Surrogacy and persistence in reserve selection: landscape prioritization for multiple taxa in Britain

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Summary

1. A principal goal of protected-area networks is to maintain viable populations of as many species as possible, particularly those that are vulnerable to environmental change outside reserves. Ideally, one wants to be able to protect all biodiversity when selecting priority areas for conservation.

2. Using the area-prioritization algorithm ZONATION, we identified the locations where UK Biodiversity Action Plan (BAP) species of mammals, birds, herptiles, butterflies and plants occur in concentrated populations with high connectivity. Both these features are likely to be correlated with population persistence. The analyses were successful in maintaining a high proportion of the connectivity of narrow-range species, and large total amounts of the connectivity of wider-range species over 10% of the land surface of Great Britain.

3. Biodiversity Action Plan (BAP – high priority) species of one taxonomic group were not particularly good surrogates (indicators) for BAP species of other taxonomic groups. Hence, maintaining population concentrations of one taxonomic group did not guarantee doing likewise for other taxa.

4. Species with narrow geographic ranges were most effective at predicting conservation success for other species, probably because they represent the range of environmental conditions required by other species.

5. *Synthesis and applications.* This study identifies landscape-scale priority areas for conservation of priority species from several taxonomic groups, using the Zonation software. 'Indicator groups' were only partially successful as predictors of priority areas for other taxonomic groups, and therefore, the identification of priority areas for biodiversity conservation should include information from all taxonomic groups available. Larger areas should be protected to account for species not included in the analyses. Conservation solutions based on data for many different species, and particularly those species with narrowly defined ranges, appear to be most effective at protecting other rare taxa.

Key-words: amphibians, birds, butterflies, conservation, mammals, plants, protected areas, reptiles, Zonation, biodiversity

Introduction

Reserve selection and area prioritization approaches aim to identify locations where species are most likely to persist (Margules & Pressey 2000; Rodrigues *et al.* 2004). Prioritization approaches require some knowledge of the distribution of species. A major constraint is that there is no region in the

world where the distribution and abundance patterns of every species is known. Thus, relatively well-known taxa, vegetation types or physical attributes of the environment are often used to guide conservation planning (Howard *et al.* 1998; Margules & Pressey 2000; Margules, Pressey & Williams 2002). The efficacy of this approach, for biodiversity as a whole, depends on how well the conservation of these surrogates will protect taxa that were not included within the original planning process (Moritz *et al.* 2001; Gladstone 2002; Margules *et al.*

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2002; Kati *et al.* 2004; Lamoreux *et al.* 2006), especially at the spatial resolution required for on-the-ground conservation planning.

The second major constraint is the difficulty in identifying the locations where species are most likely to persist. The potential value of reserve networks built on one taxonomic group for another (test) group has most commonly been measured by a 'species counting approach', whereby one representation of each test species within the reserve network counts as 'inclusion'. Few studies have considered the amount of representation in the context of analysing the efficacy of surrogates (Rondinini & Boitani 2006). In addition, reserve selection methods tend to select for overdispersed protected area networks and sites at the edges of species' distributions (Branch, Benn & Lombard 1995; Araújo & Williams 2000; Gaston et al. 2001), rather than protecting core areas where populations might be most likely to persist (e.g. Araújo & Williams 2001; Cabeza & Moilanen 2001; Moilanen et al. 2005; van Teeffelen, Cabeza & Moilanen 2006). It is largely unknown whether reserve selection approaches based on selecting regions where species of the building taxonomic group are more likely to persist will also protect areas where other taxa are most likely to persist (Bonn, Rodrigues & Gaston 2002; Kremen et al. 2008). In this study, we evaluate how well reserve networks designed to maintain concentrations of populations (i.e. those more likely to be viable and persist) for one taxonomic group are likely to protect concentrations of populations of other taxa.

