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PAUL WILLIAMS,* DAVID GIBBONS,†¶ CHRIS MARGULES,‡ ANTHONY REBELO,§
CHRIS HUMPHRIES,* AND ROBERT PRESSEY‖

*Biogeography & Conservation Laboratory, The Natural History Museum, London SW7 5BD, U.K.,
email paw@nhm.ac.uk
†British Trust for Ornithology, The Nunnery, Nunnery Place, Thetford, Norfolk IP24 2PU, U.K.
‡CSIRO Division of Wildlife & Ecology, P.O. Box 84, Lyneham, ACT 2602, Australia
§Conservation Biology Unit, National Botanical Institute, Kirstenbosch, Claremont 7735, South Africa
‖NSW National Parks & Wildlife Service, PO Box 1967, Hurstville, New South Wales 2220, Australia

Abstract: *Biodiversity conservation requires efficient methods for choosing priority areas for in situ conservation management. We compared three quantitative methods for choosing 5% (an arbitrary figure) of all the 10 × 10 km grid cells in Britain to represent the diversity of breeding birds: (1) hotspots of richness, which selects the areas richest in species; (2) hotspots of range-size rarity (narrow endemism), which selects areas richest in those species with the most restricted ranges; and (3) sets of complementary areas, which selects areas with the greatest combined species richness. Our results show that richness hotspots contained the highest number of species-in-grid-cell records (with many representations of the more widespread species), whereas the method of complementary areas obtained the lowest number. However, whereas richness hotspots included representation of 89% of British species of breeding birds, and rarity hotspots included 98%, the areas chosen using complementarity represented all the species, where possible, at least six times over. The method of complementary areas was also well suited to supplementing the existing conservation network. For example, starting with grid cells with over 50% area cover by existing "Sites of Special Scientific Interest," we searched for a set of areas that could complete the representation of all the most threatened birds in Britain, the Red Data species. The method of complementary areas distinguishes between irreplaceable and flexible areas, which helps planners by providing alternatives for negotiation. This method can also show which particular species justify the choice of each area. Yet the complementary areas method will not be fully able to select the best areas for conservation management until we achieve integration of some of the more important factors affecting viability, threat, and cost.*

Comparación de los puntos máximos de riqueza de especies, máxima concentración de especies raras y areas complementarias para conservar la diversidad de aves Británicas

Resumen: *La conservación de la biodiversidad requiere la utilización de métodos eficientes para la elección de áreas prioritarias para el manejo de la conservación "in situ." Comparamos tres métodos cuantitativos para la elección de un 5% (cantidad arbitraria) del número total de cuadrículas de 10 × 10 km para representar la diversidad de aves que se reproducen en Gran Bretaña: (1) puntos de máxima riqueza, los cuales seleccionan las áreas más ricas en especies; (2) puntos de máxima rareza en rangos de tamaños (endemismos locales), los cuales seleccionan las areas más ricas únicamente en aquellas especies con los rangos más restringidos y (3) grupos de areas complementarias, las cuales seleccionan áreas con mayor riqueza en combinaciones de especies. Nuestros resultandos muestran que los puntos de máxima riqueza obtuvieron el mayor número de registros de especies por caudrícula (con muchas representaciones de las especies más ex-*

¶ *Current address: The Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, U.K.*

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tendidas), mientras que la aproximación de complementaredad obtuvo el número más bajo. Sin embargo, mientras que los puntos de máxima riqueza incluyeron una representación del 89% de las especies de aves británicas y los puntos de máxima rareza incluyeron el 98% de las especies, las áreas elegidas utilizando complementariedad, representaron todas las especies, hasta donde fue posible, al menos seis veces más. El método de complementariedad está bien adaptado para suplementar las redes de conservación existentes. Empezando con cuadrículas con más de un 50% de área cubierta por sitios existentes de interes científico especial, buscamos areas que pudieran completar la representación de todas las aves más amenazadas en Gran Bretaña, la red dedatos de especies en peligro. Estos análisis de complementariedad distinguen entre areas irremplazables y flexibles, lo cual sirve a los planificadores proveyendo alternativas para la negociacion. Este método puede mostrar que especie en particular justifica la elección de cada área. Sin embargo, antes de que el análisis de complementariedad sea completamente capaz de seleccionar las mejores areas para la gestión de la conservación, sera necesario un desarrollo posterior para integrar algunos de los factores más importantes que afectan la viabilidad, amenaza y costo.

Introduction

Conservation of species diversity in situ requires networks of areas for conservation management. Several methods for selecting areas of high value for biodiversity conservation have been advocated, but a broad range of quantitative approaches, including hotspots of richness, hotspots of rarity, and complementary areas have not been compared using the same data.

Setting priorities for conservation is unavoidable. Competition for land limits the area available, so conservation goals have to be attained within these limits (Pressey 1994; Pressey & Tully 1994). The purpose of assigning priority is not to dictate the only areas with conservation value, but rather to recognize a necessary, though not sufficient, foundation for achieving a particular conservation goal within the limits of available information. Priority areas in this sense are relative and graded in multiple levels. Each may be considered one as yet unspecified alternative among flexible choices and priority may be subject to revision as information changes. Priority areas for biodiversity will then form part of the broader network of areas that represents many other conservation interests.

Areas important to many conservation values are already recognized in most parts of the world (Grimmett & Jones 1989; Pritchard et al. 1992). In Britain, "Sites of Special Scientific Interest" (SSSIs) form the backbone of statutory protection (Her Majesty's Government 1981; Department of the Environment/Welsh Office/Ministry of Agriculture, Fisheries and Food 1985). Most are in private ownership, even though they have been selected by the government. The selection criteria include not only floristic and faunistic interest, but also nonbiological criteria such as geological and landform value (Nature Conservancy Council 1989). Nonetheless, existing SSSIs would not be expected to represent all of Britain's biodiversity. We still must know which areas of Britain are needed to supplement the existing network in order to conserve biodiversity (Department of the Environment 1994).

Any practical method for planning should highlight flexibility in choice among areas (Williams et al. 1991; Bedward et al. 1992). Conservation planners need tools that enable them to explore alternatives quickly and easily, because for any one area there may be many competing land-use demands (Usher 1986; Reid et al. 1992). It is essential that all the values for an area be explicit and rational, not hidden in general subjective judgements (Morowitz 1991; Margules et al. 1994). The attraction of such quantitative rigor is that it can, particularly with the growing availability of high-speed computers, allow more people to discover how balancing their values will affect difficult conservation decisions and to see what the consequences of their actions might be.

In trying to meet the need for explicit and rational assessment of areas for conservation, many scoring systems have been developed to combine criteria (Usher 1986). These have not been widely adopted, in part because the criteria hidden behind the scores are often considered highly subjective (Nature Conservancy Council 1989), but also because they implicitly weight some criteria more heavily than others (Margules 1989). But because representation of biodiversity has become one of the more pressing conservation concerns, some researchers have begun to focus on this goal by using species-occurrence data with greater quantitative rigor. Among these quantitative methods we distinguish three groups: (1) choosing hotspots of richness, areas that individually have the highest species richness (Gibbons et al. 1993; Prendergast et al. 1993*a*, 1993*b*; Lawton et al. 1994; Sisk et al. 1994); (2) choosing hotspots of rarity, areas that individually are richest in the species with the most restricted distribution ranges (Terborgh & Winter 1983; Myers 1988, 1990; Bibby et al. 1992; Sætersdal et al. 1993; Sisk et al. 1994); and (3) choosing areas of complementary richness, areas that in combination have the highest species richness (Kirkpatrick 1983; Ackery &

Vane-Wright 1984; Thomas & Mallorie 1985; Margules & Nicholls 1987; Burley 1988; Margules et al. 1988; Pressey & Nicholls 1989; Rebelo & Siegfried 1990; Daniels et al. 1991; Vane-Wright et al. 1991; Ryti 1992; Pressey et al. 1993; Sætersdal et al. 1993; Scott et al. 1993; Kershaw et al. 1994; Underhill 1994; Humphries et al. 1996). In principle, all three methods could be and in some cases have been applied to attributes of areas other than species, such as vegetation formations or habitat classes, and should be combined with a treatment of threat and factors influencing viability.

British bird data provide a particularly good opportunity to compare area-selection methods using information based directly on species. Britain is fortunate in having some of the best species-based distribution data in the world (Prendergast et al. 1993*b*; Lawton et al. 1994). Birds are not only among some of the best-recorded organisms (Sharrock 1976; Lack 1986; Gibbons et al. 1993), but they are also one of the most highly valued groups of organisms; about 1.5% of people in Britain are members of the Royal Society for the Protection of Birds.

