BTO Research Report No. 677

An assessment of the potential benefits of additional stratification of BBS squares by habitat and accessibility to enhance the monitoring of rare species and habitats

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EXECUTIVE SUMMARY

1. Every year approximately 3000 volunteers across the UK take part in the BTO/RSPB/JNCC Breeding Bird Survey (BBS), recording breeding birds in randomly selected 1-km squares (stratified regionally by observer availability) to robustly monitor population trends of some 110 UK bird species. However, the chances of randomly selected squares containing rarer bird species and the habitats of interest that only cover a small proportion of the landscape are low, limiting our ability to monitor population changes. Here we examine options for increasing coverage of rare species and of assemblages occupying certain habitats of interest within the BBS framework, by including additional strata based on habitat type. We also assess the benefits and risks of including an additional stratum based on accessibility to increase volunteer uptake in large regions with low observer density and many inaccessible areas. Currently, volunteer recruitment is often difficult in these regions because randomly selected unmonitored BBS squares may require long drives, difficult walks and over-night camping.

2. We identified species and habitats of interest and assessed the potential for enhanced monitoring of these using a range of realistic options to increase the sampling frequency of habitats of interest through stratification of BBS squares by habitat. We examined the impact of additional sampling strata on current BBS trends and simulated the effect of these scenarios on our ability to monitor species and habitats. Our simulations explored the potential addition of 100, 300 and 600 additional BBS squares.

3. We identified wetlands, open non-intensively managed habitats and woodlands as being habitats that are of interest themselves, and supporting species for which better monitoring is required at a national level. We compared BBS population indices estimated with model weights based on the current regional strata with indices estimated with model weights based on both regional strata and additional habitat and/or accessibility strata. Differences between current BBS population indices and alternative ones could be indicative of improved modelling because of increased stratification or could be indicative of amplification of data noise. We found that for common species additional strata made little difference to the trends but the impact increased for rarer species, suggesting that the differences are largely a precision issue. Adding an additional stratum of open semi-natural habitats or a combination of habitat and accessibility strata altered the BBS trends from their current estimates more than an accessibility stratum alone, or a wetland or woodland stratum. There is therefore less risk of noise amplification from adding a single combined habitat stratum or an accessibility stratum than adding both a habitat-based stratum and an accessibility stratum.

4. Placing additional squares on habitat of interest instead of randomly made no measurable difference to our ability to monitor target species. Additional monitoring in habitats of interest did increase our ability to produce habitat-specific trends in woodland but not in other habitats of interest. Our simulations suggested that an additional 600 squares would be required to make a notable difference to our ability to monitor target species. Additional monitoring would be most effective if additional squares were preferentially allocated in the regions with least monitoring currently, but this is a less realistic option than increasing coverage in already relatively well covered regions. We did not simulate the impact of placing additional squares within an accessibility stratum because the desired outcome of adding an accessibility stratum would be to increase the number of volunteers willing to carry out BBS by increasing the supply of accessible BBS squares.

5. We compared the habitat and uptake of accessible and inaccessible BBS squares in Scotland. A lower proportion of inaccessible squares were sampled compared to accessible ones and inaccessible squares included more open non-intensively managed habitat and less wetland and woodland than accessible squares. Given this, adding an accessibility stratum could correct for the current bias in monitoring. However, it would not be appropriate to add an accessibility stratum to all Scottish regions and further work is required to ensure we identify the regions where an accessibility stratum would be beneficial and define accessibility to maximise volunteer uptake while minimizing the risks of noise amplification.

6. We conclude that adding a habitat-based stratum to increase monitoring in habitats of interest would not improve our ability to monitor species nationally but could increase our ability to monitor habitat-specific trends in a single habitat of interest, particularly in woodlands. We also found that to meaningfully improve monitoring of rare species an additional 600 squares would be required. We would therefore not recommend an additional stratum of habitats of interest. An additional layer of stratification could be a useful tool to increase monitoring of accessible regions of Scotland, where less accessible unmonitored squares currently prevent more squares being allocated. However, this should be done in consultation with BBS regional organisers to ensure an accessibility stratum is introduced only in regions where necessary. The risk of data noise amplification in inaccessible regions with very little monitoring could be reduced by increasing monitoring in these regions and by altering the accessibility designation criteria.

1. INTRODUCTION

Every year approximately 3000 volunteers across the UK take part in the BTO/RSPB/JNCC Breeding Bird Survey (BBS), recording breeding birds in randomly selected 1-km squares. The BBS began in 1994 and provides robust data to monitor population trends of approximately 110 common UK bird species. We also produce country, regional and/or habitat-specific trends for a number of these (Newson *et al.* 2009). However, rarer bird species and habitats of interest are often poorly monitored by BBS and fall below the sample size threshold for which we report trends. Increasing sample size would increase the number of species for which we can produce trends, increase confidence in the trends and enable us to do more analyses, for example produce regional trends, mapped trends and habitat-specific trends for a greater number of species (Harris *et al*. 2014; Sullivan *et al*. 2015; http://www.bto.org/volunteer-surveys/bbs/latest-results/maps-population-density-and-trends; http://www.bto.org/volunteer-surveys/bbs/latest-results/population-trends). There is also a need to increase coverage so as to continue monitoring of declining species such as Nightingale and Willow Tit that are currently above the sample size threshold but may not be in the future. Here we examine whether the benefits of greater coverage could be enhanced by the targeting of additional strata, directing the additional coverage to where it will most effectively monitor scarce species and habitats of interest. We also assess the benefits and risks of including an additional stratum based on accessibility to increase volunteer uptake in large regions with low observer density and many inaccessible areas. Volunteer recruitment is often difficult in these regions because the remaining vacant randomly selected BBS squares may require long drives, difficult walks and over-night camping.

Currently, BBS 1-km squares are selected randomly within 83 regional strata which roughly correspond to counties. Volunteers are allocated one or more BBS squares from the random selection and once all or almost all of these squares within a region are allocated, more BBS squares are randomly generated within the region. To model BBS population trends, counts are initially modelled in relation to factors of year and square with Poisson error terms and each square is weighted by the size of the region it comes from divided by the number of squares surveyed in that region (Freeman *et al*. 2006). A smoothed population trend is then computed by fitting a thin plate smoothing spline to the annual indices. This approach avoids making any assumptions about the form of the underlying population trend. Confidence intervals for the smoothed population trend are produced by bootstrapping. The basic underlying sites x years model is a modification of the approach adopted by the computer program TRIM (Trends & Indices for Monitoring Data), for the analysis of time series of counts with missing observations (Pannekoek & van Strien 1996). The smoothing approach was originally developed by Siriwardena *et al*. (1998). Ideally such analyses should be implemented within a Generalized Additive Modelling framework (Fewster *et al*. 2000) but this is not applied routinely to BBS trend due to the high computational demand generated by the bootstrapping.

This report assesses the advantages and disadvantages of using two alternative types of additional strata in the current stratified sampling method to improve monitoring. Firstly, we tested the potential for additional habitat strata, focussed on priority habitats to increase the sample of squares from those habitats, and to increase the coverage of rare species associated with those habitats. Secondly, we tested the potential for introducing an additional stratum in large and sparsely populated BTO regions, such as the Scottish Highlands, as a means of increasing the number of accessible squares available to volunteers.

In doing this work, we also take account of previous projects where additional surveys have been undertaken within specific habitats in order to deliver additional monitoring that has been requested within the BBS framework. In a three-year project funded by the Forestry Commission and

Scottish Natural Heritage additional Scottish woodland squares were monitored. These have been included in the main BBS trends for all species since 2014 by including an additional woodland stratum in Scotland. The 'What's Up' scheme and the Upland BBS funded by Natural England have provided additional upland BBS monitoring and these squares are now also included in BBS trends using an upland stratum. These additional habitat-specific squares are currently analysed with the standard BBS squares to create the BBS trends for all species. However, these arrangements have arisen from short-term policy needs and funding opportunities and there is a need to identify the optimal stratification approaches in terms of long-term strategic planning.

Here we examined the potential to create coherent improvements in BBS sampling at a UK scale, focussed on increasing the number of species for which we can produce national trends and on increasing the number of species for which we can estimate habitat-specific trends for habitats of interest. We aim to identify which types of habitat stratification would be most effective and the effect of a range of additional monitoring scenarios on the level of additional coverage of species and habitats of interest. We also tested whether additional levels of stratification will alter current trends. Differences between current BBS population indices and alternative ones could be indicative of improved modelling because of increased stratification or could be indicative of lower precision because of amplification of data noise. Large differences between current BBS trends and trends run with additional strata will indicate a high risk of noise amplification.

We examined the effect of additional stratification on coverage of rare species and habitats using the following steps:

- *Identifying target species*: We defined target species as species for which additional coverage could have a big impact on our ability to monitor them. These were species which are currently observed on between 20 and 90 BBS squares per year, thus near to the threshold of 40 squares per year, below which we do not produce trends due to poor precision.
- *Identifying habitats of interest*: We identified habitats of interest by identifying under-monitored habitats, habitats that target species were predominantly in and through discussions between authors and the BBS Steering Group of which habitats we wish to increase our ability to monitor habitat-specific changes in species and assemblages.
- *Identifying percentage habitat cut-off*: In the Scottish Woodland project, which aims to increase BBS coverage of Scottish woodlands, squares are considered to be woodland squares if >15% of the square is woodland. We examined the optimal threshold for other habitats of interest and whether a 15% threshold was appropriate for these habitats.
- *Impact of increased stratification on current trends*: We tested whether adding more levels of stratification significantly changed the current national BBS trends for a random selection of example species. Increasing the number of subdivisions by dividing regions into habitat types will decrease the number of squares monitored in each subdivision. With fewer squares monitored in each subdivision stochasticity could be amplified and precision reduced.
- *Identifying simulation scenarios*: Discussion lead us to identify six realistic scenarios for increasing coverage of rare species and habitats in the future. These were combinations of varying numbers of additional squares monitored and varying the method used to allocated additional squares, either as currently allocated or within habitat strata.
- *Simulating the impact of stratification scenarios on target species*: We simulated the scenarios identified above including a null scenario in which the current system for allocating BBS squares was used. We compared our predicted ability to monitor target species at a national scale in each of the simulated scenarios.
- *Simulating the impact of stratification scenarios on habitat community change*: Currently habitat-specific BBS trends are produced for some species to monitor communities within

habitats. We also compared our ability to monitor species in habitats of interest under each of the scenarios.

- *Identifying the risks and benefits of accessibility strata:* We compared the habitats of inaccessible and accessible squares in Scotland, identified whether there has been a bias in selection of accessible squares and identified where an additional accessibility stratum could amplify noise in the data.

