# The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide?

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South Africa urgently requires a national strategic plan for the conservation of the country's biodiversity. The formulation of such a plan would be relatively easy if centres (hotspots) of richness, endemism and rarity were congruent, both within and among many different taxa, if these hotspots captured a large proportion of the total species, and if hotspots fell within existing reserves. The investigation of six vertebrate taxa (*viz* freshwater fish, frogs, tortoises and terrapins, snakes, birds, and various mammal orders) at a national scale reveals that hotspots are not coincident within taxa. Centres of richness are concentrated in the north-eastern areas of the country, whereas endemism is concentrated in the south-west, and centres of rare and threatened (Red Data Book) species can be in either area. Paired comparisons among taxa reveal greatly varying proportional overlaps of species richness hotspots (0–72%). The proportion of total species falling in hotspots ranges from low (66% for fish) to high (92% for birds). Hotspots are thus not an efficient method of siting representative (ideal) reserves. In order to design a more representative reserve system to protect all vertebrate species, a complementarity algorithm was applied to all taxa separately, and then to all taxa combined. The combined analysis yielded more efficient results (66 reserves are required to represent all 1074 species at least once) than the separate analyses (97 reserves). Many of these representative reserves coincide with both hotspots and existing reserves, and over 85% of the hotspots of most taxa coincide with existing reserves, thus South Africa's vertebrate fauna could be more effectively protected with only moderate acquisition of new, well-sited reserves. A biome analysis reveals that these reserves will also have to incorporate areas of those biomes that are currently inadequately protected, *viz* grassland, Succulent Karoo and Nama-Karoo. The methods outlined in this paper should be applied to as many other taxa as possible, in order to aid the formulation of a national strategic plan for biodiversity conservation.

Suid-Afrika benodig dringend 'n nasionale strategiese plan vir die bewaring van die land se biodiversiteit. Die formulering van so 'n plan sou maklik wees as sentra (brandpunte) van spesierykheid, endemisme en skaarsheid ooreenstem binne, sowel as tussen, verskillende taksa, en as hierdie brandpunte 'n groot hoeveelheid van die totale spesies bevat en binne bewaringsgebiede voorkom. 'n Ondersoek van ses werweldiertaksa (naamlik varswatervisse, paddas, skilpaaie en varswaterskilpaaie, slange, voëls, en verskeie soogdierordes) op 'n nasionale skaal het aan die lig gebring dat brandpunte nie binne taksa ooreenstem nie. Brandpunte van spesierykheid is in die noord-oostelike gebiede gekonsentreer, endemisme in die suid-westelike gebiede, en sentra van skaars en bedreigde (Rooi Data-boek) spesies kom in al twee gebiede voor. Gekoppelde vergelykings tussen taksa openbaar groot variasies in die proporsionele oorvleueling van spesierykheidbrandpunte (0–72%). Die hoeveelheid van totale spesies wat binne brandpunte val varieer van laag (66% vir visse) tot hoog (92% vir voëls). Brandpunte is dus nie doeltreffend vir die plasing van verteenwoordigende (ideale) bewaringsgebiede nie. Om 'n meer verteenwoordigende bewaringsisteem te ontwerp, wat alle werweldierspesies bewaar, is 'n aanvullende algoritme toegepas, eerstens vir elke takson apart, en dan vir alle taksa gekombineerd. Die gekombineerde analise het meer doeltreffende resultate opgelewer (66 bewaringsgebiede is benodig om al 1074 spesies minstens een keer te verteenwoordig), as die aparte analise (97 bewaringsgebiede). Baie van hierdie bewaringsgebiede oorvleuel met brandpunte en bestaande bewaringsgebiede, en meer as 85% van die brandpunte van die meeste taksa oorvleuel met bestaande bewaringsgebiede, dus kan Suid-Afrika se werweldierfauna meer effektief bewaar word met matige verkryging van nuwe, goed geplaasde bewaringsgebiede. 'n Bioomanalise toon dat hierdie nuwe bewaringsgebiede ook biome wat huidig onvoldoende bewaar word, moet insluit, naamlik graslande, Sukkulente Karoo en Nama-Karoo. Die metodes uiteengesit in hierdie referaat moet op soveel moontlik ander taksa toegepas word om 'n nasionale strategiese plan vir die bewaring van biodiversiteit te help formuleer.

As part of its new Reconstruction and Development Programme (RDP), South Africa is currently undergoing a land reform process that will undoubtedly generate many conflicts of interest between conservation bodies and developers. The country, however, has no national strategic plan for the conservation of its biodiversity, and conservation biologists would be hard pressed to provide decision-makers with sound recommendations to help solve these conflicts of interest. Moreover, the World Conservation Union (IUCN) has recommended that at least 10% of the land area of each country should be protected, and South Africa has less than 6% of its land area protected (Siegfried 1989). South Africa also has exceptional biological wealth, and is subject to many international contractual obligations in terms of biodiversity conservation (Lombard 1995). Thus, the two important questions are: first, is the biodiversity of the country adequately protected in existing reserves, and second; if not, where are additional reserves required? South Africa clearly requires a strategic plan to address these two questions. This strategic plan should also address the current threats to biodiversity, and those species and ecosystems that are most threatened need to be identified. Some of these species and ecosystems may require conservation management outside of reserves.

In order to provide some preliminary answers to the above questions, a group of conservation biologists undertook a collaborative effort to assess the current protection status of six vertebrate taxa in greater South Africa (includes the kingdoms of Lesotho and Swaziland). Their results are reported in this volume of the *South African Journal of Zoology* (Lombard 1995; Skelton, Cambray, Lombard & Benn 1995; Drinkrow & Cherry 1995; Branch, Benn & Lombard 1995; Gelderblom, Bronner, Lombard & Taylor 1995; Mugo, Lombard, Bronner, Gelderblom & Benn 1995). A similar analysis for snakes is provided in Lombard, Nicholls & August (1995), and a separate analysis for birds is in prep. (Lombard & Hockey).

The recommendations resulting from all of these separate analyses are specific for each taxon. The aim of the present study is to compare patterns of distribution among the taxa at a national scale. The task of the reserve designer, faced with a national multi-species database, would be greatly simplified if centres (hotspots) of richness, endemism and rarity were coincident, both within and among many different taxa. However, many studies, for example Williams, Gibbons, Margules, Rebelo, Humphries & Pressey (unpubl.), and Prendergast, Quinn, Lawton, Eversham & Gibbons (1993) have demonstrated that there is little evidence for the coincidence of hotspots among taxa, and that rare species are not well represented in hotspots of total species richness. In this study, I quantify the overlap of three types of hotspots (total species, endemic species, and Red Data Book species) both within, and among, six vertebrate taxa in greater South Africa, and calculate the proportional representation of species in hotspots. The current protection status of hotspots is also reviewed.

Owing to the fact that there is often little congruency among the hotspots of different taxa, and that many species are not present in hotspots (especially rare species), the use of the hotspot approach in the design of representative (ideal) reserve systems has been widely criticized (Margules 1989; Vane-Wright, Humphries & Williams 1991; Kershaw, Williams & Mace 1994; Lombard *et al.* 1995; Williams *et al.*, unpubl.). Many other methods are available for the prioritization of areas for conservation (these are reviewed in Lombard 1995). Most authors, however, advocate the use of complementarity algorithms (Kirkpatrick 1983; Margules & Nicholls 1987; Margules 1989; Pressey & Nicholls 1989; Rebelo & Siegfried 1992; Nicholls & Margules 1993), which address complementarity and total species representation in reserve design. The algorithms generally identify irreplaceable sites (Pressey, Johnson & Wilson, in press), and produce flexible results, i.e. many alternative systems of reserves can often protect all species (Pressey, Humphries, Margules, Vane-Wright & Williams 1993). In this study, I use a complementarity algorithm to identify a representative reserve system for greater South Africa, that would represent all the vertebrate species under investigation, at least once. The current protection status of these representative reserves is reviewed.

The major stumbling block in the formulation of conservation strategies, especially at a national scale, is the lack of complete databases on species and ecosystem distributions, and threats. This study, as well as many previous papers (Lombard, August & Siegfried 1992; Lombard 1993; Lombard 1994; van Jaarsveld & Lombard 1995), reiterate the urgent need for complete, up to date, national data sets describing South Africa's biodiversity, ecosystems and threats. Unless these data can be included in national conservation planning, the effective prioritization of areas for conservation will be difficult. Nonetheless, the results reported here and in the separate papers in this volume, can be useful as preliminary analyses. In order to formulate an effective national strategic plan to ensure the long-term survival of South Africa's biodiversity, the methods outlined in this study should be applied to more complete vertebrate data, and to as many other taxa as possible. The additional components of population viability and threats will also have to be addressed.

## Methods

Details regarding the data used for this study are provided in the introductory paper in this volume (Lombard 1995), thus each database will be described only briefly here. Presence-only data, at a quarter-degree scale (QDS = 15 min × 15 min), were obtained for 1074 species of vertebrates, within greater South Africa. Table 1 shows the number of species per taxon of vertebrates that was examined. Data for all taxa (except snakes and birds) were obtained from museum and literature records. Snake data were digitized from Jacobson (1989), Broadley (1990) and Bourquin (1992), and augmented with museum records. Bird data were obtained from the southern African Bird Atlas Project (SABAP) (Harrison 1992). Data for all groups were as complete as possible (non-digital museum data were excluded), but mammal data were compiled for selected groups only: orders Carnivora, Insectivora and Chiroptera, and the endemic or Red Data Book species (Smithers 1986) within the orders Lagomorpha, Macroscelidea and Rodentia. Remaining mammal orders or species were excluded on the basis of incomplete taxonomy or inadequate distribution data. Bird data were obtained for only those species that breed in greater South Africa (P.A.R. Hockey,

**Table 1** Summary data for species occurrences, hotspots (HS) and coldspots (CS) of six vertebrate taxa in greater South Africa. Data are provided for *all* species, endemic (E) species only, and Red Data Book (RDB) species only

| | Fish | Frogs | Tortoises | Snakes | Birds | Mammals |
|---|---|---|---|---|---|---|
| **All species** | | | | | | |
| No. of species | 98 | 97 | 18 | 122 | 595 | 144 |
| No. of QDS | 727 | 1024 | 954 | 1229 | 1971 | 1372 |
| No. of records | 3918 | 5709 | 1596 | 7646 | 295981 | 8689 |
| No. of HS | 31 | 47 | 12 | 61 | 97 | 68 |
| No. of species in HS | 17–32 | 19–38 | 5–5 | 23–39 | 282–382 | 19–51 |
| No. of CS | 182 | 230 | 555 | 268 | 98 | 335 |
| No. of species in CS | 1 | 1 | 1 | 1 | 4-52 | 1 |
| **Endemic species** | | | | | | |
| No. of species | 44 | 49 | 8 | 36 | 55 | 37 |
| No. of QDS | 564 | 758 | 420 | 675 | 1938 | 525 |
| No. of EHS | 22 | 34 | 15 | 25 | 79 | 20 |
| No. of species in EHS | 6–8 | 8–15 | 3–3 | 9–14 | 27–34 | 6–9 |
| **Red Data Book species** | | | | | | |
| No. of species | 36 | 15 | 6 | 27 | 92 | 72 |
| No. of QDS | 283 | 61 | 117 | 265 | 1850 | 815 |
| No. of RDBHS | 9 | 3 | 3 | 8 | 84 | 35 |
| No. of species in RDBHS | 4–7 | 4–5 | 2–2 | 4–8 | 19–43 | 7–21 |

pers. comm.). 'Tortoises' refer to both tortoises and terrapins.

