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Size matters: the value of small populations for wintering waterbirds

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Abstract

Protecting systematically selected areas of land is a major step towards biodiversity conservation worldwide. Indeed, the identification and designation of protected areas more often than not forms a core component of both national and international conservation policies. In this paper we provide an overview of those Special Protection Areas and Ramsar Sites that have been classified in Great Britain as of 1998/99 for a selection of wintering waterbird species, using bird count data from the Wetland Bird Survey. The performance of this network of sites is remarkable, particularly in comparison with published analyses of networks elsewhere in the world. Nevertheless, the current site-based approach, whilst having the great benefit of simplicity, is deliberately biased towards aggregating species at the expense of the more dispersed distribution species. To ensure that the network continues successfully to protect nationally and internationally important waterbird populations, efforts now need to concentrate on the derivation of species-specific representation targets and, in particular, the ways in which these can be incorporated into the site selection process. Although these analyses concern the performance of protected areas for waterbirds in Great Britain, the results have wide-ranging importance for conservation planning in general and the design of protected area networks.

INTRODUCTION

The designation and management of priority conservation areas has become a central theme for many national and indeed international conservation strategies. To date, more than a tenth of the world's land surface is within some form of protected area (Hocklings, Stolton & Dudley, 2000) and the World Conservation Monitoring Centre (WCMC) database holds records for in excess of 44 000 official protected areas (as defined by the IUCN in 1994) covering 14 million km² (World Conservation Monitoring Centre, 2002). However, despite this excellent achievement, information is lacking as to the current status of many of these reservations (Hocklings *et al.*, 2000). Successful conservation of biodiversity requires the evaluation of existing protected areas and the incorporation of findings into an adaptive management framework.

The coastal and inland wetlands of the United Kingdom are of outstanding international importance for their wintering waterbird populations, which number more than three million individuals (Pollitt *et al.*, 2000). Many of these are arctic and north temperate nesting species, making their conservation a matter of both national and international concern. The designation of Ramsar sites under the Ramsar Convention on Wetlands of International

Importance (Ramsar Convention Bureau, 2002) and the classification of Special Protection Areas (SPAs) under the Directive on the Conservation of Wild Birds (the 'Birds Directive': 79/409/EEC) are important vehicles for the conservation of sites necessary for waterbird conservation in the UK. Ramsar sites are identified on the basis of internationally agreed criteria (Ramsar Convention Bureau, 1980, 1990, 1996, 1999). Several of these relate specifically to waterbirds, such that sites that regularly hold at least 1% of the individuals in a biogeographical population of one species or subspecies of waterbird (Criterion 5 as defined by the Conference of Parties to the Ramsar Convention: Ramsar Convention Bureau, 1980), or that regularly hold a total of 20 000 or more waterbirds qualify as Ramsar Sites (Criterion 6: Ramsar Convention Bureau, 1999). By contrast, the Birds Directive does not state specifically how SPAs are to be selected, rather the exact mechanisms depend on the Member States (Stroud *et al.*, 2001).

In the UK, sites qualify for SPA status under guidelines published by the Joint Nature Conservation Committee (JNCC, 1999). These follow a two-stage process and include a number of possible grounds for classification, notably Stage 1.1 (relating to species listed on Annex I of the Birds Directive), Stage 1.2 (regularly occurring migratory species), Stage 1.3 ($\geq 20\,000$ waterbird assemblage) or Stage 1.4 (an adequate suite of sites holding an Annex I or regularly occurring

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migratory species). For the Annex I species, Stage 1.1 guidelines state that an area must be used regularly by 1% or more of the Great Britain or all-Ireland population of these species in any one season. Stage 1.2 requires that an area regularly support at least 1% of the individuals in the biogeographical population of one species or subspecies of migratory waterbird. To qualify under the waterbird assemblage guideline (Stage 1.3) a site must regularly support $\geq 20\,000$ individuals. Finally, Stage 1.4 selects for those areas where the application of Stage 1.1, 1.2 and 1.3 guidelines for a species does not identify an adequate suite of sites for the conservation of that species. Within these assemblages, those species that regularly occur in nationally important numbers (1% or more of the national total present, or 50 birds where the national 1% threshold is < 50 individuals), or which number ≥ 2000 individuals, are listed as the main component species of the assemblage. Under national legislation, those sites supporting nationally important numbers of birds qualify as Sites of Special Scientific Interest (SSSIs). Finally (on those sites selected as assemblages under guideline 1.3), those species that regularly occur in nationally important numbers within sites (1% or more of the national population size present, or 50 birds where the national 1% threshold is < 50 individuals), or which number 2000 or more individuals within an assemblage, are listed as the main component species of the assemblage. This Listed Site suite, where each component site should be managed so as to maintain numbers of that species, should fulfil the relevant site-protection requirements for that particular species or population (Stroud *et al.*, 2001). The Listed Sites for each species, therefore, consists of those sites that have been selected as 'most favourable' for the species concerned in the context of the Birds Directive. Under national legislation, those sites supporting nationally important numbers of birds qualify as Sites of Special Scientific Interest (SSSIs).

As of March 2003 there were 144 Ramsar sites in the UK, the first of which was designated in 1976, and 239 SPAs (both wetland and non-wetland), many having been designated very recently, with 96 of the SPAs also being designated as Ramsar sites (JNCC, 2001). The first SPA was classified in 1982 and the first wetland SPA in 1985.

An attractive feature of these guidelines is their simplicity, which enables them to be applied widely. However, they may not take sufficient account of many features of wetland sites that may contribute to their importance for the long-term maintenance of waterbird populations, nor do they necessarily account for the seasonal and long-term dynamics of species numbers (Moser, 1987; Kirby, 1995; Kershaw & Cranswick, 2003). Moreover, the emphasis is placed on a site-by-site approach rather than one that views the conservation network in its entirety. The focus tends towards single species numbers and, as a result, incorporation of maximum biodiversity (although not a specific requirement of the Birds Directive) is incidental rather than an explicit selection objective (Lee, Woddy & Thompson, 2001).