2. METHODS

2.1. Identifying Target Species

National BBS trends are currently produced for all species that are present in more than on average 40 squares annually. Below this threshold the trends are not considered to be sufficiently robust for regular reporting. There are currently 110 species that meet this criterion. To increase the number of species for which we can produce national trends and to increase the robustness of trends for species marginally within this threshold, target species were identified as being those recorded in between 20 and 90 (inclusive) BBS squares per year on average. We identified 31 target species that met this criterion: Cetti's Warbler, Peacock, Twite, Marsh Harrier, Lesser Spotted Woodpecker, Ring Ouzel, Dunlin, Mandarin, Teal, Nightingale, Gadwall, Goosander, Pied Flycatcher, Hobby, Peregrine, Barn Owl, Crossbill, Wood Warbler, Willow Tit, Kingfisher, Dipper, Golden Plover, Ring-necked Parakeet, Common Sandpiper, Common Tern, Whinchat, Little Grebe, Great Crested Grebe, Redshank, Grasshopper Warbler and Tawny Owl.

Fulmar, Ringed Plover, Whimbrel, Little Egret and Fieldfare also met the target species criteria but were excluded following discussion because non-breeding flocks can be recorded. To exclude non-breeding flocks of Golden Plover and Dunlin we excluded transects with counts of over 10 individuals and counts from lowland sites.

2.2. Identifying Habitats of Interest

To identify habitats of interest we firstly identified habitats that are poorly represented in the current sample of BBS squares. To do this we compared the percentage cover of each of the habitat classes identified in the Land Cover Map 2000 (LCM2000) in monitored BBS squares with the percentage cover across Britain (GB).

Secondly we determined the average number of target species seen per BBS square in each habitat class. The mean annual sum of target species in a square was multiplied by the fraction of the square covered by each habitat class.

Finally we used the results from these two exercises above and ecological knowledge to simplify the number of habitat classes that were evaluated as potential strata within any revised BBS sampling strategy.

2.3. Identifying Percentage Habitat Cut-Off

Robust habitat-specific species trends are required to identify changes in assemblages within habitats of interest. Habitat-specific trends are reported currently if the species in question is recorded in an average of >30 squares annually. The number of BBS squares of a specific habitat type will depend on how we categorise habitats, i.e. what proportion of a 1-km BBS square must be woodland for the square to be considered a woodland square. In the Scottish woodland survey squares must be at least 15% woodland to be considered a woodland square and thus available for additional monitoring. Here we examined the effect of varying this 15% cut-off point on our ability to monitor habitat-specific community change. Habitat-specific BBS trends are based on habitat class at the transect section level not at the square level so the percentage cut-off point relates only to selection of squares for monitoring.

We identified the number of GB 1-km squares available of each habitat of interest given 5%, 10%, 15%, 20% and 25% cut-offs. In each habitat of interest we then identified the number of species that are adequately monitored (species that are currently recorded in >30 squares on average of this each habitat per year), at these cut-off points both under current levels of monitoring and under a scenario of increased monitoring. To do this we found the proportion of habitat-squares in which each species was seen. We multiplied this proportion by the number of habitat-squares monitored between 1994 and 2012 then assumed that the number of habitat-squares monitored would remain as observed in 2012 for 20 years and the proportion of squares that species were observed in would remain constant. This allowed us to estimate the mean annual number of habitat-squares each species would be observed in between 1994 and 2032. To estimate the number of additional species that would be well-monitored with 50 additional habitat-squares per year monitored we assumed that during 2012–2032 monitoring was carried out on 50 additional habitat-squares and repeated the steps described above.

2.4. Impact of Increased Stratification on Current Trends

If BBS squares were to be allocated within additional strata, the weighting of squares when analysing BBS trends would need to reflect this. We examined whether the inclusion of additional layers of stratification significantly impacts current BBS trends. We calculated BBS trends for 10 species selected to cover a range of prevalence: Common Sandpiper (currently observed in 61 BBS squares per year), Siskin (149 squares/year), Mute Swan (244 squares/year), Wheatear (303 squares/year), , Cuckoo (696 squares/year), Buzzard (894 squares/year), Pied Wagtail (1209 squares/year), Goldfinch (1553 squares/year), Swallow (1895 squares/year) and Chaffinch (2391 squares/year). Firstly we calculated trends using the standard method: we modelled the count against year and square, both as factors, and used a Poisson error distribution. Counts were weighted 1/the annual coverage in their region (i.e. area of the region/number of BBS squares monitored in that region and year).

Log(count) ~ square + factor(year)

We ran six additional models for each species using six alternative divisions of regions. The first (alternative 1) subdivided each Scottish region into accessible and inaccessible parts. Inaccessible 1-km squares were defined as those in which the centre point of the square was over 3 km from road, or included in 10-km square with 25 or fewer atlas volunteers within 50 km (Fig 1). The second, third, fourth and fifth models subdivided each British region into parts with more or less that 15% of four habitat types. The four habitat types were wetland (inland water, saltmarsh or fen, marsh and swamp) (alternative 2), non-intensively managed open habitat (bog, dense/open dwarf shrub heath, montane habitats, bracken and acid grassland) (alternative 3), broad-leaved or mixed woodland only (alternative 4) and finally, any type of woodland (alternative 5). The habitat types were defined by LCM2000. The final model combined all of the subdivisions described above (alternative 6). In this model regions were subdivided into parts with more or less than 15% of at least one of the habitat of interest (>15% wetland, >15% woodland or >15% non-intensively managed open habitat) and in Scotland regions were further subdivided by accessibility. Thus Scottish regions were divided into four sub-regions, and regions in the rest of the UK into two sub-regions.

We compared the resulting population trends, plotting the population indices calculated from alternative regional divisions alongside the current BBS indices. To reduce computational time, the confidence intervals we present for current trends are calculated from the standard errors associated with the year effect, rather than using the bootstrapping method routinely used to calculate the confidence intervals on smoothed indices. We also calculated the R^2 value for the association between indices from alternative regional divisions and the standard BBS indices. We modelled log-transformed R^2 values against the strata and the species' mean squares per year in which they are observed in a linear model to test whether any of the alternative strata altered the population indices significantly more than others.

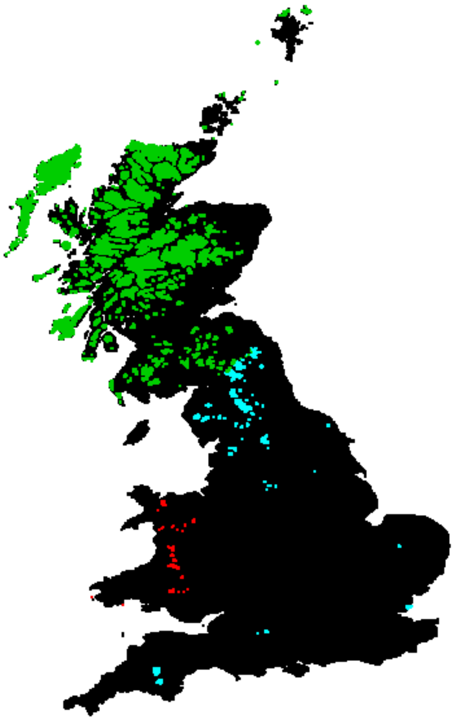

Figure 1 Map of accessible (black) and inaccessible 1-km squares in England (pale blue), Wales (red) and Scotland (green).

2.5. Identifying Simulation Scenarios

We carried out a number of simulations to estimate the effectiveness of a variety of options to increase the number of species we can robustly monitor nationally and in habitats of interest. The aim of the simulations was to identify our monitoring ability for species over 25 years under a number of scenarios. The scenarios were selected to identify the best strategy for increasing the number of species for which we can produce UK trends and habitat-specific trends within habitats of interest.

We identified seven scenarios for simulation resulting from all combinations of the following variables: zero, 100, 300 and 600 extra squares monitored and extra squares selected randomly or randomly from habitats of interest. In the first instance all squares were selected in regions in proportion to the current regional coverage (i.e. additional squares are more likely to be monitored in regions with currently high coverage). We also identified a further six “best-case” scenarios where the extra squares are selected randomly or randomly from habitats of interest as before, but with additional squares selected in regions in inverse proportion to current regional coverage (methods described below). These are the “best-case” scenarios, in which additional squares would be monitored primarily in currently under-monitored regions. It is highly unlikely that it would be possible to achieve these best-case scenarios without additional funding for professional field workers but it is useful to compare the benefits of additional monitoring in under-monitored regions compared to in habitats of interest. Numbers of additional squares were based on the range of values that BBS staff felt might be realistic to achieve. We did not simulate the impact of placing additional squares with an accessibility stratum because the desired outcome of adding an accessibility stratum would be to increase the number of volunteers willing to carry out BBS, because of an increased supply of accessible BBS squares.

2.6. Simulating the Impact of Stratification Scenarios on Target Species

The simulations carried out to test the impact of stratified or non-stratified additional squares assumed that each square had a species-specific suitability that can change over time. The suitability of a square influenced the probability of occupation (present where previously unmonitored), colonisation (present where previously absent), extinction (absent where previously present) and the probability of counting additional individuals where one individual was seen. We used BBS data to parameterize these factors as described below, using the Common Sandpiper as an example species.

1. First we randomly generated square suitability scores from an exponentially transformed normal distribution. These were assigned to BBS squares (real, not simulated) in order of the mean number of Common Sandpipers (as example species here) counted per year on squares. Hence the square with most sandpipers was assigned the highest of the randomly generated suitability scores. The order among squares with tied counts was assigned randomly. Squares were thus assigned a suitability score based on a predictable distribution instead of just using the mean number of birds, allowing random generation of square suitability in the simulations.

2. We parameterized the probabilities of occupation and colonisation by modelling the probability of the event against square suitability. The response variable in each case was the number of times each event happened on each square out of the total number of times the event could have happened: e.g. a square would have to be monitored two years in a row for a colonisation or extinction to occur. In both cases the response variable was modelled against square suitability with a quadratic term (square suitability^2) to allow for a non-linear relationship. If the quadratic term was not significant it was removed. In each model a binomial error distribution was used. We report on the significance of occupation and colonisation parameter estimates, and for the extinction and number of observation parameters described below to identify species for which the simulations may have high uncertainty.

3. To parameterize the chance of extinction on squares where there was a presence in the previous year, a binary response factor of presence or absence was modelled against the square suitability score with a quadratic term and the number of observations in the previous year. Non-significant variables were removed in a step-wise manner.

4. To parameterize the chance of multiple sighting on occupied squares, occupied squares were scored on the presence or absence of two or more individuals in each of the years they were occupied in. This dataset was added to: on all squares where two individuals were seen squares were scored on the presence or absence of three or more individuals. This was continued: on all squares where three individuals were seen squares were scored on the presence or absence of four or more individual, etc. Thus a response factor was created of the probability (0 or 1) of seeing another individual. This response variable was modelled against square suitability, a quadratic term for square suitability and the number of individuals already counted (i.e. there may be a different probability of seeing an additional individual if three have already been sighted compared to if only one has already been sighted). Here the square was included as a random factor and a binomial error distribution was used. Non-significant explanatory variables were removed from the model.

5. We also used BBS data to parameterize the probability of a square switching from being monitored to not being monitored or vice versa.

6. We identified the difference in suitability between squares with more or less than 15% of any of the three identified habitats of interest, hence identifying the mean and standard deviation of log-transformed square suitability scores on habitats of interest.

