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Deriving population estimates for wintering wildfowl in Great Britain

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Information on the numbers of individuals in a population represents some of the most basic data that are needed to conserve populations effectively. Over the past decades, many wildfowl populations have undergone rapid changes in numbers as well as changes in distribution in response to the creation of refuges, management of populations, the creation of man-made wetlands and climate change. These continuing changes make it necessary to update population estimates on a regular basis. Data on the numbers of wildfowl wintering on wetland sites in Great Britain come primarily from the Wetland Bird Survey (WeBS), a joint scheme of the British Trust for Ornithology, the Wildfowl & Wetlands Trust, the Royal Society for the Protection of Birds and the Joint Nature Conservation Committee to monitor non-breeding waterbirds in the UK. Coordinated monthly counts by volunteers at wetland sites throughout Great Britain form the basis of the scheme, which focuses mainly on the months September through to March. It is not a simple task to calculate population sizes from extensive, volunteer-based surveys such as WeBS. In particular there are three main problems associated with the derivation of population estimates from WeBS data. Firstly, not all wetlands are covered by the scheme. Secondly, those that are covered do not represent a random selection of wetland sites. Thirdly, on any one count occasion there will be a number of missing counts from individual sites. In this paper we discuss methods for deriving population estimates for wintering wildfowl in Great Britain, by using WeBS data and evaluating past assessments of population sizes. A variety of different methods have been used to generate previous estimates and so it is important to distinguish whether a perceived change in population size is a real biological phenomenon or arises due to differences in the sampling method, the extrapolation method or the formula used to derive the estimate. The results of this analysis would suggest that previous population estimates have tended to underestimate the number of wintering wildfowl, and the resultant implications for conservation are discussed.

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1. Introduction

The Ramsar Convention on Wetlands of International Importance especially as Waterfowl Habitat, adopted in 1971, is the intergovernmental treaty that provides the framework for international cooperation for conservation and wise use of wetlands (Davis 1994). Contracting Parties are obliged to designate wetlands of international importance within their territory. The criteria for identifying wetlands of international importance were developed in 1974 and place particular emphasis on the importance of a site to waterfowl. Several criteria relate specifically to the numbers of waterfowl on a site. Those sites that regularly support 1% of the individuals in a population of one species or subspecies of waterfowl qualify as internationally important. The adoption of this 1% criterion has necessitated the generation of absolute measures of population size for waterfowl species and subspecies.

Generating an absolute measure of population size is not straightforward, especially for highly mobile, migratory species whose ranges span a number of political units. However, in northwest Europe waterfowl do tend to concentrate on discrete wetland sites during winter, thus offering the opportunity to survey a large proportion of the individuals of many species at one time. International population sizes are reviewed every three years (Rose & Stroud 1994, Rose & Scott 1997). In line with the international timetable, national population estimates for waterfowl wintering in Great Britain are scheduled for review every three years (Pollitt et al. 2000).

Great Britain is of outstanding importance for wintering waterfowl, over a million individuals being recorded in the peak winter months. In the UK, many Ramsar sites have been designated under the 1% criterion, which has also been used to identify wetland Special Protection Areas under the EU Birds Directive (79/409/EEC) (European Comission, 1979). Although Great Britain does not hold the total biogeographic population of most waterfowl species, sites which regularly hold 1% of the British population can be designated as nationally important and qualify for Sites of Special Scientific Interest (SSSI) status under the Wildlife and Countryside Act (Wildlife and Countryside Act 1981).

In this paper, we review past methods for calculating population estimates for wintering waterfowl in Great Britain and develop new methods for generating population estimates, which have been used to produce the most recent suite of population estimates for waterfowl in Great Britain (Kershaw & Cranswick 2003). In particular we look at the use of data from an extensive volunteer waterbird survey (WeBS) for generating population estimates.

2. Methods

Before it is possible to calculate population sizes it is necessary to define the term 'population'. This is relatively straightforward when the total biological population of a species is being considered, in which case the population size can be defined as the sum total of all the individuals in the population at a given time. A coordinated count of all locations where the population occurs would give the total population size at any one time.