In this paper, we examine the numbers of individuals of selected waterbird species that are found in the overall

Ramsar and wetland SPA network in Great Britain (as of 1998/99) and on the suites of SPAs that have been classified for individual species (Listed Sites). The current effectiveness of these protected area networks is evaluated in relation to the patterns of distribution shown by different species, with the emphasis on the numbers of birds of each of the species contained within the national network rather than looking at the explicit selection criteria detailed by the Birds Directive and the Ramsar Convention, or the extent to which these have been successfully implemented. The findings are of interest more widely than the bounds of the European Union, since they bear on the criteria for the selection of priority areas for waterbirds elsewhere.

METHODS

Analyses were conducted using data from the Wetland Bird Survey (WeBS). This scheme, a joint venture by the British Trust for Ornithology (BTO), Wildfowl and Wetlands Trust (WWT), Royal Society for the Protection of Birds (RSPB) and the Joint Nature Conservation Committee (JNCC), aims to monitor the populations of non-breeding waterbirds in the UK. Details of WeBS are given by Kirby (1995), Cranswick *et al.* (1997) and Pollitt *et al.* (2003). In brief, the survey relies on volunteers visiting sites on pre-selected dates in each month, with an emphasis on the winter months of September to March, and recording the numbers of all waterbird species present. More than 2000 wetlands are included in the scheme annually and over 8000 have been counted at least once since 1960 (Cranswick *et al.*, 1997).

Twenty-one species of waterbird considered to be well represented by the WeBS and for which this is the principal source of data used for the selection of SPA and Ramsar sites in the UK, were analysed separately (Table 1). We included data for the years 1960/61 (earliest computerised waterbird data) to 1998/99 (latest available data in September 2001) inclusive, for little grebe (*Tachybaptus ruficollis*: data only available from 1985/86), great crested grebe (*Podiceps cristatus*: data only available from 1982/83), cormorant (*Phalacrocorax carbo*: data only available from 1986/87), Bewick's swan (*Cygnus columbianus bewickii*), whooper swan (*Cygnus cygnus*), European white-fronted goose (*Anser albifrons albifrons*), dark-bellied brent goose (*Branta bernicla bernicla*), shelduck (*Tadorna tadorna*), wigeon (*Anas penelope*), gadwall (*Anas strepera*), teal (*Anas crecca*), mallard (*Anas platyrhynchos*), pintail (*Anas acuta*), shoveler (*Anas clypeata*), pochard (*Aythya ferina*), tufted duck (*Aythya fuligula*), goldeneye (*Bucephala clangula*), smew (*Mergellus albellus*), red-breasted merganser (*Mergus serrator*), goosander (*Mergus merganser*) and coot (*Fulica atra* data only available from 1982/83). Given that WeBS counts in Northern Ireland did not begin until 1985 these analyses use British data only (excluding the Channel Islands and the Isle of Man).

To qualify as an SPA under Stage 1.3 of the JNCC site-selection guidelines requires a site to support $\geq 20\,000$ waterbirds (all WeBS species, excluding waders)

Table 1. The current number of Listed Sites (as of 1998/99), the numbers of Listed Sites classified using selection criteria 1.1, 1.2, 1.3 and 1.4, the biogeographical and national population estimates and the Protected Site and Listed Site totals for 21 species of waterbird

Species		Current number of Listed Sites	Numbers of Listed Sites classified using criteria Stages:				Biogeographical population	National population	Protected Site total	Listed Site total
			1.1	1.2	1.3	1.4				
Little grebe	<i>Tachybaptus ruficollis</i>	7			7	†	7700	933	548	
Great crested grebe	<i>Podiceps cristatus</i>	10			10	150 000	15 900	2238	1193	
Cormorant	<i>Phalacrocorax carbo</i>	23			23	120 000	23 000	4492	2866	
Bewick's swan	<i>Cygnus columbianus bewickii</i>	12	12			17 000	8070	5870	5449	
Whooper swan	<i>Cygnus cygnus</i>	12	12			16 000	5720	2419	2195	
European white- fronted goose	<i>Anser albifrons albifrons</i>	7			6	1	600 000	5790	4988	4006
Dark-bellied brent goose	<i>Branta bernicla bernicla</i>	18		6	12		300 000	98 100	83 010	73 719
Shelduck	<i>Tadorna tadorna</i>	22		9	13		300 000	78 200	53 180	49 613
Wigeon	<i>Anas penelope</i>	34		5	27	2	1 250 000	40 600	260 577	190 608
Gadwall	<i>Anas strepera</i>	12		5	7		30 000	17 100	3082	2237
Teal	<i>Anas crecca</i>	22		8	14		400 000	192 000	68 797	53 128
Mallard	<i>Anas platyrhynchos</i>	7			7		2 000 000	1 352 000	44 946	16 065
Pintail	<i>Anas acuta</i>	21		16	5		60 000	27 900	18 780	17 586
Shoveler	<i>Anas clypeata</i>	17		7	10		40 000	14 800	3705	2686
Pochard	<i>Aythya ferina</i>	8		2	6		350 000	59 500	13 190	8889
Tufted duck	<i>Aythya fuligula</i>	4		1	3		1 000 000	90 100	8139	5617
Goldeneye	<i>Bucephala clangula</i>	6			6		300 000	24 900	3604	1299
Smew	<i>Mergellus albellus</i>	0					25 000	370	52	‡
Red-breasted merganser	<i>Mergus serrator</i>	6			6		125 000	3840	1603	614
Goosander	<i>Mergus merganser</i>	0					200 000	16 100	595	‡
Coot	<i>Fulica atra</i>	3			3		1 500 000	173 000	20 283	12 791

The Protected Site and Listed Site totals were calculated using 1994/95–1998/99 peak mean counts for (1) all SPA or Ramsar sites (Protected Site total) and (2) the suite of sites listed as nationally important (Listed Site total) for each species individually.

† No biogeographical population estimate available.

‡ No Listed Sites.

irrespective of the actual species present (i.e. the total across all species present and not simply those listed as targets by the Ramsar Convention and/or the Birds Directive). Therefore, for each wetland site, in addition to the 21 species separately, totals were taken across all WeBS species.