7. In 2012, 3336 BBS squares were monitored (excluding Northern Ireland and the Channel Islands). To make our simulations realistic we generated 5875 squares: the current number of squares monitored, 3336, plus the turnover (there was a mean turnover of 101.56 squares per year between 1994 and 2012 multiplied by 25, the number of years the simulations were run for). The position of these squares was randomly selected, with the probability of them being positioned in each region equal to the current proportion of squares monitored in each region. The habitat of each square (wetland, open non-intensively managed habitat, woodland or other) was randomly generated, with the probability of each habitat type based on the percentage cover of habitat types in the square's region. This is the realistic distribution of additional squares if they were carried out by volunteers and we report on the proportion of monitored squares in each habitat given this distribution of squares. We randomly assigned each square with a value from normal distributions with the mean and standard deviation as observed in the distribution of log-transformed suitability scores in the habitat type assigned to the square. We exponentially transformed these values to assign the simulated squares with suitability scores.

8. We selected 3336 squares randomly from the 5179 generated squares for the first simulation type. For the other simulation types 100, 300 and 600 additional squares were also selected, either randomly or stratified by a habitat of interest.

9. The presence or absence of sandpipers on the square was assigned randomly according to the probability of occupation, based on the coefficients of the model of occupation probability. On occupied squares the probability of counting a second individual was calculated and the presence of a second individually assigned randomly given the probability. The same approach was used to determine whether a third individual was counted on squares with two, and so on until no more squares remained with an unknown number of individuals.

10. In the second year of the simulation all monitored squares were randomly assigned as re-monitored or not according to the probability of squares switching monitored status. New squares were selected at random from unmonitored squares to replace squares where monitoring ceased. The presence in newly monitored squares was assigned as described above for the first year of monitoring. For squares which had been monitored in the previous year, their new status was assigned according to their probability of extinction and colonisation. This process was repeated for 25 years.

11. For each simulation type, 100 simulations were run and we identified the number of squares that the species was observed in each year.

12. To quantify the effect of adding squares randomly or within habitats of interest we modelled the mean annual number of squares with observations in each simulation with the number of additional squares and the type of simulation (squares added randomly or by habitat) and the interaction between additional squares and simulation type as explanatory variables with species as a random factor.

13. We use a chi-squared test to determine whether species' habitat preference influenced whether habitat stratification significantly improved monitoring, worsened or made no

difference to monitoring. We divided target species into wetland species (Cetti's Warbler, Marsh Harrier, Mandarin, Teal, Gadwall, Goosander, Kingfisher, Dipper, Common Sandpiper, Common Tern, Little Grebe, Great Crested Grebe, Redshank, Grasshopper Warbler), species specialising in open semi-natural habitats (Twite, Ring Ouzel, Dunlin, Hobby, Peregrine, Golden Plover, Whinchat), woodland habitats (Lesser Spotted Woodpecker, Nightingale, Pied Flycatcher, Crossbill, Wood Warbler, Willow Tit, Tawny Owl) or other/non-specific (Peacock, Barn Owl, Ring-necked Parakeet).

14. We repeated the simulations described above but assuming instead that the additional squares would be allocated in inverse proportion to the current regional distribution of BBS squares, thus simulating a 'best-case' scenario, to determine if additional squares in under-monitored regions would give additional benefits. We compare the four scenarios (each combination of squares selected randomly or randomly on habitats of interest, and squares selected regionally in proportion to current regional monitoring levels or by inverse proportion to current regional monitoring levels) by calculating the mean annual observation for each target species given 600 additional squares monitored. We then modelled these mean values in a mixed model with the scenario type as the explanatory variable and species as a random factor.

2.7. Simulating the Impact of Stratification Scenarios on Habitat Community Change

We currently produce habitat-specific trends for a selection of more common species, allowing us to monitor community change within habitats. Sample sizes limit the number of species for which we can produce habitat trends. We examined whether selecting additional BBS squares within habitats of interest could increase our ability to monitor community change within habitats using the 31 target species as a proxy for other species within the habitats. To examine the effectiveness of adding habitat-specific BBS squares to improve monitoring of habitat-specific community trends we used the simulations described above to compare the mean number of observations per year of target species on woodland, wetland and open non-intensively managed habitats, given randomly assigned additional BBS squares or habitat-specific additional BBS squares. For each habitat we used a linear model to model the mean observations per year in each simulation against number of additional square and the type of simulation (squares added randomly or by habitat) and the interaction between additional squares and type, with species included as a random factor.

2.8. Risks and Benefits of Accessibility Strata

Creating population indices with an additional accessibility stratum in Scotland could improve robustness of indices if the uptake of randomly allocated squares is biased by accessibility and assuming that there are habitat differences between accessible and inaccessible squares. With an accessibility stratum, counts from inaccessible habitats would be upweighted, reducing a habitat selection bias. However, there is a risk that BBS squares in large, poorly monitored inaccessible areas would be given extremely high weights, thus amplifying any noise in the data. To assess the risks and benefits of introducing an accessibility stratum in Scotland we first determined whether there were habitat differences between accessible and inaccessible squares. We created three general linear mixed models (GLMMs) which modelled the percentage cover of wetland, semi-natural open habitats and woodland in each 1-km square against the accessibility of the squares, including the region as a random effect and using a binomial error distribution.

Secondly we compared the weights of BBS squares under the current regional strata with those incorporating an additional accessibility stratum to identify if there is currently a monitoring bias towards accessible squares. We used a paired T-test to compare the average weight of accessible and inaccessible squares in regions. We also used the calculated weights to identify regions in which there is a high risk of noise amplification if an accessibility stratum is introduced. The risks could be reduced by ensuring higher monitoring of the large, under-monitored regions, either by volunteers or professionals, although the latter is unlikely under current funding constraints.

3. RESULTS

3.1. Identifying Habitats of Interest

We found that there were a few habitats that were notably under-monitored by BBS relative to their coverage of Britain. These were open and dense dwarf shrub heath, coniferous woodland, acid grassland bog and montane habitats, bracken and littoral sediment (Fig 2). Low monitoring on these habitats is likely to be a result of regional variation in BBS sampling so overall results should not be biased with response to trends in these habitats once weights are incorporated. The number of sightings of target species per 1-km square varied between 2.9 and 0.4 between habitat types. The habitats with high numbers of sightings of target species (see methods for list) could broadly be divided into four groups: wetland, coastal, open non-intensively managed habitats and woodland (Table 1). As the BBS methods is not ideal for monitoring coast lines, we did not consider linear coastal habitats further, but we did include saltmarshes in a wetland category as saltmarshes are classified as being within the same broad habitat type as fens, marshes and swamps in the BBS habitat survey. The three habitats of interest that we identified were wetland (inland water, saltmarsh and fen, marsh and swamp), open non-intensively managed habitats (bog, bracken, montane, open and dense dwarf shrub heath and acid grassland) and woodland (coniferous and broad-leaved and mixed).

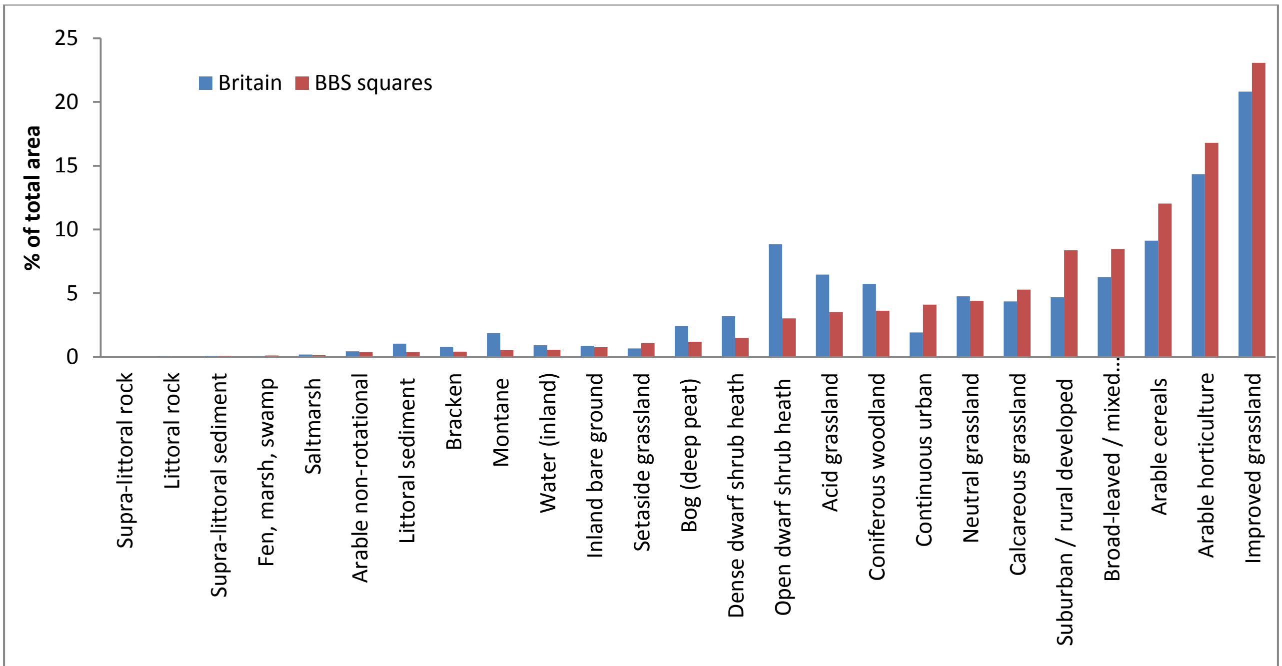

Figure 2 Land Cover Map 2000 habitat types as a proportion of the total area of Great Britain (blue) and surveyed BBS squares between 1994 and 2012 (red), assuming BBS transects cover habitats within 1-km squares evenly. Results not corrected of variable sampling intensity across regions.

Table 1 Mean density of individuals per km^2 of the 31 target species in each habitat class in BBS squares monitored between 1994 and 2012.

Habitat classes from Land Cover Map 2000	Sightings per sq km of target species
Water (inland)	7.31
Supra-littoral rock	6.73
Saltmarsh	6.69
Fen, marsh, swamp	5.64
Supra-littoral sediment	4.40
Bog (deep peat)	4.29
Littoral sediment	3.93
Littoral rock	3.46
Dense dwarf shrub heath	3.15
Open dwarf shrub heath	2.73
Montane	2.59
Coniferous woodland	2.57
Bracken	2.54
Acid grassland	2.50
Neutral grassland	2.22
Continuous urban	1.92
Inland bare ground	1.58
Setaside grassland	1.50
Broad-leaved / mixed woodland	1.41
Suburban / rural developed	1.21
Calcareous grassland	1.21
Arable non-rotational	1.12
Improved grassland	1.07
Arable horticulture	0.82
Arable cereals	0.74
All habitats	1.45

3.2. Identifying Percentage Habitat Cut-Off

The coverage of habitats of interest declined with an increasing cut-off threshold (Table 2). With a 15% cut-off 3.2% of habitats of interest were wetland, 53.1% were open habitats and 43.7% were woodland habitats.