Choosing the methods of area selection must be distinguished carefully from choosing the goals of area selection. Which taxonomic group (or other area attributes) to use, which species to include (e.g., all species or only the most threatened native species), and which areas or spatial scale to score them for, are questions that shape the goals and hence govern the kind of data required (as a matrix of attributes and areas). Goals are not universal but depend on the values of the person setting them. Consequently they are not tied to a particular method and may be specific to a particular study. For our comparison of methods, we adopt a goal based on the need to represent all species of breeding birds. Our goal easily could have been to represent only native species, and not to include introduced species (e.g., Wood Duck (*Aix sponsa*) and Ring-necked Parakeet (*Psittacula krameri*)). Many other goals are possible. For example, we also include an analysis in which we seek to represent only the threatened species of breeding birds. Similarly, deciding the spatial scale for analysis is a question of goal and can have a pronounced effect on results (Stoms 1994). For our comparison of methods we follow the approach of Prendergast et al. (1993*a*) at the scale of 10 × 10 km grid cells. As with our choice of organisms, goals at many other spatial scales are possible. But it must be emphasized that area-selection methods, unlike goals, are in themselves essentially scale-independent. It is clearly important for the success of conservation that, when future studies apply area-selection methods in making management decisions, they then pursue goals based on explicit and broadly agreed upon values.

Our purpose is to compare the success of three quantitative methods in representing breeding bird species in a limited number of areas of particular size. Comparisons of the results are made on the basis that, if all other factors were equal, then obtaining more species with more representations in an area network is likely to be better for the conservation of diversity than obtaining fewer species with fewer representations. The results are discussed in the context of major patterns of bird diversity and rarity.

Materials and Methods

The parts of the British Isles included in these analyses are England, Wales, Scotland, the Isles of Scilly, the Isle of Man, the Western Isles, and the Orkney and Shetland Islands. We excluded Northern Ireland and the Republic of Ireland because they have been less intensively surveyed and have different systems of conservation areas. The Channel Islands were also excluded because they are usually considered together with continental Europe (Batten et al. 1990). Britain was surveyed between 1988–1991 for birds by means of the 10 × 10 km cells of the British National Grid (Health & Scott 1972) by the British Trust for Ornithology and the Scottish Ornithologists' Club to compile the *New Atlas of Breeding Birds* (Gibbons et al. 1993). Although efforts were made to reduce problems in sampling (Gibbons et al. 1993), such as variation in observer effort, these problems inevitably have some effect on the data. We modified the published data only (1) by amalgamating records for the subspecies Carrion Crow (*Corvus corone corone*), Hybrid Crow, and Hooded Crow (*Corvus corone cornix*) within the single species, *Corvus corone*; (2) by deleting all records other than breeding records; and (3) by deleting all records for "crossbills of uncertain species" and feral species without self-sustaining populations (Brant Goose (*Branta bernicula*), Pink-footed Goose (*Anser brachyrhynchus*), and Snow Goose (*Anser caerulescens*)). A total of 170,098 breeding records (species-in-grid-cell records) for 218 species in 2827 grid cells (only one cell within the coastline has no breeding records, in South Wales) remained for Britain as defined in this manner (see Appendix).

Sites of Special Scientific Interest are sites recognized by the UK government as requiring management for conservation. Many of the other categories of conservation areas (National Nature Reserves, Ramsar sites, and reserves of the County Wildlife Trust and The Royal Society for the Protection of Birds) are also SSSIs or are included within them (Nature Conservancy Council 1989). The total area of all SSSIs is probably much greater than that of all other kinds of areas managed for conservation, with more than 5800 SSSIs within the data available to us, covering approximately 18,500 km^2, or about 8% of Britain. Areas of SSSIs within each 10 × 10 km grid cell were estimated from data on location (on a 1 × 1 km grid) and extent provided by the "sites and species" database of the Royal Society for the Protection of Birds (I. Fisher, personal communication). For the purpose of comparing methods we arbitrarily treat grid cells where SSSI coverage exceeds 50% of a cell by area as having adequate conservation management for the local fauna of breeding birds (this criterion is met by 65 grid cells). Clearly this interpretation of SSSI value and permanence should be refined on an area-by-area basis before analysis for any practical implementation. For example, it undervalues some small islands of great importance for seabirds.

Before investigating methods of area selection, it is useful to have some knowledge of the major patterns in diversity and rarity among the target organisms. We measured diversity as species richness. This is justified both as a direct measure of one popular aspect of diversity (Noss 1990) and as an approximation, when dealing with large numbers of species, of character (phylogenetic) diversity (Williams & Humphries 1996). Character diversity is equivalent to genetic diversity in the sense of expressed or expressible genes, which can be related most directly to option value for the future (Williams et al. 1994*a*), a value of biodiversity favored by The World Conservation Union et al. (1980).

Apart from showing the points of maximum and minimum richness, maps are often used to communicate broad regional trends in richness. In regions where local heterogeneity in richness scores is particularly great—whether due to heterogeneity of sampling effort, heterogeneity of habitat, or disequilibrium of organisms with suitable habitat—broad trends can be made clearer by smoothing techniques. We adopted one of the simplest, which takes the mean of the grid-cell scores across the neighborhood of occupied grid cells surrounding any one cell (up to eight adjoining cells) (Eversham et al. 1992; Lawton et al. 1994). These techniques lose information on species identities in the smoothed scores (unlike techniques for modeling the expected distributions for individual species; Williams et al. in press) and so are not suitable for subsequent analysis using complementarity.

We use rarity solely in reference to species of restricted range size (measured as area of occupancy in numbers of grid cells), with no reference to abundance. Two approaches to measuring rarity in this sense are in common use (Gaston 1994). The first is discontinuous, counting species as rare if they have distributions more restricted than some threshold. The second is continuous, scoring the range-size rarity of the species in an area on a sliding scale. In contrast to rarity, endemism originally referred to the property of being restricted to a particular area, irrespective of its size. Its meaning has frequently been extended to refer particularly to species that are restricted to small areas (narrow endemics). In this sense it is conceptually similar to range-size rarity, at least when range size is measured on a global scale.

Terborgh and Winter (1983) introduced a threshold criterion for narrowly endemic birds, accepting species that have total ranges of less than 50,000 km^2. Crowe and Siegfried (1993) criticized the choice of any single threshold because it is essentially arbitrary and could miss important endemics with marginally larger ranges. This problem will also occur at other scales, such as within Britain, where Harding (1985) used a threshold criterion of less than 16 of the 10 × 10 km grid cells occupied to define nationally rare species.

In our technique for finding complementary areas we use a measure of rarity that is a continuous function of range size. Like the threshold approach, it is most strongly influenced by the most restricted species, but it differs in that all species make some contribution to the scores on a sliding scale. This is calculated for all the species in a grid cell as the sum of each species' inverse number of grid-cell records (Usher 1986; Avery & Leslie 1990; Howard 1991; Williams 1993):

$$\text{Rarity score} = \sum_{\{i: c_i \neq 0,\ 1 \leq i \leq n\}} (1/c_i) \qquad (1)$$

where c_i is the number of grid cells occupied by species i. We measured range size only within Britain, even though all of these species have broader distribution. The rarity score can also be divided by the local species richness to give a measure of mean rarity, which reflects the average range size among all of the species in the area (this mean score has to be interpreted with care because with increasing richness, scores tend toward the overall mean, whereas extreme values in some areas may result from under-recording of widespread species).

Method 1: Richness Hotspots

Hotspots is a term used by Myers (1988, 1990) for areas world-wide that (1) have exceptional concentrations of species richness, with (2) exceptional concentrations of narrow endemics, and that (3) face exceptional degrees of threat. Subsequently, the term has been used in the narrower sense of areas of richness by Prendergast et al. (1993*a*, 1993*b*). It is also applied more generally to areas with high scores on any scale. Therefore, to avoid confusion, we use the term hotspots for high values and qualify it by specifying the scale as one of richness or rarity.

In quantitative studies of birds and other taxa in Britain, Prendergast et al. (1993*a*) identified richness hotspots as the top 5% of grid cells ranked by species richness. Five percent of the 2827 occupied grid cells in our dataset is 141 grid cells. This number is arbitrary but convenient for comparing the results from the three methods of area selection.

Method 2: Rarity Hotspots

In an influential, quantitative study of important areas for the conservation of bird diversity, Terborgh and Winter (1983) introduced a threshold criterion to define bird species as narrow endemics if they had range sizes of less than 50,000 km^2. They reported that in South America roughly 25% of the resident species fell within this group, although in North America the figure was less than 2%. The International Council for Bird Preservation (now BirdLife International) carried out the first quantitative analysis world-wide (Bibby et al. 1992). They found that narrowly endemic species by the same criterion amounted to 27% of all bird species world-wide (their analysis identified no endemic bird area within either Britain or northwestern Europe). These figures are consistent with most other studies of rarity, which generally recognize rare species as the 20–30% of species most restricted in range size or abundance (Gaston 1994).

For Britain we suggest that a technique comparable in effect to that used for endemic bird areas is to include only the 25% of species with the most restricted breeding ranges within Britain (rather than world-wide) and to search for the areas richest in just these species. A data set for species of restricted British range was prepared by ranking all species by the number of grid cells with breeding records for each and then selecting the 25% of species with the fewest records (this data set contains 819 species-in-grid-cell records for 54 species in 539 grid cells). To make comparisons with the richness hotspots method the 141 grid cells richest in restricted species are identified as area choices.

