
Performance of Sub-Saharan Vertebrates as Indicator Groups for Identifying Priority Areas for Conservation

JOSLIN L. MOORE,*†† ANDREW BALMFORD,† THOMAS BROOKS,‡
NEIL D. BURGESS,†§ LOUIS A. HANSEN,* CARSTEN RAHBK,* AND PAUL H. WILLIAMS**

*Zoological Museum of the University of Copenhagen, Universitetsparken 15, Copenhagen, Denmark

†Conservation Biology Group, Zoology Department, University of Cambridge, 15 Downing Street, Cambridge CB2 3EJ, United Kingdom

‡Center for Applied Biodiversity Science, Conservation International, 1919 M Street NW, Washington, D.C. 20036, U.S.A.

§World Wildlife Fund-U.S., 1250 24th Street NW, Washington, D.C. 20037-1132, U.S.A.

**The Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom

Abstract: *The aim of continental and global identification of priority areas for conservation is to identify particularly valuable areas for conservation on which to focus more-detailed effort. Often, these sets of important areas, referred to as priority sets, have been identified through use of data on a single taxon (e.g., birds), which is assumed to act as an indicator for all biodiversity. Using a database of the distributions of 3882 vertebrate species in sub-Saharan Africa, we conducted one of very few large-scale tests of this assumption. We used six potential indicator groups—birds, mammals, amphibians, snakes, threatened birds, and threatened mammals—to find priority sets of 200 areas that best represent the species in that group. Priority sets of grid cells designed to maximize representation of a single indicator group captured 83–93% of species in the other groups. This high degree of representation is consistent with observed high levels of overlap in the patterns of distribution of species in different groups. Those species of highest conservation interest were more poorly represented, however, with only 75–88% of other groups' threatened species and 63–76% of other groups' narrow-range species represented in the priority sets. We conclude that existing priority sets based on indicator groups provide a pragmatic basis for the immediate assessment of priorities for conservation at a continental scale. However, complete and efficient representation—especially of narrow-range species—will not be achieved through indicator groups alone. Therefore, priority-setting procedures must remain flexible so that new areas important for other taxa can be incorporated as data become available.*

La Efectividad de los Vertebrados del Sub-Sahara como Grupos Indicadores para Identificar Áreas Prioritarias para la Conservación

Resumen: *La meta de la identificación de prioridades globales y continentales de conservación es la identificación de áreas particularmente valiosas para la conservación en las cuales enfocar esfuerzos más detallados. A menudo, estos conjuntos de áreas importantes (referidas como conjuntos prioritarios) han sido identificados utilizando datos de un solo taxón (e. g. aves), el cual se supone que actúa como indicador de toda la biodiversidad. Utilizando una base de datos de la distribución de 3882 especies de vertebrados en África sub-Sahara, realizamos una de las pocas pruebas a gran escala de este supuesto. Utilizamos seis grupos de indicadores potenciales (aves, mamíferos, anfibios, serpientes, aves amenazadas y mamíferos amenazados) para encontrar conjuntos prioritarios de 200 áreas que mejor representan las especies de ese grupo. Conjuntos prioritarios de celdas matriciales diseñadas para maximizar la representatividad de un grupo indicador capturaron 83–93% de las especies de los otros grupos. Este alto grado de representatividad es consistente*

††Address for correspondence: CSIRO Entomology, GPO Box 1700, Canberra ACT 2601, Australia, email joslin.moore@csiro.au
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con los altos niveles de superposición observados en los patrones de distribución de especies en los diferentes grupos. Sin embargo, las especies de mayor interés para la conservación estaban poco representadas, con solo 75–88% de las especies amenazadas de otros grupos y 63–76% de las especies de distribución restringida de otros grupos representados en los conjuntos prioritarios. Concluimos que los conjuntos prioritarios existentes, basados en grupos indicadores, proporcionan una base pragmática para la evaluación inmediata de las prioridades de conservación a escala continental. Sin embargo, no se logrará la representación completa y eficiente—especialmente de especies de distribución restringida—solo con grupos indicadores. Por lo tanto, los procedimientos de definición de prioridades deben permanecer flexibles para que se puedan incorporar nuevas áreas importantes para otros taxones a medida que se obtienen los datos.

Introduction

Systematic strategies for conserving biodiversity need to be developed and applied if widespread extinctions are to be avoided (Mace et al. 2000; Margules & Pressey 2000). Numerous priority-setting approaches have been used to identify areas of disproportionately high conservation value, where conservation efforts might yield the greatest efficiency and effectiveness (Williams 1998). These methods are used at many spatial scales. At large scales, such as continents, the goal is not to identify areas for reserves but to identify regions of high conservation value that are significant in a global or continental context. Once identified, these areas should then become foci for more-detailed conservation effort (Brooks et al. 2001a) and should be targeted for regional conservation investment.

Priority-setting methods usually rely on species distribution data, but most biodiversity still remains undescribed. Hence, we are faced with the task of identifying priority areas for conservation based on partial information. One approach has been to use a subset of species as surrogates for all species (Gaston 1996). The nature of the subset varies widely from a small group of charismatic flagship species, to umbrella species that require such large areas of habitat that their protection may result in the protection of other species, to indicator groups, which usually consist of those species in a relatively speciose single taxon thought to represent biodiversity as a whole. It is this third class of surrogate that we focus on here. In general we expect that indicator groups will be effective surrogates for poorly known biodiversity only if patterns of distribution coincide across taxa.