We found that with current BBS monitoring there were between zero and 106 species adequately monitored (monitored in over 30 habitat-specific squares per year on average) within habitats of interest, depending on the habitat type and the % cover cut-off threshold (Fig 3). As the percentage habitat cut-off point increased fewer squares were classified as belonging to each of the habitat types and therefore species were recorded in fewer habitat-specific squares. This has the effect of reducing data, thus increasing confidence limits on trends and making trends more difficult to detect. However, the lower the percentage habitat cut-off, the less habitat-specific these species will be. For any species to be recorded in over 30 squares per year on wetland squares with current BBS monitoring, a percentage habitat cut-off of 15% or lower was required. With more restrictive cut-off points (i.e. higher cut-offs) there were fewer squares hence less data, while with less restrictive cut-offs, additional squares may not be specific enough to the habitat of interest to monitor habitat-specific species. There was no indication that altering the percentage habitat cut-off value from 15% would lead to greater gains in well monitored species under increased monitoring.

Table 2 The number of GB 1-km squares available for monitoring given % cut-off values.

	% of habitat in 1-km square				
	5%	**10%**	**15%**	**20%**	**25%**
Wetland	10606	6283	4350	3293	2568
Open	89822	78798	71699	66609	62535
Broad-leaved & mixed woodland	87902	53567	33406	21133	13504
Woodland	112675	79817	59001	45081	35394

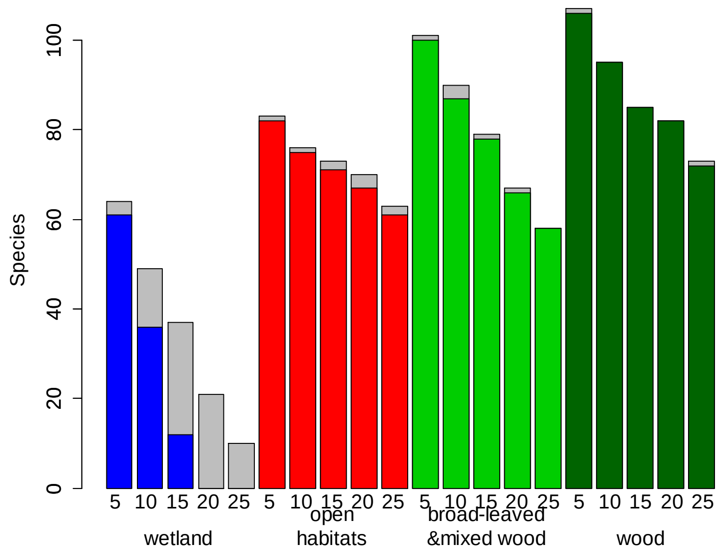

Figure 3 The number of species that are currently (coloured bars) recorded in over 30 habitat-specific squares per year on four habitat types; wetland (blue), open habitats (red), broad-leaved and mixed woodland (pale green) and all woodland (dark green). Additional species that are likely to reach the 30-squares/year threshold if an additional 50 squares were monitored of the specified habitat are shown in grey.

3.3. Impact of Increased Stratification on Current Trends

For all species the alternative trends closely matched the current trends and were well within confidence intervals (Fig 4). Confidence intervals were based on 1.96*S.E of the modelled year effect, rather than the bootstrapping method routinely used to produce confidence intervals for smoothed BBS indices. The confidence intervals here are rather larger than for smoothed and bootstrapped BBS trends but are still useful to highlight the similarity between the current and alternative trends. The mean square differences (R^2) between the alternative trends and the current trends for each species were above 0.1 (10%) for three species; Common Sandpiper (for all stratification options), Mute Swan (when stratified by wetland, woodland and a combination of habitat and accessibility) and Wheatear (when stratified by open non-intensively managed habitats and a combination of habitat and accessibility) (Fig 5).

Population indices produced with three of the alternative strata: accessibility, wetland and woodland, were more similar to current BBS trends than the other three: open habitats, broad-leaved woodland and a combination of habitat and accessibility (R^2 difference = -0.616 ± 0.180, t = -3.41, P = 0.001). Population indices of rarer species were more affected by additional strata than those of more common species (R^2 declined by $-1.07 \times 10^{-3} \pm 2.38 \times 10^{-4}$ per additional observation, t = -4.49, P < 0.001). As the additional strata have more influence of smaller sample sizes the differences are likely to be due to stochastic effects.

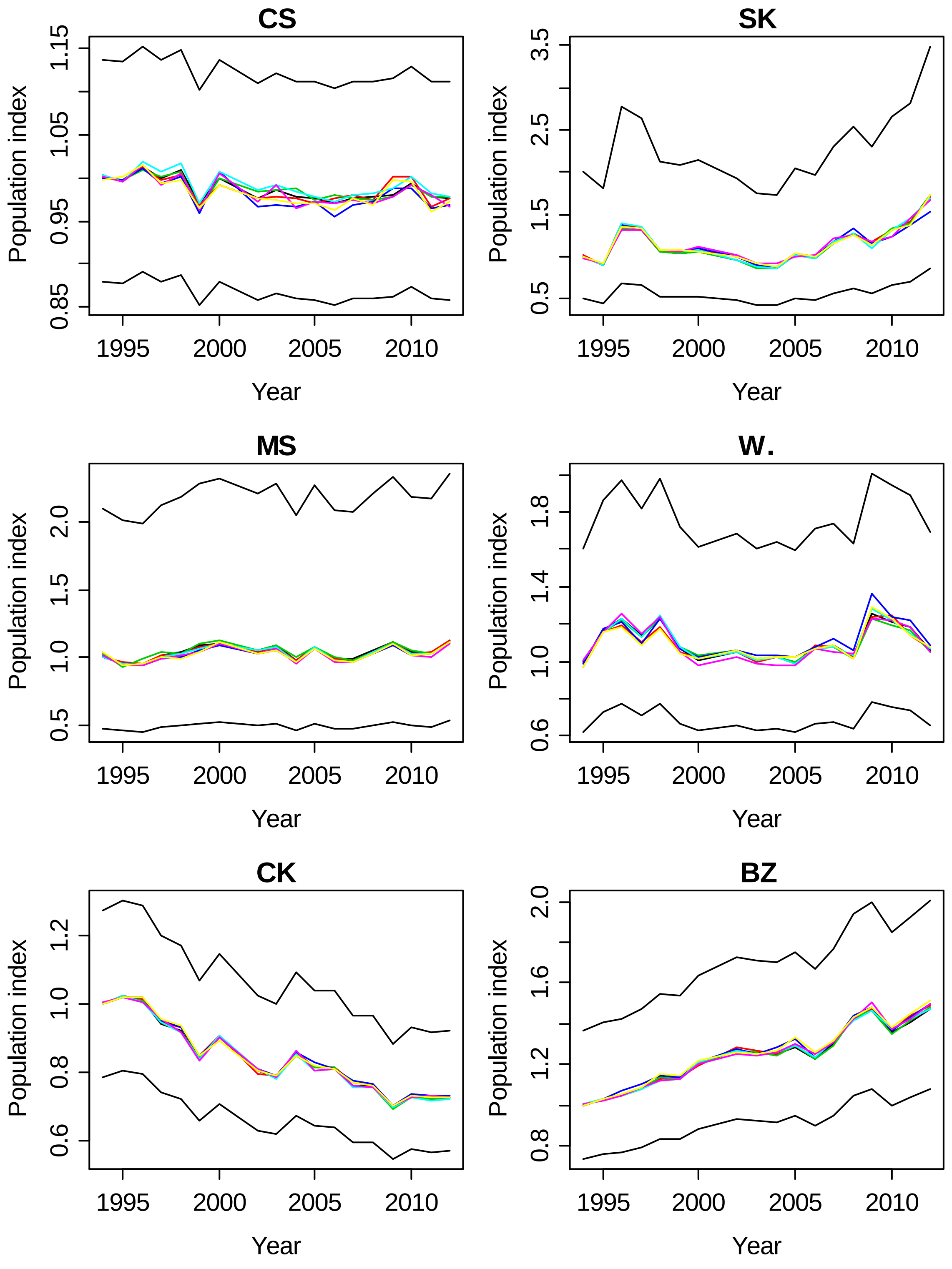

Figure 4 Population trends for ten example species (Common Sandpiper: CS, Siskin: SK, Mute Swan: MS, Wheatear: W., Cuckoo: CK, Buzzard: BZ, Pied Wagtail: PW, Goldfinch: GO, Swallow: SL and Chaffinch: CH) calculated using weights from current BBS regions ± S.E. (black), with trends estimated from six alternative regional divisions, accessibility in Scotland (red), wetland (blue), open non-intensively managed habitats (green), broad-leaved and mixed woodland (pale blue), all woodland (pink) and Scottish accessibility and habitats of interest combined (yellow).

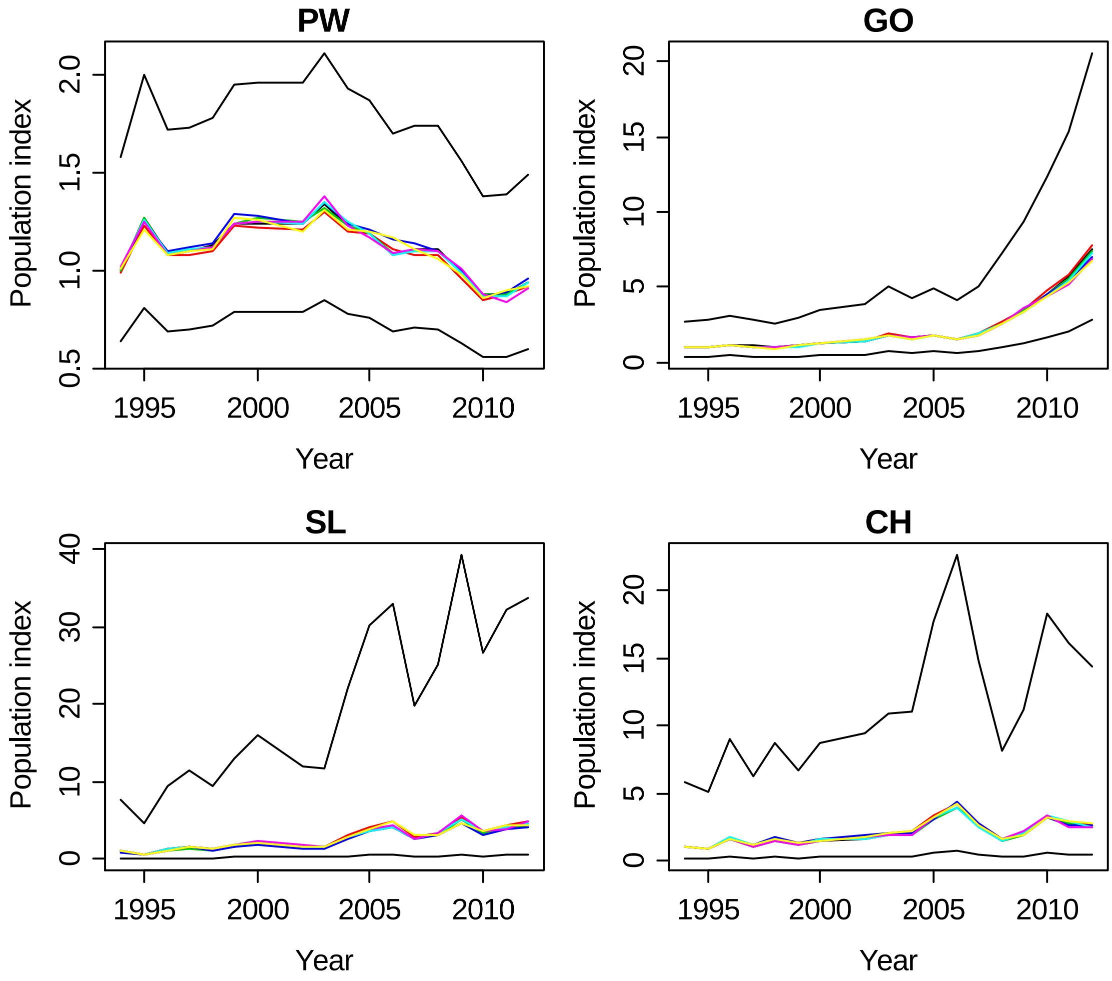

Figure 4 Continued.

