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Consequences of population change for local abundance and site occupancy of wintering waterbirds

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Abstract

Aim: Population size changes can lead to changes in local abundance and/or site occupancy, depending on the processes influencing site use by individuals. Here, we quantify such changes for wintering waterbirds and assess their implications for widely used conservation strategies in which sites that support in excess of a given proportion of a population are prioritized for protection.

Location: Britain.

Methods: We use long-term survey data to quantify changes in population size and distribution for 19 waterbird species across Britain.

Results: Population changes in these species have varied greatly (from declines of ~25% to increases of >1,600%) over 26 years, and we show that change in local abundance was the predominant consequence of these changes, while colonization of new sites mainly occurred in response to large population increases. For most species, changes in abundance and occupancy were spatially dependent over relatively short distances, consistent with (but not conclusive of) density-dependent spillover. Levels of occupancy among species were negatively associated with proportions of sites, and populations within sites, exceeding the 1% of total population threshold for site protection. For species increasing in overall population size, the occurrence of small incipient populations at new sites resulted in declines in the number of sites supporting >1% of the total population and the proportion of the population supported by these sites.

Main conclusions: Fluctuations in waterbird population size are more likely to result in changes in local abundance than distribution. Consequences of population change for site protection when abundance thresholds are used for site designation depend on shifts in the evenness of distribution of abundances across sites, and whether occupancy is increasing or decreasing. Range-expanding species have an increased likelihood of losing some sites, and populations within sites, exceeding the 1% of total population threshold for site protection.

KEYWORDS

local abundance, occupancy, population dynamics, population threshold, shorebirds, site protection

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1 | INTRODUCTION

Understanding the dynamic ecological processes through which species' distribution, site occupancy and abundances alter with changes in population size is a key issue in ecology and conservation (Borregaard & Rahbek, 2010; Gaston et al., 2000). In the face of increasing anthropogenic pressures on the planet, prioritizing the protection of sites supporting substantial and viable populations is a key component of species conservation interventions. Designating sites for protection is aimed at maintaining or enhancing important populations by alleviating within-site threats from land-use and exploitation, and thus prioritizing sites that support larger populations is a common feature of conservation strategies. Consequently, international and national conservation conventions and directives often use abundance criteria to identify important sites for protection. Abundance threshold criteria are highly effective tools for identifying areas of importance for species, but their sensitivity to changes in population sizes and associated changes in distribution is less clear. There is unequivocal evidence that species' range distributions, site occupancies and abundances are changing globally in response to changing habitat availability, direct exploitation, invasive species and climate change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Parmesan, 2006), but the consequences of these changes for site protection thresholds have not been explored.

Criteria for assessing the international importance of wetlands have been agreed by the Contracting Parties to the Ramsar Convention on Wetlands of International Importance (Ramsar Convention Bureau, 1988). Under criteria 5 and 6, respectively, a wetland is considered internationally important if it regularly supports at least 20,000 individuals of waterbirds or at least 1% of the individuals in a population of a species or subspecies of waterbirds. These abundance thresholds have also been followed in criteria used for the selection of Biological Sites of Special Scientific Interest (SSSIs; Drewitt et al., 2015) in the UK and Special Protection Areas (SPAs) (Stroud et al., 2001) in Europe. However, changes in distribution accompanying overall population changes can influence the number of sites qualifying for site designation and therefore the proportions of the population that are protected or unprotected at specific sites.

The dynamics of intraspecific abundance–occupancy relationships are central to how population changes play out in the numbers and locations of sites qualifying for site designation. A number of proposed mechanisms for positive intraspecific abundance–occupancy relationships indicate causality working in either or both directions (Borregaard & Rahbek, 2010; Gaston et al., 2000). For example, local abundances may drive changes in occupancy via density-dependent effects (Gaston, Blackburn, & Gregory, 1999), while metapopulation structures may counter the isolation of any given occupied patch and allow rescue effects (Gaston et al., 2000; Hanski, 1991). Alternatively, both abundance and occupancy may be simultaneously influenced by external drivers (Borregaard & Rahbek, 2010). Whether species are common or rare, expanding or contracting in range (Webb, Noble, & Freckleton, 2007), and the prevalence or not of time-lags between abundance and occupancy change, all influence the strength of temporal intraspecific abundance–occupancy relationships, making them highly variable and less consistently positive than interspecific relationships (Gaston et al., 1999). Migratory species such as wading birds may be viewed as a particular case where external drivers potentially act on both abundance and occupancy (e.g., at wintering sites) via impacts on overall population numbers occurring at a remote distance (e.g., at breeding sites, Newton, 1997).

The extent to which changes in abundance and/or occupancy are spatially dependent, for example as a result of density-dependent population spillover effects (Gaston, Blackburn, & Lawton, 1997; Gregory, 1998; Newton, 1997), has a bearing on which sites are likely to exceed threshold population numbers through time, as overall population size fluctuates (Gill et al., 2001). The consequences of population fluctuations for the proportions of populations and sites exceeding thresholds for protection will depend on the consequent changes in abundance and distribution across species' ranges.

Great Britain (hereafter "Britain") holds globally important numbers of waterbirds (Musgrove et al., 2011), attracted in large part because of its position on one of the major flyways for species breeding at higher latitudes, its relatively mild winters and its extensive areas of highly productive estuarine environments (van de Kam, Ens, Piersma, & Zwarts, 2004; Rehfisch et al., 2003). Numbers of non-breeding waterbirds on wetlands across the UK are monitored annually and so the importance of these sites for different populations can be assessed (Frost et al., 2016). Populations of many waterbird species have changed in recent decades (Frost et al., 2016), but the extent to which these changes are manifested as either changes in local abundance or site occupancy, and the implications for population and site protection for different species, remain uncertain.

Here, we use long-term abundance data for non-breeding waterbirds across Britain to examine the consequences of overall changes in wintering population sizes for changes in local abundance and/or site occupancy for each species, and the extent to which these changes are spatially autocorrelated and thus likely to reflect local spillover effects. We go on to explore interspecific relationships between changes in abundance and occupancy with initial levels of population and occupancy across species. We then evaluate the consequences of variation in abundance and occupancy changes across species for the 1% population threshold and levels of population and site protection.

