Mapping and Modelling the Population and Habitat of the Roan Antelope (*Hippotragus equinus langheldi*) in Ruma National Park, Kenya

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Declaration

No portion of the work presented in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning

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Abstract

Wildlife-based tourism, which is Kenya's second largest economic sector, is threatened by the risk of extinction of many wildlife species in the country. The endemic roan antelope (*Hippotragus equinus langheldi*) now only survives in Ruma National Park (RNP) where its population has been declining continuously since 1976. This thesis investigates the roan's habitat use and selection, causes of population decline and population viability in RNP with the aim of recommending scientifically-based management interventions for population recovery and sustainable conservation.

Roan movement patterns and habitat use were investigated using 4 home range estimation techniques. Habitat selection was studied at multi-spatial scales using compositional analysis, logistic regression, and information-theoretic (IT) and multi-model inference (MMI) techniques. Data for this study consisted of population estimates for roans and other grazers, Landsat images, soil maps, digital terrain data, rainfall records, snare distribution records, and roan ground tracking data. Identification of causes of population decline was carried out using both multivariate and univariate techniques. A generic population viability analysis (PVA) package was used to (i) estimate the likelihood of roan extinction under various management options; and (2) rank the management alternatives for roan population recovery.

All 4 home range estimators are useful in characterizing different aspects of the roan home range, but overall the local convex hull method produced the most realistic home ranges. The three habitat selection methods yielded similar results but the IT techniques demonstrated superior qualities as they identified important habitat variables and produced the most accurate model predictions. MMI averaged models coupled with GIS data developed very informative habitat suitability and poaching risk maps. Analysis of habitat selection indicated different usage in seasons and spatial scales depending on water availability, habitat composition and burned status, and distribution of eco-geographical features. High adult mortality due to poaching with snares was identified as the main cause of roan population decline. Other important factors included habitat change and rainfall variability with its associated droughts and floods. PVA showed that under the current conditions, the roan population cannot persist more than 3 decades. Several anti-poaching and prioritized management interventions to curb poaching and promote population recovery are described.

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GENERAL INTRODUCTION

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CHAPTER 1: General Introduction

1.1 The roan antelope: Description, biology, population status and distribution

1.1.1 Physical description

The roan is a large antelope, second only in size to eland. The roan antelope attains an average mass of 260 - 300 kg for adult males and 225 - 275 kg for adult females, and a shoulder height of 1.5-1.6 m for adult males and 1.4 – 1.5 m for adult females (Grzimek, 1990). Both sexes carry horns which rise from the head in a uniform backward curve, ridged almost to the tips and are often described as scimitar-shaped. Males are larger and built more sturdily than females, with longer, thicker horns. The body coat is greyish brown with touches of rufous colouring which varies amongst individuals. The underparts are white. The legs are darker brown than the remainder of the body and the neck has an erect, dark-tipped mane. The most distinctive features are the facial markings which resemble a black balaclava mask with elongated white 'cut-outs' around the eyes. The ears are unusually long with dark brown tufts on the tips. Authoritative descriptions are given by (1990) and Smithers (1983).

1.1.2 The roan biology

The gestation period for roan antelopes is 260 to 280 days and there is no specific calving season (Smithers, 1983). Usually a single calf is born but in a few cases two calves have been observed (Poche, 1974). Females go into oestrous 2 to 3 weeks after giving birth and are capable of having young every 10 to 10.5 months. Females become reproductively active after they reach 32 to 34 months of age. Females leave the herd for about 1 or 2 weeks before giving birth. After giving birth they return to the herd during the day and leave the newborn in a concealed area for the day. An effective camouflage colouring and absence of characteristic odour probably make isolated calves more difficult to locate by predators. The females return to their calves at dusk and spend the night with them. Calves stay hidden for about 4 to 6 weeks after birth and join the herd when they are strong enough to outrun danger (Wilson and Hirst, 1977).

The roan antelope associate in herds of up to 35 individuals, though herd sizes of 5 - 15 are more common (Smithers, 1983). However, herd size and structure changes in times of drought when herds of over 100 animals can be seen. These herds are composed of an adult dominant male and a group of females with their young. A hierarchy exists among the females of the herd with one dominant female playing a leading role in initiating such group activities as feeding, drinking, moving and flight (Wilson and Hirst, 1977). Juvenile males are forced to disperse at about 3 years of age. Juvenile females remain with the herd until the herd becomes too large, when some of the cows and calves leave to form a new herd. Juvenile males that are driven out of the herd join together to form bachelor herds of usually 3 to 5 individuals, though as many as 12 individuals have been observed (Joubert, 1974). At about 5 to 6 years of age, bachelor herds break up and those males try to take over a herd of females. The most dominant male of the bachelor group is the first to obtain a herd of females. Fights break out between males for dominance but they rarely result in physical harm to either individual. Males defend an area of about 300 to 500 meters outward from their herd against potential rivals. Herds generally range across 6,400 to 10,400 hectares per year, with the average area used at any one time being 200 to 400 hectares (Joubert, 1974).

Roan antelopes are mainly active during the cooler parts of the day, in the morning and evening, and during the hottest hour they prefer to hide in dense woodland (Schuette et al., 1998). Herds run for a short distance when disturbed, and then look back to investigate the disturbance but when pressured they can run as fast as 57 km/hr (Stuart, 1996). Grzimek (1990) asserts that roans are not elusive animals and that they tend to stand their ground when threatened or startled, which makes them easy to hunt. The call of the roan is a usually musical whistle, which changes in adulthood with 3 basic sounds having been recorded: a high-pitched squeal signifying anger, an equine snort for alarm, and a low hissing sound when wounded (Joubert, 1974).

Roan antelopes live in small herds and fight aggressively when threatened. Healthy adults are likely to be relatively invulnerable to predation but the young, ill and elderly adults are taken by large predators such as lions, hyenas, leopard and wild dogs (Kingdon, 1984). Old females act as sentinels against predators, standing on the periphery of the herd while the others feed. Lions are the principal natural enemies of adult roan antelope, although a single lion facing a roan has to be careful not to be gored by the antelope's horns (Joubert, 1974).

A typical habitat for the roan consists of open savannah woodland with extensive open areas of medium to tall grasses, where water is available (Dorst and Dandelot, 1990). Permanent water is so important for roan such that the species rarely moves further than 2-4 km from a drinking site (Wilson and Hirst, 1977). Joubert (1976) noted that they avoid woodland where the trees form a closed canopy or where the underbrush forms thick closed stands. They tolerate low bush growth up to 1.5 m in the grassland provided this forms an open scattered association but they avoid areas of short grass. Bush encroachment or over utilization of the grass degrades their habitat. Roan antelope are grazers that prefer leaves over stems in tall grasslands. They browse if grazing forage is poor. The preferred feeding height is 15 – 150 cm and green shoots are often grazed down to a height of 2 cm. Twenty percent of their diet consists of herbs and foliage (Schuette et al., 1998). As a result of these habitat requirements the distribution of the roan antelope is patchy and discontinuous.

1.1.3 Population status and distribution in Africa

The roan antelope, which is endemic to Africa, was formerly one of the most widely distributed antelopes found essentially throughout the African savannas where water was adequate (Kingdon, 1984). Originally the roan antelope used to occur in

34 African countries (East, 1988) but now possibly remains in 30 countries (IUCN, 2010): Angola; Benin; Botswana; Burkina Faso; Cameroon; Central African Republic; Chad; The Democratic Republic of Congo; Cote d'Ivoire; Ethiopia; Ghana; Guinea; Guinea-Bissau; Kenya; Malawi; Mali; Mauritania; Mozambique; Namibia; Niger; Nigeria; Rwanda; Senegal; South Africa; Sudan; Tanzania; United Republic of Togo; Uganda; Zambia and Zimbabwe. The species is now locally extinct in Burundi, Eritrea and possibly in Gambia. It was also extinct in Swaziland and later reintroduced to the privately owned Mkhaya Nature Reserve (East, 1999).

The total number of roans is estimated to be 76,000, with one-third of this total concentrated in only 4 countries: Burkina Faso, Cameroon, Zambia and Tanzania (IUCN, 2010). The species remains locally common in West and Central Africa, while in East and Southern Africa, the species is now very rare. The overall population trend is decreasing, with two-thirds decreasing and one-third either stable or increasing. However, the only population increasing is that of roans in private reserves in South Africa. Although, the roans are currently classified by the IUCN (2010) as of 'Least Concern', if the present trends continue, the roan antelope's status may eventually decline to threatened status as it disappears from large parts of its current range due to poaching and loss of habitat to the expansion of settlement. It is worth noting that in 1996 the same species was listed in the IUCN red list (IUCN, 1996) as threatened and its survival dependent on active conservation measures.

There are various classifications of the roan antelope subspecies based on phenotypic and geographic characteristics, which caused confusion and contradictions (Barrie, 2009). The roan was first officially classified by Desmarest in 1804 (Harris, 1852), and further classifications were made by Sclater and Thomas (1899), Dollman and Burlace (1922), Ansell (1971), Dorst and Dandelot (1990)**,** and Skinner and Smithers (1990)**.** Some of these authors often contradict each other with regard to the location of the various subspecies and the general appearance of the subspecies (Barrie, 2009). However, Ansell (1971), who is also referred to by

Dorst and Dandelot (1990), and Skinner and Smithers (1990), listed six subspecies of *Hippotragus equinus: H. e .koba, H. e. bakeri*, *H. e. Charicus, H. e. equinus, H. e. cottoni*, and *H. e. Langheldi.* His results are considered by many modern day taxonomists to be the best investigation into the taxonomic status of the alleged subspecies (Barrie, 2009). The geographical distribution of the six subspecies can be seen in figure 1.1. However, confusion still exists concerning what the differences between these subspecies actually are and their exact geographical distribution.

Two recent studies by Mathee and Robinson (1999) and Alpers et al (2004) to investigate the authenticity and geographical distribution of these 6 subspecies have yielded contradicting results. Mathee and Robinson (1999) concluded that the 4 subspecies they investigated (*equinus, koba, cottoni*, and *langheldi*) are genetically different. Contrary, Alpers et al (2004) concluded that out of the 5 subspecies they investigated (*equinus, koba, cottoni*, *langheldi, and charicus*), there are only two genetically distinct subspecies; one in West Africa (*H .e. koba*) and another in the rest of Africa. However, Alpers et al (2004) further noted that the subspecies in the rest of Africa can be subdivided into sub-subspecies or management units (East African group, South Eastern group and South Western group). Nevertheless, there still seems to be an agreement by these two studies that the 6 subspecies should be managed as independent management units until further research is done to resolve the issue of roan subspecies and to define the geographical coverage of each subspecies.

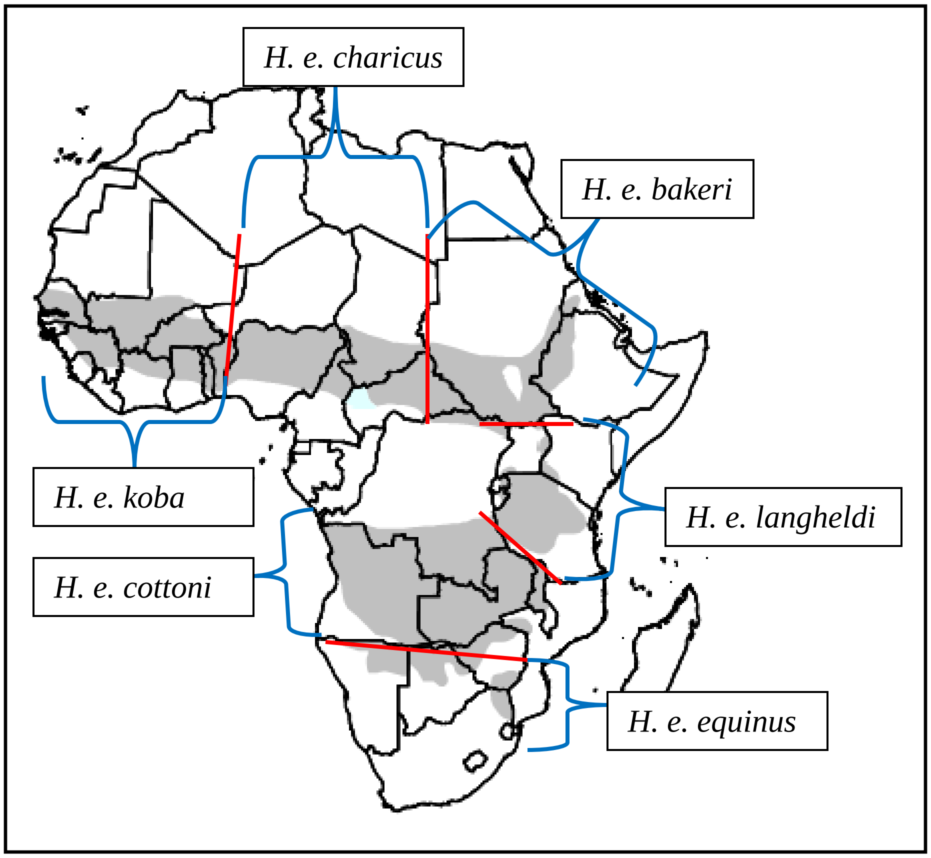


Figure 1.1: Distribution of roan antelope subspecies according to Ansell (1971)

1.2 The rationale of the research

Wildlife-based tourism is the backbone of many economies in African countries that still harbour high diversity of wildlife species. For instance, wildlife-based tourism is Kenya's second largest economic sector after agriculture, contributing over 12% to the country's Gross Domestic Product (Akama and Kieti, 2003). Sustainable tourism is dependent on maintenance of high wildlife diversity in Kenya's protected areas, but its sustainability is threatened by the risk of extinction of many wildlife species in the country. One of the species of concern is the roan antelope (*Hippotragus equinus*), whose distribution range is so drastically reduced throughout Africa that the species is faced with the risk of extinction in some localities (Benedetti, 2001). Most of the roan subspecies are threatened apart from the *H. e. koba* and *H. e. charicus* that are common in West African countries (East, 1990; Poche, 1974). For example, the roan antelope became locally extinct in the Serengeti National Park in Tanzania (Campbell and Borner, 1995) and has recently been reported to be locally endangered in South Africa's Kruger National Park (Harrington et al., 1999) and Nylsvley Nature Reserve (Dorgeloh, 2001).