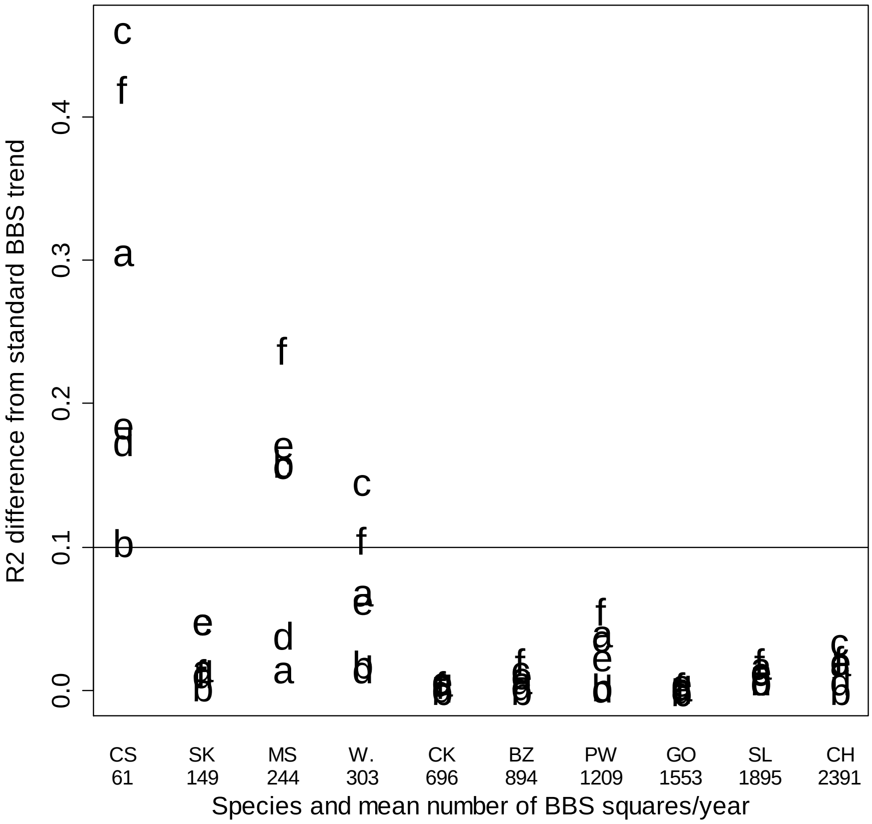

Figure 5 The mean squared difference between current BBS trends and alternative trends (R^2) for 10 example species (Common Sandpiper: CS, Siskin: SK, Mute Swan: MS, Wheatear: W., Cuckoo: CK, Buzzard: BZ, Pied Wagtail: PW, Goldfinch: GO, Swallow: SL and Chaffinch: CH). Alternative BBS trends were calculated with six variations of weightings based on combinations of regional, habitat and accessibility strata: (a) regional + Scottish access, (b) regional and wetland, (c) regional and open non-intensively managed habitats, (d) regional and broad-leaved and mixed woodland, (e) regional and woodland and (f) regional, Scottish access and 'habitats of interest' (i.e. any square with over 15% of wetland, open or woodland habitats).

3.4. Simulating the Impact of Stratification Scenarios on Target Species

For each species we parameterised the probability of occupation, colonisation, extinction and the number of observations in an occupied square using GLMs and GLMMs to model these against the site suitability scores (and the count in the previous year for the extinction probability). We examined the significance of the relationships between these parameter estimates and the explanatory variables to identify species for which the simulations may have high uncertainties. For all species the probability of colonisation and occupation (on previously unmonitored squares) varied with the site suitability score and the quadratic site suitability score. The probability of extinction varied with site suitability score for only one species (Great Crested Grebe) but varied with the count in the previous year for all but six species (Twite, Ring Ouzel, Dunlin, Hobby, Crossbill and Tawny Owl). The number of observations per occupied square varied with site suitability score for all species and the quadratic site suitability score for 21 species. In the appendix we present for each species the probability of occupation, colonisation, additional observations where present and extinction, given mean site suitability and the upper and lower quartiles of site suitability.

The majority of the squares selected in the simulations were not on habitats of interest if squares were allocated randomly and regionally in proportion to current monitoring levels (Table 3). 72% of squares selected on habitats of interest were on woodland squares, 23.4% on open habitats and only 4.6% on wetland habitats. If squares were allocated regionally in inverse proportion to current monitoring levels (i.e. the 'best-case' scenario) then the majority of squares were placed on open non-intensively managed habitats, reducing the number of additional squares being placed in woodland habitats while the coverage of wetland squares remained low (Table 3).

For each additional 100 random BBS squares monitored, each target species was observed on average in an extra 1.43 ± 0.015 squares per year (Table 4, Fig 6). Hence an additional 600 squares would lead to target species being observed in an average of 8.58 additional squares per year. Adding squares on habitats of interest only did not significantly change our ability to monitor target species (Table 4). Where additional squares were added in inverse proportion to current regional BBS coverage our ability to monitor target species increased irrespective of whether the squares were placed randomly or on habitats of interest (Table 4).

We compared the predicted impact of habitat stratification on species of different habitat specialisations, comparing the number of wetland, open, forest species and non-specialists for which habitat stratification was predicted to have a significantly positive effect on the number of observations, no effect or a significantly negative effect. The habitat preferences of species did not alter the predicted effect of habitat stratification (χ^2 = 6.16, df = 6, P = 0.405) (Table 5).

Table 3 The habitat classification of 100 additional squares monitored in BBS simulations when selected randomly or within habitats of interest and when selected regionally in proportion or in inverse proportion to current coverage.

	Additional squares placed by regional monitoring level		**Additional squares placed by inverse of regional monitoring level**	
Habitat	**Random selection**	**habitats of interest selected**	**Random selection**	**habitats of interest selected**
wetland	1.24	4.96	2.06	4.4
open habitats	11.73	22.67	39.93	52.87
woodland	24.52	72.38	19.15	42.72
other squares	62.51	0	38.86	0

Table 4 Comparison of four scenarios of placement of additional squares.

Regional placement compared to current regional distribution	**Habitat placement**	**Mean additional observations for target species given 100 additional squares**	**Additional benefit from stratification or inverse regional placement**
In proportion	Random	1.43 ± 0.015	
In proportion	Habitats of interest	1.47 ± 0.021	t = 0.02, P = 0.983
Inverse proportion	Random	1.69 ± 0.021	t = 2.57, P = 0.012
Inverse proportion	Habitats of interest	1.54 ± 0.021	t = 2.31, P = 0.023

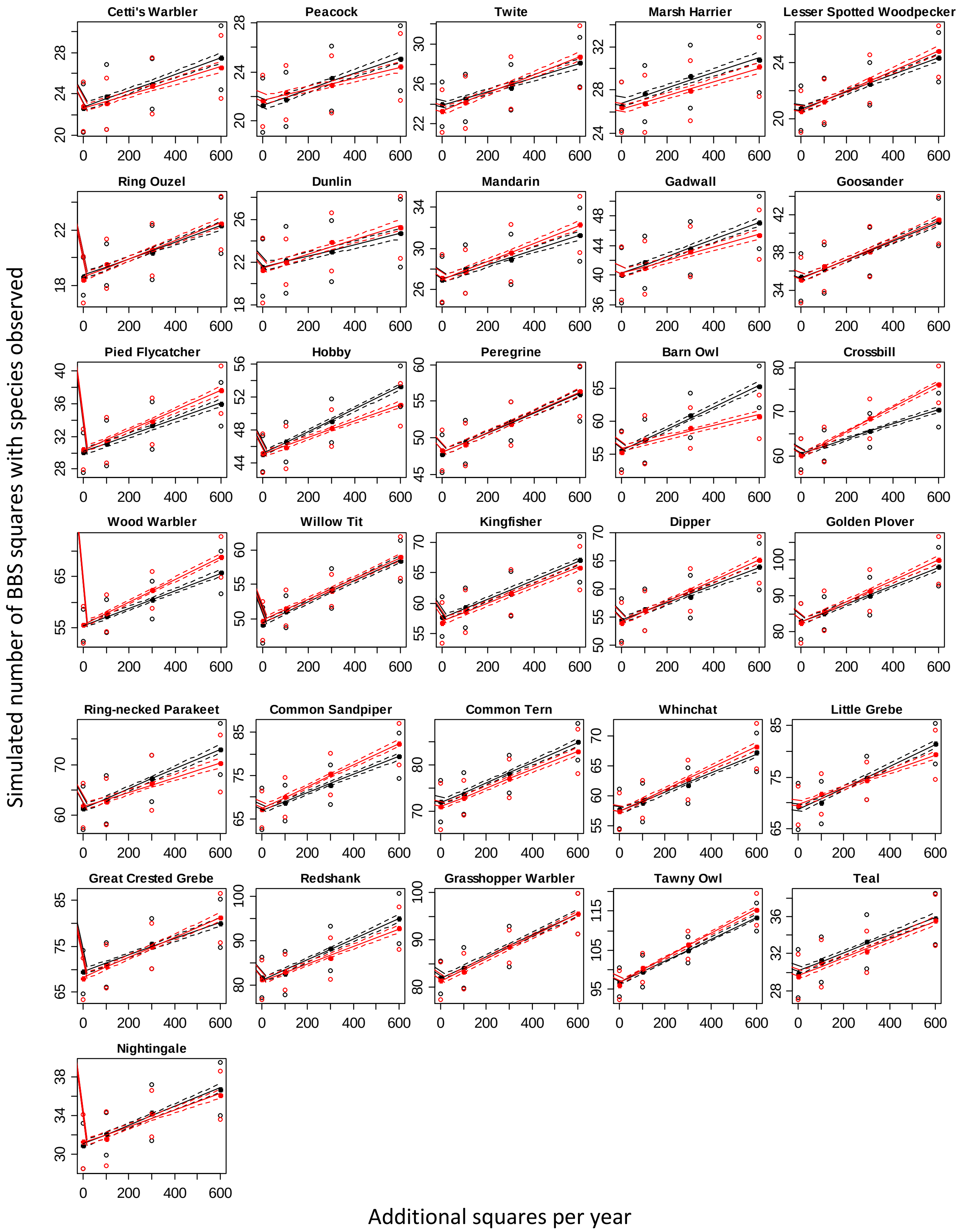

Figure 6 The mean simulated number of BBS squares per year each target species is observed in given current levels of BBS monitoring and with an additional 100, 300 and 600 squares monitored (closed circles) ± S.E (open circles). Black circles show simulations where squares were added at random, red circles show simulations where additional squares were only placed within a habitat stratum. The solid lines indicate the modelled relationships between observations, additional squares, type of simulation (random additional squares or habitat-selected additional squares) ± 95% confidence intervals (dashed lines).