A number of global and continent-wide priority sets for conservation have been produced, often based on data for single taxa. For example, global conservation priorities have been proposed on the basis of the distributions of plants (World Conservation Union [IUCN] 1994–1997), mammals (Ceballos & Brown 1995), and birds (Stattersfield et al. 1998). Myers et al. (2000) defined conservation hotspots based on plant distributions and patterns of land clearance, and demonstrated a high

number of tetrapod vertebrates in these areas. But few such large-scale studies have systematically addressed representation of nontarget taxa in conservation priority sets based on indicator groups.

This gap in our knowledge is at least partially due to the lack of appropriate data. However, the recent development of a distributional database for 3882 species of terrestrial vertebrates across all of sub-Saharan Africa (Burgess et al. 1998) provides us with an unprecedented opportunity to test the performance of different indicator groups on a continental scale. We asked how well six major taxonomic groups can identify priority areas for continental-scale conservation for all vertebrate diversity combined, and we then examined whether the performance of an indicator group can be linked to the extent of cross-taxon congruence in species distributions.

A common approach to measuring the performance of priority sets based on indicator groups is to calculate the degree of overlap of selected areas in priority sets defined in terms of different indicator taxa. Overlap of areas selected for priority sets based on different indicator groups may be poor (Lombard 1995; van Jaarsveld et al. 1998; Virolainen et al. 2000), but representation of nontarget taxa can nonetheless be high (Howard et al. 1998; Burgess et al. 2000; Reyers et al. 2000). Hence, instead we used the effectiveness of indicators to represent other groups to evaluate the performance of priority sets based on indicators (Rodrigues et al. 1999). Effectiveness measures how well a priority set represents species and is calculated as the proportion of species in the region of interest represented in the priority set. We also compared this representation with that expected if areas were chosen at random, which provides a measure of their usefulness in guiding decisions.

Considerable effort has been made to link the performance of an indicator group with patterns of species distribution. If priority sets are identified according to hotspots of species richness or endemism, then the performance of an indicator group will likely depend on cross-taxon congruence in species richness and endemism (Prendergast et al. 1993). The results of global or continental studies suggest congruence in species rich-

ness and endemism in some cases (Pearson & Cassola 1992; Williams & Gaston 1994; Pearson & Carroll 1998; Pearson & Carroll 1999) but not in all (Schall & Pianka 1978; Ryti 1992; Flather et al. 1997; Robbins & Opler 1997). The results are similarly variable at smaller scales (Lombard 1995; Weaver 1995; Lawton et al. 1998; Oliver et al. 1998). A further complication is that area selection is most efficient if explicit attention is paid not only to species richness but also to complementarity—that is, to how distinctive a site's species are compared with those of other candidate areas (Rebelo & Siegfried 1990; Lombard 1995; Williams et al. 1996; Csuti et al. 1997; Pimm & Lawton 1998; Margules & Pressey 2000). Hence, if two groups show high congruence in complementarity, then regardless of patterns of species richness or endemism, complementarity-based selection methods based on indicator groups should result in the effective representation of all groups (Howard et al. 1998). We evaluated how well congruence in species richness, congruence in the species richness of narrow-range species (defined as the 25% of species with the smallest ranges in each taxon), and congruence in complementarity predict the performance of different taxa as indicators for continental priority setting.

Methods

Distributional Databases and Area-Selection Methods

We used distributional data for 1921 bird species, 939 mammal species, 405 snake species, and 617 amphibian species, compiled at the Zoological Museum of the University of Copenhagen, for all 1° cells of mainland sub-Saharan Africa. Sources included 1115 primary publications and unpublished reports and consultation with 74 taxon specialists (see acknowledgments). For the larger and better-known species (birds and large mammals), the data are estimates of distributions taken from standard publications, including atlases, and modified from the specialist literature where necessary. For smaller and less well-known species (many small mammals, snakes, and amphibians), we interpolated expected distributions by assuming a continuous distribution among confirmed records within relatively uniform suitable habitat. For the interpolations, we used available information on species' habitat associations and took care to exclude known gaps in distribution. Interpolation was checked through consultation with taxon specialists. For the least well-known species, records were plotted without interpolation. For the 1957 1° grid cells across the continent for which we had data, there were 828,506 species-in-grid-cell data entries (for full details of sources, taxonomy, and methods, see Brooks et al. 2001a, Burgess et al. 1998, and <http://www.zmuc.dk/commonweb/research/biodata.htm> [accessed September 2000]). For each potential in-

dicator group—birds, mammals, amphibians, snakes, threatened birds, and threatened mammals—we generated a near-minimum set in which as few cells as possible were chosen such that all species were represented. We also generated near-maximum coverage sets of 200 cells that represented all species in the indicator group as many times as possible. We studied sets of 200 cells because these represent approximately 10% of the total area of sub-Saharan Africa. We selected areas using the progressive rarity algorithm (Margules et al. 1988; Williams 1998) of the computer program WORLDMAP (Williams 1996). This algorithm provides close-to-optimal solutions under the conditions we encountered (Csuti et al. 1997). First, it selects all areas with taxa that are equally restricted or more restricted than the representation goal. For example, if the goal is to represent each species at least once, the algorithm begins by selecting all areas that contain records for species that occur only once and thus are irreplaceable. Areas are chosen to represent the rarest as-yet-unrepresented species until either the target number of areas has been reached (near-maximum coverage set) or all species are represented (near-minimum set). Once the set of cells has been selected, the areas are reordered according to complementary richness (Williams 1996).

