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BIODIVERSITY RESEARCH

A pragmatic approach to estimating the distributions and spatial requirements of the medium- to large-sized mammals in the Cape Floristic Region, South Africa

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Abstract. Conservation planning in the Cape Floristic Region, a recognized world plant diversity hotspot, required systematic information on the estimated distributions and spatial requirements of the medium- to large-sized mammals within each of 102 Broad Habitat Units delineated according to key biophysical parameters. As a consequence of a general lack of data, we derived a pragmatic approach for obtaining estimates of these two parameters. Distribution estimates were based on a combination of a literature survey (with emphasis on early texts) and the ecological requirements of the species. Spatial requirement estimates were derived from a simple spreadsheet model that is based on forage availability estimates and the metabolic requirements of the mammals in question. Our analysis incorporated adaptations of the agriculture-based Large Stock Unit or Animal Unit approach. The predictions of the model were tested by comparing them with actual density data. The outcomes provided realistic estimates of the two parameters. However, they should be considered as testable hypotheses and the concept of adaptive management — or management by hypothesis — must apply. Examples of the outcomes are provided in the form of maps and tables.

Key words. Cape Floristic Region, conservation planning, distributions, mammals, modelling, spatial requirements.

INTRODUCTION

The strategic placement of protected areas is necessary to capture maximum biological diversity but this can only be undertaken by conservation planners on the basis of solid inventory data on biological diversity, i.e. distribution and abundance of species in time and space. The Cape Floristic Region (CFR) of South Africa, a region of exceptional plant diversity and one of the world's six floral kingdoms (Goldblatt, 1978; Cowling & Holmes, 1992), encompasses three of southern Africa's centres of plant endemism (Cowling & Hilton-Taylor, 1997). This globally recognized biodiversity hotspot (Myers, 1990), covering some 90,000 km^2, is currently the focus of a strategic conservation planning exercise (Cowling *et al.*, 1998). The main focus of this study is to identify the priorities for conservation on the basis of biodiversity value and threats, identify a notional system of conservation areas to achieve explicit reservation targets, draw up scenarios for the development of new reserves, and develop guidelines for effective conservation strategies outside reserves. The implementation of a conservation planning exercise in the spatially extensive CFR accords with recent emphasis on the need for conservation biology principles to be applied to large spatial scales (May, 1994). This will, for example, cater for altitudinal and horizontal nomadic and migratory patterns of certain faunal taxa.

While the spectacular plant diversity remains the major focus of conservation planning in the CFR, other biota and ecological processes which impact on the region's flora have also been taken into account in attempting to achieve the broad aims outlined above. These include the medium- to large-sized mammals, many of which (a) are in need of conservation intervention, and (b) may have an important impact on the region's flora, at the species, community and ecosystem functioning levels. Herbivory is known to have an impact on the species composition, structure and dynamics of CFR vegetation (Campbell, 1986; Johnson, 1992).

The medium- to large-sized mammals were selected as 'target' species (*sensu* Wilcox, 1982) for the CFR exercise because it is likely that if their minimum area requirements are met, adequate survival conditions will simultaneously be met for other biota. In this regard, many of these mammals qualify as 'umbrella' species (*sensu* Wilcox, 1982), since their minimum area requirements are likely to be at least as comprehensive as those for the remainder of the community. Mammals (which generally have high metabolic requirements) with a large body size (e.g. some ungulates) and which occupy a high trophic level (e.g. carnivores) are regarded as good candidates for target species acting as 'umbrella' species (see Wilcox, 1982). In addition, the distributions and spatial requirements of the larger mammals are probably better known, or can be better estimated, than those of the small-sized mammals in the CFR. In any case, realistic data for these two demographic parameters are essential for any conservation exercise that deals with the establishment and maintenance of minimum viable populations of the larger mammalian fauna (see, for example, Lande & Barrowclough, 1987; Caughley & Sinclair, 1994; Caughley, 1994).

Given the inadequate understanding and lack of information on the distribution, ecology, demography and genetics of the larger mammals of the CFR, a pragmatic approach is required to obtain data, at the appropriate scale and coverage, for achieving the overall objectives of the present planning exercise. This paper describes the approach taken to estimate the distributions and spatial requirements of each species. The detailed results are available elsewhere (Boshoff & Kerley, 1999).

APPROACH AND METHODS

The information on distributions and spatial requirements needs to be presented at the level of the 102 Broad Habitat Units (BHUs), which are the biodiversity entities for the conservation planning component of the CFR project. These BHUs were delineated according to a number of biological and environmental characteristics, including vegetation type, geology, mean annual rainfall, rainfall seasonality, modal altitude and ruggedness (Cowling & Heijnis, 2001).

