HABITAT SUITABILITY ASSESSMENTS FOR SABLE ANTELOPE

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ABSTRACT

Relationships between occurrence of a species and features of habitats occupied are central to establish factors that influence its distribution. Within large protected areas extinction processes may cause retractions of species distributions to areas that are still suitable or to locations least affected by a negative influence. The aim of the project was to identify factors that influence the suitability of areas where sable antelope occur. Climate and geographic barriers have overriding influences over biotic factors to identify regions that lie outside a species range. Abiotic factors (e.g. geology and rainfall) indicate places with environmental conditions that allow a species to persist (spatial extent of a fundamental niche). However, biotic interactions can constrain occupation to a limited proportion of those conditions (subset of fundamental niche). I used aerial census data (1977-93) in Kruger National Park to: (1) model distribution patterns commonly exhibited by large ungulate species with the objective of identifying methods most suitable for assessing different aspects of species distributions; (2) assess how distribution patterns of 12 antelope species have apparently changed since around 1960 and how these changes may be related to sable distribution shifts or abundance decline; (3) assess whether a climate effect could have caused contractions of range and abundance of sable and other rare antelopes and (4) identify features that restricted a widespread distribution of sable in KNP using logistic regression models.

In chapter 2, I compared and contrasted performance of LoCoH and kernel methods for constructing distributions for species exhibiting (i) wide and continuous distributions with a few gaps, (ii) broad distribution with local concentrations and absences, (iii) linear distribution pattern associated with rivers, and (iv) a patchy distribution pattern. The methods have valuable capabilities for assessing different objectives of species distributions. The type of spatial distribution exhibited by a species influences the performance of these methods. This contrasts generalizations from home range studies that suggest superiority of one method over the other. The LoCoH method tends not to include areas where a species was not recorded. In contrast, kernel method exhibited the opposite bias. However, their differences were not large enough to lead to a diverse interpretation of range extents or occupancy patterns. Automatic procedures of choosing *h* appeared not adequate for mapping distribution patterns of species that occur in patches where outlines of outer

boundaries are not clearly defined or for those species exhibiting clumped occurrences in places and widespread occurrences elsewhere. A different *h* value may be necessary for each section of such a distribution with fixed kernel method. This is achieved by dividing a study area into separate sections and mapping the ranges independently. The LoCoH is suitable for indicating gaps and/or fine-scale range shifts. However, LoCoH method may have to be applied with caution for species exhibiting continuous distributions because there is a possibility of emphasizing unimportant gaps.

Despite the fact that distribution patterns around 1960 were vaguely complied, it appeared that common species have increased occupation of northern half of KNP and several species (impala, buffalo, wildebeest, warthog, and waterbuck) have been sighted during dry season (1980-1993) in areas indicated around 1960 as wet season range. The 1980-1993 distribution of impala, warthog, and waterbuck appeared more widespread away from rivers than around 1960. Distributions of sable, tsessebe, eland, and roan contracted in northern half and in central region of KNP. Fences that blocked migrations of wildebeest and zebra outside the park to the west of central KNP appeared associated with distributional changes of herbivores in this area. Augmenting surface waterpoints was a key influence in expansions of distributions of common species into northern half of KNP and for occurrences of some species during dry season in areas previously used during wet season. The contractions of distributions of rarer antelopes occurred concurrently with expansions of common species into northern half of KNP where rare antelopes mainly occur. The above suggests that some areas of northern half of KNP may have become less suitable to rare antelopes.

Despite that the exact influence of climate on rarer antelopes could not be established, distribution pattern changes were characteristic of an influence consistent with that of climate. Range contractions were evident for all three species (sable, roan and Tsessebe), associated with local herd extirpations, especially following the severe 1991/2 drought. Herds of sable, roan, or tsessebe that occurred in isolated locations disappeared and ranges contracted even in the relatively wetter southern section of the park. Sable herds persisted in discrete patches after a widespread contraction of their formerly contiguous range in northern section.

Sable prevalence was highest on nutrient poor granite and sandstone rather than nutrient rich basalt and gabbro. Distances from perennial water sources did not

have overriding influences on where sable herds occurred. Sable prevalence was higher in mopane savanna woodland and sour bushveld than shrubland, dense bush savanna, or grassland with few trees. Sable herds were prevalent in localities that exhibited relatively low predation risk and low effects of competition from abundant grazers, implying that at the edge of a range, interactions involving biotic factors appear more important than searching for areas which potentially have more forage resources. Predation risk appeared more influential to sable distribution than competition. Findings showed that biotic factors strongly modify effects of abiotic factors on where rare and sedentary species establish.

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"No one can get far in any journey by just taking an aimless lazy stroll"–Milton Kamwendo

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CHAPTER 1

Introduction

AIMS AND OBJECTIVES

Broad Aim

The main aim of the project was to identify factors that influenced habitat suitability for sable antelope.

The starting objectives were

1. To identify environmental features associated with the historical sable distribution in Kruger National Park.
2. To identify environmental features associated with the recent distribution of sable.
3. To identify environmental features associated with variation in presence of sable within their recent distribution range.
4. From this basis, to develop a habitat suitability model for sable for the Kruger National Park.
5. To test the model by applying it to data for sable distribution and habitat features in Hwange National Park.

The study was designed as part of a research programme undertaken by the Centre for African Ecology at the University of the Witwatersrand. The aim of the programme was to understand the ecology of the rare antelope species that are declining in the Kruger National Park (KNP).

Initially, the research plan consisted of two major phases; i) developing a habitat suitability model for Kruger National Park and ii) testing the model using sable distribution data for Hwange National Park, Zimbabwe. The original plan was later modified because of time constraints. Objective number 5 was put on hold and objective number 1 was changed to: “to establish recent changes to historical distributions of large ungulate species in the KNP”. The focus of the new objective was (a) to assess whether perceived contractions of distribution and abundance had occurred only to sable antelope, and to document distribution patterns of other large ungulate species in KNP reliably as a basis for assessing future changes, and b) to assess if changes in distribution patterns of common species and changes in sable antelope distribution and abundance were associated. Another two objectives were incorporated into the study; first, to compare performances of Local convex hull and kernel methods in estimating large scale distribution ranges across KNP using species that exhibited different spatial patterns of occurrences. The motivation for this new objective was that obtaining information on how a probability of occupation of an area changes over time could be important in addressing concerns on range shifts and/or species losses in most conservation areas. The latter is important because it helps distinguish concentration areas from marginal sections within occupied regions and helps identifying localities where a species is likely to disappear. The second new objective was "to establish if climate influences were implicated in the perceived shifts in distributions and declines in abundances of sable and other rare antelopes in KNP". The motivation for this objective was that since KNP is at the edge of the geographic distribution of sable in Africa then climate change effects could be implicated in their population decline.

THE NEED FOR THE STUDY

Sable antelope (*Hippotragus niger*) numbers have progressively declined in parts of Southern Africa. Since 1986, abundance of sable in KNP dropped from 2 240 individuals in 1987 to an estimated 550 in 1995. Tsessebe counts that peaked at 1 163 in 1986 had dropped to an estimated 250 animals by 1995. During the same period, roan that numbered about 450 animals in 1986 dropped to an estimated 25 free-ranging animals by 1995 (Grant *et al*. 2002, Ogutu & Owen-Smith 2003, Owen-Smith & Ogutu 2003). Evidence from previous studies implicated an increase in abundance of lion, coupled with shifts in prey selection as being responsible for the downturn in population trend of these species after 1987 (Harrington *et al*. 1999, Owen-Smith & Mills 2006, 2008). Underlying this was expanded surface water availability through the provision of artificial waterpoints. A drought in 1991/2 may have additionally contributed to decline of these species through limiting availability of forage resources (Ogutu & Owen-Smith 2003). Such stressful conditions could be associated with increased susceptibility of ungulates to predation (Ogutu & Owen-Smith 2005, Owen-Smith *et al*. 2005). Some artificial waterpoints have been closed since 1993, but populations of the rarer antelope have not recovered (Grant and van der Walt 2000). Surveys in the KNP show that kudu (*Tragelaphus strepsiceros*) and waterbuck (*Kobus* *ellipsiprymnus*) that declined during periods of low rainfall (Owen-Smith & Ogutu 2003) have recovered.

The sable antelope constitutes an interesting model species because it occurs more commonly in wetter regions of Africa, but is at the southern edge of its distribution in KNP (Skinner & Chimimba 2005), the species forms sedentary and cohesive breeding herds (Estes 1991). Sable antelope exhibits a patchy distribution in KNP (Pienaar 1963). This provides an opportunity to distinguish factors such as resources or biotic influences that are associated with areas the species occupy, or factors that could exclude occupation of certain areas within the park. The present study covers a period when sable numbers were declining in the park; hence, it contributes to exploring potential causal mechanisms.

LITERATURE REVIEW

Sable distribution in Africa

There are three subspecies of sable in Africa: *Hippotragus niger niger, H. n. roosevelti* and *H. n. variani.* The subspecies *H. n. roosevelti* and *H. n. variani* occur in Kenya and Angola respectively. The subspecies *H. n. niger* exhibits the largest distribution occurring in Zimbabwe, Botswana, South Africa, Zambia, Mozambique, and Malawi (Stuart & Stuart 2000, Skinner & Chimimba 2005). The Crocodile River forming KNP's southern boundary was the historical southern limit in sable distribution, while south eastern Kenya was the limit in the north (Wilson & Hirst 1977). The sable western limit extended from Botswana into regions of Angola (Wilson & Hirst 1977). The giant sable (*H. n. variani*) was limited to the area between the Cuanza and Londo Rivers in Angola (Wilson & Hirst 1977).

Landscape and habitat selection

Gertenbach (1983) defined a landscape as an area that exhibit a specific geomorphology, climate, soil, and vegetation pattern together with associated fauna. Landscapes are composed of mosaics containing inter-linked patches of different shapes and sizes (Garshelis 2000, Wiens 1985). A patch is an area that differs from neighbouring areas (Wiens 1985). The above defines a patch as a discrete and homogenous entity, but in reality, such patches are rarely encountered. Instead, natural landscapes contain mosaics of patches within patches over broad scales (Wiens 1985, Garshelis 2000). Thus, mosaics of patches reflect spatial heterogeneity, and changes in the pattern and process over time reflect temporal heterogeneity of the system (Pickett *et al*. 2003). Processes determining heterogeneity include different plant and animal species occurring over time, foraging behaviour, predator-prey interactions, dispersal, nutrient dynamics, and disturbances (Belsky 1995). The above processes have two important and implicit properties of landscapes: namely heterogeneity and scale (Garshelis 2000). Thus, issues of habitat selection in a heterogeneous environment require sensitivity to spatial and temporal scale.

In semi-arid environments, selection of a habitat and its utilization by grazers (Western 1975) and cattle (Scoones 1995) is primarily dependent on location relative to water. Different habitat choices result in animals being non-randomly distributed in space (Dugatkin 2004). Habitat is an area with a combination of resources (such as food, water, etc) and environmental conditions (temperature, precipitation, presence or absence of predators) that enables occupancy and use by individuals of a given species or population and allows those individuals to survive and reproduce successfully (Morris *et al*. 1992). The patterns of habitat distribution can be seen as a consequence of decisions by animals in selecting a place in which to live or feed perhaps during unfavourable times. These decisions can be based on biological factors such as predation, location of mates etc, or be based on environmental factors such as food or availability of water etc.

Suitable areas are those that afford conditions necessary for maintaining a viable population. Some places support more individuals of the same species than areas that are marginally suitable. The preference for an area can change seasonally in relation to seasonal availability of food plants. For example, an area with palatable deciduous species for browsers may not be preferred in the dry season when plant species lose their leaves but become preferred during the growing season (Owen-Smith & Cooper 1987).

Studies of factors influencing habitat selection and resource use arrive at different conclusions at different scales of analysis (Johnson 1980). This is because habitat selection is a hierarchical process (Senft *et al*.1987, Bailey *et al*. 1996). From a broader scale, an animal occurs in a range but then makes decisions as to which habitat to occupy and when to use it at much finer and narrower scales (Rosenzweig 1985, Senft *et al*. 1987).

As habitat selection occurs in a hierarchical fashion, a number of orders of selection have been assigned (Senft *et al*. 1987, Bailey *et al*.1996, Owen-Smith 2002). The fifth order is the procurement of food items (Bailey *et al*.1996, Owen-Smith 2002). The fourth order pertains to a feeding station. For example, food at a feeding station could be an extended herbaceous sward (Bailey *et al*. 1996). The distribution of feeding stations within a locality forms a patch, which constitutes the third order of selection (Senft *et al*. 1987). A patch is defined as a cluster of feeding stations different from its surroundings and other clusters in appearance, and size (Bailey *et al*. 1996). Patches require search time and assessment of risks before occupation. The second level is the home range, which encompasses various patches. Animal activities can last for several months, years or a lifetime in a home range. The geographic region (first order of selection) is the broadest scale and species occurrences at this level are influenced by the climatic conditions under which a species can persist (Johnson 1980). Thus, at this very broad scale, certain regions lie outside a particular species range.

Habitat choice models have been produced to explain how animals distribute themselves in space and time with respect to resources in the environment (Rosenzweig 1985, Morris 1991). The Ideal Free Distribution (IFD) is a density-dependent habitat selection model (Rosenzweig 1991). The IFD assumes that individuals select a habitat in relation to fitness (i.e. reproductive success) (Morris 1989, Pulliam & Danielson 1991) and assumes that fitness is a function of density. In this model, species distribute individuals proportionately as regards to resources that can be obtained from the habitats (Rosenzweig 1991)

The despotic model incorporates species interactions such as monopolization of resources through dominance and/or territorial behaviour, and exclusion of other individuals from exploiting resources, thus relegating these less dominant individuals to less suitable habitats (Rosenzweig 1985). Pulliam (1988) documented that animals in different habitat types exhibited differences in reproductive success. Therefore, habitats that offer better reproduction and survival chances are occupied by more individuals compared with those that offer lower reproduction and survival chances. Thus, a proportion of individuals may occur in a “source” habitat (i.e. one that over a long period presents no net change in population size but exports its surplus of individuals to sink habitats) (Pulliam 1988). A "sink" habitat is where within-habitat reproduction is insufficient to balance local mortality. Nevertheless, populations may persist in such marginal habitats, their numbers being locally maintained by immigration from source areas (Pulliam1988, Morris 1991).

In a source-sink situation, individuals occupying better habitats achieve higher fitness through interactions such as dominance and exclusion. In the source, through increased density and competition, animals redistribute themselves among the remaining habitats. However, the IFD model assumes that gains are experienced immediately as resources are exploited (Owen-Smith 2002). The model assumes that food renewal is continuous and so no depletion occurs. Neither assumption is close to the real situation for herbivores where the effects and consequences of competition may not be immediately felt (Owen-Smith 2002). For herbivores, competition results from resource exploitation and its effects are not experienced immediately but at a later stage when less food remains as a result of feeding by competitors. In semi-arid areas, effects of resource depression on habitat choice may not be that important during the wet season as compared with the dry season (Owen-Smith 2002). Thus, habitat distribution models have to accommodate resource variability for herbivores in semi-arid areas of Africa. The models should incorporate different mosaics of resources and related benefits of exploiting heterogeneous food types such as a) high-quality and quick growing foods in wet season, b) reserve resource sustaining herbivores during early dry season, and c) poor-quality, high bulk foods serving as a buffer during late dry season. Therefore, depletion of resources is selective and habitats vary in the value of food they offer at different stages in the seasonal cycle as well as in productive potential. Furthermore, density of animals could be a misleading indicator of habitat suitability. An increase in predation risk may cause animals to crowd in safe areas although those areas may not be suitable. Besides, simple comparisons of densities between two areas may not produce information on whether it is a sink or a source habitat (Pulliam 1988). Other habitat selection models consider areas most frequently occupied by animals as representing "high quality" habitats or contributing more to fitness (Garshelis 2000, McLoughlin *et al*. 2002, Osborne *et al*. 2001). However, in certain circumstances areas with large herbivore concentrations may attract presence of predators, thus increasing the risks of mortality (Brown *et al*. 1999). Therefore, simply identifying habitats with high herbivore densities and considering them as suitable may be misleading.

Vegetation structure, season, and resource components that bridged critical periods were central in a habitat suitability model for greater kudu (*Tragelaphus strepsiceros*) (Owen-Smith 2002). The model identified the important contribution by previously less preferred food resources in the wet season through buffering animals during critical times of the dry season. Thus, resource preference and selection is dependent upon time of year and abundance of other resources. These less preferred resources sustain herbivore population levels.

Resource selection function models

These models are increasingly becoming important in conservation because they allow quantitative characterization of resource use, estimate occurrence of animals by habitat type (Boyce *et al*. 2002) between large and small scales in a form conducive for management purposes (Boyce & McDonald 1999).

Resource selection models developed for habitat selection by moose (*Alces alces*) (Neu *et al*. 1974, Erickson *et al*. 1998) and for pronghorn antelope (*Antilocapra americana*) (Ryder 1983 cited in Manly *et al*. 2002) and a habitat suitability index developed for moose (Dettki *et al*. 2003) have demonstrated the potential offered by these tools. Habitat selection was influenced by seasonal shifts in food species composition and availability.

Boyce *et al*. (2003) documented seasonal differences in habitat selection by elk. Summer habitat selection was determined by nutrient content of the food (quality) and vegetation species composition. Species richness or quality of the resource was not important during winter periods. Snow depth influenced habitat choice in winter. Elk selected habitats with little accumulation of snow. This model identified that management by burning benefited elk in summer but reduced use of the same habitats in winter as burnt areas were avoided.

Ecological Niche Factor Analysis (Hirzel *et al*. 2002) has also been used to assess habitat suitability for ibex (*Capra ibex nubiana*). Hirzel *et al*. (2002) reported that ibex selected high altitudes, steep and rocky slope habitats. The model identified habitats close to human activities and dense forest habitats as marginal for ibex. However, the model did not satisfactorily explain why some suitable and quality habitats were not selected. Another concern with ENFA techniques is that they can only handle linear relationships (Hirzel *et al*. 2002). In ecology there are very few linear relationships. Habitat selection by an ungulate is certainly affected by several factors, which may show non-linear influences and at times the same factors present interactions amongst themselves.

Remotely sensed NDVI (Normalized Difference Vegetation Index) has been used in landscape vegetation classifications being based on similarities of reflected radiation of the phenological attributes of vegetation (Nemani & Running 1997). NDVI is derived from the red: near infrared reflectance ratio [NDVI = (NIR – RED)/ (NIR + RED)] (Pettorelli *et al*. 2005), where NIR and RED are values of near-infrared and red light respectively as reflected by vegetation and picked up by satellite sensors. NDVI has yielded positive correlations with vegetation biomass and shown spatial and temporal distribution of vegetation communities (Pettorelli *et al*. 2005). The NDVI can be used for quantitative characterization of green biomass (Oesterheld *et al*.1998). The latter is possible since green vegetation can be spectrally distinguished from senescent vegetation, soil and rock by chlorophyll's absorption of red wavelengths and by high reflectance of near-infrared (NIR) wavelengths due to leaf and canopy structure (Wessman *et al*. 1997). Remotely sensed NDVI data sets are available from the Advanced Very High Resolution Radiometer (AVHRR) onboard the National Oceanic and Atmospheric Administration (NOAA) polar satellites (Kerr & Ostrovsky 2003).

High NDVI values are typically associated with green vegetation such as closed canopy woodland or a continuous layer of green grass and low NDVI values are generally associated with non-continuous vegetation cover, sparse shrub cover, dry grass or exposed bare soil (Oesterheld *et al*. 1998, van Bommel *et al*. 2006). Enhanced Vegetation Index (EVI) is incorporated in Moderate Resolution Imaging Spectroradiometer (MODIS) and provides better quality and much higher spatial resolution (up to 250 m), while also matching AVHRR's almost-daily global coverage. In other words, MODIS will provide images over a given pixel of land just as often as AVHRR, but in much finer detail, hence this data can be applied for monitoring canopy type, canopy structural variations, and architecture (Nemani & Running 1997, Pettorelli *et al*. 2005, Oesterheld *et al*. 1998). A temporal analysis of NDVI values can provide information on the effects of a delayed or an early start of the growing season to vegetation abundance. This provides clues to the expected performance of herbivore populations in relation to available food (Pettorelli *et al*.

2005). NDVI values were correlated with reindeer calf condition in spring and used to predict calf winter survival (Pettorelli *et al*. 2005).

Griffith *et al.* (2002) cited in Pettorelli *et al.* (2005) showed that caribou (*Rangifer tarandus*) selected annual calving areas with higher rates of vegetation greening. The above studies show the potential of NDVI values to become better predictors of herbivore biomass than annual rainfall. This is because satellite information has greater coverage for each area than rainfall data. Rainfall and other field data are challenging to use for predicting regional changes because such data are generally collected at small spatial and temporal scales, and vary in their reliability in different places.

Herbivore habitat selection in Africa

Catenas present soil sequences that are associated with different plant communities from uplands to bottomlands (Belsky 1995). This topography has effects on water availability for plants and determines the proportion of green leaf that remains in the sward through the dry season (Owen-Smith 2002). Bell (1971) found that buffalo, zebra, wildebeest (*Connochaetes taurinus*), topi (*Damalicus lunatus*), and Thomson’s gazelle (*Gazella thomsonii*) selected habitats on high ground in the wet season where nutritious short grass dominated. With the progression of the dry season the herbivores selected habitats towards the bottom of the catena where tall and medium grasses of poor quality prevailed. This habitat selection down the catena occurred in a determined sequence with bigger sized herbivores going first (Duncan 1975). Bell (1971) referred to this as “grazing succession”.

Dry season is critical for herbivores in Africa and they have to adapt their habitat choices or feeding strategies to cope with the limited forage (Scoones 1995) and limited drinking water availability. Scoones (1995) termed cattle feeding areas used during the dry season as “Key resource areas”. Thus, in seasonal systems herbivores are limited by their ability to survive the dry season when most plants are dormant (Illius & O’Connor 2000). Dry season water availability influences habitat selection in seasonal savannas because it contributes to the retention of green vegetation. Western (1975) described herbivores as either “water-dependent or water-independent” depending on their distributions in relation to distance from permanent water sources. Water-independent species are mainly browsers that rely on high water content in their diet and grazers are mostly water-dependent since they have to frequently drink water.

The same patterns were also reported by Lamprey (1963) who observed zebra, wildebeest, hartebeest (*Alcelaphus buselaphus cokii*) using areas close to water sources, but impala (*Aepyceros melampus*), oryx (*Oryx besia callotis*), and Grant's gazelle remaining in habitats without free water for long periods. Animals used wider home ranges in the wet season because they were not restricted by localized distribution of water (Western 1975). However, with pools drying out in the dry season grazers shifted back into areas within 4 km distances of permanent water but browsers showed little change in biomass or densities with distance from water. Similar patterns were documented by Ayeni (1975) for Tsavo National Park, Kenya and Redfern *et al*. (2003) for KNP, South Africa. Ayeni (1975) documented herbivores remaining within 5 km of water sources throughout the dry period.

Landscapes in KNP are on soils originating from varied geological substrates (Gertenbach 1983, Venter *et al*. 2003) and vegetation structure and composition changes with respect to these broad soil types. Generally, the main substrates are granite, basalt, gabbro, karoo sediments, ecca shales, rhyolite, and sandstone. Basalt gives origin to clay soils and sandy soils originate from granite. Clays hold water molecules strongly in contrast with sandy soils where water infiltrates the soils and remains available longer to plants (Scholes & Walker 1993).

In Kyle National Park, Zimbabwe, Ferrar and Walker (1974) observed that duiker selected woodland areas while tsessebe, warthog, and wildebeest used open areas with short grass. Impala, sable, zebra, and kudu selected for sparsely wooded and shrubland with tall grass. Herbivore ranges overlapped during use of green vegetation after burns.

Predation

Predation risks are related to habitat structure and have been reported to influence ungulate spatial distributions (Kie 1999). Mule deer (*Odocoileus hemionus*) and black-tailed deer (*O. h. columbianus*) avoided good feeding areas that occurred away from hiding and escape cover when mountain lions (*Felis concolor*) were within their range (Kie 1999). Sinclair (1977) reported that wildebeest herds avoided places surrounded by thick vegetation, which might conceal predators when approaching a river. Ungulates can reduce risk of predation by aggregating in open areas with increased visibility, and group sizes increase with predator abundance (Durant 1998, Kie 1999). It is not easy for a predator to approach a bigger group of ungulates without being detected (Sinclair 1977).

Studies on carnivores in KNP (Mills & Funston 2003) confirmed that lions were less successful in open areas and with larger groups of herbivores. Changes in vegetation structure caused by high rainfall (1972-1977) resulted in wildebeest and zebra making use of medium-height or tall grass for longer periods and consequently influenced their vulnerability to predation (Smuts 1978).

Artificial perennial water points keep animals resident in an area and thus predation risk may increase. If predators do not follow migratory herds, such herbivores become unavailable to those predators during part of the year. This may limit the number of predators and thus prey can escape predator regulation (Fryxell and Sinclair 1988).

Interactions between predation, resources, and habitat use may arise, with resource deficiencies causing animals to move into more risky areas, and predation risk causing them to crowd into depleted areas (Lingle 2002). Herbivores with similar food, environmental and resource requirements may end up selecting different habitats because they differ in their susceptibilities to predation (Lingle 2002).

Sable habitat selection

Sable herds in Kenya selected habitats on edges of forests with tall grass and sparse tree canopy cover (Sekulic 1981). Sekulic (1981) observed three factors influencing sable habitat choice; 1- grass height (sable showed preference for medium-tall grass), 2- density of trees and bushes (sable preferred open areas with sparsely distributed trees and bushes), 3- plateau or hills (sable used mid-slopes frequently). Sable herds did not use thick woodland areas and avoided upland slopes during the dry season. The avoidance of slopes and selection for valley habitats by sable in the dry season was ascribed to green leaf still available in valleys.

Stevenson-Hamilton (1947) indicated that sable preferred areas interspersed with thickets for shade and open valleys for grazing. Joubert (1974) documented a home range of 20 – 40 km^2 for sable in KNP (cited in Harrington *et al.* 1999).

Another home range estimate of 44 km^2 was reported in Pilanesberg National Park, South Africa (Magome 1991). Movement of sable outside their home range into areas that have recently been burned to take advantage of new green flushes of food have been documented (Magome, 1991, Sekulic 1981). Sable showed seasonal habitat selection in Angola (Estes & Estes 1974). Wet season habitats included the miombo (*Brachystegia*) woodlands and the ecotone between woodlands and grasslands with grass species containing higher nutrients contents. In the dry season sable selected for green marshes.

In Pilanesberg National Park, South Africa, Magome (1991) observed that sable avoided open savannas and secondary grasslands. At the same time, those avoided habitats were selected by wildebeest, white rhino, hartebeest, and zebra. Hence, this separation partially reduced competition between sable and these other ungulates. Avoidance of open grasslands is consistent with observations by Grobler (1974), and Wilson and Hirst (1977). However, selection for more open grassland by sable in Kenya was attributed to absence of their favoured open woodland in the area (Sekulic 1978). In Pilanesberg National Park, sable used slopes in the wet season and bottomlands during dry season (Magome 1991). Bottomlands were avoided possibly due to tall grass stands with high stem to leaf ratio during the growing season. Sable females selected for valley savanna thickets and valley habitats during the calving period (February-March). Possibly this choice was influenced by the need for cover from the long grass to hide calves (Magome 1991). Thus, calving influenced this habitat choice. There was no selection for any vegetation type in the dry season since sable randomly used the valley savannas and thickets. Sable still continued to use the hill slopes during the dry season and this partially separated them from other grazers, except for zebra and hartebeest, which used the hill slopes towards the end of the dry season. Magome (1991) reported a feeding preference by sable for grass height between 100 mm and 300 mm.

In Kgaswane Mountain Reserve, South Africa sable were reported to be selecting open woodland areas in the early and mid dry season and vlei grassland at the end of the dry season (Parrini 2006). In this area, Parrini reported that sable selected grasses that were green and with less stems. Sable avoided short grass (<100 mm) and tended to take more medium to tall grass (100 - 200 mm) but without avoiding tall grass (> 400 mm).

Competition

According to Ecological Aerial Surveys (EAS) of KNP (1980-1993) and Redfern *et al.* (2006), zebra, impala, wildebeest, and buffalo are abundant and widely distributed across the park including northern section of the park where sable mainly occur. Zebra selected for medium to tall grass heights in Serengeti (Bell 1971). Zebra used both uplands and bottomlands but made more use of bottomlands in dry season on a game ranch in Northern Province of South Africa (Gureja & Owen-Smith 2002). Preference for bottomlands in dry season by buffalo has also been reported (Sinclair 1977, Macandza *et al*. 2004). Buffalo have been reported to use tall riverine grass in East Africa although actual measurements are not available (Sinclair 1977). Thus, competition may occur for grass heights and space on the landscape. In Matopos, Zimbabwe, Grobler (1981) observed that impala and wildebeest grazing kept grass heights below 40 mm, a fact he suggested excluded sable from using the same patches. Estes and Estes (1974) noted that impala and wildebeest shared range with sable in Angola suggesting a possibility that the species could compete for some resources. Competitive effects among these species may be important during the dry season when resources are sparsely available, and less abundant (Owen-Smith 2002) and animals may expand their diets to include less formerly preferred resources.

Thesis Structure

This thesis has been written in a style whereby the majority of the chapters have been written as individual papers. Each chapter (except Introduction and Conclusion) contains an Abstract, Introduction, Methods, Discussion, and References. As a result of adopting this style, there is some degree of repetition between chapters (i.e. study area, data source, and references). Different time segments from the period 1977-2007 were selected for assessing the specific objectives outlined in different chapters of this thesis. Broadly, consideration of which time segment to use for assessing which particular objective was depended upon (a) the EAS survey coverage, (b) time when extreme events such as droughts occurred, (c) time of initial rare antelope decline, and (d) time of changes in distribution patterns of abundant species. For example, I used the period 1980-1993 for investigating potential methods that could be applied to asses large scale distribution patterns and used the same period for documenting changes within distribution patterns of all 12 species because EAS surveys covered all sections of KNP during that time. The complete survey coverage offered an opportunity to identify all habitats occupied by a particular ungulate. I used the period 1977-1997 for assessing rare antelopes range contractions and for documenting factors that restricted a widespread distribution of sable antelope because the focus here was a) to characterize features associated with all areas that sable occupied and b) to note all areas where sable and other rare antelope had lost ranges. It would have been not accurate to consider locations where sable were sighted after 1993 as not part of their range. Thus, the main focus here was to use all records of where sable herds were sighted regardless of whether EAS covered the whole park or no for reliable inferences on range losses and identifying where sable do not occur. Changes in distribution of certain herbivore species after 1984 were associated with contraction of sable abundance and distribution after 1988, hence I assed competition and predation effects up to 1984. This period offered an opportunity to investigate what factors limited distribution of sable antelope before the population declined.

The general plan was to submit each chapter to peer reviewed journals as they were finished. Two chapters: 2 and 4 have already been circulated out to some colleagues for comments. Please note that chapter 4 has been co-authored by Norman Owen-Smith, Valerio Macandza, and Elizabeth Le Roux with the aim of publication. Valerio Macandza and Elizabeth Le Roux supplied data for sable herds collared at Punda Maria and Pretorius Kop respectively. I analysed all the data and wrote the drafts. Valerio and Elizabeth suggested comments on how to improve those drafts. Professor Owen-Smith contributed to the final draft helping editing and tightening the overall story. Roughly, my contribution is about 55-60% in the co-authored paper.

Despite a widespread use of the concept of “distribution range” and concerns on reducing rates of species loss amongst conservationists, there was no study that clearly outlined how variation in probability of a species occurrence within occupied landscapes was determined. There was no indication on how concentration areas (core ranges) might be distinguished from other sections of a range. I concluded that whilst the concept of “distribution range” is fundamental in ecology, uncertainty in its estimation is primarily associated with data scarcity, poor data quality, and limited abilities to depict actual areas of occupancy. Thus, generally, all parts of a landscape where individuals have been sighted are assumed suitable for the species. However, in reality this is not the case because gaps exist within occupied ranges (Getz *et al*.

2007). Two concepts are critical in describing and quantifying distribution ranges, first, the area within the outermost limits to occurrence of a species (i.e. potential range), and second, the areas over which the species is actually found (i.e. actual occupied) (Gaston 2003).

In chapter 2, different methods (LoCoH algorithm and kernel) were examined with the aim of finding an appropriate method that could be applied to address some of the mentioned methodological challenges encountered during studying large scale distributions. Real and long term data of animal herd locations were used to compare and contrast performances of the two methods at estimating distribution ranges for species of various spatial patterns. Performances of the two methods were compared with that of the commonly used tile/grid based approach. This chapter was fundamental in providing a base to the other chapters because it suggested which method was appropriate for each of the various objectives set out in this thesis.

Next, chapter 3 provides an example of a purpose for which the fixed kernel method might be preferable over the LoCoH algorithm. The chapter addresses the objective concerning establishing recent changes to historical distributions of large ungulates in KNP. Because fixed kernel method was unlikely to underestimate distribution range extents (i.e. is not sensitive to gaps, and minimizes type I errors with spatially sparse data, with small sample sizes and/or with data that present lower spatial accuracies), it was appropriate for documenting all areas where a species could possibly have occurred from 1980-1993. The fixed kernel method was thus appropriate to reveal changes in distributions when recent patterns were compared with estimates of around 1960 when non rigorous scientific methods of data collection were employed. Distribution patterns of large herbivores in KNP were examined in relation to landscapes favoured and avoided as a basis for assessing future changes. In addition, chapter 3 examined changes in proportional distribution of each species in the four census regions in KNP (1980-1993).

Chapter 4 provides an example of a purpose for when the LoCoH algorithm (i.e. both sensitive to gaps and less influenced by outliers) could be preferred over kernel method. Chapter 4 addresses the objective concerning establishing if climate influences were implicated in the perceived shifts of sable or other rare antelope distributions. In this chapter, mechanisms contributing to rare antelope population decreases were explored further by assessing changes in distribution patterns associated with them. The purpose was to reliably examine fine scale changes of occupancy including changes in extents of areas occupied by individual herds. The analysis was based on two sources of data: (a) aerial censuses of large herbivores carried out annually from 1977 to 1997, and (b) sizes of areas occupied by surviving herds of sable antelope tracked in two regions between 2001 and 2007. Changes to annual calf recruitment and herd sizes were also examined. The expectation was that, if habitat deterioration as a consequence of lowered rainfall was the main influence, range contraction would be greater in the drier northern section of KNP than in the wetter south-western region. However, if effects other than rainfall were the main influence, then contractions of range, herd sizes, and recruitment would be patchy because such influences would unlikely be evenly spread in the park.

Chapter 5 addresses two objectives concerned with identifying environmental features associated with recent sable distribution and variation of sable presence within their recent distribution. Chapter 5 provided an example of the purpose for when the tile based approach is the preferred choice over kernel or LoCoH methods. The purpose for which the tile based approach could be preferable over kernel or LoCoH methods is for example when the objective is to assess factors influencing occupation, change in occupation or lack of occupation of specified areas plus when there is a need to maintain the sizes of those areas constant over time (e.g. perhaps size of home ranges). A tile size scale can easily be maintained constant across the whole park and over time. The latter allows an opportunity to apply rigorous statistical tests to the data. The aim was to determine which factors restricted a wider distribution of sable in KNP. Tile sizes that approximate sable home range estimates were maintained across KNP. Competition and predation effects were estimated in each of those tiles across the 20 000 km^2 of KNP. A proxy for competition using biomass of species (impala, wildebeest, buffalo, and zebra) was developed. A proxy of predation risk was developed using prey available for lions. Vegetation and geological zones distinguished by Gertenbach (1983) and Venter (1990) were used to distinguish specific vegetation attributes in those tiles. Geographical positions of herds and herd sizes were obtained from EAS surveys of larger animal species (1978–1983) in KNP. Park-wide aerial surveys (1978-1988) were used to distinguish 25 km^2 tiles occupied by sable herds from unoccupied regions. Logistic regression models were fitted to estimate the probability of presences/absence of sable herds as a function of the biotic and abiotic factors.

Chapter 6 (conclusion and recommendations) is an overview of all the findings and links each chapter in the bigger picture of sable ecology and distribution patterns in KNP. The chapter pointed out main differences between distribution of sable and that of abundant grazers in response to effects of competition, predation, rainfall, and distribution of waterpoints, and how these could help understand why sable are rare and why they exhibit a restricted distribution in Kruger Park. Areas that still need further research were noted. Consideration was also given to what this study has achieved in terms of sable management and conservation.

There are four appendices, which cover (i) details of methods, (ii) figures from the methods chapter (2) that illustrate several issues on performance of each technique, (iii) summary of simplified landscape and land type categories based on Gertenbach (1983) and Venter (1990), and (iv) a table of prey species considered in developing the predation proxy, prey body mass, a weighting factor in terms of how much each prey species contributes to lion diet.

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CHAPTER 2

Comparison of kernel density and local convex hull methods for assessing distribution ranges of large mammalian herbivores using aerial survey data

ABSTRACT

Distribution ranges and factors limiting them remain scantily documented for most protected areas partly because of lack of methods that indicate variation in presence and gaps where the species is absent. The aim was to compare and contrast performance of LoCoH and kernel methods in representing distribution patterns for different objectives. The chosen species exhibited; (i) a wide and continuous distribution with few gaps (impala), (ii) a broad distribution with local concentrations and absences (wildebeest), (iii) linear pattern associated with rivers (waterbuck), and (iv) a patchy pattern (sable). I used animal herd locations recorded during aerial surveys in Kruger Park (1980-1993). The methods are suitable for assessing different purposes with species distributions. The LoCoH method tends not to extend outer limits of ranges to areas where a species was not recorded. The kernel method exhibits the opposite tendency. However, performances of these methods do not lead to different interpretations of occupancy patterns and range extents. Performance of a method is also influenced by type of spatial patterns. I recommended both LoCoH and kernel methods for representing occupation patterns of species presenting continuous distributions, and linear patterns. I recommended the LoCoH for patchy distribution patterns and for identifying gaps or shifts of distributions. I found that the band-width (h) obtained for the kernel method through cross-validation was not optimal in the case where regional abundance was widely disparate, and hence had be adjusted subjectively. Despite some subjectivity in the choice of the optimal values for the parameters k and α for the LoCoH method, it seems generally superior when the sample of location records for mapping distributions is sufficiently large and organisms are readily visible, so that gaps and sharp boundaries in the mapped distribution become meaningful.

Introduction

Physical barriers such as rivers (Heller 1918, Gaston 1990) and forage resource availability (Caughley *et al*. 1988, Quinn *et al*. 1997) may limit species distributions. Climate has influences through affecting local conditions under which a population can persist (Caughley *et al*. 1988). Predation or competition can exclude species from areas that otherwise could maintain a population (Soberón and Peterson 2005). Assessment of distribution patterns is of value because it provides a basis for detecting shifts in range caused by climate change effects (Parmesan *et al*. 1999) and indicates species that might be experiencing range losses. Species that occur at lower abundance and experience shrinkage of range are more likely to be at higher risk of extinction than widely distributed and abundant species (Pimm *et al*. 1995). To clarify factors restricting a species distribution, it is crucial to assess variation in presence and gaps where absent within a distribution using a hierarchical framework (Johnston 1980, Gaston 1991). This includes, first, distinguishing a 1st order range (i.e. geographic extent of occurrence) that encompasses all sightings of a species, and then a 2nd order range, which is a subset of the geographic extent of occurrence because it exclude gaps that may be unsuitable habitat or not yet colonised (Gaston 1991). A focus on 1st order range obscures local contractions in actual areas of occupancy and local declines in abundance within this range (Channel & Lomolino 2000, Gaston 1991). The 2nd order range indicates areas where conditions are suitable for a species (Manly *et al*. 2002). Challenges from recent global warming effects call attention to a need for conservationists to establish shifts in occupancy as a response to climate change or other factors. Rosenzweig and Lomolino (1997) suggested that climate change effects could reduce extent or distribution of certain forage resource types while expanding others. Should climate change reduce the distribution of forage resources that support species that exhibit restricted distributions, then the latter may easily become threatened.

Uncertainty in estimating distribution ranges is primarily associated with data scarcity, poor data quality (Boyce & Pearce 2006), and limited abilities to depict actual areas of occupancy. The 1st order range assumes that distribution of a species is continuous within its extreme sightings, but, in actuality discontinuities and gaps exist (Getz & Wilmers 2004) and distributions can shift through time (Caughley *et al*.

1988). Outliers represented by animals wandering outside their usual range might exaggerate the range extent.

Two approaches developed for home range analysis could be applied to distribution ranges: 1) an analysis that delineates the outside limits to occurrence (Aebischer & Robertson 1993), and 2) an analysis that yields differences in density of occupation within the outer boundaries (Getz & Wilmers 2004). Commonly distribution ranges are constructed applying a tile/grid based approach that shows densities of occupation and extreme limits to a species range (White & Garrott 1990). Kernel smoothing method (Hemson *et al*. 2005) and local convex hull or LoCoH family of algorithms (Getz *et al.* 2007) show outside boundaries of location records and construct isopleths that join areas which exhibit same probability of use by an individual animal or herd. The kernel method uses a smoothing parameter *h* that controls the search radius or the distance over which a data point influences the grid intersections and therefore the density estimate at that point (Silverman 1986, Worton 1995). The LoCoH method constructs local hulls from a user-specified number of nearest points to each location in a data set. The fixed *k*-LoCoH constructs polygons to a subset of data localized in space, and is a generalization of the minimum convex polygon approach (Getz & Wilmers 2004). Comparisons of performances of LoCoH and kernel methods have been limited to home range usage (Dunn & Gipson 1977, Seaman & Powell 1996, White, Saunders & Harris 1996, Millspaugh *et al*. 2000, Getz & Wilmers 2004).

Capabilities to reduce type I (exclusion of areas where species really occurred) and type II (inclusion of areas where species did not occur) errors are desired in a method to improve reliability of distribution range estimations. It is not likely that any method can be equally good in reducing both type I and II errors. The LoCoH method appears to minimize type II errors (Getz *et al*. 2007) but could be prone to type I errors, whilst the kernel method appears to show the opposite bias (Worton 1989, Blundel *et al*. 2001). Therefore, the LoCoH method should better represent fine scale structure in distributions caused by topographic discrepancies within landscapes for example by features such as cliffs or rivers (Getz & Wilmers 2004), whilst the kernel method should better represent distributions of highly mobile or migratory species.

In this article, I compare and contrast the performance of two alternative approaches, the LoCoH algorithm, and the kernel method, to estimate distribution ranges of four ungulate species that exhibited different spatial patterns. These species were chosen to represent (1) a wide and continuous distribution with few gaps (impala *Aepyceros melampus*), (2) a fairly broad distribution with local concentrations and absences (wildebeest *Connochaetes taurinus*), (3) linear pattern associated with rivers (waterbuck *Kobus ellipsiprymnus*), and (4) a patchy pattern of distribution (sable *Hippotragus niger*). I compare performance of the LoCoH and the kernel methods with the tile based approach that is widely used for mapping species distributions. I compared and contrasted the techniques based on five criteria:

1. Ability to represent local differences in occupation.
2. Ability to identify gaps within range i.e. areas where the species was not present.
3. Not unduly influenced by outliers (type II errors) and propensity for type I errors).
4. Ability to handle distribution ranges of particular shapes.
5. Extent of potential bias in estimating range extents

I expected the LoCoH method to be superior in showing fine-scale variation in patterns of occupancy, and better represent local discontinuities in distributions (Getz *et al*. 2007). I expected adaptive the kernel method to less precisely define outer range edges, and to represent fine-scale variation in occupancy better than its fixed kernel counterpart (Kernohan *et al*. 2001, Gitzen, Millspaugh & Kernohan 2006). The fixed kernel method was expected to better delineate outer edges of the distribution ranges, and less precisely define fine-scale discontinuities in occupancy patterns than its adaptive counterpart.