For each of the 21 species and for all WeBS species (excluding waders) together (see Pollitt *et al.*, 2003 for details), following the procedure adopted by the WeBS (Pollitt *et al.*, 2003), the total numbers of birds on WeBS sites in Great Britain (henceforth referred to as the WeBS total) for a given month was taken to be the sum of the individual counts for that month across all WeBS sites. The peak monthly count in each year was then taken to represent the WeBS total for each species. Individual site counts were then taken as the maximum number of individuals recorded on each site between September and March for each year 1960/61–1998/99. For all analyses, unless otherwise stated, the identity and numbers of WeBS sites ($n = 1962$) and Protected Sites ($n = 138$) remained constant in all years for each species analysed. These WeBS sites are those for which at least 60% of the monthly and annual abundance records were available. Missing values were imputed using linear interpolation (SPSS version 11), based on the method adopted by WeBS

for the calculation of annual population indices for Great Britain (Kershaw & Cranswick, 2003; Pollitt *et al.*, 2003).

Aside from sources of error introduced through the use of volunteers, there are a number of systematic biases to WeBS that should be borne in mind (described in detail in Pollitt *et al.*, 2003). These relate, in particular, to the incomplete WeBS coverage of all wetland areas (missing counts and the fact that not all wetland sites are covered) and the distribution patterns of individual species. First, the coverage of widely dispersed species (e.g. little grebe, cormorant, mute swan, mallard, teal and goosander) is likely to be under-represented given the concentration of efforts towards estuarine habitats and large, standing waters. Second, numbers of cryptic or secretive species (e.g. little grebe and teal) are likely to be overlooked given the problems associated with their detection. Third, numbers of passage species are also likely to be underestimated given the high turnover of individuals in a short period of time. By contrast, counts of the numbers of particularly mobile flocks are likely to be over-estimates, particularly where individuals move between sites, which may result in the same individuals being counted more than once for a given month. In consequence, in addition to the calculation of WeBS totals, estimates of the current size of the national (Great Britain) population for each

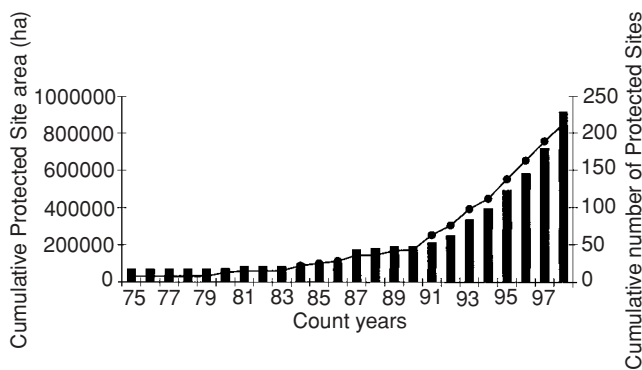


Fig. 1. The cumulative number of Special Protected Areas (SPA) and Ramsar sites (—●—) and their total area (bars) in each count year (1984/85–1998/99: JNCC, 2001). The first Ramsar site was designated in 1976 and the first SPA was classified in 1975/76.

of the 21 species were taken from Kershaw & Cranswick (2003). These published population estimates were used in an attempt to reduce the problems of incomplete WeBS coverage, both spatially and temporally.

Annual totals for all sites designated as Ramsar sites or classified as SPAs (up to and including those classified in 1998/99), taken as the sum of the individual site counts, were calculated for each count year from 1960/61 to 1998/99. These are henceforth referred to as Protected Site totals.

Finally, the peak number of birds on the Listed Sites for each species in each year (1960/61 to 1998/99) was also calculated from the sum of the individual annual counts for all sites listed as nationally important for a species, and is referred to as the Listed Site total. This will generally be smaller than, although it may equal, the Protected Site total. Since the number of Protected Sites has increased over time (Fig. 1), the Protected Site and Listed Site totals were calculated for each year using data from only those sites that were formally classified as SPAs or designated as Ramsar sites in that year. Table 1 lists the number of SPA/Ramsar sites that have been classified/designated in Great Britain for each species using each of the different selection criteria as of 1998/99 (JNCC, 2001). The Protected Site and Listed Site totals therefore reflect the peak numbers of individuals using sites officially classified/designated as SPAs and Ramsar sites in Great Britain in each year. It should be borne in mind that the protected site network in Great Britain is constantly evolving and will now include additional sites, but given that data were not available these have not been included here.

Estimates of the current size of the biogeographical populations of each species were obtained from Rose & Scott (1997), the biogeographical population being defined as a species' population inhabiting a defined area or areas that freely interbreeds but tends not to exchange individuals with other populations (Mayr, 1970). For example, for white-fronted goose two biogeographical populations are described: Greenland white-fronted goose (*Anser albifrons flavirostris*) and European white-fronted goose (*Anser albifrons albifrons*).

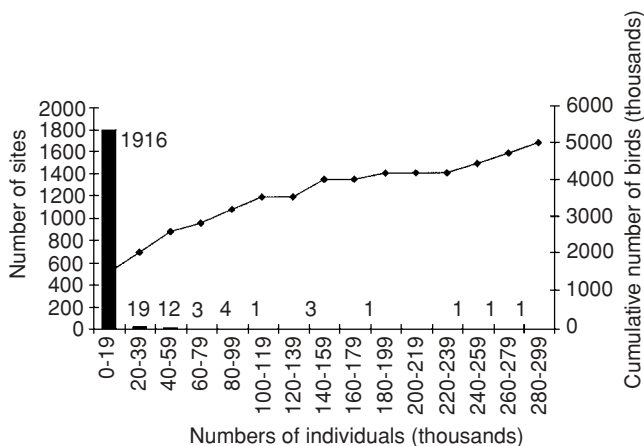


Fig. 2. The performance of the Special Protected Areas (SPA) and Ramsar site network in terms of the number of Wetland Bird Survey (WeBS) sites (bars) and the cumulative number of birds present (—●—) (in thousands) for equally sized classes (numbers in thousands) in 1998/99 across all waterbird and wader species included in the WeBS scheme. Numbers indicate the numbers of sites in each category.

