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Simulating Range Shifts of African Mammals under Predicted Climate Change: Potential Conservation and Economic Consequences

Georgina Palmer B.Sc. (Hons)

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Institute of Ecosystem Science,

School of Biological and Biomedical Sciences,

Durham University

2008

This thesis is submitted in candidature for the degree of

Master of Science

1 8 DEC 2008

Declaration

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Abstract

Simulated present-day ranges of 281 African mammal species were produced using climate-envelope models. This modeling approach was robust and was therefore used to simulate potential future ranges of 281 African mammals in response to nine future climate change scenarios (three general circulation models for 2020, 2050 and 2080). The size of species' ranges were projected to decrease only slightly (-4.41%) on average by 2080. Species' future ranges were projected to overlap current ranges by only 75.7% on average by 2080.

The effectiveness of the African protected area (PA) network under projected future climate change was then assessed by intersecting simulated ranges with PA outlines at the quarter degree scale. By 2080, the mean decrease in species richness was projected to be 7.18% under a best-case scenario of range shift, which is greater that that projected for areas of Africa beyond PAs (-4.41%). By 2080, mean species persistence and turnover within PAs were projected to be, on average, 79% and 26% respectively. Species turnover will be unevenly spread across the PA network; PAs in South Africa and Namibia will be affected most by climate change.

Simulations indicated the loss of keystone and charismatic species from a number of PAs, including Kruger National Park (KNP). The value of two keystone species in KNP was assessed using the contingent valuation method. Significant factors influencing willingness-to-pay included respondents' age, employment status and experience of visiting the PA. Aggregated willingness-to-pay values were R87.3million (± R17.4million) per year for ensemble species conservation, R41.1million (± R17.8million) for giraffe (*Giraffa camelopardalis*) and R42.4million (± R14.3million) for elephant (*Loxodonta africana*) conservation.

Until greenhouse gas emissions are stabilised (or reduced), it is inevitable that further climate change, and therefore further alterations of species distributions will occur. Efforts such as increasing the extent and connectedness of the PA network may help to protect species threatened by projected climate change by allowing them the opportunity of tracking climate change.

Acknowledgements

This thesis is written and analysed wholly by myself, (unless referenced) however the production of this work could not have happened without the support of a number of people. Special thanks must go especially to Dr Stephen Willis, my primary supervisor, whose support has been invaluable throughout the past year, and also to my co-supervisors, Prof Brian Huntley and Prof Nicholas Hanley. Many thanks also to my colleagues in the Institute of Ecosystem Science; Andy, Andy, Jemma, Jon, Judy, Nat, and Rachael as well as Yvonne and Dave for all of their technical support – plus endless offers of coffee.

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PART ONE: MODELLING CURRENT AND FUTURE DISTRIBUTIONS OF AFRICAN MAMMALS

CHAPTER ONE: INTRODUCTION

1.1.1. Climate Change

1.1.1.1. Past and Current Changes

The Earth's climate is highly variable, both temporally and spatially (Mann *et al.*, 1995). However, there is strong evidence that during the past century climate change is occurring at an unprecedented rate and magnitude (IPCC, 2007a). For example, eleven of the twelve past years (1995 – 2006) were the warmest on record, 1998 being the warmest yet with a record of 0.52°C above the 1961-1990 average temperature of 14°C (IPCC, 2001; 2007a; Figure 1.1). However, temperatures are still rising; the UK's Met Office recorded temperatures of a record-beating 0.54°C above average in 2006, and has predicted that average surface temperatures in 2007 will exceed this record yet again (Met Office, 2007).

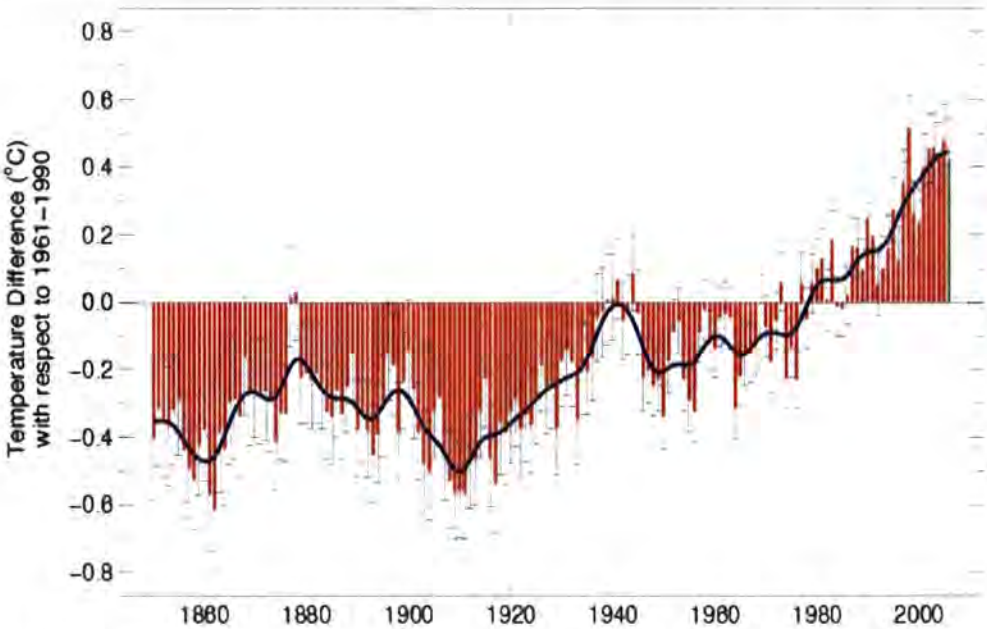


Figure 1.1. Variations in the Earth's surface temperature (Met Office, 2007). Temperature difference (°C) from the average global mean temperature (1961 – 1900) from 1850. Red bars represent the global temperature value for each year. The blue line is the 10-year running average and the green bar is the provisional 2006 value.

Global temperatures over the past 50 years have risen at a rate (0.13°C [0.10°C to 0.16°C] per decade) nearly double that of the last hundred years (IPCC, 2007a). Furthermore, the

IPCC (Intergovernmental Panel on Climate Change) Fourth Assessment Report recorded an average global temperature rise of 0.74°C (0.56 – 0.92°C) between 1906 and 2005; larger than the trend described in the IPCC Third Assessment Report which reported a rise of 0.6°C (0.4 – 0.8°C) between 1901 and 2000 (IPCC, 2001; 2007a). During the same period, the extent of rainfall has decreased in the tropics while increasing in the mid-latitudes, plus there have also been an increase in the number of extreme weather events, such as hurricanes (Landsea & Gray, 1992) and droughts (Dai *et al.,* 1998). Sea levels have risen 3.1 (2.4 – 3.8) mm per year between 1993 and 2003. This is considerably more than the average 1.8 (1.3 – 2.3) mm per year rise observed between 1961 and 2003. There is now 'high confidence' that observed sea level rise has increased in the twentieth century at a rate higher than observed in the nineteenth century (IPCC, 2007a). Many of these changes have been attributed to human activities (IPCC, 2007a) specifically via an increase in greenhouse gas emissions. The level of gases (such as carbon dioxide, methane and nitrous oxide) in the atmosphere has been increasing year-on-year since the 1950's: from 315ppm carbon dioxide in 1950 to 379ppm in 2005 (Solomon *et al.,* 2007). The IPCC have projected the levels of carbon dioxide in the atmosphere to increase to between 650 and 970ppm by 2100 (IPCC, 2001). This is especially worrying as such accumulations of gases, as well as an increasing concentration of aerosol particles, have detectable effects on the global climate system (Lovett *et al.,* 2000; Houghton *et al.,* 2001).

As with the rest of the world, the climate of the African continent is naturally variable, and recent trends on this continent have been similar to those recorded globally. For example the most rapid periods of warming on record are similar, with the 1910's to 1930's and the post 1970's being the warmest on record (Hulme *et al.,* 2001). In addition, during the last century the African continent has experienced warming of an average of 0.5°C (close to the mean global temperature rise) (Hulme *et al.,* 2001) and a general decrease in rainfall (Viner & Agnew, 1999) as well as a series of serious droughts. The IPCC Fourth Assessment Report has recorded decadal rates of warming for South Africa of between 0.1 and 0.3°C as well as decadal warming of 0.29°C in the tropics. Conversely, in Eastern Africa decreases in air temperatures in locations close to the ocean and inland lakes have been noted (Boko *et al.,* 2007). There has also been an increase in the number of warm

spells and a decrease in extremely cold days in Western and Southern Africa between 1961 and 2000 (New *et al.,* 2006). Recent precipitation trends are more complicated to observe due to spatial and temporal (e.g. interannual, decadal, multi-decadal) variability. Even so, recent reports have suggested that since the 1960's precipitation has decreased in Western Africa by between 20 and 40% whereas the Guinean coast has experienced a 10% increase in precipitation in the past 30 years. In South Africa, no precipitation trend has been noted (Boko *et al.,* 2007), yet in adjacent regions of southern Africa (e.g. Namibia, Mozamique and Zambia) large increases in heavy precipitation events have been recorded (Usman & Reason, 2004).

1.1.1.2. Potential Future Changes

General circulation model (GCM) simulations have been used to simulate potential future patterns of precipitation and temperature change globally (e.g. IPCC, 2001; 2007a). Examples of GCMs include ECHAM4/OPYC3 (Roeckner *et al.,* 1996; ECHAM4), GFDL_R30_c (Knutson *et al.,* 1999; GFDL) and HadCM3 (Gordon *et al.,* 2000), which are to be used in this study, each projecting different temperature and precipitation changes by the year 2100. GCMs such as these are used alongside the IPCC emissions scenarios (Nakićenović *et al.,* 2000) in order to predict future changes in climate. The four emission scenarios approved by the IPCC are given in Table 1.1; these storylines encompass forty different future emission scenarios with differing resource, technology, social development and demographic assumptions (Nakićenović *et al.,* 2000) thereby covering many different potential futures.

Table 1.1. IPCC Emission Scenarios (SRES; Nakićenović *et al.,* 2000).

Emission Scenario	
A1	Rapid economic growth and population growth that peaks mid-century then falls, plus the development of new technologies. This family incorporates three groups with differing technological emphases; fossil intensive (A1FI), non-fossil energy sources (A1T), or a balance across all sources (A1B).
A2	Continuously growing global population with regionally oriented economic and technological growth which is slower and more fragmented than other scenarios.
B1	As with the A1 family, global population will peak mid-century with a fall thereafter, but technological advances will be resource-efficient and clean while material technologies decline.
B2	Focuses on regional emphasis on economic, environmental and social sustainability. Population growth continues (but less than the A2 scenario) with less rapid technological change.

The Fourth Assessment Report of the IPCC projected decadal warming of 0.2°C for the next two decades and a best estimate of warming of between 1.1°C (lowest scenario) and 6.4°C (highest scenario) by the end of the century (IPCC, 2007a). These estimates are fairly consistent with those reported in the Third Assessment Report which projected an increase in global temperatures of between 1.4 and 5.8°C by the end of this century (IPCC, 2001). In addition to temperature rise, the IPCC has also predicted an increase in precipitation in equatorial areas and a decrease in the subtropics (Gitay *et al.,* 2002; IPCC, 2007a), plus a best estimate of sea level rise of between 0.2 and 0.43m at 2090 – 2099 compared to 1980 – 1999 under an intermediate emission scenario (IPCC, 2007a).

Tadross *et al.* (2005) have shown that projected changes in average temperatures (or rainfall) do not always mirror seasonal changes. Across the African continent, a general increase in the intensity of high-rainfall events is projected. In areas where models have predicted a mean drying effect, they have also predicted a larger decrease in the number of rain days (in proportion to the rest of the continent). All seasons are projected to be extremely warm by the end of the century; there will also be an increase in the number of extremely wet seasons (Christensen *et al.* 2007*)*. Results published by the IPCC (Christensen *et al.,* 2007) project that by 2100, one-in-five seasons will be extremely wet, as compared to one-in-twenty in the late twentieth century. In southern Africa, the frequency of extremely wet (austral) summers is projected to double while the number of extremely dry winters and springs will increase to one-in-five.

Future climate change scenarios generated by the IPCC suggest that the African continent is one of the most vulnerable to climate variability as well as climate change (Boko *et al.,* 2007). The IPCC have reported a predicted increase in temperature for the period 2080 - 2099 of approximately 3 – 4°C in comparison to the 1980 – 1999 period; this is approximately 1.5 times the global mean response (Boko *et al.,* 2007). In addition to this, coastal regions of the continent are projected to warm more slowly than interior areas of Africa due to the rise of sea surface temperatures (SST) of oceans surrounding Africa at levels less than the global mean (Christensen *et al.,* 2007). Ruosteenoja *et al.,* (2003), have predicted even larger increases in temperature in certain geographic areas; for example an

increase of up to 7°C in southern Africa between September and November and an increase of up to 9°C in North Africa between June and August (Figure 1.2). Bounoua *et al.,* (2000) have suggested an increase in vegetation density in response to climate warming may in fact have a cooling effect of up to 0.8°C per year which may compensate for some of the warming suggested by Ruosteenoja *et al.,* (2003). However, a simultaneous increase in habitat conversion is also expected to occur (DeFries *et al.,* 2002) which will in turn temper the increase in vegetation density in some areas (Boko *et al.,* 2007). Temperature increases are expected to lead to an increase in water evaporation (be it open water or from plants/soil) of between 5 and 10% by 2050 (IPCC, 1997). This is expected to have knock-on effects on mammals as the availability of plant matter for food and for habitats will undoubtedly change.

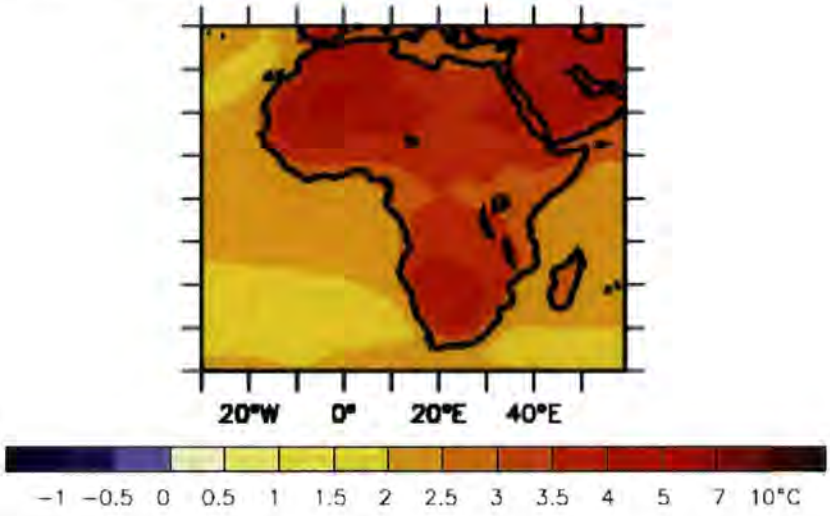


Figure 1.2. Mean potential annual surface air temperature change in Africa (averaged across 21 model projections). Temperature change (°C) is from the years 1980 – 1999 to 2080 – 99 under the A1B SRES scenario (Christensen *et al.,* 2007).

The most prominent change will be that of the precipitation regime, however reports of precipitation changes are often less consistent than those of temperature change due to large differences between models (Boko *et al.,* 2007); average precipitation changes across 21 model projections are given in Figure 1.3. In general, Africa is expected to experience an increase in precipitation (Hulme *et al.,* 2001). The IPCC Third Assessment Report expected Northern, Southern and parts of West Africa to experience decreases in annual precipitation of up to 10% by 2050 (IPCC, 2001) while equatorial areas are

expected to experience increases in annual precipitation (up to 15% by 2050). The latter overall increase masks more extreme seasonal decreases (June to August) and increases (December to February) (Desanker *et al.,* 2001). The more recent Fourth Assessment Report is fairly similar; for example, equatorial areas are expected to experience increases in summer (December to February) precipitation as well as East Africa which is predicted to experience 7% increase in precipitation. However, areas of southern Africa and southern equatorial regions are expected to experience decreases in precipitation. This decrease will be especially intense along the Mediterranean coast and in (Western) South Africa during the austral winter (June and August), with predicted decreases in rainfall of 20% and 30% respectively (Boko *et al.,* 2007). Therefore, even though the amount of precipitation is expected to increase, seasonal extremes in the austral summer and winter will be more pronounced. This will have dramatic effects upon mammals, both indirectly via changes in e.g. plants growing seasons and ranges, and directly via e.g. physiological tolerances of species to drought and/or heat stress. Decreases in annual precipitation (as well as increases in temperature) are likely to have knock-on impacts on plant growth via the reduction in available soil moisture during the growing seasons (IPCC, 2001b). Changes in land-cover patterns (both human- and climate-induced) will also have significant effects on regional climates within Africa. Changes are expected to cause the decreases in precipitation and soil moisture as well as increases in air temperature (Xue, 1997). The possible consequences of such changes in Africa may cause serious problems for the conservation of biodiversity (Skov & Svenning, 2004), especially if these changes render current protected areas unsuitable for maintaining biological diversity. Potential changes in climate are expected to induce species-level changes such as changes in the geographical arrangement (Root *et al.,* 2003), phenology, physiology, and growth of species (Cannel, 1998). In order to understand the possible consequences of climate changes upon mammals further, one must observe how species respond to climatic changes.

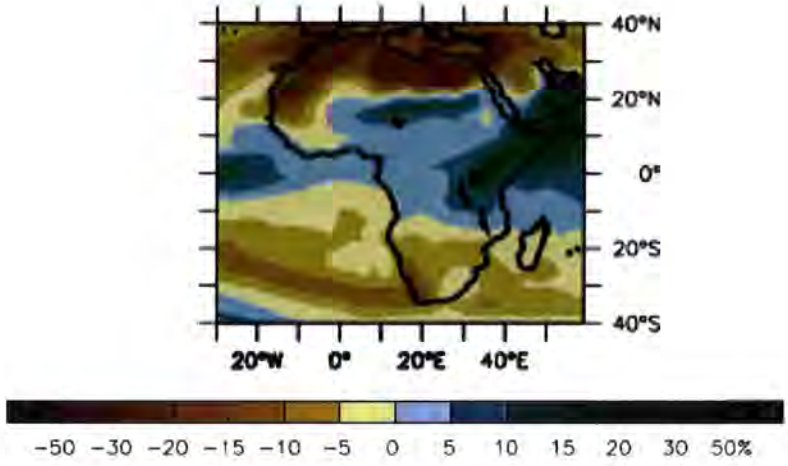


Figure 1.3. Mean potential annual precipitation response in Africa (averaged across 21 model projections). Percentage precipitation change is from the years 1980 – 1999 to 2080 – 99 under the A1B SRES scenario (Christensen *et al.*, 2007).

1.1.2. Species' Responses to Climate Change

Species' distributions and abundances are strongly influenced by climate (Walther *et al.*, 2002). Climate can affect species either directly, by affecting the physiology of organisms (Stenseth *et al.*, 2002) which in turn may e.g. influence the development and fecundity of the species (Post *et al.*, 1997) or indirectly by affecting aspects of the ecosystem which the species inhabits, e.g. by affecting the availability of food resources on which the species depend (Stenseth *et al.*, 2002; Thomas *et al.*, 2004).

Extreme climate events (such as drought and periods of cold weather) also have an effect on species (Stenseth *et al.*, 2002). Studies on red deer (*Cervus elaphus*) in Norway have found that sexual dimorphism has become more pronounced over the past 40 years due to climate variation influenced by the Northern Atlantic Oscillation (NAO) (Easterling *et al.*, 2000; Post *et al.*, 1997). Extreme weather events can also have effects on juvenile survival (Forchhammer *et al.*, 2001) and breeding systems in mammals (Simmonds & Isaac, 2007).

Gradual changes in climate as well as increases in extreme events can therefore impose direct and indirect effects on species. Gradual changes may affect species' morphology, behaviour, abundances and distributions as well as the timing of key events such as

breeding and migration (Easterling *et al.*, 2000). Changes in climate that affect life history responses (such as developmental rates, adult survival and parental care behaviours) could have community-wide effects years later when species reach sexual maturity (Forchhammer *et al.*, 2001). For example, map turtles (*Graptemys* spp) exposed to temperatures above 30°C during incubation produce only females whereas those exposed to temperatures below 28°C produce only males (Bull & Vogt, 1979). As climate changes it is likely that the sex ratio of these turtles (and many other reptiles) will become highly skewed (Parmesan *et al.*, 2000) potentially causing problems when these cohorts reach maturity.

Species are able to respond to changes in climate in three major ways; adapting to the change, exhibiting a spatial response or, if both of these responses fail, the species will be committed to extinction (Huntley *et al.*, 2006). Extinction may occur if the species becomes isolated (either temporally or spatially) from the climatic conditions it is adapted to (Huntley *et al.*, 2006). This situation is thought to have occurred with the Woolly Mammoth (*Mammuthus primigenius*) at the end of the ice age when conditions became drier and seasonal weather became more extreme (Oard, 2000). It is thought that climate change has already been held responsible for the extinction of one species, the golden toad (*Bufo periglenes*) (Pounds *et al.*, 1999) and may cause the extinction of a number of species in the near future.

Species may exhibit a spatial response i.e. they may alter their distribution so they continue to occupy areas of habitat with climate to which they are adapted. However, migration will not be instantaneous or unlimited (Midgley *et al.*, 2006); rapid changes in local conditions may outpace some species' dispersal ability, which may ultimately reduce species' persistence. If climate changes at a rate faster than a species is able to disperse out of a climatically unsuitable area (and into climatically suitable one), then it may be driven to (local) extinction. Measures such as ensuring the presence of habitat corridors will help to promote survival while species disperse. However, where species are at their altitudinal, elevational or poleward extent, then a change in climate may render dispersal impossible. Today, spatial discontinuity can be rectified by translocating animals from climatically

unsuitable areas to climatically suitable ones. However, it is harder to rectify temporal discontinuity, whereby there is a period of time when the habitats they occupy are climatically unsuitable for the survival of the species. In this case, captive breeding is the only option to save these species until a time in the future when climatic conditions have altered once again to ones the species are adapted to (Huntley *et al.*, 2006).

The final possible response, adaptation, states that instead of a spatial response species stay in the same geographic location and instead adapt to the changes by altering either their phenology (e.g. timing of egg laying/breeding/hibernation) or genetics (e.g. increasing the number of individuals tolerant to temperature extremes) (IPCC, 2001). These mechanisms of species responses to climate change have been documented in recent scientific literature (see e.g. Walther *et al.*, 2002 for an overview). However, as Huntley *et al.*, (2006) discuss, the vast majority of species responses to climate change, from palaeoecological and recent evidence, have been spatial i.e. shifting distributions in order to inhabit habitat conditions to which the species is adapted.

Changes in species' phenology, physiology, morphology and behaviour in response to recent climate change have already been recorded (Walther *et al.*, 2002; Parmesan & Yohe, 2003). Such documentations in the scientific literature span major groups of plants (e.g. Pauli *et al.*, 2007) and animals (e.g. mammals (Reale *et al.*, 2003), birds (Hitch & Leberg, 2007) and amphibians (Beebee, 1995)), and across many different habitats, from the deserts of Africa to the aquatic habitats at the Earth's poles (Walther *et al.*, 2002).

Several studies provide evidence of species altering their distributions, mainly poleward and towards higher elevations (but see Hickling *et al.*, 2006), as well as changes in timing of phenological events (Burns *et al.*, 2003; Jiguet, 2007; Suttle *et al.*, 2007) in response to recent climate change; many of these changes were predicted by climate models over a decade ago (Easterling *et al.*, 2000).

Species' responses to recent climate change have been grouped into two categories; (i) changes in the phenology of organisms, (ii) changes in the ranges, distributions and abundances of organisms (Walther *et al.*, 2002).

i. Changes in the Phenology of Organisms

There is a large body of literature providing evidence of advances in phenology (the timing of seasonal activities such as breeding or migration) in response to recent climate change (van Asch *et al.*, 2007). Much of this literature focuses on the responses of insects, birds and plants partly due to the fact that there is a multitude of long-term datasets for these species (Walther *et al.*, 2002). Examples of phenological changes of birds include earlier breeding (e.g. Dunn & Winkler, 1999), laying dates (Crick *et al.*, 1997) and the earlier arrival at breeding grounds (e.g. Tryjanowski *et al.*, 2002; Jonzen *et al.*, 2006). Examples of phenological changes of other taxon include the advanced flowering date of plants (Fritter & Fritter, 2002), earlier appearance of butterflies (Roy & Sparks, 2000) and the earlier migration of marine mammals (Robinson *et al.*, 2005; Walther *et al.*, 2002). Such responses have been shown to be associated with temperatures the species are exposed to in preceding months (Walther *et al.*, 2002), with warmer temperatures in late winter initiating earlier spring events. There is much less evidence of phenological changes of species resident in the Southern hemisphere. One example is reported by Barbraud & Weimerskirch (2006) who found an inverse trend to that found in the Northern hemisphere; their results indicating that Antarctic seabirds are arriving and laying eggs later (c. 9.1 and c. 2.1 days respectively) than they were in the 1950's. There are also a small number of papers providing evidence for the later onset of autumnal events (such as hibernation; Walther *et al.*, 2002), although these changes are less prominent than the advancement of spring events.

Phenological changes of one organism may have consequences for other species in the food chain for example the distribution and migration patterns of the Bluefin tuna (*Thunnus thynnus*) are affected by changes in the abundance of prey as a result of climate change (Walther *et al.*, 2002). Some species may not be able to track changes in prey distribution, for example, van Asch *et al.*, (2007) found that over the past two decades

winter moth (*Operophtera brumata)* egg hatch date has become asynchronous with pedunculate oak (*Quercus robur)* bud burst which has subsequently lead to disrupted synchrony between these species.

ii. Changes in the Ranges, Distributions and Abundances of Organisms

There is copious evidence that species ranges and distributions have changed in response to changes in climate; it is the most reported response of species to climate change (Parmesan, 2001). The vast proportion of these studies report shifts in ranges mainly poleward and towards higher elevations (Beaumont *et al.*, 2007; Parmesan & Yohe, 2003; Root *et al.*, 2003). Examples of poleward shifts include the northward range expansion of the green skink bug (*Nezara viridula*) (Musolin, 2007), Edith's Checkerspot butterfly (*Euphydryas editha*) (Parmesan *et al.*, 2000), breeding birds in North America (Hitch & Leberg, 2007) as well as many species resident in Britain including birds, butterflies, spiders, dragonflies and fishes (see Hickling *et al.*, 2006). Additionally, Wilson *et al.*, (2005) have provided evidence for the retreat of butterflies from their southern margins in Spain towards cooler locations as a result of climate warming, thereby reducing their range sizes and increasing extinction risk. Examples of altitudinal shifts include those by butterflies in the Czech Republic (Konvicka *et al.*, 2003), alpine plants (Grabherr *et al.*, 1994) and amphibians in Cost Rica (Pounds *et al.*, 1999). However, Archaux (2004) found alpine birds were showing no altitudinal response to temperature increases in spring of 2.3 °C. For species exhibiting altitudinal or poleward shifts, there will come a point when they will not be able to move either further polewards (e.g. species endemic to the South African Cape) or upslope (due to limits of altitude). Species in these situations, especially those endemic to such areas, will be at risk of extinction as climate changes. Changes in species abundances in response to climate change have also been documented, for example the abundance of Emperor penguins (*Aptenodytes forsteri*) was halved as a result of the reduction of sea ice in response to abnormally warm weather in the 1970's (Barbraud & Weimerskirch, 2001).

1.2.1.1. Changes in Community and Ecosystem Composition.

Species are predicted to respond to changes in climate individualistically (Hannah & Salm, 2003). Consequently, community and ecosystem composition is expected to change when species move out of (or into) specific areas (Walther *et al.*, 2002) in response to climate change. This may affect certain species more dramatically that others, especially where one species depends on another for a specific resource (e.g. the winter moth - pedunculate oak system as described previously (section i)).

Changes in community composition may occur if a species 'invades' a new area of habitat as it becomes climatically suitable. For example, as the density of the collared flycatcher (*Ficedula albicollis*) in the Czech Republic decreased due to adverse effects of the NAO, the abundance of the pied flycatcher (*F. hypoleuca*), which is a weak competitor and unaffected by the NAO, increased (Stenseth *et al.*, 2002).

Extreme weather events also have the capacity to alter community composition, for example the 1982-1983 El Niño caused widespread disruption of coral communities (Coffroth *et al.*, 1990) due to an increase in sea temperatures. Since then, the intensity and frequency of mass coral bleaching has increased, with a peak in 1998 when c.16% of the world's corals died (Wilkinson, 2000). Another example is the severe droughts of the late 1980's in the United States of America which caused population crashes of many insects which had impacts throughout the food chain (Hawkins & Holyoak, 1998). As community composition is expected to change as species' respond to climate change, so is ecosystem composition. For example, using the example of coral bleaching, the effect of mass disruption of coral communities is likely to substantially alter species richness throughout this delicate ecosystem (Walther *et al.*, 2002).

1.1.2.2. Responses of Terrestrial Mammals to Climate Change

Ecothermic organisms such as insects, reptiles and amphibians can to a large extent maintain their body temperature by environmental means e.g. the sun, air or water. During extreme weather conditions they can move to more equitable microclimates, but they are still largely dependent on ambient conditions. This means that these species are

particularly sensitive to environmental temperature change. However, changes in environmental temperatures also have the potential to affect endothermic organisms (such as mammals) by affecting their physiological processes such as homeostasis, reproduction and growth, and can in extreme kill individuals due to heat and water stress. Porter *et al.* (2000) found that increases in environmental temperature affect the foraging behaviour of mammals, which in turn means a reduction in their food intake and ultimately their mass. Post *et al.* (1997) showed that warmer air temperatures have been associated with lower body size and condition of ungulate species in Europe (in Dunn & Winkler, 1999). Similarly, Huynh *et al.* (2005) showed that for pigs ambient temperature strongly affects physiological changes such as food intake, heat loss, and respiration rate. Rising temperatures may also affect embryonic development of mammals; Thwaites (1985) has shown that unacclimatised ewes experienced high levels (up to 100%) of embryo mortality due to increases in the female's core temperature. This may subsequently have affects upon the fitness of whole populations of mammals. Endotherms most vulnerable to changes in environmental temperatures are those with low rates of reproduction, as they are less able to increase their rates of reproduction in response to temperature-related mortality (McNab, 2006). Most of these species are characterised by a low basal rate of metabolism and large body mass.

Changes in precipitation may also affect freshwater species (e.g. the hippopotamus, *Hippopotamus amphibius*) which rely on freshwater rivers and lakes to remain cool, as well as for birthing and reproduction (Thuiller *et al.*, 2006). Changes in fire regimes mediated by climate change may also have effects on mammal species, by altering dominant vegetation species on which the mammals depend (Thuiller *et al.*, 2006).

Climate change may also have indirect effects on mammal species, by altering the abundance of competitors and predators. For example, Humphries *et al.*, (2004) have predicted that the abundance and distribution of seasonally inactive larger mammal species (e.g. badgers, racoons and skunks) will increase in the Canadian arctic as summers lengthen and winters shorten in response to climate change. This is because seasonal species such as these are expected to expand their ranges northwards into areas where they

are currently absent. This is likely to have negative impacts on mammal species such as wolves, foxes and weasels which are found continuously (i.e. not seasonally) in the Canadian arctic at present.

i. Responses of Mammals to Recent Climatic Changes

Studies reporting phenological changes of mammals in response to recent climate change include those by Inouye *et al.* (2000) who have found that yellow-bellied marmots are emerging significantly earlier (23 days) than they were in 1976 in apparent response to warmer spring air temperatures, and Reale *et al.,* (2003) who observed an 18 day average advancement of breeding of the red squirrel (*Sciurus vulgaris*) in Canada. Changes in species' abundances and ranges have also been documented; for example, studies of the red fox (*Vulpes vulpes)* and the Arctic fox (*Alopex lagopus*) have reported the expansion the red fox range northwards which in turn is limiting the southern extent of the arctic fox range (Hersteinsson & MacDonald, 1992) in Canada. Extreme climate events have also been associated with changes in the physical and reproductive development of red deer (*Cervus elaphus*) and Soay sheep (*Ovis aries*) in Norway and the UK respectively (Post *et al.,* 1997; Coulson *et al.,* 2001). Twiss *et al.,* (2007) have also found that local climatic variation affects the proportion of male grey seals (*Halichoerus grypus*) contributing to the effective population size.

ii. Responses of Mammals to Climatic Changes in the Past

The Pleistocene Epoch is an important and widely documented period in prehistory with reference to large mammal populations. By the end of this era, a vast proportion (nearly two thirds) of the world's large mammal genera (megafauna; animals >44 kg) had become extinct (Owen-Smith, 1989; Barnosky *et al.,* 2004), including species of horses, cats, wolves, camels, sloths and lions (Barnosky *et al.,* 2004). A large proportion of these extinctions occurred in Australia, Northern Eurasia, South America and North America (Owen-Smith, 1989; Wroe *et al,* 2006); these areas lost 88%, 36%, 83% and 72% of their megafauna respectively. Although less substantial when compared to extinctions on these continents, Africa still experienced extinction of 18% of its megafaunal species (Barnosky *et al,* 2004). A large number of these animals were herbivores, which lead indirectly to the

disappearance of many mammalian carnivores which were dependent on those herbivores as prey.

Three hypotheses have been put forward to try and explain the reasons for the megafaunal extinctions at the end of the Pleistocene Epoch; these are

1) human settlement and consequent predation on the megafaunal species,
2) severe and sudden climate change, and
3) the spread of human-associated disease.

The first of these hypotheses is widely cited as a reason for megafaunal extinctions and has much support specifically in the cases of extinctions in Australia and the Americas; it is hypothesised that a large proportion of the extinctions in Australia and the Americas were primarily caused by the effect of the 'invasive' human population on species not adapted to such interference (Owen-Smith, 1989; Wroe *et al*, 2006). However, the 'human settlement' theory cannot fully explain the Pleistocene extinctions. For example, in some places (e.g. North America) megafaunal species started to decline before humans settled there and there is also a lack of evidence in the archaeological record. Barnosky *et al*, (2004) conclude that the effect of human settlement on mammal extinctions in Africa was minimal. This is because humans were not an immigrant species as in Australia and the Americas; therefore humans and mammals had coevolved on the African continent.

The most recent explanation, that the spread of human-associated diseases (MacPhee & Marx, 1997) caused the extinction of the megafauna has yet to gain enough evidence for credibility. Consequently, the second theory, that climate change (specifically increases in temperature) drove many species to extinction, holds the most credibility. Support for this theory comes from the finding that extinctions of large mammals in mainland Alaska occurred as a result of climate change and not the input of significant human intervention (Guthrie, 2003; Barnosky *et al.*, 2004). Changes in climate are thought to have caused extinctions by a number of mechanisms such as changing the composition of plant and animal communities as well as altering predator-prey dynamics. However, as no single theory successfully and conclusively explains the late Pleistocene extinctions one must

conclude that interplay between climate and human- associated behaviour drove these extinctions (Barnosky *et al.*, 2004). So while humans are thought to have initiated the extinctions, climate change was expected to play a central role in determining the extent, timing and distribution of these extinctions (Murray-Clay, 2006). Unfortunately, these drivers are still occurring today but with one new facet, huge human population growth is forcing the transformation of large mammal habitats into human settlements. This means that in some areas it will become increasingly difficult for the already impoverished large mammal populations to alter their distributions in response to recent rapid climate change. One must also consider the effect of changes in the abundance and distribution of the large mammal fauna on smaller mammals as well as the wider community and ecosystems they inhabit. As Thomas *et al.*, (2004) discuss, "the responsiveness of species to recent and past climate change raises the possibility that anthropogenic climate change could act as a major cause of extinctions in the near future." It is therefore crucial to evaluate how species will respond to potential future climate changes so that we can work towards conserving these species in the future (Musolin, 2007), especially as warming of 0.2° C per year for the past three decades means the Earth is now the hottest it has been since the end of the Pleistocene era approximately 12,000 years ago (Hansen *et al.* 2006). As the vast majority of responses of species to climate change are expected to be spatial (Huntley *et al.*, 2006), plus the fact that species are expected to respond to changes in climate individualistically (Hannah & Salm, 2003), predictive models anticipating species spatial responses are certain to play an important role (Berteaux *et al.*, 2006) in biodiversity conservation, especially in the short term.

1.1.3. Species Distribution Modelling

The importance of the relationship between climate and species' distributions was realised and recorded in the scientific literature over two centuries ago (e.g. Humpbold & Bonpland, 1807). Consequently, the modelling of this species-environment relationship is widely used in ecology and is based on the assumption that environmental variables (including climate) significantly influence the distribution of many species (Lischke *et al.*, 1998). Today, such modelling approaches are used for a variety of applications, for example the setting of conservation priorities (Margules & Austin, 1994) and for assessing the selection of (e.g. Hannah *et al.*, 2007) and efficiency of (e.g. Abellan *et al.*, 2007) protected areas for maintaining biodiversity.

In order to be able to model species' potential future distributions well, we need to be able to produce accurate models relating current species' distributions to climate, and to have good simulation of future climate to which the resultant models can be applied. Reliable current climate (Chapter 1.1.1.2) and current species-distribution data need to be used, as well as making the assumption that species distributions are at equilibrium with the environment (Lischke *et al.*, 1998). Species' distribution data can be obtained from a number of sources including museum collections, expert opinion, atlases and/or via direct observations in the field. With the exception of direct observations which provide presence/absence data, these methods provide details of species' presences only. A major drawback of using presence/absence data is the difficulty in conclusively recording true absences of a species in any given area, as false negatives can decrease the reliability of models (Loiselle *et al.*, 2003). This is made more difficult when little is known about a given species, or for terrestrial species which are nocturnal, highly mobile, secretive or rare. Even so, if the presence/absence data is reliable, it is preferable (over presence-only data) when predicting species' future distributions (Brotons *et al.*, 2004). Another problem in predictive modelling is the amount of species data available. Data is often patchy (temporally and spatially) and sometimes biased, it is therefore necessary to choose the most appropriate modelling technique for the species data available.

There are a number of modelling techniques available to explore relationships between species distributions and climate (Guisan & Zimmermann, 2000); however there is still

little guidance as to which technique is best (but see Elith *et al.*, 2006). Examples of modelling techniques include locally weighted approaches such as generalised linear and generalised additive models (GLM and GAM respectively), Gower-similarity models, ecological niche factor analysis (ENFA), artificial neural networks (ANN), classification and regression trees (Brotons *et al.*, 2004; Segurado & Araujo, 2004) and maximum entropy models e.g. maxent (Phillips *et al.*, 2006). A criticism of all of these methods is that they do not incorporate the possibility that as species distributions change, species interactions may change too (Tokumine, 2002). However as long as this is considered when using these methods, they still provide useful simulations of how species distributions may change as climate changes. Which technique is best to use depends on the type of species' distribution data available plus the aims and scale of the study in question.

Methods such as ENFA and Gower-similarity models were developed for cases where presence/absence data were not available and therefore use presence-only data whereas methods such as GLM, GAM and ANN use presence/absence species data (Brotons *et al.*, 2004). It is widely believed that the latter techniques (those using presence/absence data) are more robust than those using presence-only data. For example, Brotons *et al.*, (2004) found that GLM predictions were more accurate than when using ENFA, particularly in cases where absence data was reliable (i.e. true negatives). However, those species with restricted ranges were modelled better than those with less restricted ranges independent of the modelling method used. Furthermore, species with large ranges were modelled better using presence/absence methods than presence-only methods as these species were increasingly responsive to absence data (Brotons *et al.*, 2004). Therefore in most cases it is best to use presence/absence data where available.

Niche-based modelling has been adopted in this study. The climate response surfaces (CRS) for each species are fitted, using locally weighted regression, to a selection of environmental variables (or raw climate data) by producing a set of probabilities of occurrence defining the distribution and abundance of a species (Bartlein *et al.* 1986). Niche theory assumes symmetric Gaussian-shaped unimodal species response curves, which represent the probability of species' presence along an ecological gradient (Austin

2007), such as temperature or precipitation. The modelling approach adopted here has previously been used by e.g. Huntley *et al.* (1995 and 2004). It uses a narrow smoothing window, meaning that the value of the grid point depends primarily on observations near (i.e. 'local') to it, resulting in a 'spikey' species response curve. A larger smoothing window would result in additional smoothing of data rendering the response surfaces less able to simulate species' distributions (Huntley *et al.* 1995). The CRS can then be used to simulate species' potential future distributions using potential future climate scenarios (Huntley, 1995). As with other methods, this method has its limitations; many of these centre upon the fact that climate does not solely determine species distributions. However, as long as this is considered, CRS (and other climate envelope approaches) are still a very useful 'first approximation' in determining how species distributions may change in the future (Pearson & Dawson, 2003). In addition, this technique is preferential to other methods as it makes no assumption about *how* species distributions are linked to climate. CRS have already successfully been used to simulate a number of species' distributions for example butterflies (Hill *et al.,* 1995; 1999), plants (Beerling *et al.,* 1995; Huntley *et al.,* 1995; Watrin *et al.,* 2007) and birds (Huntley *et al.,* 2006; 2008; Willis *et al., in press*).

Models can be placed into three categories; mathematical models (which focus on the generality and precision of the model), mechanistic models (focusing on the generality and reality of the model) and statistical models (which focus on the precision and reality of the model) (Levins, 1966). In recent years Levins' (1966) classifications have been shown to be inadequate as models occasionally fall into more than one of these original groups. Even so, Guisan & Zimmermann (2000) still promote the use of these classifications when creating the conceptual theory of the model. Once the concept of the model has been reviewed, the model can then be designed. At this stage, the scale of the study as well as which environmental variables to use in the model is decided (Guisan & Zimmermann, 2000). One of the most difficult tasks is to decide which subset of variables are of importance when creating species-distribution models (Segurado & Araujo, 2004) especially as there are potentially huge numbers of environmental factors which affect species' distributions.

Austin & Smith (1989) define three types of environmental variables used in ecological modelling. The first of these are 'resource gradients' which refer to matter consumed or used by the species in order to survive (such as water, light and nutrients): secondly, 'direct gradients' which have physiological importance (such as the temperature and pH of the species' surroundings) and finally, 'indirect gradients' which refer to variables with no direct physiological or resource importance to the species (e.g. slope, elevation and geology) (Guisan & Zimmermann, 2000).

In the case of a large scale study such as this, (assessing multiple species responses to climate change on a continental scale), modelling using direct and resource variables are preferable over the use of indirect variables. In the case of CRS (which is to be used in this study), species distributions can be fitted using bioclimatic variables which are considered to limit species distributions in some way. Examples include measures of extreme temperatures such as mean temperature of the warmest and coldest month which may limit species distributions directly via species' tolerances to these temperatures, plus measures of seasonality (e.g. ranges of precipitation and temperature) which may limit distributions indirectly e.g. via altering vegetation growth. These variables are derived from monthly values of temperature and precipitation, and represent different trends which may be of importance in limiting species distributions (WORLDCLIM, 2005). Although the use of direct and resource variables means the model is more general than when using indirect variables, this means that the model can be used over larger areas (such as the African continent; Guisan & Zimmermann, 2000). Indirect variables cause significant errors when used over larger areas as the other variables (direct and resource) often alter significantly between different geographic locations which have the same topography (Guisan & Zimmermann, 2000).

Another requirement for large-scale modelling is the assumption that species distributions and environmental variables are at equilibrium (Lischke *et al.*, 1998). The alternative (dynamic distribution modelling) requires detailed knowledge of each species being modelled, which is beyond the capacity of this study. Indeed, only a few studies on at the scale of this one have used dynamic modelling (e.g. He *et al.*, 1999 and Roberts, 1996). In

addition, species-distribution models are preferentially used over community-distribution models, especially in light of recent evidenced stating that species are expected to respond to changes in climate individualistically (Hannah & Salm, 2003) and therefore it is highly unlikely that communities will alter their distributions 'as one' (Huntley & Webb, 1988).

1.1.3.1. Evaluating the Accuracy of Species-Distribution Models

Species-distribution models are only useful at predicting species' potential future distributions if they are shown to accurately simulate species' current (or past) distributions using accurate climate data for that time period. Model performance can be evaluated by observing how well the model predicts species' current distributions. However, one cannot be sure that the simulations of species' potential future distributions are accurate (Hijmans & Graham, 2006) as one cannot be certain in the projections of how the climate will change.

Model performance can be evaluated in a number of ways, either quantitatively or qualitatively, however, in the vast majority of cases qualitative assessments are the only option (Segurado & Araujo, 2004). There are numerous qualitative methods used for evaluating (sometimes referred to as validating) the accuracy of predictive models. The choice of which method is used depends on a number of factors such as the study objectives (Fielding & Bell, 1997) and the choice of response variables used (Guisan & Zimmermann, 2000).

The first category (re-sampling techniques) uses the same set of input data to both calibrate and evaluate the model. This approach is used if the data available is too small to be split into two datasets, or where it is preferential that all data is used to calibrate the model (Guisan & Zimmermann, 2000). Examples of re-sampling techniques include bootstrapping (sampling without replacement; Efron & Tibshirani, 1993), jack-knifing (leave-one-out) and cross-validation (Manel *et al.*, 1999).

The second category differs from re-sampling techniques as these methods use two sets of data from different sources to evaluate model performance; one set is used to calibrate the model and one to evaluate it (Guisan & Zimmermann, 2000). Examples of these methods

include split-sample approaches e.g. 70/30 split (which uses 70% of the original data to calibrate the model and 30% of it to evaluate it). Data-splitting is a commonly used alternative to the more complex re-sampling techniques such as cross-validation and bootstrapping, particularly when the dataset is large. However, this method becomes unsuitable when only small datasets are available as the statistical accuracy of evaluation is decreased (Guisan & Zimmermann, 2000).

The evaluation of species-distribution models is complicated by the occurrence of spatial autocorrelation (Dormann, 2007), which exists if "the presence of a factor [e.g. a species] in a place makes its presence in a neighbouring place more or less likely" (Cliff & Ord, 1973). This may cause an increase in the number of false positives predicted by the model and therefore reduce the performance of that model (Dormann *et al.,* 2007). These methods should therefore be used with caution, at least until further investigative study has been undertaken.

If the model produces probabilistic predictions, these need to be converted into the original scale (i.e. presence/absence format) in order to evaluate its performance (Guisan & Zimmermann, 2000). This is achieved by applying a threshold value to non-dichotomous scores (Allouche *et al.,* 2006). Numerous studies have used an arbitrary value of 0.5 as the cut-off but in many cases this is inadequate as different species will have different threshold values due to differences in their prevalence (Segurado & Araujo, 2004). Therefore, some studies use the maximum value of Cohen's kappa (κ) produced for each species as the threshold value; Cohen's kappa (κ) "assesses the extent to which models predict occurrence at a rate higher than expected by chance" (Segurado & Araujo, 2004). Cohen's kappa can also be used to evaluate the fit of a model simulation in relation to observed presence-absence data. However, this statistic has been shown to be affected by species' prevalence, so instead, techniques such as the True Skill Statistic (TSS; Allouche *et al.,* 2006) the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding & Bell, 1997) are now commonly advocated.

The True Skill Statistic, Sensitivity and Specificity

After transformation of the data into a dichotomous (presence/absence) format, the generation of a confusion matrix (Table 1.2) is required in order to compare simulated presences and absences against actual presences and absences (Allouche *et al.*, 2006). In the case of models using presence/absence data, the table is 2 x 2 in size (Guisan & Zimmermann, 2000).

Table 1.2. A confusion matrix used to evaluate the accuracy of presence/absence models in ecology. Where a = number of true positives, b = number of false positives, c = number of false negatives and d = number of true negatives.

		Validation Data Set	
		Presence	Absence
Model	Presence	a	b
	Absence	c	d

This confusion matrix can subsequently be used to measure the kappa statistic (κ) and the TSS as well as overall accuracy, sensitivity and specificity by using the formulae shown in Table 1.3.

Table 1.3. Equations used to evaluate the accuracy of presence/absence models in ecology. a, b, c, and d refer to values given in Table 2.2.

Measure	Formula
Overall Accuracy	$\frac{a+d}{n}$
Sensitivity	$\frac{a}{a+c}$
Specificity	$\frac{d}{b+d}$
Kappa Statistic	$\frac{\left(\frac{a+d}{n}\right) - \frac{(a+b)(a+c)+(c+d)(d+b)}{n^2}}{1 - \frac{(a+b)(a+c)+(c+d)(d+b)}{n^2}}$
True Skill	Sensitivity + specificity – 1

Specificity is described as the proportion of species correctly simulated as absent and sensitivity is described as the proportion of species correctly simulated as present; these measures quantify commission (number of false positives) and omission (number of false negatives) errors respectively (Allouche *et al.,* 2006). In conservation terms, poor specificity is more detrimental than poor sensitivity as failure to predict species' observed presences (Guisan & Zimmermann, 2000) could mean measures to protect those species may be targeted towards the wrong location. The true skill statistic (also known as the Hanssen-Kuipers' performance index) is a measure of discrimination and is used preferentially over the kappa statistic as it is not affected by either the size of the dataset used for model evaluation or the prevalence of the species (Allouche *et al.,* 2006). TSS values range from +1 to -1, with values the +1 being a perfect agreement and values of less than zero showing an agreement no better than random (Allouche *et al.,* 2006).

An alternative method of evaluating the accuracy of models is to use the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding & Bell, 1997) which has been used extensively in medicinal studies (Zweig & Campbell, 1993). As with the TSS, the original non-dichotomous data needs to be transformed into presence-absence data by the selection of a threshold (Allouche *et al.,* 2006). AUC values generated from the ROC plot can range between 0 and 1. The conservative guide suggested by Thuiller *et al.,* (2006) suggests that AUC values of <0.8 are defined as a null model; 0.8<AUC<0.9, a fair model; 0.90<AUC<0.95, a good model and 0.95<AUC<1.00, a very good model. The use of AUC values to evaluate model performance is considered highly effective (Fielding, 2002; Allouche *et al.,* 2006).

1.2. Aims

The aims of this study are:

- To map the ranges of African mammalian fauna using species-climate modelling;
- to examine the potential consequences of changing climate upon mammalian ranges in Africa, identifying those at most risk;
- to project potential changes in the occurrence of keystone or charismatic species in protected areas as a result of future predictions of climatic change;
- to examine the ability of the current protected area network across African to continue to protect large mammals under future climate change scenarios; and
- to assess, by means of willingness-to-pay questionnaires, the potential loss of income to protected areas that could result from the loss of charismatic species as a consequence of future climate change.

1.3. Thesis Plan

Part one of the remainder of this study will assess the effects of projected future climate change on African mammals. This section has been split into four chapters; the first chapter introduces aspects of climate change and climate modelling; the second chapter (page 26) will report on modelling the current range of African mammals; the third (page 46) will report on modelling the future distributions of African mammals in response to projected climate change; and the fourth (page 88) will assess the impacts of projected climate change in African protected areas.

In chapter five (page 115) I will assess economic consequences of species range shifts using the contingent valuation method. The two parts of this thesis are then brought together and discussed in a final conclusions chapter (chapter six; page 162).

CHAPTER TWO: Simulating the Current Range of African Mammals

2.1. INTRODUCTION

Models which simulate species' potential future distributions in relation to projected climate change are only useful in doing so if their results are as accurate as possible i.e. they can accurately simulate species current distributions. Therefore a simple test of these models is to use observed climate and species distribution data to simulate species current distributions (Huntley *et al.*, 1995). This simple step is used as one cannot be sure that the simulations of species' potential future distributions are accurate (Hijmans & Graham, 2006). The performance of these models can then be evaluated using methods such as the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding & Bell 1997) or the true skill statistic (Chapter 1.1.3.2). These evaluation methods have been used in a number of studies based on modeling the distribution of species in Africa. For example the TSS has been used by Hole *et al.*, (unpub) to evaluate the accuracy of predicted avian species inventories in Important Bird Areas (IBAs). Additionally, Erasmus *et al.*, (2002), Huntley *et al.*, (2006) and Thuiller *et al.*, (2006) have used AUC values to evaluate the predictive power of their models in simulating the distributions of African mammals and birds.