The LoCoH algorithms might be applied for fine-grain evaluation of shifts in distributions caused perhaps by increased effects from predation or competition, and climatic change effects. Kernel methods might be appropriate for assessing the extent of distribution particularly with lower survey intensities and/or with aerial survey data that have spatial inaccuracies (i.e. > several hundred meters).

Getz and Wilmers (2004) illustrated that kernel method failed to indicate gaps that represented unused areas in generated “donut” distributions. Such gaps may be consistent with e.g. areas where a change from forest to grassland or a change in geology type creates a discontinuity within a species distribution. This implies that kernel method could overestimate range area for the patchily distributed sable through inclusion of gaps where the species might be absent. Kernel method fundamentally assumes that underlying distributions lack sharp boundaries between used and unused areas (Getz & Wilmers 2004, Millspaugh *et al*. 2006). Thus, the method could overestimate total range area for wildebeest that exhibit a broad distribution but with gaps in places. The kernel method did not precisely mark the outline of circular boundaries that surrounded simulated home range patterns (Getz & Wilmers 2004). Thus, this method may also overestimate waterbuck total range extent area through extending range margin well beyond where the species was sighted. LoCoH method could potentially be less biased with estimates of total range area extents occupied by sable, waterbuck, and wildebeest because it is sensitive to non-occurrence gaps. The LoCoH method could underestimate range extent for the continuously distributed impala because it may reveal gaps that may not be important or that could be spurious. The tile based approach should produce the largest range estimates with all species because it is crude for defining boundaries or gaps.

Study Area

The following is a brief description of Kruger National Park (KNP); further details are in Venter *et al.* (2003). Kruger National Park covers nearly 20 000 km^2 and is broadly divided into granite-derived soils in the west and basaltic clays in the east (Fig. 1). The vegetation is predominantly wooded savanna with knob thorn (*Acacia nigrescens*) predominating on basalt substrates and *Combretum* spp. and *Terminalia* spp. species on granites in the southern half. Mopane (*Colophospermum mopane*) predominates in the northern half of the park. On average, the elevation is 300 m. Annual rainfall decreases from 750 mm in the south-west to 400 mm in the north-east.

Methods

KNP Census data collection

Ecological aerial surveys covering almost the entire park for large animal species were conducted annually from 1980 to 1993 (Joubert 1983, Viljoen & Retief 1994). Surveys were done using a fixed-wing aircraft in parallel strips 800 m apart. Sighting probabilities were estimated to be 80-90% for species that were easily seen from the air such as wildebeest, but 50-60% for less visible species (e.g. waterbuck and impala) (Redfern *et al*. 2002). The surveys were done during the dry season

(May-August) (Joubert 1983, Viljoen 1989) when visibility was considered best. Prior to 1987, herd locations were recorded directly by hand onto a 1:100 000 scale topographical maps and from these maps; the locations were transferred to a computerized grid system of 2 × 2 km^2 squares (Joubert 1983). In the post-1987 period, a palmtop computer coupled with a GPS unit was used to record coordinates of the position of each herd (Joubert 2007). Therefore, positional accuracies would be uncertain up to ± 2 km prior to 1987 and within 0.8 km post-87 (Viljoen & Retief 1994).

Data analysis

One location for per herd annually was used for this analysis because herd locations represent distribution of the breeding segment. The spatial position of one herd was independent from the position of another herd during the same survey. Solitary animals were excluded from the analysis because they included lone adult males distributed beyond breeding range. The distribution range extent was defined as the area that encompassed 0.99 (impala or wildebeest) or 0.95 (sable or waterbuck) of the probability density of herd locations by species with LoCoH and kernel methods. However, the distribution range extent encompassed all areas with herd location records for tile method. I did not apply 0.95 to abundant species because 4 092 (4% of 102 299) impala location points were greater than the sable total sample size (N = 3 182 locations). Hence, I judged that 0.95 would lead to underestimating area of occurrence for impala. However, for less abundant sable or waterbuck a 0.99 level stretched the range margin widely beyond where the species was sighted, hence I opted for a 0.95 level.

I applied 0.75 probability level estimated from all locations by species to represent concentration areas, instead of 0.50 that is commonly used for home range core areas. This was because the 0.50 level yielded highly fragmented concentration areas for buffalo in north-west (i.e. known buffalo concentration area) and for wildebeest in central-east region on basalt (i.e. known wildebeest concentration area). In addition, the 0.50 probability level marked distinct concentration areas separated by distances < 2 km. Because breeding buffalo commonly occur as large herds that roam widely (Sinclair 1977), such patterns may be misleading. I applied a procedure outlined by Powell (2000) to decide on the 0.75 probability level as appropriate to represent concentration areas. The procedure has three steps; i) calculate several distribution range areas using probability levels from 0.1, 0.2, 0.3, up to 1.0 (100%). ii) Plot a graph of these range areas vs. the respective probability levels. If occurrence is random, then this graph of range area vs. probability level is a straight line drawn from 100% range area to 0 percent probability of occurrence. However, if occurrence is non random, the graph sags below the line of random occurrence (Powell 2000). iii) A line drawn perpendicular from the x-axis to a point on the sagging curve (i.e. to a point located furthest away from the straight line of random occurrence) indicates the probability level for core area (Powell 2000).

It was not possible to process 102 229 impala data points all at once because of limited processing capacity of my computer. Therefore, I divided KNP into two halves, and estimated the distribution ranges independently. I later merged the two distribution range estimates in Arc Map 9.1 (GIS) for displaying on a single map (Price 2004). However, estimating distribution ranges separately in two halves of the park necessitated that interpretation of patterns be done independently for each half because the probabilities of herd occurrences were calculated based on two different regional abundance levels. The above mainly leads to biases on where concentration areas may be marked particularly for the section of the park that has fewer location points, which are used to estimate the distribution range.

Point distribution

I plotted locations (latitude-longitude) of species on maps to get the observed point distributions in Arc Map. Annual shape files were created for each species then merged using the ET-Geowizard to make “queries” easier with tile techniques in subsequent stages (Price 2004). Point distribution maps of these original data were included for comparisons with the distribution ranges estimated from the same points.

Tile method

Two tile scales, (5 × 5 and 10 × 10 km) were applied. The 10 × 10 km tile size was chosen to allow comparisons with previous studies elsewhere on species distributions (Parmesan *et al*. 1999) and on herbivore assemblages in KNP (Redfern *et al*. 2006). A minimum tile scale size of 5 × 5 km was based on home range size estimates reported for sable (Joubert 1974, Sekulic 1981, Estes 1991), a focal species in this study, hence allowing comparisons with subsequent chapters in the thesis. Shape files were created separately for each tile scale using ET-Geowizard (Price 2004). Each shape file was overlaid onto the map of KNP, and then clipped to fit park boundaries. Relative herd densities for each species were determined by overlaying the tile shape file on herd positions. First, I identified and coded in a different colour tiles with zero records. Then I calculated species herd densities per tile in each of the remaining tiles. I used the densities per tile to construct frequency distribution plots for each species. I divided the frequency distribution into 3 natural clusters depending on the density levels (i.e. low, medium, and high). I assigned to all tiles within the same density cluster one colour code. Thus, I produced a map showing four density related colours (zero, low, medium, and high). I calculated sizes of areas covered by each of the above categories in GIS using Hawth's Tools for each species (Beyer 2004).

Kernel methods

I applied the kernel method as an extension to Arc Map 9.1 (Rodgers *et al.* 2005) using least–squares cross-validation (LSCV) techniques in estimating the smoothing parameter *h* (Silverman 1986, Worton 1989). The smoothing parameter controlled how continuous a range could be (Worton, 1989). Small *h* values reveal fine-scale gaps but produce ranges that appear more disjointed; larger values obscure those details and yield more continuous range patterns. The fixed kernel method maintains the same value of *h* for all points. The adaptive kernel method allows *h* to vary such that areas with low concentration of locations have a higher *h* values than areas with high concentration of locations, and are thus smoothed more (Silverman 1986, Worton 1989).

A shape file of herd locations for each species was loaded onto the Home Range Extension Spatial Analyst Tool to estimate the distribution range (Rodgers *et al.* 2005). The kernel method extended distribution ranges beyond KNP fence boundaries and ranges had to be clipped to fit park boundaries. The fixed kernel method with least-squares cross-validation procedures proved problematic for wildebeest distribution pattern. The method yielded a higher *h* (0.0540) value compared to the one produced with adaptive kernel method (0.0196). For other three species considered here, the smoothing parameters from both methods were about the same value. That bigger *h* value appeared to be associated with extending concentration areas of wildebeest in north-west to areas where densities of wildebeest were known to be low. Additionally, the bigger *h* obscured the sparse distribution pattern exhibited in the area. The next step was to investigate whether problems noted with wildebeest distribution were due to technical details of the method design or due to *h* effects. Thus, user defined procedures available in Arc Map were used to model distribution of wildebeest applying an *h* value equal to the one applied with adaptive kernel and then comparing all the range outputs. The latter attempt yielded a fragmented range pattern for central KNP (known continuous range for wildebeest) and yielded extensive core range areas in the Far north, where only about 10% of wildebeest occur. I then chose several *h* values manually and used each of them to estimate wildebeest range area. Then I plotted a graph of range area against the value of *h* used to produce it. At first, an increase in *h* leads to huge increases in area of range. I started with smaller values of *h* and gradually increased them until the curve of area vs. *h* was stable (i.e. minor change in areas). This technique follows a procedure proposed by Getz & Wilmers (2004) to calculate a minimum spurious hole covering value (see details under Local Convex Hull Algorithm). Then, I calculated the average smoothing parameter (h = 0.0264) of values around the point when the area stabilized and used that value with a user defined option available in Arc Map with the kernel method.

Local Convex Hull Algorithms

A shape file of animal herd locations was loaded onto the LoCoH home range spatial analyst tool in Arc Map 9.1 for distribution range estimations (Ryan *et al.* 2006). Local hulls were constructed from a user-specified number of nearest points to each location in the data set that were either fixed at *k* (*k*-LoCoH) or constrained such that the sum of their distances to the root point was less than or equal to *a* (*a*-LoCoH). The fixed *k*-LoCoH applies a generalized approach of the minimum convex polygon by constructing isopleths to a localized subset of data (Getz & Wilmers 2004). Local hulls were constructed for each point and selected neighbouring points, and the union of these hulls moving up from the smallest were used to construct isopleths (Getz *et al.* 2007). In the case of *k*-LoCoH, the minimum number of points required for constructing a hull is 3 while the largest is the sample size itself. For *a*-LoCoH, initially I fixed the value of *k* (minimum number of points used to construct a polygon) at 3, and the value of *a* (distance from the root point) at 1 m. I then plotted the area of the estimated distribution range versus increasing values of *a* to find the point where the area began to level off (the minimum spurious hole covering or MSHC value of *a*, Getz *et al*. 2007). With *a* fixed at this value, I then varied *k* to find its MSHC value. Thereafter I used these joint values of *a* and *k* to construct the final distribution ranges. Hulls are joined from smallest to largest into isopleths. Values of *k* or *a* that are too large produce ranges that do not indicate small gaps within a range where the species was not recorded, and thus appear influenced by outliers. Conversely, small values of *k* and *a* may exclude areas that are part of a range. Each isopleth encompasses a determined proportion of the statistical distribution of locations-for example, the 100 % isopleth covered all the distribution. A general guiding principle is that a lower isopleth e.g. 0.50 marks sections of a range that are used more compared to a higher isopleth e.g. 0.95.

Extent of potential bias in estimating range extents

To assess extent of potential bias in each method I generated a 1 000 range extent values applying sampling with replacements techniques (Manly 1994) available in R-software from four values of range extents per species obtained from two variants of kernel method and two variants of LoCoH method. I excluded range extents estimated by applying the tile method because these encompassed all areas where a species was recorded, and thus potentially included outlying locations. I calculated a grand mean for each set of a 1 000 values of range extents per species. Then I calculated 99% confidence intervals around their means. I considered that if a range estimate obtained from each method was outside the 99% confidence interval then that could potentially underestimate or overestimate range extent leading to a biased interpretation of distribution patterns, and thus did not recommend the method to be applied for that specific pattern. The difference between each range estimate and the grand mean was expressed as a percentage to show how different were the range estimates obtained by each method.

Results

1 Impala

Impala (N = 102 229 herd locations) showed a continuous distribution of dense points in south, central and north-west, and a few gaps in eastern Kruger (Fig. 2a).

1.1Tile method

Tiles showed high densities in south and central regions compared to generally lower to medium densities in northern half (Fig. 2b). Tiles depicted a completely continuous range in the entire southern half and showed one section of northern half to the east where impala did not occur (Fig. 2b)

1.2 Kernel method

Estimating distribution ranges separately in two halves of KNP required that interpretation of range patterns in one half be independent of patterns in the other half. The above approach revealed several high concentration areas in northern half of KNP (Figs. 2c-d). Kernel method indicated that impala continuously occupied western KNP with exception of south-west that exhibited gaps. Both variants of kernel method produced identical patterns of local occupancy (Fig. 2c). Kernel method showed concentration areas as linear patterns associated with rivers in northern half, but concentration areas were widespread in southern half of KNP. Gaps within impala distribution were indicated in eastern KNP. However, the extreme south-east and extreme central-east of KNP were indicated as concentration areas for impala.

1.3 Local convex hull method

The LoCoH method produced patterns of local occupancy that were largely similar to those by kernel method. However, gaps indicated in north-east, south-west and central-west of the park appeared bigger than those mapped with kernel method (Fig. 2d). The LoCoH mapped a discontinuous impala distribution in far north-east of KNP contrary to the pattern indicated with kernel method for that area.

2 Wildebeest

Wildebeest (N = 11 630 locations) occurred densely through central Kruger Park but density of points was lower in south, north, and far north. Sparse locations occurred in south-west and far north-west of the park (Fig. 3a).

2.1 Kernel

Both variants of kernel method depicted high occurrences of wildebeest herds in central region of KNP (Fig. 3c). After manually setting h to ($h = 0.0264$) (closest patterns to those for LoCoH and adaptive kernel), the fixed kernel method still did not reveal gaps in contrast to patterns shown with adaptive kernel method within the sparsely occupied south and northern regions of KNP. The smoothing parameter applied with adaptive kernel method indicated a discontinuous wildebeest range in those south-west and north-western areas of KNP. Both variants of kernel method produced identical patterns in central region where wildebeest was continuously distributed (Figs. 3c, d).

2.2 LoCoH

The northern half and south-western sections of wildebeest range as indicated by LoCoH method appeared narrower compared with representations of same sections using kernel method (Fig. 3b-d). The LoCoH method produced a range pattern that was nearly identical to the one produced by adaptive kernel method.

3 Waterbuck

Waterbuck (N = 5 868 locations) showed linear concentrations along perennial rivers as well as seasonal rivers in central and northern half of KNP (Fig. 4a).

3.1 Kernel

Both variants of kernel method produced almost identical waterbuck patterns applying identical h values. Kernel method appeared to extend waterbuck range a bit further away from perennial rivers in central-east and south-western KNP (Fig. 4a).

3.2 LoCoH

The LoCoH method produced distribution ranges that appeared generally similar to those shown by kernel methods (Fig. 4e, f). Range pattern from adaptive a-

LoCoH appeared slightly narrower and discontinuous in central-east region of KNP compared to those from kernel method (Fig. 4e, f).

4 Sable antelope

Sable antelope (N = 3 182 points) showed locally concentrated locations in western KNP. Sable occurred on few isolated locations in north-east and in central-east of the park (Fig. 5a).

4.1 Kernel

Both variants of the kernel method produced almost identical sable distribution patterns (Figs 5c, d). The kernel method showed that concentration areas of sable occurred in western KNP.

4.2 LoCoH

The LoCoH method and kernel produced almost identical range estimates for sable in the southern half of KNP (Fig. 5d). However, the LoCoH method showed more discontinuity and bigger gaps in sable distribution than represented with kernel method in north-west and far north-west of KNP. In central-west, LoCoH method depicted three distinct locations occupied by sable whilst kernel method showed one continuous sable area. In northern half of KNP, the kernel method indicated a broader sable range than was shown with the LoCoH method (Fig. 5a-d).

5 Extent of potential bias in estimating range extents

The average 1st order range (0.99 isopleth) estimated for impala was 15 379 km^2. Range estimate values from the fixed LoCoH and fixed kernel methods were within the 99% confidence interval (14 516.25 to 16 320.5 km^2) (Table 1). Range estimates from *a*-LoCoH method were outside the lower limit of the confidence interval, whilst range estimates by adaptive kernel method showed the opposite bias (i.e. outside the upper limit). The above pattern was consistent for waterbuck and sable antelope 1st order range estimates (Table 3-4). The average 1st order range (0.95 isopleth) estimate for waterbuck was 6 742 km^2. The confidence interval for waterbuck was from 4 336.25 to 8 859.5 km^2. The average range estimate for sable antelope (0.95 isopleth) was 6 853 km^2. The confidence interval for sable antelope was 5 086 to 8 518.5 km^2. The average 1st order range estimate (0.99 isopleth) for wildebeest was 12 340 km^2. All range estimates by kernel and LoCoH methods were within the calculated confidence interval for wildebeest (11 342.25 to 14 530 km^2) (Table 2). Largest differences between the calculated grand means and range estimates for all methods were observed with waterbuck and sable (Table 5). The adaptive LoCoH consistently produced the narrowest ranges for all species and the adaptive kernel method showed the opposite bias. The least differences between the grand mean and 1st order range estimates for all methods were with impala range.

Discussion

Findings presented here confirmed that the LoCoH approach is more revealing of unoccupied regions within a distribution range than kernel methods. However, finer details of an occupancy pattern can potentially be revealed using kernel methods by reducing the value of the bandwidth h below the estimate obtained using least cross-validation techniques. The adaptive kernel method was most misleading through extending the distribution range much widely beyond the location points. Second-order distributions based on home range occupation can be expected to have more abrupt limits than the utilization patterns within home ranges with diffuse boundaries for which the method was designed. The superiority of LoCoH over kernel methods became greater for the two species showing patchily or linearly restricted ranges within the study area. The a-LoCoH method based on a variable sphere for joining points seemed better than k-LoCoH based on joining a fixed number of points, because the latter tended to merge the regions spanned by sparse points in outlying locations. The latter variant was also more prone to omitting outliers constituted by relatively few points. Findings presented here about the relative merits of these variants confirm conclusions of Getz *et al*. (2007) with respect to home range estimation.

Important aspects emergent in this study are; first, the purpose for which a method should be used is important when considering choices of which method to apply for assessing large scale animal distribution patterns. This is in contrast to current knowledge that suggests superiority or otherwise of certain methods for assessing all aspects of range use by animals (Powell *et al*. 2000, Getz & Wilmers 2004, Gitzen *et al*. 2006, Millspaugh *et al*. 2006). Second, the type of spatial pattern exhibited by a study species influence the success of any of the methods for whatever purpose.

Despite that, differences in estimates of range extent between methods resulted in up to two-fold differences in population density estimates within the occupied range. Nevertheless, the expected relationship between range extent and ecological density within this range was consistently shown for the four ungulate species.

In this study, little attention was given to issues of spatial accuracy of herd locations upon which the distribution ranges were estimated. However, indications are that the latter appeared to influence the choice of which method to use. Findings here indicated that no method is good for all purposes. For documenting differences in range occupancy patterns, tradeoffs between minimizing type I vs. type II errors have to be considered before the choice of which method to apply. The kernel method consistently indicated larger 1st order range extents for all distributions in this study than the LoCoH approach. The latter suggests the LoCoH approach offers a better likelihood of minimizing type I error than the kernel method. However, differences in distribution patterns mapped for all the four species were generally slight and considered not to affect interpretation of occupancy patterns, with wildebeest patterns in northern KNP being the only exception. In that area, the kernel method appeared influenced by perhaps effects of selecting a big smoothing parameter or effects of outlying wildebeest points. The kernel approach indicated a widespread range for wildebeest suggesting continuous occupation of the area (see Table 5 for percentage differences). In contrast, the LoCoH method represented a disrupted distribution for the same location points. It is not clear whether outliers pulled outer boundaries of the range into areas where the species was not recorded. Several attempts to apply a smaller value of *h* with fixed kernel method improved on revealing where gaps could potentially occur in this section of the park. However, a small *h* value depicted a fragmented wildebeest distribution pattern in central region (a known area of continuous wildebeest occurrences). Thus, a trade-off between a small vs. big value of bandwidth improves depicting patterns only in a one section of wildebeest range and not across the whole range. Thus, wildebeest distribution patterns shown here may somehow support Silverman (1986), Worton (1989) and Seaman *et al*. (1999) who documented that the adaptive kernel method better represented fine-scale variation in home range use than its fixed kernel counterpart. However, distributions depicted for the other species presented here are clearly consistent with observations by Borger *et al*. (2006), who documented that both adaptive kernel and fixed kernel method were equally unbiased in mapping home range use for roe deer (*Capreolus*

capreolus) and kestrels (*Falco tinnuculus*). Therefore, it appears that the fixed kernel method has to be applied with some caution for "complex spatial patterns" (i.e. species exhibiting continuous occupation of one section of a range but sparse occurrences elsewhere). Such complex patterns appear to require that bandwidth *h* be adjusted independently for each section through perhaps dividing a study area into two separate sections and then mapping the range independently.

For the purpose of identifying gaps within a species distribution that may occur over time, the LoCoH method appears superior, providing sampling is sufficiently complete, with the *a*-LoCoH variant appearing better than *k*-LoCoH for this purpose. Thus, the LoCoH approach can reliably be used to reveal where population centres are isolated or fragmented. Kernel methods may prove sufficiently reliable simply for documenting and comparing current occupied areas, especially if allowance has to be made for incomplete location records. However, although they reliably indicate multimodal concentrations of use within the occupied range, this feature is less meaningful for distribution ranges than for utilization patterns within home ranges. The fixed kernel variant should be preferred, because accommodating an adaptive kernel spreads the probability distribution unduly far beyond the true occupancy by home ranges. However, indications suggest that the LoCoH method may have to be applied with some caution for species such as impala that are continuously distributed because there is a possibility of emphasizing perhaps unimportant gaps.

The decision to use 99% isopleths to delineate the ranges of impala and wildebeest, but 95% isopleths for waterbuck and sable antelope, may seem somewhat arbitrary. It was based on the recognition that omitting 5% of impala herds would amount to overlooking a number of herds exceeding the total number of sable herds recorded in the park. For the two abundant species, the 99% range size estimates remained below that provided by amalgamating occupied tiles, and thus not unduly biased, but for the less abundant species, this was not the case. Range size estimates provided by the LoCoH variants using the 99% isopleths can be judged accurate providing location records are sufficient such that few presences are likely to be unrecorded, a condition met in this study. Kernel methods become more reliable as location records diminish such that gaps in locations become questionable indications of species absence. Except for the most abundant species, impala, the difference in range extent obtained using 95% versus 99% isopleths was quite substantial, indicating that some attention is needed to deciding which demarcation is most meaningful. The LoCoH approach generally yielded smaller estimates for the same isopleths than kernel method, through emphasising gaps. The core of the distribution range demarcated using the 75% isopleth seemed more meaningful than a 50% isopleths would have been, but we did not explore this issue further.

Getz *et al*. (2007) showed that the LoCoH algorithm is sensitive to gaps, thus fixed LoCoH method should be preferred ahead of the fixed kernel method if data has high spatial accuracy otherwise gaps that may be unimportant or that may be spurious could be emphasized. The fixed kernel method reportedly does well with lower survey intensities for home range use analysis (fewer than 50 location points) (Borger *et al*. 2006). Thus, accordingly, fixed kernel method could be preferred with lower survey intensity. If the main concern is reducing type II error, patterns presented here indicate the LoCoH algorithm should be recommended. All range estimates for distributions considered here using LoCoH method were at the lower end of the confidence intervals (i.e. near the lower limit). Indications are that both variants of LoCoH method and only the fixed kernel method can be recommended for the purpose of estimating range extents. However, in this study I highly recommended that *a*-LoCoH be considered for this purpose because it consistently produced least range estimates for all distributions assessed here. This is important because it implies that if there were any change noted in extent of occupied areas, then one would be more confident by using *a*-LoCoH than the other methods to conclude that a real change occurred. The kernel method would likely obscure changes that may be important

A change from LSCV to h_{REF} techniques of choosing the smoothing parameter with the kernel approach appeared not appropriate because the latter did not show fine scale variation of presences, concentration areas, or gaps for all the species considered here (see Appendix for $\mathrm{h_{REF}}$). As already indicated, both kernel and LoCoH approaches do not lead to generally divergent interpretations of distribution patterns. Both approaches produced almost identical range patterns for species that exhibited continuous distribution patterns (e.g. impala), clear distinct patches (e.g. sable in southern half of KNP) and those exhibiting linear occurrence patterns. For the above patterns, variants of kernel method applied same value of *h*. In central region that exhibits a continuous occupation of wildebeest, both kernel and LoCoH methods represented identical patterns. The patchy pattern of sable occurrence was less distinct in northern half of KNP with estimates from kernel method. The above just confirms that when the concern is to reduce type I error, kernel approach should be the choice.

Studies have reported that the fixed kernel method could be better (Powell *et al*. 2000, Gitzen *et al*. 2006, Millspaugh *et al*. 2006) or in cases worse (Worton 1989, Seaman *et al*. 1999) than the adaptive kernel. Getz and Wilmers (2004) and Getz *et al*. (2007) showed that the LoCoH algorithm was better than the kernel method for constructing home ranges. Emerging in this study is that both LoCoH and kernel methods have different capabilities with different issues regarding assessing range occupation by animals. Some methods are better recommended with patchy distributions whilst others perform well with a wide range of spatial patterns. Therefore, reported generalizations in literature in support or not of a method were not surprising, because conclusions were based on different purposes, which were analysed. Because the LoCoH method can reveal gaps with all distribution patterns considered here it is recommended for assessing shifts or disruptions of distributions. The above supports observations by Getz and Wilmers (2004) that showed that kernel method failed to represent holes with their small-scale home range use simulations.

As recognised by others, problems arise when choosing the optimal value for the bandwidth *h* when using kernel smoothing (Seaman *et al*. 1999, Gitzen & Millspaugh 2003, Citizen *et al*. 2006, Getz *et al*. 2007). In this situation, this problem emerged for wildebeest. Wide regional disparities in their presence led to smoothing that was deemed excessive in the range core using a fixed kernel, while an adaptive kernel spread the mapped distribution far too widely in the more sparsely occupied region. Hence a compromise was devised manually. Ad-hoc methods and user-defined choices of smoothing parameters to improve the performance of kernel method for complex patterns have been advocated (Hemson *et al*. 2005). A basic problem with the LoCoH method is that optimal values for the parameters are derived somewhat subjectively, but this did not prove to be a problem for the purposes of this study. Usually there were two to three suitable MSHC values for *k* and *a* that produce similar location of gaps, similar variation in presence and similar distribution shapes that differ slightly in range area sizes.

Studies that compared and contrasted these methods for estimating extent of areas covered by location points for any species are not available at the scale considered in this paper. Powell *et al*. (2000) reported that fixed kernel method better represented outer boundaries of a home range and based on that the method should be in a better position to be applied for this purpose. Results presented here suggest that adaptive kernel method has a propensity to overestimate range extents than the fixed kernel method, but the overall difference appeared not large enough to affect interpretation of the outcome (Table 5). The range estimates of adaptive kernel consistently fell outside the confidence interval for all species (i.e. towards the upper limit). The LoCoH method consistently showed smaller range size extents than kernel method, suggesting that it could be prone to type I error. For example, LoCoH method showed a sable area south-west of northern region of KNP as disconnected from the rest of areas occupied by sable in this region. Kernel methods showed a connected range for the same area. It is clear that increased sensitivity to gaps may as well lead to LoCoH method picking up gaps that may well be spurious within distributions and consequently lead to a smaller range extent estimates for species that roam widely such as buffalo. In this study, it is suspected that real gaps do exist within sable range. However, interpretations of those gaps with large-scale distribution range examinations need caution because our data was collected during dry seasons, and generally before midday (Joubert 1983). Such regular sampling might coincide with certain routine activities for example drinking, and that could bias core range locations.

Although “distribution range” is a fundamental ecological concept, there is surprisingly little documentation on how best it is measured. This study was the first to apply methods developed for small-scale home range assessments to large-scale distributions across an entire protected area. Hence the recommendation is that *a*-LoCoH should be preferred for studies addressing changes in occupation patterns within geographic ranges, provided a sufficient coverage of records is available to reliably identify gaps. In other circumstances, the fixed kernel method should be adequate, and its ability to reveal gaps can be enhanced by reducing the bandwidth parameter manually to produce a finer resolution. However, findings for wildebeest suggested that different bandwidths might be appropriate in different regions within the distribution range differing in herd occupancy, and not only around the margins. Borger *et al*. (2006) found that the fixed kernel method performed well for assessing the home range extent even when there were fewer than 50 location points, and this finding may be extended to the geographic range. The adaptive kernel method does not seem appropriate for demarcating second-order ranges defined by home range occupation patterns with limits that may be somewhat abrupt. However, these conclusions are specific to large mammals that are sufficiently conspicuous for location records to be a reliable measure of presence. For identifying gaps and shift in areas occupied by individual herds that might have occurred over time, the LoCoH approach reduces levels of uncertainty on whether noted changes are real or not. The study illustrated that understanding of distribution patterns can be improved with respect to estimating the relative change in probability of occupation of an area. The latter is important for improvements on management and conservation of species because it allows identification of areas that can be prioritized for managing of target species (Sagarin *et al*. 2006). Future applications that could additionally improve on management and conservation of species would be carrying out studies to identify which resources can be related to changes in probability of occurrence and linking patterns of distributions and abundance to vital rates of birth, and death.

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FIGURE CAPTIONS

FIG. 1. Kruger National Park (KNP) showing four census regions, Far-north, North, Central, and South divided by major rivers.

FIG. 2 (a) Impala original data are illustrated for the cases (b) Tile 5 × 5 km (c) Fixed kernel $h = 0.0222$, (d) Fixed LoCoH $k = 26$

FIG. 3 (a) Wildebeest original data are illustrated for the cases (b) Fixed kernel $h = 0.0265$, (c) Adaptive kernel $h = 0.0169$, (d) Adaptive LoCoH $a = 38000$; $k = 3$

FIG. 4 (a) waterbuck original data are illustrated for the cases (b) Adaptive kernel $h = 0.0264$ (c) Fixed LoCoH $k = 24$, (d) Adaptive LoCoH $a = 29000$; $k = 3$

FIG. 5 (a) sable original data are illustrated for the cases (b) Fixed kernel $h = 0.0279$, (c) Adaptive LoCoH $a = 35700$; $k = 3$

Table 1 Distribution range estimates (km^2) for impala herd locations (*n* = 102 229)

	Fixed LoCoH	Adaptive LoCoH	Fixed Kernel	Adaptive Kernel	Tile 5 × 5	Tile 10 × 10
Area of low occurrence	-	-	-	-	4 041	1 646
Area of medium occurrence	-	-	-	-	2 922	4 298
Core areas	-	-	-	-	10 510	12 337
Core areas 0.75	7 170	6 462	7 770	7 656	-	-
General Range 0.95	14 351	12 860	13 557	14 329		
General Range 0.99	14 808	14 419	15 698	16 528		
Range extent 1.0 (all points)	17 129	17 034	19 019	19 231	17 473	18 281

Table 2 Distribution range estimates (km^2) for wildebeest herd locations (n = 11 630)

	Fixed LoCoH	Adaptive LoCoH	Fixed Kernel	Adaptive Kernel	Tile 5 × 5	Tile 10 × 10
Area of low occurrence	-	-	-	-	6 525	2 936
Area of medium occurrence	-	-	-	-	4 733	4 744
Core areas	-	-	-	-	4 171	9 637
Core areas 0.75	3 890	4 015	6 724	4 051	-	-
General Range 0.95	9 473	8 303	10 735	11 122		
General Range 0.99	12 397	11 316	14 530	11 421		
Range extent 1.0 (all points)	15 378	13 439	19 105	17 944	15 430	17 318

Table 3 Distribution range estimates (km^2) for waterbuck herd locations (n = 5 868)

	Fixed LoCoH	Adaptive LoCoH	Fixed Kernel	Adaptive Kernel	Tile 5 × 5	Tile 10 × 10
Area of low occurrence	-	-		-	3 644	4 510
Area of medium occurrence	-	-		-	3 808	5 257
Core areas	-	-		-	3 807	6 047
Core areas 0.75	2 151	2 077	4 295	3 328	-	-
General Range 0.95	5 699	3 882	8 459	8 993		
General Range 0.99	7 445	5 680	11 913	12 722		
Range extent 1.0 (all points)	11 820	7 194	17 257	16 020	11 259	15 814

Table 4 Distribution range estimates (km^2) for sable herd locations (n = 3 182)

	Fixed LoCoH	Adaptive LoCoH	Fixed Kernel	Adaptive Kernel	Tile 5 × 5	Tile 10 × 10
Area of low occurrence	-	-	-	-	2 354	2 354
Area of medium occurrence	-	-	-	-	2 181	3 625
Core areas	-	-	-	-	2 816	4 227
Core areas 0.75	2 161	2 595	4 073	4 095	-	-
General Range 0.95	6 137	4 738	7 947	8 709		
General Range 0.99	7 223	6 609	10 561	12 498		
Range extent 1.0 (all points)	10 799	7 281	15 767	15 761	7 352	11 775

Table 5 Differences between the 1st order ranges estimated using each method from the grand mean (expressed as a percent)

Species	Fixed LoCoH	Adaptive LoCoH	Fixed Kernel	Adaptive Kernel
Impala	-3.7	-6	+2	+7
Wildebeest	+0.46	-8	+17	-7
Waterbuck	-15	-42	+25	+33
Sable	-10	-30	+15	+27

Figure. 1

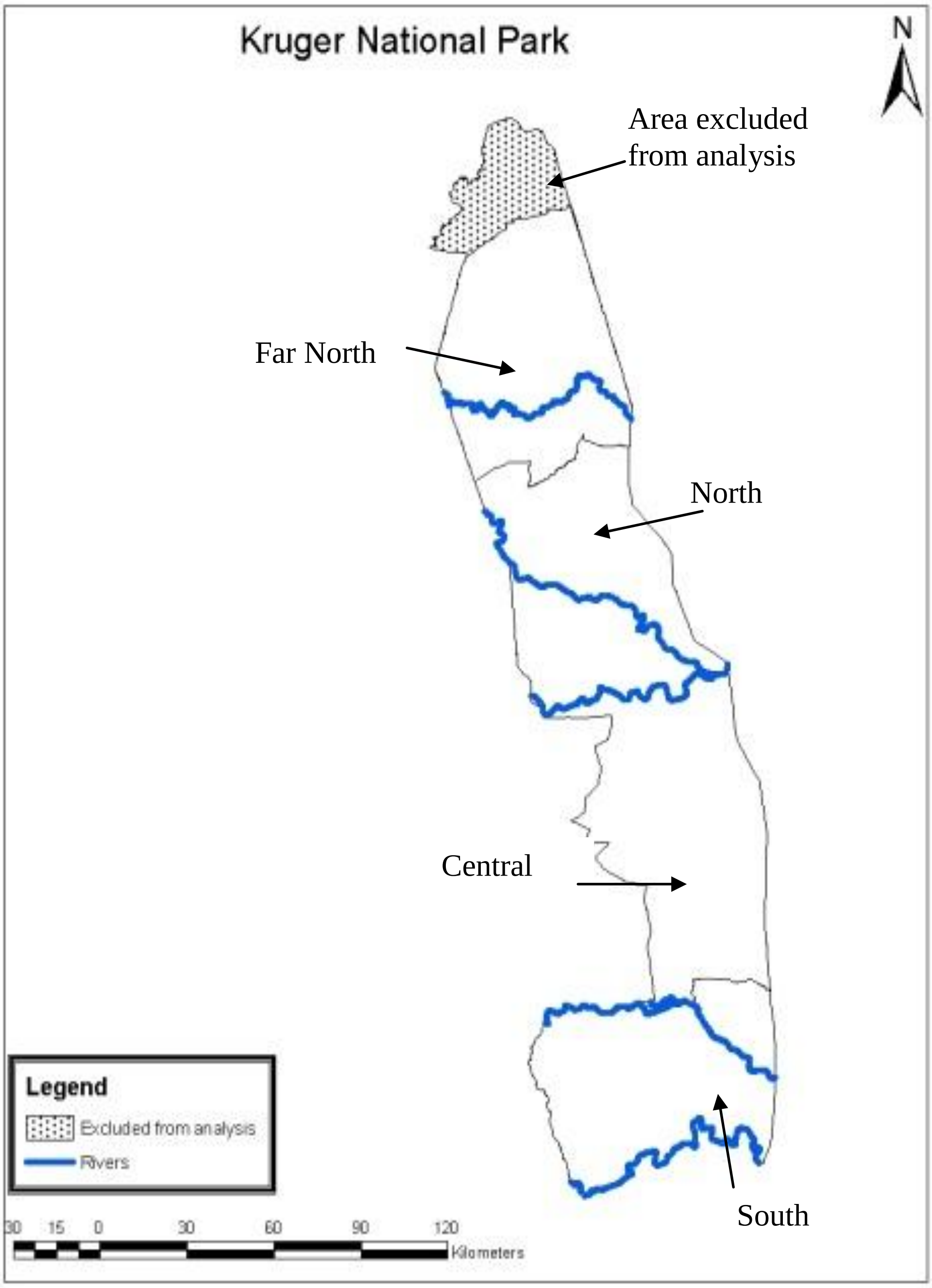
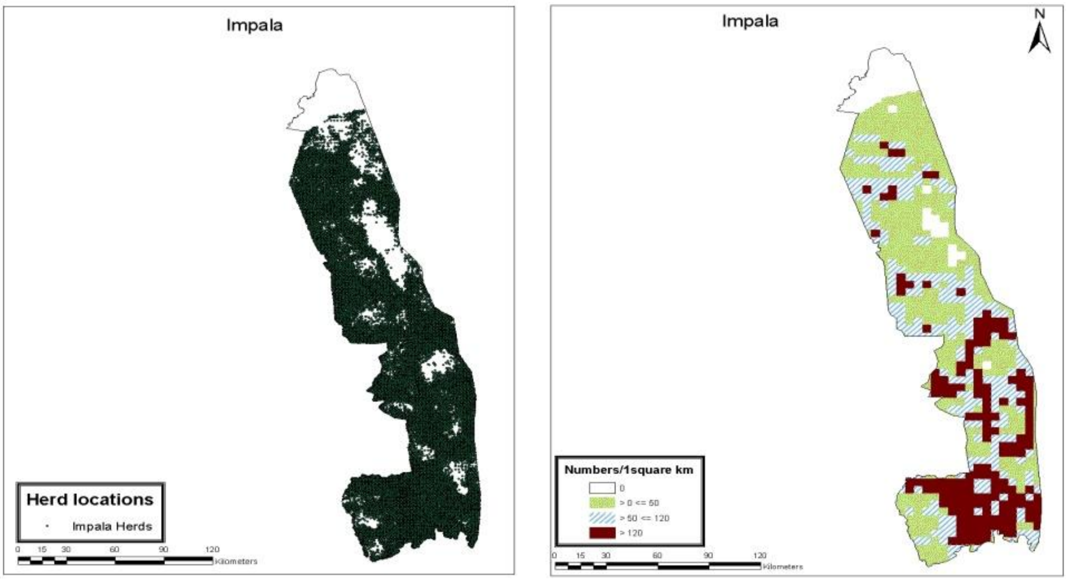

Kruger National Park
N
Area excluded from analysis
Far North
North
Central
South
Legend
Excluded from analysis
Rivers
30 15 0 30 60 90 120
Kilometers

Figure. 2

a. Data impala b. Tile 5 × 5



c. Fixed kernel *h* = 0.0222 d. Fixed *k* LoCoH *k* = 26

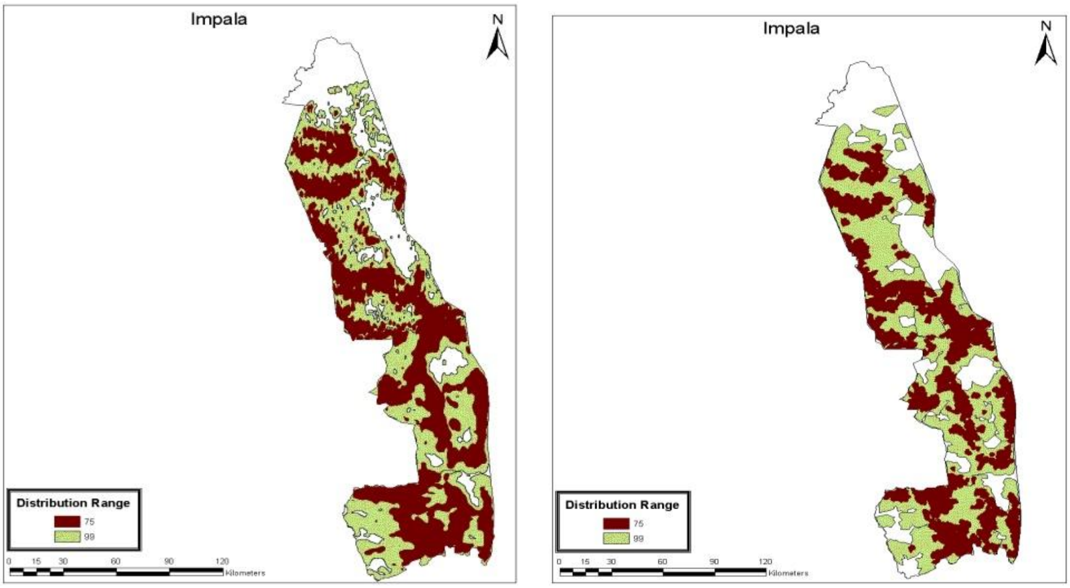
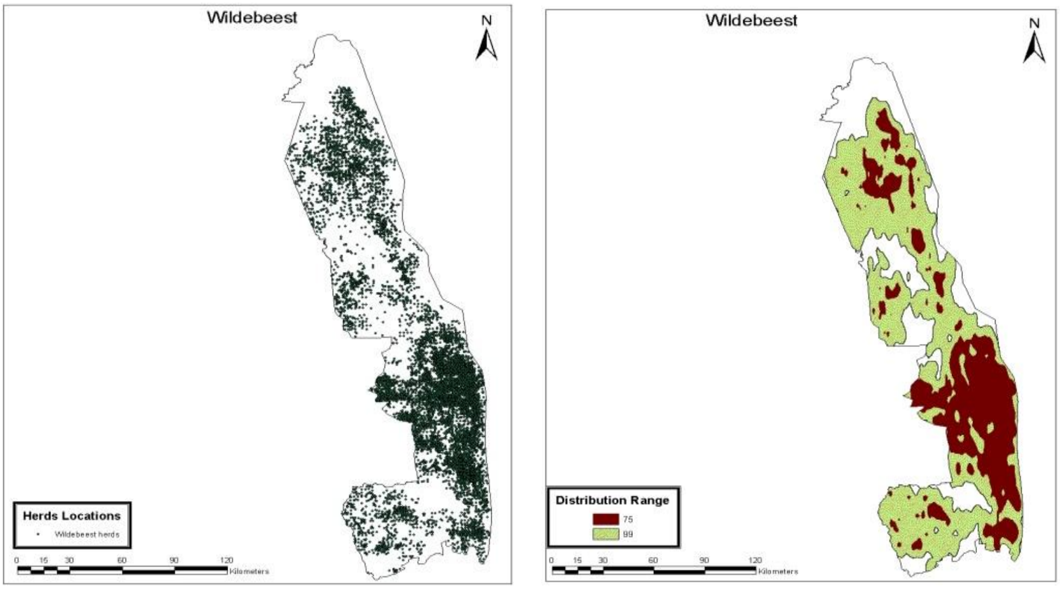
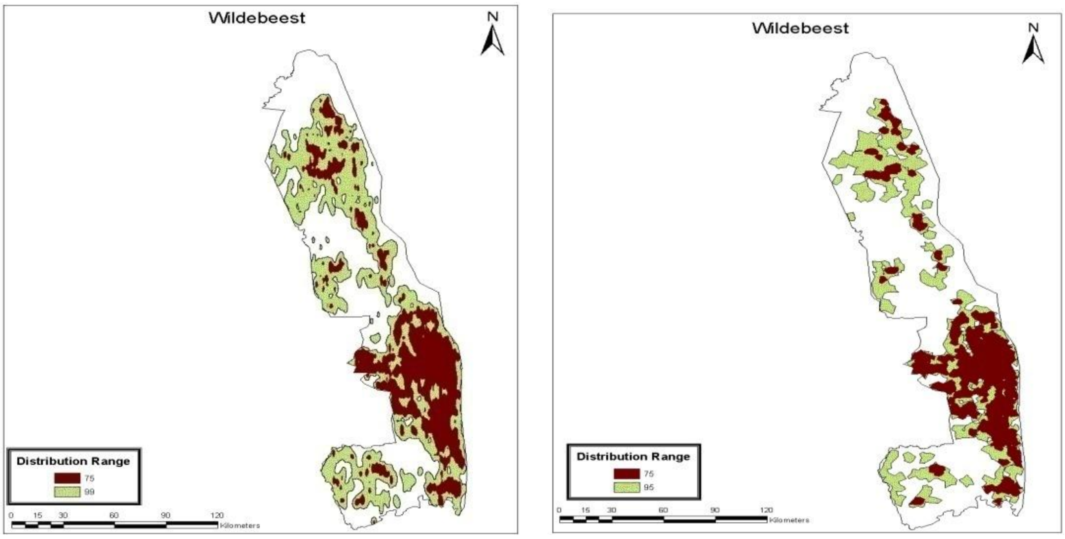