Method 3: Complementary Areas

In the present context, complementarity refers to the degree to which an area contributes otherwise unrepresented species to a set of areas (Vane-Wright et al. 1991; Colwell & Coddington 1994). As a concept it is independent of spatial scale, although actual numbers of complementary species are not.

Our use of complementarity is to seek (1) representation of all species of British breeding birds at least once in the least number of grid cells and (2), for more direct comparison with the above methods, representation of the species as many times as possible within approximately 141 grid cells. These goals require two separate analyses: one for a single representation of each species and another for multiple representations.

To find complementary area sets we used a heuristic technique. These techniques are popular for carrying out complementary areas analyses (Kirkpatrick 1983; Ackery & Vane-Wright 1984; Margules et al. 1988; Pressey & Nicholls 1989; Rebelo & Siegfried 1990; Vane-Wright et al. 1991; Kershaw et al. 1994; Margules et al. 1994) because they provide reasonable approximations to minimum sets that can be found quickly. For each analysis our technique proceeds in three stages. First, all grid cells with species that are at least as narrowly distributed as the representation goal must be selected because they are irreplaceable to achieving that goal (for example, for a goal of representing every species at least once, this means choosing all grid cells with unique species records). In the second stage, a series of grid cells is chosen to give at each step the maximum range-size rarity score from their complementary, unrepresented species (measured using equation 1). This use of rarity is just one of several techniques for finding a relatively small set of grid cells to represent all species. When there are ties among grid cells in the rarity score, the grid cell with greatest complementary species richness is chosen (to increase the overall number of species represented at a particular step). Any persistent ties are broken by accepting the most northwesterly grid cell (this is an arbitrary rule adopted here for the sake of repeatability; it might otherwise be replaced with selection by random draw). In the third stage, a backwards check is made for any chosen grid cells in which all species are already represented elsewhere in the grid-cell set. This last stage identifies which species occur in only one grid cell within the set, justifying the choice of that grid cell. It is also used to eliminate redundant grid cells from the set found by the first two stages of the heuristic technique, thereby reducing the size of the set. But this is not sufficient to ensure that a truly minimum set is obtained, which requires a combination of grid cells that heuristic techniques cannot always be guaranteed to find.

To illustrate how complementarity can work with existing conservation areas we performed an additional complementary areas analysis. The goal was to supplement the existing network of grid cells with more than 50% cover by SSSIs in order to represent the birds of most immediate conservation concern, the British Red Data species (Batten et al. 1990). A data set was prepared by including just the breeding records of Red Data birds (10,544 records, 81 species, 2576 grid cells).

The richness, rarity, and complementarity methods described were automated, and maps were plotted using WORLDMAP software, version 3.19 (Williams 1994).

Results

Distribution of Bird Diversity and Rarity

Geographical variation in the species richness of British breeding birds is shown in Figs. 1a and 1b, the latter being a smoothed representation of the former. Species richness is highest on the east coast of southeastern Britain (Blythburgh area, arrow in Fig. 1a) but is otherwise generally high around the New Forest and the southeast, and from south Wales through the southern Pennines, Lake District, Cheviot and Moorfoot Hills to Tayside (Fig. 1b).

Areas rich in species with restricted ranges within Britain include the band from Hampshire to Norwich in the southeast, just as for total species richness, but central and northern England are poor, and the highest

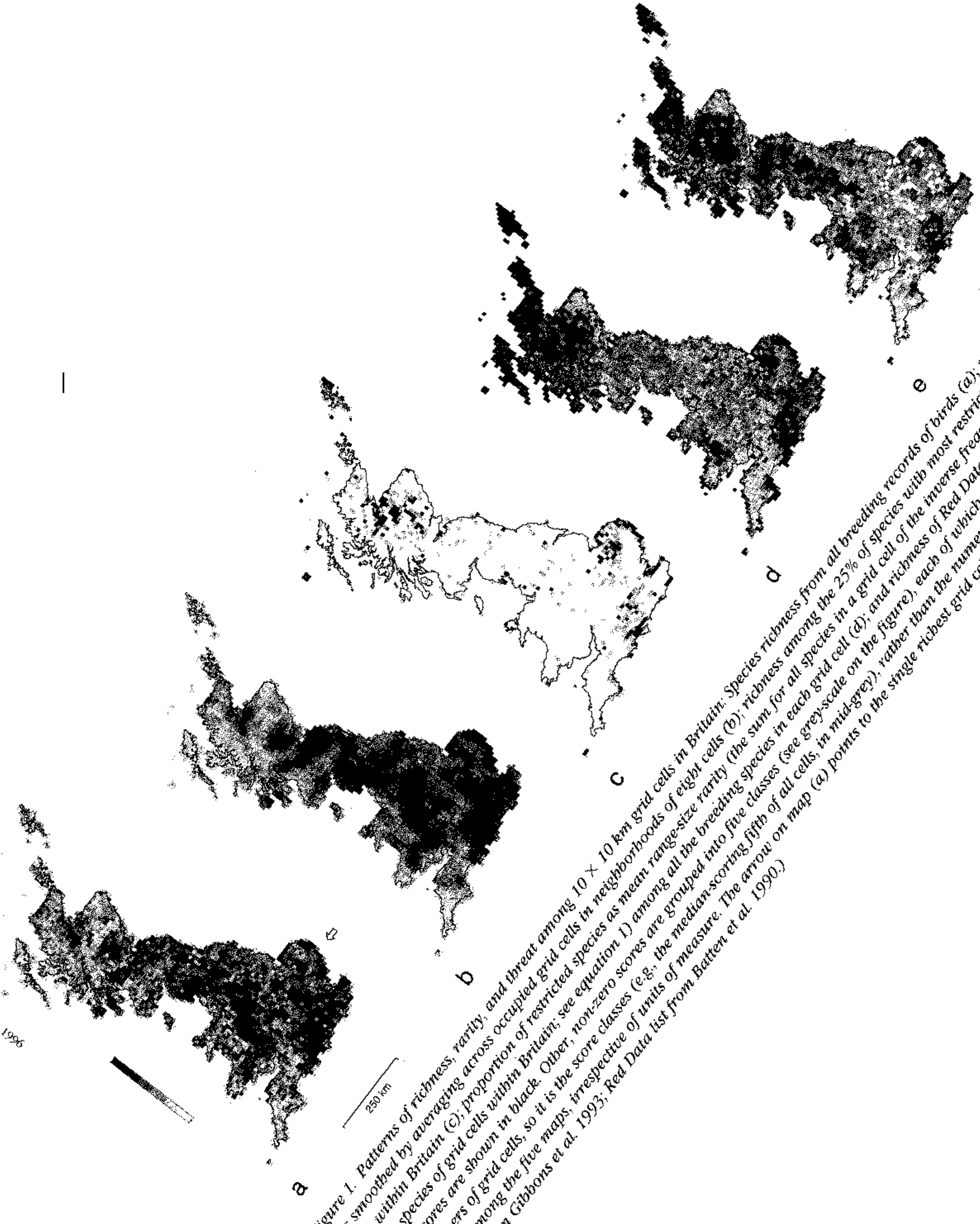


Figure 1. Patterns of richness, rarity, and threat among 10 × 10 km grid cells in Britain: Species richness from all breeding records of birds (a); species richness smoothed by averaging across occupied grid cells in neighborhoods of eight cells (b); richness among the 25% of species with most restricted breeding range within Britain (c); proportion of restricted species as mean range-size rarity (the sum for all species in a grid cell of the inverse frequency of occ by each species of grid cells within Britain; see equation 1) among all the breeding species in each grid cell (d); and richness of Red Data species (e). grid-cell scores are shown in black. Other, non-zero scores are grouped into five classes (see grey-scale on the figure), each of which contains ap equal numbers of grid cells, so it is the score classes (e.g., the median-scoring fifth of all cells, in mid-grey), rather than the numerical values f comparable among the five maps, irrespective of units of measure. The arrow on map (a) points to the single richest grid cell in Britain. bution data from Gibbons et al. 1993; Red Data list from Batten et al. 1990.)