2 | METHODS

2.1 | Data collection

Our analyses encompass 19 species of waterbird whose UK wintering populations are monitored by the Wetland Bird Survey (WeBS, Frost et al., 2016). The species are all waders with the exception of shelduck (*Tadorna tadorna*), which (as elsewhere, e.g., Mendez et al., 2012) is included because of its high dependence on estuaries and its similarity in feeding ecology to waders. Under the WeBS monitoring scheme (and its predecessor schemes), synchronized monthly counts are carried out at wetlands of all habitat types across the UK on predetermined dates, minimizing the likelihood of double-counting or missing individuals, and the resulting site and national totals for all species are published annually (Frost et al., 2016). National population estimates are periodically updated using these counts (e.g., Musgrove et al., 2011).

We used count data for 83 sites across Britain (Fig. S1) for which monthly counts were available annually between the winters of 1980/1981 and 2006/2007. Winter mean abundance for each species at each site was calculated using counts from November to February, when the numbers of birds using a site more accurately reflect stable non-breeding population numbers. For each species, wintering population size was calculated as the sum of the winter mean abundances (local populations) across sites. Note that these estimates do not equate to complete Great Britain population estimates (published in Musgrove et al. (2011)), and changes in population sizes on these 83 sites might differ slightly from published population trends (Frost et al., 2016). The 1% thresholds are measured from the wintering population estimates on our 83 sites and therefore also differ slightly from those used in the designation of Sites of Special Scientific Interest (SSSI), Special Protection Areas (SPAs) or Ramsar sites (e.g., Musgrove et al., 2011).

2.2 | Data analysis

To quantify changes in local abundance (i.e., number of individuals at a single site) and compare population changes across time between species, a five-year mean abundance at each site was calculated for two periods: at the start (1980/1981-1984/1985) and the end (2002/2003-2006/2007) of the time series. Five-year means are used in site designations to define numbers of a regularly occurring species (Stroud et al., 2001). Variation among population trends was firstly assessed using population growth indices, which provide a measure of population size on an arithmetic scale relative to one, and result from dividing the population size in the second time period by the population size in the first period.

To understand the consequences of population change for local abundances and site occupancy, we used Rank Occupancy-Abundance Profiles (ROAPs; Collins, Holt, Foster, Ollins, & Olt, 2009). ROAP uses a graphical representation of abundances across space, by displaying the distribution of local abundances and site occupancy. To generate a ROAP for a single species at a given time, all sites are ordered and ranked by the species' local abundance (here using five-year means, as described above), from the highest (site rank 1) to the lowest local abundance. The rank position of a given site is divided by the total number of sites (83) to determine its relative rank. This allows comparisons between species with different distributions (some species are present across the majority of sites whereas others have a more restricted distribution). Species-specific ROAPs can then be generated by plotting the local abundance at each site (y-axis) against the relative rank of the sites (x-axis) (Fig. S2).

To test for differences between ROAPs at different time periods, we used the nonparametric statistic D^* (Collins et al., 2009), calculated as the area between the two ROAPs, that is the difference in total population size between two time periods. Total population size was calculated as the sum of the local abundances across all sites for each time period (i.e., the area under each ROAP). Therefore, D^* represents the number of birds gained/lost between two time periods. We tested for statistical significance of D^* using a randomization protocol (Collins et al., 2009). For each pair of ROAPs, we combined the dataset of each time period into one, re-sampled the data 1,000 times, randomly assigning each abundance to a time period without replacement, and calculated D^* for each randomization. This generates a statistical distribution of D^* values that could have been generated by chance, given the observed data. We compared the empirical D^* (increase or decrease) to the distribution generated from the randomizations and considered the results to be significantly different at $\alpha = 0.05$.

We then quantified the changes in local abundance and site occupancy resulting from changes in the overall population for each species. First, we divided the area between ROAPs into different sectors (Collins, 2009) according to where the lower ROAP intersects with the higher ROAP in the plot (Fig. S2). Changes in (1) site occupancy were assessed from the intersection between ROAPs on the x-axis and calculated as the sum of individuals at sites where a species had colonized or gone locally extinct between the two time periods. Changes in local abundance were explored for both maximum and intermediate local abundance. Changes in (2) maximum local abundance were quantified using the intersection between ROAPs and the y-axis, summing the populations at sites that, at the end of the time period, had higher/lower abundances than the maximum local abundance at the beginning of the time period. Changes in (3) intermediate local abundances were calculated as the sum of local populations that had not been included in the other two changes. Finally, all changes in local abundance and occupancy were transformed into proportions of the initial population. For example, to understand shifts in maximum local abundance between periods, we divided changes in maximum local abundance by D^* and multiplied by the growth index previously calculated (% population change between 1980/1981-1984/1985 and 2002/2003-2006/2007), resulting in the proportionate amount by which the population had increased or decreased due to changes in maximum abundance.

ROAPs are not spatially explicit and hence reveal nothing about the spatial structuring of changes in abundance and/or occupancy of sites through time. However, such changes are expected to be spatially non-independent if they are the result of density-dependent spillover effects of abundance changes at a particular site or sites (Melles, Fortin, Lindsay, & Badzinski, 2011; Newton, 1997). In other words, it is likely that newly colonized sites or sites showing abundance increases are in geographical proximity to each other, as is common with range-expanding (or -contracting) systems (Bartón, Phillips, Morales, & Travis, 2009; Yvonne, Mark, Collingham, Hill, & Huntley, 1996). To test this, we looked for evidence of positive spatial autocorrelation in the distribution of changes across sites using Moran's I correlograms. Sites lying within a lag distance were defined as neighbours using a binary weighting matrix for each distance class, using the *ncf* package

TABLE 1 Wintering wader population changes on British estuaries between 1980/1981-1984/1985 and 2002/2003-2006/2007