Climate response surfaces will be used in this study to simulate species' current and future distributions. CRS have already successfully been used to simulate a number of species' distributions for example butterflies (Hill *et al.*, 1995; 1999), plants (Beerling *et al.*, 1995; Huntley *et al.*, 1995; Watrin *et al.*, 2007) and birds (Huntley *et al.*, 2006; 2008; Willis *et al.*, unpub). This method relates species distributions to a limited set of environmental variables which are chosen as they are thought to limit the species distributions in some way. For example bioclimatic variables such as mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA) and the ratio of actual to potential evapotranspiration (A/PET) are thought to affect species distributions both directly (e.g. by affecting species' physiological tolerances) and indirectly (e.g. by affecting plant growth and therefore food availability). Rather than simulating species' current and potential future distributions directly, these models simulate areas of

climatically suitable habitat for each species. Consequently this does not necessarily indicate where the species will be found because an area of land may be classed as climatically suitable by the models but, in reality, may be unsuitable for a specific species to live. For example, the models may predict a species to be present in an area of human habitation which may limit species distributions to outside of that area. It is therefore assumed that predictions of species distributions using this method will not be defined perfectly. However they are expected to provide a good estimation of how species ranges may alter in relation to projected climate change, especially as we can evaluate these results using methods such as the AUC. This means we can be more confident with the findings of this study if their accuracy at simulating species' current distributions is shown to be good.

Even if the models do well in predicting species distributions overall, it is expected that species with smaller distributions will be modelled better than species with larger distributions (Segurado & Araujo, 2004). This is because generalists tend to inhabit a wider range of habitats than specialists (i.e. species with smaller prevalence and/or biome endemics) and therefore an increasing number of environmental variables may affect their distribution (Osborne & Suarez-Seoane, 2002). As the very nature of CRS means that species distributions are fitted to a small number of environmental variables this is very likely to be the case. This phenomena has been observed in a number of studies; for example Segurado & Araujo (2004) recorded smaller errors in simulations for amphibian and reptilian species with restricted distributions; Brotons *et al.,* (2004) found that birds with more widespread distributions were modelled 'less accurately than more marginal selective species' and finally, Hepinstall *et al.,* (2002) recorded that simulations of generalist avian species' distributions were inferior to simulations of specialists' distributions. Despite the fact that 'specialists' are expected to be modelled better than 'generalists', the overall performance of the models in simulating the current distributions of African mammals is expected to be good; especially as other studies have successfully used these modelling techniques when simulating the distribution of species in relation to climate in Africa (e.g. Hole *et al., unpub*; Huntley *et al.,* 2006).

2.2. METHODOLOGY

2.2.1. Species Datasets

Extent of occurrence (EO) data for 280 African mammals belonging to 12 orders and 28 families covering the whole African continent (excluding Madagascar) were downloaded from the African Mammals Databank (AMD) website (www.gisbau.uniroma1.it/amd, accessed November 2006). This is a GIS-based databank which holds information on the distribution (*c.* 1998) and conservation of medium and large mammals on the African continent (IEA, 1998).

The species included in the databank belong to a number of different orders; these are Artiodactyla, Carnivora, Hydracoidea, Insectivora, Lagomorpha, Macroscelidea, Perissodactyla, Pholidota, Primates, Rodentia, Sirenia and Tubulidentata. Data on the location of the two species of rhinoceros (*Diceros bicornis* and *Ceratotherium simum*) are not included in the databank in order to keep the location of these species private (IEA, 1998). Data for the African elephant (*Loxodonta africana*) were also excluded from this databank and were obtained separately from the Elephant Specialist Group (AfESG) of the Species Survival Commission SSC/IUCN - World Conservation Union (Blanc *et al.*, 2003).

EO data from the AMD were downloaded and viewed as polygon coverages in ArcGIS (ESRI ArcGIS Version 9.0). The EO coverage files were then transformed into presence-absence data by overlapping the EO polygon with 0.25° (15') longitude x 0.25° latitude points for the whole of Africa. Points overlaying a polygon were defined as 'presence points', those not overlaying a polygon were defined as 'absence points'.

Data on the species' Red List Category & Criteria were obtained from the 'IUCN Red List of Threatened Species' (IUCN, 2006). Species names, reference numbers and red list categories are given in the appendices (Table A1). Species lists for protected areas were obtained from a number of sources (the Central African Republic species list was from UNEP (2002); Côte d'Ivoire lists from [1]Gartshore *et al.*, (1995) and [2]UNEP (2003); Kenya and Tanzania lists from Williams *et al.*, (1994); South African lists from SanParks (2007; www.sanparks.org) and Ugandan lists from the Uganda Wildlife Authority (2007)).

2.2.2. Climatic Datasets

Climatic data representing the present day (1961–90) were downloaded from WORLDCLIM (www.worldclim.org; Version 1.4 Release 3) at a resolution of 2.5 arc-minutes. In order to match the resolution of the species distribution data, the climatic data was scaled up to a resolution of 0.25° (15').

2.2.3. Climate Response Surfaces

Climate response surfaces were not fitted to the raw climatic data; instead, a series of bioclimatic variables were computed from the climate data. Initially, climate response surfaces were fitted using species presence-absence points and three bioclimatic variables; mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA) and the ratio of actual to potential evapotranspiration (A/PET). These variables represent measures of extreme annual temperatures (winter cold and summer warmth) and extent of moisture availability respectively and were derived using monthly climatic values of insolation, precipitation and temperature (Huntley *et al.,* 2006). Measures of mean annual precipitation tend to mask wider seasonal extremes of climate change at the height of the wet and dry seasons (Erasmus *et al.,* 2000). Therefore for each species, the climate response surfaces were fitted using the three variables above as well as an additional four variables which describe seasonality across the African continent. These four seasonality variables were calculated to measure both the length and intensity of dry and wet seasons (total wet intensity, total dry intensity, total wet duration and total dry duration). The length and intensity of the dry and wet seasons were estimated using daily values of the ratio of precipitation to potential evapotranspiration (P/PE) as in Huntley *et al.,* (2006). The start and end of these seasons were defined by applying a threshold to daily moisture availability values; above a certain value was defined as the start of the wet season, and conversely below a certain value was defined as the start of the dry season (Willis *et al., unpub*). Only one of these seasonality variables were used, selecting the one which optimised the performance of the model (in combination with MTWO, MTCO and A/PET) for modelling species future distributions.

Climate response surfaces were fitted using locally weighted regression (LWR) (Cleveland & Devlin, 1988). LWR was chosen as it makes no assumptions about the relationship between the bioclimatic variables and each species' probability of occurrence (Huntley *et al.*, 2006). A disadvantage of using LWR is the requirement to make an "*a priori*" choice of bioclimatic variables (Burns *et al.*, 2003; Huntley *et al.*, 2004). However, all of the bioclimatic variables chosen in this study have been shown to have mechanisms which limit species distributions and have been used to successfully model distributions of species including mammals (e.g. Erasmus *et al.*, 2002; Thuiller *et al.*, 2004; Huntley *et al.*, 2006). For example, duration and intensity of the dry and wet seasons may affect mammals by limiting the availability of food and/or water; temperature extremes may have direct effects upon individual species' physiological tolerances; ratio of A/PET may affect mammals indirectly by affecting plant growth and therefore food availability.

The species-climate response surface models were applied to current climate data to simulate probabilities for the occurrence of each species across the African continent; as Huntley *et al.*, (1995) discuss, this is a simple test of the ability of response surface. However, due to a degree of smoothing when fitting the response surface, it is expected there will be some simulated presences which are false positives. Therefore the kappa (κ) statistic was calculated for each simulation for each species in order to produce the optimal cut-off threshold for converting the continuous simulated suitability into presence-absence data (Collingham *et al.*, 2000); this maximises sensitivity and specificity of the simulations. Above this threshold value the simulated values represent presences and below this threshold value the simulated values represent absences in that cell. This is better than using an arbitrary value for all species (Allouche *et al.*, 2006).

Model fit was assessed using the values obtained from the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding & Bell 1997; Thuiller *et al.*, 2006). This is used rather than kappa, as kappa is affected by species' prevalence (Chapter 1) much more than AUC (Manel *et al.*, 2001), although Huntley *et al.*, (2004) found a small but significant positive correlation between prevalence and AUC ($F_{(1,294)} = 2.83$, $P < 0.001$).

Simulations of species' current distributions were also assessed by comparing simulated inventories of mammal species in protected areas to observed mammal inventories for each site. Observed inventories were obtained for 28 protected areas in six countries (Table 2.2). Sensitivity and specificity of species' current- versus simulated current distributions as well as the true skill statistic were calculated using the equations in Table 1.3 (page 23). Comparisons were also made between species' observed extent of occurrence (EO) and the occurrence predicted by the models; a good agreement between these two indicating a good simulation of observed species EO.

A one-way ANOVA was used to establish if geographic location of species had an effect on model performance, and a Spearman's rank order correlation was used to correlate model performance and species' extent of occurrence.

2.3. RESULTS

2.3.1. Model Validation

2.3.1.1. The Receiver Operating Characteristic (ROC) Curve

AUC values from this study ranged from 0.915 to 1.000 (n = 281, $\bar{x}$ = 0.989) (Figure 2.1).

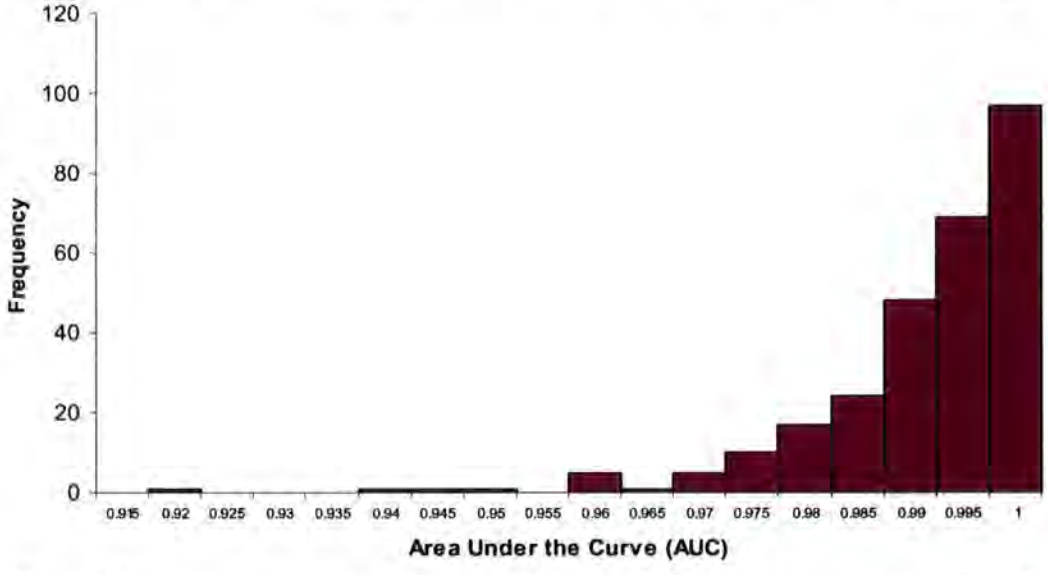


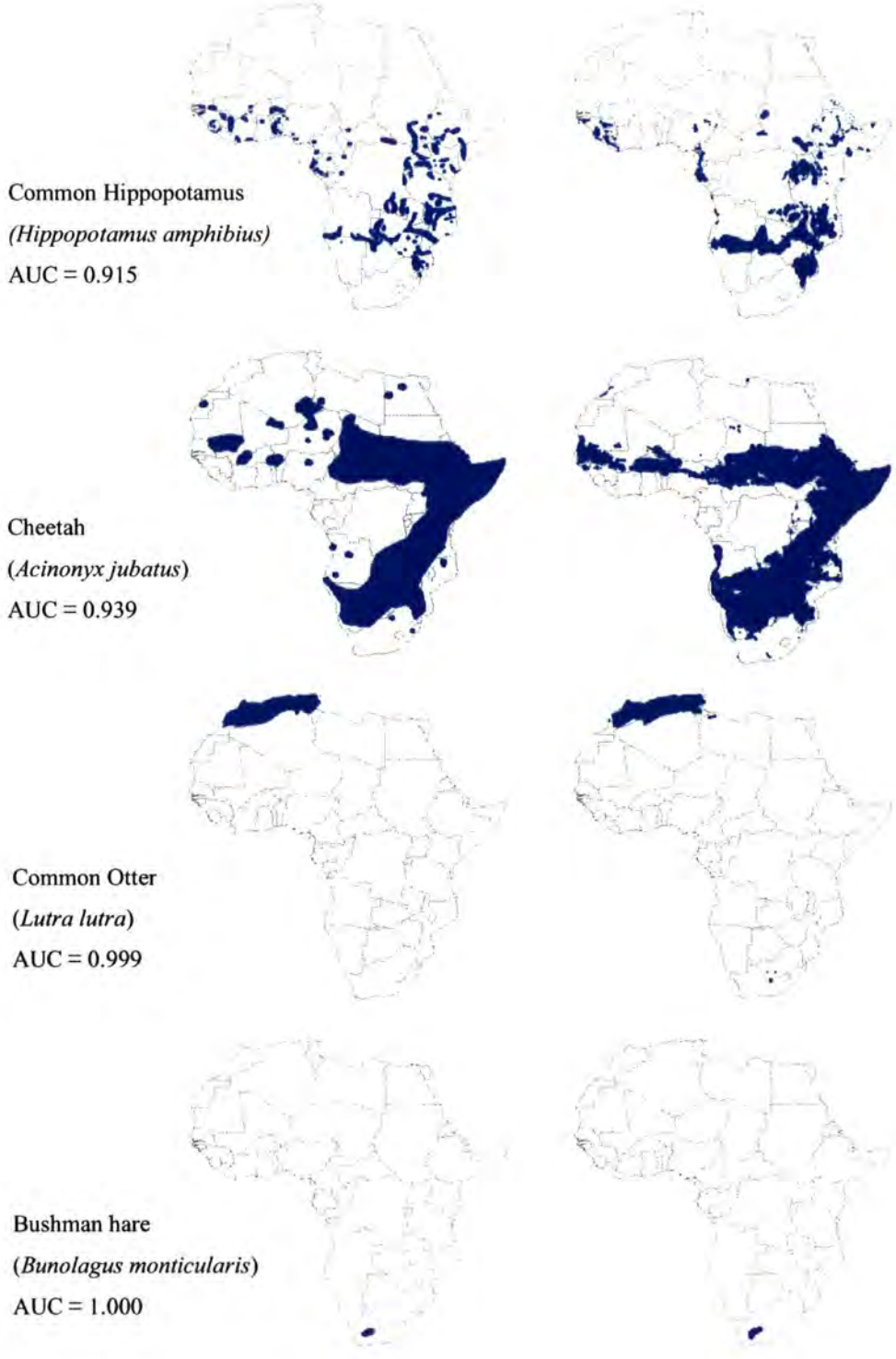
Figure 2.1. Frequency histogram of species AUC values. Each AUC value is representative of the optimal performance of the model using four variables (MTCO, MTWO, A/PET plus one of totwetint, totwetdur, totdrvint and totdrvdur.

Following the definitions of Thuiller *et al.*, (2006) (page 24), for four species, models were classed as 'good' and for the other two hundred and seventy seven species models were 'very good' in predicting species' ranges (see Table A1 in the appendices). The minimum accuracy value was 0.915 recorded for the common hippopotamus (*Hippopotamus amphibious)* whilst an accuracy of 1.000 (correct to 3 d.p.) was recorded for seven species (Table 2.1). Some examples of simulations of species' present-day distributions are shown in Figure 2.2 (see appendices, page 182, for instructions on how to view present-day distributions of all species in ArcMap). Table A1 in the appendices shows individual species AUC values.

Table 2.1. Species with the highest AUC values, all of which rounded to 1.000.

Species Ref.	Scientific Name	Common Name
8	*Capra walie*	Walia Ibex
9	*Cephalophus adersi*	Aders' Duiker
20	*Cephalophus rubidus*	Red Duiker
101	*Canis simensis*	Ethiopian Wolf
181	*Bunolagus monticularis*	Bushman Hare
190	*Pronolagus randensis*	Jameson's Red Rockhare
238	*Cercopithecus solatus*	Sun-tailed Monkey

Figure 2.2. Observed (left hand maps) and simulated (right hand maps) current distributions of a sample of 4 species (names on the left of each map) along with their corresponding AUC value. Blue indicates the observed/simulated distribution of each species.



2.3.1.2. Using CRS Models to Simulate Species Occurrences in Protected Areas

Twenty-eight protected areas from six different countries (Figure 2.3) were used to test the ability o the models to simulate species occurrences in protected areas. The simulated species inventories in these protected areas were shown to have high specificity and sensitivity as well as a correspondingly high true skill statistic (see Table 2.2). As TSS values range from +1 to -1, the mean TSS value of 0.74 supports the view that this modelling approach is robust.

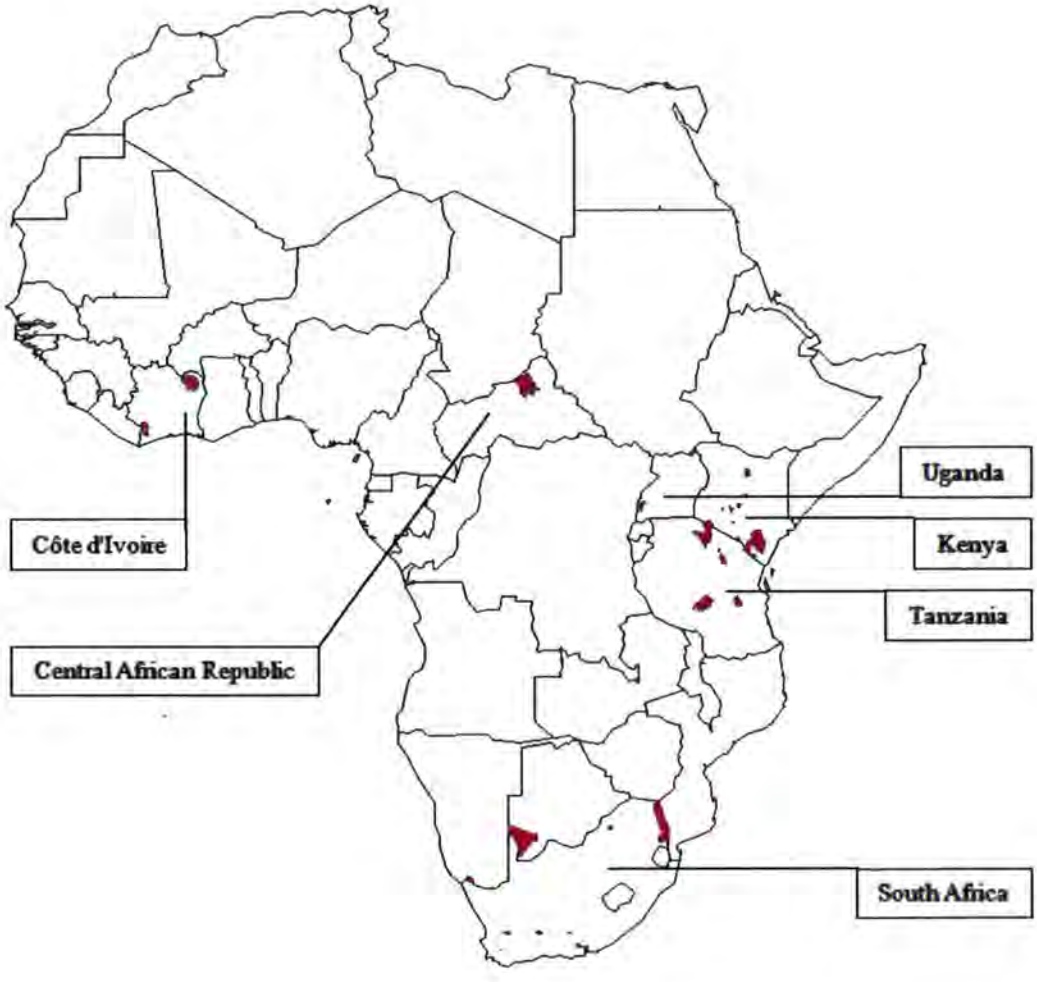


Figure 2.3. Location of the 28 protected areas whose species lists were used to calculate the TSS. Black lines indicate country borders, red areas indicate the protected areas used in this analysis.

Table 2.2. Performance of climate response surface models in producing mammal species inventories for 28 protected areas. Summary of values used to calculate the TSS are also given. Species lists from a variety of sources were used: see page 26.

Protected Area	Location	Proportion of species correctly classified (%)	Sensitivity	Specificity	True Skill Statistic	Mean TSS
Manovo-Gounda-Saint Floris National Park	Central African Republic	86.48	0.81	0.87	0.68	0.68
Comoé National Park	Côte d'Ivoire[2]	81.85	0.62	0.84	0.45	
Tai National Park	Côte d'Ivoire[1]	83.63	0.82	0.84	0.66	0.56
Aberdare National Park	Kenya	77.22	1.00	0.73	0.73	
Amboseli National Park	Kenya	91.81	0.95	0.91	0.86	
Lake Nakuru National Park	Kenya	88.26	0.88	0.88	0.76	
Marsabit National Reserve	Kenya	90.39	0.91	0.90	0.81	
Masai Mara National Reserve	Kenya	85.05	0.85	0.85	0.70	
Mount Elgon National Park	Kenya	85.05	0.67	0.87	0.53	
Mount Kenya National Park	Kenya	80.78	0.97	0.79	0.76	
Nairobi National Park	Kenya	88.61	0.80	0.90	0.71	
Samburu - Shaba Reserves	Kenya	81.49	0.88	0.80	0.67	
Tsavo National Park	Kenya	90.04	0.96	0.88	0.84	0.74
Addo Elephant National Park	South Africa	91.46	0.88	0.92	0.80	
Karoo National Park	South Africa	88.61	0.85	0.89	0.74	
Kgalagadi Transfrontier Park	South Africa	94.66	0.86	0.96	0.82	
Kruger National Park	South Africa	93.59	0.93	0.94	0.87	
Marakele National Park	South Africa	82.56	0.79	0.83	0.62	
Richtersveld Transfrontier National Park	South Africa	95.37	0.89	0.96	0.85	
Tankwa Karoo National Park	South Africa	91.46	0.87	0.92	0.79	
Tsitsikama National Park	South Africa	91.10	1.00	0.91	0.91	0.80
Lake Manyara National Park	Tanzania	85.05	0.88	0.84	0.73	
Mikumi National Park	Tanzania	80.43	0.76	0.81	0.57	
Ruaha National Park	Tanzania	84.34	0.90	0.83	0.73	
Serengeti National Park	Tanzania	78.29	0.87	0.75	0.62	
Tarangire National Park	Tanzania	85.41	0.98	0.83	0.81	0.69
Kidepo Valley National Park	Uganda	88.97	0.98	0.87	0.85	
Rwenzori Mountains	Uganda	83.27	0.96	0.80	0.77	0.81
	MEAN	86.62	0.88	0.86	0.74	

2.3.2. Model Performance

The maximum AUC values for each species were arcsine transformed (Sokal & Rohlf, 1995) after which they approximated to a normal distribution (One-Sample Kolmogorov-Smirnov Test: KS = 1.011, n = 281, P = 0.259). Consequently, parametric tests were chosen when analysing the data further. Interestingly, for some groups of species such as the African antelopes (*Damaliscus* spp.), gazelles (*Gazella* spp.), foxes (*Vulpes* spp.), colobus monkeys (*Colobus* spp.) and the zebras (*Equus* spp.) the fourth variable which maximised AUC was constant within each genus. In the first four genera listed above, 'total dry intensity' maximised AUC whereas for the zebras 'total wet intensity' maximised AUC values.

There was a strong positive correlation between species' present-day extent of occurrence and the occurrence predicted by the models (correlation = .964, $P < 0.001$, Figure 2.4) i.e. models did well in predicting species' current distributions and there was no consistent over- or under-prediction of range extent by the models.

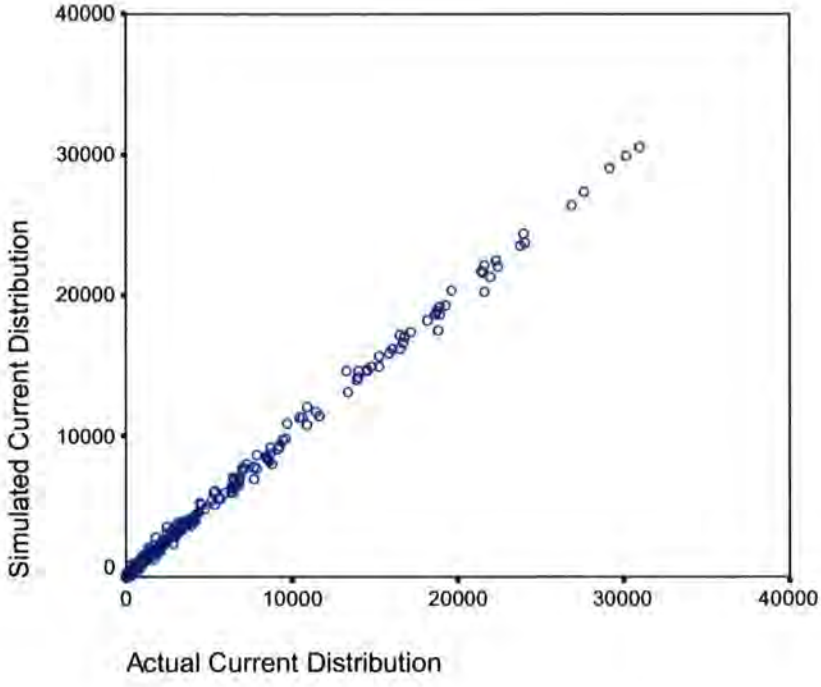


Figure 2.4. Correlation between species' present-day extent of occurrence and the occurrence predicted by the models. Species distribution is defined by number of quarter-degree cells in which the species is observed or simulated to occur.

Although overall the models did well in predicting species present-day distribution, there were a few anomalies such as the Walia Ibex (*Capra walie*) and the Golden-rumped elephant shrew (*Rhynchocyon chrysopygus*) which were simulated to occupy 42% and 50% less than observed, and the Lechwe (*Kobus leche)* which was simulated to occupy 289% more than their actual distributions (Figure 2.5). The overestimate of the distribution of the Lechwe is due to the model's inability to account for its inhabitance of swamps in low rainfall areas, with the conventional climatic variables used in this assessment.

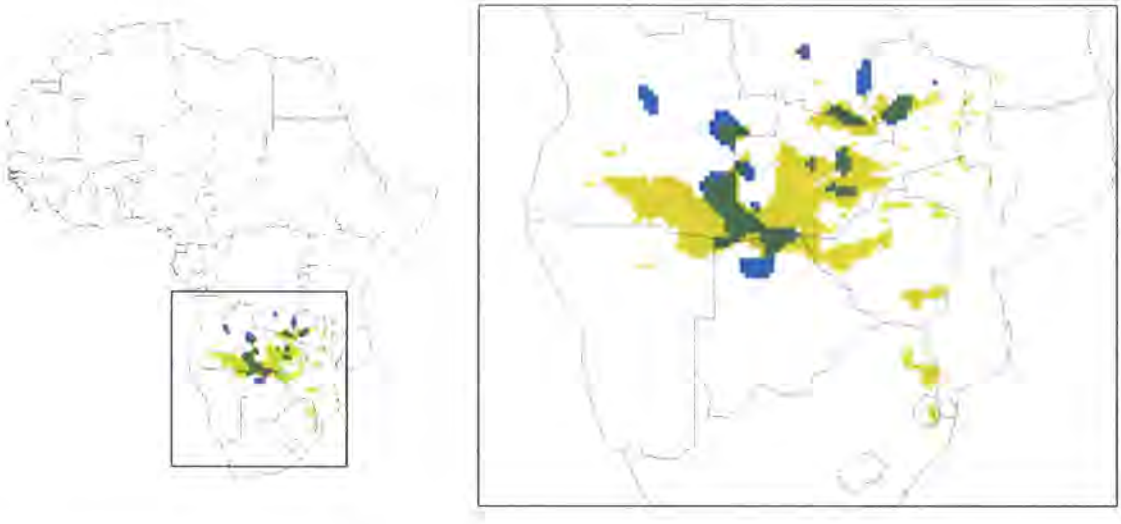


Figure 2.5. Present-day and simulated present-day distributions of the Lechwe (*K. leche)*. .Present-day distributions are taken from the African Mammals Databank (IEA, 1998). Blue dots represent present-day distribution, yellow dots represent simulated present-day distribution and green dots represent overlap between observed and simulated distributions for each species.

For each species, only the combination of four variables (MTCO, MTWA, APET plus one of total wet intensity (totwetint), total dry intensity (totdryint), total wet duration (totwetint) and total dry duration (totwetdur)) which maximised AUC were used for modeling the future distributions of each species. This was decided as there were

differences between the performances of the simulations using each of the fourth variables. For that reason, the decision of choosing one of the fourth variables to remain constant for all 281 species would have been counterproductive, as it would have reduced the robustness of the future predictions of species' ranges.

Figure 2.6 and Table 2.3 show a summary of AUC values from models of current species' distributions. Each AUC value is the maximum recorded for each species from the four different combinations; MTCO, MTWA and A/PET were kept constant and the fourth variable changed between total wet intensity (totwetint), total dry intensity (totdryint), total wet duration (totwetint) and total dry duration (totwetdur).

Table 2.3. Summary of the area under the curve (AUC) values for four variable models simulating current distributions. 'Total number of species' is the sum of species for which that specific bioclimatic variable combination maximised AUC; i.e. MTCO, MTWA, APET and that particular fourth variable. (See main text for descriptions of totwetint, totdryint, totwetint and totwetdur).

	AUC Value			
Fourth Variable	TotDryDur	TotDryInt	TotWetDur	TotWetInt
Maximum AUC	1.000	1.000	1.000	1.000
Minimum AUC	0.910	0.911	0.913	0.915
Mean AUC	0.984	0.987	0.985	0.987
Median AUC	0.988	0.990	0.989	0.990
Total Number of Species	5	138	23	115

The combinations of MTCO, MTWA and APET and the fourth variables representing total intensity of the wet and dry seasons maximised the AUC values in the majority of cases; however, the range of AUC values were also larger for these variables (Table 2.3; Figure 2.6).

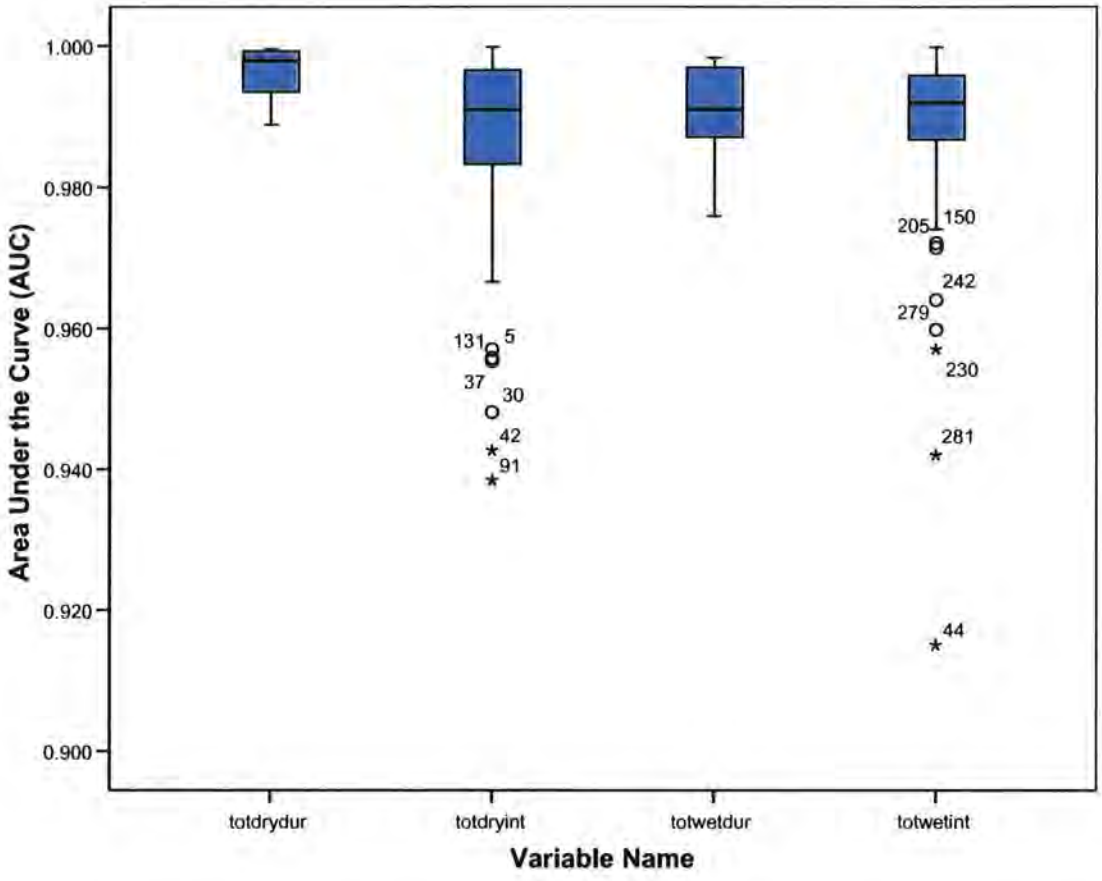


Figure 2.6. Summary of the area under the curve (AUC) values from climate response surface models simulating current range extent. Totdrydur, totdryint, totwetdur and totwetint represent the AUC values of those species for which that specific bioclimatic variable combination maximised AUC; i.e. MTCO, MTWA, APET and that particular fourth variable. Numbers adjacent to the outliers correspond to species' reference numbers as defined in Table A1 of the appendix. Median values are indicated by the bold black horizontal line; upper and lower quartiles are denoted as the ends of the boxes; maximum and minimum values are represented by whiskers; outliners (values ≥ 1.5 ≤ three box lengths from the ends of the box) are given as circles; and extreme values (> 3 box lengths away) are given as asterisks..

2.3.3. The Effect of Species' Extent of Occurrence on Model Performance

Analyses were carried out using all species; ranging from the extremely restricted (less than ten quarter degree cells), up to the most widespread species (up to 30,000 quarter degree cells). Results of a Spearman's Rank-Order Correlation suggested there was a significant negative correlation between extent of occurrence and model performance (r = -.388, d.f. = 280, $P < 0.001$) such that as extent of occurrence increases, model performance decreases (Figure 2.7). After the removal of restricted species (those whose extent of occurrence is less than 100 quarter-degree cells) this association remained significant (r = -0.328, d.f. = 262, $P < 0.001$).

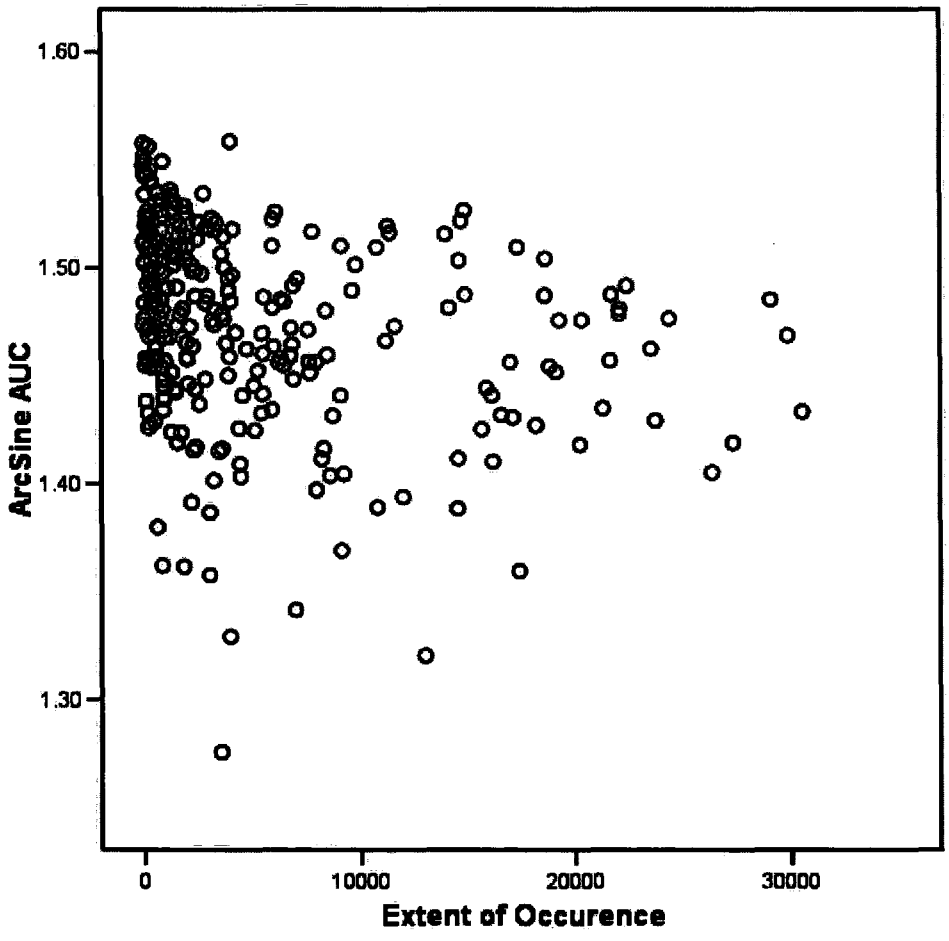


Figure 2.7. Correlation between species' extent of occurrence and model performance. Extent of occurrence is defined as the number of presence points in which the species is observed to occur. Arcsine AUC values are a measure of model performance (higher values indicate better performance).

2.3.4. The Effect of Species' Geographic Location on Model Performance

The whole of Africa was divided into five geographic areas as shown on Figure 2.8. Using the presence-absence maps of the 281 species, each species was categorised into the most relevant geographic area(s).

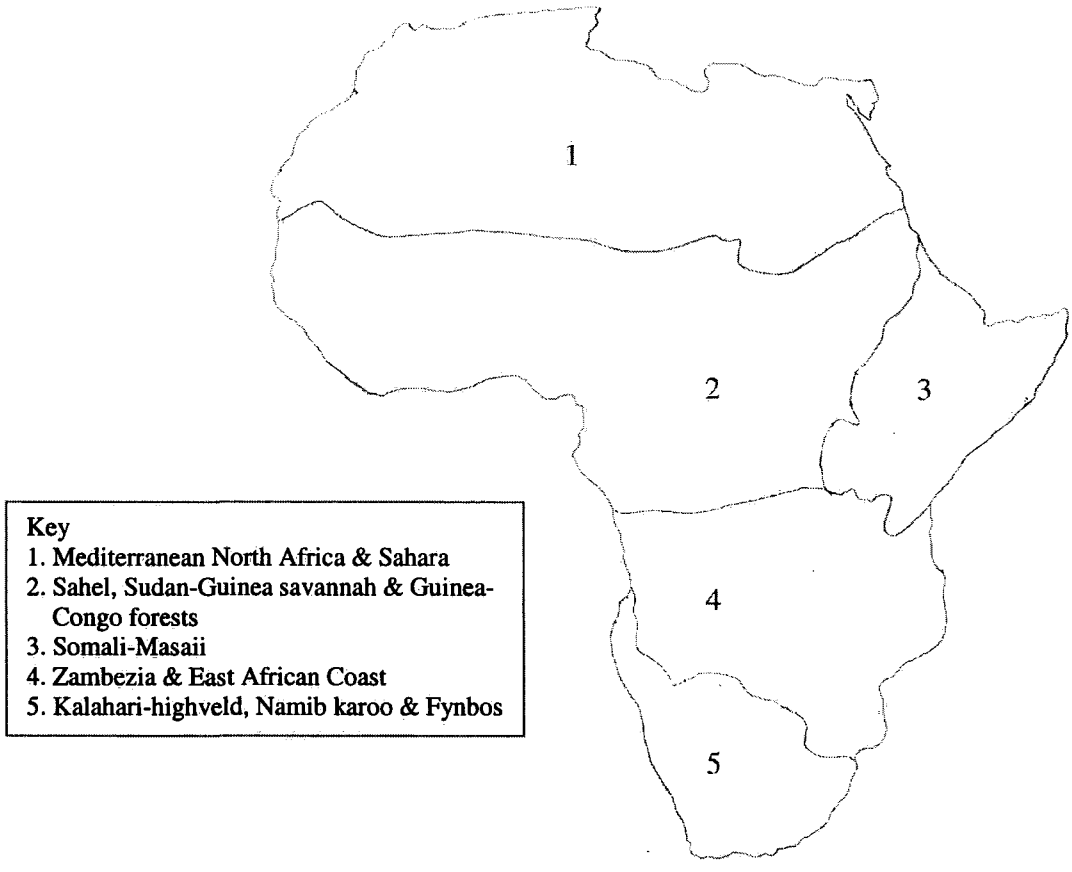


Figure 2.8. Biomes in Africa, adapted from Fishpool & Evans (2001).

A one-way ANOVA was carried out to determine if there was a significant difference between AUC values of species endemic (defined by the species' occupying only one of the five areas depicted in figure 2.8) to the five different areas; 181 species were endemic to one of the five zones in Figure 2.8, the other 100 occupied two or more areas. The results of the one-way ANOVA provided evidence that geographic origin of species ranges affected model performance ($F_{(4,180)} = 7.323$, $P < 0.001$); equal variances were not assumed as a Levene's test was significant (Levene Statistic = 4.852, $d.f. = 4$, $P < 0.001$).

Post hoc tests (assuming unequal variances i.e. Games-Howell) indicated model performance of species endemic to zone two (Sahel, Sudan-Guinea savannah & Guinea-Congo forests) differed significantly from species endemic to zones four (Zambezia & East African Coast) and five (the Kalahari-highveld, Namib karoo & Fynbos) ($P < 0.05$). Species endemic to zone four differed significantly from species endemic to zone three (Somali-Masai) and five (Table 2.4).

Table 2.4. Posthoc tests of the effect of geographical occurrence of species on model performance. Geographic locations are numbered as follows: 1 = Mediterranean North Africa and Sahara; 2 = Sahel, Sudan-Guinea Savannah and Guinea-Congo forests; 3 = Somali-Masai; 4 = Zambezia and East African coast and 5 = Kalahari-highveld, Namib karoo, Fynbos. * denotes the mean difference is significant at the .05 level.

Geographic Location (A)	Geographic Location (B)	Mean Difference (A-B)	Sig.
1	2	-.007660	.959
	3	-.024152	.286
	4	.020682	.517
	5	-.032274	.066
2	1	.007660	.959
	3	-.016492	.082
	4	.028342(*)	.019
	5	-.024614(*)	.000
3	1	.024152	.286
	2	.016492	.082
	4	.044833(*)	.000
	5	-.008123	.770
4	1	-.020682	.517
	2	-.028342(*)	.019
	3	-.044833(*)	.000
	5	-.052956(*)	.000
5	1	.032274	.066
	2	.024614(*)	.000
	3	.008123	.770
	4	.052956(*)	.000

An Independent Samples T-test was carried out to compare AUC values of biome endemic species with widespread species (widespread being defined as occupying two or more of the five core areas shown in Figure 2.8). There was a significant difference between AUC values of endemics and widespread species ($T = 8.64$, $d.f. = 162$, $P < 0.001$), with biome endemics modelled better than more widespread species.

2.4. DISCUSSION

Model fit was assessed using two methods; the AUC of a ROC plot and the TSS. These methods have been used in other studies (e.g. Huntley *et al.*, 2006; Thuiller *et al.*, 2006) and are considered highly effective in evaluating model performance (Fielding, 2002; Allouche *et al.*, 2006). Both of these methods produced results indicating the modelling approach chosen in this study is robust and therefore better than a random model. The mean AUC value of 0.99 (to 2 d.p.) recorded in this study (similar to 0.98 recorded by Thuiller *et al.*, 2006) indicates that the present-day distribution of African mammals can be simulated very successfully using this modelling approach. Thuiller *et al.*, (2006) recorded an AUC of 1.0 for only one species, the Silver dik-dik (*Madoqua piacentini*) while this study recorded the maximum AUC of 1.0 for seven species (Table 2.1), indicating a perfect simulation of those species' present-day distribution using the chosen set of environmental variables. In addition to these findings, the minimum AUC value recorded in Thuiller *et al.*,'s (2006) study was 0.85 for the common hippopotamus (*Hippopotamus amphibious*); which was also the case in this study, albeit with a higher maximum AUC value of 0.92. Models may have poor predictive ability for the hippopotamus (*H. amphibious*) in particular as this species relies on freshwater to remain cool, as well as for birthing and reproduction. As in Thuiller *et al.*,'s (2006) paper, this parameter was not used as one of the variables in the modelling procedure as only a limited set of environmental variables could be used as model parameters.

Reliable and accurate species lists within protected areas were difficult to obtain, leading to the possibility that the high mean TSS values for South African and Ugandan protected areas were a result of better quality lists than those for other areas. Even so, the overall mean TSS value (mean TSS = 0.74) indicated that the modeling approach adopted was robust and could be reliably used to model species' potential future distributions. Specificity (mean specificity = 0.86) and sensitivity (mean sensitivity = 0.88) of the models were also high, indicating that the number of commission (number of false positives) and omission (number of false negatives) errors was low. The high sensitivity and specificity is encouraging as one would expect a larger number of false positives in particular, if factors other than climate (such as topographical barriers, human

encroachment, habitat modification or competition between species) were preventing species realising their climatically suitable niches. However, it seems climate is the primary determinant of mammal species distributions with other possible variables playing a secondary role. The high specificity value is particularly encouraging, as poor specificity could mean measures to protect species could be positioned in the wrong place. These results are similar to those reported by Hole *et al.*, (*unpub*) (median TSS = 0.718; median sensitivity = 88%) who simulated the current distribution of avifauna within African Important Bird areas (IBAs) in order to project the impacts of climate change on a continent-wide protected area network using analogous modelling approaches. The success rates of predicting occurrences here are also similar to those found by Willis *et al.*, (2008) using a similar approach to simulate birds of concern in South African important bird areas (TSS = 0.74). Willis *et al.*, (2008) also added a habitat layer to filter out false presences and found TSS increased to 0.78. Such an approach could also improve the mammal models, especially for those species such as the hippopotamus which are known to be habitat restricted in many areas.

The fourth bioclimatic variables which maximized AUC were, overwhelmingly, the total intensity of the wet (n = 115 species) and dry (n = 138 species) seasons rather than the duration of the wet or dry seasons (n = 23 and n = 5 species respectively). It is therefore likely that the intensity of the wet and dry seasons play a more important role in limiting mammal species distributions than the duration of the wet or dry seasons.

For some groups of species such as the African antelopes (*Damaliscus* spp.), gazelles (*Gazella* spp.), foxes (*Vulpes* spp.), colobus monkeys (*Colobus* spp.) and the zebras (*Equus* spp.) the fourth variable which maximised AUC was constant within that genus. In the first four genera listed above, total dry intensity maximised AUC whereas for the zebras total wet intensity maximised their AUC values. This could be due to the fact that all species within that genus inhabit similar climatic niches and are therefore exposed to similar climatic conditions, or it could be because their geographic locations are similar.

Results suggest that species with smaller extents of occurrence were modelled better than those species with larger distributions. For example, the seven species whose present-day

distributions were simulated perfectly (i.e. AUC = 1.0) all had extremely restricted ranges (mean simulated range size = 52 quarter degree cells) compared to the overall mean range size (mean = 5151 cells). In addition, species endemic to one area (of the five biomes in Figure 2.8) were modelled better than those species whose distributions were more widespread. Although Huntley *et al.*, (2004) found a significant positive relationship between model performance and species' prevalence; other studies have the found opposite. For example Segurado & Araujo (2004), Brotons *et al.*, (2004) and Hepinstall *et al.*, (2002) found that species with widespread distributions were modeled less well than those with restricted distributions (Chapter 1.1.3). As we are only using a limited set of environmental variables (four for each species) to fit the CRS, it is likely that 'specialists' were modelled significantly better than 'generalists' because they inhabit a smaller variety of habitats (Osborne & Suarez-Seoane, 2002).

Although there were a few anomalous results (e.g. the simulated distributions of the Walia Ibex (*C. walie*), Golden-rumped elephant shrew (*R. chrysopygus*) and the Lechwe (*Kobus leche*)), on average this modeling approach appears useful in investigating the role of climate in determining African mammal ranges, and demonstrates climate to be an important factor in the distributions of mammals. As we have confidence in this modelling approach, climate response surfaces can now be used to model the projected impacts of potential future climate change on the African mammals.

CHAPTER THREE: Simulating Range Shifts of African Mammals under Projected Climate Change

3.1. INTRODUCTION

Improved estimates of the rate and magnitude of projected climate change have recently been reported in the IPCC Fourth Assessment Report (IPCC, 2007a). These estimates indicate that the African continent is one of the most vulnerable continents to climate change; with rates of warming 1.5 times the projected global response, and while precipitation is expected to increase, seasonal extremes in the austral summer and winter are expected to be more pronounced (Boko *et al.*, 2007; Chapter 1). It is expected that these changes will have dramatic effects upon the distribution of African mammals; mainly via the impacts of climate change upon vegetation growth (IPCC, 2001b). Indeed, there is a large amount of literature detailing how species ranges and distributions have already changed in response recent anthropogenic climate change; most reporting ranges shifts primarily polewards and towards higher elevations (Beaumont *et al.*, 2007; Parmesan & Yohe, 2003; Root *et al.*, 2003 but see Hickling *et al.*, 2006).

Species-distribution models are now widely used as first approximations in determining the potential impacts of future climate change upon species (Levinsky *et al.*, 2007). However these are only useful if they can predict species' ranges accurately (see Chapter 1.1.3.1). Such models have been used to simulate potential changes in the distributions of a wide variety of species in response to potential future climate change; from aquatic and terrestrial plants (Hill, 1991; Huntley *et al.*, 1995) and trees (Iverson *et al.*, 2004) to birds (Huntley *et al.*, 2006; Manel *et al.*, 1999) and fishes (Lek *et al.*, 1996). In many cases, such modelling approaches remain the only option for assessing the effects of changes in climate on species distributions. This is because only a small number of species' responses to environmental change have been studied in detail (Woodward & Cramer, 1996). Species-distribution models have also been used to determine the impacts of climate change upon the distribution of mammals. Examples of these studies include Burns *et al.*, (2003) who modelled shifts of 213 mammal species resident in the United States of America in response to a doubling of atmospheric carbon dioxide. They found that vegetation changes influenced the extent of species diversity loss/gain in national parks;

however a general shift of community composition is expected to occur at a magnitude "unprecedented in recent geological time" (Burns *et al.*, 2003). Another example is the recent study by Levinsky *et al.*, (2007) who used bioclimatic envelope models to investigate the potential impact of climate change on 120 native terrestrial European mammals. Assuming unlimited dispersal, they found that 1% of mammals modelled faced risk of extinction, and 32 – 46% may be severely threatened as a result of projected climate change.

As Africa is expected to be one of the most vulnerable contients to climate change (Boko *et al.*, 2007), and the fact that it holds nearly a quarter (n = 8; 24%) of the world's biodiversity hotspots (CI, 2007), one would expect studies on this continent to be the most numerous. Yet there are few studies focusing on the effects of climate changes on the distribution of species (especially mammals) resident in Africa (but see Erasmus *et al.*, (2002) and Thullier *et al.*, (2006)). Thullier *et al.*, (2006) used generalised additive models (GAM) to assess the sensitivity of 277 African mammals to climate change and anthropogenic land transformation under two climate change scenarios for 2050 and 2080 (HadCM3 A2 and B2 scenarios), as well as to estimate species richness gain and loss across the continent plus within the African protected area network. Thuiller *et al.*, predicted substantial decreases in species richness in central Africa (60 – 75% by 2080), and southern Africa (Kalahari region, northern South Africa and Namibia; 80 – 100% by 2080) in response to potential climate change and land transformation. They also predicted that a substantial number of African mammals will become "severely threatened by future climate change and land transformation." Assuming unlimited dispersal of species, 30% of species would become listed as critically endangered under the HadCM3 A2 scenario for 2080. Thuiller *et al.*, (2006) concluded that the effects of climate change on mammal species may be seen as a change in community composition as well as loss of species from their current ranges. They predicted median range contraction to be -49% (mean = -18%), which is a cause for concern as range size is negatively correlated to extinction risk (Gatson, 1994). So, as range size decreases, the risk of local extinctions is predicted to increase (Thomas *et al.*, 2004). This is particularly so when decreases in range cause the overall population to become fragmented into smaller sub-populations as these smaller

populations tend to be less stable and are therefore more likely to become extinct during extreme events such as disease outbreaks and drought (Erasmus *et al.*, 2002).