Figure. 3



3 a. Data Wildebeest

b Wildebeest Fixed kernel $h = 0.0265$

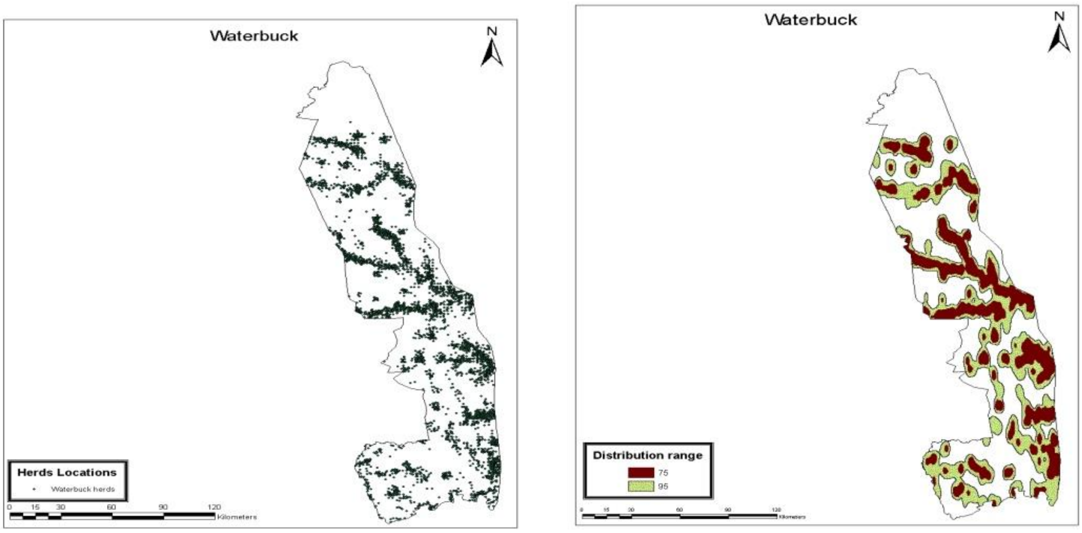


c. Adaptive Kernel $h = 0.0197$

d. Adaptive LoCoH: $a = 38000$, $k = 3$

Figure. 4

4. a. Data waterbuck b. Adaptive kernel *h* = 0.0244



c. Fixed *k* LoCoH *k* = 24 d. Adaptive LoCoH *a* = 29 000; k = 3

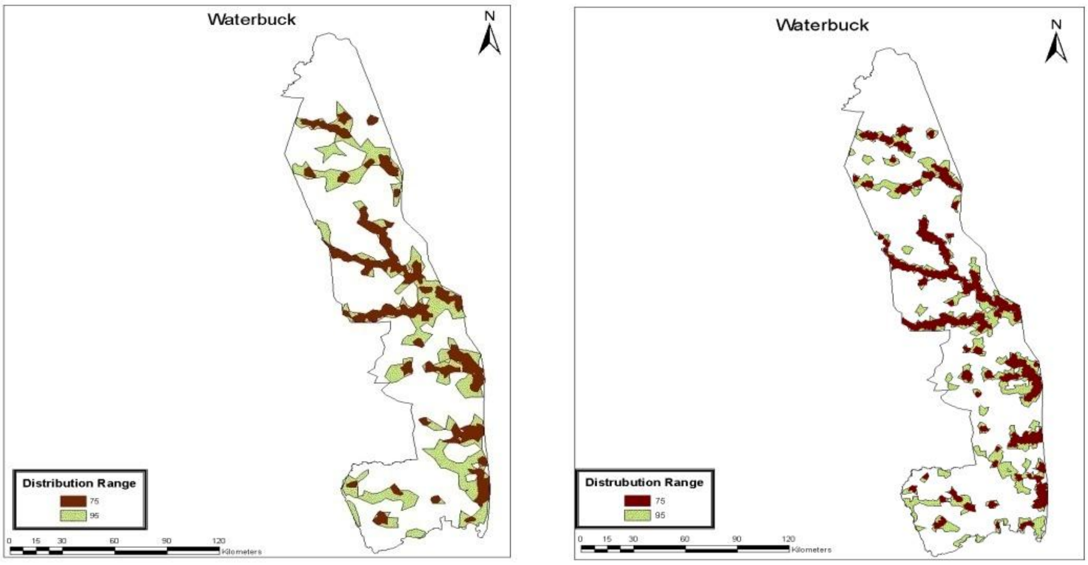
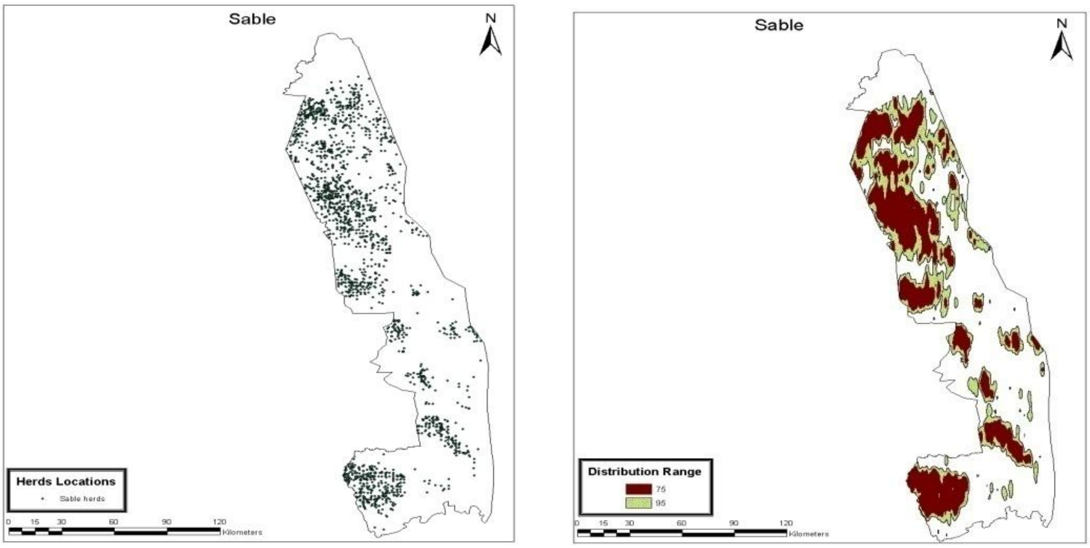


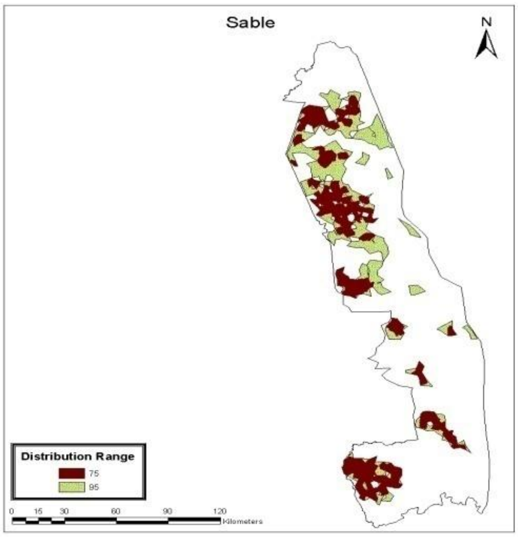
Figure. 5



5. a Data sable

b. Fixed kernel *h* = 0.0279

c. Adaptive LoCoH *a* = 35700; *k* = 3



CHAPTER 3

Recent distribution of large ungulates in the Kruger National Park from ecological aerial survey data

ABSTRACT

Spatial locations of resources and a suitable climate appear to set broad limits on extent of distributions of large ungulate species. Effects of competitors, predators, and parasites can limit occupation to sections of a potential range. Increasing concerns on conservation of species under climate change requires documenting current distribution patterns as a basis for assessing range shifts. I applied the fixed kernel method to construct recent distribution ranges of 12 large ungulate species using geographical positions of animal herds recorded during aerial surveys conducted during dry seasons (1980-1993). I compared recent patterns to those mapped crudely around 1960. I also assessed changes in proportional distribution of each species in four census regions for periods 1979-1983, 1984-1988, and 1989-1993. Buffalo, zebra, kudu, and warthog were continuously distributed throughout KNP. Impala were absent from some localized areas in eastern granites. Wildebeest were absent from sections in western granites. Giraffe were continuously distributed in southern half of KNP but were absent in some places in northern half. Waterbuck were associated with rivers across KNP. Sable were more prevalent on western granite, but occurred on distinct patches on basalt areas to the east. Roan and tsessebe occurred mainly throughout north-eastern and far north-eastern basalt areas but occurred on isolated areas in north-west. Eland occurred through most of far north, were not recorded in some places in northern region and were largely absent in southern KNP. Comparison of recent patterns with those around 1960 indicate (i) an increase in occupation of northern half by common species i.e. impala, zebra, buffalo, wildebeest, warthog and giraffe. (ii) Zebra, warthog, buffalo, waterbuck, and wildebeest occurred during dry season in areas indicated around 1960 as wet season range. (iii) Distributions of rarer grazers contracted in northern half of KNP and in central-western region. Management effects that included blocking migration outside the park by fencing and augmentation of waterpoints appeared associated with changes in distributions of these species.

Introduction

Distributions of species are affected by physical barriers, climate and by spatial distribution of resources they are able to exploit (Grinnell 1917, Hirzel & Le Lay 2008). Factors such as competitors, predators, and parasites may further constrain occurrences within these broad limits (Grinnell 1917, Hirzel & Le Lay 2008). With increasing concern for conservation of species under climate change scenarios, it is important to document current distribution patterns as a basis for assessing range shifts, and thus provide information for management purposes (Lawton 1993). Recently, studies on climate change effects have highlighted impacts that include shifts in distributions for birds (Thomas & Lennon 1999), insects, (Parmesan *et al*. 1999), amphibians (Pounds *et al*. 1999), and a mammalian carnivore (Walther *et al* 2002). Therefore, distribution patterns could provide insights on how effects of climatic changes might influence range occupation (Gaston 1990) and provide a basis for identifying factors that could impact negatively on persistence of species (Brown *et al*. 1997).

In Kruger National Park (KNP), Pienaar (1963) mapped distribution patterns for the larger ungulate species. These serve as the basis for assessing subsequent distribution patterns to identify changes in distributions. Factors that could have contributed to changes in distribution patterns of these large ungulates included (i) fencing of the KNP, particularly the southern and western boundaries, which were completed in 1961 (Pienaar 1982 cited in Whyte & Joubert 1988, Joubert 2007), (ii) provision of 50 dams, and 300 boreholes and troughs fed by windmills between 1930s and 1980s aimed at reducing effects of droughts and to ensure a reliable network of surface water all year round (Joubert 2007, Smit *et al*. 2007), (iii) cessation of culling involving wildebeest, zebra, and impala that ended in early 1970s, and of buffalo and elephant ending in 1993 (Joubert 2007), (iv) two severe drought episodes in 1982/3 and 1991/2 (Walker *et al*. 1987), and (v) doubling in elephant abundance from an estimated 1 186 in 1962 to around 2 374 in 1964. By 1968, there were over 7000 elephants in the park (Whyte *et al*. 1999).

In this article, I established recent distribution ranges of twelve large ungulate species in KNP, using geographical positions of animal herds recorded during aerial surveys (May–August) from 1980 to 1993, and compared these with previous distributions as presented by Pienaar (1963). Information on animal locations and distributions reported by Pienaar was obtained through rangers' diaries and reports, monthly road strip counts (1956-61) and two aerial counts targeted at elephant and buffalo in central KNP (1960 and 1962) (Joubert 2007). Pienaar (1963) produced a map that showed dry and wet season range for each species. My aims were 1) to document distribution patterns for the period 1980-1993 reliably as a basis for assessing future changes, 2) note how distribution patterns have apparently changed since around 1960, and 3) relate distribution patterns to landscapes favoured and avoided.

Methods

1.1 Study Area

Kruger National Park is nearly 20 000 km^2 in extent and located in the eastern lowveld region of South Africa. Detailed descriptions of climate, vegetation, and geology are outlined elsewhere (Gertenbach 1983, Venter *et al.* 2003, du Toit *et al.* 2003). Briefly, precipitation decreases in a north-south gradient, with annual rainfall averaging about 750 mm in the south-west and around 400 mm in north-east (Venter *et al.* 2003). In the southern half, knob thorn (*Acacia nigrescens*) and marula (*Sclerocarya birrea*) predominate on basalt substrates, and *Combretum* spp. and *Terminalia* spp. species predominate on granites. Mopane (*Colophospermum mopane*) predominates on both granitic and basaltic substrates in the northern half.

1.2 Data source

I assessed recent distribution patterns using Ecological Aerial Survey (EAS) data (1980-1993). Detailed descriptions of the EAS survey procedure have been documented extensively (see Joubert 1983, Viljoen & Retief 1994, Joubert 2007). I excluded an area north of Punda Maria from this analysis because it was irregularly surveyed (Viljoen 1992). The mountainous corner of south-western Kruger was a difficult terrain to survey, and data from this section might not be reliable (Viljoen 1992). Positional accuracy of locating animal herds from the air was within 2 km prior to 1987 when locations were recorded directly by hand on to topographical maps and latter computerized using a grid system of 2 × 2 km^2 squares (Joubert 1983). Positional accuracy improved to within 0.8 km after 1987 when a palmtop computer coupled with a GPS unit was used to capture coordinates of the position of each herd (Viljoen & Retief 1994, Joubert 2007).

Data analysis

1.3.1 Distribution range estimates

I applied the fixed kernel method (Silverman 1986) in constructing distribution ranges with least-squares cross-validation procedures to choose the smoothing parameter (*h*) (Gitzen *et al*. 2006, Horne & Garton 2006). The smoothing parameter is the bandwidth or the width of a kernel constructed over a reference location point (chapter 2). I did not use the adaptive kernel method because it attaches some level of uncertainty to range edges by applying a bigger smoothing parameter (*h*) for locations at the edge (Kernohan *et al*. 2001, Gitzen *et al*. 2006). However, the fixed kernel method selecting the value for *h* from least-squares cross-validation procedures proved problematic for distribution pattern of wildebeest (see chapter 2 for details). Briefly, least squares cross validation yielded a higher *h* value compared to the one produced with adaptive kernel method, a situation which did not occur with the other 11 species whereby smoothing parameters from both methods were nearly of the same value (chapter 2). To choose the final smoothing parameter for wildebeest patterns I plotted a graph of range area against value of a smoothing parameter (Powell 2000). I gradually increased values of *h* until the curve of area vs. *h* was stable, and I used the average ($h = 0.0264$) of the values around the point when the area stabilized (chapter 2).

I excluded solitary animals from my analysis because they included lone adult males that may be dispersed outside breeding ranges. I used 0.95 probability kernel to estimate range extents for the less abundant waterbuck, sable, eland, tsessebe, and roan, but used 0.99 probability levels for the abundant buffalo, kudu, zebra, warthog (*Phacochoerus aethiopicus*), impala (*Aepyceros melampus*), wildebeest, and giraffe. I represented concentration areas (core sections) consistently by 0.75 probability kernel (see chapter 2 for details). I created shape files of positions of herds recorded during aerial surveys in Arc Map 9.1. I loaded a shape file of locations of herds for each species onto the Home Range Extension Spatial Analyst Tool (Rodgers *et al*. 2005) and constructed distribution ranges. I did not have sufficient computing power to compute all impala positions (N = 102 229) in one batch and therefore I divided KNP into two halves to estimate that distribution range. The two separate analyses were later merged in GIS for displaying a complete impala range on one map, but isopleths refer to different abundance levels in these two sections of the park, and thus cannot be compared.

1.3.2 Analysis of favoured or avoided landscapes

Kruger National Park is divided into fifteen ecological zones that are based on general landscapes features (Gertenbach 1983). I reduced the 15 to 9 entities to represent habitat types in this study (Fig. 1). I merged (a) the predominantly mopane areas (mopane and bushwillow savanna and tree mopane savanna) to form the mopane woodland, (b) knob thorn and marula savanna and stunted knob thorn savanna to form the knob thorn-marula parkland and (c) Pretorius Kop sourveld and Malelane mountain bushveld to form the sour bushveld. Smaller landscapes including Olifants rugged veld, sandveld and thorn veld were grouped into a new category, others. I estimated relative availability of each landscape by calculating the area a particular landscape covered in KNP then dividing that by total area of the park. I used the ET Geowizard tool in Arc Map to determine records of animal sightings per species in 0.95 or 0.99 probability isopleths within each landscape type. To determine whether a landscape type was occupied in proportion to its availability, avoided or preferred, I assessed proportion of animal records in an isopleth per landscape in relation to proportion of total records in the whole park. I indicated strongly favoured habitats if the proportion of occupation was twice or more than the proportional availability, and avoidance if the proportion of records was less than 0.5 of the proportion available. I did not apply statistical tests for comparisons of current distribution ranges with ranges depicted in the 1960s because Pienaar’s maps were vaguely complied and thus may not be scientifically rigorous to form a basis for inferring distributional changes. Furthermore, the very large sample sizes for most species spanning the period (1980-1993) may most likely show significant relationships anyway.

1.3.3 Changes in proportional distribution in various regions

I assessed changes in the proportional distribution of each species in each of the four census regions for the period 1979-1993 when aerial censuses covered most of the park except for a small section in centre of the southern region of KNP which was not covered in 1979. Kruger National Park has four regions south, central, north and far northern region which are separated by rivers. I subdivided the period (1979-1993) into three periods consisting of 5 years each: (a) 1979-1983 (representing pre-1982/3 drought), (b) 1984-1988 (representing period prior to decline of rare antelopes abundances and prior to a second drought (1992/3), and (c) 1989-1993 (after abundance decline had started and a period that included a second drought in 1992/3). I calculated an average of animals sighted for each 5 year period in each region, but divided by 4 years in southern region where records were not available for 1979. I plotted proportion of animal records in each region in relation to total records in the whole park during a specific time period.

Results

1. Impala

The concentration areas for impala must be interpreted independently in each half of KNP as distribution patterns in the two halves were analyzed separately. Impala were notably absent from some localized areas of the eastern half of KNP (north-east of central region and most sections of north-east region except near Shingwedzi River) (Fig. 2a). Concentration areas of impala were associated with seasonal and perennial rivers on western granite areas in northern half, but more widespread away from rivers in the southern half. Concentration areas of impala were not represented in south-western KNP. The proportion of impala was approximately two times more in central and southern KNP than in northern sections (Fig. 3a). The proportion of impala occurring in northern region increased from an estimated 0.164 during 1979-1983 to about 0.187 during 1989-1993 and the proportion occurring in far north increased from 0.063 to 0.094, but declined largely in southern region of KNP during the same period.

Impala favoured thorn thickets near Sabie and Crocodile rivers, and thorn thickets on karoo sediments of central region (Table 1).

1.2 Zebra

Zebra distribution was continuous across KNP apart from a gap in a section in central-north of southern region near the Sabie River where zebra were not recorded. Concentrations of zebra were mainly in western granite areas in northern half of KNP, but occurred mostly in basalt areas in the southern half. However, concentrations of zebra occurred in granite areas in the extreme south-west of KNP. Proportion of zebra increased in far north from an estimated 14% during 1979-1983 to about 20% during 1989-1993 (Fig. 3b). In contrast, 34% and 10% of the proportion of zebra occurred in north and southern regions in 1979-1983 but decreased to 10% and 7% respectively during in 1989-1993.

Zebra did not show strong preference for any particular landscape, but tended to avoid thorn thickets along Sabie River and the sour bushveld around Pretorius Kop (Table 1).

1.3 Buffalo

Buffalo were distributed throughout KNP but concentrations during dry seasons were associated with seasonal and perennial rivers mainly in the western half of KNP on granitic substrates (Fig. 3a). The proportion of buffalo relative to total population size in northern region increased from an estimated 26% to 34% and 13% to 15% in southern region between 1979-1983 and 1989-1993 (Fig. 3c). The proportion of buffalo occurring in far north and central regions declined from 30% to 23% and from 30% to 27% respectively relative to other regions of KNP during same period.

Buffalo showed no strong preference for any particular landscape, but avoided thorn thickets near Sabie River, sour bushveld around Pretorius Kop, and mountain bushveld on rhyolite (Table 1)

1.4 Wildebeest

Wildebeest were highly concentrated in central region where > 70% of the population occurred (Fig. 2d). Other local dry season concentration areas were on basalt in far north-east and south-eastern KNP. Gaps occurred in a section in central-north areas of southern region near Sabie River and along Crocodile River where wildebeest were not recorded. Gaps also occurred in north-west of KNP on granite. Proportion of wildebeest increased in far north from 8% during 1979-1983 to 10% during 1989-1993 and from 68% to 74% in central region during this period. Proportion of total wildebeest showed a decrease of similar magnitude per region in south (11% to 7%) and northern (12% to 8%) regions during this period (Fig. 3d).

Wildebeest strongly favoured knob thorn and marula parkland on basalt in central region (Table 1). Wildebeest avoided mopane woodlands, sour bushveld, and thorn thickets near Sabie and Crocodile rivers (Table 1).

1.5 Kudu

Kudu occurred continuously across nearly the whole park and concentration areas were indicated throughout most of central and southern regions (Fig. 2b). The proportion of kudu in southern region increased from about 22% in 1979-1983 to about 30% in 1989-1993 and the proportion in central region increased from 38% to 41% during the same period. The proportion of kudu declined 26% to 18% north (0.26 to 0.18) and from 13% to 11% in far north respectively during the same period.
Kudu favoured mountain bushveld in eastern KNP, but did not avoid any particular landscape (Table 1).

1. 6 Giraffe

Giraffe range covered all the southern half of KNP. Concentrations of giraffe occurred in central region extending into southern region to the east (Fig. 2g). Giraffe were not recorded in parts of both granite and basalt areas of northern region, but from granite areas of the far north region. Proportion of giraffe doubled in far north from 27% in 1979-1983 to 54% in 1989-1993 periods and decreased from 63% to 61% in central region. The proportion of giraffe in southern region decreased by about the same magnitude as was the central region.
Giraffe favoured the knob thorn and marula parkland in central region and mountain bushveld (Table 1). Giraffe avoided sour bushveld around Pretorius Kop and mopane shrubveld in north and far north sections of KNP (Fig. 2e).

1.7 Waterbuck

Waterbuck distribution was associated with perennial and seasonal rivers (Fig. 2h). Concentrations occurred along Olifants and Letaba rivers, and on seasonal rivers in central-east. The proportion of waterbuck in central region increased from 37% to 46% and from 11% to 14% in far north regions between the periods 1979-1983 and 1989-1993 (Fig. 4h). The proportion of waterbuck in the north region decreased from 41% to 28% during the same periods.

Waterbuck favoured mountain bushveld in eastern Kruger, but showed no avoidance of any landscape (Table 1).

1.8 Warthog

Warthog were distributed throughout most of KNP with concentrations across the central region, south-east, and in granite areas of south-central and west of northern half of KNP (Fig. 2g). Proportion of warthog in the north region increased from 22% to 25% and increased from 7% to 11% in far north region between the periods 1979-1983 and 1989-1993 (Fig. 3g). Proportion of warthog in south declined from about 28% to 20% during the same periods.

Warthog favoured knob thorn and marula parkland in central region and did not appear to avoid any particular landscape (Table 1).

1.9 Sable antelope

Sable distribution was continuous in most of the western granite section of the north and far north and extended out to basalt areas in far north-east, but distribution was patchy in the southern half, and sable mostly occurred on granite (Fig. 2i). Concentrations of sable occurred in the north-west, south-west plus localized areas west of the central region (Fig. 3i). The proportion of sable increased from 30% to 37% and from 13% to 16% in far north and central regions between 1979-1983 and 1989-1993 (Fig. 3i). However, the proportion of sable decreased from 32% to 24% in northern region during the same period.

Sable favoured mopane woodland in north-west and sour bushveld around Pretorius Kop in south-west. Sable avoided knob thorn and marula parkland in eastern parts of the central region and the mountain bushveld of eastern Kruger (Table 1).

1.1.0 Tsessebe

Tsessebe were continuously distributed through north-eastern basalt areas, but their occurrence was isolated in north-west (Fig. 3k). Tsessebe occurred on isolated patches in central region and north-east of southern KNP. The proportions of tsessebe showed little change, declining from 55% to 52% in far north but increasing in south region from 3% to 5% between 1979-9183 and 1989-1993.

Tsessebe strongly favoured mopane shrubveld in north-eastern basalt areas (Table 1).

1.1.1 Eland

Eland occurred through most of the far north, but distribution was patchy in northern region. Eland were absent from southern KNP except for the south-west where some eland were introduced (Fig. 2j). The proportion of eland in far north increased from 51% to 59% between 1979-1983 and 1989-1993 (Fig. 3j). The proportion of eland declined in the north from 48% to 37% during the same periods.

Eland favoured mopane woodlands and mopane shrubveld (Table 1).

1.1.2 Roan antelope

Roan showed a patchy distribution, with most concentrated in the eastern region of the North and Far North sections, plus isolated patches occupied by single herds in the western region of the northern part of KNP and in the south-west (Fig. 3l). Those recorded in the east of the Central section were introduced there. Roan concentrated especially in mopane shrubland (Table 1), and isolated herds in the west tended to be associated with gabbro intrusions into this predominantly granitic region. The roan antelope population declined equally through all sections of KNP after 1986 (Figs. 6l). However, the proportion of roan in central region increased from 0.0 to 0.3 but declined from 60% to 56% in far north region during the same period.

Roan strongly favoured mopane shrubveld in north-eastern Kruger (Table 1).

Discussion

This paper established that amongst the six common species, buffalo and zebra occurred throughout KNP. Impala distribution exhibited gaps in a few localized areas on basalt in eastern KNP whilst wildebeest were not recorded in some places on granite to the north-west. Amongst common browsers, kudu occurred throughout KNP, and giraffe occurred throughout southern half, but were absent in some places in northern half. Of the two “intermediate species” (abundance level somewhere between the common and rare species), waterbuck were associated with rivers in all four regions and warthog were distributed throughout KNP. Amongst the four rarer antelopes, sable antelope were more prevalent on western granite, but occurred on distinct patches on basalt areas in the east of KNP. Roan and tsessebe occurred mainly in areas on basalt in north-eastern and far north-eastern KNP. Eland occurred through most of far north, were not recorded in parts of northern region and were largely absent in southern KNP.

Assessment of changes in proportional distribution indicated two contrasting patterns amongst the different species. First, an initial (1979-1983 to 1984-1988) upward trend of population sizes for all species (except buffalo) which was characterized by evident increases in proportions of their numbers in northern half relative to southern half of the park. Second, a decline of all species (except wildebeest and zebra) after 1988, which was again associated with shifts in regional proportions of these populations. Between 1979-1983 and 1989-1993, the common species i.e. impala, zebra, buffalo, wildebeest, giraffe, and warthog all increased proportionately in northern half of KNP relative to the southern half. In contrast, proportions of rarer antelopes, kudu, and waterbuck decreased in northern half of KNP relative to the southern half. Changes in proportional distribution of common species appeared less associated with specific vegetation characteristics. Instead, the proportional changes and the expansions of distributions of common species appeared closely linked to lower abundances of these species in the northern half of KNP relative to the southern half. This suggests that perhaps proportional changes were somehow linked with lower competition or predation risks in those northern sections of KNP. Furthermore, the common species expanded on both nutrient rich basaltic and nutrient poor granitic substrates in this northern half of KNP. In addition, the same common species occurred on both granite and basalt substrates in the southern half of KNP.

Comparisons of recent distributions (1980-1993) to those mapped around 1960 indicate these basic features. (1) An increased occupation of northern half of KNP by common species (zebra, buffalo, impala, warthog, giraffe, and wildebeest). (2) Several species (1980-1993) occurred during dry season in areas indicated around 1960 as wet season range (zebra, warthog, buffalo, waterbuck, and wildebeest). (3) Distributions of rarer grazers contracted in northern half of KNP and west central region.

Impala appeared more widespread away from rivers in northern and central regions due to increases in their numbers in these sections. Warthog also appeared more widely distributed in the northern half of KNP than was shown around 1960. Apparently, some range expansion for waterbuck away from rivers occurred in central-east, south-east, and south-west.

Areas in east central region shown around 1960 as part of wet season range for zebra and wildebeest had become dry season concentration areas. Wildebeest appeared more widespread in north region than was indicated around 1960. There were more wildebeest and zebra in KNP in 1989-1993 than 1979-1983, while their populations showed little change after 1988. Therefore, proportional distribution shifts suggest a higher local increase of their numbers in northern half of KNP. Dry season concentrations for buffalo were indicated along the central-western boundary, which was indicated as wet season range around 1960. An increase in proportion of buffalo in northern half relative to southern half during a period when buffalo were declining suggests that proportional distribution shifts were due to decline of numbers in northern region relative to southern sections. Kudu showed a similar pattern to buffalo. Giraffe expanded their presence in northern half of KNP to areas not occupied prior to 1963, so their proportion increased in this region.

Recent (1980-1993) distribution patterns indicated a shrinkage of ranges of rarer antelope species associated with a decline in their relative numbers in northern half of KNP. Areas occupied by sable in west-central region around 1960 appeared fragmented into discrete patches. Tsessebe were absent from western granite areas in the central region where Pienaar had shown them to be present. Eland range had apparently shrunk north of Letaba River. Roan disappeared from north-west of central region and from most of the western section of northern regions where Pienaar indicated their presence.

Distributions of browsers are less influenced by surface water availability in dry season in comparison to those of grazers (Western 1975, Ayeni 1975). Therefore, giraffe in KNP may have expanded their distribution northward because of food availability there. Patterns suggest that impala, zebra, buffalo, wildebeest, waterbuck, and warthog likely increased occupation of areas away from perennial rivers after waterpoints were added. Persistence during dry season in areas marked as wet season range around 1960 suggests that provision of permanent water to those areas may have led to these changes. The number of boreholes and drinking troughs amounted to about 300 plus 50 earth dams by the 1980s (Joubert 2007). Stevenson-Hamilton

(1947) suggested that lack of surface water during dry season limited occupation of northern KNP.

It has been suggested that widespread provision of artificial surface water in semi-arid savannas may result in homogenisation of animal distributions (Owen-Smith 1996, Smit *et al*. 2007). Based on this view, distributional shifts presented here could be explained by widespread provision of waterpoints. Smit *et al*. (2007) reported that grazers in KNP were more associated with artificial waterpoints than browsers and mixed feeders. Patterns presented here appear to support those observations. Grant *et al*. (2002) recorded that radio-collared zebras in KNP moved away from areas where waterholes were closed towards areas where waterholes were still operational. Harrington *et al*. (1999) noted that there was a zebra influx in roan range shortly prior to roan decline. The strong influence that surface water has on where grazers occur on the landscape was shown for Tsavo National Park and in the Amboseli, Kenya, where most grazers occurred within 4 km from a water source during the dry season (Ayeni 1975, Western 1975)

I expected dry season distributions for previously migratory wildebeest and zebra to shift in central region where fences blocked movement westwards outside the park. Patterns shown here appear to show some support for this expectation for wildebeest and zebra, although availability of water in dry season in those areas may potentially be an additional factor. Results presented here suggest tsessebe had disappeared from the area. Roan and tsessebe disappeared from west central KNP while sable distribution became patchy in this area.

This study provides support for previous conclusions (Whyte & Joubert 1988, Grant *et al*. 2000) that management effects that included blocking migration outside the park by fencing and augmenting artificial water may lead to grazer species remaining in areas where waterpoints were added during dry season. Expansions of ungulate distribution northwards and occurrence in areas previously used during wet season suggest that shifting distributions may have been associated with effects of providing permanent surface water to those areas. Range shrinkages and fragmentation of rare antelope distributions may have occurred because common species had become resident on areas which then became less suitable to rare antelopes.

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FIGURE CAPTIONS

FIG. 1. Main ecological zones in Kruger National Park. 1-Bushveld (Pretorius Kop/Malelane), 2-Thorn thickets around Sabi and Crocodile Rivers, 3- Mopane shrubveld, 4-Mopane woodlands 5-Mountain bushveld (Lebombo), 6-Knob thorn and marula park land, 7-Mixed bushwillow woodlands, 8- Others, 9-Thorn thickest (Delagoa)

FIG. 2. Distribution ranges (1980-1993) (a) impala (h = 0.0222), (b) zebra (h = 0.0498), (c) buffalo(h = 0.0651), (d) wildebeest (h = 0.0265) (e) giraffe (f) kudu (h = 0.0196) (g) warthog (h = 0.0222), (h), waterbuck (h = 0.0244) (i) sable (h = 0.0279), (j) eland (h = 0.0364), (k) tsessebe (h = 0.0288), (l) roan (h = 0.0357).

FIG. 3. Changes in proportional distribution in various regions. 1-Complete fill with small dots represent the Far North, 2-diamonds represent the North region, 3-vertical lines represent the Central region and 4-slanted lines represent the Southern region (a) impala, (b) zebra, (c) buffalo, (d) wildebeest, (e) kudu, (f) giraffe, (g) waterbuck, (h) warthog, (i) sable, (j) tsessebe, (k) eland, (l) roan.

Table 1. - Proportion of animal sightings in all herds in 0.95/.099 probability isopleths within each landscape type expressed as a percentage relative to its proportional extent in Kruger National Park. 1- Bold represent favoured landscapes, 2- Brackets represent avoided landscapes.

		Impala	Zebra	Buffalo	Wildebeest	Giraffe	Kudu	Warthog	Sable	Waterbuck	Eland	Tsessebe	Roan
Landscape Type	Avail.	Proportion of use											
Mopane Woodland	30	21	26	35	(9)	13	21	28	**49**	26	**57**	11	17
Mopane Shrubveld	17	7	23	23	12	(6)	12	8	10	20	**35**	**78**	**75**
Mixed Bushwillow woodland	12	17	7	8	11	16	15	16	15	8	(0)	(1)	(0)
Knob thorn-marula parkland	11	11	**20**	14	**45**	**21**	15	**22**	(4)	16	(0)	(2)	(0)
Others	9	10	8	8	7	12	9	8	12	5	6	5	5
Mountain bushveld	7	10	11	(3)	7	**13**	**14**	4	(1)	17	(1)	(1)	(2)
Thorn thickets (near Sabie & Crocodile Rivers	7	**15**	(1)	(3)	(1)	8	6	7	(0)	(2)	(0)	(0)	(0)
Sour bushveld	5	3	**(2)**	(2)	(1)	(3)	6	(2)	**10**	3	(1)	(1)	(1)
Delagoa thorn thicket	3	**6**	3	4	5	**7**	2	5	(0)	3	(0)	(0)	(0)

Figure. 1.

Excluded from Analysis

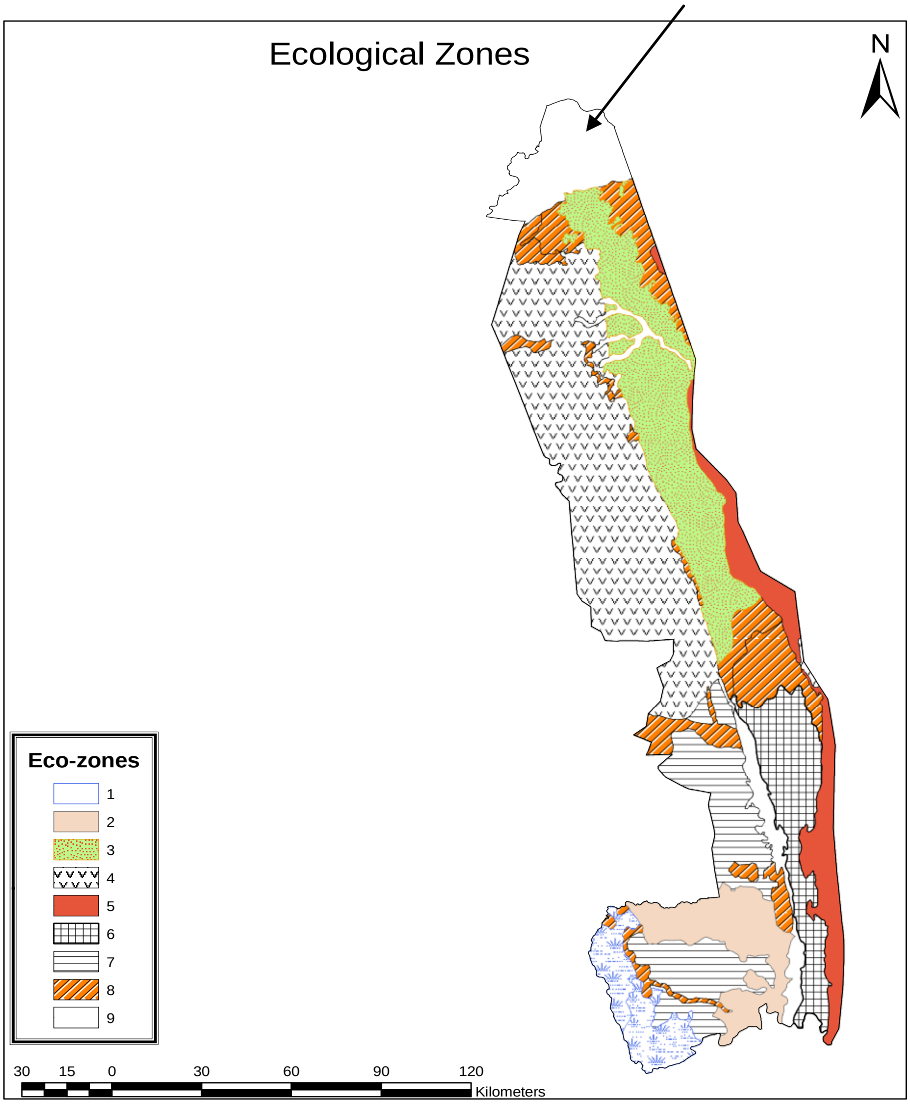
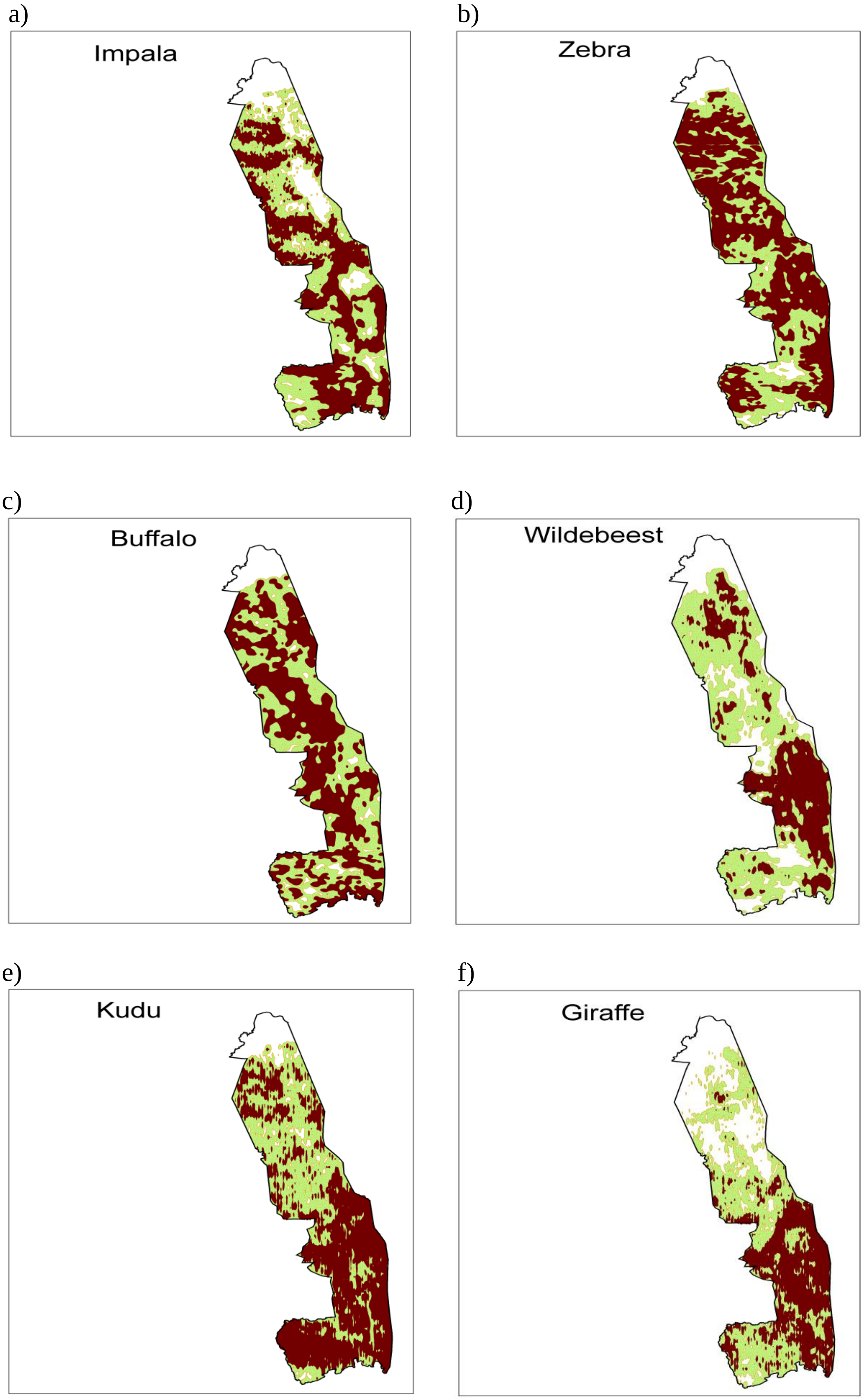
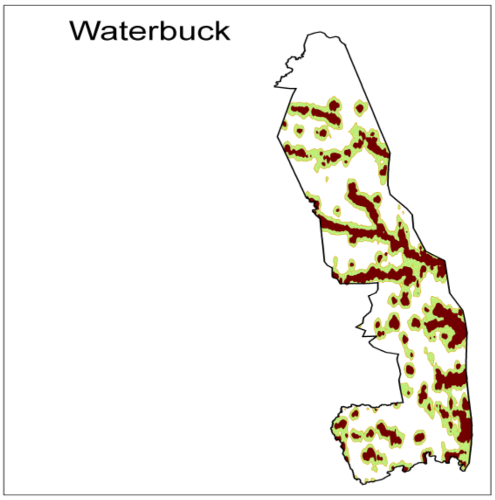


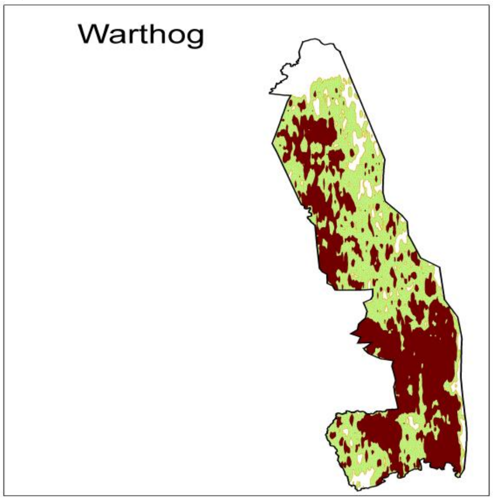
Figure. 2.