Surrogates can never be perfect, and thus, it is important to identify the characteristics of taxa that make them reliable indicators of conservation value for other species. For example, geographically localized species may act as more successful surrogates than random draws of species (Moritz et al. 2001; Lawler et al. 2003; Tognelli 2005). Whatever the 'ideal' surrogates might be, in practice, country conservation bodies identify priority species (e.g. national Red Lists) using a diversity of criteria, enact legislation to protect them, and set targets to maintain populations of these taxa [e.g. 2010 targets (www.cbd.int/2010-target/)]. Therefore, it is important to identify whether reserve networks built to protect such species will protect the sites where non-listed species are more likely to persist and, given the strong taxonomic bias in red listing, whether they will protect threatened species of other taxonomic groups (Brooks et al. 2001; Lawler et al. 2003; Moore et al. 2003).

The first major goal of this study is to analyse whether reserve networks designed to protect concentrations of populations of one taxonomic group (indicator group species) also protect concentrations of populations of other groups (test group species). The second major goal is to evaluate the extent to which variation in taxonomic affiliation, range size, and number of species included in the analysis influence the efficiency with which surrogates protect concentrations of test species. All analyses are carried out using 2-km grid resolution data for mammals, birds, amphibians and reptiles, butterflies and plants in Britain.

Materials and methods

DISTRIBUTION DATA AND MODELLING APPROACHES

We used the species listed as priorities for conservation action under the UK Biodiversity Action Plan (UK BAP). This plan was the UK's response to the Convention of Biological Diversity. Distribution data was available at 2×2 km (tetrad) grid for 62 plant species, 11 mammals, 4 herptiles (1 reptile and 3 amphibian species were grouped together), 9 butterflies and 22 birds. The data sets include distribution information from the recent atlases: 1970 to 2000 data for mammals (Arnold 1993), herptiles (Arnold 1995), and plants (Preston, Pearmanm & Dines 2002), 1995–1999 for butterflies (Asher *et al.* 2001) and 1988–1991 for birds (Gibbons, Reid & Chapman 1993). Presence/absence data were used. Marine species, and birds that strictly depend on marine resources for feeding, were excluded.

In the bird atlas, volunteer recorders were asked to visit at least 8 of the 25 tetrads in each 10×10 -km grid square (Gibbons *et al.* 1993). We modelled species distributions to obtain a probability of occurrence value for all tetrads including the unsurveyed tetrads. Models were built using the amount of each of 13 classes (Supporting Information, Table S1) from the 1990 Land Cover Map (original resolution 25 m) (Fuller, Groom & Jones 1994) in the square, plus altitude and geographical location (x and y coordinates, Ordnance Survey grid reference) as predictors. For more details, see Supporting Information, Appendix S1.

SELECTION OF PRIORITY AREAS FOR CONSERVATION

Priority areas were selected using Zonation (Moilanen et al. 2005; Moilanen 2007), a reserve selection software designed to identify networks of areas with concentrations of populations for many species simultaneously. The algorithm incorporates the dispersal ability of each species which determines whether separate sites are 'connected', and whether unoccupied sites can be colonized. Cells where species are present have high connectivity values. Empty neighbouring cells also have some connectivity, their connectivity 'value' (below) increases with the number and proximity (weighted by each species' ability to disperse) of nearby occupied cells. Areas with aggregations of population/s have high connectivity as individuals can easily disperse between neighbouring sites. Connectivity values were calculated for every cell, for each species separately, to provide population connectivity surfaces of individual species (correlated with the likelihood that populations will persist; Hanski 1998; Hanski & Ovaskainen 2000), and these surfaces were then used within the Zonation software. The Zonation meta-algorithm (Moilanen 2007) determines the proportion of the total connectivity of each species summed across the study area (Britain) that is contained within each grid cell and then iteratively discards locations (grid cells) of lowest proportional connectivity value across all species. The removal process starts from the edge of the area, thus maintaining a high degree of structural connectivity in the remaining area. Once a cell is removed from a species' distribution, a part of the species' connectivity is removed; thus, the remaining grid cells will contain a higher proportion of the species' overall remaining connectivity. This causes those cells to increase in value and become harder to remove (Moilanen et al. 2005; Moilanen 2007). In the final steps of the ranking process, a small percentage of grid cells remain but all species are still represented, following the principle of complementarity (Williams et al. 1996; Margules & Pressey 2000;

Cabeza & Moilanen 2001). These cells represent the top priority core areas for species conservation and contain high connectivity areas for all species. The Zonation software and user manual (Moilanen & Kujala 2006) are freely available from www.helsinki.fi/bioscience/ consplan.