While Thuiller *et al.*,'s (2006) study had a continent-wide focus, Erasmus *et al.*, (2002) concentrated on the vulnerability of only South African taxa to climate change. In this study, a multivariate climate envelope approach was used to predict range changes of 179 animal species (including birds, mammals, reptiles, butterflies, beetles, antlions and termites) in response to a global temperature rise of 2°C via a doubling of CO_2 in the atmosphere. Changes in species richness, as well as shifts and contractions of species' ranges were predicted. Erasmus *et al.*, (2002) predict that the majority (78%) of species will experience range contraction, whereas 17% species will experience range expansion. 25% of species were projected to experience range shifts of over 90%, especially reptiles and invertebrate species. Many of the mammals, birds and butterflies showed an overlap between current and potential future ranges of over 50%. The majority (41%) of expected range shifts will be in the easterly direction, triggering the highest species losses in western South Africa. Species listed as vulnerable or red-listed were more likely to experience changes in range (a composite measure reflecting range contraction and displacement; 58% and 43% respectively). Erasmus *et al.*, (2002) concluded that the majority of species will experience a reduction as well as a significant displacement of their ranges in response to projected future climate change. These studies both state that their results may be conservative estimates of predicted distribution changes; if species are unable to track projected climate changes or adapt (behaviourally or physiologically) the impacts could be more pronounced than those estimated (Erasmus *et al.*, 2002; Thuiller *et al.*, 2006). Despite this, studies such as these provide initial estimates of how climate may affect species across the African continent. These are useful guides of the scale and type of conservation action which is necessary to save these species, until a time in the future when more detailed data on species interactions and climate change is collected (Thuiller *et al.*, 2006).

3.1.1. Objectives

The modelling approach used to simulate species' present day distributions using bioclimatic variables chosen was previously shown to be robust (Chapter 2.3) In this chapter I use these models but apply them to future climate scenarios to investigate how species richness, prevalence and overlap between species' current and potential future ranges may change by considering to what extent mammalian species will alter their distributions in response to projected climate change. This can be used to guide conservation action required to limit detrimental effects of climate change on mammal species.

3.2. METHODOLOGY

3.2.1. Climatic Datasets

Future climate projections were produced for three different time periods (2020, 2050 and 2080) and for three different General Circulation Models (GCMs). The time slice 2020 refers to the years 2010 – 2039; similarly, 2050 refers to the period 2040 – 2069 and 2080 refers to 2070 – 2099 (IPCC, 2007b). The GCMs used were ECHAM4/OPYC3 (Roeckner *et al.*, 1996; ECHAM4), GFDL_R30_c (Knutson *et al.*, 1999; GFDL) and HadCM3 (Gordon *et al.*, 2000), all utilising the B2 IPCC SRES future emissions scenarios (Nakićenović *et al.*, 2000). The GCM data was obtained from the IPCC Third Assessment Report (TAR, 2001). The B2 emissions scenario was chosen as it takes an optimistic view of change in the future; economic development is at an intermediate level and while population is set to increase it will increase at a decreasing rate. Consequently, change under the B2 scenario would result in relatively moderate climate change when compared to more drastic states closer to the 'business as usual' scenarios (Huntley *et al.*, 2006). The hottest scenario is A1F1 and the coolest is B1; the B2 scenario lies as an intermediate of these scenarios (A2, A1B, B2, A1T). The IPCC B2 storyline and scenario describes:

> *"a world in which the emphasis is on local solutions to economic, social, and environmental sustainability. It is a world with continuously increasing global population at a rate lower than A2, intermediate levels of economic development, and less rapid and more diverse technological*

change than in the B1 and A1 storylines. While the scenario is also oriented toward environmental protection and social equity, it focuses on local and regional levels" (Kagramanian *et al.*, 2000).

The three GCMs were chosen because their projections of future global warming are approximately 2.5 °C by 2100; this is the modal value of projections from the nine GCMs (CGCM1, CCSR/NIES, CSIRO Mk2, ECHAM3/LSG, GFDL_R15_a, HadCM2, HadCM3, ECHAM4/OPYC and DOE PCM) included by Cubasch *et al.*, (2001). Additionally, their predictions of global precipitation change by the year 2100 represent 'medium' (HadCM3), 'dry' (ECHAM4) and 'wet' (GFDL) scenarios (Huntley *et al.*, 2006), which will provide scope for investigating the range of potential future precipitation changes on the potential distribution of mammals. As with birds (Huntley *et al.*, 2006), seasonal changes in precipitation patterns have been shown to be important in modelling mammalian species' distributions successfully; length and intensity of dry and wet seasons affecting mammals for example, by directly limiting the availability of food and/or water (Chapter 2.2).

For each GCM, precipitation and temperature anomalies between present and future time periods were interpolated to 2.5' resolution and applied to the values of the WORLDCLIM present-day climate. Data were then re-sampled to a resolution of 0.25° to match the resolution of the species datasets. These values were then used to calculate the values of the bioclimatic variables used for modelling the potential distribution of each species; these variables were 'mean temperature of the coldest month' (MTCO), 'mean temperature of the warmest month' (MTWA), 'ratio of actual to potential evapotranspiration' (APET) plus the variable which maximised AUC for the current climate simulations (totdrydur, totdryint, totwetdur or totwetint) (Chapter 2). APET was calculated using data relating to soil water capacity and the calculated daily potential insolation (as in Huntley *et al.* 1995). Bioclimatic variables representing length and intensity of the dry and wet seasons were derived using daily values of the ratio of precipitation to potential evapotranspiration (P/PE) (Willis *et al.* 2008).

Climate response surfaces were fitted using the species' simulated present day presence-absence points plus and recent climate (Chapter 2) and were used to simulate the potential future ranges of each species for each of the nine future climate scenarios. Presence-absence values for species' future distributions were produced by transforming species' probabilities of occurrence using the same threshold values (κ) obtained when simulating the present day species' distributions.

3.2.2. Assessing the potential future distributions of African mammals

3.2.2.1. Species richness

The sum of species in each 0.25° cell across Africa was calculated for the present-day and all nine future scenarios using species' presence-absence data. Mean species richness across the continent for all scenarios was calculated as well as the change in species richness between the current and nine future scenarios.

3.2.2.2. Species Prevalence

Species prevalence describes a species' extent of occurrence. It was obtained by calculating the number of 0.25° cells in which a species was simulated to be at present and in the nine future scenarios. Changes in species' prevalence were calculated (i.e. potential future prevalence as a percentage of simulated current prevalence) for the three GCMs for each time slice (2020, 2050 and 2080). Individual species- and collective species responses were analysed.

3.2.2.3. Species Range Shifts – in Space and Time

Size and overlap between current and future ranges were investigated by overlaying simulated occurrence under different scenarios and at different time periods. By examining range changes at intermediate time points (e.g. 2020 and 2050) rather than just at the start and end of the century, it was also possible to look for temporal changes in range sizes. In this case, the species might have to be maintained *ex situ* until a time in the future when the climate becomes suitable again.

In order to examine disparity between species current and potential future ranges, every 0.25° cell where an individual species' current and potential future range overlapped was noted. Then for each species individually, the percentage overlap between current and future range was recorded; some examples of these were visualised in ArcMap. Collective species' responses were also recorded so as to gain an idea of spatial and temporal disparity of mammalian species' distributions as a whole as climate changes.

3.3. RESULTS: Species Responses to Potential Future Climate Change

3.3.1. Species Richness

Average species richness across the African continent decreased from the present day to the 2020's (-1.09%), 2050's (-2.78%) and 2080's, with the scenarios for the 2080's projecting the highest decrease species richness of 4.41% (HadCM3 = -6.86%, ECHAM4 = -5.51% and GFDL = -0.87%). These are optimistic estimates as we have made the assumption that all species will be able to fulfil their potential future distributions (Huntley *et al.*, 2006), so the potential decreases could be greater. For all time periods, the GFDL scenarios predict smaller decreases in overall species richness than either the HadCM3 or ECHAM4 GCMs (Table 3.1).

Table 3.1. Simulated species richness across Africa under nine potential future climate change scenarios. Species richness is defined as the average number of species per 0.25° cell in Africa.

	Scenario									
	Simulated Current	HadCM3 B2			ECHAM4 B2			GFDL B2		
		2020	2050	2080	2020	2050	2080	2020	2050	2080
Species Richness	36.24	35.75	35.13	33.75	35.74	34.84	34.24	36.04	35.74	35.93
Percentage Change (%)		-1.34	-3.06	-6.86	-1.37	-3.87	-5.51	-0.55	-1.40	-0.87

Areas of Africa with highest species richness at present are in Eastern Africa; in countries such as Kenya, Tanzania and Uganda. This remains the case in all three future scenarios for the 2080s (i.e. highest species richness remains in Uganda). However, species richness is projected to decrease in Zambia, Malawi and northern Mozambique when compared to the present-day pattern; this is most pronounced under the HadCM3 B2 scenario for 2080

(Figure 3.1). Western Africa (e.g. Liberia, Sierra Leone and Guinea) is projected to experience potential decreases in species richness as is much of Northern Sub-Saharan Africa (e.g. Cameroon, Central African Republic, southern Sudan and the Democratic Republic of the Congo).

Areas of relatively moderate species richness at the northern tip of Africa (Morocco, Algeria and Tunisia) remain fairly similar in the future, as do the relatively low species richness areas across North Africa (e.g. Egypt, Mauritania and the northerly parts of Malawi, Niger, Chad and Sudan). Conversely, in South-Western Africa (i.e. South Africa and Southern Namibia) species richness decreases under all future scenarios for 2080, being most pronounced under the ECHAM4 and HadCM3 B2 scenarios. However, species richness at the tip of the South African Cape increases slightly (Figure 3.1), presumably due to the poleward movement of species in order to track climate conditions to which they are adapted.

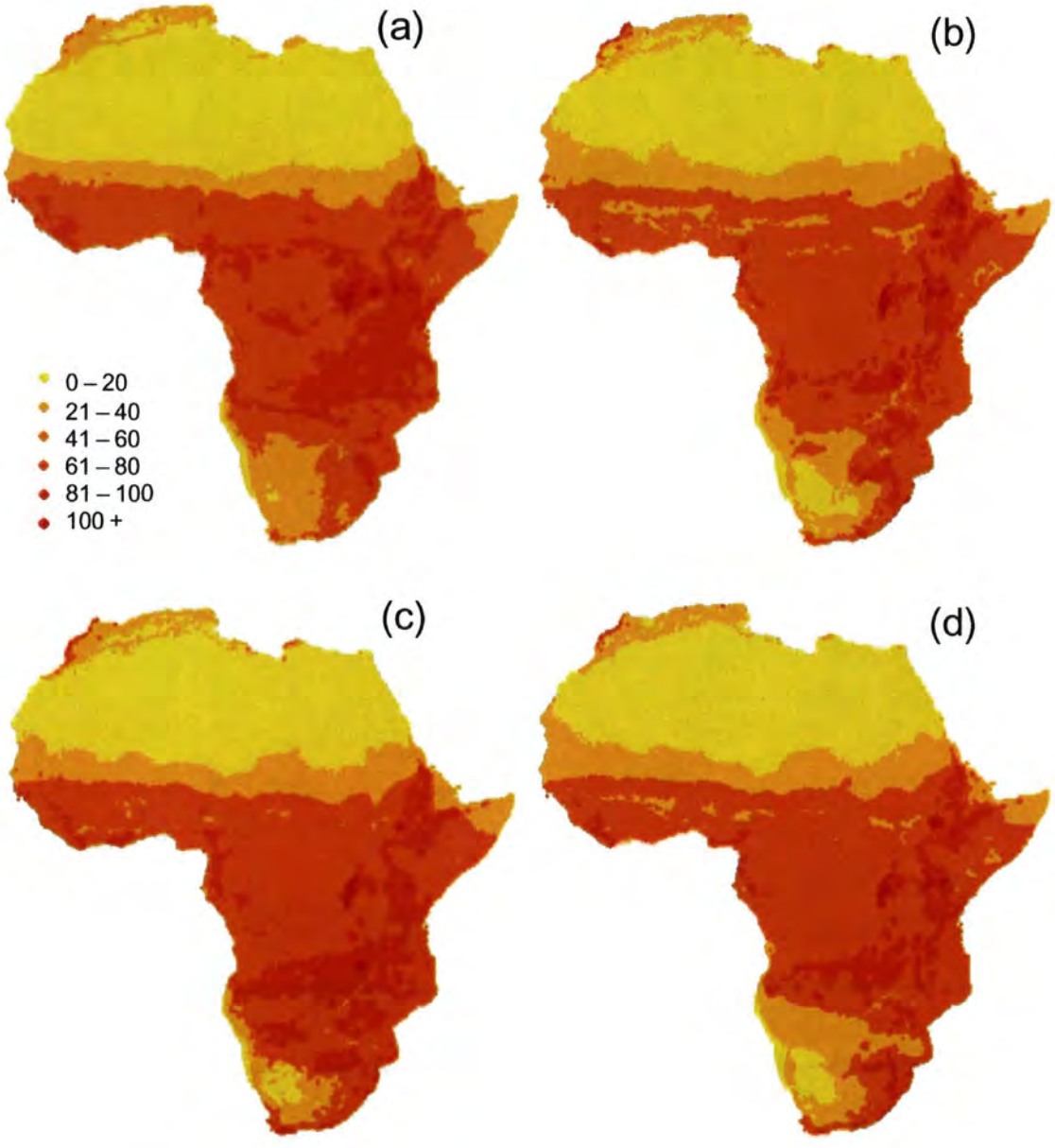


Figure 3.1. Simulated current and potential future diversity of African mammals.

Each 0.25° grid cell shows the diversity of species simulated to be present in each cell. The maps depict simulated current (a) and potential future species diversity for the year 2080 (years 2070-99) and under the (b) ECHAM4 B2, (c) GFDL B2 and (d) HadCM3 B2 scenarios. The key represents number of species in each grid cell. Increasingly darker areas on these maps depict areas of increasing species richness.

3.3.2. Species Prevalence

3.3.2.1. Individual Species Responses

Simulated-present and potential-future distributions of several species in response to predicted climate change are shown in Figure 3.2i to 3.2ix. These figures illustrate the potential extent and nature of individual species spatial responses to climate change (see appendices for instructions on how to view distributions of all 281 species). For example the Lesser Egyptian Jerboa (*Jaculus jaculus*) is projected to experience large decreases in climatically suitable habitat in the Western parts of its range (i.e. Namibia, Angola and Zambia) by the 2080s, especially under the ECHAM4 and HadCM3 B2 scenarios (Figure 3.2i). Whereas the Greater Egyptian Jerboa (*Jaculus orientalis*) is projected to lose habitat currently suitable in Egypt and Libya while simultaneously experiencing increases in parts of South Africa (Figure 3.2viii).

The Common Jackal (*Canis aureus*) is predicted to have a fairly stable northerly range, including the Horn of Africa, while experiencing an increase in climatically suitable habitat in Namibia, Botswana and South Africa (Figure 3.2iii). The location of suitable habitat for the Bush Pig (*Potamochoerus larvatus*) remains fairly static, however the extent of climatically suitable area is reduced and becomes increasingly fragmented by the 2080s (Figure 3.2iv). This is similar to the Elephant (*Loxodonta africana*) which is predicted to experience contraction of climatically suitable area southwards from its northern range in the Central African Republic and Southern Sudan while the general pattern and location of the rest of suitable habitat remains fairly static.

Some species are predicted to experience massive increases in range, especially by 2080. For example, the Red-Bellied Monkey's (*Cercopithecus erythrogaster*) relative extent is predicted to increase by 966% by 2080 as it's potential range increases in the easterly direction (Figure 3.3). Collectively, over half (n = 144) of the 281 species are predicted to potentially experience an increase in extent for at least one future scenario (i.e. over 100% of current distribution), whereas sixty-eight species are predicted to potentially experience an increase in extent for all nine future scenarios. See Table A2 (appendices) for species' projected prevalence at present and under the nine projected future climate change scenarios.

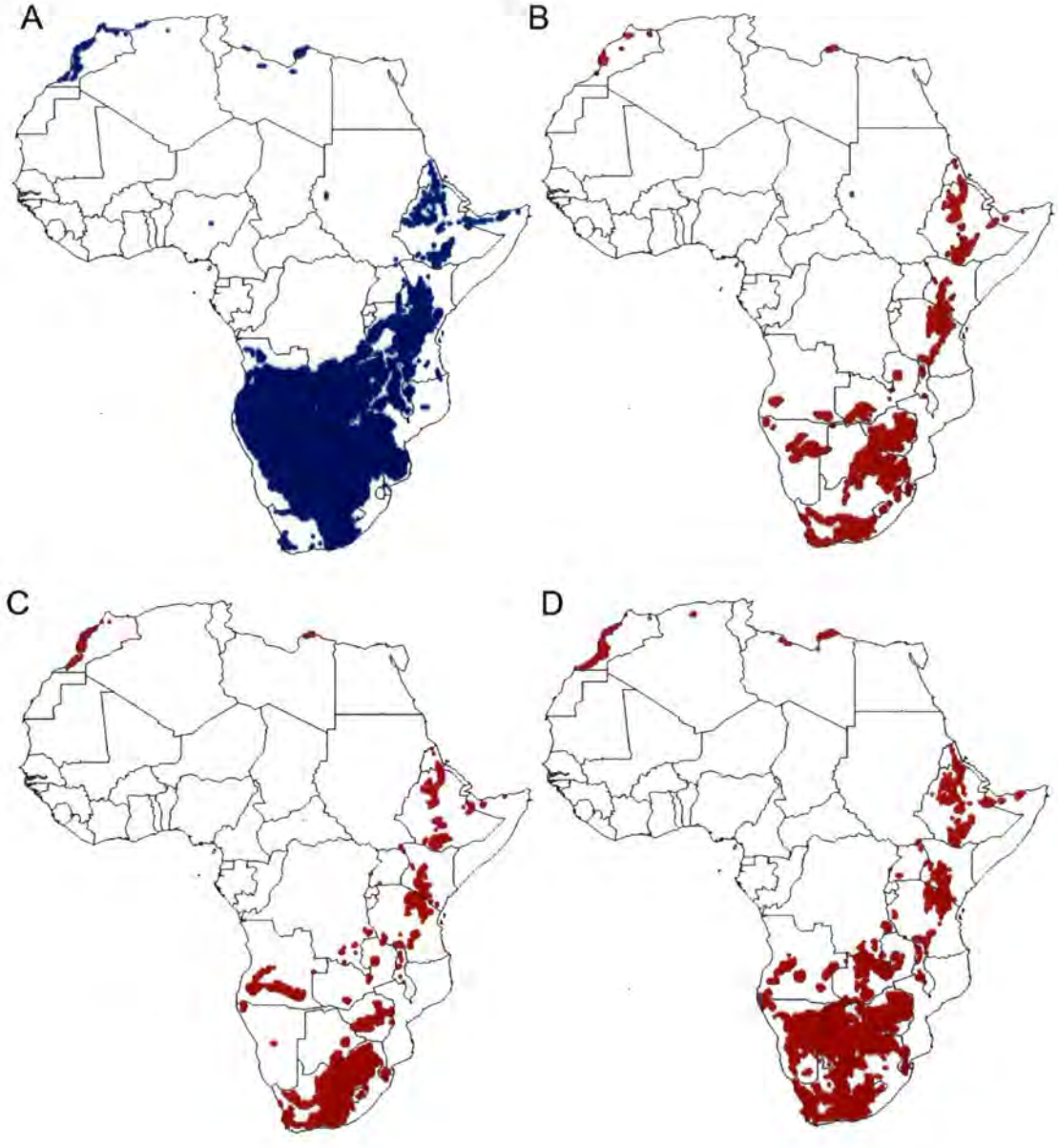


Figure 3.2i. Simulated current and potential future distribution of the Lesser Egyptian Jerboa (*Jaculus jaculus)*. The maps depict simulated current (A) and potential future distribution of *J. jaculus* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.998.

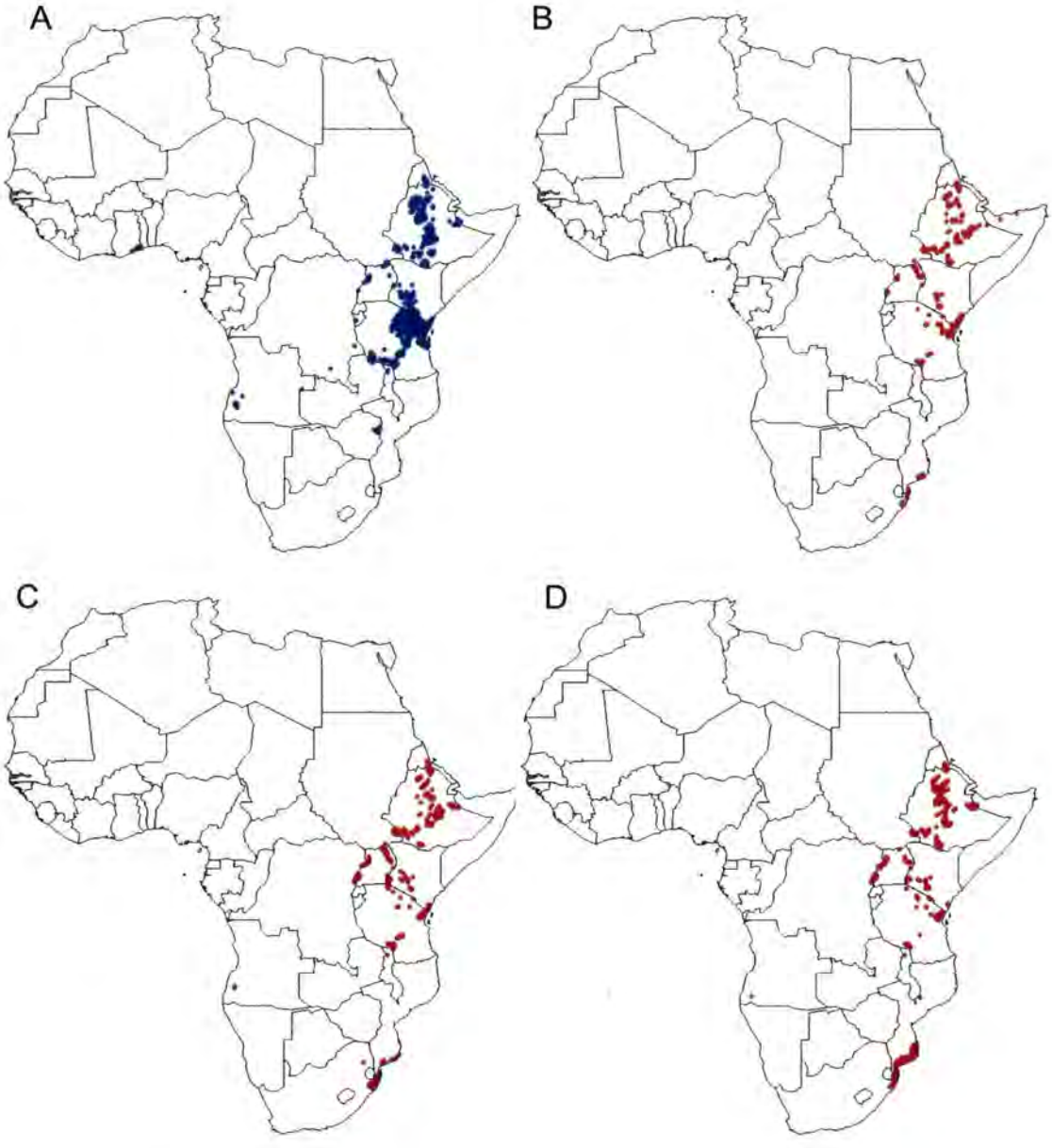


Figure 3.2ii. Simulated current and potential future distribution of the Harvey's Duiker (*Cephalophus harvey)*. The maps depict simulated current (A) and potential future distribution of *C. harvey* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.986.

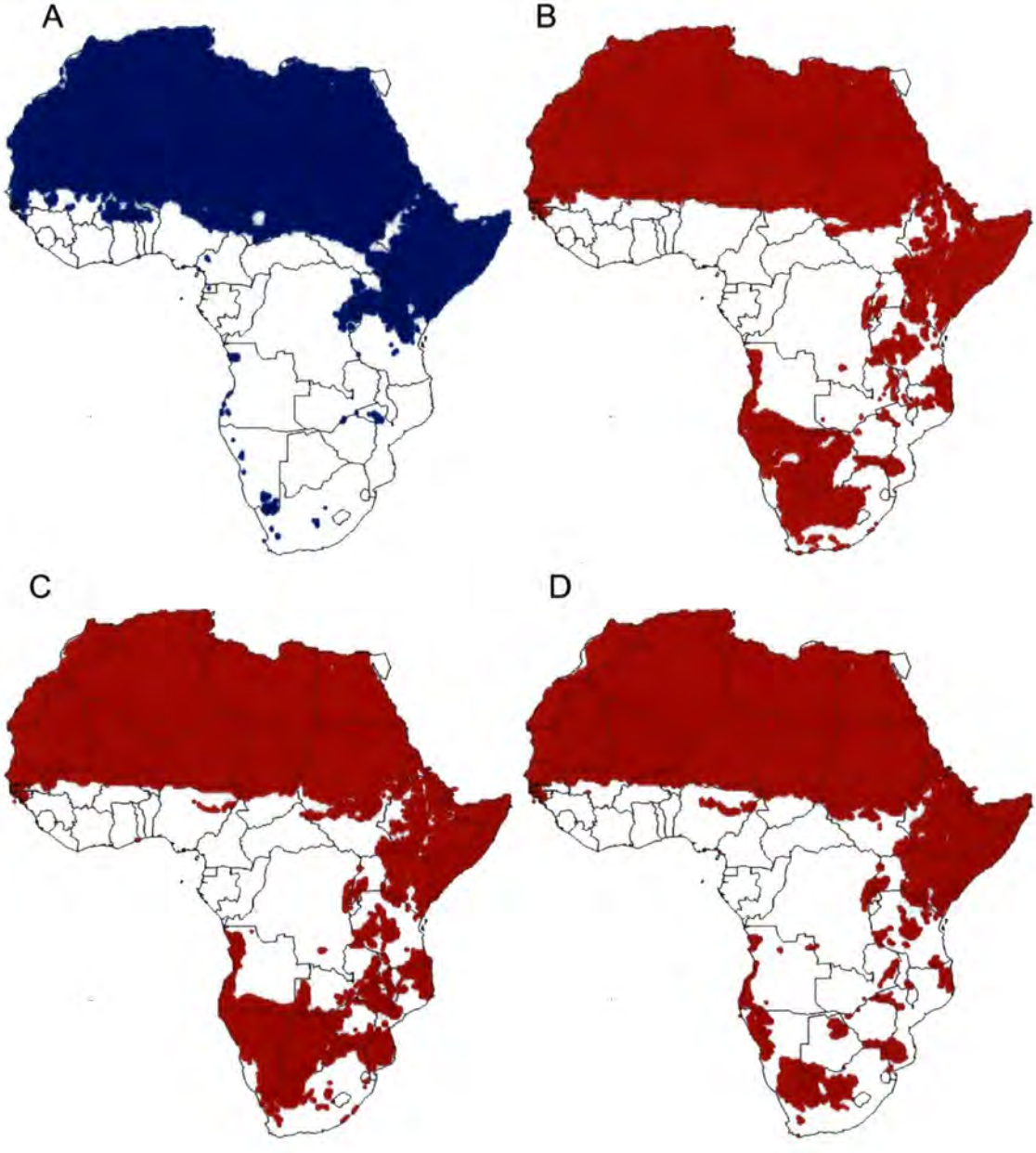


Figure 3.2iii. Simulated current and potential future distribution of the Common Jackal (*Canis aureus)*. The maps depict simulated current (A) and potential future distribution of *C. aureus* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.982

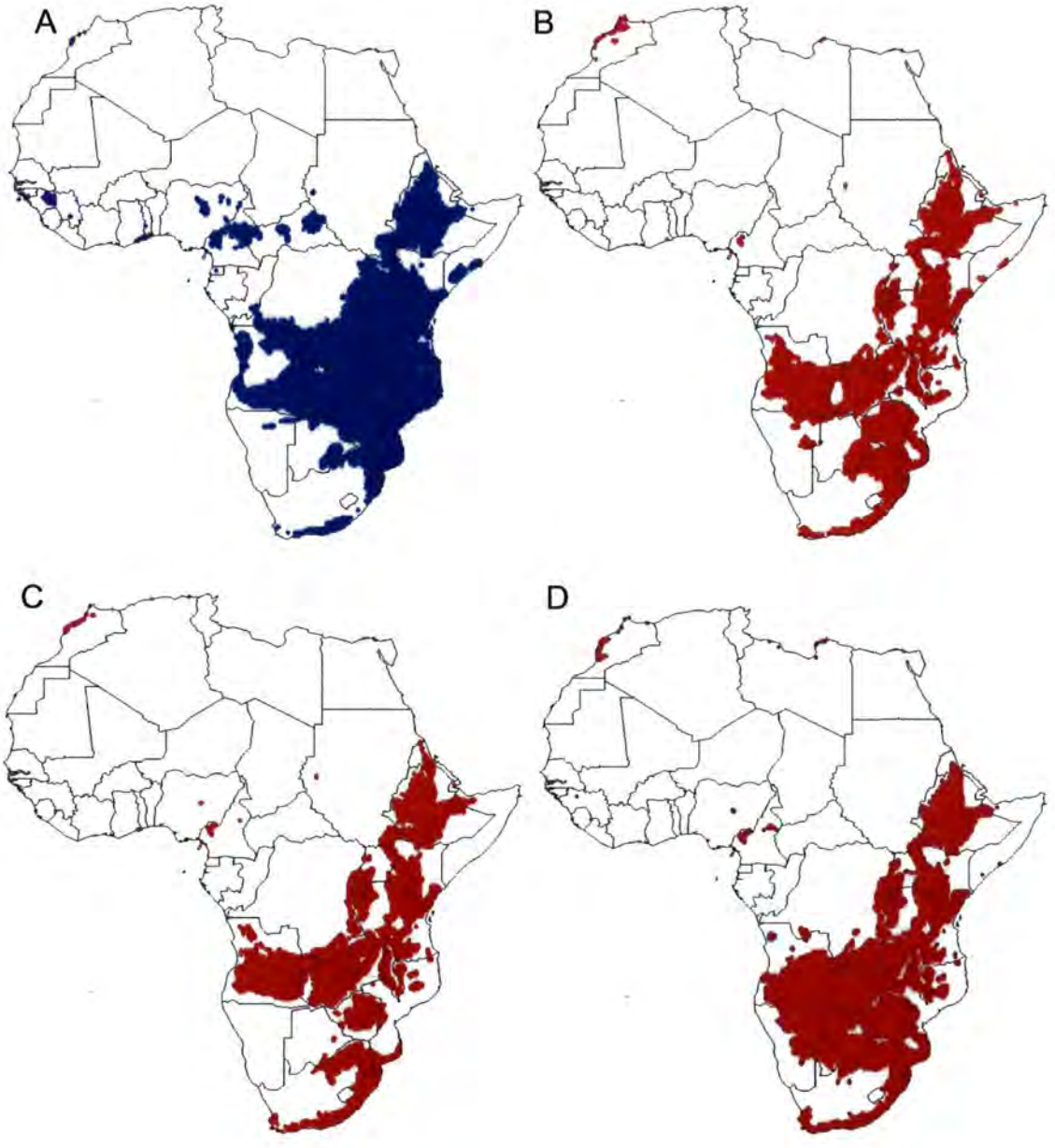


Figure 3.2iv. Simulated current and potential future distribution of the Bush Pig (*Potamochoerus larvatus)*. The maps depict simulated current (A) and potential future distribution of *P. larvatus* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.972

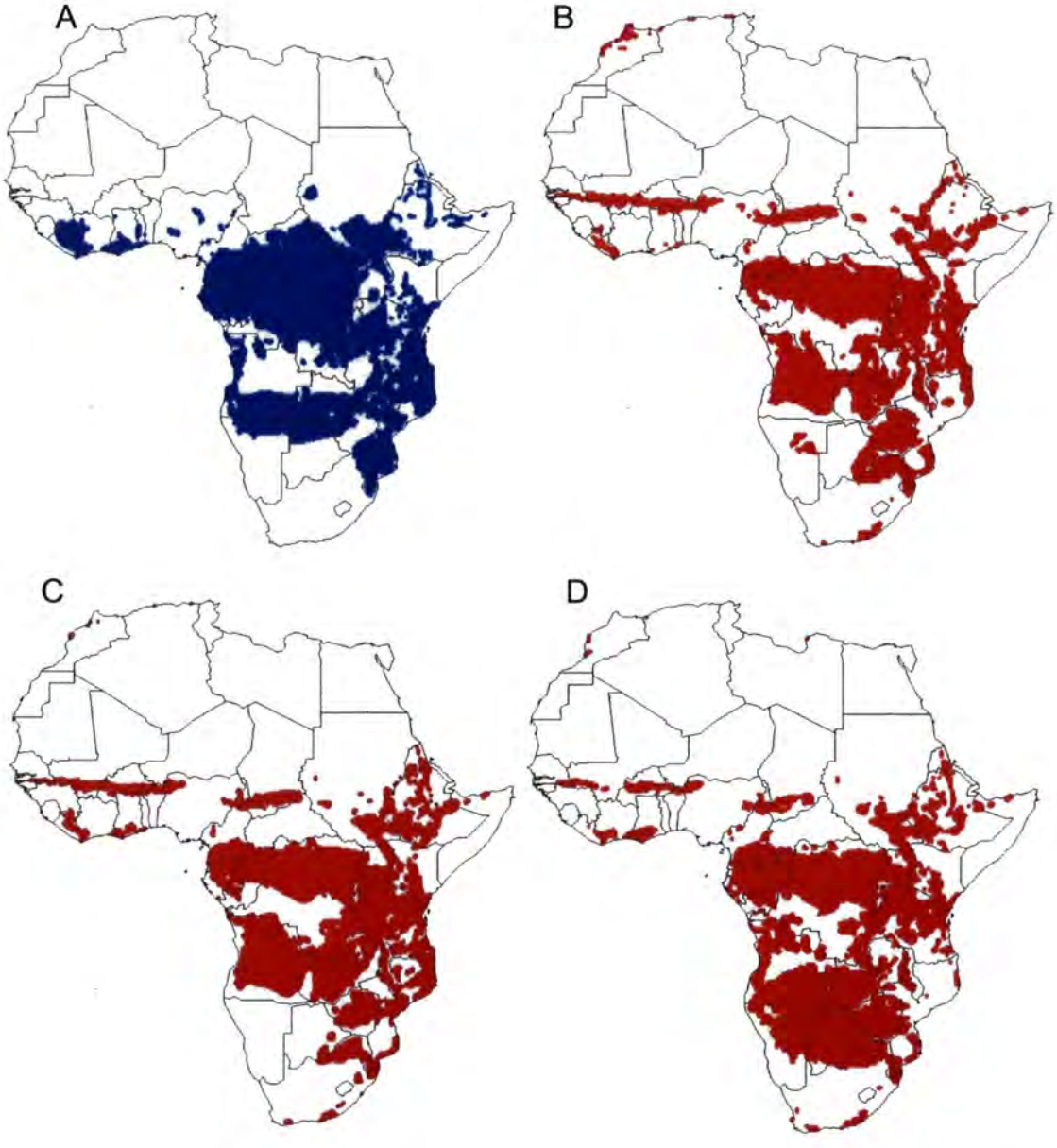


Figure 3.2v. Simulated current and potential future distribution of the Elephant (*Loxodonta africana*). The maps depict simulated current (A) and potential future distribution of *L. africana* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.988.

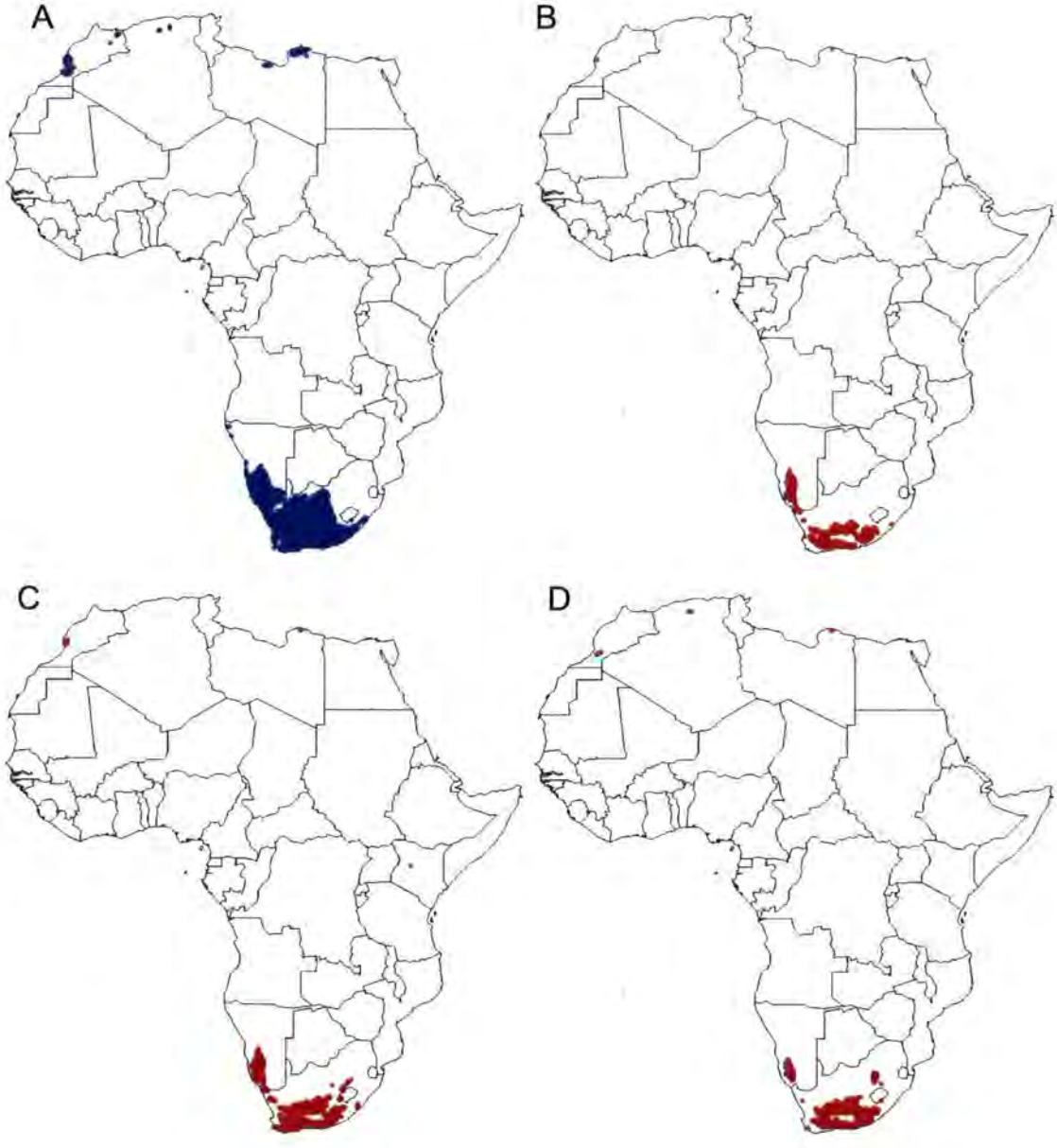


Figure 3.2vi. Simulated current and potential future distribution of the Scrub Hare (*Lepus saxatilis)*. The maps depict simulated current (A) and potential future distribution of *L. saxatilis* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.998.

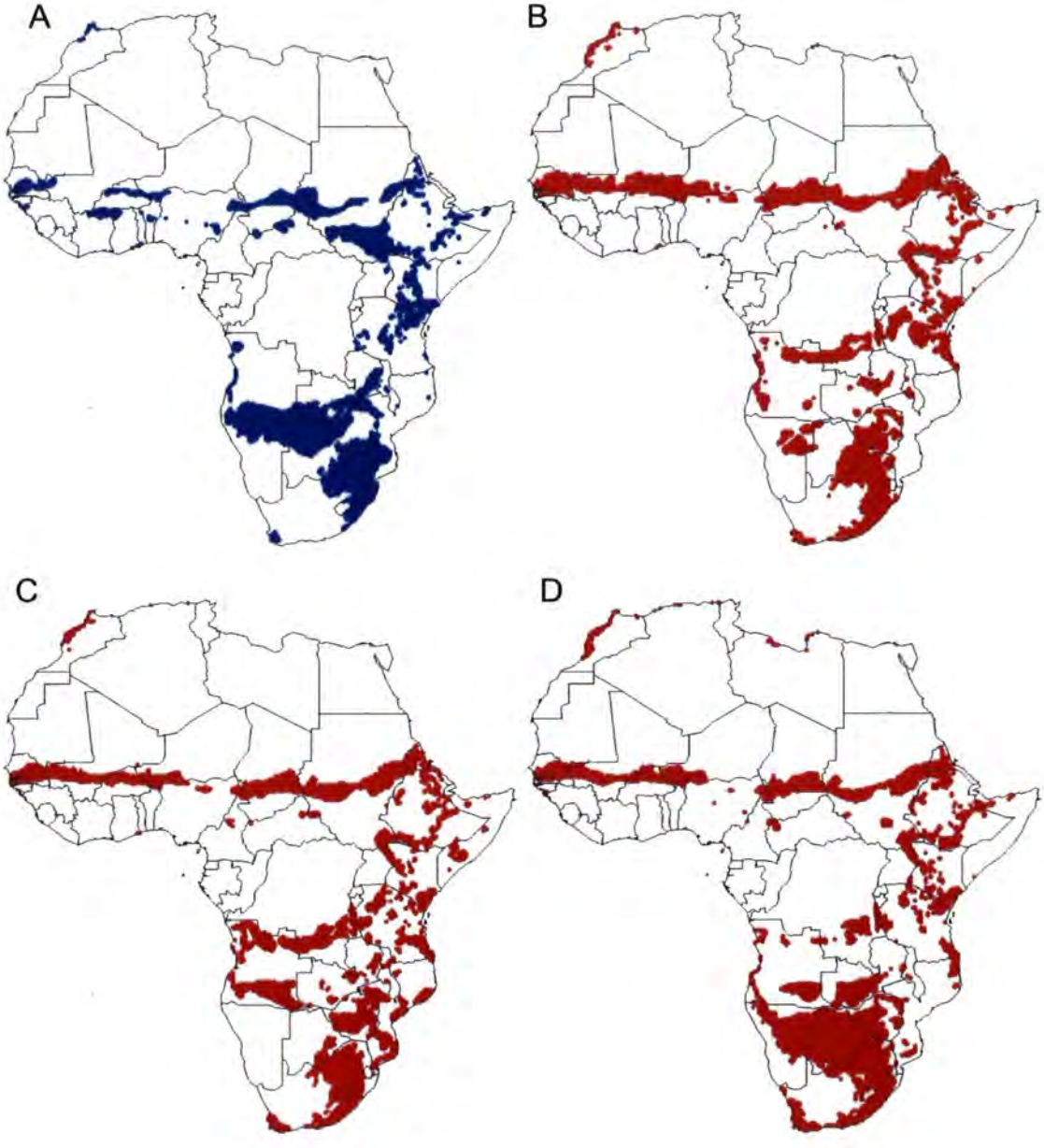


Figure 3.2vii. Simulated current and potential future distribution of the Giraffe (*Giraffa camelopardalis)*. The maps depict simulated current (A) and potential future distribution of *G. camelopardalis* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.942.

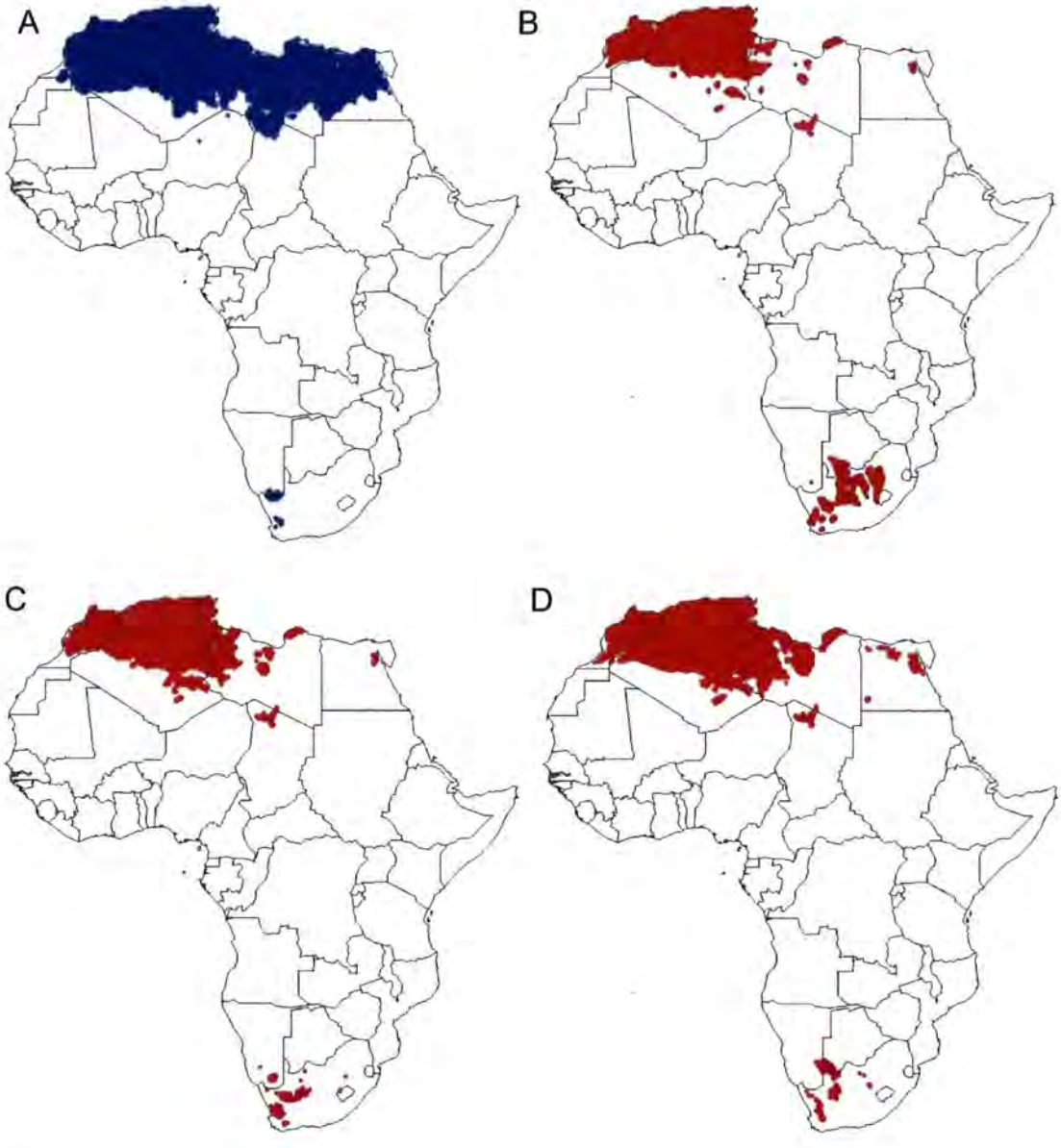


Figure 3.2viii. Simulated current and potential future distribution of the Greater Egyptian Jerboa (*Jaculus orientalis*). The maps depict simulated current (A) and potential future distribution of *J. orientalis* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.991.

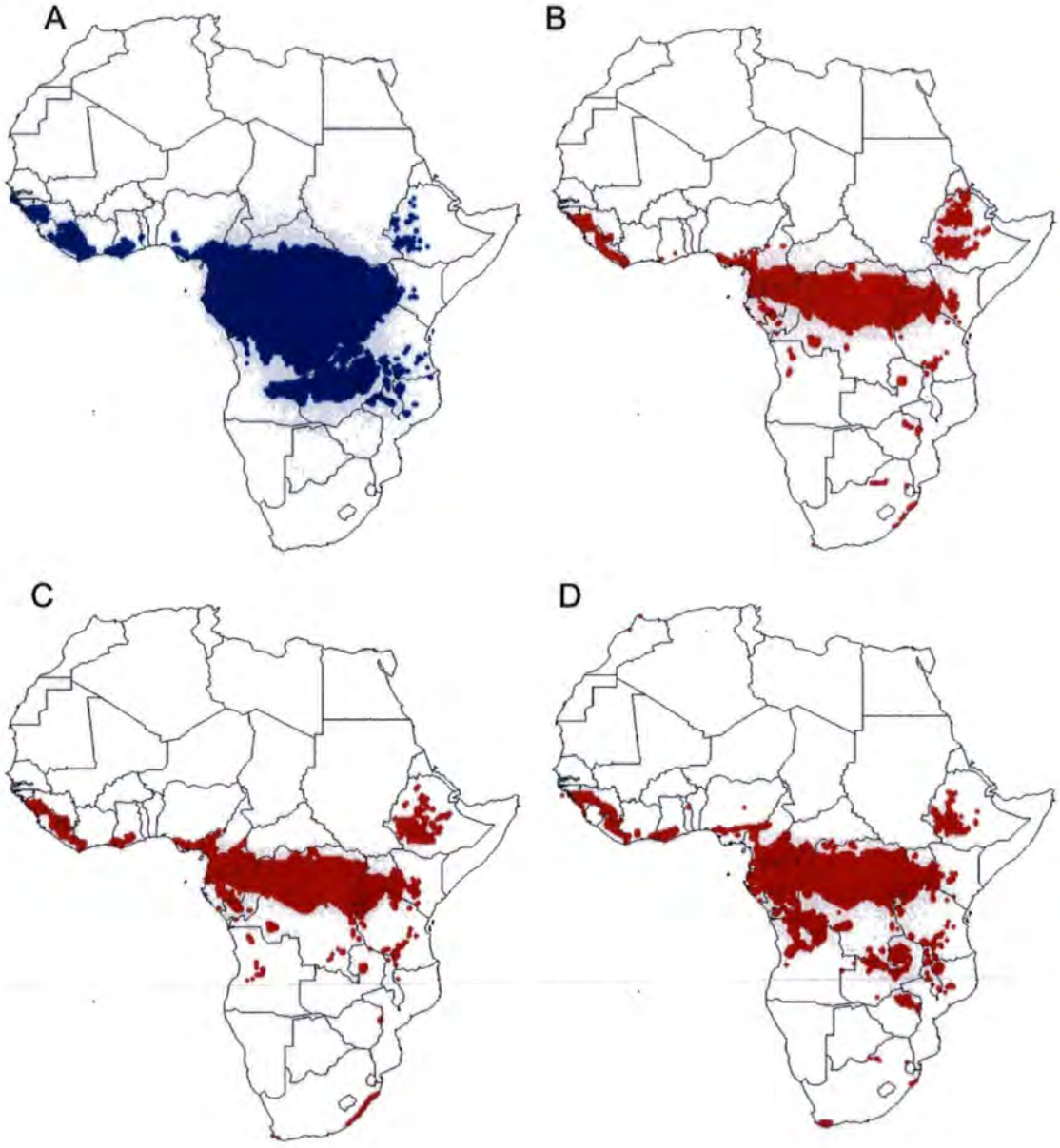


Figure 3.2ix. Simulated current and potential future distribution of the Marshbuck (*Tragelaphus spekii*). The maps depict simulated current (A) and potential future distribution of *T. spekii* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.979.

