The potential distributions, and estimated spatial requirements and population sizes, of the medium to large-sized mammals in the planning domain of the Greater Addo Elephant National Park project

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The Greater Addo Elephant National Park project (GAENP) involves the establishment of a mega biodiversity reserve in the Eastern Cape, South Africa. Conservation planning in the GAENP planning domain requires systematic information on the potential distributions and estimated spatial requirements, and population sizes of the medium to large-sized mammals. The potential distribution of each species is based on a combination of literature survey, a review of their ecological requirements, and consultation with conservation scientists and managers. Spatial requirements were estimated within 21 Mammal Habitat Classes derived from 43 Land Classes delineated by expert-based vegetation and river mapping procedures. These estimates were derived from spreadsheet models based on forage availability estimates and the metabolic requirements of the respective mammal species, and that incorporate modifications of the agriculture-based Large Stock Unit approach. The potential population size of each species was calculated by multiplying its density estimate with the area of suitable habitat. Population sizes were calculated for pristine, or near pristine, habitats alone, and then for these habitats together with potentially restorable habitats for two park planning domain scenarios. These data will enable (a) the measurement of the effectiveness of the GAENP in achieving predetermined demographic, genetic and evolutionary targets for mammals that can potentially occur in selected park sizes and configurations, (b) decisions regarding acquisition of additional land to achieve these targets to be informed, (c) the identification of species for which targets can only be met through metapopulation management, (d) park managers to be guided regarding the re-introduction of appropriate species, and (e) the application of realistic stocking rates. Where possible, the model predictions were tested by comparison with empirical data, which in general corroborated the predictions. All estimates should be considered as testable hypotheses.

Key words: conservation planning, mammals, distribution, density, population estimates, Addo, South Africa.

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Introduction

In November 2000, the Global Environment Facility (GEF) approved a grant to South African National Parks (SANParks) to research and prepare a full proposal to the GEF for the planning and establishment of a "greater" Addo Elephant National Park (GAENP). The SW boundary of the Addo Elephant National Park (AENP) is some 35 km east of the city of Port Elizabeth (33°58'S, 25°31'E), South Africa. The vision for an expanded Addo Elephant National

Park was developed and documented by Kerley & Boshoff (1997, 2002, www.zoo.upe.ac.za/teru). Systematic conservation planning forms an integral and critical component of the implementation of the GAENP project, managed by South African National Parks ("http://www.addoelephantpark.com" www.addoelephantpark.com). Note that the original boundary of the proposed expansion to the AENP (Kerley & Boshoff 1997) has been modified, by SANParks, for the purposes of the conservation planning exercise for GAENP, by the addition of a 5-km buffer that follows cadastral boundaries.

While the impressive plant diversity remains a major focus of conservation planning in the establishment of a GAENP (Kerley & Boshoff 1997), other biota and ecological processes which impact on the park's biodiversity must be taken into account in attempting to achieve its broad conservation objectives. The species' patterns and ecological and evolutionary processes in the GAENP planning domain include the medium to large-sized mammals and the processes that they drive, many of which (a) are in need of conservation intervention, and (b) may have an important impact on the park's biota, at the species, community and ecosystem functioning levels. Herbivory is known to have an impact on the species composition, structure and dynamics of fynbos vegetation (Campbell 1986; Johnson 1992) and thicket vegetation (Barratt & Hall-Martin 1991; Johnson *et al.* 1999; Lombard *et al*. 2001; Moolman & Cowling 1994; Penzhorn *et al.* 1974; Stuart-Hill 1992; Stuart-Hill & Aucamp 1993). The important role that the proposed mega reserve will play in conserving a diverse array of larger mammals, including the top predators and a number of megaherbivores, is emphasised by Kerley & Boshoff (1997). The numerous ecological processes that are mediated by the larger mammals, or that they participate in, are reported on elsewhere (Boshoff *et al*. 2001a).

The medium to large-sized mammals were selected as "target" species (*sensu* Wilcox 1982) for the GAENP planning exercise because it is likely that if their minimum area requirements are met, adequate survival conditions will be simultaneously 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 with a large body size (e.g., some ungulates) or which occupy a high trophic level (e.g., carnivores) are regarded as good candidates for target species acting as "umbrella" species (Wilcox 1982). In addition, the distributions and spatial requirements/densities of the larger mammals are probably better known, or can be better estimated, than those of the small-sized mammals in the GAENP planning domain. In any case, realistic data for these two population parameters are essential for any conservation exercise that deals with the establishment and maintenance of minimum viable populations of the larger mammalian fauna (Caughley 1994; Caughley & Sinclair 1994; Lande & Barrowclough 1987).

An additional consideration for determining minimum area requirements for preserving biological diversity is that of the estimation of minimum viable populations (MVP) for "target" species (Wilcox 1982; Soulé 1987). The MVP is a set of specifications concerning the size and structure of the populations of a species that is necessary to provide a margin of safety from extinction. The MVP for a species can be translated into the minimum area requirements by determining the amount and type of habitat that will satisfy the MVP. In view of this, it is necessary for realistic estimates of the spatial requirements/densities of each the selected species in the GAENP planning domain to be obtained.

In summary, systematic data and information are required to enable conservation planners to calculate the potential numbers of individuals of each mammal species, within the mammal habitats within various park configuration scenarios. These data will enable planners to measure the effectiveness of the proposed GAENP in achieving predetermined demographic, genetic and evolutionary targets for medium to large-sized mammals that can potentially occur in the park. In addition, they will inform decisions regarding acquisition of additional land, where necessary, to achieve these targets, and help identify species for which targets can only be met through metapopulation management.

APPROACH

The indigenous mammal species included in this study (Table 1) are those with a mass greater than ca. 2 kg (cf. Chew 1978), that are the most prominent on the landscape, and which are generally amenable to direct management. As part of a separate exercise, 43 Land Classes were delineated through field mapping by Kruger & Sykes (2002), using as a basis the hierarchical classification of Subtropical Thicket by Vlok & Euston-Brown (2002). It was considered impractical to use this detailed classification for deriving the potential distributions and estimated spatial requirements/densities of the larger mammals. It was consequently decided to collapse the 43 Land Classes into a practical number (21) of Mammal Habitat Classes (MHCs) and to use these as the biodiversity surrogates for the mammal conservation planning component of the Greater Addo Elephant National Park. Only those Land Classes that exhibited a generally high degree of similarity, in terms of vegetation structure (and hence mammal habitat) and productivity (determining mammal densities), and for which any differences that exist are considered unlikely to impact significantly on the known and potential presence and densities of mammal species, were combined. The potential distributions and estimated spatial requirements of the two otter species are based exclusively on aquatic habitats, i.e., coastline and rivers, where appropriate.

DISTRIBUTIONS

Methods

Two steps were followed in determining the potential distribution of each species, within each MHC in the GAENP planning domain.

1. *Collation and interpretation of evidence that a species occurred, or could potentially occur in all, or in a specific part, of the GAENP planning domain.*

The early and recent published literature was consulted, as were conservation scientists and managers with a good knowledge of the macro fauna of the existing Addo Elephant National Park (AENP) and close environs (see Boshoff & Kerley 2001 and Boshoff *et al*. 2001b for details of the methods used). The mammal checklist for the AENP was also consulted, as were the mammal collection registers of the Amatole Museum in King William's Town, where the terrestrial mammal collections from the four provincial museums in the Eastern Cape are now housed.

The present study attempts to reconstruct the distributions of indigenous herbivores in the period prior to arrival of European settlers, in the GAENP planning domain, in the mid 17th century. These distributions thus represent a situation where the patterns and processes exhibited by the mammals of the region were presumably still fairly intact. Thus, domestic herbivores, maintained by Khoi pastoralists in the period prior to European settlement, have not been taken into account in this analysis, owing to a lack of information on their distributions, nomadic movements and densities.

Zoological and explorer's records from the 17th, 18th and 19th centuries have been well reviewed by Du Plessis (1969), Rookmaaker (1989) and Skead (1987). These reviews were useful in determining the general presence or absence of most species in all or parts of the GAENP planning domain, but they generally proved to be 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 mammal occurrences 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 1987).

The following additional sources were consulted for information on the historical occurrence of mammals in the broader area around the GAENP: Coetzee (1979); Hewitt (1931); Lloyd & Millar (1983); Shortridge (1942); Skinner & Smithers (1990); Smithers (1986); Stuart (1981); Stuart (1985); Stuart *et a*l. (1985).

A review of the recent (20th century) literature revealed that surveys 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 sub-region (Skinner & Smithers 1990) allows only generalised 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 GAENP planning domain, and they do not take into account the possible migratory or nomadic patterns of some species.

2. *Estimation of potential presence of the species, based on their ecological requirements*

The potential presence/absence of each species in each MHC was determined according to our understanding of their ecological requirements, including a review of published habitat requirements (in the general GAENP area and further afield), our personal field knowledge, and the respective habitat characteristics of each MHC. These characteristics included dominant plant species, vegetation structure, grass component, soil nutrients, geology, topography, modal altitude, mean rainfall and rainfall seasonality). See Boshoff & Kerley (2001) and Boshoff *et al*. (2001b) for details of the methods used. As part of this exercise, AENP conservation scientists and managers, with ecological knowledge of mammals of the area, were consulted.