The 40 indigenous terrestrial mammal species included in this study are those with a mass greater than ≈ 2 kg (cf. Chew, 1978), which are the most prominent in the landscape, and which are generally amenable to direct management. Two species that fall into this category, namely the hippopotamus *Hippopotamus amphibius* and the Cape clawless otter *Aonyx capensis*, have been excluded from this study since they occur exclusively in aquatic habitats and their associated riparian areas; the riparian habitat was not mapped as a separate habitat unit by Cowling & Heijnis (2001). The scientific names of the species referred to in this paper are provided in Tables 1 and 2.

Distributions

Zoological and explorer's records from the 17th, 18th and 19th centuries have been well reviewed by Du Plessis (1969), Rookmaaker (1989) and Skead (1980, 1987). These reviews were useful in determining the general presence or absence of most species in all or parts of the CFR, but they proved to be frustratingly vague in terms of the exact areas and habitats occupied by the various species. This resulted mainly from the fact that most early hunters and naturalists only recorded occurrence along well-travelled, or passable, routes and few travelled at night, thereby missing the nocturnal species. Other problems arose with interpreting the early published accounts with regard to the accurate identification of some species (see Skead, 1980).

A review of the recent (20th century) literature revealed that noteworthy surveys, namely those by Hewitt (1931), Shortridge (1942), Bateman (1961), Lloyd & Millar (1983), Stuart (1981, 1985) and Stuart *et al.* (1985), are incomplete in terms of species and/or area covered and tend to use political boundaries rather than ecological zones as the basic mapping units. The scale of the distribution maps in the standard account of the mammals in the southern African subregion (Skinner & Smithers, 1990) allows only generalized

Table 1 Sample (selected section) of a table providing estimated spatial requirements for omnivores and carnivores in the Cape Floristic Region

Species	Calculation basis
Chacma baboon *Papio cynocephalus*	Cape Point NR: 1 troop of 80 uses 3400 ha
Vervet monkey *Cercopithecus aethiops*	25/troop, 8 troops required for 200 individuals at 80 ha/troop
Aardwolf *Proteles cristatus*	Males and females share territories of up to 1000 ha
Brown hyaena *Hyaenna brunnea*	Clan of 8 members has territory size of about 25 000 ha
Spotted hyaena *Crocuta crocuta*	A clan of 15 would require territory of around 40 000 ha
Cheetah *Acinonyx jubatus*	Est. home range for 5 animals (2m, 3f) at 100 000 ha, with 75% overlap; 50 animals = 100 000 + 25% for 10 iterations
Leopard *Panthera pardus*	1 pair requires a home range of about 20 000 ha
Lion *Panthera leo*	A pride of 10 animals (adults, subadults and young) require a territory of about 50 000 ha

ranges (extents of occurrence) to be determined. Similarly, distributions of threatened mammal species are illustrated on a broad regional basis (Smithers, 1986).

Museum specimens and records provide useful point data but are biased in that they only provide 'presence' data, i.e. they do not represent the results of systematic data collection throughout the CFR, and they do not take into account the possible migratory or nomadic patterns of some species.

To address the above issues, two steps were followed in the determination of potential species' distributions, in terms of BHUs:

1. Evidence that a species occurred, or could potentially occur, in all, or in a specific part, of the CFR, according to the early and recent literature.
2. The presence/absence of each species in each BHU, according to our understanding of their ecological requirements, including a review of published habitat requirements (in the CFR and elsewhere in their range), our personal field knowledge, and the respective habitat characteristics of each BHU (mainly dominant plant species and vegetation structure, grass component, soil nutrients, geology, topography, modal altitude, mean rainfall, rainfall seasonality). As part of this exercise, wildlife scientists with knowledge of mammals in the CFR were consulted.

Output is in the form of a distribution map for each species, with three distribution categories being used:

(a) BHUs with the potential to sustain significant resident (i.e. present all year round and breeding) populations;
(b) BHUs which may be used on an ephemeral (i.e. seasonal) basis, or which may carry small populations in habitat refugia (patchy basis); and
(c) BHUs where the species is unlikely to occur, except perhaps for vagrants or during rare and short incursions.

The approach described above, which involves a simple model based on the estimated range of each species and its association with mappable environmental features, and expressed as a series of polygons, is broadly similar to that used in other studies (e.g. Butterfield *et al.*, 1994).

Table 2 Sample (selected section) of model-generated spatial requirement estimates (in ha/animal) for medium- to large-sized herbivores in the Cape Floristic Region. Shown here are data for the Riversdale Coast Renosterveld Broad Habitat Unit (BHU no. 34), with a total area of 316,300 ha, and adjusted stocking rate of 70 ha/Large Stock Unit (LSU), and total LSUs of 4519. Note that values in columns 5 and 7–10 differ slightly from those in the spreadsheet model owing to the reduced number of decimal places used here