The endemic East African subspecies (*H. e. langheldi)* has declined rapidly throughout much of its range but no comprehensive study on the subspecies has ever been conducted in East Africa (East, 1997). There are less than 100 individuals in both Uganda and Kenya and around 250 roans in north-western Tanzania whilst the current situation in Rwanda is unknown (Musyoki, 2010). There are more roans in southern and central Tanzania, but these are suspected to belong to another subspecies, probably the *H. e. cottoni*. In Kenya, the roan antelopes formerly occupied large areas around Lake Victoria, Mt Elgon, Cherangani Hills, Ithanga Hills, Chyulu Hills, Ololo (or Isuria) escarpment, and eastern Mara (Stewart and Stewart, 1963). However, by 1990s the species became locally extinct in Masai Mara National Reserve (Broten and Said, 1995) and all other areas in Kenya except Ruma National Park (Olubayo et al., 1997). In this park the roan antelope is now critically locally endangered. Its population declined continuously from 202 individuals in 1976 to about 45 roans in 2005 (Kones, 2005). This is of serious concern to the Park management because a population of less than 50 roan antelopes is not considered viable according to population genetic criteria (Soule, 1980). The park authorities need to act fast to halt further decline, and promote population recovery back to sustainable levels.

Many studies have been done on roan antelopes in Africa to identify the factors that led to their decline and to identify means of mitigating their effects. However, research over the last three decades (Kroger and Rogers, 2005; McLoughlin and Owen-Smith, 2003; Harrington et al., 1999; Allsopp, 1979; Joubert, 1976) has so far failed to identify either the key roan habitat requirements or the precise factors causing population decline. This is evidenced by the lack of effective measures to halt roan population declines at least in the researched protected areas (McLoughlin and Owen-Smith, 2003). Many hypotheses have been put forward to explain the roan decline including predation, poaching, habitat loss and deterioration, competition with other grazers, diseases, human settlement and agricultural encroachment (Harrington et al., 1999; Parkinson, 1972). Other potential causes of roan population decline include extreme droughts, fires, floods and inbreeding depression. However, most of the causes identified seem to be site-specific. Research is needed to establish which of these factors are most relevant to the Kenyan situation and Ruma N. Park in particular. Also, previous studies were conducted mainly on the South African subspecies (*H. e. equinus*) as opposed to the East African subspecies (*H. e. langheldi*), which this research is studying.

No comprehensive research has ever been done on roans in Kenya. Most of the past studies (Allsopp, 1979; Parkinson, 1972) are based on observations without any statistical analysis whilst others are brief unpublished reports (Kones, 2005; Olubayo et al., 1997; Muriuki, 1995). There is a need to conduct a detailed study using modern techniques such as modelling, Geographic Information Systems (GIS) and Remote Sensing (RS) techniques coupled with ground-based methods and historical data to identify the specific causes of decline of the Kenyan roan population in Ruma National Park. These techniques could then be used to develop models, scenarios and simulations upon which appropriate management practices and recommendations could be made to ensure the sustainable conservation and management of the roan population in Kenya.

Interventions to save the drastically declining roans in Kenya from extinction may not be successful without prior research. For example, in 1970 a group of 37 roans were translocated to Shimba Hills National Reserve from Tana Ranch in Ithanga Hills in Kenya where their habitat had faced serious threat from human settlement (Parkinson, 1972). However, the roans reduced to 12 within five years (Allsopp, 1979) and they became locally extinct by 1985 (Litoroh, 1989). The causal factors leading to their extinction are still not well known. However, reports indicate that the roans perished at the hands of poachers while exploring the reserve environs in search of suitable habitat (Olubayo et al., 1997; Litoroh, 1989). They are said to have lacked water and optimum food and cover inside the reserve that led them to move outside where they were killed by poachers. Hence without proper detailed research, translocations of roan will continue to be unsuccessful. There is a need for detailed research on roan habitat suitability before translocations and possibly re-introductions into known ranges in Kenya.

A number of studies have been conducted in Ruma National Park on the vegetation (Okita-Ouma and Njue, 2006; Muriuki et al., 2005; Waweru et al., 1995) but none has been done to characterize the specific habitat for roan antelopes. However, studies by Joubert (1976), Schuette et al (1998) and Smithers (1983) in other parts of Africa showed that roans have strictly defined habitat requirements:

- dependent on a regular supply of water (within 3 - 5km);
- prefer lightly wooded savannah with open areas of medium /tall grasses up to 1.5m;
- avoid closed canopy woodland and thick closed stands of bush 1.5-4m high;
- avoid burns and subsequent green flush; and
- graze on leaves rather than stems in tall grasslands but browse if grazing forage is poor, showing sensitivity to apparently minor habitat changes.

This study seeks to identify which of these habitat features are important in RNP and recommend measures of ensuring sustainable habitat conservation. Mapping of detailed roan habitat in RNP with high accuracy is vital to help the Park managers and planners in zoning and ensuring core areas of the roan home range are protected as well as in monitoring the effect of different management practices on roan habitat change.

There is no effective monitoring program or documentation system for the declining roan population in RNP. The information on roan population has a lot of gaps between consecutive years and the available records are stored in a format that is not easily accessible and these records are likely to get lost. The exact numbers of roans in RNP are still unknown as numbers are always stated as estimates. With a small endangered population, it is imperative that the exact numbers be known for the purpose of management. There is a need to design a systematic way of carrying out a total roan count to ascertain their exact numbers, ages, sex structure and distribution in both dry and wet seasons. Also, cost-effective long-term methods of monitoring the roan population and habitat in RNP need to be established. The monitoring program should be backed with an efficient method of storing the data for easy access and sharing.

In summary, the research problems are:

- The rapidly declining small isolated roan population in RNP is likely to become extinct soon without effective management interventions;
- The factors responsible for the roan population decline in RNP are not known;
- Information on the preferred habitat features by roans and their distribution in RNP is lacking;
- No comprehensive study on the various aspects of the roan antelopes in Kenya has ever been done;
- Available data on the roan antelopes in RNP is inadequate and stored in forms that are not easily accessible to researchers and park authorities;
- Cost-effective and reliable methods for long-term monitoring of roan habitat, population, movement and distribution patterns in RNP are lacking.

It is anticipated that the successful completion of this study and implementation of its findings will halt further roan decline and promote quick population recovery in RNP. With the RNP being in the Western Kenya tourist circuit, this will boost tourist flow into the park to see the endemic species of roan. In the long term, this will lead to poverty reduction in the local communities surrounding the park through the tourism industry in particular and also promote the local and national economy in general. This study will contribute towards Kenya's achievement of two vital Millennium Development Goals (poverty reduction and environmental sustainability). The lessons learned from this study will contribute scientific knowledge to aid in saving other roan populations that are facing similar threats. This study will also aid in evaluating the usefulness of managing a small population in an isolated park with the aim of saving an endangered ungulate population.

1.3 Research objectives

The overall aim of this research is to evaluate the roan habitat and population through mapping and modelling, and recommend scientifically-based interventions for population recovery and sustainable conservation of the endangered roan antelopes in RNP. The research was designed to achieve the following six objectives:

- To identify the factors responsible for population decline of roan and other antelopes in RNP;
- To analyze and map the spatio-temporal changes in roan habitat and population;
- To model the relationships between the roan presence and the biotic factors (such as habitat types), abiotic environmental factors (water, slope, soil and snares) and park infrastructure (roads, gates and fence);
- To determine the cost-effective and sustainable methods for long-term monitoring of roan habitat, population, movement and distribution patterns;
- To analyze the probability of persistence of the roan population under the current conditions as well as under various management options;
- To determine the factors influencing the distribution of snares and recommend management strategies to curb poaching activities.

1.4 Outline of thesis

This thesis consists of eight chapters which are linked together as shown in Figure 1.2. Chapter 1 gives a brief background of the study. Chapter 2 analyzes population dynamics of 6 antelope species. Chapter 3 explores different sampling protocols and home range estimation techniques for monitoring of roan movement patterns and habitat use. Chapter 4 and 5 evaluate roan habitat selection and suitability using compositional analysis (chapter 4) and logistic regression and information-theoretic approach (chapter 5). Chapter 6 estimates the probability of persistence and identifies the factors influencing the persistence using population viability analysis. It is a further analysis of roan population dynamics using the findings of chapter 2, 3, and 5. Chapter 7 is a relatively independent chapter that investigates the issue of poaching with snares. The last chapter presents general discussion and conclusion arising from the other chapters and recommends the way forward for the sustainable conservation of the roan antelope in Kenya. More specific information about each chapter is provided below.

Chapter 1 presents a brief research background, outlines the research problems, states the research objectives, outlines the thesis structure, and describes the study area: Ruma National Park.

Chapter 2 analyzes how the grazing habitat and populations of roan and 5 other antelopes have changed over the last 3 decades. The effect of rainfall variation and habitat on the population of these antelopes is explored using redundancy analysis and negative binomial regression.

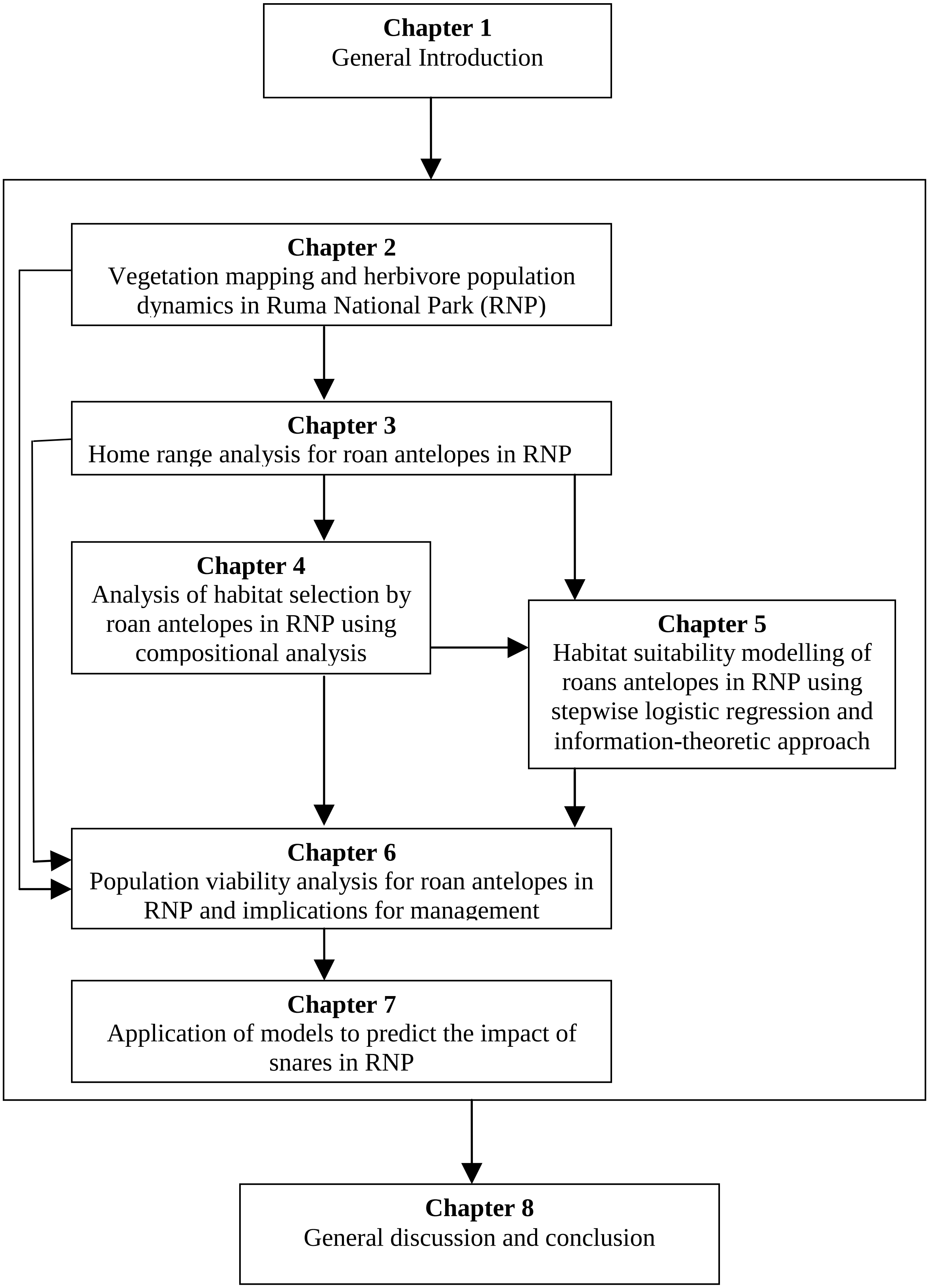


Figure 1.2: Thesis layout and the link between chapters

Chapter 3 compares the performance and effectiveness of 4 home range estimators (Minimum Convex Polygon, Incremental cluster polygons, Fixed kernel density, and Local convex hull) in varying samples sizes and sampling protocols (random or systematic sampling, varying sampling time intervals). It also highlights the differences in home range estimates (i) calculated in Adehabitat and RANGES software packages and (ii) between roan groups and lone males. These comparisons aim at identifying the most cost-effective methods for long-term monitoring of roan movement and distribution patterns.