The potential distribution of each species is presented according to three categories:

- MHCs with the potential to sustain significant resident (i.e., present all year round and breeding) populations. In these MHCs the animals are generally homogeneously distributed across the landscape;
- MHCs which may be used on a seasonal basis, or which may carry small populations in habitat refugia (i.e., patchy basis). In these MHCs the animals are generally not homogeneously distributed, temporally and spatially, across the landscape;
- MHCs where the species is unlikely to occur, except perhaps for vagrants or during rare and short incursions. In such cases the species was considered to be absent, and the MHC in question could not be relied upon to contribute to the conservation of that species.

The hippopotamus potentially occurs, in suitable habitat, in and along major rivers and dams. These waterbodies must be perennial in nature and must contain pools at least 1.5 m deep. The distance travelled from watercourses to feeding grounds depends on forage availability and can vary widely. Hippopotamus generally forage within about 1.5 km from waterbodies but will move freely up to eight or 10 km, and are known to move much further when forage is scarce (Skinner & Smithers 1990). Potential hippopotamus habitat was marked on a digital terrain map produced by CSIR-Environmentek. For practical reasons, the overall distribution of this species is presented, rather than its distribution according to Mammal Habitat Class. Using GIS, those parts of MHCs that overlap with potential hippopotamus habitat are considered as additional (i.e., additional to the original 21 MHCs) MHCs and are treated as such for the calculation of estimated spatial requirements and densities (see "Spatial Requirements").

The potential distributions (that are linear in nature) of the two otter species were marked on a digital terrain map that identifies the major rivers and dams. A conservative approach was adopted in determining these distributions; only waterbodies that can be confidently classified as being perennial were included.

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

Results

Of the 44 indigenous, non-marine mammal species that occur, or can potentially occur in the proposed GAENP (Table 1), 41 species occur exclusively in terrestrial habitats, whereas three species, the Cape clawless and spotted-necked otters and the hippopotamus are associated with aquatic habitats. Three species are omnivores, 18 are carnivores and 23 are herbivores. Of the 44 species, 35 are

Table 1
The common and scientific names, foraging guild classifications and current (2001) presence of potentially occurring medium- to large-sized omnivorous, carnivorous and herbivorous mammals in the GAENP planning domain. P = Present in 2001. Taxonomic order (except for aardvark – see text) and nomenclature (scientific and common names) follow Skinner & Smithers (1990)

Common name	Scientific name	Foraging guild	Presence in 2001
OMNIVORES			
Chacma baboon	*Papio cynocephalus*		P
Vervet monkey	*Cercopithecus aethiops*		P
Porcupine	*Hystrix africaeaustralis*		P
Aardvark	*Orycteropus afer*		P
CARNIVORES			
Aardwolf	*Proteles cristatus*		P
Brown hyaena	*Hyaenna brunnea*		
Spotted hyaena	*Crocuta crocuta*		
Cheetah	*Acinonyx jubatus*		
Leopard	*Panthera pardus*		P
Lion	*Panthera leo*		
Caracal	*Felis caracal*		P
African wild cat	*Felis lybica*		P
Small spotted cat	*Felis nigripes*		P
Serval	*Felis serval*		
Bat-eared fox	*Otocyon megalotis*		P
Wild dog	*Lycaon pictus*		
Cape fox	*Vulpes chama*		P
Black-backed jackal	*Canis mesomelas*		P
Cape clawless otter	*Aonyx capensis*		P
Spotted-necked otter	*Lutra maculicollis*		P
Honey badger	*Mellivora capensis*		P
HERBIVORES			
African elephant	*Loxodonta africana*	Mixed feeder	P
Black rhinoceros	*Diceros bicornis*	Browser	P
Cape mountain zebra	*Equus zebra zebra*	Bulk grazer	P
Burchell's zebra	*Equus burchelli*	Bulk grazer	P
Bushpig	*Potamochoerus porcus*	Mixed feeder	P
Warthog	*Phacochoerus aethiopicus*	Concentrate grazer	P
Hippopotamus	*Hippopotamus amphibius*	Bulk grazer	P
Black wildebeest	*Connochaetes gnou*	Concentrate grazer	
Red hartebeest	*Alcelaphus buselaphus*	Concentrate grazer	P
Blue duiker	*Philantomba monticola*	Browser	P
Common duiker	*Sylvicapra grimmia*	Browser	P
Springbok	*Antidorcas marsupialis*	Mixed feeder	P
Klipspringer	*Oreotragus oreotragus*	Browser	P
Oribi	*Ourebia ourebi*	Concentrate grazer	
Steenbok	*Raphicerus campestris*	Browser	P
Grysbok	*Raphicerus melanotis*	Browser	P
Grey rhebok	*Pelea capreolus*	Concentrate grazer	P
African buffalo	*Syncerus caffer*	Bulk grazer	P
Kudu	*Tragelaphus strepsiceros*	Browser	P
Bushbuck	*Tragelaphus scriptus*	Browser	P
Eland	*Taurotragus oryx*	Mixed feeder	P
Reedbuck	*Redunca arundinum*	Concentrate grazer	
Mountain reedbuck	*Redunca fulvorufula*	Concentrate grazer	P

already present and nine could be considered for re-introduction.

The 21 MHCs delineated for this study are mapped in Fig. 1 and listed in Table 2. The potential occurrence of each species in each MHC, on a "resident" or "seasonal/patchy" basis (Table 2), is illustrated in a series of distribution maps (Figs. 2–44). Due to a lack of detailed habitat information, the hippopotamus and the two otter species are considered to be potentially resident in all habitats mapped for these species.

Discussion

Notwithstanding the constraints inherent in the approach used here, the maps provided in this report are considered to represent realistic potential distributions of the medium to large-sized mammals in the GAENP planning domain. We stress, however, that these data are underpinned by putative habitat-mammal relationships that are testable in the future. Nonetheless, the data provide new information that is essential for effective conservation planning in the GAENP, and for developing a greater understanding of the larger terrestrial vertebrates as indicators of environmental change in the proposed park (Macdonald 1992).

The black wildebeest is the only species for which the greater part of its distribution range within the GAENP planning domain falls within the 5-km buffer zone. For two other species, namely oribi and reedbuck, a significant proportion of their distribution range within the planning domain falls within the 5-km buffer.

It is emphasised that the allocation of species to specific MHCs should not be interpreted to imply that the distributions of the mammals are spatially and temporally fixed in the planning domain. Because of the dearth of ecological information from the region, any reconstruction of the demographics and dynamics of the medium to large mammal populations must be based on the collection of new information.

Owing, in part, to the expansion of the AENP, there are currently seven extralimital species in the park, namely gemsbok *Oryx gazella*, impala *Aepyceros melampus*, waterbuck *Kobus ellipsiprymnus*, blesbok *Damaliscus dorcas phillipsi*, blue wildebeest *Connochaetes taurinus*, red lechwe *Kobus leche* and nyala *Tragelaphus angasii*. It is recommended that these species be removed from the AENP, in view of the real and potential ecological and economic costs of keeping them in the park (Castley *et al*. 2001).

SPATIAL REQUIREMENTS

Methods

The estimated spatial requirements of each species, and the associated density estimates, refer exclusively to those MHCs in the GAENP planning domain where the species is likely to occur, on a "resident" or "seasonal/patchy" basis.

Omnivores and carnivores

The overall lack of information from the GAENP domain precluded an estimation of the spatial requirements of the omnivores and carnivores according to individual Mammal Habitat Classes. Consequently, the planning domain 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 MHC were based on a review of available information on densities, social structures, breeding units, territory sizes and home ranges. However, since published ecological information for the region is not available (cf. Boshoff *et al*. 2001b) for any of the species that can potentially occur there, estimates based on the interpretation and extrapolation of information on the relevant species from other regions in South Africa, mainly the Nama-Karoo, Grassland and Savanna biomes (*sensu* Low & Rebelo 1996), were used as surrogates. 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. For the sake

Table 2

The presence/absence of the medium- to large-sized mammals in the GAENP planning domain, according to Mammal Habitat Class (R = Resident, SP = Seasonal/Patchy)