Potential species	Foraging guild	LSU equivalent	Proportion (%) of total LSUs[1]	Allocated LSUs	Seasonality[2]	Released LSUs, from E/P species	Adjusted LSUs	No. of animals	Ha/ animal
Black rhinoceros *Diceros bicornis*	Browser	1.65	11.25	508.4	R		660.9	401	789
Common duiker *Sylvicapra grimmia*	Browser	0.09	11.25	508.4	R		660.9	7343	43
Steenbok *Raphicerus campestris*	Browser	0.06	11.25	508.4	E/P	457.6	50.8	847	373
Grysbok *Raphicerus melanotis*	Browser	0.06	11.25	508.4	R		660.9	11 015	29
Cape mountain zebra *Equus zebra*	Bulk grazer	0.63	5	226	E/P	203.4	22.6	36	8786
Burchell's zebra *Equus burchelli*	Bulk grazer	0.66	5	226	R		327.7	497	636
African buffalo *Syncerus caffer*	Bulk grazer	1.07	5	226	R		327.7	306	1034
Red hartebeest *Alcelaphus buselaphus*	Concentrate grazer	0.37	5	226	R		327.7	886	357
Bontebok *Damaliscus dorcas*	Concentrate grazer	0.21	5	226	R		327.7	1560	203
Grey rhebok *Pelea capreolus*	Concentrate grazer	0.1	5	226	E/P	203.4	22.6	226	1400
African elephant *Loxodonta africana*	Mixed feeder	2.78	12.5	564.9	E/P	508.4[3]	56.4	20	15 815
Eland *Taurotragus oryx*	Mixed feeder	1.08	12.5	564.9	E/P	508.4[3]	56.4	52	6083
Totals			100	4519			3502.3		

[1] From Table 1.
[2] R = Resident; E/P = Ephemeral/patchy.
[3] Unallocated LSUs ('floaters').

Spatial requirements

The estimated spatial requirements refer exclusively to those BHUs where the species is likely to occur, on a 'resident' or 'ephemeral/patchy' basis.

Omnivores and carnivores

The overall lack of information from the CFR precluded a standardized approach to an estimation of the spatial requirements of the omnivores and carnivores, according to individual BHUs. Consequently, the CFR was treated as a homogeneous unit for this purpose. This is likely to be more appropriate for the smaller species than for the larger ones; the abundance of the latter will generally reflect the abundance and spatial distribution of the larger herbivores.

Estimates of the spatial requirements of each species in each BHU were based on a review of available information on densities, social structures, breeding units, territory sizes and home ranges. However, published ecological information for the CFR is available for only four of the 19 species in this category, little of which deals specifically with spatial requirements in more than one habitat type in the CFR. Consequently, estimates based on the interpretation and extrapolation of information on the relevant species from other biomes in South Africa, mainly the Nama-Karoo, Grassland and Savanna biomes (*sensu* Low & Rebelo, 1996), were used for many of the species. In the case of the carnivores (especially the large predators and scavengers such as lion and spotted hyaena) the assumption is made that predator–prey systems are in operation and that sufficient food is available.

A conservative approach to the estimation of the spatial requirements of the omnivores and carnivores in the CFR was adopted because of the naturally, and relatively low, herbivore carrying capacity (Teague, 1999) and a very poor understanding of the ecology of the species concerned. This was achieved by (a) usually adopting the lowest densities or largest territories or home ranges provided in the literature, (b) using the home range when territory size is not known, (c) basing, in appropriate cases, the estimates only on the sizes of the territories or home ranges of breeding adults; in these cases effective densities may be higher when non-territorial individuals (e.g. subadults, immatures and juveniles) are taken into account, and (d) reducing the densities in the ephemeral/patchy habitats to 20% of those calculated for the 'core' habitats.

Herbivores

In the general absence of data on the spatial requirements for herbivores, we took a pragmatic approach in the derivation of the necessary estimates. This involves a simple spreadsheet model, based on forage availability estimates and the metabolic requirements of the mammal species in question. The sequential components of the model are described below.

1. Allocation of species to foraging guilds. Each herbivore species was classified according to one of four foraging guilds (adapted from Collinson & Goodman, 1982), namely:

- Bulk grazer;
- Concentrate grazer;
- Mixed feeder (grazer/browser);
- Browser.

2. Adjustment of the agricultural stocking rate. The recommended agricultural stocking rates (SRs) for the respective land/agricultural units, as calculated by the South African Department of Agriculture on the basis of Large Stock Units (LSUs) (Anonymous, 1985), were used as guidelines for estimating forage production, and ultimately the spatial requirements in the BHUs. It must be emphasized that the term 'spatial requirements' normally refers to an ecological response, whereas the term 'stocking rates' normally refers to an operator/manager response.

An LSU is the equivalent of a steer with a mass of 450 kg and a mass gain of 500 g per day on grass pasture with a mean digestible energy concentration of 55%; to maintain this, 75 megajoules of metabolizable energy per day is required (Meissner, 1982). The concept of the LSU, or AU (Animal Unit), was developed for the livestock industry to determine grazing capacity (e.g. Anonymous, 1985) and has been defined as 'the area of natural vegetation (ha) required to carry a single LSU for the normal grazeable period without deterioration of the grazing or the soil' (Edwards, 1981).

