

Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa

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Abstract

More biodiversity could be protected *in situ* if the few species that attract the most popular support (the ‘flagship’ species) had distributions that also covered the broader diversity of organisms. We studied how well different groups of mammals performed for representing the diversity of mammals and breeding birds among 1° areas of sub-Saharan Africa. We demonstrate that choosing areas of sub-Saharan Africa using either conservationists’ six primary flagship mammals, or the six ‘Big Five’ mammals popular with wildlife tourists, is not significantly better for representing the diversity of mammals and birds than choosing areas at random. Furthermore, neither of these groups is significantly better for representing the diversity of mammals and birds than groups of the same number of species chosen at random. We show that in order to succeed in representing many mammals and birds in area selection, it is not sufficient for the groups used for selection to occur in many different ecoregions, they must also have low overlaps in distribution, so as to provide high ecological complementarity (a similar pattern of ecological complementarity must be shared by the larger group of species to be represented). Therefore there may be a need for an explicit policy to balance the requirements of flagship conservation and broader biodiversity conservation, which will have implications for the distribution of resources.

INTRODUCTION

Conservationists often choose ‘flagship’ species strategically from among the largest and most charismatic threatened mammals in order to raise public support for conservation (for a review, see Leader-Williams & Dublin, 2000). It is often argued that these flagships might also act as ‘umbrellas’ for conserving many other species, if the flagships have particularly broad ecological requirements (e.g. Shrader-Frechette & McCoy, 1993). More recently, the effectiveness of this approach for conserving biodiversity has been called into question, although suitable data were unavailable for tests (Simberloff, 1998). This might not be a problem if it were not apparent that even the smaller and less charismatic species are becoming increasingly threatened (Entwistle & Stephenson, 2000). We investigated the consequences of selecting areas for flagships using new data for the highly valued fauna of sub-Saharan Africa.

Which are the principal flagship species for raising support for conservation in sub-Saharan Africa? There are many conservation organizations with their own

favourites. Among the most broadly accepted are six species, including the two species of rhinos (*Ceratotherium simum* and *Diceros bicornis*), elephant (*Loxodonta africana*), gorilla (*Gorilla gorilla*), and the two species of chimps (*Pan troglodytes* and *Pan paniscus*).

However, most conservation effort is currently directed towards parks and reserves because of their importance for wildlife tourism revenue (direct and indirect). The overwhelming proportion of tourist spending goes on seeing the ‘Big Five’ animals (MacKinnon & MacKinnon, 1986; Stuart, Adams & Jenkins, 1990; Perrings & Lovett, 1999). These ‘five’ actually consist of six species: lion (*Panthera leo*), leopard (*Panthera pardus*), buffalo (*Syncerus caffer*), elephant and the two rhinos. Although the Big Five were chosen originally neither as flagships nor as indicators for biodiversity (but as large-bodied game animals), we regard them, from their promotion in travel brochures and their consequent gross earnings, to be *in effect* the most important flagship species for conservation in Africa.

The flagship concept, or at least its extension to the idea of umbrellas, might also be stretched to include all of the larger-bodied mammals (Entwistle & Stephenson, 2000). One reason for expecting larger species to

perform better than others for representing biodiversity for conservation would be if they were to have particularly broad home ranges (or other habitat requirements), which might then encompass the habitats of many other organisms (as 'umbrella' species: e.g. Shrader-Frechette & McCoy, 1993; Simberloff, 1998; Leader-Williams & Dublin, 2000). In sub-Saharan Africa, larger mammal species belong to the orders Primates (monkeys, apes, etc), Carnivora (dogs, cats, mongooses etc), Proboscidea (elephant), Perissodactyla (zebra, rhinos, etc) and Artiodactyla (pigs, giraffe, antelope etc). Together, these orders include 224 of the 938 mammal species in our analyses.

In this study, we assessed the consequences of selecting areas using flagship species for representing mammals and breeding birds as a highly valued part of the biodiversity of sub-Saharan Africa. We were concerned not with past practices for choosing conservation areas, but with assessing the possible consequences of applying variations on the flagship approach in the future, and particularly with the constraints imposed by their ecology and biogeography. This is a form of surrogacy or 'indicator' problem (Reid *et al.*, 1993), along with examining similarity in richness distributions (e.g. Pearson & Cassola, 1992; Pomeroy, 1993; Gaston, 1996; Pearson & Carroll, 1998; Williams & Gaston, 1998) or overlap in selected-area networks (e.g. Ryti, 1992; Pomeroy, 1993; Prendergast *et al.*, 1993; Lombard, 1995). However, our approach, of assessing the amount of biodiversity represented within areas selected using surrogates, addresses more directly the conservation goal of how to represent as much biodiversity as possible.

METHODS

Data on the distribution of 938 mammal species (following the taxonomy of Wilson & Reeder, 1993) were entered on a 1° grid across mainland sub-Saharan Africa (each cell measured approximately 105 × 105 km) in collaboration with an international network of mammalogists. For the larger and better-known species, the data were an estimate of distribution ranges in the period 1970–1989 (see Fig. 1 for examples). For smaller and less well-known species, expected distribution ranges were interpolated by assuming a continuous distribution between confirmed records within relatively uniform habitat, using available information on species' habitat associations, and taking into account specialist opinion, especially concerning any known gaps in distribution. For the least well-known species, records were plotted without interpolation because of lack of information, which would make interpolation unreliable (all area-selection methods using species data will be most strongly constrained by these most restricted species). Similarly, to represent another highly valued part of biodiversity, data on the distribution of 1749 breeding bird species were entered on the same grid using similar methods (Burgess *et al.*, 1997; Fjeldså *et al.*, 1999). Thus, for the 1961 1° grid cells with records of both mammals and breeding birds, there was a total of

663 003 species-in-grid-cell records for 2687 species (referred to below as all mammals and birds). As a coarse-grained approach for classifying species' habitats, we used the ecoregions mapped by Itoua *et al.* (1997), of which 98 classes are represented within sub-Saharan Africa.

