% within three days either side. In the Republic of Ireland, counts were undertaken between 10 January and 4 February, of which 48% ($n = 379$) took place on the scheduled dates and 45% during three days either side.

In Iceland, counts were undertaken between 25 December 2014 and 3 February 2015. Coverage was good for all regions, with the exception of two areas in west Iceland (Mýrar and part of Breiðarfjörður), which are thought to hold a few tens of birds, although these areas have also not been covered during previous censuses (Ó. Einarsson, pers. comm.).

Numbers and distribution

A total of 34,004 Whooper Swans was recorded in Britain, Ireland and Iceland during the January 2015 census (Table 1). Since the publication of the results from the January 2010 census (Hall *et al.* 2012), additional counts totalling 68 birds were received from four sites in the Republic of Ireland resulting in a revised 2010 population estimate of 29,300. The total recorded in 2015 thus represents a 16% increase on this revised 2010 figure (Table 1 & Fig. 1).

During the 2015 census, all countries with the exception of Northern Ireland recorded an increase in the number of wintering Whooper Swans compared to the previous census (Table 1 & Fig. 1). Britain and Ireland each held an almost equal proportion of the

overall population (47.4% and 45.2%, respectively), whilst Iceland held 7.4%. In England, there was a significant increase in the proportion of the total population recorded in 2015 (35.5%), compared to the 2010 census (30.8%; $\chi^2_1 = 164.7$, $P < 0.001$; Table 1 & Fig. 2). Swans were recorded at 111 sub-sites within 51 sites across England, distributed from Northumberland to Cornwall (Fig. 3a). Counties containing the key sites continue to support the majority of birds, whilst there was some variation in those holding smaller numbers compared with the previous census (Table 1): seven counties which held birds in 2010 recorded no birds in 2015 (accounting for < 1% of the total for England), and four held birds in 2015 where none were seen in 2010 (accounting for 1% of the English

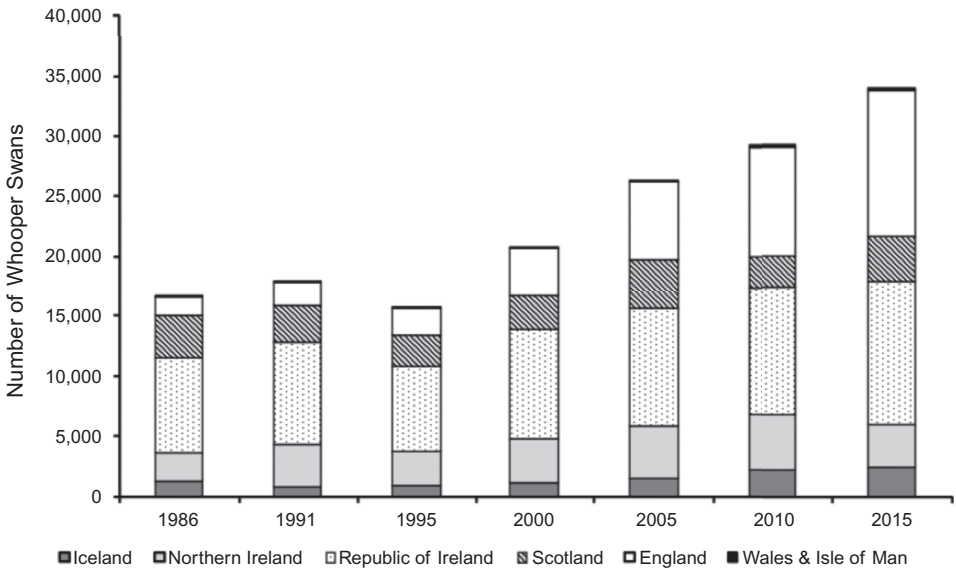


Figure 1. Number of Whooper Swans recorded in Iceland, Ireland and Britain during the international censuses of the Icelandic-breeding population from 1986–2015. Note: Wales and the Isle of Man have been combined as each held less than 1% of the population during each census.

Table 1. Numbers of Whooper Swans recorded in Iceland, Ireland and Britain during the international census in January 2015, and the percentage change compared with the January 2010 census.