However, when attempting to measure the number of individuals in a political unit (for example Great Britain), a coordinated count of all locations might represent only a fraction of the total numbers of individuals using the country during a winter season. There may be considerable turnover of individuals as birds move into and out of the political unit over the winter. Furthermore, there may be regional differences in the timing of arrival and departure of individuals. For these reasons national population estimates based on count data can represent only the peak number of individuals present in the region during the course of a winter and indicate only a minimum proportion of the species' biological population that uses the country.

Tab. 1. Estimates derived using the three methods used in the previous assessment of population size (see methods for details). The figure used to extrapolate the WeBS counts for each species is given in brackets in the last column. The overall population estimate is calculated as the mean of these figures for each species (see Tab. 3).

Species	Peak Sum	Mean of Estimated	Extrapolated Estimate
-	Monthly Means	Peak Count	(extrapolation figure)
Little Grebe Tachybaptus ruficollis	4623	4387	5360 (1.43)
Great Crested Grebe Podiceps cristatus	9970	9777	12494 (1.4)
Cormorant Phalacrocorax carbo	17410	16158	18311 (1.24)
Mute Swan Cygnus olor	20549	19031	28817 (1.65)
Bewick's Swan Cygnus columbianus	6405	6004	-
Whooper Swan Cygnus cygnus	4613	3525	-
European White-fronted Goose Anser	5499	5419	-
albifrons albifrons			
Greylag Goose (naturalised) Anser anser	19365	19494	-
Canada Goose Branta canadensis	49956	49931	65605 (1.55)
Dark-bellied Brent Goose Branta bernicla	90678	88857	-
bernicla			
Shelduck Tadorna tadorna	73312	72587	-
Wigeon Anas penelope	381853	372037	-
Gadwall Anas strepera	13857	12055	14280 (1.16)
Teal Anas crecca	145369	138736	161739 (1.21)
Mallard Anas platyrhynchos	184550	174197	259441 (1.71)
Pintail Anas acuta	23701	23512	-
Shoveler Anas clypeata	10868	10083	12437 (1.22)
Pochard Aythya ferina	47682	41869	49204 (1.18)
Tufted Duck Aythya fuligula	62903	59632	70405 (1.32)
Goldeneye Bucephala clangula	19123	18368	20282 (1.21)
Smew Mergellus albellus	323	304	-
Red-breasted Merganser Mergus serrator	4730	4745	5296 (1.18)
Goosander Mergus merganser	5203	4656	11329 (2.62)
Ruddy Duck Oxyura jamaicensis	3625	3588	-
Coot Fulica atra	124756	109539	140462 (1.3)

- no extrapolation

Data

Data on the numbers of waterfowl wintering on wetland sites in Great Britain come primarily from the Wetland Bird Survey (WeBS), a scheme to monitor non-breeding waterbirds in the U.K. The main aims of WeBS are to:

- 1. Obtain population sizes.
- 2. Identify important sites.
- Monitor trends in numbers and distribution.
- 4. Conduct research into population dynamics and ecology of waterfowl.

WeBS core counts are made at around 2000 wetland sites (3500 count units) of all habitats each year, coordinated counts at

each site being made mainly between September and March. WeBS incorporates long-term count data that date back to 1947 for waterfowl. Data from 1960/61 have been computerised and comprise more than 400 000 visits to 8800 count areas, over 180 million wildfowl having been counted. Approximately 3000 volunteer counters contribute annually to the scheme, making 25 000 visits to WeBS sites each year. WeBS is not suitable for monitoring all species of wildfowl (e.g. seaducks) and so this paper considers methods for generating population estimates only for those species that are reasonably well represented by WeBS (Tab. 1).

When attempting to use WeBS data to

derive population estimates, there are a number of factors that affect the accuracy and representativeness of the estimates and the methods that can be used. Firstly, WeBS is a volunteer scheme and the sites counted are largely those that the counters choose to cover. For example, it is not possible to dictate which sites are counted or to assign a random selection of sites to counters, and so the main sites holding the largest number of waterfowl tend to receive good coverage, whereas smaller wetlands (or those habitat types that hold lower numbers of birds) tend to be underrepresented or omitted.