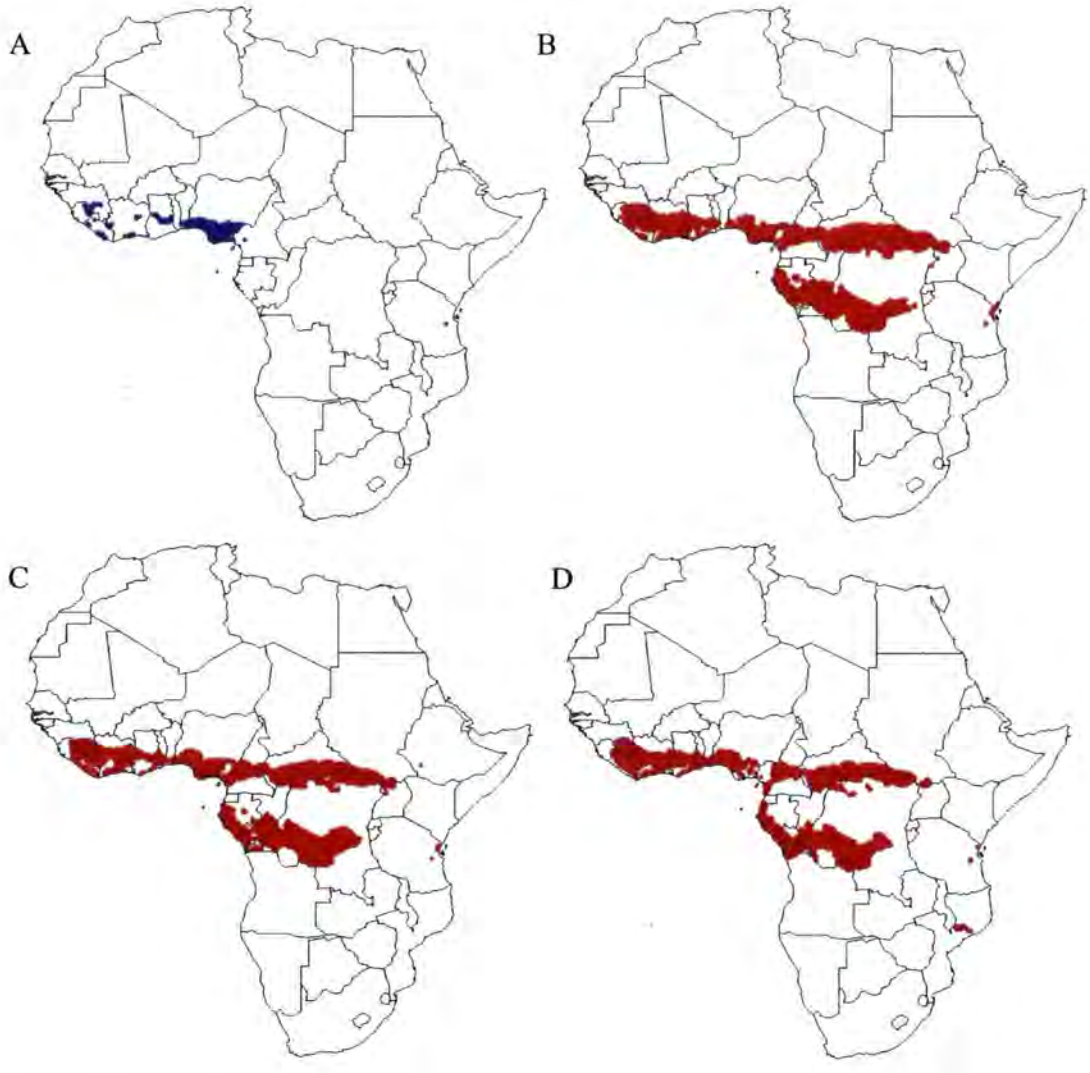


Figure 3.3. Simulated current and potential future distribution of the Red-Bellied Monkey (*Cercopithecus erythrogaster*). The maps depict simulated current (a) and potential future species distribution of *C. erythrogaster* for the year 2080 under the (b) ECHAM4 B2, (c) HadCM3 B2 and (d) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. AUC = 0.997.

Conversely, a handful of species are predicted to experience massive range decreases. The potential future distributions of five species are predicted to be reduced to zero for at least one future scenario (Table 3.2); five others are predicted to occupy less than 10% of their simulated present distribution for at least one future scenario. Distribution maps for these species are given in Figure 3.4i to 3.4x. These ten species include species already listed as vulnerable, endangered or critically endangered in the IUCN red list (IUCN, 2006) such as the critically endangered Bushman hare (*Bunolagus monticularis*) and Walia Ibex (*Capra walie*) (Table 3.2).

Table 3.2. Species whose potential future distributions are predicted to occupy less than 10% of their simulated present distribution (for at least one future scenario (GFDL, ECHAM4, HadCM3 for 2020, 2050 or 2080)). Extent of occurrence (EO) is expressed as future distribution as a percentage of simulated current distribution either as 0% (0) or less than 10% (<10). Also shown is the current IUCN red list categories for each species.

Ref. Number	Scientific Name	Common Name	Red List Category	EO
181	*Bunolagus monticularis*	Bushman Hare	Critically Endangered	0
8	*Capra walie*	Walia Ibex	Critically Endangered	0
7	*Capra nubiana*	Nubian Ibex	Endangered	0
238	*Cercopithecus solatus*	Sun-tailed Monkey	Vulnerable	0
159	*Vulpes cana*	Steppe Fox	Vulnerable	0
177	*Hemiechinus auritus*	Long-eared Hedgehog	Lower Risk	<10
62	*Okapia johnstoni*	Okapi	Lower Risk	<10
111	*Felis chaus*	Jungle Cat	Least Concern	<10
272	*Allactaga tetradactyla*	Four-toed Jerboa	Data Deficient	<10
225	*Cercopithecus dryas*	Dryad Monkey	Data Deficient	<10

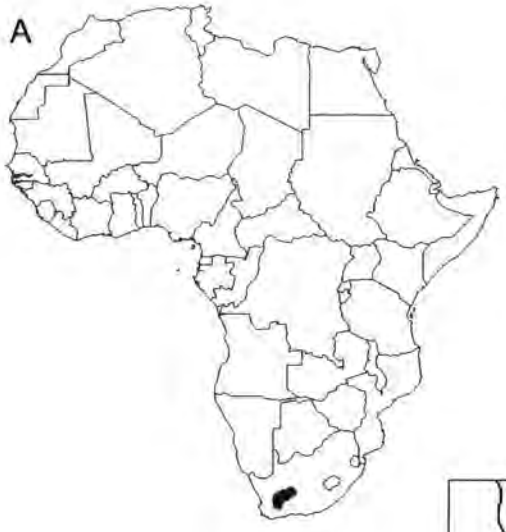
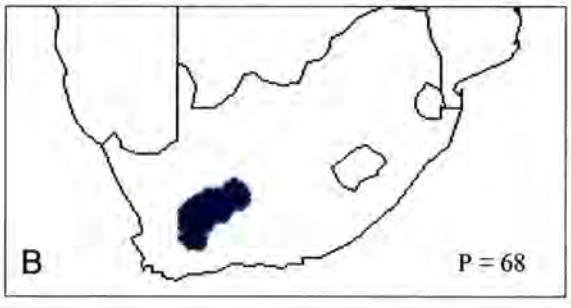


Figure 3.4i. Simulated current and potential future distribution of the Bushman Hare (*Bunolagus monticularis*). The maps depict simulated current (A and B) and potential future distribution of *B. monticularis* for the year 2080 under the (C) ECHAM4 B2 and (D) HadCM3 B2 scenarios. (GFDL B2 2080 scenario not included as *B. monticularis* is simulated to be absent). Blue/red areas depict where the species is simulated to occur.

AUC = 1.000



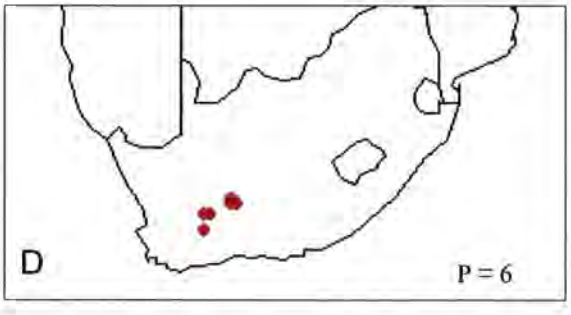


Figure 3.4ii. Simulated current and potential future distribution of the Walia Ibex (*Capra walie*). The map depicts only the simulated current distribution of *C.walie* as this species was simulated to be absent for the potential future scenarios for the year 2080. Blue areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 1.000.

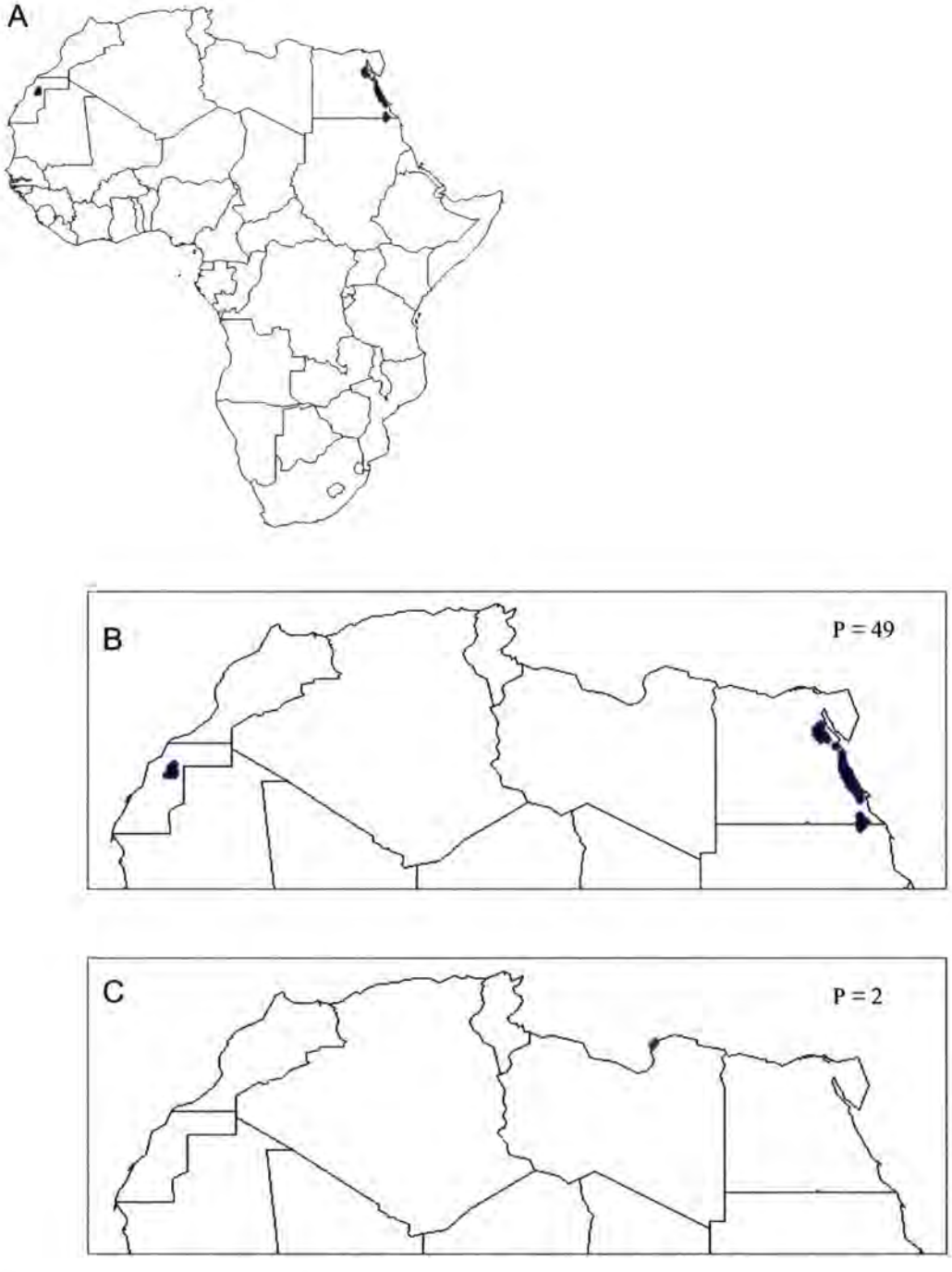


Figure 3.4iii. Simulated current and potential future distribution of the Nubian Ibex (*Capra nubiana).* The maps depict simulated current (A and B) and potential future distribution of *C.nubiana* for the year 2080 under the (C) ECHAM4 B2 scenario. (HadCM3 B2 and GFDL B2 scenarios not included as *C.nubiana* is simulated to be absent). Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 0.992.

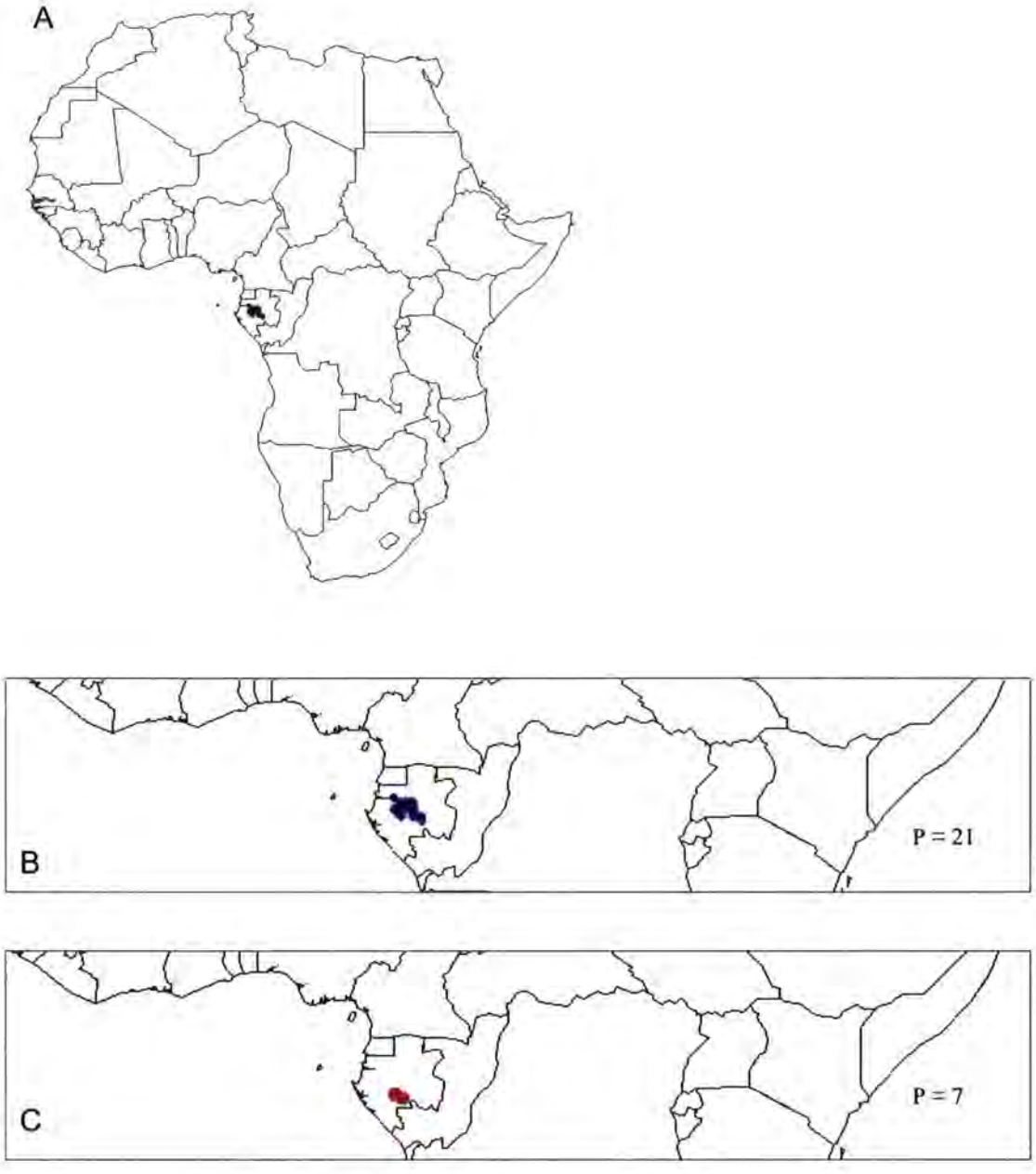


Figure 3.4iv. Simulated current and potential future distribution of the Sun-tailed Monkey (*Cercopithecus solatus)*. The maps depict simulated current (A and B) and potential future distribution of *C.solatus* for the year 2080 under the (C) GFDL B2 scenario. (ECHAM4 B2 and HadCM3 B2 2080 scenarios not included as *C.solatus* is simulated to be absent). Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 1.000.

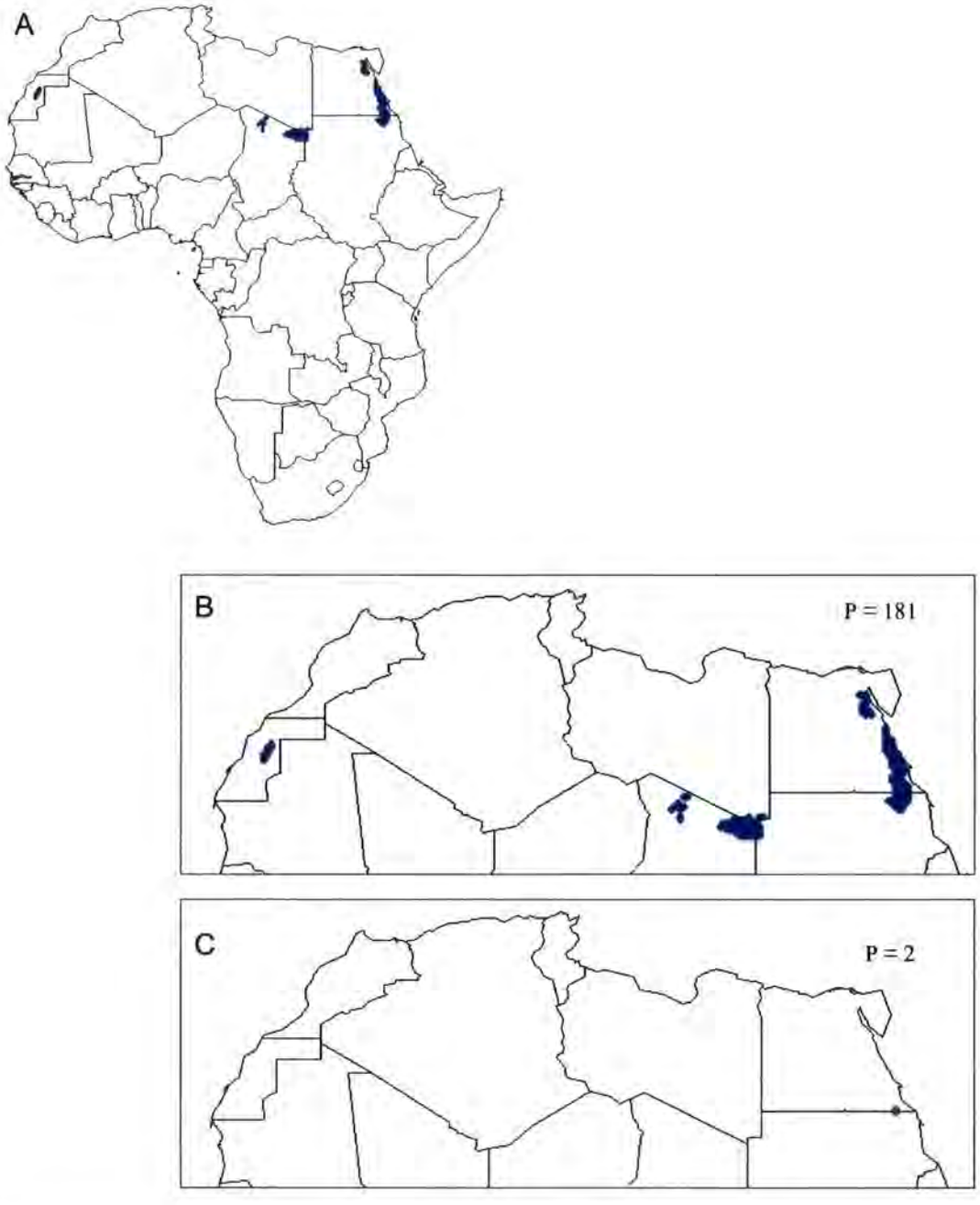


Figure 3.4v. Simulated current and potential future distribution of the Steppe Fox (*Vulpes cana*). The maps depict simulated current (A and B) and potential future distribution of *V. cana* for the year 2080 under the (C) GFDL B2 scenario. (ECHAM4 B2 and HadCM3 B2 2080 scenarios not included as *V.cana* is simulated to be absent). Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 0.994.

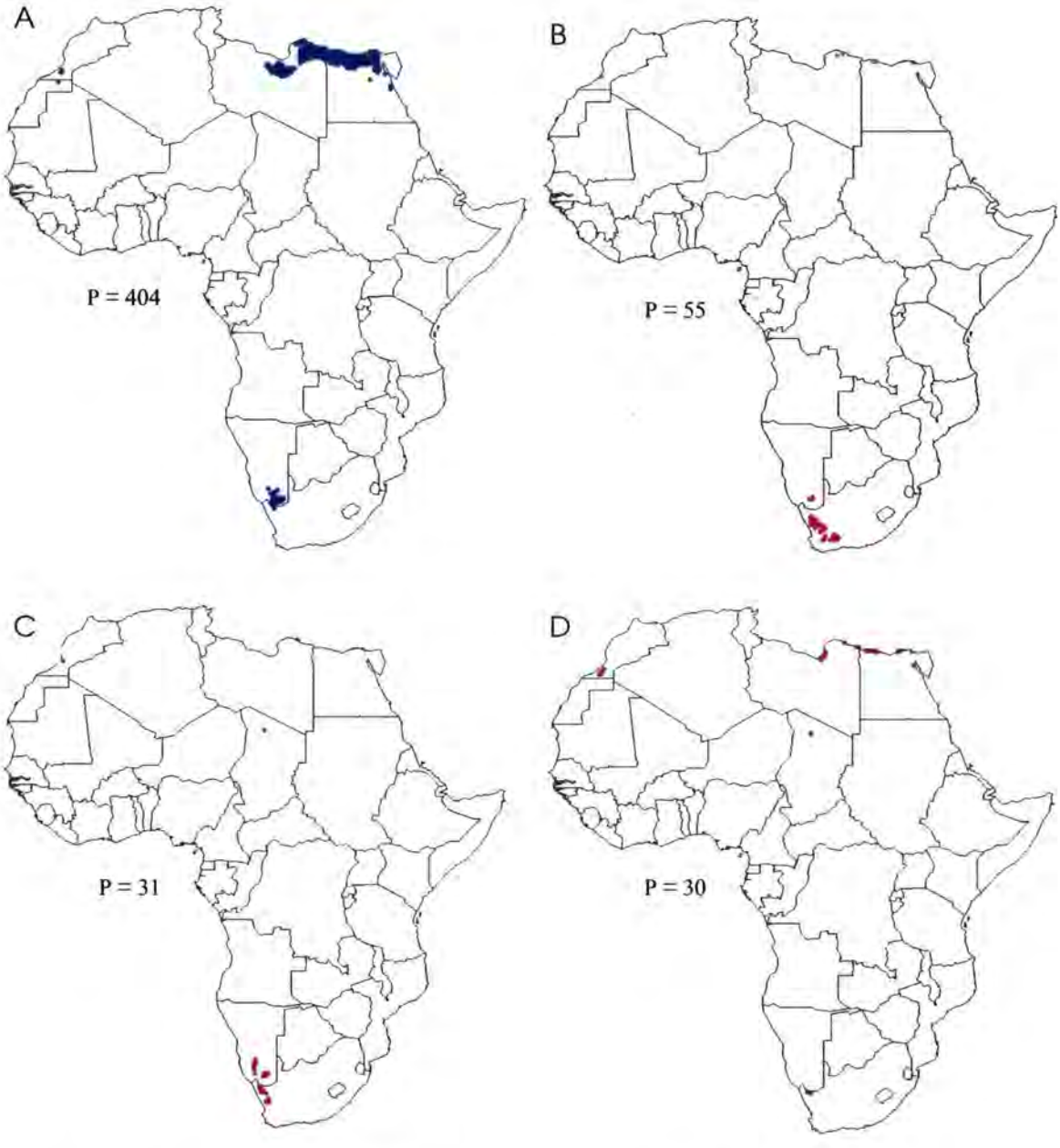
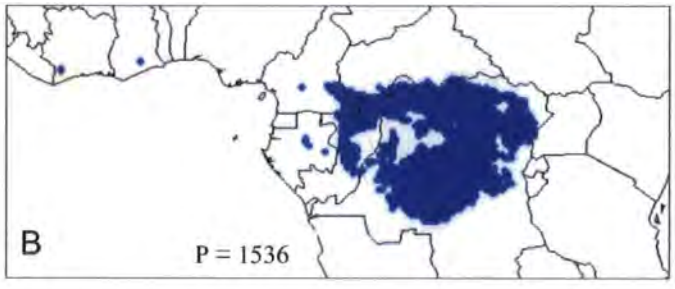
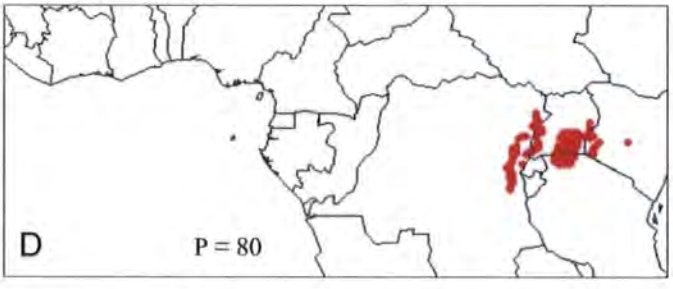


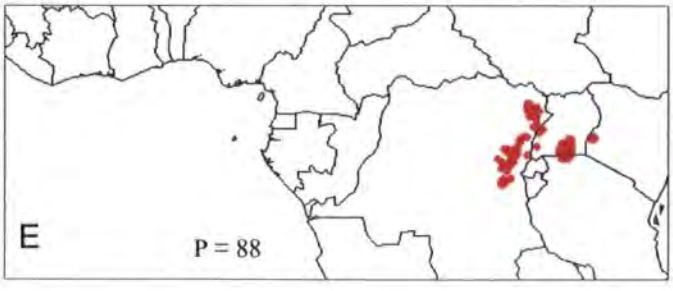
Figure 3.4vi. Simulated current and potential future distribution of the Long-eared Hedgehog (*Hemiechinus auritus)*. The maps depict simulated current (A) and potential future distribution of *H. auritus* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. (ECHAM4 B2 2080 scenario not included as *H. auritus* is simulated to be absent). Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 0.994.

Figure 3.4vii. Simulated current and potential future distribution of the Okapi (*Okapia johnstoni).*

The maps depict simulated current (A and B) and potential future distribution of *O. johnstoni* for the year 2080 under the (C) ECHAM4 B2, (D) HadCM3 B2 and (E) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 0.967.







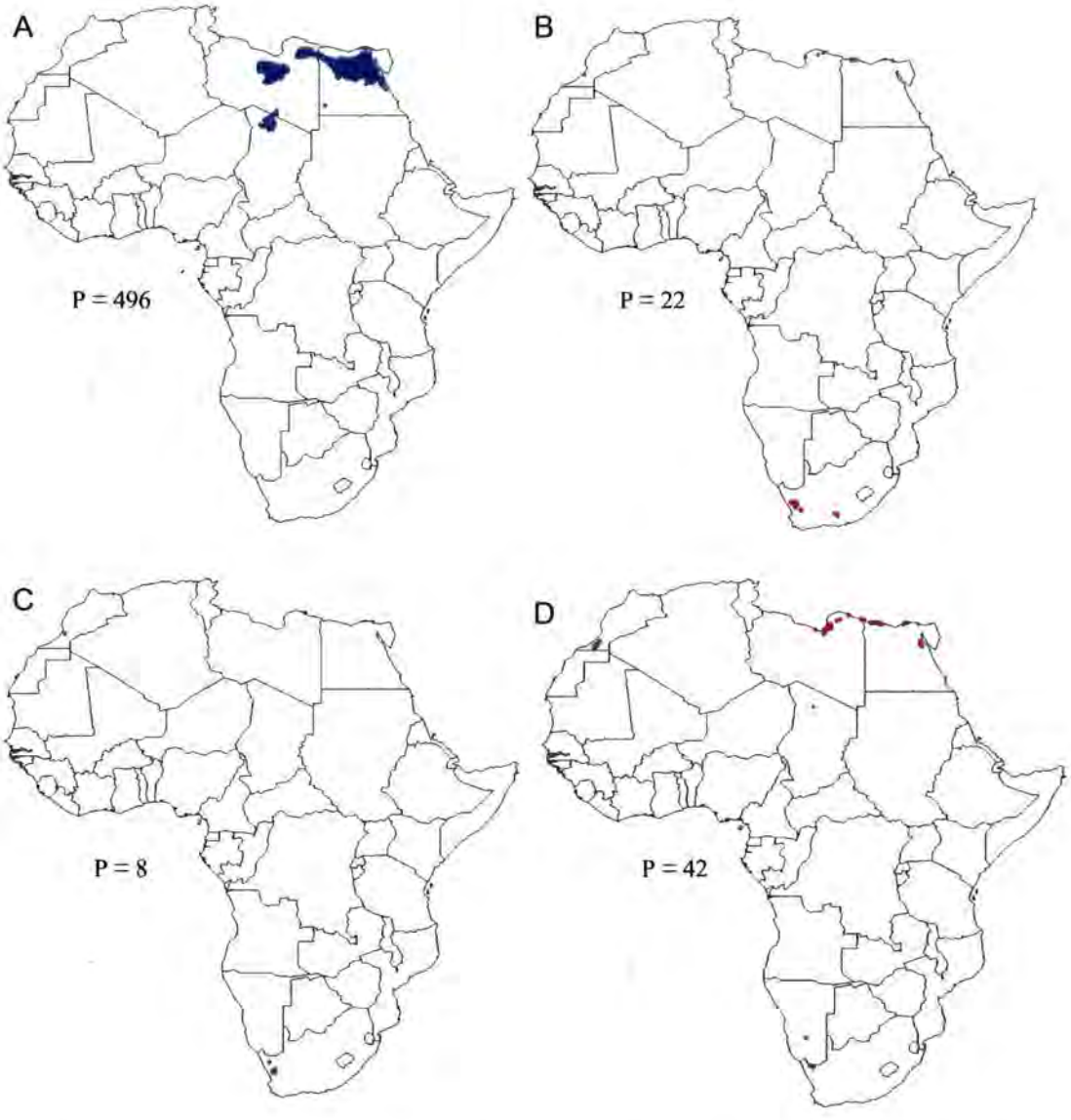


Figure 3.4viii. Simulated current and potential future distribution of the Jungle Cat (*Felis chaus).* The maps depict simulated current (A) and potential future distribution of *F. chaus* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 0.980.

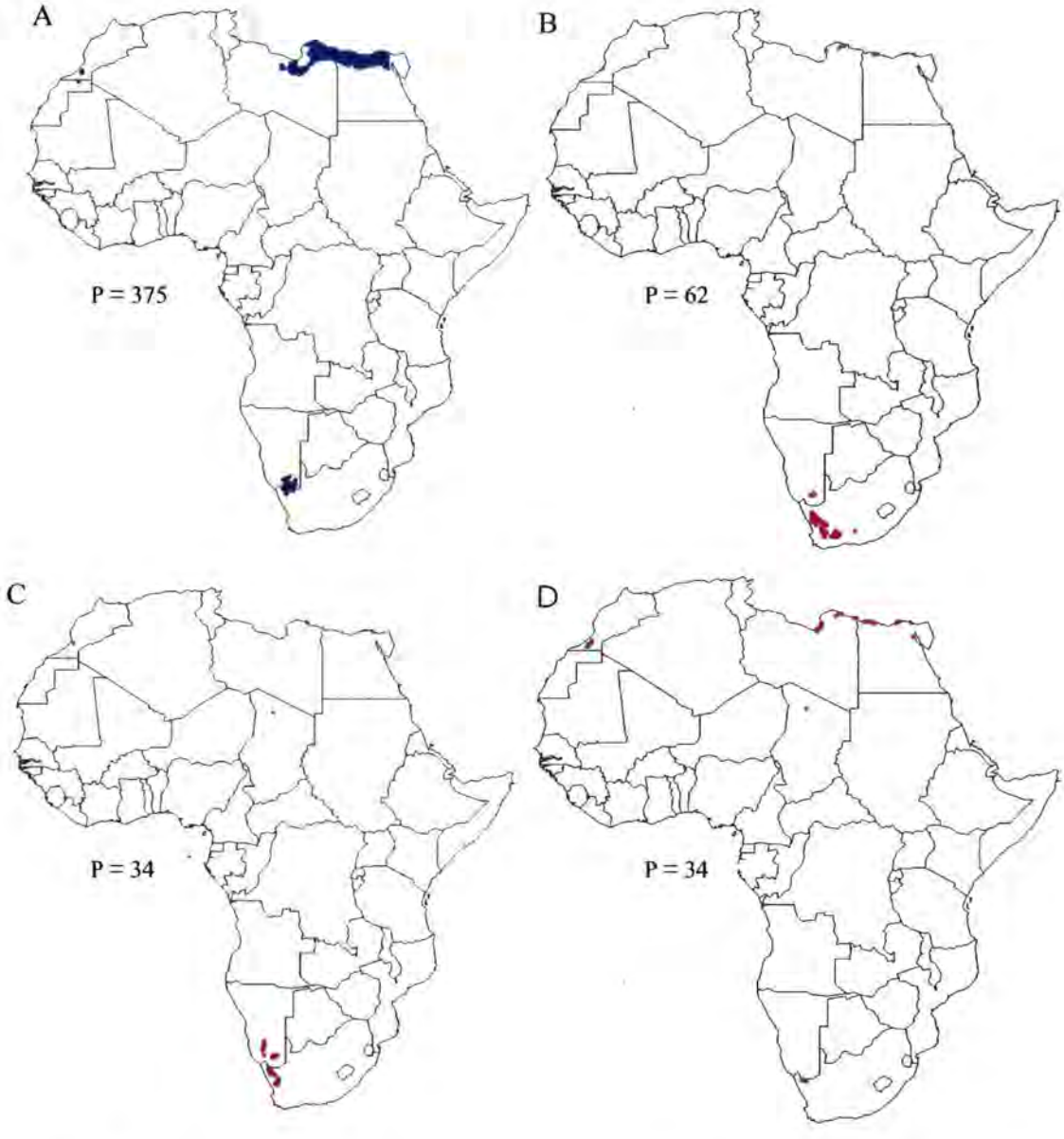
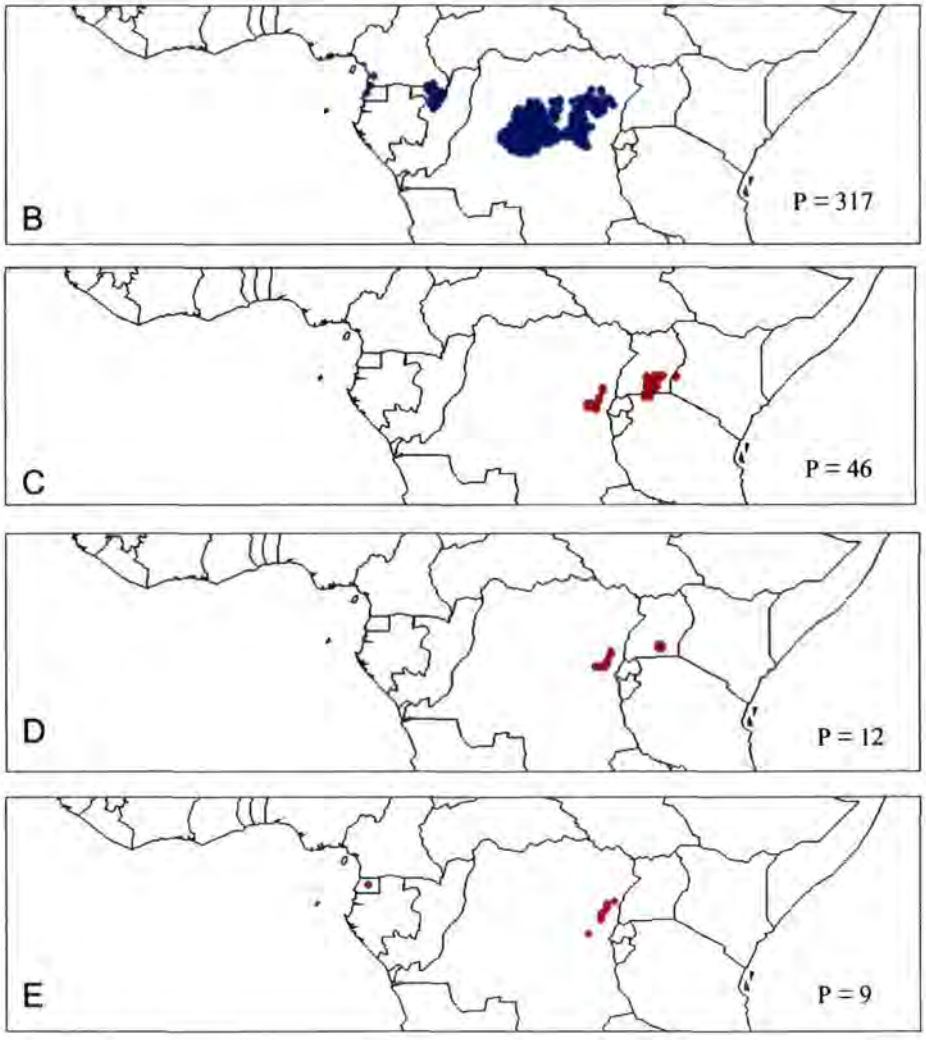


Figure 3.4ix. Simulated current and potential future distribution of the Four-toed Jeroba (*Allactaga tetradactyla).* The maps depict simulated current (A) and potential future distribution of *A. tetradactyla* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence i.e. the number of 0.25° cells the species is simulated to be present. AUC = 0.992.

Figure 3.4x. Simulated current and potential future distribution of the Dryad Monkey (*Cercopithecus dryas*).

The maps depict simulated current (A and B) and potential future distribution of *C. dryas* for the year 2080 under the (C) ECHAM4 B2, (D) HadCM3 B2 and (E) GFDL B2 scenarios. Blue/red areas depict where the species is simulated to occur, black lines represent country borders. 'P' is species prevalence *i.e.* the number of 0.25° cells the species is simulated to be present. AUC = 0.994.



3.3.2.2. Collective Species Responses

The extents of the potential future distributions of the 281 African mammal species modelled were slightly reduced when compared to their current distributions; the HadCM3 B2 scenario modelled simulated ranges to be on average 6.86% smaller than present-day ranges. Those simulated under ECHAM4 B2 simulated ranges showed a reduction of 5.51% and those simulated under GFDL B2 showed a reduction of 0.87% (Table 3.3).

Table 3.3. Simulated current and future prevalence, averaged across the 281 species for each potential future scenario.

	Scenario									
	Simulated Current	HadCM3 B2			GFDL B2			ECHAM4 B2		
		2020	2050	2080	2020	2050	2080	2020	2050	2080
Prevalence	5151	5082	4994	4798	5123	5080	5107	5081	4952	4868
Percentage Change (%)		-1.34	-3.06	-6.86	-0.55	-1.40	-0.87	-1.37	-3.87	-5.51

By 2080, 41% species (n = 114) are expected to have a range size greater than their current range. Conversely, 59% species (n = 167) are expected to experience range contraction (Table 3.4).

Table 3.4. Changes in species ranges in response to three potential future climate change scenarios.

	Number of Species								
GCM	HadCM3 B2			GFDL B2			ECHAM4 B2		
Year	2020	2050	2080	2020	2050	2080	2020	2050	2080
Expanded Range Size	118	116	100	124	127	129	111	109	113
Decreased Range Size	161	165	180	156	154	152	169	171	168
Constant Range Size	2	0	1	1	0	0	1	1	0

An examination of the ratio of future projected to current projected range sizes (using future projections for the period 2080-2099 using the HadCM3 GCM) among species of different biogeographic regions (as defined in Figure 2.8) indicated that there were systematic differences in the projected relative range size dependent upon the region in which a species occurs (ANOVA of relative range size [projected future/projected current

range] df = 4,175, F = 4.83, P<0.001, using species than only occur in a single biogeographic region). An examination of mean relative range size for each biogeographic area suggests, on average, range loss for species of southern Africa (biomes 4 & 5 in Figure 2.8: mean ratio =0.58 and 0.36 respectively). Those species of central Africa show an average increase in potential range extent (biomes 2 & 3 in Figure 2.8: mean ratio = 1.47 and 1.29 respectively). Species occurring in North Africa show an intermediate change in potential range extent (Biome 1: mean ratio = 0.85). Thus it appears that species of more xeric biomes (e.g. biomes 1 & 5) are more likely to have reduced range extent in the future. However, these results are confounded by the fact that many North African desert species have been hunted such that their range extents are now much reduced and hence current range limits may not reflect actual climatic limitations. Similarly, because there are systematic differences in model performance (as measured by AUC, Figure 2.4) between species of differing biogeographic affinities this confounds any attempts to generalize as which species will fare best under future climate projections.

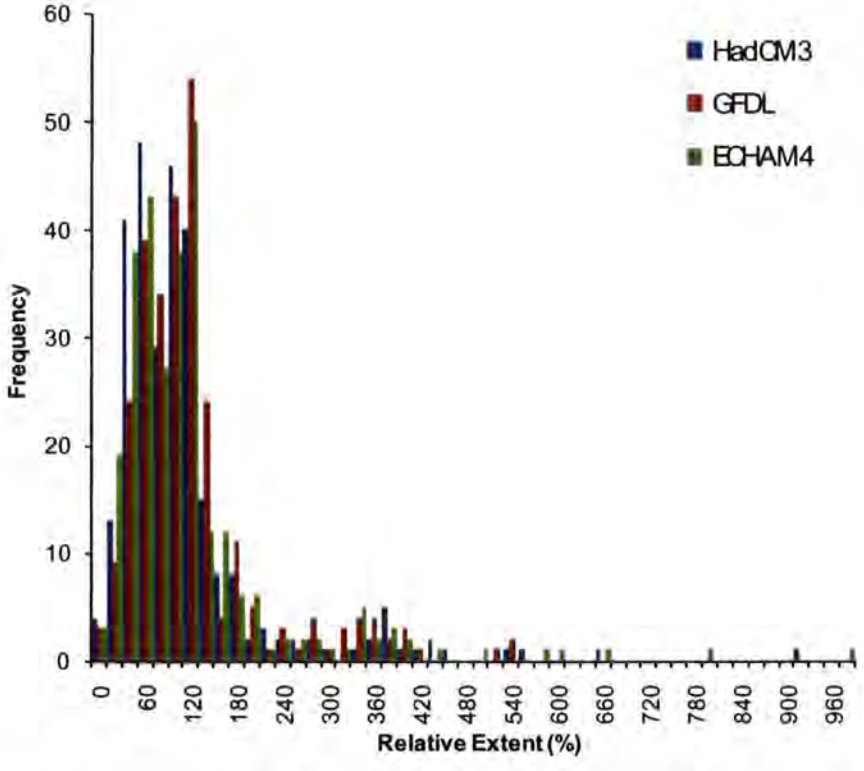


Figure 3.5. Frequency plot of the relative extent of the potential future distributions of African mammals in the year 2080.

3.3.3. Spatial Disparity between Species Current and Potential Future Distributions

3.3.3.1. Individual Species Responses

Over a third of species (n =111) are predicted to have over 90% overlap between their current ranges in at least one future scenario; thirty species have over 90% overlap for all nine future scenarios. Conversely, forty-three species have less than 10% overlap between their current range and future ranges under at least one future scenario; two species have less than 10% overlap for all nine scenarios (the Dryad Monkey (*Cercopithecus dryas*; Figure 3.6), and Nubian Ibex (*Capra nubiana*)). Eighteen species have no overlap between current distribution and at least one future scenario. As Figure 3.6 shows, the potential future extent of occurrence of the Dryad Monkey is decreased, its range is shifted eastwards, and there is no overlap between current and potential future (2080) ranges. See Table A3 (appendices) for details of projected overlap between individual species' current and projected future ranges.

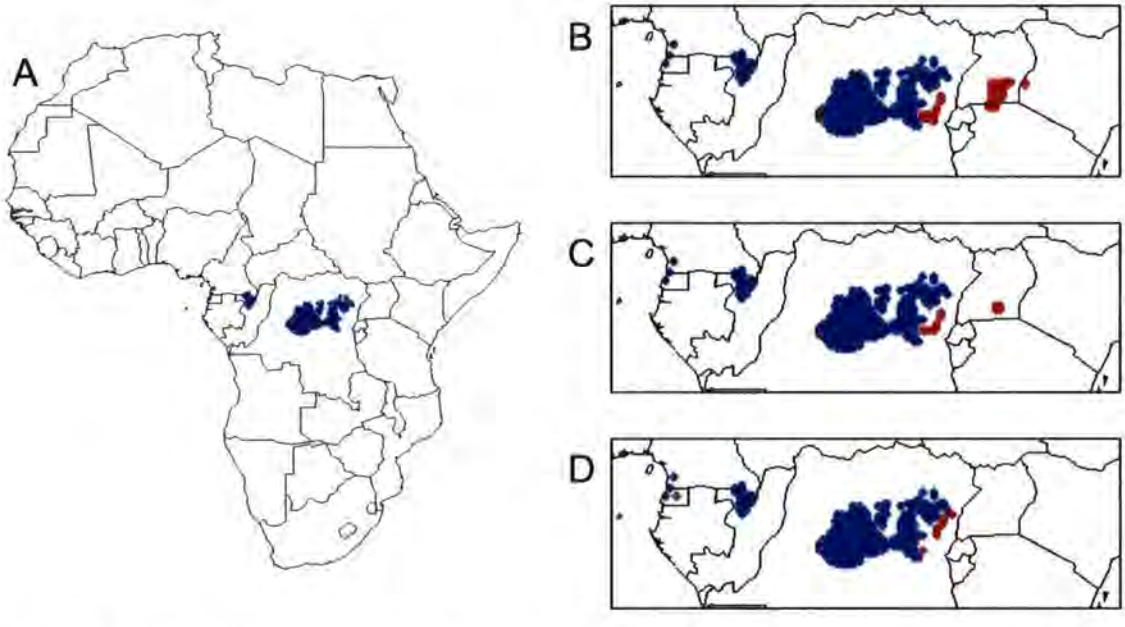


Figure 3.6. Current and potential future distribution of the Dryad Monkey (*Cercopithecus dryas*). Blue dots indicate simulated current distribution (A; AUC = 0.994); red dots indicate potential distribution under B2 emissions scenarios for the year 2080 (B is ECHAM4, C is HadCM3 and D is GFDL). The right hand side maps (B, C and D) are magnified.

3.3.3.2. Collective Species Responses

On average, the overlap between species' current ranges and their potential future ranges decreases from 89.3% in 2020, to 81.7% in 2050 to 75.7% by 2080 (Table 3.5). However, by 2080, seventy-three species still have overlap > 90% between their current and potential future distributions (Figure 3.7).

Table 3.5. Summary of overlap between species' current and potential future distributions. Values are given for overall change and percentage change for nine potential future scenarios. Overall change is defined as the number of 0.25° cells which overlap between current and future scenarios.

	Number of 0.25° Cells									
GCM		HadCM3 B2			GFDL B2			ECHAM4 B2		
Time Period	Current	2020	2050	2080	2020	2050	2080	2020	2050	2080
Overall	5151	4632	4246	3806	4645	4312	4110	4535	4071	3789
Overlap (%)		89.92	82.42	73.88	90.16	83.71	79.79	88.02	79.02	73.55

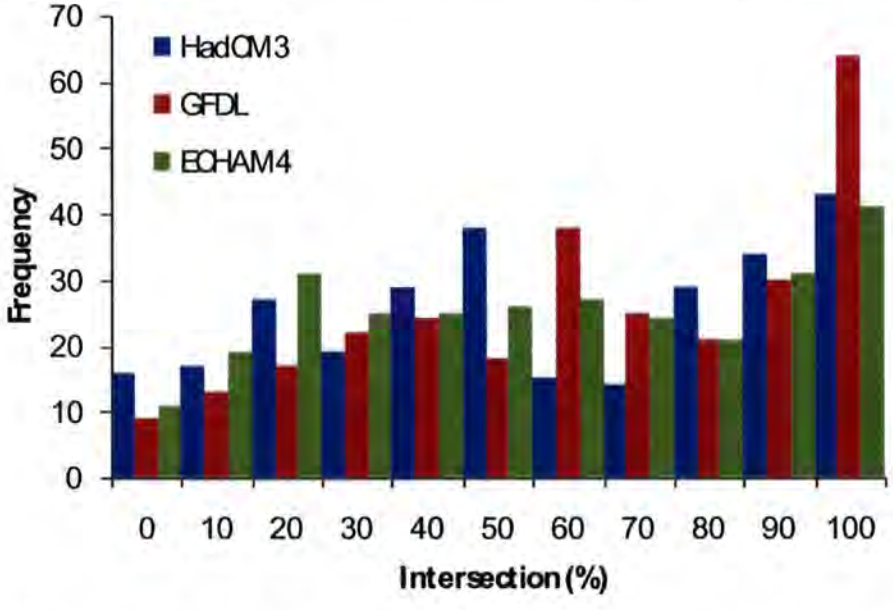


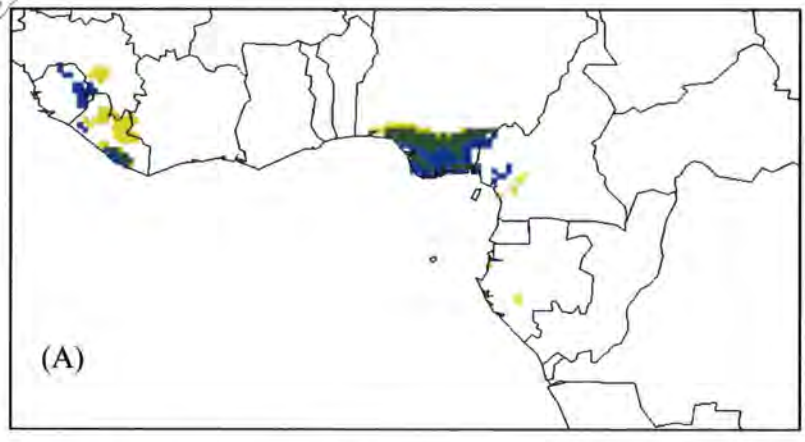
Figure 3.7. Frequency plot of intersection of species simulated current and potential future distributions in the year 2080. Intersection is the number of 0.25° cells in which each species' current and potential future distribution overlaps, given as a percentage of current distribution.

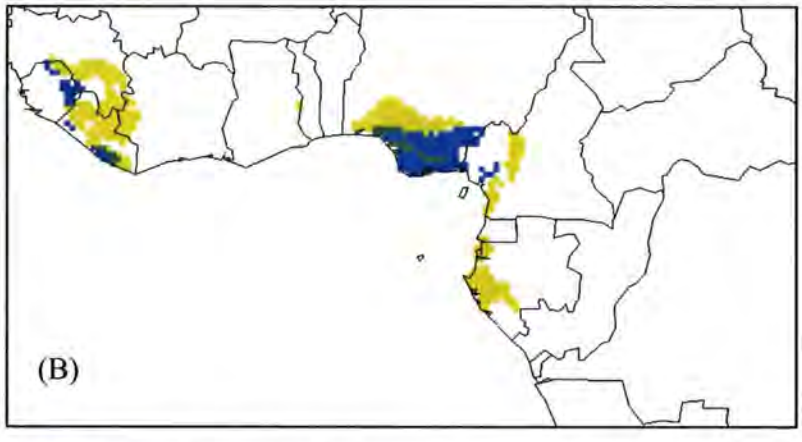
3.3.4. Temporal Disparity between Species Current and Potential Future Distributions

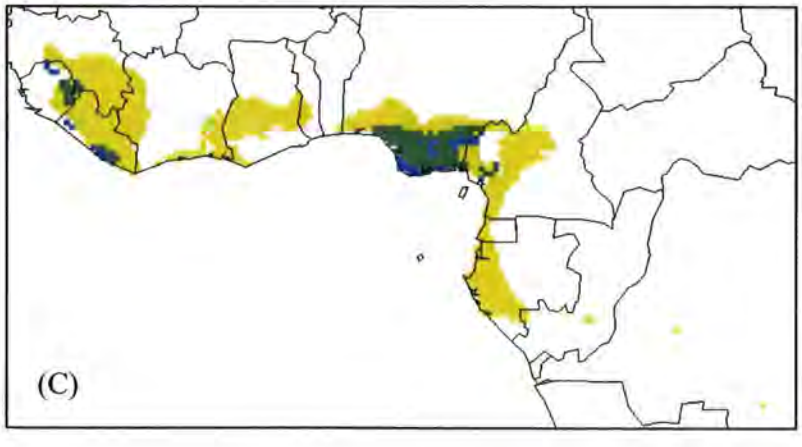
On average, overlap between species' simulated current and potential future distribution decreased as time progressed, from 2020 to 2050 and 2080 (Section 3.3.3.2). In all cases, species where overlap drops to zero in 2020 or 2050, the overlap remains at zero in 2080, suggesting there will be no examples of temporal bottlenecks where there is no suitable climate but only for a short period. However, a number of species saw substantial decreases in overlap (although not to zero) between the present day and the year 2020 (or 2050) and then subsequent increases in overlap between 2020 and the future scenarios. The best example of this is the endangered Sclater's monkey *(Cercopithecus sclateri)* whose overlap between simulated current distribution and future distribution decreased to 43% in 2020, decreased again to 17% in 2050 but then increased to 73% by 2080 (Figure 3.8) under the GFDL B2 scenarios.

