Long-term population trends and shifts in distribution of Bewick's Swans *Cygnus columbianus bewickii* wintering in northwest Europe

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Abstract

Coordinated international censuses of the Northwest European Bewick's Swan *Cygnus columbianus bewickii* population have been undertaken across the swans' wintering range at *c.* 5-year intervals since 1984. During the early years of the study, numbers increased steadily to a peak of 29,780 individuals in January 1995, but then declined by 39.4% to 18,057 swans counted in January 2010 before showing a partial recovery to 20,149 recorded in January 2015. Changes in distribution across the wintering range were also recorded; a higher proportion of the population now remains in more easterly countries (notably Germany) in mid-winter, whilst only a handful of birds migrated to Ireland (at the western edge of the range) during the 2000s compared to >1,000 wintering there at the start of the study. Variation between censuses in the proportion of swans recorded in different parts of the range were attributable to weather conditions, with more swans wintering further north in warmer years. The overall percentage of cygnets recorded in each of the census years ranged from 9.6% in 2010 to 13.2% in 2005, with no obvious consistency over time in the distribution of cygnets across the wintering range. There were however changes between 1990 and 2015 in the swans' use of feeding habitats, with a decline in the proportion of birds on pasture and a corresponding increase in those on arable land. Decreases in the total population size and changes in distribution in the 21st century have implications for the designation and resultant protection of sites of international importance for the species.

Key words: habitat use, population increase and decline, short-stopping, species threshold levels, weather conditions.

Systematic surveys of waterbirds at wetland sites, undertaken by national count programmes since the mid-20th century, have been coordinated internationally since 1967 through the International Waterbird Census (IWC) (Delany *et al.* 1999). The IWC provides valuable data on trends in waterbird numbers and distribution at the population level, which serve to inform the protection of key sites used by these species. That the IWC focuses on regularly counted wetlands is however less well-suited for determining total population sizes, particularly for species including many of the geese and swans which disperse to feed on terrestrial habitats such as farmland outside the IWC network (Nagy *et al.* 2014). Yet a population size estimate is fundamental for identifying sites that meet criteria for protection under national and international legislation. Sites which regularly support 1% of the individuals in a population of one species or subspecies of waterbird are classed as being of international importance under the terms of the Ramsar Convention (Criterion 6 of the Convention; Scott 1980), and this classification requires data both on population size and on numbers using particular sites. The 1% threshold is also used to inform designation of Special Protection Areas (SPAs) under the terms of the European Union (EU) Birds Directive, which currently provides the highest level of site protection for birds within EU Member States. Population size therefore should be determined and these estimates updated regularly, particularly for a declining population such as the Northwest European Bewick's Swans (described in this paper). Otherwise, sites of international importance may be missed if the population size is set at an earlier higher level, because a 1% threshold based on the elevated population estimates may exclude sites with fewer birds than would otherwise be found to be of international importance if the lower population size was known.

From the mid-20th century onwards, continued drainage of wetlands and an expansion of arable landscapes saw migratory swans and geese increasingly switch from feeding mainly on aquatic vegetation and pasture to using arable land (Kear 1963; Van Eerden *et al.* 1996; Rees 2006), enabling the birds to maximise their nutrient and energy intake (Fox *et al.* 2017; Fox & Abraham 2017; Wood *et al.* 2019a,b). Additional species-specific censuses therefore were instigated, covering farmland as well as wetlands, to confirm their population sizes and trends. These monitoring programmes have found a growth in numbers since the 1980s for most of the northwest European swan populations (Delany *et al.* 1999; Hall *et al.* 2016; Laubek *et al.* 2019) and also some of the goose populations (*e.g.* Fox *et al.* 2010; Mitchell & Hall 2013; Brides *et al.* 2018). Their results have had major input into various conservation measures, such as the development of protected areas networks (Fox & Madsen 2017). More recently, however, some arctic- and taiga-breeding goose populations have gone into decline (Fox *et al.* 2010) and a number of International Single Species Action Plans (ISSAPs) have been issued, for instance for the Red-breasted Goose *Branta ruficollis*, Taiga Bean Goose *Anser fabalis fabalis* and the Lesser and Greenland White-fronted Geese *A. erythropus* and *A. albifrons flavirostris* (Jones *et al.* 2008; Cranswick *et al.* 2012; Stroud *et al.* 2012; Marjakangas *et al.* 2015). Careful monitoring of population size is also a key component of the adaptive harvest management programmes, such as recently put in place for the Svalbard Pink-footed Goose *Anser brachyrhynchus* population (Madsen & Williams 2012).

The migratory Bewick's Swan *Cygnus columbianus bewickii*, which breeds across arctic Russia from the Kola Peninsula in the west to the Chukotka Autonomous Okrug in the east, numbers around 120,000 birds globally (Rees *et al.* 2019). There is relatively little long-term data for the Eastern and Caspian populations (estimated at *c.* 90,000 and *c.* 800–3,000 individuals respectively, Jia *et al.* 2016; Wetlands International 2017; Rees *et al.* 2019), but the Northwest European population has been monitored for *c.* 50 years through the IWC (Rees 2006). The IWC indicated that the number of Bewick's Swans wintering in Europe rose from *c.* 6,000–7,000 birds in the late 1960s (Atkinson-Willes 1976) to 9,000–10,000 by the mid-1970s (Mullie & Poorter 1977), and to 17,000–18,000 by the mid-1980s (Rüger *et al.* 1986; Monval & Pirot 1989), but as Bewick's Swans increasingly fed on arable land from the early 1970s onwards (Rees 2006) the total size of the Northwest European population remained uncertain. A new research initiative – the "Dutch Bewick's Swan Project 1982–84" – therefore called for additional counts of the species across northwest Europe, timed to coincide with the mid-January IWC (to avoid duplication of count effort) in winters 1983/84 to 1986/87, to obtain a more accurate total population size estimate through comprehensive coverage of areas where Bewick's Swans were known to occur, including relevant farmland areas. These, the first species-specific, International Bewick's Swan Censuses (IBSC), suggested a rather stable population of about 16,000–17,000 birds in the mid-1980s (Dirksen & Beekman 1991).

From January 1990 onwards, IBSC have continued to be made at 5-yearly intervals under the auspices of the Wetlands International/IUCN-Species Survival Commission's Swan Specialist Group, to verify trends in numbers, monitor shifts in winter distribution and identify changes in habitat use by the Northwest European Bewick's Swan population over time. Since 1995, the IBSC have been undertaken as part of a larger census made of migratory swans across Europe, which also provides population estimates for Whooper Swans *Cygnus cygnus* from the Icelandic and the Northwest Mainland European populations, whose winter distribution overlaps with that of Bewick's Swans in northwest Europe (Hall *et al.* 2016; Laubek *et al.* 2019). Preliminary results indicated that Bewick's Swan numbers increased from the mid-1980s to a peak of more than 29,000 birds in January 1995 (Beekman 1997; Rees & Beekman 2010), but evidence for a subsequent decline triggered the development of an ISSAP for the population (Nagy *et al.* 2012). More recent national indices for Ireland, Britain and the Netherlands have indicated that declines in Bewick's Swan numbers are continuing in the western part of their range (Crowe & Holt 2013; Koffijberg & Tijsen 2018; Frost *et al.* 2019; Hornman *et al.* 2019). The extent to which trends in the western part of the range were attributable to the decline in the population as a whole, or to birds "short-stopping" (Elmberg *et al.* 2014) and wintering further east in milder winters, was unclear. Moreover, the situation was confounded by numbers wintering on the Evros/Meriç Delta on the Greek-Turkish border increasing from just a handful of birds present up to the mid-1990s (Handrinos 1996) to 8,400 counted in February 2016 (Vangeluwe *et al.* 2016). Whether this accounted for the drop in numbers in the swans' core wintering areas elsewhere in Europe, or reflected a westward redistribution of swans from the Caspian population, therefore remained to be determined.

This paper presents the first detailed analysis of the International Bewick's

Swan Census (IBSC) data, with the aim of confirming long-term trends in the numbers and distribution of the Northwest European Bewick's Swan population since the mid-1980s. Changes in distribution were analysed in relation to weather conditions recorded during the census years, to identify any possible short-stopping in the wintering range attributable to weather variables. The habitats on which swan flocks were recorded during each of the censuses were also investigated, to describe any change over time or between countries in their use of farmlands and wetlands as mid-winter feeding sites. Furthermore, we investigated how many of the sites of international importance for Bewick's Swans were used in the midwinter period (based on Ramsar guidelines of regularly supporting ≥ 1% of the total population; Ramsar Convention 2017), and in which part of the flyway they were situated, to provide a general overview of how many swans concentrate at protected sites.

Methods

Study population

The Northwest European population of Bewick's Swans breeds mainly on the Russian arctic tundra to the west of the Ural Mountains and migrates to wintering sites in the lowland areas of northwest Europe, from Denmark and Germany through the Netherlands and Belgium to Great Britain and Ireland, with smaller numbers regularly reaching southern France (Rees 2006; Nagy *et al.* 2012). Birds wintering in the Evros/Meriç Delta of Greece and Turkey have previously been thought to be part of the Caspian-wintering group, a view supported by recent tracking of swans tagged on the Yamal Penisula through the Caspian region to Greece (Vangeluwe *et al.* 2018), though re-sightings in Greece of a few (< 10) individuals ringed in western Europe indicates some linkage to the population wintering in northwest Europe (Rees 2006; Hellenic Rarities Committee 2007; Nagy *et al.* 2012).

Counting methods

The IBSC were undertaken by a network of volunteer and professional ornithologists involved in national waterbird count programmes across the core wintering range of the Northwest European Bewick's Swan population, notably in Belgium, Denmark, France, Germany, Ireland, the Netherlands, Poland and the UK. Countries further north and east along the migration route – Estonia, Latvia, Lithuania and Sweden – also participated in the census along with Switzerland and Norway because small numbers occasionally occur there in mid-winter and in order to measure any redistribution of the population over time. Greece was formally included in the 2015 IBSC, with IWC data for Greece available for earlier census years.

National counts were coordinated and collated by the national count coordinator, usually following the process put in place for the IWC (Delany *et al.* 1999) but extended in an attempt to obtain complete coverage in each country. Hence, counts were carried out during the daytime and focussed on feeding sites. Census forms were provided to the counters for reporting the numbers recorded and additional data on the swans' breeding success (percentage of cygnets and brood sizes) and the habitat being used.

Counters were also asked to visit additional (farmland) areas, not well-covered by the existing schemes, but known (from local information or previous censuses) or suspected (on the basis of habitat suitability) to support Bewick's Swans. The recommended weekend count dates of 13/14 January 1990, 21/22 January 1995, 15/16 January 2000, 15/16 January 2005, 16/17 January 2010 and 17/18 January 2015 were timed to coincide with the dates of the national waterbird monitoring schemes contributing to the IWC, to avoid asking the counters to make two surveys in the January of census years. Counts made up to two weeks either side of the census dates were included for sites not surveyed on the census weekend but only when the risk of duplicate counts was considered low by the national coordinator, for instance where previous counts and information provided by counters indicated that a flock had been missed and that bird movement from censused sites was unlikely. January was considered the optimal time for conducting censuses to determine population size and mid-winter distribution because migratory movement is relatively limited at this time of year (Evans 1982; Beekman *et al.* 1985; Dirksen & Beekman 1991; Rees 2006), whilst coordinating with the IWC provided high spatial coverage including sites not used by Bewick's Swans in previous censuses.