In Zonation, the connectivity value S of cell *i*, for each species *j*, is commonly modelled using an exponential function of the distance d(in km) from all k cells that are occupied by the same species, taking into account the species' ability to disperse (α_i) and the size of the population in cell $k(A_{ki})$: $S_{ii} = \sum_{k} \exp(-\alpha_{i}d_{ik}) A_{ki}$ (Moilanen & Nieminen 2002). In this study, presence/absence data were used for all taxonomic groups (except the birds for which the probability of occurrence from modelled distributions was used), and thus, the population in cell (A_{ki}) is a value between 0 and 1 in all cases. Connectivity values are calculated for all cells for each species. With modelled bird distributions, cells *i* are weighted by the probability of occurrence value obtained from the model outcome. The values of α correspond to movements of individuals: these ranged from 0.25 for the most dispersive species (10% of individuals disperse more than 9.2 km), to 3 (10% move more than 0.76 km). These alpha values were based on prior knowledge of species dispersal capacities for butterflies (Cowley et al. 2001) and birds (Wernham et al. 2002). For other taxa, we attributed an alpha value within this range, taking into account the relative ability of each species to disperse (Supporting Information, Table S2). This procedure was an approximation and not based on dispersal studies. The plants are the group with the lowest average dispersal value and correspondingly, the highest α (average 2.71) and the birds have the highest dispersal ability and the lowest average α (0.36).

Maps (Fig. 1) show the highest priority 10% of Britain for the BAP species in each taxonomic group. We evaluated how the best 10% areas obtained for each taxonomic group protected the connectivity of the remaining groups. We display 10% of Britain as an example, although this is not necessarily the target for conservation (Rodrigues & Gaston 2001). Information used for red-listing inevitably varies among taxonomic groups because different types of data are available. Birds and mammals could be classified as UK BAP priority species on the basis of small range or population size or large population declines (for which data exist), whereas range size criteria predominate for taxa with less complete data. To understand the consequences of this effect, we determined the 95% range size quartile of all species from the other taxonomic groups and carried out the selection of priority areas for bird and mammal species with a range size below this threshold.

Distribution information at 2-km resolution is available for *all* resident breeding butterflies and birds in Britain (57 butterfly and 176 bird species, as defined above), allowing us to carry out additional analyses. We evaluated how the best 10% of the landscape obtained for the BAP species performed at protecting the connectivity of non-BAP species.

FACTORS AFFECTING THE EFFICIENCY OF SURROGATES AT SMALL-SCALE RESOLUTION

We assessed the efficacy of surrogates by gradually adding more taxonomic groups, more species and species with different range sizes (building species) to the analysis and quantified how the solutions protected the remaining species (test species). Generalized linear models (GLM) with a *normal* error distribution and *identity* link function (Venables & Ripley 2002) were used to determine which attributes of the building species were most important for maximizing the connectivity of the test species.

For birds and butterflies, we tested the effect of range size, and carried out a sub-sampling approach. All 57 butterflies and 176 birds (analysed separately) were sorted according to range size, with the first half designated LARGE range size species and the second half SMALL range size species. Large-range species were then randomly split in two sub-samples, as were the small-range species. The randomization procedure ensured comparable sub-samples (for range size averages and variances): the two smallest range species were taken first and one of them was randomly assigned to each of the two sub-samples, then proceeding to the next pair of species, and so on. A Zonation solution was built for each sub-sample. Thus, we could assess the extent to which the Zonation solution built using half the small-range butterfly species protected the connectivity of the remaining small-range butterfly species, and of the large-range butterfly species, etc. To test the similarity between solutions, we used Spearman rank correlations.