Table 5 Number of species for which stratification significantly improved, did not change or significantly worsened monitoring by species habitat preference. See text for methods and Fig 6 for species-specific plots.

Species habitat preference	Monitoring improved by habitat stratification	Monitoring not changed by habitat stratification	Monitoring worsened by habitat stratification
Wetland	4	5	5
Open semi-natural habitats	4	2	1
Woodland	2	5	0
Non-specific	1	1	1

3.5. Simulating the Impact of Stratification Scenarios on Habitat Community Change

Adding squares of habitat of interest instead of adding squares randomly improved our ability to monitor populations within woodlands but not in other habitats of interest. Adding squares in habitats of interest rather than adding squares randomly changed the slope of increasing observations with additional squares in woodlands by 0.142 ± 0.061 (t = 2.33, P = 0.020) while in wetland and open non-intensively managed habitats it change respectively by 0.010 ± 0.016 (t = 0.60, P = 0.548) and -0.073 ± 0.070 (t = -1.04, P = 0.297).

3.6. Risks and Benefits of Introducing a Scottish Accessibility Stratum

We defined accessible 1-km squares as those within 3 km from road and had more than 25 atlas volunteers within 50 km. In Scotland 59,639 km^2 was defined as accessible and 16,742 km^2 as inaccessible (Fig 1). We found that inaccessible 1-km squares in Scotland had less wetland cover than accessible squares (0.88% compared to 1.23%, z = 147.7, P < 0.001), more open non-intensively managed habitat (73.8% compared to 35.3%, z = -2040, P < 0.001) and less woodland (2.79% compared to 7.93%, z = 964.6, P < 0.001).

The mean weight that would be given to inaccessible BBS squares if an accessibility stratum was introduced was more than double the weight of accessible squares (mean weight of accessible squares = 357.5, mean weight of inaccessible squares = 747.7, t = -2.44, P = 0.026) (Table 6).

Here we used the area of the smaller subdivision within regions and weights given to BBS squares with regional and accessibility strata to determine the recommendation for introducing an accessibility stratum within each region (Fig 7 for map of Scottish BBS regions). In seven regions, the smaller subdivision within the region (i.e. number of accessible or inaccessible 1-km squares) was fewer than 100 1-km squares so no additional accessibility strata are recommended (Table 6). If regional BBS organisers report a problem in of volunteers without suitable squares available in these regions then the accessibility definition could be narrowed to define more of the region as inaccessible.

In seven regions the number of accessible or inaccessible 1-km squares was between 100 and 200 so an accessibility stratum may not be required. In four of these, uneven sampling would lead to very high weights (>1000) for some squares so additional monitoring of inaccessible squares may be required (accessible in the ISLA region). In fourteen regions there were over 200 1-km squares in both strata so an accessibility stratum is likely to be beneficial but in the five of these regions where high weights would increase the risk of noise amplification additional monitoring in inaccessible areas may be required (Table 6).

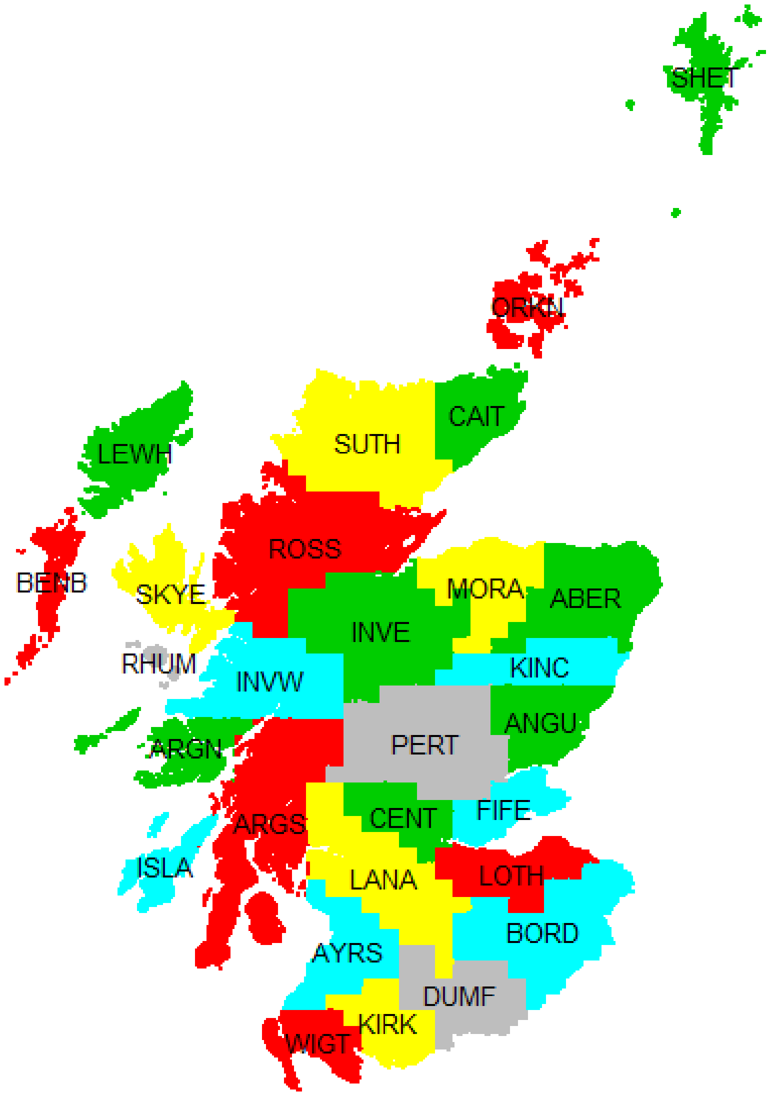

Figure 7 Map of Scottish BBS regions.

Table 6 Mean number of BBS squares monitored per year, areas and weight (area/squares monitored) in accessible (access) and inaccessible (inaccess) areas of Scottish regions. Recommendations were based on the area of the smaller subdivision in regions and the larger weight within regions: A: no accessibility stratum required (area of smaller subdivision < 100), B: accessibility stratum recommended (area of smaller subdivision > 200) but additional monitoring on inaccessible squares required (larger weight > 1000 or some strata currently have no squares monitored and would therefore be likely to have a high weight if only a small number of squares are monitored), C: accessibility stratum recommended (area of smaller subdivision > 200). Weight calculations are based on current numbers of squares, and therefore cannot be calculated for strata with no BBS squares monitored.

Scottish BBS region	Mean BBS squares monitored/year		Area (km^2)		Current mean weight	Weight in BBS trends with added accessibility stratum		Recommendation
	access	inaccess	access	inaccess	All squares	access	inaccess	
RHUM	0	1.56	37	120	100.93	no squares	77.14	A
BENB	0	2.94	24	822	287.32	no squares	279.17	A
FIFE	36.17	0	1532	0	42.36	42.36	NA	A
ABER	17.83	0	3703	82	212.24	207.64	no squares	A
LOTH	22.06	0	2235	61	104.1	101.34	no squares	A
ORKN	6.67	0	955	54	151.35	143.25	no squares	A
LEWH	0	5.22	0	2223	425.86	no squares	425.86	A
ISLA	0	2.56	186	852	406.17	no squares	333.39	A or B
AYRS	5.94	0	2352	138	418.88	395.66	no squares	A or B
ANGU	5.89	0	2222	180	407.89	377.32	no squares	A or B
WIGT	2	0.06	1462	120	769.62	731	2160	A or B
DUMF	11.78	0.28	2756	133	239.64	234	478.8	A or C
SHET	1.44	0.67	1026	117	541.42	710.31	175.5	A or C
CENT	22	3.67	1679	178	72.35	76.32	48.55	A or C
SKYE	5.33	0.11	1527	215	319.96	286.31	1935	B
ARGN	3.72	0.33	1127	402	377.01	302.78	1206	B
PERT	7.89	0.44	4118	1261	645.48	522	2837.25	B
INVW	3.44	0.94	2168	1429	819.57	629.42	1513.06	B
ARGS	8.06	1.17	4294	1185	594.11	533.05	1015.71	B
MORA	7.39	0.61	2397	444	355.12	324.41	726.55	C
KIRK	2.78	0.72	1698	255	558	611.28	353.08	C
ROSS	14.28	3.56	4006	2337	355.68	280.58	657.28	C
INVE	11.11	4.72	3279	2207	346.48	295.11	467.36	C
SUTH	6.39	3.44	2887	2436	541.32	451.88	707.23	C
KINC	15.06	3.11	1722	688	132.66	114.38	221.14	C
BORD	13.33	1.44	4351	280	313.38	326.33	193.85	C
LANA	18.17	1.44	4317	263	233.54	237.63	182.08	C
CAIT	2.78	3.61	1579	483	322.75	568.44	133.75	C

4. CONCLUSIONS

We identified wetlands, open non-intensively managed habitats and woodlands as being habitats that are of interest themselves, and habitats in which increased monitoring may lead to better monitoring at a national level of 31 species of currently low coverage. We compared BBS population indices of 10 example species estimated with model weights based on the current regional stratum with indices estimated with model weights based on regional stratum and an additional habitat and/or accessibility stratum. Differences between current BBS population indices and alternative ones could be indicative of improved modelling because of increased stratification or could be indicative of amplification of data noise. We found that for common species additional strata made little difference to the trends but the impact increased for rarer species, suggesting that the inclusion of additional strata could potentially impact upon national population trends for rarer species, although it is difficult to assess if this is because of reduced bias with new stratification, or amplification of stochasticity in the data from smaller, habitat-specific strata. Adding an additional open semi-natural habitat stratum, or a combination of habitat and accessibility strata altered the BBS trends from their current estimates more than an accessibility stratum alone or a wetland or woodland stratum. There is therefore less risk of noise amplification from adding a single combined habitat stratum or an accessibility stratum than adding both a habitat-based stratum and an accessibility stratum. If habitat stratification and stratification by accessibility were both to be considered, habitat stratification could be restricted, for instance to England where accessibility stratification is not required, or to the most well monitored regions to reduce the amplification of stochasticity.