Data recorded during the IBSC included in the analysis were: country, site name/location and coordinates, count date and the total number of birds counted. Sub-site names and coordinates were also recorded if birds were observed at feeding sites around a central roost. The number of adults and cygnets in the flocks, family sizes (*i.e.* number of cygnets associating with their parents), and the habitat used by the swans for feeding during the day, were determined for as many birds as possible, in some cases on the days immediately following the main count if peak numbers were recorded at the roost site. Habitat types were grouped into three main categories for analysis – pasture, arable and waterbodies – with the condition of the pasture (wet/dry; rough/improved), crop type (*e.g.* sugar beet, potatoes, maize, winter cereals) and whether the swans were on freshwater or coastal sites also recorded. During the 20th century "stubble fields" tended to refer to fields with spilt grain following a cereal harvest, but cereal stubbles are now ploughed more rapidly in most countries by farmers in autumn to early winter, so the original crop in fields reported as "stubbles" by observers is unclear for recent censuses, unless they were specifically classed as maize. National counts recorded during the earlier international swan censuses of 1984 and 1987, described by Beekman *et al.* (1985) and Dirksen & Beekman (1991), were used along with the IBSC data on analysing population trends over time. National Bewick's Swan totals were estimated for the Republic of Ireland in 1990, and details of numbers per site were not provided, because the main census of migratory swans in Ireland was undertaken the following year (in 1991), for an international census of the Icelandic Whooper Swan population in that year (Kirby *et al.* 1992). Similarly, totals reported to the IBSC for Germany in 1990 and 1995 and for Britain in 1990, published in Beekman (1997), are slightly higher (by a few hundred birds) than the sum of the counts per site reported to the IWC. Here we therefore use the national totals published by Beekman (1997) in presenting population trends, as these are considered to be more comprehensive than the IWC data for the reasons described above.

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. 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. On considering the importance of sites for the species, the highest count recorded at each site was used for comparison with the 1% of the population size at the time.

Treatment of the data

The total number of Bewick's Swans counted in all countries censused excepting Greece were summed for each census year to describe population size and trends for the Northwest European population. We lacked information on which sites had been counted on each occasion, required to confirm zero swans present, so were unable to fit boot-strapped confidence intervals to the census totals (as also found by Laubek *et al.* 2019), but considered that the level of coverage combined with the tendency for Bewick's Swans to congregate at a relatively limited number of sites (Beekman *et al.* 1994) means that the sum of the counts is a realistic indication of total population size. For countries with > 5% of the population in at least one year, Pearson correlations were used to test the association between national totals and the total population size, to determine whether trends in the national counts followed trends in the total population size in some countries but not in others. Counts made in Greece were considered separately because Greece was not originally included in the IBSC, and also because the proportion emanating from the Northwest European population *vs.* the Caspian population remains uncertain. Numbers recorded in Greece have tended to be higher towards the end of the winter, for instance with peak counts made in February in 2015 and 2016 (Litvin & Vangeluwe 2016; D. Vangeleuwe pers. comm. in Eggers 2018), but whether this is attributable to a late winter influx of swans or to increased observer effort at this time remains to be determined. To allow for either possibility, both the mid-January counts (from the IWC) and also the peak winter counts recorded for Greece (from published reports: Handrinos 1996; Hellenic Rarities Committee 2007, 2010; Litvin & Vangeluwe 2016; Vangeluwe *et al.* 2016) therefore are described in relation to the numbers recorded in the swans' core wintering range.

Changes in distribution were first described as the proportion of the population recorded within each country each year, because the national boundaries provided a rough overview of whether the swans were in the northeast (Germany and the Baltic countries), central (Netherlands and Belgium), or southwest (Britain, Ireland and France) parts of their wintering range. For the main wintering areas (*i.e.* countries with > 5% of the population in at least one year), linear regressions (in Minitab version 14.1) were used to analyse variation in the proportion of the total population (arcsine transformed for normality of residuals) recorded in the country across census years, to assess whether there was a shift in the distribution of the swans from the southwest to the northeast part of the range indicative of short-stopping over the study period. Linear regressions likewise analysed trends in the proportion of birds (arcsine transformed) using the three main habitat categories (pasture, arable crops and waterbodies) over the course of the study.

Maps of the Bewick's Swans' distribution were also generated for the 6 census years for which we had counts recorded to site level (*i.e.* the IBSC from 1990 onwards) using ESRI ArcGIS® software, with data grouped onto 1 degree grids (geographic coordinates), to illustrate changes in the location of sites used by the swans over time. To analyse the change in distribution we estimated the mean for each census year. For that we first converted geographic coordinates to a projected coordinate system, using the European Terrestrial Reference System (ETRS89) datum, then calculated the mean point and standard deviation ellipses for each year, using not only the coordinates but also the number of swans counted at each site. Regression analysis was used to test whether variation in these central locations were related to the mean January temperature at the centre of the Netherlands in census years (van der Schrier *et al.* 2011), as a proxy for conditions experienced by a high proportion of the population at the time of the censuses, using data from the Royal Netherlands Meteorological Institute website (KNMI 2016). This was done to test the hypothesis that swans may remain further north and east (closer to their breeding grounds) in warmer winters (*e.g.* Fox *et al.* 2016; Nuijten *et al.*, unpubl. data). A regression analysis of mean latitude (and also mean longitude) in relation to year similarly was used to determine whether there was a significant trend for any shifts in the swans' distribution over time.

The 95% confidence intervals (CIs) for the proportion of cygnets in a given sample (either country-specific totals or census totals) were estimated using binomial tests, whilst the CIs associated with mean brood sizes were estimated based on a normal distribution where sample size (*i.e.* the number of broods assessed) was ≥ 30 and a Student's *t* distribution where sample size was < 30 (Crawley 2015). Finally, temporal trends in the two measures of productivity (the proportion of cygnets within the population and mean brood size) were examined using linear regression analyses, and analysis of variance was used to test whether variation in the proportion of cygnets recorded within each country across censuses differed consistently with the values recorded for the population as a whole. The proportion of cygnets and mean brood size were arcsine and $\log_{10}$ transformed, respectively, so that residuals met the test assumptions.

Results

Population size and trends

The comprehensive Bewick's Swan censuses (IBSC) made across Europe found a marked increase in numbers recorded in the main wintering areas from 16,300–16,400 in 1984–1987, to 26,748 in 1990 and 29,780 in 1995, before declining to 23,816 in 2000, 21,702 in 2005 and 18,057 in 2010. The most recent census showed a slight recovery to 20,149 birds in 2015 (Table 1, Fig. 1). No Bewick's Swans were recorded in Greece during the IWC in 1987, 1990, 1995, 2000 and 2005, but a mid-January count of 76 was made for the IWC in 2010, rising to 2,110 during the IBSC in 2015. Even if peak (February) counts for Greece of 2,250 in 2010 and 4,200 in 2015 are included in the census totals, there was still a decline in total numbers from 1995 onwards (Fig. 1).

The main change in total population size over the study period was a 62.8% increase between the numbers estimated in 1987 and 1990 (Table 1, Fig. 1), equivalent to population growth of 20.9% *per annum*

Table 1. Total number of Bewick's Swans recorded during coordinated international censuses of the Northwest European population from 1984 onwards. n/a = no data available. The 1987 number for Denmark has been revised (from a previously published total of 22 birds) following Nielsen *et al.* (2019).

Country	1984	1987	1990	1995	2000	2005	2010	2015
Belgium	43	120	25	266	325	175	496	806
Britain	4,995	8,018	8,754	6,983	7,215	6,992	6,999	4,371
Denmark	427	91	606	928	363	402	7	747
Estonia	n/a	n/a	4	5	29	12	1	6
France	88	77	19	52	41	206	274	569
Germany	678	321	1,183	1,118	1,450	3,390	637	5,444
Ireland (Northern)	130	107	504	145	35	13	1	0
Ireland (Republic of)	1,114	1,041	1,500	435	347	211	100	21
Latvia	0	1	0	0	2	0	0	0
Lithuania	1	n/a	32	12	0	2	2	0
Netherlands	8,801	6,650	14,003	19,822	14,003	10,218	9,527	8,113
Poland	5	4	116	12	1	74	2	70
Sweden	0	1	0	0	1	0	1	0
Switzerland	1	5	2	2	2	3	8	1
Norway	1	0	0	0	2	4	2	1
TOTAL	**16,284**	**16,436**	**26,748**	**29,780**	**23,816**	**21,702**	**18,057**	**20,149**

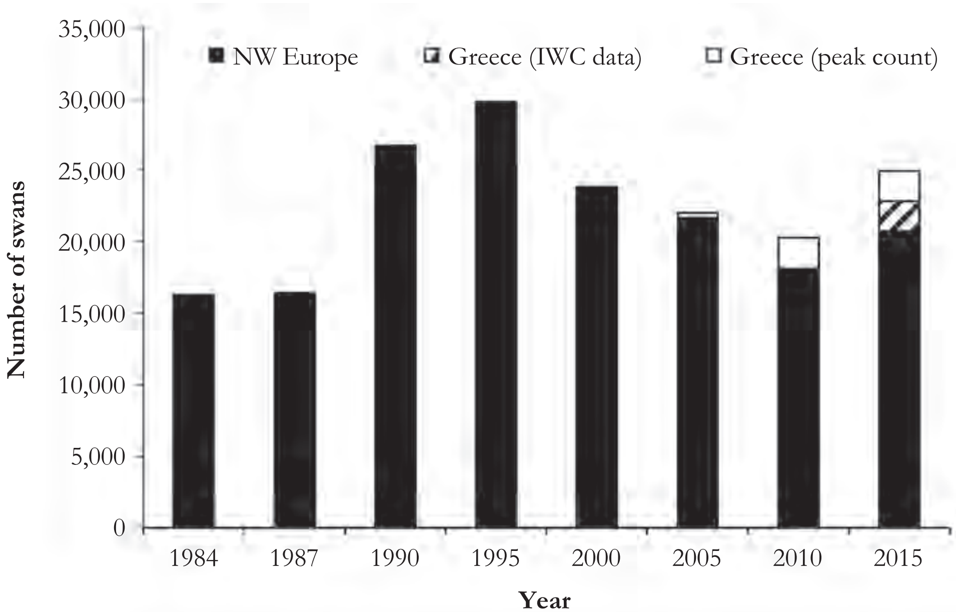

Figure 1. Numbers of Bewick's Swans counted during the international censuses in northwest Europe (black columns), for Greece during the mid-January international waterbird censuses (IWC; hatched columns) and also the maximum numbers recorded in Greece during census winters (hatch and open columns combined; from Handrinos 1996; Hellenic Rarities Committee 2016; Litvin & Vangeluwe 2016).

over this 3-year period, but this may reflect difficult counting conditions in the Netherlands during the cold January 1987, which was thought at the time to have had a negative effect on the quality of that census (Dirksen & Beekman 1991). The increase of 21.3% between 1984 and 1990 (averaging at 10.7% *per annum*) and of 82.9% between 1984 and 1995 (7.5% *per annum*; Table 1) therefore is considered to be more realistic. The subsequent decline was less rapid but nonetheless the numbers recorded in 2010 were 39.4% below the peak count of 29,780 swans counted in 1995, giving an annual average decrease of 2.6% per year over the 15-year period (Table 1).