Effectiveness of Priority Setting

We evaluated the effectiveness of representation of non-target taxa in priority sets based on each indicator group by comparing representation with two benchmarks: (1) representation in an all-vertebrate priority set based on the maximum amount of information available and (2) representation in randomly chosen priority sets when no information was used. We used all the species data combined to generate all-vertebrate priority sets (a near-maximum set of 200 cells and a near-minimum set). These sets contributed the best solution to the problem of representing all the vertebrates in the database. Random-area selections were drawn, without replacement, 1000 times. Median species representation and 95% confidence intervals of the random selections are presented in the results.

Effectiveness of representation in a priority set was measured by calculating the percentage of nontarget species represented in each priority set. This measure assumes that the representation goal is a single representation of each species. Because the groups differed in species richness, we evaluated both the total percentage of species represented (i.e., weighting each species equally regardless of its taxon) and the mean percent representation per taxon (i.e., weighting representation in each taxonomic group equally). For threatened mammals and threatened birds, we also included the representation of nonthreatened mammals and birds, respectively.

Indicator Groups and Narrow-Range Species

We evaluated each of the four major taxonomic divisions—mammals, birds, snakes, and amphibians—as potential indicator groups. We also considered globally threatened mammals and birds as indicator groups because these groups are immediate priorities for conservation and thus are likely to drive priority-setting exercises in the near future. We defined threatened mammals and birds according to the 2000 IUCN Red List (available at <http://www.redlist.org/> [accessed September 2000]). In Africa, few snake or amphibian species are listed as threatened because these groups have not yet been systematically assessed. Hence, we did not use threatened amphibians and snakes as indicator groups in the analysis.

Narrow-range species for each of the four major taxonomic divisions were defined as the 25% most narrowly distributed species. Range size was estimated by summing the number of 1° cells in which each species was present. Because of ties in the range size of different species, in practice the largest range size of a narrow-range species in each group was set at 6 cells for mammals (24% of species), 39 cells for birds (26% of species), 5 cells for snakes (27% of species), and 2 cells for amphibians (27% of species).

Measures of Congruence in Distribution

We used four measures of species distribution—species richness, richness of narrow-range species, mean complementarity, and local complementarity—to assess congruence between taxa. Each measure was calculated separately for each grid cell. Species richness and narrow-range species richness was calculated simply as the number of species in the group of interest in each grid cell.

For two areas, *A* and *B*, complementarity is (Colwell & Coddington 1994)

$$C(A,B) = 1 - \frac{\text{number of species common to both areas}}{\text{total number of species in both areas}}$$

This formula is equivalent to Jaccard's dissimilarity index (Jongman et al. 1995). High values of complementarity imply that areas have a low proportion of their species in common. We computed complementarity for all possible comparisons between the focal grid cell and all other 1956 grid cells. Mean complementarity of the focal grid cell was the mean of these 1956 complementarity values. This measure is likely to be dominated by the large number of comparisons between distant grid cells from very different environmental conditions, where complementarity will necessarily be high for all groups considered (e.g., comparing the Kalahari Desert and the Congo Basin). Hence, we also considered a more localized measure of complementarity. We calculated the local complementarity of a focal grid cell as the mean complementarity value when the focal grid cell was compared with its eight adjacent neighbors.

For each measure, we calculated congruence in scores across taxa using Spearman rank correlations. All measures exhibited high spatial autocorrelation. The presence of autocorrelation does not affect the value of the correlation coefficient but may alter the outcome of significance tests because of the inflated degrees of freedom caused by falsely assuming that all samples are independent (Cliff & Ord 1981; Haining 1990). Hence, we conducted significance tests with a degrees-of-freedom correction (Dutilleul 1993) that estimates the effective number of independent samples in the data sets (program MODTTEST; P. Legendre, available at <http://www.fas.umontreal.ca/biol/legendre/> [accessed September 2000]).

Results

Effectiveness of Indicator Groups

When the results of selection based on different indicator groups were compared, some areas were important in all priority sets (Fig. 1): the Cameroon Highlands, the Eastern Arc, the Ethiopian Highlands, the Albertine Rift, the lower Congo River, and Upper Guinea. Sets based on indicator groups, however, all missed some important areas for other taxa. When birds are used as indicators, these areas included the Ivory Coast and Ghana, the inner Congo Basin, the Karoo-Namib scrubland, and the Kalahari region. The mammal set failed to identify the upper Kalahari and miombo woodland in Angola and areas in Mozambique and Malawi. The snake set missed the Sahel, the lower portion of the Albertine Rift, and the whole length of the South African coast, whereas the amphibian set poorly represented the Kalahari region along with Horn of Africa, much of the Sahel, and the Mozambique coast. Sets for both threatened species groups were focused in areas of high habitat heterogeneity and relatively rare habitats. Again, the dry southwest of Africa stood out as being particularly poorly covered by these groups.

The near-maximum sets of 200 areas based on any of the four major indicator groups represented nontarget taxa better than would be expected at random (Fig. 2). Thus, including species-distribution information even on a single taxon significantly improved our ability to select areas of high conservation value. In all cases, however, these near-maximum sets represented nontarget taxa less well than the all-vertebrate near-maximum set (88–93% cf. 99%; Table 1), so, depending on the indicator group, 212–270 species of a total of 3882 species were missed. Threatened mammals and birds were least effective as indicator groups, with priority sets based on these groups representing 86% and 83% of all species, respectively. Priority sets based on threatened groups represented snakes and amphibians particularly poorly.