Figure 3.8. Overlap between current and potential future distributions of the endangered Sclater's monkey *(C. sclateri)*.

Blue squares denote simulated current distribution; yellow squares denote potential future distribution (GFDL B2 scenario for 2020 (A), 2050 (B) and 2080 (C)); green squares denote overlap between current and future distribution. AUC = 0.999.







3.4. DISCUSSION

Levels of species richness in northern Africa (e.g. Morocco, Algeria, Tunisia and Egypt) are predicted to remain fairly constant; although this is may be an artefact of low species richness there at present. Similarly, eastern parts of Africa (such as Kenya, Tanzania and Uganda) are predicted to remain the most speciose in all future climate change scenarios. However, species richness is predicted to decrease in western areas of Africa (such as Liberia, Sierra Leone, Guinea, South Africa and Namibia) which may indicate a general eastward shift of species' ranges along an aridity gradient towards moister areas in the east in response to predicted climate change. In this sense, these results mirror projections by Thuiller *et al.*, (2006) and Erasmus *et al.*, (2002) who reported a west-east shift of species in response to potential climate change. The shifts predicted in this study were most pronounced under the HadCM3 and ECHAM4 scenarios; it is likely that the GFDL scenario predicts less distinct movements as it is the 'wettest' future scenario used in this study and therefore the aridity gradient is projected to be less pronounced.

Collectively, overlap between species' current and potential future ranges is predicted to decrease as time progresses; by 2020, species' ranges are predicted to overlap current ranges by 89.3%, 81.7% by 2050 and only 75.7% by 2080. Species with little (or no) overlap between their current and future ranges are at a greater risk of extinction than those with large overlap between ranges. This means the forty-three large mammals whose overlap between their current and future ranges is less than 10% (Chapter 3.3.3) may become critically endangered in the future. If their current range becomes climatically unsuitable, and they are not able to adapt to the potential future changes in climate and/or consequently alter their ranges, these species may only be able to occupy those areas where current and future ranges overlap (Huntley *et al.*, 2006). This may have serious consequences for the survival (both genetic and absolute) of the species.

A number of species saw substantial decreases in overlap between the present day and the year 2020 (or 2050) and then subsequent increases in overlap between 2020 and the 2050's and 2080's. The best example of this is the endangered Sclater's monkey *(C. sclateri)* whose overlap between simulated current distribution and future distribution

decreased to 43% of its current range in 2020, decreased again to 17% in 2050 but then increased to 73% by 2080 (Figure 3.8) under the GFDL B2 scenarios. This could cause problems if such species are only expected to maintain viable populations in places where areas of suitable climate space overlap. Consequently, if they are unable to maintain viable populations until the time in the future when simulated overlap is predicted to be much greater, the species may be at risk of local extinction.

However, it is range contraction rather than range overlap which is of most concern with regards to the possible future of African mammals (Erasmus *et al.*, 2002; Thuiller *et al.*, 2006). This is because of the association between range size and extinction risk (Jablonski, 1991; Gaston, 1994). As population size and range size are positively correlated, it is expected that as range size decreases population size will decrease too (Thuiller *et al.*, 2006). Therefore a reduction in range size could mean species are at a higher risk of local extinction (Thomas *et al.*, 2004). This could occur for a number of reasons, for example, smaller catastrophic events such as drought or disease outbreaks may negatively affect a larger proportion of the population (Erasmus *et al.*, 2002). Land transformation may additionally increase this risk of extinction (Lawton & May, 1998) because the absolute population may be fragmented into smaller sub-populations. Also, land transformation may bring humans and wild animals into increasingly close contact and possible conflict (Thuiller *et al.*, 2006). However, for some species human intervention is the only opportunity for their survival in the future. For example if a species' current and potential future ranges do not overlap, only artificial translocation or *ex situ* conservation will help these species to persist into the future (Huntley *et al.*, 2006).

Of the 281 species examined in this study, the majority (n = 167, 59%) of species are predicted to experience range contraction whereas 41% (n = 111) species are predicted to experience range expansion and only a very small number of species (<1%) experienced no change. These results are similar but slightly more conservative than those predicted by Erasmus *et al.*, (2002) who found 78% species' ranges declined and 17% expanded. It is likely that the more conservative results of this study are more robust, as the whole climate envelope for each species (rather than just the South African portion), have been

taken into account when modelling species' potential future ranges. This probably reflects the fact that Erasmus *et al.'s* area of study was in South Africa – a region whose climate is projected to change markedly compared to the average changes across Africa. In addition, Erasmus *et al.*, (2002) modelled the distributions of a number of taxon other than mammals (birds, butterflies, reptiles and invertebrates) which may show more pronounced range contractions than mammals in response to climate change.

While the majority of species' are predicted to experience reductions of climatically suitable habitat, the magnitude of this reduction is relatively small (-4.41% by 2080). This is especially so when compared to a similar study by Thuiller *et al.*, (2006) which predicted the mean range contraction of African mammals to be more than four times this amount (18%) by 2080. However, this is likely to have arisen because Thuiller *et al.*, (2006) used a more severe scenario of potential future climate change (HadCM3 A2 as opposed to B2). It is therefore possible that under this more extreme emissions scenario we would report similar results; which is the most robust prediction depends on the scale of potential future climate change. In addition these estimates are relatively low compared to a similar study focussing on birds, which simulated a potential decrease in range of approximately 19% for the three GCM scenarios for 2080 (Huntley *et al.*, 2006), although this could reflect the more extreme changes in climate forecast at higher latitudes.

As the extent of occurrence of the 281 species is, on average, predicted to decrease only slightly (Chapter 3.3.2) many of these species, especially for those with large ranges, are likely to be able to cope with such a decrease (assuming they can get to the new range, and that suitable habitat occurs there). However, the situation may be different for those species which depend on slow growing and restricted habitats such as tropical forest, which may not be present in the future and is unlikely to rapidly spread to newly suitable areas. Additionally, those species whose current ranges are already quite small (e.g. the sun-tailed monkey (*C. solatus*) or the red duiker (*C. rubidus*)), as well as those species who are already listed as threatened (vulnerable, endangered or critically endangered) in the IUCN red list (IUCN, 2006) will also be at a greater risk of extinction; any decrease in their already small ranges could prove disastrous due to the negative correlation between

range size and extinction risk (Gaston, 1994). However, those species with large decreases in extent of occurrence that also simultaneously experience small overlaps between current and future distributions are at the greatest risk of extinction. For example, the ten species who were predicted to have prevalence of <10% of their current distribution (Table 3.2) all occupy relatively small current ranges and half of them are already listed as threatened in the IUCN red list (IUCN, 2006). In addition, these ten species all have less than 10% overlap between their current and future (2080) ranges.

Three GCMs (which contrasted in their precipitation projections) were chosen in this study because other studies found moisture availability to be important when modelling potential distribution of species in Africa (e.g. Huntley *et al.*, 2006). Indeed, the scale of potential impacts of climate change on African mammals was found to change depending on which future climate change scenario was used. For example, when comparing the results of this study to Thuiller *et al.'s* (2006), one concludes that the A2 SRES emissions scenario will have a more dramatic effect upon mammal species in Africa than change under the B2 SRES emissions scenario. Additionally, differences between GCMs were also shown to result in differing projections of impacts of climate change on mammal species. As these GCMs differ in their projections of precipitation in the future, it is likely that moisture availability is a key factor in determining species distributions. More specifically, the wettest scenarios (GFDL) consistently projected smaller potential decreases in species' prevalence and overlap than the HadCM3 and ECHAM4 models. This indicates that 'drying' in particular, will be detrimental to mammalian species; most probably via negative impacts of decreased precipitation on vegetation growth. These findings therefore defend the decision of choosing these models (as well as precipitation variables) in this study.

The impacts of climate change on African mammals vary between species, with some (such as the red-bellied monkey, *C. erythrogaster*) potentially benefiting from climate change while others (such as the bushman hare, *B. monticularis*) will be potentially quite severely affected. However, the majority of species are predicted to experience decreases in their absolute range size as well as simultaneous decreases in overlap between their

current and potential future ranges. These estimates are likely to be conservative, because the likelihood is that some species may not be able to realise their potential future ranges. We have assumed 'unlimited dispersal' i.e. species will be unobstructed from tracking changes in climate. This is highly unlikely as human pressures are expected to increase in the future, with the likelihood that land transformation will increase as well as the interactions between humans and wild animals. Many of the large mammals in this study can pose threats to humans, be it directly or indirectly for example the use of resources saved for domestic livestock such as water and pasture (Thuiller *et al.,* 2006). It is therefore likely that as species move to track climate changes they will come under increased persecution by humans, thereby increasing the risks of local extinctions. In addition, this study has only looked at the effect of climate change on the distribution of African mammals, and while climate has been shown to be important in predicting species' potential future distributions it is likely that other factors may play an important role too. For example, changes in land-use may cause additional species loss, particularly those species resident in tropical countries (Jetz *et al.,* 2007). In order to reduce these possible impacts one must work hard to protect these species through efforts such as increasing the extent of the protected area network, educating the public about the predicted plight of these animals, but also primarily to reduce climate change in the future (Jetz *et al.,* 2007).

CHAPTER FOUR: Projected Impacts of Climate Change in African Protected Areas

4.1. INTRODUCTION: Protected Areas

The World Conservation Union (IUCN) defines a protected area (PA) as:

> "*an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means*" (IUCN, 1994).

PAs are consequently regarded as the most important and effective means of *in situ* conservation of biodiversity (Bruner *et al.*, 2001; Burns *et al.*, 2003; Rodrigues *et al.*, 2004; Thuiller *et al.*, 2006). However, in addition to maintaining biodiversity, PAs are managed for other roles concurrently for example education, research, tourism, recreation, and to maintain cultural integrity. As a consequence, huge amounts of resources are ploughed into the establishment and maintenance of PAs (Green & Pain, 1997).

The IUCN have grouped PAs into seven broad categories based on how each area is managed ranging from category Ia (strict nature reserves) which are managed first and foremost for scientific research and environmental monitoring, to category VI (managed resource PAs) which are mostly unmodified natural habitats managed with both the protection of biodiversity and the provision of resources to local communities in mind. In this study, PAs will be defined as those which fall into management categories Ia to VI (Table 4.1).

Table 4.1. Protected Area Management Categories, taken from IUCN (1994).

Category	Definition
Ia	Strict Nature Reserve
Ib	Wilderness Area
II	National Park
III	Natural Monument
IV	Habitat/Species Management Area
V	Protected Landscape/Seascape
VI	Managed Resource Protected Area

Yellowstone National Park, USA, (established in 1872) was the first PA of the modern era. Since then, the number, size and extent of PAs worldwide has grown rapidly, especially in the past few decades (Figure 4.1). In 1993 the meeting of the IUCN Fifth World Parks Congress in Durban, South Africa set a target that 10% of each nation should be protected (IUCN, 1993). By 2003, this was surpassed in nine of fourteen terrestrial biomes, with a total of 11.5% of the world's surface designated as protected (Chape *et al.*, 2003).

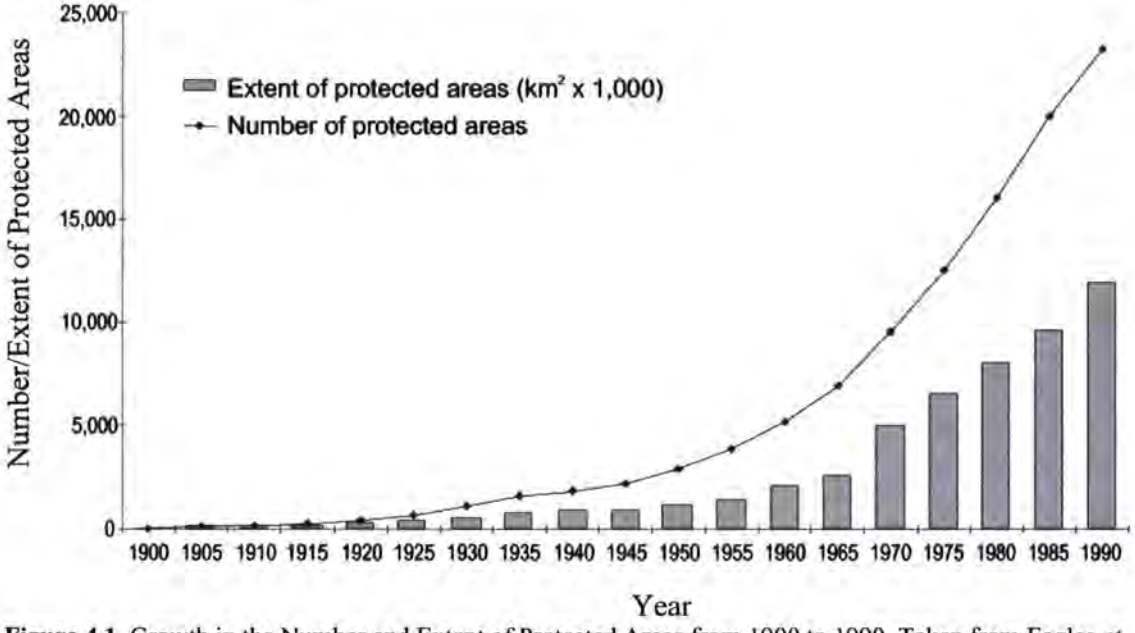


Figure 4.1. Growth in the Number and Extent of Protected Areas from 1900 to 1990. Taken from Eagles *et al.*, (2002).

Table 4.2. Number, area and extent of Protected Areas within Africa (Green & Pain, 1997).

		Total	
Region	Area of Region (Km^2)	Number	Extent (%)
North Africa/Middle East	12,866,541	542	8.06
Africa (Western/Central)	12,352,849	343	5.66
Africa (Eastern/Southern)	10,773,580	927	12.24

Matching the global trend of an increase in the number and size of PAs, PAs within Africa have also grown immensely over the past century; from being virtually absent 110 years ago to covering over two million km^2 today (Table 4.2; Burgess *et al.,* 2007). The large increase in area protected in Northern Africa was due a small number of extensive PAs being created (Green & Pain, 1997). New governmental policies have also helped with the creation and expansion of reserves. For example, the Government of South Africa created a new property rates bill which exempts PAs from land taxes thereby allowing this money to remain within the PA's control for other purposes such as biodiversity conservation. Since this bill, five new national parks in South Africa have been established covering a total of 130,000 hectares. This has pushed the total of land protected in South Africa from 6.6% to over the IUCN target of 10% (IUCN, 2003). However, while the IUCN target is met in South Africa (and Eastern Africa) it is not reached in North Africa and 'Western & Central' Africa, where only 8.06% and 5.66% land is protected respectively (Green & Pain, 1997).

There is much debate as to the feasibility and effectiveness of the IUCN's (1993) target; it has been criticised for being too uniform as it does not take into account each country's ability (or indeed aspiration) to meet such targets (Rodrigues *et al.,* 2004). Others believe this target is insufficient (e.g. Soulé & Sanjayan, 1998) but in spite of this there has still been little debate as to what would constitute a more appropriate target (Rodrigues *et al.,* 2004). One thing is for certain, PAs will only remain effective at maintaining biodiversity if they are able to encapsulate species' potential future ranges as climate changes (Hannah *et al.,* 2007). Therefore in order for PAs to preserve biodiversity as climate changes, PA networks need to represent those species for which they were designed to protect at present, as well as protecting newly colonising species for which PAs become climatically suitable. PAs must therefore be sufficiently large and connected to guarantee species persistence in the PA network in the future (Rodrigues & Gaston, 2001).

While the establishment of new PAs and the expansion of existing ones have been driven by the desire of protecting and increasing wildlife abundances, there is some debate as to how successful these PAs have been in protecting biodiversity (Johannesen, 2007) with some studies suggesting that many PAs already do not fully or efficiently achieve this

(Hannah *et al.,* 2007). As the majority of PAs have been established according only to political feasibility and space availability (Hannah *et al.,* 2002) the dynamic nature of either the climate or the distribution of species they were built to protect has not been kept in mind (Araújo *et al.,* 2004; Hannah *et al.,* 2002; McClean *et al.,* 2006).

Species are predicted to respond to changes in climate individualistically and in one of several ways: by adaptation to the new climate, by movement of their ranges to track climatic conditions to which they are suited or, if neither of these is possible, the species is likely to be driven to extinction. Species richness and composition within PAs is therefore expected to be altered as climate changes (Midgely *et al.,* 2002; Burns *et al.,* 2003; Hannah & Salm, 2003).

As the majority of species' responses to climate change are expected to be spatial (Huntley *et al.,* 2006), the effectiveness of PA networks in safeguarding the future of these species comes into question (Burns *et al.,* 2003), especially as a large number of PAs have not been designed with the dynamic nature of the climate, or species ranges, in mind. As climate changes, species may shift their ranges out of PAs if these areas become climatically unsuitable (Hannah *et al.,* 2007). Equally, new species may enter a PA if the previously unsuitable climate within the PA becomes suitable in the future (Peters & Darling, 1985). Another response, which relies heavily on the connectedness of PAs, is for a species to exchange a PA in its current range for one that becomes climatically suitable in the future (Hannah *et al.,* 2005). In every case, the community composition of PAs in the future will almost certainly be altered (Hannah *et al.,* 2005). In addition, due to the fixed nature of PAs many of these are becoming increasingly isolated due to human-associated activities (e.g. habitat destruction, encroachment) which are set to increase in the future as the human population grows (CI, 2006). This could have serious negative impacts on both the species within- and the economic revenue of the PAs, especially if climate within the PA becomes unsuitable in the future for charismatic or keystone species which hold either ecosystem or economic roles within the PA.

In recent years, there have been a number of multispecies modelling efforts looking into the impacts of climate change on the selection and efficiency of PAs for maintaining biodiversity (e.g. Lemieux & Scott, 2005; Williams *et al.,* 2005; Abellan *et al.,* 2007).

Studies such as Hannah *et al.* (2005) used bioclimatic modelling to calculate the effect of climate change on species composition within PAs. This is possible because as climate changes, species' range boundaries are expected (and have been shown) to move; one can therefore determine if this movement will result in species moving out of (or into) a PA.

A number of studies report that PAs across the world, from Europe and America to Africa and Australia, are not expected to fully protect the species for which they were designed (e.g. Burns *et al.*, 2003; Araújo *et al.*, 2004). Burns *et al.* (2003) found that the eight United States PAs they studied stood to lose up to 20% of their current mammalian species diversity, and that the average loss for these parks was projected to be 8.3% under a scenario of a doubling of carbon dioxide levels. Araújo *et al.* (2004) found that the European reserve system, which is geared towards protecting species' current ranges, is predicted to lose between 6 and 11% of species within its boundaries within fifty years as climate (and therefore species distribution) changes. Furthermore McDonald & Brown (1992) predicted that 9 – 62% of mammal species living in montane regions of the Great Basin of the USA will be lost with a warming of 3°C.

Studies focussing on African PAs have also predicted a progressive loss of species representation in PAs (e.g. Hannah *et al.* (2005) in the Southern African Cape). On a finer scale, Erasmus *et al.* (2002) reported that the flagship Kruger National Park, South Africa, could lose up to 66% of the 179 animal species included in their analysis under a doubling of CO_2 (and therefore a mean temperature increase of 2°C). A more recent study by Hannah *et al.* (2007) using predictive species' distribution modelling found that under the HadCM3 A1 emissions scenario for the year 2050, the majority of species' future ranges were represented within PAs in the three regions studied (Mexico, the South African Cape and Western Europe). However this included the assumption that supplementary areas to compensate for species' range changes would be added to the existing PA network. Even under the moderate HadCM3 A1 future climate scenario, 11% of species studied in the South African Cape were not fully represented within the PA network in 2050 (Hannah *et al.*, 2007). Furthermore, Rutherford *et al.* (1999) reported that the Succulent Karoo and Cape Floristic Regions of South Africa will experience major vegetation shifts; a doubling of carbon dioxide resulting in a loss of up to 80% of the succulent karoo range. In a more

recent study by Rutherford *et al.* (2000), five parks in South Africa were projected to lose more than 40% of their plant species.

As the area needed to maintain and protect current species diversity within PAs in the future is larger than area of PAs now, studies suggest the expansion/creation of PAs will be needed to maximise the conservation of species diversity in the face of climate change (Hannah & Salm, 2003; Hannah *et al.*, 2007). The view widely held is that premeditative action based on climate model predictions and direct observations will be both better for species (i.e. by avoiding species extinctions (Hannah *et al.*, 2002)) and less costly in the long run when compared to restorative action (Hannah *et al.*, 2007).

4.1.1. Objectives

As the modelling approach to be used in this study has been shown to be robust (Chapter 2.3) we can have some confidence in applying it to assess the ability of the current network of African PAs to protect mammalian species diversity under a number of future climate scenarios. It is recognised that other modelling approaches may produce different results (Araújo & New, 2006; Pearson *et al.*, 2006), and therefore ideally multiple models and scenarios should be used (i.e. ensemble forecasting). However due to the limited time available to complete this study, I use one modelling technique with multiple climate change scenarios. In this chapter I investigate how mammalian species richness, persistence and turnover may change in African PAs (IUCN categories I to VI) by considering to what extent mammalian species will alter their distributions in response to predicted climate change.

4.2. METHODOLOGY

4.2.1. Protected Areas Data

Data relating to the location, sizes and World Conservation Union (IUCN) classifications of PAs worldwide were downloaded from the World Database on PAs (http://sea.unep-wcmc.org/wdbpa/, WDPA, 2006) as shapefiles in order to be viewed in ArcMAP (ESRI, 2003). Only those shapefiles for PAs which fell within the African continent were included. This amounted to 900 PAs in total; the majority of these being national parks (n = 216), nature reserves (n = 191), state forests (n = 81) and game reserves (n = 59). These PAs fell into IUCN PA management categories, I to VI (Table 4.1).

Longitude-latitude coordinates for the PAs were obtained by firstly buffering the African PA polygons by 0.125° in all directions in ArcMap (ESRI, 2003) and then spatially joining (i.e. appending the fields of the buffered PA polygons to those of the corresponding quarter-degree cells; Breslin *et al.,* 1999) these polygons to longitude-latitude (0.25°) points for the whole of Africa. PAs were buffered in order to maximise the number of smaller PAs (e.g. Groenkloof National Park, South Africa) included in the later analyses, and allowing the calculation of species loss/gain in the core area of each park (Burns *et al.,* 2003). Subsequently, the number of quarter-degree cells which fell within the buffered protected areas totalled 4877. Seven-hundred and seventeen PAs were subsequently included in this analysis (see appendices Table A4); the other 183 PAs in Africa were overlapping another PA already included (e.g. the Kafue Flats Game Management Area, Zambia, which holds the Blue Lagoon National Park within its boundaries).

4.2.2. Species Richness in African Protected Areas

The total number of species in each 0.25° cell across Africa has already been simulatedfor the current- and nine future scenarios (Section 3.3.2.1). Subsequently, the total number of species in each 0.25° cell within protected areas was calculated. Mean species richness for all scenarios for each PA was then calculated by summing predicted presence for all species in each PA. Changes in species richness between current and the nine future scenarios were then calculated.

4.2.3. Species Turnover in African Protected Areas

Species turnover is a measure of community disruption (Thuiller, 2004). Areas with high turnover indicate where community composition differs markedly between the present time and the projected future (i.e. 2080) climate change scenario. It is presumed that where simulated turnover is high, future climate change will have its greatest effect.

The number of colonisers and emigrants in each PA was calculated, as well as the number of species present in each PA both at present and in the future (the time period 2080) (in order to calculate the total number of species which the PA is simulated to be climatically suitable for, in the present and future). Species turnover in PAs was then calculated using the equation given below:

$$\text{Turnover} = ((\Sigma C + \Sigma E) / (\Sigma P + \Sigma F)) * 100$$

Where C = the potential colonisers of that area (i.e. species for which the climate becomes suitable in the future)

E = the simulated emigrants of that area (i.e. species for which the climate becomes unsuitable in the future)

P = the total number of species for which the PA is simulate climatically suitable in the present

F = the total number of species for which the PA is simulated climatically suitable in the future.

Jaccard similarity coefficients (Jaccard, 1901) were calculated to compare similarity and diversity between outputs of the three GCM scenarios (in 2080) using the equation below:

$$\text{Jaccard similarity coefficient} = \frac{a}{(a + b + c)}$$

Where a = the number of taxa simulated in a PA in both periods (e.g. currently and in 2080)

b = the number of taxa simulated in a PA in the present only

c = the number of taxa simulated in the future only.

Possible values range from 0 to 1, where 0 represents communities with totally different species lists, and 1 represents communities with identical species lists (Arnott *et al.*, 1999).

4.2.4. Species Persistence in African Protected Areas

Species persistence (i.e. the survival of the species in each PA between now and the potential future scenario) can be defined using the equation below:

$$\text{Persistence} = (\sum B \ / \ \sum P)*100$$

Where B is the number of species for which the climate is suitable in the present as well as the future and P is the number of species in the PA at present. If species persistence is high, the complement of species within the PA at present is predicted to be similar to community composition in the future. Persistence was calculated using the equation given above.

Values of average persistence and turnover for each PA across the three GCMs for the year 2080 were placed into one of five classes (0 – 20%, 20 – 40%, 40 – 60%, 60 – 80% or 80 – 100%) and visualised in ArcMAP (ESRI, 2003). Instructions on how to visualise individual species' present day and projected future distributions in ArcMap can be found in the appendices (page 182).

As there is some variability between outputs of the three GCMs used in this study, values of species turnover and species persistence were averaged across these three GCMs for the year 2080 and were expressed as mean, median and range of the three scenarios.

4.3. RESULTS

4.3.1. Species Richness in African Protected Areas

Current species richness in PAs is simulated to be higher than areas of Africa which are currently not protected (on average (mean) 47 species per quarter degree cell in PAs compared to 36 species per cell across the whole of Africa) (t = -40.09, $d.f.$ = 6522, p = < 0.001; equal variances not assumed). By 2080, the reduction in species richness within quarter-degree cells enclosed by PAs is projected to be greater (-7.18%) than the reduction in species richness within all quarter-degree cells across the African continent (-4.41%; Table 4.3).

Table 4.3. Changes in species richness across the whole of Africa and in African PAs under nine potential future climate scenarios.

	SCENARIO									
	Simulated Current	HadCM3 B2			ECHAM4 B2			GFDL B2		
		2020	2050	2080	2020	2050	2080	2020	2050	2080
Overall Species Diversity Across Africa	36.24	35.75	35.13	33.75	35.74	34.84	34.24	36.04	35.74	35.93
Percentage Change (%)		-1.34	-3.06	-6.86	-1.37	-3.87	-5.51	-0.55	-1.40	-0.87
Species Diversity within PAs	46.66	45.53	44.21	42.13	45.41	43.46	42.41	46.11	44.96	45.38
Percentage Change (%)		-2.42	-5.25	-9.70	-2.68	-6.86	-9.10	-1.19	-3.65	-2.75

4.3.2. Species Turnover in African Protected Areas

Mean projected turnover of species in the 717 PAs included in this analysis increases from 10% by 2020, to 18% by 2050, up to 26% by the year 2080 (see appendices Table A2; Figure 4.2). Median projected turnover in PAs by 2080 is 21% (18 – 21%; Figure 4.3). There were significant differences in species turnover calculated using the three GCMs (Huynh-Feldt repeated measures ANOVA; $F = 44.62$, $d.f. = 2$, $p < 0.001$); the ECHAM4 B2 scenario projected a slightly higher mean species turnover (25%) than the other scenarios (HadCM3 B2 = 23%, GFDL B2 = 20%; Figure 4.3). However, Jaccard similarity coefficients comparing similarity between outputs of these three GCM scenarios (in 2080) indicate a high level of agreement among the GCM scenarios (Table 4.4). Therefore, despite differences in turnover, community composition within individual PAs is predicted to be fairly similar between GCM scenarios for the year 2080.

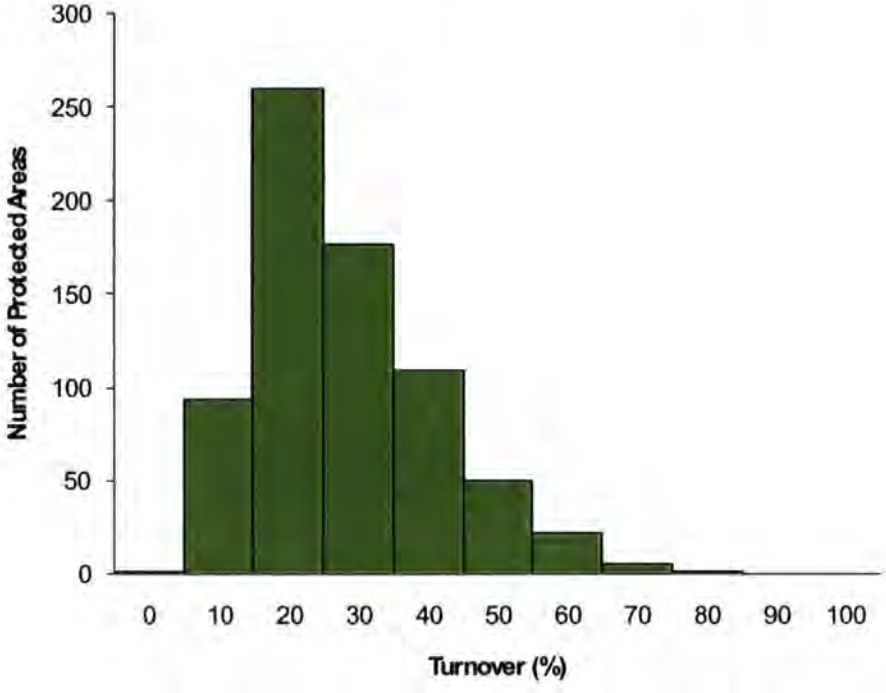


Figure 4.2. Frequency distribution of turnover in PAs averaged across three future climate scenarios (ECHAM4 B2, HadCM3 B2 and GFDL B2) for the year 2080.

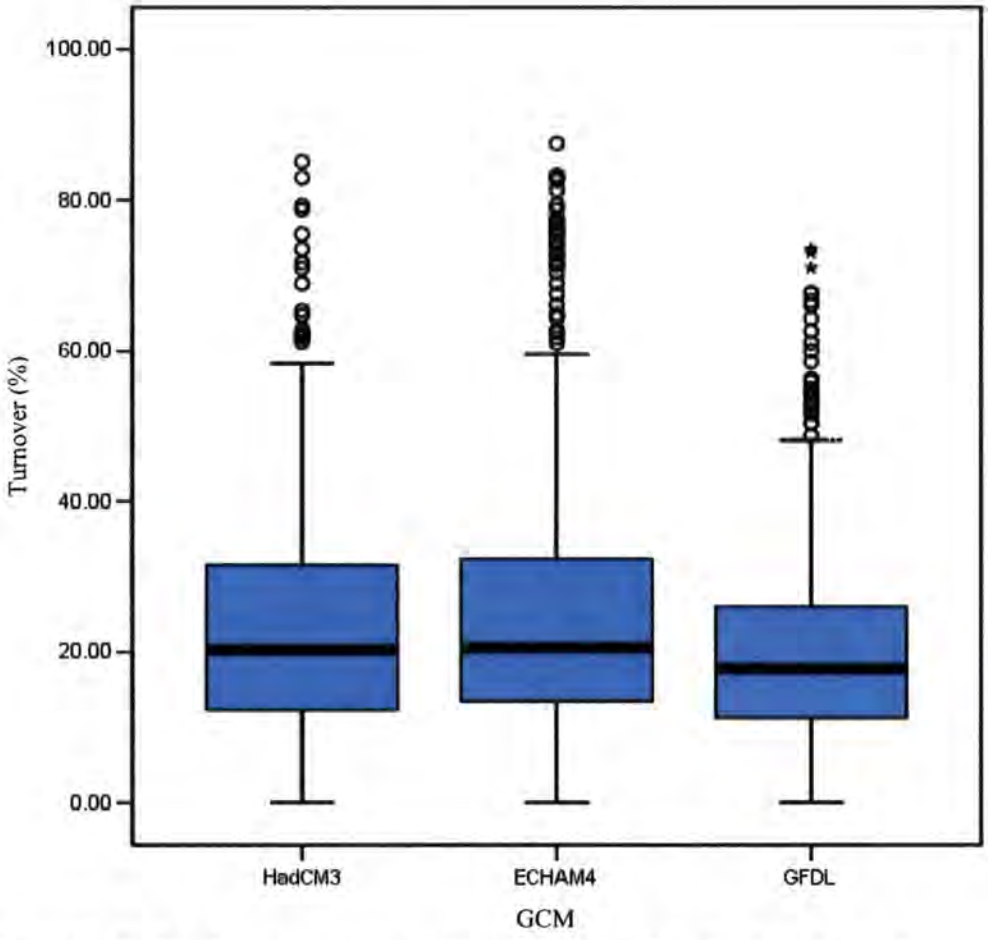


Figure 4.3. Predicted species turnover (%) within African PAs for three future climate scenarios (HadCM3, ECHAM4 and GFDL) B2 for the year 2080. Median values are indicated by the bold black horizontal line; upper and lower quartiles are denoted as the ends of the boxes; maximum and minimum values are represented by whiskers; outliners (values ≥ 1.5 ≤ three box lengths from the ends of the box) are given as circles; and extreme values (> 3 box lengths away) are given as asterisks.

Table 4.4. Jaccard similarity coefficients between 'expected' species inventories across all PAs used in this study for three future climate scenarios for 2080. Possible values range from 0 to 1, where 0 represents communities with totally different species lists, and 1 represents communities with identical species lists (Arnott *et al.*, 1999).

GCM	Jaccard Similarity Coefficient
HadCM3	0.63
ECHAM4	0.62
GFDL	0.67
Mean	0.64
Median	0.63

By the 2020's, the majority of PAs have relatively low species turnover (Figure 4.6); only a few PAs have turnover of over 20%. However, by the 2050's turnover in PAs has increased in a large number of PAs, especially in southern Africa (Figure 4.5). This situation seems to remain fairly stable by the 2080's (Figure 4.4).

By 2080, the PAs with highest median turnover are Augrabies Falls National Park (78%; $\bar{x}$ = 93%), Hardap Dam (69%; $\bar{x}$ = 83), Witsand (65%; $\bar{x}$ = 75%), Molopo Green Belt (65%; $\bar{x}$ = 75%) and the Kalahari Gemsbok Park (64%; $\bar{x}$ = 75%). With the exception of Hardap Dam (Namibia), these PAs are located within South Africa. Conversely, areas with the lowest simulated turnover were Boukornine (1%; $\bar{x}$ = 1%), W du Niger (1%; $\bar{x}$ = 1%) Cape Mount (2%; $\bar{x}$ = 2%) and Tamou (2%; $\bar{x}$ = 2%). These PAs are in Tunisia, Niger, Liberia and Niger respectively (Table 4.5; Table A2). These results indicate that species turnover is not distributed evenly within PAs across the African continent. This is demonstrated visually in Figure 4.4. For example, PAs in Botswana, Namibia and Northern South Africa are projected to have the highest species turnover, especially areas such as the Kgalagadi Transfrontier Park and the Augrabies Falls National Park (dark blue areas in Figure 4.4). Whereas PAs in North Africa, North Western Africa, Ethipopia, Kenya, Tanzania and Milawe are predicted to have low species turnover in 2080 (Figure 4.4).

Areas with highest turnover have relatively high numbers of species gain (colonisers) and loss (emigrants) (Table 4.5) therefore turnover is not a function of low species richness. Conversely, areas with lowest turnover in 2080 have low number of species gain and loss but higher species richness at the present time.

Table 4.5. Summary of number of colonisers, emigrants, number of species and turnover in selected PAs. PAs were selected to demonstrate those with either high or low predicted turnover for possible future climate scenarios in the year 2080.

Protected Area	Number of Species Currently	GCM	Number of Colonisers	Number of Emigrants	Median Turnover (%)
Augrabies Falls	32	HadCM3	11	28	83
		ECHAM4	10	27	79
		GFDL	13	25	73
Hardap Dam	32	HadCM3	10	27	79
		ECHAM4	12	26	76
		GFDL	16	17	52
Kalahari Gemsbok	38	HadCM3	14	32	79
		ECHAM4	14	31	76
		GFDL	14	14	37
Witsand	33	HadCM3	10	27	76
		ECHAM4	13	25	70
		GFDL	7	19	48
Molopo Green Belt	36	HadCM3	13	27	69
		ECHAM4	13	27	69
		GFDL	10	23	56
Boukornine	22	HadCM3	0	0	0
		ECHAM4	0	0	0
		GFDL	1	0	2
W du Niger	44	HadCM3	0	0	0
		ECHAM4	0	1	1
		GFDL	1	1	2
Cape Mount	46	HadCM3	0	0	0
		ECHAM4	5	0	5
		GFDL	0	0	0
Tamou	45	HadCM3	0	1	1
		ECHAM4	0	2	2
		GFDL	1	1	2

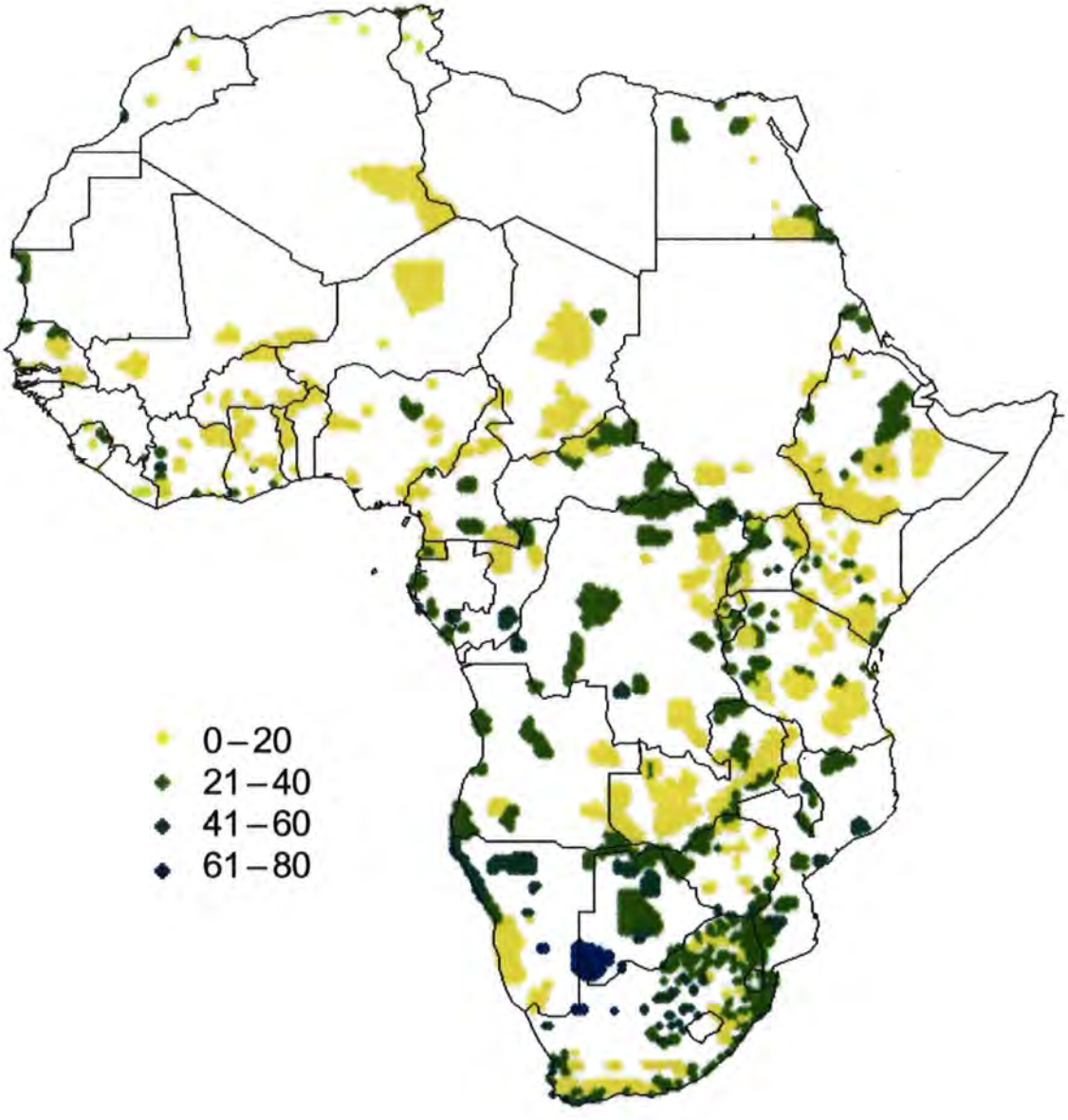


Figure 4.4. Predicted species turnover (%) in African protected areas by 2080. Turnover in each PA is calculated as the mean turnover of species under the three GCM scenarios for the year 2080 (see appendices Table A4). These values were placed into one of five distinct classes (see key), with darker colours representing higher predicted turnover. NB in this case there were no PAs with turnover in the class 81- 100%.

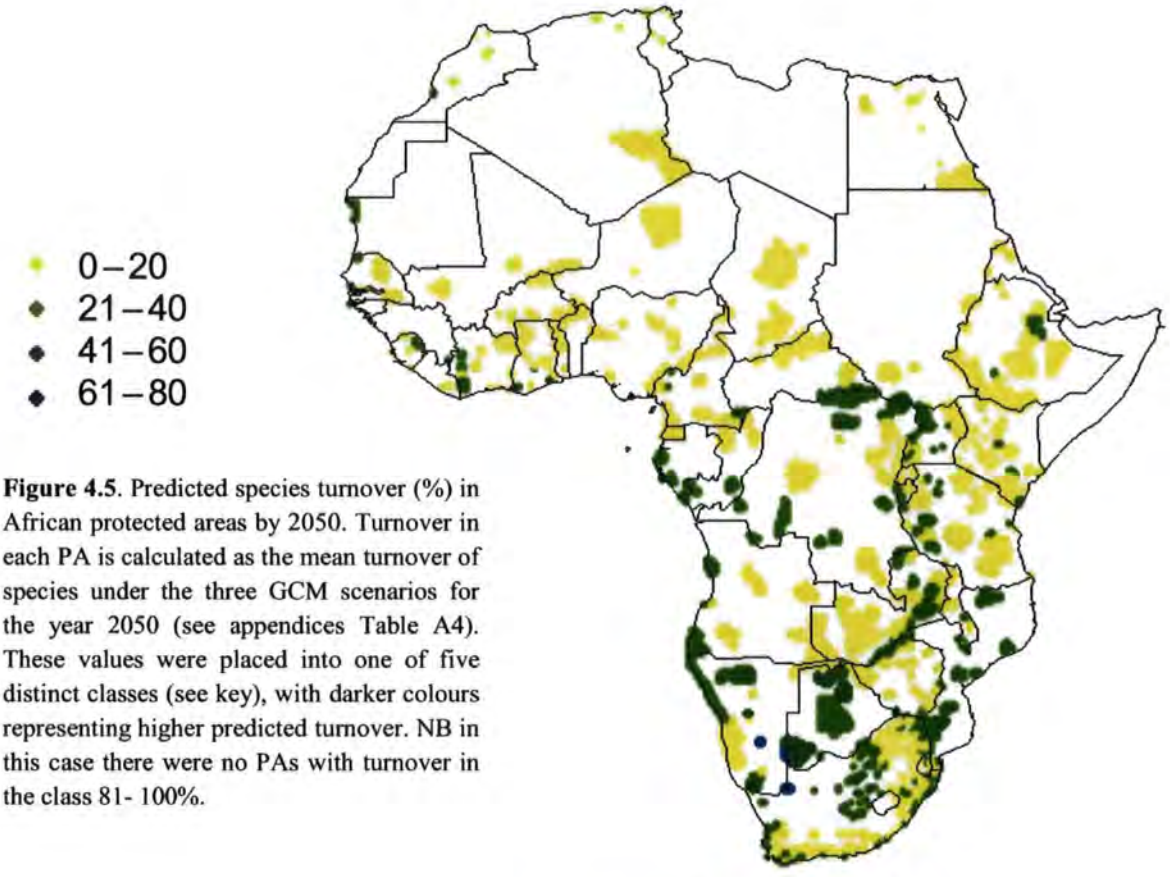


Figure 4.5. Predicted species turnover (%) in African protected areas by 2050. Turnover in each PA is calculated as the mean turnover of species under the three GCM scenarios for the year 2050 (see appendices Table A4). These values were placed into one of five distinct classes (see key), with darker colours representing higher predicted turnover. NB in this case there were no PAs with turnover in the class 81- 100%.

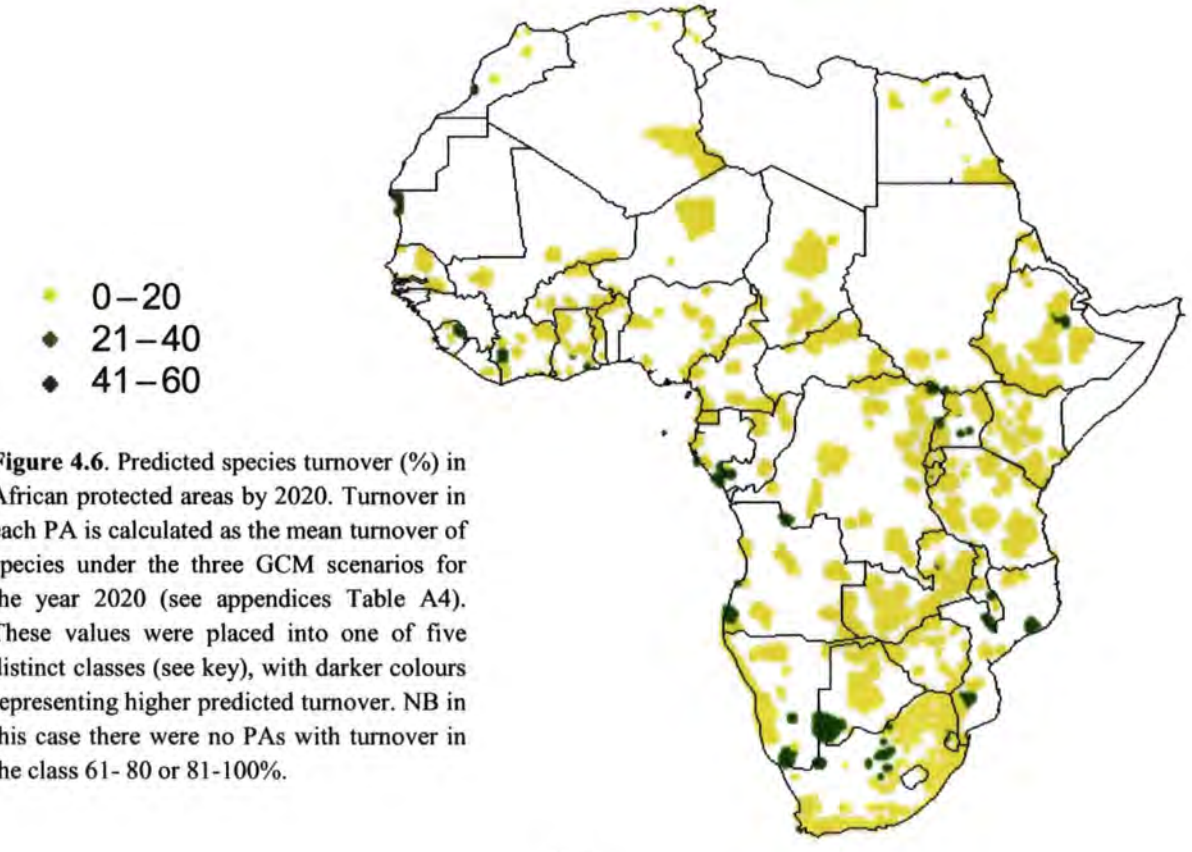


Figure 4.6. Predicted species turnover (%) in African protected areas by 2020. Turnover in each PA is calculated as the mean turnover of species under the three GCM scenarios for the year 2020 (see appendices Table A4). These values were placed into one of five distinct classes (see key), with darker colours representing higher predicted turnover. NB in this case there were no PAs with turnover in the class 61- 80 or 81-100%.

A Spearman's Rank Correlation indicates a significant negative association between size (area in Hectares) of PA and species turnover; suggesting larger protected areas have slightly lower levels of species turnover than smaller ones (r = -0.210, $d.f.$ = 716, P < 0.001, Figure 4.7).

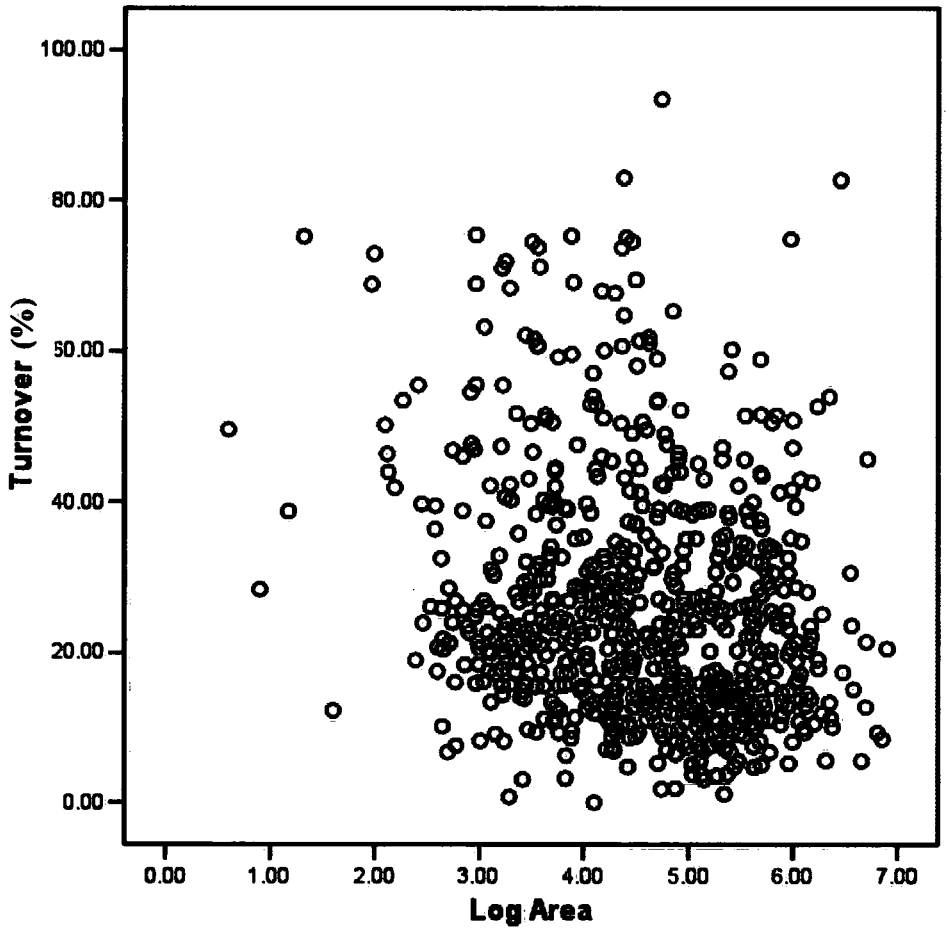


Figure 4.7. Scatter diagram of the relationship between species turnover and log area (measured in Hectares) of protected areas in Africa.

4.3.3. Species Persistence in African Protected Areas

Mean projected persistence of species in the 717 PAs included in this analysis is 81% by 2080. Persistence in PAs then decreases to 74% by the 2050s before increasing to 79% by 2080 (see appendices Table A4; Figure 4.8). Median persistence by 2080 is 84% (82 – 86%). There were significant differences in species persistence calculated using the three separate GCMs (Huynh-Feldt repeated measures ANOVA; $F = 53.82$, $d.f. = 2$, $p < 0.001$); the GFDL B2 scenario projected higher median persistence (86%) than the other scenarios (ECHAM4 B2 = 83%, GFDL B2 = 82%) (Figure 4.9).