Changes in distribution

National totals recorded during each of the mid-winter censuses found that most birds were in the Netherlands (range = 40.3–66.6% of the total), confirming the Netherlands as the main wintering area for the species in northwest Europe, followed by Britain (21.7%–49.0%) and Germany (4.2%–27.0% Fig. 2, Fig. 3a,b,c). A further 7.0–7.5% were recorded in Ireland during the 1980s, but only 0.1% of the population was recorded there in 2015 (Fig. 3d). Other countries in northwest Europe each recorded < 5% of the population during the IBSC, although numbers have been increasing in Belgium and in France, whilst in Denmark numbers have fluctuated ranging from as low as seven birds in 2010 during exceptionally cold conditions up to a maximum of 928 in 1995 (Table 1).

The increase and subsequent decrease in total population size was reflected mainly in the numbers counted in the Netherlands (Fig. 2). The correlation between the national count and total population size was statistically significant for the Netherlands (Pearson correlation: $r_6 = 0.934$, $P = 0.001$; Fig. 2), but not for the other countries (Britain, Ireland and Germany) where at least 5% of the population was recorded (Britain: $r_6 = 0.372$, $P = 0.36$; Ireland: $r_6 = 0.09$, $P = 0.78$; Germany: $r_6 = 0.052$, $P = 0.90$; n.s. in each case). In contrast to the Netherlands, Bewick's Swan counts for Britain remained relatively constant at around 7,000 individuals during the first years of the population decline (*i.e.* from 1995–2010 inclusive), before dropping by 37% to 4,400 in 2015 (Fig. 2, Table 2).

The increase in the total number of Bewick's Swans remaining in Germany in mid-winter, from fewer than 1,000 birds in the mid-1980s to just over 5,400 in 2015, was statistically significant (linear regression: $F_{1,6} = 6.06$, $P = 0.049$; Fig. 2), and the proportion of the population (arcsine transformed) wintering in Germany also increased over time ($F_{1,6} = 6.05$, $P = 0.049$; Fig. 3c, Fig. 4a). Conversely, the massive (98.1%) decline in numbers wintering in Ireland from > 1,000 swans recorded during 1984–1990 to just 21 individuals in 2015 was also significant ($F_{1,6} = 13.96$, $P = 0.010$; Table 1, Fig. 4a), resulting in a concomitant drop in the proportion of the population wintering in this the westernmost part of the range ($F_{1,6} = 29.71$, $P = 0.002$; Fig. 3d). There were no significant linear trends

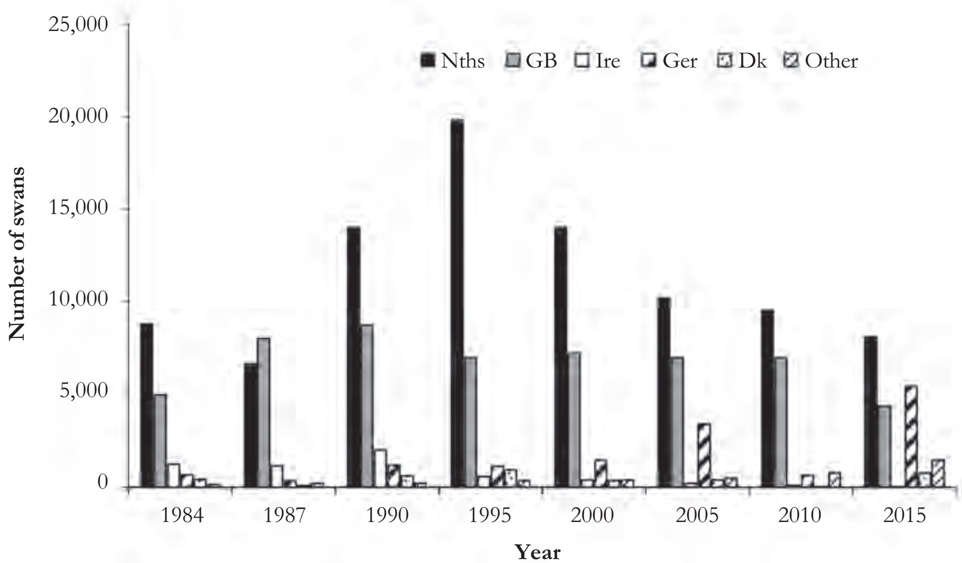

Figure 2. Total number of Bewick's Swans recorded in each range country during the International Bewick's Swan Censuses (IBSC).

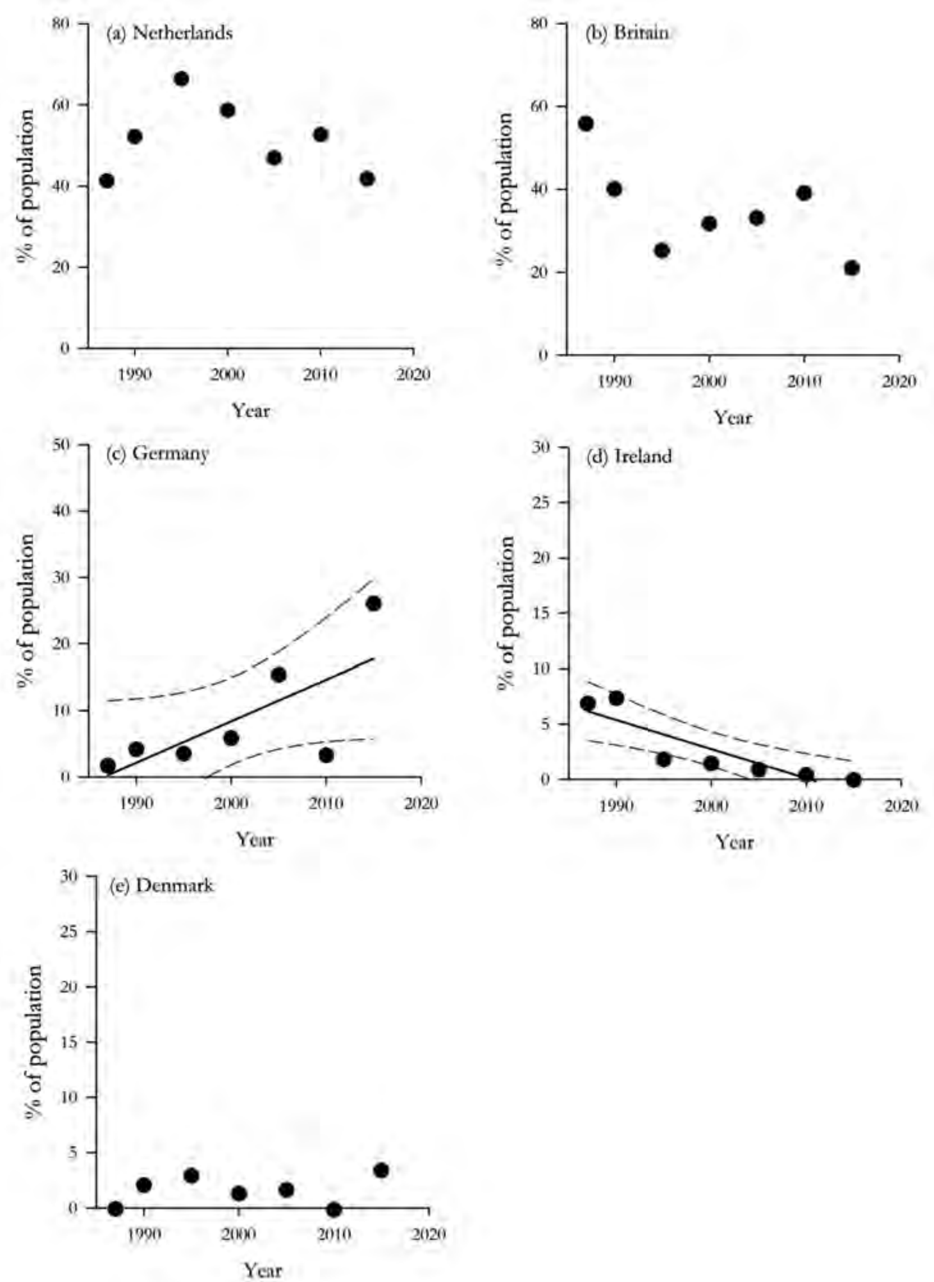

Figure 3. Variation over time in the proportion of Bewick's Swans recorded in different countries during mid-winter, in (a) the Netherlands, (b) Britain, (c) Germany, (d) Ireland, and (e) Denmark. Mean ± 95% CI statistically significant linear relationships are indicated by the solid and dashed lines, respectively.

over time in the proportion of the population recorded in the Netherlands, Britain and Denmark ($F_{1,6}$ = 0.28, 0.98 and 0.04 respectively, $P > 0.05$, n.s. in each case; Fig. 3a,b,e).

Analysis of the mean latitudes and longitude recorded for the population in relation to the mean January temperatures for the centre of the Netherlands in census years found that the centre of the population was significantly further north in milder winters ($F_{1,5}$ = 106.65, $P < 0.001$; Figs. 4b & 5a), but not significantly further east ($F_{1,5}$ = 0.49, P = 0.52, n.s.; Figs. 4b & 5b). There was also no evidence, on analysing temporal trends in the mean latitudes and longitude data, for a north-easterly shift in the swans' distribution in the census years ($F_{1,5}$ = 1.34, P = 0.31 and $F_{1,5}$ = 1.37, P = 0.31 for latitude and longitude respectively; n.s. in each case).

Productivity

The overall percentage of cygnets recorded during the censuses ranged from 9.6% in 2010 to 13.2% in 2005, and mean brood sizes ranged from 1.5 in 2010 to 1.9 in 1995, 2000 and 2005 (Table 2). Although the proportion of cygnets recorded varied between countries, no country had a consistently higher or lower proportion of juveniles in the flocks over the years (ANOVA: $F_{4,24}$ = 1.95, P = 0.142, n.s.; Fig. 6). Variation between censuses in the percentage of cygnets recorded was most marked in Belgium, but relatively few Bewick's Swans wintered there in the early years of the study so sample sizes were low from 1995–2005 inclusive (Table 2). There was no statistically significant trend in either the proportion of cygnets ($F_{1,3}$ = 0.58, P = 0.500, n.s.) or mean brood size ($F_{1,3}$ = 2.74, P = 0.196, n.s.) in the censuses of 1995 to 2015.

Productivity data for the Netherlands, the main wintering area for the population, were available only for the January 2015 census, because Dutch annual age assessments are generally made earlier in the winter (in November–December). The 10.1% juveniles recorded in the Netherlands in 2015 was however similar to results of age counts made concurrently in Britain (10.2%) and Germany (10.0%), whereas the percentage of juveniles recorded nationally earlier in the winter tended to be lower (Table 2).