The effectiveness of the indicator groups depended

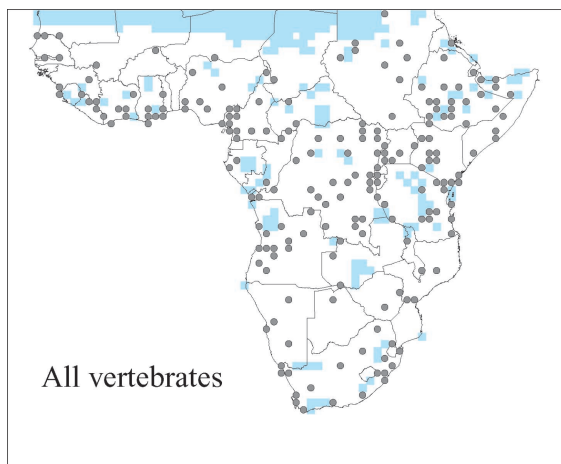


Figure 1. Distribution of maximum-coverage sets (grey dots) and the proportion of all species not represented in the maximum-coverage set (colored squares). The colored squares indicate the proportion of unrepresented species in each cell on an equal-frequency scale (lowest proportion pale blue, highest red). Note that the total number of species unrepresented differs among maps (Table 1). The indicator group used to determine the maximum-coverage set is written on each map.

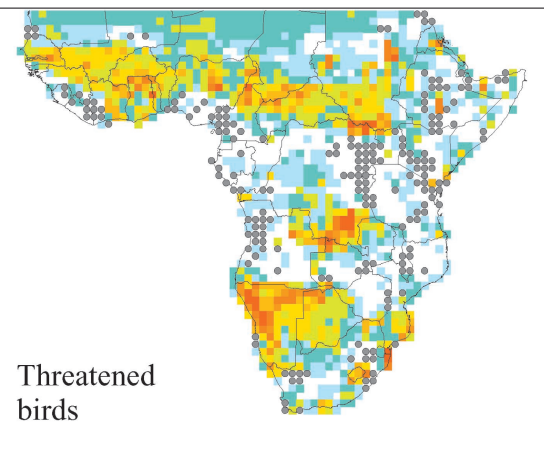
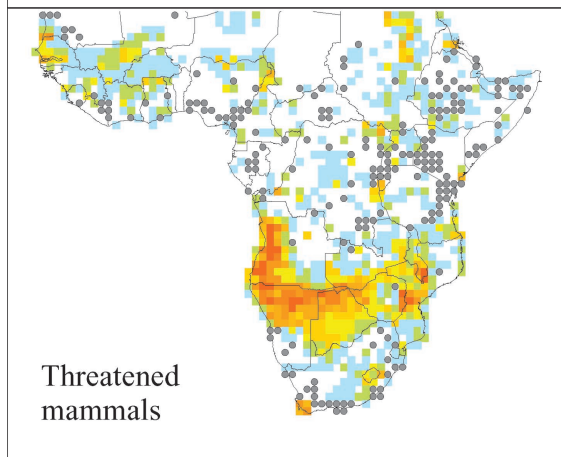
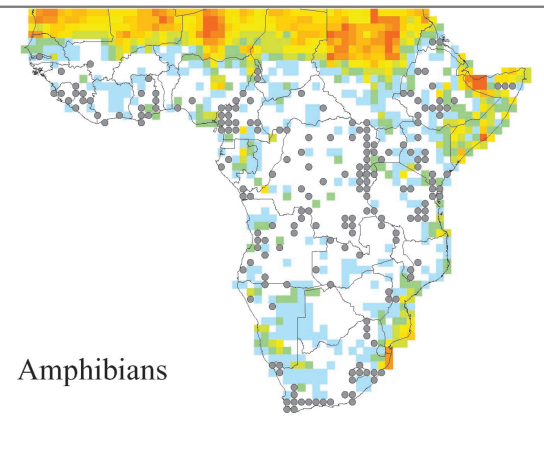
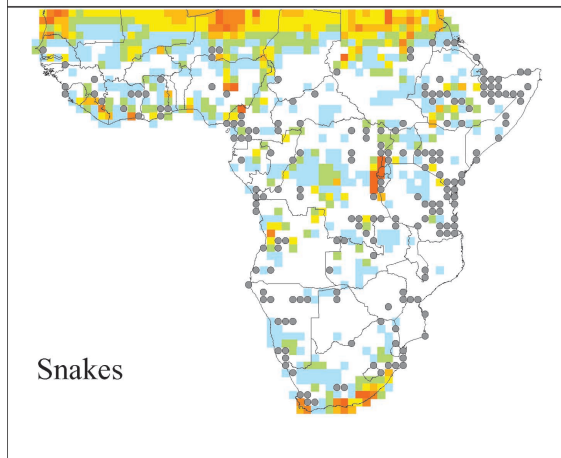
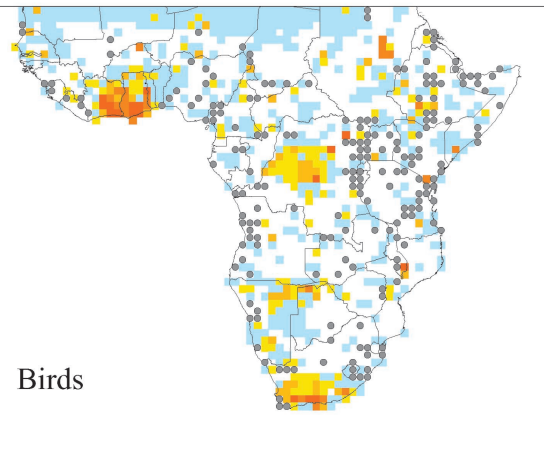
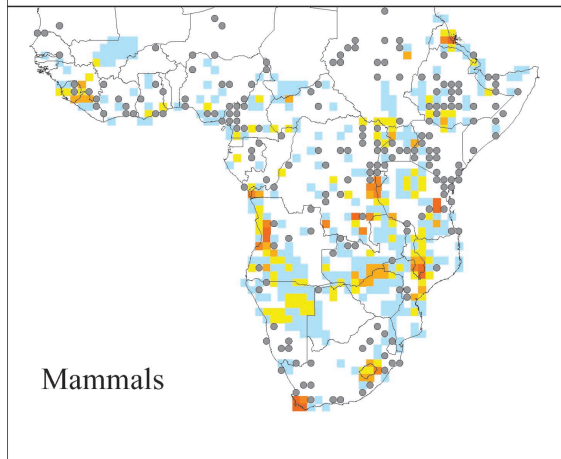