Chapter 4 analyzes habitat selection by roans using compositional analysis at the second- and third-order selection in different seasons, times of the day and for different activities.

Chapter 5 models habitat suitability for roans using stepwise logistic regression and information-theoretic approach at the study area and home range spatial scales. The results are used to illustrate the differences in seasonal habitat suitability, to map the suitable habitat and test the effect of scale in habitat selection by roan antelopes.

Chapter 6 performs a population viability analysis in VORTEX software to estimate the probability of persistence of the roan population under the current conditions and other alternative management options. The simulated model also identifies the factors responsible for roan population decline.

Chapter 7 investigates the problem of poaching with snares in the park. It analyzes how snares are spatially distributed and what factors influence such distribution. Models on the probability of snare occurrence are developed and used to map the poaching risk in the park.

Chapter 8 summarises all the major research findings and conclusions of this study; collates different methods used in analyzing habitat selection; and recommends prioritised interventions for poaching control, habitat management, population recovery and sustainable conservation of the roan antelopes not only in Ruma National Park but also in the whole of the country. It ends with an outline of future research topics.

1.5 Description of the study area

Location

Ruma National Park is located close to the southern shores of Lake Victoria in Suba District of Nyanza province, between 0^{o} 33' - 0^{o} 44' S, and 34^{o} 10' - 34^{o} 22'E (Figure 1.3). It is 23km south-west of Homa Bay Town and 425km west of Nairobi. The park covers an area of 120km^{2}.

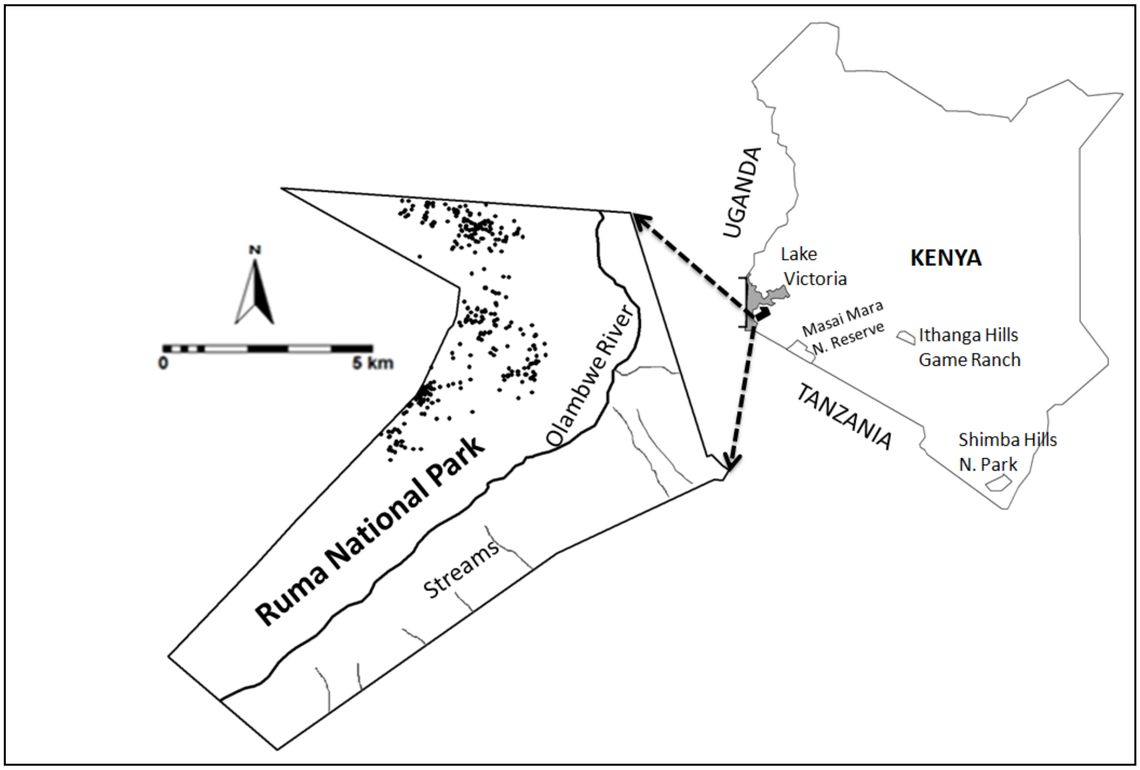


Figure 1.3: Location of study area showing other reserves in Kenya where roans became locally extinct and the current roan locations recorded during this study's fieldwork in Ruma National Park as indicated by black dots

History of Ruma National Park

Ruma National Park was initially established as the Lambwe Valley Game Reserve in 1966 and acquired national park status in 1983 (KWS, 1990). It was mainly established to protect the endangered population of the endemic roan antelopes (*Hippotragus equinus langheldi*), which is not found anywhere else in Kenya. In the past, the park has experienced high frequency of fire outbreaks, poaching incidences and human-wildlife conflicts with the surrounding community (KWS, 2006). A wire fence was erected in 1994 to resolve the problem of poaching and human-wildlife conflicts. The fence almost totally encloses the park leaving only 23 km unfenced, although many portions of the original fence have been vandalised by the local community. Therefore, the park is almost completely isolated from its former surrounding environment by the fence and dense human settlement. However, the fence has not achieved its purpose because poaching and human-wildlife conflicts still persists. Another historical problem of the park and its environs is the presence of high levels of tsetse flies (*Glossina pallidipes*) that cause trypanosomiasis in livestock and sleeping sickness in humans. The area was uninhabited until the 1930s when a tsetse fly eradication program was started (Waweru et al., 1995). Continued habitation of the area by both man and livestock depends on the success of the on-going tsetse fly control programs.

Topology and drainage

The park lies in the valley floor between Gwasi hills to the west, Kanyamwa escarpment to the east and Gembe and Ruri hills to the north. It is at an altitude of 1170-1750m above sea level. The Park is drained by Olambwe river, which flows across the park and into Lake Victoria. Olambwe is a seasonal river with a few permanent water pools along its course throughout the year. There are numerous water springs along the Kanyamwa escarpment from where a number of seasonal streams originate.

Soils

Omoto (1994) showed that most of the park valley bottom is covered by Pleistocene lacustrine sedimentary depositions overlain by alluvian clays washed from surrounding escarpment and hills of volcanic origin. Because the valley is surrounded by alkali rock formations, the ground waters are rich in sodium and many of the lower-lying sub-soils are consequently alkaline. All the water in the park is muddy and salty. Deep layers of fertile black cotton soil are also found in the valley. During the long rains the black cotton soil becomes waterlogged, which makes transportation almost impossible even with four wheel drive vehicles. The availability of water is mainly determined by rainfall and during the dry season water is scarce to wildlife in the park.

Vegetation

The park vegetation is dominated by savannah grassland and woodland with extensive thickets or forest and bushes. Waweru et al (1995) described the vegetation briefly. They estimated that about 20% of the park is an evergreen forest situated at the lowest point of the valley mainly along the Olambwe River. The rest of the habitat falls under wooded grassland dominated by *Balanites aegyptica* or *Acacia drepanolobium*, *Acacia seyal* woodland or bushland. In the wooded grassland the dominant grass species are *Themeda triandra* or *Setaria sphacelata*. *Themeda triandra* is dominant in the bushland whilst *Hyparrhenia filipendula* is dominant in the woodland.

Climate

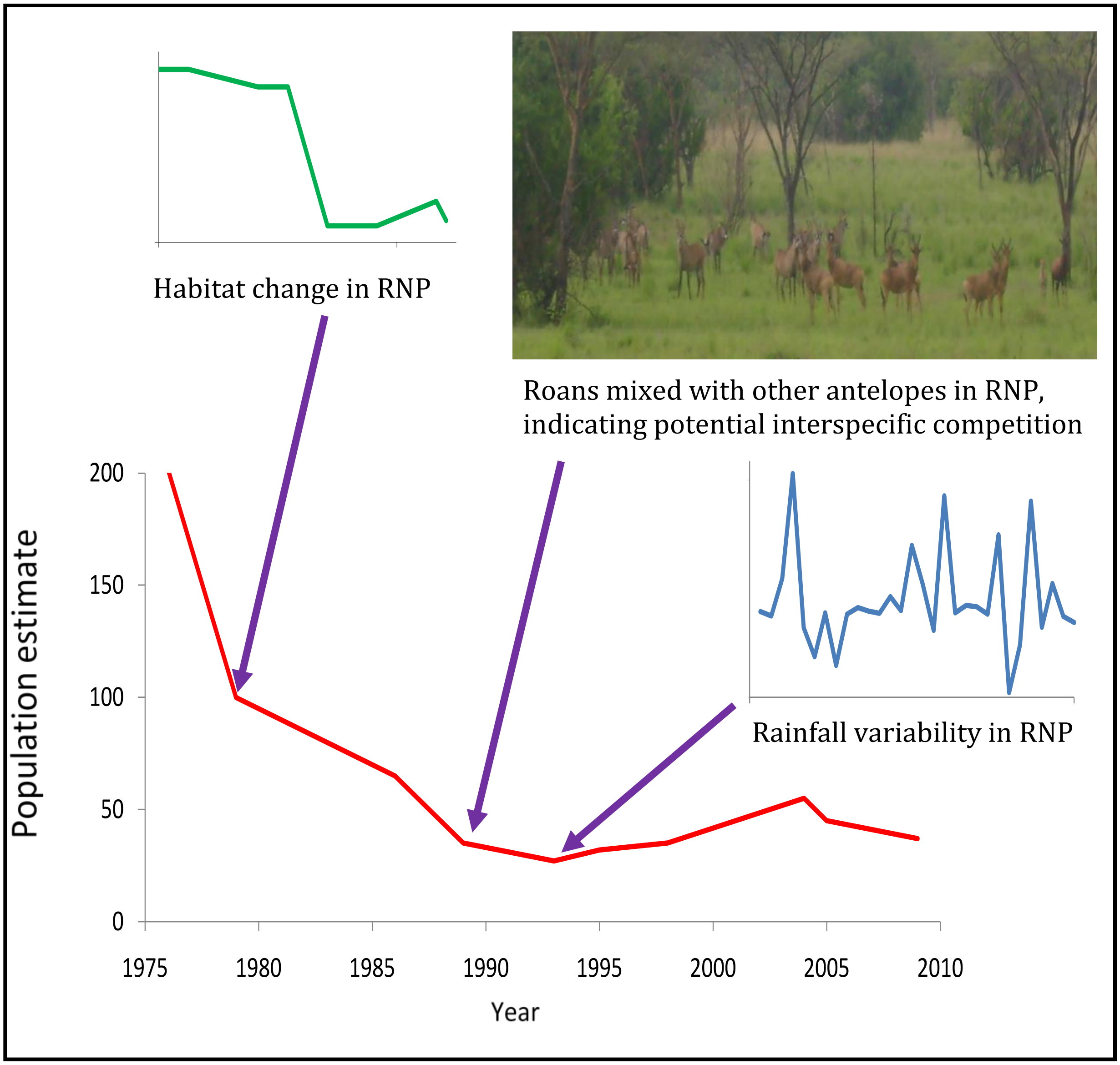
The park lies in a region classified as sub-humid to semi-arid with medium agricultural potential. Long rains occur March-June and short rains fall September-November. The average annual rainfall is 875 mm and 1125 mm for the short and long rains, respectively (Omoto, 1994). The park experiences high temperatures throughout the year that range from 17^0C to 34^0C (Omoto, 1994). June and July are the coldest months whilst February is the hottest month of the year. Greatest wind movements occur during the driest season of the year from January to February, a time when fire outbreaks are frequent.