We tested the effectiveness of additional monitoring, either by placing additional squares randomly or by placing them in habitats of interest. Placing additional squares on habitat of interest instead of randomly made no significant difference overall to our ability to monitor target species. Additional monitoring in habitats of interest did increase our ability to produce habitat-specific trends in woodland but not in other habitats of interest. Increasing BBS monitoring by 300 squares would increase monitoring of target species (species currently on the borderline of adequately monitored) by a mean of 4.29 squares with observation per year. This would not make a great difference to our ability to produce trends for these species. An additional 600 squares would be required to increase the number of squares species are observed on by 8.6 squares per year, or 8.8 squares if those squares are targeted on habitats of interest, further suggesting that the magnitude of benefit associated with habitat stratification is fairly limited. There was no significant difference in effect of habitat stratification between species of different habitat specialisms. We also examined whether habitat stratification would be more effective if additional squares were placed in regions in inverse proportion to current coverage. We found that our ability to monitor target species increased under this placement of additional squares, irrespective of whether the squares were placed on random habitats or on habitats of interest. This suggests that the most important mechanism for improved coverage of species which are currently relatively poorly covered is to target the monitoring of squares in poorly surveyed regions. However, the impact would be relatively small: if 600 additional squares were placed in regions in inverse proportion to current regional coverage target species would only be observed in an additional 1.5 squares on average, compared to if 600 additional squares were selected in regions in proportion to current regional coverage. These low impact of additional monitoring on these target species can be attributed to the low probability of target species being observed on squares irrespective of the site quality (see Appendix).

We did not simulate the impact of placing additional squares with an accessibility stratum because the desired outcome of adding an accessibility stratum would be to increase the number of volunteers willing to carry out BBS by increasing the supply of accessible BBS squares. We compared the habitat and uptake of accessible and inaccessible BBS squares in Scotland. Inaccessible squares were less well monitored than the accessible ones and included more open non-intensively managed habitat and less wetland and woodland than accessible squares. Given this, adding an accessibility stratum could correct for the current bias in monitoring. However, it would not be appropriate to add an accessibility stratum to all Scottish regions and we identified a number of Scottish regions which could benefit from an accessibility stratum as they have large areas of inaccessible land that may currently reduce volunteer uptake. Further work is required to identify the regions where additional volunteers would be recruited if there were more accessible squares and to ensure we define accessibility optimally to maximise volunteer uptake while reducing the risks of noise amplification.

We conclude that adding a habitat-based stratum to increase monitoring in habitats of interest would not improve our ability to monitor species nationally, but could increase our ability to monitor habitat specific trends in a single habitat of interest, in this case in woodlands. We would therefore not recommend an additional stratum of all habitats of interest, but it may be worth considering the inclusion of a woodland strata to increase our ability to monitor woodland trends. To meaningfully improve monitoring of scarce species an additional 600 squares would be required irrespective of whether habitat stratification is applied. Our results suggest that a our ability to monitor target species would be better improved by increasing monitoring in currently under-monitored but this would be difficult to achieve without funding for professional surveyors. An additional layer of stratification could be a useful tool to increase monitoring of accessible regions of Scotland where inaccessible unmonitored squares currently prevent more squares being allocated. This should be done in consultation with BBS and regional organisers to ensure an accessibility stratum is introduced only in regions where it is most likely to result in a significant benefit. The risk of data noise amplification in inaccessible regions with very little monitoring could be reduced by increasing monitoring in these regions and by altering the accessibility designation criteria. A list of the highest priority regions where the introduction of accessibility criteria should be considered is given in Table 6.

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APPENDIX

Predicted probabilities of (Table A) occupation, (Table B) colonisation, (Table C) additional observations and extinctions of target species ± confidence intervals at mean site suitability and upper and lower quartiles of site suitability. Confidence intervals are not presented for the probability of extinction and probability of observing a second individual on squares where the species is present because these were predicted using mixed models.

Table A	Occupation probability on previously unmonitored squares		
Species	**Lower quartile of sites**	**Mean site suitability**	**Upper quartile of sites**
Cetti's Warbler	$4.62 \times 10^{-5} \pm 2.76 \times 10^{-5}$	$1.56 \times 10^{-4} \pm 8.02 \times 10^{-5}$	$2.19 \times 10^{-4} \pm 1.07 \times 10^{-4}$
Peacock	$2.47 \times 10^{-4} \pm 9.04 \times 10^{-5}$	$6.17 \times 10^{-4} \pm 1.97 \times 10^{-4}$	$7.95 \times 10^{-4} \pm 2.43 \times 10^{-4}$
Twite	$1.44 \times 10^{-4} \pm 6.41 \times 10^{-5}$	$3.85 \times 10^{-4} \pm 1.48 \times 10^{-4}$	$5.05 \times 10^{-4} \pm 1.86 \times 10^{-4}$
Marsh Harrier	$1.20 \times 10^{-4} \pm 5.49 \times 10^{-5}$	$3.57 \times 10^{-4} \pm 1.39 \times 10^{-4}$	$4.81 \times 10^{-4} \pm 1.79 \times 10^{-4}$
Lesser Spotted Woodpecker	$5.55 \times 10^{-4} \pm 1.56 \times 10^{-4}$	$1.41 \times 10^{-3} \pm 3.26 \times 10^{-4}$	$1.82 \times 10^{-3} \pm 3.98 \times 10^{-4}$
Ring Ouzel	$2.22 \times 10^{-16} \pm 1.59 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.35 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.38 \times 10^{-10}$
Dunlin	$2.18 \times 10^{-6} \pm 2.34 \times 10^{-6}$	$1.17 \times 10^{-5} \pm 1.06 \times 10^{-5}$	$1.86 \times 10^{-5} \pm 1.59 \times 10^{-5}$
Mandarin	$2.89 \times 10^{-4} \pm 9.91 \times 10^{-5}$	$8.12 \times 10^{-4} \pm 2.33 \times 10^{-4}$	$1.08 \times 10^{-3} \pm 2.94 \times 10^{-4}$
Teal	$1.51 \times 10^{-3} \pm 2.86 \times 10^{-4}$	$2.89 \times 10^{-3} \pm 4.75 \times 10^{-4}$	$3.47 \times 10^{-3} \pm 5.47 \times 10^{-4}$
Nightingale	$1.86 \times 10^{-4} \pm 7.12 \times 10^{-5}$	$6.09 \times 10^{-4} \pm 1.92 \times 10^{-4}$	$8.43 \times 10^{-4} \pm 2.51 \times 10^{-4}$
Gadwall	$2.22 \times 10^{-16} \pm 1.60 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.36 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.42 \times 10^{-10}$
Goosander	$3.89 \times 10^{-4} \pm 1.19 \times 10^{-4}$	$1.22 \times 10^{-3} \pm 3.00 \times 10^{-4}$	$1.66 \times 10^{-3} \pm 3.83 \times 10^{-4}$
Pied Flycatcher	$2.22 \times 10^{-16} \pm 1.60 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.35 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.38 \times 10^{-10}$
Hobby	$1.07 \times 10^{-3} \pm 2.44 \times 10^{-4}$	$3.50 \times 10^{-3} \pm 5.80 \times 10^{-4}$	$4.79 \times 10^{-3} \pm 7.23 \times 10^{-4}$
Peregrine	$1.30 \times 10^{-3} \pm 2.48 \times 10^{-4}$	$3.57 \times 10^{-3} \pm 5.42 \times 10^{-4}$	$4.70 \times 10^{-3} \pm 6.67 \times 10^{4}$
Barn Owl	$7.61 \times 10^{-4} \pm 1.75 \times 10^{-4}$	$2.57 \times 10^{-3} \pm 4.59 \times 10^{-4}$	$3.57 \times 10^{-3} \pm 5.91 \times 10^{-4}$
Crossbill	$4.56 \times 10^{-4} \pm 1.23 \times 10^{-4}$	$1.78 \times 10^{-3} \pm 3.72 \times 10^{-4}$	$2.56 \times 10^{-3} \pm 4.97 \times 10^{-4}$
Wood Warbler	$8.78 \times 10^{-4} \pm 1.85 \times 10^{-4}$	$2.43 \times 10^{-3} \pm 4.24 \times 10^{-4}$	$3.22 \times 10^{-3} \pm 5.30 \times 10^{-4}$
Willow Tit	$1.70 \times 10^{-3} \pm 3.08 \times 10^{-4}$	$4.51 \times 10^{-3} \pm 6.35 \times 10^{-4}$	$5.87 \times 10^{-3} \pm 7.69 \times 10^{-4}$
Kingfisher	$8.69 \times 10^{-4} \pm 1.93 \times 10^{-4}$	$2.84 \times 10^{-3} \pm 4.87 \times 10^{-4}$	$3.90 \times 10^{-3} \pm 6.21 \times 10^{-4}$
Dipper	$5.28 \times 10^{-4} \pm 1.30 \times 10^{-4}$	$1.75 \times 10^{-3} \pm 3.50 \times 10^{-4}$	$2.43 \times 10^{-3} \pm 4.57 \times 10^{-4}$
Golden Plover	$1.46 \times 10^{-4} \pm 4.74 \times 10^{-5}$	$8.61 \times 10^{-4} \pm 2.17 \times 10^{-4}$	$1.41 \times 10^{-3} \pm 3.27 \times 10^{-4}$
Ring-necked Parakeet	$2.22 \times 10^{-16} \pm 1.65 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.40 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.50 \times 10^{-10}$
Common Sandpiper	$2.22 \times 10^{-16} \pm 1.59 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.34 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.37 \times 10^{-10}$
Common Tern	$6.81 \times 10^{-4} \pm 1.51 \times 10^{-4}$	$2.41 \times 10^{-3} \pm 4.28 \times 10^{-4}$	$3.40 \times 10^{-3} \pm 5.65 \times 10^{-4}$
Whinchat	$2.22 \times 10^{-16} \pm 1.61 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.35 \times 10^{-10}$	$2.22 \times 10^{-16} \pm 1.39 \times 10^{-10}$
Little Grebe	$8.39 \times 10^{-4} \pm 1.81 \times 10^{-4}$	$2.81 \times 10^{-3} \pm 4.76 \times 10^{-4}$	$3.90 \times 10^{-3} \pm 6.14 \times 10^{-4}$
Great Crested Grebe	$5.94 \times 10^{-5} \pm 2.51 \times 10^{-5}$	$3.47 \times 10^{-4} \pm 1.18 \times 10^{-4}$	$5.63 \times 10^{-4} \pm 1.78 \times 10^{-4}$
Redshank	$6.53 \times 10^{-4} \pm 1.45 \times 10^{-4}$	$2.60 \times 10^{-3} \pm 4.53 \times 10^{-4}$	$3.80 \times 10^{-3} \pm 6.14 \times 10^{-4}$
Grasshopper Warbler	$1.58 \times 10^{-3} \pm 2.70 \times 10^{-4}$	$5.54 \times 10^{-3} \pm 7.05 \times 10^{-4}$	$7.76 \times 10^{-3} \pm 9.05 \times 10^{-4}$
Tawny Owl	$5.50 \times 10^{-3} \pm 6.34 \times 10^{-4}$	$1.42 \times 10^{-2} \pm 1.16 \times 10^{-3}$	$1.82 \times 10^{-2} \pm 1.37 \times 10^{-3}$