Habitat use

The proportion of Bewick's Swans recorded feeding on grasslands decreased significantly across the census years, from 64.1% in 1995 to 42.2% in 2015 (linear regression: $F_{1,5}$ = 9.17, P = 0.039), and there was a corresponding increase from 23.0% to 46.7% in the proportion using arable land over the same period ($F_{1,5}$ = 21.79, P = 0.01; Fig. 7a). The swans' daytime use of waterbodies varied between 1.2% and 13.0% during the censuses and did not show a significant trend over time ($F_{1,5}$ = 1.86, P = 0.245, n.s.). Other habitats, primarily saltmarshes, were used relatively infrequently with 0.0–4.2% of birds recorded on these habitats.

Inspection of data crop type, available for a subset of the arable sites, indicated that the proportion of birds using different arable crops varied quite markedly between years (Fig. 7b). This may however reflect crop type being recorded in some countries in some years and not in others; for instance,

Table 2. Percentage of cygnets and mean brood sizes recorded in each country during the International Bewick's Swan Censuses. Comparable data for the Netherlands (*i.e.* recorded during the censuses) were available only in 2015, because age counts are made there earlier in the winter. *Data from the Netherlands (in *italics*) are for November (winters 1994/95, 1999/2000) and December (winters 2004/05, 2009/2010; Hornman *et al.* 2019) and therefore are not included in the totals for each year. **Brood size figure reported in the Netherlands report for 1999/2000 are for swans in several countries in November, not just the Netherlands.

Year	Country	Aged	Cygs	% cygs	(95% CI)	No. broods	No. cygs in broods	Mean brood size (95% CI)
1995	Belgium	60	9	18.0	(7.1–26.6)	n/a	n/a	n/a (n/a)
	Denmark	818	59	7.2	(5.5–9.2)	33	59	1.8 (1.5–2.1)
	Estonia	5	0	0.0	(0.0–52.2)	0	0	n/a (n/a)
	GB	1,631	203	12.4	(10.9–14.1)	71	140	2.0 (1.8–2.2)
	Ireland	580	52	9.0	(6.8–11.6)	18	35	1.9 (1.3–2.5)
	Lithuania	12	3	25.0	(5.5–57.2)	–	–	–
	*Netherlands**	*8,070*	*670*	*8.3*	–	–	–	–
	Poland	10	5	50.0	(18.7–81.3)	1	5	5.0 (n/a)
	Total	**3,116**	**331**	**10.6**	**(9.6–11.8)**	**123**	**239**	**1.9 (1.8–2.1)**
2000	Belgium	89	5	5.6	(1.8–12.6)	1	1	1.0 (n/a)
	Estonia	29	1	3.4	(0.1–17.8)	1	1	1.0 (n/a)
	GB	704	91	12.9	(10.5–15.6)	45	85	1.9 (1.6–2.2)
	Germany	965	123	12.7	(10.7–15.0)	23	47	2.0 (1.6–2.4)
	Ireland	120	20	16.7	(10.5–24.6)	9	17	1.9 (1.3–2.5)
	*Netherlands**	*6,033*	*452*	*7.7*	–	*237*	*377*	*1.6***
	Poland	30	1	3.3	(0.1–17.2)	1	1	1.0 (n/a)
	Total	**1,937**	**241**	**12.4**	**(11.0–14.0)**	**80**	**152**	**1.9 (1.7–2.1)**
2005	Belgium	51	12	23.5	(12.8–37.5)	4	9	2.3 (1.5–3.0)
	Denmark	396	46	11.6	(8.6–15.2)	24	42	1.8 (1.4–2.1)
	Estonia	12	6	50.0	(21.1–78.9)	2	6	3.0 (n/a)
	GB	420	61	14.5	(11.3–18.3)	22	44	2.0 (1.6–2.4)
	Germany	3,319	422	12.7	(11.6–13.9)	99	189	1.9 (1.8–2.1)
	Ireland	201	34	16.9	(12.0–22.8)	19	34	1.8 (1.4–2.3)
	Lithuania	2	0	0.0	(0.0–84.2)	0	0	0
	*Netherlands**	*3,000*	*288*	*9.6*	–	*200*	*312*	*1.6*
	Poland	74	9	12.2	(5.7–21.8)	4	7	1.8 (0.3–3.3)
	Total	**4,475**	**590**	**13.2**	**(12.2–14.2)**	**174**	**331**	**1.9 (1.8–2.0)**

Table 2 (*continued*).

Year	**Country**	**Aged**	**Cygs**	**% cygs**	**(95% CI)**	**No. broods**	**No. cygs in broods**	**Mean brood size (95% CI)**
2010	Belgium	492	64	13.0	(10.2–16.3)	11	21	1.9 (1.1–2.7)
	Denmark	7	0	0.0	(0.0–41.0)	0	0	0
	Estonia	1	0	0.0	(0.0–97.5)	0	0	0
	GB	5,491	504	9.2	(8.4–10.0)	327	489	1.5 (1.4–1.6)
	Germany	440	48	10.9	(8.2–14.2)	21	42	2.0 (1.4–2.6)
	Ireland	34	4	11.8	(3.3–27.5)	2	4	2.0 (0.0–4.0)
	Lithuania	2	0	0.0	(0.0–84.2)	0	0	0
	*Netherlands**	*2,600*	*174*	*6.7*	–	*90*	*161*	*1.8*
	Poland	2	0	0.0	(0.0–84.2)	0	0	0
	Total	**6,469**	**620**	**9.6**	**(8.9–10.3)**	**361**	**556**	**1.5 (1.4–1.6)**
2015	Belgium	687	59	8.6	(6.6–10.9)	6	10	1.7 (0.8–2.5)
	Denmark	308	33	10.7	(7.5–14.7)	14	33	2.4 (1.7–3.1)
	Estonia	6	0	0.0	(0.0–45.9)	0	0	0
	GB	3,690	377	10.2	(9.3–11.2)	222	334	1.5 (1.4–1.6)
	Germany	4,967	499	10.0	(9.2–10.9)	91	175	1.9 (1.7–2.1)
	Ireland	16	2	12.5	(1.6–38.3)	2	2	1.0 (n/a)
	Netherlands	1,554	157	10.1	(8.6–11.7)	–	–	–
	Switzerland	1	0	0.0	(0.0–97.5)	0	0	0
	Total	**11,229**	**1,127**	**10.0**	**(9.5–10.6)**	**335**	**554**	**1.7 (1.6–1.8)**

data from the Netherlands were available only for 2015 when all of the birds were seen on stubble fields. Additionally, substantial changes between years in the availability of crops and habitat types due to changes in subsidy schemes may have resulted in significant changes in crop compositions. Overall, however, of the swans seen on arable land where crop type was recorded (n = 24,379 for all censuses), 42.3% were on winter cereals, 24.9% on sugar beet, 13.6% on stubble fields (crop type not recorded), 9.9% on oilseed rape, 3.1% on potatoes and 2.5% on maize (Fig. 7b).

Sites of international importance

A total of 22 sites were found to hold at least 1% of the total population in at least two of the six January-censuses between 1990 and 2015, of which most (17 sites; 77%) were in the Netherlands, four in Britain and one in Belgium (Krekengebied Noord-Oost-Vlaanderen) (Fig. 4). Three sites were found to hold at least 1% of the total population in all of the six censuses

(a)

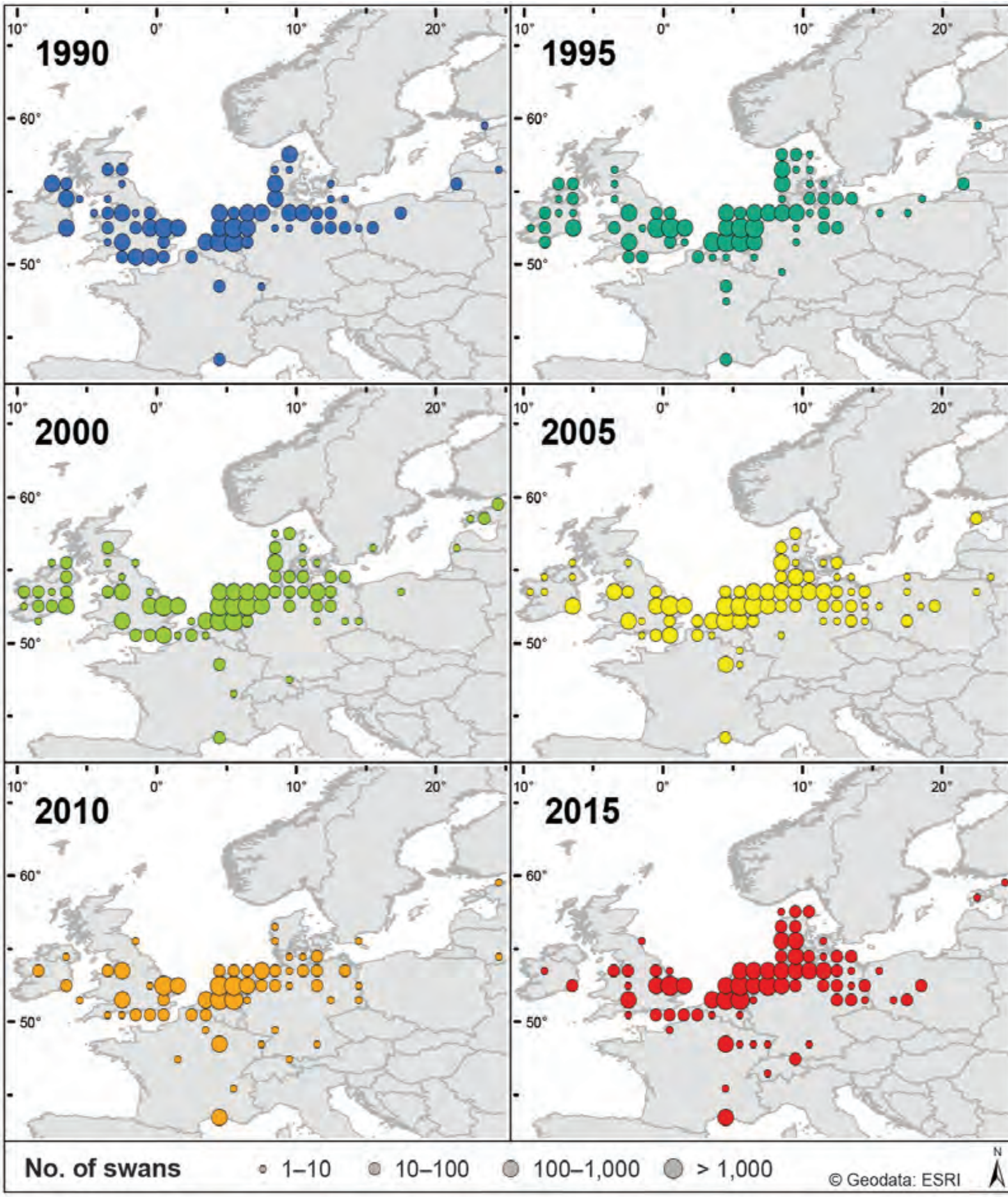

Figure 4. Distribution of Bewick's Swans during the international censuses in January 1990, 1995, 2000, 2005, 2010 and 2015: (a) aggregated into 1° × 1° grid squares (geographic coordinates; upper maps), and (b) the central point (mean location) of the population in each year (lower map).