	No. of swans	% change (2010)		No. of swans	% change (2010)
England			Northern Ireland		
Cambridgeshire	6,513	43.3	Fermanagh	784	-23.1
Lancashire	2,172	-9.7	Antrim	769	47.9
Norfolk	2,154	51.1	Londonderry	648	-61.3
Cumbria	471	50.5	Down	515	-6.0
Lincolnshire	247	>1,000	Armagh	465	-8.5
Northumberland	170	70.0	Tyrone	337	-2.9
South Yorkshire	144	585.7	Total	3,518	-23.8
North Yorkshire	104	+	Republic of Ireland		
Nottinghamshire	37	+	Galway	1,793	62.9
Cheshire	24	-66.2	Roscommon	1,367	34.4
Derbyshire	15	+	Mayo	1,259	38.7
Shropshire	12	20.0	Cavan	1,053	19.9
Humberside	9	-75.0	Wexford	785	22.5
Gloucestershire	4	-50.0	Clare	632	20.4
Somerset	3	50.0	Donegal	522	-38.9
Bedfordshire	2	-66.7	Monaghan	496	22.8
Cornwall	1	-50.0	Offaly	489	19.6
East Sussex	1	+	Kerry	470	-12.5
Total	12,083	34.3	Waterford	435	-2.2
Isle of Man			Westmeath	389	-38.4
			Tipperary	304	10.1
			Leitrim	302	123.7
Scotland			Cork	244	-5.4
Highland	846	115.3	Longford	213	10.9
Dumfries and Galloway	558	-40.6	Meath	209	-18.4
Strathclyde	491	85.3	Sligo	198	6.5
Grampian	479	839.2	Limerick	179	-52.4
Tayside	346	36.8	Kildare	162	44.6
Borders	259	292.4	Laois	120	-20.5
Lothians	253	107.4	Wicklow	116	182.9
Western Isles	154	30.5	Louth	93	-49.7
Orkney	150	-9.6	Kilkenny	22	>1,000
Fife	122	-12.2	Total	11,852	12.7
Shetland	90	-33.8	Iceland		
Central	36	260.0	South	1,387	0.1
Total	3,784	42.3	Southwest	551	-0.2
Wales			West	370	6.4
Gwynedd	83	-26.5	Northeast	208	-0.4
Dyfed	45	0.0	Southeast	4	-0.8
Powys	39	95.0	Total	2,520	10.6
Clwyd	38	65.2	Overall total		
Total	205	2.0		34,004	16.0

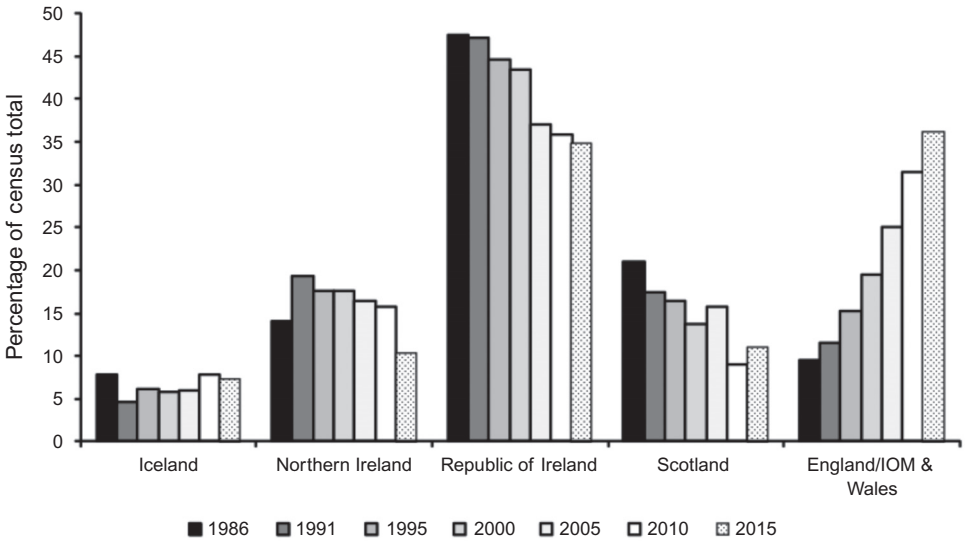


Figure 2. Changes in the distribution of Whooper Swans across Iceland, Ireland and Britain during the international censuses of 1986–2015. Note: Wales and the Isle of Man have been combined with England as each only contributes <1% to the census totals each year.

total). The largest concentrations of Whooper Swans were at the Ouse Washes, Cambridgeshire/Norfolk (7,171 birds), WWT Martin Mere, Lancashire (1,462) and the Nene Washes, Cambridgeshire (1,173), which together accounted for 81% of the swans recorded in England (Fig. 3a). Of particular note was the increase at the Nene Washes where just 337 swans were recorded in 2010. Of the other sites where swans were recorded, seven held between 100 and 307 birds and six held between 50 and 100, whilst the remainder held fewer than 100.

Scotland held 11.1% of the population, which was also a significantly higher proportion than recorded during the 2010 census (9.1%; $\chi^2_1 = 72.6$, $P < 0.001$; Table 1), albeit still below the proportion of the population recorded wintering there during the late 20th century (Fig. 2). Birds were

observed at 189 sub-sites within 185 sites across the country from the Shetland Isles to Dumfries & Galloway, with many counties holding notably higher numbers compared with 2010, particularly those in the northeast (Table 1 & Fig. 3a). The largest concentrations were reported from the Solway Estuary in Dumfries & Galloway (382) and Lower Pitkerrie (near Loch Eye) in the Highlands (247), whilst a further eight sites held between 100 and 180 birds and the remainder <100 swans.