All species distributions were loaded into a geographic information system (GIS, see Lombard 1995). Hotspots of total species richness (HS), endemic species richness (EHS) and Red Data Book species richness (RDBHS) were identified for each taxon. Endemic species are those that have at least 90% of their known range within greater South Africa, and Red Data Book species are those listed in the most recent South African Red Data Books (Foundation for Research Development, Pretoria). Hotspots were defined as the top 5% of data-containing QDS (i.e. species-rich QDS). However, the threshold of 5% of species-rich QDS for each taxon fell mostly in a group of QDS with equal species richness counts. The final hotspots were thus selected using the method described by Prendergast *et al.* (1993). For example, 727 QDS contained fish data (see Table 1), and the top 5% of these would be the 36 richest squares (i.e. squares 1–36). Squares 32–39, however, contained equal species counts (i.e. 16 species). These squares were then excluded from hotspots, and all squares with a greater species richness were classified as hotspots. Endemic hotspots and Red Data Book hotspots were identified by the same method, using data for endemic or Red Data Book species only. Species-poor areas, or coldspots (CS), were also identified for each taxon. These were the most species poor 5% of all data-containing QDS. Numbers of coldspots within a taxon were far higher than numbers of hotspots, owing to the large number of QDS containing only one species record. The desired threshold of exactly 5% of the poorest data-containing QDS always fell in a group of QDS with a species richness of one (except for birds), thus all of these had to be selected as coldspots.

Representative reserves for all taxa were identified using the complementarity algorithm developed by Rebelo & Siegfried (1992). This algorithm identifies a set of reserves (QDS) that would represent all species in the database at least once. Although the algorithm can produce flexible results (i.e. alternative systems of reserves can also represent all species), a flexibility analysis was not performed. Such an analysis is recommended once data on additional taxa, land uses and threats become available. For all taxa, excluding birds, all available data were used for reserve selection, owing to the verification procedure that all museum data were subjected to (see Lombard 1995). The bird data, however, were subjected to an 'outlier-exclusion' program within the GIS, where all species occurrences that had no adjacent or diagonal neighbouring QDS with the same species, were excluded from the analysis. This procedure was followed because verification of the bird data had not been completed at the time.

There has been some debate regarding the best method for selecting representative reserves (Underhill 1994; Pressey, Possingham & Margules, in press). Owing to the fact that linear programming was not used in the present study, I refer to 'representative', rather than 'ideal' or 'optimal' reserves. Williams *et al.* (unpubl.) refer to these as 'complementary areas'. The method used in this paper was tested against the method described by Nicholls & Margules (1993), and was found to be equally efficient (Pressey & Nicholls 1989).

Existing reserves are defined as all publicly owned protected areas in greater South Africa. The database used in this study was at a QDS scale and is described in Lombard (1995). Reserve authorities are those that existed before South Africa's transition to a new government in April 1994. New data are not available as yet. The biome map used was based on Rutherford & Westfall (1986). The savanna category was split into arid and woodland savanna by G.N. Bronner. Forests were not analysed because they occur at scales finer than a QDS.

## Results

### Hotspots and coldspots

Summary data for hotspots and coldspots in all vertebrate taxa are provided in Table 1. The total number of data-containing QDS per taxon is shown in Table 1 and Figure 1. Fish, frogs and snakes have been well sampled in the eastern and coastal areas, but inadequately sampled in the western arid areas. Many species, however, may well be absent from the western areas (especially in the case of fish and frogs), but the presence of false negatives in the database does not allow one to distinguish between unsampled areas and confirmed absence of species. The gap in tortoise data in the east may be real (Branch *et al.* 1995). Mammals have been relatively well sampled throughout the country, with gaps in the Nama-Karoo. The coverage of bird data is excellent, given that data were obtained from SABAP which collates bird data from both public and professional sources.

Figure 2 shows the position of HS, EHS and RDBHS for each taxon. HS of all groups (except tortoises) are concentrated in the north-east of the country, whereas EHS are concentrated in the south and south-west (except snakes). RDBHS of fish and frogs are concentrated in the south-west, whereas those of the other four taxa are found mainly in the north-east.

### Coincidence of HS, EHS and RDBHS within taxa

The degree of overlap of the three types of hotspots within each taxon is listed in Table 2. Proportional overlaps were calculated as the number of overlapping hotspots in a paired comparison (e.g. there are three overlaps of fish HS and fish EHS), divided by the smallest number of hotspots in the pair (e.g. there are 31 fish HS, and 22 fish EHS, thus 22 is chosen).

The overlap of HS and EHS is less than 15% in fish and birds, between 35–42% in frogs, tortoises and mammals, and there is a high overlap in snakes (68%). There is no overlap between HS and RDBHS in tortoises, there is a 22–33% overlap in fish and frogs, and a high overlap in snakes, birds and mammals (64–88%). There is no overlap between EHS and RDBHS in tortoises and snakes, there is little overlap in birds and mammals (4–10%), there is a high overlap in fish (56%), and there is total overlap in frogs. The six QDS in which all three types of hotspots overlap within taxa are listed at the base of Table 2.

### Coincidence of HS, EHS and RDBHS among taxa

The degree of overlap of the three types of hotspots among the six taxa is shown in Table 3 (above diagonal). Data are proportional overlaps, and the number in parentheses is the maximum number of possible overlaps. Proportional overlaps were calculated as the number of overlapping hotspots in a

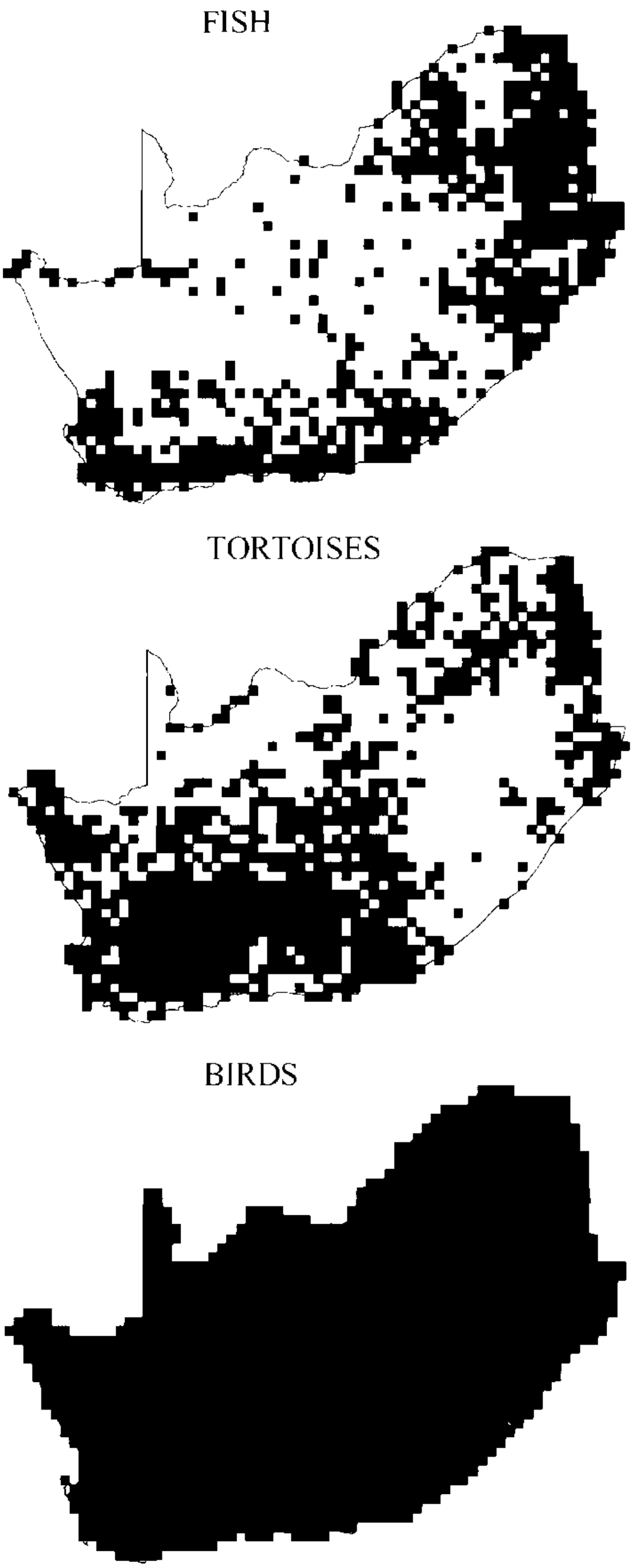


**Figure 1** Data coverage for six vertebrate taxa in greater South Africa. Each square = 1 QDS (quarter-degree square; 15 min × 15 min).

paired comparison (e.g. there are 10 overlaps of fish HS and mammal HS), divided by the maximum number of possible overlaps (28 in this paired comparison). This maximum number of possible overlaps was calculated as the smallest number of hotspots in the pair of taxa (there are 31 fish HS, and 68 mammal HS, thus 31 is chosen), excluding those hotspots that do not contain species of the other taxon (3 fish hotspots do not contain any mammal data, thus 31−3 =28,

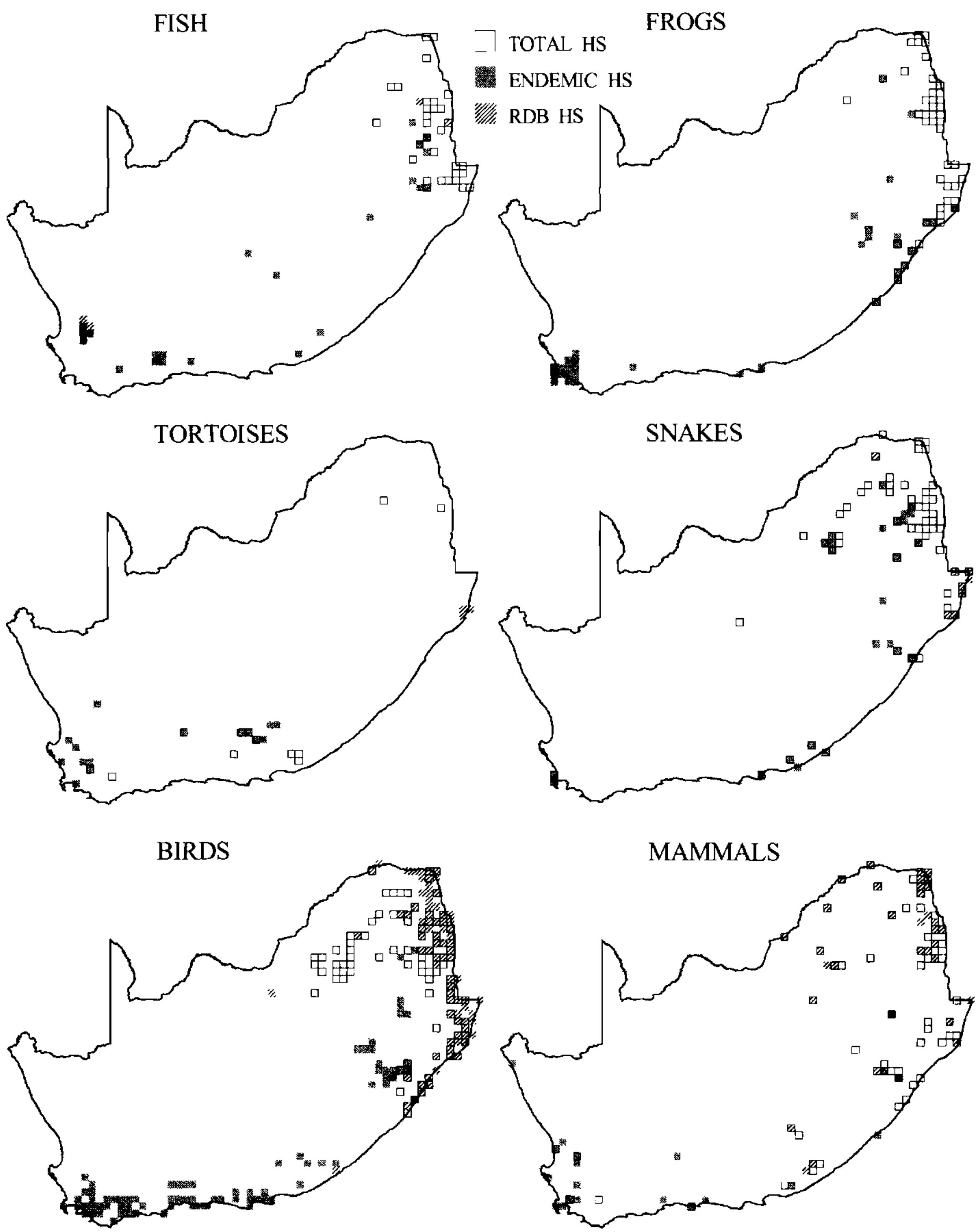


**Figure 2** The coincidence of species richness hotspots (TOTAL HS), endemic species hotspots (ENDEMIC HS) and Red Data Book species hotspots (RDB HS) within six vertebrate taxa in greater South Africa.

and 28 is the maximum number of possible overlaps). Data have been presented in the same format as that of Prendergast *et al.* (1993) to facilitate comparisons.