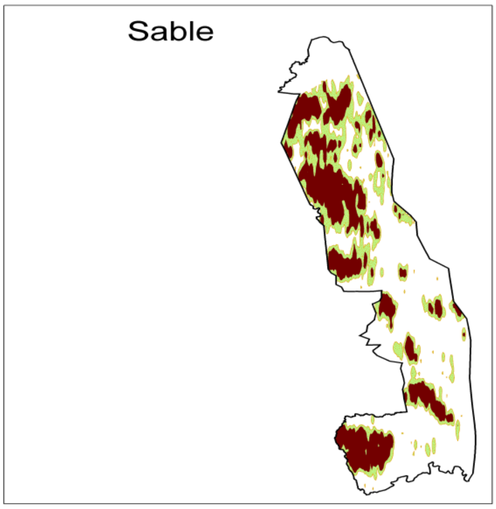
g)


Waterbuck

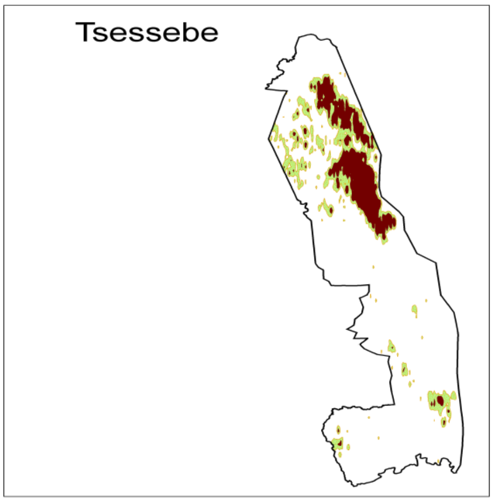
h)


Warthog

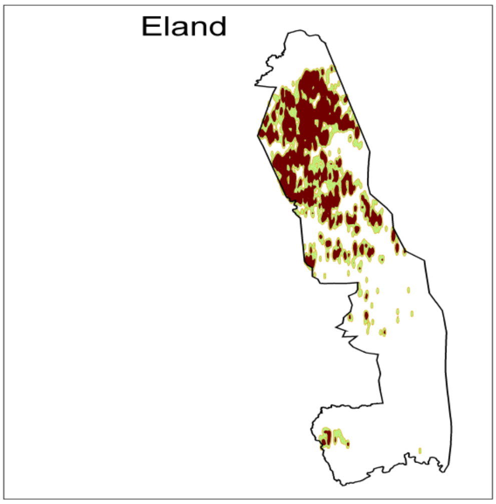
i)


Sable

j)


Tsessebe

k)


Eland

l)

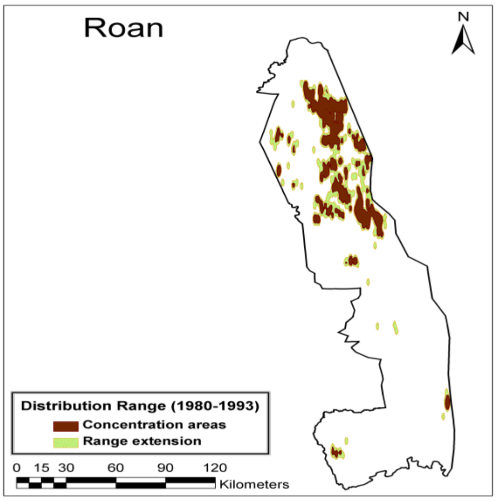
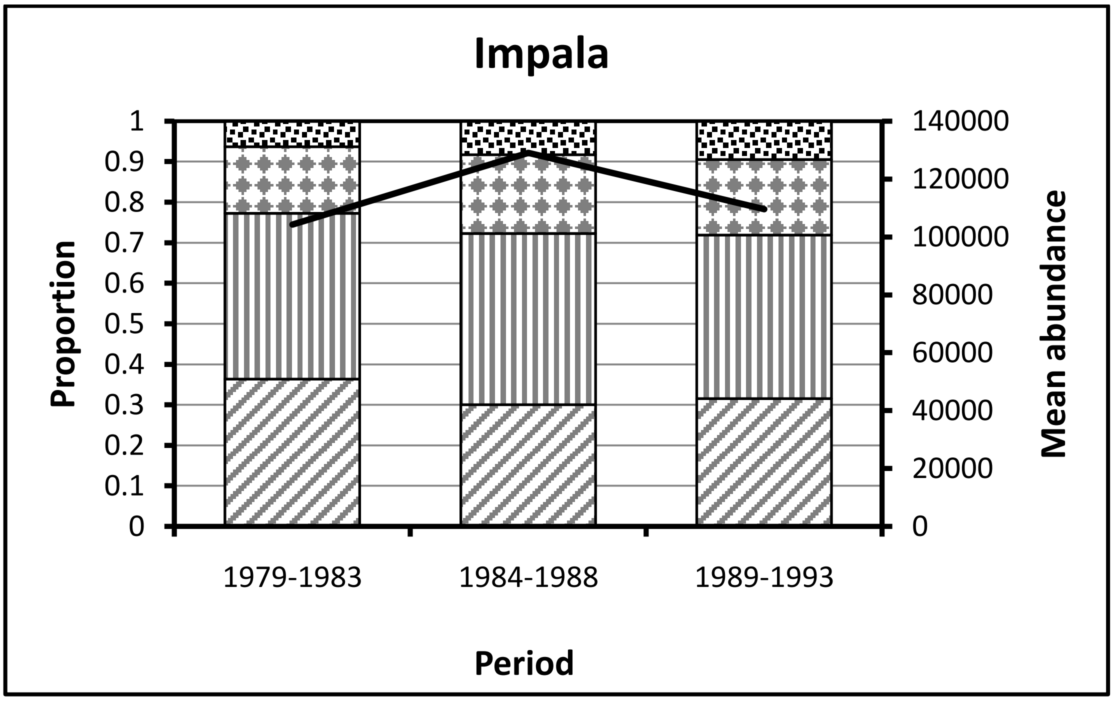
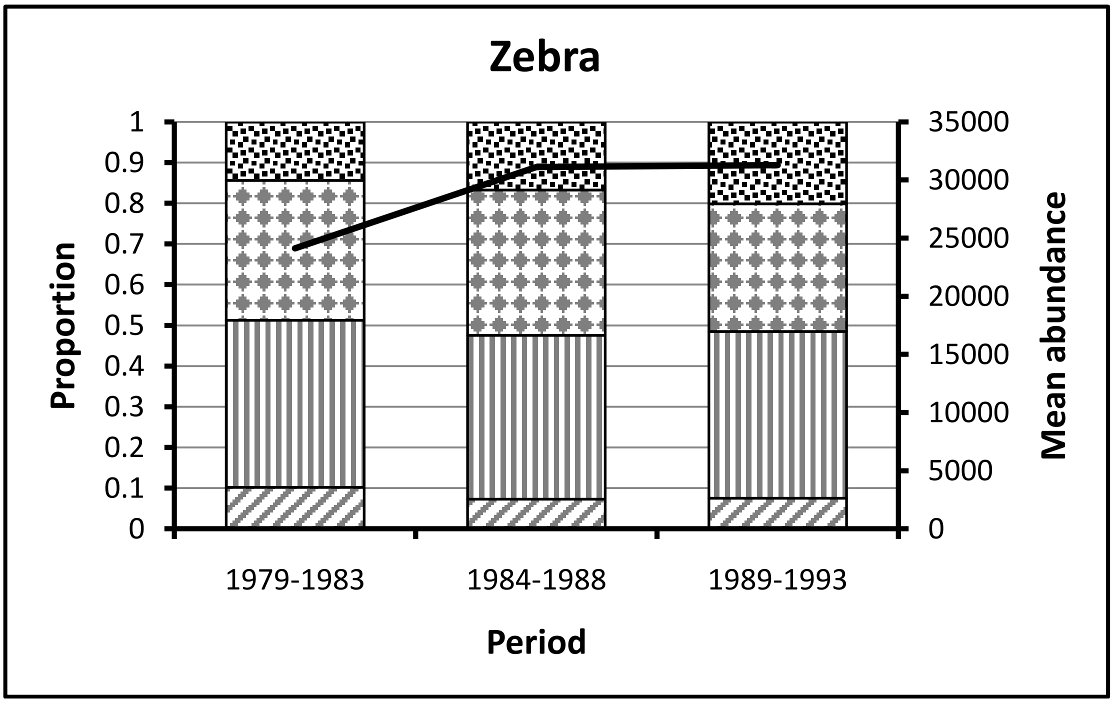

Roan
N
Distribution Range (1980-1993)
Concentration areas
Range extension
0 15 30 60 90 120
Kilometers

Figure 3

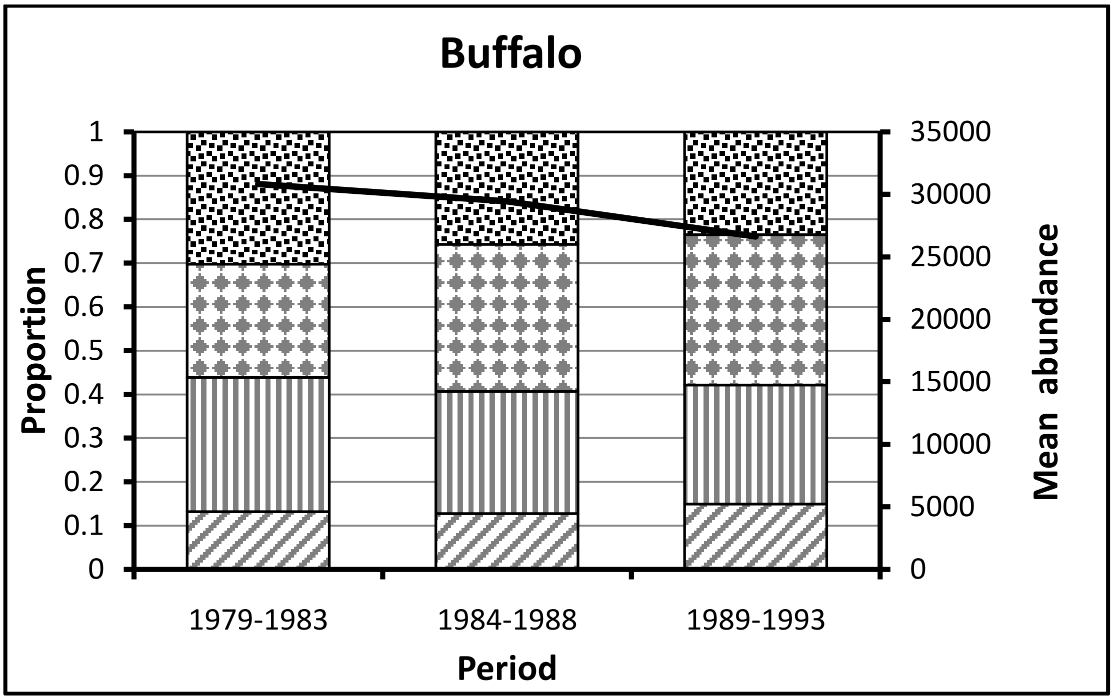
a) Impala



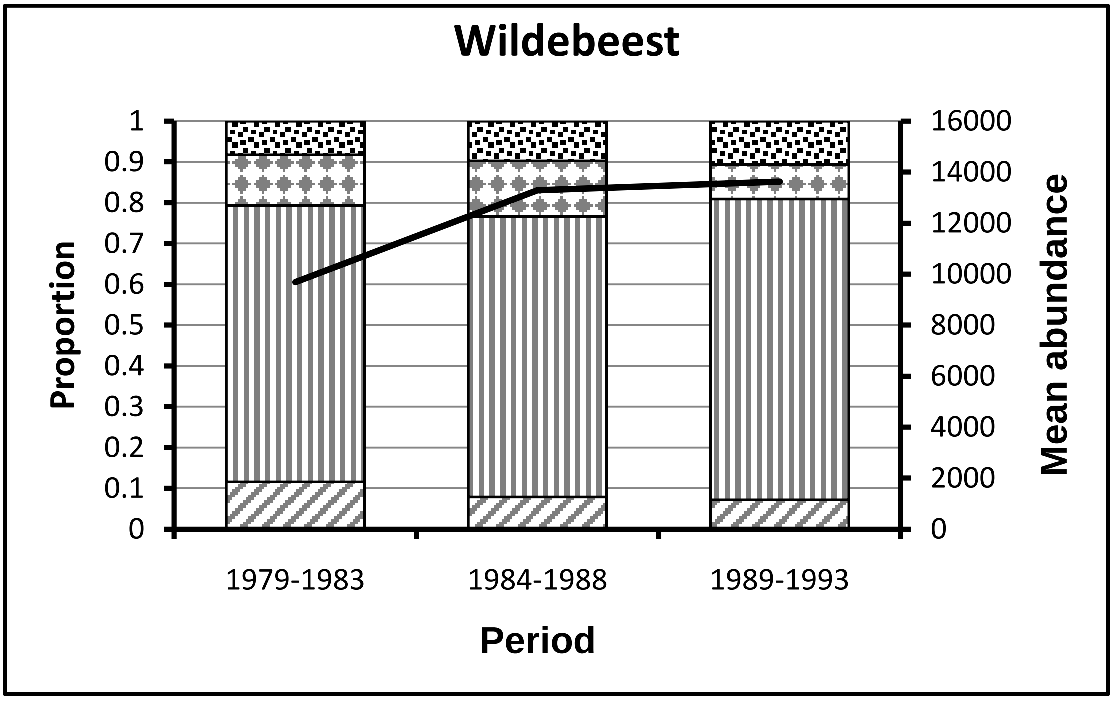
b) Zebra



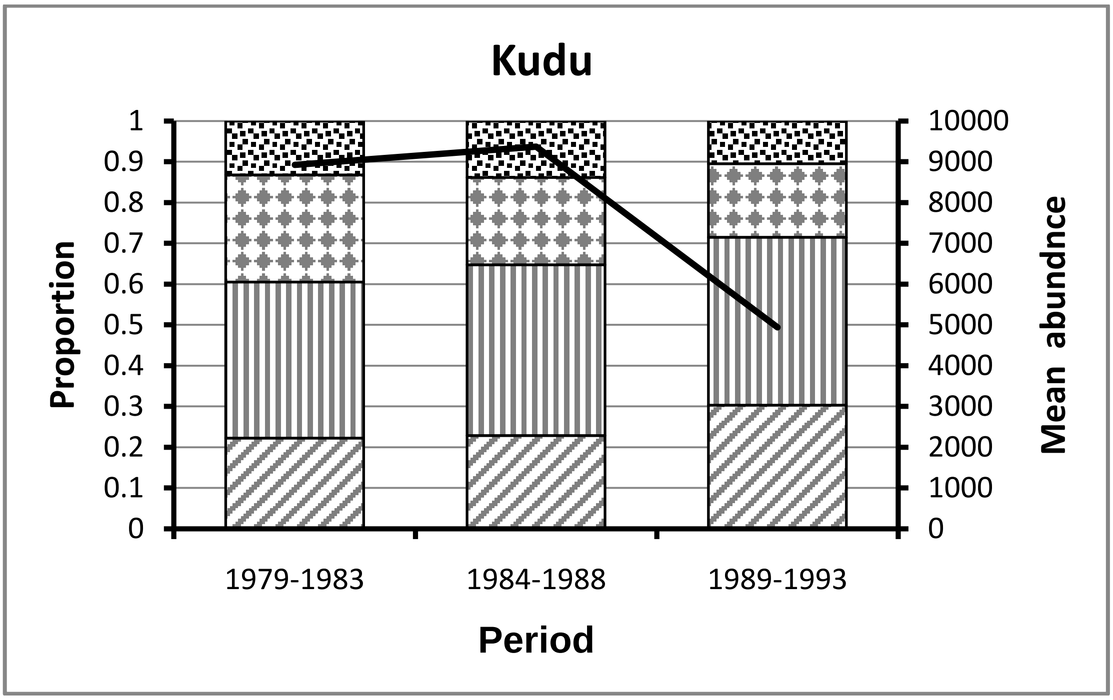
c) Buffalo



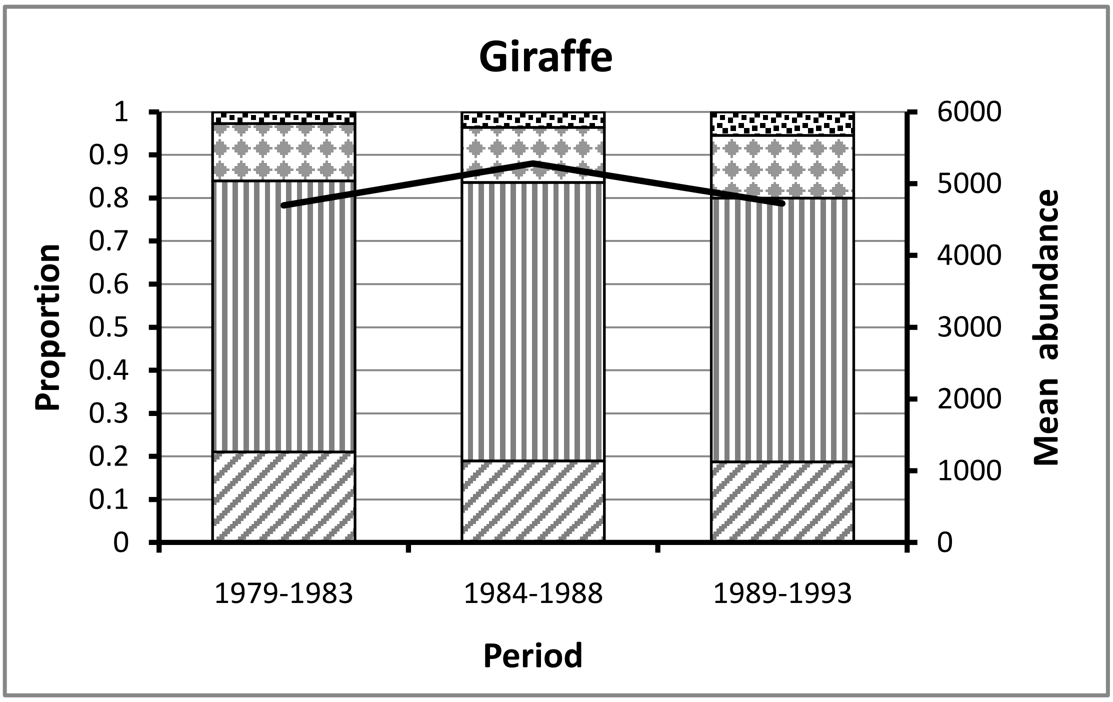
d) Wildebeest



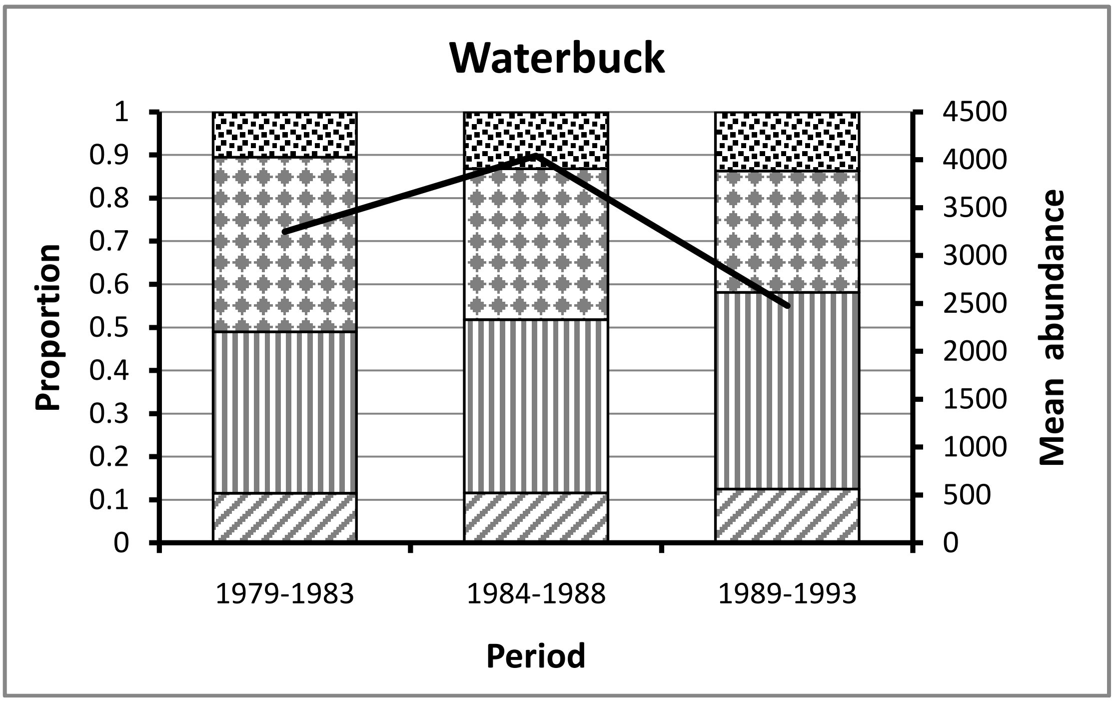
e) Kudu



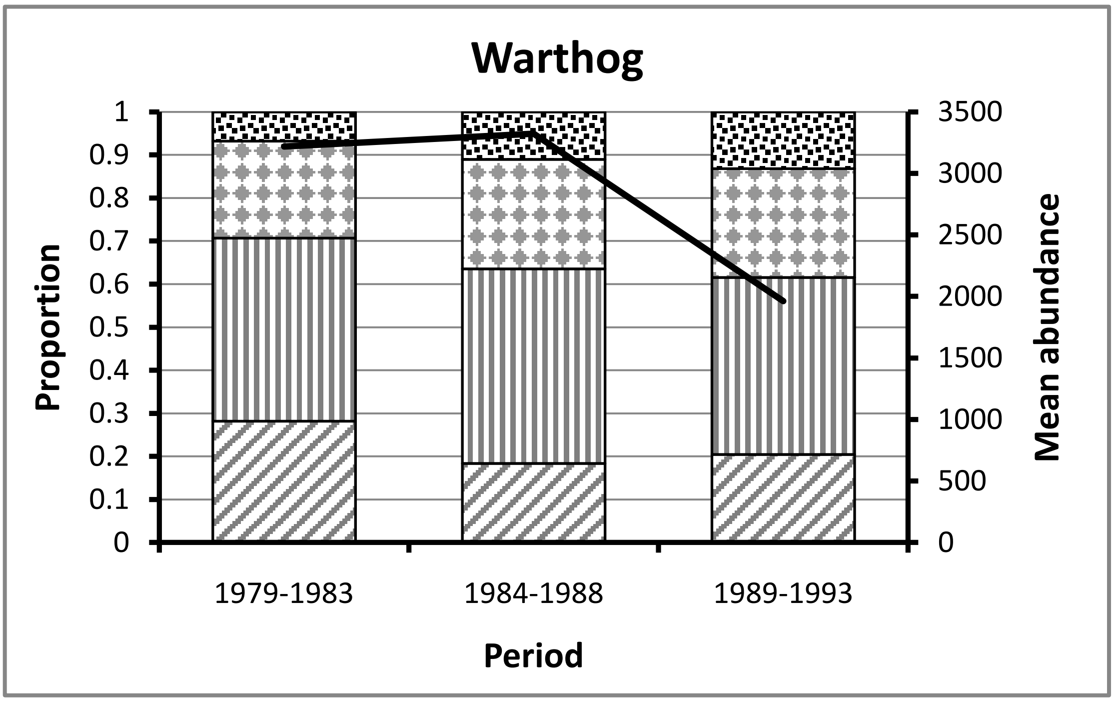
f) Giraffe



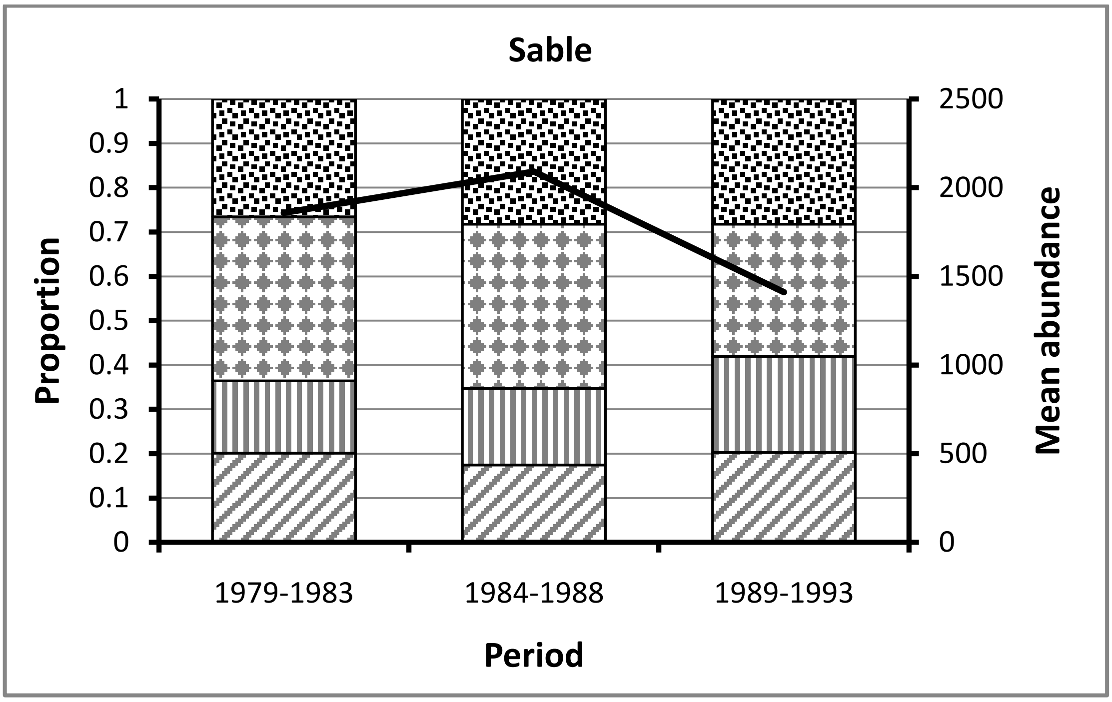
g) Waterbuck



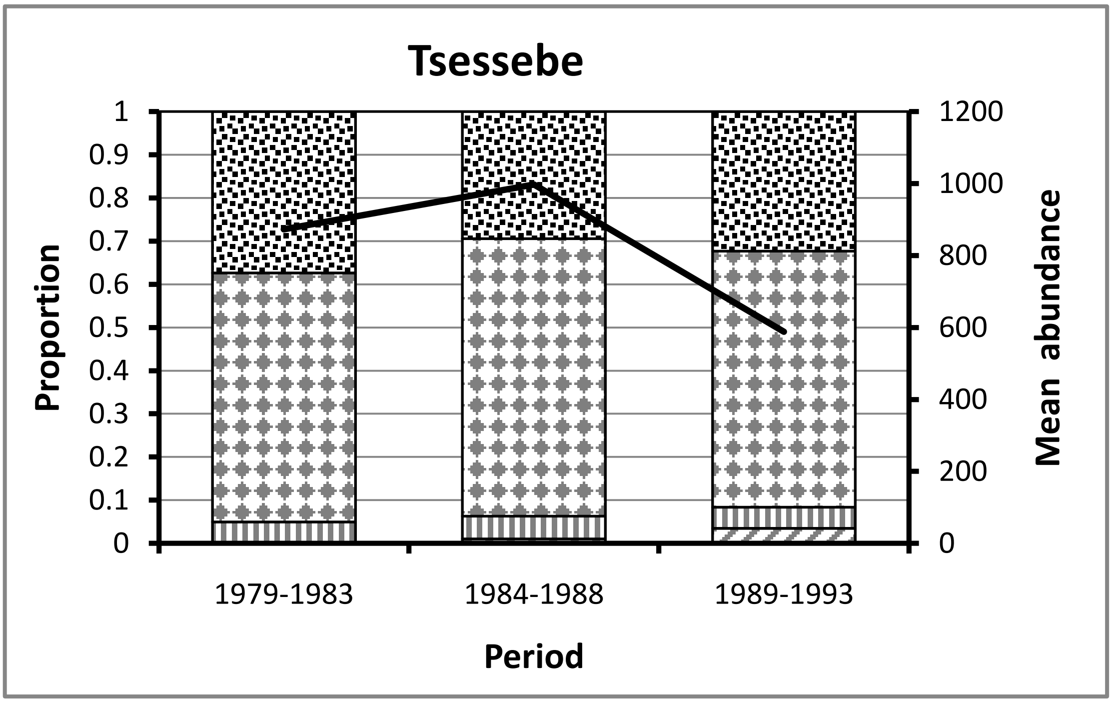
h) Warthog



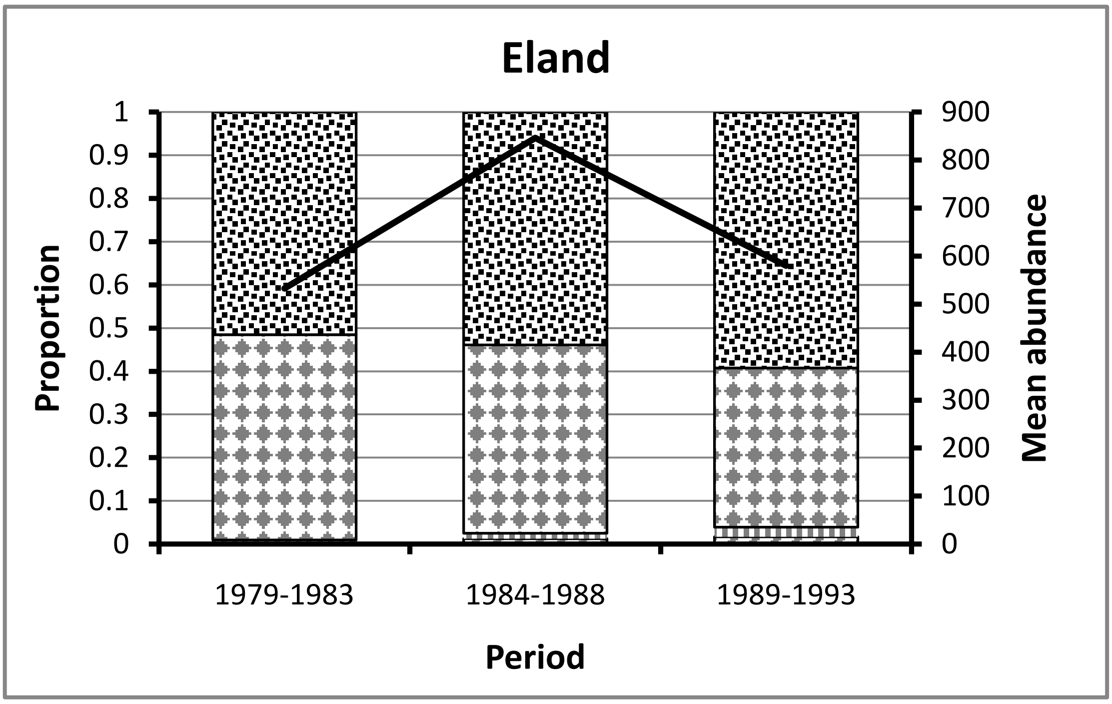
i) Sable



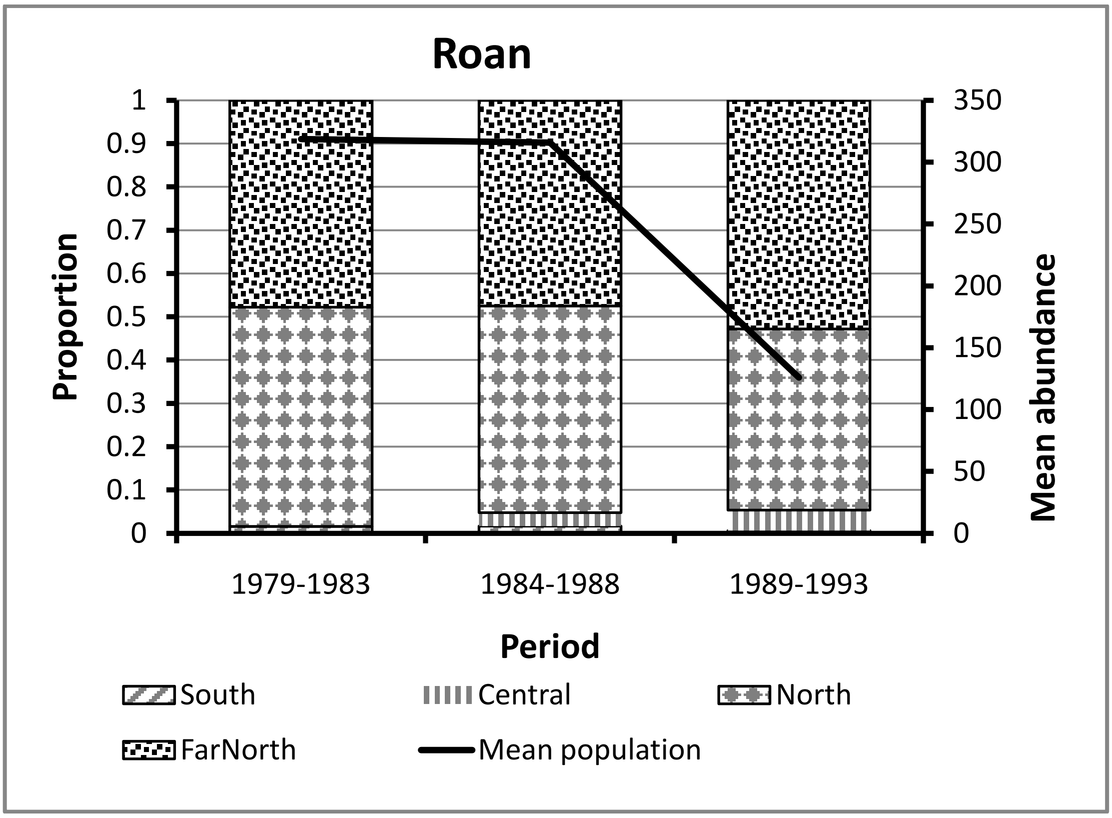
j) Tsessebe



k) Eland



l) Roan



CHAPTER 4

Contracting distributions at the edge of the range: rarer antelope species in Kruger National Park, South Africa.

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ABSTRACT

Distributional changes in response to global warming documented for several taxa involve a range shift towards higher latitudes or elevations. At range edges, changes may be complex. Species may disappear from less suitable patches while persisting where conditions remain sufficiently favourable. Less documented are range shifts related to changing rainfall amount and seasonal distribution influencing vegetation composition and productivity, and hence food resources for herbivores. Roan antelope, sable antelope, and tsessebe declined to 20% or less of their prior abundance during recurrent droughts between 1982 and 1995 in Kruger Park at the southern limit of their geographical distribution. We assessed changes in their distribution ranges associated with these population declines using location records obtained from (1) park-wide annual aerial surveys (1977–1997), and (2) locations of sable herds tracked by GPS in two regions of Kruger Park (2001-2007). Range contractions were evident for all three antelope species, associated with local herd extirpations, especially following the severe 1991/2 drought. Range shifts up the rainfall gradient did not occur, and roan and tsessebe became locally extirpated in the wetter southern section of the park. Small sable herds persisted in discrete remnants of their former distribution in the park. Populations of these three species have not recovered despite more favourable rainfall in recent years. It remains uncertain whether heightened predation risk, increased competition from more abundant grazers, or a regime shift in habitat conditions following persistent El Nino conditions through 1982-1995, is holding back the recovery of these rarer antelope species.

Introduction

Distributional shifts in response to global warming have been documented for insects (Parmesan *et al.*, 1999), amphibians (Janzen, 1994), fish (Brander *et al.*, 2003), birds (Thomas & Lennon, 1999), and mammalian carnivores (Walther *et al.*, 2002). These typically involve a range shift towards higher, and hence cooler, latitudes or elevations. However, spatial patterns may be more complex around the margin of the distribution range due to local variation in habitat conditions and other influences ranges (Caughley *et al.*, 1988; Gaston, 1990; Lawton, 1993). Species may become extirpated from localities representing marginal habitat, while persisting in places where conditions remain more suitable (Lomolino & Channel, 1995). Changes in occurrence may be mediated through interactions with competitors or predators rather than being simply a response to changing climatic conditions (Gaston, 1990; Channel & Lomolino, 2000a).

Relatively poorly documented are range shifts related to changing rainfall patterns. The amount and seasonal distribution of rainfall strongly influences vegetation structure, composition and productivity in drier regions (Woodward, 1987), with consequences for the distribution and abundance of large herbivores dependent on this vegetation as food (Walker, 1991; Brown *et al.*, 1997). Moreover, the presence of these large mammals has become restricted largely to protected areas, which may be fenced or surrounded by human settlements and livestock preventing dispersal. Three large herbivore species occur at the southern limit of their historical distributions within the Kruger National Park (KNP) in South Africa: roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*) and tsessebe (*Damaliscus lunatus*) (Skinner & Chimimba, 2005). All three remain widely prevalent in wetter savanna regions further north in Africa. Their populations within KNP declined to 20% or less of their peak abundance during the recurrent droughts that occurred between 1982 and 1995 (Ogutu & Owen-Smith, 2003). Various lines of evidence implicate an increase in abundance of their major predator, plus shifts in prey selection, as primarily responsible for the sharp downturn in population trends of these species apparent after 1986, rather than simply low rainfall (Owen-Smith *et al.*, 2005; Owen-Smith & Mills, 2006, 2008). Underlying this pattern was expanded surface water availability through the provision of numerous artificial waterpoints in form of boreholes and dams by park managers. The result was expanded populations of the ungulate species that form the principal prey of lions. Nevertheless, the rarer antelope species have not recovered despite more favourable rainfall conditions since 1995, and the closure of many water points. This suggests that some lasting effect of the prolonged dry conditions, persistent high predation pressure, or increased competition from the more abundant grazers, may be restricting their population recovery.

In this paper, we assess distributional changes within the park associated with the population decreases by these relatively rare antelope species in order to unravel the contributory mechanisms further. We draw on two sources of data: (a) aerial censuses of all large herbivores within KNP, carried out annually from 1977 to 1997, including spatially explicit herd locations, and (b) locations of surviving herds of sable antelope tracked by telemetry in two regions of the park between 2001 and 2007. We expected that, if habitat deterioration as a consequence of lowered rainfall was the main influence, the range shrinkage would be greater in the drier northern section of the park than in the wetter southern region. However, the increase in water points putatively leading to heightened predation was also proportionally greatest in the northern section of the park (Grant *et al.*, 2002), potentially confounding relationships with rainfall. We also extracted supporting information on changes in herd numbers, herd sizes, and calf proportions recorded during the aerial censuses. All three antelope species form cohesive breeding herds occupying distinct and spatially fixed home ranges (Skinner & Chimimba, 2005). Hence distributional shifts occur through the local extirpation of herds. While predation by lions affects especially adult mortality (Owen-Smith *et al.*, 2005), a reduction in food availability due to less effective rainfall, or predation by smaller carnivores, should lead mainly to reduced calf survival (Gaillard *et al*. (1998). We expected that, if effects besides rainfall (e.g. predation) were overriding, contractions of distribution range, herd sizes and recruitment would be spatially disparate. If rainfall was the main cause, reductions in recruitment and herd size should be consistently greater in the drier north. Variation in the timing, regional location, and spatial extent of range reductions could provide further clues to the causal mechanisms.

Methods

Study area and species

Kruger National Park (KNP) covers almost 20,000 km^2 in the eastern Lowveld region of South Africa. Its boundaries became completely fenced in 1976, but in 1993 a section of the fence separating the park from private wildlife reserves to the west was removed. Precipitation ranges from 750 mm in the south-west to around 450 mm in the north-east (Venter *et al*., 2003). Granite-derived sandy soils prevail in the west and basaltic clays in the east. In the southern half, the vegetation is predominantly knob thorn (*Acacia nigrescens*) - marula (*Sclerocarya birrea*) parkland on basalt, and bush willow (*Combretum* spp.) - silver cluster-leaf (*Terminalia sericea*) savanna on granite. In the northern half, mopane (*Colophospermum mopane*) savanna woodland or shrubland predominates on both substrates. Towards the north-west, rainfall rises locally to 600 mm, and largely sandstone substrates support *Combretum*-dominated savanna in the Punda Maria area.

Sable antelope typically occur in herds of females plus young numbering 20-50 animals, frequently accompanied by the local territorial male. Herd home ranges cover 3-15 km^2, with little overlap among neighbouring groups (Estes & Estes, 1974; Grobler, 1974). Roan antelope form somewhat smaller herds of 6-12 animals, and move over discrete ranges of up to 100 km^2 (Joubert, 1974). Tsessebe also form discrete herds, typically numbering 3-12 animals including the accompanying territorial male, occupying discrete ranges of 2-4 km^2 with herd aggregations sometimes forming in favoured feeding areas (Joubert, 1972; Grobler, 1973). For all three species, there are no historical records of their presence south of the Crocodile River, which forms the southern boundary of the Kruger National Park (Du Plessis, 1969).

Data collection

Annual ecological aerial surveys (EAS) of KNP have been conducted by fixed-wing aircraft carrying the pilot, a recorder and four observers (Viljoen & Retief, 1994). Adjacent transects 800 m apart were flown from May to August when visibility was best. For interpretation, the park area is divided into four broad regions, separated by major rivers (Fig. 1). The entire extent of the park was covered from 1980 to 1993, except for hilly regions in the extreme north and south-west. However, the South was covered only partially through 1977-1979 and omitted through 1994-1996, while the Central section was left out in 1977 and covered only partially in 1994-1996. Parts of the northern half were omitted in 1995 and 1996, while in 1997 only South was censused.

The geographical locations of animals seen had an uncertainty of up to 2 km prior to 1987 when sightings were mapped by hand, but subsequently were within 0.8 km enabled by a Global Positioning System (GPS) unit in the aircraft coupled to a palmtop computer. Herd size was recorded, as well as the number of calves less than a year old that were visible. All-male groups were distinguished from herds including females plus young where possible. The fraction of animals of medium-sized antelope species detected from the air was estimated to be 60-80% (Redfern *et al.*, 2002).

Locations of the two sable herds remaining within a 400 km^2 area near Punda Maria camp in Far North were tracked using Very High Frequency (VHF) radio collars from October 2001 to September 2003, and thereafter by Global Positioning System (GPS) - cellular phone (GSM) collars. In June 2006, GPS-GSM collars were used to track the movements of the four sable herds that remained in a 1,500 km^2 region around Pretorius Kop camp in the south-west. GPS units were scheduled to record herd locations at 6 hour intervals.