(b)

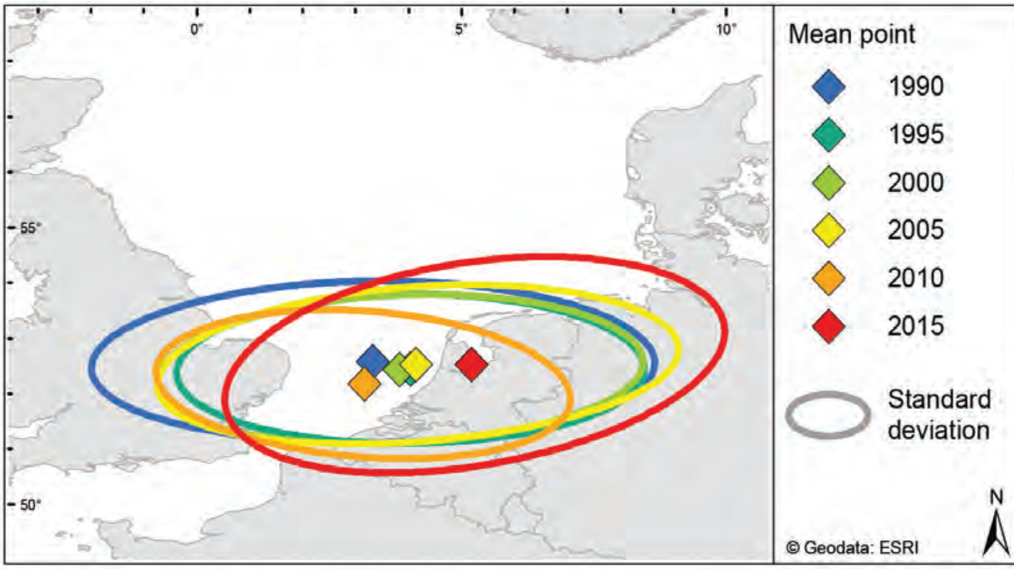

Figure 4 (*continued*).

between 1990 and 2015, of which two were in the Netherlands (Alblasserwaard and the Eempolders) and one (the Ouse Washes) in Britain. Four more sites, all in the Netherlands, held > 1% of the population in four census years (Arkemheen/Putterpolder, Krimpenerwaard, Maasland Oss – Den Bosch and Wieringermeer) and just two additional sites held internationally important numbers in three census years (Lopikerwaard in the Netherlands and the Nene Washes in Britain). All of the sites in Britain and Belgium were identified as key sites for the species in the ISSAP for the Northwest European Bewick's Swans (Nagy *et al.* 2012), and have also been designated as SPAs, but 12 (71%) of the 17 sites in the Netherlands with > 1% of the Bewick's Swans counted in at least two of the censuses have not yet been protected as SPAs under the EU Birds Directive, including nine sites listed within the ISSAP for the Netherlands.

Germany has been important for Bewick's Swans mainly during their spring staging period rather than in mid-winter, but it is worth noting that seven sites in Germany with > 1% population were all recorded with these numbers in January 2015, reflecting the more northerly distribution of the population in warmer winters. This almost certainly underestimates the number of sites in Germany now receiving ≥ 1% of the total population in mid-winter, over and above the sites known to have internationally important numbers during spring migration (listed in Nagy *et al.* 2012), because the German count data were provided at the flock/subsite level.

Overall, the number of sites recorded with internationally important numbers

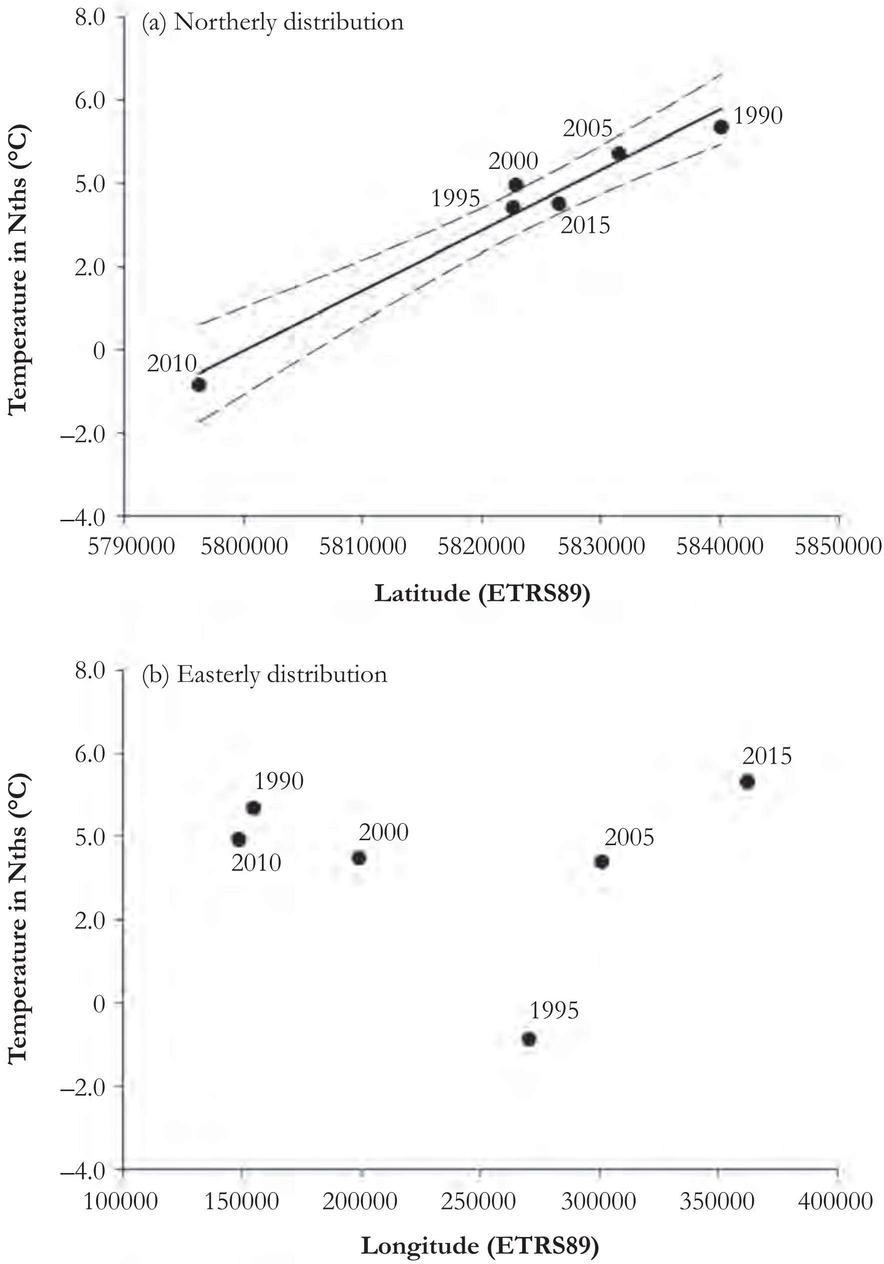

Figure 5. Mean coordinates (ETRS89) recorded for the Northwest Bewick's Swan population in relation to the mean January temperatures for the centre of the Netherlands during census years. The mean ± 95% CI relationships are indicated by the solid and dashed lines, respectively.

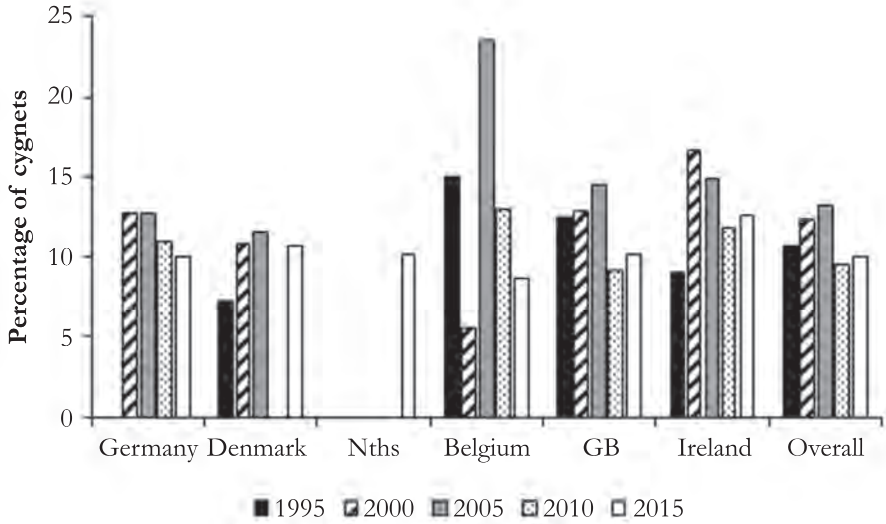

Figure 6. Percentage of cygnets recorded in flocks counted during the International Bewick's Swan Censuses. Note: age counts were recorded during the censuses (in mid-January) in the Netherlands only in 2015, because Dutch age-counts generally are made in November–December each year. Sample sizes are described in Table 2.

during the IBSC were 19 in 1990, 19 in 1995, 17 in 2000, 16 in 2005, 16 in 2010 and 20 in 2015. These sites held a total of 16,525 swans (61.8% of the population), 18,429 (61.9%), 14,255 (59.9%), 12,919 (59.5%), 14,222 (78.8%) and 9,762 (48.5%) during each of the censuses, illustrating their importance for the species, although further investigation of the precise locations of feeding flocks is required to determine the proportion observed within SPA boundaries.

Discussion

Population size and trends

The International Bewick's Swan Censuses confirmed that an increase in the total population size from 16,000–17,000 swans in the mid-1980s to a peak of 29,780 birds in 1995 was followed by a decline of 39.4% to 18,057 individuals by 2010. The population growth of 21.3% between 1984 and 1990 (averaging at 10.7% *per annum*) and of 82.9% between 1984 and 1995 (7.5% *per annum*) recorded in our study seems very rapid for a long-lived species with low annual productivity and where onset of successful breeding (*i.e.* bringing a brood to the wintering grounds) is not usually until 4–6 years of age (Rees 2006). Annual mortality has been estimated at 14.7% for swans in the Northwest European population during the 1980s (Wood *et al.* 2018), suggesting that annual productivity would need to be at *c.* 22.2% to offset mortality and achieve even the lower population growth rate indicated for the late 1980s, although a population model is required to analyse this more rigorously. In contrast, the mean percentage of juveniles recorded in winters