Table 1. Representation (%) of different taxa in near-maximum coverage sets of 200 grid cells generated using indicator groups.

<i>Indicator</i>	<i>Mammals</i>	<i>Birds</i>	<i>Snakes</i>	<i>Amphibians</i>	<i>All^a</i>	<i>Mean^b</i>	<i>SD^c</i>
All species							
all vertebrates	97	99	100	99	99	99	1.2
mammals	100	97	85	84	93	89	7.3
birds	89	100	89	86	88	88	1.9
snakes	88	97	100	83	92	90	6.9
amphibians	89	97	84	100	93	90	6.3
threatened mammals	91	96	84	83	86	89	6.4
threatened birds	88	95	80	83	83	86	6.7
random	75	92	73	60	81	75	13.3
Narrow-range species							
all vertebrates	96	98	90	100	97	96	4.5
mammals	100	89	57	51	76	66	20.2
birds	66	100	64	57	63	62	4.8
snakes	61	89	100	48	74	66	21.2
amphibians	64	89	53	100	77	69	18.6
threatened mammals	65 ^d	85	58	51	73	65	14.6
threatened birds	63	90 ^d	46	58	71	64	18.5
random	24	69	22	12	44	32	25.2

^aPercent representation of species in all taxa except the indicator group.

^bMean value per group (excluding the indicator group). When selection was based on all vertebrates or selection at random, the mean was calculated using all groups. For threatened mammals and threatened birds the mean was based on representation in the four groups but did not include those species classified as threatened.

^cStandard deviation of the mean.

^dPercentages calculated for only those species classified as rare but not threatened: 121 and 385 species for mammals and birds, respectively.

on the way in which representation was evaluated. If effectiveness was measured as the total percentage of species represented (Fig. 2), then amphibians, snakes, and mammals were the most effective groups, with birds and threatened groups being less effective. The disparity between indicator groups diminished if effectiveness was measured as the mean percentage of species represented in each taxon (Fig. 2). The difference between all groups decreased, and, notably, birds no longer stood out as poor indicators. This result can be attributed to the high representation of birds in priority sets based on other indicator groups, which inflated the species totals relative to the mean for all indicator groups except birds.

The near-minimum set for all vertebrate species in the database was at least twice as large as the near-minimum set for any group alone (Table 2). Therefore, full repre-

sentation of nontarget taxa could never be achieved in the near-minimum set for any single indicator group. Nevertheless, for all indicator groups, the near-minimum sets represented between 80% and 90% of the nontarget species (with the exception of threatened birds, which represented only 71% of nontarget species), which was only 4–12% less than representation in corresponding near-maximum sets. Considering that these near-minimum sets were less than half the size of the near-maximum sets, they represented nontarget species remarkably well.

Representation of Nontarget Taxa

The mean representation of each of the four taxa in sets identified by use of other taxa as indicator groups revealed some variation (mean representation of each group by the other three groups: birds, 97%; mammals,

Table 2. Representation (%) of different taxa in near-minimum sets (NMS) generated using indicator groups.^a

<i>Indicator</i>	<i>NMS size^b</i>	<i>Representation in NMS (%)</i>						<i>SD</i>
		<i>mammals</i>	<i>birds</i>	<i>snakes</i>	<i>amphibians</i>	<i>all</i>	<i>mean</i>	
All vertebrates	235	100	100	100	100	100	100	0.00
Mammals	115	100	95	79	78	90	84	9.77
Birds	86	82	100	81	76	80	80	3.38
Snakes	75	78	94	100	72	86	81	11.17
Amphibians	108	84	95	77	100	90	86	9.07
Threatened mammals	73	86	94	72	74	81	81	10.52
Threatened birds	43	72	87	64	64	71	72	10.65

^aFor definitions of measures, see footnotes of Table 1.

^bThe number of 1° grid cells in the near-minimum set for the indicator group.