Data analysis

To include data from years with incomplete spatial coverage (1977-1979) and still ensure unbiased estimates of distribution changes, I duplicated data from the same census block in preceding or subsequent years to represent the missing data. I considered duplication of data appropriate because the focus here was to document if a herd had disappeared from a previously occupied geographic area. Sable antelope are sedentary and form stable cohesive groups. Thus, it is reasonable to assume that two sightings of a sable herd in the same home range area in a space of two years represent persistence of that same herd. Furthermore, construction of distribution ranges only uses geographical positions of herds and not numbers of animals per herd.

Because our concern was with the distribution of breeding herds, we excluded data for single animals and herds recorded as including only males, which might occupy outlying home ranges. To estimate distribution ranges, we used the Adaptive Local Convex Hull (*a*-LoCoH) method (Getz *et al.*, 2007) as Spatial Analyst Extension in Arc Map 9.1 (GIS). This method is more sensitive to gaps in occurrence, and less influenced by outliers, than kernel methods (Getz & Wilmers, 2004; Chirima & Owen-Smith in preparation). Initially, we fixed the value of *k* (minimum number of points used to construct a polygon) at 3, and the value of *a* (distance from the root point) at 1 m. We then plotted the area of the estimated distribution range versus increasing values of *a* to find the point where the area began to level off (the minimum spurious hole covering or MSHC value of *a*, Getz *et al.*, 2007). With *a* fixed at this value, we then varied *k* to find its MSHC value. Thereafter we used these joint values of *a* and *k* to construct the final distribution ranges. Hulls are joined from smallest to largest into isopleths. We represented total distribution ranges by the 95% isopleths, and distinguished core from marginal regions using 75% isopleths. The same approach was used to construct range utilization distributions for sable herds at Punda Maria and Pretorius Kop, using location records from either EAS surveys and VHF or GPS telemetry.

Distribution ranges were plotted from the EAS data distinguishing four periods: (1) 1977-1981, prior to the low-rainfall conditions; (2) 1982-1986, through the 1982/3 drought but before the population declines; (3) 1987-1991, through the initial population declines, and (4) 1992-1997, following the severe 1991/2 drought. Assuming a sighting probability of 0.7, the chance of a herd being missed for five consecutive years is 0.24%, while if only four years were covered this chance is around 0.8%. For Punda Maria and Pretorius Kop, local distribution ranges were estimated from the EAS data for these same periods and in addition from radio-telemetric locations for three divisions of the period between late 2001 and 2007. Rainfall was exceptionally high in 1999/2000 (July-June), thereafter alternating between high and low rainfall years.

Changes in mean herd size and number of herds recorded in the EAS were analysed by year for South, Central, North, and Far North sections (excluding single animals and all-male herds). Annual calf recruitment was calculated by dividing the number of animals estimated to be less than a year old by the total number of animals in breeding herds besides calves. While the calf proportion is underestimated because of the smaller size of these animals relative to adults, this bias should remain fairly consistent between years. For roan antelope, we also plotted annual changes in number of animals recorded in the spatially discrete subpopulation units.

Results

Sable antelope

Sable antelope showed a patchy distribution spread throughout the KNP, but with a concentration towards the west. Their distribution range showed some expansion in the northern half of the park between 1977 and 1986, associated with a 50% increase in population size. Following their population decline after 1987, their range contracted in western and southern regions of the northern half of the park, and eastern margin of the south-western patch, accentuated after 1991 (Fig. 2, Table 1). The increase in population size between 1977 and 1986 was coupled with a substantial increase in number of herds recorded in both northern sections, while mean herd size showed little overall change (Fig. 3). Herd size but not herd numbers increased in the Central section during this period, while in the South there was little change in either measure. Herd numbers as well as size declined slightly in northern sections after 1986, followed by a precipitous drop in herd numbers after 1992. By 1995, only 22 herds were recorded in Far North and 13 herds in North, compared with 57 and 49 herds respectively when the population had peaked around 1985-6. Herd size also decreased substantially, from earlier means of about 15 to around 5 in both northern sections. Calf proportion fluctuated between years without any trend from 1980 through 1991, being low in dry years and high in years with good rainfall, except in South where it remained relatively constant (Fig. 3 (c)). After 1991, calf recruitment dropped most notably in South where it had previously been consistently highest.

A detailed examination of distribution changes in the Pretorius Kop region in the south-west showed initial signs of herd disappearances towards the north-eastern edge after 1987, which was accentuated after 1992 (Fig. 4). By 1997, only 8 herds were counted in this region, down from the peak of over 20 herds seen around 1987. When GPS collars were fitted in 2006, only four herds of 7-12 animals were found in this section, with gaps between their home ranges that had formerly been occupied by other herds. However, chance sightings indicated that 2-3 additional herds remained to the south of the GPS study area. In the Punda Maria study area, the concentration of sable that had been present in the south disappeared after 1991 (Fig. 5). Only 4 herds were counted from the air in 1995, down from a peak of 12-15 herds around 1987. When VHF collars were placed in 2001, only two herds totalling about 30 animals were found in this region. After 2003 when GPS tracking was undertaken, the remaining animals formed a single herd of around 20 animals, with their movement range having shrunk towards a north-west core by 2006.

Roan antelope

Prior to 1986, roan antelope occurred in two fairly distinct core ranges, including about 100 animals each, in the east of North and Far North, plus three isolated herds within the western region of the northern half, and a remotely situated herd in South (Fig. 6). Range shrinkage was evident across the whole park after 1986 (Table 1(b)). Specifically, the isolated herd in the South plus the herd in the south-western region of North had disappeared by 1989, followed by all remaining herds in North, including the core subpopulation, by 1996 (Fig. 7). The four herds remaining in Far North in 1992 had decreased to two herds, totalling around 20 animals, plus some lone males, by 1996, representing the entire free-ranging population in the park.

Tsessebe

Tsessebe occurred fairly continuously through the eastern region of the northern half of KNP, plus an isolated subpopulation in the south-eastern region of the Central section (Fig. 8). No range contraction took place until after 1991, when the northern range shrunk and the south-western herds disappeared (Table 1(c)). The number of tsessebe herds increased in KNP between 1977 and 1991, after which herd counts exhibited a downward trend (Fig. 9 (a)). Tsessebe herd size showed a slight downward trend over this period (Fig.9 (b)). The appearance of an occupied patch in the south-west after 1986 was as a result of animals moved there by park managers.

Discussion

Reductions in the distribution ranges of the three antelope species occurred throughout KNP, rather than being manifested mainly in the drier northern half, after 1986. Nevertheless, the initial range shrinkage became evident during a sequence of years with generally below-average rainfall when populations of these species declined, initiated by a severe drought in 1982/3 (Ogutu & Owen-Smith, 2003). For sable, much of this range reduction was associated with the loss of herds that had established during the sequence of high rainfall years extending through 1981. Range contraction by all three species became accentuated following the extremely severe drought experienced in 1991/2, involving the disappearance of isolated herds of roan and tsessebe, as well as herds within continuously occupied regions for all three antelope species. In the Punda Maria area, up to 15 sable herds totalling over 200 animals present around 1987 had become reduced to a single herd of about 20 animals after 2003. In the Pretorius Kop area, herd numbers changed little until the severe 1991/2 drought, after which many long-standing herds were no longer recorded. Peak numbers of around 450 sable in over 30 breeding herds recorded in this region around 1987 had declined to under 100 animals in no more than seven herds by 2004 (Whyte, 2006). Hence for sable the range contraction was almost as severe in this wettest region of KNP as in the drier north. Furthermore, all tsessebe herds plus the single roan herd were extirpated from the southern half of KNP.

For sable, calf recruitment fluctuated in response to annual rainfall variation. A persistent downward shift was evident in the south-west and far north of the park after 1991, but not in other sections. Hence poor recruitment probably accentuated the shrinkage and ultimately the disappearance of sable herds in the former two sections. In the Central section where no range contraction by sable was evident, calf recruitment remained constant and herd numbers showed no change, although herd size declined. Roan antelope showed annual variation in calf recruitment without any trend, meaning that the downward population trend was an outcome of the elevated adult mortality related to herd disappearances (Harrington *et al.*, 1999). Tsessebe recruitment indicated little variation prior to 1991 but exhibited a persistent downward trend thereafter.

Historical records indicate that contractions in the distribution ranges of sable, roan, and tsessebe became evident prior to 1977. During the 1920s, sable had been among the most common antelope species within and beyond the western boundary of KNP, being frequently shot for meat (Roche, 2002; Joubert, 2007). Distribution ranges mapped by Pienaar (1963) from rangers' reports plus ground surveys show sable more widely distributed in west-central and far north-east regions of KNP around 1960 than documented after 1977. Roan antelope evidently occurred more widely in the western region of the northern half of the park at that time. Tsessebe were recorded through much of the west-central region of KNP, as well as in western sections of Far North. Eight hundred sable were reported to be present on in private nature reserves to the west of KNP around 1962, along with numerous tsessebe and several herds of roan antelope, but all of these animals have subsequently vanished (Roche, 2002).

A widespread decline in tall trees, and thickening of woody shrubs especially on granite substrates, occurred in parts of KNP between 1940 and 1998 (Trollope *et al*., 1998; Eckhardt *et al*., 2000). A thickening of woody vegetation in private nature reserves to the west of KNP was also evidently under way during the 1960s (Roche, 2002). This vegetation transformation could make animals more vulnerable to being killed by lions (Funston *et al*., 1998). Nevertheless, wildebeest and zebra, which form the principal prey species for lions, remain abundant within the park, although not in the private nature reserves. The drastic decline of roan antelope and disappearance of sable in the north-eastern basalt plains of KNP appeared to be related to increased predation on adult females. This was associated with an increase in the local abundance of lions following an influx of zebra, in turn attracted by artificial waterholes when drought conditions prevailed (Harrington *et al*., 1999; Owen-Smith & Mills, 2006). Zebra numbers also increased more than two-fold in the far north-western region of Kruger Park between 1983 and 1987. Within the Punda Maria area, zebra herds appeared to concentrate towards the south, i.e. the zone from which sable herds disappeared. In the Pretorius Kop area, a temporary doubling of zebra numbers was recorded in 1992, just prior to the sable decline there. Apart from the role of zebra in attracting lions, their competitive grazing at times when grass was in short supply during droughts cannot be discounted. An increase in the number of buffalo around Pretorius Kop was also evident between 1982 and 1990, adding their competitive grazing pressure as well as expanding the prey base for lions. A buffalo herd totalling around 400 animals shared the Punda Maria study area with the surviving sable herd.

Evidence for the role of predation in the decline after 1986 of the rarer antelope species, as well as relatively more common species like kudu (*Tragelaphus strepsiceros*) and waterbuck (*Kobus elipsiprimnus*), came from increases in adult rather than juvenile mortality (Owen-Smith & Mason, 2005; Owen-Smith *et al.*, 2005), plus increased representation of these species in lion kills (Owen-Smith & Mills, 2008). Elevated adult mortality was also associated with the reduction of herd sizes of the rarer antelope species, as documented above. Localities that had formerly supported herds no longer did so following the persistently dry conditions prevailing over 1982-1993, whether because of greater predation numbers, bush thickening, or grassland deterioration. In the northern section of KNP, new sable herds became established during the high rainfall conditions that prevailed through the late 1970s, indicating a general improvement in habitat suitability in this region of predominantly low rainfall. Earlier estimates of sable numbers from aerial plus ground counts indicated a fairly consistent total of around 1000-1200 sable in KNP from 1954 through 1975, with little decline during the drought years of the late 1960s (Joubert, 2007). The steep decline across all regions after 1991 reduced the sable population to an unprecedented low of under 500 animals, with little or no recovery evident 15 years later (Whyte, 2006). The sable pattern is closely paralleled by both tsessebe and roan antelope, with the latter reduced to numbers where a vortex of genetic and demographic stochasticity (Gilpin & Soule, 1986) could lead to local extirpation. The long-term viability of the sable population is also insecure, despite its larger total, because remaining herds could be more susceptible to predation because of their small size, as an Allee effect (Stephens & Sutherland, 1999). The recent alternation of good and bad rainfall years could also be holding back recovery, through allowing little opportunity for rebound from the poor calf survival in the dry years.

Whilst outbreaks of anthrax in the past have been associated with mortality among roan, buffalo, and kudu, the occurrence of anthrax related deaths is closely monitored in KNP (Furnis & Hahn 1981) with none recorded at the time the rare antelope population declines were initiated. Diseases can potential reduce abundances of species, however, there was no evidence that this was the case for KNP concerning the rare antelope. There were no reports in KNP that suggested an outbreak of diseases during the initial decline of rare antelopes. Elephant impacts were associated with a decline of other antelope species elsewhere through modifications of habitat structure (Valeix *et al*. 2006). However, there is no evidence that this is the case in KNP, instead, sable herds persisted in the north west, areas which, have been categorized as high elephant density zones (Whyte *et al*. 1999). The shrinkage in the distribution ranges of the rarer antelope species that occurred after 1986 has been documented in greater detail elsewhere (Chirima et al. submitted). Furthermore, the spatial distribution of these species within KNP appears to be related primarily to the available prey biomass for lions, rather than to the geological and vegetation features expected to govern habitat suitability for the three grazers (sable antelope, roan antelope, and tsessebe). However, the shrinkage in distribution ranges of these species were associated with persistently low rainfall conditions, including an especially severe drought in 1991/2, suggesting that habitat deterioration was a contributory factor. There is also evidence of a generally thickening in the shrub layer in the western granitic section of KNP, while the eastern basaltic region in the southern half, although not in the mopane-dominated north, has become more open as a result of the destruction of canopy trees by elephants (Trollope *et al*. 1998, Eckhardt *et al*. 2000). This change may also have heightened the risk of predation for the rarer antelope species where they mostly occurred.

The pervasive lack of recovery by these rarer antelope populations raises the possibility that a tipping point or “regime shift” in habitat conditions occurred when the severe 1991/2 drought accentuated the generally dry, El Nino-related conditions that had prevailed over most of the preceding decade (Holmgren *et al*., 2006). The habitat transformation could be the bush thickening alluded to above, changes in grass composition and seasonal forage value, or a general aridification exacerbated by woody plant expansion coupled with low rainfall. Notably, all three species commonly occur in wetter savannas than represented within the boundaries of KNP. Nevertheless, sable herds, as well as the sole roan herd, disappeared in the south-western region of KNP which approached moist savanna conditions. This is also an area where relatively few artificial waterpoints were added. It is possible that persistently aridity led to the drying up of natural springs and streams in this region of granite inselbergs, forcing the emigration of some sable herds into unsuitable habitat and hence their demise. Ogutu and Owen-Smith (2003) related widespread declines among less common ungulate populations in KNP after 1986 to extremely little rainfall during the normally dry season months, but unusually low rainfall during the dry season has not persisted. These authors also noted that prevailing temperature conditions rose by about 0.4^{o}C around the time of the population declines, as a local reflection of global warming. Persistently warmer conditions especially at night could elevate plant respiration and hence lead to a more rapid loss of green foliage during the dry season, to the detriment of forage quality. The atmospheric CO_2 increase contributing to global warming could also be promoting bush thickening, through benefiting the growth of woody plants at the expense of grasses (Walker, 1991; Bond & Midgley, 2000). Furthermore, warmer conditions could cause more rapid evaporation of soil moisture.

Whether changes in woody-grass balance, grass species composition or grass phenology underlie the shrinkage in the distribution of rarer antelope species in KNP cannot be established reliably because of the lack of adequate records of vegetation features prior to the onset of low rainfall conditions in 1982. Hence, the suggested shift in habitat conditions remains speculative. Moreover, it is difficult to disentangle the direct effects of predation on prey populations from factors predisposing animals to a greater risk of predation, whether through inadequate nutrition, denser vegetation cover, or more predators following changes in populations of common ungulate species. Aerial censuses completely covering the KNP were discontinued after 1994, so that information on subsequent population changes by the rare antelope species is fragmentary. Surveys of population structure also ended. This lack of information prevents us from making more confident statements about causal processes bringing about the range and population contractions.

Nevertheless, our study has documented how adverse conditions, through whatever cause, both contracted and fragmented the distribution of these three antelope species in a region representing the southern margin of their historic distribution ranges. Range contractions were associated with local herd extirpations, but no distributional shift up the rainfall gradient. The fence blocking dispersal towards the west was of little consequence, since no movement of sable in this direction has taken place following the removal of this fence in 1993. Recolonization from animals occupying wetter habitats further west is no longer possible, because these three antelope species occur there only within tightly fenced wildlife ranches. Climate variation affects these species not only through changing food resources, but also indirectly through ramifying interactions related to susceptibility to predation and competition linked to surface water access. All of these mechanisms play out within a changing spatial template. Comprehensive information on spatial variation in these influences is needed in order for confident conclusions to be drawn about contracting species distribution ranges.

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FIGURE CAPTIONS

Figure 1 Map of Kruger National Park, South Africa, showing the four sections distinguished as well as location of the two intensive study areas. Grey lines indicate rivers forming boundaries between these sections; shading indicates areas in north and south not covered during aerial surveys.

Figure 2 Changes in sable antelope herd distribution in Kruger National Park mapped by Local Convex Hull method: (a) 1977-81, (b) 1982-1986, (c) 1987-1991, (d) 1992-1997. Darker grey represent core region within 75% isopleths, with lighter grey bounded by 95% isopleths.

Figure 3 Trends in (a) herd counts, (b) mean herd size, and (c) calf proportions for sable antelope in the four sections of Kruger National Park, recorded in aerial surveys.

Figure 4 Changes in sable antelope herd distribution in Pretorius Kop region of south-western Kruger National Park between 1977 and 1997, recorded in aerial surveys (a-d), and between 2006 and 2007, from GPS tracking of collared herds, mapped by Local Convex Hull method (e; shading as in Figure 2).

Figure 5 Changes in sable antelope herd distribution in Punda Maria region of north-western Kruger National Park between 1977 and 1995, recorded in aerial surveys (a-d), and between 2001 and 2007, from VHF or GPS tracking of movements of collared herds, mapped by Local Convex Hull method (e-g; shading as in Figure 2).

Figure 6 Changes in roan antelope herd distribution in Kruger National Park mapped by Local Convex Hull method (shading as in Figure 2): (a) 1977-81, (b) 1982-1986, (c) 1987-1991, (d) 1992-1995.

Figure 7 Annual changes in the number of roan antelope recorded in discrete patches within the distribution range (FN – Far North, N - North, S – South; -E – eastern region, -W – western region, -NW = north-western region, SW = south-western region).

Figure 8 Changes in tsessebe herd distribution in Kruger National Park mapped by Local Convex Hull method (shading as in Figure 2): (a) 1977-81, (b) 1982-1986, (c) 1987-1991, (d) 1992-1995.

Figure 9 Trends in (a) herd counts and (b) mean herd size for tsessebe in three sections of Kruger National Park, recorded in aerial surveys.

Table1a. Area covered by estimated 95% distribution ranges (km^2) during four blocked periods for each antelope species within each section of Kruger National Park (Total extent: Far North - ; North - ; Central - : South - .

(a) Sable antelope

Period	Region				
	Far North	North	Central	South	Entire park
1977-1981	1800	1179	322	785	4086
1982-1986	1865	1641	426	807	4739
1987-1991	1519	1123	402	724	3768
1992-1997	1272	879	515	426	3092

(b) Roan antelope

Period	Region				
	Far North	North	Central	South	Entire park
1977-1981	1046	666	0	46	1758
1982-1986	1660	1059	0	58	2777
1987-1991	1148	815	0	0	1963
1992-1995	544	247	0	0	791

(c) Tsessebe

Period	Region				
	Far North	North	Central	South	Entire park
1977-1981	1683	663	3	79	2428
1982-1986	1729	735	7	100	2571
1987-1991	1714	713	21	192	2640
1992-1995	1038	583	0	36	1657

Figure 1

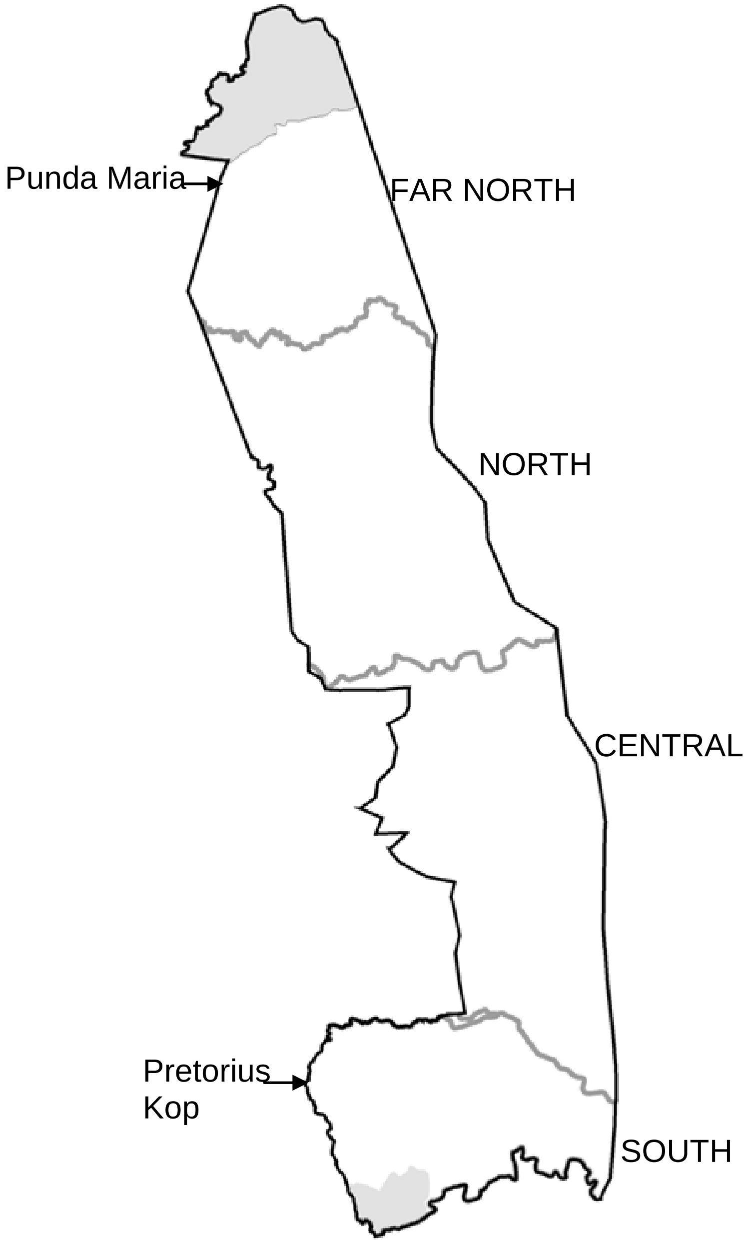


Figure 2

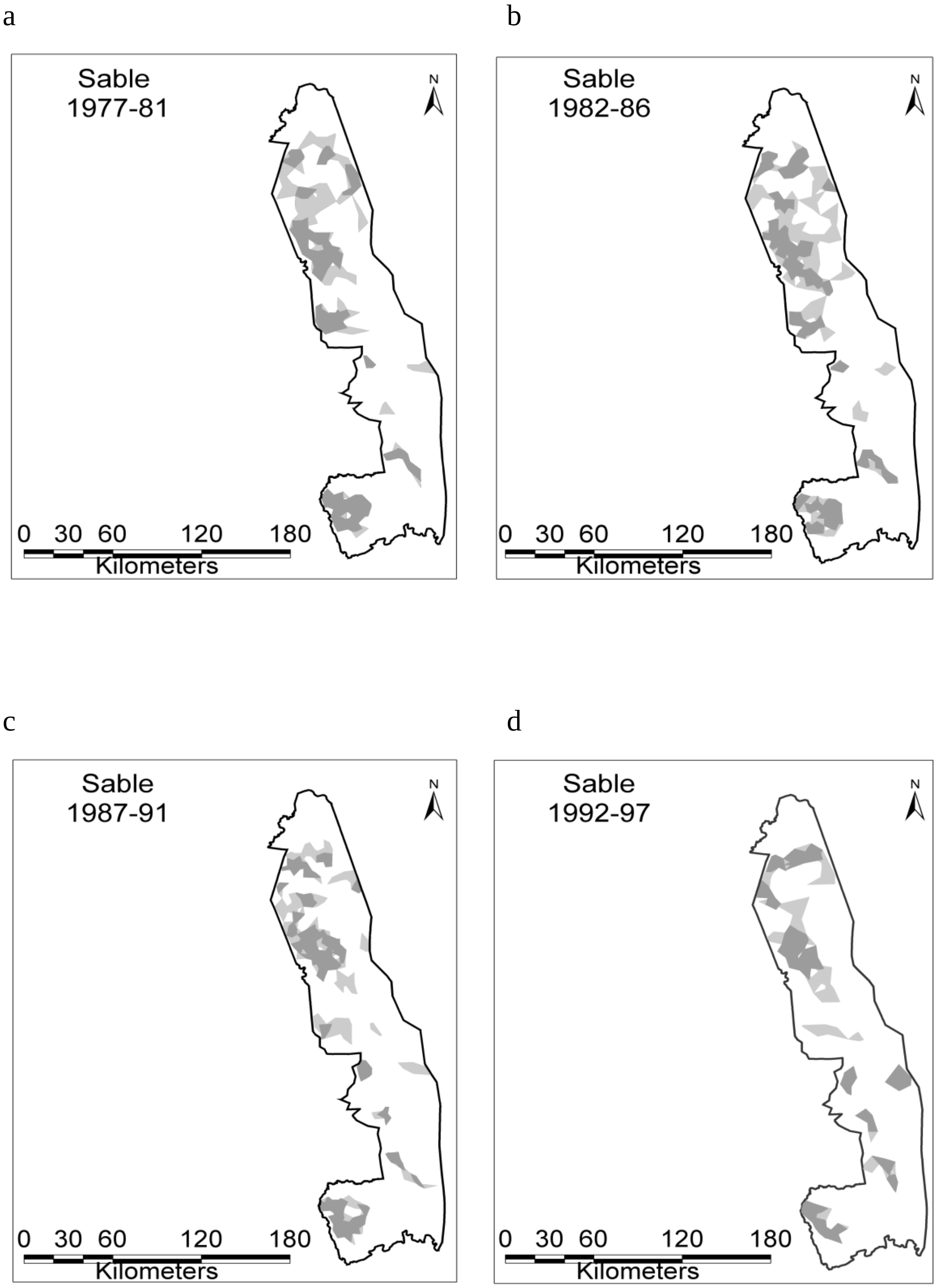
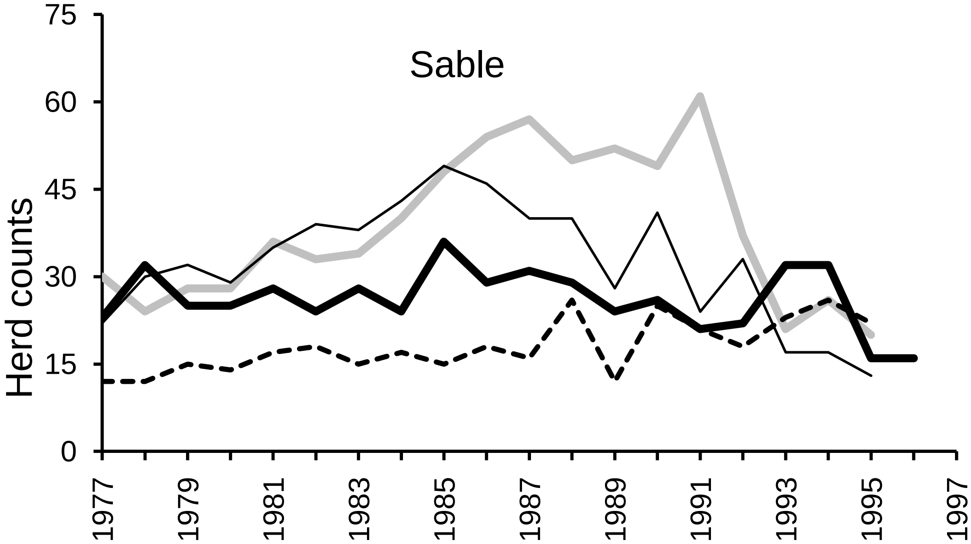
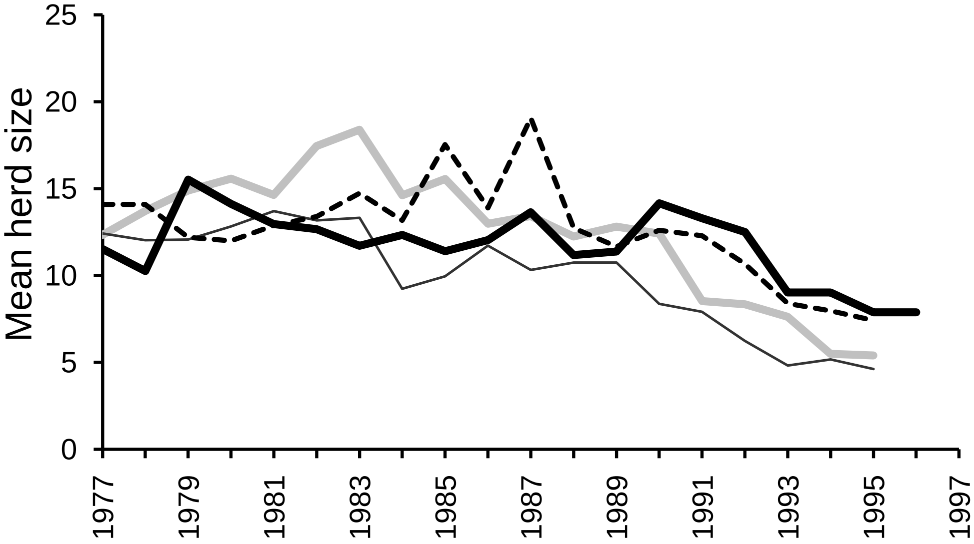

a
b
c
d
Sable
1977-81
Sable
1982-86
Sable
1987-91
Sable
1992-97
N
0 30 60 120 180
Kilometers

Figure 3

a


Sable
Herd counts
75
60
45
30
15
0
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997

b


Mean herd size
25
20
15
10
5
0
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997

c

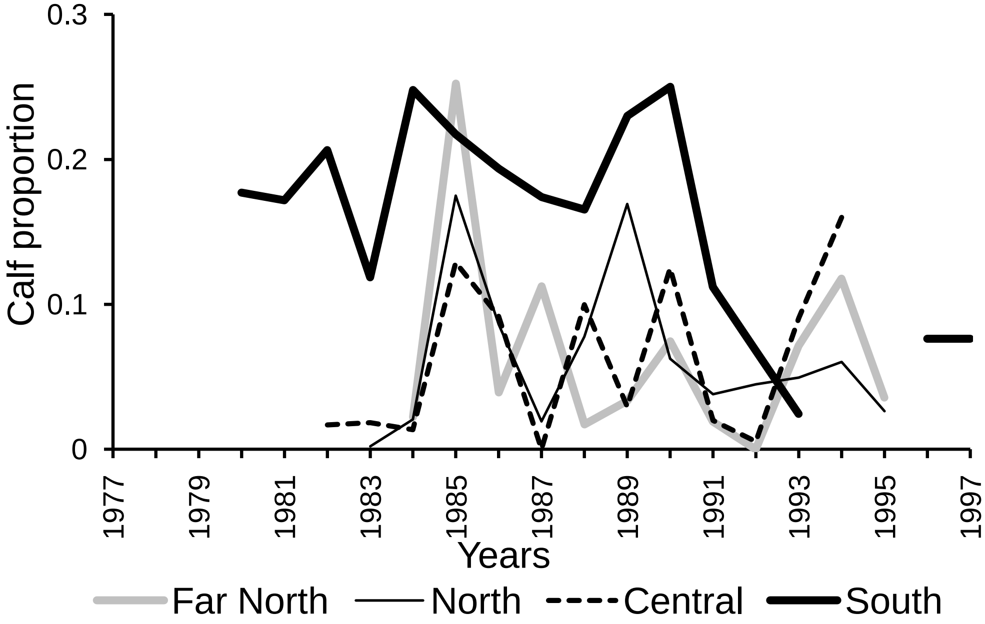

0.3
0.2
0.1
0
Calf proportion
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997
Years
Far North
North
Central
South

Figure 4

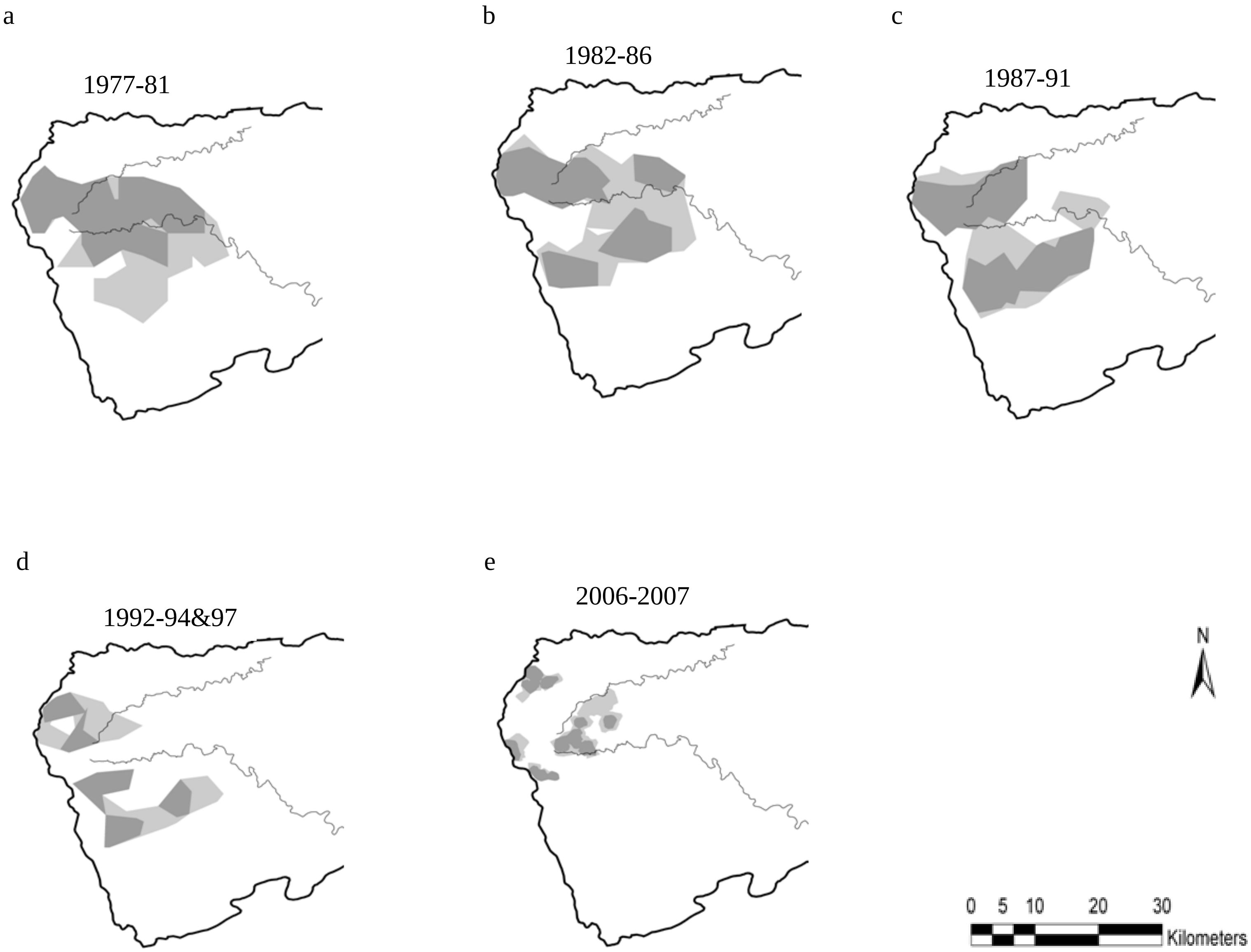

a
1977-81
b
1982-86
c
1987-91
d
1992-94&97
e
2006-2007
N
0 5 10 20 30
Kilometers

Figure 5

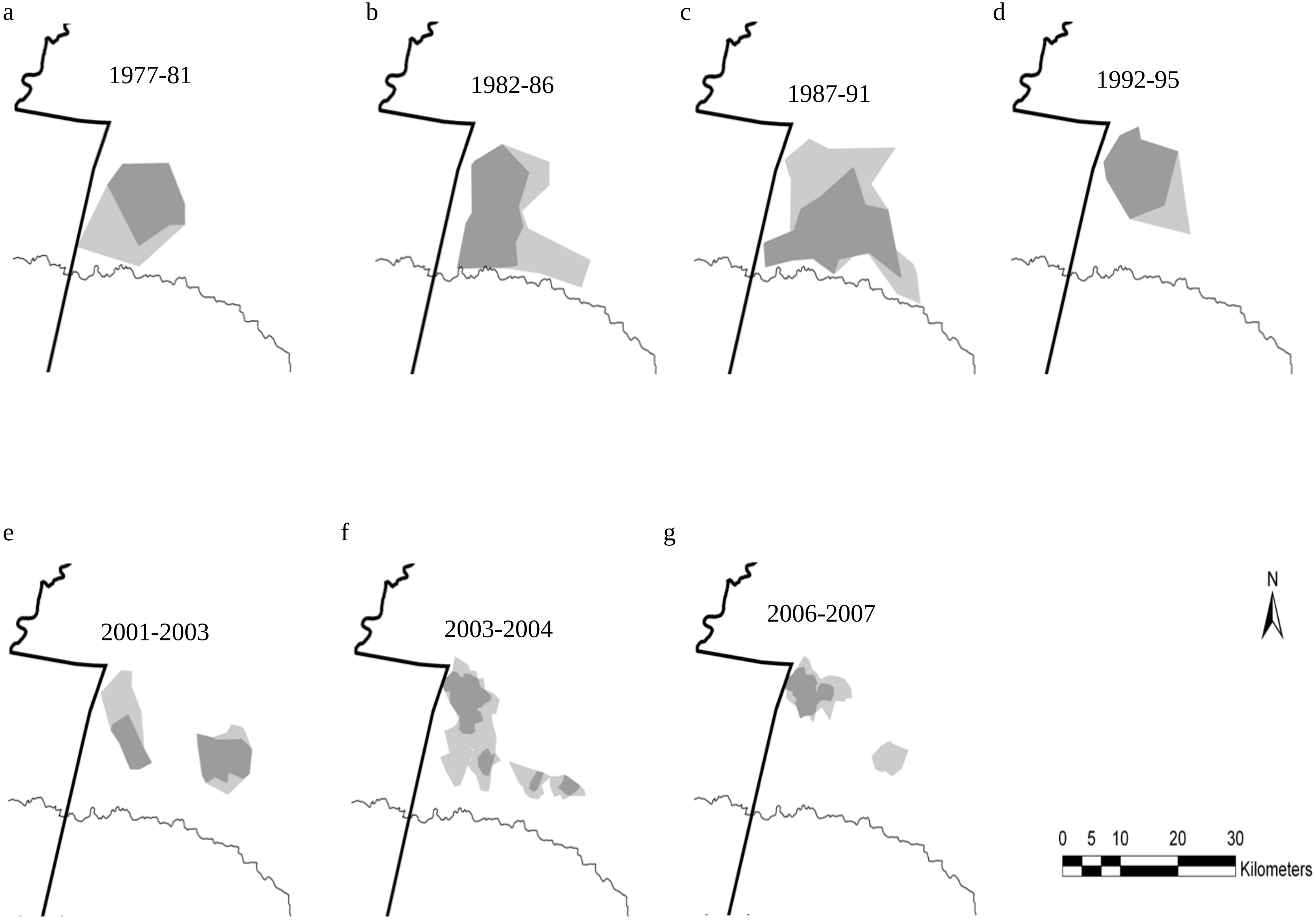

a
1977-81
b
1982-86
c
1987-91
d
1992-95
e
2001-2003
f
2003-2004
g
2006-2007
N
0
5
10
20
30
Kilometers

Figure 6

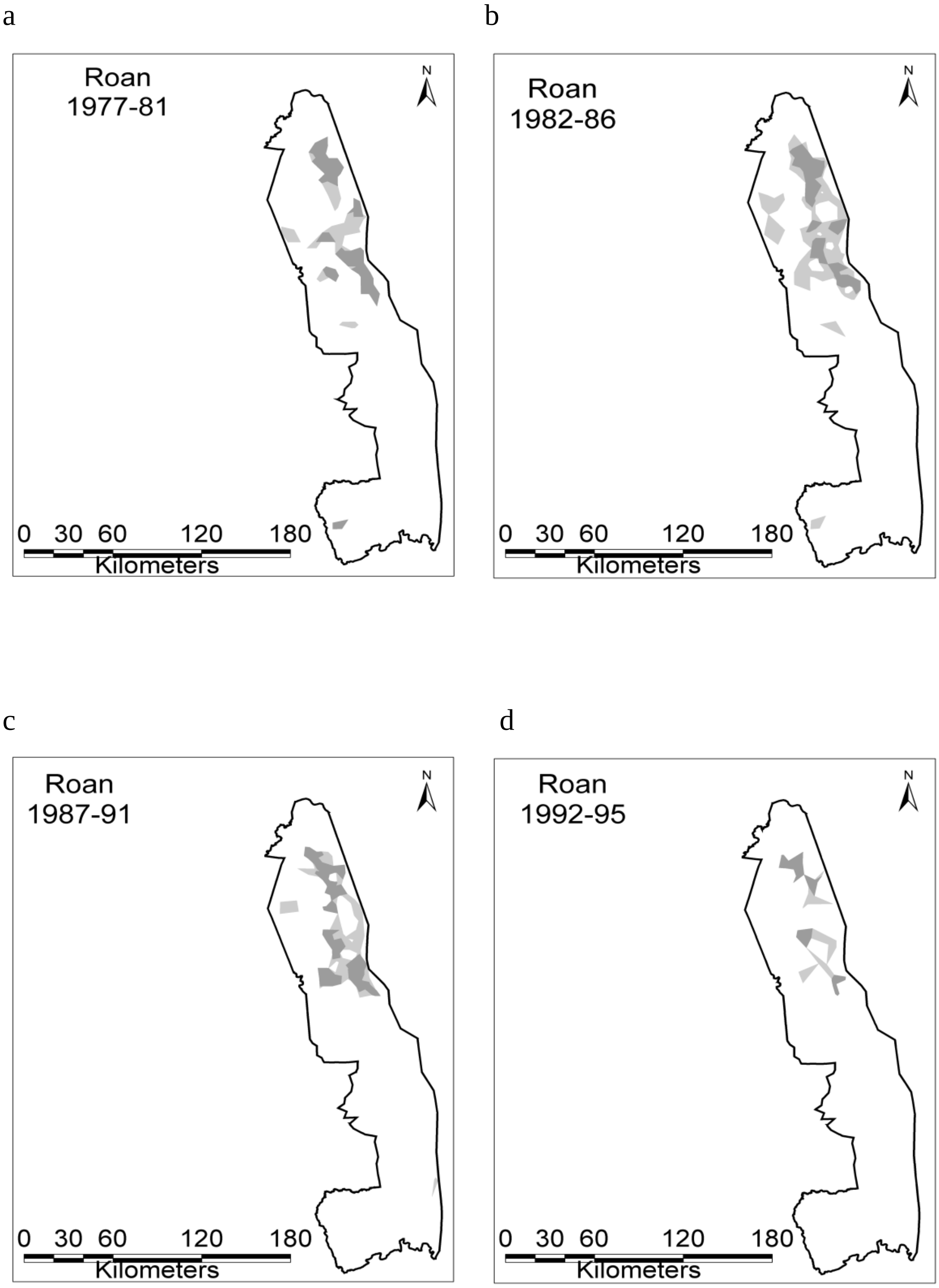

a
Roan
1977-81
N
0 30 60 120 180
Kilometers
b
Roan
1982-86
N
0 30 60 120 180
Kilometers
c
Roan
1987-91
N
0 30 60 120 180
Kilometers
d
Roan
1992-95
N
0 30 60 120 180
Kilometers