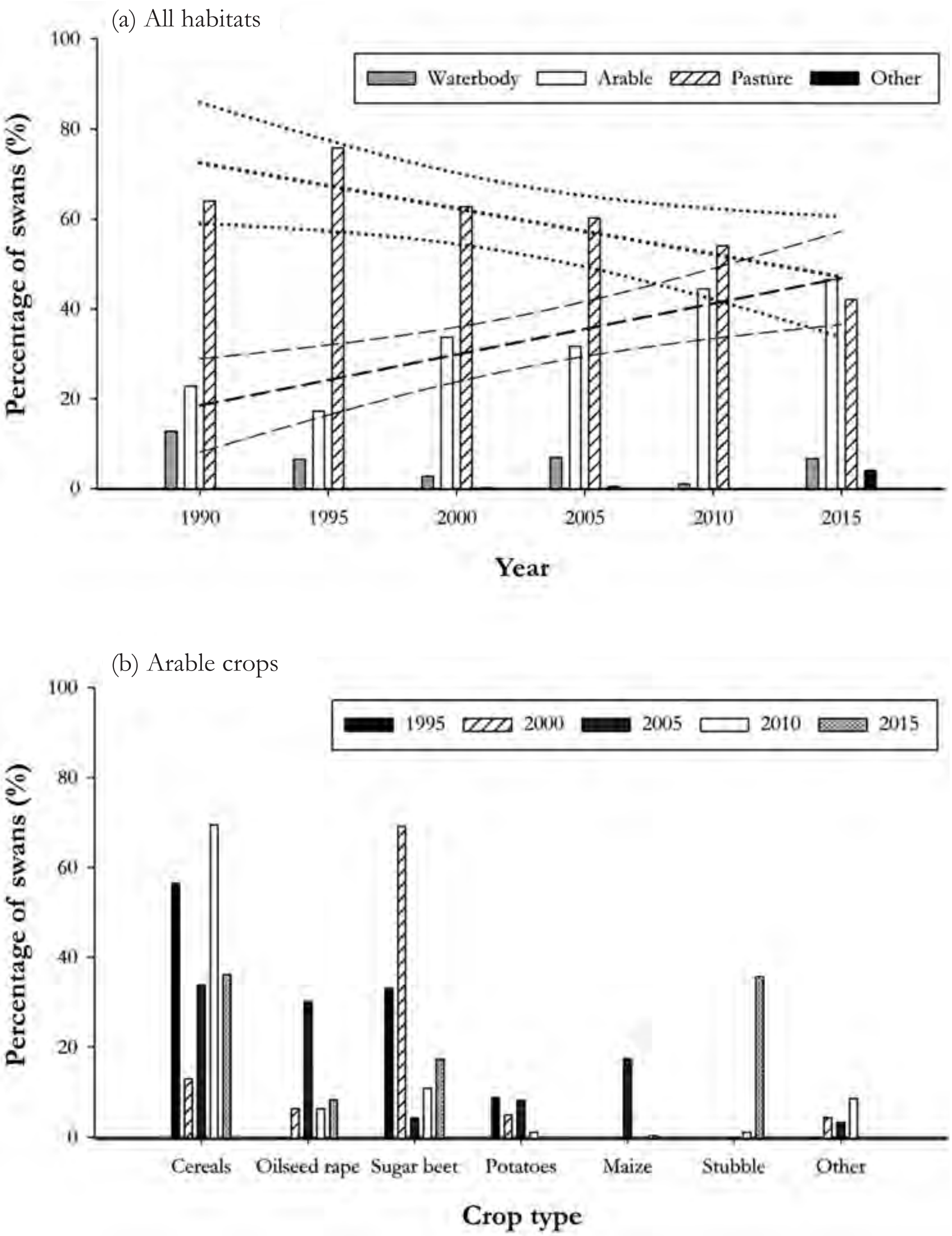

Figure 7. Percentage of Bewick's Swans recorded on different habitat categories during the International Bewick's Swan Censuses: (a) the relative use of different habitats (dotted line = mean ± 95% CI trend for swans on pasture; dashed line = mean ± 95% CI trend for swans on arable crops), and (b) the relative use of different types of arable crops in each census year.

1983/84–1994/95 inclusive was 15.1% (s.d. ± 5.2%) among Bewick's Swans observed near-daily at Slimbridge in southwest England, for which breeding success estimates tend to be higher than elsewhere (Rees *et al.* 1997; Wood *et al.* 2016). While survival may have shown some decreases over time, the productivity data from the censuses, in terms of the proportion of cygnets in the population and mean brood size, showed no temporal changes in common with long-term analysis of annual productivity data from Britain (Wood *et al.* 2016).

The decrease in numbers by 39.4% between 1995 and 2010 (*i.e.* indicating that mortality exceeded recruitment by 2.6% *per annum* over this period) appears to provide a better fit to productivity and survival rate estimates. However, population modelling again is required to determine whether four very poor breeding years (in 1997, 2002, 2007 and 2014; Wood *et al.* 2016) together with a slight drop in survival rates between the 1980s and 1990s followed by a more major decrease in apparent survival from winter 2008/09 onwards (Wood *et al.* 2018) accounts for the decline, or if some emigration of birds to the Caspian or Eastern populations may have occurred as well. The accuracy of each of the three variables (survival rates, productivity and total counts) should also be considered, particularly for the early years with rapid population growth. It is possible that the January 1984 census underestimated population size (as was thought to occur in 1987; Dirksen & Beekman 1991), perhaps if counters were not fully familiar with sites used by the swans at the start of the study, though there was no obvious reason for an undercount and it was considered that near complete coverage had been achieved between 13–15 January 1984 (Beekman *et al.* 1985).

Changes in distribution

Despite a shortening of migration distances reported for a number of other species in western Europe, including Greylag Geese *Anser anser* (Podhrázský *et al.* 2017) and Eurasian Wigeon *Anas penelope* (Fox *et al.* 2016), analysis of the coordinates recorded for Bewick's Swans counted during the censuses did not find evidence for the swans remaining closer to their breeding grounds in more recent years. The birds did however occur further north in milder winters, suggesting that the swans may be able to make increased use of more northerly sites should warmer winters become more frequent as a result of climate change. Annual rather than 5-yearly data would provide a better indication of such a trend as the less frequent censuses may coincide with colder conditions, as occurred in 2010. For instance, this pattern is evident in count data from Denmark, where complete national censuses have been carried out annually during 1983–2019 (except in 1986). In this time-series, eight years have national totals of > 1,000 birds, which is higher than Danish totals for all of the ISC years (Table 1) (Nielsen *et al.* 2019 supplemented with preliminary data for 2018 and 2019; P. Clausen, unpubl. data). All counts of > 1,000 birds in Denmark were from mild winters: one in the 1980s, two in the 1990s, one in the 2000s and four in the 2010s (all four with > 1,500 swans), confirming the populations' recent expansion to the northeast. Elsewhere in the wintering range, the marked decrease in numbers migrating to Ireland described in this paper and by Worden *et al.* (2006) suggests that short-stopping might be occurring, and analyses of colour-marked swans have likewise found a northeast shift in distribution over time for individual swans (Nuijten *et al.*, unpubl. data), although no firm evidence of short-stopping was found in the current study.

Changes in habitat use

Assessment of the swans' use of different habitats found that an increasing proportion of the population were using arable land in mid-winter, with a corresponding decline in the proportion on grasslands. In contrast, the proportion feeding in waterbodies showed little variation, although individual countries have reported an increasing proportion of the swans feeding on submerged macrophytes during midwinter, following ecological restoration of aquatic ecosystems (*e.g.* in the Netherlands; Tijsen & Koffijberg 2015). The obvious increase in use of arable habitats between 1995 and 2015 has also been recorded for the Icelandic Whooper Swan population, although a slightly higher proportion of the Whooper Swans were using pasture than arable land in 2015 (39.0% *vs.* 30.8%; Hall *et al.* 2016) whereas fewer Bewick's Swans were on pasture than arable for the first time (42.2% *vs.* 46.7%) in 2015. Whilst the use of different types of arable crop was somewhat variable, perhaps reflecting the timing of the harvest and whether the farmers had ploughed in preparation for the next planting, the Bewick's Swans were seen on fields of winter cereals, sugar beet, oilseed rape and potatoes in each census year, with maize also used in the 21st century. It is likely, at least in some countries (*e.g.* the Netherlands), that birds recorded on stubble during the most recent censuses were actually feeding on maize stubble. Arable crops are now the predominant food resources used by Bewick's Swans at many key winter sites (*e.g.* Wood *et al.* 2019a,b; this study). The trend towards greater use of arable feeding areas presents a conservation challenge, as whilst roost sites near major arable feeding areas may be protected for the birds (for example, as SPAs or Ramsar sites), the arable fields themselves are not protected directly. Therefore, it is important for the long-term future of the Bewick's Swan that these arable feeding resources are not degraded or lost due to development or other land-use changes, bearing in mind that changes in farming practice may occur quite rapidly across a wide area if changes in government policy (*e.g.* the EU's Common Agriculture Policy) promote the planting of different crops less suitable for swans, and shifts in farming activity may also occur with climate change (as indicated by Porter *et al.* 2014). The availability of suitable wetland roost sites for the swans close to their feeding areas continues to be a crucial component of site-use by the species. The restoration of dozens of large lakes in Denmark have changed the distribution of several goose and swan species (including Bewick's Swans), as new roosts have been established in several inland areas making new farming areas accessible to the swans (Clausen *et al.* 2019).

Population interchange

The extent to which the recent population decline in northwest Europe is attributable to a redistribution of swans to the Evros/Meriç Delta remains debatable, but there is good evidence from different sources that at least some of these birds are linked to the population which traditionally winters on the Caspian Sea, and thus not primarily connected to the declining Northwest European population. Moreover, even when Bewick's Swan counts for Greece were included in the Northwest European population totals, there was a decline from 1995 onwards, though the population recovery in 2015 would be more substantial in the event that the vast majority of the birds in Greece emanated from the population wintering in northwest Europe. This seems very unlikely, however, because tracking of 11 Bewick's Swans tagged on the Yamal peninsula in 2015–2016 showed that at least some of the swans wintering in Greece migrate along the River Ob and Turgai lowlands to the north Caspian region before continuing to the Evros Delta (Vangeluwe *et al.* 2018), suggesting a westward shift of swans from the Caspian population. Several recent studies have reported increased numbers of Caspian population Bewick's Swans migrating through the Volgograd region of southern Russia towards wintering areas in the Black Sea region (Belik *et al.* 2012; Belik & Gugueva 2016). Moreover, annual changes in the peak numbers counted in Greece were not found to be an important explanatory variable on analysing the swans' apparent survival rates, indicative of relatively few marked birds from the Northwest European population emigrating to the region (Wood *et al.* 2018), a view supported by relatively few swans marked with leg-rings or neck-collars being resighted in Greece in recent years (Rees 2006; Vangeluwe *et al.* 2016; Eggers 2018). Further investigation through ringing and tracking programmes into the migration routes taken by Bewick's Swans wintering in southeast Europe nonetheless is required to determine the proportion of swans following different routes to reach this destination. Genetic analysis (*e.g.* assessment of haplotype diversity in mitochondrial DNA) would also provide a valuable indication of whether the birds wintering in Greece are primarily from the Northwest European or the Caspian population. Monitoring numbers on the Evros Delta throughout the winter would additionally help to assess whether the mid-January counts underestimate the numbers present at the time if observer effort is relatively low, or alternatively if the peak counts recorded in February reflect a late-winter influx of swans using sites further east in the Black Sea or Caspian regions in mid-January. Overall, better monitoring of Bewick's Swans in the Caspian and Black Sea regions would be highly beneficial for understanding (and disentangling) trends for both the Northwest European and the Caspian populations.