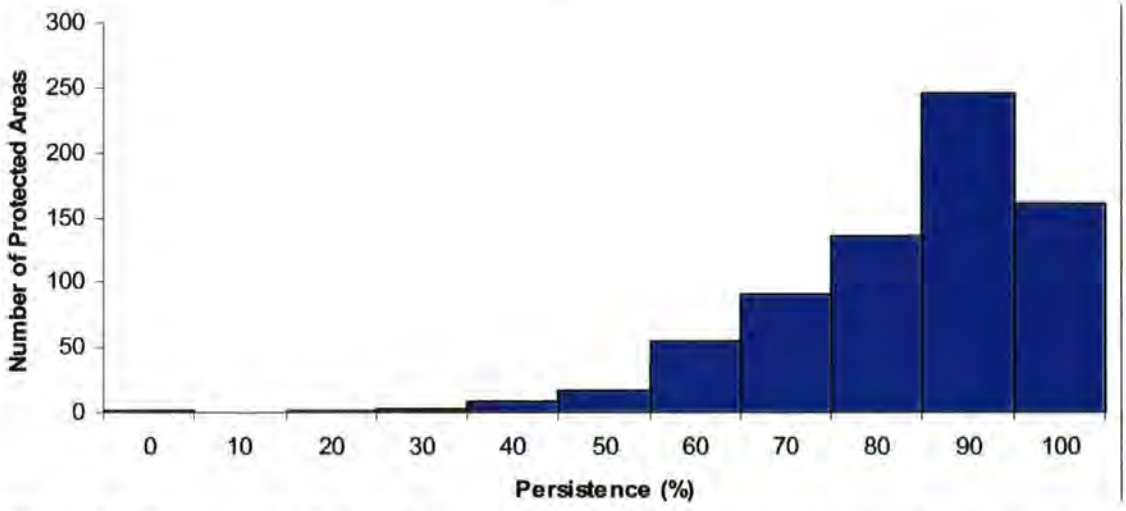


Figure 4.8. Frequency distribution of turnover in PAs averaged across three future climate scenarios (ECHAM4 B2, HadCM3 B2 and GFDL B2) for the year 2080.

Results indicate that persistence follows an inverse geographic pattern to species turnover, i.e. areas with highest turnover have low persistence (Table 4.6) and vice versa (Figure 4.10, compare to Figure 4.4).

Table 4.6. PAs where species turnover is high and persistence is low. Values for species turnover and persistence are averaged across three GCMs (HadCM3, ECHAM4 and GFDL) for the time period 2080.

Protected Area	Persistence (%)	Turnover (%)
Augrabies Falls	16.67	78.26
Hardap Dam	27.08	69.03
Kalahari Gemsbok	32.46	64.14
Molopo Green Belt	28.70	64.62
Witsand	28.28	64.68

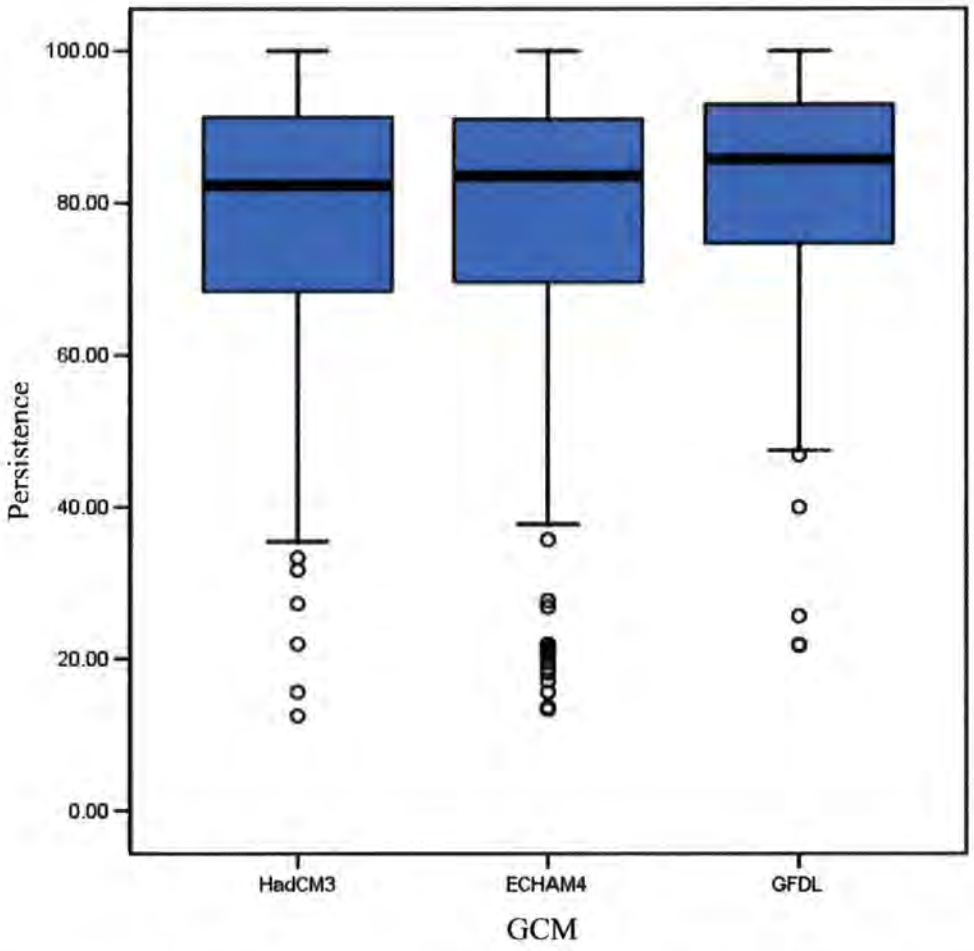


Figure 4.9. Predicted species persistence (%) in African PAs for three future climate scenarios (HadCM3, ECHAM4 and GFDL) B2 for the year 2080. Median values are indicated by the bold black horizontal line; upper and lower quartiles are denoted as the ends of the boxes; maximum and minimum values are represented by whiskers; outliners (values ≥ 1.5 ≤ three box lengths from the ends of the box) are given as circles; and extreme values (> 3 box lengths away) are given as asterisks.

Figures 4.10, 4.11 and 4.12 depict the location and extent of species persistence in PAs in 2080, 2050 and 2020 respectively. By the 2080's a large number of PAs have high levels of species persistence (i.e. over 60% persistence; Figure 4.10). There are five PAs which are projected to retain suitable climate for all species resident at present (i.e. 100% persistence); these are Boukornine Mountain Nature Park, Cape Mount Nature Reserve, Chambi National Park, El Kala National Park and Gadabedji Faunal Reserve (Table 4.7). These PAs are located in northern and western Africa (Table 4.7). However, in Southern Africa there are a number of PAs with relatively low species persistence (i.e. <40% persistence; Figure 4.10); examples include Augrabies Falls (17%; $\bar{x}$ = 17%), Hardap

Dam (27%; $\bar{x}$ = 27%), Witsand (28%; $\bar{x}$ = 28%), Molopo Green Belt (28%; $\bar{x}$ = 29%) and the Kalahari Gemsbok Park (32%; $\bar{x}$ = 32%).

Table 4.7. Protected areas chosen with predicted persistence of 100% by the year 2080. (B) is the sum of species for which the climate is suitable in the present as well as the future and (P) is the sum of species in the protected area at present.

Protected Area	Location	Number of Species Currently (P)	Present and Future (B)
Boukornine	Tunisia	22	22
Cape Mount	Liberia	46	46
Chambi	Tunisia	20	20
El Kala	Algeria	21	21
Gadabedji	Niger	23	23

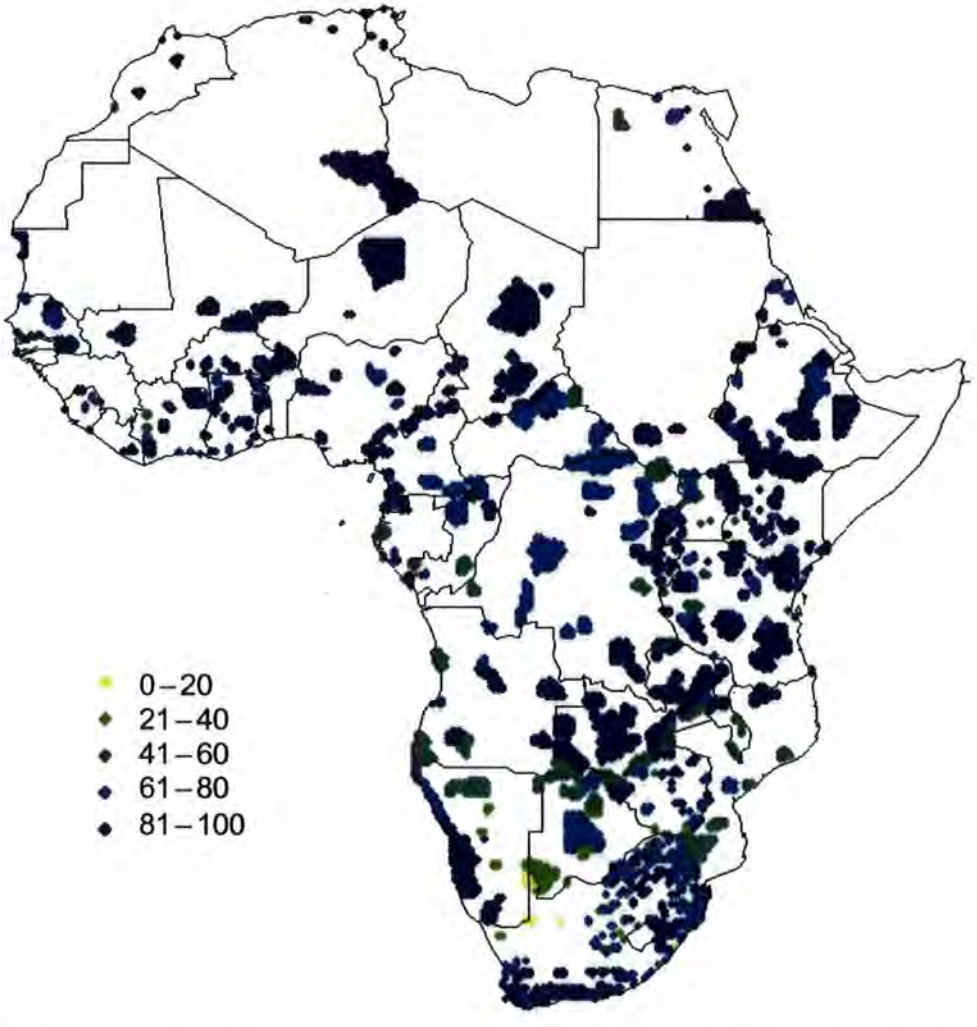


Figure 4.10. Predicted species persistence (%) in African protected areas by 2080. Persistence in each PA is calculated as the mean persistence of species under the three GCM scenarios for the year 2080 (see appendices Table A4). These values were placed into one of five distinct classes (see key), with darker colours representing higher predicted persistence.

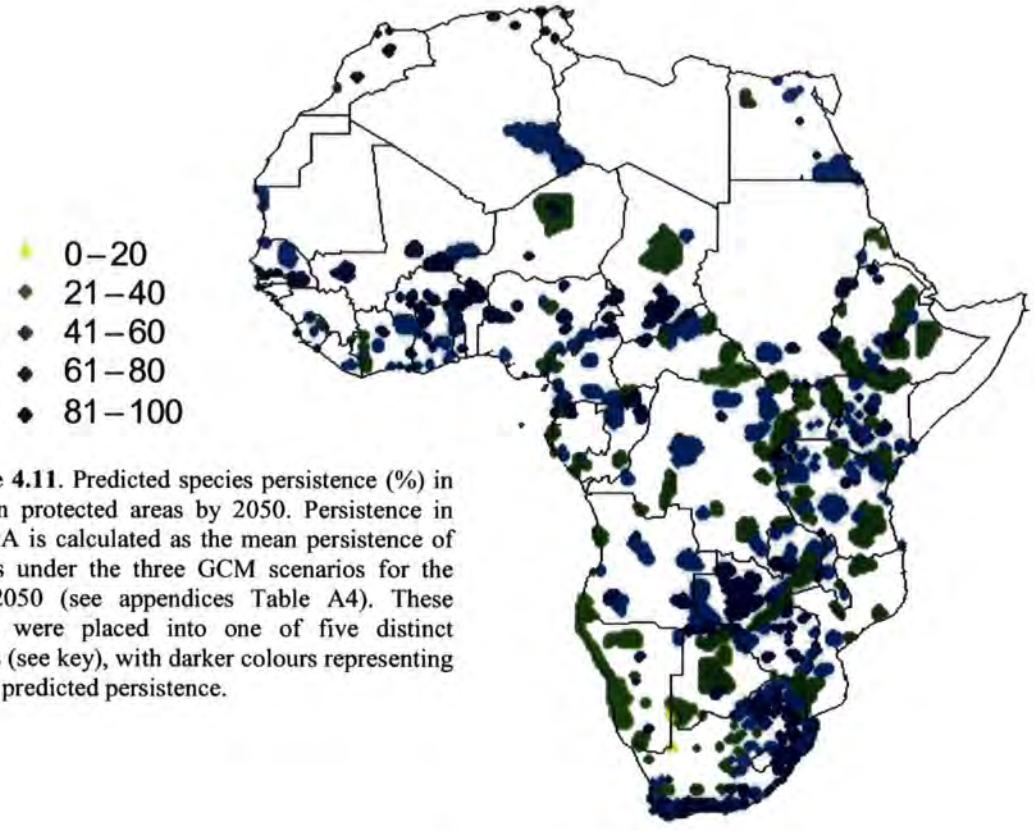


Figure 4.11. Predicted species persistence (%) in African protected areas by 2050. Persistence in each PA is calculated as the mean persistence of species under the three GCM scenarios for the year 2050 (see appendices Table A4). These values were placed into one of five distinct classes (see key), with darker colours representing higher predicted persistence.

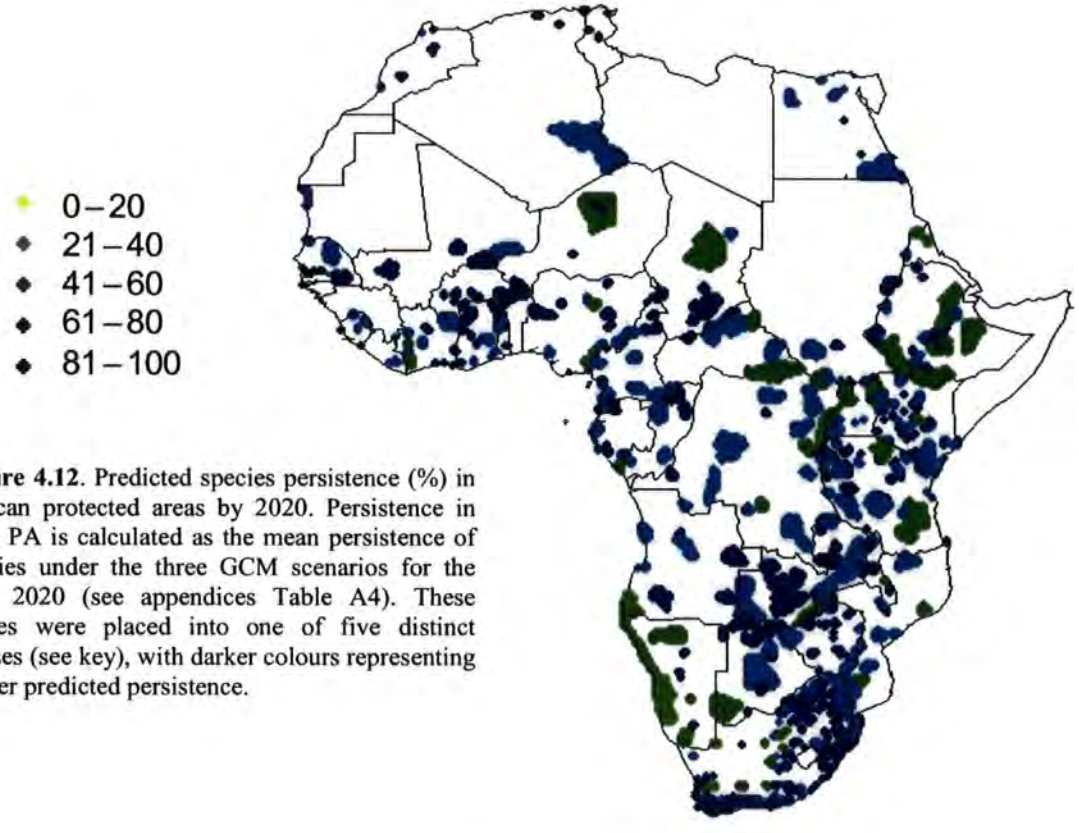


Figure 4.12. Predicted species persistence (%) in African protected areas by 2020. Persistence in each PA is calculated as the mean persistence of species under the three GCM scenarios for the year 2020 (see appendices Table A4). These values were placed into one of five distinct classes (see key), with darker colours representing higher predicted persistence.

A Spearman's Rank Correlation indicated there was a slight significant positive association between PA size and species persistence; a larger protected area having a slightly higher species persistence ($r = 0.048$, $d.f. = 716$, $p < 0.05$) (Figure 4.13).

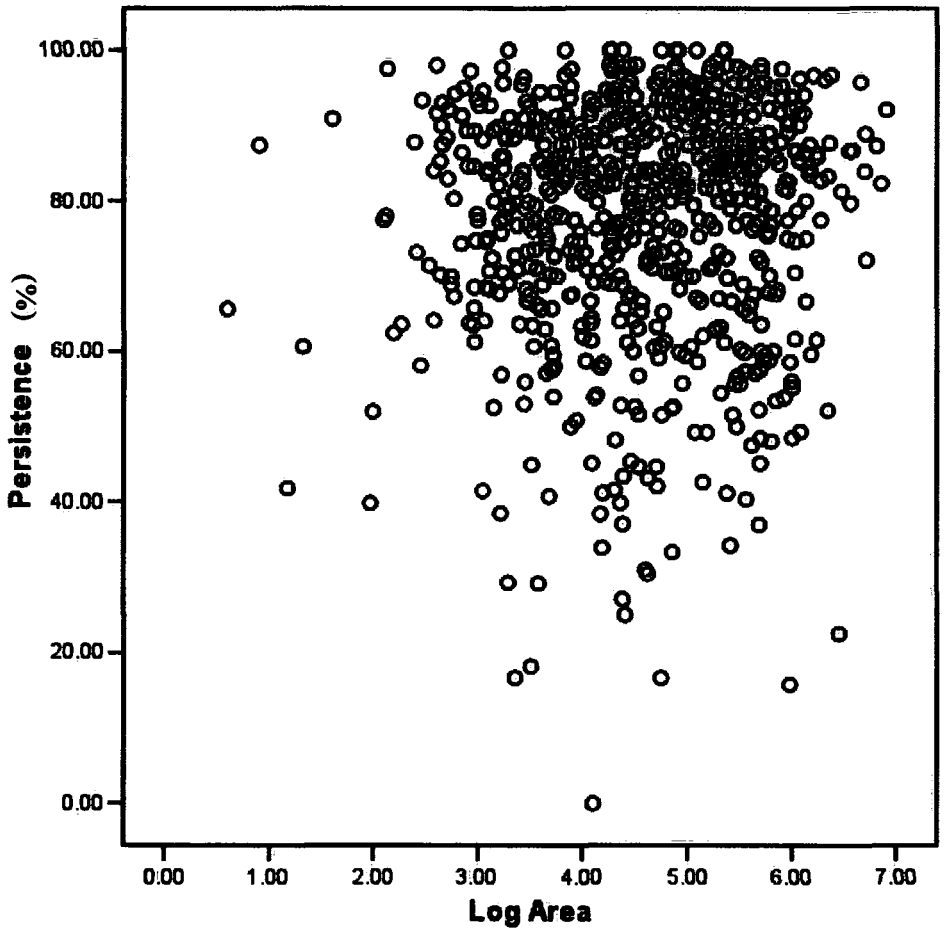


Figure 4.13. Scatter diagram of the relationship between species persistence and log area (measured in Hectares) of protected areas in Africa.

4.4. DISCUSSION

Species' range boundaries have already been observed to be shifting in response to contemporary climate change (see Chapter 1.1.2.1). Consequently there is the potential for species ranges to move out of (or into) protected areas which would mean that as climate changes, species richness and composition within PAs will change (Hannah *et al.,* 2007). Mean projected turnover of species within African PAs is projected to increase from 10% by 2020, to 18% by 2050, to 26% by 2080. At the same time, mean species persistence within PAs is predicted to be fairly high in all future scenarios; 81% in 2020, 74% in 2050, and 79% by 2080. These results are similar to work on avian species richness in African Important Bird Areas (IBAs) by Hole *et al.,* (unpublished) which predicted species turnover within IBAs of 10 – 12% by 2025, and 20 – 25% by 2085. They also predicted that avian species persistence within IBAs will remain high (75 – 81%), even under late 21st Century predictions of climate change. Subsequently, on the whole the African PA network seems to be robust in the face of predicted climate change. However, species turnover (and persistence) will be unevenly spread across the PA network; by 2080, PAs in South Africa and Namibia are projected to experience the high turnover (64 – 78%) while PAs in Tunisia, Niger, Liberia and Niger experience the low turnover (1 – 2%). As high turnover indicates that community composition will differ markedly between the present and the projected future scenario, this would suggest that PAs in South Africa and Namibia will be affected most by climate change. Similarly, Thuiller *et al.,* (2006) predicted that national parks in South-Western African will be the most sensitive to climate change; with parks such as the Kalahari Gemsbok Park and Tassili N'Ajjer experiencing high numbers of mammalian species losses (approximately 50%) and little immigration (approximately 10%). Like this study, Thuiller *et al.,* (2006) simulated that the Kalahari Gemsbok Park will experience high turnover of mammal species by 2080; although we predict this park will have more colonizers and less emigrants than Thuiller *et al.* did. This could be due to the fact that Thuiller *et al.* used only one GCM (HadCM3) while our study calculated turnover as the mean of three different GCM outputs (HadCM3, GFDL and ECHAM4), as well as a different emissions scenarios (A2 and B2 rather than just B2). Consequently, average turnover in this study may be a better estimate than Thuiller *et al.'s.*

The results of this study suggest that species richness within protected areas will change as climate changes. By ~2080, mean species richness at the quarter degree scale is greater in protected areas (47 species) than mean species richness across the whole of Africa (36 species). Similar results have been recorded by Midgley *et al.,* (2002); who predicted that by ~2050, mean species richness in PAs (also at the quarter degree scale) is significantly greater than species richness in areas lost to the Fynbos biome. We also predict that by 2080, decreases in species richness within PAs will be larger than the decrease in species richness in areas beyond PA boundaries. If the current PA network remains the same (i.e. in size, location and extent) until at least 2080, the mean decrease in species richness at the quarter degree scale within PAs will be 7.18%, which is greater than that experienced overall across areas of Africa beyond PA boundaries (-4.41%). Similarly, Burns *et al.,* (2003) recorded the average loss of mammalian species richness in selected PAs in America to be 8.3%. Therefore the PA network is predicted to fare worse than Africa as a whole as climate changes.

The findings of this study are based on an 'unlimited dispersal' scenario which, in reality is unlikely to be possible for all species; some may not be able to track such changes fast enough, especially relatively slow dispersing organisms such as plants. For example many of the Cape Proteacaeae in South Africa are ant dispersed which therefore limits their dispersal rates (Midgley *et al.,* 2002). However, for mammals, the idea of relatively rapid (~20 – 50 years) range shifts are not out of the question (Thuiller *et al.,* 2006). Despite this, other factors such as habitat fragmentation and human-wildlife conflict are likely to be key factors determining mammals' opportunity to track climate changes (WWF, 2007). For example, agricultural activities such as the growth of crops are expected to track climate change by moving polewards and upslope thereby coming into direct competition with wild animals as they also track changes in this way (Hannah *et al.,* 2005). For example, it is projected that between 2000 and 2050, 10 – 20% of grassland and forestland in Africa will be converted, primarily for agricultural activities. Furthermore, as climate changes human-wildlife conflict is almost certain to increase as increasing human populations exert increased pressure upon natural resources (Millennium Ecosystem Assessment, 2005). It is expected that conversion of land to agriculture will cause a decrease in the extent of natural ecosystems, as well as causing increased contamination of

groundwater which would impact negatively upon aquatic ecosystems (Millennium Ecosystem Assessment, 2005). Some species may be able to adapt to potential future climates within PAs (Thomas *et al.,* 2001). Despite this, one would expect changes of species richness, turnover and persistence in PAs in the future if factors such as barriers to dispersal, continued habitat loss and ecosystem lags are into account (Root & Schneider, 1995; Hannah *et al.,* 2005). In a worst case scenario, species diversity in PAs would simply be the sum of the species persisting in an area, i.e. no immigration of colonist species but loss of those for which the climate becomes unsuitable.

PAs within areas which are projected to incur high species turnover and decreasing species richness will require significant attention from PA managers and policy makers in the future. Especially as PAs with high turnover were projected to simultaneously incur low species persistence when compared to the average (79%) for the African PA network (Table 4.7). Consequently, PAs which are predicted to experience high turnover and low persistence (e.g. Augrabies Falls, Hardap Dam, Kalahari Gemsbok, Molopo Green Belt and Witsand) will be most severely affected by climate change as they will no longer retain suitable climate for the species they were designed and built to protect (Hole *et al.,* unpub). So, while on average the African PA network seems to be robust in the face of predicted climate change (i.e. high persistence ($\bar{x}$ = 79%) and low turnover ($\bar{x}$ = 26%)), it is expected that a few areas will need intensive management (e.g. expansion, connection to other PAs and/or artificial habitat modification) in order for species to persist there in the future.

Changes in community composition within PAs will have far-reaching effects within ecosystems by for example altering interspecific interactions such as predator – prey dynamics, or by affecting species which rely on mammals for ecosystem roles such as seed dispersal and habitat modification (Burns *et al.,* 2003; Thuiller *et al.,* 2006). Some mammal species have a more significant role in ecosystem processes than others; these species are termed 'keystone species' because they exert an influence on the environment disproportionate to their size or abundance (Paine, 1995). For example, the loss of zebras and giraffes, as well as other large herbivorous mammals in African savannas may cause substantial population shifts of other species (Pringle *et al.,* 2007). African elephants

(*Loxodonta africana*) are termed 'super keystone species' (Shoshani, 1993); without them, African grasslands become overgrown with woody plants and shrubs (Chaplin *et al.*, 1997). This negatively impacts upon species such as grazing antelopes and carnivorous predators of those antelopes. Therefore if the distribution of keystone species such as elephants were to change as a result of climate change, this could have potential effects upon many other species within (and outside of) PAs. Additionally, as elephants are large charismatic species the public visit PAs to see, the loss (or gain) of these from PAs may impact upon visitor numbers and associated revenues to those PAs (Walpole & Leader-Williams, 2002).

As PAs are regarded the mainstay for *in situ* conservation efforts managers and policy makers must take the dynamic nature of the climate into account when selecting new reserves and managing existing ones in order to remain an integral conservation tool in the future (Hannah *et al.*, 2005). It seems that increasing the size of existing PAs will increase the stability of community composition within PAs by decreasing turnover (page 104) (and increasing persistence; page 109) within them, especially as many species require relatively large areas of habitat to maintain viable populations (Shaffer, 1981). However, increasing the connections between PAs by creating wildlife corridors will also be of benefit by allowing species the option of tracking climate change (Hannah *et al.*, 2002). For example, wildlife corridors between Ghana and Burkina Faso, as well as Mali and Burkina Faso, are currently being planned in order to aid the survival of West African elephants (IUCN, 2005). Corridors allowing mammals to track climate change would simultaneously have positive impacts on other species such as birds, plants, reptiles and amphibians whose survival is partly dependant on mammals e.g. for ecosystem services such as seed dispersal or habitat modification. In addition to extending and connecting existing PAs, the creation of new PAs, especially in areas which are expected to be altered substantially with climate change, will be a key tool in protecting species well into the future. While these proposals require huge resources (both economic and personnel) in order to become viable, it will be of great benefit for mammalian species in African PAs in the future. Additionally, the creation of transfrontier parks between protected areas in multiple countries will aid species conservation in the face of projected climate change. Examples of transfrontier parks established in Africa are the Greater Limpopo

Transfrontier Park (www.greatlimpopopark.com) which encompasses area in South Africa, Mozambique and Zimbabwe; and the Kavango-Zambesi Transfrontier Park (www.kazapark.com) which connects Angola, Zambia, Botswana, Namibia and Zimbabwe. These parks allow the re-formation of larger ecosystems, which aid species migration and genetic mixing, as well as addressing threats facing biodiversity including habitat loss, fragmentation, over hunting and the impacts of climate change (Reyers, 2003). However, in addition to addressing the *potential* impacts of climate change, we also need to stabilise greenhouse gas emissions *now* in order to halt this change (IPCC, 2001).

CHAPTER FIVE: Willingness-to-pay towards the conservation of threatened mammals in South Africa; a case study in Kruger National Park

5.1. INTRODUCTION

Africa is extremely rich in biological diversity; nearly a quarter of the world's biodiversity hotspots are located within this continent (CI, 2007). Conservation strategies within these areas are often prioritised according to traditional criteria such as species richness and diversity (Spellerberg, 1992), or ranking overall threat and decline of species (White *et al.*, 1997). However, these methods of prioritisation may not necessarily reflect human preferences and values (White *et al.*, 2001). Compounding this problem is the fact that relatively little is known about the social value of biodiversity within these areas (Turpie, 2003). As a result, understanding human preferences towards conservation and placing an economic value on biodiversity has gained increasing emphasis in recent years, which is crucial if the conservation of biodiversity is to compete for funding against other issues (Edwards & Abivardi, 1998).

Biodiversity worldwide is threatened by a number of processes including land transformation, the invasion of non-native species, and human population pressures (White *et al.*, 2001). However, it is climate change which is the most significant threat to biodiversity today, not only because of the unprecedented rate and magnitude of the change but also the relatively more complex and costly action required to prevent it (White *et al.*, 2001). Previous chapters have demonstrated the possible consequences of climate change upon the potential distribution of large mammal species in the future; species' ranges are predicted to (on average) decrease and mean overlap between current and future ranges is also predicted to decline (Chapter 3). The impact of climate change on the effectiveness of African protected areas has also been investigated (Chapter 4), and while on the whole PAs are predicted to be fairly robust to climate change in relation to large mammal distributions, some protected areas are predicted fare worse than others in terms of large mammal species' turnover and persistence within them.

The vast majority of research into the economic effects of climate change has focused on market impacts of climate change e.g. the effects of climate change upon the productivity

of crops, or the costs associated with rises in sea levels (e.g. Frankhauser *et al.*, 1998; Mendelsohn & Neumann, 2004). However, much less focus has been placed upon estimating the non-market impacts of climate change (e.g. social impacts of biodiversity loss), presumably because non-market impacts are more controversial and harder to measure (Turpie, 2003). The non-market value of a good may have economic values in terms of both use and non-use values (Hanley *et al.*, 2004). Use values compromise direct use, indirect use and option values; non-use values compromise bequest values and existence values (White *et al.*, 1997; Figure 5.1). Although deriving economic values of non-market goods can be controversial, environmental valuation remains a useful tool in providing estimates of the social benefits of these resources (White *et al.*, 2001)

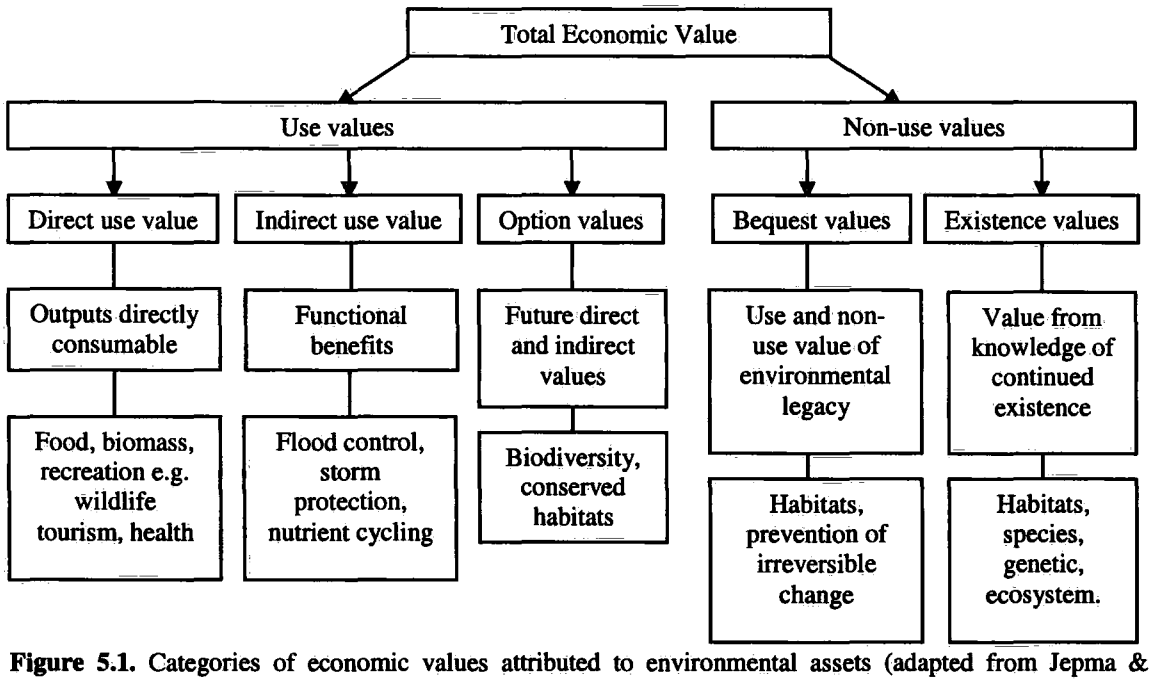


Figure 5.1. Categories of economic values attributed to environmental assets (adapted from Jepma & Munasinghe (1998).

Economic values of non-market environmental goods and/or services are often elicited in terms of people's willingness-to-pay for conservation, using a type of stated preference method called contingent valuation (CV) (Turpie, 2003). Other stated preference (SP) methods include choice experiments and contingent ranking however by CV is by far the most widely used (Hanley *et al.*, 2004). CV surveys (Mitchell & Carson 1989; Bateman & Willis 1999) question participants directly about the amount they are willing-to-pay to

prevent (WTP) or willing-to-accept compensation for (WTAC) hypothetical changes in environmental quality (Hanley *et al.*, 2004). One can extrapolate the estimates of WTP (or WTAC) from the sample population up to the local, regional or national population in order to gain estimates of the losses that would be accrued if the stated environmental change transpires e.g. loss of a particular species or degradation of a natural feature. Subsequently, the results of such studies provide useful estimates of the value of species conservation and can easily be compared to the 'actual' amount set aside for conservation (see e.g. White *et al.*, 1997). However, care must be taken when interpreting these results as such estimates may be affected by the presence of similar or complementary species (Hoehn & Loomis, 1993). A consequence of this is the possibility that aggregated values for a group of species may differ if the total is calculated directly or indirectly (i.e. if individual species values are summed) (Nunes & van den Bergh, 2001).

As part of the CV study design, one must decide who the target population are, and how many people in this population should be questioned. Bateman *et al.*, (2002) suggest that the minimum sample size for CV studies is about 250. However, they also stipulate that smaller sample sizes can be used when multiple valuations are elicited from each respondent. Additionally, they suggest the target population should be those people who will be affected by the change, and are thought to have some knowledge of the change. In the case of this study, the target population will be the 'user population' i.e. those people who are visiting Kruger National Park (KNP). However, it is possible that the loss of species from KNP as a result of climate change may affect a wider population that this e.g. non-visitors to KNP. These people may hold existence/bequest values of the good (i.e. species). Therefore, if time permitted, an extension of this study could be to assess WTP of people who are not visitors to KNP.

Methods of sampling the target population in CV studies can be by in-person interviews, telephone or mail surveys. All three have their advantages and disadvantages for example postal surveys are much more economical than the others, and also reduce possible interviewer biases but they suffer from low response rates; phone surveys reduce non-response bias (Loomis & King, 1994) and consequently have slightly higher response

rates than postal surveys but there are still problems such as the bias assoicated with different levels of telephone ownership. Consequently, in-person interviews are the preferable sampling method in CV studies (Arrow *et al.,* 1993). Although this method secures much higher response rates than postal or telepone surveys, it is the most costly sampling strategy. In a recent metaanalysis by White *et al.,* (2005), mean (±SE) response rate from in person interviews was 97.5 ± 1.4%; postal and telephone interviews presented much lower response rates of 51.9 ± 2.7% and 58.1 ± 5.4% respectively. Babbie (1990) has suggested that the minimum response rate adequate for analysis is 50%. However, more recently Hanley *et al.* (2004) have suggested the minimum response rate from the target population should be over 70%, which in-person interviews clearly obtain. This facet of in person interviews is a definite advantage of this method of data collection; low response rates indicate that the issue in question is not particularly important to the respondents, in which case either the WTP/WTAC question or the choice of target population is almost certainly unsuitable (White *et al.,* 2005).

As part of a CV study, the respondents are asked about the level of sacrifice they would be prepared to make (or compensation they would be willing to accept) in order to prevent the hypothetical change in environmental quality (Arrow *et al.,* 1993). These WTP (or WTAC) questions can either be in an open-ended (e.g. what is the most you are WTP to conserve species Z?) or closed format. Examples of closed format questions include dichotomous choice (are you you WTP 'X' amount to conserve species Z?) or using payment cards to indiciate the respondents maximum WTP from a set number of given amounts. The latter two methods are generally preferred as they result in less uncertainty (White *et al.,* 2005) and reduce the occurence of very high (or low) WTP values (Arrow *et al.,* 1993). Additionally, respondents often find open-ended questions more difficult to answer compared to closed-ended questions. Despite this, open-ended questions are generally easier to constuct and analyse statistically (Barnes *et al.,* 1999). Moreover, Loomis & White (1996) found the format of WTP questions to be "relatively unimportant" in determining WTP for the conservation of endangered species.

Results of CV studies were often previously considered as controversial, for example some critics believed that respondents often did not understand the good they were being asked to value, and that CV questions were often taken lightly as they were seen as being non-binding (Arrow *et al.,* 1993). Additionally, CV is prone to a number of other biases such as scenario misspecification (whereby the respondent does not understand the scenario and therefore values the wrong good) and non-response bias (whereby a respondent does not answer key questions such as their income or WTP). Additionally, the respondent may give a WTP amount that differs from their true WTP amount in order to influence the level of payment for the good (strategic bias) or in order to please the interviewer (interviewer bias) (Hanley *et al.,* 2004). However, the most noteworthy bias in CV studies is the problem of embedding (Turpie, 2003), whereby 'WTP for a good is approximately the same for a more inclusive good' (Fisher, 1996). However, amendments and improvements to CV methods plus the introduction of guidelines set out by e.g. Arrow *et al.,* (1993) have reduced these biases and therefore improved the reliability of CV studies. Examples of recommendations set out by the Arrow *et al.,* (1993) panel on contingent valuation include that interviews should be in-person rather than by mail or telephone, a WTP rather than a WTAC format should be used, there should be yes/no follow up questions after the WTP question, the questionnaire should be extensively pre-tested, it should hold adequate information about the hypothetical change in the environmental good and finally that respondents must be reminded of their budget constraints and undamaged substitutes of the environmental good in question before the valuation question. Consequently, with careful design of the CV questionnaire to prevent (or reduce) potential biases and problems, CV is deemed an acceptable method to determine non-market values of environmental goods and/or services (Arrow *et al.,* 1993). So much so that many governments have now commissioned the use of CV studies to seek the views of stakeholders and the general public before deciding on environmental policies (White *et al.,* 2005). For example, the United States Department of Agriculture commissioned studies using CV to estimate the economic value to the public of protecting ecosystems from fire (Loomis *et al.,* 1996); the Department for Environment, Food and Rural Affairs in the U.K. has used CV to gage public views about hunting with dogs (Burns *et al.,* 2000), to inform the design of agri-environmental schemes (Hanley *et al.,*

1999; DEFRA, 2002) and in setting waste management options and eco-taxes (Turner *et al.*, 2004; also see www.defra.gov.uk/Environment/economics). CV studies have also been used to assess water quality improvement schemes in the U.K. (Hope & Palmer, 2004).

CV methods have been used in numerous other studies over the past thirty years; however there has been a dramatic increase in the amount of scientific papers particularly in the past twenty years (Arrow *et al.*, 1993). A major reason for this increase comes from the increased availability of reference texts (e.g. Mitchell & Carson, 1989) and guidelines (e.g. Arrow *et al.*, 1993), as well as a huge increase of the interest of the general public towards environmental problems and biodiversity conservation (Edwards & Abivardi, 1998). The majority of CV studies tend to value a single environmental resource such as a habitat, a species or an ecosystem service (Christie *et al.*, 2006). For example the majority of studies valuing species conservation focus on a single species rather than multiple species ensembles (Nunes & van den Bergh, 2001). Studies focusing on single species conservation often ask respondents their WTP to avoid the loss of that particular species. For example, White *et al.*, (1997, 2001) estimated the value of otter, water vole, red squirrel and brown hare conservation in the U.K.; Loomis & Larson (1994) estimated the mean household WTP for the conservation of the endangered grey whale; Brookshire *et al.*, (1983) valued WTP for the conservation of the grizzly bear and bighorn sheep in Wyoming; and Boman & Bostedt (1995) estimated the mean WTP per household for the conservation of the wolf in Sweden. The majority of studies valuing species have been undertaken in America (Christie *et al.*, 2006); only a small number of studies in Africa have assessed the public's willingness-to-pay towards biodiversity conservation. One such study is by Barnes *et al.*, (1999), who assessed 'tourists' willingness-to-pay for wildlife viewing and wildlife conservation in Namibia'. Overall, the majority (72%) of respondents were WTP towards wildlife conservation. The aggregated mean amount these people were WTP was N$28.7 million (275 912 tourists at N$104 each) per year.

A relatively small number of studies have assessed the impacts of climate change upon African biodiversity in economic terms. An example of such a study is Verlarde *et al.*,

(2005), who valued the predicted ecosystem shifts resulting from climate change in protected areas in Africa; their results indicated a negative economic impact of climate change upon African protected areas by the year 2100. Other examples include Turpie *et al.*, (2002) and Turpie (2003) who estimated the economic impacts of climate change in South Africa; more specifically, the loss of existence value attached to biodiversity. Turpie's (2003) study focused on the fynbos biome in the Western cape, which Kiker (2000) predicted to lose over a third of its present range due to climate change; such changes were expected to have impacts upon biodiversity in this region. Results indicated that the majority (76%) of respondents were WTP towards biodiversity conservation in South Africa. Additionally, the amount respondents were WTP for biodiversity conservation increased dramatically when the possible impacts of climate change were explained ($3.3 million up to $15 million per year for fynbos and $58 million up to $263 million per year for South African biodiversity).

5.1.1. Aims

The aim of this chapter is to use contingent valuation to estimate people's willingness-to-pay towards the conservation of mammals threatened by climate change in Kruger National Park. This study will also investigate significant factors affecting people's willingness-to-pay towards these schemes. It is hoped these results will contribute towards biodiversity conservation in Kruger; data on the response of the public towards the conservation of mammal species as well as attitudes and preferences towards certain mammalian species will be useful as a reference for management decisions.

5.2 METHODOLOGY

5.2.1. Choice of protected area and focal species

It is predicted that as climate changes, protected areas in Southern Africa will be worst affected in terms of species persistence and turnover within them (Chapter 4), therefore this case study had a focus on protected areas within this geographic region. The majority of national parks in South Africa are controlled by South African National Parks (SANParks). In total nineteen national parks, one national lake area and one Transfrontier Park are under the control of SANParks (SANParks, 2007a - www.sanparks.org/parks). In

order to choose a suitable venue for this study, a number of requirements needed to be met. Firstly, the protected area(s) chosen had to currently hold the large mammal species studied in this project. Secondly, large numbers and high turnover of visitors were required in order to gain sufficient data on people's willingness-to-pay towards large mammal conservation. Finally, permission from the specific park authorities to carry out this research needed to be granted. Consequently, Kruger National Park in South Africa was chosen as it met all of these requirements.

Simulated future turnover and persistence of species in Kruger was close to the average values for the whole PA network studied (Chapter 4). By 2080 the level of species turnover in Kruger was simulated to be 25% and persistence 80%, when compared to the current species composition. These values are similar to the median turnover of 21% and median persistence of 84% across the PA network studied. While these results give a positive outlook for the majority of large mammal species in Kruger at present, the future of others in Kruger may be increasingly uncertain as climate changes. After investigation into how the current large mammal diversity of Kruger is projected to change in the future, a few charismatic large mammal species predicted to experience large (or total) decreases in climatically suitable habitat in Kruger in the future (i.e. the 2080s) were identified. Consequently, the species chosen in this study were the giraffe (*G. camelopardalis*) and elephant (*L. africana*); the distribution of both of these species in Kruger are projected to decrease substantially under all three scenarios for 2080 (Figure 5.5 and 5.7).

A large number of protected areas which are climatically unsuitable for the giraffe (n = 144) and elephant (n = 165) at present are projected to become climatically suitable by 2080 (Table 5.1). Conversely, 19% (n = 56) of the protected areas where giraffes are currently found (n = 290) are projected to become climatically unsuitable for this species by 2080. Similarly, 20% (n = 54) of the protected areas where elephants are currently found (n = 290) are projected to become climatically unsuitable for this species by 2080 (Figures 5.2 and 5.3; Table 5.1). Kruger National Park is an example of a protected area which is projected to become largely climatically unsuitable for the giraffe and elephant

by 2080. The potential future distribution of giraffes in southern Africa is projected to contract in eastern areas of Africa (southern Mozambique and eastern South Africa) under all three GCM scenarios for 2080 (Figure 5.4). The distribution of giraffes in Kruger is projected to decrease substantially under all three scenarios for 2080 (Figure 5.5). This is most pronounced under the HadCM3 B2 scenario whereby giraffes are projected to be absent from Kruger completely by 2080 (Figure 5.5c); the ECHAM4 and GFDL scenarios predict retention of climatically suitable range in the middle portion of the Park (Figure 5.5b & 5.5d). The distribution of elephants in southern Africa is projected to also decrease in south-eastern areas of Africa (southern Mozambique and into eastern South Africa); decreases in these areas are most pronounced under the HadCM3 B2 scenario for 2080 (Figure 5.6). As with the giraffe, the potential future distribution of the elephant in Kruger is projected to be reduced in all three future scenarios for 2080, but in this case particularly from the northern areas of Kruger (Figure 5.7). This reduction is most pronounced under the HadCM3 B2 scenario (Figure 5.7c), although under this scenario the elephant is not predicted to be totally absent in Kruger as was the giraffe.

Table 5.1. Persistence of the giraffe (*Giraffa camelopardalis*) and elephant (*Loxodonta africana*) within protected areas across the African continent. A species is noted as being present in a protected area if it is simulated to have at least one 0.25° presence point within the boundary of the protected area at the given time.

		Number of Protected Areas The Species is Simulated to Occur			
Species	Year	Current And Future	Current not Future	Future Not Current	Persistence in Protected Areas (%)
Giraffe	2020	277	13	79	95.52
	2050	255	35	129	87.93
	2080	234	56	144	80.69
Elephant	2020	254	14	99	94.78
	2050	230	38	142	85.82
	2080	214	54	165	79.85

By 2080, the mean prevalence of the giraffe across the whole of Africa is projected to increase by 12% whereas the mean prevalence of the elephant is projected to decrease by 14%. The overlaps between the current and potential future (2080) range of the giraffe and elephant are predicted to decrease to only 40% and 47% of the respective species current distribution (see Figure 3.2v (elephant) and Figure 3.2vii (giraffe)). These estimates are

substantially lower than the mean overlap between current and potential future distribution of 76% calculated for all 281 species (Chapter 3).

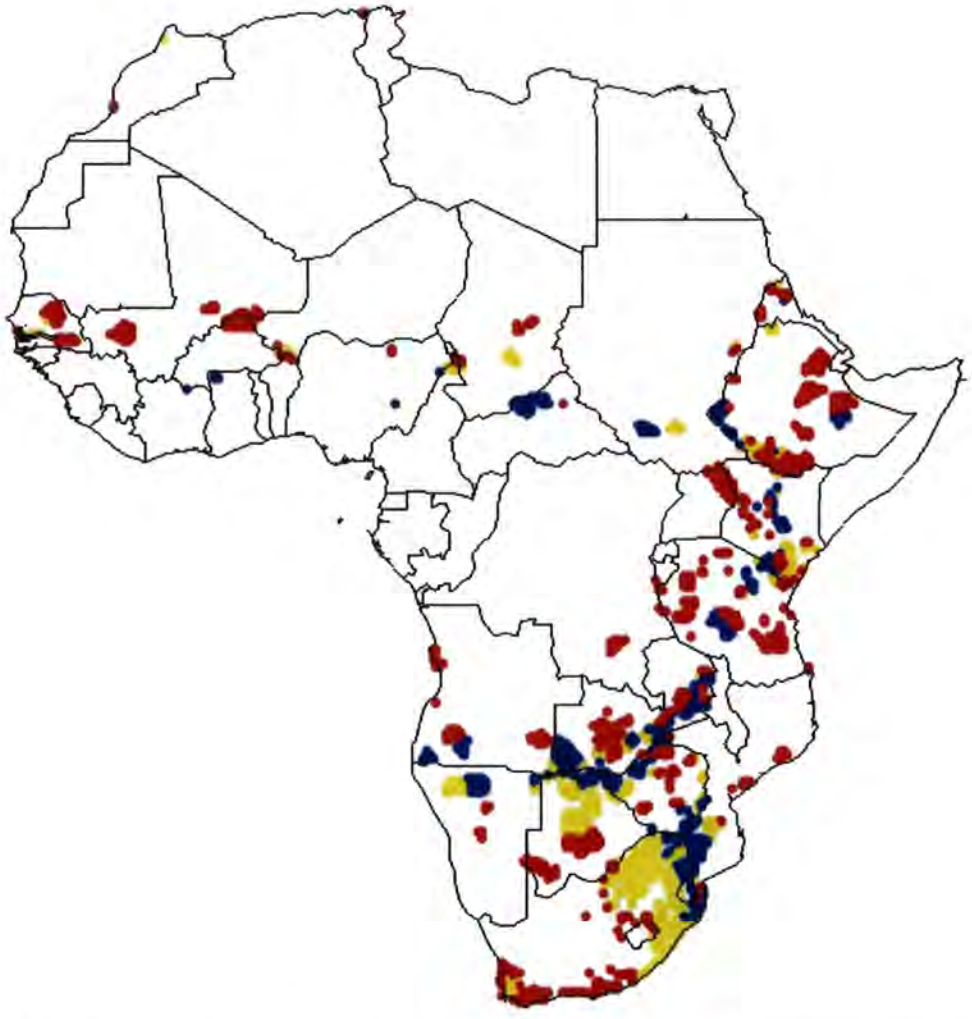


Figure 5.2. The simulated suitability of protected areas for the giraffe (*Giraffa camelopardalis*) in 2080. Red areas: indicate where giraffes are simulated to be present within protected areas in 2080 only. Blue areas indicate where giraffes are simulated to be present within protected areas at present only. Yellow areas indicate where giraffes are simulated to remain within protected areas between the present and 2080. Black lines represent country borders.

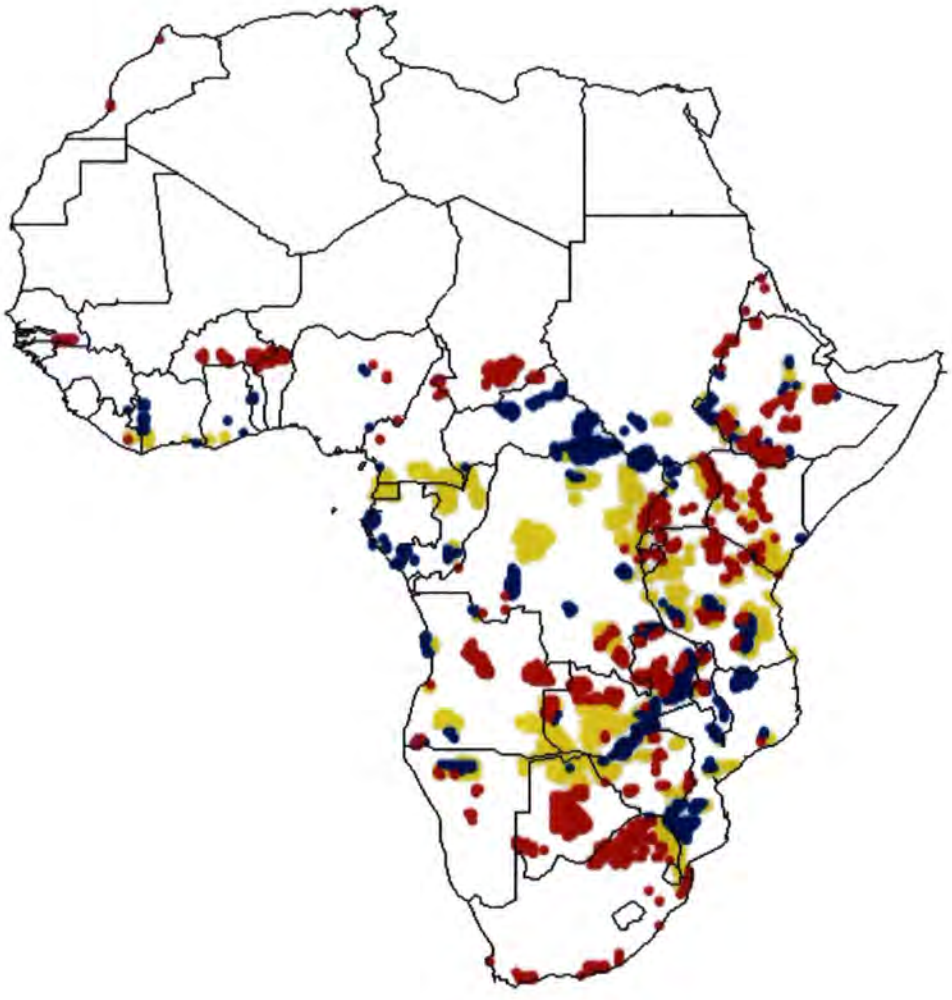


Figure 5.3. The simulated suitability of protected areas for the elephant (*Loxondonta africana*) in 2080. Red areas: indicate where elephants are simulated to be present within protected areas in 2080 only. Blue areas indicate where elephants are simulated to be present within protected areas at present only. Yellow areas indicate where elephants are simulated to remain within protected areas between the present and 2080. Black lines represent country borders.