					% change in:			
Species	Species code	Initial population	*D**	*p*	Total population	Maximum abundance	Intermediate abundance	Occupancy
Avocet (*Recurvirostra avosetta*)	av	327	5,525	<.001	1,690	829.05	636.39	224.85
Bar-tailed godwit (*Limosa lapponica*)	ba	38,092	−3,322	.37	−9	7.85	−16.58	0.005
Black-tailed godwit (*Limosa limosa*)	bw	4,060	16,971	<.001	418	214.67	187.16	16.15
Curlew (*Numenius arquata*)	cu	43,422	18,891	.009	43	4.29	39.04	0.16
Dunlin (*Calidris alpina*)	dn	357,848	−27,661	.36	−8	1.13	−8.86	0
Spotted redshank (*Tringa erythropus*)	dr	41	11	.20	27	−7.31	31.7	2.43
Greenshank (*Tringa nebularia*)	gk	136	92	.015	67	19.63	44.36	2.90
Golden plover (*Pluvialis apricaria*)	gp	19,329	107,026	<.001	554	274.75	278.79	0.15
Grey plover (*Pluvialis squatarola*)	gv	18,297	13,922	.005	76	13.72	62.37	−0.01
Knot (*Calidris canutus*)	kn	189,824	55,844	.24	29	3.03	26.38	0
Lapwing (*Vanellus vanellus*)	l_	76,074	125,535	<.001	165	50.96	114.04	0
Oystercatcher (*Haematopus ostralegus*)	oc	196,028	32,350	.29	16	7.01	9.48	0.0005
Purple sandpiper (*Calidris maritima*)	ps	557	−147	.22	−26	−45.6	19.03	0
Redshank (*Tringa totanus*)	rk	51,349	17,027	.037	33	3.36	29.78	0.005
Ringed plover (*Charadrius hiaticula*)	rp	5,757	−123	.43	−2	3.634	−5.76	0
Ruff (*Calidris pugnax*)	ru	120	56	.24	47	16.66	30	0
Sanderling (*Calidris alba*)	ss	3,979	3,122	.035	78	11.3	66.67	0.47
Shelduck (*Tadorna tadorna*)	su	69,160	−17,859	.11	−26	−29.79	3.95	0.01
Turnstone (*Arenaria interpres*)	tt	9,331	329	.41	4	0.39	3.12	0.01

Initial population is the sum of all individuals across all sites. *D** is the difference in population abundance between the two time periods and represents the number of individuals lost (with negative sign) or gained between time periods.

The percentage change is calculated in relation to the initial population abundance and indicates the total population change and the changes in maximum and intermediate local abundances and site occupancy.

*The p values are derived using a randomization protocol by comparing empirical *D** with the random distribution of *D**.

(Bjornstad, 2016). We investigated changes in abundance and occupancy separately, in both cases carrying out a sensitivity analysis using lag distance intervals of 0–40, 40–80 and 80–120 km. In each case, significant positive Moran's *I* ($p < .05$) at shorter pairwise site distance intervals up to 120 km was taken as an indication of local spillover effects. We do not explore the occasional incidence of significant negative Moran's *I* as negative autocorrelation was not of interest here, and occurred mostly at intermediate- to long-distance intervals. Similarly, because of the focus of interest on short-distance autocorrelation, we did not use global Moran's *I* tests. Given that large differences in absolute abundance change between neighbouring sites as a result of site-area effects could potentially swamp any signal of spatial autocorrelation in population changes, we re-assigned change scores for sites as abundance increase =+1; abundance decrease =−1; no change = 0.

We examined interspecific trends in intraspecific change in local abundances and site occupancy in relation to overall population change using Spearman's rank correlations. To understand how changes in occupancy and population size lead to changes in proportions of populations and sites qualifying for protection, we examined the relationship between numbers of sites occupied by species in each time period and the proportions of sites, and total proportions of populations within those sites, exceeding the 1% population threshold for site protection. All analyses were conducted in R (R Core Team 2014).

3 | RESULTS

3.1 | Variation in population trends

Populations of the 19 waterbird species fluctuated by varying amounts between 1980/1981-1984/1985 and 2002/2003-2006/2007. Five species declined over this period, with the greatest losses occurring in purple sandpiper (*Calidris maritima*) and shelduck (both declined by ~25%). Conversely, avocet (*Recurvirostra avosetta*), golden plover (*Pluvialis apricaria*) and black-tailed godwit (*Limosa limosa*) experienced the greatest population increases, of 1,690%, 554% and 418% of the initial population sizes, respectively (Table 1).

Nine of the 19 species showed statistically significant differences between ROAPs in 1980/1981-1984/1985 and 2002/2003-2006/2007