There are also differences in coverage relating to habitat and region. In general, estuaries, reservoirs and gravel pits are well covered whereas linear waterways such as rivers and canals are poorly represented relative to their extent in Great Britain. There are also biases in WeBS coverage relating to geographical region, with remote areas and those of low population density having lower coverage. Furthermore, we do not know what proportion of the total wetland resource in Great Britain receives coverage, making it difficult to extrapolate results from WeBS sites to all wetlands. Other biases relate to the nature of the data collected by WeBS, in particular the presence of missing counts from individual sites throughout the data series and incomplete counts from complex sites (e.g. large estuaries that comprise a number of individual count units).

The major advantage of this type of extensive volunteer-based survey is that a large proportion of the waterfowl present in Great Britain at any one time are probably counted. The major disadvantage is that it cannot be treated as a random sample and extrapolated to the total resource to produce an estimate. Additionally, there is the problem of how to deal with missing and incomplete counts within the scheme's sites.

Waterfowl tend to be highly mobile in winter, moving to other sites in response to factors such as cold weather and changes in water levels and in food resources. Numbers on sites can also fluctuate substantially from year to year. Traditionally, methods for assessing population size have used a window spanning (typically) five years to dampen shortterm fluctuations in numbers. The previous assessment of population size for waterfowl in Great Britain covered the five-year period 1987/88 to 1991/92 and introduced a new methodology for calculating population sizes (Kirby 1995). The new methods recognised not only the need to account for missing values within the normal WeBS count but also that WeBS does not cover the whole of the wetland resource in Great Britain. For those species where WeBS achieves a reasonable level of coverage, three different methods were used and the mean of these was taken to produce a population estimate (Kirby 1995, Stone et al. 1997). Two of these methods used only WeBS count data, but attempted to take into account that on any count occasion, there will be counts missing from some of the WeBS sites. The third method recognised that WeBS sites do not represent all wetlands and so even if all WeBS counts were complete, a certain proportion of the population would still go uncounted.

Two methods were employed to account for the problem of missing values in the WeBS dataset (Kirby 1995):

1. Peak sum of monthly means. This method took the mean site count for

each month over the five-year period and then summed this value across all sites. The population estimate selected is then that for the month with the highest value.

2. Mean of estimated peak counts. This method involved selecting the month of peak abundance for each species (derived from index values; see Kirby [1995]). If the count for a site in the peak month was missing, then the count from the next available month in that year was selected, or if none of the alternative counts was available, then a count from the preceding year was selected. The population estimate was then calculated by summing the counts across all sites for each year and then taking the five-year mean.

To estimate the number of birds occurring outside WeBS sites, the previous analysis of population sizes used data from three regional intensive surveys, of northwest England, northeast England and southwest London (Quinn & Kirby 1995, WWT unpublished data). In these surveys an attempt was made to count every waterbody in the region concerned, enabling a calculation to be made of the number of birds on WeBS sites in the region, relative to the total regional population. The mean proportion of birds on WeBS sites relative to the regional total from these three intensive surveys was then used to correct the WeBS five year peak mean for each species nationally, to derive a total population estimate for Great Britain. The assumption was that the blitz survey regions were representative of all regions in terms of the relationship between birds on WeBS sites and total bird numbers

The mean of the three different meth-

ods was used to generate a single population estimate for each species (Kirby 1995). These same methods were used to generate new population estimates for waterfowl wintering in Great Britain. The most recent data available were from the period September 1994 to March 1999 and included data from only the WeBS core winter months September through to March in each year.