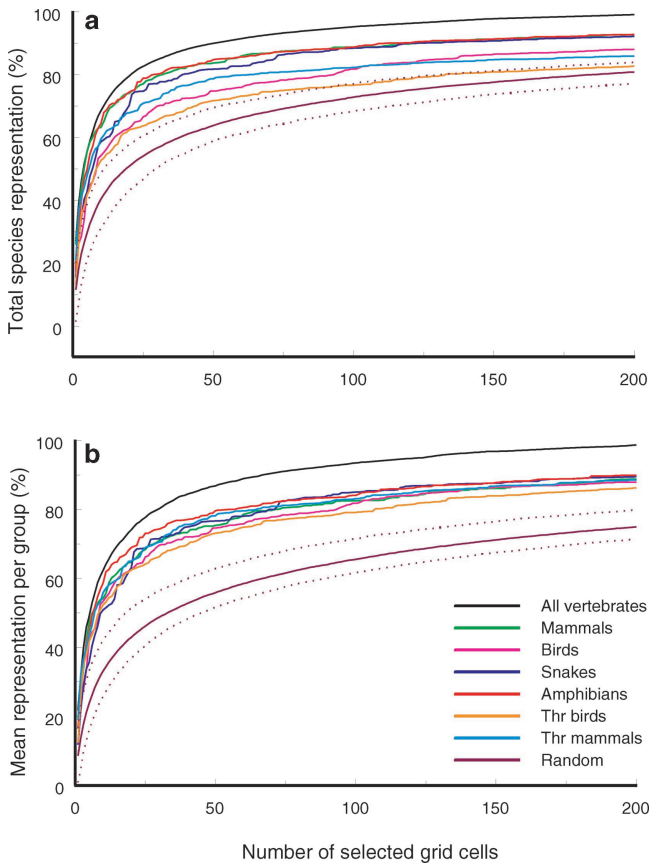


Figure 2. Cumulative percent representation of (a) all species and (b) the mean proportion of species per taxon in the maximum-coverage set of 200 cells (excluding the indicator taxon) when the set has been generated by different indicator groups. When individual taxa are used as indicators, the subsequent calculations include only those species not in the indicator taxon. The median representation of all species in sets selected at random is also presented. Dotted lines indicate 95% confidence intervals.

89%; snakes, 86%; amphibians, 84%). Birds were well represented in all sets, whereas amphibians and snakes were less well represented. This difference can be attributed to differences in the distribution of range sizes among the groups (Brooks et al. 2001a). Groups that contain many localized species were less well indicated by other taxa. In our database, birds had a much larger median range size than the other groups, particularly amphibians (in descending order, median range size measured as number of grid cells was birds, 144; mammals, 33; snakes, 30; amphibians, 10).

Although the overall effectiveness of using an indicator group to represent all vertebrates was high, representation of more vulnerable groups such as narrow-range and threatened species was lower (Table 1). In contrast to the case where all species were considered,

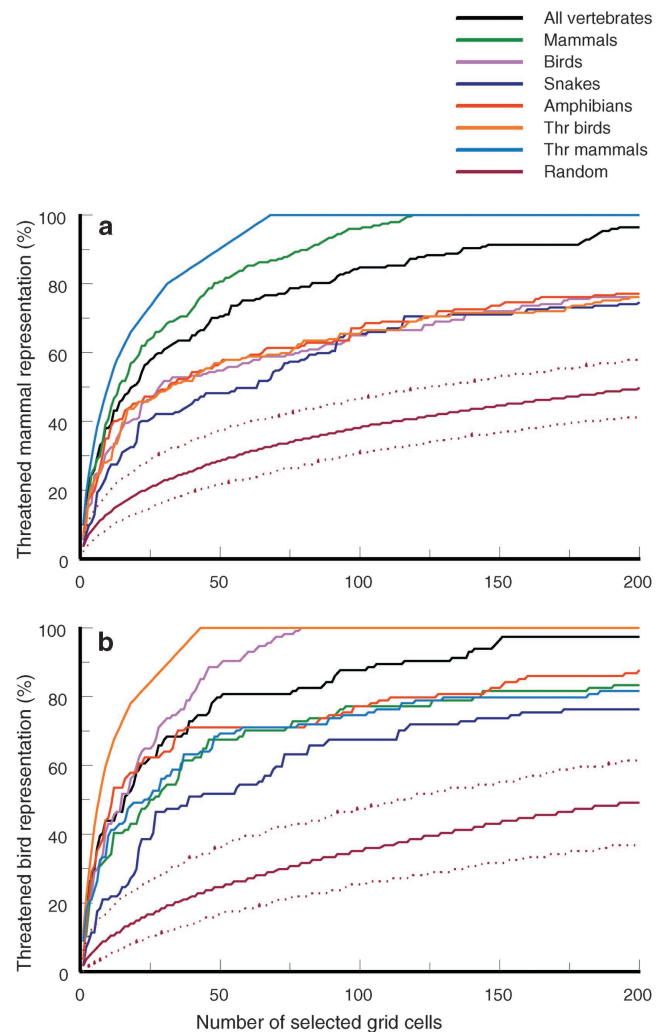


Figure 3. Representation of (a) threatened mammals and (b) threatened birds in maximum-coverage sets of 200 cells generated from different indicator groups. Threatened birds and threatened mammals are also included in the bird and mammal indicator groups, respectively.

the degree of representation of narrow-range species was more dependent on the identity of the indicator group (the values in a single column vary more across rows in the lower portion of Table 1). For example, although sets based on birds or snakes represented roughly the same total number of amphibian species, the bird set captured almost 10% more narrow-range amphibians.

Threatened mammals and birds were also less well represented in sets based on other taxa (Fig. 3). It was noticeable that representation of threatened species was poor even in the early stages of priority setting based on their own taxon, indicating that threatened species are not necessarily in the cells with the highest complementary species richness for their group.