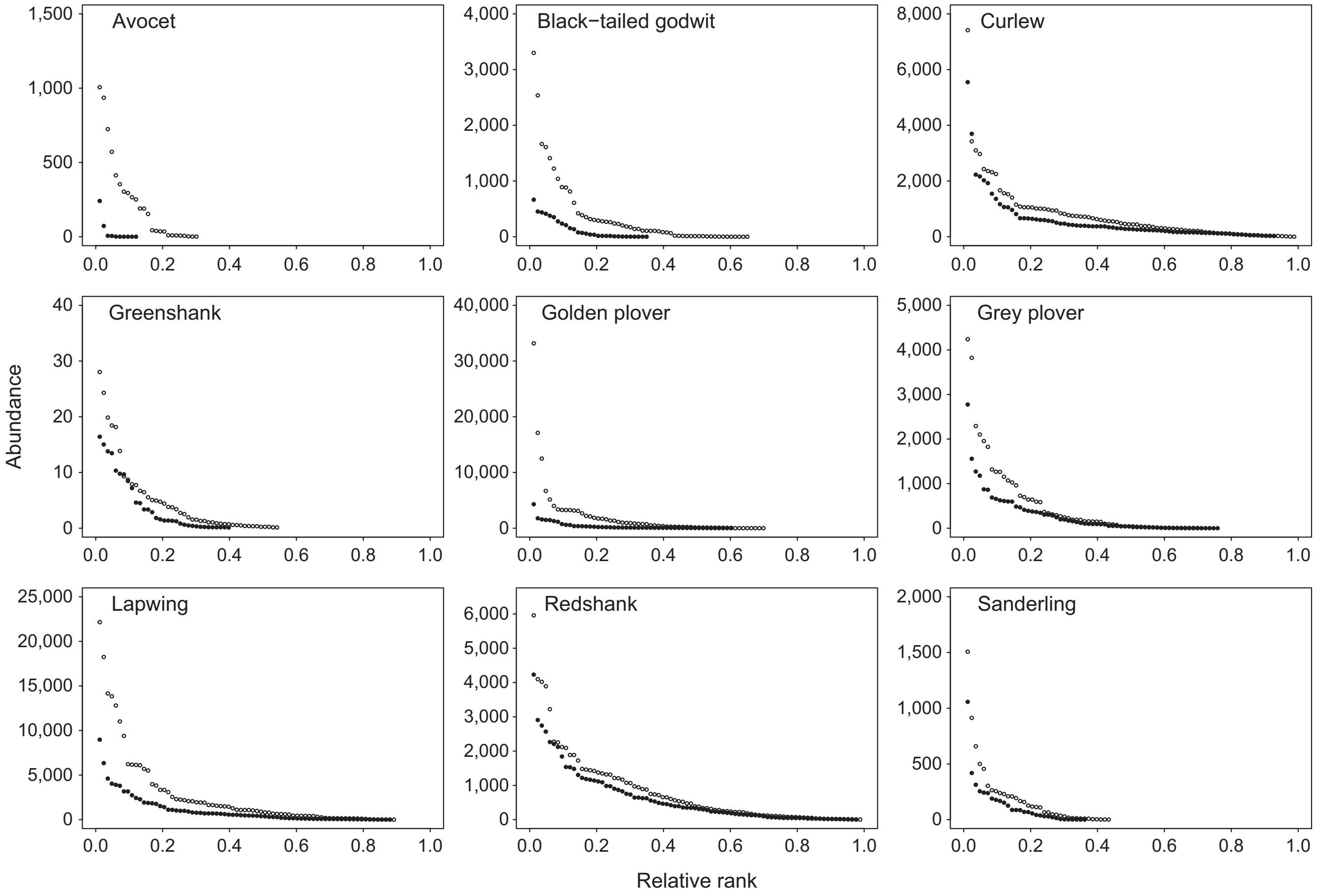

FIGURE 1 Rank occupancy-abundance profiles (ROAP) at two time periods, 1980/1981-1984/1985 (filled circles) and 2002/2003-2006/2007 (open circles), for all species that showed significant population changes (D^*—see Table 1). Local abundance was measured as the five-year mean abundance of winter means for the two time periods at each site. Relative rank was calculated by dividing the rank order of sites by the total number of sites surveyed ($n = 83$). Each site in which the species was present is represented by a single point. For ease of interpretation, sites where species were not present (local abundance=0) are not shown

(Table 1), all having increased population sizes over this period (Figure 1). Black-tailed godwit showed the greatest increase in wintering site occupancy (25 new sites, with local abundances up to approximately 100 individuals), followed by avocet (15 new sites, with local abundances ranging from a few individuals to 200). Other species that also occupied new sites during this period were greenshank (*Tringa nebularia*), golden plover and sanderling (*Calidris alba*). Grey plover (*Pluvialis squatarola*) was the only species that increased significantly in population size but decreased in site occupancy, being present at five fewer sites in 2002/2003-2006/2007 than in 1980/1981-1984/1985 (Figure 1). Common species such as curlew (*Numenius arquata*), redshank (*Tringa totanus*) and lapwing (*Vanellus vanellus*) were present in at least 90% of the sites considered in this study (Figure 1).

3.2 | Consequences of population change for changes in local abundance and site occupancy

Overall, changes in wintering populations have largely resulted in changes in local abundances rather than changes in site occupancy, with only four species showing changes in occupancy of >2% (Table 1). Of the species with statistically significant D^*, most of the population increase was manifested as increases in local abundances, both maximum and intermediate, rather than in site occupancy (Table 1). Wintering populations of avocet and black-tailed godwit increased their maximum local abundances by 829% and 215%, respectively, between time periods. For the remaining species with significant D^*, changes in intermediate local populations were greater than changes in maximum local abundance (Table 1). Although the number of sites occupied by some species has changed greatly (e.g., black-tailed godwit and avocet), local abundances in colonized sites were mostly small in comparison to the increases in local abundances in sites already occupied (Table 1, Figure 1). While bar-tailed godwit and shelduck both experienced declines in overall population size, these were not statistically significant and their site occupancy increased slightly through time (Table 1).

Sensitivity analyses for the spatial autocorrelation tests showed that all three distance class intervals gave very similar results; hence, for brevity, we report results using only the 40 km interval. The correlograms revealed significant positive spatial autocorrelation at one or more of the three shortest lag distance intervals for eight species showing an overall population increase (circles in Figure 2) and three experiencing an overall population decline (triangles in Figure 2). Six species that increased in site occupancy showed significant spatial autocorrelation at one or more of the first three distance class intervals, and one (spotted redshank, *Tringa erythropus*) showed spatial autocorrelation at intermediate distance intervals (>120 km) (circles in Figure 3). Of the species showing a decline in the number of sites occupied, only purple sandpiper showed significant spatial autocorrelation at one or more of the first three distance class intervals (triangles in Figure 3). One species (ruff, *Calidris pugnax*) showed significant short-scale spatially autocorrelated changes in occupancy with no changes in the total number of sites occupied.

3.3 | Correlates of population change

There was no significant correlation between changes in maximum or intermediate local abundance and initial population size (Figure 4a,d). However, for species with significant changes in population size (D^*), those with smaller initial population sizes showed significantly greater changes in site occupancy (Figure 4g), and those that initially occupied fewer sites had significantly greater changes in maximum and intermediate local abundances and site occupancy (Figure 4b,e,h). Therefore, for species with significant changes in population size, those that were initially rare have colonized larger numbers of new sites.

Changes in local abundances—maximum and intermediate—were significantly positively correlated with total population change; the greater the total population change, the greater the change in local abundance (Figure 4c,f). This correlation was consistent for analyses including all species and those excluding species with non-significant D^*. In contrast, there was no significant correlation between changes in site occupancy and total population change (Figure 4i).

3.4 | Consequences of occupancy and population changes for population thresholds

We found that total occupancy is strongly negatively associated with the proportion of sites where numbers exceeded 1% of the defined total population across the 83 sites studied (Fig. S3a), and with the total proportion of the population occurring within these sites (Fig. S3b). Nevertheless, a high proportion of the wintering populations (>75%) of individual species were supported on sites where numbers exceeded 1% of the defined total population in the given time period. However, changes in population size and associated changes in local abundance and site occupancy in these wintering populations have resulted in changes in the number of sites exceeding this 1% threshold, and thus changes in the total proportion of the population that might be targeted for protection using such a threshold (Figures 5 and 6). The proportion of sites (and proportion of the population in these sites) exceeding the 1% of the defined total population has decreased for eight species and, with the exception of ringed plover (*Charadrius hiaticula*), all are species that have experienced increases in their population size (bottom left quadrant in Figure 6). In contrast, increases in the proportion of sites (and proportion of the population in these sites) where numbers exceeded 1% of the defined total population have been observed for eight other species, three of which have shown overall declines in their population size (top right, Figure 6). For only two species (with contrasting population changes) has the proportion of population in sites above the threshold decreased while the number of sites above the threshold increased (top left, Figure 6). No species showed a decrease in the number of sites above the threshold combined with an increased proportion of population in sites above the threshold (bottom right, Figure 6).