As in previous censuses, Wales and the Isle of Man each held <1% of the total population (Table 1 & Fig. 2). Birds were seen at eight sites in Wales and one in the Isle of Man, with all counts being of < 100 individuals (Fig. 3a).

In Ireland, the majority of birds was seen in the Republic of Ireland (34.9% of the



Figure 3. Distribution of Whooper Swans recorded during the international census in January 2015
a) Britain and Ireland; b) Iceland. Symbols represent total numbers at a site.

total population), with Northern Ireland holding 10.3% (Table 1 & Fig. 1). Both countries saw a significant reduction in the proportion of the population wintering there compared with 2010 (decreasing from 35.9% in 2010 for the Republic of Ireland, $\chi^2_1 = 7.59$, $P = 0.006$; and from 15.8% in Northern Ireland, $\chi^2_1 = 411.1$, $P < 0.001$, Fig. 2), but it is notable that only in Northern Ireland was there a drop in total numbers of swans recorded between 2010 and 2015 (Table 1). Swans were recorded at 473 sub-sites within 253 sites across all counties in Ireland, with the exception of Dublin and Carlow. There was substantial variation for most counties in the numbers recorded between censuses although, given that county totals depended on the precise location of the flocks at a site, some of the variation can be accounted for by changes in swan distribution within sites that span multiple counties, such as Loughs Neagh & Beg in Antrim/Londonderry/Tyrone/Armagh/Down. Counties Galway, Mayo and Roscommon saw the largest increases in numbers (by 692, 351 and 350 birds, respectively), whilst Londonderry and Donegal saw the largest declines (by 1,025 and 332 birds, respectively). Highest numbers were recorded at Loughs Neagh & Beg (1,587) and Upper Lough Erne in Fermanagh (676): counts at these two sites accounted for 64% of the Northern Ireland total. Elsewhere in Ireland, counts at 42 sites ranged from 100 to 465 birds whilst the rest held fewer than 100.

The proportion of Whooper Swans wintering in Iceland in 2015 (7.4% of the population) was very similar to that of 2010 (7.8%; $\chi^2_1 = 2.98$, n.s.; Table 1 & Fig. 2).

Birds were recorded at 135 sites and were predominately seen in the south, west and northeast of the country (Table 1 & Fig. 3b). The distribution of birds within Iceland was also similar to that seen during the 2010 census, although a notably greater number of birds was recorded in west Iceland (370 in 2015 *cf.* 50 in 2010) with swans recorded at 11 sites there in 2015 compared with three in 2010. The largest concentrations were noted at Hólsá (southern Iceland; 462) and Beruförður (west Iceland; 170). Counts at all other sites ranged from 1 to 92 birds.

Sites of conservation importance

Six sites in Britain and eight in Ireland held numbers exceeding the published 1% threshold for international importance, which was based on the January 2010 census (*i.e.* 270 birds; Wetlands International 2016) during the 2015 census (Appendix 1). Twelve of these 14 sites also held at least 1% of the total count of Whooper Swans recorded in 2015 (340). A further 10 sites in Britain and 16 in Ireland supported nationally important numbers (110 and 150, respectively; Musgrove *et al.* 2011; Crowe & Holt 2013), although only six of the 10 British sites would be of national importance on the basis of numbers counted in 2015 (*i.e.* a 1% threshold for Britain of 161; Table 1; Appendix 1). It should be noted, however, that the assessment of site importance was based on counts from January 2015 only, and does not reflect the importance of sites during other months or over several years.

There was notable change to the sites holding nationally or international important numbers compared with 2010 (Appendix 1).

Five sites moved down from international importance to being of national importance in Ireland, whilst 15 sites (10 in Ireland and five in Britain) no longer held numbers above either the national or international thresholds. However, 19 sites entered the table in 2015, with two qualifying as internationally importance and a further nine in Ireland and eight in Britain holding nationally important numbers.

Most sites in Iceland considered to be of international importance for Whooper Swans are used by the birds during the breeding season or as staging sites during spring and/or autumn migration (Einarsson 2000). Nevertheless, the total of 462 birds recorded at Hólsá during the mid-winter census exceeds 1% of the total population and thus internationally important levels.

Age and brood size data

During the 2015 census, a total of 26,576 Whooper Swans were aged (78% of the census total), with the majority assessed in England/Isle of Man (37%) and the Republic of Ireland (34%) (Table 2). Overall, the percentage of cygnets was 19.9%, ranging from 13.8% in Wales to 22.5% in the Republic of Ireland. This equates to a population containing 27,236 adults and 6,768 cygnets.

The overall mean brood size was 2.18 cygnets per successful pair for the 1,710 families assessed (Table 2), ranging from 1.33 in Wales to 2.49 in the Republic of Ireland. The majority of families (66%) consisted of broods of one or two cygnets, 30% had three or four cygnets, whilst the remaining families (4%) contained five to seven cygnets.