The AU approach has been used in North America (e.g. Robinson & Bolen, 1989; Heady &

Child, 1994) and in Australia (e.g. Landsberg *et al.*, 1992) to standardize measures for both livestock and wildlife, including an assessment of foraging pressure; in North America (USA) 1 AU is the taken as the equivalent of one cow and a calf, or 454 kg.

Given that agricultural management is usually aimed at maximizing production (Morris *et al.*, 1999), we adopted a highly conservative approach in the calculations for the indigenous ungulates, for the purpose of sustaining populations and protecting biodiversity. This took the form of adjusting (i.e. reducing) the Department of Agriculture stocking rate applicable to each BHU by a proportion which was estimated following a subjective assessment of the biophysical attributes, as surrogates for the productivity of forage, for the BHU in question. Key surrogates here are dominant vegetation, grass component, soil nutrient status, mean annual rainfall, rainfall seasonality, modal altitude and general topography. In this way, the agricultural SRs of BHUs characterized by winter rain (low productivity), low nutrient soils and a limited grass component which occur in the far western parts of the CFR, were reduced by a higher percentage than those BHUs characterized by a higher percentage of summer rain (higher productivity), relatively higher soil nutrient status and a relatively high grass component which occur in the eastern parts of the CFR (see Campbell, 1983).

Thus:

$$Adj_{sr} = X^* \ (1 + Y) \qquad (1)$$

where Adj_{sr} = Adjusted stocking rate, X = agricultural carrying capacity/stocking rate (ha/LSU), Y = adjustment value (where, e.g. 60% = 0.4), and LSU = Large Stock Unit.

Department of Agriculture stocking rates were not available for some BHUs, nor could they be determined, owing due to mapping scale differences. In these cases, stocking rates were estimated according to: an interpretation of the key biophysical attributes (as listed above); the stocking rates for similar BHUs; the stocking rates for neighbouring BHUs; our broad understanding of the general ecological requirements of mammal species in question.

3. Allocation of available forage to foraging guilds, within BHUs. The total available forage within each BHU was allocated to each of the four foraging guilds. To achieve this, forage allocations (as percentage) were made for each of the 17 Primary BHUs (i.e. groupings of related BHUs) (Cowling & Heijnis, 2001) within the six biomes represented in the CFR (Table 3) based on subjective estimations of the graze/browse proportions, as suggested by the BHU biophysical descriptions and our personal knowledge of these habitats. The allocation for an individual Primary BHU is then used for all the BHUs falling within that class (Table 3).

4. Allocation of available forage to individual species within foraging guilds, within BHUs. The available forage within each BHU was expressed as 'total number of LSUs' and calculated as follows:

$$LSU_t = A/SR_{(adj)} \qquad (2)$$

where LSU_t = total LSUs in a BHU, A = total area [ha] of BHU and $SR_{(adj)}$ = adjusted stocking rate for same BHU.

For each BHU the total LSUs were allocated to the herbivores within each foraging guild, in proportion to the percentage of forage available to each guild. Where > 1 species occurs within a single foraging guild, the LSUs accorded to that guild are allocated to these species in equal proportions.

5. Adjustment for seasonality patchiness. Species that are resident in a BHU will most likely have different forage requirements (and possibly other ecological requirements, e.g. presence/absence of surface water, shelter/cover) than species that are highly spatially localized or that may only be present for a limited part of a year (i.e. nomads or migrants). Therefore, there was a requirement for the model to incorporate seasonality or habitat patchiness. This was addressed by reducing by 90% the amount of forage allocated to ephemeral/patchy species. We assumed that the amount, and indeed quality, of resources was limiting, rather than their seasonal availability or total absence.

Thus, each species in each BHU is classified as 'Resident' or 'Ephemeral/Patchy' (see 'Distributions'). The LSUs which were 'released' by an ephemeral species were re-allocated, in equal proportions, to other species within the same foraging guild. This gives the adjusted number of LSUs available to each species within a BHU. In cases where other species are not present in the same

Table 3 Suggested allocations (%) of available forage among the four herbivore foraging guilds in 17 primary Broad Habitat Units in the Cape Floristic Region (see text for details)

Biome	Primary BHU	Bulk grazer	Concentrate grazer	Mixed feeder	Browser
Azonal	Dune pioneer	5	10	40	45
Fynbos	Fynbos/thicket mosaic	10	10	30	50
	Sand plain fynbos	5	5	45	45
	Limestone fynbos	15	15	15	55
	Grassy fynbos	20	20	30	30
	Fynbos/renosterveld mosaic	5	5	45	45
	Coast renosterveld	15	15	25	45
	Inland renosterveld	10	10	40	40
	Mountain complexes	5	5	20	70
Succulent Karoo	Vygieveld	5	5	20	70
	Strandveld	5	5	20	70
	Broken veld	5	10	25	60
Nama Karoo	Broken veld	5	10	40	45
Thicket	Mesic succulent thicket	5	5	40	50
	Xeric succulent thicket	5	5	40	50
Forest	Afromontane	5	5	40	50
	Indian Ocean	5	5	40	50

guild, the 'released' forage equivalents (LSUs) were considered as 'floaters' within that BHU — to be utilized across the graze/browse spectrum by the remaining species in the BHU.