Selecting areas for biodiversity conservation can be approached as a 'maximal covering' problem (Church, Stoms & Davis, 1996), where the representation of flagship species has to be maximized when choosing a limited number (or cost) of areas. The numbers of all mammal and bird species represented can then be counted. We used three popular quantitative area-selection methods to choose areas. First, hotspots of richness were chosen by counting the numbers of species in each grid cell, ranking the grid cells by this count, and selecting the highest scoring cells (e.g. Myers, 1988; Prendergast *et al.*, 1993; WWF & IUCN, 1994; Lombard, 1995; Mittermeier *et al.*, 1998). Second, hotspots of narrow endemism were chosen in a similar way, but based on just the most restricted species (e.g. Terborgh & Winter, 1983; Myers, 1988; ICBP, 1992; WWF & IUCN, 1994; Lombard, 1995; Mittermeier *et al.*, 1998). Rather than identifying narrowly endemic species by applying an absolute threshold of range size (Terborgh & Winter, 1983; ICBP, 1992), we identified the rare quartile (25%) of species with most restricted distributions by numbers of grid cells (after Gaston, 1994) and searched for hotspots of richness for them (Williams *et al.*, 1996). Third, hotspots of complementary richness (e.g. Ackery & Vane-Wright, 1984; Margules, Nicholls & Pressey, 1988; Pressey *et al.*, 1993; Scott *et al.*, 1993; Witting & Loeschcke, 1993; Lombard, 1995; Church *et al.*, 1996; Freitag, Nicholls & van Jaarsveld, 1996; Williams *et al.*, 1996; Fjeldså & Rahbek, 1997, 1998; Howard, Davenport & Kigenyi, 1997) were chosen so that in combination they represented the largest number of species (in this context, complementarity refers to the degree to which the fauna of an area contributes otherwise unrepresented species to a set of area faunas, Vane-Wright, Humphries & Williams, 1991). Our maximal covering procedure was based on a heuristic algorithm for near-minimum-area sets (Margules *et al.*, 1988), but was extended for (1) tests to reject redundant areas; (2) re-ordering of areas by complementary richness (Table 1).

When using one group of species as a surrogate to represent another group in area selection, it is essential to take account of flexibility in area choices. This is not a concern when the group of species used to select areas is the same as the group to be represented, because any fully flexible areas are, by definition, equivalent in that they will represent the same total number of species in the same number of areas (Pressey *et al.*, 1993). But when these areas are used to represent a second group of species, their representation could vary substantially among even fully flexible area choices (Hopkinson *et al.*, in press), because the distributions of the two groups are likely to be different. Fully flexible areas for representing a particular set of species can be found after the

areas have been selected by identifying the ‘goal-essential’ species within each area (Williams, 1998: figure 10.6). For minimum-area sets with a goal of representing each species at least once, the goal-essential species are the ones that occur in only one area within the selected-area set (Rebelo, 1994). However, here we considered maximal covering problems, which often require n multiple representations of species to achieve solu-

tions. In this case, the goal-essential species can be identified as the species recorded in each area that occur within the entire selected-area set from one to n times. For each selected area, any other single area that has the same set of goal-essential species will be a *fully flexible* alternative (*partially flexible* areas have just some of these species, so that more than one partially flexible area has to be substituted to represent all of the species).