Wildlife

The park harbours a variety of wildlife with the most notable being the endangered roan antelope. Other species include Oribi, Jackson's hartebeest, Mountain reedbuck, Buffalo, impala, Rothschild's giraffe, deffasa waterbuck, leopard, hyaena, and vervet monkey. More than 400 bird species have been recorded in the park and it is renowned by ornithologists for its rare migratory blue swallow (KWS, 2006). The park harboured many other wildlife species in the past, which either became locally extinct or emigrated to other protected areas especially Masai Mara National Reserve. The most notable of these species are elephants, rhinos, zebra, lions and cheetah (Sutherland, 1972).

CHAPTER 2

VEGETATION MAPPING AND HERBIVORE POPULATION DYNAMICS IN RUMA NATIONAL PARK (RNP)


Habitat change in RNP

Roans mixed with other antelopes in RNP, indicating potential interspecific competition

Rainfall variability in RNP

Roan population decline in Ruma National Park and potential factors driving the decline

CHAPTER 2: Vegetation mapping and herbivore population dynamics in Ruma National park (RNP)

2.1 Introduction

Establishing and understanding causal influences on population dynamics is essential in order to make effective decisions on how to counteract effects of population decline (Owen-Smith and Mills, 2006). Successful intervention approaches are dependent on how well the causes of population decline are understood. There is need to employ robust statistical and modelling techniques capable of distinguishing among potential causes of population decline (Coulson et al., 2000), since causal processes do not operate in isolation especially in multispecies assemblages (Owen-Smith and Mills, 2006).

Past studies on mammal population dynamics have shown that population decline is caused by various factors including: rainfall fluctuation, predation, competition for food, habitat change, extreme weather conditions, diseases, and poaching (including bush meat hunting). Rainfall is the main climatic factor governing herbivore population dynamics in African savannas (Ogutu et al., 2008; Ogutu and Owen-Smith, 2003; Owen-Smith and Ogutu, 2003). Ungulates have been shown to respond both to cumulative past rainfall and seasonal fluctuations in rainfall through changes in movements, reproduction and survival (Ogutu et al., 2008; Owen-Smith and Mills, 2006). For instance, variability in wet season rainfall controlled the population dynamics of Kudu (*Tragelaphus strepsiceros*) through its effects on food resources in Kruger National Park (Owen-Smith, 1990) whilst annual population changes in many African ungulates are dependent on variation in dry season rainfall (Ogutu et al., 2008; Ogutu and Owen-Smith, 2003). Food availability affected by dry season rainfall limits the growth of the migratory wildebeest population in Serengeti-Mara ecosystem (Mduma et al., 1999). These findings suggest that changes in rainfall due to global warming may greatly alter the abundance and diversity of many African ungulates in future (Ogutu et al., 2008).

Predation can be difficult to disentangle from other factors, because its effects are often interactive with nutritional status, habitat conditions, parasite loads, and weather (Post et al., 2002). Ogutu et al (2008) recommends that fluctuations in rainfall should be evaluated and accounted for before the effects of other factors such as predation can be revealed. However, past studies have been able to demonstrate that predation plays a key role in structuring a number of ungulate populations. For example, predation has been identified as the main cause of population decline of several ungulate populations in Etosha National Park in Namibia (Gasaway et al., 1996), roan antelopes (*Hippotragus equinus*) in Kruger National Park in South Africa (Harrington et al., 1999), Thomson's gazelles (*Gazella thomsoni*) and Grant's gazelles (*Gazella granti*) in Masai Mara National Reserve (Sinclair, 1985).

Although competition can be best studied by subjecting small mammals to experimental conditions (Neill, 1975; Park, 1962), past studies have documented competition for food among ungulates in natural conditions (Sinclair, 1985; Singer, 1979; Hudson, 1976). For example, the migratory wildebeests (*Connochaetus taurinus*) of Serengeti-Mara ecosystem are regulated by intraspecific competition (Sinclair, 1985). However, interspecific competition seems to work together with other factors to shape the structure and size of ungulate populations. Sinclair (1985) concluded that the populations of zebra (*Equus burchelli*), topi (*Damaliscus korrigum*), impala (*Aepyceros melampus*), waterbuck (*Kobus defassa*) and warthog (*Phacochaerus aethiopicus*) in the Serengeti-Mara ecosystem are influenced by both interspecific competition and predation.

Habitat changes that reduce or fragment suitable habitat are likely to negatively affect the survival of relevant species. This may occur due to habitat alterations by (i) other species through overgrazing, removal of cover, or trampling of grass by large mammals, (ii) anthropogenic activities such as burning or cutting of vegetation or (iii) natural causes such as bush encroachment. Such habitat changes will ultimately reduce the species range of available or accessible habitat. The inverse relationship between range size and extinction probability (Gaston, 1994) suggests that range contractions will probably amplify the risk of local extinctions of species, including ungulates (Thuiller et al., 2005). The current advancement in geographical information systems (GIS) and readily available spatio-temporal remotely sensed data has made it feasible to assess more accurately habitat changes in multi-spatial landscapes. Understanding such changes is a vital prerequisite for effective habitat management interventions for species recovery.

Extreme weather conditions such as droughts and floods have devastating effects on ungulate populations. They cause death of animals directly through starvation and indirectly by weakening them and thus amplifying their vulnerability to predation, diseases, and parasites (Ogutu et al., 2008). For example, during the 1997 drought and 1997-1998 El Niño floods, there were mass deaths of impalas attributed to anthrax outbreak in Serengeti (Ogutu et al., 2008), and high incidences of livestock diseases in northern Kenya and southern Somali (Little et al., 2001). Understanding the intensity and frequency of such droughts and floods in a region can aid in formulation of management plans and policies that minimize their mortalities. Such policies should promote mobility and flexible access of resources by wildlife through maintaining open dispersal and migratory routes (Ogutu et al., 2008), emergency supply of resources such as water, or construction of ridges to prevent extensive and destructive spread of floods.

Disease outbreaks can have catastrophic effects on wildlife populations. Diseases affect populations directly by killing the infected animals or indirectly by weakening and making them vulnerable to starvation, predation, parasites and intraspecific competition. For example an outbreak of distemper almost wiped out the only remaining population of the black-footed ferret (*Mustela nigripes*) in Philadelphia (Clark, 1989). Also, an anthrax outbreak drastically reduced the roan population in Kruger National Park in 1960s and 1970s (Harrington et al., 1999; Pienaar, 1967). Unfortunately, in many protected areas in Africa there is no long-term veterinary monitoring, which makes it hard to assess the role of diseases unless there are sudden mass wildlife deaths that can be easily linked to disease outbreak.

Bushmeat hunting is a widespread form of resource extraction in tropical forests, nature reserves and parks (Fa et al., 2007). Past studies have shown that game harvests in Africa greatly exceed the wildlife production (Robinson and Bodmer, 1999). The continuing uncontrolled exploitation will inevitably lead to population declines and eventually extinction of many game species. Uncontrolled bushmeat hunting in Africa is influenced by several factors such as food insecurity, poverty, economic market failures, slow development and lack of political and institutional understanding or goodwill (Fa et al., 2007). Bushmeat hunting has been a historical feature in and around Kenya's Ruma National Park (KWS, 2006; Allsopp, 1979; Allsopp, 1972) and therefore a whole chapter of this study (chapter 7) has been devoted to studying this problem with the aim of coming up with long term solutions. Fa et al (2007) recommends that effective solutions should satisfy both wildlife conservation goals and development needs of the human populations involved.

The aforementioned factors influencing ungulate population dynamics affect different ages and sexes differently. This is because vital rates of particular population segments and sexes respond differently to environmental influences (Owen-Smith and Mason, 2005; Owen-Smith et al., 2005). For example, young animals which are normally less adapted are likely to be more affected by short-term abrupt environmental changes than the adults. Owen-smith and Mason (2005) found out that for large mammalian herbivores in Kruger National Park, survival rates of adults vary more over multi-year periods whilst juvenile survival is more prone to annual variability in resources or weather conditions. Pienaar (1969) showed that male ungulates are more vulnerable to lion predation than their female counterparts. Effects of malnutrition seem to affect juveniles (Owen-Smith, 1990) whilst predation can affect either adults or juveniles depending on the predator concerned and the relative size of the prey species (Kunkel and Pletscher, 1999;

Pienaar, 1969). However, many past studies have investigated the influence of these factors on overall abundance as opposed to abundance of different age and sex classes within species. Other long-term studies have been conducted on temperate-zone ungulates in environments lacking predators and therefore the findings cannot be applied to population dynamics of African tropical ungulates living with diverse predators (Owen-Smith et al., 2005). Further long-term studies are needed in this field, as many African ungulates have not been studied. Understanding the variability in age- and sex-specific responses to environmental changes could aid in disentangling the specific causes of population decline in affected species, and consequently ensure implementation of effective population recovery strategies.

In most cases the factors causing population decline act together to reduce populations and isolate the once contiguous populations. Even if some or all of the causes of decline are removed, a small, isolated, and localized population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Soule, 1987). In such populations chance events may dominate the long-term dynamics and fate of a population (Miller and Lacy, 2005). Management interventions for such small populations should entail not only addressing the primary causal factors of species vulnerability but also extra measures such as establishment of other populations in known ranges, protection sanctuaries, translocations, and captive breeding, among others.

Large ungulate populations in RNP are subjected to unique environmental factors, as the park is fenced, isolated and surrounded by land uses such as farming and settlement that are incompatible with wildlife conservation. Potential causal factors include poaching, habitat change, predation, lack of surface water, rainfall fluctuations, fires, interspecific competition, and inadequate management regime. Figure 2.1 presents a flow diagram summarizing the various interactions of how these factors could be driving ungulate population fluctuations in RNP.

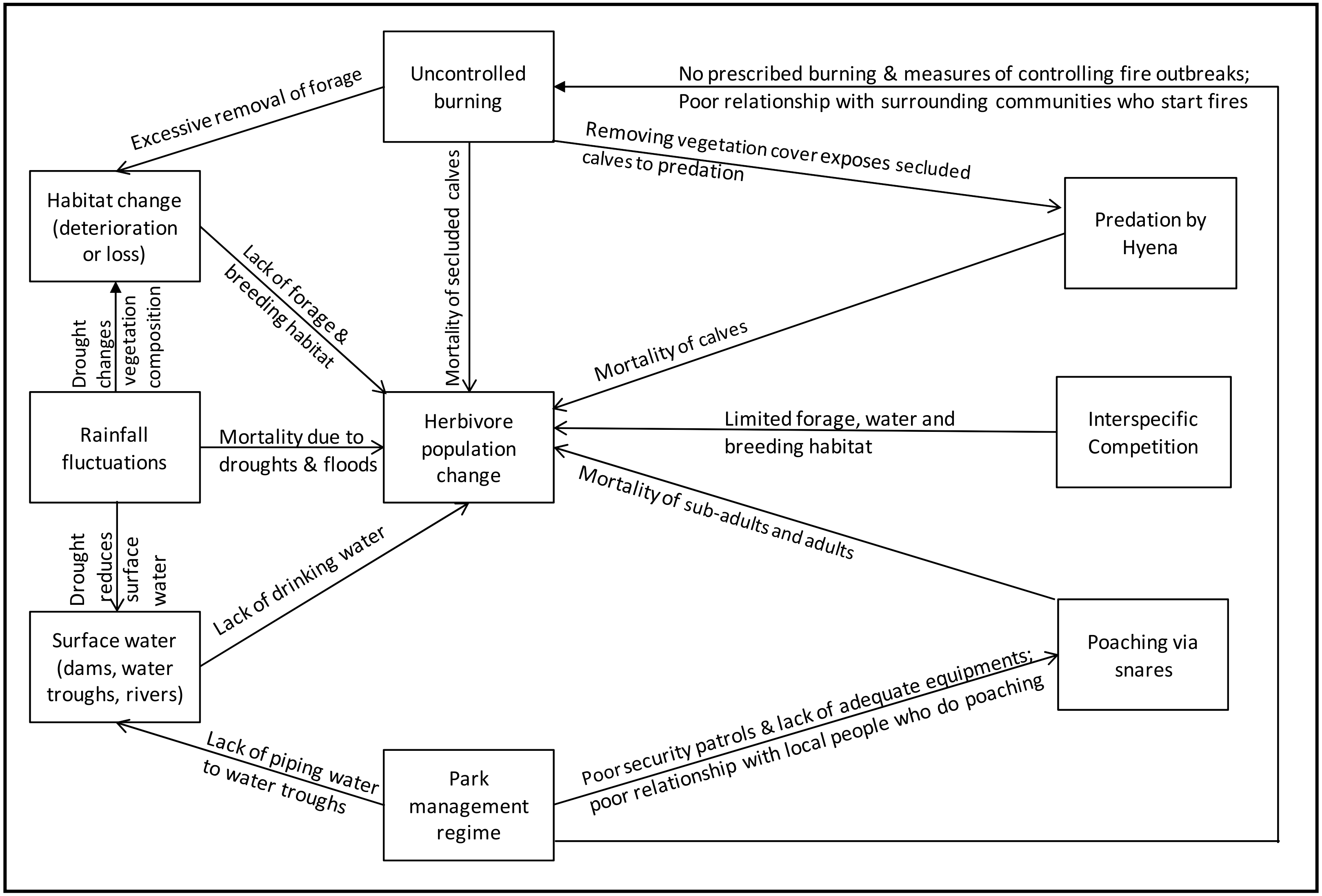


Figure 2.1: Potential factors influencing herbivore population dynamics in RNP and how they interact

Apart from the roan antelope (*Hippotragus equinus langheldi*), five other ungulates were investigated in RNP because past studies have shown that different ungulate species respond differently to environmental changes and perturbations (Ogutu et al., 2008; Owen-Smith et al., 2005). The five ungulates were selected based on availability of data and they include: topi (*Damaliscus korrigum*), bohor reedbuck (*Redunca redunca*), Jackson's hartebeest (*Damaliscus jacksoni*), impala (*Aepyceros melampus*) and oribi (*Ourebia ourebi*). However, not all the factors were considered in this study due to lack of data. This chapter investigates how the 6 ungulate species respond to changes in rainfall, habitat change and competition with other grazers using data for the past 30 years.