Common name	Mammal Habitat Class																				
	Forest	Thicket Forest Mosaic	Thicket Savanna Mosaic	Zuurberg Mesic Thicket	Addo Heights Mesic Thicket	Succulent Thicket	Spekboomveld	Eastern Spekboom Noorsveld	Western Spekboom Noorsveld	Noorsveld	Grassy Bontveld	Karroid Bontveld	Karoo Thicket Mosaic	Karroid Dwarf Shrubland	Karroid Broken Veld	Sour Grassland	Mixed Grassy Shrubland	Fynbos	Riparian Woodland	Dunefield	Sundays Saltmarsh
Chacma baboon				R		R		R	R	R			R	SP	R	R	R	R	R		
Vervet monkey	R	R	R	R	R	R	R	R	R	SP	SP	SP	R	SP	SP				R	SP	
Porcupine	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	SP	
Aardwolf			SP	SP	SP	SP	SP	SP	SP	SP	R	R	R	R	R	R	R	SP	SP		
Brown hyaena		SP	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	SP
Spotted hyaena			SP	SP	SP	SP	SP	R	R	R	R	R	R	R	R	SP	R	SP	R	SP	SP
Cheetah								R	R	R				R	R						
Leopard	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	SP	SP
Lion			R	SP	SP	R	SP	R	R	R	R	R	R	R	R	SP	R	SP	R	SP	SP
Caracal	SP	SP	R	R	R	R	R	R	R	R	R	R	R	R	R	SP	R	SP	R	SP	SP
African wild cat		SP	R	R	R	R	R	R	R	R	R	R	R	R	R	SP	R	SP	R	SP	SP
Small spotted cat						SP		R	R	R	R	R	R	R	R		R				
Serval			SP			SP		SP	SP		SP		SP				SP	SP	R		
Bat-eared fox			SP			SP	SP	R	R	R	R	R	R	R	R		SP		SP		
Wild dog			R	R	R	R	R	R	R	R	R	R	R	R	R	SP	R	SP	R	SP	SP
Cape fox						SP	SP	R	R	R	R	R	R	R	R		SP		SP		
Black-backed jackal	SP	R	R	R	R	R	R	R	R	R	R	R	R	R	R	SP	R	SP	R	SP	SP
Honey badger	SP	SP	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	SP	SP
Aardvark			R	SP	SP	R	R	R	R	R	R	R	R	R	R	SP	R		R		
African elephant	SP	R	R	R	R	R	R	SP	SP	SP	R	R	R	SP	SP		SP		R		
Black rhinoceros		SP	R	R	R	R	R	R	R	R	R	R	R	R	R		R		R		
Mountain zebra				SP		SP		SP	SP	SP			SP	SP	SP	R	R	R			
Plains zebra			SP		SP		SP	R	R	R	R	R		R	R				SP		
Bushpig	R	R	SP	R	R	R	R				SP	SP	SP						R	SP	
Warthog			SP		SP	SP	SP	R	R	R	R	R	SP	R	R				R		
Black wildebeest								SP							SP						
Red hartebeest			SP			SP		R	R	R	R	R	SP	R	R	SP	R	SP	SP		
Blue duiker	R	R	SP	R	R	SP	SP												SP		
Common duiker	SP	SP	R	R	R	R	R	R	R	R	SP	SP	R	SP	SP	SP	R	SP	R	SP	
Springbok			SP					R	SP	R	SP	SP	SP	R	R				SP		
Klipspringer						R		SP	SP				R	SP	SP		R				
Oribi			SP								SP					SP					
Steenbok			SP					R	R	R		SP	SP	R	R		SP		P		
Grysbok		R	SP	R	R	SP	R				SP	SP				SP	R	R		SP	
Grey rhebok																R	R	R			
Cape buffalo		SP	R	SP	SP	SP	SP	SP	SP	SP	R	R	R	SP	SP	SP	SP		R		
Kudu			R	R	R	R	R	R	R	R	SP	R	R	SP	R		R		R		
Bushbuck	R	R	R	R	R	R	R				SP	SP	SP						SP	SP	
Eland			SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP	SP		
Reedbuck			SP																		
Mountain reedbuck								R	R				SP		R	R	R	SP			

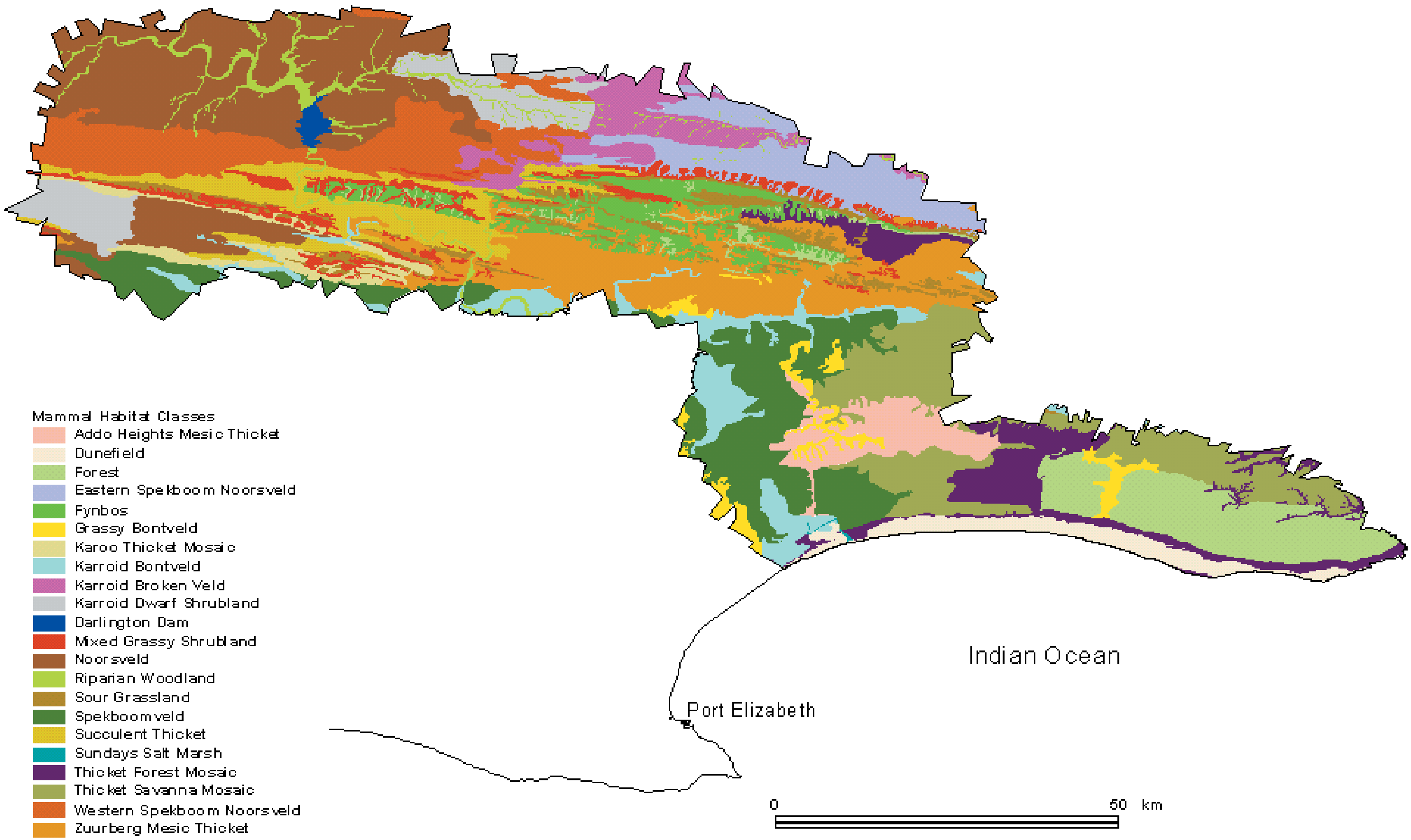

Fig. 1. The mammal habitat classes in the planning domain for the Greater Addo National Park Initiative. See text for details.

of brevity, the sources of the data used to estimate the spatial requirements have not been included in this paper.

Given that they occur along rivers or along the coastline, the density estimates for the two otter species are expressed in linear terms (individuals/km). Where the distribution of the Cape clawless otter potentially overlaps with that of the spotted-necked otter, the food resources have been equally apportioned between them, thereby reducing the potential density of each species.

A conservative approach to the estimation of the spatial requirements of the omnivores and carnivores in the GAENP planning domain was adopted because of the naturally, and relatively, low herbivore carrying capacity in some habitats, and a generally 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., sub-adults, immatures and juveniles) are taken into account; and (d) reducing the densities in the seasonal/patchy habitats to 20 % of those calculated for the "core" habitats (Boshoff *et al*. 2001b).

Herbivores

Given the virtual absence of information on the spatial requirements of herbivores in the GAENP planning domain, we followed a pragmatic approach in the derivation of the necessary estimates. This involves a spreadsheet model, based on forage availability estimates and the metabolic requirements of the mammal species in question. The approach followed is very similar to that described by Boshoff *et al*. (2001b) but some adjustments have been made to accommodate the GAENP requirements and characteristics. Although the porcupine is predominantly a herbivore, we have treated it as an omnivore and excluded it from the spreadsheet model, since it does not fit in the conventional grazer/browser classification.

The six 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 (Table 1, adapted from Collinson & Goodman 1982), namely: bulk grazer; concentrate grazer; mixed feeder (grazer/browser); and 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) (Anon. 1985), were used as guidelines for estimating forage production, and ultimately the spatial requirements of herbivores within each Mammal Habitat Class. It must be emphasised that the term "spatial requirements" normally refers to an ecological response, whereas the term "stocking rates" normally refers to an operator/manager response. The definition and use of the LSU concept to determine stocking rates for livestock and wildlife is discussed in some detail by Boshoff *et al*. (2001b).

Where available data (cf. Stuart-Hill & Aucamp 1993) have permitted a comparison, the agricultural stocking rate broadly agrees with published empirical data.

Agricultural management is usually aimed at maximising production (Morris *et al*. 1999), and therefore 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 MHC by a proportion which was estimated following a subjective assessment of the biophysical attributes, as surrogates for the productivity of forage, for the MHC 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 MHCs characterised by low productivity, low nutrient soils and a limited grass component, were reduced by a higher percentage than those MHCs characterised by a higher productivity, relatively higher soil nutrient status and a relatively high grass component.

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.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Figs. 2–44. The potential distribution of the different mammals in the Greater Addo Elephant National Park planning domain, according to Mammal Habitat Class (MHC). Solid shading denotes MHCs with the potential to sustain significant resident (i.e., present all year round and breeding) populations; grey shading denotes MHCs 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 MHCs where the species is unlikely to occur, except perhaps for vagrants or during rare and short-lived incursions.

Department of Agriculture stocking rates were not available for some MHCs, nor could they be determined, owing 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 MHCs; and the stocking rates for neighbouring Mammal Habitat Classes.

For the purposes of the model, these adjusted stocking rates (ha/LSU) were expressed as animal unit densities (LSU/ha).