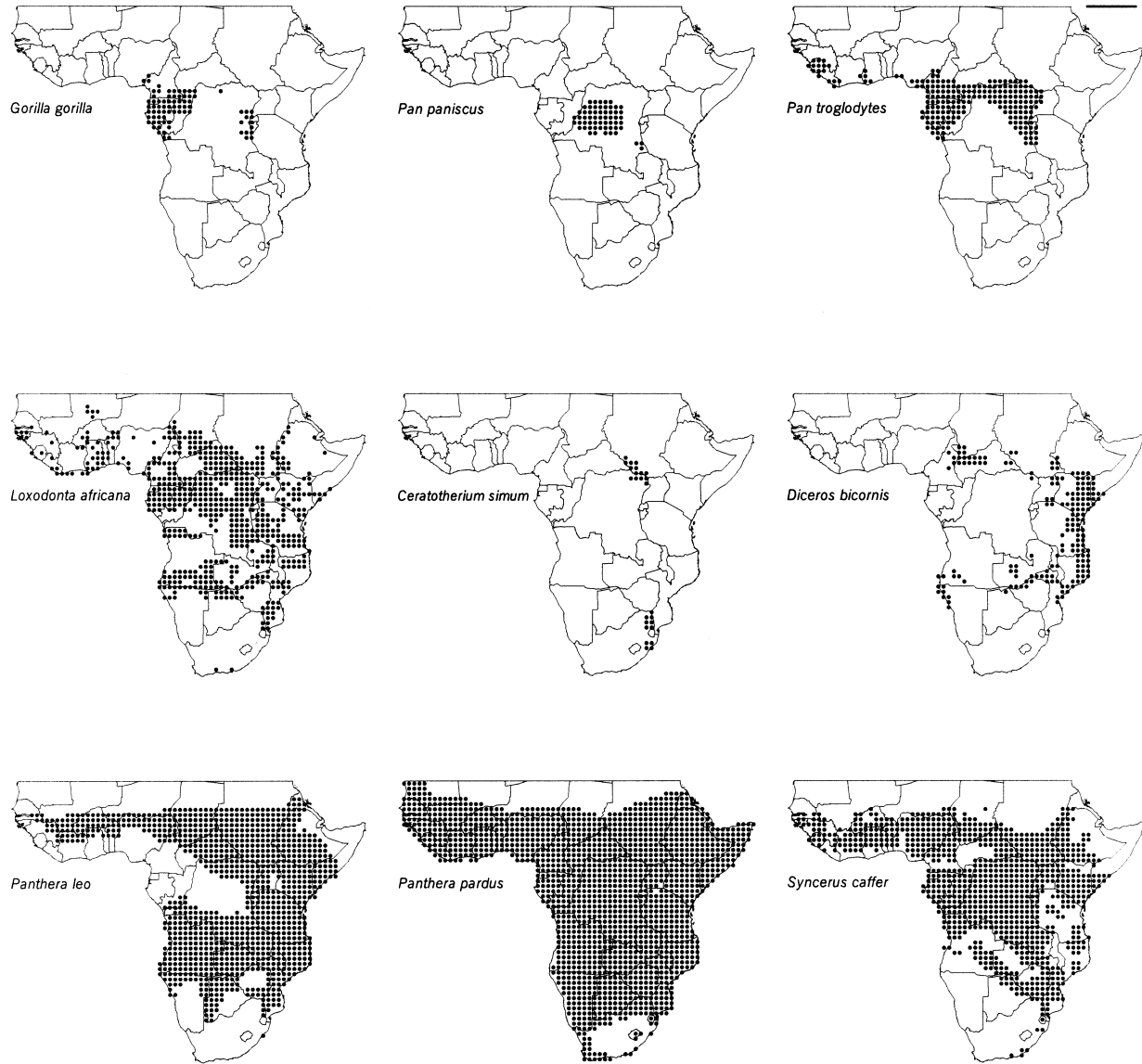


Fig. 1. Maps summarizing the distribution data for flagship and Big Five mammal species among 1° grid cells in sub-Saharan Africa. The six flagship species are *Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Loxodonta africana*, *Ceratotherium simum* and *Diceros bicornis*. The Big Five species (actually six species) are *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*, *Panthera leo*, *Panthera pardus* and *Syncerus caffer*. Filled circles represent estimates of distribution ranges for the period 1970–1989. The horizontal scale bar (upper right) represents 10° of longitude, or approximately 1100 km at the equator. Data sources: *Gorilla gorilla* (Kingdon, 1971, 1997), *Pan paniscus* (Wolfheim, 1983; Kingdon, 1997), *Pan troglodytes* (Wolfheim, 1983; Kingdon, 1997), *Loxodonta africana* (Working Group on the distribution and status of East African mammals, 1977; Kingdon, 1997), *Ceratotherium simum* (Cumming, Du Toit & Stuart, 1990), *Diceros bicornis* (Smithers, 1983), *Panthera leo* (Working Group on the distribution and status of East African mammals, 1977; Smithers, 1983), *Panthera pardus* (Smithers, 1983), and *Syncerus caffer* (Dorst & Dandelot, 1970; Working Group on the distribution and status of East African mammals, 1977; Smithers, 1983).

Table 1. The set of rules for selecting a given number (n) of hotspots of complementary richness in order to provide a near-maximum coverage of species

Step	Rule
1	Select all areas for species that are more restricted than the representation goal (for representing all species at least once, this means selecting all areas with unique species records)
2	The following rules are applied repeatedly until all species are represented: <ul style="list-style-type: none"> A Select areas with the greatest complementary richness in just the rarest species (ignoring less rare species), if there are ties (areas with equal scores), then: B Select areas among ties with the greatest complementary richness in the next-rarest species, if there are persistent ties, then: C Select areas among persistent ties at random (this is an arbitrary rule; other criteria, such as proximity to previously selected cells, or number of records in surrounding cells, could be substituted) Repeat steps A-C until all species are represented
3	Identify and reject any areas that with hindsight are unnecessary to represent all species (this includes a fast check of whether pairs of selected areas can be replaced by a single area)
4	Repeat steps 1–3 for representing every species at least once, twice and so on, until the required number of areas, n , is attained or exceeded, disregarding the results of one iteration of steps 1–3 before moving on to the next
5	The following rules are applied repeatedly until all selected areas are re-ordered by complementary richness: <ul style="list-style-type: none"> a Choose the previously selected area with the greatest complementary richness, then: b If, before all areas are re-ordered, the maximum complementary richness increment declines to 0, continue to re-order areas (step a, above) after re-setting the cumulative richness to 0, but starting to score complementary richness again from the current position on the area list (ignoring: previously re-ordered areas; species more restricted than the current multiple representation target; species that are already represented the required number of times within a smaller number of areas) Repeat steps a-b until all previously selected areas are re-ordered
6	Choose the first n areas from the re-ordered area list

In this context, 'areas' are grid cells, and the rarest species is taken to be the one with the fewest grid-cell records. This procedure can also be used to complement an existing set of protected areas, as a form of 'gap' analysis.

The total number of alternative fully flexible sets for the same species representation is then estimated as the product of the number of fully flexible alternatives for each area within the selected set. It is only an estimate, because exchanging even one fully flexible area may change the pattern of goal-essential species, causing the pattern of fully flexible areas for other selected areas to change. Unfortunately, the number of alternative sets is often far too large to assess exhaustively, so a sample of 1000 sets (checked to ensure the same number of species is represented) is drawn at random.

To assess the success of the area-selection methods, areas were chosen using random draws without replacement 1000 times for each number of areas required, and the number of all sub-Saharan mammal and bird species represented in these area sets was counted. To assess how well any six species might be expected to perform for representing biodiversity in area selection, six species of mammals and birds were chosen using random draws without replacement 1000 times, maximum coverage sets of 50 areas were selected for each, and the numbers of all sub-Saharan mammal and bird species represented in these area sets were counted. All methods were implemented using the *WORLDMAP* software (Williams, 1999).

RESULTS

First, Fig. 2 shows that, when selecting more than three areas, the only area-selection methods that succeed in representing significantly more sub-Saharan mammal

and bird species than would be expected by chance (single-tailed test) are hotspots of narrow endemism (Fig. 2(b); using all species) and hotspots of complementary richness (Fig. 2(c); using all species, or the large mammals). These results come from considering only one near-maximal covering set for each number of areas, which ignores the variation that may arise from flexibility in area sets (but see below). The highest species representation is obtained when using hotspots of complementary richness and all species of mammals and birds (Fig. 2(c)).

Second, Table 2 shows that when using hotspots of complementary richness to select near-maximal covering sets of 50 areas, there are often very large numbers of alternative area sets. Figure 3 is equivalent to a vertical section of Fig. 2(c) for 50 areas, but with alternative fully flexible area sets included in the scoring. Taking this flexibility into account, flagships tend to represent more species than the Big Five (Fig. 3), the opposite of the results for the single sets shown in Fig. 2(c). Figure 3 also shows that even when flexibility is considered, the flagship species and the Big Five species still usually (99.1% of sets sampled) fail to represent more species of sub-Saharan mammals and birds in 50 areas than would be expected from selecting areas at random (single-tailed test).