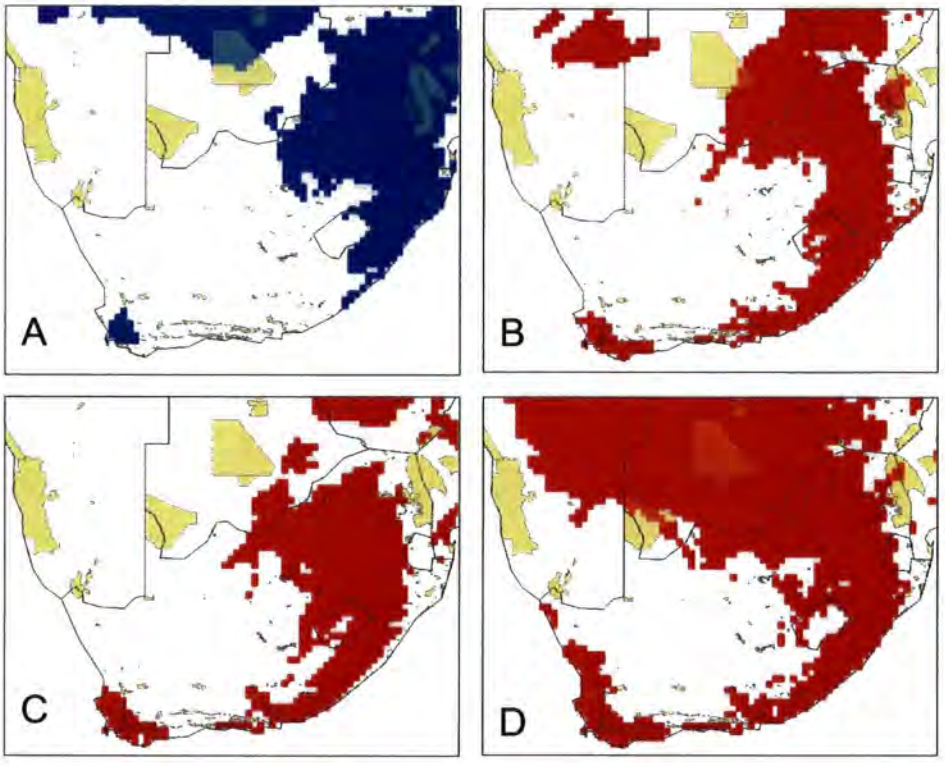


Figure 5.4. Simulated current and future distribution of the giraffe (*Giraffa camelopardalis)* in relation to protected areas in southern Africa. The maps depict simulated current (A) and potential future distribution of *G. camelopardalis* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Red/blue squares indicate the simulated presence of elephants in that area at that time; protected areas are shown in yellow; black lines indicate country borders/coasts; an overlap between protected areas and *G. camelopardalis* distribution is shown in green (Figure Ta) or orange (Figure Tb – Td).

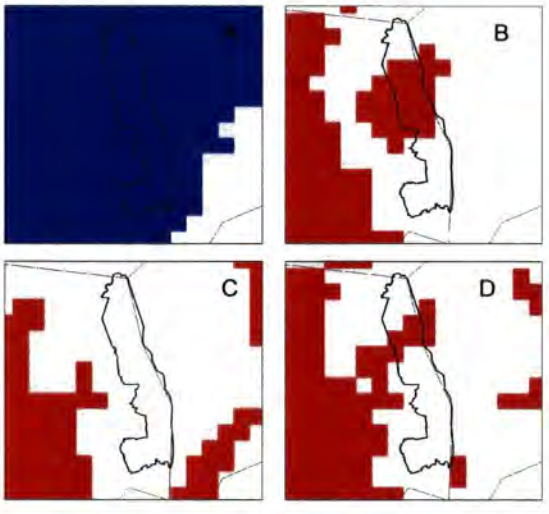


Figure 5.5. Simulated current and future distribution of the giraffe (*Giraffa camelopardalis)* in Kruger National Park, South Africa. The maps depict simulated current (A) and potential future distribution of *G. camelopardalis* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Red/blue squares indicate the simulated presence of giraffes in that area at that time; bold black lines indicate the border of Kruger National Park; other black lines indicate country borders.

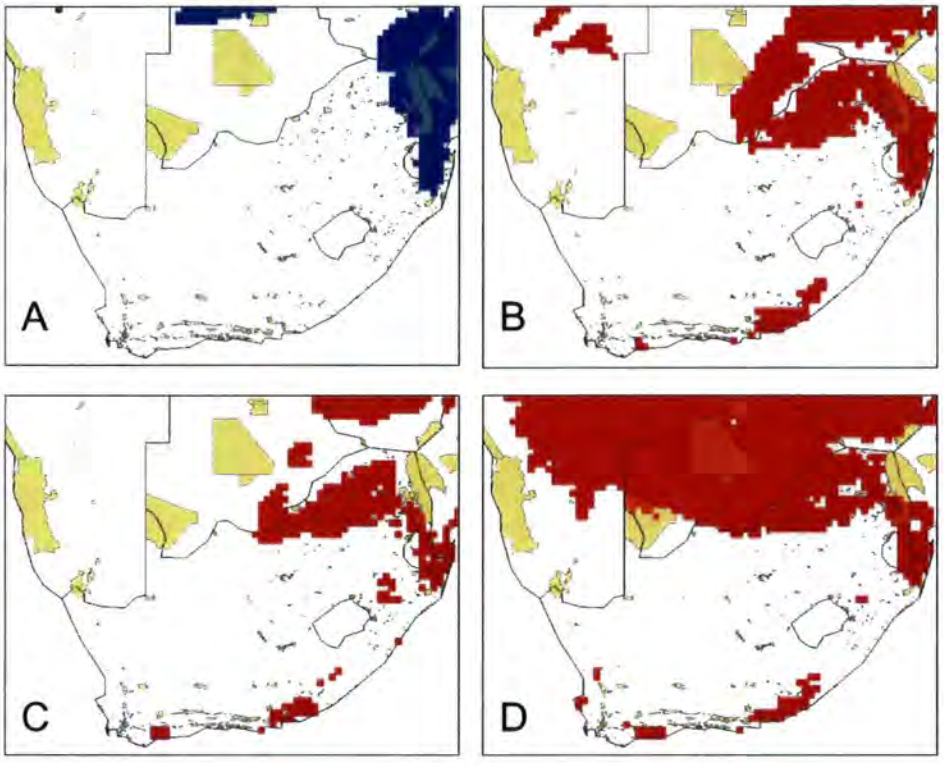


Figure 5.6. Simulated current and future distribution of the elephant (*Loxodonta africana)* in relation to protected areas in southern Africa. The maps depict simulated current (A) and potential future distribution of *L. africana* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Red/blue squares indicate the simulated presence of elephants in that area at that time; protected areas are shown in yellow; black lines indicate country borders/coasts; an overlap between protected areas and *L. africana* distribution is shown in green (Figure Ta) or orange (Figure Tb – Td).

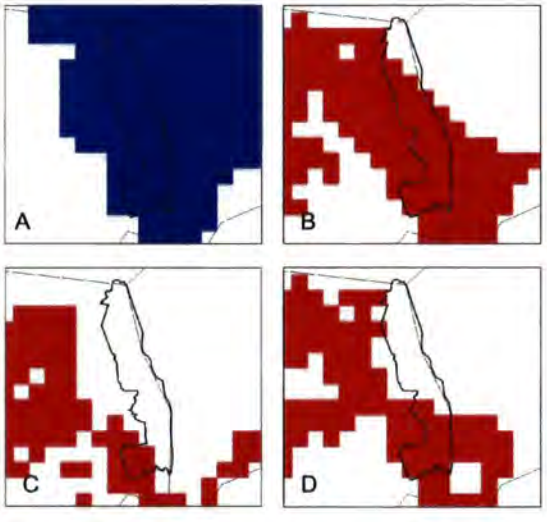


Figure 5.7. Simulated current and future distribution of the elephant (*Loxodonta africana)* in Kruger National Park, South Africa. The maps depict simulated current (A) and potential future distribution of *L. africana* for the year 2080 under the (B) ECHAM4 B2, (C) HadCM3 B2 and (D) GFDL B2 scenarios. Red/blue squares indicate the simulated presence of elephants in that area at that time; bold black lines indicate the border of Kruger National Park; other black lines indicate country borders.

5.2.2. Overview of Kruger National Park, South Africa

Kruger National Park (KNP) is described as "one of the premier game-watching destinations in the world" and is consequently one of the most popular game parks worldwide as reflected by the large number of visitors to KNP each year (SANParks, 2007). Of the 21 parks controlled by South African National Parks, KNP is the most visited of these by far (SANParks, 2007). In the year ending 31st March 2007, a total of 1,313,185 people visited KNP. This total compromised 76% of the total number of visitors (n = 1,725,451) to the fifteen major parks controlled by SANParks, indicating that KNP is a very important revenue generator for SANParks.

A major factor in the popularity of the park is that it holds a large variety of species, including 507 bird species, 147 mammalian species, 336 tree species, 114 reptile species, 49 fish species and 34 amphibian species (SANParks, 2007b - www.sanparks.org/parks/kruger/tourism/general). Examples of the mammalian species which can be seen include all of the typical African big game such as elephant, buffalo, leopard, lion, cheetah, giraffe, zebra, hippopotamus and the two species of African rhinoceros as well as a number of smaller species. A full checklist of mammalian species found in KNP can be found at:

www.sanparks.org./parks/kruger/conservation/ff/lists/mammals (SANParks, 2007).

KNP is situated in north-eastern South Africa, and is characterised by savanna, woodland and thornveld eco-zones (SANParks, 2007). The park is 350km long, on average 65km wide and compromises an area of 20,000km^2 (see Figure 5.8). It borders Mozambique and Zimbabwe; both of which have agreed to remove fences between KNP and parks within their borders in order to create connected wilderness areas (SANParks, 2007). Within KNP there are 12 main rest camps, 2 bush lodges and 4 satellite camps open to the general public, as well as some private lodges within and at the borders of the park.

Entrance fees to KNP are given in Table 5.2. Instead of paying a daily fee, all visitors also had the option of purchasing a WILD Card; this is a one-off yearly payment which allows the holder free entrance into all national parks controlled by SANParks, as well as Cape Nature Conservation Reserves (CNC) and Msinsi Resorts. International visitors can only

buy the 'all clusters' WILD Card, whereas South African residents can buy a card that covers 'all clusters' or just one cluster (Bushveld, Dry, River, Cape or Swazi). The WILD Card can be bought for individual use, for a couple to use or a family to use. For more details on WILD Cards see www.wildinafrica.com.

Table 5.2. Entrance Fees to Kruger National Park. Entrance fee information from www.sanparks.org. WILD Card information taken from http://www.sanparks.org/tourism/wild/wild_brochure_sept06.pdf, (only types of WILD Cards suitable for entry into KNP included in table). All Prices VAT inclusive and all tariffs in South African Rand. Entrance fees Valid from 1 November 2006 to 31 October 2007.

Type of Payment			
Daily Conservation Fee (entrance fee)	Individual		
South African Citizens and Residents	R30		
South African Development Community (SADC) Nationals	R60		
Standard Conservation Fee (international visitors)	R120		
WILD Card	Individual	Couple	Family
All Clusters (international visitors)	R795	R1395	R1795
All Clusters (national visitors)	R195	R335	R440
Bushveld Cluster (nationals only)	R170	R295	R395

5.2.3. Study Design

This study used stated-preference techniques to determine the existence value of two large mammal species currently in KNP, the giraffe and elephant, which are projected to lose a significant amount of climatically suitable habitat in KNP by 2080 (see Chapter 5.1.). Data were collected in-person using questionnaires; two questionnaires were developed, one for each of the chosen species. The first environmental change (in both versions of the questionnaire) to be valued was the possible loss of the current number and variety of large mammal species in KNP as a result of climate change. Questionnaire version one (V1) then asked respondents' to value the possible loss of elephants in KNP as a result of climate change, and version two (V2) valued the possible loss of giraffe in KNP as a result of climate change. The remainder of the two questionnaires were identical.

Ethical considerations were discussed and the questionnaire approved by Dr. B. Banks (Feb 2007), a member of the Durham University Ethics Advisory Committee. The questionnaire was also ethically approved by SANPARKs.

Once developed, the questionnaires were pre-tested by colleagues, friends and family with experience of visiting national parks in Africa. Replies and suggestions were noted and ambiguities clarified and re-checked. Once finalised, each questionnaire held 25 questions, split into three main sections. The first section (the tourism interest questions) of the questionnaire was intended as a warm-up section, with questions intended to get the respondents thinking about their trip and the animal species they had seen. The second section asked payment questions and included the open-ended WTP question. The bid vehicle chosen was an addition to the entrance fee to KNP as the respondents were familiar with the amount they had paid to enter the park. The final section of the questionnaire was used to collect socioeconomic data (Demographic Information). A copy of the whole questionnaire is given in Figure A1 of the appendices.

5.2.4. Sampling Strategy

International and domestic visitors to the restaurant/picnic area of Skukuza Rest Camp in KNP (Figure 5.8) were randomly selected to complete the questionnaire. The research was conducted between approximately 9am and 3pm daily from the 28th June to the 14th July 2007. The interviews were conducted either by myself or a student volunteer assistant from Durham University. In-person interviews were conducted with the interviewer leading the respondent through a pre-designed questionnaire. The version of the questionnaire to be completed was also chosen randomly. Interviews lasted approximately ten minutes each. Only adults were questioned as they have a defined source of income and were expected to be familiar with both the animals questioned and the amount of money they had already paid to enter the park. However, children (<18years) also place a value on wildlife conservation therefore results of this study are expected to be conservative estimates (Navrud & Mungatana, 1994).

Respondents were asked if they would answer the questionnaire, if yes they were then given a general introduction about the research. Respondents were then guided through the rest of the questionnaire. Directly preceding questions 14, 20 and 23 the respondents were shown the relevant supporting materials (current and potential distribution of giraffe/elephants in KNP (Figure 5.10*i* and 5.10*ii*), ethnic origin options (Appendix, Figure A2) and income bracket options (Appendix, Figure A3) respectively). At the end of

the questionnaire respondents were thanked for their time and given an opportunity to leave their name and email address in order to obtain a summary of results. Time, date and interviewer name were noted by the interviewer at the end of the questionnaire.

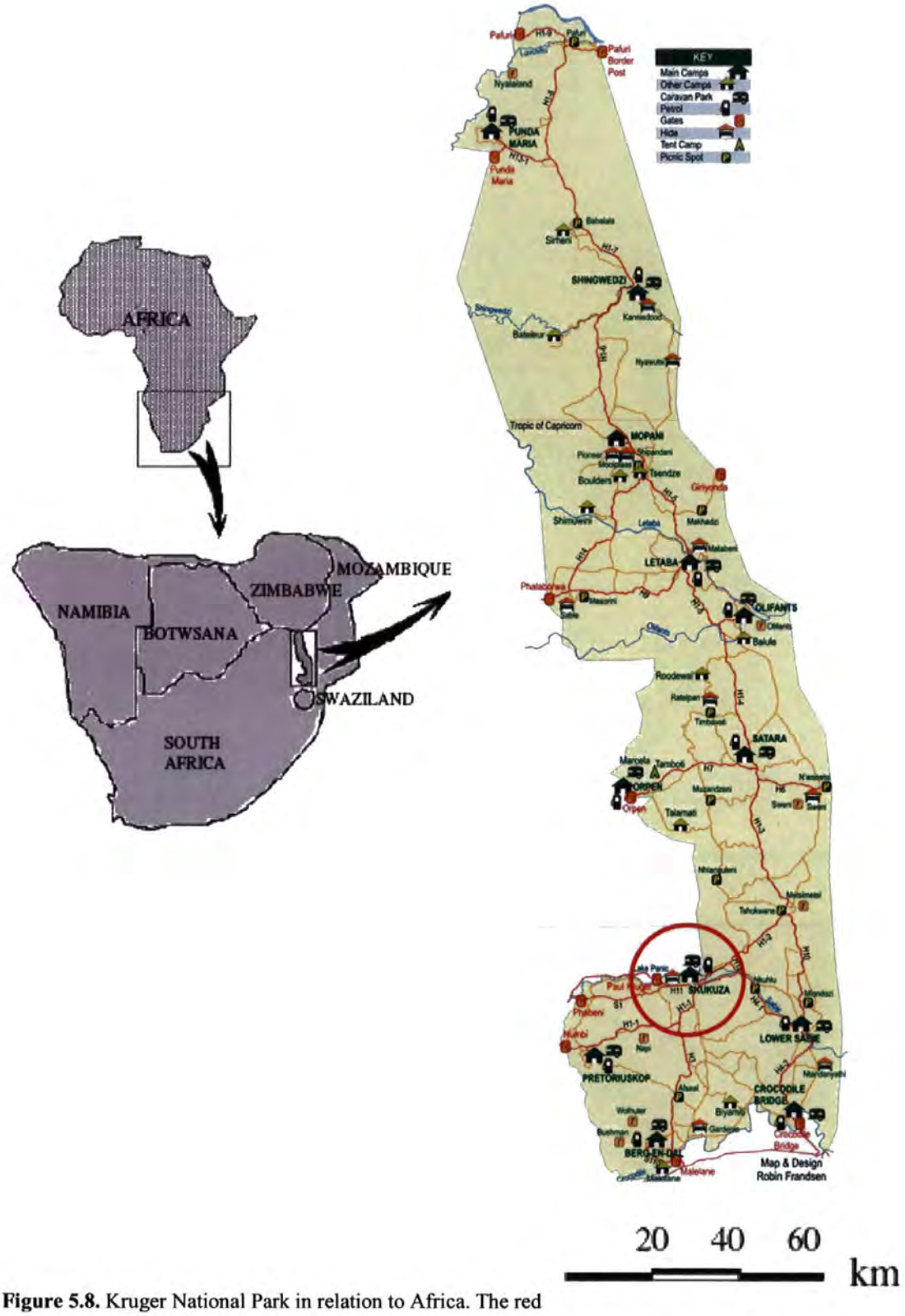


Figure 5.8. Kruger National Park in relation to Africa. The red circle indicates Skukuza Rest Camp. Pictures courtesy of www.sanparks.org and Fornara (2005).

5.2.5. Structure of the Questionnaire

The questionnaire started with a general introduction detailing for whom the research was being carried out and describing the aims of the research. Potential participants were also told that their responses would be anonymous and confidential. The introduction is shown below:

> This survey is being undertaken by **Durham University**, UK, as a piece of **independent** research to find out ***your*** views and values towards animals in National Parks in Africa. We would also like to find out ***your*** attitudes about the possible future changes in the variety of these animals. Finally, we would like to find out about your visit to the National Park today.
>
> Your help in answering this questionnaire would be greatly appreciated; your responses are anonymous and will be kept confidential.

The respondents were then guided through section one of the questionnaire; the tourism interest questions. Respondents were asked how many times, if any, they had visited KNP in the last two years; if they were visiting as a day or overnight visitor; their main reason for visiting KNP as well as the highlights of their trip to KNP so far. As this study focused on KNP, and did not mention other national parks, there may have been potential embedding effects. To reduce this effect, respondents were also asked if they were intending to visit (or had visited) any other national parks on their trip, and if so, to name them. This section concluded by asking respondents how many people they were travelling with, accommodation they were staying in and their type of holiday e.g. independent travel, part of an organised tour, backpacking or overland.

The second section (Payment Questions) started by asking respondents if they had used a WILD Card during their trip, if yes they were then asked which clusters it was for and whom it was valid for. They were then asked how much money they were spending on entrance fees per day (see Figure 5.9) and finally if they thought that this fee was too high, just right or two low. For both of the previous two questions they were given the option of stating they were unsure of the price they paid to enter the park. Entrance fees and prices for WILD Cards at the time of the study are shown in Table 5.2.

11. How much money are you spending on entrance fees to Kruger National Park per day? *Please tick one only.*

SA Citizens and Residents	R30 per day	☐
SADC Nationals	R60 per day	☐
Standard Conservation Fee (foreign visitors)	R120 per day	☐
WILD card (one off payment)		☐
Don't know/ Part of Inclusive Holiday Price		☐

Figure 5.9. Question 11 of the questionnaire.

The final questions in the Payment Section asked about respondents' willingness-to-pay an increased entrance fee in order to maintain the current number and variety of animals in KNP and then, more specifically, willingness-to-pay to help conserve only elephants (V1) or giraffes (V2) in KNP. These statements were designed to elicit a value response from the participants, and are not intended to imply that additional fees would solve climatic change problems such as these.

The first of these two questions was preceded by the text below:

> 'Effective conservation requires immense financial and human resources. South African National Parks (SANParks) needs to receive sufficient revenue to be able to successfully manage the 23 parks under its control. These parks, including Kruger, currently hold a wide variety and number of species; the following questions aim to try to find out how much *you value* these species.
>
> Imagine that in the next few years the variety and number of species may change as a result of climate change affecting habitat quality. If this were the case, SANParks would need extra money to manage the park to protect such species e.g. by identifying and averting threats to these species, the provision of artificial habitats etc. As there are only limited governmental resources available, a possible extra source of revenue to SANParks is to increase entrance fees. This increased fee would be in place for the foreseeable future.'

The second payment question was preceded by the text below (as well as a separate laminated sheet as shown in Figure 5.10*i* and 5.11*ii*):

Certain species are at a greaterrisk from the effects of changes in climate, for example the number of elephants [giraffe] in this park is expected to decrease in the next few years (see attached sheet). SANParks would be able to stabilise or even reverse this change using the extra revenues from an increase in entrance fees.

The laminate showed maps of the current and potential future distribution of elephants (V1) or giraffes (V2) in KNP, as well as a photograph of the respective species. No date was given for the potential future scenario as it was predicted that respondents would struggle to 'visualise' a scenario set too far in the future (in this case, 2080) (Parson *et al.*, 2003).

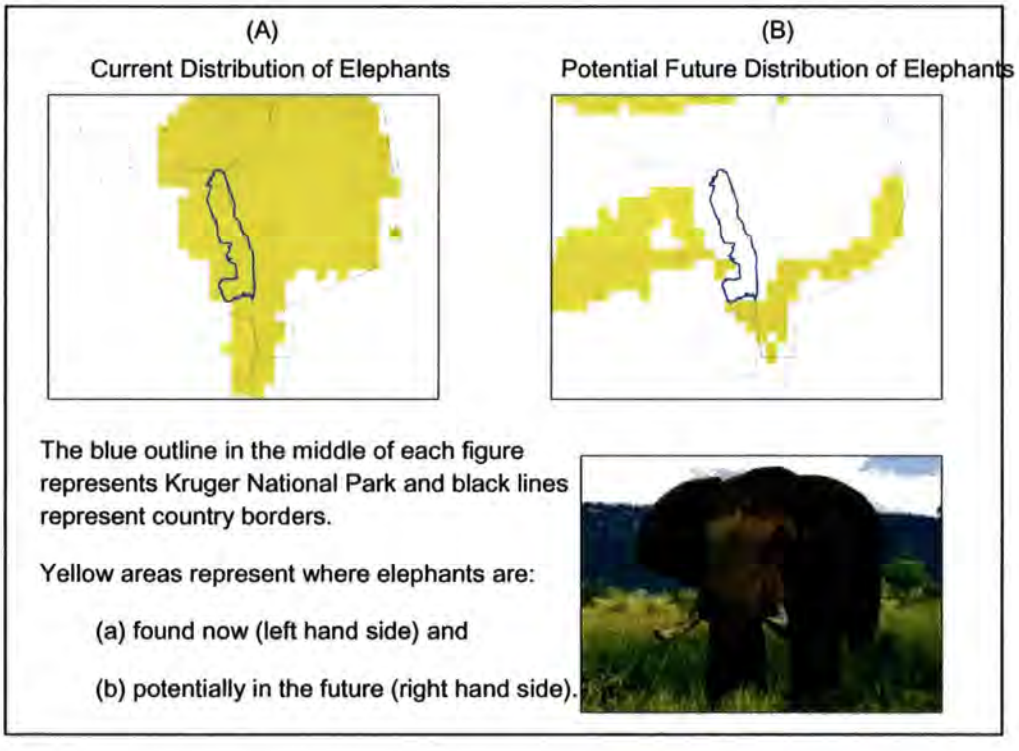


Figure 5.10*i*. Handout given to respondents before answering Q14 (V1).

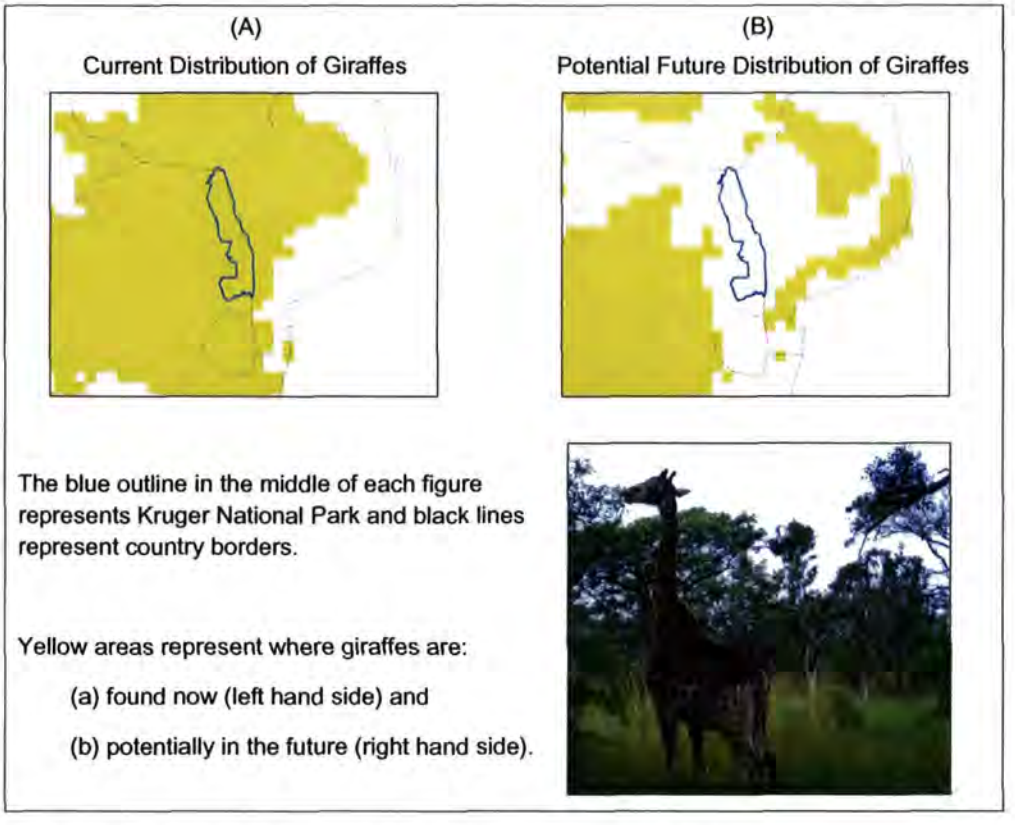


Figure 5.11*ii*. Handout given to respondents before answering Q14 (V2).

If the respondents answered no to either/both of the WTP questions they were asked to give an explanation why they were not willing to pay; if the respondents answered yes to either/both of these questions they were then asked to state how much they were willing-to-pay on top of the fees they had already paid to enter KNP. This WTP question took an open-ended format rather than the widely used dichotomous choice method (Navrud & Mungatana, 1994). This format was chosen as it allows the researcher to elicit direct measures of respondent's WTP without the need for sophisticated statistical techniques (Barnes *et al.,* 1999). The currency used in these questions was South African Rand (ZAR) because respondents were familiar with this currency as it was used in previous questions (e.g. the amount the respondent's paid to enter the park; Q11).

Socioeconomic data were collected in the final section if the questionnaire (Demographic Information). Respondents' were first asked their sex (Q16) and their age (Q17); ages were split into six categories (18 – 24, 25 – 34, 35 – 44, 44 – 54, 55 – 64 and 65 +). They were then asked their nationality, country and province/state of residence, ethnic origin, level of education and employment status. The respondents' were given a choice of different levels/options for the latter two questions (Table 5.3). The respondents' household income was then ascertained, by asking the respondents which one of eight income brackets they fell into (Table 5.3). The respondents were also given the option of answering in one of four currencies (South African Rand, Euros, US Dollars or Pounds Sterling) as it was presumed people would be able to give a more accurate answer if they were able to answer in the currency in which they received their income. In the year ending 31st March 2007, 76.6% of visitors to KNP were SA residents and therefore used to working in ZAR. The top five origins of international visitors were Germany, United Kingdom, Holland, France and the United States of America. For this reason ZAR, Euros, GBP and USD were chosen as most appropriate currency options. Respondents were then asked how many adults and children lived in their household, and finally if they were a member of a conservation organisation.

The questionnaire ended by thanking the respondents for their time and giving them the opportunity to leave their name and email address in order to receive a summary of the results.

5.2.6. Data collation and analysis

Data from the questionnaires were input into Microsoft Office Excel. Representativeness of the sample was checked against statistics relating to visitor statistics obtained by SANParks. The average exchange rate for the year to 30th March 2007 was R14.22 per £1, $1.96 per £1 and €1.47 per £1 (HM Revenue & Customs, 2007).

The data included in the questionnaires of respondents giving protest bids to the WTP question were excluded. These respondents were protesting to the concept of WTP and were therefore refusing to partake in the hypothetical exercise (Shackley & Donaldson, 2002). A total of eight protest bids were identified (4 were in version one and 4 were in version two). The main reasons for respondents' claimed unwillingness-to-pay included

the belief that the extra fee would not go to the stated cause; that the government should allocate more money towards this cause instead; and that an increased entrance fee may impact negatively on their business as a tour guide. A further three people who answered version one (elephant) were unsure if they were WTP or not; these questionnaires were also removed. This left a total of 170 questionnaires which were used in further statistical analysis (giraffe $n = 85$, elephant $n = 85$). Seven respondents who answered questionnaire V2 (giraffe) and six who answered questionnaire V1 (elephant) were WTP but unsure of the amount. These questionnaires were therefore not used when calculating descriptive statistics (mean, median, etc). However these thirteen questionnaires were suitable for use in the binary logistic regression models as the amount they were WTP was not needed.

Differences between respondents' answering the two versions of the questionnaire, in terms of the respondents' age, gender, employment status, income, level of education, nationality and country of residence were assessed using Chi^2 tests.

Logistic regression was used to determine the significant factors affecting peoples' willingness-to-pay towards conserving the current level of species diversity in KNP (model 1) as well as towards the conservation of solely giraffes/elephants in KNP (model 2). Willingness-to-pay (WTP) was a dichotomous dependent variable with two possible states: yes (1) and no (0) (Hanemann, 1984). Independent variables included in the analysis are given in Table 5.2.

Mean and median WTP for each species was estimated for each of the different scenarios (all species, giraffe and elephant). The median WTP for each species was then aggregated over the total number of visitors to KNP by multiplication, giving the total WTP for the conservation of large mammal species in KNP.

Table 5.3. Independent variables used in the logistic regression models to determine significant factors affecting peoples' willingness-to-pay. Numbers in brackets indicate numerical code for each possible answer. *For equivalent amount in different currencies see Appendix Figure A3. ^Entrance Fees are given in South African Rand (R).

Variable Name	Description
Gender	Gender of the Respondent: Female (0), Male (1)
Nationality	Nationality of the Respondent. Dummy variables were used for British, American, Australian, German, and Other. Reference group was 'South African'.
Employment	Employment Status of the Respondent: Dummy variables were used for Part-Time, Retired, Unemployed and In Full-Time Education. 'Full Time' was used as the reference group.
FirstTripSA	Whether it was the respondent's first trip to South Africa: Yes (1), No (0)
FirstTripKruger	Whether it was the respondent's first trip to Kruger: Yes (1), No (0)
Length	Whether respondent was visiting Kruger as a Day (0) or Overnight (1) visitor
Reason	The main reason for the respondent's visit to Kruger: To see wildlife (1) Other (0)
Interviewer	Person who interviewed that respondent: Georgina (0) George (1)
Species	Which version of the questionnaire the respondent answered; Giraffe (V2) (0) or Elephant (V1) (1)
Age	Respondent's age group in years, the midpoint for each was used in the model: 18 – 24, 25 – 34, 35 – 44, 45 – 54, 55 – 64, 65+
Education	The respondent's level of education. Dummy variables were used for University Higher Degree, Secondary School Completion, College Completion and No formal Qualifications. The reference group was 'University First Degree.'
Income*	The respondent's household income bracket: the reference number for each was used in the model: <£5000 (1), £5001 - £9999 (2), £10000 - £19999 (3), £20000 - £29999 (4), £30000 - £39999 (5), £40000 - £49999 (6), £50000 - £59999 (7), £60000 + (8)
TypeTrip	Type of trip the respondent was on. Dummy variables were used for Overland, Backpacking and Organised Tour. Independent Travel was the reference group. (0),
EntranceFee^	The amount the respondent paid to enter Kruger. Dummy variables were used for Standard Conservation Fee R120, WildCard and Don't Know. The reference group was 'SA Citizen R30.'
AttitudeFee	The respondent's attitude towards the cost of the entrance fee. Dummy variables were used for 'Too Low', 'Too High' and 'Unsure.' 'Just Right' was used as the reference group.

5.3. RESULTS

5.3.1. Socioeconomic Characteristics

A total of 181 questionnaires were completed (elephant n = 92, giraffe n = 89) from 203 attempts giving a response rate of 89%. As 1,313,185 people visited KNP in the financial year ending 31/03/2007 (SANParks), this sample of respondents represents 0.014% of the yearly visitors to KNP. Of the 181 respondents, 45% (n = 81) were female and 55% (n = 100) were male. The majority of respondents were in the age class 25 – 34 (24%, n = 43); 59% of respondents were younger than 45 years old and 59% had annual household income of less than £30,000 (or equivalent). A breakdown of gender, age, income, nationality, country of residence and employment status of respondents to the questionnaires is shown in Table 5.4.

The visitor data obtained from KNP did not contain a breakdown about variables such as sex, ages, income and level of education so it is impossible to check if the sample was representative in these respects. However, it was possible to assess if the respondents were representative of the overall visitors to KNP in terms of nationality. Of those who gave their nationality, 58% (n = 102) were South African citizens 42% (n = 74) were international visitors. Official data from the gate access system shows that 77% of visitors for the year ending 31st March 2007 were South African residents, and 23% were international (excluding SADC nationals) (Table 5.4). There was no significant difference between the survey sample and the overall KNP visitors in terms of nationality (t = -0.40, $d.f.$ = 5, p = 0.970) therefore indicating our sample was representative in this respect.

Table 5.5. Comparison of nationalities of the respondents to the breakdown of nationalities of visitors to Kruger National Park.

Nationality	Respondents (%)	KNP Visitors (%)
South African	58	76.6
British	16	2.2
American	10	1.0
Australian	6	0.5
German	6	10.6
Other	4	8.3

Table 5.4. Comparison of gender, age, income, nationality, country of residence and employment status of respondents to the questionnaires. Income is given as £ sterling. However respondents were able to answer in four different currencies: for equivalents in Rand (R), US Dollars ($) or Euros (€) see Appendix Figure A3.

Variable	Category	Overall (%)	Version of the Questionnaire	
			Elephant (%)	Giraffe (%)
Gender	Male	100 (55)	48 (52)	52 (58)
	Female	81 (45)	44 (48)	37 (42)
Age (years)	18 – 24	23 (13)	10 (11)	13 (15)
	25 – 34	43 (24)	22 (24)	21 (24)
	35 – 44	39 (22)	20 (22)	19 (21)
	45 – 54	28 (16)	16 (18)	12 (13)
	55 – 64	35 (19)	17 (19)	18 (20)
	65 +	12 (7)	6 (7)	6 (7)
Income (£)	< 5,000	20 (11)	8 (9)	12 (14)
	5,001 – 9,999	18 (10)	12 (14)	6 (7)
	10,000 – 19,999	27 (15)	13 (15)	14 (16)
	20,000 – 29,999	41 (23)	24 (28)	17 (19)
	30,000 – 39,999	22 (13)	6 (7)	16 (18)
	40,000 – 49,999	12 (7)	7 (8)	5 (6)
	50,000 – 59,999	8 (5)	2 (2)	6 (7)
	60,000 +	27 (15)	15 (17)	12 (14)
Nationality	South African	102 (58)	50 (54)	52 (58)
	British	28 (16)	15 (16)	13 (15)
	American	17 (10)	8 (9)	9 (10)
	Australian	11 (6)	7 (8)	4 (4)
	German	11 (6)	7 (8)	4 (4)
	Other	7 (4)	5 (5)	7 (8)
Country of Residence	South Africa	111 (61)	57 (62)	54 (61)
	United Kingdom	19 (10)	10 (11)	9 (10)
	United States of America	18 (10)	9 (10)	9 (10)
	Australia	9 (5)	5 (5)	4 (4)
	Germany	9 (5)	6 (7)	3 (3)
	Other	15 (8)	5 (5)	10 (11)
Employment Status	Part-Time	13 (7)	8 (9)	5 (6)
	Full-Time	113 (62)	58 (63)	55 (62)
	Retired	24 (13)	11 (12)	13 (15)
	Unemployed	12 (7)	7 (8)	5 (6)
	In Full Time Education	18 (10)	8 (9)	10 (11)

There were no significant differences between the respondents answering the two versions of the questionnaires in terms of gender (X^2 = 0.398, *d.f.* = 1, *n.s.*), income (X^2 = 11.24, *d.f.* = 7, *n.s.*; Figure 5.12), age (X^2 = 1.02, *d.f.* = 5, *n.s.*; Figure 5.13), nationality (X^2 = 2.16, *d.f.* = 5, n.s.), country of residence (X^2 = 2.86, *d.f.* = 5, *n.s.*) or employment status (X^2 = 1.41, *d.f.* = 4, *n.s.*) (Table 5.4).

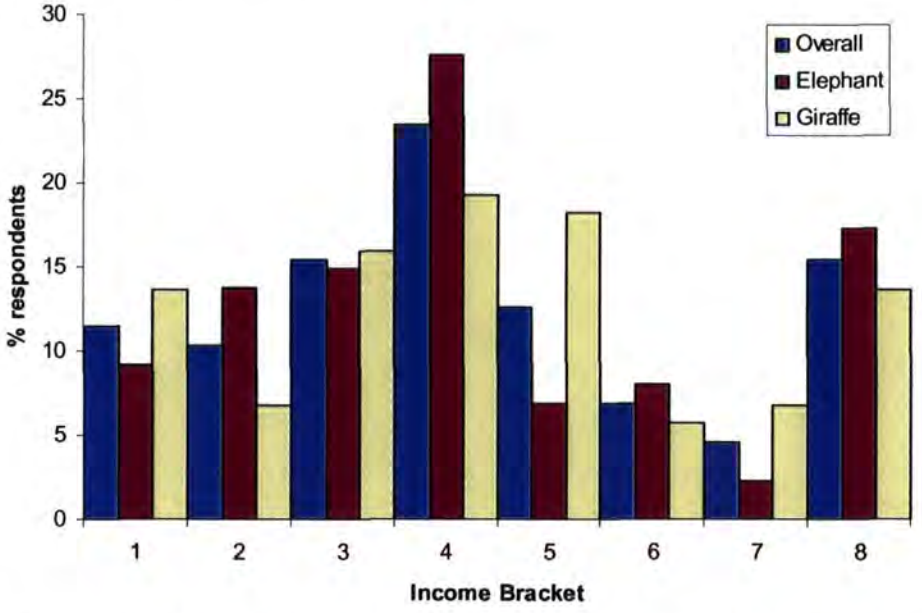


Figure 5.12. Percentage of respondents to each of the questionnaires (Elephant = Version 1, Giraffe = Version 2) in terms of income. Numbers 1 – 8 correspond to income brackets given in Table 5.3.

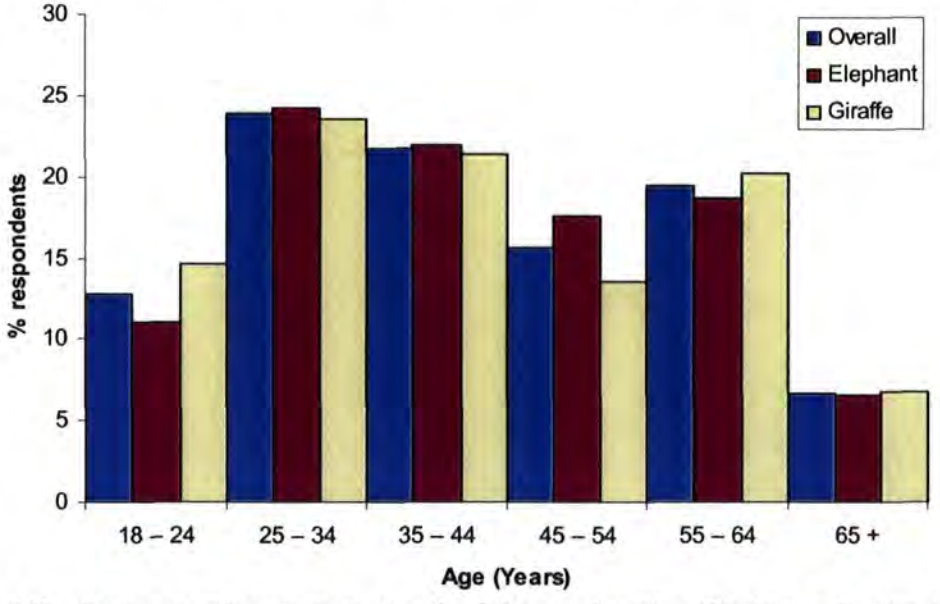


Figure 5.13. Percentage of respondents to each of the questionnaires (Elephant = Version 1, Giraffe = Version 2) in terms of their age.

5.3.2. General Awareness

62% (n = 112) of respondents had visited KNP previously, 33% (n = 60) were visiting KNP for the first time, and 5% (n = 9) did not answer that question. 41% (n = 74) of respondents were intending to visit other national parks during their trip, the rest of respondents (59%, n = 107) either left no response or said they were visiting only KNP on their trip. The main reason for visiting for the majority of people was to view and photograph the wildlife (42%, n = 76), followed by rest and relaxation (18%, n = 33), study or research (6%, n = 10), business (3%, n = 5) or other reasons (4%, n = 8) such as 'visiting family'. The rest of respondents (24%, n = 44) chose multiple reasons for visiting KNP. Of the 76 people who chose to visit KNP primarily to see and photograph the wildlife, 42 (55%) people stated 'seeing a large number of different wildlife species' as the best description of the reason for their visit, 15 (20%) people stated 'seeing the big 5', 11 (14%) people stated 'seeing a particular species' and 8 (11%) people chose both 'seeing a large number of different wildlife species' plus 'seeing the big 5'.

There was a general enthusiasm towards the topics included in the questionnaire; over half (54%, n = 97) of the respondents left their email address to gain a summary of the results.

5.3.3. Payment Questions

27% (n = 48) of respondents paid the standard fee for South African citizens and residents (R30) to enter KNP; 21% (n = 37) paid the standard conservation fee of R120 (for foreign visitors); 17% (n = 30) people didn't know how much they paid to enter the park and 35% (n = 64) respondents used a WILD Card. Of those who used a WILD Card, 22% (n = 14) were exclusively for the bushveld cluster, 53% (n = 34) for South African citizens visiting all clusters, and 25% (n = 16) were for international individuals visiting all clusters. In total 15 were solely for individual use, 28 were part of a couple and 21 were part of a family. The majority of respondents (62%) thought the entrance fee they paid was 'just right'; 10% thought it was 'too low', 11% 'too high' and '17% were 'unsure'.

5.3.4. Respondents' Willingness-to-Pay

There was an overall positive attitude towards conserving the current complement of large mammal species in KNP; 70% (n = 119) respondents were WTP towards this scheme. The numbers of people WTP towards giraffe and elephant conservation were both less; of the 119 respondents WTP for the conservation of the current large mammal biodiversity in KNP, 31 of these were subsequently not WTP for the conservation of just the elephant, and 29 were subsequently not WTP for the conservation of just the giraffe. Consequently, 44% of the people answering V2 were WTP for giraffe conservation (n = 34) and 44% answering V1 were WTP for elephant conservation (n = 35). A summary of descriptive statistics are given in Table 5.6.

Table 5.6. Willingness-to-pay values (given in South African Rand, R) for conservation scenarios in Kruger National Park, South Africa.

Scenario	*N* WTP	% WTP	Median (R)	Range of WTP values (R)	Mean (R)	Std. Error	95% confidence interval
All Species	119	70%	60	5 – 600	94.92	9.57	75.97 – 113.87
Giraffe	34	44%	50	3 – 450	72.12	15.16	41.28 – 102.96
Elephant	35	44%	50	4 – 300	73.40	12.18	48.64 – 98.16

19% respondents (n = 33) were not WTP for the conservation of the current complement of large mammals in KNP. In this case, the most common reason for not WTP was that the '*South African residents are paying too much already.*' 56% (n = 44) people were not WTP for the conservation of giraffes and 56% (n = 44) people were not WTP for the conservation of elephants; the main reasons for not paying included that *'conservation must adopt a broad multi-species approach'* and therefore they *'prefer to see a balanced distribution of funds amongst all species'* rather than *'just one species.'*

Mean WTP for the conservation of all species was highest, at R94.94 (equivalent to ~£6.68) in increased entrance fees. Mean WTP for giraffe conservation was R72.12 (~ £5.07) and mean WTP for elephant conservation was only slightly higher, at R73.40 (~£5.16). However, differences between the amounts people were WTP for different scenarios was not significant; an independent t-test showed that there was no significant difference between the amount people were willing-to-pay for elephant or giraffe

conservation ($t = 0.066$, $d.f. = 67$, $p = 0.947$). Additionally, a one-way ANOVA indicated there was no significant difference between the average amount people were willing-to-pay for the conservation of all species, giraffes or elephants in KNP ($F = 1.153$, $d.f. = 2$, $p = 0.318$). Figures 5.14, 5.15, and 5.16 show the amount people were WTP (in South African Rand, R) for each scenario. In all cases, median WTP was less than mean WTP by approximately a third of the mean amount (Table 5.6). The finding that median WTP is 'considerably' less than mean WTP is a common occurrence in CV studies (Christie *et al.*, 2006), and is due to the fact that people giving high values of WTP distort the mean value.

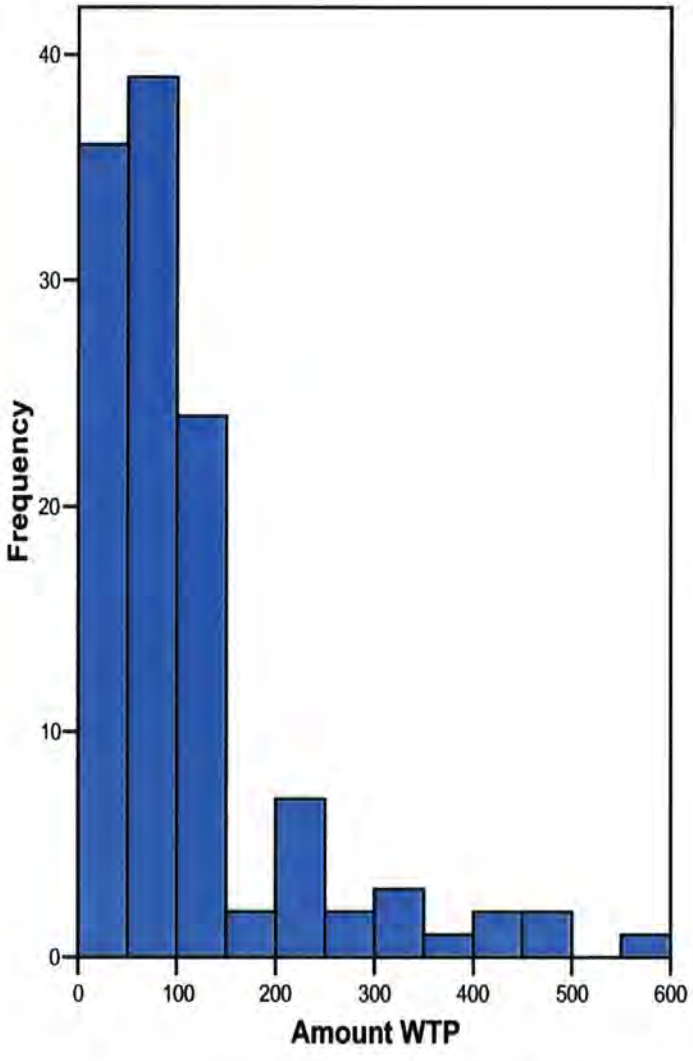


Figure 5.14. Frequency histograms showing the amount of money (South African Rand, R) respondents were WTP in increased entrance fees in order to conserve the number and variety of large mammals currently in Kruger.

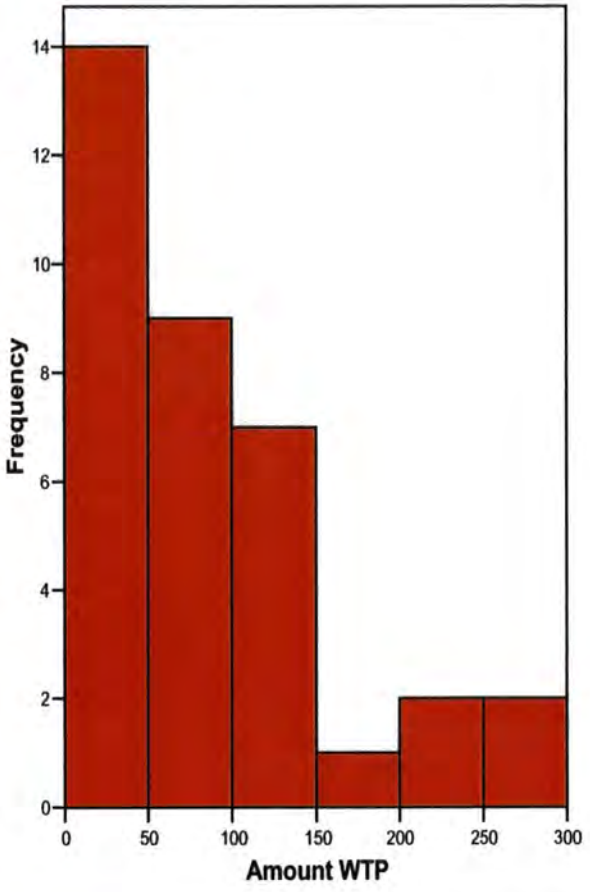


Figure 5.15. Frequency histograms showing the amount of money (South African Rand, R) respondents were WTP in increased entrance fees in order to conserve elephants in Kruger.