Overall, the proportion of cygnets in 2015 was higher than that recorded during the 2010 census (16.3%), a feature that was mirrored across all countries with the exception of Wales. Similarly, the overall mean brood size was marginally higher in 2015 than during the previous census (2.08), with all countries, except Iceland and Wales, seeing a slight increase.

There was a significant difference in the proportion of juveniles recorded across the individual countries ($\chi^2_4 = 148.4$, $P < 0.001$, Wales omitted because the sample size was small; Table 2), with the highest proportion of cygnets being recorded in Scotland and the Republic of Ireland, the latter also reporting the highest mean brood size (Table 2). The proportion of cygnets also varied across regions within countries; however, generally, flocks in northern regions of Scotland and Ireland held higher proportions of young. A high proportion of cygnets was also recorded among swans counted in Iceland, albeit not significantly greater than in Britain and Ireland combined ($\chi^2_1 = 0.74$, n.s.). Mean brood size was highest amongst flocks in regions of the Republic of Ireland (Table 2).

Habitat use

Data on the habitat being used by the birds were collected for 28,477 (> 80%) of the swans counted, with 391 (1.4%) of these observations made at sites recorded as being used only to roost. A further 1,462 (5.1%) were recorded as a “dawn count” at Martin Mere (a permanent inland water), but Martin Mere is used for feeding as well as roosting. Overall, the majority of the birds were seen on pasture (39.0%) and arable

Table 2. Percentage young, mean brood size and frequency of broods of Whooper Swans in Iceland, Ireland and Britain in January 2015 (see Appendix 1 in Worden *et al.* 2009 for regional definitions).

	Number aged	% young	Mean brood size	Broods						
				1	2	3	4	5	6	7
Iceland										
North	188	30.3	3.31	1	3	6	3	2	1	
South West	358	24.0	2.95	2	6	6	5	2		
Southeast	3	33.3	1.00	1						
Southern	1,101	17.3	2.12	30	27	19	6	3		
West	57	35.1	2.22	1	5	3				
Total	1,707	20.7	2.39	35	41	34	14	7	1	
Northern Ireland	3,158	21.8	2.23	96	89	58	27	13	3	
Republic of Ireland										
Northeast	1,886	22.3	2.55	14	19	27	8	2	1	
Northwest	4,165	22.5	2.45	44	51	39	23	7	2	1
Southeast	1,712	26.6	2.59	19	41	26	20	5	1	
Southwest	1,336	17.7	2.27	14	16	6	7	2		
Total	9,099	22.5	2.49	91	127	98	58	16	4	1
Ireland total	12,257	22.3	2.38	187	216	156	85	29	7	1
England										
East Central	7,410	14.2	1.93	197	198	103	24	3		
Northeast	170	21.8	2.00	2	3	2				
Northwest	2,140	21.8	2.02	73	55	36	13	5		
South	5	20.0								
Total	9,725	16.0	1.95	272	256	141	37	8		
Scotland										
Northeast	1,023	22.3	2.25	17	7	7	7	2		
Northern Isles	217	21.2	2.06	7	5	5		1		
Northwest	178	31.5	2.13	5	5	3	2			
Southeast	602	24.9	2.24	12	16	8	4	2		
Southwest	773	18.2	2.06	27	17	13	6	2		
Total	2,793	22.2	2.15	68	50	36	19	7		
Wales	94	13.8	1.33	2	1					
Britain total	12,612	17.4	1.99	342	307	177	56	15		
Overall total	26,576	19.9	2.18	564	564	367	155	51	8	1

land (30.8%) (Table 3). However, there was a notable difference in the habitats used between countries, with a significantly higher proportion of swans found on

permanent waters in Iceland than in Britain and Ireland (93.8% *versus* 19.6%; $\chi^2_1 = 6,563$, $P < 0.001$) and with substantially more swans on arable land in Britain than in

Table 3. Percentage of Whooper Swans recorded on different habitat types in January 2015. Definitions of habitat classifications: 1) Permanent standing water = natural permanent lake, artificial lake/reservoir, gravel pit; 2) River = non-tidal river, freshmarsh; 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 not specified in one of the other categories.

	Iceland	Northern Ireland	Republic of Ireland	Britain
Number of swans (<i>n</i>)	2,520	3,518	9,512	12,927
Permanent waterbodies	93.8	11.0	17.9	23.2
Permanent standing water	9.0	9.7	11.4	8.7
River	51.1	1.1	6	13
Coastal	33.7	0.2	0.5	1.5
All pasture	0.0	81.2	69.4	12.8
Improved pasture (dry)	0.0	56.8	30.5	9.2
Improved pasture (wet)	0.0	19.3	23.9	2.9
Rough/ unimproved pasture (dry)	0.0	2.6	0.3	<0.1
Rough/unimproved pasture (wet)	0.0	2.5	14.7	0.6
All arable	0.2	7.4	3.1	63.6
Arable growing			2	34.1
Arable waste	0.2	7.4	1.1	29.5
Other	6.0	0.4	9.6	0.4

Ireland (63.6% versus 4.3%; $\chi^2_1 = 10,218$, $P < 0.001$; Table 3). Although the 2015 census found that pasture and arable land remained the habitats most frequently used by Whooper Swans in Britain and Ireland, the proportion of the population occurring on these habitats was lower than in 2010, whereas a slightly higher proportion was seen on permanent standing water and riverine habitats (Fig. 4).