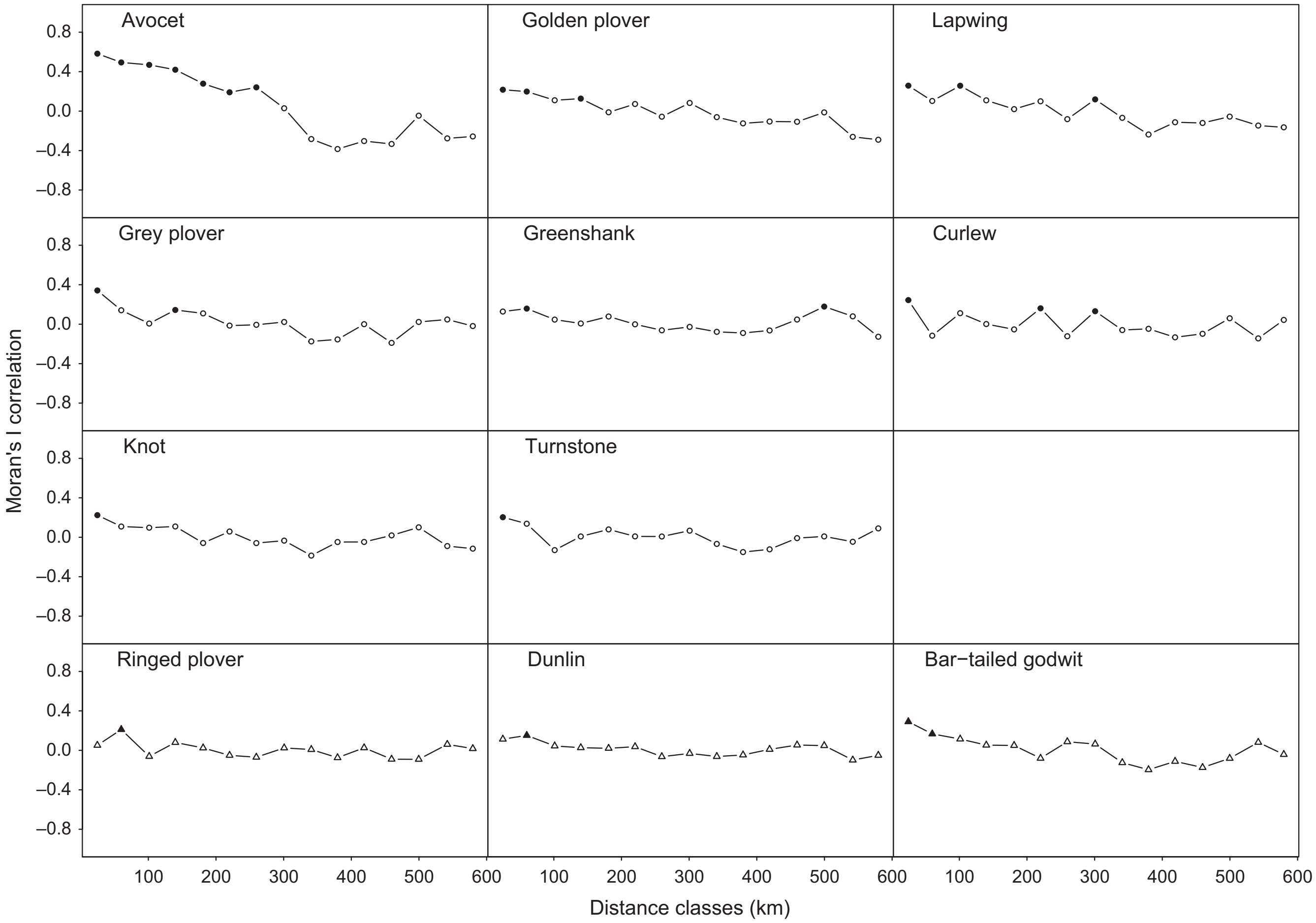

FIGURE 2 Moran's I correlograms for the changes in species' local abundances. Only species with significant spatial autocorrelation at one or more of the three shortest lag distance intervals are shown. For species showing an overall population increase, significant spatial autocorrelation is indicated with black filled circles, while for species showing an overall population decline, significant autocorrelation is indicated with black filled triangles

4 | DISCUSSSION

4.1 | Consequences of population change for species distribution and local abundances

The substantial variability in population changes of waterbird species wintering across Britain over the last 40 years provides an unusual opportunity to assess the consequences for local abundance and distribution at large spatial scales. Most species have undergone increases in population abundance, and our analyses reveal that this has primarily lead to increases in local abundance rather than in site occupancy. In addition, for species in which ranges have expanded, increases in site occupancy were always accompanied by increases in local abundance in occupied sites. Thus, population changes in these systems are largely manifested as changes in local abundance, and changes in site occupancy typically only follow substantial changes in abundance. Our findings are consistent with broader theory and evidence concerning temporal intraspecific abundance–occupancy relationships (Borregaard & Rahbek, 2006; Gaston et al., 2000). Notably, weaker intraspecific relationships between abundance and occupancy change are predicted for longer lived, site-faithful species such as wading birds, resulting in time-lags between changes in local abundances and eventual changes in occupancy of sites (Borregaard & Rahbek, 2010; Gaston et al., 1999).

Despite the large increase in number of sites occupied by some species (e.g., black-tailed godwit and avocet), the number of individuals occupying newly colonized sites was small in relation to the increases in local abundance in occupied sites. As shown for other waterbird species (Jackson, Kershaw, & Gaston, 2004a), site fidelity can strongly influence patterns of occupancy (e.g., Burton, 2000; Burton & Evans, 1997 and references therein), particularly given the potential life span of these birds (~7-40 years, British Trust for Ornithology, 2015). Site choice by individuals may also be influenced by the performance and abundance of conspecifics, resulting in aggregations around areas of abundant resources (Brown, Brown, & Danchin, 2000; Doligez, Danchin, Clobert, & Gustafsson, 1999; Jackson et al., 2004a). Thus, juvenile settlement decisions may be influenced by the distribution of conspecifics, resulting in increased local abundances rather than colonization of new sites (Gunnarsson, Gill, Newton, Potts, & Sutherland, 2005).