However, there were several problems with the methods used in the final population assessment. The two methods for accounting for missing counts will tend to underestimate the true number of birds. Using the Peak sum of monthly means method, it is possible for a site to have no counts at all in a particular month in each of the five years and so the site will not feature in the population estimate. Furthermore, a site's mean count for a particular month could be based on just one or two counts, which could result in an under- or overestimate of the average fiveyear population size, especially if numbers have changed substantially over the fiveyear period. Moreover, this method assumes that the seasonal phenology is similar across years, but if the peak count occurs in different months across the fiveyear period, then averaging the monthly count across years, summing across sites and selecting the highest value will produce a figure that is lower than the method of taking the five-year peak mean value. Using the Mean of estimated peak counts method, there remains a number of sites where no counts are available to impute, either from another month in the same winter or from the previous winter (in other words some counts are still missing). Furthermore, even if a count can be substituted using a count from another month

or year, this count will tend to be lower (because it is not from the month of peak abundance).

Neither of the above methods attempts to compensate for missing counts within complex sites: ie the situation where a site count is incomplete (site counts were treated as complete even if some units within them remained uncounted). Both methods will therefore always produce an underestimate of the number of birds on WeBS sites.

Extrapolation based on enhanced coverage on its own is likely to give the best indication of national population size. However, the intensive surveys were restricted in terms of geographical region or in the case of the southwest London survey, habitat type covered. The northwest England survey was carried out during a period of cold weather when birds were likely to be more concentrated (on to the bigger, and in many cases, WeBS sites). Additionally, in calculating the relationship between birds on WeBS sites and total birds, the extrapolation figure was derived by comparing the surveyed birds that were on WeBS sites with the total counted. However, this assumes complete coverage of the WeBS sites, whereas on a typical WeBS count occasion some of the WeBS sites will go uncounted. Therefore the extrapolation should only be applied to the WeBS count, after accounting for missing values.

The population estimates generated by the two methods that accounted for missing values in WeBS counts give a population estimate only for birds on WeBS sites. For some species like Pintail *Anas acuta* this will be close to the national population size, but for other species like Mallard *A. platyrhynchos* the figure will be much lower. The extrapolated counts based on enhanced coverage surveys give an indication of the national population estimate, across all sites, not just WeBS sites. For this reason it is not valid to calculate a mean across all three methods. A mean value based just on WeBS counts is valid to produce an estimate of the number of birds on WeBS sites (although it might be better to select the maximum value since we know that the methods are more likely to underestimate numbers), but this should not be treated as comparable with the extrapolation method based on intensive coverage which produces a national estimate of population size across all wetland sites.

Despite these methodological problems, WeBS data remain the best available data on the numbers and distribution of the majority of waterfowl species wintering in Great Britain. However, there is a need to account for missing counts within the WeBS database in a more comprehensive manner than in the previous population assessment. It is necessary also to be able to extrapolate from WeBS sites to the total wetlands resource in order to generate a national population estimate, but WeBS estimates should not be combined with the extrapolated estimates. For this assessment of British population sizes, new methods were used which aim to address the above deficiencies.

In an attempt to account for missing counts in the data, an indexing technique was used to impute values where a count was missing using a simple multiplicative model having site, year and month factors (Underhill 1989, Underhill & Prŷs-Jones 1994). Indexing was also used to compensate for the effect of incomplete site counts when some sectors of complex Tab. 2. Comparison of the % of missing counts imputed by the mean of estimated peak count and the index model methods. The "% missing after estimation" gives the % of the potential, complete dataset that remains missing after the addition of available estimated counts by the mean of estimated peak counts method. The "% of total count imputed" gives the % of the total number of birds that consists of estimated counts. The "% of actual counts imputed" gives the % of the available counts (correct plus imputed) that were estimated counts. Under the index model method, the first column is the total % of counts that were missing or incomplete 94/95 - 98/99 and the second column gives the % of birds that were imputed.