Third, Fig. 4 shows that the flagship species and the Big Five species are not significantly better or worse (two-tailed test) for representing the diversity of all sub-Saharan mammals and birds than would be expected

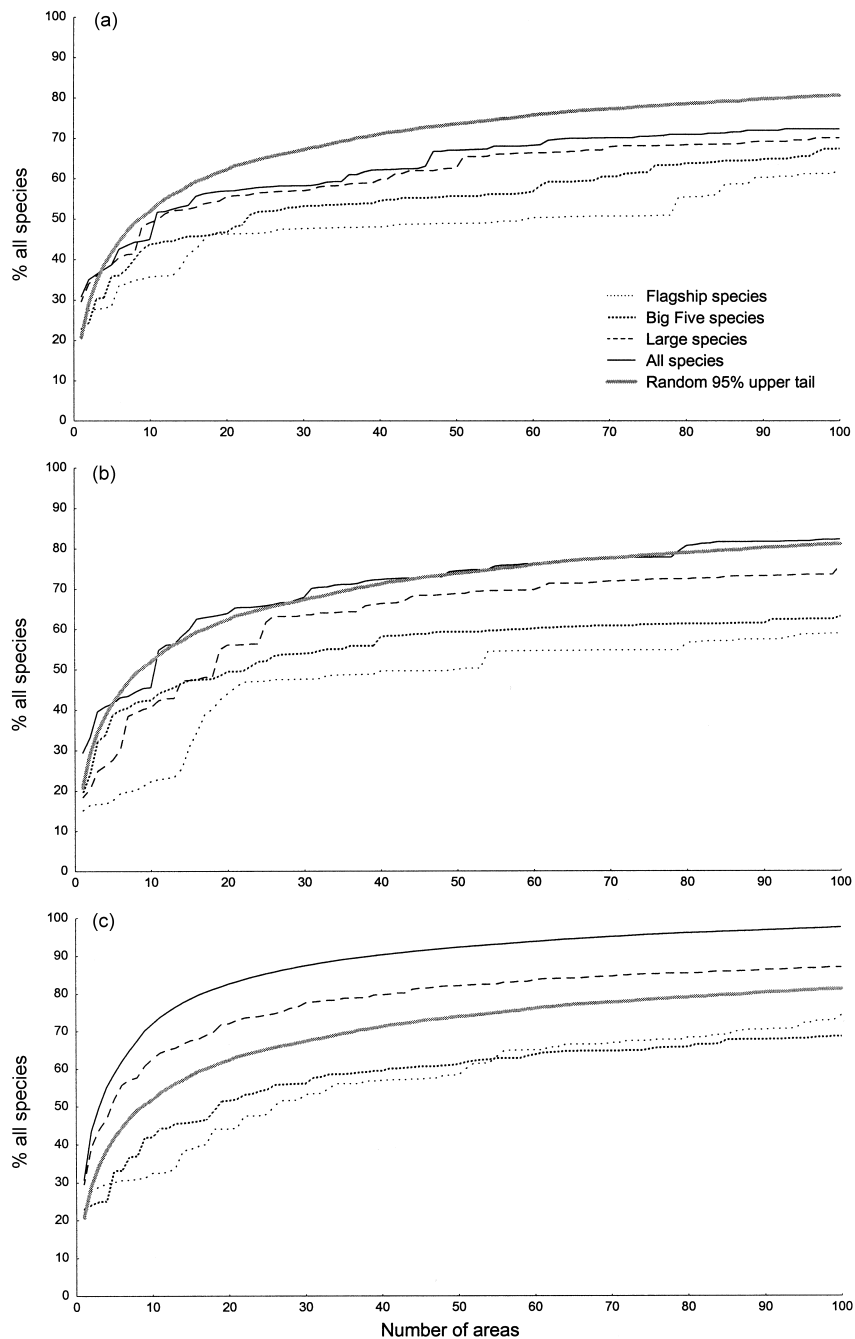


Fig. 2. Percentage of all sub-Saharan mammal and bird species represented in from 1 to 100 grid cells selected for maximal coverage by three methods: (a) hotspots of richness; (b) hotspots of narrow endemism; and (c) hotspots of complementary richness. Data used to make the selection are from the six flagship species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*); the Big Five species (actually six species: *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*, *Panthera leo*, *Panthera pardus*, *Syncerus caffer*); the five orders of larger mammal species (224 sub-Saharan species of Primates, Carnivora, Proboscidea, Perissodactyla and Artiodactyla); and all 2687 sub-Saharan mammal and breeding bird species. Scores below the continuous thick line are within the range expected when choosing grid cells at random.

from a group of six species chosen at random. Among the sample of randomly drawn combinations of six species shown in Fig. 4, the best group found for representing the diversity of all sub-Saharan mammals and birds in 50 areas consisted of a bat (*Chaerephon bemmeleni*), gerbil (*Microdillus peeli*), rat (*Aethomys stannarius*), crane (*Porzana pusilla*), barn owl (*Tyto*

alba) and an oriole (*Oriolus larvatus*). This is very unlikely to be the best possible group of six species, because a sample of just 1000 groups was tested among a possible 3.7×10^{20} combinations of six from among 2687 species (the best group of six species is also likely to differ when different numbers of areas are to be selected). None the less, this best group within the

Table 2. Flexibility in sets of 50 grid cells selected for maximal coverage of different area attributes (species or ecoregions)

Area attributes used in area selection	Number of area attributes (species or ecoregions)	Estimated number of fully flexible sets of 50 grid cells	Maximum number of fully flexible alternatives per grid cell among all selected areas	Median number of mammal and bird species represented
Big Five mammal species	6	1.41×10^{81}	174	1675 [†]
Flagship mammal species	6	2.12×10^{86}	174	1755 [†]
Best six species from random draws	6	1.59×10^{73}	547	2121 [†]
Five orders of larger mammals	224	6.54×10^{41}	344	2171 [†]
Ecoregions	98	1.89×10^{27}	62	2194 [†]
All mammal and bird species	2687	120	5	2473 [‡]

The sets were chosen to represent: the six flagship species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*); the Big Five species (actually six species: *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*, *Panthera leo*, *Panthera pardus*, *Syncerus caffer*); the six species found to represent most mammals and birds from a sample of six species drawn at random without replacement 1000 times (*Chaerephon bemmeleni*, *Microdillus peeli*, *Aethomys stannarius*, *Porzana pusilla*, *Tyto alba*, *Oriolus larvatus*); the five orders of larger mammal species (sub-Saharan species of Primates, Carnivora, Proboscidea, Perissodactyla, Artiodactyla); sub-Saharan ecoregions from Itoua *et al.* (1997); all sub-Saharan mammal and breeding bird species with records. See Methods for a definition of fully flexible areas and for methods for estimating them.