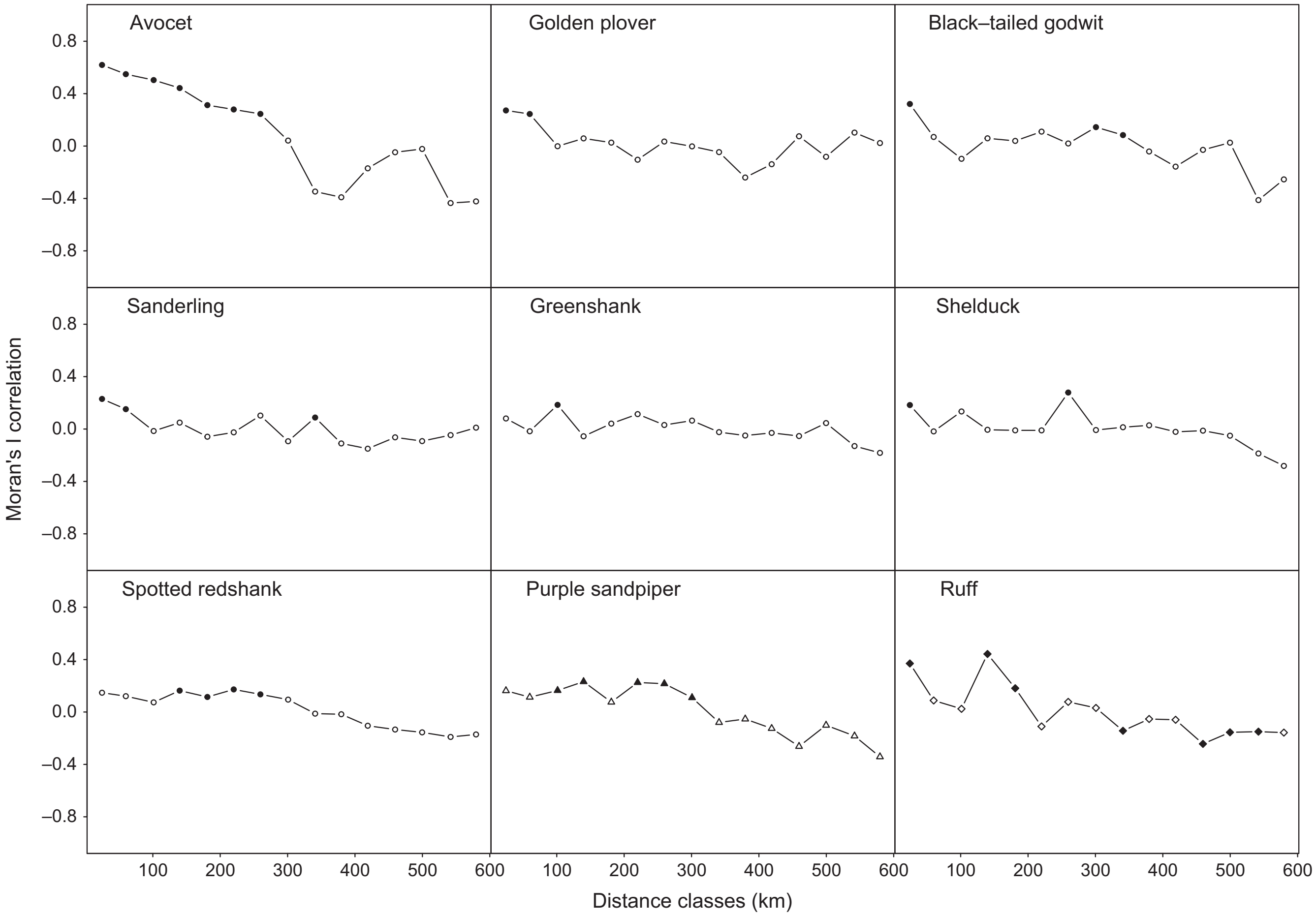

FIGURE 3 Moran's I correlograms for the changes in species' occupancy. Only species with significant spatial autocorrelation at one or more of the three shortest lag distance intervals are shown. For species that experienced increases in site occupancy, significant spatial autocorrelation is indicated with black filled circles, for species with decreases in occupancy, significant autocorrelation is indicated with black filled triangles, and for species with no changes in occupancy, significant autocorrelation is indicated with black filled diamonds

The extent of initial occupancy proved to be an important factor influencing patterns of change in local abundance and occupancy, as has been found elsewhere (Borregaard & Rahbek, 2006; Zuckerberg, Porter, & Corwin, 2009). While range expansions occurred in initially rare and narrowly distributed species (e.g., avocet), abundant and widespread species (e.g., lapwing) have changed little in occupancy but have increased in local abundances. This pattern would be expected as widespread species were already present across the majority of sites, and thus, the potential for colonization was limited (Gaston et al., 2000; Newton, 1997). However, it is worth noting that changes in distribution outside of the British wintering range may be occurring in some species (Maclean et al., 2008). Colonization of new sites is likely to be a density-dependent response to increases in population size. Patterns of change in abundance and occupancy are spatially non-independent at relatively short distances (0-120 km pairwise site distances) for the majority of species, suggesting that both increases in local abundance and colonization events tend to occur as a result of population spillover between neighbouring occupied sites or from occupied to neighbouring unoccupied sites, respectively. However, this does not necessarily imply that the factors driving the population changes are local, as changes in abundance and occupancy in winter may be a consequence of changes operating in the breeding season. For example, range expansion of black-tailed godwits has occurred on both the breeding and the wintering grounds (Gill et al., 2001; Gunnarsson et al., 2005), and strong links between breeding and non-breeding locations mean that changes in one could be a consequence of changes in the other (Gunnarsson et al., 2005). Thus, in addition to density-dependent pressures, range expansion can depend on the amount and distribution of suitable areas, the distances over which individuals will disperse and the strength of links between breeding and non-breeding sites.