Species	Mean of Estimated Peak Method			Imputing using Index Model	
	% missing	% of total	% of actual	% counts	0/ total hird
	after	count	counts	missing or	70 total bild
	estimation	imputed	imputed	incomplete	numbers imputed
Little Grebe	14.7	20.3	35.2	33.9	28.1
Great Crested Grebe	13.2	17.4	32.1	32	21.2
Cormorant	15.0	11.6	20.9	34.5	25.2
Mute Swan	17.5	25.8	37.6	37.6	26.6
Bewick's Swan	6.48	0.900	9.77	24.4	10.9
Whooper Swan	13.2	14.1	16.5	32.6	24.2
European White-fronted Goose	5.80	0.148	6.88	21.4	4.5
Greylag Goose naturalised	11.2	24.5	32.0	29.7	25.8
Canada Goose	15.6	22.6	34.8	33.9	28
Dark-bellied Brent Goose	3.67	0.518	5.78	18.2	10.7
Shelduck	11.7	1.17	12.8	29.4	15.3
Wigeon	13.4	2.83	15.9	32.7	15.8
Gadwall	10.7	6.52	13.8	27.6	20.7
Teal	15.1	5.32	19.6	34.9	23
Mallard	20.7	14.2	24.0	45	30.6
Pintail	8.07	2.48	11.2	24	13.2
Shoveler	10.0	5.85	16.2	27.1	21.3
Pochard	13.8	10.3	18.9	33.3	22.6
Tufted Duck	16.9	11.8	20.6	36.9	26.3
Goldeneye	14.8	9.31	18.0	34.8	22.8
Smew	4.90	3.68	9.05	21	20.3
Red-breasted Merganser	14.4	5.83	16.8	34.5	23.6
Goosander	13.3	12.3	15.1	31.4	32.8
Ruddy Duck	8.07	9.40	13.3	24.5	15.5
Coot	17.1	13.0	22.8	37.1	25.4

sites went uncounted on a particular occasion. Here, a count was flagged as potentially incomplete if less than 75% of the total sectors and less than 75% of the maximum bird numbers for a particular month had been recorded. The imputed value from the indexing model, where this was greater than the incomplete count recorded, was then substituted for the actual count. Otherwise, the actual count was retained. The five-year peak mean count for each species was then calculated using the real count where it existed and imputed values where counts were missing or incomplete. This figure gives an estimate of the total number of individuals on WeBS sites.

In order to generate an estimate of the national population size, it is necessary to extrapolate the WeBS total according to the proportion of the population that WeBS covers. This is largely a matter of conjecture since it is not known what proportion of populations, or indeed wetland sites, that WeBS covers. The best indication of the proportion of birds on WeBS sites comes from regional intensive surveys carried out in the early 1990s.

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Tab. 3. Population estimates derived using alternative methods. The first two columns give the minimum and maximum population estimates on WeBS sites for each population. The minimum population estimates represent the highest value out of 1) the peak sum of monthly means, 2) the mean of the estimated peak count and 3) the five year peak mean. The maximum estimated population represents the five year peak mean, calculated with all missing counts imputed according to an index model. The third column gives the population estimates that would be derived using the previous methods of (Kirby 1995). The final column is the estimate derived using the new methods. All values rounded to the nearest 1000 for estimates >100,000, the nearest 100 for estimates <1001-100,000, the nearest 10 for estimates <1001-10,000 and the nearest one for estimates <1001.

Spacing	Minimum	Maximum	Population using	Population using
Species	WeBS	WeBS	previous methods	new methods
Little Grebe	4,620	5,430	4,790	7,770
Great Crested Grebe	9,970	11,400	10,700	15,900
Cormorant	17,400	18,600	17,300	23,000
Mute Swan	20,500	22,700	22,800	37,500
Bewick's Swan	7,180	8,070	6,210	8,070
Whooper Swan	4,610	4,850	4,070	5,720 ^a
European White-fronted Goose	5,600	5,790	5,460	5,790
Greylag Goose (naturalised)	19,500	22,900	19,400	28,500 ^a
Canada Goose	50,000	62,000	55,200	96,100
Dark-bellied Brent Goose	95,900	98,100	89,800	98,100
Shelduck	73,300	78,200	73,000	78,200
Wigeon	382,000	406,000	377,000	406,000
Gadwall	13,900	14,700	13,400	17,100
Teal	145,000	159,000	149,000	192,000
Mallard	185,000	206,000	206,000	352,000
Pintail	25,600	27,900	23,600	27,900
Shoveler	10,900	12,100	11,100	14,800
Pochard	47,700	50,500	46,300	59,500
Tufted Duck	62,900	68,300	64,300	90,100
Goldeneye	19,100	20,600	19,300	24,900
Smew	323	370	314	370
Red-breasted Merganser	4,750	5,520	4,920	6,510 ^b
Goosander	5,200	6,140	7,060	16,100
Ruddy Duck	3,630	4,110	3,610	4,110
Coot	125,000	133,000	125,000	173,000