In Ireland, pasture was found to be the main habitat used by the Whooper Swans (72.6%), particularly dry, improved pasture (56.8% in Northern Ireland and 30.5% in the Republic of Ireland; Table 3). Although most birds in Britain were found on arable land (including growing crops particularly of winter cereals or harvest waste such as cereal stubbles, oil seed rape and sugar beet;

63.6%), the large concentration of birds at the Ouse Washes accounted for a high percentage (54.8%) of those birds found on this habitat type in Britain. Away from the Ouse Washes there was a more even distribution across arable land (27.3%), pasture (25.6%) and river habitat (including non-tidal river and freshwater marsh; 26.0%).

In Iceland, the majority of birds were recorded using rivers and coastal sites (including open coast and coastal river outlets) (51.1% and 33.7%, respectively; Table 3). There was a notably smaller proportion of birds using permanent standing water compared with the 2010 census (9.0% in 2015 compared with 38.7% in 2010), whilst a higher proportion was observed using riverine habitats (51.1% in 2015 compared with 29.1% in 2010).

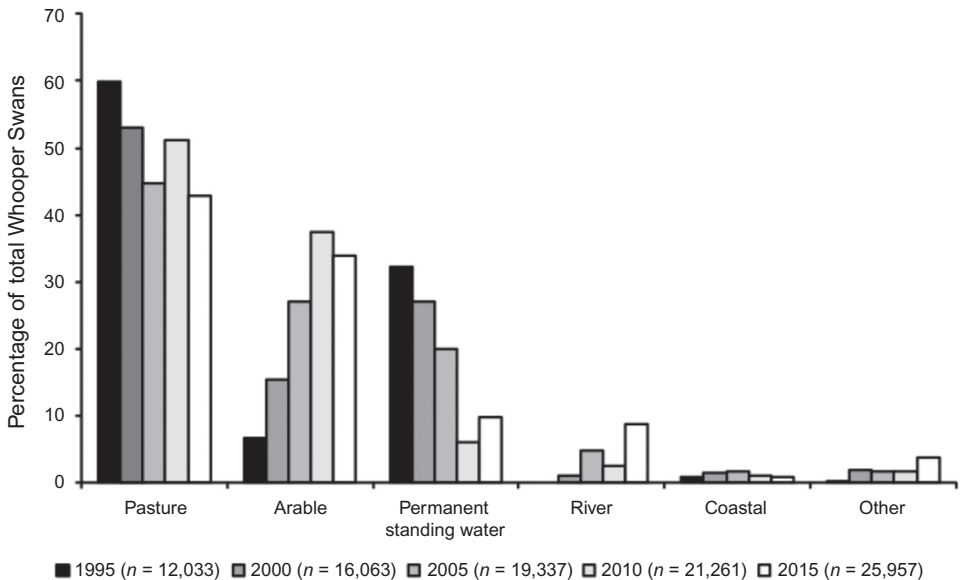


Figure 4. Distribution of Whooper Swans across habitat types in Britain and Ireland during the January 1995, 2000, 2005, 2010 and 2015 censuses.

Discussion

Population size and changes in distribution

Results of the 2015 census clearly indicated a continued growth in the Icelandic Whooper Swan population. The total of 34,004 birds is the highest recorded to date, represents a 16% increase on the previous population size estimate (29,232) recorded in 2010 and a 115% increase on the lowest census total (15,842) recorded in 1995. The largest change was in Britain, where wintering numbers have increased 3.2 fold since 1995, compared with 1.6 and 2.6 fold increases in Ireland and Iceland, respectively, over the same period. The more substantial increase in Britain has also resulted in a gradual shift in the population's centre of distribution. For the first time since the international Whooper Swan censuses commenced in 1986 (Salmon & Black 1986), Britain held a higher proportion of the population than Ireland, albeit by just a small percentage. Between censuses, Britain has seen a gradual increase in the proportion of the population it supports, whilst conversely Ireland has seen a continued decline.

On comparing individual countries across the range, it is evident that England has sustained the highest rate of increase in Whooper Swan numbers, with this rate being consistently higher than that of the population as a whole. Numbers in England have increased 5.3 fold since 1995, and during the 2015 census it held the majority of the population, whereas previously the Republic of Ireland had always supported the highest proportion. The rate of growth

in England has, however, been slowing, with an increase of 34% recorded between 2010–2015 compared with 74% between 1995–2000 (Cranswick *et al.* 2002), 65% between 2000–2005 (Worden *et al.* 2009) and 39% between 2005–2010 (Hall *et al.* 2012).