Results

SELECTION OF PRIORITY AREAS FOR CONSERVATION FOR DIFFERENT TAXONOMIC GROUPS

Figure 1 shows the top-ranked (hereafter 'best') 10% of Britain, resulting from the landscape prioritization algorithm, for each taxonomic group (BAP species). Solutions were especially effective for plants, butterflies and herptiles, maintaining an average of over 95% of the connectivity of the target species within 10% of the land surface, and reasonably effective for mammals and birds (italicized diagonal in Table 1).

When all species were included simultaneously in the analysis (Fig. 1f), on average 72% of the connectivity of all 108 BAP species was contained within the best 10% of the land surface. This all-species analysis contained 94% and 76% of the connectivity of BAP plants and herptiles, respectively, but only 30% and 31% of the connectivity of the more widespread BAP birds and mammals (underlined values in Table 1).

Birds lost the highest proportion of their connectivity per unit area lost, whereas 80% of the landscape could be removed without causing any depletion/loss to the BAP plants' connectivity (Fig. 2a). This difference arose because BAP plants have much smaller range sizes than BAP birds: loss of a part of the landscape will eliminate some of the bird species' connectivity. Due to the widespread ranges of BAP birds and mammals, protection of 10% of the landscape was not enough to maintain high proportions of their connectivities. Nonetheless, because BAP birds and mammals had relatively large range sizes to start with, these groups, and especially birds, had high average total amounts (as opposed to proportion) of connectivity in the best 10% solution obtained when using all BAP species in the analysis (Fig. 2b). It is only possible to maintain a relatively small proportion of the connectivity of large-range species in a small reserve network, but the total amount of their connectivity protected is higher than for small-range species (Fig. 3).

To understand if the Zonation solutions are equally good for small- and large-range size species, the 95% quartile of the range size of all BAP species (except birds and mammals) was



Fig. 1. The highest-ranking 10% of Britain to protect the connectivity of the BAP species of each taxonomic group, ordered by average range sizes: (a) plants (smallest average range sizes), (b) butterflies, (c) herptiles, (d) mammals, (e) birds (largest average range sizes), (f) solution obtained using all groups in the analysis.

determined: a figure of 327 10 × 10-km grid squares. When only the small-range size BAP bird and mammal species are included in the analyses (species that occur in less than 327 grid squares), the Zonation solutions show an improvement, relative to all-bird and all-mammal solutions, in protecting the connectivity of the other taxonomic groups (Table 1). This improvement is significant for birds ($Z_{(2)57} = -3.029$, P = 0.002), but marginal for small-range size mammals ($Z_{(2)98} = -1.773$, P = 0.07). The map with the best 10% of Britain obtained for plants (Fig. 1a) showed a high degree of fragmentation in the distribution of the threatened plant species at this scale, while the map obtained for birds was the least fragmented. This difference could have arisen because of: the much smaller range sizes of BAP plants than birds, the larger number of BAP plant species (62 vs. 22 BAP bird species), the lower dispersal ability of plants (average $\alpha = 2.7$ for plants; 0.3 for birds; Table 1), or because the birds had modelled distributions