3. Allocation of animal units to foraging guilds, within MHCs

The available animal units, per hectare, within each MHC (expressed as adjusted LSU/ha) were allocated to each of the four foraging guilds, where appropriate (i.e., for each guild that was represented in that MHC). To achieve this, allocations of forage (as percentages) were made for each guild within each MHC, based on subjective estimations of the proportions and nature (e.g., sweet or sour grassveld) of graze and browse, as suggested by the MHC biophysical descriptions and our personal knowledge of these habitats (Appendix 1). These allocations were then corroborated with the guild structures of the herbivores occurring in each Mammal Habitat Class. For example, a check was made that the distribution patterns described earlier indicated that grazers were the dominant herbivores in MHCs dominated by grass.

For pragmatic reasons, no distinction was made between the pre- and post-Darlington Dam scenarios, i.e., the dam was considered to be a permanent feature. Since the dam itself (water area) it does not contribute any forage, it has been subtracted from the total area of Riparian Woodland that provides suitable hippopotamus habitat.

4. Allocation of available animal units to individual species within foraging guilds, within MHCs

For each MHC the available animal units, calculated in Step 3 above and expressed as adjusted LSU/ha, were allocated to the herbivore species within each foraging guild. Thus, where more than one species occurs within a single foraging guild within an MHC, the LSUs accorded to that guild are allocated to these species in equal proportions. This course was chosen owing to the paucity of information on resource partitioning within these guilds.

5. Adjustment for seasonality/ patchiness

Species that are resident in a MHC will most likely have different forage requirements (and possibly other ecological requirements, e.g., availability of surface water, shelter/cover) than species that are highly spatially localised 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 and habitat patchiness. This was addressed by reducing by 60 % the amount of forage

Fig. 7.

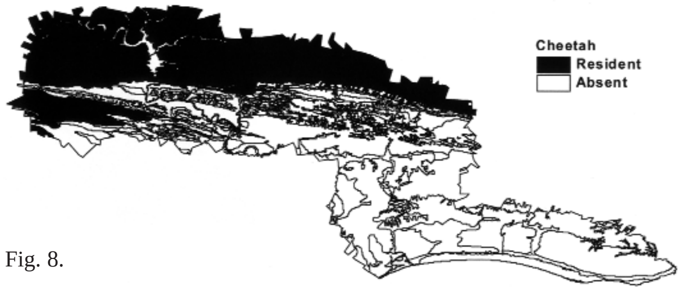

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13

Fig. 14.

Fig. 15.

Fig. 16.

allocated (expressed as adjusted LSU/ha) to seasonal/patchy species. We assumed that the amount, and indeed quality, of resources was limiting, rather than their seasonal availability or total absence. The basis for using a value of 60 % is the same as that used for a similar study in the Cape Floristic Region, where a value of 90 % was used (Boshoff *et al*. 2001b). A value of 60 % was used here to reflect the probable higher and more reliable year-round forage productivity.

Thus, each species in each MHC is classified as "resident" or "seasonal/ patchy" (see "Distributions"). The LSUs that were "released" by a "seasonal/patchy" species were re-allocated, in equal proportions, to other species within the same foraging guild. This gives the recalculated number of LSUs available to each species within a Mammal Habitat Class. In cases where other species are not present in the same guild, the "released" animal equivalents (LSU/ha) were considered as "floaters" within that MHC—to be utilised across the graze/browse spectrum by the remaining species in the Mammal Habitat Class.

6. *Calculation of species specific densities and spatial requirements, within each MHC*

The number of individuals of a species per ha (density), within each MHC, was calculated as follows:

$$D = LSU_{rec} / S_{equ} \qquad (2)$$

where D = density (number of individuals/ ha), LSU_{rec} = recalculated LSUs per species (as calculated in steps 1-5 above) and S_{equ} = species' LSU equivalent.

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

The estimated spatial requirement for an individual of each species, within each MHC, is calculated as follows:

$$SpRq_i = 1/D \qquad (3)$$

where $SpRq_i$ = spatial requirement (ha/individual) of an individual, D = density (individuals/ha - from equation 2).

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), and for some species the availability of food, water and shelter is superseded 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.

Model testing

The outputs of the model were tested by comparing spatial requirement estimates derived from the model with published, empirically derived observations of densities of species for which appropriate data are available. Such data are not available for complete species assemblages.

Hippopotamus

For those parts of MHCs where hippopotamus can potentially occur, a separate spreadsheet model was constructed. It differs from the model for the MHCs without hippopotamus in that hippopotamus has been inserted as an additional herbivore (it is a bulk grazer). This results in adjustments to the allocation of forage between bulk grazers within these parts of MHCs, and ultimately the densities of all species within this foraging guild.

There is no published information on the densities and spatial requirements of hippopotamus in the GAENP domain, or even in the Eastern Cape,

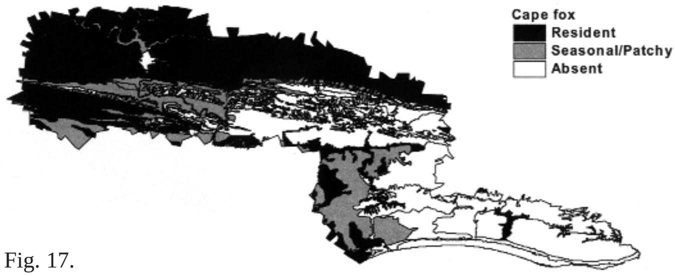

Fig. 17.

Fig. 18.

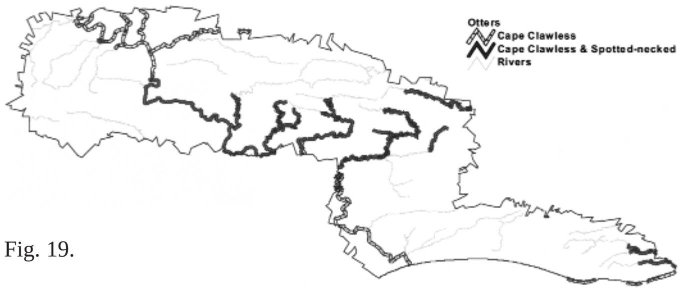

Fig. 19.

Fig. 20.

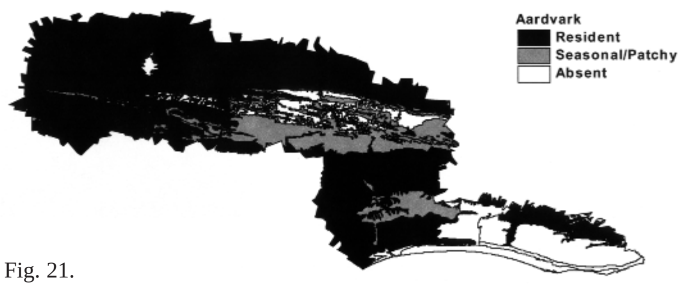

Fig. 21.

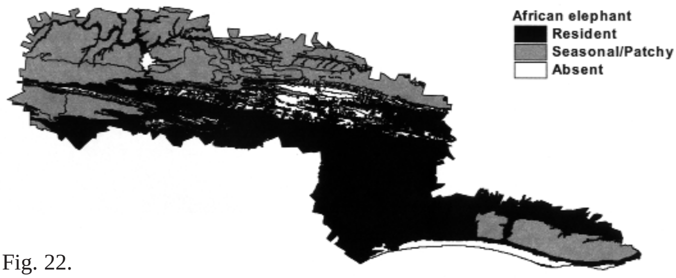

Fig. 22.

Fig. 23.

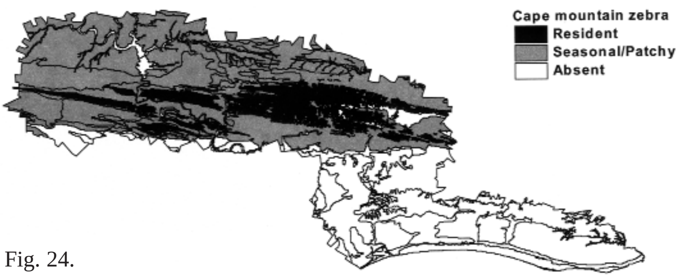

Fig. 24.

Fig. 25.

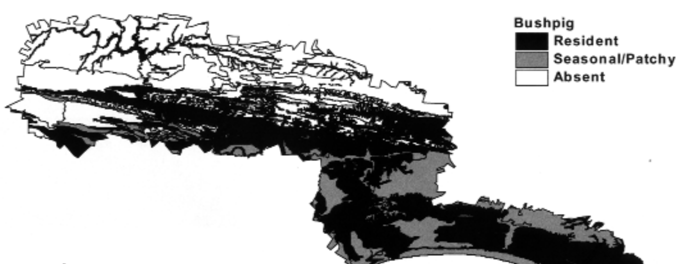

Fig. 26.

to validate the estimates provided by the model.

Results

Omnivores and carnivores

The estimates of the spatial requirements/densities for the omnivores and carnivores are provided in Table 3. As an example of the basis for the estimation of the spatial requirements, the case of the chacma baboon is given (Box 1; cf. Table 3). The

***Box 1**: Estimation of the spatial requirements of the chacma baboon.*

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 home ranges of three troops of 20, 35 and 80 baboons were 9.1, 14.8 and 33.7 km², respectively, with home range being related to size of troop (Devore & Hall 1965). Home ranges of 400-4000 ha have been recorded.