Table 1. Surrogacy among measures of diversity and rarity.*

Pairwise comparisons between measures of richness and rarity	*Raw species richness*	*Smoothed species richness*	*25% rarest species richness*	*Mean range-size rarity score*	*Red Data species richness*	*SSSI area coverage per grid cell*
Raw species richness	1					
Smoothed species richness	0.757	1				
25% rarest species richness	0.140	0.084	1			
Mean range-size rarity score	0.001	−0.138	0.604	1		
Red Data species richness	0.246	0.053	0.352	0.619	1	
SSSI area coverage per grid cell	0.134	0.055	0.190	0.255	0.289	1

**Spearman rank correlation coefficients among scores for species richness, restricted species richness, mean range-size rarity, Red Data species richness, and existing SSSI conservation area coverage for breeding bird species across 2827, 10 × 10 km grid cells in Britain. Original bird distribution data taken from Gibbons et al. 1993; Red Data list from Batten et al. 1990; estimates of SSSI coverage per grid cell based on information in Royal Society for the Protection of Birds "sites and species" database from I. Fisher, personal communication. (Our primary interest is in the relative strength of correlations, and formal statistical tests are not appropriate.)*

scores overall are in the highlands of the north, the Orkneys and Shetland. The same result is obtained irrespective of whether rarity is mapped using the 25% of most restricted species (Fig. 1c) or mean range-size rarity (Fig. 1d). These are broadly the same areas that are rich in Red Data species (Fig. 1e), although there are more Red Data species in the uplands of northwestern England and southern Scotland.

Pairwise correlations between our measures of diversity and range-size rarity in Table 1 are generally weak (apart from the correlation between raw and smoothed species richness), although the two rarity measures show more agreement both with one another and with the richness of Red Data species.

Species Representation with the Three Area-Selection Methods

The richness hotspots method (Fig. 2a) inevitably captures the largest numbers of species-in-grid-cell records (Table 2) but fails to represent all of the species of birds breeding in Britain within the limit of 141 grid cells. This is because many of the species-in-grid-cell records come from multiple representations of the most widespread species (Fig. 3a; see also Appendix). The rarity hotspots method (Fig. 2b) captures fewer species-in-grid-cell records (Table 2), particularly of the most widespread species (Fig. 3b), but it boosts representation of the more restricted species (Fig. 3b), so it is more successful in capturing some representation of nearly all of the species (Table 2). In contrast, the complementary areas method could represent all of the birds at least once within just 27 grid cells. More usefully, it was found that within a total of 139 grid cells (marginally less than our limit of 141 grid cells) this method can represent all species that have six or more breeding records at least six times, as well as including all representations of the species with one, two, three, four, or five breeding records. It accounts for fewer species-in-grid-cell records than the richness method (Table 2), but, like rarity hotspots, these records are more evenly distributed among the species. However, because the goal of six representations maximizes representation of the most restricted species, there are even fewer species in the class with least representations (Fig. 3c). From a planning viewpoint the complementary areas analysis recognizes that, although 49 of the 139 grid cells chosen are irreplaceable for achieving the goal (the black cells in Fig. 2c), nonetheless by exploiting flexibility among ties for the remaining 90 grid-cell choices, there are many more possible combinations of 139 grid cells that permit six representations. Therefore, the pattern of grid cells in Fig. 2c is only one among many equivalent sets of grid cells found by this technique.

Table 2. Results of the three area-selection methods in representing breeding birds among 10 × 10 km grid cells in Britain.*

	Area-selection methods			
			Complementary areas for	
Representation achieved (%)	*Richness hotspots*	*Rarity hotspots*	*1 representation*	*6 representations*
Occupied grid cells chosen (n = 2827)	5.0 (141)	5.0 (141)	1.0 (27)	4.9 (139)
Total species represented (n = 218)	89.0 (194)	97.7 (213)	100.0 (218)	100.0 (218)
Total species-in-grid-cell records represented (n = 170,098)	7.8 (13,208)	6.1 (10,329)	1.1 (1954)	6.0 (10,141)

**Representation results are shown as percentages of the UK totals, with numbers of records in parentheses. For a listing of the representation achieved by species see Appendix (original bird distribution data from Gibbons et al. 1993).*

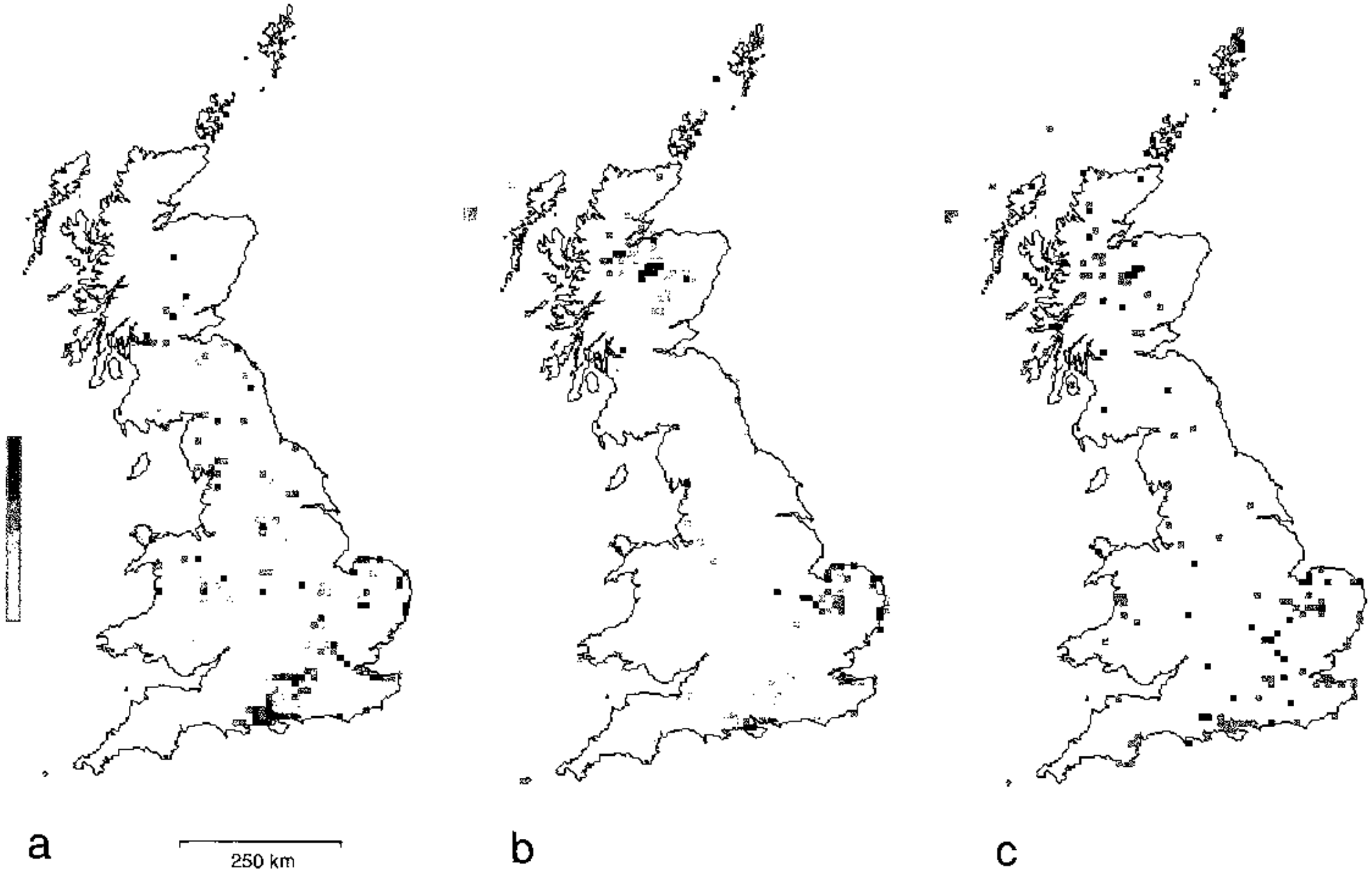
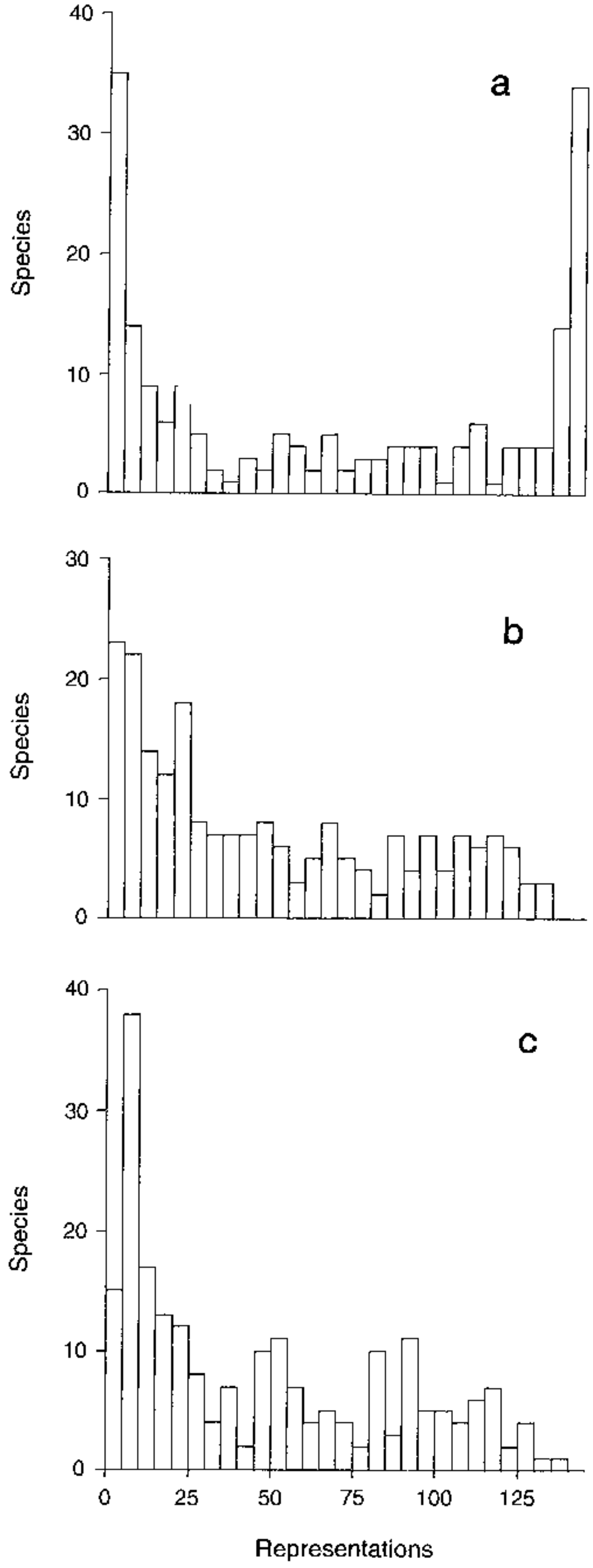