	Indicator group (used to build Zonation solution)							
	Plants	Butterflies	Herptiles	Mammals	Mammals*	Birds	Birds*	All BAP species
Test group	Average	Average proportion of connectivity in 10% solution						
Plants	0.991	0.184	0.130	0.137	0.185	0.143	0.150	0.944
Butterflies	0.207	0.951	0.202	0.202	0.249	0.167	0.204	0.667
Herptiles	0.292	0.249	0.993	0.175	0.206	0.228	0.237	0.763
Mammals	0.185	0.255	0.208	0.612	0.503	0.139	0.160	0.315
Mammals*	0.259	0.375	0.278	0.721	0.878	0.179	0.225	0.466
Birds	0.122	0.127	0.102	0.125	0.146	0.417	0.398	0.307
Birds*	0.141	0.163	0.082	0.140	0.191	0.626	0.667	0.453
All BAP species†	0.168	0.182	0.138	0.142	0.183	0.149	0.161	0.720
	Characteristics of the taxonomic group							
No. of species	62	9	4	11	5	22	12	108
Average range size [‡]	58.8	102.3	242.3	464.5	73.0	784.9	65.7	285.5
Average total connectivity	104.7	210.5	611.1	1557.6	563.3	10 611.6	713.6	2419.7
Average α value	2.7	1.1	2	0.7	0.45	0.3	0.35	1.9

Table 1. Average proportion of connectivity included in each group's best 10% solution, using BAP species from each taxonomic group

*subset with small range size species (species present in $<327 10 \times 10$ km grid squares which corresponds to the 95% quartile of the range size of plants, butterflies and herptiles).

†average for all BAP species excluding the indicator group used to run the analysis.

 \ddagger average number of 10×10 km grid squares per BAP species.

Values in *italics* are for analyses where indicator and test species are the same as one another; for underlined values, test species are a subset of the indicator species.



Fig. 2. Amount of original distribution (connectivity) retained for each taxonomic group when determining priority areas for BAP species in those taxonomic groups. (a) Proportion of original distribution as a function of proportion of the landscape remaining as lower priority areas are removed. (b) Relationship between average proportion of connectivity retained in the best 10% of the landscape and the average total connectivity retained.

(and a different sampling strategy). Our solutions were not particularly sensitive to estimated dispersal parameters, as assessed by comparing the order in which cells were removed by Zonation using species-specific α values (the main results)



Fig. 3. The (a) proportions and (b) total amounts of connectivity of each species in the within-taxon Zonation solutions when selecting the 'best' 10% of Britain. Range size is the number of 10×10 km grid squares occupied by each species in Britain.

with the order of removal when every species was assigned $\alpha = 2$ (Spearman $\rho = 0.96$ for plants and butterflies; $\rho = 0.86$ for mammals, $\rho = 0.80$ for birds, and $\rho = 0.81$ for all BAP species; the original herptile solution already used $\alpha = 2$ for every species).

EFFICACY OF INDICATOR GROUPS

There was some overlap in Zonation solutions (Fig. 1) obtained for each taxonomic group, but indicator taxa maintained only a fairly small proportion (0.18 on average; compared to the null expectation of 0.10) of the connectivity of test species in the top 10% of Britain (Table 1). The best areas for maintaining the largest proportion of the connectivity of one group did not coincide particularly well with the best areas for protecting the connectivity of other groups. Butterflies (and small-range mammals) were the best indicator groups, and herptiles the worst, although none of the groups was particularly good. The best 10% of Britain for butterflies protected 96% of the BAP butterflies' connectivity, but only 18% (about twice as good as choosing locations at random) of the connectivity of BAP species in all other taxonomic groups (Table 1). In contrast, when all BAP species were included in the analysis, on average 72% of the connectivity of all species was protected, still in 10% of the land surface.

ARE BAP SPECIES GOOD AT PROTECTING THE CONNECTIVITY OF NON-BAP SPECIES?

For butterflies, the BAP-species and all-species Zonation solutions were correlated (Spearman $\rho = 0.77$, n = 6136, P < 0.001, comparing the removal order of the best 10% of cells). The solution obtained with all butterfly species is better than the solution obtained with only the BAP species at protecting the connectivity of all species of butterflies ($Z_{(2)57} = -4.108$, P < 0.001). The BAP species maintained on average 26% of the connectivity of the 46 non-BAP butterflies and 96% of the connectivity of the BAP species in the best 10% of cells (Table 2). If all butterfly species are included, 43% and 83% of the connectivity of non-BAP and BAP species is maintained in the best 10% of cells, respectively. The same pattern can be seen for birds, albeit with lower average proportional protection, and there is no significant difference between the connectivity of all birds protected by the all-bird species and BAP-bird solutions ($Z_{(2)176} = -0.517$, P = 0.605).