Five of the 19 species decreased in number between 1980/1981-1984/1985 and 2002/2003-2006/2007, although these changes were not statistically significant. These decreases in the wintering population resulted primarily in declines in abundance at sites with maximum or intermediate local abundances, rather than reductions in site occupancy. Bar-tailed godwit (*Limosa lapponica*) and shelduck showed increases in site occupancy, suggesting a possible redistribution on their wintering grounds, whereas dunlin (*Calidris alpina*), ringed plover and purple sandpiper showed small declines in occupancy (local

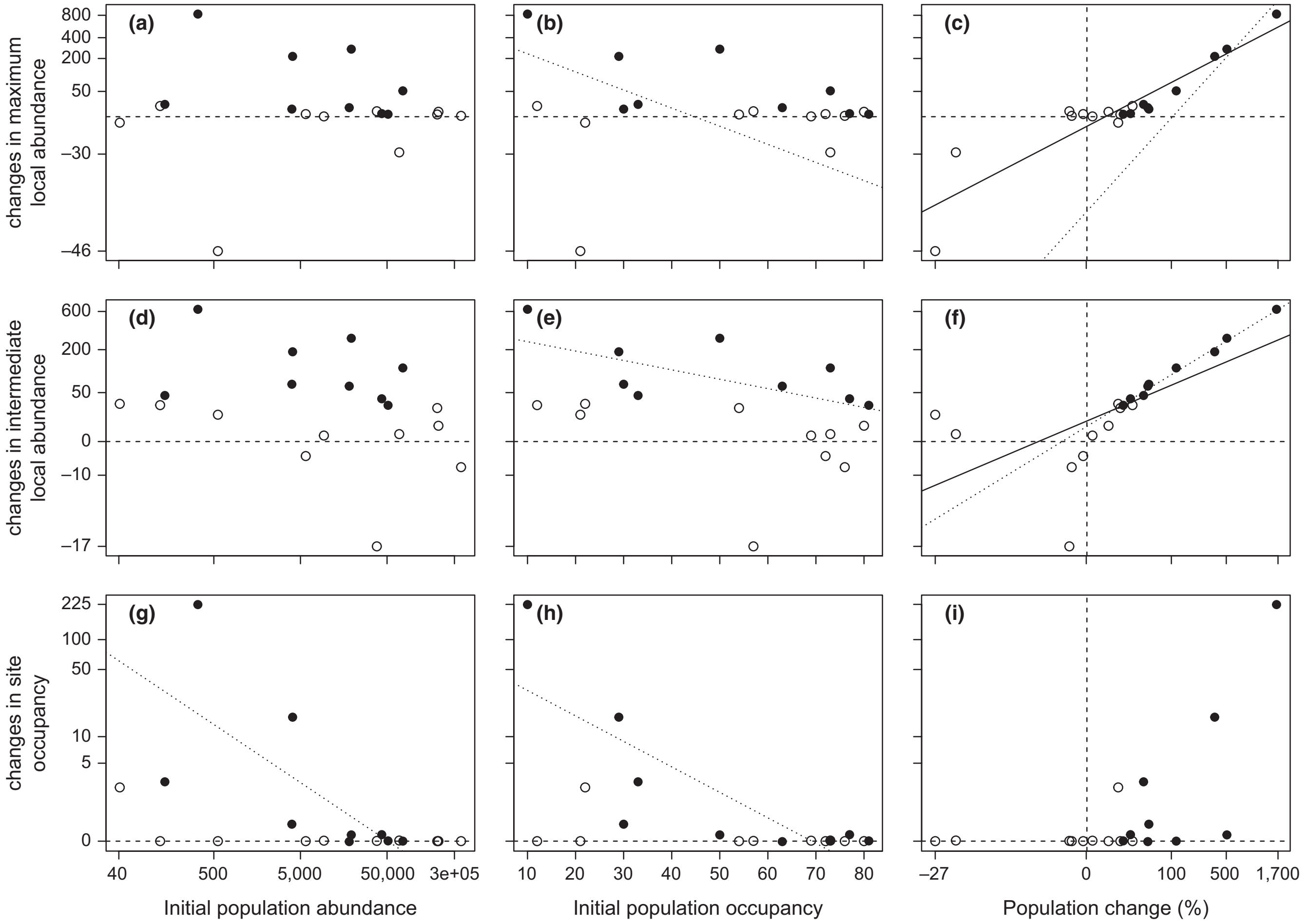

FIGURE 4 *Top row*: relationships between changes in maximum local abundance and (a) initial population abundance, (b) initial population occupancy (ρ = −0.7, *n* = 9, *p* = .04) and (c) total population change (solid line, ρ = 0.86, *n* = 19, *p* < .001; dotted line, ρ = 0.93, *n* = 9, *p* < .001). *Middle row*: relationships between changes in intermediate local abundance and (d) initial population abundance, (e) initial population occupancy (ρ = −0.73, *n* = 9, *p* = .03) and (f) total population change (solid line, ρ = 0.93, *n* = 19, *p* < .001; dotted line, ρ = 1, *n* = 9, *p* < .001). *Bottom row*: Relationships between changes in site occupancy and (g) initial population abundance (ρ = −0.7, *n* = 9, *p* = .03), (h) initial population occupancy (ρ = −0.78, *n* = 9, *p* = .01) and (i) total population change. Black solid lines show the correlation when all the species are included, while dotted lines show the correlation when only species with statistically significant change in *D** are analysed (filled circles). Open circles are species with no statistically significant change in D* (see Table 1 for details)

extinction on one site only) in the latter period. This study spans a time period of 26 years, which might be insufficient to capture many local extinctions, given the longevity of wader species, their typically high levels of fidelity to wintering sites, and thus, the likelihood that changes in distributions result primarily from differential juvenile settlement and survival. According to the extinction debt concept, local extinction may occur with delay following an environmental perturbation (Tilman, May, Lehman, & Nowak, 1994), and long-lived species would be expected to show a longer time-lag between declines in local abundances and loss of site occupancy (reviewed in Kuussaari et al., 2009). That such lagged effects potentially explain the weak linkage between changes in abundance and occupancy observed here highlights the importance of population monitoring programmes to detect not only losses in site occupancy but the early warnings that declines in abundance within and across sites represent. While site fidelity and longevity mean that it is very likely that small populations will persist at traditional wintering sites for an extended time, it also means that losses in site occupancy will be slower to reverse for species sharing these life histories. Indeed, theory predicts that, whether delayed or otherwise, the two-way causality between falling population numbers and declining range occupancy means species under either pressure face a "double jeopardy" (Borregaard & Rahbek, 2010; Gaston et al., 1999).