[†] Median number of mammal and bird species represented among a sample of 1000 fully flexible sets.

[‡] Median number of mammal and bird species represented among all fully flexible sets.

sample succeeded in representing > 20% more mammals and birds within 50 areas than when using the flagship species (from medians in Table 2), and significantly more species than when choosing areas at random (Fig. 3). Among these 'best' six species, none is a large-bodied mammal, but compared to the flagships and the Big Five, they cover many ecoregions, the median range size is small, and overlaps among species are low (Table 3).

DISCUSSION

Area selection for conservation is a complex problem that has to take account of many constraints. In contrast, analytical studies usually have to simplify the problem

in order to disentangle the effect of particular factors. Here, we were concerned not with identifying specific priority areas, but with exploring the consequences of ecological and biogeographical patterns of species distribution for the performance of flagships in representing broader diversity. We did not consider information on existing conservation areas in sub-Saharan Africa, information on cost, or the information on viability and threat for populations within realistic management areas that is necessary for ensuring the persistence of species (Pressey *et al.*, 1993; Witting & Loeschcke, 1993; Lombard, 1995; Freitag *et al.*, 1996; Howard *et al.*, 1997; Nicholls, 1998; Williams, 1998). Information on these constraints was unavailable or unreliable at pre-

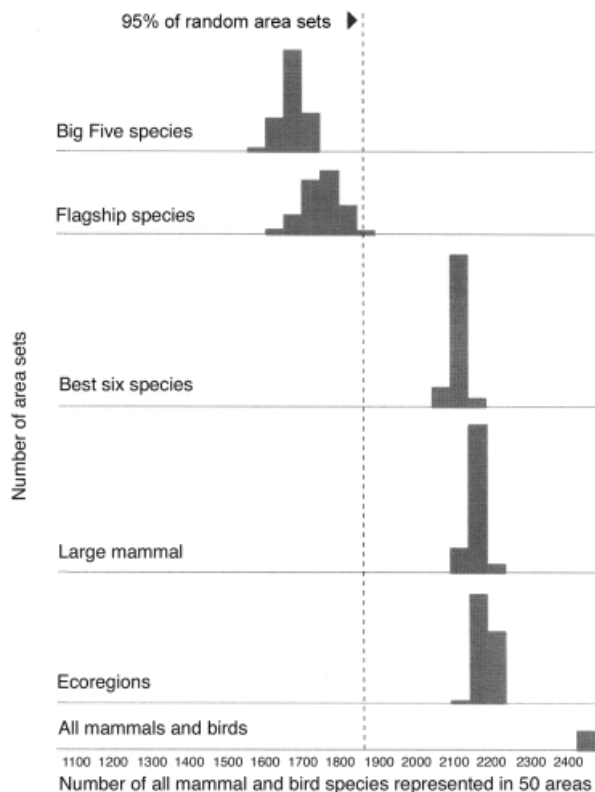


Fig. 3. Frequency with which fully flexible sets of 50 grid cells represent different numbers of all sub-Saharan mammal and breeding bird species when the grid cells are selected for maximal coverage (hotspots of complementary richness) of different area attributes. Area attributes used to make the selections are the six flagship species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*); the Big Five species (actually six species: *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*, *Panthera leo*, *Panthera pardus*, *Syncerus caffer*); the six species found to represent most mammals and birds from a sample of six species drawn at random without replacement 1000 times (*Chaerephon bemmeleni*, *Microdillus peeli*, *Aethomys stannarius*, *Porzana pusilla*, *Tyto alba*, *Oriolus larvatus*); the 98 sub-Saharan ecoregions from Itoua *et al.* (1997); the five orders of larger mammal species (224 sub-Saharan species of Primates, Carnivora, Proboscidea, Perissodactyla and Artiodactyla); and all 2687 sub-Saharan mammal and breeding bird species records. With the exception of the histogram at the bottom, which shows all fully flexible sets, scores are taken from a randomly drawn sample of 1000 alternative fully flexible sets checked to ensure that they represent the same number of species from the groups used to make the selection. Scores to the left of the dotted line are within the range expected when choosing 50 grid cells at random.

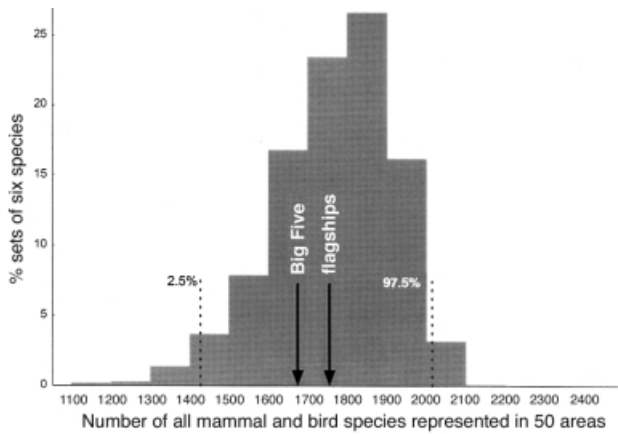


Fig. 4. Frequency with which numbers of all 2687 sub-Saharan mammal and breeding bird species are represented in sets of 50 grid cells selected for maximal coverage (using hotspots of complementary richness) of groups of six mammal and/or bird species, which were drawn randomly 1000 times. For comparison, arrows show the median numbers of mammal and breeding bird species represented in 50 grid cells, when these are selected using the Big Five species (actually six species: *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*, *Panthera leo*, *Panthera pardus*, *Syncerus caffer*) or the six flagship species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*), taken from random samples of 1000 alternative fully flexible sets (from Fig. 3). Dotted lines show the lower 2.5% and upper 97.5% tails of the frequency distribution.

sent for the vast majority of species and areas (the software used here can accommodate all of these when appropriate data become available). Consequently, our analyses should provide an approximate estimate for the upper bound to species representation that can be attained by area-selection using flagship species, which is the central issue of this paper. Even when starting with an existing conservation-area network, which already contributes some degree of species representation, it will not remove the responsibility for seeking the best methods for identifying new important areas for biodiversity where opportunities do occur, because resources and land availability are limited (Pressey *et al.*, 1993). We see the aims of quantitative methods as being to provide a fully accountable process for recognizing the most important areas in need of some conservation policy, in

order to keep track of the most complementary choices when faced with complex data. Eventually, this may amount to no more than putting good autecological and synecological information within a larger framework, in order to help fill ‘gaps’ in the conservation system. Consequently, the kind of action that is appropriate in each case is not prejudged. Actions could be anywhere on a spectrum from complete protection in some instances, to support for minimal matrix management in many others (e.g. Vane-Wright, 1996; Balmford, Mace & Ginsberg, 1998).