Table 3

Estimated densities and spatial requirements for selected medium- to large omnivores and carnivores in (a) "seasonal/patchy" and (b) "resident" occurrence categories in the GAENP planning domain. See text and Boshoff et al. (2001a) for assumptions and calculations. Scientific names in Table 1

Species	Extrapolated densities and spatial requirements	Est. density (ind./ha)		Est. spat./req. (ha/ind.)	
		Seas./patchy	Resident	Seas./patchy	Resident
Chacma baboon	1 troop of 80 uses 3400 ha.	0.01299	0.02326	77	43
Vervet monkey	25/troop, 8 troops required for 200 individuals at ca. 80 ha/troop.	0.18519	0.33333	5.4	3
Porcupine	Family group of 5 individuals; territory size of 80 ha	0.03448	0.06250	29	16
Aardwolf	Males and females share territories of up to 800 ha.	0.00139	0.00250	720	400
Brown hyaena	Clan of 4 members has a territory size of about 25 000 ha.	0.00009	0.00016	11250	6250
Spotted hyaena	A clan of 9 would require a territory of around 40 000 ha.	0.00013	0.00023	7999	4444
Cheetah	Est. home range for 5 animals (2m, 3f) at 100 000 ha, with 75% overlap. 50 animals = 100 000 + 25% for 10 iterations	0.00003	0.00005	33480	18600
Leopard	1 pair requires a home range of about 20 000 ha	0.00006	0.00010	18000	10000
Lion	A pride of 10 animals (adults, sub-adults and young) may require a territory of about 45 000 ha.	0.00012	0.00022	8100	4500
Caracal	Pairs have overlapping (by up to 20%) home ranges of about 6 600 ha.	0.00021	0.00038	4752	2640
African wild cat	1 pair has a home range of approximately 250 ha.	0.00444	0.00800	225	125
Small spotted cat	Males and females have overlapping (ca 20%) territories of about 900 ha. Thus, 1 pair has a territory of about 1500 ha.	0.00074	0.00133	1350	750
Serval	Males and females occur in home ranges of up to 3000 ha, taking overlap into account.	0.00037	0.00067	2700	1500
Bat-eared fox	Density of 3 animals/100 ha	0.01667	0.02941	60	34
Wild dog	0.017 animals per 100ha	0.00009	0.00017	10588	5882
Cape fox	Only information for hunting range (up to 500 ha); overlapping home ranges. Say 1 pr needs 750 ha.	0.00148	0.00267	675	375
Black-backed jackal	Territory/home range of about 1100 ha/pr.	0.00101	0.00182	990	550
Cape clawless otter	1 per 3.5 km of river; 1 per 2 km of coastline				
Spotted-necked otter	1 per 2.5 km of river				
Honey badger	Male and female have overlapping home ranges of about 10 000 ha.	0.00011	0.00020	9000	5000
Aardvark	Est. home ranges for 1 male and 1 female of 7 500 ha.	0.00015	0.00027	6750	3750

Table 4
Estimated densities and spatial requirements of the larger mammalian herbivores in areas of 20 Mammalian Habitat Classes in the GAENP planning domain that do not contain hippopotamus habitat. Data derived from a spreadsheet model. See text for calculations and assumptions. Scientific names in Table 1

Mammal Habitat Class	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)
Forest	African elephant	0.00035	2876	Common duiker	0.01704	59
	Bushpig	0.01758	57	Bushbuck	0.03833	26
	Blue duiker	0.16611	6			
Thicket Forest Mosaic	African elephant	0.00540	185	Common duiker	0.06617	15
	Black rhinoceros	0.00361	277	Grysbok	0.34740	3
	Bushpig	0.06818	15	Cape buffalo	0.00208	482
	Blue duiker	0.69481	1	Bushbuck	0.16034	6
Thicket Savanna Mosaic	African elephant	0.00540	185	Oribi	0.04082	25
	Black rhinoceros	0.00807	124	Steenbok	0.06122	16
	Burchell's zebra	0.00866	116	Grysbok	0.06122	16
	Bushpig	0.00974	103	Cape buffalo	0.02136	47
	Warthog	0.01143	88	Kudu	0.02466	41
	Red hartebeest	0.00772	130	Bushbuck	0.10243	10
	Blue duiker	0.12245	8	Eland	0.00198	504
	Common duiker	0.14796	7	Reedbuck	0.01143	88
	Springbok	0.01429	70			
Zuurberg Mesic Thicket	African elephant	0.00229	436	Grysbok	0.10621	9
	Black rhinoceros	0.00386	259	Cape buffalo	0.00099	1011
	Cape mtn. zebra	0.00168	595	Kudu	0.01180	85
	Bushpig	0.02897	35	Bushbuck	0.04902	20
	Blue duiker	0.21242	5	Eland	0.00182	551
	Common duiker	0.07081	14			
Addo Heights Mesic Thicket	African elephant	0.00229	436	Common duiker	0.07081	14
	Black rhinoceros	0.00386	259	Grysbok	0.10621	9
	Burchell's zebra	0.00160	623	Cape buffalo	0.00099	1011
	Bushpig	0.02897	35	Kudu	0.01180	85
	Warthog	0.00094	1063	Bushbuck	0.04902	20
	Blue duiker	0.21242	5	Eland	0.00182	551
Succulent Thicket	African elephant	0.00111	898	Common duiker	0.06092	16
	Black rhinoceros	0.00332	301	Klipspringer	0.07833	13
	Cape mtn. zebra	0.00076	1323	Grysbok	0.02948	34
	Bushpig	0.01407	71	Cape buffalo	0.00045	2247
	Warthog	0.00571	175	Kudu	0.01015	98
	Red hartebeest	0.00386	259	Bushbuck	0.04218	24
	Blue duiker	0.05896	17	Eland	0.00088	1134
Spekboomveld	African elephant	0.00142	706	Common duiker	0.06128	16
	Black rhinoceros	0.00334	299	Grysbok	0.09192	11
	Burchell's zebra	0.00069	1452	Cape buffalo	0.00042	2354
	Bushpig	0.01791	56	Kudu	0.01021	98
	Warthog	0.00727	138	Bushbuck	0.04242	24
	Blue duiker	0.06566	15	Eland	0.00112	891
Eastern Spekboom Noorsveld	African elephant	0.00027	3753	Springbok	0.02716	37
	Black rhinoceros	0.00387	258	Klipspringer	0.03175	32
	Cape mtn. zebra	0.00353	284	Steenbok	0.10648	9

Table 4 (continued)

Mammal Habitat Class	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)
	Burchell's zebra	0.01852	54	Cape buffalo	0.00208	482
	Warthog	0.00667	150	Kudu	0.01183	85
	Black wildebeest	0.00121	828	Eland	0.00069	1458
	Red hartebeest	0.00450	222	Mtn. reedbuck	0.01282	78
	Common duiker	0.07099	14			
Western Spekboom Noorsveld	African elephant	0.0002	24587	Springbok	0.00404	248
	Black rhinoceros	0.00348	287	Klipspringer	0.02857	35
	Cape mtn. zebra	0.00241	416	Steenbok	0.09583	10
	Burchell's zebra	0.01263	79	Cape buffalo	0.00142	706
	Warthog	0.00606	165	Kudu	0.01065	94
	Red hartebeest	0.00410	244	Eland	0.00056	1782
	Common duiker	0.06389	16	Mtn. reedbuck	0.01166	86
Noorsveld	African elephant	0.00020	5004	Common duiker	0.06366	16
	Black rhinoceros	0.00347	288	Springbok	0.02037	49
	Cape mtn. zebra	0.00220	454	Steenbok	0.09549	10
	Burchell's zebra	0.01157	86	Cape buffalo	0.00130	770
	Warthog	0.00833	120	Kudu	0.01061	94
	Red hartebeest	0.00563	178	Eland	0.00051	1944
Grassy Bontveld	African elephant	0.00252	397	Springbok	0.00667	150
	Black rhinoceros	0.00801	125	Oribi	0.01905	53
	Burchell's zebra	0.01221	82	Grysbok	0.02593	39
	Bushpig	0.00455	220	Cape buffalo	0.00753	133
	Warthog	0.01733	58	Kudu	0.00288	347
	Red hartebeest	0.01171	85	Bushbuck	0.01197	84
	Common duiker	0.01728	58	Eland	0.00093	1080
Karroid Bontveld	African elephant	0.00210	477	Springbok	0.00556	180
	Black rhinoceros	0.00617	162	Steenbok	0.03086	32
	Burchell's zebra	0.00842	119	Grysbok	0.03086	32
	Bushpig	0.00379	264	Cape buffalo	0.00519	193
	Warthog	0.01667	60	Kudu	0.01886	53
	Red hartebeest	0.01126	89	Bushbuck	0.01425	70
	Common duiker	0.02058	49	Eland	0.00077	1296
Karoo Thicket Mosaic	African elephant	0.00157	635	Klipspringer	0.07093	14
	Black rhinoceros	0.00301	332	Steenbok	0.02546	39
	Cape mtn. zebra	0.00198	504	Cape buffalo	0.00467	214
	Bushpig	0.00284	352	Kudu	0.00919	109
	Warthog	0.00333	300	Bushbuck	0.01175	85
	Red hartebeest	0.00225	444	Eland	0.00058	1728
	Common duiker	0.05517	18	Mtn. reedbuck	0.00641	156
	Springbok	0.00417	240			
Karroid Dwarf Shrubland	African elephant	0.00030	3336	Springbok	0.03055	33
	Black rhinoceros	0.00480	208	Klipspringer	0.02381	42
	Cape mtn. zebra	0.00176	567	Steenbok	0.13194	8
	Burchell's zebra	0.00926	108	Cape buffalo	0.00104	963
	Warthog	0.01250	80	Kudu	0.00309	324
	Red hartebeest	0.00845	118	Eland	0.00077	1296
	Common duiker	0.01852	54			