For conservation planning it is necessary to consider such biogeographical populations separately, given the differing circumstances encountered by each in the wintering and breeding areas (Stroud, Mudge & Pienkowski, 1990). These biogeographical estimates are calculated from available waterbird count data, drawn primarily from the Wetlands International's International Waterbirds Census (which has inputs from WeBS) as well as supplementary data, information and interpretation from Wetlands International's Specialist Groups (Rose & Scott, 1997). These population estimates are then used to calculate the 1% thresholds for sites of international importance. International estimates and 1% levels were produced/revised in 1980 (Scott, 1980), 1989 (Boyd & Piro, 1989), 1994 (Rose, 1994) and 1997 (Rose & Scott, 1997), and these were used to derive estimates of the biogeographical population size for the relevant years. However, estimates were unavailable for several species in some or all of the count years used in this investigation; for cormorant, comparisons with the biogeographical population were possible from 1994 and for great crested grebe from 1997, while no biogeographical population estimates are available for little grebe.

RESULTS

Current population distributions

Considering all waterbirds (as defined by the Ramsar Convention Bureau, 2002; excluding waders) included by the WeBS and not just the 21 species examined separately, in the most recent year for which data were analysed (1998/99) the vast majority of sites contained relatively small numbers of birds (Fig. 2). Specifically, for 97.5% of the Great Britain WeBS sites < 20 000 birds, the threshold level for consideration as a site of international importance

as a waterbird assemblage, were recorded. However, in aggregate, these sites (with < 20 000 birds) only contained 32.3% or 1 531 719 of the 4 743 615 waterbirds summed across all sites, the remainder being concentrated on 2.5% of the sites (Fig. 2).

A similar pattern was evident for the 21 selected species of waterbird considered individually. In 1998/99 most sites contained only small numbers of individuals of a given species. Indeed, for all of these species, > 90% of sites individually contained 0–10% of the maximum count (i.e. the range of values for individual site counts subdivided into ten equal size classes) for that species. For example, this was true for 99.8% of sites for Bewick's swan, 99.1% of sites for dark-bellied brent goose, 98.3% of sites for red-breasted merganser and 97.1% of sites for shoveler. However, for ten species (little grebe, great crested grebe, whooper swan, wigeon, teal, mallard, pochard, tufted duck, goldeneye and coot), those sites that individually contained 0–10% of the maximum count, in aggregate accounted for > 50% of the WeBS total, and for four of these species this was > 60% (60.1% for great crested grebe, 60.6% for pochard, 64% for tufted duck and 71.5% for goldeneye). Despite, in sum, containing so many individuals, very few of those sites with low numbers of individuals were protected as SPA or Ramsar sites, as demonstrated by the small contribution these sites made to the Protected Site total, compared to the total number of individuals on these sites (Fig. 3). For example, only 4.9% (87, $n = 1768$) of the sites with ≤ 345 mallard (0–10% range) were either SPA or Ramsar sites. However, these sites, in combination, account for 53.4% of the WeBS total for mallard. Thus, from a total number of 124 551 mallard on these sites, only 10 223 (8.2%) were recorded on Protected Sites (Fig. 3(a)). In contrast, 70.9% of mallard on sites with between 1036 and 1380 birds (31–40% range) were in the Protected Site network, but these sites only hold 6.9% of the WeBS total for this species (Fig. 3(a)). Similarly, sites supporting 0–10% of the maximum count for goldeneye (< 233 birds) and pochard (< 583 birds) account for 71.5% and 60.5% of the WeBS total, respectively and represent 99% of sites for these species; nevertheless, less than 25% of these sites are SPAs (24% for goldeneye and 14% for pochard).

For several species, the distribution of individuals was highly aggregated (Bewick's swan, European white-fronted goose, dark-bellied brent goose and pintail). In addition, for these species more birds actually occur on the most populous sites than on the sum total of the sites with the lowest numbers of individuals. For example, individual sites with 0–10% of the maximum count, in sum held < 20% of the WeBS total for Bewick's swan (19.4%) and European white-fronted goose (12.8%). Those species that tend to be more aggregated also had a higher representation within the protected site network. For example, while 65% and 70%, respectively, of the WeBS total of dark-bellied brent goose and pintail occurred on sites with large numbers, a significant proportion of the total numbers of birds included in the remaining size groups was also protected, including the smaller size categories (Figs. 3(b) & (c)). Specifically, for dark-

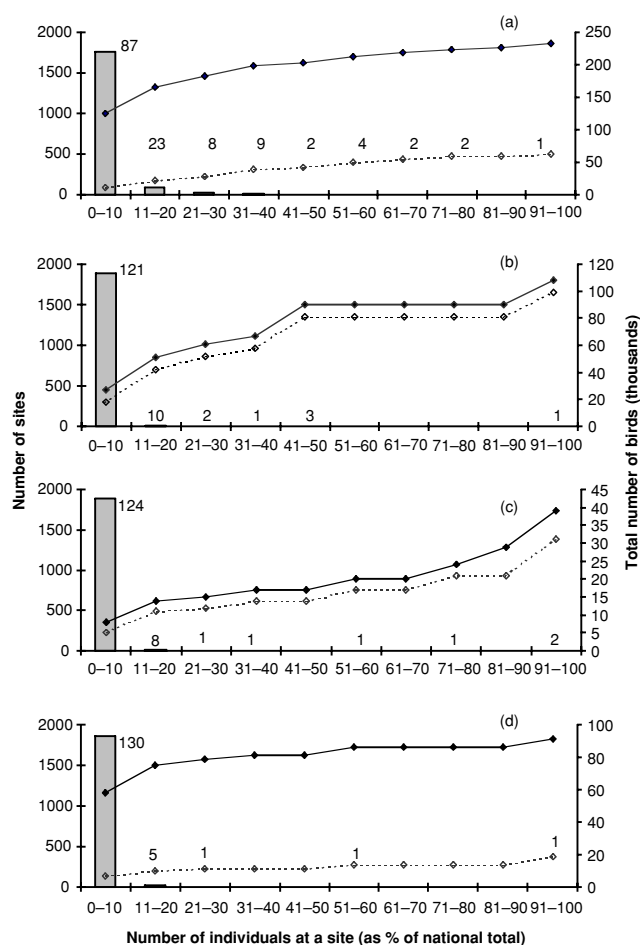


Fig. 3. The number of Wetland Bird Survey (WeBS) sites for: (a) mallard, (b) dark-bellied brent goose, (c) pintail and (d) tufted duck (bars), the numbers of Protected Sites (numbers above bars), the cumulative numbers of birds (\blacklozenge) and the Protected Site total (\blacklozenge) in 1998/99 for 10 equally sized classes. The categories vary depending on the overall number of individuals recorded for each species, each equate to 10% of the total range.

bellied brent goose, 80.7% of the WeBS total for sites with ≤ 2000 birds (0–10% range) and all individuals from the larger size classes were counted on Protected Sites (Fig. 3(b)). For pintail, 65.6% of the 0–10% range was recorded on Protected Sites (Fig. 3(c)).