2.1.1Research objectives

This chapter aimed at achieving the following research objectives:

- To assess how the vegetation, grazing habitat, rainfall and herbivore populations in RNP have changed over the past 30 years.
- To investigate how the changes in rainfall and grazing habitat have affected the abundance of various antelope species in RNP.
- To investigate if the roan population decline correlates with changes in the population of other competing grazers.

2.1.2 Hypotheses and predictions

This chapter had the following hypotheses:

- The vegetation, rainfall, roan and other antelope populations in RNP have changed over the past 30 years. It was predicted that over the past 30 years the vegetation (and therefore the grazing habitat), rainfall and all antelope populations would have decreased.
- The change in roan and other herbivores in RNP is associated with change in rainfall and grazing habitat. It was predicted that due to the effect of these two factors (i) the population of topi, with their highly synchronized and

seasonal births, would have decreased less than that of other species that calf throughout the year; (ii) the strongly water-dependant roan antelopes would have experienced more population decline than the weakly water-dependant species; (iii) the populations of pure grazers would have decreased more than those of mixed feeders; and (iv) population decline varied among different age and sex groups of the roan antelopes.

- The antelope species in RNP are experiencing interspecific competition. It was predicted that roan population decline was associated with the increase in the population of other antelopes in the park.

2.2 Methods

2.2.1Data collection

This chapter uses data on three aspects: herbivore populations, vegetation types, and rainfall. The following sections describe in detail how each data type was collected.

2.2.1.1 Herbivore population census

The population estimates of herbivores were collected by park personnel once or twice per year from 1976 to 2009, but records for some years were missing. Total ground counts were conducted in 10 animal counting blocks (Figure 2.2) using the method described by Sutherland (1996). Teams counted the animals in the 10 blocks simultaneously using vehicles as well as walking. To minimize counting bias the ground counts were conducted in the morning when most animals were actively feeding. More time was spent in areas with dense vegetation and rock outcrops. The searching exercise was designed to avoid double counting, and brief identification notes of the counted individuals were taken for this purpose. The drive paths and locations of all counted groups were indicated on a map. The data recorded during counts included census block, number of animals in each age group and by sex where feasible.

Animals were visually identified to sex and age classes with the aid of binoculars using combinations of sexually dimorphic physical characteristics, such as dimorphic morphology of the external genitalia, coat colour, age-specific differences in body size, presence, shape and size of horns as described by Sinclair (Sinclair, 1995). For instance, Male impala have horns, but females do not. Contrary, male topi and hartebeest have larger thicker horns than females. The calves of all species were not sexed because the males and females were indistinguishable in the field, except in a few cases. Therefore, animals were classified as young, male sub-adults, female sub-adults, male adults and female adults. However, in some cases there were unidentified and unsexed sub-adult and adult animals. The young age group consisted of calves that had no visible horns. These were usually less than 1 year old. The sub-adults had visible horns but less than the length of the ears. For the adults the horns were fully grown and distinctly curved.

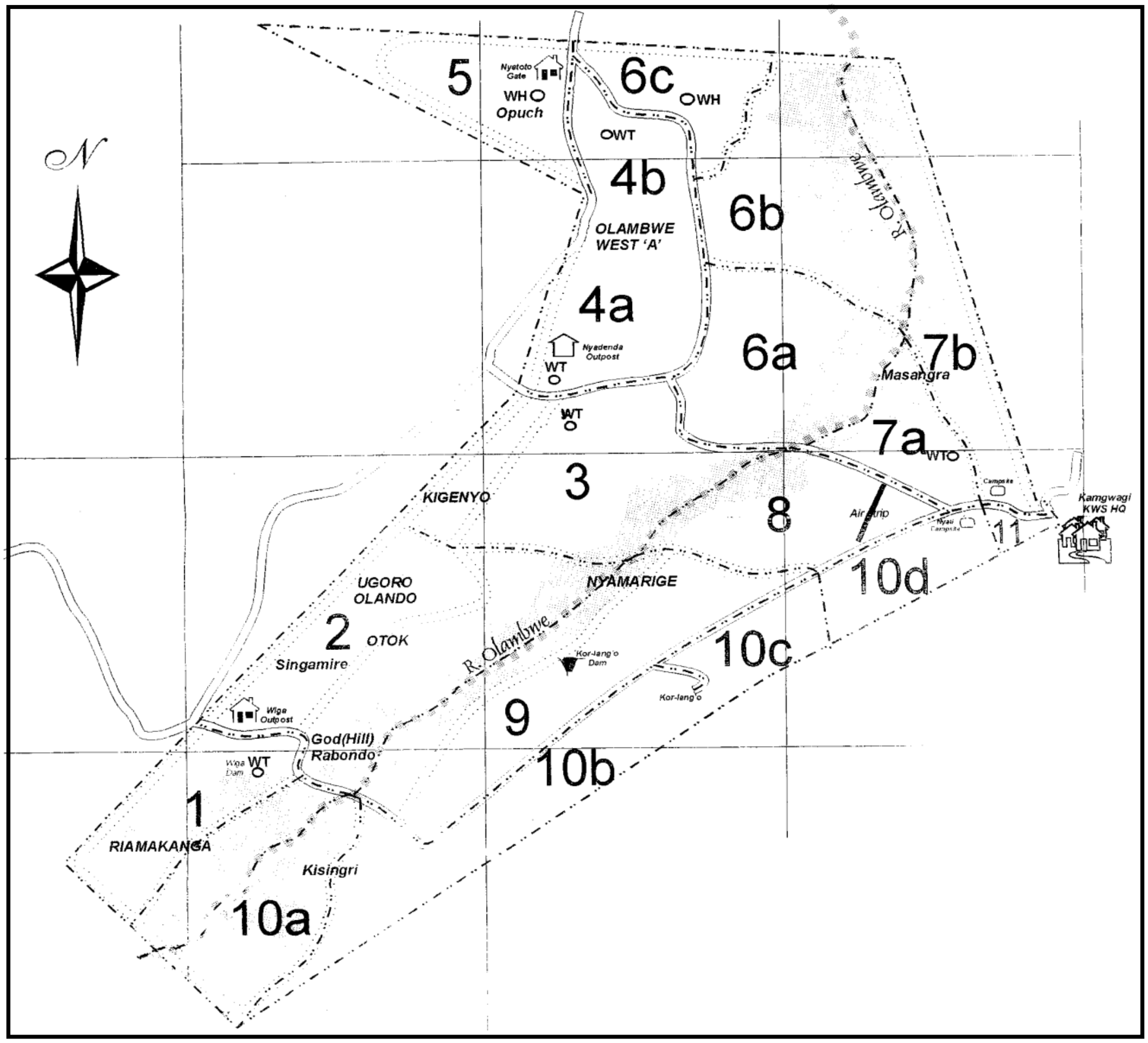


Figure 2.2: Animal counting blocks in Ruma National Park. Block boundaries are marked by Olambwe river, major roads and fire-break tracks.

2.2.1.2 Vegetation mapping

Vegetation mapping was done using the method described by Janssen and Huurneman (2001), which involves six major steps: pre-processing satellite images, visual image interpretation, field data collection (ground truth), field data analysis, digital image classification and map accuracy assessment. Figure 2.3 presents a chart summarising all the steps used in preparations of vegetation maps. Four multi-temporal Landsat imageries were purchased from the Regional Centre for Mapping Resources for Development (RCMRD) in Kenya (Table 2.1). The Landsat imageries were already processed to level 8 according to the National Landsat Archive Production System (NLAPS) (USGS, 2008). This means that the images were systematically corrected, radiometrically and geometrically corrected using the satellite model and platform/ephemeris information, and rotated and aligned to the WGS84 projection. The images were obtained in geotiff format and imported into ILWIS software.

2.2.1.2.1 Image pre-processing

For the purpose of multi-temporal image analysis, atmospheric corrections (distortions due to haze and sun elevation angle) were performed using the techniques described by Janssen and Huurneman (2001). This was necessary because in change detection studies such distortions have an additive or subtractive effect, since by nature multi-temporal images are affected by different atmospheric conditions. Therefore, if images are not corrected for such effects, a change in land cover detected by such studies cannot (totally) be attributed to actual change. In correction for haze, haze contribution for each band was estimated and that value subtracted from all measurements (pixels) in the relevant band. This was done by using a single band (by computing the histogram and subtracting the minimum value from all values). Sun elevation angle correction was performed to have all images corrected for the same illumination angle. The Landsat image for 2005 (ETM05) was used as the reference image since it had the highest sun elevation angle in comparison with the rest of the images. The procedure involves selecting a stable ground cover (for this case a bare rock in the study area) and its reflections plotted for same band, from different dates. A correction factor (r) is calculated by dividing the mean of the reference image by the mean of the image being corrected. This correction factor is used as a multiplier for all pixel values in the image.

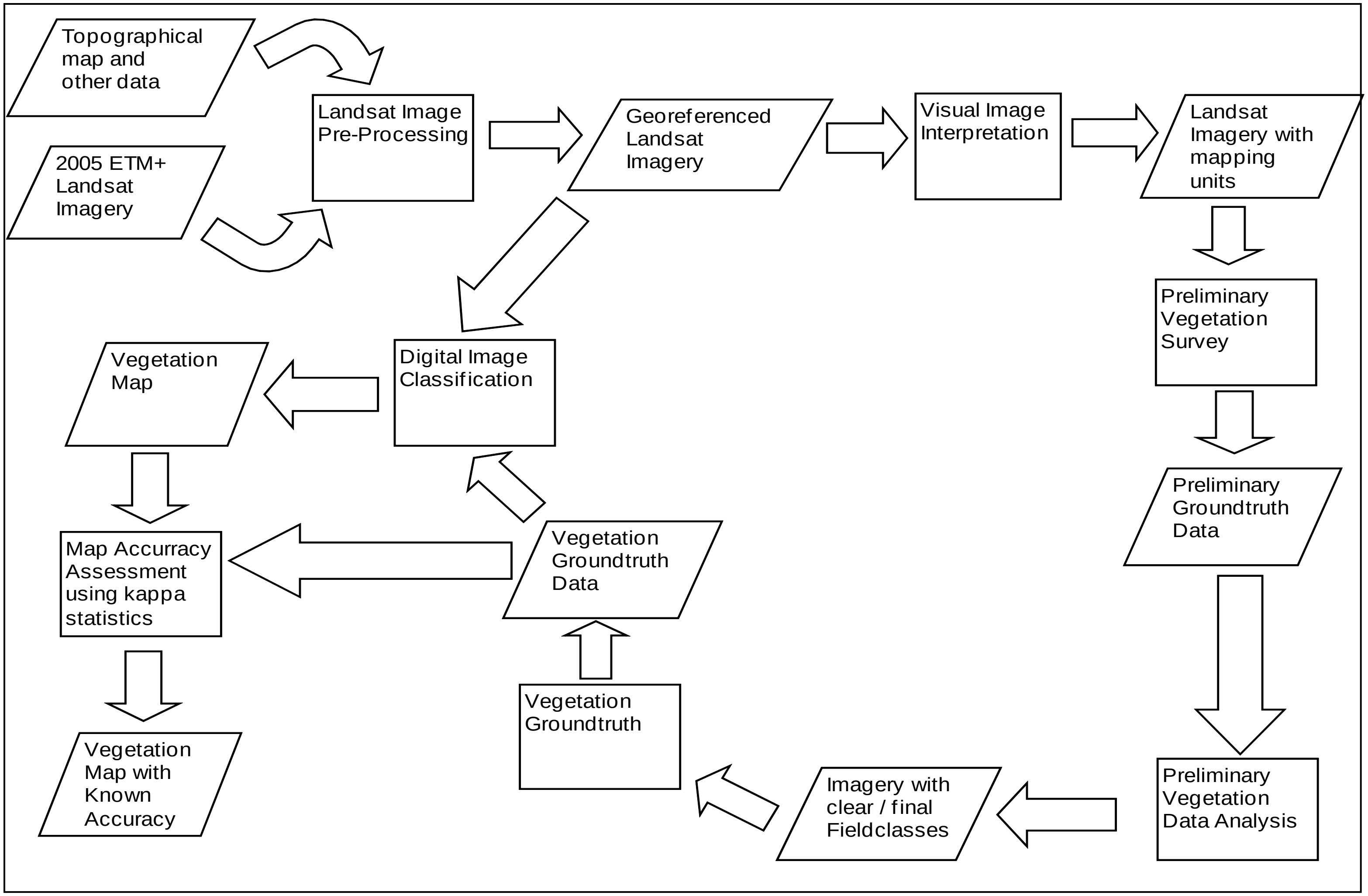


Figure 2.3: A summary of steps used in preparation of vegetation maps using ILWIS Academic 3.6. The parallelograms indicate data or end products, the rectangles indicate processes and the arrows show the sequence of activities.