Figure 2. Distribution of grid cells chosen by three methods for selecting 5% from among all (2827) 10 × 10 km grid cells to represent British breeding birds: Richness hotspots (a), rarity hotspots (b), and complementary areas (c). For maps (a) and (b), see Fig. 1 legend for description of scores and grey scale. For map (c) grid cells that must be chosen to achieve the goal are shown in black and grid cells for which there are alternative choices are shown in grey. (Original bird distribution data from Gibbons et al. 1993.)



Complementing Existing Areas to Represent All Threatened Species

Eighty-seven percent of the 10 × 10 km grid cells with breeding birds across Britain have some cover by SSSIs in the data available (Fig. 4a). But Table 1 shows that the extent of SSSI cover is only weakly related to the diversity or range-size rarity of birds within Britain (although the strongest agreement is between SSSI cover and richness in the most threatened birds, the Red Data species). Using the data for all breeding birds in Britain and, for illustrative purposes only, accepting that faunas of the 65 grid cells with more than 50% cover by SSSIs are managed effectively for conservation, the residual fauna in need of conservation areas is 31 species (14%; Fig. 4b).

The complementary areas method can represent all of these remaining species at least once within an additional 20 grid cells. If interest were concentrated on the Red Data species (Fig. 1e), however, as being of the most immediate conservation concern, then the set of areas required most urgently to supplement the 65 SSSI-rich grid cells for complete representation of Red Data species is a set of 16 grid cells (Fig. 4c), of which six are irreplaceable. All 16 of these grid cells already enjoy limited SSSI coverage.

Discussion

Diversity, Rarity, and Area Choices

Unfortunately for hard-pressed conservationists, hotspots of species richness, although easily identified, do not represent all bird species in Britain. This is because the distributions of rarer species are not strongly nested within the distributions of more-widespread species, as shown by the low correlations in Table 1 and by the lack of success of even our rarity hotspots in representing all species. The low correlations between our measures of diversity and rarity in Table 1 show that they do not provide reliable surrogates for one another. Furthermore, area cover per grid cell by existing SSSIs does not coincide closely with either of these patterns, although it is at least reassuring that the best agreement is with the richness of Red Data birds. Explanations for why richness and rarity are not closely related in these data have been sought from disturbance and fragmentation of habitats at this fine scale within Britain (Prendergast et al. 1993*a*; Lawton et al. 1994). It has been suggested that

Figure 3. Frequency of species representation in the results by each of the three area-selection methods: richness hotspots method (a), rarity hotspots method (b), and complementary areas method (for six representations of each species; c). (Original bird distribution data from Gibbons et al. 1993.)

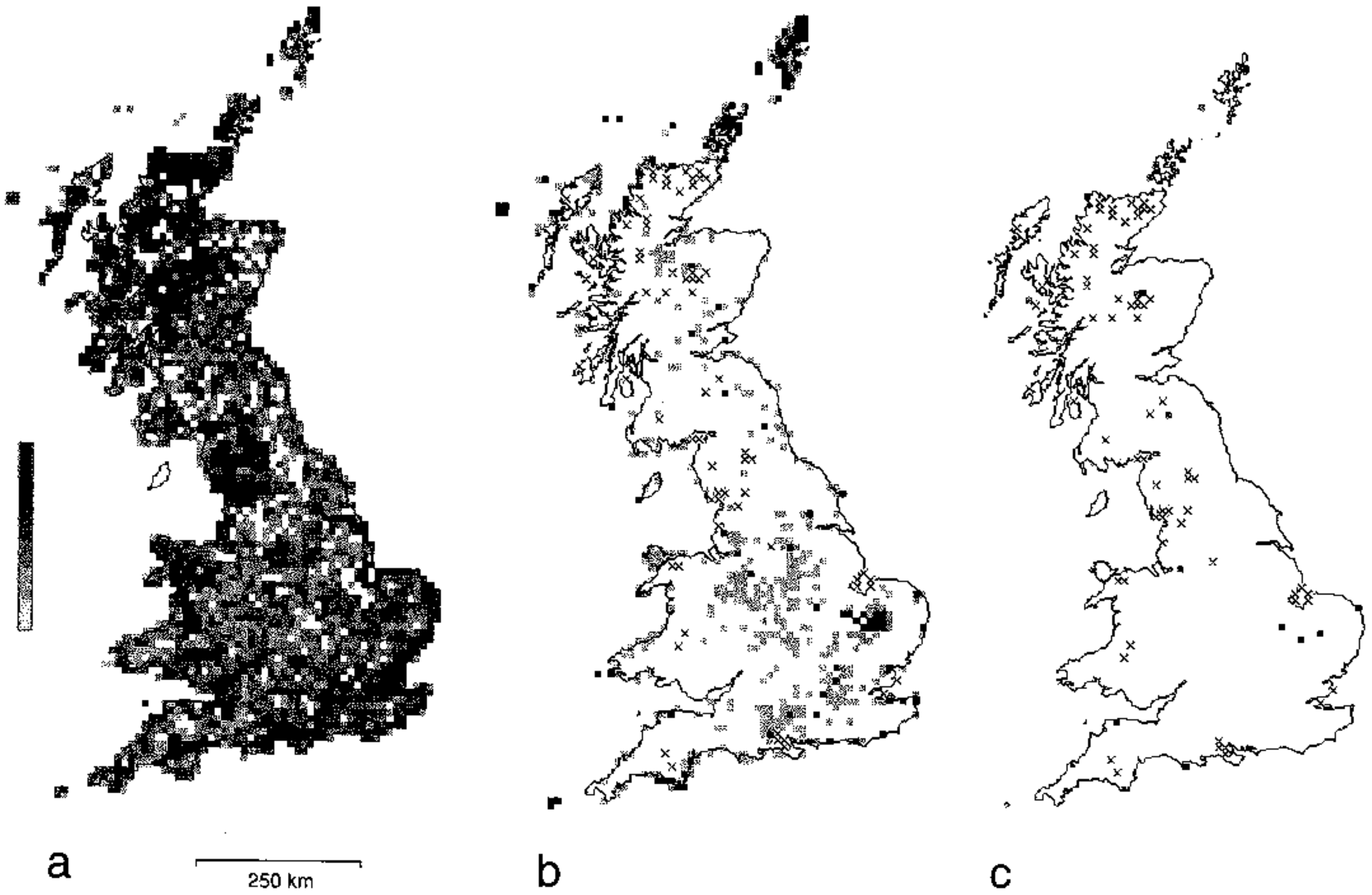


Figure 4. Example of the use of the complementary areas method for supplementing previously recognized areas of conservation interest: proportion of the area of each 10 × 10 km grid cell across Britain that lies within existing Sites of Special Scientific Interest (SSSIs) (a); complementary species richness of breeding birds (species not represented) after removing the fauna of the grid cells with more than 50% of their area within SSSIs (b); and an example of one near-minimum-area set of grid cells for representing just the Red Data species at least once to supplement the grid cells with more than 50% of their area within SSSIs (c). For maps (a) and (b) see Fig. 1 legend for description of scores and grey scale. In maps (b) and (c) crosses mark the 65 grid cells with more than 50% of their area within SSSIs. In map (c) grid cells that must be chosen to achieve the goal are shown in black and grid cells for which there are alternative choices are shown in grey. (Estimates of SSSI coverage per grid cell based on information in the "sites and species" database of the Royal Society for the Protection of Birds from I. Fisher, personal communication; original bird distribution data from Gibbons et al. 1993; Red Data list from Batten et al. 1990.)

the coincidence of hotspots of richness and rarity might improve at larger spatial scales (Bibby et al. 1992; Prendergast et al. 1993*a*; Curnutt et al. 1994). Consequently, in order to represent all species, all threatened species, or any other set of area attributes chosen as a goal, our results for Britain show that some explicit implementation of the complementary areas method will be required if we are to avoid selecting large numbers of areas that merely duplicate the representation of widespread species. Such methods may themselves be independent of scale, but this is not necessarily true of the results, so great care must still be taken in formulating the goals of an analysis.