Future prospects

The partial recovery of the population to 20,700 birds in 2015 is in line with the initial remit of the Bewick's Swan Action Plan, which was to halt the ongoing decline, though the overall goal of holding the population minimally at its 2000 level (*i.e.*

23,000 birds) in the long-term (Nagy *et al.* 2012) has yet to be achieved. National trends, however, indicate that the decline in numbers is continuing in the western part of the range, most notably in Britain to winter 2017/18 (Frost *et al.* 2019), although there appears to have been some recovery of numbers in the Netherlands in winter 2016/17 (Hornman *et al.* 2019). Evidence from the next census, scheduled for January 2020, is therefore required to determine whether the 2015 counts reflect a reversal of the population trend or if the decline is continuing. Ensuring good coverage in countries outside the main wintering areas for the species is important to confirm the situation. Whether more swans are remaining further northeast along the flyway, for instance in Poland, therefore should be addressed in the next census. So far, numbers of Bewick's Swans in Poland during mid-winter reached only 116 birds (during the 1990 census), despite swan sites being apparently well covered for the Whooper Swan census (with *c.* 5,000 Whooper Swans counted in Poland in January 2015) which is undertaken at the same time (Laubek *et al.* 2019).

Whilst a number of sites important for Bewick's Swans in mid-winter are listed as being protected as SPAs and/or Ramsar sites, the tendency for swans to feed on arable land generally results in them flying outside the boundaries of the SPA during the day, whereas protection is mainly at the wetland roosts. Farmland outside an SPA may be ecologically important for supporting species for which the site has been designated, and thus maintaining the integrity of the SPA. In such cases, these habitats are considered to be "functionally linked" to the site, resulting in protection extending to these areas under the Habitats Regulations Assessment process of the European Union (EU) Habitats Directive (*e.g.* Chapman & Tyldesley 2016). For sites identified as being used by internationally important numbers of Bewick's Swans, which are not protected either directly or through linkage with an SPA, further consideration should be given by governments to designating these areas, bearing in mind that "*maintaining favourable conditions at key foraging and roosting sites through appropriate management and/or protection measures according to the species requirements*" is a high priority action for all range countries within the ISSAP (Nagy *et al.* 2012).

The censuses are particularly important for providing updated estimates of the total population size, which are used to identify sites of international importance (*i.e.* receiving ≥ 1% of the total population) for Bewick's Swans, and thus determine areas that should be protected for the species. Updated estimates therefore should be considered by government environmental agencies as they become available, to identify key areas for conservation. Moreover, bearing in mind that a key result within the ISSAP is that "*A chain of key sites, sufficient to support the population throughout its annual cycle, is sustained across the flyway*" (Nagy *et al.* 2012), annual national count data should also be considered for sites used by the species throughout its range, along with an assessment of the swans' dispersal to feeding areas around a core roost, with a view to appropriate protection measures being put in place under national and EU legislation. Important sites used by the swans not only in winter but also at key staging areas will be missed if only January counts are considered. For instance, an overview of counts made across the entire SPA network for migratory waterbirds in Denmark (Clausen *et al.* 2019) includes several notations of Bewick's Swan numbers exceeding the international or national 1% criteria being recorded outside the midwinter census periods, usually in October–November or March, when numbers are highest in Denmark. We therefore recommend that the list of internationally important sites for Bewick's Swans included in the ISSAP (which was compiled nearly 10 years ago; Nagy *et al.* 2012) is updated as a key action under the remit of the Bewick's Swan Action Plan.

Acknowledgements

This study would not have been possible without the dedicated network of volunteer and professional ornithologists in each country, who undertook the fieldwork and submitted the count data, which enabled us to describe variation in the numbers and distribution of the Bewick's Swan population. We are immensely grateful to each counter for their time and effort, to the organisers of the counts networks for collating the data, and to the statutory agencies and conservation organisations who have supported the five-yearly International Bewick's Swan Censuses under the auspices of the Wetlands International/IUCN-SSC Swan Specialist Group. In particular we thank SOVON (the Dutch Centre for Field Ornithology), the DDA Federation of German Avifaunists, the Research Institute for Nature and Forest in Belgium and the Department of Bioscience at Aarhus University, Denmark. Counts within the UK were undertaken and coordinated in association with WeBS (a partnership between the British Trust for Ornithology, the Royal Society for the Protection of Birds and the Joint Nature Conservation Committee, in association with the Wildfowl & Wetlands Trust) and funded by the Goose & Swan Monitoring Programme (GSMP) (on behalf of the WWT, the Joint Nature Conservation Committee and Scottish Natural Heritage). The censuses in Ireland were funded through I-WeBS, which is funded and supported by the National Parks and Wildlife Service of the Department of Arts, Heritage, Regional, Rural and Gaeltacht Affairs, and is managed by BirdWatch Ireland. ECR is indebted to WWT colleagues supporting the Bewick's Swan study, and to Stratis Bourdakis (Hellenic Ornithological Society) and Didier Vangeluwe (Royal Belgian Institute of Natural Sciences) for valuable information on key reports and the number of Bewick's Swans wintering in Greece. PC acknowledges funding from the Danish Environmental Protection Agency to help finalise the Danish contribution to the paper.

References

Atkinson-Willes, G. 1976. The numerical distribution of ducks, swans and coots as a guide to assessing the importance of wetlands. *In* M. Smart (ed.), *Proceedings International Conference on the Conservation of Wetlands and Waterfowl, Heiligenhafen 1974*, pp. 199–254. International Waterfowl Research Bureau, Slimbridge, UK.

Beekman, J.H. 1997. Censuses of NW European Bewick's Swan population January 1990 and 1995. *Swan Specialist Group Newsletter* 6: 7–9.

Beekman, J.H., Dirksen, S. & Slagboom, T.H. 1985. Population size and breeding success of Bewick's Swans wintering in Europe in 1983–4. *Wildfowl* 36: 5–12.

Beekman, J.H., Rees, E.C. & Bacon, P.J. 1994. Bewick's Swan *Cygnus columbianus bewickii*. *In* G.M. Tucker & M.F. Heath (eds.), *Birds in Europe: their Conservation Status*, pp. 108–109. Birdlife Conservation Series No. 3. Birdlife International, Cambridge, UK.

Belik, V.P. & Gugueva, E.V. 2016. Goose and swan fauna of Volgograd Oblast. *Casarca* 19: 105–141.

Belik, V.P., Gugueva, E.V., Vetrov, V.V. & Makhmutov, R. 2012. Migration of the Bewick's Swan (*Cygnus bewickii*) in the Volga-Akhtuba floodplain. *Casarca* 15: 13–29.

Brides, K., Mitchell, C., Sigfússon, A. & Auhage, S.N.V. 2018. Status and distribution of Icelandic-breeding geese: results of the 2017 international census. Wildfowl & Wetlands Trust Report, Slimbridge, Gloucestershire, UK.

Clausen, P., Petersen, I.K., Bregnballe, T. & Nielsen, R.D. 2019. *Numbers of Non-breeding Birds in Special Protection Areas for Birds in Denmark, 2004 to 2017*. Danish Centre for The Environment and Energy Technical Report No. 148. Aarhus University, Rønde, Denmark. [In Danish with English summary.]

Cranswick, P.A., Raducescu, L., Hilton G.M. & Petkov, N. 2012. International Single Species Action Plan for the Conservation of the Red-breasted Goose (*Branta ruficollis*). AEWA Technical Series No. 46. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Crawley, M.J. 2015. *Statistics: An Introduction Using R* (*Second Edition*). Wiley, Chichester, UK.

Crowe, O. & Holt, C. 2013. Estimates of waterbird numbers wintering in Ireland, 2006/07–2010/11. *Irish Birds* 9: 545–552.

Delany, S., Reyes, C., Hubert, E., Pihl, S., Rees, E., Haanstra, L. & van Strien, A. 1999. *Results from the International Waterbird Census in the Western Palearctic and Southwest Asia 1995 and 1996*. Wetlands International Publication No. 54, Wetlands International, Wageningen, The Netherlands.

Dirksen, S. & Beekman, J.H. 1991. Population size, breeding success and distribution of Bewick's Swans *Cygnus columbianus bewickii* wintering in Europe in 1986–87. *Wildfowl* (Supplement No. 1): 120–124.

Eggers, H. 2018. Observations of Bewick's Swans at the Evros Delta, in Greece and Turkey, in February 2017. *Swan News* 14: 18–21.

Elmberg, J., Hessel, R., Fox, A.D., & Dalby, L. 2014. Interpreting seasonal range shifts in migratory birds: A critical assessment of "short-stopping" and a suggested terminology. *Journal of Ornithology* 155: 571–579.

Evans, M.E. 1982. Movements of Bewick's Swans, *Cygnus columbianus bewickii* marked at Slimbridge, England from 1960 to 1979. *Ardea* 70: 59–75.

Fox, A.D. & Abraham, K.F. 2017. Why geese benefit from the transition from natural vegetation to agriculture. *Ambio* 46 (Supplement No. 2): S188–S197.

Fox, A.D. & Madsen, J. 2017. Why geese benefit from the transition from natural vegetation to agriculture. *Ambio* 46 (Supplement No. 2): S179–S187.

Fox, A.D, Ebbinge, B.S., Mitchell, C., Heinicke, T., Aarvak, T., Colhoun, K., Clausen, P., Dereliev, S., Farago, S., Koffijberg, K., Kruckenberg, H., Loonen, M.J.J.E., Madsen, J., Mooij, J., Musil, P., Nilsson, L., Pihl, S. & van der Jeugd, H. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. *Ornis Svecica* 20: 115–127.

Fox, A.D., Dalby L., Christensen T.K., Nagy S., Balsby T.J.S., Crowe O., Clausen, P., Deceuninck, B., Devos, K., Holt, C.A, Hornman, M., Keller, V., Langendoen, T., Lehikoinen, A., Lorentsen, S.-H., Molina, B., Nilsson, L., Stīpniece, A., Jens-Christian Svenning, J.-C. & Wahl J. 2016. Seeking explanations for recent changes in abundance of wintering Eurasian Wigeon (*Anas penelope*) in northwest Europe. *Ornis Fennica* 93: 12–25.

Fox, A.D., Elmberg, J., Tombre, I. & Hessel, R. 2017. Agriculture and herbivorous waterfowl: A review of the scientific basis for improved management. *Biological Reviews* 92: 854–877.

Frost, T.M., Austin, G.E., Calbrade, N.A., Mellan, H.J., Hearn, R.D., Robinson, A.E., Stroud, D.A., Wotton, S.R. & Balmer, D.E. 2019. *Waterbirds in the UK 2017/18: The Wetland Bird Survey*. BTO, RSPB and JNCC, in association with WWT. British Trust for Ornithology, Thetford, UK. Available at https://www.bto.org/sites/default/files/wituk-2017-18.pdf (last accessed 18 September 2019).

Hall C., Crowe, O., McElwaine, G., Einarsson, Ó., Calbrade, N. & Rees. E. 2016. Population size and breeding success of the Icelandic Whooper Swan *Cygnus cygnus*: results of the 2015 international census. *Wildfowl* 66: 75–97.

Handrinos, G.I. 1996. Numbers and distribution of swans wintering in Greece. *In* M. Birkan, J. van Vessem, P. Havet, J. Madsen, B. Troillet & M. Moser (eds.), *Proceedings of the Anatidae 2000 Conference, Strasbourg, France, 5–9 December 1994*. *Gibier Faune Sauvage, Game Wildlife* 13: 463–476.

Hellenic Rarities Committee. 2007. *Annual Report – 2006*. Hellenic Ornithological Society Themistokleous 80, GR-10681 Athens, Greece. Available at http://files.ornithologiki.gr/docs/rarities/annual_report_2006_en.pdf (last accessed 18 September 2019).