Figure 7

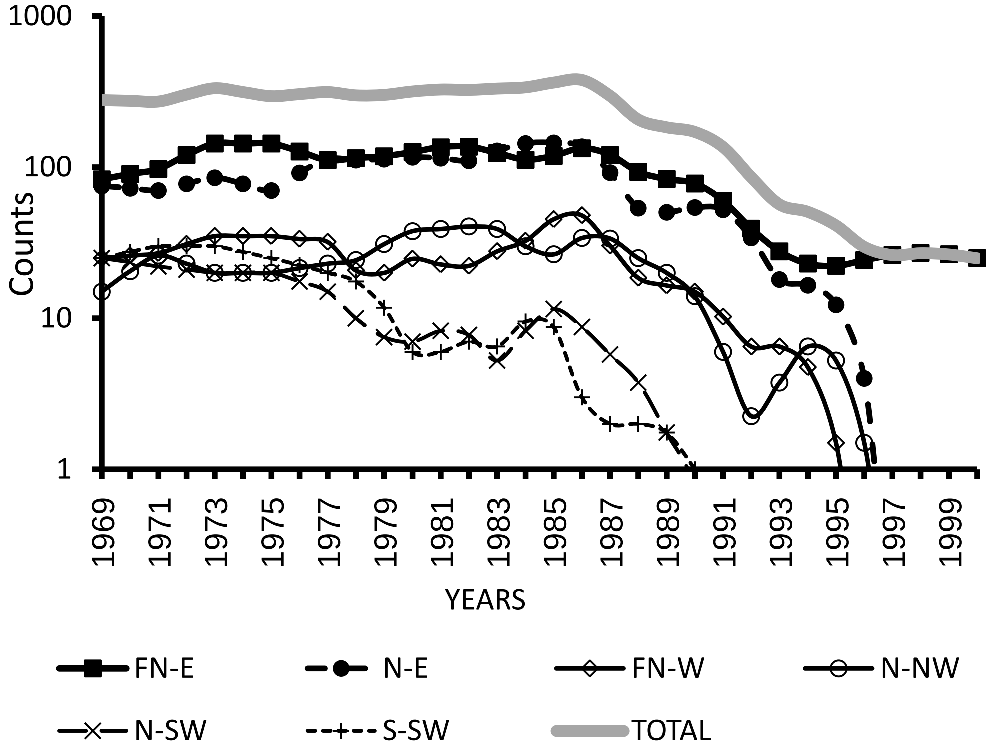

1000
100
10
1
Counts
1969
1971
1973
1975
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997
1999
YEARS
FN-E
N-E
FN-W
N-NW
N-SW
S-SW
TOTAL

Figure 8

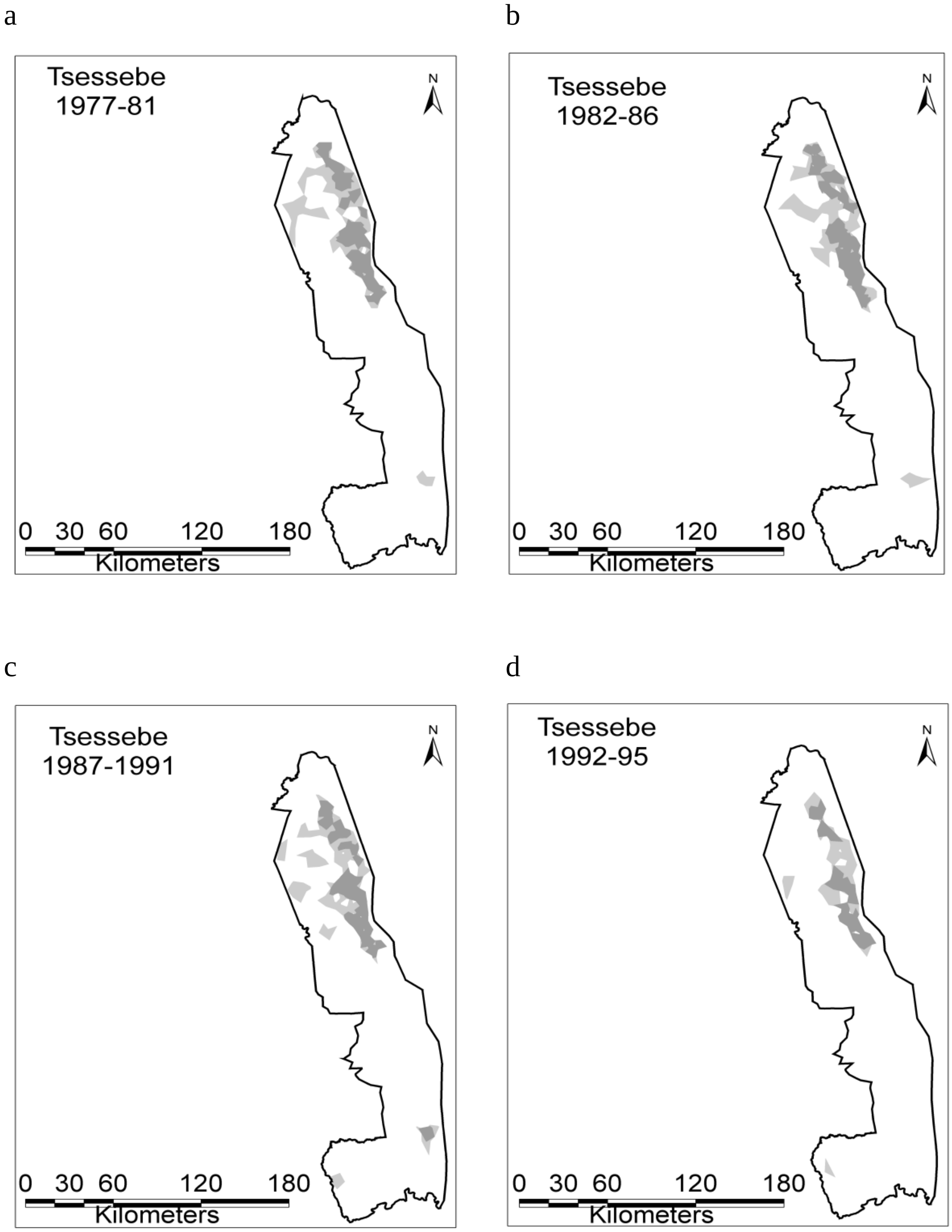
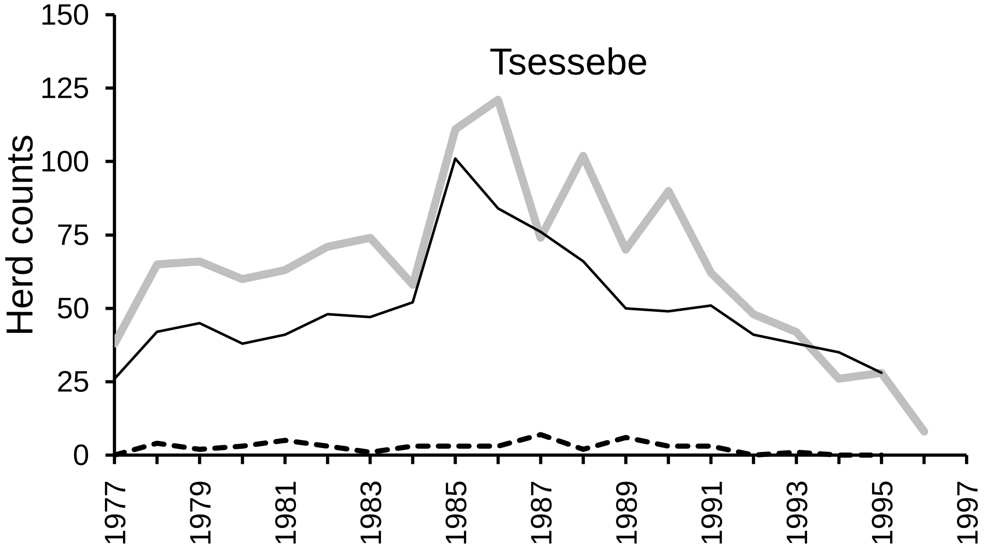
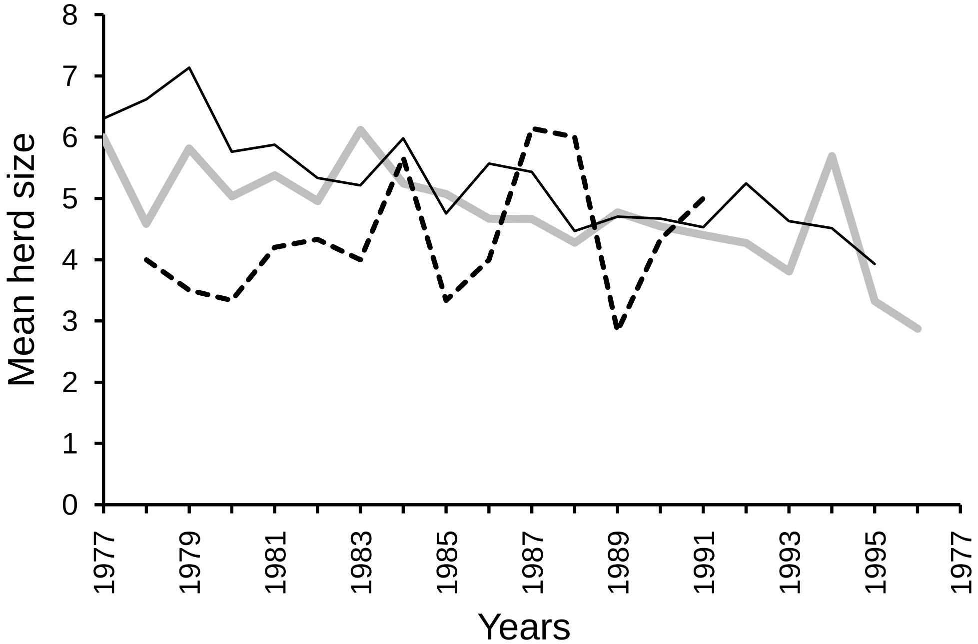

a
Tsessebe
1977-81
N
0 30 60 120 180
Kilometers
b
Tsessebe
1982-86
N
0 30 60 120 180
Kilometers
c
Tsessebe
1987-1991
N
0 30 60 120 180
Kilometers
d
Tsessebe
1992-95
N
0 30 60 120 180
Kilometers

Figure 9

a


Tsessebe
Herd counts
150
125
100
75
50
25
0
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1997

b


Mean herd size
8
7
6
5
4
3
2
1
0
1977
1979
1981
1983
1985
1987
1989
1991
1993
1995
1977
Years
Far north
North
Central

CHAPTER 5

Biotic vs. abiotic determinants of the local distribution of a low-density large herbivore in the Kruger National Park.

ASBTRACT

The aim was to determine which factors restricted a wider distribution of sable antelope in Kruger National Park. I used park-wide aerial surveys (1978–1988) to distinguish 25 km^2 cells occupied by sable herds from unoccupied regions. I fitted logistic regression models using geology, rainfall, vegetation type, and distance from water sources as abiotic predictors. I used biomass of the most abundant grazers impala, wildebeest, buffalo, and zebra to assess competition. As a proxy for predation risk, I used prey available for lions calculated as the product of each species abundance, carcass mass and relative selection by lions, summed over prey species. I fitted logistic regression models to biotic predictors (competition and predation). Sable prevalence differed from expectation for geology because prevalence was highest on nutrient poor granite and sandstone instead of nutrient rich basalt and gabbro. Distances of up to 5 km from perennial water sources did not appear to exert limiting influences on where sable herds occurred in Kruger Park. Land type was the best supported abiotic factor in explaining distribution of sable herds. Sable favoured mopane/bushwillow (tree/bush) savanna, mopane/knob thorn savanna, and sour bushveld over thorn veld, mountain bushveld and knob thorn/bushwillow/silver cluster-leaf bush savanna. Sable prevalence was most negatively associated with impala and wildebeest which favoured different habitat types. Sable were not excluded from areas of high biomass of buffalo or zebra, with most similar food selection, suggesting that sable herds established home ranges within wider range occupied by buffalo and zebra. Sable were more prevalent in areas where predation risks appeared lower than elsewhere. Predation risks appeared more influential on sable distribution compared to competition. Results presented here show that biotic factors modify effects of abiotic factors on where rare and sedentary species establish.

Introduction

Relationships between occurrence of a species and features of the types of habitats it occupies are central to establishing factors that influence the distribution of a species (Johnson 1980, Heglund 2001, Johnson *et al*. 2004). Predicting where a species could occur and determining which resources are favoured is achieved through quantifying occupied areas and used resources in relation to their availabilities to the animals (Manly *et al*. 2002, Boyce *et al*. 2002, Johnson *et al*. 2004). Senft *et al*. (1987) suggested that resource selection requires multi-scale considerations because animals use different sets of selection criteria at different scales. Johnson (1980) outlined a hierarchical fashion in which selection could occur from a geographic range, (1st order), home range (2nd order), usage of various components within home ranges (3rd order) (e.g. feeding sites) to procurement of items (e.g. food) from those available at a site (4th order).

At the 1st order of selection, a species distribution range is represented as a continuous unit, which encompasses all regions in which individuals have been recorded (Heller 1918, Gaston 1991, Hill *et al*. 1999). Broad abiotic factors such as climate and geographic barriers have overriding influences over biotic influences to identify regions that lie outside a species range (Heller 1918, Palmeirim 1988, Olson *et al*. 2001, Pearson *et al*. 2002). Distribution models developed at this selection level are helpful to provide insights into range losses under changing climate effects (Peterson 2006)

Less studied is the 2nd order of selection, which relates to how herbivores select where to establish home ranges and how interactions between abiotic and biotic factors, including predation or competition, influence occupation patterns. Studies at this scale clarify the different influences that resource types exert at each order of selection, and reveal factors that could constrain use of those resource types; aspects that have received little attention in resource selection studies (Boyce *et al*. 2002). The 2nd order of selection may expose which species might be of concern to conservationists because of shrinking distributions (Pim *et al*. 1995, Lawton *et al*. 1994). Important for conservation is that the 2nd order of selection reveals which areas may be suitable, and which are unsuitable, for the establishment of home ranges (Gaston 1991). Soberón and Peterson (2005), and Soberón (2007) propose three conditions that could be pertinent to establishment of a home range: (i) a local environment that allows the species population to grow, (ii) interactions with other local species that allow the species to persist, and (iii) an accessible location in terms of dispersal.

At 2nd order of selection, abiotic factors particularly temperature and precipitation in association with topographic conditions, which influence vegetation growth, could impose physiological limits to species occurrence (Grinnell 1917, Soberón & Peterson 2005). Animals respond to plants as food and because they provide breeding sites or shelter. Rainfall also influences plant distributions, composition and structure, and hence prevalence of open grasslands, thickets, forest, and tree savannas. Larger herbivores may select from among these vegetation structures or from among attributes such as shrub density, percentage cover, or distance from water (Funston *et al*. 1994, Manly *et al*. 2002). For example, caribou (*Rangifer tarandus*) favour vegetation patches of alpine forest distributed at mid-elevations on moderate to steep slopes (Johnson *et al*. 2004), whilst ibex (*Capra ibex nubiana*) establish in high altitude, steep and rocky slope habitats (Hirzel *et al*. 2002). Interactions between vegetation structure and predation through visibility issues might reduce security from predation (Walker 1991, Brown *et al*. 1999). Buffalo (*Syncerus caffer*) in a reserve bordering central Kruger favoured tree savanna with better visibility than thorn thickets, which possibly reduced predation risk from lion (*Panthera leo*) (Funston *et al*. 1994).

Identifying which factors have primary influences on where animals establish home ranges is tricky because their influences vary at different scales. Whilst location of food could be basic (Quinn *et al*. 1997), predation risks associated with some locations modify selection of where animals can occur. In many parts of Africa, elephant range selection is modified by locations of dry season water, because water exerts constraints on where elephants can occur during dry seasons (Chamaille-Jammes *et al*. 2007, Harris *et al*. 2008). Grazers are water dependent (Western 1975, Gaylard *et al*. 2003), and therefore selection of where to locate home ranges should be modified by distance to nearest water source. Pienaar (1963, 1970), reported a gradual colonisation by herbivores of drier northern Kruger Park after provision of artificial water. A superior competitor may relegate inferior competitors to establish residency in areas where the former species is less abundant (Harrison *et al*. 1995, Soberón & Peterson 2005). If an abundant primary prey locally maintains a predator population, an alternative prey species could be restricted to low abundance levels or even excluded from some areas (Holt 1977, Bergerud & Elliot 1986).

In African savanna regions, food production indexed by rainfall (Coe *et al*. 1976, Owen-Smith 1990), or normalized difference vegetation index (NDVI) (Van Bommel *et al*. 2006, Chammaille-James *et al*. 2007) correlates with herbivore biomass. Areas with too little vegetation productivity may not provide sufficient forage that remains to carry animals through the dry season. However, Mueller *et al*. (2007) noted that highest vegetation productivity was associated with mature forage that provided a poor quality resource for gazelles (*Procapra gutturosa*) because grasses decline in nutritional quality as they grow. Higher NDVI values may be associated with more mature and hence less nutritious grasses (Van Bommel *et al*. 2006, Mueller *et al*. 2007). Thus, sable antelope may favour intermediate to high NDVI ranges that could allow for both sufficient forage quantity as well as quality during wet season**.** Sable antelope might establish home ranges in locations that retain more green leaves during dry seasons. Alternatively, locations of higher food production could attract superior competitors and hence might not be favoured by sable antelope. Geological substrates are strong drivers of large-scale heterogeneity in savannas (Scholes *et al*. 2003, Venter *et al*. 2003). Differences in nutrient status of soils originating from diverse geological substrate types influence plant growth, biomass, and quality of food for herbivores (Scholes *et al*. 2003). Clays from basalt are richer in nutrients and lead to more vegetation growth than sandier soils from granite (Scholes *et al*. 2003). Interactions of geological substrates with climate yield spatial variation in vegetation structure and composition, thus implying differences in distribution of forage quality and quantity for grazers (Venter *et al*. 2003).

Modelling distributions of large mammalian herbivores at scales relevant to 2nd order selection is faced with challenges because commonly data on absences are not reliable (Hirzel & Le Lay 2008). Survey errors might result in false absences (Hirzel & Le Lay 2008). The data set used in this study reliably accounts for absences. Redfern *et al*. (2002) estimated that the fraction of animals detected during aerial surveys of Kruger Park is 60-80% for medium-sized ungulates such as sable antelope. However, the likelihood of missing a sable herd if present is very small ($(0.3)^{10}$) over 10 years of repeated surveys. Sable antelope constitute an interesting model species because it occurs more commonly in wetter regions of Africa, but are at the southern edge of their distribution in Kruger (Skinner & Chimimba 2005). Furthermore, sable antelope form sedentary and cohesive breeding herds (Estes 1991), and occur in distinct patches in Kruger Park (Pienaar 1963), which provides an opportunity to distinguish variables such as resources or biotic influences that are associated with patches they occupy, or that could exclude occupation of other areas within the park. Since 1988, the abundance of sable antelope has declined dramatically from a peak of 2 240 individuals in 1986 to probably less than 500 in 1993 (Grant *et al*. 2002, Ogutu & Owen-Smith 2003). Thus, this study contributes to exploring causal mechanisms behind sable antelope decline in Kruger.

Factors that might influence where sable can establish home ranges include (i) distance from water, considering that Kruger Park has augmented water sources in the park by providing dams and drinking troughs fed by windmills since the 1930s (Grant *et al*. 2002, Smit *et al*. 2007), (ii) distribution of locations that retain more green leaves in dry season when food quality drops, (iii) competition from the numerically most abundant grazers in the park, which include impala (*Aepyceros melampus*), buffalo, wildebeest (*Connochaetes taurinus*), and zebra (*Equus burchelli*), and (iv) predation risks associated with spatial distribution of prey supporting lions. I excluded megaherbivores (>1000 kg) that included hippopotamus (*Hippopotamus amphibious*), white rhinoceros (*Ceratoherium simum*), and elephant (*Loxodonta africana*) because the differences in body mass between sable (220 kg) and for example a white rhinoceros (>1 000 kg) (Owen-Smith 1998) yield high body mass ratios of around 4.5. According to Prins and Olff (1998), such a ratio could be too high for competition to occur, but instead is suggestive of facilitation. In addition, megaherbivores are not common prey for lions.

It is important to separate effects of abiotic factors from those of biotic factors on sable distribution to identify those factors that exert the most influence on where sable herds occur. Abiotic factors such as geology and rainfall can indicate places with environmental conditions that allow a species population to persist (i.e. spatial extent of a fundamental niche) (Soberón & Peterson 2005, Hirzel & Le Lay 2008). However, biotic interactions can constrain occupation to a limited proportion of those conditions (i.e. subset of fundamental niche) (Soberón & Peterson 2005, Hirzel & Le Lay 2008). For example, presence of a superior competitor or predators may prevent a species from occupying some part of its potential range (Hirzel & Le Lay 2008).

The aim was to determine which factors restricted a wider distribution of sable in Kruger Park. I used geographical positions of herds from aerial surveys of larger animal species (1978–88). This period was chosen in order to investigate what factors limited distribution of sable antelope before the population declined. In chapter 4, it was evident that changes in distribution of certain herbivore species after 1984 were associated with contraction of sable abundance and distribution after 1988. I used landscapes (representing specific vegetation type) distinguished by Gertenbach (1983) and Venter (1990) that are available as GIS files in KNP database to distinguish factors that were most influential on sable home range distribution. Specific questions and hypotheses were:

1. Does geology influence sable distribution, and if that is the case, which geological substrates appear most influential?
    - H1: Sable home ranges are more prevalent on fertile basalt substrates than on nutrient poor substrates such as granites, sandstone or aeloian sands because nutrient richer locations will support more production of forage resources.

2) Does rainfall influence sable distribution?
    - H2: Sable home ranges are more prevalent in areas with higher annual rainfall which indicate locations that produce more food and subsequently retain more forage resources through the dormant season.
    - H3: Dry season rainfall is a better predictor of sable distribution than annual rainfall because it indicates locations that retain more green foliage during the period when food quality is lower

3) Does vegetation production or retention of green foliage through the dry season influence sable distribution?
    - H4: Sable home ranges are more prevalent on areas with higher dry season NDVI, which indicates locations that retain more green foliage when food quality is low.
    - H5: Sable home ranges are more prevalent on areas with higher wet season NDVI, which indicates locations that produce more food and subsequently retain more food later when plants stop growing in dry season.

- H6: NDVI is a better predictor of sable distribution than rainfall because primary production and retention of green foliage not only depend upon rainfall, but also on soil moisture availability, which varies between soil types.

4) Does distance from water sources influence sable distribution?

- H7: Sable are less prevalent > 5 km from perennial water sources.

5) Does landscape type influence sable distribution, and if that is the case, which landscapes are most influential?

- H8: Sable home ranges are more prevalent in woodland savanna over shrubland and dense bush savanna or areas that are predominantly grassland with sparse trees.

6) Does competition influence sable distribution, and if that is the case, which potential competitors appear most influential?

- H9: Sable home ranges are more prevalent on areas with lower competition from the most abundant grazers, buffalo, wildebeest, zebra, and impala. Competition should be greatest from buffalo and zebra**,** because as medium tall grass grazers, they compete for similar forage with sable**.**

7) Does predation influence sable distribution?

1. H10: Sable home ranges are more prevalent on areas with lower prey base supporting lion because such areas support fewer lions and thus, have lower predation risks.

METHODS

1. Study area

Kruger National Park covers nearly 20 000 km^2 in eastern lowveld region of South Africa. The park was entirely fenced from 1976 to 1993. In 1993, a section of the western fence separating KNP from private wildlife reserves was removed (Joubert 2007). Eighty percent of the annual precipitation falls during the wet season (October–March). Annual rainfall distribution averages 750 mm in south-west and decreasing to 450 mm in north-east (Ogutu & Owen-Smith 2003). During dry season, surface water remain in perennial rivers or waterholes fed by windmills (Redfern *et al*. 2003). The western half of KNP is principally underlain by granite, although gabbro intrusions occur in south, central, and northern regions, whilst sandstone occurs in north-west. The eastern half is primarily basalt, although rhyolite occurs along the eastern park boundary (Gertenbach 1983, Venter 1990). Granite derived soils are sandier and generally less fertile than soils from basalt (Scholes *et al*. 2003).

Different vegetation communities occur on the different geological substrates (Venter 2003). Mopane (*Colophospermum mopane*) predominates in northern half with tree savanna on granite and shrub savanna on basalt. Marula (*Sclerocarya birrea*) and knob thorn (*Acacia nigrescens*) savanna occur on basalt, and Delagoa thorn (*Acacia welwitschii*) and magic guarri (*Euclea divinorum*) woodland on karoo sediments and ecca shales in central and southern regions to the east. Red bushwillow (*Combretum apiculatum*) dominates in mountain bushveld on rhyolite extreme east of central and southern regions (along park boundary), and in west of central region in mixed woodland dominated by *Combretum* spp. on granite. In southern region, sour bushveld dominated by silver cluster-leaf (*Terminalia sericea*) and sickle bush (*Dichrostachys cinerea*) occur on granite to the west. Mountain bushveld dominated by *C. apiculatum* occurs on granite to the south and dense mixed savanna woodland dominated by *Combretum* spp. occur on granite to the north and central. Gertenbach (1983) distinguished 35 landscapes based on finer details of vegetation patterns and outlined plant community features that distinguish one landscape from the next. Venter (1990) produced a hierarchical classification system based on soil characteristics that distinguished 56 land types. Boundaries of landscapes delineated by Gertenbach (1983) and land types delineated by Venter (1990) are equivalent in many cases. However, differences exist in places that Gertenbach (1983) represented as single landscapes, whilst Venter (1990) subdivided those areas into distinct units (Appendix Table 5). The Venter (1990) system has more divisions than were delineated by Gertenbach (1983).

1.1 Source data

Details of methods used during Kruger National Park's annual Ecological Aerial Surveys (EAS) are outlined elsewhere (Joubert 1983**,** Viljoen 1989, Viljoen & Retief 1994). Ecological aerial surveys were conducted between May and August when visibility conditions were best (Viljoen 1989, Redfern *et al*. 2002). I analysed presence /absence of sable herds from 1978 up to 1988 covering a period when sable abundance peaked in the park (Grant *et al*. 2002) in order identify factors that affected sable distribution before declines started (post-1988). I analysed data on lion abundance that was recorded during EAS surveys covering a period (pre-1989) before lion range expanded into northern Kruger Park following an influx of zebra (Harrington *et al*. 1999). Surveys periods considered here covered most of KNP except for an area in far north that is hilly and was not regularly surveyed. That part of far north was excluded from this analysis. In 1978 and 1979, some areas of central southern region were not covered. Census transects were 800 m apart, and four observers, two on each side of a fixed wing aircraft recorded geographical locations of herds, herd size and composition. Prior to 1987, accuracy of locating herds was uncertain up to 2 km because sightings were mapped by hand, but the uncertainty decreased to within 0.8 km after incorporating a palmtop computer coupled to a GPS unit during the surveys from 1987 onwards (Viljoen & Retief 1994).

1.3 Data analysis

1.3.1 Tiles

Sable is a sedentary species and assuming an annual herd sighting probability of 0.7 based on estimates by Redfern *et al*. (2002), the chance of a herd being missed if resident in an area for two incomplete surveys is small (0.09). Therefore, I accounted for areas not surveyed in 1978 and 1979 (southern region) by duplicating herds location data recorded in those areas in 1980. I created a shape file of 5 × 5 km tiles in Arc Map (version 9.1) a Geographical Information System software (GIS), using a map of KNP as a template. I overlaid the tile shape file on a map of KNP that showed geographical positions of herds and classified each tile as showing presence/absence of a sable herd record. I considered a herd was resident (i.e. present) if a tile presented at least 2 records of sable herds from 1978-1993 a period when EAS surveys covered all KNP. I considered 2 sightings (for different years) as enough to exclude records when a herd may have been sighted outside usual home range. Tiles that contained multiple records of herds over the same period (1978-1988) were treated as a single “presence”. I chose the 25 km^2 scale to form the basis for this analysis because it approximates home range size estimates for sable (Joubert 1974, Sekulic 1981, Estes 1991). Hence, the presence of a resident herd in one home range is independent of the presence of neighbouring herds during the same aerial survey. I used 25%, 50%, 75% and greater than 75% percentiles to distinguish different levels for each categorical variable. The above levels (percentiles) were deemed appropriates because frequency distribution plots constructed for sable herd occurrences against most of my predictor variables exhibited natural breaks in these bands.

2. Abiotic factors

I formed two groups of abiotic factors: i) broad factors consisting of geology, dry and wet season rainfall, dry and wet season NDVI index and distance from perennial water source, and ii) specific vegetation composition and structure represented by landscapes (Gertenbach 1983) and land types (Venter 1990). Because the two classification systems are different concerning delineation of boundaries, and descriptions representing certain vegetation types (Appendix 3), I fitted them in separate models to assess which one explained better where sable herds occurred.

2.1 Broad abiotic factors

2.1.1 Rainfall

I derived two predictors from Kruger National Park’s long-term rainfall records (ranging from 18 to 85 years of data per station), 1) mean annual rainfall and 2) mean dry season rainfall, but fitted models separately because the two are dependent. The wet season extended from October to March, and dry season from April to September following distinctions by Venter and Gertenbach (1986). I used ordinary kriging techniques in Arc GIS on rainfall records at each rainfall station to predict values that I assigned to neighbouring tiles. Kriging carries out interpolation functions of random or regularly spaced out points to predict values for neighbouring tiles (Oliver 1990). I calculated percentiles (25%, 50%, 75% and > 75%) of all rainfall values in the 718 grids considered in this study to create categorical predictors each with four levels (Mean annual rainfall; up to 475 mm; > 475 to 525 mm; 525 to 575 mm; and > 575; Dry season rain; up to 40 mm; > 40 to 47; > 47 to 56 and > 56 mm).

2.1.2 NDVI

I used NDVI 10 days composite data sets acquired by the National Oceanic and Atmospheric Administration (NOAA) Very High Resolution Radiometer (AVHRR) from 1984 to 1995 (1994 excluded due to satellite failure). The 1 × 1 km spatial resolution of these images was resampled to a 5 × 5 km resolution to match the scale used for all other analysis in this study. I processed the data, as described below, to (a) minimize cloud contamination effects, and (b) define metrics such dry season NDVI and wet season NDVI following Reed *et al*. (1994) and White *et al*. (1997, 2000). Clouds and poor atmospheric conditions result in low NDVI values, or NDVI values in a series that drop suddenly but peak again suddenly, thus can be considered as noise, and removed. I applied a line smoothing algorithm to the time series NDVI data, following Chen *et al*. (2000). The smoothing consisted of 1) calculating the mean NDVI value for each of the thirty six 10-days composite data sets in a year and 2) comparing the mean of a 10-day period under consideration with the mean of a previous and the following 10-day period in the series. If the mean value under consideration was greater than the previous one, the previous one was replaced; if the mean value was smaller, then the previous NDVI value was retained. This technique preserves the essence of the NDVI time series, whilst eliminates much of the contaminated data (Chen *et al*. 2000). I calculated percentiles (25%, 50%, 75% and > 75%) of NDVI values using the same procedure as with rainfall, and created categorical predictors each with four levels (Wet season NDVI; up to 987; > 987 to 1105; > 1105 to 1228; and > 1228; Dry season NDVI; up to 675; > 675 to 776; > 776 to 874 and > 874).

2.1.3 Distance to water points

Locations of water sources were recorded simultaneously during herbivore EAS surveys (Viljoen 1996). I excluded temporary water sources from the analysis because I consider their influences would be more pertinent to movement patterns within a home range rather than to large scale sable distribution patterns. I created a shape file of distance from a perennial water source to the centre of each tile yielding five categories (0-1 km, 1-2 km, 2-3 km, 3-5 km) and greater than 5 km. Five kilometres was proposed as within the daily movement range of water dependent medium sized herbivores such as wildebeests and zebra (Owen-Smith 1996). I used the distance from each water source as the explanatory variable.

2.1.4 Geology

First, I reduced the 15 geological zones distinguished by Venter (1990) to just 7 major geological entities; granite, basalt, gabbro, karoo sediments, aeolian sand, and rhyolite with distinctive soil types and vegetation structure. The above was achieved through lumping geology types that yielded soils with similar characteristics. For example, I lumped together geology types that yielded sandy soils from granite origin, and geology types that yielded clays from basalt origin. I included an additional 8th category, others, which consisted of tiles that covered more than one geological substrate.

3. Fine abiotic factors

3.1 Landscapes and land types

Landscapes and land types are not independent from effects of geology. However, a decreasing rainfall gradient (north to south) has been associated with different vegetation formations on same type of geological substrate in areas that differ in mean annual rainfall. I reduced land type categories to 14 from the 56 categories proposed by Venter (2003), and reduced 35 landscape categories of Gertenbach (1983) to 13 (see Appendix Table 5). I included an additional category, others, in each case, to represent tiles that covered more than one land type or landscape. I used names based on dominant woody species and geology to represent these simplified land types/landscapes.

4. Biotic factors

4.1 Competition

Changes in distribution patterns of certain herbivore species after 1984 were associated with changes in distributions of sable and other rare antelopes after 1988 (Chapter 4). Therefore, I considered competition and predation effects for the period pre-

1984. I considered competitive effects of a single species (impala, buffalo, wildebeest, or zebra) first, and then later considered combined effects of the sum of the biomass for the four competitors on distribution of sable. I multiplied the average body mass of each potential competitor by the number of individuals of that species in each 5 × 5 km tile after down weighting the biomass of impala (mixed grazer-browser) to 50% (approximate contribution of grass to impala diet in KNP) (Sponheimer *et al*. 2003, Codron *et al*. 2005). Because buffalo herds move over wider areas relative to the other species, I buffered buffalo biomass in each 5 × 5 tile using surrounding biomasses in 5 × 5 tiles and calculated a moving focal mean in Arc Map 9.1. The focal mean is a neighbourhood statistical function in GIS that creates output values for each considered location based on the value for that location plus values identified in a specified neighbourhood. I used predictor "aggregate biomass" to represent the combined biomasses of the four species. Competitor biomass in 5 × 5 tiles was the predictor variable. I derived four categories for the competition index by calculating percentiles (25%, 50%, 75% and >75%) of the biomass values in all the 718 tiles.

4.2 Predation

The predation risk proxy and competition proxy were both derived using biomass of species. However, the predation proxy differs from the competition index because it includes browsers, grazers, and mixed feeders (browser-grazers) that constitute prey for lions (Owen-Smith & Mills 2006, 2008). Each species was weighted based on relative selection shown by lions for these species (Owen-Smith & Mills 2008) (i.e. a species was weighted relative to how much it contributed to lion diet). The relative degree of selection for different prey species by lion was derived by comparing the proportion in the prey killed with the proportion in the herbivore assemblage. I estimated the spatial distribution of predation risk in each 5 × 5 km tile using a proxy following Owen-Smith and Mills (2006, 2008). The proxy was calculated as the product of each species numbers, carcase mass, and relative selection by lions, summed over all prey species. Accordingly, the relative kill likelihood was calculated by assigning the prey species showing the highest selection ratio for lion a value of 1 and adjusting the selection ratios for other species relative to this maximum.

The most favoured prey species for lion; wildebeest, was assigned a relative selection of 1.0, and comparative values for other species were calculated as a proportion of this fixed maximum (Owen-Smith & Mills 2008) (see Appendix Table 2 for list of prey species and relative likelihood of selection by lions considered in the predation proxy). The predation risk proxy incorporates aspects related to prey capture, search, and effects of prey herd sizes, and locations where the lions hunt (Owen-Smith & Mills 2008). I excluded megaherbivores (>1000 kg) such as elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), black rhino (*Diceros bicornis* and white rhinoceros (*Ceratoherium simum*) because mortality of these species attributable to lion kills is very low. I derived four categories of the predation risk by calculating 25%, 50%, 75%, and > 75% percentiles of the spatial predation risk values in all the 718 tiles. Then, each 5 x 5 km tile was allocated one of four predation risk categories from 1 = least risk to 4 = most risk. I used EAS lion counts (pre-1989) to derive four categories representing distribution of lions by calculating 25%, 50%, 75%, and > 75% percentiles of lion biomass values in all the 718 tiles. The four lion biomass levels were; 0; > 0 to 320; > 320 to 960; and > 960 kg. Buffalo contributed less to lion diet prior to 1984 compared to post-1984 (Owen-Smith & Mills 2008), thus, I down weighted buffalo to 25% of its potential contribution to lion diet by biomass during the period up to 1984.

Sightings of lions and number of individuals in a pride were recorded during aerial surveys in KNP. However, lion is subject to greater undercounting bias because the species is cryptic and thus not easily seen from the air. I calculated the spatial distribution of lion biomass. Then I estimated the probability of sable presence in relation to distribution of lion biomass. I also calculated the correlation between the distribution of lion biomass and the predation proxy.

5. Statistical procedures

5.1 Model fitting

I used the 5 × 5 km tile shape file as the base for all the statistical analyses. I excluded tiles covering less than 12.5 km^2 (i.e. half sable home range area), which occurred along the park fences. I considered that sable home range was present if a herd was recorded on at least two occasions from 1978-1988 in the same tile. The latter minimized chances of including in the analysis sable herd locations recorded outside usual home range. I defined a sable herd as two or more individuals, including males and breeding herds seen at any one particular location at the same time.

I fitted logistic regression models because the technique is considered appropriate for modelling dichotomous outcomes (Hosmer & Lemeshow 2000) (i.e. presence/absence of a sable herd) defined for this analysis. I preferred logistic regression to log linear analyses because the latter do not allow for defining a response variable (Agresti 1996). I fitted models in a hierarchical fashion (Agresti 1996, Manly *et al*. 2002) to assess the distribution of sable as a function of (i) broad abiotic factors (geology, rainfall, NDVI), (ii) fine abiotic factors (vegetation structure) and (iii) biotic factors (competition and predation). First, I fitted models to single terms within each grouping in order to determine a) which factors influenced sable distribution, and b) in a factor, which distinctions (i.e. levels) were most influential? I did not fit NDVI and rainfall predictors in the same model because the two terms are both indices of (i) vegetation production (wet season) and (ii) retention of green leaves (dry season) and thus are dependent. Land types (Venter 2003) and landscape systems (Gertenbach 1983), both indices of vegetation structure and composition, were considered non-independent, and thus I did not incorporate both of them in one model. I did not fit geology and indices of vegetation composition and structure in the same model because these were also non-independent. I also did not fit the predation proxy with competition terms in same models, and did not fit the aggregate competition term in same model with competition terms representing single species because they are dependent.

I used the step down procedure in SPSS 13.0 to investigate which of the predictors was closely associated with a probability of sable herd presence, and I evaluated the contribution of each predictor in the model using the log-likelihood statistic (Agresti 1996). Akaike Information Criterion (AIC) model selection procedures provided the relative support for each individual model by comparing, AIC values, and delta Akaike (AIC Δ_i) amongst the various models (Burnham & Anderson 2002). Burnham and Anderson (2002) proposed that models with delta AIC values < 2 have equally good fit and in the event of several models presenting delta AIC values of < 2, the model with the fewest parameters (i.e. the most parsimonious) is the best (Anderson & Burnham

2002). Models with substantial support that should be considered candidates for the best model should be within 4-7 AIC units of the best model. Burnham and Anderson (2002) proposed that models with delta AIC values >10 are not supported. I calculated AIC using the formula AIC = -2(log-likelihood) + 2*K*, where *K* is the number of estimable parameters included in the model + intercept (Burnham & Anderson 2002) (2nd edition page 60-62). For categorical predictors, number of estimable parameters equal number of categories in each predictor minus 1 summed over all categories. The above AIC formula yields identical relative AIC values, delta AIC and evidence ratios to an alternative formula (AIC = -2LL-2df), where LL is the log likelihood of the model and df is degrees of freedom proposed for log linear analysis Quinn and Keogh (2002) (pages 393-399).

At first, I fitted models to address the following questions; A; i) Does geology, rainfall, NDVI and distance from water influence sable distribution? ii) Which geological substrates, which rainfall components and which NDVI aspect is most influential? iii) At what range of distance from water source do sable antelope favour to establish home ranges? B; i) Do effects of geology on sable distribution depend on distance from water source? ii) Do effects of geology on sable distribution depend on rainfall or NDVI? iii) Do effects of rainfall or NDVI on sable distribution depend on distance from water source? To answer questions (A) i, ii, and iii, I fitted models that estimated probability of presence/absence of resident sable herds as a function of effects of individual broad abiotic factors. To answer questions (B) i, ii, and iii, I fitted models that estimated probability of presence/absence of resident herds as a function of i) additive effects of geology and distance from water, and ii) additive effects of geology and rainfall or NDVI. I also estimated probability of presence/absence of resident sable herds as a function of additive effects of distance from water and rainfall or NDVI. Furthermore, I fitted models that estimated the probability of presence/absence of sable herds as a function of additive effects of distance from water, geology and rainfall or NDVI.

At the second stage, I fitted models to address the following questions. A) Do landscapes or land types influence where sable herds occur, if so, which landscapes are most influential? B) I then considered the best supported specific vegetation type predictor, and fitted models to address the following question: i) Does effect of landscape on sable distribution depend on effects of distance from water, rainfall, or NDVI? To answer the first question, I fitted two models, first, to assess contributions of effects of landscape alone and second, assess contributions of effects of land type alone to sable distribution. To answer question B (i) I fitted models that predicted sable distribution as a function of additive effects of land types and effects of broad abiotic predictors.

At the third stage, I fitted models to address the following questions, A) Does competition influence sable distribution, if so, which competitors are most influential? I fitted models that estimated the probability of presence/absence of resident sable herds as a function of effects of; i) single competitors and ii) aggregate biomass of competitors. During the fourth stage, I fitted models to address the following questions; A) i) Does predation additionally influence sable distribution? ii) Does predation risk have a stronger influence on sable distribution than competition? B) Does competition or predation risk override influences of abiotic conditions? I lumped categories of geology that presented a prevalence level of < 0.1 into one category, other. I lumped levels of land type using the same criteria. I then modelled the modified geology with 5 levels instead of 8 and the land type predictor with 10 levels instead of 15. First, I fitted models to assess if effects of the modified geology and land type predictors were better than effects of the unmodified counterparts in predicting where sable herds established. Second, I fitted models to estimate probability of presence/absence of resident herds as a function of predation effects alone. Third, I fitted models of effects of competitors with land type. Fourth, I compared effects of competition vs. effects of predation risk on where sable herds occurred. Fifth, I fitted models to estimate the probability of presence/absence of sable herds as a function of i) effects of competition and land type and ii) as a function of effects of predation risk and land type. Sixth, I fitted models of presence/absence of sable herds as a function of i) effects of competition, land type and distance from water, and ii) effects of predation risk, land type and distance from water.

RESULTS

1. Broad Abiotic factors

Sable herds were recorded on 301 (42%) of the 718 tiles that were equal or greater than the minimum size (12.5 km^2) considered in this analysis. Amongst effects of single broad abiotic factors on where sable herds occurred, geology was the most influential followed by dry season NDVI, dry season rainfall, and wet season NDVI (Table 1). Sable were more prevalent on granite and sandstone rather than the more nutrient rich basalt or gabbro substrates (Fig. 2a). Models that combined modifying effects of dry season NDVI/wet season NDVI, dry season rainfall, and distance from water with effects of geology received more statistical support for explaining where sable herds occurred compared to models that incorporated solely effects of single abiotic factors. The "best" model that explained where sable herds occurred consisted of effects of geology combined with effects of wet season NDVI and distance from water.