Three popular area-selection methods

The result that higher representation of sub-Saharan mammal and bird species was achieved using hotspots of complementary richness (Fig. 2) supports many previous studies, which have shown that complementarity performs better than scoring methods (e.g. Pressey & Nicholls, 1989), and more particularly, that it performs better than hotspots of richness or hotspots of narrow endemism (e.g. Williams *et al.*, 1996). Indeed, hotspots of complementary richness should, in principle, always give maximal representation of species (at least whenever selection is made directly using all of the species to be represented, Fig. 2(c)), so that any exceptions must be due to sub-optimality in the algorithms (for examples and discussion, see Pressey, Possingham & Margules, 1996; Pressey, Possingham & Day, 1997; Csuti *et al.*, 1997). Despite this, hotspots of richness and of narrow endemism are popular among conservation agencies (ICBP, 1992; WWF & IUCN, 1994; Mittermeier *et al.*, 1998). However, our results go further in showing that hotspots of richness are actually no better at representing the diversity of sub-Saharan mammals and birds than would be expected for the same number of areas chosen at random (Fig. 2(a)). A similar result has been found for the atlased European vascular plants and terrestrial vertebrates at the scale of 50 × 50 km grid cells (Williams *et al.*, 2000).

Why should hotspots of richness perform so poorly with these data? These areas are particularly strongly clustered around the East African highlands (the richness of these faunas is presumably partly an effect of high habitat heterogeneity caused by the large variation in altitude and climate of these areas), where they share

Table 3. Patterns of co-occupancy of grid cells (overlap) for species within the groups of six species used to select areas (see Table 2 for details), together with numbers of species of all sub-Saharan mammals and breeding birds represented in example sets of 50 grid cells selected using the hotspots of complementary richness method

Groups of 6 species used for area selection	Median range size (cells)	Number of ecoregions within combined range of six species	Mean number of species per cell from the group of six species	Median number of mammal and bird species among sample of 1000 fully flexible sets
Big Five species	757	95	2.63	1675
Flagship species	125	81	1.50	1755
‘Best’ six species	13	94	1.35	2121
Total	1961	98	6	2687

Range sizes are measured as numbers of grid cells with presence records. Ecoregions are from Itoua *et al.* (1997). Geographical overlap is measured as the mean richness within each group of six species, counted only for grid cells that have records for at least one of these six species. Totals refer to the area mapped in Fig. 1.

many of the same habitats and species. Table 4 shows that hotspots of richness are more highly clustered in their geographical distribution than areas selected by other methods, both at the scale of neighbourhoods of grid cells, and at the scale of $10^\circ \times 10^\circ$ grid cells, and that they represent fewer ecoregions (fewer than expected by chance from 1000 random draws of 50 areas, $P < 0.025$) and fewer biogeographical provinces. Selecting areas repeatedly within the same few ecoregions and biogeographical provinces is likely to capture a reduced underlying diversity in aspects of the ecology and history of the chosen faunas. This leaves many other ecoregions, provinces and species in northern and southern Africa unrepresented. Hotspots of narrow endemism can perform better than choosing areas at random, but only when the smaller species are included. This is because many smaller species have narrower distribution ranges (species in the five orders of large mammals have larger sub-Saharan range sizes than the remaining, smaller species, log-transformed numbers of 1° grid cells, $t = 24$, $P < 0.001$) that are often restricted to different regions, so that more regions are represented in total (Table 4). In achieving representation of a greater number of species, hotspots of complementary richness are less clustered, and represent more ecoregions and more biogeographical provinces (Table 4). The broad scatter of chosen areas may also be important politically, because it shows that all countries have a valuable contribution to make (Fig. 5(b)), especially when flexibility among complementary areas is considered.

Flagships and representing biodiversity

Why do the six flagship species not perform better in area selection for representing broader biodiversity? At first sight they are an ecologically diverse group, representing many ecoregions within their broad distributions (Table 3), and therefore might appear well suited for representing much of biodiversity (e.g. Wikramanayake *et al.*, 1998). The three apes are forest species, the elephant is distributed among a broad range of habitats from savannah to forest, and the two rhinos are primarily savannah species (Estes, 1991). However, when a limited number of areas is chosen to represent these species as many times as possible, selection will tend to favour the areas where they are co-recorded (irrespective of whether or not they co-occur at finer scales). One cause

of species apparently sharing areas is an overlap in their habitat requirements. The flagship species not only overlap broadly in distribution (Fig. 1), but also share habitats in the more open forests and woodlands (Estes, 1991). Similarly, the Big Five species also perform poorly in area selection, despite occurring in a variety of habitats. For these species it appears to be a pattern of coincidence within the savannah biome (Estes, 1991) that is influencing area selection, both by our methods and in practice. In this case, any bias towards selecting savannah rather than forest areas for these species might be exacerbated by the preferences of tourists, who demand areas where animals are more accessible and more visible. For both the flagship species and the Big Five species, a tendency for selection to favour relatively few kinds of shared habitat might explain the low representation achieved for different ecoregions and biogeographical provinces, as well as the geographical clumping of selected areas and the clumped distribution of unrepresented species in particular ecoregions (Table 5, Fig. 5). Thus, while Table 5 shows that the number of species ultimately represented within an area set may be most consistently related to the number of ecoregions represented, Table 3 shows that this is not simply a consequence of making the selection using species whose combined distribution covers more ecoregions.