There is very little overlap between tortoise HS and HS of the other taxa (0–10%) (Table 3a). There is a large overlap between HS of three pairs of taxa: frogs and birds (72%);

**Table 2** The proportional overlap between hotspots (HS), endemic species hotspots (EHS), and Red Data Book species hotspots (RDBHS) within six vertebrate taxa in greater South Africa. Numbers of overlapping hotspots are shown in parentheses. The six quarter-degree squares in which all three categories of HS overlap within a taxon are listed at the base of the table

| | Fish | Frogs | Tortoises | Snakes | Birds | Mammals |
|---|---|---|---|---|---|---|
| Prop. of HS=EHS | 0,14 (3) | 0,35 (12) | 0,42 (5) | 0,68 (17) | 0,05 (4) | 0.40 (8) |
| Prop. of HS=RDBHS | 0,22 (2) | 0,33 (1) | 0,00 (0) | 0,88 (7) | 0,64 (54) | 0.86 (30) |
| Prop. of EHS=RDBHS | 0,56 (5) | 1,00 (3) | 0,00 (0) | 0,00 (0) | 0,04 (3) | 0.10 (2) |
| Prop. of HS=EHS=RDBHS | 0,11 (1) | 0,33 (1) | 0,00 (0) | 0,00 (0) | 0,03 (2) | 0.10 (2) |
| | 2531CC | 3318CD | | | 2930AD | 2730AC |
| | | | | | 3030BC | 2930CB |

**Table 3** The proportional overlap of hotspots, endemic species hotspots and Red Data Book species hotspots among six vertebrate taxa in greater South Africa (data above diagonals). Data below diagonal in section (a) are proportional overlaps of coldspots among the six taxa. Numbers in parentheses are total possible overlaps (see text for explanation)

| | Fish | Frogs | Tortoises | Snakes | Birds | Mammals |
|---|---|---|---|---|---|---|
| **(a) Hotspots and coldspots** | | | | | | |
| Fish | – | 0,35 (31) | 0,00 (5) | 0,35 (31) | 0,48 (31) | 0,36 (28) |
| Frogs | 0,24 (110) | – | 0,00 (9) | 0,49 (47) | 0,72 (47) | 0,62 (47) |
| Tortoises | 0,54 (98) | 0,61 (128) | – | 0,10 (10) | 0,00 (12) | 0,08 (12) |
| Snakes | 0,19 (118) | 0,25 (153) | 0,62 (133) | – | 0,59 (61) | 0,42 (59) |
| Birds | 0,67 (3) | 1,00 (2) | 0,88 (32) | 0,47 (19) | – | 0,47 (68) |
| Mammals | 0,19 (144) | 0,22 (172) | 0,65 (155) | 0,34 (177) | 0,41 (39) | – |
| **(b) Endemic hotspots** | | | | | | |
| Fish | – | 0,00 (21) | 0,00 (7) | 0,14 (14) | 0,18 (22) | 0,19 (16) |
| Frogs | | – | 0,20 (10) | 0,25 (24) | 0,42 (33) | 0,44 (18) |
| Tortoises | | | – | 0,00 (10) | 0,20 (15) | 0,22 (9) |
| Snakes | | | | – | 0,24 (25) | 0,16 (19) |
| Birds | | | | | – | 0,40 (20) |
| Mammals | | | | | | – |
| **(c) Red Data Book hotspots** | | | | | | |
| Fish | – | 0.00 (0) | 0,00 (2) | 0,00 (6) | 0,22 (9) | 0,00 (8) |
| Frogs | | – | 0,00 (1) | 0,00 (2) | 0,00 (2) | 0,00 (1) |
| Tortoises | | | – | 0,33 (3) | 1,00 (3) | 0,33 (3) |
| Snakes | | | | – | 0,75 (8) | 0,38 (8) |
| Birds | | | | | – | 0,54 (35) |
| Mammals | | | | | | – |

frogs and mammals (62%); and snakes and birds (59%). Table 4 shows that no HS is common to all taxa, whereas six HS are common to five taxa: 2231AC, 2231AD, 2431DC, 2531BD, 2431CB and 2632CD.

EHS show no overlap between the two aquatic taxa as well as between the two reptilian taxa (Table 3b). Highest overlap occurs between frogs and birds (42%), frogs and mammals (44%) and birds and mammals (40%). Table 4 shows that two EHS are common to four taxa (3418AB and 3326BC), and a further six are common to three taxa (3318DD, 3418BB, 3319AC, 3325DC, 2730AC and 2930CB).

RDBHS show very little overlap among taxa, with the exception of three pairs: tortoises and birds (100%); snakes and birds (75%); and birds and mammals (54%) (Table 3c). Table 4 shows that only one RDBHS is common to four taxa (2832AD), and another is common to three taxa (2632DD).

## Coincidence of CS among taxa

Coldspot overlap is shown in Table 3a (below diagonal). The high percentage of overlap of coldspots among most pairs of taxa is expected, given the high number of coldspots per taxon. Lowest coldspot overlaps were found between fish and snakes, and fish and mammals (both 19%), indicating large differences in their patterns of distribution.

## Coincidence of HS and CS among taxa

The degree of overlap of HS versus CS among all taxa is shown in Table 5. Proportional overlaps and total number of possible overlaps were calculated as in Table 3. Generally, there is a low overlap: 10 pair-wise comparisons are = 0, and 12 pair-wise comparisons are less than 10%. Highest overlaps occur between fish HS and tortoise CS (36%), and bird HS and tortoise CS (43%).

## Proportion of species in HS, EHS, RDBHS and CS

The proportion of species in each taxon that falls within hotspots of all taxa, is shown in Figure 3. In all taxa, the highest proportion of species fall in mammal HS, with the exception of snakes, which are best represented in their own HS. Snake HS capture the second highest number of species of four of the six taxa. The lowest proportion of species of all taxa, except tortoises, fall in tortoise HS.

These results are biased by the total number of hotspots per taxon (Table 1), thus a second analysis, which standardized for the number of hotspots per taxon, was undertaken (Figure 4). In this analysis, a standard number of hotspots was chosen from each taxon, and the proportion of species within these hotspots was calculated. This standard number was as close to 61 as possible, because 61 is the mean of 5% of all data-containing QDS for each taxon. The number of QDS closest to 61, that represented a cut-off in the number of species counts, was chosen for each taxon. In fish hotspots, for example, the richest 61 QDS did not represent a cut-off in species richness. QDS numbers 44–57 contained 14 species each, and QDS numbers 58–72 contained 13 species each. QDS number 57 was closer to the desired number 61, than was QDS number 72. The final number of hotspots resulting from this process was: fish — 57; frog — 56; tortoises — 57; snakes —61; birds — 58; and mammals — 58. Figure 4 shows that if the number of hotspots is standardized, the species of four taxa are best represented in their own hotspots, with the exception of fish, which are represented best in snake HS, and birds, which are represented best in mammal HS. Mammal and snake HS, however, still capture the first and second highest

**Table 4** Numbers of hotspots (HS), endemic species hotspots (EHS) and Red Data Book species hotspots (RDBHS) common among six vertebrate taxa in greater South Africa

| No. of taxa | No. of HS in common | No. of EHS in common | No. of RDBHS in common |
|---|---|---|---|
| 6 | 0 | 0 | 0 |
| 5 | 6 | 0 | 0 |
| 4 | 11 | 2 | 1 |
| 3 | 22 | 6 | 1 |
| 2 | 36 | 31 | 26 |

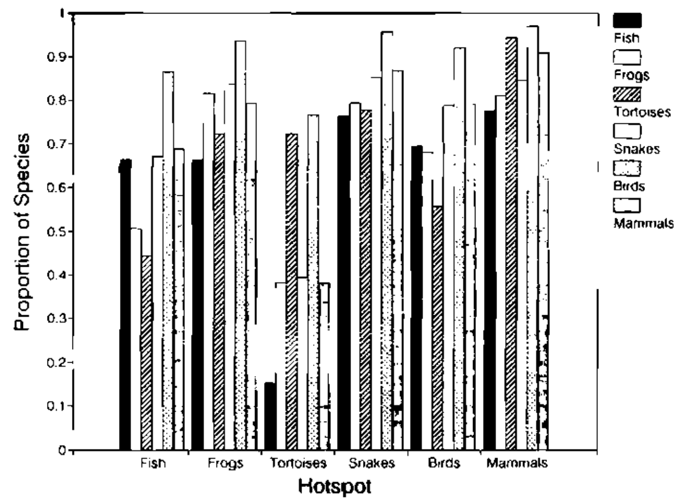


**Figure 3** The proportion of species in six vertebrate taxa in greater South Africa, that fall in the hotspots of their own taxon, as well as the hotspots of other taxa.

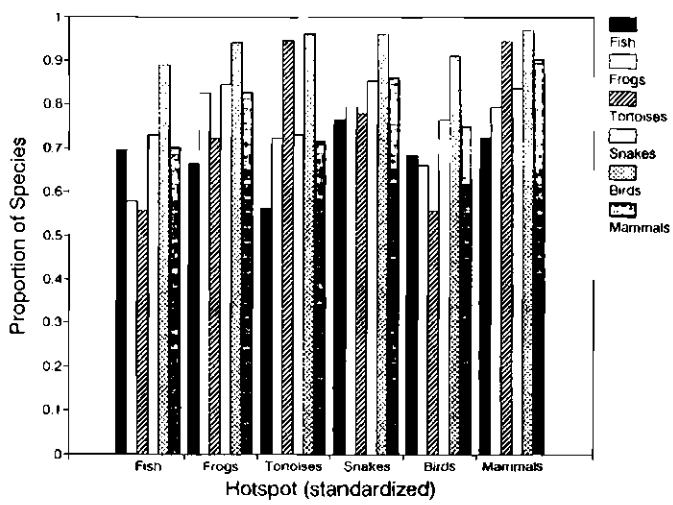


**Figure 4** The proportion of species in six vertebrate taxa in greater South Africa, that fall in a standardized number of hotspots for each taxon (see text for standardization procedure).