Table B	Colonisation probability on previously unoccupied squares		
Species	**Lower quartile of sites**	**Mean site suitability**	**Upper quartile of sites**
Cetti's Warbler	$1.02x10^{-5} \pm 1.21x10^{-5}$	$4.85x10^{-5} \pm 4.71x10^{-5}$	$7.40x10^{-5} \pm 6.76x10^{-5}$
Peacock	$2.18x10^{-5} \pm 2.15x10^{-5}$	$1.10x10^{-4} \pm 8.50x10^{-5}$	$1.70x10^{-4} \pm 1.22x10^{-4}$
Twite	$4.28x10^{-5} \pm 3.95x10^{-5}$	$1.49x10^{-4} \pm 1.10x10^{-4}$	$2.09x10^{-4} \pm 1.45x10^{-4}$
Marsh Harrier	$2.74x10^{-5} \pm 2.35x10^{-5}$	$1.21x10^{-4} \pm 8.37x10^{-5}$	$1.80x10^{-4} \pm 1.17x10^{-4}$
Lesser Spotted Woodpecker	$2.93x10^{-4} \pm 1.31x10^{-4}$	$8.92x10^{-4} \pm 3.07x10^{-4}$	$1.21x10^{-3} \pm 3.84x10^{-4}$
Ring Ouzel	$1.23x10^{-5} \pm 1.45x10^{-5}$	$7.64x10^{-5} \pm 6.90x10^{-5}$	$1.25x10^{-4} \pm 1.04x10^{-4}$
Dunlin	$5.03x10^{-8} \pm 1.29x10^{-7}$	$5.69x10^{-7} \pm 1.19x10^{-6}$	$1.10x10^{-6} \pm 2.15x10^{-6}$
Mandarin	$1.78x10^{-4} \pm 8.76x10^{-5}$	$5.75x10^{-4} \pm 2.26x10^{-4}$	$7.90x10^{-4} \pm 2.92x10^{-4}$
Teal	$9.32x10^{-4} \pm 2.44x10^{-4}$	$2.03x10^{-3} \pm 4.48x10^{-4}$	$2.52x10^{-3} \pm 5.29x10^{-4}$
Nightingale	$5.75x10^{-5} \pm 3.81x10^{-5}$	$2.65x10^{-4} \pm 1.38x10^{-4}$	$4.00x10^{-4} \pm 1.93x10^{-4}$
Gadwall	$5.81x10^{-6} \pm 6.35x10^{-6}$	$5.73x10^{-5} \pm 4.73x10^{-5}$	$1.05x10^{-4} \pm 7.96x10^{-5}$
Goosander	$1.19x10^{-4} \pm 6.16x10^{-5}$	$5.53x10^{-4} \pm 2.18x10^{-4}$	$8.34x10^{-4} \pm 3.03x10^{-4}$
Pied Flycatcher	$4.15x10^{-6} \pm 5.18x10^{-6}$	$4.43x10^{-5} \pm 4.10x10^{-5}$	$8.28x10^{-5} \pm 7.00x10^{-5}$
Hobby	$6.18x10^{-4} \pm 1.91x10^{-4}$	$2.79x10^{-3} \pm 5.90x10^{-4}$	$4.12x10^{-3} \pm 7.81x10^{-4}$
Peregrine	$8.57x10^{-4} \pm 2.25x10^{-4}$	$2.90x10^{-3} \pm 5.65x10^{-4}$	$4.02x10^{-3} \pm 7.18x10^{-4}$
Barn Owl	$3.48x10^{-4} \pm 1.28x10^{-4}$	$1.67x10^{-3} \pm 4.35x10^{-4}$	$2.53x10^{-3} \pm 5.94x10^{-4}$
Crossbill	$3.53x10^{-4} \pm 1.22x10^{-4}$	$1.47x10^{-3} \pm 3.88x10^{-4}$	$2.16x10^{-3} \pm 5.24x10^{-4}$
Wood Warbler	$4.41x10^{-4} \pm 1.62x10^{-4}$	$1.54x10^{-3} \pm 4.14x10^{-4}$	$2.16x10^{-3} \pm 5.30x10^{-4}$
Willow Tit	$6.10x10^{-4} \pm 1.88x10^{-4}$	$2.40x10^{-3} \pm 5.34x10^{-4}$	$3.44x10^{-3} \pm 6.97x10^{-4}$
Kingfisher	$2.90x10^{-4} \pm 1.08x10^{-4}$	$1.50x10^{-3} \pm 4.01x10^{-4}$	$2.31x10^{-3} \pm 5.59x10^{-4}$
Dipper	$1.26x10^{-5} \pm 1.09x10^{-5}$	$1.60x10^{-4} \pm 9.72x10^{-5}$	$3.12x10^{-4} \pm 1.69x10^{-4}$
Golden Plover	$3.94x10^{-6} \pm 4.51x10^{-6}$	$1.08x10^{-4} \pm 7.82x10^{-5}$	$2.53x10^{-4} \pm 1.58x10^{-4}$
Ring-necked Parakeet	$8.62x10^{-7} \pm 1.29x10^{-6}$	$2.51x10^{-5} \pm 2.60x10^{-5}$	$6.00x10^{-5} \pm 5.51x10^{-5}$
Common Sandpiper	$1.99x10^{-5} \pm 1.59x10^{-5}$	$2.44x10^{-4} \pm 1.31x10^{-4}$	$4.70x10^{-4} \pm 2.24x10^{-4}$
Common Tern	$4.85x10^{-4} \pm 1.46x10^{-4}$	$1.84x10^{-3} \pm 4.30x10^{-4}$	$2.66x10^{-3} \pm 5.74x10^{-4}$
Whinchat	$1.16x10^{-4} \pm 6.20x10^{-5}$	$9.66x10^{-4} \pm 3.39x10^{-4}$	$1.67x10^{-3} \pm 5.13x10^{-4}$
Little Grebe	$1.97x10^{-4} \pm 8.12x10^{-5}$	$1.09x10^{-3} \pm 3.29x10^{-4}$	$1.72x10^{-3} \pm 4.71x10^{-4}$
Great Crested Grebe	$1.61x10^{-5} \pm 1.28x10^{-5}$	$1.37x10^{-4} \pm 8.21x10^{-5}$	$2.44x10^{-4} \pm 1.34x10^{-4}$
Redshank	$3.12x10^{-4} \pm 1.37x10^{-4}$	$1.65x10^{-3} \pm 4.70x10^{-4}$	$2.58x10^{-3} \pm 6.45x10^{-4}$
Grasshopper Warbler	$5.66x10^{-4} \pm 1.72x10^{-4}$	$3.34x10^{-3} \pm 6.63x10^{-4}$	$5.29x10^{-3} \pm 9.23x10^{-4}$
Tawny Owl	$2.53x10^{-3} \pm 4.49x10^{-4}$	$1.08x10^{-2} \pm 1.21x10^{-3}$	$1.56x10^{-2} \pm 1.55x10^{-3}$

Table C	Extinction probability (after a single individual observed in previous year)			Probability of a second observation on occupied squares		
Species	**Lower quartile of sites**	**Mean site suitability**	**Upper quartile of sites**	**Lower quartile of sites**	**Mean site suitability**	**Upper quartile of sites**
Cetti's Warbler	0.430	0.430	0.430	$6.23x10^{-2}$	$7.63x10^{-2}$	$8.07x10^{-2}$
Peacock	0.103	0.103	0.103	$5.73x10^{-3}$	$7.80x10^{-3}$	$8.52x10^{-3}$
Twite	0.207	0.207	0.207	$3.18x10^{-1}$	$3.51x10^{-1}$	$3.61x10^{-1}$
Marsh Harrier	0.433	0.370	0.353	$3.17x10^{-2}$	$3.76x10^{-2}$	$3.94x10^{-2}$
Lesser Spotted Woodpecker	0.032	0.032	0.032	$3.05x10^{-2}$	$3.60x10^{-2}$	$3.78x10^{-2}$
Ring Ouzel	0.005	0.005	0.005	$1.66x10^{-9}$	$3.72x10^{-5}$	$1.32x10^{-4}$
Dunlin	0.255	0.255	0.255	$1.08x10^{-1}$	$1.31x10^{-1}$	$1.38x10^{-1}$
Mandarin	0.262	0.200	0.184	$2.88x10^{-1}$	$3.12x10^{-1}$	$3.20x10^{-1}$
Teal	0.667	0.667	0.667	$1.92x10^{-4}$	$1.69x10^{-2}$	$2.99x10^{-2}$
Nightingale	0.346	0.346	0.346	$6.46x10^{-9}$	$4.42x10^{-5}$	$1.38x10^{-4}$
Gadwall	0.334	0.334	0.334	$1.52x10^{-4}$	$1.45x10^{-2}$	$2.61x10^{-2}$
Goosander	0.104	0.104	0.104	$2.20x10^{-6}$	$2.36x10^{-3}$	$5.62x10^{-3}$
Pied Flycatcher	0.196	0.196	0.196	$3.12x10^{-8}$	$1.37x10^{-4}$	$4.05x10^{-4}$
Hobby	0.028	0.028	0.028	$4.76x10^{-11}$	$1.72x10^{-5}$	$7.88x10^{-5}$
Peregrine	0.043	0.048	0.049	$5.18x10^{-9}$	$1.09x10^{-4}$	$3.62x10^{-4}$
Barn Owl	0.201	0.201	0.201	$3.13x10^{-2}$	$3.73x10^{-2}$	$3.92x10^{-2}$
Crossbill	0.399	0.437	0.448	$8.30x10^{-6}$	$1.36x10^{-2}$	$3.26x10^{-2}$
Wood Warbler	0.086	0.086	0.086	$1.06x10^{-6}$	$9.16x10^{-4}$	$2.19x10^{-3}$
Willow Tit	0.241	0.241	0.241	$1.53x10^{-5}$	$4.64x10^{-3}$	$9.48x10^{-3}$
Kingfisher	0.472	0.472	0.472	$6.13x10^{-2}$	$7.01x10^{-2}$	$7.29x10^{-2}$
Dipper	0.327	0.327	0.327	$3.53x10^{-8}$	$1.74x10^{-4}$	$5.07x10^{-4}$
Golden Plover	0.678	0.678	0.678	$1.49x10^{-4}$	$1.70x10^{-2}$	$3.21x10^{-2}$
Ring-necked Parakeet	0.816	0.816	0.816	$4.61x10^{-9}$	$2.72x10^{-4}$	$1.07x10^{-3}$
Common Sandpiper	0.507	0.507	0.507	$8.16x10^{-6}$	$2.75x10^{-3}$	$5.98x10^{-3}$
Common Tern	0.217	0.217	0.217	$9.31x10^{-5}$	$1.39x10^{-2}$	$2.66x10^{-2}$
Whinchat	0.227	0.227	0.227	$1.23x10^{-1}$	$1.56x10^{-1}$	$1.67x10^{-1}$
Little Grebe	0.731	0.731	0.731	$1.88x10^{-5}$	$3.72x10^{-3}$	$7.36x10^{-3}$
Great Crested Grebe	0.341	0.341	0.341	$5.74x10^{-7}$	$1.04x10^{-3}$	$2.75x10^{-3}$
Redshank	0.679	0.679	0.679	$2.65x10^{-6}$	$2.89x10^{-3}$	$7.05x10^{-3}$
Grasshopper Warbler	0.491	0.491	0.491	$8.09x10^{-7}$	$1.03x10^{-3}$	$2.56x10^{-3}$
Tawny Owl	0.217	0.217	0.217	$7.55x10^{-6}$	$1.88x10^{-3}$	$3.68x10^{-3}$