The grid cells chosen by the richness hotspots method are mainly in south and central Britain, with few grid cells being chosen in the north of Scotland (Fig. 2a). This reflects the general trend for increasing species richness of breeding birds toward the south of Britain (Fig. 1a, 1b). This pattern is familiar from previous studies of all breeding birds (Sharrock 1976; Turner et al. 1988; Gibbons et al. 1993; Prendergast et al. 1993*a*), butterflies (Heath et al. 1984; Turner et al. 1987; Eversham et al. 1992; Prendergast et al. 1993*a*; Lawton et al. 1994), and dragonflies (Prendergast et al. 1993*a*, 1993*b*; Lawton et al. 1994). (Except for the two separate bird atlases, the data referred to for each group are not from independent samples but were drawn from the same UK Biological Records Centre databases). This north-south trend is not universal among taxa, however: liverworts (Prendergast et al. 1993*a*, 1993*b*; Lawton et al. 1994), ferns (Lawton et al. 1994), and even some subgroups within the birds (Fig. 5) are richest in the north and west.

In contrast, the grid cells chosen by the rarity hotspots method are concentrated in two clusters, one in the south and one in the north of Britain, with few grid cells being chosen in central and northern England (Fig. 2b). This reflects the higher concentrations of restricted species that occur separately in the north and south of Britain (Fig. 1c, 1d). Among the different rarity scores the higher scores for central Wales in Fig. 1d (mean range-size rarity among all species) illustrate how the threshold approach in Fig. 1c (richness among only the 25% species with the most restricted ranges) can exclude a potentially informative part of the pattern. The clusters of restricted species at the two ends of the country tend to be contributed by different subgroups of birds, such as seabirds (e.g., parvorder Charadriida, Fig. 5a) and upland waders (e.g., parvorder Scolopacida; Fig. 5b) in the north, and warblers (superfamily Sylvoidea; Fig. 5c) in the south. Although a few of these species may be genuinely restricted on a global scale, many are merely on the edge of their range in Britain and are much more widespread elsewhere in the world. For example, among the northern species some seabirds have a northwestern Atlantic distribution (e.g., Leach's Storm-petrel *Oceanodroma leucorhoa*), and some upland species have a subarctic distribution (e.g., Snow Bunting (*Plectrophenax nivalis*)), whereas some southern species have a more Mediterranean distribution (e.g., Dartford Warbler (*Sylvia undata*)) (Batten et al. 1990; Gibbons et al. 1993). In part, the information on the relative importance of the British populations in the global context is taken into account in the Red Data listing (Batten et al. 1990). The criteria for the Red Data list are currently under review for birds (Avery et al. 1995) and will ultimately consider the proportion of the European population of each species within Britain. Richness in Red Data species (Fig. 1e) is relatively high in northern England and low in the southeast (in comparison with our measure of national range-size rarity, Fig. 1d), which shows that, of the more restricted species within Britain, the northern species are considered more threatened and the southern species less threatened. Possible explanations are that the southern species may tend to be more widespread outside Britain or are declining less rapidly. If the information were made available, then the pattern of global range-size rarity (Williams et al. 1994*b*) could be mapped for bird faunas within Britain, summarizing information from all species across their entire range.

The grid cells chosen by the complementary areas method are more evenly dispersed across Britain, with some grid cells being chosen in all regions (Fig. 2c). Many of the irreplaceable grid cells are necessarily concentrated in the south and north, where most of the more restricted species are to be found, but a few are located in Wales, northern England, and southern Scotland. These central grid cells account for only two of the five species that are represented by the complementary areas but not the hotspots of rarity; the other choices in central Britain possess combinations of more-widespread species that are required to achieve the goal of six representations of species.

Techniques for Finding Complementary Areas

We are seeking to maximize the number of species that can be represented within a limited area of land (a "maximal coverage" problem). We use near-minimum-area sets, not to reduce the amount of land required for conservation but as a rough approach to increasing the amount of diversity represented. We regard land area as a surrogate for cost (a common index of competing land-use values), so the result should be the conservation of more diversity for the same cost. Ultimately, however, some of the more important factors for determining the contribution of an area to biodiversity persistence include viability and threat (Witting & Loeschcke 1993; Margules et al. 1994; Kershaw et al. 1995). We would prefer quick techniques that discover all sets that have a truly optimal combination of these factors and show where any flexibility lies. Unfortunately, suitable data are not yet available.

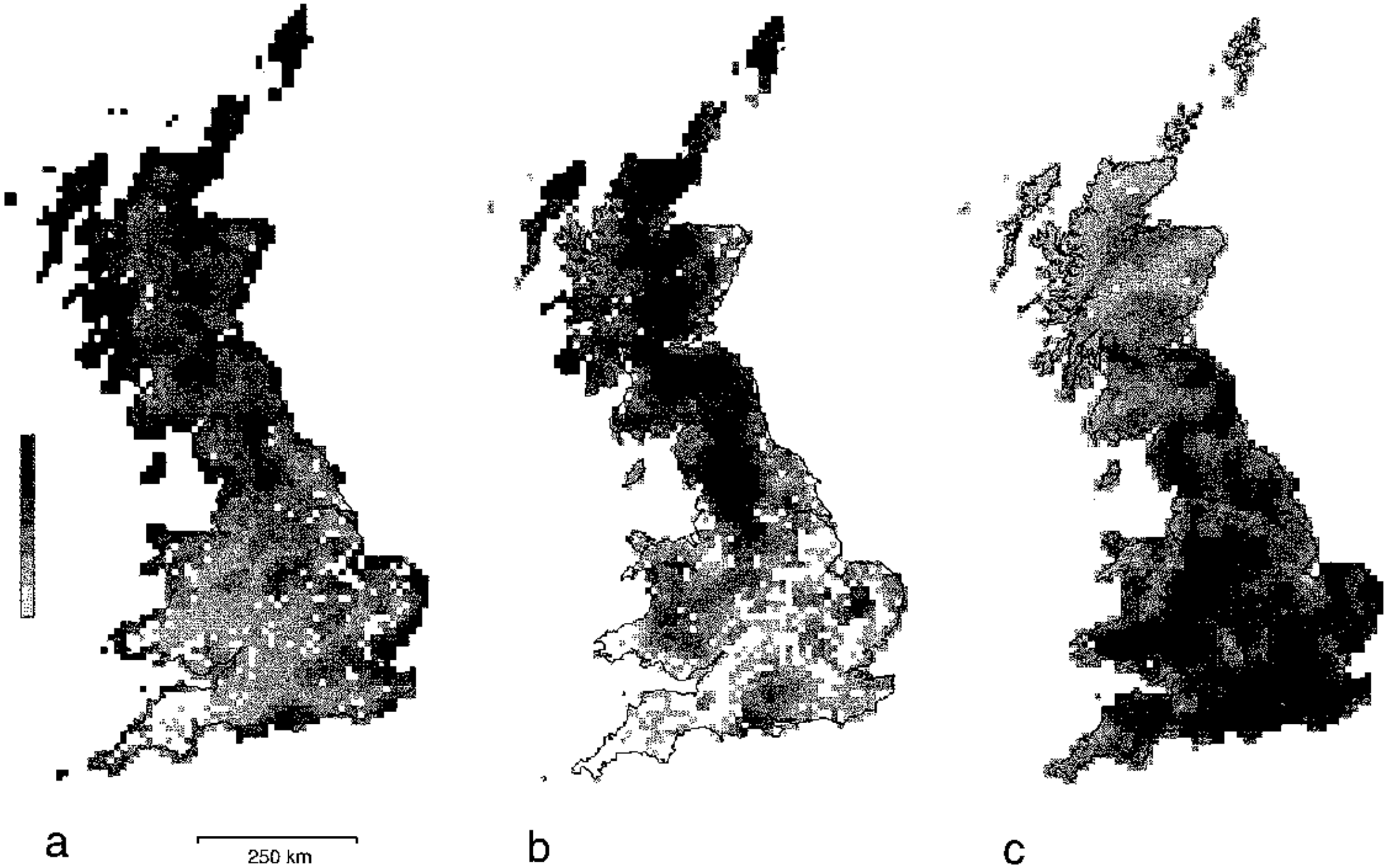


Figure 5. Species richness for examples of regionally restricted groups of breeding birds across 10 × 10 km grid cells in Britain, smoothed by averaging among occupied grid cells in neighborhoods of eight cells: seabirds of the parvorder Charadriida, including the Oystercatcher (Haematopus ostralegus), *plovers, gulls, and terns (a); upland waders of the parvorder Scolopacida, including the Woodcock* (Scolopax rusticola), *godwits, sandpipers, and Curlew* (Numenius arquata) *(b); and warblers of the superfamily Sylvoidea, including the Nuthatch* (Sitta europoea), *tits, and warblers (c). See Fig 1 legend for description of scores and grey scale. (Original bird distribution data from Gibbons et al. 1993; higher classification follows Sibley & Ahlquist 1990.)*

Underhill (1994) has critized the use of "near-minimum" sets in complementary areas analysis, on the grounds that sets are either of minimum area or they are not. But finding and confirming all truly minimum sets is guaranteed only by complete enumeration and testing of all possible sets, at least for sets with a number of areas greater than the irreplaceable set (such as all the areas with unique species) and less than the size of the near-minimum set found by a heuristic technique. Such extensive testing is often beyond practicality for all but a small number of areas and species. In systematics, where similar problems are encountered in trying to find the shortest trees to account for all of the character changes among species, it is widely accepted that partial solutions or approximations are unavoidable in practice with all but the smallest of data sets (Swofford 1990). For all techniques speed will depend in part on the characteristics of particular data sets.