**Table 5** The proportional overlap of hotspots with coldspots among six vertebrate taxa in greater South Africa. Numbers in parentheses are total possible overlaps. The table should be read as hotspots across the top, versus coldspots down the left hand column

| | Fish | Frogs | Tortoises | Snakes | Birds | Mammals |
|---|---|---|---|---|---|---|
| Fish | – | 0,07 (44) | 0,20 (5) | 0,14 (57) | 0,07 (90) | 0,05 (65) |
| Frogs | 0,03 (31) | – | 0,00 (9) | 0,00 (60) | 0,02 (93) | 0,02 (62) |
| Tortoises | 0,36 (25) | 0,24 (38) | – | 0,18 (50) | 0,43 (67) | 0,19 (52) |
| Snakes | 0,00 (31) | 0,00 (47) | 0,20 (10) | – | 0,05 (97) | 0,02 (66) |
| Birds | 0,00 (31) | 0,00 (47) | 0,00 (12) | 0,00 (61) | – | 0,00 (68) |
| Mammals | 0,04 (28) | 0,02 (47) | 0,08 (12) | 0,00 (59) | 0,06 (90) | – |

proportion of species in all taxa, respectively.

Figure 5 shows the proportion of species within HS, EHS, RDBHS and CS of their own taxon. Fish, tortoises, snakes and mammals have the greatest proportion of species in HS, frog species are best represented in EHS, whereas birds are best represented in RDBHS.

Similar data for endemic species only are provided in Figure 6. Endemic fish, frog and bird species are best represented in EHS, whereas endemic tortoises, snakes and mammals are best represented in HS. HS represent endemic species with varying degrees of success (39–92% of species).

Figure 7 shows the same data for RDB species. No RDBHS for any taxon captures the greatest proportion of RDB species. Fish and frog RDB species are best represented in EHS, whereas RDB snakes, birds and mammals are best represented in HS. RDB tortoises are found mainly in CS, but

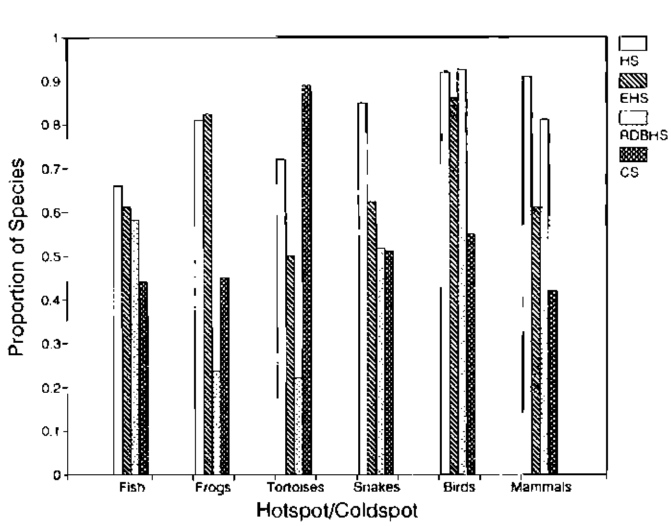


**Figure 5** The proportion of all species in six vertebrate taxa in greater South Africa, that fall in the hotspots (HS), endemic species hotspots (EHS), Red Data Book species hotspots (RDBHS) and coldspots (CS) of their own taxon.

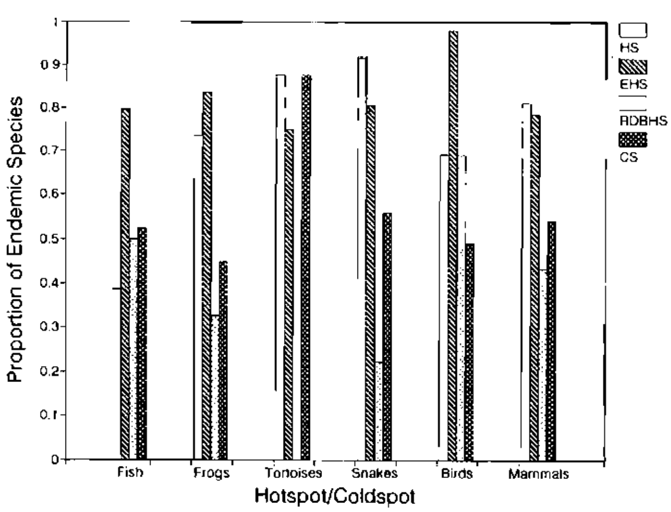


**Figure 6** The proportion of endemic species in six vertebrate taxa in greater South Africa, that fall in the hotspots (HS), endemic species hotspots (EHS), Red Data Book species hotspots (RDBHS) and coldspots (CS) of their own taxon.

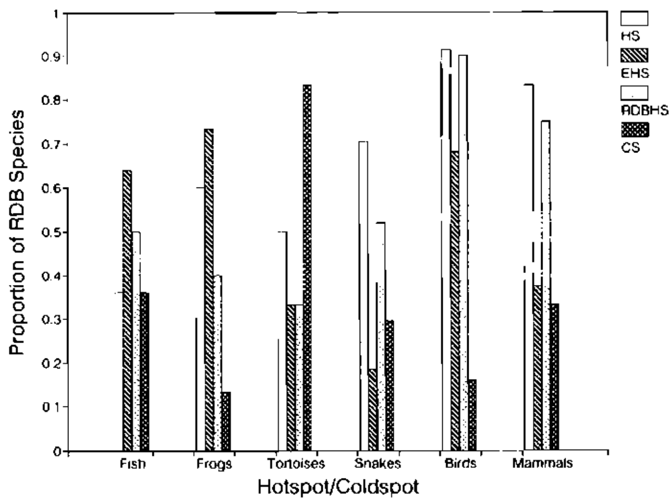


**Figure 7** The proportion of Red Data Book species in six vertebrate taxa in greater South Africa, that fall in the hotspots (HS), endemic species hotspots (EHS), Red Data Book species hotspots (RDBHS) and coldspots (CS) of their own taxon.

this may be explained by the exceptionally high number of tortoise CS (Table 1). In all taxa, except fish, HS represent RDB species better than RDBHS do, and capture 50–91% of species.

## Hotspots and species versus existing reserves

A comparison of hotspots of all taxa with existing reserves is shown in Table 6a. Over 80% of HS of all taxa are protected, except tortoise HS, of which only 67% are protected (assuming that the actual HS within a QDS falls within the reserve found in that QDS). Within all taxa, between 17–40% of HS fall in National Parks, and 42–58% of HS fall in provincial reserves. Thus between 59–84% of all HS enjoy some degree of national or provincial protective legislation.

Similar data for EHS are shown in Table 6b. Over 85% of EHS of all taxa are protected, except tortoise EHS, of which only 73% are protected. Within all taxa, very few EHS fall in National Parks (7–20%), and most EHS fall in provincial reserves (47–88%). No fish, frog or snake EHS fall in National Parks. Local authority reserves play an important role in protecting EHS, and five of the six taxa have between 5–30% of their EHS in these reserves.

Data for RDBHS are shown in Table 6c. Over 76% of RDBHS of all taxa are protected. All taxa have between 50–100% of their RDBHS in provincial reserves, with the exception of mammals. National Parks protect only 11–40% of the RDBHS of three taxa. Frogs, tortoises and snakes have no RDBHS in a National Park. Local authority reserves are important for frog RDBHS.

Table 7 lists those eleven species that do not occur in any QDS containing an existing reserve (according to the data used in this study).

## Important QDS

Twenty very important QDS were identified in the HS analyses. Six of these are QDS where the three types of hotspots coincide within each taxon (Table 2), and 16 QDS are where the three types of hotspots are common to a large number of

**Table 6** The proportion (or number) of hotspots, endemic species hotspots and Red Data Book species hotspots that coincide with existing reserves (owned by different public authorities) in greater South Africa

| | National Parks Board | Provincial Reserves | State Forests | Local Authorities | Other Authorities | No existing Reserve | Total No. |
|---|---|---|---|---|---|---|---|
| **(a) Hotspots** | | | | | | | |
| Fish | 0,23 (7) | 0,58 (18) | | | | 0,19 (6) | 31 |
| Frogs | 0,40 (19) | 0,57 (27) | | | | 0,02 (1) | 47 |
| Tortoises | 0,17 (2) | 0,42 (5) | | | 0,08 (1) | 0,33 (4) | 12 |
| Snakes | 0,26 (16) | 0,49 (30) | 0,02 (1) | 0,13 (8) | 0,02 (1) | 0,08 (5) | 61 |
| Birds | 0,18 (17) | 0,57 (55) | 0,02 (2) | 0,07 (7) | 0,02 (2) | 0,14 (14) | 97 |
| Mammals | 0,34 (23) | 0,50 (34) | 0,01 (1) | 0,03 (2) | | 0,12 (8) | 68 |
| **(b) Endemic hotspots** | | | | | | | |
| Fish | | 0,82 (18) | 0,05 (1) | | | 0,14 (3) | 22 |
| Frogs | | 0,88 (30) | | 0,12 (4) | | | 34 |
| Tortoises | 0,07 (1) | 0,47 (7) | | 0,13 (2) | 0,07 (1) | 0,27 (4) | 15 |
| Snakes | | 0,72 (18) | | 0,20 (5) | | 0,08 (22) | 25 |
| Birds | 0,11 (9) | 0,70 (55) | 0,01 (1) | 0,13 (10) | | 0,05 (4) | 79 |
| Mammals | 0,20 (4) | 0,65 (13) | | 0,05 (1) | | 0,10 (2) | 20 |
| **(c) Red Data Book hotspots** | | | | | | | |
| Fish | 0,11 (1) | 0,67 (6) | 0,11 (1) | | | 0,11 (1) | 9 |
| Frogs | | 0,67 (2) | | 0,33 (1) | | | 3 |
| Tortoises | | 1,00 (3) | | | | | 3 |
| Snakes | | 1,00 (8) | | | | | 8 |
| Birds | 0,33 (28) | 0,50 (42) | | | 0,06 (5) | 0,11 (9) | 84 |
| Mammals | 0,40 (14) | 0,29 (10) | | 0,09 (3) | | 0,23 (8) | 35 |

**Table 7** Species which may not occur in existing publicly owned reserves in greater South Africa

| Taxon | Species | Red Data Book status | Endemism status |
|---|---|---|---|
| Fish | *Serranochromis robustus* (nembwe) | | |
| Frogs | *Breviceps macrops* (desert rain frog) | Restricted | Endemic |
| | *Arthroleptella ngongoniensis* (chirping frog) | | Endemic |
| Snakes | *Bitis schneideri* (Namaqua dwarf adder) | Vulnerable | |
| Birds | *Vanellus crassirostris* (longtoed plover) | | |
| | *Mirafra burra* (red lark) | Indeterminate | Endemic |
| | *Spizocorys sclateri* (Sclater's lark) | Indeterminate | |
| Mammals | *Cryptochloris wintoni* (De Winton's golden mole) | Indeterminate | Endemic |
| | *Myotis seabrai* (Angola hairy bat) | Indeterminate | |
| | *Bathyergus janetta* (Namaqua dune molerat) | Rare | Endemic |
| | *Petromyscus collinus* (pygmy rock mouse) | Indeterminate | |

taxa (Table 4: the six HS common to five taxa, and the EHS and RDBHS common to three or four taxa). Two of these 16 QDS are repeats of the former six. Fortunately, all of these QDS coincide with existing reserves: five fall in the Kruger National Park; five fall in Natal Parks Board reserves; five fall in Western Cape Nature Conservation reserves; and the remaining five fall in reserves owned by the Kwazulu Bureau of Natural Resources, Eastern Transvaal Nature Conservation, Eastern Cape Nature Conservation and local authorities.