CAN SELECTION OF SURROGATES BE IMPROVED?

Inclusion of three or more different taxonomic groups (forming 'mixed taxon' indicator groups) arguably provided an improvement on using just one or two taxonomic groups (Fig. 4), but the improvement was modest (average proportion of test species' connectivity increased from 0.16 to 0.2) and not significant (Mann–Whitney Z = -1.597, P > 0.05). These values were very low compared to the average proportion of connectivity protected when all groups were included in the analysis directly (0.72, Fig. 4).

When different groups are combined, this produces building sets of species that vary in average range size and number of species, as well as in taxonomic affiliation. In GLM analyses, the number of species included in the analysis was the most important factor determining the average *proportion of connectivity* of test species maintained in the best 10% of



Fig. 4. Mean (\pm SE) proportion of the connectivity of the nontargeted species (*y* axis) protected by the 10% solution obtained from all possible combinations of taxonomic groups (the *y* axis has a minimum value 0·1 which is the random value expected). The all taxa solution (five taxa included) represents the maximum proportion of connectivity that could be maintained, that is, when all test species are included in the Zonation analysis.

obtained	when different groups of	f species (indicator groups) are used	to prioritize areas			
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Table 2.	Performance of indicato	r groups in protecting other species.	Values give the average	proportion of the co	onnectivity in the !	10% solution

	Indicator group (used to build Zonation solution)				
Test group	BAP butterflies	All butterfly species	BAP birds	All bird species	
All BAP species	0.957	0.830	0.417	0.355	
All species	0.372	$\overline{0.496}$	0.164	$\overline{0.201}$	
All non-BAP species*	0.262	0.434	0.128	0.179	
No. of species with more than 50% of connectivity in solution	15	29	11	20	
No. of species with less than 15% of connectivity in solution	13	0	142	113	
	Characteristics of the taxonomic group				
No. of species	9	57	22	176	
Average range size [†]	102.3	893.3	784.9	909.0	
Average α value	1.1	1.9	0.3	0.3	

Values in *italics* are for analyses where indicator and test species are the same as one another; for underlined values, test species are a subset of the indicator species.

†average number of 10×10 km grid squares per BAP species.

	Characteristics of indicator group						
GLM	No. of taxonomic groups	Average range size	No. of species	β			
Average total connectivity Average proportion of connectivity	-0·224 (n.s.) 0·006 (n.s.)	-5·756 (<0·001) 0·975 (n.s.)	-0·133 (n.s.) 3·093 (0·004)	9·430 (<0·001) 11·923 (<0·001)			

Table 3. Results of the GLM analysis. Effects of the characteristics of the indicator group on average total and proportion of connectivity in the 10% solution. β is the constant value obtained in the GLM



Fig. 5. Efficacy of Zonation solutions built using random samples of small- and large-range species at maintaining the connectivity of non-target small and large-range species. Each line represents a separate random selection of species.

the land surface. For average *total connectivity*, species range size was most important (Table 3). The most effective indicator groups contained large numbers of small-range species, regardless of the taxonomic group to which they belonged.

Effects of range size were also seen in additional analyses of all bird and all butterfly species (Fig. 5). For butterflies, large- and small-range size (building) species were equally good at predicting the best areas for protecting small-range size test species (solid and dashed black lines are intermingled: Fig. 5). For birds, small-range size species were the best predictors of other small-range size species (solid black lines lie above the dashed black lines: Fig. 5). The connectivity of smallrange size species is better predicted by other species (black lines) than is the connectivity of large-range size species (grey lines), which is useful since small-range size species are usually more important for conservation actions. In general, the results show that small-range size species are more effective than large-range size species in prioritizing areas for conservation, with small-range building species on average protecting some 29% (birds) to 45% (butterflies) of the connectivity of small-range testing species in the best 10% solutions.