Considering only the overall Protected Site and Listed Site networks in 1998/99, again for some species those Protected Sites containing small numbers of individuals contained large numbers in aggregate (e.g. cormorant, mallard, shoveler and tufted duck). Although the Protected Site totals for these species were large, few of the sites are listed as nationally important for the species and therefore do not contribute to their Listed Site suite. For mallard, none of the sites with a 5-year mean population of < 2000 birds within a ≥ 20000 assemblage qualify as SPA or Ramsar sites for that species (i.e. for its Listed Site suite). Collectively, however, such sites (0–50% range) held 89.9% of the WeBS total and 79.1% of the Protected Site total of mallard in 1998/99 (Fig. 4(a)). Similarly, for the tufted duck no site with < 1% (600 birds) of the

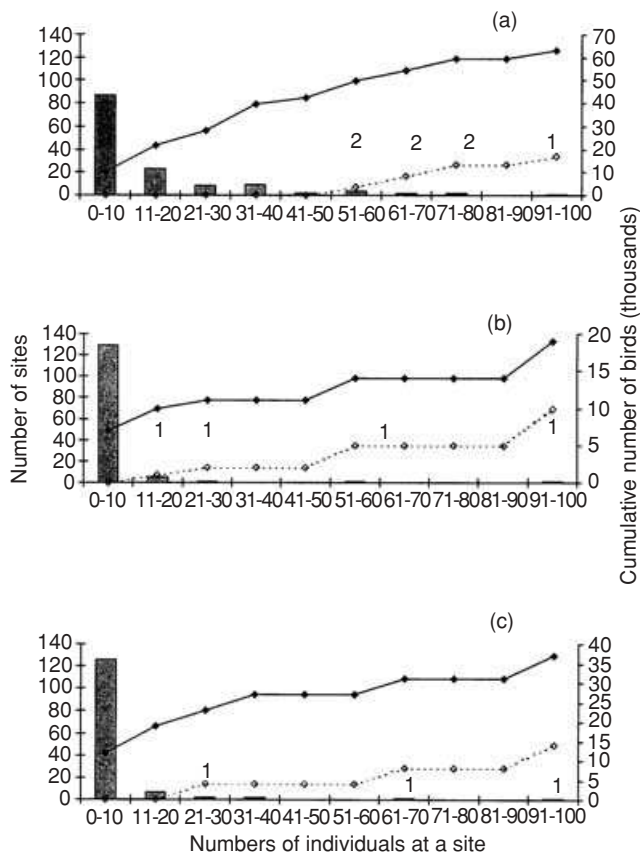


Fig. 4. The relationship between the number of Protected Sites for equally sized classes (bars), the numbers of Listed Sites (numbers above bars), the cumulative Protected Site total in each category (—●—), and the cumulative Listed Site total (---◇---) in 1998/99 for: (a) mallard, (b) tufted duck and (c) coot. Each percentage category is the same as that shown in Fig. 3.

national population is eligible for listing (0–10% range), yet these sites contained 70.4% of the WeBS total and 39.5% of the Protected Site total in 1998/99 (Fig. 4(b)). For the coot, 66.1% of the WeBS total and 41.2% of the Protected Site total was recorded on sites outside the coot Listed Site suite, where the total fell below the threshold for listing as sites of national importance in 1998/99 (1100 birds: Fig. 4(c)).

Proportions of a species' biogeographical population, national population estimate and Protected Site total within the Protected Site and Listed Site networks

Protected Site totals

Calculating the percentage of a species' biogeographical population and the percentage of the national population estimate within the Protected Site and Listed Site networks, based on the most recent 5-year peak mean data (1994/95–1998/99; Kershaw & Cranswick, 2003), provides an indication of the relative effectiveness of the current suite of SPAs and Ramsar sites at both an international and national level. These 5-year means are traditionally used to assess site importance, as a way of

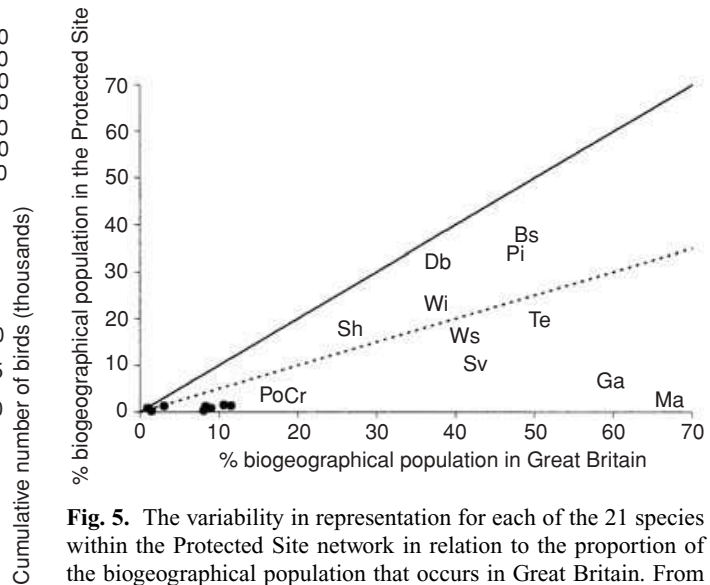


Fig. 5. The variability in representation for each of the 21 species within the Protected Site network in relation to the proportion of the biogeographical population that occurs in Great Britain. From left to right the first 11 data points refer to species Ew, Sm, Rm, Gs, Ge, Td, Gg, Co. The continuous line depicts the maximum possible level of representation, while the dashed line, depicts 50% of the national population estimate. The symbols used are: Bs, Bewick's swan; Cr, cormorant; Co, coot; Db, dark-bellied brent goose; Ew, European white-fronted goose; Ga, gadwall; Ge, goldeneye; Gg, great crested grebe; Gs, goosander; Ma, mallard; Pi, pintail; Po, pochard; Rm, red-breasted merganser; Sh, shelduck; Sm, smew; Sv, shoveler; Td, tufted duck; Te, teal; Wi, wigeon; Ws, whooper swan. No biogeographical population estimate was available for little grebe (Lg).