^a New population estimate calculated using an extrapolation figure derived from additional census data (see Kershaw & Cranswick 2003)

^b This estimate derived from WeBS data was not the final adopted population estimate for Red-breasted Merganser (see Kershaw & Cranswick 2003)

Unfortunately there have been no intensive surveys since, so in the current assessment of population size the extrapolation figures from in the previous assessment (Tab. 1) were used. The five-year peak mean, calculated with all the missing and incomplete values imputed using an index model, was multiplied by the extrapolation figure to generate an estimate of the national population size for each species.

3. Results

During the five-year period 1994/95 to 1998/99, a total of 2773 wetland sites (comprising 4328 individual count units) was counted during the winter period September through to March. More than 30% of these sites had five or fewer missing counts out of the potential thirty-five for the period, although 15% of sites had more than thirty missing counts. However, the sites with the most complete coverage were also the numerically most important for waterbirds, holding, on average, almost five times the number of birds compared to sites with more than thirty counts missing. This means that the percentage of the count missing for most species was in fact much lower than the overall coverage achieved would suggest.

At a species level, if only sites where a species was present between 1994/95 and 1998/99 are included, between 18 and 45% of site level counts were missing or incomplete (Tab. 2). Those species that have restricted distributions (and so occur on relatively few sites), such as Bewick's Swan Cygnus columbianus and Dark-bellied Brent Goose Branta bernicla berni*cla*, and those that show highly aggregated distributions, such as Pintail, tended to have the lowest percentage of counts missing or incomplete. In contrast, widely distributed, dispersed species like Mallard and Mute Swan Cygnus olor have a higher percentage of counts missing or incomplete because they are more likely to occur on sites that are poorly covered.

The population estimates derived using the three methods used in the previous assessment are given in Tab. 1 and the mean population estimate is given in Tab. 3. For the majority of species the Mean of the estimated peak count produced an estimate that was on average 6% lower compared to the Peak sum of monthly means. Tab. 2 shows the percentage of potential counts that consisted of estimated values using the Mean of estimated peak counts method to impute missing values, and the percentage of counts that remained missing after the estimation procedure had been applied. Between 4 and 21% of counts remained missing after the addition of available counts from months outside the peak month, depending on the species. The percentage of the total count that consisted of imputed values was always substantially lower than the percentage of counts that these imputed values represented. For example, 16% of Wigeon Anas penelope counts were imputed, but these only represented 3% of the birds. Although the missing counts came disproportionately from the less important sites (so it would be expected that the counts would be of lower magnitude), coupled with the missing counts remaining after imputing, the Mean of estimated peak counts method of accounting for missing counts will tend to produce an underestimate of the total number of birds.

Since the methods used in the previous assessment of population sizes to account for missing counts were considered likely to produce underestimates, an alternative method was used to impute missing values. An index model was used to produce estimated counts based on a 'site, year and month' factor and these estimated counts were used to fill the missing values. Tab. 2 shows the percentage of counts missing and incomplete and the percentage of the total bird numbers that represent imputed values for each species for the whole period 1994/95 to 1998/99. Most species had between 20 and 35% of counts missing or incomplete, but the percentage of the total count that this imputed element represented varied by more, partly dependent on factors such as how dispersed or widespread the species was. For example, 33% of Wigeon counts were missing or incomplete, but only 16% of the count was imputed, because the species tends to be aggregated on well-

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covered sites, so that most of the imputed counts were of small numbers on the less important, less well-covered sites. In contrast, 34% of Little Grebe *Tachybaptus ruficollis* counts and 32% of Goosander *Mergus merganser* counts were missing or incomplete and imputed values represented 28% and 33% of the total count respectively. Both these species are more dispersed than Wigeon.