Table 3. Spearman correlation coefficients measuring congruence between taxa in species richness (above the diagonal) and mean complementarity (below the diagonal).^a

	<i>Mammals</i>	<i>Birds</i>	<i>Snakes</i>	<i>Amphibians</i>
<i>Mammals</i>	—	0.86 (0.34)	0.82 (0.23)	0.82 (0.23)
<i>Birds</i>	0.82 (0.43)	—	0.71 (0.26)	0.76 (0.28)
<i>Snakes</i>	0.76 (0.53)	0.77 (0.42)	—	0.74 (0.16)
<i>Amphibians</i>	0.63 (0.33)	0.54 (0.19 ^b)	0.38 ^c (0.27)	—

^a Correlations between species richness of narrow-range species and local complementarity are shown in parentheses. Unless marked otherwise, correlations are significant (two-tailed, modified *t* test to control for autocorrelation and Bonferroni correction for multiple comparisons), with $p < 0.001$.

^b Correlation not significant.

^c $p < 0.01$.

Patterns of Congruence

Species richness was significantly correlated between pairs of taxa (Table 3). Congruence in species richness of narrow-range species was much weaker, however, explaining the poorer representation of narrow-range species in priority sets based on indicator groups. Mean complementarity was also significantly and positively correlated between taxa, with the correlations being slightly weaker than for species richness (Table 3). Correlations for local complementarity were generally much weaker than correlations for mean complementarity. Nevertheless, all correlations were significant except that between birds and amphibians. Despite this last result these two groups were nevertheless well represented in each other's priority sets (Table 1). Thus, low congruence in complementarity did not necessarily lead to poor cross-taxon representation.

The overall congruence in the distribution patterns of the different groups matched the relatively high rates of representation of nontarget species in priority sets identified based on indicator groups. However, none of our measures of distributional congruence acted as a consistent predictor of the performance of the different taxa as indicators of overall priorities for vertebrate conservation. For example, the correlation in mean complementarity between snakes and amphibians was much poorer (0.38) than that between snakes and mammals (0.76), yet the representation of snakes in amphibian- and mammal-derived priority sets was very similar (84% vs. 85%).

Discussion

Our analyses suggest that the use of indicator groups to select priority sets of areas of high conservation value can be effective and that these sets will represent significantly more nontarget richness than can be expected at random. Hence, the assumption that areas of high conservation value for one group also represent the diversity of other groups seems well supported in this case (Prendergast et al. 1993; Howard et al. 1998; Burgess et al. 2000; Reyers et al. 2000; Virolainen et al. 2000). Any

of the sets identified based on a single indicator group, especially one of the four major taxonomic divisions, would provide a useful initial basis for setting large-scale conservation priorities in Africa.

It is interesting that the difference between the all-vertebrate set and random selection was large. This result contrasts with the findings of smaller-scale studies (Howard et al. 1998; Virolainen et al. 2000) in which little difference between the near-optimal solution and random selection has been found. Indicator groups will be most useful when the difference between optimal and random representation is great. Understanding why the difference between random and optimal representation varies and being able to predict when it will be great would do much toward targeting the use of indicators to those circumstances where they will be most useful.

Representation of Nontarget Taxa

A number of factors may contribute to the high degree of representation of nontarget taxa in priority sets for indicator groups. One obvious factor is the relatively close taxonomic and ecological similarities between the different groups. We can expect indicator groups to work well only when they have ecological requirements similar to those of the taxa they are meant to represent (Kremen 1992; Caro & Odoherly 1999). The high degree of representation between taxa may decline if other more ecologically and evolutionarily diverse groups, such as plants, fish, or invertebrates, were also considered.

Second, the number of species in the indicator groups was large and represented much of the variation in geographical distribution, range size, and ecological adaptation found in Africa. Good representation of nontarget taxa when priority setting is based on indicator groups contrasts with studies that focus on small groups of flagship or umbrella species, for which representation is often low (Andelman & Fagan 2000) or not better than random (Williams et al. 2000). This is not surprising, because a small number of species are unlikely to accurately reflect the distribution patterns of many species, are unlikely to inhabit the entire range of habitat types

in the region, and will likely require conservation effort in less total area than all species combined.

Third, we measured representation rather than comparing particular areas in different priority sets or the coincidence of hot spots. High representation of other species in priority sets based on indicator groups has been reported in a number of other studies at a variety of other scales (Ryti 1992; Howard et al. 1998; Burgess et al. 2000; Virolainen et al. 2000; Brooks et al. 2001b; Hopkinson et al. 2001). But high representation does not guarantee correspondence between the identity of areas in priority sets for different taxa, nor does it necessarily mean that there is consistently high cross-taxon agreement in patterns of species richness or endemism between taxa (Prendergast et al. 1993; Lombard 1995; Dobson et al. 1997; van Jaarsveld et al. 1998). Hence, previous studies that examined surrogate performance based on these other criteria may well have drawn more pessimistic conclusions.

A fourth likely factor is the large scale of the study, which may have increased the overall effectiveness or efficiency of priority-setting exercises. For example, the near-minimum set to represent all vertebrates required little more than 10% of the entire area, which is considerably less than has been required to achieve full representation in other, smaller-scale studies (Howard et al. 1998; Virolainen et al. 2000). There are a number of possible reasons for this difference in overall efficiency. It may be a result of the choice of taxa: plant and invertebrate groups were included in the other studies, and their inclusion may have driven the increase in required area. Another possible explanation is the inevitable increase in species richness per grid cell (or planning unit) as grid-cell size increases. This in turn means that the probability that any two species occur in the same cell will increase with grid-cell size. At the scale considered here, co-occurrence in a grid cell does not guarantee co-occurrence at smaller scales. In this respect, the apparent efficiency of these priority sets may be inflated. Finally, large-scale planning is associated with increased efficiency because one is not constrained to seek representation of species in each of several pre-defined areas. Regional studies aim to represent every taxon in the study area, whereas across all of Africa many of these species may be more easily represented elsewhere. Therefore, fewer areas are required under continent-wide selection than under region-wide selection.