6. Calculation of total numbers of individuals per BHU. The total number of individuals of a species within a BHU was calculated as follows:

$$N = LSU_{adj}/S_{equ} \tag{3}$$

where N = number of individuals, LSU_{adj} = adjusted LSUs per species and S_{equ} = species' LSU equivalent.

The LSU equivalents for the species follow Grossman (1991); that for African elephant follows Meissner (1982).

7. Calculation of estimated spatial requirements. The estimated spatial requirement for an individual of each species, within each BHU, is calculated as follows:

$$SpRq_i = A/N \tag{4}$$

where $SpRq_i$ = spatial requirement [ha] of an individual, A = total area of BHU [ha] and N = total number of individuals.

8. Constraints. A limitation on the spatial requirements of some herbivores is provided by social interaction, namely intolerance of conspecifics, as well as a number of other constraints, e.g. presence of surface water, seasonal food availability. It is known that, irrespective of the availability of forage, social and other constraints can limit the densities of ungulates (e.g. see Moen, 1973). For some species availability of food, water and shelter could be superceded by social factors in determining densities. In this regard, the spatial requirements predicted by our model were compared, where possible, with available information to investigate whether species' social constraints had been violated.

9. Model testing. The outputs of the model were tested by comparing density estimates derived from the model with published, empirically derived observations of densities of species for which acceptable data are available. Such data are not available for complete species assemblages.

RESULTS

Distributions

Figures 1–3 illustrate the distribution-related outputs of the study; the maps represent the known and potential distribution of each species. Although not shown here, the distributions of the large predators mirror closely those of their main prey items.

Spatial requirements

Omnivores and carnivores

A sample of the estimates of the spatial requirements for the omnivores and carnivores is provided in Table 1. As an example of the basis for the estimation of the spatial requirements, the case of the chacma baboon is given (Table 1, Box 1). The estimated requirement of 3400 ha for a troop of 80 individuals (Table 1) is derived from this information.

Box 1. Estimation of the spatial requirements of the chacma baboon *Papio cyanocephalus ursinus*

Breeding unit/social structure

Baboons are highly social, living in female bonded troops of between four and around 100–130 individuals, with one adult male in small troops and up to 12 males in large troops; average troop size is 40 (Skinner & Smithers, 1990; Apps, 1996) and troop size is apparently correlated with habitat quality.

Breeding density/home range/territory size

Troops have home ranges but they are not territorial and rather tend to avoid other troops (Apps, 1996). In the Good Hope section of the Cape Peninsula National Park (in the CFR) home ranges of three troops of 20, 35 and 80 baboons were 9.1, 14.8 and 33.7 km^2, respectively, with home range being related to size of troop (Devore & Hall, 1965). Home ranges of 400–4000 ha have been recorded (various published sources — omitted here for brevity).

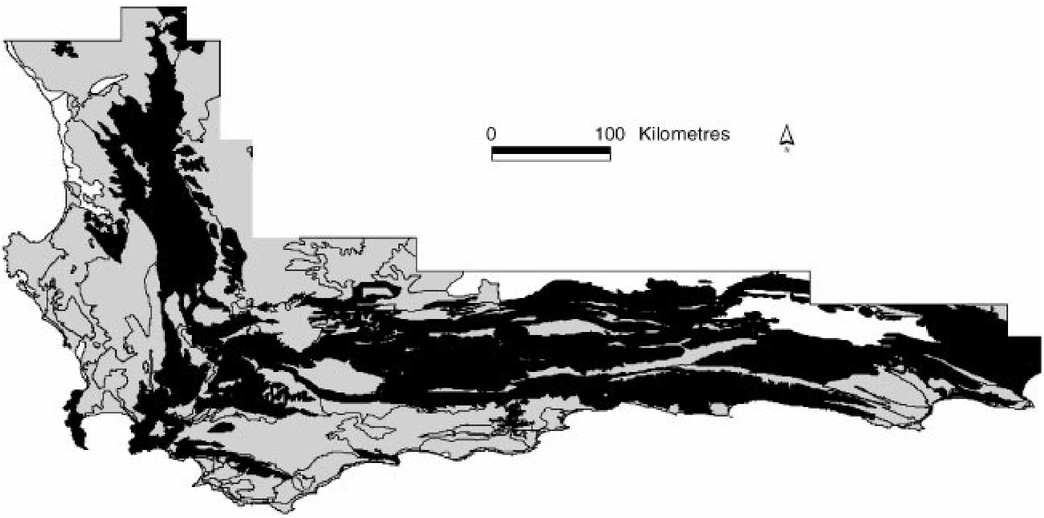

Fig. 1 The potential distribution of the leopard *Panthera pardus* in the Cape Floristic Region, according to the Broad Habitat Unit (BHU). The polygons on the map represent the BHUs; see Cowling & Heijnis (2001) for names of BHUs. Solid shading denotes BHUs with the potential to sustain significant resident (i.e. present all year round and breeding) populations, grey shading denotes BHUs which may be used on an ephemeral (i.e. seasonal) basis, or which may carry small populations in habitat refugia (patchy basis), and no shading denotes BHUs where the species is unlikely to occur, except perhaps for vagrants or during rare and short-lived incursions.