Table 4 (continued)

Mammal Habitat Class	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)
Karroid Broken Veld	African elephant	0.00034	2919	Springbok	0.03492	29
	Black rhinoceros	0.00364	275	Klipspringer	0.02449	41
	Cape mtn. zebra	0.00252	397	Steenbok	0.10000	10
	Burchell's zebra	0.01323	76	Cape buffalo	0.00148	674
	Warthog	0.00857	117	Kudu	0.01111	90
	Black wildebeest	0.00155	644	Eland	0.00088	1134
	Red hartebeest	0.00579	173	Mtn. reedbuck	0.01648	61
	Common duiker	0.01905	53			
Sour Grassland	Cape mtn. zebra	0.01905	53	Grey rhebok	0.06000	17
	Red hartebeest	0.00405	247	Cape buffalo	0.00280	357
	Common duiker	0.02222	45	Eland	0.00370	270
	Oribi	0.02143	47	Mtn. reedbuck	0.04615	22
	Grysbok	0.03333	30			
Mixed Grassy Shrubland	African elephant	0.00085	1182	Grysbok	0.07320	14
	Black rhinoceros	0.00266	376	Grey rhebok	0.03922	26
	Cape mtn. zebra	0.01494	67	Cape buffalo	0.00220	455
	Red hartebeest	0.01060	94	Kudu	0.00813	123
	Common duiker	0.04880	20	Eland	0.00218	459
	Klipspringer	0.06274	16	Mtn. reedbuck	0.03017	33
	Steenbok	0.02614	38			
Fynbos	Cape mtn. zebra	0.00756	132	Grey rhebok	0.03492	29
	Red hartebeest	0.00172	583	Eland	0.00353	284
	Common duiker	0.06349	16	Mtn. reedbuck	0.00488	205
	Grysbok	0.38094	3			
Riparian Woodland	African elephant	0.00308	324	Common duiker	0.16931	6
	Black rhinoceros	0.00924	108	Springbok	0.01429	70
	Burchell's zebra	0.01299	77	Steenbok	0.06349	16
	Bushpig	0.03896	26	Cape buffalo	0.03204	31
	Warthog	0.06857	15	Kudu	0.02822	35
	Red hartebeest	0.01158	86	Bushbuck	0.02930	34
	Blue duiker	0.12698	8	Eland	0.00198	504
Dunefield	Bushpig	0.00135	743	Grysbok	0.00658	152
	Common duiker	0.00439	228	Bushbuck	0.00304	329

estimated requirement of 3400 ha for a troop of 80 individuals is derived from this information.

Herbivores

The model's estimations of the spatial requirements (and densities) for all species, except hippopotamus, in a single MHC are listed in Table 4. The estimations for MHCs that can potentially carry hippopotamus are listed in Table 5. The inclusion of hippopotamus within certain MHCs has, predictably, had the effect of lowering the densities and increasing the spatial requirements of all the bulk grazers in these habitats.

Thicket forest mosaic and thicket savanna mosaic can potentially carry the highest densities of elephant (0.54 individuals/km²). Riparian woodland and thicket savanna mosaic can potentially carry the highest densities (0.8–0.9 individuals/km²) of black rhinoceros, as they can Cape buffalo

(2.1–3.2 individuals/km²) and common duiker (14.7–16.9 individuals/km²).

In the case of the African elephant, a megaherbivore, social constraints (e.g., inter-bull aggression–Kerley & Boshoff 1997; Whitehouse & Kerley 2002) have not been violated by the model's predictions. Interaction between individuals of another megaherbivore, the black rhinoceros, provides a major constraint (Adcock 1994) and a general minimum spatial (social) requirement of 200 ha/ animal has been suggested (see Hall-Martin & Knight 1994). Only four of the 16 density estimates provided by the model are above this suggested maximum density for this species; given the nature of the habitats in question, these estimates require field testing. It is noteworthy that in xeric succulent thicket in the Andries Vosloo Kudu Reserve, a density of as high as 1 male rhino/50 ha has been recorded (Adcock 1994).

It is difficult to obtain empirical data to test the estimates provided by the spreadsheet models. There is virtually no information for the study area, and where information is available, it is normally unsuitable due to a number of constraints. For example, populations of the larger mammal species in the current AENP (including the Zuurberg portion), and indeed in other national parks and nature reserves in the region, are not natural and are influenced by factors such as presence of fencing (affecting population numbers, and limiting natural movements), and the absence of the large predators (influencing population structure and causing behavioural aberrations). Thus, densities may be relatively high in protected areas due to a combination of pristine, or near-pristine, habitats and absence of the larger predators. In addition, the spatial requirements of the herbivores are known to vary between habitats, owing to spatial variation in forage quality and availability, and shelter. Thus, until empirical studies have been conducted in the MHCs in the GAENP planning domain, testing of the model's predictions is always going to be problematic.

Notwithstanding the contraints mentioned above, an attempt was made to compare empirically obtained spatial requirement data with the predictions from the model (Table 6). With few exceptions, the data derived from the model were broadly corroborated for those herbivore species for which published information is available, thereby indicating that realistic values were generated by the model. It is again emphasised that the predictions from the model should be regarded as hypotheses and should be tested through field studies and modified where necessary (see also General Discussion).

Discussion

The spatial requirement and density data generated by the model described here are considered to be realistic. They can therefore be meaningfully used in the conservation planning exercise for the larger mammals in the GAENP planning domain. These data also provide useful information for guiding conservation management decisions, for example, determining multi-species assemblages and preliminary stocking rates of herbivores in the proposed GAENP.

It is emphasised that the estimated densities or spatial requirements refer to a situation where the entire suite of potentially occurring species is available and present, and the habitats in which they can occur are in an "intact" or "potentially restorable" state. Any deviation from this scenario, e.g., due to the unavailability of a species (for various reasons) or total habitat transformation, will require manipulation of the data and rerunning of the model.

We recognise, 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 being influenced by seasonality. There are, however, no alternatives when working at this scale, and with so little ecological information available for the species concerned.

Table 5

Estimated densities and spatial requirements values of the larger mammalian herbivores in areas of nine Mammalian Habitat Classes in the GAENP planning domain that contain hippopotamus habitat. Data derived from a spreadsheet model. See text for calculations and assumptions. Scientific names in Table 1

Mammal Habitat Class	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)
Thicket Forest Mosaic	African elephant	0.00540	185	Common duiker	0.06617	15
	Black rhinoceros	0.00361	277	Grysbok	0.34740	3
	Bushpig	0.06818	15	Cape buffalo	0.00104	963
	Hippopotamus	0.00198	504	Bushbuck	0.16034	6
	Blue duiker	0.69481	1			
Thicket Savanna Mosaic	African elephant	0.005395	185	Springbok	0.014286	70
	Black rhinoceros	0.00807	124	Oribi	0.040816	25
	Burchell's zebra	0.005772	173	Steenbok	0.061224	16
	Bushpig	0.00974	103	Grysbok	0.061224	16
	Warthog	0.011429	88	Cape buffalo	0.011571	86
	Hippopotamus	0.005527	181	Kudu	0.02466	41
	Red hartebeest	0.007722	130	Bushbuck	0.102432	10
	Blue duiker	0.122449	8	Eland	0.001984	504
	Common duiker	0.147958	7	Reedbuck	0.011429	88
Zuurberg Mesic Thicket	African elephant	0.00229	436	Common duiker	0.07081	14
	Black rhinoceros	0.00386	259	Grysbok	0.10621	9
	Cape mtn. zebra	0.00112	893	Cape buffalo	0.00066	1516
	Bushpig	0.02897	35	Kudu	0.01180	85
	Hippopotamus	0.00173	577	Bushbuck	0.04902	20
	Blue duiker	0.21242	5	Eland	0.00182	551
Succulent Thicket	African elephant	0.00111	898	Common duiker	0.06092	16
	Black rhinoceros	0.00332	301	Klipspringer	0.07833	13
	Cape mtn. zebra	0.00050	1985	Grysbok	0.02948	34
	Bushpig	0.01407	71	Cape buffalo	0.00030	3371
	Warthog	0.00571	175	Kudu	0.01015	98
	Hippopotamus	0.00078	1283	Bushbuck	0.04218	24
	Red hartebeest	0.00386	259	Eland	0.00088	1134
	Blue duiker	0.05896	17			
Spekboomveld	African elephant	0.00142	706	Common duiker	0.06128	16
	Black rhinoceros	0.00334	299	Grysbok	0.09192	11
	Burchell's zebra	0.00046	2178	Cape buffalo	0.00028	3531
	Bushpig	0.01791	56	Kudu	0.01021	98
	Warthog	0.00727	138	Bushbuck	0.04242	24
	Hippopotamus	0.00074	1344	Eland	0.00112	891
	Blue duiker	0.06566	15			
Western Spekboom Noorsveld	African elephant	0.00022	4587	Springbok	0.00404	248
	Black rhinoceros	0.00348	287	Klipspringer	0.02857	35
	Cape mtn. zebra	0.00180	554	Steenbok	0.09583	10
	Burchell's zebra	0.00689	145	Cape buffalo	0.00106	942
	Warthog	0.00606	165	Kudu	0.01065	94
	Hippopotamus	0.00203	493	Eland	0.00056	1782
	Red hartebeest	0.00410	244	Mtn. reedbuck	0.01166	86
	Common duiker	0.06389	16			
Noorsveld	African elephant	0.00020	5004	Common duiker	0.06366	16
	Black rhinoceros	0.00347	288	Springbok	0.02037	49