Table 2.1: The metadata for the Landsat Images used in vegetation mapping

Landsat Imagery	Sensor	Satellite	Bands	Resolution (meters)	Date of acquisition
MSS73	Multispectral Sensor (MSS)	Landsat 1	4	57	01/02/1973
TM86	Thematic Mapper (TM)	Landsat 5	7	Band1-5&7(28.5) Band 6 (57)	08/03/1986
ETM01	Enhanced Thematic Mapper (ETM+)	Landsat 7	8	Band1-5&7(28.5) Band 6 (57) Band 8 (14.25)	05/02/2001
ETM05	ETM+	Landsat 7	8	Same as above	21/04/2005

A Coordinate system was created using the ILWIS software (ILWIS, 2009) with the following specifications: Name = KenyaRuma; Projection = UTM Zone 36; Datum = Arc 1960; Datum Area = Kenya; Ellipsoid = Clarke 1880. This coordinate system is the same as that used in Kenya (study area) and hence GPS coordinates collected from the field could match with those in the Landsat images and existing topographical maps. A Georeference corners object was created with the following specifications: Name = KenyaRuma; Spatial resolution (pixel size) = 30m; Minimum X and Y = (632000, 9920040) and Maximum X and Y = (650000, 9937350). The georeference corners object formed a baseline layer of the area of interest (study area) where all other maps should fit in. All the images were georeferenced using the KenyaRuma coordinate system and resampled into the KenyaRuma georeference object

2.2.1.2.2 Vegetation ground truthing

Before the vegetation ground truth, the 2005 Landsat ETM+ image was visually interpreted to define the mapping units for use in the field. Mapping units were delineated based on image interpretation elements such as colour, shape, size and texture as described by Janssen and Huurneman (2001). Ten mapping units were identified using the above image elements. Ground truthing was done using stratified random sampling technique as described by Westinga (2001). However, a preliminary vegetation survey was performed first to help in implementation of the sampling design. Five samples per mapping unit were selected at random for the preliminary study and data analyzed using a correlation matrix to assess homogeneity of mapping units. During the pilot study, the researcher learned how to measure plant heights using a Sunto Hypsometer as described by Kangas and Maltamo (2006). Training was done on how to measure vegetation canopy cover using a forest spherical densiometer using the guidelines given by Lemmon (1957). The forest densiometer is suitable for measuring the percentage canopy cover of a single vegetation layer such as artificial plantation forest. Since natural vegetation in the park is multi-layered, the densiometer could not be used to measure the canopy cover in all the vegetation layers. Therefore, the knowledge and experience gained from the forest densiometer was used in this study to estimate the percentage cover in the different vegetation layers. Estimation of vegetation canopy cover has been shown to be accurate when done by trained or experienced observers (Murphy and Lodge, 2002).

Preliminary vegetation survey and characterization identified 10 mapping units as distinct vegetation classes in RNP. In each mapping unit, 30 circular sample plots were selected at random and located in the field using a GPS. The plots ranged in radius from 10m to 30m depending on the vegetation type of the mapping unit. Circular plots were used because they are easy and convenient to estimate in the field and they are also recommended by Kangas and Maltamo (2006) for fieldwork in natural vegetation where the rows of trees are not distinct. For each selected sample plot, the following data were recorded: percentage cover and average height of different vegetation layers (trees, shrubs, herbs and grasses) and dominant plant species per vegetation layer. It was made sure that the selected random points were at least 150m apart and away from the mapping unit boundary. This was to compensate for any GPS errors, georeference error and ensure that points are separated by at least 1 pixel.

After analysis of the field data from vegetation ground truth, the 10 mapping units were assigned the following vegetation names based on percentage canopy cover, dominant species and vegetation height: grassland, dwarf shrub grassland, sparsely shrub grassland, shrub grassland, thin-wooded grassland, wooded grassland, sparsely wooded grassland, woodland, bushland and forest. These vegetation names are derived from the recommendation of the East African Range Classification Committee (Pratt and Gwynne, 1977) with a few amendments to suit the study area. Similar vegetation names were used to describe vegetation of Masai Mara National Reserve (Broten and Said, 1995). Table 2.2 gives a detailed criterion used in classifying the vegetation. Each vegetation type is also described in more details below.

Table 2.2: Criterion for vegetation classification in Ruma N. Park. N.A stands for 'Not Applicable', meaning that the canopy cover for that vegetation layer is negligible

Structural type		Percentage Cover			
		Trees (Height>5m)	Shrubs (Height 1 - 5m)	Dwarf shrubs (height<1m)	Grass & Herbs
I	Forest	>60	N.A.	N.A.	N.A.
II	Bushland	15 – 25	20 - 40	N.A.	N.A.
III	Woodland	25 – 50	<10	N.A.	<40
IV	Grassland	<2	<2	<2	>75
V	Shrub grassland	<5	10 - 20	<2	>50
VI	Sparsely shrub grassland	<2	2 - 10	<2	>60
VII	Dwarf shrub grassland	<5	<5	10 - 20	>60
VIII	Wooded grassland	10 – 20	<5	<2	>50
IX	Thin-wooded grassland	10 - 20 (Thin trees)	<5	<2	>50
X	Sparsely wooded grassland	2 – 10	<2	<2	>60

I. Forest

Land covered by closed stand of trees of one or more storeys, with an interlaced upper canopy cover of more than 60% and rising to 10 – 20 m in height. The ground cover is mainly bare with a few herbs, shrubs, lianas and epiphytes. This vegetation layer never experiences fire outbreaks throughout the year. The tree species found here are varied and mainly evergreen.

II. Bushland

Land supporting an assemblage of trees and shrubs, often dominated by plants of shrubby habit but trees more conspicuous, with layered canopy, not exceeding 15m in height except for occasional emergents, and a total canopy cover of more than 30%. The trees comprise of 15 – 25% of the canopy cover whilst the shrubs comprise of 20 – 40%. The trees are mainly dominated by Acacia species such as *Acacia seyal* and *Acacia tortilis* whilst the shrubs are of diverse species but the dominant are Rhus, Grewia and Euphorbia species. Fires are infrequent in this vegetation type and the ground cover is poor; but epiphytes can occur.

III. Woodland

Land supporting a stand of trees, up to 20m in height, with open or continuous but thickly interlaced canopy, and a canopy cover of between 25 – 50%. The tree found here are mainly dominated by Acacia species such as *Acacia seyal* and *Acacia tortilis*. Shrubs, if present, contribute less than 10% of the canopy cover. Grasses and other herbs dominate the ground with a total cover of less than 40%. This vegetation type is affected by periodic burning.

IV. Grassland

Land dominated by diverse grass species and occasionally other herbs with a total ground cover of more than 75%, sometimes with widely scattered or grouped trees and shrubs, the canopy of which does not exceed 2%. This vegetation type is frequently affected by periodic fires. The dominant grasses include: Setaria, Themeda, and Hyparrhenia species.

V. Shrub grassland

Grassland with scattered or grouped shrubs, the shrubs always conspicuous, but having a canopy cover of between 10 - 20%, and ground grass cover of more than 50%. The dominant shrubs are Rhus, Grewia and Maerua species whilst dominant grasses include Setaria, Themeda, and Hyparrhenia species. It is often subjected to infrequent burning.

VI. Sparsely shrub grassland

Grassland with very scattered or grouped shrubs, the shrubs always conspicuous, but having a canopy cover of between 2 - 10% and ground grass cover of more than 60%. Dominant shrub and grass species are the same as those of the shrub grassland. It is often subjected to periodic burning.

VII. Dwarf shrub grassland

Grassland set with *Acacia drepanolobium* dwarf shrubs not exceeding 1 m in height, sometimes with widely scattered larger shrubs or stunted trees. The shrubs canopy cover is between 10 – 20 % while the ground grass cover is more than 60%. Fire outbreaks are rare in this type of vegetation. It can also be termed as *Themeda triandra* – Setaria – *Acacia drepanolobium* shrub grassland

VIII. Wooded grassland

Grassland with scattered or grouped trees, the trees always conspicuous, but having a canopy cover of less than 20% and ground grass cover of more than 50%. Most of the trees are mature. Most of it consists of *Themeda triandra* – Balanites wooded grassland or *Themeda triandra* – Combretum wooded grassland. Other dominant grass species are Setaria, and Hyparrhenia. It is often subjected to periodic burning.

IX. Thin-wooded grassland

Grassland with scattered or grouped thin trees, the trees always conspicuous, but having a canopy cover of less than 20% and ground grass cover of more than 50%. This vegetation type is similar to wooded grassland except that all the trees are young, thin and black stemmed Acacia species. This vegetation type is greatly influenced by frequent fires. It is mainly found near park boundaries as a result of frequent fires crossing from the community land into the park.

X. Sparsely wooded grassland

Grassland with scattered or grouped trees, with a canopy cover of between 2-10% and ground grass cover of more than 60%. Most of the trees are mature and mainly *Balanites aegyptica*. The dominant grass species are the same as those of the wooded grassland. It is often subjected to periodic burning.

2.2.1.2.3 Vegetation changes

To assess how the vegetation has changed over the past 30 years, the Landsat imageries of 1973, 1986, and 2001 were digitally classified into maps using the same procedure as that of baseline image of 2005. However, the Landsat images of 1973 and 1986 could not be classified into the same 10 vegetation classes as those of 2001 and 2005, due to differences in the sensors used in different years. The 1973 Landsat used the Multispectral Sensor (MSS) whilst the 1986 Landsat used the Thematic Mapper (TM). The other two Landsat images of 2001 and 2005 used the Enhanced Thematic Mapper (ETM+). Therefore, for the purpose of assessing the change in the habitat that is relevant to the herbivore species studied, all the four maps were reclassified into two broad vegetation classes: the grazing habitat (all grassland types) and non-grazing habitat (forest, bushland and woodland). These two vegetation classes were adequate because the hypothesis in question was to investigate if decrease in grazing habitat was associated with decline in the population of grazing herbivores in Ruma National Park.

2.2.1.3 Rainfall measurements

Rainfall was obtained from park records that were collected from daily gauges located at the park headquarters. Data was available from 1976 up to 2005. Monthly means were computed for the 30 year-period and used to define four rainfall seasons: long wet season (March to June), short wet season (September to November), short dry season (July and August), and long dry season (December to February) as shown in Figure 2.4. The year starts from March when the animals in this study were counted. Apart from these four seasons the park rainfall was also summarized into two other components: annual and prior rainfall. The annual rainfall consisted of rainfall from March to February whilst the prior rainfall consisted of cumulative annual rainfall for 5 years preceding the animal count year. The 5 years were used because Owen-Smith and Mills (2006) showed that the effect of prior rainfall on roan antelopes is highest about 5 years prior to the count year. Prior rainfall could have a cumulative lagged influence on the state of the vegetation and hence, on productive capacity of the vegetation (Owen-Smith and Mills, 2006). This will consequently affect the rate of population growth and hence population size.