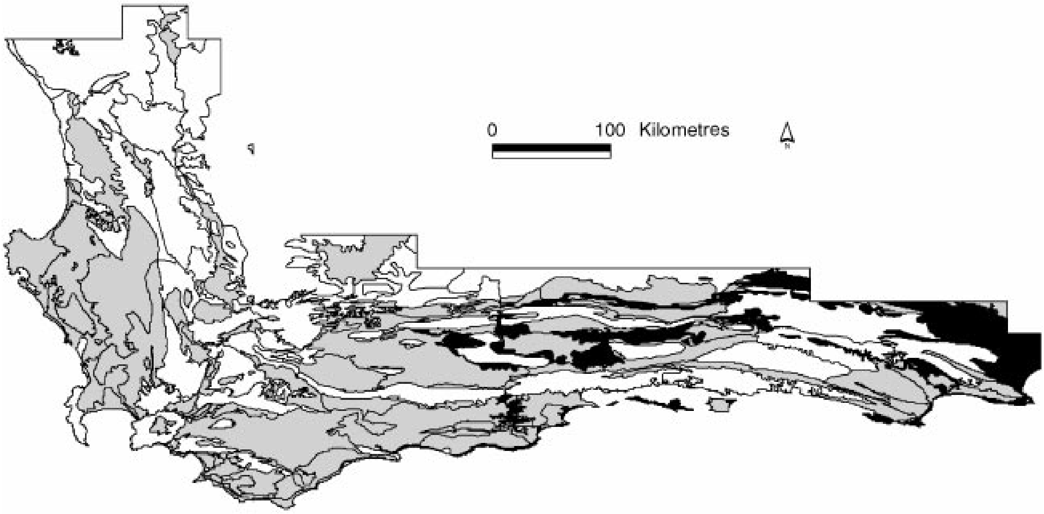

Fig. 2 The potential distribution of the African elephant *Loxodonta africana* in the Cape Floristic Region, according to the Broad Habitat Unit (BHU). The polygons on the map represent the BHUs; see Cowling & Heijnis (2001) for names of BHUs. Shading conventions as for Fig. 1.

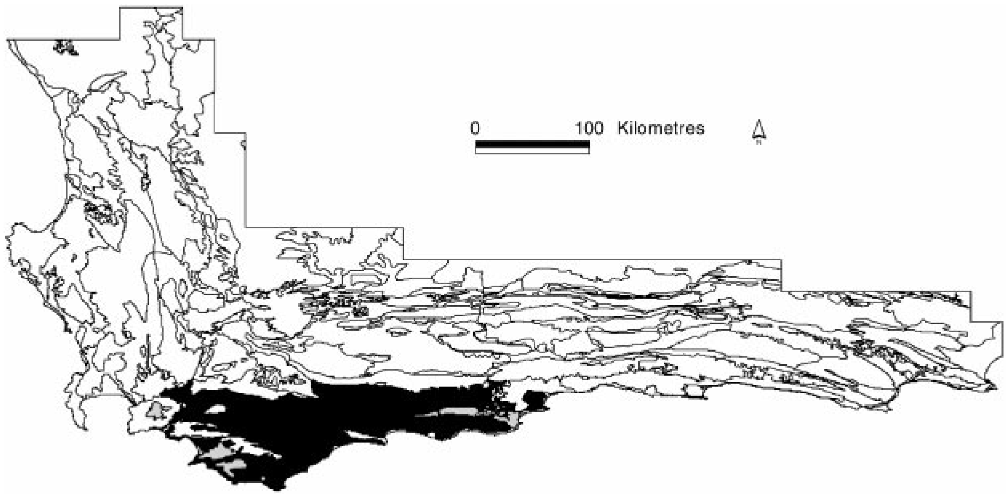

Fig. 3 The potential distribution of the bontebok *Damaliscus dorcas dorcas* in the Cape Floristic Region, according to the Broad Habitat Unit (BHU). The polygons on the map represent the BHUs; see Cowling & Heijnis (2001) for names of BHUs. Shading conventions as for Fig. 1.

Herbivores

Table 4 shows a sample of the adjustments to the agricultural stocking rates in the CFR, according to BHU, and Table 2 shows a sample of the model predictions of the spatial requirements for all species in a single BHU.