In comparison, Scotland has seen fluctuating numbers in recent years, having recorded a 44% increase during the 2005 census, a 36% decline in 2010, followed by a 42% increase in 2015. It is unclear why these fluctuations occur in Scotland, albeit weather conditions are thought to be one of the contributing factors (see below).

The rate of growth in Ireland has fallen during the 21st century, with an increase of just 2% recorded between 2010–2015, compared with 29% between 1995–2000, 11% between 2000–2005 and 6% between 2005–2010. Despite the continued population increase, numbers in Ireland appear to be stabilising, with the total of 15,068 in 2010 (Hall *et al.* 2012) only 300 birds fewer than the 15,370 counted across Ireland in 2015. Whether the disproportionate increase in numbers in England in particular stems individual birds migrating further south and east or to different growth rates for different parts of the population remains unclear, though the relatively low proportion of cygnets recorded in England compared with elsewhere in the wintering range is perhaps more indicative of the former than the latter.

Although Iceland has seen an increase in the number of wintering Whooper Swans, there has only been a small increase in the proportion of the population remaining there to overwinter. There has been some evidence of other species of waterbirds

showing a northerly shift in their wintering distribution, mainly in response to climate change and the resulting milder winters. For example, a higher proportion of the Icelandic Greylag Goose population is now wintering in Orkney compared to elsewhere in the UK (*e.g.* Mitchell 2016), and there has also been a decline in the use of southern and eastern sites in Britain by a number of wader species in preference of more northerly sites closer to their breeding grounds (*e.g.* Rehfish *et al.* 2004; Higgins & Holt 2013). However, results from the Whooper Swan censuses provide little evidence to suggest that this is occurring for the Icelandic population – indeed, the results show a continued south-easterly shift in their wintering distribution. Further evidence for this shift in the Whooper Swan population has also been highlighted in the *Bird Atlas* (Balmer *et al.* 2013), which shows some range expansion in southern areas of Britain compared with the mid-1980s, particularly in southeast England.

Distribution across sites

Although the 2015 census found that sites of national and international importance for Whooper Swans in Britain and Ireland continued to hold the majority of birds (Appendix 1), elsewhere there was an obvious change in the swans' distribution compared with 2010, particularly for the sites that receive fewer swans within the Republic of Ireland and Scotland. Conceivably, this may be partly due to the difference in weather conditions experienced during the censuses. The winter of 2009/10 was especially cold in Britain and Ireland, with many wetlands frozen over and much

of the land covered in snow when the census took place. These poor conditions are believed to have forced flocks away from their traditional sites to previously unknown and unusual locations, which was observed in Ireland in particular (Boland *et al.* 2010), as well as pushing birds south away from northerly areas, which was most noted in Scotland (Hall *et al.* 2012). In contrast, the weather during the 2014/15 winter was relatively mild and wet, resulting in more available wetlands and generally better habitat conditions.

In Ireland and Scotland, Whooper Swans were more widely distributed across a greater number of sites when compared with 2010. In contrast, in England, the majority of swans continue to be concentrated at just a few sites, principally Martin Mere and the Ouse Washes. Numbers at both of these sites have increased substantially, with two-fold and seven-fold increases occurring, respectively, since the 1995 census.

The disproportionate increase seen in England is predominately due to the continued increase at the Ouse Washes. During the 2015 census, the increase at the site accounted for 50% of the overall increase in England. However, this is notably lower than in 2010 (89%) and in general the rate of increase at the site has slowed to a greater extent than that for the country as a whole. It is possible that in 2010 numbers at the Ouse Washes were inflated by flocks moving south to avoid the colder conditions in the north. Also, the Nene Washes, which neighbours the Ouse Washes, has seen a growth in numbers between 2005 the 2015 censuses (79 birds in 2005, 337 in 2010 and 1,173 in 2015), with

the increase there in 2015 accounting for 27% of the overall increase in England. This may suggest a dispersal of birds away from the Ouse Washes as numbers in the area increase.

Distribution across habitats

Comparison of habitat data recorded during the 5-yearly censuses from 1995 to 2015 suggests a general decline in the use of permanent standing water and pasture, and an increasing tendency for swans to be recorded on arable land, although the proportion of the swans recorded at arable sites was a little lower in 2015 than in 2010. The gradual change in habitat use may also be related to the decreasing proportion of the population wintering in Ireland, where pasture has continued to be the main feeding habitat used by the swans, whilst the increasing numbers at the Ouse Washes coincides with the movement on to arable land, which is abundant around that site.