damping fluctuations in count data (Pollitt *et al.*, 2000; Ramsar Convention Bureau, 2002). When considering the proportion of a species' biogeographical population within the Protected Site and Listed Site networks it should be noted that for each species there is an upper limit, dependent upon the fraction of this population that winters in Great Britain, which varies considerably. Indeed, for the 5-year period 1994/95 to 1998/99 the percentage of the biogeographical population recorded on the British WeBS sites for the 21 species ranged from < 1% for the European white-fronted goose to 67.6% for the mallard (Table 2).

The percentage of the biogeographical population within the Protected Site network was small for many species (Fig. 5). For example, < 5% of the biogeographical population was included in the Protected Site network for 11 species (Table 2). However, in general where the percentage of the biogeographical population recorded in Great Britain was larger, the percentage within the Protected Site network was also larger ($r = 0.59$, $n = 20$, $P < 0.01$). However, there were exceptions to this trend, e.g. 67.6% of the biogeographical population of mallard winters in Great Britain, however, < 3% of this total are in the Protected Site network (Fig. 5). Similarly, shoveler and gadwall have > 30% of their respective biogeographical populations in Great Britain, but < 15% of the total numbers in Great Britain are in the Protected Site network (Table 2).

Considering the percentage of a species' national population estimate within the Protected Site network,

Table 2. The % of the biogeographical population in Great Britain (nationally), recorded in the Protected Site network and in the Listed Site network, the % of the national population estimate supported by the Protected Site network and the Listed Site network and the % of the Protected Site total supported by the Listed Site network for each of the 21 waterbird species individually

Species	% Biogeographical population in:			% National population in:		% Protected Site total in Listed Sites
	National population	Protected Sites	Listed Sites	Protected Sites	Listed Sites	
Little grebe	a	a	a	12.12	7.12	58.74
Great crested grebe	10.60	1.49	0.80	14.08	7.50	53.31
Cormorant	19.17	3.74	2.39	19.53	12.46	63.80
Bewick's swan	47.47	34.53	32.05	72.74	67.52	92.83
Whooper swan	35.75	15.12	13.72	42.29	38.37	90.74
European white-fronted goose	0.97	0.83	0.67	86.15	69.19	80.31
Dark-bellied brent goose	32.70	27.67	24.57	84.62	75.15	88.81
Shelduck	26.07	17.73	16.54	68.01	63.44	93.29
Wigeon	32.48	20.85	15.25	64.18	46.95	73.15
Gadwall	57.00	10.27	7.46	18.02	13.08	72.58
Teal	48.00	17.20	13.28	35.83	27.67	77.22
Mallard	67.60	2.25	0.80	3.32	1.19	35.74
Pintail	46.50	31.30	29.31	67.31	63.03	93.64
Shoveler	37.00	9.26	6.72	25.03	18.15	72.50
Pochard	17.00	3.77	2.54	22.17	14.94	67.39
Tufted duck	9.01	0.81	0.56	9.03	6.23	69.01
Goldeneye	8.30	1.20	0.43	14.47	5.22	36.04
Smew	1.48	0.21	b	14.05	b	b
Red-breasted merganser	3.07	1.28	0.49	41.74	15.99	38.30
Goosander	8.05	0.30	b	3.70	b	b
Coot	11.53	1.35	0.85	11.72	7.39	63.06

there was considerable variation between the 21 species analysed, from 3.3% for mallard to 86.2% for European white-fronted goose. In addition, there was a positive relationship ($r=0.86$, $n=21$, $P<0.0001$) between the percentage of a species' national population estimate within the Protected Site network and the percentage of the national population estimate in the top ten sites for that species, whether these sites were in the Protected Site network or not (Fig. 6). For those species with a high proportion of the national population estimate

within the top ten sites for that species, such as the European white-fronted goose, dark-bellied brent goose, Bewick's swan, whooper swan, shelduck and pintail, the Protected Site network supported a greater percentage of the national population estimate (Fig. 6). Specifically, >70% of the national population was recorded in the Protected Site network for Bewick's swan (72.7%), dark-bellied brent goose (84.6%) and European white-fronted goose (86.2%). In addition, for a further three species, Protected Sites supported >50% (Table 2). Conversely,

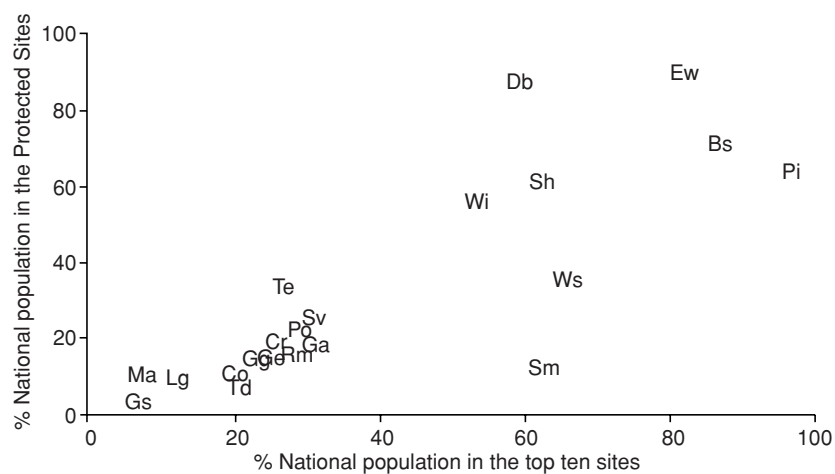


Fig. 6. The effect of aggregation and dispersal on the level of representation of each species within the Protected Site in terms of the percentage of the national population estimate that occurs in the top ten Wetland Bird Survey (WeBS) sites for population size (these are not necessarily all Protected Sites) and the percentage of the national population estimate found in the Protected Sites. Protected Site totals and national population estimates are based on the 1994/95–1998/99 peak means. For species labels see the legend to Fig. 5.

for those species with a more dispersed distribution, the Protected Site network supported a lower proportion of the national population estimate. Indeed, for 13 species < 30% of the national population estimate was supported by the Protected Site network (Table 2).