Sable prevalence was associated positively with both dry season and wet season NDVI (Fig 2e-f). As single factors, effects of dry season NDVI received more statistical support than effects of dry season rainfall and effects of wet season NDVI. However, a model that combined effects of dry season rainfall with effects of geology plus effects of distance from water, received equivalent statistical support in explaining where sable herds occurred to a model that combined effects of dry season NDVI with effects of geology plus effects of distance from water (Table 1). Prevalence of sable was highest in areas of highest NDVI values, but prevalence increased with an increase of rainfall and slightly dropped in areas of highest rainfall (Fig. 2b-c). Although effect of distance from water solely on where sable herds occurred appeared weak, it nevertheless improved the fit of a model that included effects of geology plus effects of wet season NDVI, dry season rainfall, or dry season NDVI (Table 1).

2. Landscape and land types

Land type received better statistical support than landscape or geology for predicting where sable herds occurred (Table 2). Effects of wet season NDVI, dry season rainfall and dry season NDVI appeared most influential in addition to effects of land type in predicting where sable herds occurred. In addition, models that combined effects of dry season rainfall, dry season NDVI and wet season NDVI with effects of land type made up the best seven supported models that could best explain sable antelope distribution. Distance from water made little contribution to model fit either when added to effects of land type or when combined with effects of land type plus effects of dry season rainfall. Effects of land type and effects of dry season rainfall contributed to the best supported model, although a model with effects of land type and wet season NDVI could not be excluded as an alternative. Effects of wet or dry season NDVI were statistically better supported than effects of dry season rainfall when these factors were combined with effects geology. Most favoured land types were; i) mopane/bushwillow (tree/bush) savanna on sandstone, ii) mopane/knob thorn savanna on granite, iii) sour bushveld on granite, iv) mopane savanna on granite, and v) mixed bushwillow/silver cluster-leaf woodland. Least favoured were i) mountain bushveld on rhyolite, ii) delagoa thorn thickets on karoo sediments, iii) sand camwood/silver cluster-leaf (shrubveld/bush) savanna on aeolian sands and iv) knob thorn/bushwillow/silver cluster-leaf on granite (Fig. 3).

3 Biotic factors

3.1 Competition

Amongst single effects of potential competitors, impala and wildebeest appeared most influential on where sable herds occurred. Effects of zebra and buffalo appeared least influential on where sable herds occurred (Table 3). Sable prevalence was lowest in areas of highest impala and wildebeest biomass, but not in areas of highest buffalo or zebra biomass as anticipated (Fig. 4a-e). Additive influences of impala, wildebeest, zebra, and buffalo contributed to the “best” model for competition. However, models with additive effects of either buffalo or zebra plus effects of impala and wildebeest could not be discounted as alternatives. Additive effects of buffalo or zebra received equivalent statistical support in explaining where sable herds occurred when combined with effects of impala. Sable prevalence peaked at intermediate levels of zebra biomass. Sable prevalence dropped from 0.53 (45%) to 029 for areas of their intermediate biomass to areas of their highest biomass. Aggregate competition was less strongly supported compared to impala or wildebeest alone in explaining where sable herds established. Effects from competitors were less influential to where sable herds occurred compared to land type. Adding effects of aggregate competition and land type marginally improved the fit of the model relative to effects of land type alone (Table 4).

3.2 Predation

Predation risk was an additional factor that influenced sable distribution and was better supported as a predictor of where sable herds occurred than aggregate competition (Table 4). Amongst effects of single competitors, only effects of impala were better supported than predation. Effects of predation and effects of wildebeest received equivalent statistical support for explaining where sable herds occurred. Sable prevalence dropped from about 0.50 (50%) in areas of lowest predation risk to 0.25 in highest predation risk areas (Fig. 5a). Additive effects of predation risk with effects of land type received equivalent statistical support to additive effects of zebra and buffalo with effects of land type. Prevalence of sable in relation to lion abundance exhibited patterns equivalent to those shown by our predation index (Fig. 5b). The predation proxy was positively correlated to lion presence records (Pearson correlation coefficient, 0.252, $P = 0.01$). Sable herds mostly occurred in the northern half of Kruger and on western side of the southern half where predation risks appeared lower than elsewhere (Fig. 6a-b).

Discussion

Sable prevalence differed from expectation for geology because prevalence was highest on nutrient poor granite and sandstone instead of nutrient rich basalt and gabbro. Distances of up to 5 km from perennial water sources did not appear to exert limiting influences on where sable herds occurred in Kruger Park. Land type was the best supported abiotic factor in explaining distribution of sable herds. Sable herds established more in mopane/bushwillow savanna, mopane/knob thorn savanna, and sour bushveld than mopane shrubveld, mountain bushveld, and Delagoa thorn thickets. Despite that, models with additive effects of places that could potentially produce more food in wet season and places that retain green foliage in dry season combined to effects of land type were amongst the top statistically supported. Additive effects of competition or predation modified effects of land type and all other factors on where sable herds occurred. Sable prevalence was most negatively associated with impala and wildebeest. The statistical support exhibited for effects of zebra, impala, and those of wildebeest when combined with effects of land type suggested existence of competitive influences on where sable herds occurred. Sable were not excluded from areas of high biomass of buffalo or zebra suggesting that sable herds established home ranges within wider range occupied by buffalo and zebra. Predation risks appeared more influential on sable distribution compared to competition.

Evidence from NDVI and rainfall suggested that on the nutrient poor substrates, sable were prevalent on areas of high rainfall and those that retained high NDVI during dry seasons. In theory, this implied that sable in a way conform to what is known for large African herbivores (Coe *et al*. 1976). Food production indexed by rainfall correlates with herbivore biomass. Why then were sable relegated to nutrient poor granite and sandstone in Kruger Park? In Angola, sable range encompassed both nutrient poor and richer areas. Sable range covered a mixture of gritty sandstones of the karoo sediments, deep aeolian sands of Kalahari system and granite in uplands but heavy clays in low lands (Estes & Estes 1974). Reddish ferralitic clays and sandy clay loams also occurred in parts of sable range in woodland areas (Estes & Estes 1974). At Loskop dam and Percy Fyfe Reserve, South Africa, sable occurred on soils of low organic matter and poor in macronutrients originating from granite. In Zimbabwe, sable in Matetsi occur on basalt of the karoo system whilst in Hwange and Matopos sable occur on aeolian Kalahari sands and granites respectively (Wilson & Hirst 1977).

Additive effects of rainfall appeared not to be consistent on the effect of land type. Whilst additive effects of dry season rainfall plus effects of land type received statistical support to explain sable distribution, a model with additive effects of mean annual rainfall and effects of land type did not receive enough statistical support and did not improve fit of the model. Consistent with prediction, retention of green foliage in dry season (dry season NDVI/rainfall) and vegetation production in growing season (wet season NDVI) was positively associated with where sable herds occurred. Dry season NDVI/rainfall may have been more reliable at indicating locations that retain quality food during critical periods of the year, whilst wet season NDVI would have shown locations that produced enough food to last through the dry season when plants stop growing. Dry season NDVI would also indicate locations with a high component of woody cover. The preference for areas with high dry season retention of green foliage by sable is also in agreement with patterns observed for many African grazers such as zebra, topi, and buffalo that use bottomlands during the dry season (Bell 1970, Duncan 1975, Sinclair 1977). Estes and Estes (1974) documented that sable range in Angola covered upland woodland (wet season areas) and the fertile lowlands (dry season areas).

Sable prevalence increased with corresponding increase of rainfall and peaked at intermediate rainfall levels but dropped slightly in areas of highest rainfall. Sable prevalence peaked at highest NDVI values. The latter could (a) reflect contributions of tree canopy cover to NDVI values. Sable were more prevalent on granite than basalt, and granite areas in KNP present a higher proportion of the woody component of vegetation than basalt (Gertenbach 1983, Venter *et al*. 2003). Therefore, NDVI values on granite areas incorporate a higher proportion of NDVI from tree canopy than on basalt especially during dry season. In the Zambezi valley, Zimbabwe, sable favoured ecotone areas between grassland and woodland (Jarman 1972). The tendency by sable to favour landscapes with a high proportion of the woodland component of vegetation is in agreement with patterns observed elsewhere (Estes & Estes 1974, Wilson & Hirst 1977, Grobler 1981). Sable contrast with other African grazers such as wildebeest, zebra (Duncan 1975) and some populations of buffalo (Sinclair 1977), which favour predominantly grassland areas. In Angola, sable range covered miombo (*Brachystegia spiciformis*, *Julbernardia paniculata*) woodland with a canopy height from 7 to 15 m, and little or no shrub layer (Estes & Estes 1974). Broadly, Percy Fyfe, Rustenburg, Lospkop Dam, and Matopos are regarded as sourveld areas (Wilson & Hirst 1977). Vegetation of Loskop is mixed bushveld and sour bushveld (Wilson & Hirst 1977). Vegetation is open tree savanna, dominated by *Burkea africana* and *Combretum molle*, *Acacia caffra*. Sable preferred open savanna woodland in Matetsi (Wilson & Hirst 1977).

Avoidance of habitats in open grasslands is consistent with observations done at the 3rd and 4th orders of selection elsewhere (Grobler 1974; Estes & Estes 1974, Ferrar & Walker 1974, Wilson & Hirst 1977). In Pilanesberg, sable avoided secondary grassland, but used slopes during wet season and valley bottom during the dry season (Magome 1991). The only exception was in Kenya, where sable showed a preference from more open grasslands due to the absence of the open woodland (Sekulic 1987). The dry season use of habitat by sable at Pilanesberg (moving down the valleys) indicated the importance of valleys in terms of providing green leaf. The water table is higher in valleys compared to hillsides so that grass communities were relatively greener in valleys.

I hypothesized that sable prevalence would be higher up to 5 km from perennial water sources. Overall influence of distance from water on where sable herds occurred was found to be weaker in KNP than what was previously reported for sable or other grazers (Estes & Estes 1974, Western 1975, Wilson & Hirst 1977, Grobler 1981, Smit *et al*. 2007). Sable in Angola were documented to be water dependent, drinking every day even during wet season (Estes & Estes 1974). My results support Redfern *et al*. (2003) who reported that the KNP is well supplied with artificial water, and that less than 10% of KNP occurs further than 5 km from water. Smit *et al*. (2007) reported that sable occurred at lower numbers close to rivers and beyond 4 km from water; this does not refute my conclusions that distances within the 5 km range do not explain why sable occur on nutrient poor substrates. Collars fitted to sable herds have recorded that sable in KNP can travel more than 5 km to water (unpublished data), thus, distances within 0 - 5 km from water may not have restricting influences to a widespread of sable in Kruger Park.

Details of factors that might have overriding influences on where a species can establish a home range (2nd order of selection) are scant, but studies at finer 3rd and 4th selection orders suggest competition could have such an effect. Large herbivores can avoid other species in relation to some perceived negative competition impacts (Grobler 1981, Sinclair 1985). I predicted that competition effects would be negatively associated with sable prevalence. My results suggest that competition influences from zebra, buffalo, impala, and wildebeest could be exerting negative effects on sable prevalence, thus relegating the latter to areas of low abundances of these species. Effects from impala and wildebeest appeared more influential on where sable herds established than effects of zebra and buffalo. However, effects of impala and wildebeest competition diminish when land type is taken into account. Effects of competition from the two species need further studying because sable may avoid impala and wildebeest because these species have different habitat preferences to sable. Observations from areas such as Matopos, Zimbabwe (Grobler 1981) and Kenya (Sekulic 1978) indicate that sable generally do not favour areas dominated by bushes or shrubs. Impala in KNP predominate in thickets and along rivers (Pienaar 1963, chapter 3). In addition, competition effects of impala on sable may not be much because impala switch to browse when grasses dry out (Sponheimer *et al*. 2003, Codron *et al*. 2005). However, competition effects of impala cannot be completely discounted on sable because, first, Grobler (1981) observed that impala grazing kept grass heights below 40 mm, a fact he suggested excluded sable from using the same patches. Second, impala were the most common species sharing range with sable in Angola (Estes & Estes 1974) a fact that could perhaps suggest use of some common resource type. If that is the case, should such a resource be insufficient for both species then competition might occur. However, the negative associations of sable with wildebeest in KNP may as well be associated with distinct habitat preferences by the two species. Wildebeest in KNP were abundant in knob thorn and marula savanna, which is dominated by short grasses and a few trees in central areas of the park, whilst sable were prevalent on mopane woodland savanna areas of the western half of the park (Pienaar 1963, chapter 3). Elsewhere in Africa, wildebeest predominate on open short grasslands (Bell 1970, Ferrar & Walker 1974, Estes 1991). Alternatively, sable might avoid areas with higher concentrations of wildebeest because of predation risks associated with areas such areas. Wildebeest constitute the most preferred species for lions in KNP (Owen-Smith & Mills 2008).

The fact that zebra and buffalo range over wider areas than sable was convincing enough to explain why sable were not completely excluded from areas with high abundances of the two species. Zebra and buffalo range was not restricted suggesting that it might be difficult for sable to avoid buffalo or zebra at scales relevant to home range selection. Sable could avoid buffalo or zebra at finer scales through movement patterns within a home range. This may be particularly important during dry seasons when food quality is low and buffalo concentrate around water supplies. Sable prevalence was also low in areas where biomass of buffalo and zebra was low, implying existence of some areas that were less suitable for all three species. Observations of sable in Pilanesberg, South Africa are in agreement with findings here; sable avoided the more open habitat and grasslands that were favoured by wildebeest, white rhino, hartebeest, and zebra, thus partially reducing grazing competition (Magome 1991). In Percy Fyfe Nature Reserve, zebra spatially overlapped with sable in the dry season and early spring (August through November) (Wilson and Hirst 1977). Survey records of sable antelope in the Selous-Niassa corridor are in agreement with findings here, the population is reportedly increasing likely because abundances of impala, wildebeest, zebra, and buffalo are very low in this area (Hofer *et al*. 2004).

Elsewhere, Sinclair (1985) observed that zebra and wildebeest favoured different habitats during dry periods when food is scarce in Serengeti. Thompson & Fox (1993) suggested that larger species could be better off than smaller ones in the event of competition. Accordingly, for sable the latter implies competitive advantages for buffalo and zebra. However, my result did not show exclusion of sable by buffalo. Based on habitat models, Rosenzweig (1991) suggested that increased animal abundance in a shared habitat reduces benefits from that habitat and that at some stage it becomes beneficial for a species to establish in “inferior habitats” that are less crowded. He further suggested that spilling over into an alternative habitat may be excluded by presence there of some competing species. According to these models if sable was indeed an “inferior competitor” to wildebeest and impala, then it could be possible that sable could be relegated to poor granite areas. No sable home ranges occurred on rhyolites and aeolian sands. Considering that areas under aeolian sands also showed lower biomass of competitors, we could assume that this substrate might not support some preferred type of resource for sable. My predation risk map placed rhyolite areas in southern KNP in the high risk category, thus, I could not be entirely certain whether rhyolites areas were avoided because they do not support the required resources for sable or rhyolites are predation risky areas.

Research on African ungulates has described separation of species by habitat type (Bell 1970, Jarman 1972), by food species (Jarman 1971) and by plant parts eaten (Bell 1970), but few clarify what drives selection of where to establish home ranges for species that physically do not interfere with another. Caughley *et al*. (1987) suggested that distribution of large macropods responded strongly to rainfall and temperature, rather than outcomes of species interactions. Studies on selection generally do not clarify at which level of selection a resource type has overriding influences (Manly *et al*. 2002, Boyce *et al*. 2002, Johnson *et al*. 2004). Basic generalizations emphasize importance of abiotic factors because they are associated with provision of food (Funstone *et al*. 1994, Quinn *et al* 1997, Dettki *et al*. 2003, Hirzel *et al*. 2002) or may represent access to some key resources such as water (Chammaille-James *et al*. 2007). Predators are generally considered to influence negatively a population through direct predation or indirectly when prey species show avoidance of areas where chances of encountering predators are high (Lingle 2002, Hik 1995, Burger *et al*. 2000). Evidence presented here shows the role effects of predation and competition can play by modifying effects of abiotic factors and ultimately relegate sable a sedentary species to establish in nutrient poor areas, and preclude a wider range expansion for this species. Nutrient poor granite and sandstone might potentially be less productive (i.e. less forage resources for sable), but may have less competitors and could be relatively safer for sable herds to establish.

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FIGURE CAPTIONS

FIG. 1. Sable herd prevalence in relation to geological substrates 1-granites, 2- basalts, 3-sandstone, 4-gabbro, 5- Karroo sediments, 6- rhyolites, 7-aeliam, 8-mixed geology.

FIG. 2a. Sable herd prevalence in relation to dry season rainfall

FIG. 2b. Sable herd prevalence in relation to mean annual rainfall

FIG. 2c. Sable herd prevalence in relation to distance from water

FIG. 2d. Sable herd prevalence in relation to dry season NDVI

FIG. 2e. Sable herd prevalence in relation to wet season NDVI

FIG. 3. Sable herd prevalence in relation to land type

FIG. 4a. Sable herd prevalence in relation to impala biomass

FIG. 4b. Sable herd prevalence in relation to aggregate biomass

FIG. 4c. Probability of a sighting sable herd in relation to wildebeest biomass

FIG. 4d. Sable herd prevalence in relation to zebra biomass

FIG. 4e. Sable herd prevalence in relation to buffalo biomass

FIG. 5a. Sable herd prevalence in relation to a predation risk

FIG. 5b. Sable herd prevalence in relation to lion distribution

FIG. 6. Spatial distribution of; a) locations of sable herds, b) locations of lions, and c) predation risk.

Table 1. Sable distribution as a function of broad abiotic conditions

Predictors	-2Log likelihood	Sample size (*N*)	*K*	df	AIC	Delta AIC (Δi)	Evidence Ratio
Geol+DryNDVI+DistH2O	806.2	718	15	**702**	**836.2**	**0.0000**	**1.0000**
Geol+DryNDVI	815.9	718	11	**706**	**837.9**	**1.7930**	**0.4080**
Geol+DryRain	817.4	718	11	**706**	**839.4**	**3.2760**	**0.1944**
Geol+DryRain+DistH2O	810.8	718	15	**702**	**840.8**	**4.6830**	**0.0962**
Geol+WetNDVI+DistH2O	811.7	718	15	**702**	**841.7**	**5.5480**	**0.0624**
Geol+NDVIwet	823.1	718	11	**706**	**845.1**	**8.9590**	**0.0113**
Geol+DistH2O	837.3	718	12	705	861.3	25.1210	0.0000
Geology	846.6	718	8	709	862.6	26.4330	0.0000
Geol+WetRain+DistH2O	835.3	718	15	702	865.3	29.1930	0.0000
Geol+Mean annual rain	844.1	718	11	706	866.1	29.9820	0.0000
DryNDVI	900.2	718	4	713	908.2	72.0200	0.0000
Dryrain	917.2	718	4	713	925.2	89.0780	0.0000
WetNDVI	938.8	718	4	713	946.8	110.6640	0.0000
Mean annual rain	948.9	718	4	713	956.9	120.7260	0.0000
DistH2O	952.8	718	5	712	962.8	126.6600	0.0000

Notes: Geol- geology; DistH2O- distance from water; DryNDVI- dry season NDVI; NDVIwet- wet season NDVI; *K*- number of parameters; Supported models are indicated in boldface; Delta AIC (Δ_i) - a measure of each model relative to the best model calculated as AIC_i-min AIC where AIC_i is the AIC value for model i, and minAIC is the AIC value of the best model; Evidence Ratio –a ratio that compares one model to the other. Calculated as W_j/W_i

Table 2. Sable distribution as a function of broad abiotic factors, land types and landscapes (specific habitat predictors)

Predictors	-2Log likelihood	Sample size (*N*)	*K*	df	AIC	Delta AIC (Δi)	Evidence Ratio
Land type+DryRain	695.9	718	18	**699**	**731.9**	**0.0000**	**1.0000**
Land type+DryRain+DistH2O	691.3	718	22	**695**	**735.3**	**3.3320**	**0.1890**
Land type+NDVIwet	700.7	718	18	**699**	**736.7**	**4.7930**	**0.0910**
Land type+DryNDVI	700.9	718	18	**699**	**736.9**	**4.9850**	**0.0827**
Land type+NDVIwet+DistH2O	694.0	718	22	**695**	**738.0**	**6.0760**	**0.0479**
Land type+DryNDVI+DistH20	694.4	718	22	**695**	**738.4**	**6.4220**	**0.0403**
Land Type	710.5	718	15	**702**	**740.5**	**8.5530**	**0.0139**
Land type+DistH2O	703.8	718	19	698	741.8	9.9090	0.0071
Land type+Mean annual rain	706.5	718	18	699	742.5	10.5800	0.0050
Landscpe	722.4	718	14	703	750.4	18.4750	0.0001

Notes: DistH2O, distance from water; NDVIwet, wet season NDVI; Dryrain, dry season rainfall; DryNDVI, dry season NDVI; *K*, number of parameters

Supported models are indicated in boldface

Table 3. Sable distribution as a function of competitors

Predictors	-2Log likelihood	Sample size (*N*)	*K*	df	AIC	Delta AIC (Δi)	Evidence Ratio
Impala+Wildebeest+zebra+buffalo	830.4	718	13	**704**	**856.4**	**0.0**	**1.0000**
Impala+wildebeest +buffalo	842.6	718	10	**707**	**862.6**	**6.2**	**0.0446**
Impala+Wildebeest+zebra	842.7	718	10	**707**	**862.7**	**6.4**	**0.0415**
Impala+wildebeest	863.3	718	7	710	877.3	21.0	0.0000
Impala+zebra+buffalo	866.2	718	10	707	886.2	29.8	0.0000
Wildebeest+buffalo+Zebra	866.3	718	10	707	886.3	29.9	0.0000
Wildebeest+Zebra	875.8	718	7	710	889.8	33.4	0.0000
Impala+zebra	880.2	718	7	710	894.2	37.8	0.0000
Impala+buffalo	880.9	718	7	710	894.9	38.6	0.0000
Wildebeest+buffalo	881.9	718	7	710	895.9	39.6	0.0000
Impala	898.6	718	4	713	906.6	50.2	0.0000
Wildebeest	899.8	718	4	713	907.8	51.4	0.0000
Aggregate competition(less Buffalo)	909.8	718	4	713	917.8	61.5	0.0000
Buffalo+zebra	923.5	718	7	710	937.5	81.1	0.0000
Zebra	934.2	718	4	713	942.2	85.9	0.0000
Buffalo	948.3	718	4	713	956.3	99.916	0.0000
Aggregate competition	954.8	718	4	713	962.8	106.473	0.0000

Notes: *K*, number of parameters; Supported models are indicated in boldface

Table 4. Sable distribution as a function of distance from water, land type, competition, and predation.

Predictors	-2Log likelihood	Sample size (*N*)	*K*	df	AIC	Delta AIC (Δi)	Evidence Ratio
Land type+impala+wildebeest+zebra+buffalo	616.7	718	27	**690**	**670.7**	**0.00**	**1.0000**
Land type+impala+wildebeest+zebra	627.7	718	24	**693**	**675.7**	**5.04**	**0.0805**
Land type+impala+zebra	643.9	718	21	696	685.9	15.23	0.0005
Land type+impala+wildebeest+buffalo	640.0	718	24	693	688.0	17.33	0.0002
Land type+impala+buffalo	649.1	718	21	696	691.1	20.41	0.0000
Land type+wildebeest+impala	656.0	718	21	696	698.0	27.29	0.0000
Land type+impala	663.3	718	18	699	699.3	28.63	0.0000
Land type+wildebeest+zebra	676.2	718	21	696	718.2	47.53	0.0000
Land type+wildebeest+buffalo	688.3	718	21	696	730.3	59.63	0.0000
Land type+wildebeest	696.1	718	18	699	732.1	61.37	0.0000
Land type+zebra	700.4	718	18	699	736.4	65.74	0.0000
Land type+buffalo	703.7	718	18	699	739.7	69.02	0.0000
Land type+Predation	705.9	718	18	699	741.9	71.16	0.0000
Land type+Aggregate competition	706.8	718	18	699	742.8	72.13	0.0000
Land type 2	732.6	718	11	706	754.6	83.88	0.0000
Predation	922.6	718	4	713	930.6	259.94	0.0000
Lion	932.8	718	4	713	940.8	270.13	0.0000
Aggregate competition	954.8	718	4	713	962.8	292.16	0.0000

Notes: Supported models are indicated in boldface

Figure. 1

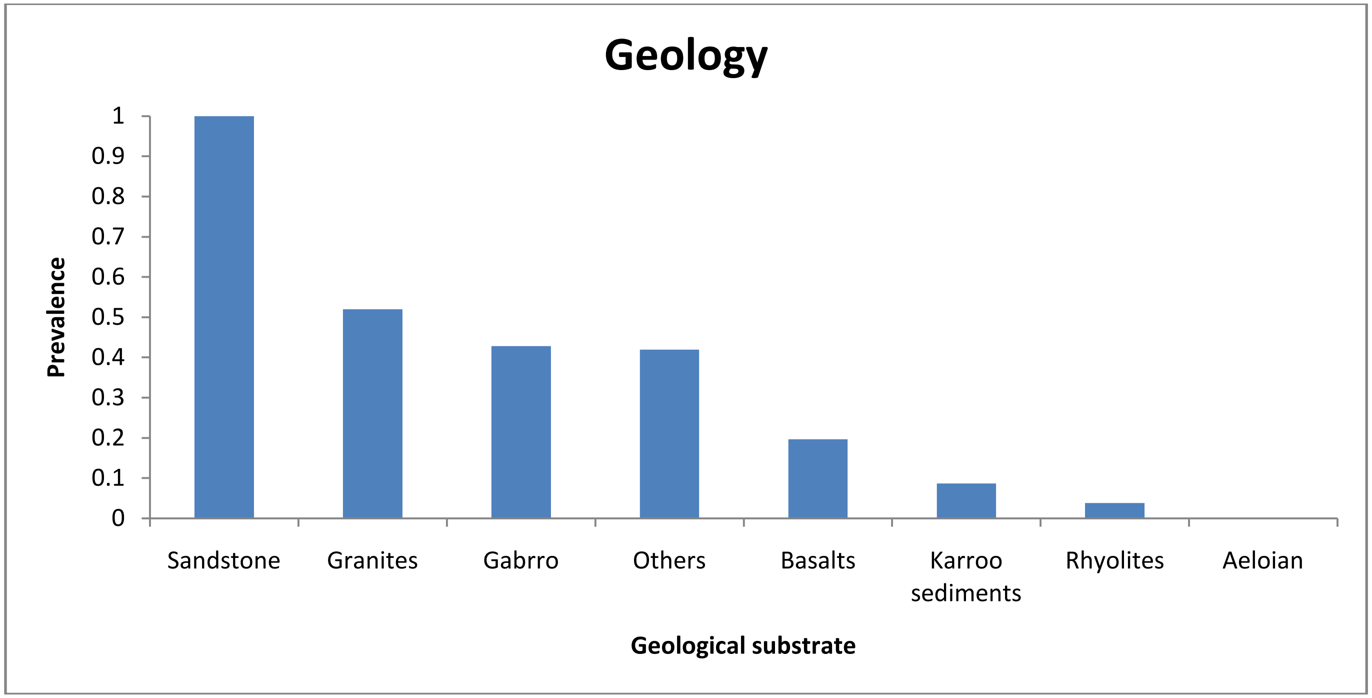
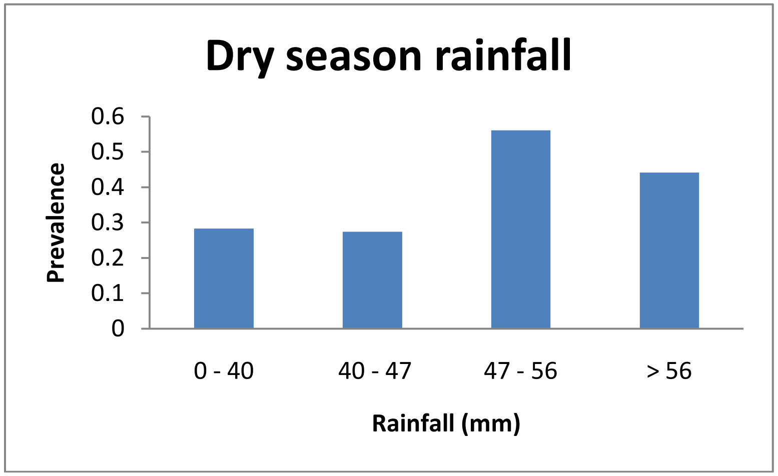

Geology
Prevalence
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Sandstone
Granites
Gabrro
Others
Basalts
Karroo sediments
Rhyolites
Aeloian
Geological substrate

Figure. 2a



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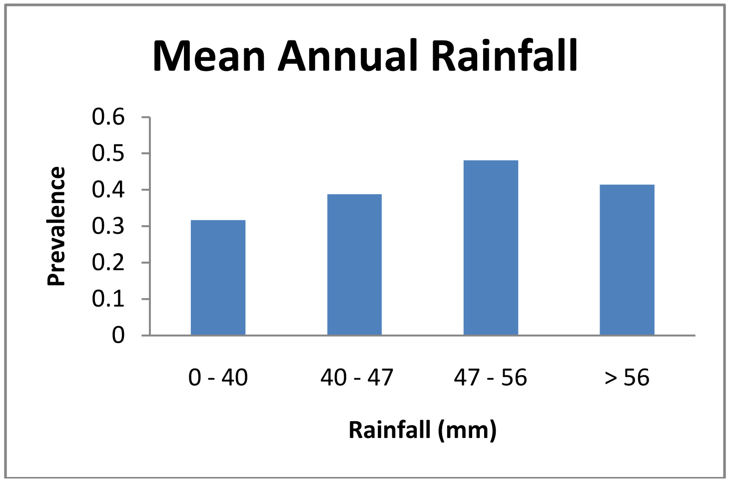
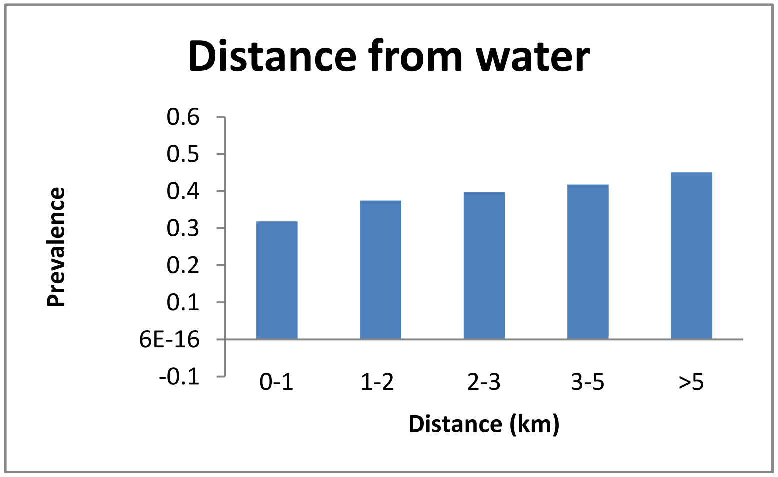
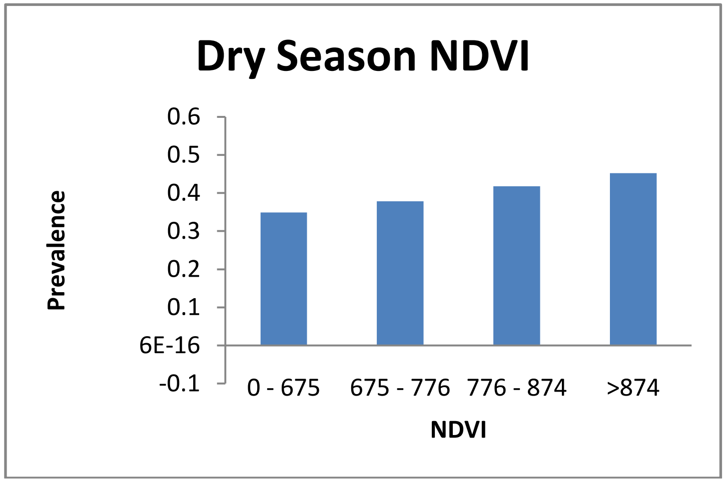


2c



d



e

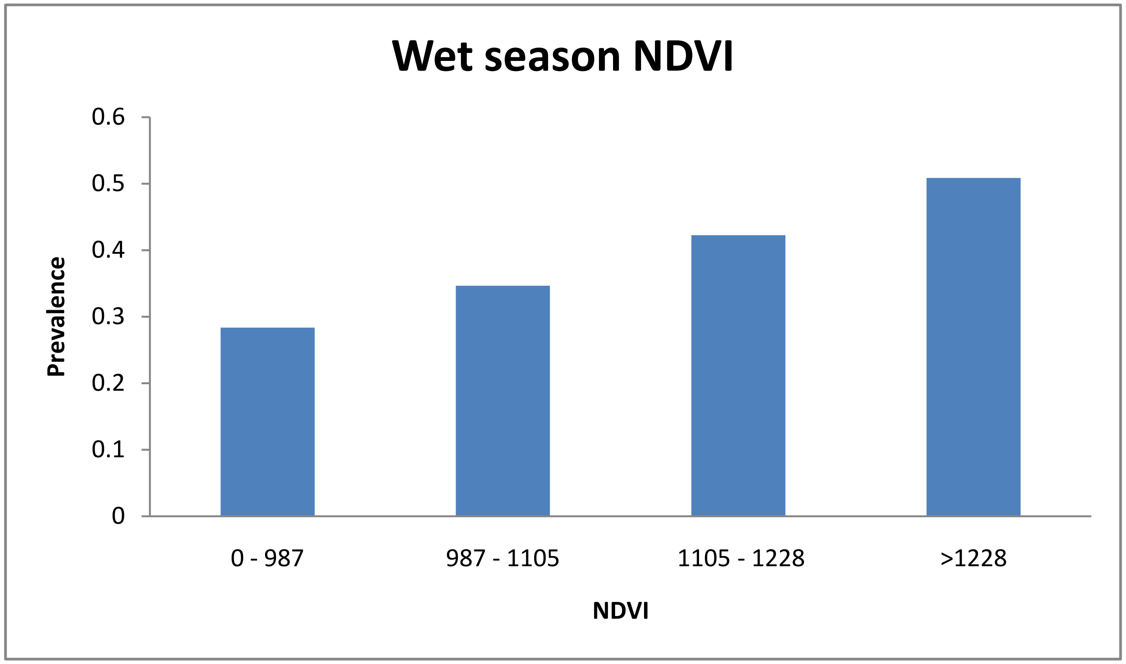
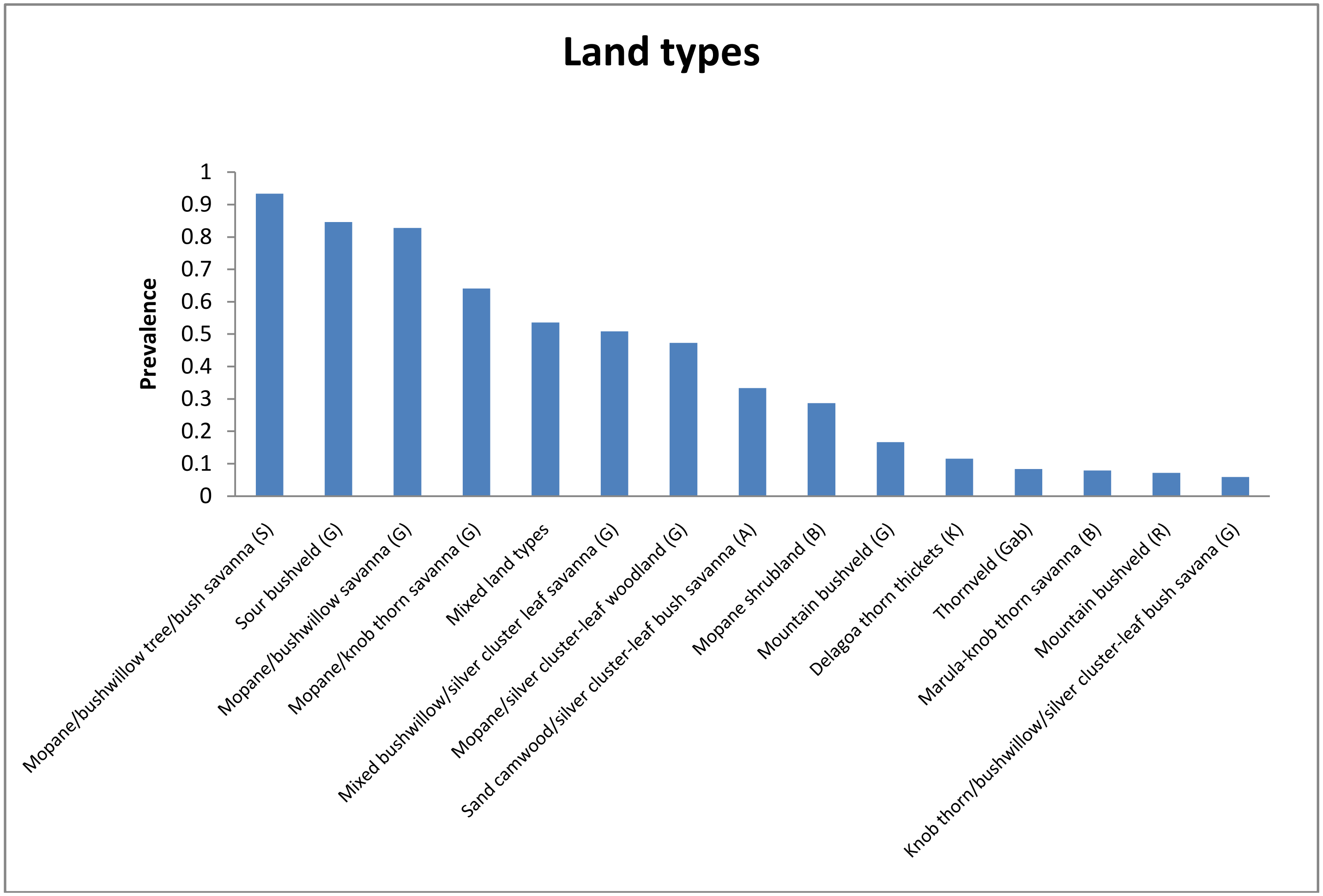
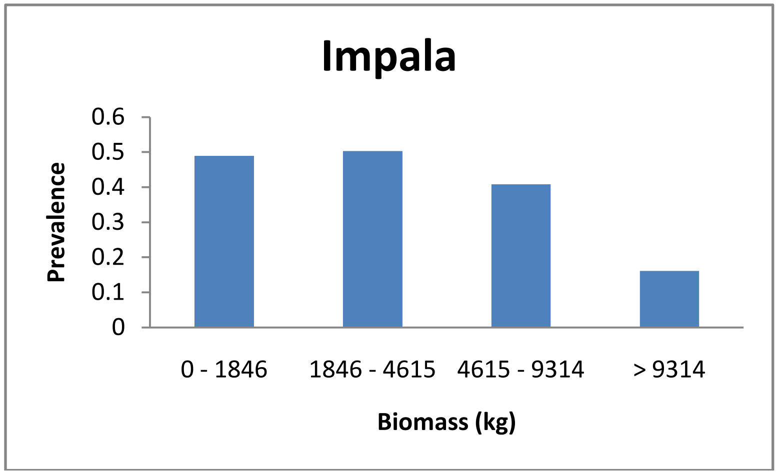

Wet season NDVI
Prevalence
0.6
0.5
0.4
0.3
0.2
0.1
0
0 - 987
987 - 1105
1105 - 1228
>1228
NDVI

Figure. 3

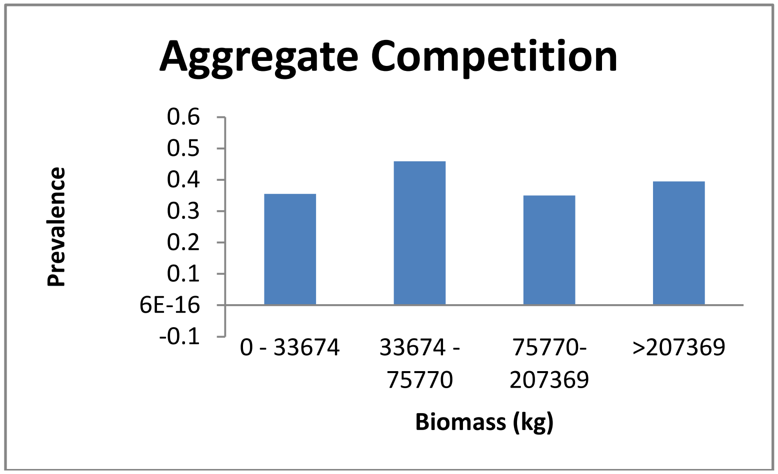


Notes: G, granites; B, basalt; K, karoo sediments; Gab, gabbros; R, rhyolite; S, sandstone

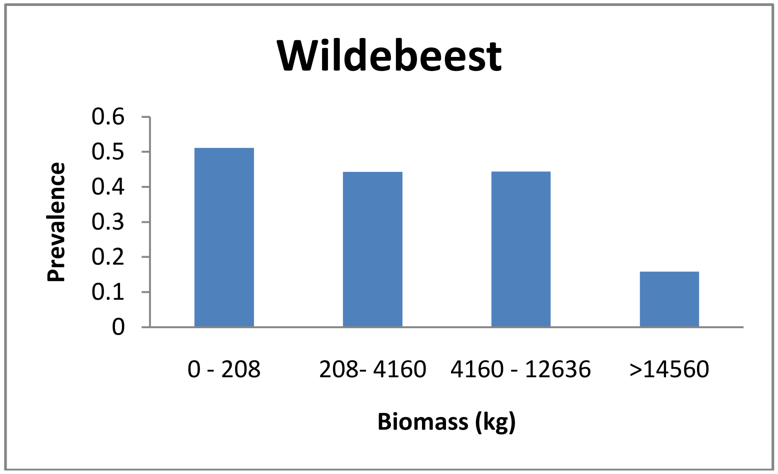
Figure. 4a



b



c



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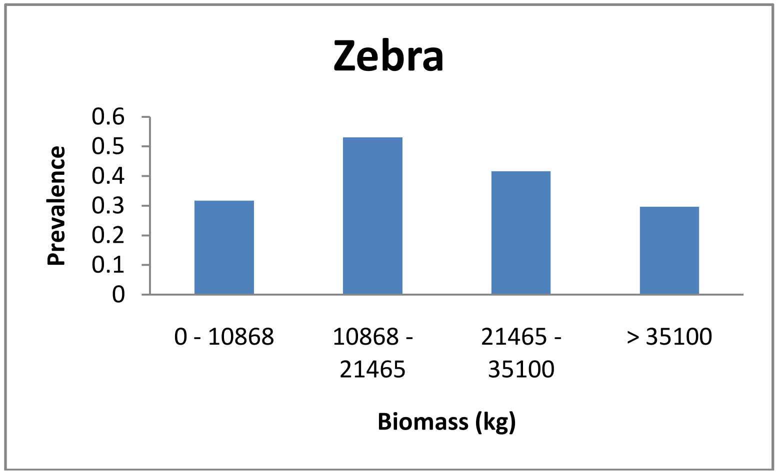