4.2 | Consequences of population change for site protection

The SPA network in Britain protects high proportions of the British populations of many wader species (Baker & Stroud, 2006; Jackson, Kershaw, & Gaston, 2004b). However, our study shows that although a high proportion of the wintering populations (>75%) of these species were supported on sites where numbers exceeded 1% of the defined total populations in the given periods, the proportion of sites (and the proportion of the population in these sites) where numbers exceeded

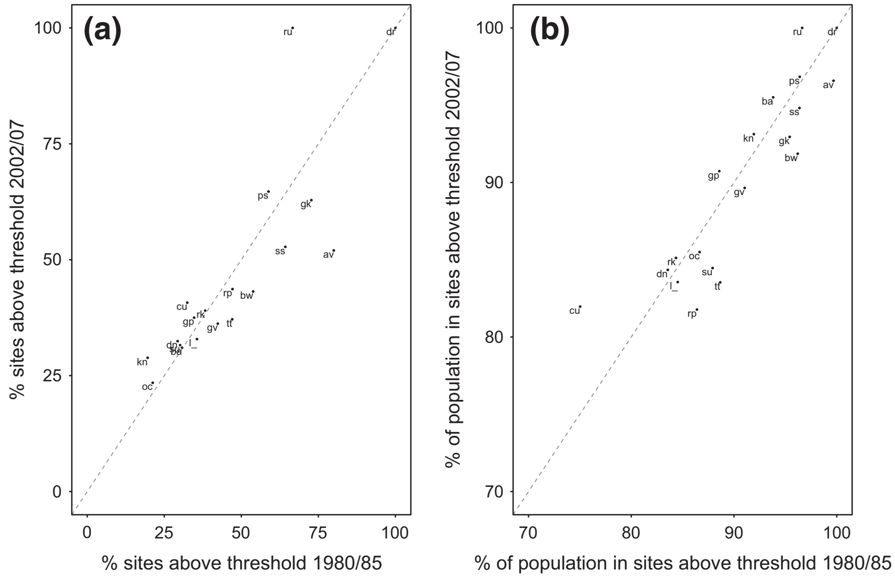

FIGURE 5 Changes in the proportion of (a) sites supporting at least 1% of the total population of wintering waders in Britain considered and (b) the proportion of the population on these sites in each time period. The dashed line is the line of unity. Species codes are given in Table 1

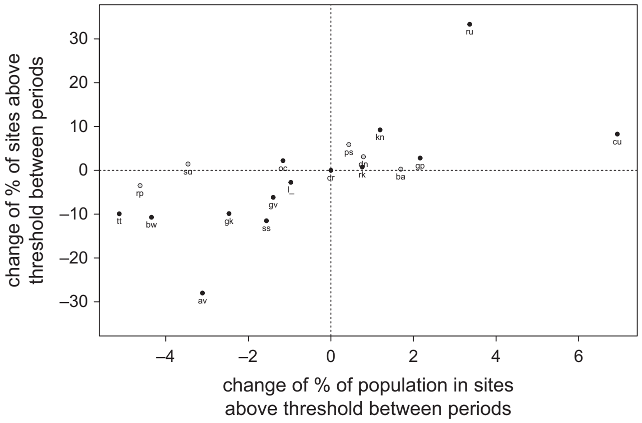

FIGURE 6 Changes in the proportion of sites supporting at least 1% of the total population of wintering waders in Britain considered in relation to changes in the proportion of the population on these sites in each time period. Species codes are given in Table 1

1% has decreased for some species, particularly those in which wintering population sizes have increased. Despite a strong negative interspecific trend, the varying directions of intraspecific temporal change among species cautions against concluding that intraspecific increase in occupancy always leads to lower percentages of sites and populations protected using population thresholds. Nevertheless, it must be the case that with increase in occupancy comes an increased probability that more sites will fall below 1% of total population. The finding that four of the five species with the largest percentage increases in occupancy (avocet, black-tailed godwit, greenshank and sanderling) show among the largest decreases in the percentage of sites, and populations within sites, exceeding the 1% threshold, supports this idea. Changes in levels of protection will also depend on changes in the shape of ROAPs, and hence, how population change alters the evenness of distribution of abundances across sites.

Spatial non-independence of changes in abundance and occupancy suggests that site colonization may largely be a function of changes in abundance in neighbouring sites, rather than sites being colonized according to their environmental conditions. This indicates that neighbouring sites, irrespective of 1% thresholds, provide important connectivity that may help to maintain long-term population stability. However, if newly colonized sites are, on average, of lower quality than occupied sites (Gill et al., 2001), then population increases and associated spillover could result in occupied sites dipping below 1% threshold levels that have been revised upwards as a result of total population increase. Regular reviewing of population estimates will help to ensure that changes in designations only follow sustained changes in abundance and distribution.

As population declines tend to be manifested in declines in local abundance rather than range contraction, the number of sites exceeding the 1% threshold is likely to depend on the variation in rates of decline in local abundance between sites. Similar declines in abundance across all sites would have little impact on the number of sites exceeding the threshold, while sharp declines in sites with relatively small populations could result in those sites no longer exceeding the threshold for designation. In our study, population declines have primarily occurred in highly abundant species and have not been sufficient to reduce local abundances below the threshold. However, the decline observed in ringed plover numbers led to a reduction of both the number of sites and the proportion of the population present in sites exceeding the threshold, and hence, this declining population could risk losing protection at those sites even while experiencing a decline. In practice, the protected status of sites will only rarely be altered by species no longer occurring in sufficient numbers, because sites are typically designated for many species. However, removal of species from site designations could reduce the capacity for statutory agencies to resource and implement conservation actions aimed at those species.

In conclusion, our study provides insights into how local abundance and site occupancy change in response to overall population change. While large changes in site occupancy are apparent for some of the species included here, changes in wintering populations have primarily resulted in changes in local abundance, and range expansion tends to follow increases in local abundance. Habitat availability and site fidelity, along with species longevity, may explain the strong tendency for local population abundance to change much more than site occupancy. The response of such species to environmental change is therefore likely to be demographic rather than behavioural, reinforcing the need to understand density-dependent effects as range change mechanisms. Given the statutory importance of maintaining waterbird populations in designated protected areas, it is important to maintain surveys for identifying changes in local abundances and distribution that are likely to result from changes in total population size. Understanding the dynamic between population change, range change and changes in local abundance is key for understanding the effectiveness of site protection criteria and for targeting of conservation actions.

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DATA ACCESSIBILITY STATEMENT

Count data used were provided by the Wetland Bird Survey (WeBS), a partnership scheme of the British Trust for Ornithology, Royal Society for the Protection of Birds and the Joint Nature Conservation Committee, in association with Wildfowl & Wetlands Trust. These data are available from the British Trust for Ornithology (www.bto.org).

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BIOSKETCH

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Author contributions: V.M and R.G.D. conceived the ideas; V.M. carried out the research and analysed the data with contributions from J.A.G., J.A.A and R.G.D; all authors contributed ideas and to writing the paper.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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