Discussion

SELECTION OF PRIORITY AREAS FOR LONG-TERM PERSISTENCE OF BAP SPECIES

Twentieth century agricultural intensification and other human activities radically transformed the UK landscape, confining many species to small areas of semi-natural habitats, and generating large population declines in others (Pain & Pienkowski 1997). Biodiversity Action Plan (BAP) species are those for which the UK government has set targets of trying to stop their decline by 2010 (www.cbd.int/2010-target). To meet the 2010 biodiversity targets (CBD 1992) and the targets and requirements of other relevant strategies and legislation, protecting areas where these species have the greatest chances of long-term survival appears to be appropriate. We had access to data from UK BAP species belonging to five taxonomic groups. Zonation identifies areas where the greatest concentrations of species populations exist, which is a relative measure of the likelihood of population/species persistence (Moilanen et al. 2005). To guarantee long-term persistence, one would ideally obtain information on the capacity of each landscape to support viable populations through detailed population viability analyses. Unfortunately this information is difficult to obtain for every species in multi-species systems (Carroll et al. 2003), even in a relatively data-rich part of the world. The connectivity approximation adopted within Zonation is probably one of the best approaches available, although solutions obtained should be tested for robustness to population extinction (Early & Thomas 2007).

Our maps represent the best 10% of the landscape for each of the five taxonomic groups analysed and also for the full set of 108 BAP species analysed. Ten per cent was selected for display purposes, and it might not be enough for the effective protection of all species (Rodrigues & Gaston 2001). As with other reserve selection algorithms, Zonation uses complementarity principles (Williams et al. 1996), but in combination with the distribution smoothing (connectivity) technique, it retains areas with larger concentrations of species populations, and not just species presences (Moilanen et al. 2005). The solution with the best 10% of Britain for all BAP species is able to maintain over three-quarters of the connectivity of small-range plants and herptiles, and twothirds of the butterfly connectivity (many of which have extremely small distributions; Cowley et al. 1999), but less than one-third of the connectivity of the more widespread mammals and birds. This indicates that a larger area needs to be managed for the effective long-term protection of these

species (alternatively, the criteria for conservation listing may have been lower for some taxa). Measures that promote species conservation in the wider countryside could be a solution for the effective protection of threatened species with large range sizes. Nevertheless, these two groups still have large total amounts of connectivity in the solutions, showing that the Zonation approach is adequate to identify priority areas for large-range size species.

The results obtained for birds are based on models of probability of occurrence and not raw distribution data, as used for the other taxonomic groups. Although the presence/ absence and modelled solutions were correlated (see Supporting Information, Appendix S1), we selected the latter because potentially good quality sites that were not surveyed could then be identified and included in the selection of priority areas for conservation.

As with other area selection algorithms, that attempt to prioritize areas where species are more likely to persist (Cabeza & Moilanen 2001; Briers 2002; Nicholson *et al.* 2006), Zonation does not assess the availability of suitable habitat within the underlying landscape, and therefore, Zonation will prioritize empty cells that are close to cells that are occupied even if no suitable habitat is available in those cells. Furthermore, Zonation assumes that species can move in all directions equally and does not take into account landscape barriers and the fact that some species may only disperse if specific habitats are available. Therefore, the priority areas should be regarded as regions within which more specific conservation measures should be undertaken (cross-checking with habitat layers; establishing conservation programmes for specific habitats; habitat restoration).

EFFICACY OF INDICATOR TAXA

The results indicate that, at 2×2 -km resolution, the best areas for maintaining the largest proportion of the connectivity of one group do not coincide well with the best areas for protecting the connectivity of the other groups; this conclusion is similar to studies based on species occurrences (Prendergast et al. 1993; van Jaarsveld et al. 1998). At this resolution, the BAP species of one taxonomic group taken together are not particularly good surrogates for determining the best areas for protecting the combined BAP species of other taxonomic groups, albeit better than random. Ideally, one should have distribution information on all species to select priority areas for their conservation. Since complete data on all taxa is rare, this implies that distribution/habitat models will often have to be used to establish priority areas (Moilanen et al. 2005; Kremen et al. 2008), as with the birds in this study.