## Representative reserves

The representative reserves selected for each taxon by the complementarity algorithm are shown in Figure 8. Any differences between these results and those reported by the individual papers in this volume can be explained by two factors: (i) data were updated for this study, and (ii) South African data only were used in this study (in the case of tortoises). It should be noted that these sets of representative reserves may be flexible. Changing the starting point of the reserve selec-

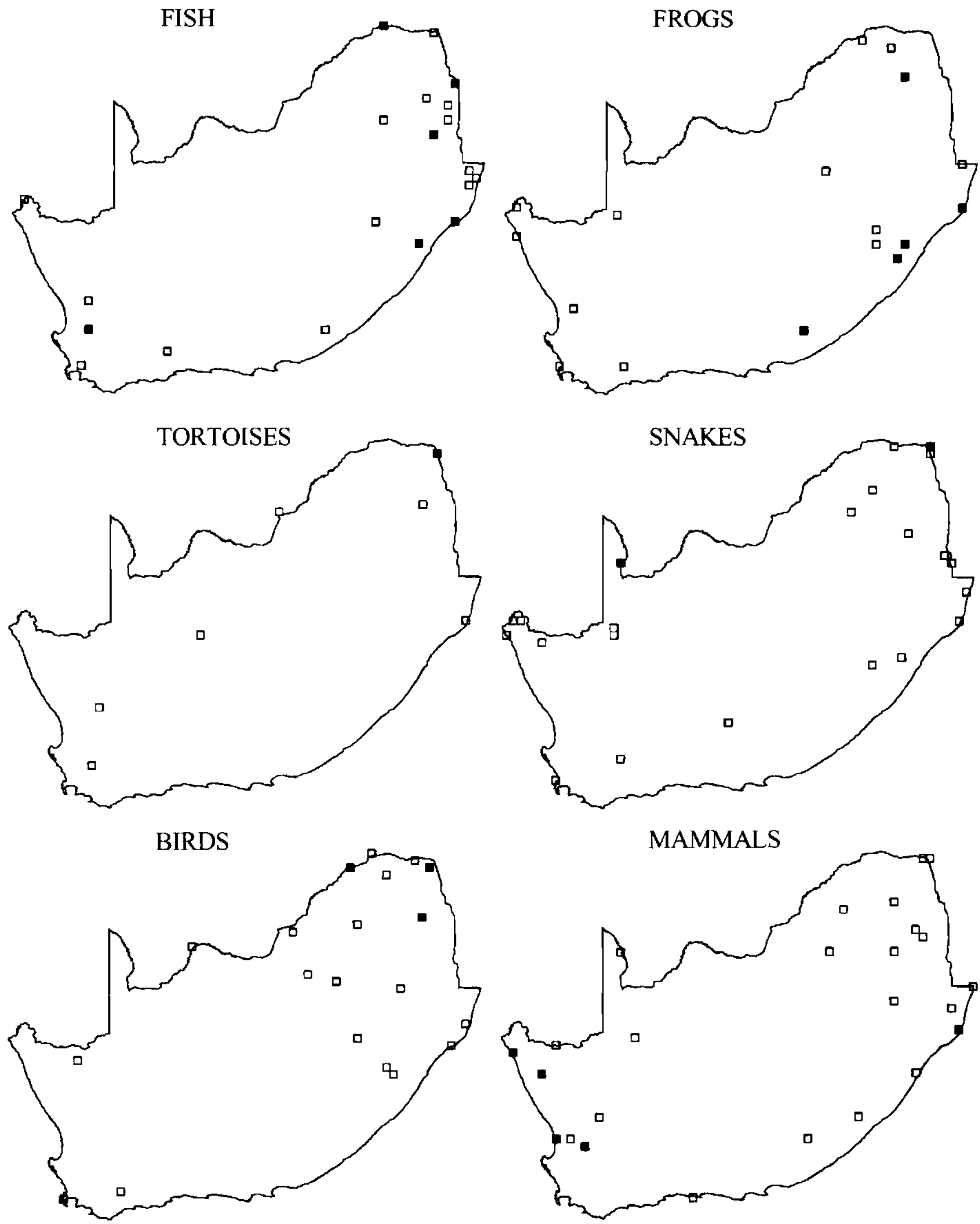


**Figure 8** Representative reserve systems for six vertebrate taxa in greater South Africa. Solid black squares are irreplaceable reserves. Each reserve system ensures that all species in the taxon's database are represented at least once.

tion algorithm, or changing some of the selection rules, results in alternative reserve systems being selected. These alternative systems may comprise the same number of reserves as chosen by the original algorithm, or many extra reserves may be required to represent all species by the required number of times. A flexibility analysis was not conducted in this study, but all irreplaceable reserves were identified. These are reserves that are not flexible, owing to the presence of a species that occurs only once in the database. Irreplaceable representative reserves are shown as solid squares in Figure 8.

Between 17–25 representative reserves can represent all species in each taxon, except tortoises, which require only seven reserves. The total number of different reserves depicted in Figure 8 is 97. It is apparent that if one combines all distribution data into a single database before selecting reserves, a more economical 66 reserves can represent all species (Figure 9). Fifty-two of these were chosen for at least one individual taxon, whereas 14 were newly selected. The 22 reserves selected here for snakes show that the reserve selection algorithm used in this analysis delivers slightly more efficient results than the algorithm used on the same snake database by Lombard *et al.* (1995) (23 reserves).

There is a concentration of representative reserves in the north-eastern savannas, with a smaller concentration in the Succulent Karoo (Figure 8). There are very few representative reserves in the interior areas (Nama-Karoo and grasslands). When all data are combined (Figure 9), this pattern remains the same, with the exception that the arid western interior contains many more reserves.

## Representative reserves and hotspots

Table 8a shows the overlap between representative reserves and the three types of hotspots within each taxon. The proportions per taxon in Table 8 do not add up to one because hotspots, endemic hotspots and Red Data Book hotspots overlap in some cases. Approximately half (45–59%) of the representative reserves in five taxa do not overlap with hotspots, whereas 71% of frog representative reserves do not overlap with hotspots.

Hotspots of total species richness coincided more frequently with representative reserves, than did EHS or RDBHS, within four of the six taxa. Tortoise and bird representative reserves coincided most frequently with tortoise EHS, and bird RDBHS, respectively.

As noted previously, the representative reserves selected by the algorithm are flexible. The comparisons shown in Table 8 would be very different if a modified algorithm was used. The most important information to be gained from Table 8 is that the hotspot method of prioritizing areas for conservation, ver-

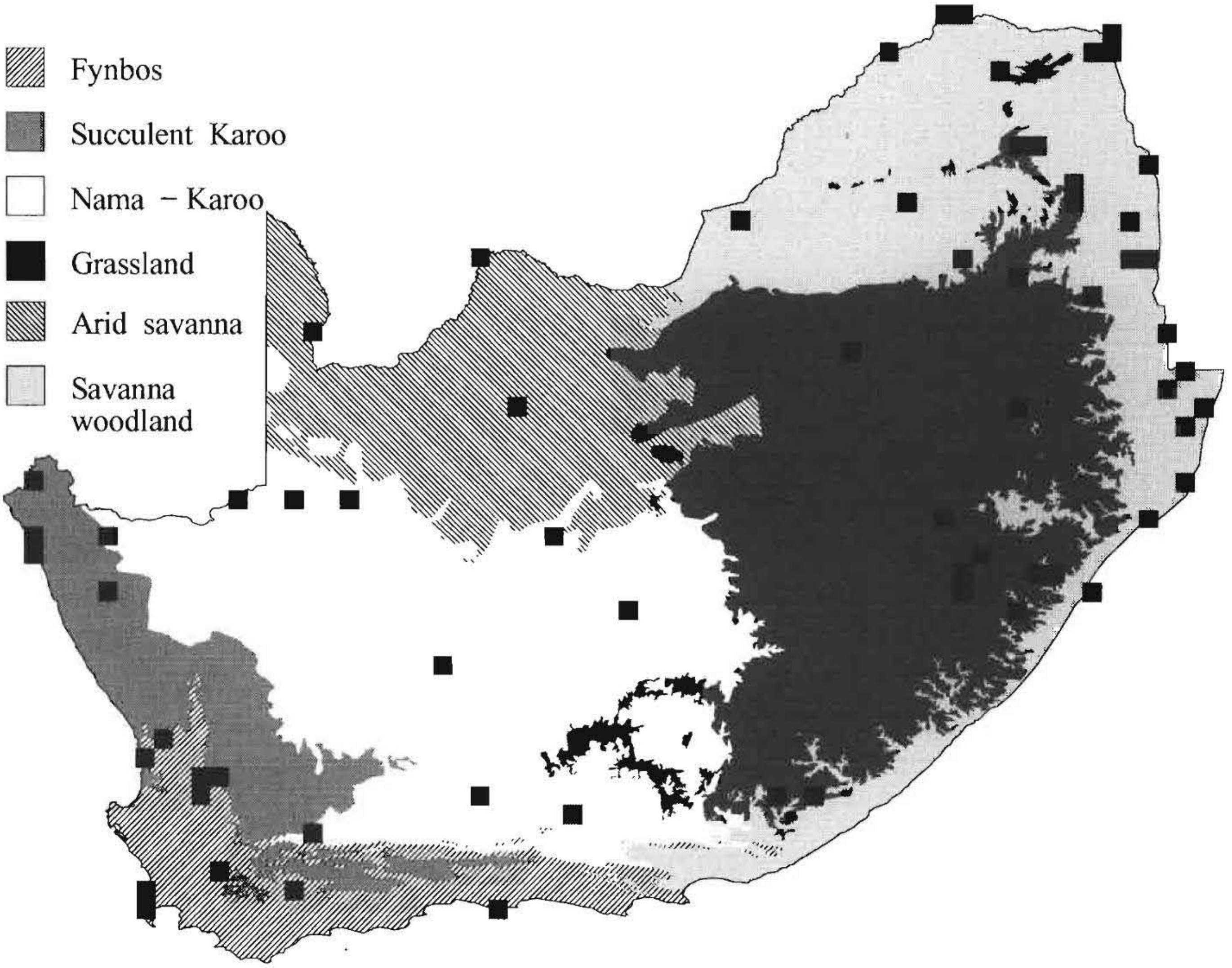


**Figure 9** A representative reserve system for the combined databases of six vertebrate taxa in greater South Africa (solid black squares). This reserve system represents all 1074 species at least once. The six biomes for greater South Africa are described by the key.