Table 5 (continued)

Mammal Habitat Class	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)	Species	Density (ind./ha)	Est. spat. req. (ha/ind.)
	Cape mtn. zebra	0.00165	605	Steenbok	0.09549	10
	Burchell's zebra	0.00631	158	Cape buffalo	0.00097	1027
	Warthog	0.00833	120	Kudu	0.01061	94
	Hippopotamus	0.00186	538	Eland	0.00051	1944
	Red hartebeest	0.00563	178			
Karroid Bontveld	African elephant	0.00210	477	Springbok	0.00556	180
	Black rhinoceros	0.00617	162	Steenbok	0.03086	32
	Burchell's zebra	0.00561	178	Grysbok	0.03086	32
	Bushpig	0.00379	264	Cape buffalo	0.00346	289
	Warthog	0.01667	60	Kudu	0.01886	53
	Hippopotamus	0.00165	605	Bushbuck	0.01425	70
	Red hartebeest	0.01126	89	Eland	0.00077	1296
	Common duiker	0.02058	49			
Riparian Woodland	African elephant	0.00308	324	Common duiker	0.16931	6
	Black rhinoceros	0.00924	108	Springbok	0.01429	70
	Burchell's zebra	0.00866	116	Steenbok	0.06349	16
	Bushpig	0.03896	26	Cape buffalo	0.01736	58
	Warthog	0.06857	15	Kudu	0.02822	35
	Hippopotamus	0.00829	121	Bushbuck	0.02930	34
	Red hartebeest	0.01158	86	Eland	0.00198	504
	Blue duiker	0.12698	8			

The advantages and disadvantages of using the LSU approach to estimate stocking rates, is discussed in some detail by Boshoff *et al*. (2001b) and Boshoff *et al*. (2002). We contend that the LSU-based approach is appropriate for estimating densities of medium to large-sized wild mammals at a mega-reserve (e.g., GAENP) scale, and that realistic values, that can be used for systematic conservation planning in the GAENP planning domain, have been generated. An alternative to the LSU approach for calculating stocking rates is the use of a standing crop biomass of animals as an index of carrying capacity. In savanna regions, often exhibiting high rainfall and nutrient rich soils, primary production and animal density are generally positively correlated with mean annual rainfall (Coe *et al*. 1976). However, soil type influences and further complicates this relationship, even in the savannas, and the biomass of large ungulates can be as much as 20 times lower on nutrient poor soils (Fritz & Duncan 1994). The fact that savannas with nutrient rich soils support different kinds of vegetation and also different types and densities of herbivores from those with nutrient poor soils has been emphasised by Bell (1982). Given the high regional variation in rainfall, soil type (ranging from nutrient poor to nutrient rich soils) and presumably primary productivity, in the GAENP planning domain, this approach was not attempted in the present study.

There is strong evidence that a high density of elephants in the "Addo bush" habitat (Spekboomveld MHC) has a negative impact on the cover, architecture and diversity of the plants (Barratt & Hall-Martin 1991; Johnson *et al*. 1999; Lombard *et al*. 2001; Moolman & Cowling 1994; Penzhorn *et al*. 1974; Stuart-Hill 1992; Stuart-Hill & Aucamp 1993), summarised in Cowling & Kerley (2002). The only published recommended density for elephant in the AENP, and specifically

Table 6

Comparisons between the predictions of spatial requirements from the spreadsheet model (see text) and from available empirical data for similar habitats beyond the GAENP planning domain. Scientific names in Table 1

Mammal species	Empirical data(ha/individual)	Predictions from the model (ha/individual)	Notes
Black rhinoceros	Andries Vosloo Kudu Reserve: 50 ha/individual to 200 ha/individual (Adcock 1994).	Range: 108-376	The estimates from the model overlap with empirical data.
Cape mountain zebra	Mean of 4.7 individuals per breeding herd in MZNP (Penzhorn 1975); mean home range per breeding herd in MZNP is 910 ha (Penzhorn 1982). = 194 ha/individual	Range: 53-1373	The empirical values fall within the model's range.
Warthog	Andries Vosloo Kudu Reserve (Somers 1992) 12.32 animals/km² (from 800 animals per 6493 ha) = 8 ha/individual	Range: 15-1063	AVKR density considered to be artificially high due to absence of the large predators, especially lion.
Blue duiker	0.5–1 ha/individual (Apps 1996) 5.5–8 ha/individual (Hanekom & Wilson 1991) 1.8–11 ha/individual (Von Gadow 1978)	Range: 1-17	The empirical values correspond well with the model's range.
Common duiker	17 ha/individual, and as low as 20–50 ha/individual (Allen-Rowlandson 1986). 20–50 ha/individual (Rowe-Rowe 1991). Eastern Cape thicket: est. less than 3 ha/individal (Furstenburg & Kleynhans 1996).	Range: 6-228	The empirical values fall within the model's range.The empirical values fall within the model's range.The empirical value is simply an estimate.
Klipspringer	11–15 ha/individual (Norton 1980)	Range: 13-42	The empirical values broadly correspond with the lower end (i.e. highest density) of the model's range.
Oribi	Eastern Cape: 12.5 ha/individual (increasing population so could be higher density) (Van Teylingen & Kerley 1995). 8 to 30 ha/individual (Rowe-Rowe 1988) and 6.3 to 57.6 ha/individual (Everett *et al.* 1991).	Range: 33-63	This empirical study was conducted in prime habitat and one with a relatively high rainfall.The empirically obtained values overlap or correspond with the model's predictions.

Table 6
(continued)

Grysbok	1.3–9.4 ha/individual (Manson 1974).	Range: 3-152	The empirically obtained values overlap with the model's predictions.
Grey rhebok	15–152 ha/individual (Ferreira 1984). 15 ha/individual (Beukes 1987).	Range: 17-29	The empirically obtained values overlap or correspond closely with the model's predictions.
Kudu	Addo Elephant National Park: mean of 527 animals in 13 642 ha = 26 ha/individal (from SANP). MZNP: ca 100 animals in 6500 ha = 65 ha/individual (from SANP). Andries Vosloo Kudu Reserve (Allen Rowlandson 1980). = 17 kudu/km² or 5.9 ha/individual.	Range: 33-324	The model predicts relatively low densities; it may be overestimating the spatial requirements, for reasons not understood but possibly linked to kudu feeding ecology, or the kudu densities in these reserves may be artificially high due to an absence of large predators.
Bushbuck	20 ha/individual (Allen-Rowlandson 1986) S Cape: 14–20 ha/individual (Seydack 1984). 33 ha/individual (Odendaal & Bigalke 1979) E Cape: 77 ha/individual (Stuart-Hill & Danckwerts 1988).	Range: 6-329	In all cases quoted, the empirical values fall within the model's range.
Mountain reedbuck	MZNP: 409 animals in 6500 ha = 16 ha/individual (from SANP).	Range: 22-205	The MZNP conserves prime habitat for this species.

Fig. 27.

Fig. 28.

Fig. 29.

Fig. 30.

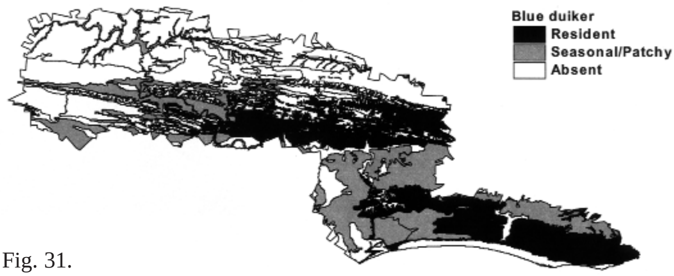

Fig. 31.

for the Spekboomveld habitat class, is derived from research by National Parks scientists during the early 1970s, when a density of 0.4 elephants per km² was proposed (Penzhorn *et al*. 1974). A significantly lower density of 0.142 elephants per km² was estimated for this habitat by our spreadsheet model. The highest densities predicted by the model, namely 0.54 elephants/km², are for the Thicket Forest Mosaic and the Thicket Savanna Mosaic. The basis for the fourfold higher density of 2 elephants/km² recommended by Hall-Martin & Barratt (1991), and adopted by Knight *et al*. (2002), is questionable (Cowling & Kerley 2002).

It needs to be emphasised that even though the model has attempted to address the issue of seasonality for certain species (by reducing the amount of allocated forage), it is important that the GAENP be managed as a single spatial unit, in order to provide maximum opportunity for movements by nomadic or migratory species, on a year-round basis. This will cater for ecological factors such as presence of surface water, seasonal food availability and the possible negative effects of selective foraging on threatened plants.

POPULATION SIZES

Methods

The potential population sizes of the 44 mammal species were calculated by simply multiplying the density estimate for each species with the area (in hectares) of the terrestrial habitats (i.e., MHCs), or length (km), in the case of rivers or coastline.

These data were calculated for two park planning scenarios, namely: slightly modified Kerley & Boshoff (1997) planning domain; and the GAENP planning domain; and according to two habitat transformation categories, namely: "Intact" and "Restorable".