Distribution of juveniles

The significant difference between countries in the percentage of young recorded is similar to the results of some previous censuses which found a bias in the distribution of families within the wintering range (*e.g.* Hall *et al.* 2012), although other censuses found no significant variation in the proportion of cygnets recorded in the different countries (*e.g.* Cranswick *et al.* 2002). We suggest that the reasons for this difference between years, which may be related to varying conditions in different parts of the Icelandic breeding range the previous summer, should be investigated in further detail. The relatively low proportion

of cygnets recorded in England in the current and some previous censuses, with higher proportions seen in northern Scotland and Ireland, may also reflect a tendency for Whooper Swan families to stay closer to their breeding grounds, with non-breeding birds migrating further south (Rees *et al.* 1997).

Comparison with WeBS counts

The WeBS peak count of Whooper Swans in Britain and Northern Ireland in January 2015 was 7,825 (WeBS, unpubl. data), which represents 40% of the combined census total for those countries, indicating that WeBS misses a notable proportion of the population. Moreover, although the WeBS programme also found an increasing trend in Whooper Swan numbers for winters 1988/89–2013/14, the 10-year trend for 2003/04–2013/14 indicated a decline at sites covered by WeBS (Frost *et al.* 2016). The varying distribution of swans between censuses, together with the increased use of habitats away from wetlands (which may account for the difference between the census results and the 2003/04–2013/14 trend indicated by WeBS), clearly show the importance of monitoring areas outside the network of sites already covered by the national schemes. This, together with the fact that numbers of swans wintering in Iceland are increasing, highlights the necessity of species-specific surveys for producing an accurate population estimate.

Demographic drivers of the population change

Results from the censuses clearly show a sustained growth in the Icelandic Whooper

Swan population but the drivers behind the increase remain unclear. Annual age assessments made at a suite of sites in Britain and Ireland suggest a mean breeding success of 14.8% (s.d. = 2.52) (WWT Waterbird Monitoring 2016) between 2005/06 and 2014/15, with the percentage of young consistently above 10% each year. It should be noted, however, that further quantification is needed to ascertain whether these data are representative of the population. Further analysis of ring re-sighting data is also required to determine whether the annual mortality rate for the population, most recently estimated at 15.3% for adult swans re-sighted in Scotland over the period 1979–2009 (WWT unpubl. data; M. Trinder, pers. comm.), has decreased in recent years, and whether this rate of breeding success may have been enough to fuel and sustain the increase in population size.

Some interchange between the Icelandic and Northwest European Whooper Swan populations is also known to occur, so it is possible that numbers in Britain, particularly in southeast England, have been inflated by birds moving across from mainland Europe. Ring re-sightings have shown that movements may occur in both directions, with swans ringed in Iceland re-sighted in Europe (Gardarsson 1991) and several individuals ringed in Europe re-sighted in the UK (Laubek *et al.* 1998). The level of immigration/emigration and the extent to which this varies from year to year is not known but is generally estimated at a few hundred birds per year (Rees *et al.* 2002). Laubek *et al.* (1999) suggested that the increase in the Northwest European

population since the 1980s may result in an increasing number of these birds are wintering in Britain, with movements also influenced by severe weather on mainland Europe. Preliminary results from the Netherlands (*i.e.* the southern end of the Northwest European population's wintering range) however suggest that numbers there were lower than average in January 2015, with the majority of birds seen in north-eastern areas (M. Hornman, pers. comm.). Numbers in the Netherlands are influenced by severe weather in northern Germany and Denmark and in mild winters numbers are found to be relatively low, which was the case in 2015 (DMI 2016; DWD 2016; KNMI 2016; M. Hornman, pers. comm.). There were also no clear indications of bird movements from mainland Europe at the time of the 2015 census, as no re-sightings of marked birds from the Northwest European population were reported in Britain during that winter (K. Brides, pers. comm.). Moreover, there have been only 31 sightings and recoveries of Whooper Swans ringed on mainland Europe reported to the British Trust for Ornithology in previous years up to December 2015 (22 from Finland, 5 from Poland, 4 from Denmark listed in Robinson *et al.* 2015), from 407 marked with neck-collars in Denmark from 1979 onwards (P. Andersen-Harild, pers. comm.), *c.* 800 ringed in Finland including several hundred swans marked with neck-collars during the mid 1990s (Laubek *et al.* 1998; M. Piha, pers. comm.), and *c.* 1,500–2,000 marked elsewhere in Europe (particularly in Latvia but also Poland, Germany, the Netherlands and Sweden) during the 21st century (*e.g.* Boiko &

Kampe-Persson 2011; D. Boiko, pers. comm.; K. Brides, pers. comm.), suggesting that an influx of birds from the Northwest European population during winter 2014/15 was unlikely to have had a major influence on the total number of swans recorded.

A census of Whooper Swans in Iceland during the late summer/autumn may help provide some insight into the level of exchange between the two populations, by estimating the size of the Icelandic-breeding population prior to their migration to their wintering grounds. However, the costs and practicalities of carrying out such a survey would need careful consideration because Whooper Swans are widely dispersed during the summer and move from moulting to staging areas in the autumn (Garðarsson & Skarphéðinsson 1984).