The effect that the imputed counts had on the population estimate for WeBS sites varied according to the species. Tab. 3 compares the maximum value that could have been derived using the previous methods for assessing population size on WeBS sites (ie the maximum value from the Peak sum of monthly means, the Mean of the estimated peak count and the fiveyear peak mean) with the five-year peak mean calculated when all the missing and incomplete counts are imputed using an index model (Columns 1 and 2 in Tab. 3. respectively). The difference between these two values varied from 2.3% (Darkbellied Brent Goose) to 24% (Canada Goose Branta canadensis). The largest differences were for dispersed species where the cumulative effect of missing counts over a large number of sites (including the smaller less well-covered sites and poorly covered habitats such as rivers) adds up to a significant number of birds missed. Such species include Goosander (18% difference between lower and upper estimates), Little Grebe (18%) and naturalised Greylag Goose Anser anser (17%). The smallest differences were for species which tend to be concentrated on the larger, well-covered sites, for example, European White-fronted Goose Anser albifrons (3.4%), Whooper Swan Cygnus cygnus (5.2%) and Wigeon (6.2%).

The estimates in columns one and two of Tab. 3 indicate only the estimated peak number of birds on WeBS sites. To generate a national population total requires extrapolation from WeBS sites to all sites in Great Britain. The figures used to extrapolate WeBS counts to produce a national population estimate were based on data from three regional blitz surveys carried out in the early 1990s, taken from Kirby (1995) (see Tab. 1). The figures represent the proportional increase (%) in the numbers of birds counted during the blitz survey compared to the number of birds that were present on the WeBS sites within the survey region. The mean value from the three intensive surveys was used to extrapolate the five-year peak mean WeBS count (with all missing values imputed [column 2 of Tab. 3]) (Tab. 3). For naturalised Greylag Goose and Whooper Swan, extrapolation figures were calculated from national surveys that had been carried out for the species (see Kershaw & Cranswick 2003 for details). The extrapolated population estimates represent the estimated peak number of birds wintering in Great Britain and are between 6% and 128% higher than the estimates calculated using the previous methodology (Tab. 3).

4. Discussion

One of the earliest assessments of the number of waterfowl wintering in Great Britain used average January waterfowl census data over the period 1967-73 as a measure of population size (Atkinson-Willes 1976). This method took no account of missing counts within the time period on sites within the census or of sites that were not included in the census at all. In the mid-1980s, a method was used to account for both missing counts in census sites and for sites not covered at all (Owen et al. 1986). To account for missing counts in the census sites, the five-year peak mean for a species was compared to the peak monthly mean summed across all sites. Using this method Owen et al. (1986) calculated that annually WeBS would cover, for example, 70% of the Pintail on WeBS sites, 76% of Wigeon, 89% of Gadwall Anas strepera, 73% of Mallard, 75% of Pochard Aythya ferina and 80% of Tufted Duck Aythya fuligula. These percentages enabled the peak annual count for each species to be corrected to compensate for sites not counted. This total was then corrected for sites completely missed in the five-year period (Owen et al. 1986). This correction was based on a 'best guess' such that, for example, 10% of Tufted Duck and Pochard and 50+% Mallard were estimated to occur on non-WeBS sites.

The previous assessment of wintering waterfowl population sizes in Great Britain (1987-1991) applied a new methodology to the problem of generating population estimates from an extensive, volunteer-based survey (Kirby 1995). However as the current analysis illustrates, these methods are likely to underestimate substantially the peak numbers of waterfowl occurring in Great Britain during the winter. In particular, insufficient accounting for missing values and calculating a mean population size using both the WeBS and national estimates will result in an underestimate of true numbers.