**Table 8** The proportion (or number) of representative reserves (RR) (a), and irreplaceable representative reserves (IRR) (b), that coincide with hotspots, endemic species hotspots and Red Data Book species hotspots, in six vertebrate taxa in greater South Africa

| | Hotspots | Endemic Hotspots | Red Data Book Hotspots | No Hotspots | Total No. of RR/IRR |
|---|---|---|---|---|---|
| **(a) All representative reserves** | | | | | |
| Fish | 0,30 (6) | 0,20 (4) | 0,15 (3) | 0,50 (10) | 20 |
| Frogs | 0,29 (5) | 0,24 (4) | 0,06 (1) | 0,71 (12) | 17 |
| Tortoises | 0 (0) | 0,29 (2) | 0,14 (1) | 0,57 (4) | 7 |
| Snakes | 0,41 (9) | 0,09 (2) | 0,09 (2) | 0,59 (13) | 22 |
| Birds | 0,25 (5) | 0,25 (5) | 0,30 (6) | 0,45 (9) | 20 |
| Mammals | 0,40 (10) | 0,16 (4) | 0,36 (9) | 0,48 (12) | 25 |
| **(b) Irreplaceable representative reserves** | | | | | |
| Fish | 0,17 (1) | 0,33 (2) | 0,33 (2) | 0,67 (4) | 6 |
| Frogs | 0,40 (2) | 0,40 (2) | 0 (0) | 0,60 (3) | 5 |
| Tortoises | 0 (0) | 0 (0) | 0 (0) | 1,00 (1) | 1 |
| Snakes | 0,50 (1) | 0 (0) | 0 (0) | 0,50 (1) | 2 |
| Birds | 0,67 (2) | 0 (0) | 0,67 (2) | 0,33 (1) | 3 |
| Mammals | 0,40 (2) | 0,40 (2) | 0,20 (1) | 0,40 (2) | 5 |

**Table 9** The proportion (or number) of (a) representative reserves, and (b) irreplaceable representative reserves only, that coincide with existing reserves (owned by different public authorities) in greater South Africa

| | National Parks Board | Provincial Reserves | State Forests | Local Authorities | Other Authorities | No existing Reserve | Total No. |
|---|---|---|---|---|---|---|---|
| **(a) All representative reserves** | | | | | | | |
| Fish | 0,25 (5) | 0,70 (14) | | | | 0,05 (1) | 20 |
| Frogs | 0,12 (2) | 0,59 (10) | 0,06 (1) | | | 0,24 (4) | 17 |
| Tortoises | 0,14 (1) | 0,43 (3) | | 0,14 (1) | | 0,29 (2) | 7 |
| Snakes | 0,27 (6) | 0,32 (7) | 0,05 (1) | 0,05 (1) | 0,05 (1) | 0,27 (6) | 22 |
| Birds | 0,10 (2) | 0,45 (9) | | 0,10 (2) | 0,05 (1) | 0,30 (6) | 20 |
| Mammals | 0,16 (4) | 0,36 (9) | | 0,16 (4) | | 0,32 (8) | 25 |
| All taxa | 0,17 (11) | 0,44 (29) | 0,03 (2) | 0,06 (4) | | 0,30 (20) | 66 |
| **(b) Irreplaceable representative reserves** | | | | | | | |
| Fish | 0,17 (1) | 0,67 (4) | | | | 0,17 (1) | 6 |
| Frogs | | 0,80 (4) | | | | 0,20 (1) | 5 |
| Tortoises | 1,00 (1) | | | | | | 1 |
| Snakes | 1,00 (2) | | | | | | 2 |
| Birds | 0,33 (1) | 0,33 (1) | | | | 0,33 (1) | 3 |
| Mammals | | 0,60 (3) | | | | 0,40 (2) | 5 |
| All taxa | 0,24 (5) | 0,52 (11) | | | | 0,24 (5) | 21 |

sus the complementarity method, produce vastly different results.

Table 8b shows a comparison between irreplaceable representative reserves and hotspots. Owing to the fact that irreplaceable representative reserves are based on rarity (singly occurring species), one would not expect a high overlap between these reserves and hotspots. The data in Table 8b support this (33–100% of irreplaceable representative reserves do not overlap with hotspots).

## Representative reserves and existing reserves

Table 9a shows that between 68–95% of the representative reserves within each taxon overlap with existing reserves. National Parks overlap with between 10–27% of representative reserves within each taxon, whereas provincial reserves overlap with between 32–70% of representative reserves. The 'all taxa' category refers to the representative reserves selected for the combined vertebrate database (as shown in Figure 9). The overlap of representative reserves with existing

**Table 10** Numbers and areas (ha) of reserves, owned by different public authorities, within six biomes (after Rutherford & Westfall 1986) in greater South Africa

| | Fynbos | | Succulent Karoo | | Nama-Karoo | | Grassland | | Arid savanna | | Savanna woodland | | Total | Total | %Total reserve |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Authority | No. | ha | No. | ha | No. | ha | No. | ha | No. | ha | No. | ha | No. | ha | estate |
| NPB | 6 | 113539 | 2 | 189509 | 4 | 129824 | 3 | 19401 | 2 | 970452 | 5 | 1998246 | 22 | 3420971 | 49,43 |
| NAT | | | | | | | 47 | 310867 | | | 42 | 405740 | 89 | 716607 | 10,36 |
| WCC | 66 | 497426 | 17 | 112319 | 2 | 11424 | | | | | | | 85 | 621169 | 8,98 |
| NDF | 13 | 30317 | 1 | 6280 | 2 | 22560 | 9 | 31248 | 8 | 233454 | 22 | 89922 | 55 | 413781 | 5,98 |
| NTE | | | | | | | 8 | 42565 | | | 49 | 300477 | 57 | 343042 | 4,96 |
| ECC | 8 | 183693 | | | | | 4 | 22091 | | | 24 | 75359 | 36 | 281143 | 4,06 |
| LA | 52 | 41380 | 6 | 5481 | 16 | 100677 | 43 | 39003 | 7 | 9096 | 28 | 12374 | 152 | 208011 | 3,01 |
| NWC | | | | | | | 7 | 26303 | 4 | 40314 | 8 | 96602 | 19 | 163219 | 2,36 |
| ETC | | | | | | | 14 | 45471 | | | 9 | 63063 | 23 | 108534 | 1,57 |
| KWA | | | | | | | 10 | 9796 | | | 19 | 89850 | 29 | 99646 | 1,44 |
| SF | 28 | 42069 | | | | | 35 | 34207 | | | 12 | 8755 | 75 | 85031 | 1,23 |
| OFS | | | | | 4 | 27043 | 13 | 45343 | 1 | 11025 | | | 18 | 83411 | 1,21 |
| KAN | | | | | | | 1 | 28000 | | | 6 | 42360 | 7 | 70360 | 1,02 |
| NCC | 1 | 5070 | 2 | 25848 | 2 | 15703 | | | 1 | 3000 | | | 6 | 49621 | 0,72 |
| KWAN | | | | | | | | | | | 5 | 40120 | 5 | 40120 | 0,58 |
| CIS | | | | | | | 10 | 30073 | | | 2 | 9625 | 12 | 39698 | 0,57 |
| PWV | | | | | | | 5 | 17746 | | | 2 | 20180 | 7 | 37926 | 0,55 |
| SNTC | | | | | | | 1 | 18000 | | | 1 | 18400 | 2 | 36400 | 0,53 |
| TRA | | | | | | | 4 | 20300 | | | 7 | 15776 | 11 | 36076 | 0,52 |
| SNT | | | | | | | | | | | 1 | 30000 | 1 | 30000 | 0,43 |
| NPA | | | | | | | 3 | 10116 | | | 2 | 9500 | 5 | 19616 | 0,28 |
| DWA | | | | | | | | | | | 1 | 7004 | 1 | 7004 | 0,10 |
| LNP | | | | | | | 1 | 6500 | | | | | 1 | 6500 | 0,09 |
| NBG | 5 | 898 | | | | | 4 | 414 | | | 2 | 220 | 11 | 1532 | 0,02 |
| MC | | | | | | | | | | | 1 | 851 | 1 | 851 | 0,01 |
| Total area protected: | | 914392 | | 339437 | | 307231 | | 757444 | | 1267341 | | 3334424 | | 6920269 | |
| Total area: | | 7603221 | | 9009682 | | 31641956 | | 36075067 | | 16253206 | | 26138408 | | 126721540 | |

* CIS = Ciskei; DWA = Dept. Water Affairs & Forestry; ECC = Eastern Cape Nature Conservation; ETC = Eastern Transvaal Nature Conservation; KAN = KaNgwane; KWA = Kwazulu; KWAN = KwaNdebele; LA = Local Authority; LNP = Lesotho National Parks; MC = Monuments Council; NAT = Natal Parks Board; NBG = National Botanical Gardens; NCC = Northern Cape Nature Conservation; NDF = National Defence Force; NPA = Natal Provincial Administration; NPB = National Parks Board; NTE = Northern Transvaal Environment & Tourism; NWC = North West Nature Conservation; OFS = OFS Nature Conservation; PWV = PWV Nature Conservation; SF = State Forests; SNT = Swaziland National Treasury; SNTC = Swaziland National Trust Commission; TRA = Transkei; WCC Western Cape Nature Conservation.

reserves could probably be improved by a flexibility analysis.

Most irreplaceable representative reserves (60–83%) overlap with either National Parks or provincial reserves (Table 9b).

## Biomes and existing reserves

The percentages of biomes currently protected by existing reserves are shown in Figure 10. The fynbos and savannas have the most area protected (7,8–12,8%). The grassland and Karoo biomes are greatly under-represented in reserves (1–3,8%). The total area of greater South Africa that falls in publicly owned reserves is 126 721 540 ha (5,46%). The representation of the different biomes in reserves managed by 25 different authorities is shown in Table 10. Data have been ranked so that the authority responsible for the most reserved areas appears at the top. The National Parks Board is responsible for just under 50% of all reserved areas. Of the provincial conservancies, the Natal Parks Board and Western Cape Nature Conservation are each responsible for approximately 10% of protected land. The National Defence Force plays the next most important role (6%), and all other authorities are responsible for 5% or less of reserved areas.

According to the National Parks Act No. 57 of 1976, National Parks should represent all of the major biomes in South Africa. It is evident from Table 10 that the fynbos, Karoo and grassland biomes have only 0,05–2,1% of their total areas protected in National Parks, whereas the arid and woodland savannas have 5,97 and 7,64% of their areas protected, respectively. Compared with the other 24 authorities,

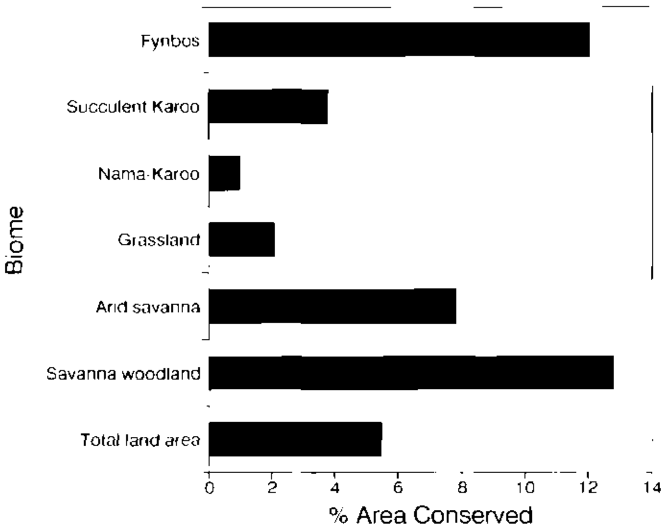


**Figure 10** The percentages of six biomes protected by existing publicly owned reserves in greater South Africa.

National Parks do, however, protect the greatest area of four of the six biomes. The two exceptions are fynbos and grasslands, which occur mostly within areas protected by Western Cape Nature Conservation and the Natal Parks Board, respectively. The role of local authority reserves in protecting the Nama-Karoo is almost as important as that of the National Parks Board.

## Discussion

South Africa's exceptional biological wealth has been discussed many times (see Lombard 1995). Within vertebrates alone, the country supports well over 1000 species, and up to 382 breeding birds have been sighted in a single QDS. Not only is the country species rich, but it also supports a high proportion of endemics (Table 1). Of the 1074 vertebrate species examined here, 229 are endemic to greater South Africa (21%). Endemism is particularly high in frogs (51%). However, there is an even larger proportion of vertebrate species listed in the South African Red Data Books (248 species, 23%). Given the large numbers of endemic and Red Data Book species, there is an urgent need for a National Strategic Plan for the conservation of South Africa's biota. The separate papers in this volume (Skelton *et al.* 1995; Drinkrow & Cherry 1995; Branch *et al.* 1995; Gelderblom & Bronner 1995; Gelderblom *et al.* 1995; Mugo *et al.* 1995; Freitag & van Jaarsveld 1995) have highlighted those vertebrate species, and areas, that are currently under the greatest threat, and which require additional protection. The conclusions reached by these papers, and the present study, can form the basis of such a strategic plan.

One component of a strategic plan would be to identify areas in need of greater sampling effort. Although South Africa has been the focus of many major collections in the past, certain areas have been greatly under-sampled. Figure 1 emphasizes the gaps in collections of the separate vertebrate taxa, but the general trend is a lack of data for the arid western areas (specifically the Nama-Karoo).