In the case of the two megaherbivores — African elephant (Kerley & Boshoff, 1997) and black rhinoceros (Adcock, 1994) — social constraints have not been violated by the model predictions. A general minimum spatial (social) requirement of 200 ha/animal has been suggested for the black

Table 4 Sample (selected section) of a table providing adjusted Department of Agriculture stocking rates (SR) for the Cape Floristic Region. *Our estimates. BHU = Broad Habitat Unit (after Cowling & Heijnis, 2001). LSU = Large Stock Unit. See Boshoff & Kerley (1999) for the full table of data

BHU no.	BHU	Agric. SR (ha/LSU)	Adjustment (%) [Alternate format in ()]	Adjusted SR (ha/LSU)
Succulent karoo biome				
Vygieveld				
75	Western Mountain	50	50* (0.5)	75
76	Klawer	39	50* (0.5)	58.5
77	Knersvlakte	47	50* (0.5)	70.5
78	Tanqua	71	50* (0.5)	106.5
79	Laingsberg	41	50* (0.5)	61.5
80	Moordenaars	37	50* (0.5)	55.5
81	Touws	54	50* (0.5)	81
Strandveld				
82	Namaqualand	50	50* (0.5)	75
83	Lamberts Bay	30	50* (0.5)	45
Broken veld				
84	Garies	39	50* (0.5)	58.5
85	Loeriesfontein	30	50* (0.5)	45
86	Witrantjies	30	60* (0.4)	42
87	Robertson	50*	60* (0.4)	70
88	Little Karoo	54	60* (0.4)	75.6
89	Oudtshoorn	50	60* (0.4)	70
90	Prince Albert	37	60* (0.4)	51.8
Nama Karoo biome				
91	Gamka Broken Veld	34	70* (0.3)	44.2
92	Steytlerville Broken Veld	21	70* (0.3)	27.3

Table 5 Sample of comparisons between the predictions of the spatial requirements model and available empirical data. Empirical data from the Cape Floristic Region in italics

Mammal species	Empirical data (ha/animal)	Predictions from the model (ha/animal)
Blue duiker *Philantomba monticola*	0.5–1 (Apps, 1996) *5.5–8 (Hanekom & Wilson, 1991)* *1.8–11 (Von Gadow, 1978)*	3–14
Common duiker *Sylvicapra grimmia*	Mean = 17; as low as 20–50 recorded (Allen-Rowlandson, 1986)	8–135
Klipspringer *Oreotragus oreotragus*	*11–15 (Norton, 1980)*	6–428
Grysbok *Raphicerus melanotis*	*1.3–9.4 (Manson, 1974)*	6–456
Grey rhebok *Pelea capreolus*	15–152 (Ferreira, 1984) *15 (Beukes, 1987)* 44–57 (Mentis, 1978)	26–2340
Bushbuck *Tragelaphus scriptus*	20 (Allen-Rowlandson, 1986) *14–20 (Seydack, 1984)* *33 (Odendaal & Bigalke, 1979)* *77 (Stuart-Hill & Danckwerts, 1988)*	12–1699

rhinoceros (see Hall-Martin & Knight, 1994); the model's highest estimated densities are 151 and 158 ha/animal, even in habitats where densities higher than 200 ha/animal are potentially feasible in terms of forage quantity and quality.

With the exception of one species in the Thicket Biome (kudu), the spatial requirements derived from the model were corroborated for those herbivore species for which published information is available, thereby indicating that realistic values were generated. A sample of the predicted values in relation to actual data is provided in Table 5; the species included in this table are those for which some information is also available from the CFR. The values in Table 5 are normally derived from specific studies in high quality habitats (e.g. conservation areas) and they therefore reflect relatively high-density situations.

DISCUSSION

Distributions

Notwithstanding the constraints inherent in the approach used here, the distribution maps are considered to represent realistic potential distributions of the medium- to large-sized mammals in the CFR. We stress, however, that the current maps are underpinned by putative habitat–mammal relationships that are testable. None the less, the maps contain new information that is essential for effective conservation planning, and for developing a greater understanding of the larger terrestrial vertebrates as indicators of environmental change in the region (see Macdonald, 1992). The maps generated here are applicable to planning and analysis at the regional scale and not to the local scale; this conforms to the findings of other similar studies (e.g. Butterfield *et al.*, 1994).

Spatial requirements

The spatial requirement data generated by the model described here can be used meaningfully in the CFR conservation planning exercise to determine the size, shape and location of the protected areas required to achieve demographically and genetically viable populations, in evolutionary terms, of each species in a multi-species assemblage.

We recognize, however, that the model greatly oversimplifies the highly complex intraspecific and inter-specific mammal interactions, and the equally complex animal–plant relationships, the latter often influenced by seasonality. There are, however, no alternatives when working at this scale, and with so little ecological information available for the species concerned.