Limitations to Cross-Taxon Surrogacy

Although indicator taxa worked well for vertebrates overall, they had a number of limitations. First, each indicator group missed at least one major region important for the other groups. In particular, the arid Kalahari region, an important region for snakes, was missed by all other indicator groups, reflecting the larger proportion

of snakes adapted to arid environments compared with that of other taxa.

In addition, narrow-range and threatened species, exactly those of greatest conservation concern, are consistently missed by using indicator taxa (Dobson et al. 1997; Fjeldsa 2000; Reyers et al. 2000). Indicator approaches may be effective in representing widespread species, but full representation of narrow-range species will often be guaranteed only through direct evaluation of their distributions.

Finally, efficient networks for indicator species will likely miss a significant proportion of nontarget species (Reyers et al. 2000). The size of the near-minimum set for all vertebrates (235 areas; Table 2) was at least twice as large as the near-minimum sets for any single indicator group (40–115 areas). Other studies (Ryti 1992; Lombard 1995; Dobson et al. 1997; Burgess et al. 2000; Reyers et al. 2000) also suggest that any near-minimum set based on a single taxon will be insufficient in size to represent all biodiversity. One possibility is to continue to use indicator species to select the estimated number of areas required to represent all species. As we continue to choose areas, however, the value of using an indicator group may decline. In the extreme, the proportion of area chosen would be so great that complete representation would become almost inevitable, and, crucially, equivalent to the case if areas were chosen at random (Brooks et al. 2001b). Hence, if we rely on indicators to provide efficient priority sets we must acknowledge that some important areas for nontarget taxa are likely to be missed. We suggest that opportunistically incorporating additional areas based on other data (even if incomplete) may be more efficient than continuing with selection based on a single indicator group once the representation goal of the indicator group has been reached.

Identifying Good Indicator Groups

Unfortunately, our study provides little insight into the identity of a good indicator group. Variation in the effectiveness of mammals, snakes, and amphibians as indicator groups was surprisingly small, whereas birds were less effective, probably because of their generally large ranges. The relatively poor performance of birds contrasts with the general perception that birds make a good indicator group (International Council for Bird Preservation 1992). Congruence in species richness and mean complementarity was strong among most groups, explaining the general pattern of high representation of nontarget species by indicator groups. These large-scale differences explain the high degree of representation of nontarget species but do little to explain the variation in the performance of different groups as indicator taxa. High congruence in cross-taxon complementarity merely indicates that in all groups different species live

in deserts than in tropical rainforests. Poorer correlations for narrow-range species and local complementarity explain the poorer representation of narrow-range and threatened species in priority sets based on indicator groups, but again do little to explain the variation in the performance of different taxa as indicator groups.

Considering the low number of species and the high degree of ecological specialization in amphibian and snake indicator groups, their representation of other taxa was surprisingly high. This may be partly due to biases in the accuracy of the distribution data. The distributions of many species, particularly amphibians, snakes, and small mammals, are poorly known. Consequently, it is likely that many of these species are mapped as more restricted in range than is actually the case. If so, we may have overestimated the number of areas required to represent these groups, which could have inflated their representational power.

The identity of a universally suitable indicator group continues to be evasive. One possibility is that taxa with small ranges are likely to make good indicator groups simply because narrow-range species are the most difficult to represent in priority sets based on other groups. For example, birds were well represented in all priority sets based on other indicator groups yet performed less well as indicators for other taxa. In contrast, snakes and amphibians, with typically smaller ranges, performed better as indicators but were more poorly represented in priority sets for other groups. But although many threatened species are narrowly distributed, threatened species were poorer indicators, suggesting that choosing an indicator group with many narrowly restricted species is not sufficient to guarantee the performance of an indicator group.

A Final Caveat

Priority-setting approaches based on minimizing area and optimizing representation need to be interpreted with care. Using representation as the criterion for priority setting fails to incorporate a number of important considerations likely to affect the success of conservation efforts. In particular, schemes that incorporate population viability, threatening processes, and costs are likely to provide a more robust set of priorities (Cowling et al. 1999; Araujo & Williams 2000; Wessels et al. 2000; Williams & Araujo 2000). It should also be remembered that particular areas within priority grid cells are unlikely to contain all species associated with their cell, and in this respect representation at a large scale is likely to overestimate representation of species at smaller scales. These issues, although important, are less critical at large scales, where the aim of priority setting is to identify areas of outstanding conservation value rather than to design a reserve network.

Conclusion

Our analysis suggests that indicator taxa may provide a useful shortcut to identifying large-scale priorities for conservation. Overall, representation of nontarget taxa was encouragingly high and much greater than representation if areas were chosen at random. It is unreasonable, however, to expect any single indicator group to provide a complete picture. It is likely that plants and invertebrates, groups with high total species richness and many narrowly distributed species, would not be so well represented in priority sets based on vertebrate taxa. Likewise, rare and threatened taxa can be guaranteed protection only by explicitly incorporating them into the goal of the network. Therefore, priority sets must remain flexible so that important areas for other taxa can be incorporated as they are identified. If we rely solely on a limited number of indicator groups to identify important regions for conservation, we surely will disenfranchise many of the narrow-range, threatened, and poorly known species in other taxa.

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