Box 2: Estimated population sizes of the two otter species

Based on the information given in Table 3, it was decided to use a linear density of 1 individual/3 km of river or coastal habitat for both species of otter, namely Cape clawless otter and spotted-necked otter. Note that the transformation of landscapes did not affect the availability of rivers for otter conservation, i.e., all rivers were considered as "intact" habitat for otters. See "Spacial Requirements" for an explanation of methodology followed.

Cape clawless otter

183 km of potentially suitable river and coastal habitat for Cape clawless otter alone = 61 individuals

342 km of potentially suitable river habitat equally shared with spotted-necked otter; results in 171 km available for Cape clawless otter = 57 individuals.

Grand total = 118 individuals

Spotted-necked otter

342 km of potentially suitable river habitat equally shared with Cape clawless otter; results in 171 km available for spotted-necked otter = 57 individuals.

Grand total = 57 individuals

Fig. 32.

Fig. 33.

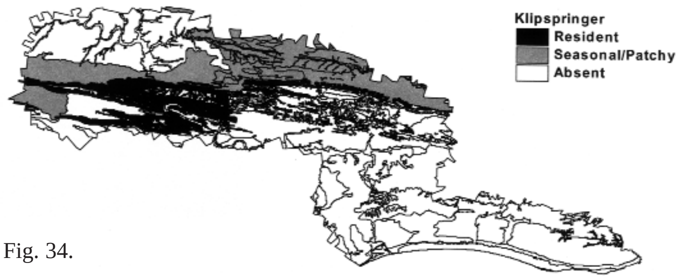

Fig. 34.

Fig. 35.

Fig. 36.

Fig. 37.

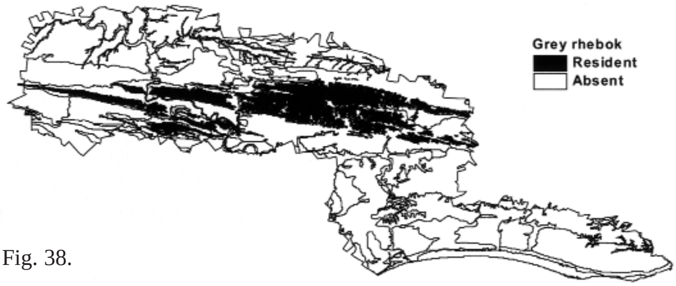

Fig. 38.

Fig. 39.

Fig. 40.

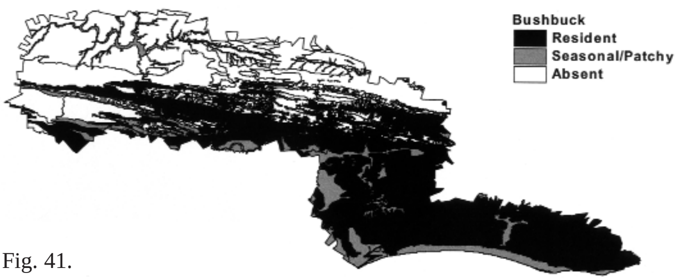

Fig. 41.

Results

The potential population sizes, according to two park planning domain scenarios are listed for all species in Table 7. The population estimates for the two otter species are presented in Box 2.

Discussion

The estimates of populations sizes provided in Table 7 and in Box 2, can be used to measure the degree to which mammal population targets, that are set as part of a separate conservation planning exercise (e.g., Kerley *et al*. *in prep*.), are met by the various planning domain scenarios, taking into account different transformation categories.

The estimated population sizes for two species require comment. First, the estimates for the klipspringer require closer scrutiny, as the values appear to be somewhat high. In the MHCs where this species has been marked as being "resident" it may be more appropriate, in a future study, to map individual habitat patches. Second, the estimates for the kudu may be too low. The reasons for this are not known but may be linked with this species' particular feeding ecology. A similar pattern was observed in the analysis for the Cape Floristic Region (Boshoff *et al*. 2002). The estimates for some of the other smaller ungulates may at face value also appear to be high (e.g., grysbok: JG Castley *pers. comm*.). We again emphasise that the model's outputs represent potential densities in intact habitats, and

Table 7

The estimated potential total population sizes of the medium- to large-sized mammals, according to two GAENP planning domain scenarios, and according to two transformation categories. Scientific names in Table 1

Species	Estimated number of animals					
	Modified Kerley & Boshoff (1997) planning domain			GAENP planning domain		
	Intact	Restorable	Total	Intact	Restorable	Total
Chacma baboon	3885	1504	5388	5477	2233	7710
Vervet monkey	60440	28480	88920	90504	46297	136801
Porcupine	15915	6328	22242	22957	10250	33207
Aardwolf	356	134	490	536	227	763
Brown hyaena	37	15	52	55	24	79
Spotted hyaena	37	17	55	56	28	84
Cheetah	3	3	6	6	4	10
Leopard	25	10	36	37	16	53
Lion	40	19	58	60	30	90
Caracal	85	36	121	126	59	184
African wild cat	1696	720	2416	2554	1189	3743
Small spotted cat	130	83	213	205	129	334
Serval	36	18	54	49	28	78
Bat-eared fox	3280	2137	5416	5291	3472	8763
Wild dog	35	15	50	52	25	77
Cape fox	282	177	458	448	282	731
Black-backed jackal	418	176	594	619	287	907
Honey badger	48	19	67	70	31	101
Aardvark	45	23	68	70	38	108
African elephant	322	141	464	523	248	771
Black rhinoceros	766	401	1167	1250	677	1927
Cape mountain zebra	851	161	1012	1083	245	1328
Burchell's zebra	996	805	1801	1724	1324	3048
Bushpig	3316	958	4274	4845	1557	6402
Warthog	1325	820	2145	2206	1362	3569
Hippopotamus	27	29	55	32	33	64
Black wildebeest	24	8	32	43	21	64
Red hartebeest	874	460	1334	1369	755	2124
Blue duiker	24849	7824	32673	36277	12352	48628
Common duiker	14479	6843	21322	21777	11204	32981
Springbok	1666	1022	2689	2929	1815	4744
Klipspringer	3574	1293	4867	4836	1954	6790
Oribi	702	510	1213	1234	929	2162
Steenbok	7967	6213	14181	13288	9958	23246
Grysbok	21964	3693	25657	28569	6296	34865
Grey rhebok	2122	88	2210	2393	106	2499
Cape buffalo	582	414	996	1058	732	1789
Kudu	2023	1120	3143	3277	1892	5169
Bushbuck	7684	2965	10649	11577	5074	16652
Eland	340	84	424	470	144	614
Reedbuck	103	128	231	219	241	460
Mountain reedbuck	1528	423	1951	1980	639	2618

Fig. 42.

Fig. 43.

Fig. 44.

therefore cannot be equated with current densities in transformed habitats.

The data in Table 7 indicate that potential populations of herbivore species that are more prevalent in the "upland" areas are less impacted by transformed (but potentially restorable) habitats than are herbivore species that are more prevalent in "lowland" areas. For example, the steenbok is markedly affected by transformation in the "lowland" areas, whereas the grey rhebok is not. This pattern is understandable, given that most of the transformation has occurred in the "lowland" areas.

GENERAL DISCUSSION

The information generated by the present study provides realistic guidelines for the testing of population targets for medium to large-sized mammals that can potentially occur in the GAENP planning domain, and for the identification of species for which metapopulation management may be required for their conservation. It will also guide park managers regarding species that are no longer present in the general GAENP domain but that can be considered for re-introduction, and in the maintenance of realistic densities. The information in this report will therefore make a significant contribution to achieving the overall conservation goals of the GAENP.

It is important that the estimates derived by this study 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/density 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 (Bowman 1995; Macnab 1983; May 1991).

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The GIS tasks involved in collapsing the 43 original land classes to form 21 Mammal Habitat Classes (MHC), and the calculation of the areas of the MHCs that comprised, or did not comprise, habitat for hippopotamus, and also the areas of "Intact" and "Restorable" habitat, were conducted by CSIR-Environmentek, in a consortium with TERU, as part of a GEF co-funded contract to South African Parks to provide conservation planning services. We thank Jeanne Nel, Inge Kotze, Sarah Davies and Dirk Roux, all of CSIR-Environmentek, for their patience and co-operation in providing TERU with these GIS outputs.

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Appendix 1

Adjusting stocking rates and proportional allocation of stocking opportunities to foraging guilds (see text for methods)

	Forest	Thicket Forest Mosaic	Thicket Savanna Mosaic	Zuurberg Mesic Thicket	Addo Heights Mesic Thicket	Succulent Thicket	Spekboomveld	Eastern Spekboom Noorsveld	Western Spekboom Noorsveld	Noorsveld	Grassy Bontveld	Karroid Bontveld	Karoo Thicket Mosaic	Karroid Dwarf Shrubland	Karroid Broken Veld	Sour Grassland	Mixed Grassy Shrubland	Fynbos	Riparian Woodland	Dunefield	Sundays Saltmarsh
Adjusted Stocking Rate (LSU/ha)	0.017	0.111	0.143	0.059	0.059	0.048	0.045	0.056	0.045	0.042	0.056	0.056	0.042	0.042	0.048	0.050	0.059	0.048	0.143	0.004	0.000
Bulk Grazer	1	5	20	9	9	5	5	30	25	25	29	20	15	20	25	30	20	10	30	0	0
Concentrate Grazer	1	1	20	1	1	15	10	10	10	10	18	15	15	15	15	30	20	10	15	0	0
Mixed Feeder	29	27	15	25	25	15	20	10	10	10	18	15	15	15	15	20	20	20	15	20	0
Browser	69	67	45	65	65	65	65	50	55	55	35	50	55	50	45	20	40	60	40	80	0