The use of the LSU concept to provide estimates of forage production and ultimately of stocking rates for multi-species stock grazing systems, let alone wildlife, have not been investigated fully, e.g. comparing the impacts of sheep and cattle (Hardy, 1996; Meissner, 1996; Peel *et al.*, 1998). Due to a number of influences the use of LSUs can be, even for domestic livestock predictions, difficult to calculate and interpret (Meissner, 1982; Peel *et al.*, 1998). In particular, estimated stocking rates derived from the LSU approach do not take spatial and temporal heterogeneity into account. These problems are exacerbated in the CFR where agricultural stocking rates are notoriously difficult to calculate (H. Lindemann, Department of Agriculture, personal communication). Nevertheless, the LSU concept is, with reservations and adaptations, considered to be sound and 'there is sufficient evidence that (this) approach has been more acceptable than almost any other approach elsewhere' (Meissner, 1996).

The LSU concept permits ready comparison of stocking rates between areas, regardless of the species occurring, and is a convenient base for calculating optimal stocking rates and combinations of species in the commercial exploitation of indigenous ungulates (Mentis, 1977). Although the LSU approach provides only a broad index of the potential stocking rate for game in a given area or habitat, it is considered a practical gauge for comparing different habitat types (Van Rooyen *et al.*, 1996).

The LSU concept, or adaptations of it, has been widely applied, through the use of the indigenous herbivore equivalents of agricultural LSUs, in South Africa for estimating stocking rates of indigenous ungulates on game ranches and nature reserves (e.g. Berry, 1975; Mentis, 1977; Collinson & Goodman, 1982; Meissner, 1982; Van Rooyen *et al.*, 1996; Grossman *et al.*, 1999). Given the virtual absence of information on forage availability (quantity, quality and seasonality) for indigenous herbivores in the CFR, the LSU approach provides the only extant measure of the influence of key biophysical factors on this parameter.

Based on the density information in Allen-Rowlandson (1980), the model appears to overestimate the spatial requirements for the kudu. The reasons for this are not understood but may be related to the species' feeding ecology. This aspect requires further investigation.

It needs to be emphasized that even though the model has attempted to address the issue of seasonality for certain species (by reducing the amount of allocated forage), it will be unwise to keep a nomadic or migratory species in a single BHU on a year-round basis. This is because there may be other ecological factors that need to be taken into account, for example, presence of surface water, seasonal food availability and possible negative effects on threatened plants through selective foraging. This concern is addressed more specifically at private landowners wishing to re-introduce normally nomadic or migratory species to their land. A good example is the eland; it may be sedentary in certain areas but highly nomadic in others (Skinner & Smithers, 1990).

General

It is important that the estimates derived by this study must be treated as hypothetical guidelines at this stage. Thus, any management action based on these estimates should be considered experimental, should be tested through adaptive management strategies and should be closely monitored. The need to test indigenous herbivore spatial requirement estimates in practice, and to adapt them in the light of field experience, has been mentioned elsewhere (Trollope, 1990). In addition, the final stocking rates for these herbivores should be conservative, in order to cope with unfavourable conditions (Trollope, 1990). We thus advocate a 'management by hypothesis' approach, with assumptions and predictions being explicitly tested. A major advantage of the estimates presented here is that the assumptions are explicitly quantitative and can be modified as these ideas are tested, allowing adaptive management principles and actions to be employed. The concepts of 'management by hypothesis' and 'adaptive management' are a generally accepted approach to dealing with management challenges associated with a paucity of information (e.g. Macnab, 1983; May, 1991; Bowman, 1995).

The use of the LSU as a basis for estimating spatial requirements and stocking rates for indigenous herbivores is not novel, and has been invoked in various counties, e.g. South Africa, United States of America, Australia (see earlier). However, there has been a tendency to use this approach only at a local level, e.g. for small (< 10 000 ha) private reserves and game ranches and, occasionally, small (< 20 000 ha) conservation areas. As far as can be established, it has not been used for conservation planning at a regional scale approaching that of the CFR study (9 million ha). Implementation at this scale introduces new challenges and assumptions. Furthermore, the LSU approach, as applied to private game ranches, is normally used to estimate high stocking rates for maximum game production, whereas the approach in the present study has been to estimate low stocking rates, i.e. non-production orientated.

We contend that the LSU-based approach is appropriate for estimating densities of medium- to large-sized wild mammals at a regional scale but not necessarily at the scale of individual protected reserves and game ranches; in the case of the latter categories, additional ecological parameters need to be addressed when estimating spatial requirements and stocking rates.

The information generated by the present study has a number of potentially useful applications, e.g.

1. Provision of information for systematic conservation planning, at a regional scale, for the setting of targets for the design of protected area systems to effectively maintain viable populations of medium- to large-sized mammals; this would include the concept of metapopulation management. In this regard, the information generated for the CFR, using the approach described in this paper, made a significant contribution to achieving the aims of the conservation planning project in this floristic region.
2. Establishment of species composition and estimation of stocking rates for the re-introduction of medium- to large-sized mammals to extant private and public reserves from which they may have been extirpated.
3. Provision of information for the drafting of translocation policies by conservation management agencies.

The value of the spatial requirements model is that it produces explicit predictions that are testable.

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