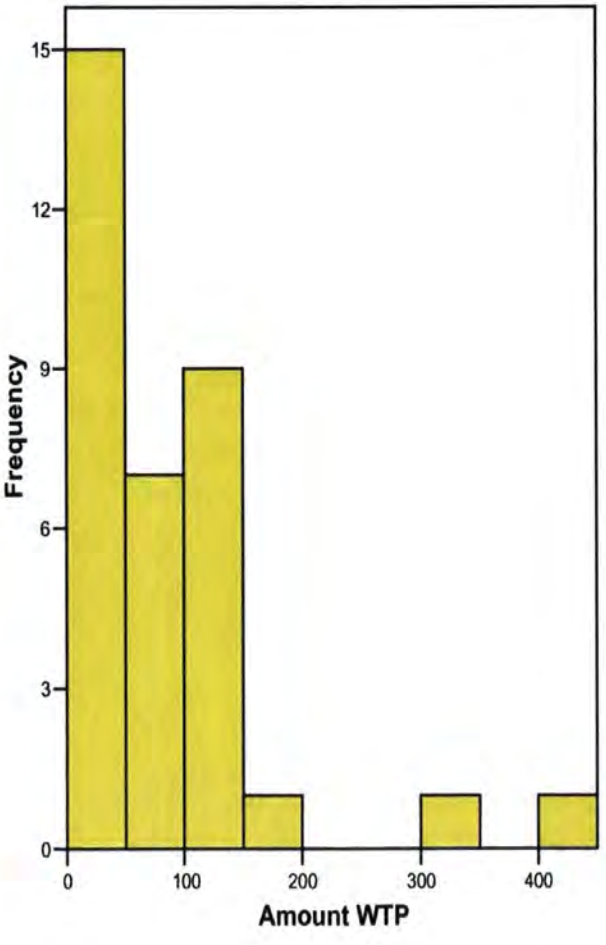


Figure 5.16. Frequency histograms showing the amount of money (South African Rand, R) respondents were WTP in increased entrance fees in order to conserve giraffes in Kruger.

5.3.5. Aggregation

In the year ending 31st March 2007, a total of 1,313,185 people visited KNP (SANParks, 2007). 70% of respondents were WTP towards the conservation of all large mammals in KNP; the mean WTP was R94.92. Therefore by multiplication, the aggregate value of WTP over the total number of KNP visitors is R87.3million (± R17.4million) per year which is equivalent to approximately £6.1million (± £1.2million) per year.

Only 44% of people interviewed were WTP for giraffe conservation, the mean amount was R71.12. Consequently, the aggregate value of WTP for giraffe conservation over the total number of KNP visitors is R41.1million (± R17.8million) per year which is equivalent to £2.9million (± £1.3million) per year. Similarly, 44% of people were WTP for elephant conservation, with a mean amount of R73.40. Therefore, the aggregated WTP values for elephant conservation is R42.4million (± R14.3million), which is equivalent to £3.0million (± £1.0million) per year.

5.3.6. Significant Factors Affecting Respondents' Willingness-to-Pay for the Conservation of Large Mammals

Logistic regression analysis was used to predict the probability that a participant would be willing-to-pay for the conservation of the current complement of large mammals in KNP. The predictor variables were age, gender, income, length of visit, reason for visit, interviewer and whether it was their first visits to South Africa and KNP. Dummy variables were also used to encode possible responses with regards to the respondents' nationality, employment status, level of education, type of travel, entrance fee paid and their attitude towards the entrance fee (Table 5.3). Reference groups for each of these dummy variables were 'South African', 'Full Time', 'University Standard Degree', 'Independent Travel', payment using a 'WildCard' and 'just right' as their attitude towards the cost of the entrance fee respectively. These groups were chosen as there were no natural numeric values for these variables, therefore the most common response was chosen as the reference group.

A test of the full 'all species' model versus a model with the intercept only was statistically significant at the 0.05 level, which implies there is a causal relationship

between the predictor variables and respondents' WTP (model $X^2 = 57.66$, $d.f. = 28$, $p < 0.01$) (Table 5.7). The full model was able to correctly classify 46.7% of people who were not willing-to-pay and 94.1% of people who were willing-to-pay, giving an overall success rate of 85.5%.

Table 5.7. Summary statistics calculated from the logistic regression models of respondents' willingness-to-pay towards conserving the current level of species diversity in Kruger ('all species') plus towards conserving only one species (giraffe/elephant) in Kruger National Park. Results are given for a full model – with all predictor variables (Table 5.2), as well as a reduced model which used only significant variables from the full models. Model X^2 is the difference between the -2log likelihood for the model with a constant only, and -2log likelihood for the current model.

	Full Model		Reduced Model	
	Giraffe/Elephant	All Species	Giraffe/Elephant	All Species
Model X^2	55.01	57.66	44.24	28.67
% Correct Classification	72.4	85.5	70.4	81.2
Significance (p)	<0.01	< 0.01	<0.01	< 0.01
Pseudo R^2 (Cox & Snell)	0.286	0.295	0.230	0.155

Table 5.8 below shows the logistic regression coefficient, Wald test and odds ratio for each of the predictor variables. Employing a 0.05 criterion of statistical significance, the respondent's age, if it was their first visit to KNP, if it was their first visit to South Africa, the interviewer and if they were travelling 'overland' all had significant effects (i.e. those with $p < 0.05$) on respondents' willingness-to-pay. The rest of the predictor variables such as income, gender and nationality had non-significant effects (Table 5.8). The odds ratios indicate that when holding all other variables constant, respondents who were interviewed by George (the student volunteer) were more likely to be WTP than those interviewed by Georgina ($X^2 = 9.17$, $B = 2.55$, $p < 0.01$); and those who were travelling 'overland' were significantly less likely to be WTP than those who were travelling independently ($X^2 = 5.01$, $B = -4.36$, $p < 0.03$; Table 5.8). An increase in age was associated with the odds of being WTP decreasing ($X^2 = 4.54$, $B = -0.63$, $p < 0.04$); this is consistent with findings in recreation economics literature (Walsh, 1986). Additionally, respondents who were visiting South Africa for the first time were 17 times more likely to be WTP than those who had visited previously (including those who live in SA) ($X^2 = 4.65$, $B = 2.84$, $p <$

0.04); however, those who were visiting KNP for the first time were less likely to be willing-to-pay than those who had visited KNP previously ($X^2 = 3.89$, $B = -2.64$, $p < 0.05$).

Table 5.8. Parameter estimates for logistic regression models of willingness-to-pay for the conservation of the current level of species diversity in Kruger. Independent variables are described in Table 5.2.

Independent Variable		Coefficient *B*	Wald X^2	Significance *p*	Odds Ratio Exp*B* (95% confidence interval)
Gender		-.418	.472	.492	.659 (.20 -2.17)
Age		-.063	4.542	.033	.939 (.89 -1.00)
Nationality	British	.419	.129	1.521 (.15 –	1.521 (.01 - .98)
	American	.145	.009	1.156 (.06 –	1.156 (.35 – 3.78)
	Australian	20.064	.000	517326900.573	517326900.573 (.38 – 4.44)*
	German	-.868	.485	.420 (.36 – 4.83)	.420 (2.46 – 66.90)
	Other	-1.663	1.748	.190(.16 – 2.23)	.190 (.89 -1.00)
Employment Status	Part-time	1.932	2.167	6.904 (.53 –	6.904 (.15 – 15.07)
	Retired	-1.108	1.260	.330 (.48 – 2.29)	.330 (.06 – 22.32)
	Unemployed	22.821	.000	8151650978.673	8151650978.673 (.0 -)*
	In Full Time	1.126	.498	3.084 (.14 –	3.084 (.36 – 4.83)
Level of Education	University Higher	1.202	2.503	3.327 (.75 –	3.327 (.16 – 2.23)
	College	1.089	1.493	2.971 (.52 –	2.971 (.75 – 14.75)
	Secondary School	1.646	2.416	5.184 (.65 –	5.184 (.52 – 17.04)
Household Income (£)		.029	.031	.861	1.029 (.75 – 1.42)
Entrance Fee	R30	-.114	.023	.892 (.20 – 3.90)	.892 (.53 – 90.41)
	R120	-.851	.793	.427 (.07 – 2.78)	.427 (.48 – 2.29)
	Unsure of Amount	.561	.149	1.753 (.10 –	1.753 (.0 -)
Attitude	Too Low	1.070	.774	2.917 (.27 –	2.917 (.14 – 70.50)
	Too High	-.936	1.663	.392 (1.0 – 1.63)	.392 (0.0 - .58)
	Unsure	-2.009	2.557	.134 (.011 –	.134 (.18 – 4.00)
TypeTravel	Overland	-4.360	5.008	.013 (0.0 - .58)	.013 (.20 – 3.90)
	Organised Tour	-.170	.046	.844 (.18 – 4.00)	.844 (.07 – 2.78)
Interviewer		2.551	9.165	.002	12.825 (2.46 – 66.90)
Reason		.257	.166	.684	1.293(.38 – 4.44)
Length		.142	.055	.815	1.153 (.35 – 3.78)
FirstTripSA		2.840	4.649	.031	17.123 (1.30 – 226.42)
FirstTripKruger		-2.641	3.891	.049	.071 (.01 - .98)

*The large odds ratios for the variables 'Australian' and 'unemployed' occur due to the presence of zero values i.e. everyone in these categories was willing-to-pay to conserve the current level of species diversity in Kruger.

5.3.7. Significant Factors Affecting Respondents' Willingness-to-Pay for Giraffe/Elephant Conservation

Logistic regression analysis was then used to predict the probability that a participant would be willing-to-pay for the conservation of a single species of large mammal (elephant or giraffe) in KNP. The predictor variables were the same as in the 'all species' model, with the exception of an additional variable encoding if the respondents answered version one or two of the questionnaire was added ('species' in Table 5.3). A test of the full model versus a model with the intercept only was statistically significant at the 0.05 level, which implies there is a causal relationship between the predictor variables and respondents' WTP (model $X^2 = 55.01$, $d.f. = 28$, $p < 0.01$) (Table 5.7). This 'single species' model was able to correctly classify 70% of people who were not willing-to-pay and 75% of people who were willing-to-pay, giving an overall success rate of 72%. Although this 'single species' model was able to correctly classify more people who were not WTP, overall the 'all species' model is better than the 'single species' model in predicting if respondents' would be WTP.

The table below shows the logistic regression coefficient, Wald test and odds ratio for each of the predictor variables (Table 5.9). Employing a 0.05 criterion of statistical significance, the respondent's age, if they were German, if they were in full time education, if they paid the daily conservation fee of R120 to enter KNP and if they believed the entrance fee was 'too low' all had significant effects (i.e. those with $p < 0.05$) on their willingness-to-pay. The odds ratios indicate that when holding all other variables constant, respondents in full time education were significantly less likely to be WTP for giraffe/elephant conservation than those in full-time employment ($X^2 = 4.88$, $B = -1.66$, $p < 0.03$). Similarly, respondents who paid R120 were significantly less likely to be WTP than those who used a WildCard ($X^2 = 4.56$, $B = -1.54$, $p < 0.04$). Those respondents who stated that the entrance fee was 'too low' were more than seven times as likely to be WTP than those who believed the entrance fee was 'just right' ($X^2 = 5.21$, $B = 2.03$, $p < 0.03$). Additionally, German respondents were more than ten times as likely to be WTP towards single species conservation than South African respondents ($X^2 = 4.15$, $B = 2.32$, $p < 0.05$). Finally, as with the 'all species' model, an increase in age was associated with the odds of being WTP decreasing ($X^2 = 8.60$, $B = -0.60$, $p < 0.01$). The version of the

questionnaire (giraffe/elephant) the respondents answered did not have a significant impact on their WTP towards conservation; the rest of the predictor variables such as gender, level of education and income also had non-significant effects (Table 5.9).

Table 5.9. Parameter estimates for logistic regression models of willingness-to-pay for the conservation of a single species of large mammal (giraffe or elephant) in Kruger. Independent variables are described in Table 5.2.

Independent Variable		Coefficient *B*	Wald X^2	Significance *p*	Odds Ratio Exp*B* (95% confidence interval)
Gender		-.697	2.385	.123	.498 (.21 – 1.21)
Age		-.060	8.596	.003	.942(.91 - .98)
Nationality	British	.842	1.195	.274	2.320(.51 – 10.50)
	American	.969	1.093	.296	2.635(.43 – 16.20)
	Australian	.761	.606	.436	2.140(.32 – 14.52)
	German	2.321	4.147	.042	10.187(1.01 – 95.12)
	Other	-1.829	2.196	.138	.161(.01 – 1.80)
Employment Status	Part-time	-.322	.158	.691	.725(.15 – 3.55)
	Retired	-1.078	1.706	.192	.340(.07 – 1.71)
	Unemployed	-.891	.853	.356	.410(.06 – 2.72)
	In Full Time	-1.658	4.884	.027	.191(.04 - .83)
Level of Education	University Higher	-.004	.000	.995	.996(.36 – 2.75)
	College	.324	.257	.612	1.382(.40 – 5.83)
	Secondary School	-.080	.013	.909	.923(.24 – 3.63)
Household Income (£)		.005	.002	.963	1.005 (.81 -1.24)
Entrance Fee	R30	-.455	.725	.394	.634(.22 – 1.81)
	R120	-1.539	4.555	.033	.215(.05 - .88)
	Unsure of Amount	.417	.154	.695	1.517(.19 – 12.17)
Attitude	Too Low	2.026	5.212	.022	7.585(1.33 – 43.19)
	Too High	-.066	.010	.918	.936(.27 – 3.30)
	Unsure	-1.049	1.067	.302	.350(.05 – 2.57)
TypeTravel	Organised Tour	-.318	.218	.641	.728(.10 – 24.02)
	Overland	.438	.098	.754	1.549(.19 – 2.77)
Interviewer		-.781	2.971	.085	.458 (.19 - 1.11)
Reason		.358	.613	.434	1.431(.58 – 3.51)
Length		-.128	.084	.772	.880(.37 – 2.10)
FirstTripSA		1.075	1.546	.214	2.931 (.54 – 15.96)
FirstTripKruger		-.872	1.156	.282	.418(.09 – 2.05)
Species		-.497	1.448	.229	.609(.27 – 1.37)

5.3.8. Reduced Models Assessing Significant Factors Affecting Respondents' Willingness-to-Pay for Conservation

Reduced models for 'all species' and 'single species' were then tested. These models included only those predictor variables which significantly affected respondents' WTP in the respective full models (Table 5.8 and Table 5.9). A test of the 'all species' reduced model versus a model with the intercept only was statistically significant at the 0.05 level, which implies there is a causal relationship between the predictor variables and respondents' WTP (model $X^2 = 28.67$, $d.f. = 6$, $p < 0.01$) (Table 5.7). The same can be said for the 'single species' reduced model versus a model with the intercept only (model $X^2 = 44.24$, $d.f. = 16$, $p < 0.01$) (Table 5.7). The 'single species' reduced model was able to correctly classify 72% of respondents who were not WTP and 68% of respondents who were WTP, giving an overall success rate of 70%. These results are slightly lower than those for the corresponding full model (Chapter 5.3.7). Similarly, the reduced model for 'all species' was able to correctly classify a smaller percentage of respondents than the full model (Chapter 5.3.6); only 10% of respondents who were not WTP were correctly classified. However, 97% of those WTP for 'all species' conservation were correctly classified, giving an overall success rate of 81%.

The logistic regression coefficient, Wald test and odds ratio for each of the predictor variables for the reduced models are given in Tables 5.10 ('all species') and 5.11 ('single species'). Employing a 0.05 criterion of statistical significance, the reduced model for 'all species' had two significant variables; the interviewer and the respondents' age. Holding all other variables constant, respondents interviewed by George were more likely to be WTP than those interviewed by Georgina ($X^2 = 7.89$, $B = 1.551$, $p < 0.01$); and an increase in age was associated with the odds of respondents being WTP decreasing ($X^2 = 12.49$, $B = -0.065$, $p < 0.001$).

The reduced model for 'single species' had four significant variables which were the respondents' age, employment status, entrance fee paid and attitude towards the entrance fee paid. Holding all other variables constant, respondents in full time education were significantly less likely to be WTP for giraffe/elephant conservation than those in full-time employment ($X^2 = 7.22$, $B = -1.784$, $p < 0.01$); respondents who paid R120 to enter KNP

were significantly less likely to be WTP than those who used a WildCard ($X^2 = 4.83$, $B = -1.366$, $p < 0.03$); respondents who believed the entrance fee they paid was 'too low' were significantly more likely to be WTP than those who believed the fee was 'just right' ($X^2 = 7.08$, $B = 2.196$, $p < 0.01$); and an increase in age was associated with the odds of respondents being WTP decreasing ($X^2 = 6.72$, $B = -0.044$, $p < 0.02$).

Table 5.10. Parameter estimates for reduced logistic regression models of willingness-to-pay for the conservation of the current level of species diversity in Kruger. This logistic regression model uses only significant variables from the corresponding full model (Table 5.8). Independent variables are described in Table 5.2.

Independent Variable		Coefficient *B*	Wald X^2	Significance *p*	Odds Ratio (Exp*B*)
Age		-.065	12.490	.000	.937
TypeTravel	Overland	-1.741	1.575	.210	.175
	Organised Tour	-.707	1.515	.218	.493
Interviewer		1.551	7.890	.005	4.714
FirstTripSA		1.222	1.563	.211	3.395
FirstTripKruger		-1.219	2.049	.152	.295

Table 5.11. Parameter estimates for reduced logistic regression models of willingness-to-pay for the conservation of a single species of large mammal (giraffe or elephant) in Kruger. This logistic regression model uses only significant variables from the corresponding full model (Table 5.9). Independent variables are described in Table 5.2.

Independent Variable		Coefficient *B*	Wald X^2	Significance *p*	Odds Ratio (Exp*B*)
Age		-.044	6.718	.010	.957
Nationality	British	.575	.905	.341	1.777
	American	.610	.675	.411	1.841
	Australian	.040	.003	.959	1.041
	German	1.675	3.381	.066	5.339
	Other	-1.924	2.842	.092	.146
Employment Status	Part-time	.085	.013	.909	1.089
	Retired	-.521	.656	.418	.594
	Unemployed	-.174	.058	.810	.840
	In Full Time Education	-1.784	7.219	.007	.168
Entrance Fee	R30	-.252	.289	.591	.777
	R120	-1.366	4.829	.028	.255
	Unsure of Amount	.876	.881	.348	2.401
Attitude	Too Low	2.196	7.081	.008	8.986
	Too High	-.159	.073	.787	.853
	Unsure	-1.161	1.675	.196	.313

5.4 Discussion

Results of this study suggest that the vast majority of visitors to KNP were in favour of protecting the current number and variety of large mammals found there; 70% of the respondent's who completed the questionnaire were WTP towards the conservation of mammals in KNP. A number of studies have recorded similar support for biodiversity/species conservation programs; Barnes *et al.,* (1999) found that 72% respondents were WTP for wildlife conservation in Namibia; White *et al.,* (1997) recorded that 58% of respondents were WTP (the amount specified in the questionnaire) for mammal conservation in Britain; and 75% of respondents in Turpie's (2003) study were WTP towards the conservation of biodiversity in South Africa. Of those respondents who were WTP, the mean amount was R92.92 (± R18.95) per person per visit. Although we cannot directly compare this mean value to the average cost respondents paid to enter the park (due to the majority (35%) of respondents using a one-off yearly fee, i.e. WILD Card, which allows unlimited visits), it is obvious the mean value people were WTP was large; over triple the fee South Africans pay to enter KNP, and just over three-quarters of the fee international visitors pay for each visit. Other studies such as Barnes *et al.,* (1999), Schultz *et al.,* (1998) and Navrud & Mungatana (1994) have also recorded undervaluation of tourists' WTP which suggests entrance fee policies have room for improvement (Naidoo & Adamowicz, 2005). Consequently, the information from this and other WTP studies may be useful in informing park managers about how to set differential charges for different types of users in order to maximise park revenues (Naidoo & Adamowicz, 2005). However, the differential setting of fees must be done carefully. Increased entrance fees deliver greater revenue for PA management, while reducing the number of tourists visiting parks. This may have positive effects, such as alleviating negative impacts of tourism upon ecosystems (Chown & Gaston, 2000; Mulligan, 1999; Naidoo & Adamowicz, 2005), but may also reduce the general public's experience and interest in protecting their native fauna in the face of projected future climate change.

The percentage of respondents WTP for giraffe/elephant conservation was less than those WTP for ensemble species conservation; only 44% of respondents were WTP for giraffe- and 44% for elephant conservation. White *et al.,* (2001) found similar results to these; 62% of their respondents were WTP for ensemble species conservation, but only 31% and

45% were WTP for brown hare *(Lepus europaeus)* or red squirrel *(Scuirus vulgaris)* conservation respectively. The fact that more people were WTP for multi-species conservation than for single species conservation is reflected in the reasons people gave for not being WTP; many people felt that conservation should adopt a broad multi-species approach and therefore not concentrate on a single species. The fact that respondents were more enthusiastic and more generous towards multi-species conservation may indicate that in recent years the public have become more in tune with the science of nature conservation, which is moving towards biodiversity conservation rather than single species conservation. However, it is reasonable to presume that visitors to KNP are more interested in nature conservation than people who do not visit national parks, due to the very fact they are visiting KNP. Therefore the general public, most of whom do not visit national parks, may still find it easier to perceive conservation in single-species terms (White *et al.*, 2001).

The mean amount respondents were WTP for giraffe and elephant conservation were similar to each other (R71.12 and R73.40 respectively). It was expected that WTP would be similar for these species. This is because elephants and giraffes are both well known and charismatic mammal species, and are also thought to be a very important part of the wildlife viewing experience (Navrud & Mungatana, 1994; Kaltenborn *et al.*, 2006). Furthermore, even though some locals often associate elephants with crop damage, to many others both giraffes and elephants are national symbols and represent the African environment (Kuriyan, 2002; Kaltenborn *et al.*, 2006). However, similar results could possibly be found when investigating visitors' WTP towards conservation of other flagship species (e.g. white and black rhinoceros' or lions). Consequently, it may not be that giraffes and elephants are perfect substitutes for each other in visitors' eyes, but that visitors want to help conserve flagship species but don't care which specific species it is. Even so, the preference for conservation of charismatic species is significantly greater than for less notable species (Loomis and White, 1996). PA managers and conservation organizations can exploit this fact and 'use' flagship species to gain funding which can then help conserve less high profile species and their associated ecosystems (Kontoleon & Swanson, 2002).

The aggregation of mean WTP values was restricted to the target population only, i.e. the visitors to KNP, rather than a wider population such as the visitors to all parks under SANParks' control or all parks in South Africa. This was due to the potential differences between respondents' WTP towards conservation programs in different protected areas in Southern Africa/Africa. The aggregated WTP values for the conservation of the current number and variety of large mammals over the KNP visitor population was R87.3million (± R17.4million). A possible reason for the high aggregated values respondents were potentially WTP towards the conservation of large mammals in KNP is that respondents were passionate about seeing a variety of animals such as these *in situ*. The majority (43%) of respondents were visiting KNP to 'see and photograph the wildlife' (Question 5); of these, 55% were visiting to 'see a large number of different wildlife species.' It is therefore assumed that the existence of large mammals in KNP would be important to them. As the number of people visiting 'to see a particular species' was less (14%) than those who were visiting to 'see a large number of different wildlife species' (55%) it was therefore expected that the number of people WTP for single species' conservation would be less than ensemble species conservation. This was the case in this study; a greater proportion (70%) of respondents was WTP towards ensemble species conservation than giraffe (44%) or elephant (44%) conservation. Consequently, the aggregated WTP values for the conservation of all species were more than double those for either giraffe or elephant conservation; the aggregated WTP values for the conservation of giraffe or elephants in KNP were R41.1million (± R17.8million) and R42.4million (± R14.3million) respectively.

Factors Affecting WTP towards Mammal Conservation in KNP

The pseudo R^2 statistics indicated that the logistic regression models with all possible predictor variables had greater explanatory power of respondents' WTP than the reduced models (Table 5.7; Bateman *et al.*, 2002). The full models were able to correctly classify a larger proportion of respondents' responses than the corresponding reduced models, for both the 'all species' and giraffe/elephant scenarios (Table 5.7). Consequently, the variables significantly associated with WTP in the logistic regression 'full' model for the ensemble species scenario were the participants' age, whether it was their first trip to KNP, their first trip to South Africa, the interviewer and if they were travelling 'overland.'

The variables significantly associated with WTP in the logistic regression 'full' model for the single species scenario were if they were in full time education, if they paid the daily conservation fee of R120, if they believed the entrance fee they paid was 'too low', as well as their nationality.

Under both scenarios (i.e. ensemble species- and single species conservation), respondents' age was negatively associated with WTP. Other studies which have assessed WTP for conservation, have also recorded negative relationships between WTP and respondents' age (e.g. Martín-López *et al.*, 2007; Kaltenborn *et al.*, 2006; White *et al.*, 2001). The negative association between WTP and age could be because younger people generally have less financial responsibilities than older people, and therefore more disposable income (White *et al.*, 2001). Additionally, younger people are generally thought of as being more aware of environmental issues, such as the potential negative effects of climate change upon species (Martín-López *et al.* 2007).

WTP for Ensemble Species Conservation

The majority (62%) of respondents had been to KNP previously and a large proportion was intending to visit other national parks on their trip (41%). As visitation to national parks was high amongst respondents, it was assumed that they were familiar with- and interested in- the good (i.e. mammal species) about which they were questioned and were consequently able to make informed decisions about their WTP. Indeed, people who had visited KNP previously were more likely to be WTP towards ensemble species conservation than those who were visiting KNP for the first time, indicating that previous experience of national parks enhance peoples' interest and WTP towards mammal species conservation (a result also found by Turpie, 2003). Turpie's (2003) study indicated that knowledge and interest were positively correlated to WTP for nature conservation. However, respondents who were visiting South Africa for the first time (i.e. international residents) were significantly more likely to be WTP than those people who had either previously visited South Africa or those who were resident in South Africa. A possible reason for this is that respondents visiting South Africa for the first time have different preferences and reasons for visiting KNP – indeed the primary purpose of international

tourists visiting South Africa was 'leisure reasons' i.e. holidays incorporating visiting PAs (South African Tourism, 2007).

Although suitable training of interviewers, as well as the inclusion of follow-up questions to the WTP question, (which Bateman *et al.*, (2002) suggest should reduce the likelihood of interviewer effects), interviewer bias was still present in this study. Respondents interviewed by George were twice as likely to be WTP towards ensemble species conservation as those interviewed by Georgina. Therefore the respondents may have been giving a WTP amount that differs from their true WTP amount in order to please either interviewer (Bateman *et al.*, 2002; Hanley *et al.*, 2004). This could be due to effects such as the interviewer's age, gender or education level. Although it was decided there were enough questionnaires for statistical analysis (and steps were taken to reduce possible interviewer effects), it would have been preferential to collect more surveys to assess such effects. This could have been achieved either by increasing the time spent in KNP or by increasing the number of interviewers. However time and money prevented both of these options in this study.

WTP for Single Species Conservation

Variables significantly associated with WTP in the logistic regression 'full' model for the single species scenario differed from those in the ensemble species scenario. Firstly, respondents who believed the entrance fee they paid was 'too low' were more than seven times as likely to be WTP as those who believed it was 'just right.' It can be assumed that those who believed the entrance fee was 'too low' consequently believed the fee should be raised. However, it is possible that respondents would be equally as willing for their increased fee to go towards other things such as education within the park, maintenance of buildings and roads etc, and therefore not necessarily solely towards biodiversity conservation.

The logistic regression models also indicated those in full-time employment were significantly more likely to be WTP than those in full-time education, possibly because of the expectation that people in employment have higher incomes (Bateman *et al.*, 2006). Additionally, Germans were more likely to be WTP than South African residents; South

Africans may be less WTP than Germans because of views towards paying to protect their native species. For example, some SA respondents were not WTP because they felt that "*South Africans should not pay excessive amounts to view their own country.*"

Another variable significantly associated with WTP was the payment given by the respondents to enter the park; those who paid R120 were less likely to be WTP than those who used a WildCard. As the WildCard allows unlimited access to all parks under SanParks' control, it is assumed that international visitors (the only people who pay the R120 entrance fee), pay a lot more *per visit* to KNP than those holding a WildCard. WildCard holders may be more likely to be WTP because as the WildCard allows unlimited access to parks, it is possible that WildCard holders visit KNP more regularly, and therefore have a greater interest in conservation within KNP than those who visit the park for a single trip.

It is possible that the estimates of WTP differed to respondents actual WTP. Firstly, respondents may have given positive WTP responses regardless of their own views in order to please the interviewer (Mitchell & Carson, 1989; Holmes & Kramer, 1995). This effect is difficult to eradicate in studies such as this (Turpie, 2003). As discussed on page 158, interviewer effects influenced respondents' WTP towards ensemble species conservation, but not single species conservation. An additional problem is that the WTP questions incorporated uncertainty; it was put to all respondents that "SANParks would be able to stabilise or even reverse this change [decrease in species] using the extra revenues from an increase in entrance fees." It is possible that respondents interpreted this last sentence differently, however we cannot tell how. A further problem associated with CV studies is the problem of embedding (Turpie, 2003). It was assumed that the embedding effect was reduced by asking respondents about other national parks they had visited/intended to visit, other mammal species they have seen, as well as explaining about the other parks controlled by SANParks in South Africa. However, it is evident that embedding effect (Kahneman & Knetsch, 1992) was still present in this study; mean WTP for 'all species' (R94.92) was considerably less than for the mean WTP for the giraffe and elephant combined (R145.52). Other studies, such as White *et al.*, (1997; 2001) have

reported the presence of the embedding effect, and have attributed this to the fact that respondents were expressing a more symbolic rather than additive WTP. White *et al.*, (1997) suggested that the value respondents give for the highest valued species in a group will be approximately the same as the value given for that whole group of species; this is known as the 'flagship' hypothesis. Consequently, the public profile of a given species may be as significant as the public's perception of the rarity or degree of threat in determining the economic value of that species (White *et al.*, 1997). Other studies, e.g. by Loomis & White (1996) have supported the idea that high profile species gain more public support for conservation than lower profile species. It is therefore likely that less well-known large mammal species, such as the Aders' Duiker (*Cephalophus adersi)* or the African Wild Ass (*Equus africanus)*, which are both critically endangered species (IUCN, 2006), would gain less public support for their conservation than higher profile species such as the elephant or giraffe. Flagship species such as the giraffe and elephant therefore play an important role in gaining public support for conservation projects (White *et al.*, 1997). Additionally, it is likely that the estimates of the aggregated WTP towards conservation in KNP are approximations; our study only asked adults (>18years) their views towards conservation within KNP, however children (<18years) also place a value on wildlife conservation (Navrud & Mungatana, 1994). Furthermore, it is likely that visitors to protected areas place higher values upon species conservation than those who do not visit protected areas (as in White *et al.*, 2001). This could be tested by comparing WTP of visitors versus non-visitors to KNP, with the assumption that WTP of visitors would be greater than non-visitors.

While this study cannot tell us what would happen to visitation rates if climate change were to cause the number of mammal species (including giraffes and/or elephants) to decline in KNP in the future, or how WTP may change if this did occur, it does provide some insight into visitors' views and willingness to pay towards mammal conservation in KNP today. The contingent valuation method proved a reliable method for assessing and quantifying respondents WTP towards species conservation. A large proportion of visitors to KNP were WTP towards such conservation programmes; aggregated WTP values across the KNP population revealed immense support (approximately R87.3 million per

year). However, as there is no information on the actual amount of money spent on large mammal (and/or giraffe/elephant) conservation in KNP, one cannot compare the findings of this study directly. We found that factors such as the respondents' age and experience of visiting KNP, as well as the costs they are paying to enter the park and their attitudes towards this fee, all had impacts upon their WTP towards the conservation scenarios. The majority of respondents who were not WTP towards ensemble species conservation gave the reason '*South Africans are paying too much already.*' There is a greater need for funding towards such conservation issues as discussed in this chapter. WTP studies may therefore be useful in informing park managers about how to set differential charges for different types of users in order to maximise park revenues (Naidoo & Adamowicz, 2005).

6.0 Conclusion

Bioclimatic modelling using climate response surfaces provides a useful 'first approximation' in determining how species distributions might change as climate changes (Pearson & Dawson, 2003). In this thesis I have used climate response surfaces to assess the potential impacts of climate change upon the majority of large African mammals. This method produced simulated current distributions that were comparable to observed distributions for the majority of species (Chapter Two) and indicated that distributions of many African mammals are ultimately determined by climate. Further investigation suggested that 'drying' in particular will be detrimental to mammalian species diversity, most probably acting via negative impacts of decreased precipitation on vegetation growth (Chapter Three, page 86). If greenhouse gas emissions are not stabilised, we would expect further changes in the precipitation regime to occur (IPCC 2007). In fact, even if emissions are stabilised are the levels of the end of the 20th century, we are still committed to climatic change of approximately 0.1°C per decade for the next two decades (IPCC 2007). One would expect this to impact upon vegetation and, therefore, mammal species abundances and distributions. In this study mean overlap between species' current and potential future ranges is projected to decrease to 89% by 2020, 81.7% by 2050, and only 75.7% by 2080. Similar results have been reported by Huntley *et al.*, (2008) who found that potential future (2070-99) range extent of 431 European breeding bird species averaged 72 – 89% of their present ranges. However, for some mammal species (~ 43), future ranges are projected to overlap current ranges by less than 10%. Similarly, Huntley *et al.*, (2008) reported that even under moderate climate change scenarios, 14% (*c.* 60) avian species suffer zero overlap, and a larger number of species had overlap <10% of their present range.

If a species current range becomes climatically unsuitable in the future, and that species is unable to adapt to the potential future changes in climate and/or consequently alter their ranges, that species may only to occupy those areas where current and future ranges overlap (Huntley *et al.*, 2006). This may have serious consequences for the survival (both genetic and absolute) of the species. Additionally, due to the association between species'

range size and extinction risk (Jablonski, 1991; Gaston, 1994), range contraction as a result of climate change may compound the problems associated with decreasing overlap.

On the whole, species ranges were projected to decrease slightly by 2080, under a best-case scenario of range alteration (Chapter Three). However, as with range overlap, the effects of climate change are expected to impact upon individual species differently. Some species are projected to face no change in range size, some will suffer range contraction and others will potentially 'profit' from climate change due to an increase in their range sizes. This is not to say that species' newly climatically suitable areas will be necessarily suitable for them to populate – potential future climatically suitable area may include areas of human settlement which could lead to human-wildlife conflict, or may contain no suitable habitat or prey sepecies. Other species may experience little or no overlap between current and future ranges, in which case only wildlife-corridors or artificial translocation will aid their survival. Consequently, it is necessary that conservation strategies aim to protect species wherever they move in response to climate change (Huntley *et al.,* 2006), be it inside or outside of protected area boundaries. Consequently, the reliance solely on the PA network to maintain biodiversity is insufficient (Huntley *et al.,* 2006). Further research into how climate change is projected to affect species distributions both within and outside of PAs is urgently required.

The current network of protected areas across Africa has been shown to be fairly robust to climate change (Chapter Four); however one cannot rely solely upon these areas to maintain biodiversity in the future. One also needs to ensure that species are given every opportunity to track projected climate changes too. This can be attained by creating corridors or 'stepping stones' (Huntley *et al.,* 2006) of suitable habitat between PAs so that species are able to adjust their distributions in response to climate changes. In addition, the design and creation of additional PAs with the dynamic nature of the climate in mind will also be of benefit.

Protected areas play an important role in maintaining biodiversity as well as acting as natural and cultural resources (IUCN, 1994). However, it is likely that as climate changes,

PAs will be unable to meet their remit of protecting the biodiversity for which they were designed (Burns *et al.,* 2003). This research has estimated that PAs will experience decreases in species richness at a greater rate than non-protected areas. Additionally, as the majority of species are projected to respond to climate change individualistically, mammalian community composition within (and outside) of PAs is expected to change as a result of changing vegetation (Burns *et al.,* 2003). This may have implications upon species which depend on another species for a specific ecosystem service or resource e.g. the winter moth - pedunculate oak system described in Chapter One. Additionally, many PAs rely heavily upon revenues gained from tourism in order to conserve resident species. If a charismatic keystone species, such as the elephant, is unable to persist in a PA in the future due to the absence of climatically suitable habitat, this may have knock-on effects upon the presence/absence of other species, as well as potentially impacting upon visitor numbers and therefore park revenues (Palmer *et al.,* 2008).

Chapter Five assessed the public's willingness-to-pay for the conservation of mammal species in Kruger National Park (KNP), which is one of the world's most popular game parks. A major factor in the popularity of the park is the variety of species resident there. Consequently, if community composition were to change as a result of climate change, one could assume that this would impact upon the number of people visiting KNP, particularly if the distribution of large charismatic mammals such as the elephant or giraffe were to decrease substantially. Results of the contingent valuation survey of visitors to KNP suggested that the vast majority were in favour of protecting the current number and variety of large mammals found there. Other studies such as Barnes *et al.,* (1999), White *et al.,* (1997) and Turpie (2003) have reported strong support for biodiversity conservation, indicating that this topic is important to the general public. Although the number of people WTP for single species conservation was less than for ensemble species conservation, this study also indicates the support for the conservation of two flagship species – the giraffe and elephant – in the face of climate change. Indeed, flagship species such as these play an important role in gaining public support for conservation projects (White *et al.,* 1997).

The contingent valuation method proved a reliable method for assessing and quantifying respondents WTP towards species conservation (Chapter 5.4). The aggregated WTP values for mammal conservation in KNP were high; R87.3million (± R17.4million) per year for ensemble species conservation, R41.1million (± R17.8million) for giraffe- and R42.4million (± R14.3million) for elephant conservation. It would be inappropriate to use the results of this study as a direct measure of public support for conservation in all PAs in Africa, therefore a potential extension of this work would be to gauge if levels of public support for conservation in KNP are comparable to other PAs in Africa. However, this study *does* show that the presence of a large number and variety of animals in their natural environment is an important factor in the public's decision to visit PAs, particularly KNP.

As there is a great need for increased funding for species conservation, WTP studies may be useful in informing park managers about how to set differential charges for different types of users in order to maximise park revenues (Naidoo & Adamowicz, 2005). A number of park authorities now set differential fees for resident and non-resident visitors – examples include South African National Parks and the Kenyan Wildlife Service. The current research found that the mean value people were WTP per visit for conservation was large when compared to the price of their entrance fee, especially the fee paid by South Africans (Chapter Five, page 154). Many other studies (e.g. Barnes *et al.*, (1999); Naidoo & Adamowicz (2005); Navrud & Mungatana (1994); Schultz *et al.*, (1998)) have also demonstrated that entrance fee policies have room for improvement.

Variables which significantly affected visitors' WTP included their age, experience of visiting the national park and employment status (Chapter 5.4). As previous experience of national parks enhances people's interest and WTP towards mammal species conservation (a result also found by Turpie, 2003), park authorities need to adjust entrance fees carefully, so that people are not discouraged from visiting. If this were the case, the general public's experience and interest in protecting African fauna in the face of projected future climate change may decrease.

If climate change were to proceed as predicted by the General Circulation Models (GCM), the bioclimatic models suggest that mammalian species composition within PAs will be altered significantly as climate changes; particularly those in South Africa and Namibia which were projected to experience high species turnover (64 – 78%) by the 2080's. This is expected to have knock-on effects upon other species. Consequently, until greenhouse gas emissions are stabilised (or reduced), it is inevitable that further climate change, (Huntley *et al.,* 2006) and therefore further alterations of species distributions will occur too. Until (and if) emissions are reduced, there are a number of ways to lessen the possible impacts of climate change upon mammals; educating the public about the predicted plight of these animals, as well as increasing the extent of the protected area network will be of key importance. Increasing public education and experience of nature will increase awareness of conservation issues and was shown in Chapter Five to increase the public's WTP towards conservation. Efforts such as increasing the extent and connectedness of the PA network will allow species the opportunity of tracking climate change, but these strategies will only be effective if the dynamic nature of climate is taken into account during PA design.

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Appendices

Figures A1, A2 and A3 start from page 185. Due to the large size of the rest of the files in the appendices, Table A1, A2, A3 and A4 can be found on the attached DVD. Also on the DVD are files needed to visualise simulated distribution maps of the 281 species for the present day and each of the nine potential future climate change scenarios used in this study.

Files on the DVD were created and written to DVD using a Dell Dimension DXC051 Intel(R) Pentium(R) 4CPU computer. The operating system used was Microsoft Windows XP Professional. The software used to access each file is given below, as are instructions on how to access selected files in ArcMap (page 184).

File Name	Description	Format	Software
africa_outline	Files needed to be able to view the outline of African country borders in ArcMap (see page 180).	DBF File	ArcMap
africa_outline.sbn		SBN File	
africa_outline.sbx		SBX File	
africa_outline.shp		SHP File	
africa_outline.shp.xml		XML Document	
africa_outline.shx		SHX File	
echam_2020_sp1-140	These files can be imported into ArcMap (see page 180) in order to view simulated distribution maps of each of the 281 species using three different GCMs (ECHAM4, GFDL, and HadCM3) for the present day ('simulatedcurrent') and for 2020, 2050 and 2080. Species reference numbers are given in Appendices Table A1. For example, 'echam_2020_sp1-140' can be used to visualise distribution maps of species number 1 to 140, under the ECHAM4 2020 scenario.	DBF File	ArcMap
echam_2020_sp141-281		DBF File	ArcMap
echam_2050_sp1-140		DBF File	ArcMap
echam_2050_sp141-281		DBF File	ArcMap
echam_2080_sp1-140		DBF File	ArcMap
echam_2080_sp141-281		DBF File	ArcMap
gfdl_2020_sp1-140		DBF File	ArcMap
gfdl_2020_sp141-281		DBF File	ArcMap
gfdl_2050_sp1-140		DBF File	ArcMap
gfdl_2050_sp141-281	These files can be imported into ArcMap (see page 180) in order to view simulated distribution maps of each of the 281 species using three different GCMs (ECHAM4, GFDL, and HadCM3) for the present day ('simulatedcurrent') and for 2020, 2050 and 2080. Species reference numbers are given in Appendices Table A1. For example, 'gfdl_2080_sp141-281' can be used to visualise distribution maps of species number 141 to 281, under the GFDL 2080 scenario.	DBF File	ArcMap
gfdl_2080_sp1-140		DBF File	ArcMap
gfdl_2080_sp141-281		DBF File	ArcMap
hadcm3_2020_sp1-140		DBF File	ArcMap
hadcm3_2020_sp141-281		DBF File	ArcMap
hadcm3_2050_sp1-140		DBF File	ArcMap
hadcm3_2050_ sp141-281		DBF File	ArcMap
hadcm3_2080_sp1-140		DBF File	ArcMap
hadcm3_2080_ sp141-281		DBF File	ArcMap
simulatedcurrent_sp1-140		DBF File	ArcMap

simulatedcurrent_sp141-281		DBF File	ArcMap
Table A1	Details of each of the 281 species, including names, red list categories, AUC values and geographic regions they occupy	Microsoft Word 97-2003 Document	Microsoft Word
Table A2	Extent of species' simulated-present and potential-future distributions.	Microsoft Word 97-2003 Document	Microsoft Word
Table A3	Extent of overlap between species' current and potential future distributions.	Microsoft Word 97-2003 Document	Microsoft Word
Table A4	Projected Persistence and Turnover in African Protected Areas by 2020, 2050 and 2080.	Microsoft Word 97-2003 Document	Microsoft Word

Instructions to View Files in ArcMap

Simulated presence-absence maps for each of the 281 species can be viewed as follows:

1. Load ArcMap.
2. Tools > Add XY Data >
3. Click and locate the chosen file (e.g. gfdl_2080_sp1-141.dbf) on the DVD.
4. Click Add.
5. Select "LONG" as the X Field.
6. Select "LAT" as the Y Field.
7. Click OK.
8. Double click on the layer just added.
9. Select the 'symbology' tab.
10. On the left-hand menu select Categories > Unique Values.
11. Under 'value field' select the chosen species you wish to view (e.g. SPECIES1).
12. Click 'add all values'* > OK.

*(N.B. presences are denoted by "1" and absences by "0")

To view African country borders:

1. Load ArcMap.
2. Click the 'Add data' button:
3. Select the file "africa_outline.shp" on the DVD.
4. Click Add.

Durham University

Figure A1. National Park Survey

This survey is being undertaken by **Durham University**, UK, as a piece of **independent** research to find out ***your*** views and values towards animals in National Parks in Africa. We would also like to find out ***your*** attitudes about the possible future changes in the variety of these animals. Finally, we would like to find out about your visit to the National Park today.

Your help in answering this questionnaire would be greatly appreciated; your responses are anonymous and will be kept confidential.

Tourism Interest Questions

1. Is this your first trip to South Africa? Yes ☐ No ☐

2. Is this your first visit to Kruger National Park? Yes ☐ No ☐

i) if no, how many times have you visited Kruger in the last two years (including today)? *Please tick one only.*

1 ☐ 2 ☐ 3 ☐ 4+ ☐

3. Are you visiting Kruger as a: day visitor ☐ overnight visitor ☐

4. Which other National Parks have you visited/ do you intend to visit on this trip? *Please list.*

.....

.....

5. What is the main reason for your visit to Kruger National Park? *Please tick one only.*

To experience South African culture ☐ Rest and relaxation ☐

To see and photograph the wildlife ☐ Honeymoon ☐

Business (commercial/workshop/conference) ☐ Study/Research ☐

Other, please specify.....

i) If the main reason for your visit is 'to see and photograph wildlife' (Question 5), which of these best describes the aim of your visit? *Please choose the one option most important to you.*

Seeing a large number of different wildlife species ☐

Seeing a particular species (please state which species) ☐ .....

Seeing the 'Big Five' (Lion, Leopard, Buffalo, Rhinoceros, Elephant) ☐

Other, please specify ☐ .....

6. What have been the highlights of your visit to Kruger so far?

.....

.....

7. How many people are you travelling with? *Please tick one only.*

On my own	☐	1 – 4 others	☐
5 – 9 others	☐	10 + others	☐

8. How would you describe your trip? *Please tick one only.*

Independent travel	☐	Backpacking	☐
Overland	☐	Organised Tour	☐

If organised tour/overland, please state which company .....

9. What type of accommodation have you stayed in/ are you staying in on your trip? *Please tick all those that apply.*

Camping (own equipment)	☐	Safari tent / Permanent tent	☐
Bungalow	☐	Mobile home/caravan	☐
Chalet	☐	Cottage	☐
Hut	☐	Guest House	☐
Houseboat	☐	Log cabin	☐
Hotel	☐	Lodge room	☐
Youth Hostel	☐	Other, please specify	

Payment Questions

10. Have you used a WILD Card on this trip? *Please tick one only.*

Yes – International all clusters	☐	Yes – WILD pass	☐
Yes – Bushveld cluster	☐	Yes – River cluster	☐
Yes – Dry cluster	☐	Yes – Cape cluster	☐
Yes – Swazi cluster	☐	No	☐

i) **if yes, is it:** Individual ☐ Couple ☐
Family ☐

11. How much money are you spending on entrance fees to Kruger National Park per day? *Please tick one only.*

SA Citizens and Residents	R30 per day	☐
SA DC Nationals	R60 per day	☐
Standard Conservation Fee (foreign visitors)	R120 per day	☐
WILD card (one off payment)		☐
Don't know/ Part of Inclusive Holiday Price		☐

12. Do you believe the entrance fee you paid to enter the park was: *(Please select one only)*

Too low Just right Too high Not sure of the amount paid

Effective conservation requires immense financial and human resources. South African National Parks (SANParks) needs to receive sufficient revenue to be able to successfully manage the 23 parks under its control. These parks, including Kruger, currently hold a wide variety and number of species; the following questions aim to try and find out how much *you value* these species.

Imagine that in the next few years the variety and number of species may change as a result of climate change affecting habitat quality. If this were the case, SANParks would need extra money to manage the park to protect such species e.g. by identifying and averting threats to these species, the provision of artificial habitats etc. As there are only limited governmental resources available, a possible extra source of revenue to SANParks is to increase entrance fees. This increased fee would be in place for the foreseeable future.

13. In order to maintain the current number and variety of animals in the face of these threats, would you be prepared to pay more to enter Kruger National Park in the future?

Yes ☐ No ☐

i) If yes, what is the most you would be willing to pay to enter Kruger on top of the entrance fee you have already paid today (as stated in Question 11)? Please keep in mind that you would not be able to spend this extra money on other things such as entry fees to other national parks/ donations to animal welfare organisations etc.

.....South African Rand

Certain species are at a greater risk from the effects of changes in climate, for example the number of elephants/giraffes in this park is expected to decrease in the next few years (see attached sheet). SANParks would be able to stabilise or even reverse this change using the extra revenues from an increase in entrance fees.

14. In the scenario described above, would you be prepared to pay more money to enter Kruger in the future if all of the extra money you would be willing to pay was used to help conserve ONLY elephants/giraffes but all other aspects of your trip remained the same?

Yes ☐ No ☐

i) if yes, how much would you be willing to pay in increased entrance fees (on top of the entrance fee you have already stated in question 11) to help conserve elephants/giraffes? .....South African Rand

15. If you stated in Question 13 and/or 14 that you are not willing to pay any extra fees, *please indicate below why you would not contribute to these programs*.....

.....

Demographic Information Finally, to help us understand visitors to Kruger we would like to ask a few questions about **you**. Please remember your answers will remain confidential and anonymous.

16. Are you: Male ☐ Female ☐

17. Age group. *Please tick one.* ☐ 18 – 24 ☐ 25 – 34 ☐ 35 – 44 ☐ 45 – 54 ☐ 55 – 64 ☐ 65+

18. Nationality .....

19. Country of residence .....

i) Province/State (if applicable).....

ii) Please state how long you have been resident there .....years

20. Ethnic Origin:.....(see attached sheet).

21. How would you describe your level of education? *Please tick one only.*

University Higher Degree (Master or Doctorate) ☐ Secondary School Completion ☐

University First Degree (Bachelor) ☐ Elementary School Completion ☐

College (no degree) ☐ No Formal Qualifications ☐

Other, *please specify* ☐ .....

22. How would you describe your current employment status? *Please tick one only.*

Part time (less than 30 hours/week) ☐ Full time (more than 30 hours/week) ☐

Retired ☐ Unemployed ☐

In full time education ☐ Other, please specify .....

23. Using the payment card attached, please indicate which group your estimated yearly household income (before tax) lies in. 1 ☐ 2 ☐ 3 ☐ 4 ☐ 5 ☐ 6 ☐ 7 ☐ 8 ☐

i) Please tick which currency you are working in:

South African Rand ☐ Pounds Sterling ☐ US Dollars ☐ Euros ☐

24. How many people live in your household? ..... Adults .....Children (under 16)

25. Are you a member of a conservation organisation (e.g. WWF, AWF)? Yes ☐ No ☐

i) if yes, please specify which .....

I would like to take this opportunity to thank you for taking the time in filling out this questionnaire.

If you would like a summary of our results, please enter your name and email address below. These details will not be passed on, and will only be used for the purpose stated.

Name .....

Email .....

Durham University

Time: __:__ Date: __/__/07 Location: Interviewer:

Figure A2. Ethnic origin options shown to the respondents preceding question 20 of the questionnaire (Figure A1).

(Question 20) Ethnic Origin

(1) White British
(2) White Irish
(3) White Other
(4) Mixed: White and Black Caribbean
(5) Mixed: White and Black African
(6) Mixed: White and Asian
(7) Mixed Other
(8) Black Caribbean
(9) Black African
(10) Black Other
(11) Asian Pakistani
(12) Asian Indian
(13) Asian Bangladeshi
(14) Asian Other
(15) Chinese
(16) Other
(17) Unknown

Figure A3. Household Income bracket options shown to the respondents preceding question 23 of the questionnaire (Figure A1). Respondents were able to choose which currency they answered in.

(Question 23) Household Income

South African Rand

(1) Less than 70,000 ZAR
(2) 70,000 - 139,999 ZAR
(3) 140,000 - 279,999 ZAR
(4) 280,000 - 424,999 ZAR
(5) 425,000 - 564,999 ZAR
(6) 565,000 - 704,999 ZAR
(7) 705,000 - 844,999 ZAR
(8) 845,000 + ZAR

€ Euros

(1) Less than € 7,500
(2) € 7,500 - € 14,999
(3) € 15,000 - € 29,999
(4) € 30,000 - € 44,999
(5) € 45,000 - € 58,999
(6) € 59,000 - € 74,999
(7) € 75,000 - € 88,999
(8) € 89,000 +

£ Sterling

(1) Less than £5,000
(2) £5,001 - £9,999
(3) £10,000 - £19,999
(4) £20,000 - £29,999
(5) £30,000 - £39,999
(6) £40,000 - £49,999
(7) £50,000 - £59,999
(8) £60,000 +

$ US

(1) Less than $10,000
(2) $10,000 - $19,999
(3) $20,000 - $39,999
(4) $40,000 - $59,999
(5) $60,000 - $79,999
(6) $80,000 - $99,999
(7) $100,000 - $119,999
(8) $120,000 +