4e

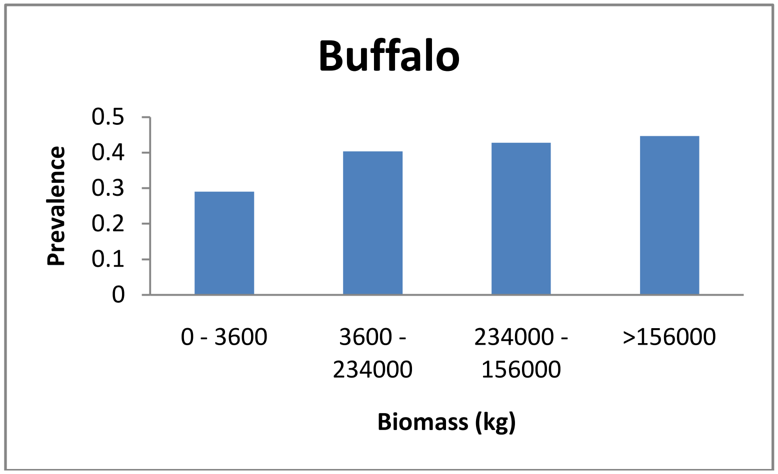
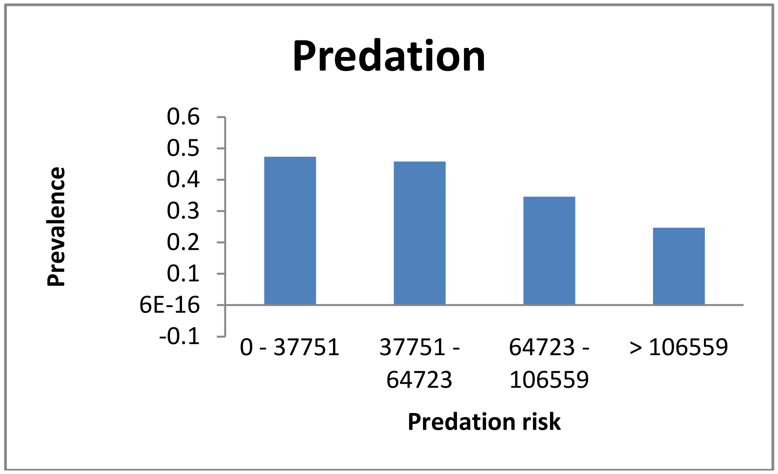

Buffalo
Prevalence
0.5
0.4
0.3
0.2
0.1
0
0 - 3600
3600 - 234000
234000 - 156000
>156000
Biomass (kg)

Figure. 5a


Predation
Prevalence
0.6
0.5
0.4
0.3
0.2
0.1
6E-16
-0.1
0 - 37751
37751 - 64723
64723 - 106559
> 106559
Predation risk

b

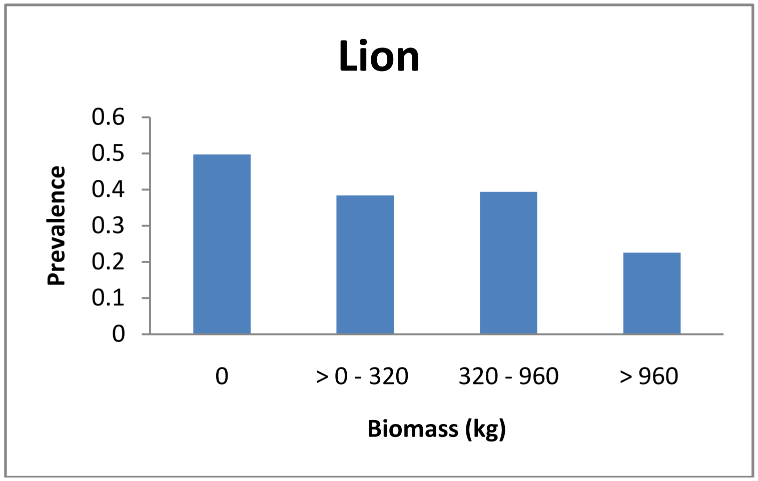
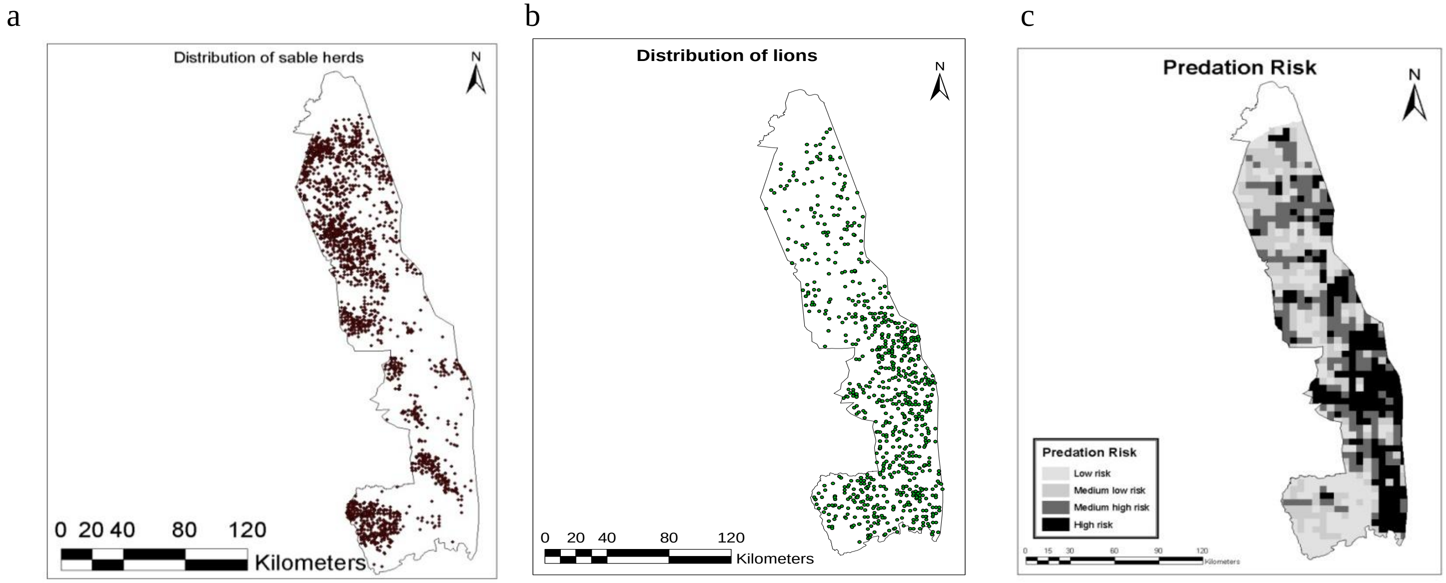

Lion
Prevalence
0.6
0.5
0.4
0.3
0.2
0.1
0
0
> 0 - 320
320 - 960
> 960
Biomass (kg)

Figure 6


a
b
c
Distribution of sable herds
N
0 20 40 80 120
Kilometers
Distribution of lions
N
0 20 40 80 120
Kilometers
Predation Risk
N
Predation Risk
Low risk
Medium low risk
Medium high risk
High risk
0 15 30 60 90 120
Kilometers

CHAPTER 6

Conclusion and recommendations

This study was complementary to a bigger research programme aimed at understanding causes of rare antelope decline or lack of recovery in KNP. The aim of my study was to identify factors that influenced habitat suitability for sable antelope. To do this I distinguished environmental features associated with localities sable occupy and where absent. I categorized key questions in this study into two groups. The first group of questions concerned the broader issues of sable distribution: (i) was the perceived contraction of sable antelope distribution and abundance limited only to this species?, and (ii) were those contractions only in certain landscape types or regions of KNP? The second set concerned specific habitat characteristics: (i) what distinguished occupied areas from unoccupied areas?, (ii) what features were associated with variation of sable presence within occupied areas?, and (iii) what restricted a wider distribution of sable in KNP?

The broader questions required use of methods capable of (a) estimating changes in probability of occupation by a species across the park and (b) revealing variation in occupancy patterns. Documenting changes of distributions and changes in probability of occupation of landscapes is important for addressing concerns relating to range shifts, range fragmentation and/or species losses (Parmesan *et al*. 1999, Thomas & Lennon 1999, Gaston 1990, Lawton 1993). The above information helps in conserving species through identifying favoured habitats and localities where probability of occurrence has severely declined. A severely declining probability of occupation suggests reduced chances of local persistence by a species. Existing methods designed for radio tracking of animals estimate probabilities of use of sections of a home range. Two broader questions presented here required methods with those capabilities adapted to use for studying distributions. Previous assessments of species distributions (Gaston 1990, Thomas & Lennon 1999, Janzen 1994, Brander *et al*. 2003,) assume that all areas where individuals have been sighted exhibit equal chances of occurrences of that species (i.e. all areas are equally suitable), but this is known not to be true (Getz *et al*. 2007). Therefore, I added a new objective to examine use of home range methods on species distributions. The new objective concerned comparing performances of Local convex hull and kernel methods in estimating some examples of commonly encountered types of distribution patterns for different objectives. This became my first task because it was fundamental to provide basis for identifying which method was appropriate to address other distinct objectives in this study.

The outcome of this comparison was that contrary to generalizations from home range studies (Silverman 1986, Seaman *et al*. 1999, Kernohan *et al*. 2001, Gitzen, Millspaugh & Kernohan 2006, Getz & Wilmers 2004, Getz *et al*. 2007), application of these methods to species distributions suggested no superiority of one method over the other. Instead, these methods have different capabilities useful for assessing different purposes of species distributions. The LoCoH method has a propensity for not including areas where a species was not recorded. The kernel method by contrast exhibited an opposite tendency. The kernel method consistently produced the largest range estimates for species assessed in this study. However, with different species distributions examined here, performances of these methods did not appear to lead to different interpretations of their occupancy patterns and range extent estimates. Furthermore, performance of a method is also influenced by type of spatial patterns exhibited by a study species. Both kernel and LoCoH methods were recommended for representing local differences in occupation patterns for species exhibiting continuous distributions, linear patterns of occurrences or patchy distributions. However, automatic procedures of choosing a smoothing parameter could lead to different interpretations of occupation patterns produced by fixed kernel method vs. those from LoCoH method for species that occur in patches which exhibit boundaries that are not clearly outlined (e.g. sable in northern half of KNP) and those exhibiting clumped occurrences in places and widespread occurrences elsewhere (e.g. wildebeest). For these type of pattern, the fixed kernel method showed evidence of a limitation pointed out during home range analyses (i.e. masking gaps and exaggerating range extents) (Getz *et al*. 2007). Evidence from the estimated wildebeest pattern was in line with observations of computer simulation models of home range where the kernel method reportedly overestimated extents of areas covered by location points (Getz & Wilmers 2004). My conclusions here are that fixed kernel method might have to be applied with different h values to different sections of that type of pattern (e.g. one h value for northern half of KNP exhibiting widespread occurrences and a distinct h value for central region where wildebeest are continuously distributed). Thus, it may be practical to divide a study area into separate sections and then mapping their ranges independently.

This study illustrated that LoCoH method is useful for identifying gaps and revealing shifts of distributions for all species examined here. However, increased sensitivity to picking up gaps may require applying this method with caution for estimating range extent sizes of species exhibiting continuous distributions or those that roam widely because the method may show narrower range extents and perhaps emphasize unimportant gaps. I recommended *a*-LoCoH method as best for showing 1^{st} order range extent estimates and for assessing distribution shifts for patchy distribution patterns because this method consistently produced least range estimates for all distribution types considered here. Thus, one would be more confident by using *a*-LoCoH than other methods to conclude that a real change in distribution has occurred or not.

Application of LoCoH or kernel method required making decisions of when to apply 0.95 vs. 0.99 statistical levels, which depended on abundance of location points. The 0.99 levels extended outermost boundaries of a distribution to areas where herd sightings were not recorded for less abundant sable and waterbuck, whilst 0.95 could potentially lead to underestimating area of occurrence for abundant species such as impala and wildebeest. Thus, there is some uncertainty on deciding the cut-off point for applying a 0.95 or a 0.99 level. The challenge appears related to automatic procedures of choosing *h*. Therefore, a further development of methods of choosing a smoothing parameter may overcome this limitation.

The application of LoCoH and kernel methods to assess species distributions was additionally of value to conservation activities because these methods (a) facilitate comparisons of distribution patterns across populations and species, (b) may help in planning which landscapes can be conserved for a focal species, and (c) show areas where distributions are disrupted. These methods enhance potential to; (i) investigate causes of disruptions of distributions, (ii) distinguish resource types related to changes in probability of occurrences, and (iii) link patterns of distributions and abundances to rates of birth, death, and dispersal.

In chapter 3, I could not identify factors associated with historical sable distribution because collection of geographical positions of animal herds and animal count records was irregular prior to 1977 (Joubert 2007). Therefore, I modified the original objective to become;- "to establish changes to historical distributions of larger ungulate species". Maps constructed by Pienaar (1963) provided an opportunity for comparing recent distributions of several large ungulate species against their respective distributions around 1960. The aim was to identify if perceived contractions noted for sable antelope distribution was limited to this species alone.

Because the concern was not to reveal fine scale variation of occurrence, but instead identify changes (at a broad landscape level) that may have occurred amongst ungulate distributions before sable declined (around 1960) and when sable declined (1980-1993), the fixed kernel method, with a tendency not to underestimate 1st order range extents (chapter 2) was applied. Furthermore, choice of fixed kernel method was appropriate because distributions mapped around 1960 are uncertain to some level, thus a method which is not prone to type I error had to be applied if those species distributions were to be compared with recent patterns.

This study has implicitly suggested an approach whereby broad distribution patterns are considered first before setting up hypotheses for small scale studies. For example, examining broader distribution patterns revealed that influences of climate may be involved in the decline of sable abundance. Climate was not initially considered as an important factor involved in the decline of sable antelope abundance. In addition, assessment of broader distributions revealed that declines in sable abundance were across the entire KNP and not just in certain landscapes. This widespread nature of effects of constraints on sable antelope had not been considered as important during the early planning of the research.

An important outcome of this assessment was that changes in distribution and abundance of sable antelope was in some way linked to changes in distributions and to an increase in proportion of common grazers (buffalo, wildebeest, zebra and impala) in northern sections of KNP after 1983, where previously they were less abundant. Thus, in some way this study supported previous findings that indicated an increase in competing or prey species that supported lions were implicated in roan antelope decline (Harrington *et al*. 1999). The same process may also have contributed to sable antelope decline. Another important outcome of this assessment was that contractions of distributions and abundance had also occurred to other rare antelopes (tsessebe and roan), which like sable are at the edge of their geographic distribution in Africa. The above factor would otherwise have been less clear if distribution patterns of other large ungulates across KNP had not been examined. Therefore, this study suggested that diagnosis of factors affecting a species should not be considered in isolation.

Chapter 3 further illustrated that impala, buffalo, wildebeest, warthog, and waterbuck appeared widespread away from rivers than was indicated around 1960 (Pienaar 1963). Because common species occurred during dry season in areas they previously used during wet season, this could have led to a decline in suitability of those areas to rarer antelope. Movement by common species from wet season ranges to dry season areas that may have previously allowed recovery of forage resources had been blocked. Broadly, the analysis highlighted that; i) fences particularly in central-west that excluded wildebeest movement outside the park appeared associated with distributional changes of herbivores as species became resident in the area. ii) Augmenting of surface waterpoints in areas that in the 1960s lacked surface water during dry season appeared influential to the increase of common grazers i.e. buffalo, wildebeest and zebra in northern half of KNP. The increase of these species appeared associated with a decrease in rarer antelopes in this northern half of KNP.

This study has contributed to conservation management in KNP by producing distribution patterns of several species based on a statistical probability of a species occurring in an area. Patterns produced here may thus be used as basis to assess future distribution changes in the park. The maps constructed here show concentration areas of each species, information that might be important in making management decisions concerning which locations to prioritize when conserving target species for example roan or sable.

Assessments of broader questions pointed towards range contractions for sable and other rarer antelopes. Thus next step was to ask specific questions such as; (1) has range losses occurred through animals shifting to other areas or herds going locally extinct. (2) Which areas were no longer parts of a range? (3) What characterized the range contractions; (a) lack of recruitment leading to declining of herd sizes and eventually disappearance, or (ii) a climate effect through making habitats perhaps less suitable? I therefore added another new objective aimed at investigating if a climate effect had caused sable range contractions and abundance decline. Elsewhere climate change effects were linked to species shifting distributions towards cooler areas and where conditions were still suitable (Bakkenes *et al*. 2002, Rodriguez 2002, Walther 2002). The motivation for this new objective followed Caughley *et al*. (1988) who proposed that patterns of how distributions shrunk could reveal the nature of causal factors. For this purpose, it was evident that LoCoH was the method of choice. My initial task in the study had revealed advantages of LoCoH for assessing gaps and changes in areas occupied by a species exhibiting a patchy distribution. The focus here was to examine changes that might have occurred at fine spatial scales including noting changes of areas occupied by specific sable herds radio collared and tracked in two regions of KNP. It was now important to pick up finer details of changes in herd sizes or recruitment in space and over time. The expectation was that if suitability of sable areas had declined as a consequence of lowered rainfall, contractions of distributions, herd sizes and recruitment of sable antelope would be widespread across KNP but be greater in drier northern sections than in the relatively wetter south-western region. Otherwise, range loses and declines in recruitment or herd sizes would be localized to some areas but show no change elsewhere.

I could not establish beyond doubt the exact influence of climate on these rarer species, but I showed that the widespread contractions of ranges, recruitment and herd sizes was characteristic of an influence consistent to that of climate. Whether climate effects contributed through changes in woody–grass balance or forage species composition that consequently could have affected suitability of the areas to rare antelopes could not reliably be established. All three rare antelope species showed evident range contractions associated with local herd extirpations especially following the severe 1991/2 drought. Some of the new herds that established during the period (1984-1988) after the first drought had disappeared. Distribution shifts through tracking perhaps suitable conditions comparable to cases documented in northern hemisphere (Bakkenes *et al*. 2002, Rodriguez 2002, Walther 2002) were not observed in KNP. Sable, roan, and tsessebe herds became locally extirpated even in the relatively wetter southern section of KNP. Small sable herds persisted in discrete remnants of their previously wider distribution in the park. For KNP tsessebe, sable and roan antelopes that occur at the edge of their geographic distribution in Africa, other influences perhaps involving biotic factors (chapter 5) appeared to restrict persistence of these species to localized patches rather than expanding distributions towards higher rainfall areas. Because I could not establish the exact nature of climate effects in KNP, I recommended further studies especially on vegetation structure changes which may be related to decreased visibility and hence increased predation risk.

Chapter 5 contributed the most to the aim and questions set out in this thesis because it involved rigorously testing (i) contributions of factors that exhibit broad scale influences (NDVI, distribution of water points, geology and specific habitat types) and ii) factors that could influence small and localized changes in species distribution (e.g. spatial differences in predation risks or influences of competition) in order to established factors that restricted distribution of sable antelope. I expected location of food to be a basic indicator of where sable antelope should establish home ranges (Soberón and Peterson 2005, Hirzel & Le lay 2008), thus, factors such as geology and rainfall should explain best where sable antelope occur because they indicate locations which potentially can support enough forage resource. Assessment of this objective necessitated the application of the tile based approach because (i) the identity of each area (i.e. tile) in the analysis had to remain the same during the analysis, and (ii) there was a need to apply rigorous statistics to estimate influence of different levels of the various factors on the same area.

The study indicated that sable prevalence differed from expectation for geology because prevalence was highest on poor nutrient granite and sandstone instead of nutrient rich basalt and gabbro. Distances of up to 5 km from perennial water sources did not appear to exert limiting influences on where sable herds occurred in KNP. Land type was the best statistically supported abiotic factor in explaining distribution of sable antelope herds. It appears there is an ecological separation between KNP sable antelope distribution with wildebeest or impala distributions. Broadly, sable antelope favoured mopane savanna woodland in north-west and far north-west and sour bushveld around Pretorius Kop in south-west. Sable antelope avoided knob thorn-marula parkland, which is favoured by wildebeest in eastern parts of the central region. Impala favoured dense areas along rivers. Sable range overlapped with buffalo and zebra ranges, hence, sable could avoid these species by movement patterns. By exploiting or establishing on such areas that are not favoured by the common grazers in KNP, sable may have been able to reduce grazing competition. Sable were more prevalent in areas where predation risks appeared lower than elsewhere. Predation risks appeared more influential on sable distribution compared to competition. The novel contribution of this objective (chapter 5) is that biotic factors exert strong modifying influences on effects of abiotic factors on distribution of sable a sedentary species. This study (chapter 5) reveals a strong modifying influence of predation risk at a higher order of selection (i.e. distribution of sable home ranges) in the KNP.

In Kruger National Park, land type was the predictor that best explained distribution of sable antelope. Predation risk and competition were important factors that modified influences from land type on where sable antelope occurred, and restricted a wider spread of this species in the park. Data from Hwange National Park was less rigorously collected compared with aerial counts in KNP. However, slight modifications to the model presented here would allow to test if sable antelope distribution in Hwange was limited by the same factors as those in KNP. The land type predictor in Hwange has the following levels: woodland, wooded bushland, bushed grassland, scrub, thicket, and woodland-bushland-grassland mosaic. The biomass of impala, wildebeest, zebra and buffalo at all waterholes in a given landscape type could be used to index competition effects in that landscape. Spatial distribution of predation risks of a given landscape type would be estimated using a proxy calculated from prey available to lions at all waterholes. Generalized linear models such as Logistic regression models could be fitted to combinations of these predictors: landscape, competition, and predation risk testing how well the predictors explain the distribution of sable antelope.

Management implications

The findings of this study provide some insights into what could be done to improve conditions for sable antelope in KNP. The knowledge that predation risk and competition have strong modifying roles on effects of abiotic factors on where sable herds occur and have restricted a widespread sable distribution can help improve management of potential competitors or prey for lions. The abundance of Roosevelt's sable antelope (*Hippotragus niger roosevelti*) in the Selous-Niassa Corridor is on the increase (Hofer *et al*. 2004). Animal census records of the Selous-Niassa corridor showed very little or no wildebeest, impala or zebra in the area. In addition, the few buffalo occurring in the corridor were considered migratory (Hofer *et al*. 2004). Therefore, in some ways sable in the Selous-Niassa corridor maybe experiencing lower competition effects from these species. The latter can also suggest lower abundances of prey species that support lions in area, thus potentially reducing predation risks. Therefore, I concluded that for successful reintroduction of sable in any area, abundances of impala, zebra, wildebeest, and buffalo should be monitored. The above could be done through variations in the current waterpoint management policy. Smaller water troughs that may not support huge buffalo herds may be maintained in sable areas. In addition, since sable is a sedentary species, home range of each sable herd should be treated as a distinct management unit so that each herd may benefit from burning programmes in the park.

To monitor and manage successfully environmental drivers of sable distribution it is fundamental to collect data on sable locations at a relevant spatial resolution. Collection of geographical locations of animal herds (during surveys) no longer occurs over the entire area of KNP, as occurred prior to 1998, but rather is based on a distance sampling method. The distance sampling method works by dividing the park into equally spaced strips. Data obtained that way have a coarse spatial resolution and leads to inability to detect local variability in occurrences of a species or detect shift of distributions. This study makes recommendations that broadly cover two issues:

1) Collecting spatial data on sable distribution without loss of spatial variability or resolution to the data.

2) Improving conditions for sable in areas where they occur

1) Data collection (adjustments to current technique)

It is unlikely that management in KNP can detect where sable distribution has shifted if they do, where sable are doing well and which landscapes are sable not recruiting from data collected using distance sampling techniques.

I recommend spatially varying intensities of surveys: instead of flying over the whole park using evenly spaced out transect for all species, more census transects should be laid out in areas which have highest value for sable persistence than outside sable areas. Areas that are important to sable have been identified and mapped in this study. Those extra transects need not be surveyed every year, but instead every 3-4 years (a reliable enough frequency to detect spatial changes in probability of occupancy or local herd size decline before it is too late for remedial action).

Other considerations

Survey flights across the 20 000 km^2 area of KNP is always going to involve high costs because large number of flying hours are required, thus future surveys are always going to be uncertain. Therefore, I recommend exploring possibilities of establishing partnerships with other parks, government, internal national partners and non-governmental organizations to set up some kind of a national authority that carries out censuses in all parks in the country. The authority could be carrying out census every 3-4 years in a park. An alternative to the above would be carrying out the census annually but only covering one region in KNP per year (i.e. flying each region alternatively). This last approach has an extra advantage in that spatial differences in recruitment across regions can be assessed. The area covered by one region is small hence counting of juveniles could be possible.

1) Improving conditions for sable in the areas where they occur

The aim should be to reduce large concentrations of competitors or prey for lions in sable areas. Thus I recommend spatially varying size dimensions of waterpoints and burnt plots.

(a) Monitoring of remaining sable herds with the help of rangers, who should other than closing waterpoints where sable core areas occur, should reduce the sizes of water troughs in these areas and maintain larger water troughs elsewhere away from sable range.

(b) Burning small patches in sable habitats that may not attract huge concentrations of competitors and prey for lions. This would be more effective if burning of bigger patches outside sable areas would be implemented at the same time in such a manner that the green flushes of grass would occur at about the same time in both areas.

The above could likely reduce competition and predation risk in habitats of highest value to sable (i.e. create refuge where sable can escape from predators and competition).

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APPENDIX I: Method Details

Tile method

The tile method is used in spatial analysis for establishing presence/absence, densities of animals per given area (White and Garrott 1990, Swihart 1992,) and assessing spatial associations between species (Doncaster 1990, Redfern *et al*. 2006). Two tile scales, (5 × 5 and 10 × 10 km) were applied. Tile size choices are flexible and dependent on the scale of study (Redfern *et al*. 2006) and might also depend on minimum home range size estimates of species understudy. A tile size that approximates home range size estimates has advantages; first, surveys are unlikely to result in omissions of herds if resident in an area over a given period, e.g. 1980-1993 in this case. Second, a record of one herd in one tile is thus independent of another herd recorded in a different tile during a survey. The 10 × 10 km tile size was chosen to allow comparisons to previous studies of spatial association in the KNP (Redfern *et al*. 2006).

For our this assessment, the 5 × 5 km was within the minimum range size requirements for each of the four species, and in addition, 5 × 5 is half the 10 × 10 km scale and therefore, ideal for assessments of effects of bigger tile sizes versus effects of smaller tiles on estimating distribution ranges.

Kernel method

I applied the kernel method using least–square cross-validation (LSCV) techniques for choosing the smoothing parameter *h* (Silverman 1986, Powell 2000 and Worton 1989). Each merged point shape file was loaded onto the Animal Movement Spatial Analyst Extension Tool where I estimated 0.99 and 0.75 kernels distributions. The technique constructed kernels through allowing *h* to vary (adaptive kernels) or remain fixed (fixed kernel) from one point to another (Silverman 1986). Following Seaman and Powell (1996) and Terrell and Scott (1992), the fixed kernel is mathematically defined as

$$f_{\text{fixed}}(\chi) = \frac{1}{nh^2}\sum_{i=1}^{n} K\left(h^{-1}(\chi - X_i)\right), \qquad (1)$$

where *n* is the number of points, *K* is a kernel density, *h* is the smoothing parameter (Silverman 1986), *X* is a random sample of *t* independent points, χ is a vector of (*x*,*y*) coordinates describing the location where the function is being evaluated and X_i is a series of vectors whose coordinates describe the location of each observation *i*.

The adaptive kernel is defined by

$$f_{\text{adaptive}}(\chi) = \frac{1}{nh^2}\sum_{i=1}^{n}\frac{1}{\lambda_i}K\left(h^{-1}\lambda_i^{-1}(\chi - X_i)\right), \qquad (1.1)$$

where λ_t is local smoothing parameter that depends on the density of points around each data point X_t and the other symbols are defined as in fixed kernel.

Local Convex Hull Algorithms

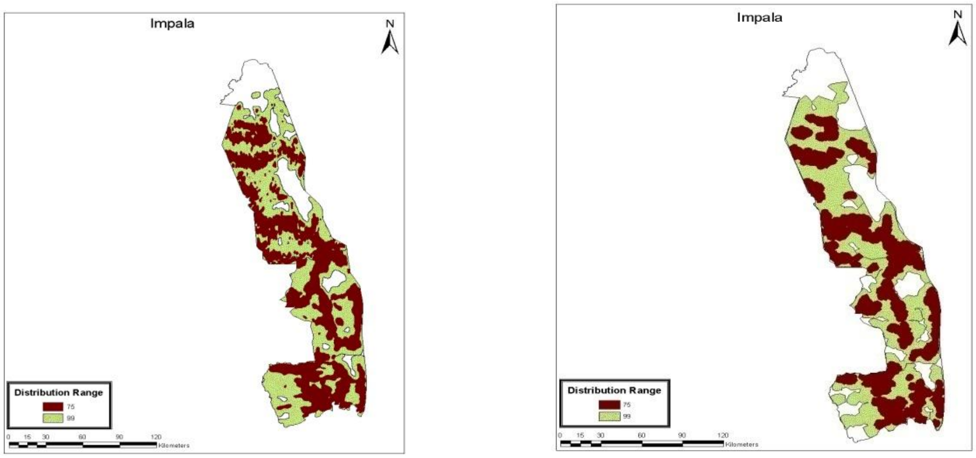
LoCoH methods following Getz *et al.* (2007) were implemented as an extension to Arc GIS (Ryan *et al*. 2006). These techniques estimated a distribution range by identifying a user-specified number of nearest points to each location in the data set that were either fixed at *k* (*k*-LoCoH) or constrained such that the sum of their distances to the root point was less than or equal to *a* (*a*-LoCoH). Then local hulls were constructed from each point and its selected neighbours, and the union of these hulls moving up from the smallest were used to construct the isopleths (Getz and Wilmers 2004, Getz *et al.* 2007). Individual isopleth levels can be calculated from 10% up to 100% depending on specific objectives of the range estimation. Each isopleth encompassed a determined proportion of the statistical distribution of locations—for example the 100 isopleth covered all the distribution, the 99 isopleth encompassed 99% the distribution and 75 isopleth covered 75%—using the principle that smaller hulls represent the more heavily used regions. Thus, isopleths provided information on the location of core areas (75%) and marginal areas (99%) across the range. We used both *k*-LoCoH and *a*-LoCoH algorithms to estimate distribution ranges in our analysis.

Selection of *k* and *a* is non trivial: values that are too large include gaps where the species were not recorded and take in outliers points, but conversely small values exclude intervening localities that are part of the range (i.e. too conservative). In the case of *k*-LoCoH, the minimum number of points required for constructing a hull is 3 while the largest is the sample size itself. In that case *k*-LoCoH yields the MCP such that the technique is also a generalization of the MCP approach to estimate the animal's home range (Getz and Wilmers 2004). For *a*-LoCoH the maximum value for *k* is 3 and *a* is the cumulative point to point distance from each point to its nearest neighbour.

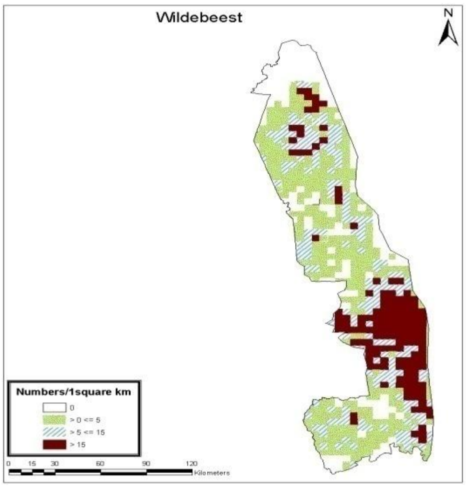
We plotted distribution range area estimates against *k* for each species for several values of *k* upwards, searching for the value of *k* where the positive relationship for range area with *k* begins to flatten out until reaching a constant (i.e. point of inflection). Prior to this point range area increased with corresponding increases in k, and after this point, increases of k do not lead to corresponding increases of range area. That k value referred to by Getz and Wilmers (2004) as the MSHC (minimum spurious hole covering) was adopted for each species. This same method was used to identify the MSHC value of a. Additionally, knowledge of gaps in the species distributions because of picnic sites, rest camps, and park residence locations was helpful and used to improve judgements on choice of h and on whether the distribution ranges created looked appropriate.

APPENDIX II: Additional methods figures (chapter 2)

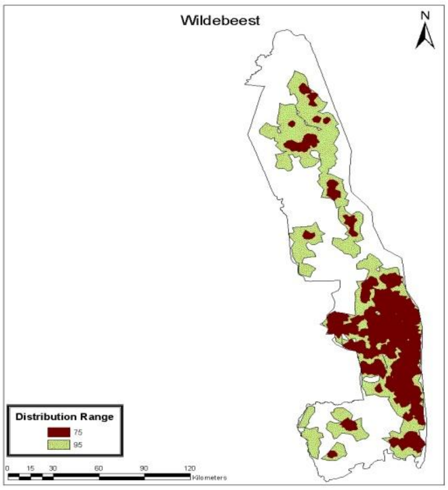
1. a. Adaptive kernel *h* = 0.0222 b. Adaptive LoCoH *a* = 150000, *k* = 3



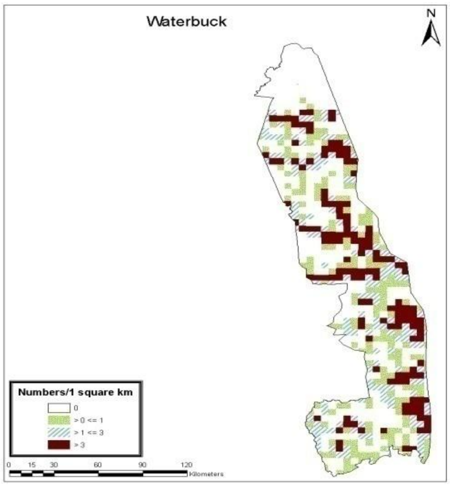
2 a. Tile 5 × 5



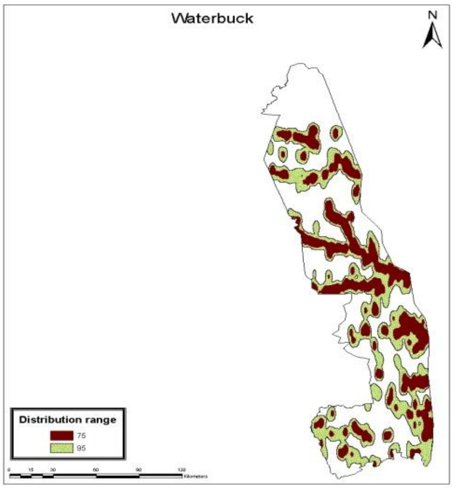
b. Fixed LoCoH *k* = 24



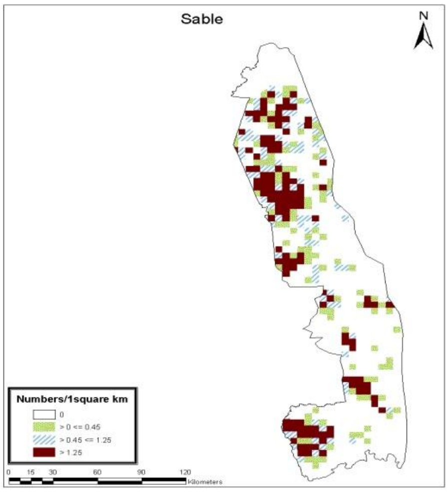
3. a Tile 5 × 5



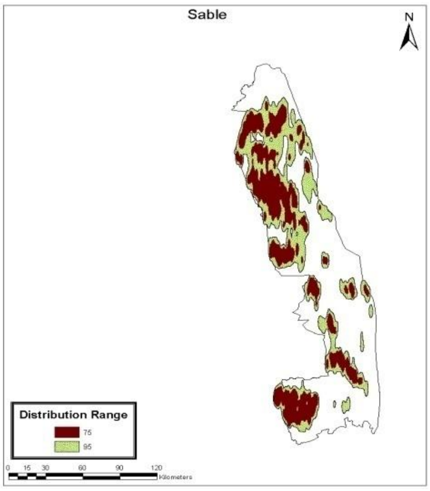
b Adaptive kernel *h* = 0.0244



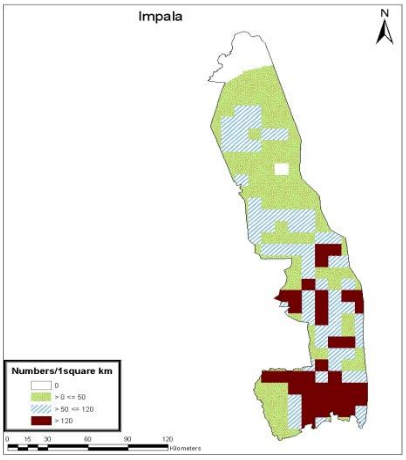
4. a. Tile 5 × 5



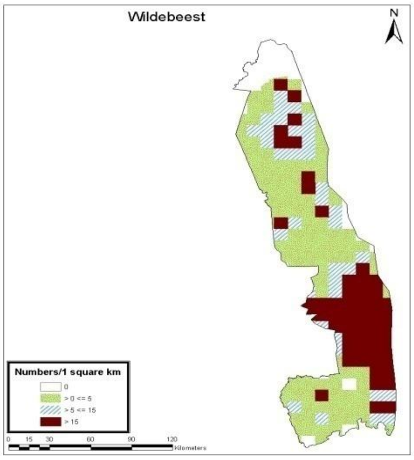
b. Adaptive kernel h = 0.0279



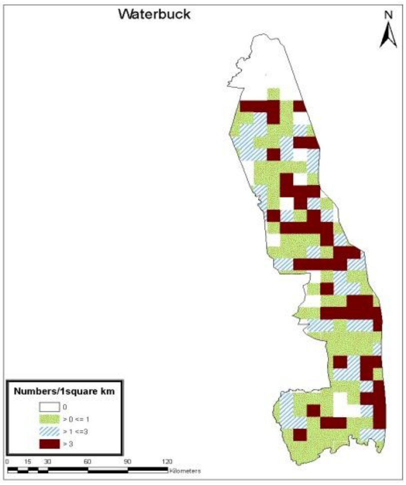
5 a. Impala Tile 10 × 10



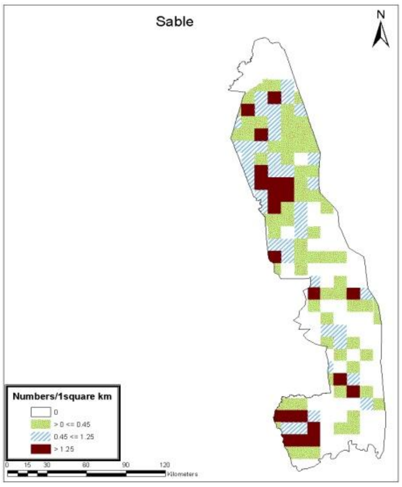
b. Wildebeest Tile 10 × 10



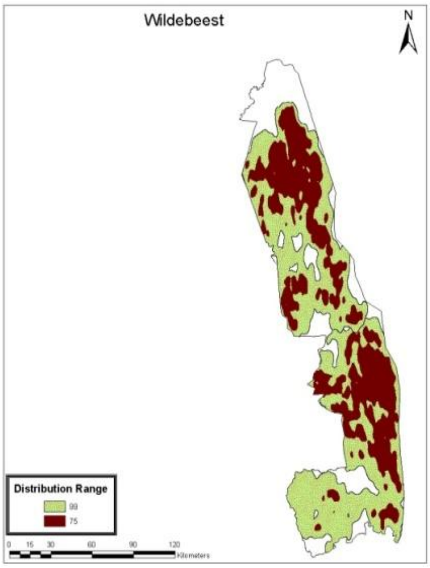
c. Waterbuck Tile 10 × 10



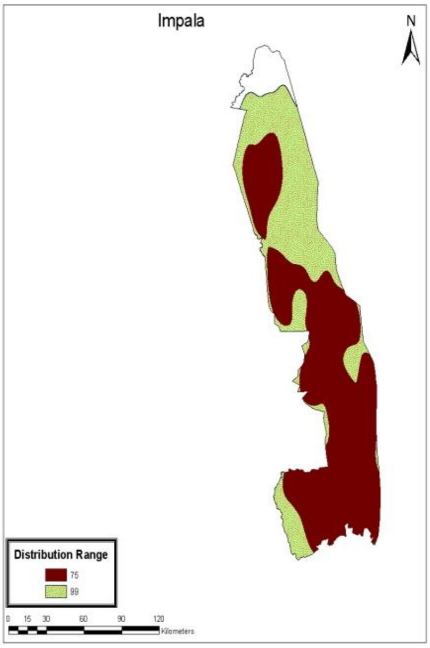
d. Sable Tile 10 × 10



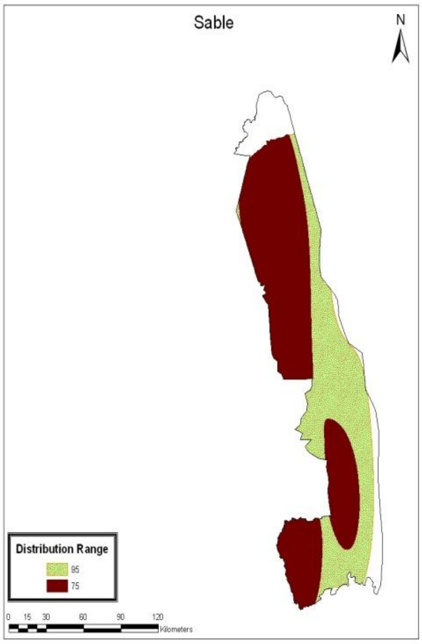
6. a Automatic choices of *h* with wildebeest



6 b. h ref, impala, *h* = 0.145058



c) h ref, sable, *h* = 0.260745



APPENDIX III Summary of landscapes and land types of Kruger (after Gertenbach 1983 and Venter 1990)

Landscape	Land type	Geology
Mixed mopane/teak/bushwillow woodland	Mopane/ teak/ bushwillow (tree/bush savanna)	sandstone
Mopane shrubveld	Mopane shrub savanna	basalt
Mountain bushveld	Mountain bushveld (eurphobia/bushwillow)	rhyolite
Sand camwood-silver cluster-leaf shrubveld or bush savanna	Sand camwood-silver cluster-leaf shrubveld or bush savanna	aeolian sands
Mopane-knob thorn savanna woodland	Mopane-knob thorn savanna	granite
	Mopane-bushwillow	granite
	Mopane-silver cluster-leaf woodland	granite
Thorn veld	Thorn veld	gabbro
Sourveld (silver cluster leaf/sickle bush)	Sour bushveld	granite
Delagoa thorn thickets	Delagoa thorn thickets	Karroo sediments & ecca shales
Marula - knob thorn	Marula-knob thorn savanna	basalt
Mountain bushveld	Mountain bushveld (bushwillow-silver cluster-leaf)	granite
Mixed bushwillow-silver cluster-leaf woodland	Mixed bushwillow /silver cluster- leaf savanna	granite
Mixed mopane - bushwillow woodland		
Thickets of the Sabi and Crocodile Rivers	Mixed dense bush savanna bushwillow/silver cluster-leaf/ knob thorn/ sickle	granite

Notes; common names of plant species following Gertenbach (1983) and Venter (1999)

APPENDIX IV Prey species for lion, body mass and weighting factor (kill likelihood) used to calculate the predation index

Species	Body mass	Weighting factor
Wildebeest	208	1
Warthog	83	0.8
Waterbuck	210	0.8
Kudu	214	0.7
Zebra	270	0.6
Giraffe	1013	0.5
Eland	463	0.5
Sable antelope	230	0.5
Tsessebe	134	0.5
Roan antelope	270	0.5
Buffalo	600	0.25
Impala	52	0.2

Notes; Body mass of prey species following Owen-Smith (1998) are available as a range. body mass values- calculated as the (sum of male and female mid-points divided by two) average of two mid-points; i) males and ii) females, and weighting factor following Owen-Smith and Mills 2006, 2008)