Accounting for missing counts using an index model and using the extrapolated totals on their own as an indication of national population totals results in some substantial increases in population size. The new methods result in population estimates that are between 6% (European Goose) White-fronted and 128% (Goosander) higher than using the previous methods. The largest increases are for those species that are widely dispersed across sites, or where a significant proportion of the individuals are on habitats that are poorly covered by WeBS. For example, compare Mallard (71%), Mute Swan (64%) and Little Grebe (62%), with more aggregated species like Wigeon (8%), Shelduck (7%) and Pintail (18%).

This result has implications in terms of sites that qualify as important. Applying the new estimates of national population size to generate national 1% levels means that almost all species would have fewer sites qualifying as nationally important. The most marked change occurs for Gadwall where the number of nationally important sites would fall from 82 sites to 27 compared to a fall from 37 sites to 25 for Wigeon. However, Mallard would show an increase from zero sites to one (based on 1998/99 data in Pollitt *et al.* 2000).

Despite the large differences between the methods used for the last assessment and the most recent, applying the same methodology as Owen *et al.* (1986) gives comparable results to the new methods presented here. For example, Pochard 59 300 (61 775 Owen), Mallard 352 000 (415 671, although Owen *et al.* used 500 000). The population sizes derived using the figures of Owen *et al.* (1986) in fact tend to be slightly higher than those presented in this paper. This might be expected, however, since WeBS coverage has improved since the late 1970s, both in terms of the coverage within WeBS sites and coverage of wetland resource in Great Britain, and so the extrapolation figures used by Owen *et al.* (1986) are now probably slightly high.

All these estimates are considerably lower than the total numbers of each species using Great Britain during each winter season. For Teal Anas crecca, the estimated hunting kill was 180 000 per annum 1979-81 (although Bertelsen & Simonsen [1989] quote a kill of 288 000 Teal for Great Britain and Northern Ireland annually) compared to a peak winter count in the region of 100 000 at the time of the bag estimate (Owen et al. 1986). Similarly, the estimated annual kill for Mallard was 600 000 compared to a population estimate of 500 000 and a peak winter count of 190 000 (Owen et al. 1986).

The need for an absolute measure of population size arises largely as a result of the 1% criterion (Atkinson-Willes 1976). Under this criterion sites that hold 1% of a population qualify as internationally important under the Ramsar Convention, and more recently the 1% criterion has been used for designating SPAs (Special Protected Area) under the EU Birds Directive. At a national level, sites in Great Britain that support 1% of the national population of a species can be designated as Sites of Special Scientific Interest. Although the 1% criterion has no biological basis (for example, sites with 1% of a population are not known to be viable compared with sites holding less than 1%) application of this criterion requires an estimate of absolute population size. This allows a major criticism of the 1% criterion, that it is dependent on an estimate of absolute population size,

something that is virtually impossible to measure, even in cases where there are very good survey data.

Despite the problems associated with generating population estimates, it is still valuable to be able to extrapolate the numbers on WeBS sites to numbers at a national level. In order to extrapolate more accurately, it is essential that new intensive surveys are carried out in Great Britain to determine the relationship between birds on WeBS sites versus the total wetland resource. Since WeBS sites tend to represent the larger more important wetlands, it is possible that if populations increase, numbers on WeBS sites may reach carrying capacity and birds will move on to less important sites which may not be counted. Conversely, management of the well-monitored sites for waterfowl populations may result in numbers faring well on these sites, masking detrimental changes in population status on smaller non-WeBS sites or the wider countryside. A major criticism of the above-mentioned methods is their inability to calculate the precision and accuracy for the population estimates. We know that the estimates are more accurate for highly clumped species like Wigeon, which occur on the larger, better-covered sites. However, we cannot quantify the levels of precision or accuracy of the estimates. One approach might be to focus counters' effort on achieving complete coverage of fewer sites so as to minimise the effect of missing counts in the data series. There is considerable scope for more work to determine the best way of using data collected from this extensive volunteer-based survey to calculate population sizes for waterfowl in Great Britain.

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