Listed Site totals

For each of the 21 species, the percentage of the biogeographical population within Listed Sites ranged from 0.4% for goldeneye to 32.1% for Bewick's swan (Table 2), with a mean (\pm SD) of 9.4% (\pm 10.6%). For seven species the total percentage of the biogeographical population, using the 1994/95–1998/99 peak means, in all Listed Sites was < 1% (one of the established classification thresholds applied to individual site populations: Table 2). This contrasts with only four species with < 1% using the 1991/92–1995/96 peak mean data (which were the data used for the recent SPA review: JNCC, 2001).

The percentage of the national population estimate of a species within the Listed Site suite is inevitably greater than that for the biogeographical population. Indeed, this percentage ranged from 1.2% for the mallard to 75.2% for the dark-bellied brent goose, with a mean (\pm SD) of 29.5% (\pm 26.1%: Table 2). In addition, the Listed Sites for nine of the species contained < 20% of the national population estimate.

The percentage of the Protected Site total within the Listed Site suite ranged from 35.7% for the mallard to 93.6% for the pintail, with an overall mean (\pm SD) of 69.5% (\pm 18.8%: Table 2). For 16 out of the 21 species the percentage of the Protected Site total within the Listed Site suite was > 50%, however for three the percentage was < 40% (Table 2).

In addition, there was a significant positive correlation between the percentage of the biogeographical population of a species in the national population estimate and the percentage of the Protected Site total in the Listed Site suite ($r=0.59$, $n=18$, $P<0.01$). This means that, for those species such as Bewick's swan, gadwall, teal and pintail where a greater percentage of the biogeographical population resides in Great Britain, the percentage of the Protected Site total within the Listed Sites is correspondingly greater.

DISCUSSION

There have been relatively few in-depth evaluations of existing protected area network performance (although see Table 3 for examples). Where these have been conducted they typically report insufficient coverage, sub-optimal species/habitat representation and inadequate selection methods. Indeed, some authors have suggested that the evaluated sites appear to be *ad hoc* collections of areas rather than systematically selected reserve networks (e.g. see Pressey, 1994; Lombard, Nicholls & August, 1995; Freitag, Nicholls & van Jaarsveld, 1998) and are, as a result, inadequate for the protection of target

species (Rebello & Siegfried, 1992). Few studies report the overall success of reserve networks; notable exceptions being for fenland SSSIs in Scotland (Rodrigues *et al.*, 1999) and RSPB reserves in Great Britain (Hopkinson *et al.*, 2000). Nevertheless, in contrast to the many negative reports for reserve network performance, the network of SPAs and Ramsar Sites in Great Britain has been shown to be extremely successful in terms of the overall numbers of waterbirds regularly supported. Indeed, considering all WeBS species, despite accounting for < 3% of the total number of wetland sites, those sites with large overall waterbird numbers ($\geq 20\,000$ birds) support approximately two-thirds of the total numbers of wintering waterbirds. Bearing in mind the extreme pressure on the classification and designation process, both from competing land use options and from the European Union to meet set quotas and targets, this level of protection is a remarkable achievement, particularly in comparison with other countries. For example, the Ramsar network in Mexico has been strongly criticised by Perez-Arteaga, Gaston & Kershaw (2002), who concluded that the seven existing Ramsar sites are not representative of Mexican wetland diversity. Furthermore, the current number of Ramsar Sites officially listed on the 'IUCN Protected areas of the world database' for Great Britain greatly exceeds that of all other signatories (e.g. Australia = 63, Canada = 36, France = 18, Greece = 10, Mexico = 7, Portugal = 12, South Africa = 17 and USA = 19) and provides an indication of the considerable effort made to adopt the targets set out both in the Birds Directive and the Ramsar Convention.

In addition to this excellent performance in total conservation, for three species (Bewick's swan, dark-bellied brent goose and European white-fronted goose) > 70% of the national population was recorded in the Protected Site network and > 50% for three additional species. These species, generally, are those where the proportion of the biogeographical population in Great Britain is greatest (with the exception of European white-fronted goose which has < 1% of the biogeographical population in Great Britain), suggesting that the SPA/Ramsar Site selection process has successfully preferentially targeted those species of international importance over others.

For several species, however, large total numbers of birds occur in low numbers on many sites (e.g. mallard, tufted duck, goldeneye and coot). Furthermore, their combined value exceeds that of sites that individually contain larger numbers of individuals. Nevertheless, such sites will not generally be classified as SPAs/Ramsar Sites following the current site-selection methodology. Given that the 1% threshold levels to determine the national and international importance of a site were devised preferentially to target aggregating species (Atkinson-Willes, Scott & Prater, 1982) such as European white-fronted goose, dark-bellied brent goose, Bewick's swan, whooper swan, shelduck and pintail this was not unexpected. Indeed, the Protected Site network better represents these aggregating species as the numbers of birds on a site regularly exceed the numerical

Table 3. Examples of published studies of the performance of existing networks of protected areas, the geographical region considered, the features analysed and the main conclusions