ARE BAP SPECIES GOOD SURROGATES FOR ALL SPECIES?

The ability of species of high conservation value (BAP species) to act as surrogates in the protection of non-threatened species apparently depends on the number of species considered

and their range sizes. While BAP birds were good surrogates of all bird species, threatened butterfly species were not particularly good surrogates for conserving population concentrations of all butterfly species, as found by other authors examining species representation (Bonn et al. 2002). Nonetheless, conservation of threatened and non-threatened species is compatible; the connectivities of both the existing BAP and non-BAP species were well-represented when we considered both groups together (Table 2). Because species with small range sizes are maintained disproportionately within Zonation, the all-butterfly analysis maintained the BAP species (most of which have small range sizes) well. The proportion of connectivity maintained for bird species was much lower than for butterflies, given that many birds (even BAP species) are widespread (and ranges sizes are possibly inflated due to the use of modelled distributions). BAP and all-species bird solutions were relatively similar, probably due to the larger number of species and to a diversity of range sizes of the BAP species.

WHAT IS A GOOD SURROGATE?

Identification of an efficient group of surrogate taxa was not feasible, and there was little direct advantage to including a diversity of taxonomic groups in the analysis. Other authors found that indicator groups work well if they have similar ecological requirements to the non-targeted species they are trying to represent (Kremen 1992; Caro & O'Doherty 1999).

We did find that including large numbers of species, and species with small-range sizes, improved the average proportion of connectivity and the total connectivity protected in the test species; just as other authors have also found that range size is important for the effectiveness of umbrella species (Brooks et al. 2001; Lawler et al. 2003). Thus, a small number of species are unlikely to represent the distribution patterns of every other species accurately. In addition, small-range species usually occupy specific types of environments, and thus, inclusion of many such species is likely to represent a wide range of environmental conditions, and therefore, coincidentally to protect other specialized species. The more detailed analyses of bird and butterfly distributions showed that species with small ranges can be effective surrogates for other small-range species, increasing the connectivity protected some three or four times over what would be expected from a random selection of protected areas (at 10% of Britain selected; Fig. 5). If this conclusion proves to be general, then population concentrations of small-range species can be used to identify the locations where population concentrations of other smallrange species are likely to be located (Vos et al. 2008).

Conclusions

Our analyses were carried out for arguably the five best-known taxonomic groups in Britain, where there is a strong tradition of wildlife survey by a large number of volunteers and, thus, high-resolution distribution information. The data are consistently collected, they are compiled by non-governmental

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organizations and governmental agencies involved in conservation, and the information is rigorously evaluated to provide the distribution maps used. Whilst the data are not perfect, it is unlikely that better data exist at such a fine resolution (2-km grid) for other countries. Even with such high quality data, the low capacity of one taxonomic group to predict priority areas for another suggests that 'indicators' are only weak surrogates for other taxa at the scale of analysis at which detailed conservation planning is typically carried out. Only increasing the total area under conservation is likely to be entirely effective at maintaining viable populations of taxa that are not included in conservation assessments directly. If surrogates are to be used, small-range size species appear to be relatively effective at protecting the connectivity of other species with small ranges, thereby increasing the expected persistence of non-target species. Our results help define British priority areas for population persistence of the species concerned, and the UK government is committed to the conservation of the designated BAP species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Modelling bird distributions

Table S1. Land cover map 1990 classes used to constructmodels for bird distributions. Classes are based on the 17'Key' cover types

Table S2. British Action Plan (BAP) species list

 Table S3. Summary statistics for model performance of GLM (Hawfinch) and GAMs (all other species) obtained for all bird species

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