Although many African mammals and birds do live in forests and savannahs, many others live in desert, temperate and high montane biomes. Therefore, in order to represent the broad diversity of organisms living in these different biomes, we might expect to need to use species for area selection that have a low overlap among themselves in habitat at the level of biome, as well as at a finer grain, to seek increased ecological complementarity. Table 3 provides some support for this, because lower spatial overlap among species in those groups of six species that succeed in representing more of all species is shown by lower mean richness in the six species. The question of which species work best, and why, is connected to other problems in identifying good indicators for biodiversity. For example, when seeking surrogates for estimating species richness in a group to be indicated, better results are expected if governing factors are shared more closely between indicator and indicated groups (Prendergast *et al.*, 1993; Faith & Walker, 1996a; Gaston, 1996; Williams & Gaston, 1998). The requirement here is that the different species

Table 4. Geographical dispersion of selected grid cells, together with numbers of biogeographical provinces (from Udvardy, 1975), ecoregions (from Itoua *et al.*, 1997), and numbers of species of all sub-Saharan mammals and breeding birds represented within 50 grid cells, selected by three methods using data for all mammal and breeding bird species

Area-selection method	Local dispersion (%)	Regional dispersion	Number of biogeographical provinces	Number of ecoregions	Number of mammal and bird species
Hotspots of richness	41	6	6	23	1810
Hotspots of narrow endemism	61	8	9	36	2002
Hotspots of complementary richness	96	21	16	57	2473
Total	–	31	20	98	2687

Local dispersion (scatter) is measured for selected grid cells as the mean percentage of the eight nearest neighbouring cells that are not themselves selected. Regional dispersion (scatter) is measured as the number of $10^\circ \times 10^\circ$ cells with selected 1° cells. Totals refer to the area mapped in Fig. 1.

Table 5. Geographical dispersion of selected grid cells, together with numbers of biogeographical provinces (from Udvardy, 1975), ecoregions (from Itoua *et al.*, 1997), and numbers of species of all sub-Saharan mammals and breeding birds represented within single example sets of 50 grid cells.

Area-selection method	Local dispersion (%)	Regional dispersion	Number of biogeographical provinces	Number of ecoregions	Number of mammal and bird species
Big Five species	72	11	8	28	1675
Flagship species	82	11	9	34	1755
Best six species from random draws	93	18	15	47	2121
Five orders of larger species	89	19	16	51	2192
All mammal and bird species	96	21	16	57	2473
Total	–	31	20	98	2687

All sets were selected using the hotspots of complementary richness method, and using data for five sets of species (see Table 2 for details). Local dispersion (scatter) is measured for selected grid cells as the mean percentage of the eight nearest neighbouring cells that are not themselves selected. Regional dispersion (scatter) is measured as the number of $10^\circ \times 10^\circ$ cells with selected 1° cells. Totals refer to the area mapped in Fig. 1.

used for selecting areas for representing biodiversity should indicate as many other different and complementary species as possible. Among the random sample of 1000 combinations of six species, as expected, the best six species occur in a broad variety of ecoregions (forest, savannah, grassland and montane) but, crucially, these six species also show relatively little spatial overlap in their distributions (Table 3). Testing this relationship among all of the randomly drawn sets of six species, we found that higher representation of all mammals and birds was indeed weakly correlated with lower overlap among the six species, as measured by lower mean richness for the species in each group (Spearman $r = -0.19$, $P < 0.001$).

So why not move to using habitat, landscape, or environmental diversity (e.g. Faith & Walker, 1996a,b) directly for area selection, particularly if the data were less expensive to collect? Figure 3 shows that selecting areas for maximal representation of Itoua *et al.*'s (1997) ecoregions represented more of the diversity of all mammals and birds than when using flagships or the Big Five species, and was comparable to using the large mammals, at least when selecting just 50 areas at the coarse scale of 1° grid cells. This representation of mammals and birds is encouragingly high, at just 11% less than when applying selection to data for all of these species directly. The shortfall can be explained because ecoregions are a relatively coarse-grained classification of habitat, and because species rarely occur in all patches of suitable habitat. Therefore, when representative data are available for all of the valued species, they would be expected to include an additional and important level of discrimination among areas.

A second kind of process that might lead to congruent patterns of complementarity between groups depends on the historical constraints to distribution (Williams, 1996), as described by vicariance biogeography (e.g. Humphries & Parenti, 1986). From the limited information available at present, this factor appears not to have dominated the patterns in these data. For example, there is little evidence for consistent vicariant patterns among the majority of sub-Saharan bird taxa at the rank of species that might be associated with events such as the opening of the Rift Valley (Williams, de Klerk & Crowe, 1999).

Numbers of species and area selection for biodiversity

Taken together, our results show that increasing the number of species used to select areas, from just six flagship species up to all 2687 species in our data, increases the diversity of sub-Saharan mammals and birds that is represented to significantly more than is expected by chance (Fig. 3). The property of the selected-area set showing the most consistent rank correlation with improving overall species representation in Table 5 is the number of ecoregions covered (mapped for comparison in Fig. 5). However, all of the factors in Table 5 are inter-related, so further analysis will be required in order to disentangle dependencies.

That using more species for selecting areas may result in representing more biodiversity is not surprising. The problem is that using species as flagships for raising public awareness and funding might be expected to be most effective when these species are relatively few in number (e.g. Leader-Williams & Dublin, 2000). But in the context of biodiversity conservation, having to rely on just a few species appears to be a serious limitation, because it constrains severely the total amount of biodiversity that can be represented.

Our study has demonstrated that protecting a few flagship species, or even the Big Five wildlife-tourism species, cannot be assumed to be sufficient on its own to ensure the conservation of broader biodiversity. Of course, it is possible that sub-Saharan Africa may differ from other parts of the world in how well a few flagships perform at representing biodiversity in area selection, partly because sub-Saharan Africa has such a very diverse mammal fauna (e.g. Cole, Reeder & Wilson, 1994), and perhaps also if in other regions more species tend to co-occur more often, for example within forests. But unless all species show highly nested patterns of distribution, species used in selection for biodiversity will have to be more numerous and will have to be chosen carefully so that they represent organisms from a broad variety of habitats. Consequently, there is likely to be a need for an explicit policy to balance the requirements of flagship conservation and conservation of biodiversity, which will have implications for the distribution of