Good approximations that find near-minimum sets are available from techniques such as branch-and-bound (although these cannot always guarantee truly minimum sets if they become trapped by local "islands" of near-minimum sets in "set space"; see Maddison 1991; Page 1993). This is the technique advocated by Underhill (1994) from the mathematical perspective. Unfortunately, Possingham et al. (1993) found that a problem of a size similar (1885 areas, 248 attributes) to that of our British analyses took about 10 days of computation using a branch-and-bound algorithm on a SUN IPX workstation. Possingham (personal communication) reports that this has recently been reduced to about 10 hours.

Faster approximations of varying reliability are provided by heuristic techniques (Pressey et al. in press). The heuristic method used in this paper certainly passes the test of Underhill's (1994) simple counter-example against the weaknesses of "greedy" algorithms (selecting his areas 2 and 3) by rejecting within-set redundant choices (although this heuristic method will fail tests with more-demanding data where optimal solutions require swapping areas with others outside the initial greedy set). It also found and mapped a near-minimum-area set of 27 grid cells and many flexible ties for Britain in just 10 seconds on a 33 MHz 486DX personal computer. From a pragmatic perspective, until adequate viability information is available from all areas for full optimization, heuristic techniques will greatly reduce the number of areas required to represent all species and are still fast enough to allow routine interactive assessment of alternative flexible areas using any available fragments of external information (on, for example, viability, threat, land availability, and other competing values) for planning and negotiation. They provide the power even with complex data (for up to around 7500 species at this scale with the present software on a PC) to explore quickly some of the consequences of particular area choices.

Flexibility and Prioritization of Areas within Sets

One advantage for conservationists of the complementary areas method is that it is possible to justify the choice of each particular area within a set. The third stage of the technique used here distinguishes whether each species in an area is irreplaceable to achieving the representation goal, or whether the species could be represented by other area choices. This interactive implementation can display the information when the cursor is clicked on a grid cell by highlighting those species within the local faunal list that are not represented elsewhere in the set and by showing for each of these species the number of alternative grid cells where it is represented. This not only enables conservationists to explore flexibility in area choice for designing networks but also enables reserve managers, for example, to know precisely which species in their area are most important in the national context, and therefore which species the management practices might favor when a conflict arises.

Financial or political constraints may demand that priorities for the order of acquiring areas be assigned within an area set. Many criteria for deciding priority could be used but the choice of criterion might depend on whether or not the pattern of threat and persistence is likely to be predictable over time (Williams 1996). If it were predictable, then prioritization by threat might ensure that those areas most at risk, or areas with species most at risk, are acquired before they are devalued (Kershaw et al. 1995). If the pattern of threat were not predictable (perhaps because it is changing too rapidly and is not sufficiently well understood to be modeled), then the present situation may not be a reliable guide to what will prove to be the worst threat to attaining the goal during the entire period of area acquisition. In this case, prioritization by diversity complement might ensure that the largest, most goal-important diversity complements are secured first (Vane-Wright et al. 1991). But threat is usually considered sufficiently predictable to define useful priorities (N. Myers, personal communication). As the situation changes with time the capacity for rapid reassessment of the potential contribution of all areas that is provided by the methods described here could be useful.

Prescriptions and Prospects

We include no prescription of specific priority areas for concentrating the effort of conservation management because this is a preliminary comparison of area-selection methods, with less emphasis on precise goals and without detailed exploration of the flexibility in area choices. No generality is claimed for the results of any one analysis to the results expected when other goals are used (e.g., other taxa or spatial scales), although preliminary results may help to identify areas for further study. Instead, our aim is that identification of better methods of area selection and their continuing refinement should aid projects dealing with other goals and with other, less well-known groups.

One reason for using birds is that the problem of selecting conservation areas has already received much consideration, so short-comings in the present methods should be most apparent. These analyses are most obviously simplistic in treating all records at the relatively coarse resolution of 10 × 10 km grid cells as equivalent or as depending simply on area extent per grid cell for SSSIs, when much detailed information about particular SSSIs and local populations of birds does exist. Small islands (e.g., Bass Rock) may be tiny and yet still support breeding colonies with enormous populations of seabirds, whereas large upland areas may support only low numbers of upland waders. Both could be of great importance for conservation depending on the particular circumstances.

A next major step in the development of complementary areas analysis is to incorporate some of the other important factors, including viability, threat, and cost. There are many possible ways of doing this as explicit components for optimization by area-selection methods. These will need to be explored in other studies. At least for birds, there is a growing wealth of information on viability factors, including migration and seasonal needs, local abundance, local rates of increase, and local habitat preferences, that should be available for integration in the future (Lack 1986; Nature Conservancy Council 1989; Batten et al. 1990; Pritchard et al. 1992; Gibbons et al. 1993).

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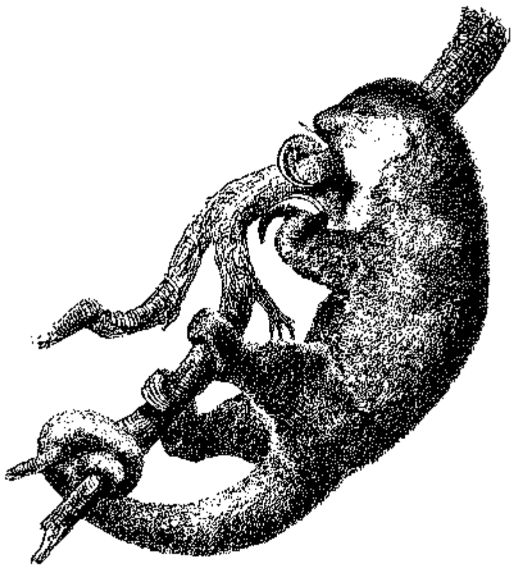

Appendix . Representation of species achieved by three area-selection methods (quantifying richness hotspots; rarity hotspots; and complementary areas) for British birds as numbers of 10 × 10 km grid cells with breeding records.[a]

	Numbers of records				
				Complementary areas[c] *for goal of*	
Species name	*Total areas*[b]	*Richness hotspots*	*Rarity hotspots*	*1-rep*	*6-reps*
Red Grouse	749	35	32	9	39
Ptarmigan	133	2	6	3	13
Black Grouse	278	19	24	5	22
Capercaillie	34	4	15	3	6
Red-legged Partridge	894	110	66	13	64
Grey Partridge	1278	124	79	14	71
Quail	233	31	10	1	12
Pheasant	1925	140	108	18	95
Golden Pheasant	15	9	9	1	6
Lady Amherst's Pheasant	4	2	0	1	4
Mute Swan	1341	125	97	17	81
Whooper Swan	4	1	1	1	4
Canada Goose	978	117	65	10	63
Barnacle Goose	17	8	7	1	6
Greylag Goose	417	72	49	11	45
Shelduck	669	81	71	9	56
Egyptian Goose	39	9	15	4	10
Mandarin	133	40	17	2	22
Mallard	2397	141	126	24	124
Gadwall	192	55	43	8	35
Wigeon	128	11	25	5	26
Teal	571	85	70	13	65
Garganey	39	16	14	2	11
Pintail	17	2	9	1	7
Shoveler	217	50	44	8	42
Wood Duck	6	1	2	1	6
Red-crested Pochard	3	1	1	1	3
Tufted Duck	1019	130	87	16	81
Scaup	3	1	2	1	3
Pochard	162	42	31	5	30
Eider	359	6	27	6	24
Common Scoter	16	1	4	1	6
Goldeneye	13	1	10	2	8
Goosander	398	24	25	5	23
Red-breasted Merganser	377	20	27	7	26
Ruddy Duck	184	29	15	4	19
Wryneck	1	0	1	1	1
Green Woodpecker	1130	130	63	13	69
Great Spotted Woodpecker	1598	137	92	18	91
Lesser Spotted Woodpecker	516	95	40	8	46
Kingfisher	816	106	42	10	53
Cuckoo	1739	139	103	22	107
Ring-necked Parakeet	15	5	4	1	6
Swift	1673	137	86	17	94
Nightjar	190	55	27	6	29
Barn Owl	748	91	53	9	54
Snowy Owl	1	0	1	1	1
Little Owl	942	111	52	10	60
Tawny Owl	1688	137	97	17	89
Long-eared Owl	307	46	39	5	31
Short-eared Owl	381	29	18	4	19
Collared Dove	1826	140	101	17	94
Turtle Dove	700	93	55	10	57
Feral Pigeon/Rock Dove	1427	121	79	17	81
Stock Dove	1423	132	77	14	80