Another component of a strategic plan would be to identify areas in need of protective legislation. Two methods of identifying such areas are hotspot analyses, and complementary algorithms. Both of these methods have been applied, and then compared, in this study. A third component of the plan would be to map the spatial distribution of threats (to both species and ecosytems). Reserves can offset only certain threats, and some species and ecosystems will have to be protected by other forms of protective legislation (see Lombard 1995).

Using hotspots as a method of siting reserves has received much criticism, mainly because hotspots are arbitrarily chosen (e.g. the top 5% of data-containing squares) and do not usually represent all species (Rebelo & Tansley 1993; Rebelo 1994; Curnutt, Lockwood, Luh, Nott & Russell 1994; Lombard *et al.* 1995; Williams *et al.*, unpubl.). Endemic and/or restricted-range species frequently do not occur in hotspots, and the hotspots of one taxon infrequently coincide with hotspots of other taxa (Ryti 1992; Sætersdal, Line & Birks 1993; Prendergast *et al.* 1993). The present study supports all of these findings.

Although the identification of hotspots alone cannot allow one to design effective reserve systems, they do have conservation value, in that they are centres of exceptional biological wealth. Many hotspots were identified in this study, but a subset of 20 of these have been given special attention, because they are centres of hotspot congruency either within or among taxa. These hotspots are described later in the section on important QDS.

### The lack of coincidence of hotspots within taxa

The lack of congruency among richness, endemism and rarity (= Red Data Book species) within taxa is demonstrated in Table 2. Only 5–42% of HS coincide with EHS, with the exception of snakes, and RDBHS may or may not be congruent with HS (0–88%). Five of the six taxa have hotspots in the north-eastern areas, whereas five taxa have centres of endemism in the south and south-west (tortoises and snakes are the two exceptions, respectively, Figure 2). The subtropical subtraction effect (the southern range extension of tropical species into north-eastern South Africa) is apparent in four taxa, which have hotspots of Red Data Book species in the north-east, coinciding with areas of total species richness.

Of special note is the high degree of overlap between EHS and RDBHS in the two aquatic groups (fish and frogs). Not only do these two taxa inhabit two of South Africa's most threatened habitats (wetlands and rivers), but they also have the highest percentage of endemic species of all six taxa studied here. The areas where their EHS and RDBHS are congruent (the Cederberg Wilderness Area and the Cape Peninsula) deserve special conservation attention.

The general lack of congruency of richness, endemism and rarity within taxa highlights the importance of examining these three distributional aspects separately in reserve design.

### The lack of coincidence of hotspots among taxa

The proportional overlap among hotspots of different taxa ranges from high (72% for frogs and birds) to low (none between tortoises and three other taxa). Prendergast *et al.* (1993) calculated values of 0–34% in their study of five taxa in Britain. This lack of congruency is important to note, because the use of indicator taxa in rapid biodiversity assessments is becoming an attractive option as budgets for conservation are cut, while increasing demands are made on land for development, afforestation and agriculture. Table 3a shows that three pairs of taxa have a relatively high proportional overlap of hotspots: frogs and birds, frogs and mammals, and snakes and birds (values range between 59–72%), thus perhaps these taxa can be used as surrogates for one another in rapid biodiversity assessments. Overall, bird hotspots are the best predictors of hotspots of other taxa. The same conclusions can be drawn from Prendergast *et al.*'s (1993) data.

There is little coincidence among endemic species hotspots (values range from 0–44%, Table 3b). As was the case for total species hotspots, the highest coincidence is found between frogs and mammals, and frogs and birds. Overall, bird or mammal endemic hotspots are the best predictors of endemic hotspots of other taxa.

There is also little coincidence among Red Data Book species hotspots (eight paired comparisons had no overlap, Table 3c). The exceptions are tortoises and birds, snakes and birds, and birds and mammals (values range from 54–100%). Overall, bird Red Data Book hotspots are the best predictors of Red Data Book hotspots of other taxa. It must thus be concluded that birds are the best indicators to use in predicting all three types of hotspots of other vertebrate taxa (exceptions can be noted from Table 3).

The general lack of congruence of hotspots among taxa is further emphasized by the high proportion of overlap between the hotspots of certain taxa, with the coldspots of others. Table 5 shows a relatively high overlap between fish HS and tortoise CS, and bird HS and tortoise CS. This emphasizes the need to investigate the distributions of as many taxa as possible in reserve design, and not to assume that richness in one taxon translates to richness in another.

## Important QDS

Six QDS that deserve special mention are those where the three types of hotspots are coincident within a taxon (Table 2). The area of varied topography between Barberton (Eastern Transvaal) and Piggs Peak (Swaziland), just south-west of Kruger National Park (KNP), is very important for fish (253ICC). The Cape Peninsula is very important for frogs (3318CD) and two areas are very important for birds: the area just north of Pietermaritzburg in Kwazulu-Natal (2930AD), and the area between Scottburgh and Mtwalume on the Kwazulu-Natal south coast (303OBC). Finally, the two important mammal areas are the Pietermaritzburg area in Kwazulu-Natal (293OCB), and the Wakkerstroom area on the border of the eastern Transvaal and Kwazulu-Natal (2730AC).

In addition, the six hotspots that are common to five taxa require priority attention (Table 4). Two of these are the two most northern QDS of the KNP, and occur at the junction of three countries (South Africa, Zimbabwe, Mozambique) and two rivers (Limpopo and Levuvhu) — 2231AC, 2231AD. Two fall partially within the KNP: 2431DC falls both in the KNP and the private Sabie-Sand game reserve; and 2531BD falls half in the KNP, while the other half incorporates the Crocodile River valley in the vicinity of Komatipoort on the Eastern Transvaal-Mozambique border. Another QDS (2431CB) is on the western border of the KNP and includes portions of three private game reserves (Timbavati, Manyeleti and Sabie-Sand), and the other is in the vicinity of Ndumu Game Reserve and the Tembe Elephant Park on the border between Kwazulu-Natal and Mozambique (2632CD). It includes the wetlands of the Rio Maputu, and the confluence of the Suthu and Phongolo rivers where they merge to form the Rio Maputu.

The two endemic hotspots that are common to five taxa require priority attention (Table 4). One is the Cape Peninsula (3418AB) and one is in the area south and south-east of Grahamstown in the Eastern Cape (3326BC). A further six endemic hotspots are common to three taxa. Two are in the Hottentots-Holland Mountain Range of the Western Cape (3318DD and 3418BB), one is on the southern slopes of the Groot Winterhoek Mountains in the Tulbagh area (3319AC), one is in the Port Elizabeth area of the Eastern Cape (3325DC), and two are in Kwazulu-Natal (2730AC and 2930CB). These last two QDS are especially important because they are also areas where the three categories of hotspots overlap within mammals (Table 2).

Two QDS are very important in terms of Red Data Book hotspot overlap among taxa. 2832AD, in the vicinity of the St Lucia estuary in Kwazulu-Natal, is common to four taxa, and 2632DD in the Kosi Bay area on the border of Kwazulu-Natal and Mozambique, is common to three taxa (Table 4).

In addition to these important QDS, many other important QDS were identified in the separate taxon analyses within this volume (Skelton *et al.* 1995; Drinkrow & Cherry 1995; Branch *et al.* 1995; Gelderblom & Bronner 1995; Gelderblom *et al.* 1995; Mugo *et al.* 1995; Freitag & van Jaarsveld 1995). More specific details can be found in the separate papers, but some examples include: the Cape Fold Mountains (for endemic and restricted range fish and mammals); the Orange River mainstream and the Drakensberg Mountains in Kwazulu-Natal (for endemic fish); the Cape Peninsula (for RDB frogs); the central Nama-Karoo, and the forests of the Eastern Cape coast (RDB endemic mammals); the Waterberg and Amatola area of the Eastern Cape (RDB bats); Wakkerstroom (all three categories of hotspots for Insectivora); and Port St Johns (endemic Insectivora).

## Proportion of species in hotspots

Not only is there a lack of congruency of hotspots within and among taxa, but the proportion of species present in hotspots of their own taxa can be as low as 66% (fish species in fish HS, Figure 3). This value improves for the other five taxa (72–92%), but the total number of species that do not fall within hotspots of their own taxa is still high (e.g. 48 bird species). Prendergast *et al.* (1993) obtained similar values (87–96%) in their analysis of the percentage of species in hotspots, in five taxa in Britain. Where previous analyses in the present study showed that bird hotspots are the best predictors of hotspots of other taxa, Figure 3 shows that mammal hotspots perform the best in representing the most number of species of other taxa (between 78–97% of all species within a taxon). Snake hotspots perform second best (77–96% of species represented).

Owing to the disparity among the different numbers of hotspots for each taxon (Table 1), the possibility existed that the success of hotspots in representing species of all taxa depended on the number of hotspots. This was tested in Figure 4, where the number of hotspots in each taxon was standardized. Results confirm that mammal, followed by snake hotspots, perform best at representing species of all taxa.

A comparison of the proportion of species that fall within a taxon's own three types of hotspots reveals two interesting results (Figure 5): slightly more frog species are found in EHS than HS (even though there are 13 fewer EHS than HS), and bird RDBHS capture as many species as bird HS do (again, there are 13 fewer RDBHS than HS). If the hotspot approach is ever used as a component of a reserve-design strategy, these results could be informative.

Figure 6 confirms that endemic species are not particularly well represented in hotspots (e.g. only 39% of endemic fish species are found in fish HS). If endemic species are the target of any conservation strategies, EHS are more important than HS in three taxa (fish, frogs and birds), whereas HS are more important than EHS in the other three taxa. Bird EHS perform the best, and capture 98% of endemic species.

Figure 7 confirms that Red Data Book species are also not well represented in hotspots. Between 36–91% of RDB species fall in hotspots of their own taxa. Although hotspots do not capture a great percentage of RDB species, they do represent more RDB species than RDBHS do (with the exception of fish). Within four taxa, RDBHS capture only 33–52% of RDB species. Thus, one should not rely on HS, or even RDBHS, to represent rare or threatened species in a database. A similar comparison by Prendergast *et al.* (1993) reported values of 50–100% (rare species) and 63–87% (uncommon species) in hotspots. The only taxon that is common to this study, and that of Prendergast et al. (1993), is breeding birds. The latter study calculated that 57% of breeding birds fall in hotspots. Bird hotspots in the present study thus do well to capture 91% of bird species.

### Hotspots and species versus existing reserves

The overlap of hotspots and existing reserves is relatively good (Table 6). With only three exceptions, more than 80% of all three types of hotspots fall in the same QDS as existing reserves do. The provincial reserves play the largest role by far, in protecting all hotspots, especially RDBHS. National Parks play the second largest role, but EHS and RDBHS are not well represented in National Parks, and two taxa (frogs and snakes) have no EHS or RDBHS in a National Park. In fact, the local authority reserves play a larger role in protecting EHS than National Parks do. As part of a new strategic plan for biodiversity conservation, the National Parks Board should place greater emphasis on the incorporation of centres of endemism and rarity into its reserve system.

Fortunately, the twenty important QDS identified in the hotspot analyses appear to be well represented in existing reserves, but this assumption needs to be ground truthed, to ensure that: (i) the species within the database are still present in the QDS; and (ii) the hotspot does actually fall within the reserve. It is also fortunate that only eleven of the 1074 species examined may currently be unprotected. Unfortunately, eight of these species are listed in the Red Data Books, and five of them are endemic (Table 7), thus deserving priority conservation attention. The list of unprotected species may be much longer, because the present study assumed that if a species and an existing reserve were present in the same QDS, the species fell in the reserve. For many species, this assumption may not be valid.