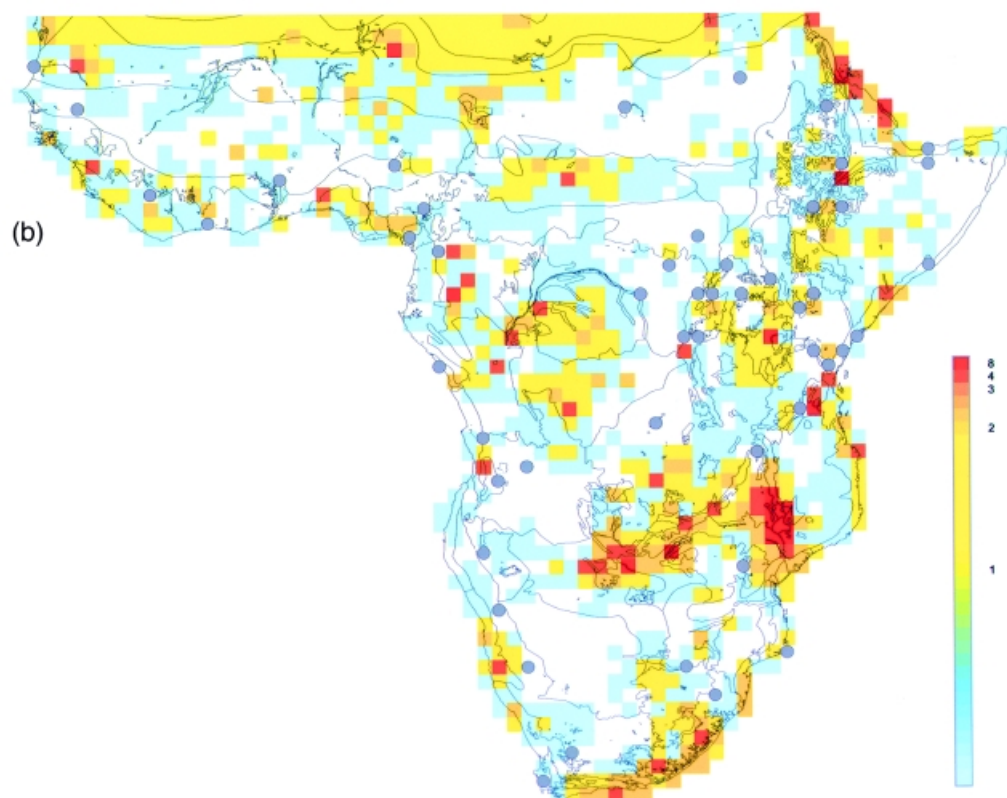
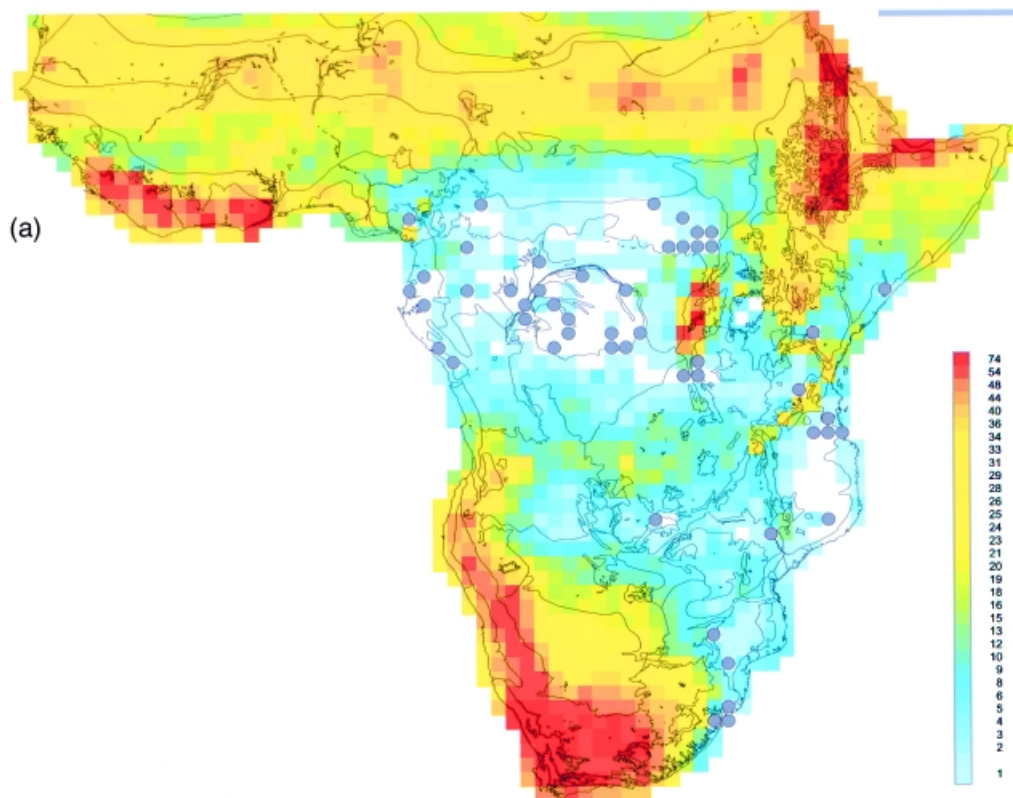


Fig. 5. Spatial distribution of 50 hotspots (grey circles) of complementary richness in mammals and birds selected using: (a) six flagship species (*Gorilla gorilla*, *Pan paniscus*, *Pan troglodytes*, *Loxodonta africana*, *Ceratotherium simum*, *Diceros bicornis*); and (b) all species, respectively. The colour scale gives the richness of species not represented in the selected hotspots. Of 2687 sub-Saharan mammals and breeding birds species, (a) 932 species and (b) 214 species were left unrepresented when using six flagship species and all species respectively. Each colour class represents a consistent part (3%) of the frequency distribution of richness scores on the maps (except where constrained by large numbers of tied scores), with red for maximum and blue for minimum non-zero scores. Ecoregion boundaries based on Itoua *et al.* (1997) are plotted on the map as black lines. The horizontal scale bar (upper right) represents 10° of longitude, or approximately 1100 km at the equator.

resources. If the political and social reality is that conservation will have to depend to a large extent on a few flagships for support, then to protect broader biodiversity, more effort will need to be directed towards identifying and promoting non-overlapping flagship organisms that represent biotas that are as different and as complementary as possible.

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