Reference	Geographical region	Feature	Main conclusions
Nilsson & Götmark (1992)	Sweden	Landscape and habitat types	< 1% of the farmland and < 2% of the coniferous forests were represented in existing protected areas. At least half the species for these areas are not represented in existing protected areas.
Rebello & Siegfried (1992)	Cape Region, South Africa	Plants	Existing reserves contain no more species than predicted by a null model.
Sætersdal, Line & Birks (1993)	Western Norway	Plants, birds	The 12 sites in the existing reserve system are, to a large extent, duplicating each other, and many species are missed from the total species list.
Fearnside & Ferraz (1995)	Brazil	Vegetation	Only one-third of terrestrial vegetation zones are protected. Need to extend the reserve network by 67%.
Pressey, Possingham & Margules (1996)	New South Wales, Australia	Land systems	Need to expand the existing network by 78% to include all systems at least once. Existing reserves lower the efficiency with which all land systems can be represented at least once (31% more sites, 44% larger area).
Williams <i>et al.</i> (1996)	Great Britain	Birds	20 additional sites are needed to represent all species at least once.
Howard, Davenport & Kigenyi (1997)	Uganda	Woody plants, birds, small mammals, butterflies and large moths	> 7% of indicator species represented in existing reserves. Adding 11 forests would increase the representation to 95%.
Barnard <i>et al.</i> (1998)	Namibia	Desert vegetation types	The existing network covers only 13.8% of the land area. Four of the 14 desert vegetation types are comprehensively protected (67–94%), but six have < 5% of their extent within protected areas.
Jaffre, Bouchet & Veillon (1998)	New Caledonia	Plants	83% do not occur within protected areas.
Rodrigues <i>et al.</i> (1999)	Scotland	Wetland plants	The current SSSI network has been selected in an inefficient manner. Although, it performed considerably better than a random set of sites where at least two representations of each species were required.
Hopkinson <i>et al.</i> (2000)	Great Britain	Ten taxonomic groups	> 94% of species in each taxonomic group were in the combined network of National nature reserves, RSPB sites and SSSIs.
Sierra, Campos & Chamberlin (2002)	Continental Ecuador	Terrestrial ecosystems	The current network is highly inefficient and only 12 out of the 22 ecosystems are represented at $\geq 50\%$ of their area.
Rouget, Richardson & Cowling (2003)	Cape Floristic Region, South Africa	Vascular plants	Approximately 20% of the region is under some form of protection. The representation bias towards upland areas has seriously constrained the representation of biodiversity pattern and process.

SSSI, Sites of Special Scientific Interest; RSPB, Royal Society for the Protection of Birds.

site-selection thresholds. In consequence, there are considerable differences between species in the proportion of the national population estimate found within the Protected Site network, which is largely a function of their national and international distribution across wetland sites.

Although protection of the sites with highest waterbird numbers means that high numbers of birds are protected with minimum site inclusion, as shown by the strongly aggregated nature of wintering waterbirds in total (i.e. considering all WeBS species together), a significant proportion of the national population estimate remains

unprotected and there is a bias towards species that tend to occur in the most populous sites. This assumes that the most important sites for target species and, therefore, a sufficient proportion of each of their overall populations, occurs within these larger assemblages. If a significant proportion of a species' population is found elsewhere, alternative approaches may be more appropriate to ensure adequate protection. Indeed, the degree of aggregation does not necessarily reflect conservation priority. In particular, those species that are widespread and abundant today may be in great need of conservation in the future, as shown by the recent declines of a number of once common

bird species characteristic of farmland habitats (Fuller, 2000; Gates & Donald, 2000). For example, although the mallard is widespread and has a large population size, it is also one of the few waterbird species where the numbers recorded in Great Britain over winter have declined in recent years (at a rate of 3% per year, 1989–99; M. Kershaw, unpubl. results). Furthermore, several dispersed distribution species, including goldeneye, pochard and shoveler, were included as species of conservation concern in the JNCC 'Birds of Conservation Concern 2002–2007' (JNCC, 2002). Specifically, for shoveler, internationally important numbers regularly winter in Great Britain (> 30% of the biogeographical population), nevertheless, protected areas support < 30% of the national population estimate. By contrast, Great Britain supports < 1% of the biogeographical population of European white-fronted goose, yet almost 90% of the estimated national population winters on protected areas.

A species' presence in the Protected Site network does not guarantee protective measures specific to that species, since only individuals on Listed Sites are targeted for active management. However, the percentage of a species' population on such sites is even smaller than on the Protected Site network and for many species is biased towards those Protected Sites that hold large numbers of waterbirds overall, rather than the most important sites for that species. The relatively low percentages of the Protected Site total within some species' Listed Site suite suggest, as is intuitively expected, that the listing of Listed Sites using the current site-selection criteria does not inevitably target the most suitable sites for protection. For those species where the population does not aggregate and are thus not the focus of the SPA/Ramsar Site selection process, the most important sites on which they occur will not necessarily hold > 1% of the biogeographical population or $\geq 20\,000$ waterbirds, as is in fact the case for several of these species. If this is so, then many potentially important wetland sites for these species will be ignored by the selection guidelines. As an example, the pochard Listed Site suite contains 11 sites in Great Britain, but four of the top ranking sites for pochard, based on the 5-year peak means for 1994/95–1998/99, are not included in the Listed Site suite because they do not contain $\geq 20\,000$ waterbirds. In addition, 34 Listed Sites have been listed as important for wigeon, a species which occurs in large numbers on many wetland sites, compared with only four for tufted duck and seven for mallard, which are more dispersed in distribution and do not occur in sufficient numbers in the larger ($\geq 20\,000$) assemblages. Nevertheless, for internationally important species (i.e. where there is a large proportion of the biogeographical population within Great Britain) there tends to be a greater percentage of the population within the Listed Sites.

In summary, the performance of the current SPA network is remarkable, particularly in comparison with published analyses of networks elsewhere in the world. Nevertheless, the current site-based approach, whilst having the great benefit of simplicity, is deliberately biased towards aggregating species at the expense of the more dispersed distribution species such as mallard,

goldeneye, shoveler, pochard and goosander, many of which are species of conservation concern (JNCC, 2002). To achieve an appropriate level of representation for all target species (as defined by the Birds Directive) will require further development of the current site-selection criteria. Specifically, to ensure that the SPA/Ramsar Site network continues successfully to protect nationally and internationally important waterbird populations, efforts now need to concentrate on the derivation of species-specific representation targets and, in particular, the ways in which these can be incorporated into the site-selection process (see Jackson, Gaston & Kershaw (2004) for details).

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