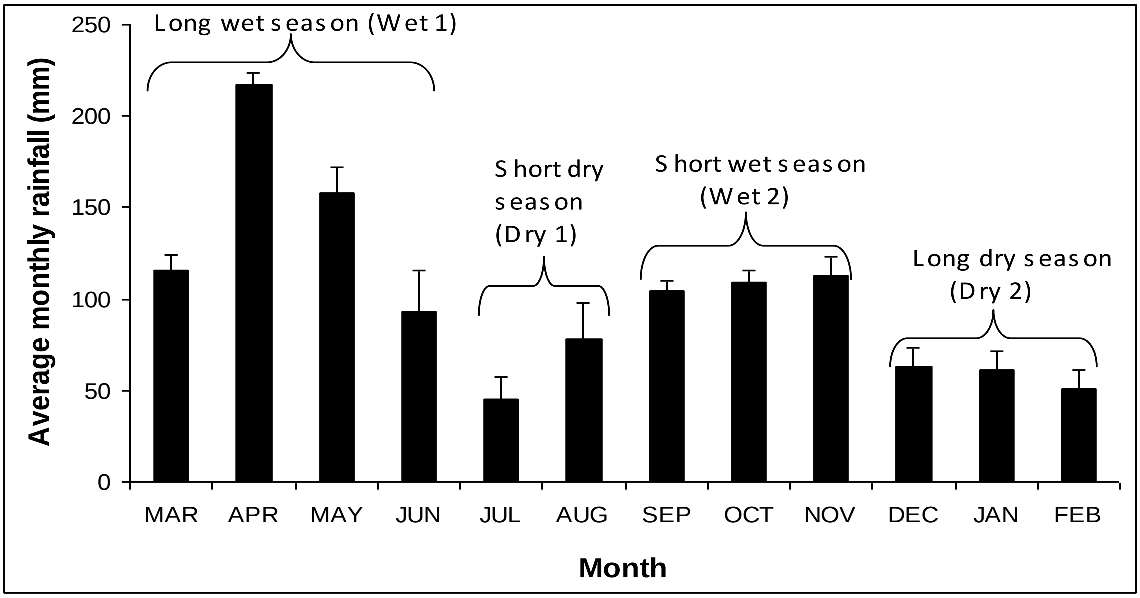


Figure 2.4: Changes in mean (± SE) monthly rainfall for 30 years (1976 to 2005) in RNP. Seasonal rainfall was divided into four seasons.

2.2.2 Statistical data analysis and modelling

Data analysis and modelling involved relating abundance to the various components of rainfall, vegetation and assessing how various herbivore populations co-vary.

Exploratory data analysis was done using graphs, correlation and regression analyses. Statistical data analysis was carried out using multivariate techniques and generalized linear models.

2.2.2.1 Vegetation map accuracy assessment

It is generally recommended that the accuracy of a map be tested using an independent data set (Mather, 1999). To achieve this, the original data set of 300 ground truth points was split into two data sets: a training set and a testing set. Thirty percent of the original data was set apart as testing data set (that is, 90 points) and the rest used as the training data set during the supervised digital image classification process. Map accuracy was assessed using the kappa statistics (Bishop et al., 1975) with the formula:

$$K = \frac{\mathrm{N} \sum_{\mathrm{i=1}}^{\mathrm{r}} \mathrm{X_{ij}} - \sum_{\mathrm{i=1}}^{\mathrm{r}} (\mathrm{X_i X_j})}{\mathrm{N}^2 - \sum_{\mathrm{i=1}}^{\mathrm{r}} (\mathrm{X_i X_j})}$$

Where, K = Kappa statistic

N = total number of samples in the confusion matrix

X_i = sum of row i (ground truth field class i)

X_j = sum of column j (vegetation class j of final map legend)

X_{ij} = diagonal element for row i and column j

r = number of rows

Confidence limits for map accuracy assessment were also computed using Jensen's (1996) formula:

Confidence limit $= P \pm [Z\sqrt{\frac{PQ}{N}} + \frac{50}{N}]$

Where, P = classification overall accuracy

Q = overall classification error (i.e. 100 – P)

Z = z score corresponding to α error (derived from standard normal curve)

N = total number of pixels used in the accuracy assessment

Apart from the overall accuracy of the map, the errors of omission and commission were also computed. Errors of omission are committed when patterns that are really class i become labelled as members of some other class whilst errors of commission occur when pixels that are really members of some other class become labelled as members of class i (Mather, 1999).

2.2.2.2 Multivariate techniques

Multivariate techniques have been widely used to analyse ecological data (Zuur et al., 2007). These methods have proven to be particularly useful in extracting the underlying data structure and relating this to explanatory (environmental) variables (Van den Brink et al., 2003). They provide a useful framework for identifying the important environmental variables driving community changes. Multivariate analysis is able to produce a diagrammatic representation of complex systems as biplots (two-dimensional scatter plot) or triplots (three-dimensional scatter plot) which display observations in relation to the attributes that characterise them. Ordination techniques are capable of summarising very complex responses because they are not restricted to a single dimension (Van den Brink et al., 2003). The advantages of using ordination methods are that (i) a large number of variables is reduced into a smaller number; (ii) it makes it easier to interpret complex multivariate data and to communicate the results effectively; and (iii) it is useful in discovering the structure in multivariate data (Van den Brink et al., 2003).

The ordination methods used in this study included Principal Component Analysis (PCA), Redundancy Analysis (RDA) and Detrended Correspondence Analysis (DCA). The decision tree advocated by Ter Braak and Smilauer, (2002) was used to guide the choice of the ordination method to use in this study, that is, whether to use linear or unimodal ordination methods. Linear ordination methods (such as PCA and RDA) utilise a species response model where the species abundances are seen to change linearly over short sections of the ordination axis, and implicitly any environmental gradient. Unimodal ordination methods (such as Canonical Correspondence Analysis (CCA) and Detrended Correspondence Analysis (DCA)) are based on a species response model that assumes a symmetrical 'bell shape' distribution of species abundances along the gradient of the axes (Ter Braak and Smilauer, 2002). These authors recommend that preliminary data analysis be done on the response variable using DCA and if the length of the first gradient is less than 3, then linear ordination methods should be used. Also if the response variable data consists of absolute abundance, linear methods are recommended as opposed to unimodal methods that are suitable for relative abundance (Van den Brink et al., 2003).

Preliminary DCA analysis on the herbivore abundances for a period of 30 years (1976 – 2005) showed that the length of the first gradient was 0.2751. Therefore, the linear methods (PCA and RDA) were employed in this study. PCA is used to analyse species data without explanatory variables whilst RDA is used to analyse both response and explanatory variables (Zuur et al., 2007). PCA was used to assess the association of the fluctuation of population abundances of 6 herbivore species. RDA was used to analyze linear relationships between the herbivore species and environmental variables (rainfall components and vegetation). Apart from interpretation of the PCA biplots and RDA triplots, significance tests were carried out to identify those significant environmental variables explaining the variation in the herbivore populations.

2.2.2.3 Generalized linear models (GLM)

Statistical modelling was carried out in R software for statistical computing (R Core Team Development, 2007) using the negative binomial regression, which has been shown to yield good results with overdispersed data (Crawley, 2007). Preliminary analysis showed that the data were overdispersed, that is, the residual deviance was far greater than the degrees of freedom. Before selection of the negative binomial regression several other models were explored. First of all, models were fit for each species using a generalized linear model with a Poisson error distribution, which was discarded because the data showed overdispersion. Secondly, a generalized linear mixed model with a penalized quasi-likelihood (glmmPQL) was used to compensate for the overdispersion and also to include the effect of year of data collection as a random effect factor for accounting for temporal autocorrelation. Results showed that the year of data collection was not a significant factor in explaining the change in herbivore populations, implying there was no temporal autocorrelation. A comparison of models developed using the negative binomial regression and the glmmPQL yielded similar results. However, the former was preferred over the latter because it includes an element of assessing spatial aggregation, that is, theta. Theta can be used to assess the differences in aggregation of animal groups in different seasons. Another disadvantage of PQL is that since it computes quasilikelihood rather than a true likelihood, it should not be used for inference with likelihood-based methods (such as hypothesis testing and AIC ranking) (Bolker et al., 2009; Pinheiro and Chao, 2006). Therefore, in this study, the negative binomial regression was used to analyze the effect of rainfall components (long wet, short wet, long dry and short dry rainfall seasons) and vegetation change on the population fluctuations of 6 antelopes: roan, topi, reedbuck, hartebeest, impala and oribi. A more thorough review of statistical methods is presented in chapter 5.

2.2.2.4 Model assessment

A bootstrapping technique described by Manly et al., (2002) was used to validate the negative binomial regression model results. The idea behind bootstrapping is that when the only information available about a statistical population consists of a random sample from that population, then the best guide to what might be obtained by resampling the population is provided by resampling the sample (Manly et al., 2002). In this study, the technique was performed by resampling (with replacement) the population data to construct bootstrap samples, by leaving out two data values at a time. The bootstrap model was run 999 times and its coefficients used to assess the variability and bias in the coefficients of the original model.

2.3 Results

2.3.1 Vegetation map of RNP

Vegetation mapping produced a map of RNP (Figure 2.5) with 10 vegetation classes: grassland (4%), dwarf shrub grassland (6%), sparsely shrub grassland (10%), shrub grassland (9%), thin-wooded grassland (12%), wooded grassland (14%), sparsely wooded grassland (7%), woodland (13%), bushland (12%) and forest (13%). Map accuracy assessment using kappa statistics a high overall accuracy of 85% (95% confidence limits of 83.05% and 86.95%). The error of omission and commission were 12% and 10%, respectively.

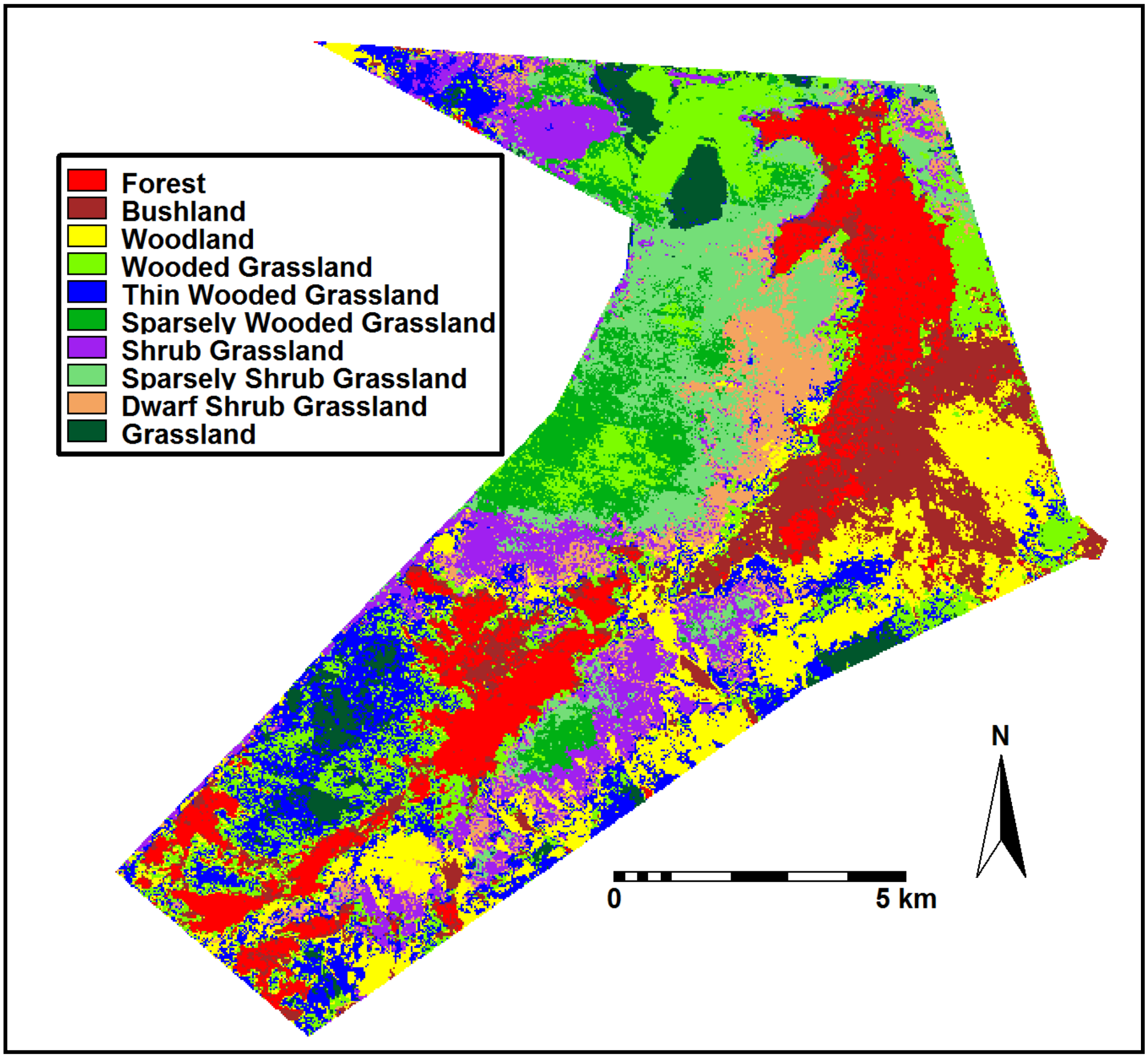


Figure 2.5: Vegetation map of Ruma National Park derived from 2005 ETM+ Landsat Image and updated with ground truth of 2008

2.3.2 Exploratory pattern seeking

2.3.2.1 Vegetation changes

Regression analysis using estimates from Landsat imageries showed that the grassland habitat decreased significantly ($R^2 = 0.913$, $p = 0.003$) from about 9750 hectares in 1976 to 7829 hectares in 2005. Due to this decrease, the roan habitat that was largely interconnected in the 1970s was consequently split into habitat patches interspersed with unpalatable forest thickets, bushes and woodlands (Figure 2.6). This decline, which was greatest between 1986 and 2001, seems to have been triggered by the long period of below-average rainfall that occurred from 1983 to 1988 as shown in section 2.3.2.2. Correlation analysis indicated a significant positive association ($r = 0.771$, $n = 15$, $p = 0.017$) between the decrease in grassland habitat and decline in roan population.