Hellenic Rarities Committee. 2010. *Annual Report – 2010*. Hellenic Ornithological Society Themistokleous 80, GR-10681 Athens, Greece. Available at http://files.ornithologiki.gr/docs/rarities/annual_report_2010_en.pdf (last accessed 18 September 2019).

Hellentic Rarities Committee. 2016. *Annual Report – 2015*. Hellenic Ornithological Society Themistokleous 80, GR-10681 Athens, Greece. Available at http://files.ornithologiki.gr/docs/rarities/annual_report_2015_en.pdf (last accessed 18 September 2019).

Hornman, M., Hustings, F., Koffijberg, K., van Winden, E., van Els, P., van Kleunen, A., SOVON Ganzen- en zwanenwerkgroep & Soldaat, L. 2019. *Watervogels in Nederland in 2016/17*. SOVON rapport 2019/01, RWS-rapport BM 19.01. SOVON Vogelonderzoek Nederland, Nijmegen, the Netherlands.

Jia, Q., Koyama, K., Choi, C.-Y., Kim, H.-J., Cao, L., Gao, D., Liu, G. & Fox, A.D. 2016. Population estimates and geographical distributions of swans and geese in East Asia based on counts during the non-breeding season. *Bird Conservation International* 26: 397–417.

Jones, T., Martin, K., Barov, B. & Nagy, S. (comps.). 2008. International Single Species Action Plan for the Conservation of the Western Palearctic Population of the Lesser White-fronted Goose *Anser erythropus*. AEWA Technical Series No. 36. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Kear, J. 1963. The history of potato-eating by wildfowl in Britain. *Wildfowl Trust Annual Report* 14: 54–65.

Kirby, J.S., Rees, E.C., Merne, O.J. & Gardarsson, A. 1992. International census of Whooper Swans *Cygnus cygnus* in Britain, Ireland and Iceland: January 1991. *Wildfowl* 43: 20–26.

KNMI. 2016. *Royal Netherlands Meteorological Institute: Central Netherlands Temperature v6*. Available on-line at http://projects.knmi.nl/klimatologie/onderzoeksgegevens/CNT/ (last accessed 18 September 2019).

Koffijberg, K. & Tijsen, W. 2018. Kleine Zwaan *Cygnus columbianus bewickii*. *In* SOVON Vogelonderzoek Nederland (ed.), *Vogelatlas von Nederland*, pp. 84–85. Kosmos Uitgevers, Utrecht/Antwerp, the Netherlands.

Laubek, B., Clausen, P., Nilsson, L., Wahl, J., Wieloch, M., Meissner, W., Shimmings, P., Larsen, B.-H., Hornman, M., Langendoen, T., Lehikoinen, A., Luigujõe, L., Stīpniece, A., Švažas, S., Sniaukstra, L., Keller, V., Gaudard, C., Devos, K., Musilová, Z., Teufelbauer, N., Rees, E.C. & Fox, A.D. 2019. Whooper Swan *Cygnus cygnus* January population censuses for Northwest Mainland Europe, 1995–2015. *Wildfowl* (Special Issue No. 5): 103–122.

Litvin, K. & Vangeluwe, D. 2016. The Bewick's Swan is a paradox. *Swan News* 12: 12.

Madsen, J. & Williams, J.H. (comps.) 2012. International Species Management Plan for the Svalbard Population of the Pink-footed Goose *Anser brachyrhynchus*. AEWA Technical Series No. 48. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Marjakangas, A., Alhainen, M., Fox, A.D., Heinicke, T., Madsen, J., Nilsson, L. & Rozenfeld, S. (comps.) 2015. International Single Species Action Plan for the Conservation of the Taiga Bean Goose (*Anser fabalis fabalis*). AEWA Technical Series No. 56. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Mitchell, C.R. & Hall, C. 2013. *Greenland Barnacle Geese* Branta leucopsis *in Britain and Ireland: Results of the International Census, Spring 2013*. Wildfowl & Wetlands Trust, Slimbridge, UK.

Monval, J.-Y. & Pirot, J.-Y. 1989. *Results of the IWRB International Waterfowl Census 1967–1986*. IWRB Special Publication No. 8. International Waterfowl & Wetlands Research Bureau, Slimbridge, UK.

Mullie, W.C. & Poorter, E.P.R. 1977. Aantallan, verspreiding en terreinkeus van de Kleine Zwaan bij vijf landelijke tellingen in 1976 en 1977. *Watervogels* 2: 85–96.

Nagy, S., Petkov, N., Rees, E.C., Solokha, A., Hilton, G., Beekman, J. & Nolet, B. 2012. International Single Species Action Plan for the Conservation of the Northwest European Population of Bewick's Swan (*Cygnus columbianus bewickii*). AEWA Technical Series No. 44. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Nagy, S., Flink, S. & Langendoen, T. 2014. *Waterbird trends 1988–2012. Results of Trend Analyses of Data from the International Waterbird Census in the African-Eurasian Flyway*. Wetlands International, Ede, the Netherlands.

Nielsen, R.D., Holm, T.E., Clausen, P., Bregnballe, T., Clausen, K.K., Petersen, I.K., Sterup, J., Balsby, T.J.S., Pedersen, C.L., Mikkelsen, P. & Bladt, J. 2019. *Fugle 2012–2017. NOVANA*. Danish Centre for the Environment and Energy Scientific Report No. 314. Aarhus University, Rønde, Denmark. [In Danish.]

Porter, J.R., Xie, L., Challinor, A.J., Cochrane, K., Howden, S.M., Iqbal, M.M., Lobell, D.B. & Travasso, M.I. 2014. Food security and food production systems. *In* C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White (eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects,* pp. 485–533. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Podhrázský, M., Musil, P., Musilová, Z., Zouhar, J., Adam, M., Závora, J. & Hudec, K. 2017. Central European Greylag Geese *Anser anser* show a shortening of migration distance and earlier spring arrival over 60 years. *Ibis* 159: 352–365.

Ramsar Convention. 2017. Strategic framework and guidelines for the future development of the list of Wetlands of International Importance of the Convention on Wetlands (Ramsar, Iran, 1971). The Ramsar Convention Secretariat, Gland, Switzerland. Available online at https://www.ramsar.org/document/strategic-framework-and-guidelines-for-the-future-development-of-the-list-of-wetlands-of-1 (last accessed 23 August 2019).

Rees, E.C. 2006. *Bewick's Swan*. T. & A.D. Poyser, London, UK.

Rees, E.C. & Beekman, J.H. 2010. Northwest European Bewick's Swans: a population in decline. *British Birds* 103: 640–650.

Rees, E.C., Kirby, J.S. & Gilburn, A. 1997. Site selection by swans wintering in Britain and Ireland: the importance of geographical location and habitat. *Ibis* 139: 337–352.

Rees, E.C., Cao, L., Clausen, P., Coleman, J.T., Cornely, J., Einarsson, O., Ely, C.R., Kingsford, R.T., Ma, M., Mitchell, C.D., Nagy, S., Shimada, T., Snyder, J., Solovyeva, D.V., Tijsen, W., Vilina, Y. & Włodarczyk, R. 2019. Conservation status of the world's swan populations, *Cygnus* sp. and *Coscoroba* sp.: a review of current trends and gaps in knowledge. *Wildfowl* (Special Issue No. 5): 35–72.

Rüger, A., Prentice, C. & Owen, M. 1986. *Results of the IWRB International Census 1967–1983*. IWRB Special Publication No. 6, International Waterfowl and Wetlands Research Bureau (IWRB), Slimbridge, UK.

Scott, D.A. 1980. A preliminary inventory of wetlands of international importance for waterfowl in Western Europe and North-west Africa. *IWRB Special Publication No. 2*. International Waterfowl Research Bureau, Slimbridge, UK.

Stroud, D.A., Fox, A.D., Urquhart, C. & Francis, I.S. (comps.). 2012. International Single Species Action Plan for the Conservation of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). AEWA Technical Series No. 45. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Tijsen, W. & Koffijberg, K. 2015. Thirty years of goose and swan counts in the north of the province of Noord-Holland. *Limosa* 88: 83–95. [In Dutch with English summary.]

Van der Schrier, G., van Ulden, A. & van Oldenborgh, G.J. 2011. The construction of a Central Netherlands temperature. *Climate of the Past* 7: 527–542.

Van Eerden M.R., Zijlstra M., van Roomen M. & Timmerman A. 1996. The response of Anatidae to changes in agricultural practice: long-term shifts in the carrying capacity for wintering waterfowl. *Gibier Faune Sauvage* 13: 681–706.

Vangeluwe, D., Rozenfeld, S. & Kazantzidis, S. 2016. The odyssey of the Bewick's Swan – another route to Greece. *Swan News* 12: 10–12.

Vangeluwe, D., Rozenfeld, S.B., Volkov, S.V., Kazantzidis, S., Morosov, V.V., Zamyatin, D.O. & Kirtaev, G.V. 2018. Migrations of Bewick's Swan (*Cygnus bewickii*): new data on tagging the migration routes, stopovers, and wintering sites. *Biology Bulletin* 45: 90–101.

Wetlands International. 2017. *Flyway Trends Analyses Based on Data from the African-Eurasian Waterbird Census from the Period of 1967–2015*. Wetlands International, Ede, the Netherlands. Accessible at http://iwc.wetlands.org/index.php/aewatrends (last accessed 30 May 2019).

Wetlands International. 2019. *Waterbird Population Estimates*. Available at wpe.wetlands.org (last accessed on 5 April 2019).

Wood, K.A., Newth, J.L., Hilton, G.M., Nolet, B.A. & Rees, E.C. 2016. Inter-annual variability and long-term trends in breeding success in a declining population of migratory swans. *Journal of Avian Biology* 47: 597–609.

Wood, K.A., Nuijten, R.J.M., Newth, J.L., Haitjema, T., Vangeluwe, D., Ioannidis, P., Harrison, A.L., Mackenzie, C., Hilton, G.M., Nolet, B.A. & Rees, E.C. 2018. Apparent survival of an Arctic-breeding migratory bird over 44 years of fluctuating population size. *Ibis* 160: 413–430.

Wood, K.A., Newth, J.L., Brides, K., Burdekin, M., Harrison, A.L., Heaven, S., Kitchin, C., Marshall, L., Mitchell, C., Ponting, J., Scott, D.K., Smith, J., Tijsen, W., Hilton, G.M. & Rees, E.C. 2019a. Are long-term trends in Bewick's Swan (*Cygnus columbianus bewickii*) numbers driven by changes in winter food resources? *Bird Conservation International* 29: 479–496.

Wood, K.A., Hilton, G.M., Newth, J.L. & Rees, E.C. 2019b. Seasonal variation in energy gain explains patterns of resources use by avian herbivores in an agricultural landscape: Insights from a mechanistic model. *Ecological Modelling* 409: 108762.

Worden, J., Cranswick, P.A., Crowe, O., McElwaine, G. & Rees, E.C. 2006. Numbers and distribution of Bewick's Swan *Cygnus columbianus bewickii* wintering in and Ireland: results of international censuses, January 1995, 2000 and 2005. *Wildfowl* 56: 3–22.

Photograph: Bewick's Swans at Meggerkoog, Schleswig-Holstein, Germany, by Hans-Joachim Augst.