### Advantages of hotspot analyses

Despite the criticisms of hotspot analyses as a tool in reserve design, the results obtained in this study can be useful, mainly because richness, endemism and rarity were treated separately, and because many taxa were investigated. Not only do the analyses identify areas of exceptional biological wealth, but the distribution patterns of various taxa become much clearer. Pairs of taxa that have similar distribution patterns are identified, thus allowing one to design sampling strategies more efficiently. This study, however, has demonstrated only that these patterns operate at a national scale. No evidence is provided that the same relationships hold at finer scales. Finally, hotspot analyses are not as sensitive to false negatives or false positives in the data as complementarity algorithms are (see below), and they do not require abundance data to identify patterns of distribution at national scales.

### Advantages of complementarity algorithms

The inefficiency of hotspots at representing all species in a taxon can be addressed by designing reserves with complementarity algorithms. Figure 8 emphasizes the efficiency of the complementarity method at representing all species in a taxon. The average number of representative reserves per taxon was 18,5, and these incorporated 100% of all species. The average number of hotspots per taxon was 53, and these incorporated between 66–92% of species only, per taxon. The one representative reserve (2832AD, St Lucia estuary) that is common to four taxa is also an area of coincidence of Red Data Book hotspots in four taxa, and is thus especially important.

Combining the data for all taxa and running only one complementarity analysis is even more efficient, and only 66 representative reserves can replace the 97 selected by individual taxon analyses. This result, however, must be viewed with caution, because many of these representative reserves contain species that are at the edges of their ranges, and in trying to minimize the number of reserves needed to capture the combined species, the algorithm often places reserves in ecotones where the ranges of many species overlap (i.e. at their margins, see Branch *et al.* 1995).

The prioritization of representative reserves should be driven by irreplaceability (between one and six representative reserves in each taxon are irreplaceable and thus require conservation attention). Of these irreplaceable reserves, five do not coincide with existing reserves (QDS 2228CB; 2916BB; 2917DD; 2930DA and 3030AA). These five irreplaceable reserves are thus especially important.

Prioritization of representative reserves can be further aided with comparisons of these reserves and hotspots (Table 8a). Of the six taxa, bird and mammal hotspots (all three categories) have the highest overlap with representative reserves. This supports the data in Figure 5 which shows that these are the two groups that have the greatest proportion of their own species in their own hotspots.

The fact that the South African reserve estate could be far more efficient at protecting all vertebrate species, with only modest acquisition of extra area, is emphasized in Table 9. Provincial reserves, followed by National Parks, have a high degree of overlap with representative reserves of all taxa. Perhaps the greatest advantage of complementarity algorithms is that they produce flexible results. If the rules of the reserve selection algorithm were changed, the overlap between representative reserves and existing reserves could probably have been increased.

## Using complementarity effectively

Each representative reserve is selected for a specific complement of species. This is usually a subset of all the species present in the reserve. The complementarity method, however, is very sensitive to false negatives and false positives in incomplete databases, and, in the absence of abundance data, all representative reserves must be carefully ground truthed to ensure that viable populations of the species that the reserve was selected for, do actually exist. This would preclude the protection of species in marginal habitats, or the protection of small and fragmented or threatened populations. Another way of avoiding the protection of species in marginal, fragmented or threatened habitats, is to exclude such data points from the iterative reserve selection procedure, *a priori*. This is more difficult, and requires an in-depth knowledge of the status of all species' populations.

The most efficient application of the complementarity method is to identify which species are currently adequately protected, and then to design a reserve system for the remaining species (bearing in mind that not all species can be conserved in protected areas). The results from the separate papers in this volume can be used to compile a database of only those species requiring further protection. Alternatively, the complementarity algorithm can be forced to choose hotspots of each taxon first, and then base further reserves on all species, or inadequately protected species only. This would build an 'insurance policy' into the final reserve system, in that many species would be protected more than once.

It should also be noted that the representative reserves shown in Figures 8 and 9 are flexible. Informed, sensible decisions regarding reserve design must exploit this flexibility, and the system of reserves that is finally chosen must also consider factors such as threat, condition of ecosystem, as well as socio-economic and political factors. A flexibility analysis was not performed here, but when national data on the above-mentioned factors (such as threat etc.) become available, such a flexibility analysis is recommended.

Once a representative reserve has been ground truthed, recommendations can be made as to the total size and shape of an appropriate conservation area, as well as its exact location. Frequently, the final conservation area will be much larger than the QDS on which it is based, especially if it has been charged with conserving large species with large areal requirements. No static, representative reserve, however, can be expected to conserve viable populations of all the species it has been chosen to represent. This is especially true for the larger, more vagile, animals, for example mammals and birds (especially raptors, nomadic or migratory species). Alternative methods of conservation are required for these species, for example, conservation and management of the matrix surrounding reserves. Another complicating factor is that the final management boundary of a reserve may contain a different complement of species to the original representative reserve (QDS). This alters the potential contribution of all other representative reserves in the initial run of the algorithm, and the algorithm may need to be rerun after each reserve boundary is finalized.

In the absence of abundance, species turnover, cost and threat data (Horowitz 1991; Margules, Nicholls & Usher 1994; Williams *et al.*, unpubl.), it is difficult to select a realistic set of representative reserves. The results of this study must thus be viewed as the first stage in a more comprehensive study, and the importance of the results obtained here is to prove that many more of our unprotected vertebrate species can be accommodated in reserves, with moderate extension of existing reserves, and moderate acquisition of new areas. As a next step, it would be useful to predict which species, and which ecosystems or geographical areas, are most threatened by processes that reserves can offset. This information can then influence the timing and form of protection given to these species and ecosystems.

## South Africa's reserve estate

Only 5,46% of greater South Africa's land area falls in publicly owned reserves. A similar figure (5,8%) was obtained by Siegfried (1989). These figures fall short of the 10% suggested by the IUCN (World Conservation Union), and the extra area required amounts to 5,75 million ha. Given current land-reform processes in the country, South Africa urgently needs to identify areas for priority conservation. The results of the present study, and the various papers within this volume can provide guidance to a (vertebrate) species-based approach, but a biome-based analysis provides further assistance on a broader scale. It is apparent from Figure 10 that three of the six biomes in South Africa probably have adequate representation within existing reserves (fynbos, arid and woodland savannas). The other three biomes, however, have less than 4% of their total area protected, and require additional protection (i.e. the grasslands, Succulent and Nama-Karoo). There are many assemblages of plants and animals that are endemic to these biomes, and their habitat needs to be protected, e.g. small mammals such as the Namaqua dune molerat, the riverine rabbit, Brant's whistling rat and the Pygmy rock mouse (Mugo *et al.* 1995).

The inadequacies of the National Parks at representing endemic and Red Data Book species is compounded by the bias of the Parks towards the savanna biomes (Table 10). In terms of total area protected, National Parks are responsible for almost 50%, but most of this area is accounted for by a few very large reserves. A more representative distribution of reserves is required, with more reserves in the other four biomes. The Natal Parks Board and Western Cape Nature Conservation are responsible for the next largest percentages of areas, a fact that should be reflected in their state budgets. In addition, the large amount of area owned by the National Defence Force needs to be examined for species, hotspots, representative reserves and biome representation. This would allow decision-makers to avoid conflicts of interest, and to allocate the land to the most appropriate and economically viable cause (e.g. conservation or subsistence farming). Finally, given the importance of local authority reserves in protecting the Nama-Karoo, some of these reserves could possibly be expanded, and/or have their status changed to provincial or national reserves.

### Prescriptions

Although the present study, and the other papers in this volume, have provided both general and specific recommendations for the additional conservation of both species and areas, the purpose of the collaborative exercise was not to provide a prescriptive national plan for biodiversity conservation. Instead, it is hoped that the conclusions, and the methods outlined, will be used as a foundation in the formulation of such a plan. In order to be totally prescriptive, three tasks must be accomplished. First, more complete databases must be collated, because the 66 reserves recommended here (Figure 9) for the protection of South Africa's vertebrates are based on incomplete distributional data and lack any information on population viability. Second, many more taxa must be investigated, because the ideal reserves for vertebrates (Figure 9), will not necessarily coincide with ideal reserves for plants (Rebelo 1994). Third, data on the spatial distribution of current land uses and threats need to be compiled for the country, and species and ecosystems that are most threatened by processes that reserves can offset must be identified. These species and ecosystems can then receive priority attention. These three tasks could easily be accomplished in a short time (less than one year), if a national effort is coordinated and adequately funded. The data collation and analyses reported in all of the collaborative papers in this volume of the *South African Journal of Zoology*, took less than five months to complete.

To be effective in the long term, a national plan will also have to take factors such as cost and socio-economics into account. The identification of inadequately conserved landscapes or ecosystems, at a finer scale than was used here, would also strengthen the plan. For example, within the fynbos biome, mountain fynbos is well protected, but lowland fynbos is not. With the inevitable changes that will be brought about by increased fragmentation and demand on land, as well as global climate change, the role of the matrix in conserving species and ecosystems will become increasingly important. A national strategic plan will have to incorporate all of these factors, and land-use planners and conservation biologists will have to work together.

## Conclusions

1. South Africa has a high proportion of endemic and Red Data Book vertebrate species that are under-represented in the current system of publicly owned reserves. The separate papers in this volume of the *South African Journal of Zoology* describe these species, within six vertebrate taxa.
2. The vertebrate fauna of the arid western part of South Africa has been inadequately sampled.
3. There is a lack of congruency among richness, endemism and rarity within vertebrate taxa. Richness is concentrated in the north-eastern areas, whereas centres of endemism are found in the south and south-west. Rarity can be in either of these two areas. This emphasizes the necessity of separating these three distributional aspects in reserve design.
4. There is a lack of congruency among richness, endemism and rarity among different vertebrate taxa. This emphasizes the need to investigate the distributions of as many taxa as possible in reserve design. Overall, bird hotspots are the best predictors of hotspots of other taxa, bird or mammal endemic hotspots are the best predictors of endemic hotspots of other taxa, and bird Red Data Book hotspots are the best predictors of Red Data Book hotspots of other taxa.
5. Hotspots of individual taxa contain only 66-92% of species. Mammal hotspots contain the most number of species of other taxa.
6. Endemic and Red Data Book species are not particularly well represented in total species hotspots.
7. Twenty hotspots are identified as being of exceptional importance, because they are centres of hotspot congruency either within or among taxa. Most of these hotspots are well protected, but before any conservation action is taken, ground truthing of the areas is necessary.
8. In general, hotspots are relatively well represented in existing reserves, but endemic and Red Data Book hotspots are not well represented in National Parks (especially for frogs and snakes). The National Parks Board should place greater emphasis on the incorporation of centres of endemism and rarity into its reserve system. In general, the South African reserve estate is biased towards richness, and certain taxa, and needs to be improved upon in order to incorporate the full suite of biodiversity in the country.
9. The complementarity method is far more efficient than the hotspot approach in designing reserve systems. As few as 66 quarter-degree squares can represent all 1074 vertebrate species studied here (Figure 9), and 70% of these squares already have some level of protection. This figure could be increased if the flexibility of selected reserves is examined. Many unprotected vertebrate species can be accommodated in reserves, with moderate extension of existing reserves, and moderate acquisition of new areas.
10. The total publicly owned reserve estate of greater South Africa is small (5,46% of land area). Additional areas need to be identified for protection, especially within the grassland, Succulent Karoo and Nama-Karoo biomes, before final decisions are made within the new land-reform process.
11. The results of this study must be viewed as the first stage towards a strategic plan for biodiversity conservation. A complete plan should: (i) identify all species and ecosystems that require additional protection; and (ii) use the complementarity method to identify where these species and ecosystems can be adequately conserved. An analysis of threats to species and ecosystems is required for final reserve placement, and alternative forms of conservation planning must be developed for species and ecosytems that cannot be protected in reserves.

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