In conclusion, whilst this paper provides some insight into the current size and distribution of the Icelandic Whooper Swan population, further investigation and research is required to gain a better understanding of the extent to which the different demographic variables, particularly survival rates and the level of exchange between the Icelandic and Northwest European Whooper Swan populations, are accounting for trends in the number of Whoopers Swans recorded in Britain, Ireland and Iceland.

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Appendix 1. Sites in Britain and Ireland which held numbers of Whooper Swans exceeding the current 1% thresholds for international importance (270; Wetlands International 2016) and national importance for Britain (110; Musgrove *et al.* 2011) and Ireland (150; Crowe & Holt 2013) in January 2015.

Site	County	No. of swans in 2015	% change from 2010
Sites exceeding threshold for international importance in Britain and Ireland			
Ouse Washes	Norfolk, Cambridgeshire	7,171	27
Loughs Neagh & Beg	Antrim, Londonderry, Tyrone, Armagh, Down	1,587	-12
Martin Mere & surrounding area	Lancashire	1,462	-29
Nene Washes	Cambridgeshire	1,173	248
Upper Lough Erne	Fermanagh	676	-15
Solway Estuary	Dumfries & Galloway, Cumbria	524	93
Shannon Callows	Galway, Offaly, Roscommon, Westmeath	465	28
Ribble Estuary [†]	Lancashire	390	228
Wexford Harbour & Slobs	Wexford	382	-7
River Suck	Roscommon, Galway	381	15
Kilmacshane [†]	Galway	365	+
Cashen River & Estuary	Kerry	341	-33
Tacumshin Lake [†]	Wexford	316	829
Morecambe Bay [†]	Cumbria, Lancashire	307	>1,000
Sites exceeding threshold for national importance in Britain			
Lakenheath Fen [†]	Norfolk	249	+
Lower Pitkerrie, near Loch Eye [†]	Highland	247	+
Crossrig West Duns [†]	Borders	190	+
Merryhatton [†]	Lothians	179	+
Upper Badenoch Sites: Aviemore to Spey Dam ¹	Highland	173	368
Dyke Gatehead West Duns [†]	Borders	165	+
Loch of Strathbeg [†]	Grampian	155	+
Hatfield Moors [†]	South Yorkshire	144	+
Tiree ²	Strathclyde	119	-14
River Nith – Keltonbank to Nunholm [†]	Dumfries & Galloway	111	>1,000

Appendix 1 (*continued*).

Site	County	No. of swans in 2015	% change from 2010
Sites exceeding threshold for All-Ireland importance in Ireland			
Shannon & Fergus Estuary [↓]	Clare, Limerick	246	-27
Brees Wetlands [†]	Mayo	231	425
Garryduff [†]	Galway	228	+
Lough Swilly [↓]	Donegal	223	-34
Glen Lough [†]	Westmeath	215	139
East Ballinamore Lakes	Cavan	210	56
Ballyhaunis Lakes [†]	Mayo, Roscommon	208	86
Castleplunket Turloughs [†]	Roscommon	195	255
Strangford Lough	Down	178	29
River Foyle [↓]	Donegal, Tyrone	178	-54
Lough Oughter Complex [↓]	Cavan	176	-51
Lower Blackwater River [†]	Waterford	175	130
Lough Gara [†]	Sligo	159	31
Lough Foyle [↓]	Londonderry, Donegal	157	-82
North East Galway Lakes [†]	Galway	157	>1,000
Finn-Lacky Catchment [†]	Monaghan	156	53

¹This site covers Loch Insh & Spey Marshes which qualified in 2010.

²The count for Tiree in 2015 was at the island level rather than for the individual sites as in 2010.

[†]Site did not qualify during the 2010 census.

[↑]Site was of higher importance during the 2015 census than the 2010 census.

[↓]Site was of lower importance during the 2015 census than the 2010 census.

⁺Site held no birds during the 2010 census.

Sites that did not maintain either internationally or nationally important numbers between 2010 and 2015 censuses.

International (Britain & Ireland): Little Brosna Callows (Offaly, Tipperary); Lough Iron (Westmeath); Blackwater Callows (Cork, Waterford); Pear Tree Grove, Pilling Moss (Lancashire); Kelton Mains (Dumfries & Galloway).

National Britain: Abbey House, Abbeystown (Cumbria); Ballone (Highland); Wigtown Bay (Dumfries & Galloway).

All-Ireland importance: Foxhall/Cloghans Hill (Galway); Mullaghmore (Moylough/L. Nalarsagh) (Galway); River Blackwater (Meath); River Boyne (Meath); River Lagan (Antrim, Down); River Moy (Mayo); The Cull & Killag (Wexford).



Photograph: Feeding Whooper Swans and Mute Swans in flood conditions at WWT Welney, by Sacha Dench.