Appendix. Continued

	Numbers of records				
				Complementary areas[c] *for goal of*	
Species name	*Total areas*[b]	*Richness hotspots*	*Rarity hotspots*	*1-rep*	*6-reps*
Woodpigeon	2308	141	117	21	111
Crane	1	1	1	1	1
Water Rail	215	60	41	5	39
Spotted Crake	11	2	6	2	6
Corncrake	105	3	5	2	6
Moorhen	1867	140	106	18	95
Coot	1470	138	95	16	90
Woodcock	917	114	69	12	69
Black-tailed Godwit	12	2	9	1	6
Snipe	1311	113	102	18	92
Stone Curlew	44	10	13	1	8
Dunlin	353	10	21	7	29
Purple Sandpiper	1	0	1	1	1
Red-necked Phalarope	5	0	3	1	5
Redshank	1046	120	94	14	86
Greenshank	149	0	8	3	11
Common Sandpiper	1057	50	41	9	45
Wood Sandpiper	4	1	2	1	4
Ruff	10	4	5	1	6
Whimbrel	36	0	9	2	7
Curlew	1354	78	68	13	74
Oystercatcher	1375	79	110	19	90
Avocet	22	10	16	3	7
Ringed Plover	812	81	75	15	65
Little Ringed Plover	323	73	28	7	28
Golden Plover	630	20	29	8	36
Dotterel	48	0	3	2	8
Lapwing	2091	141	121	23	115
Razorbill	233	3	21	6	19
Guillemot	212	3	21	6	19
Black Guillemot	383	3	19	6	23
Puffin	151	0	22	4	16
Arctic Skua	113	0	12	5	15
Great Skua	97	0	15	3	16
Kittiwake	252	6	24	6	23
Mediterranean Gull	7	3	7	1	6
Black-headed Gull	671	78	69	9	59
Common Gull	577	14	47	7	45
Lesser Black-backed Gull	434	16	32	6	26
Herring Gull	729	29	51	9	46
Great Black-backed Gull	486	8	31	9	34
Sandwich Tern	43	6	23	1	10
Roseate Tern	19	3	14	1	6
Common Tern	426	55	63	9	46
Arctic Tern	303	8	30	5	19
Little Tern	110	17	24	3	16
Kestrel	1991	141	108	23	111
Merlin	382	24	17	4	21
Hoby	230	53	24	5	24
Peregrine	720	31	36	8	45
Osprey	39	5	22	2	8
Red Kite	45	1	0	1	6
Sparrowhawk	1511	136	87	19	90
Goshawk	91	21	9	2	14
Buzzard	1174	63	56	10	57

Appendix. Continued

Species name	*Numbers of records*				
				Complementary areas[c] for goal of	
	Total areas[b]	*Richness hotspots*	*Rarity hotspots*	*1-rep*	*6-reps*
Honey Buzzard	10	6	6	2	6
Golden Eagle	216	2	9	4	15
White-tailed Eagle	3	0	1	1	3
Marsh Harrier	32	14	22	2	12
Hen Harrier	286	14	22	2	16
Montagu's Harrier	5	2	3	1	5
Little Grebe	984	126	89	13	82
Great Crested Grebe	726	97	46	11	54
Slavonian Grebe	17	0	11	1	6
Black-necked Grebe	11	1	2	1	6
Red-necked Grebe	3	0	0	1	3
Gannet	18	0	6	1	6
Cormorant	174	4	12	3	8
Shag	386	2	26	7	26
Bittern	10	6	9	1	6
Grey Heron	791	85	52	12	51
Red-throated Diver	246	2	18	7	23
Black-throated Diver	112	0	7	2	11
Storm Petrel	48	0	13	3	11
Leach's Storm-petrel	10	0	9	1	6
Manx Shearwater	22	0	10	2	7
Pulmar	550	9	38	8	33
Red-backed Shrike	2	0	1	1	2
Jay	1267	129	62	12	73
Magpie	1775	132	85	13	84
Chough	64	1	2	1	6
Jackdaw	2149	140	109	20	100
Rook	1954	135	85	15	82
Crow	2538	141	121	24	128
Raven	785	25	24	6	38
Golden Oriole	14	2	7	1	6
Starling	2498	141	132	23	124
Ring Ouzel	401	19	18	5	23
Blackbird	2583	141	127	25	126
Fieldfare	18	2	1	1	6
Song Thrush	2491	141	119	23	119
Redwing	46	2	6	2	10
Mistle Thrush	2153	141	113	20	111
Spotted Flycatcher	2097	140	111	22	111
Pied Flycatcher	547	42	10	4	18
Stonechat	850	57	49	8	50
Whinchat	1062	67	48	11	56
Wheatear	1341	65	71	16	75
Redstart	1019	84	54	12	54
Black Redstart	57	15	12	3	13
Robin	2536	141	119	22	118
Nightingale	303	65	35	6	36
Nuthatch	1063	107	49	11	59
Treecreeper	1675	138	97	15	93
Dipper	1097	50	36	10	43
Wren	2650	141	134	26	135
Marsh Tit	858	105	41	8	52
Willow Tit	789	100	38	10	50
Crested Tit	31	1	20	3	10
Coal Tit	2009	140	108	20	106

Appendix. Continued

	Numbers of records				
Species name	*Total areas*[b]	*Richness hotspots*	*Rarity hotspots*	*Complementary areas*[c] *for goal of*	
				1-rep	*6-reps*
Blue Tit	2382	141	120	21	113
Great Tit	2317	141	116	20	109
Long-tailed Tit	1868	140	108	18	101
Sand Martin	991	95	67	11	58
Swallow	2457	141	122	23	119
House Martin	2227	141	113	16	108
Dartford Warbler	40	21	12	1	9
Lesser Whitethroat	981	108	68	11	67
Whitethroat	1934	137	94	17	97
Garden Warbler	1477	137	74	13	81
Blackcap	1757	139	87	15	90
Bearded Tit	52	24	24	3	15
Cetti's Warbler	57	23	14	1	14
Grasshopper Warbler	673	91	51	10	50
Savi's Warbler	8	7	7	1	6
Goldcrest	1930	136	102	21	99
Firecrest	48	20	6	1	10
Willow Warbler	2446	141	119	23	118
Chiffchaff	1662	136	81	12	81
Wood Warbler	859	88	36	9	49
Sedge Warbler	1554	127	99	16	88
Marsh Warbler	8	1	3	1	6
Reed Warbler	638	94	64	11	60
Woodlark	55	27	15	2	13
Skylark	2571	141	130	26	131
Dunnock	2317	141	116	23	111
House Sparrow	2431	141	124	23	119
Tree Sparrow	1040	98	61	12	52
Yellow Wagtail	759	85	49	9	46
Grey Wagtail	1657	114	74	14	80
Pied Wagtail	2467	141	119	27	126
Tree Pipit	1215	113	66	11	74
Meadow Pipit	2261	136	129	24	126
Rock Pipit	554	10	31	8	36
Snow Bunting	15	0	3	1	6
Yellowhammer	1962	140	106	20	100
Cirl Bunting	18	0	1	1	6
Reed Bunting	1846	140	111	18	104
Corn Bunting	686	69	45	9	46
Chaffinch	2503	141	121	23	119
Brambling	2	0	0	1	2
Greenfinch	2056	141	112	19	100
Goldfinch	1888	141	94	17	93
Siskin	728	65	58	12	53
Bullfinch	1769	140	98	16	99
Hawfinch	170	50	23	3	24
Linnet	2002	140	97	15	91
Twite	420	12	22	6	24
Lesser Redpoll	1184	120	82	15	77
Serin	1	0	1	1	1
Scarlet Rosefinch	1	0	0	1	1
Common Crossbill	364	45	30	5	29
Scottish Crossbill	39	1	24	3	11

[a] *Original bird distribution data from Gibbons et al. 1993; sequence of species based on the classification of Sibley & Ahlquist 1990 and the convention of Nelson 1972.*

[b] *Total number of grid cells in Britain for which there are breeding records for each species.*

[c] *For complementary areas results are included for goals of both one representation and six representations of species.*