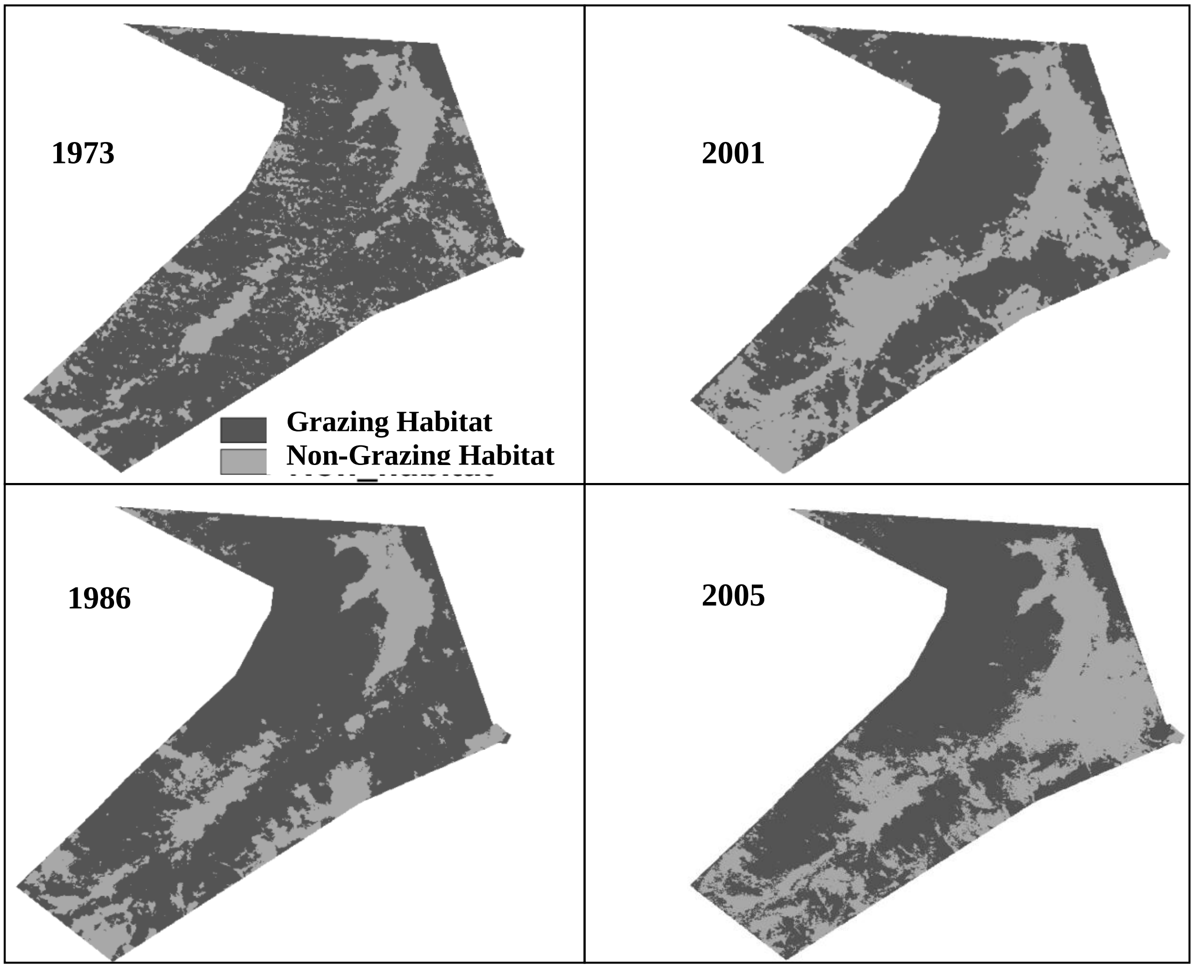


Figure 2.6: The changes in grassland habitat in RNP from 1973 to 2005. The grazing habitat was a combination of all grasslands whilst non-grazing habitat consisted of forest, bushland and woodland.

2.3.2.2 Rainfall fluctuations

Annual rainfall records (Figure 2.8) show that there were several years with poor rains in 1979 -1981, 1985-86, 1987-88, 1999 - 2001 and 2004-05. Also, during the same period (1976-2005) there were three wet years between 1981 and 1983 and in 1989-90. The fluctuations in the prior rainfall for the past 5 years before the animal count year followed a similar pattern to that of annual rainfall but with a lowest value in 1987-88 and a peak value in 1992-93 (Figure 2.7). A closer look at the seasonal rainfall records revealed diverse fluctuations in wet and dry season rainfall across the study period (Figure 2.8). With reference to the long wet season (Wet 1), there were three years with very low rainfall in 1985-86, 1987-88 and 2004-05 and five years with very high rainfall in 1990-92, 1994-95, 1998-99, and 2002-03. For the short wet season (Wet 2) there were four years with poor rains between 1978-81, 1998-99 and 2000-01. Likewise, for the short dry season (Dry 1), 2000-01 had exceptionally low rainfall whereas 1981-83 had relatively high rainfall. Also, for the long dry season (Dry 2), there were three years of poor rainfall in 1980-81, 1982-83 and 1998-1999 as well as three very wet years in 1978-79, 1992-93 and 2000-01.

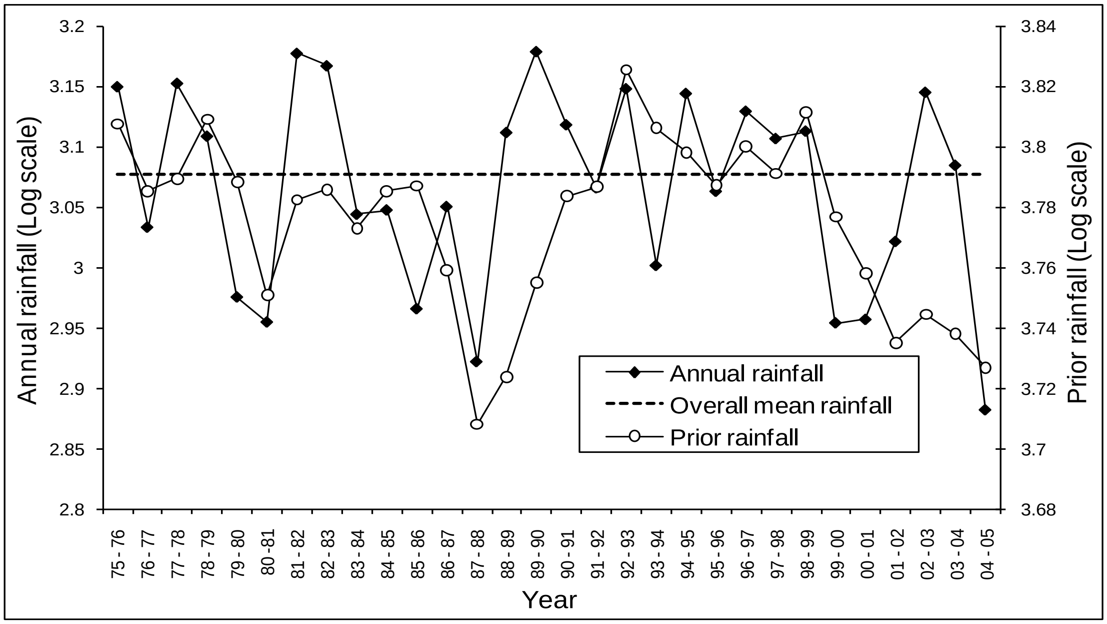


Figure 2.7: Changes in annual (March - February) rainfall (log scale) and prior rainfall for the past 5 years before the animal count year in RNP. The overall mean rainfall was computed using rainfall for 30 years (1976 – 2005).

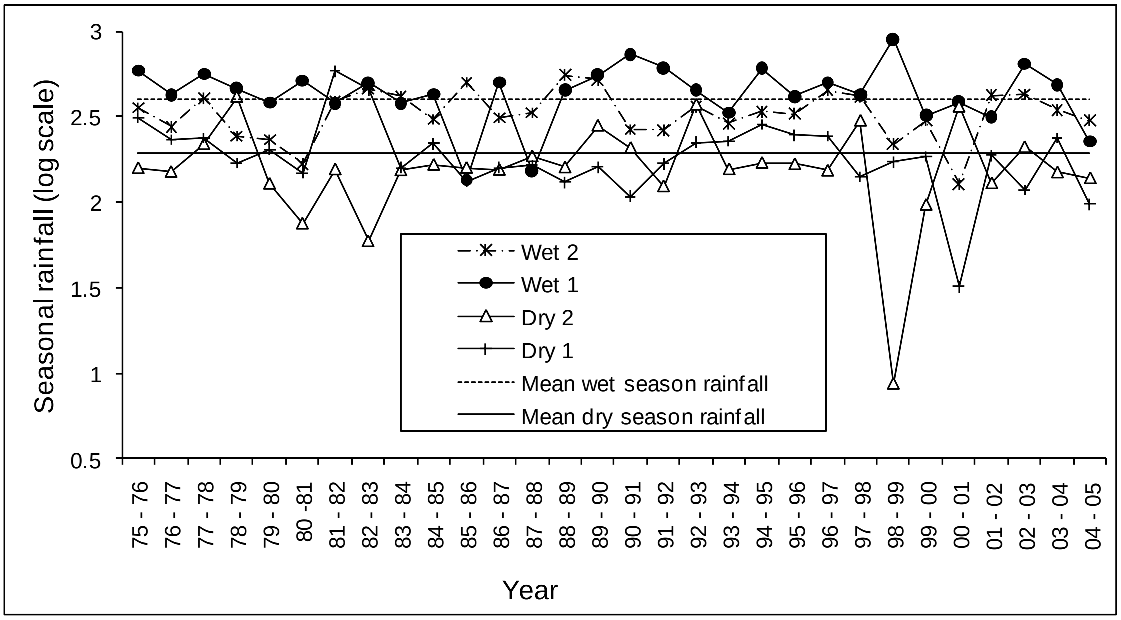


Figure 2.8: Changes in seasonal relative rainfall (log scale) in RNP. The seasonal rainfall was grouped into four seasons: Wet 1, Wet 2, Dry 1 and Dry2. Details of abbreviations are given in Figure 2.4.

Regression analysis on the rainfall fluctuations for the 30 years indicated an insignificant overall decrease in the annual rainfall, prior rainfall, long wet season rainfall, short wet season rainfall, long dry season rainfall but a significant overall decrease in the short dry season rainfall ($R^2 = 0.122$, $p = 0.029$). Correlation analysis showed significant positive correlation between the annual rainfall and short dry season rainfall ($r = 0.876$, $n = 30$, $p = 0.002$). There was also considerable but insignificant positive correlation between the prior rainfall and long dry season rainfall ($r = 0.540$, $n = 30$, $p = 0.134$) and annual rainfall ($r = 0.558$, $n = 30$, $p = 0.118$) as well as a negative correlation between the long dry season rainfall and short dry season rainfall ($r = -0.429$, $n = 30$, $p = 0.250$).

2.3.2.3 Herbivore population changes

Regression analysis of herbivore populations in RNP showed different changes from 1976 to 2008, with one species indicating an overall increase and the rest showing overall decrease (Figure 2.9). Topi showed an insignificant overall increase in population but with small declines in population in 1986 and 1993. There was an overall significant decline in the populations of roan antelopes ($R^2 = 0.477$, $p = 0.029$) and impala ($R^2 = 0.506$, $p = 0.042$). However, there was a slight increase in roan population from 1993 to 2004 and slight increase in impala population from 1998 to 2004. There was insignificant overall decline in the populations of reedbuck, hartebeest and oribi. The population of reedbuck and hartebeest showed similar fluctuations with major population increases occurring in 1989 and between 1995 and 1998. The population of oribi was steady from 1976 up to 2005 beyond which it declined precipitously. It is worth noting that for the declining herbivore populations, it is only the roans that started declining continuously from as early as 1976 and had the smallest population in RNP for almost 30 years.

Some herbivore populations were positively correlated while others were negatively correlated with each other in the park. Roan antelopes were significantly positively correlated with impala ($r = 0.705$, $n = 15$, $p = 0.023$) and almost significantly negatively correlated with reedbuck (r = -0.620, n = 15, p = 0.056). Reedbuck were significantly positively correlated with hartebeest (r = 0.721, n = 15, p = 0.023) and significantly negatively correlated with topi (r = -0.661, n = 15, p = 0.044). Hartebeest were significantly positively correlated with oribi (r = 0.716, n = 15, p = 0.020) and significantly negatively correlated with topi (r = -0.686, n = 15, p = 0.029).

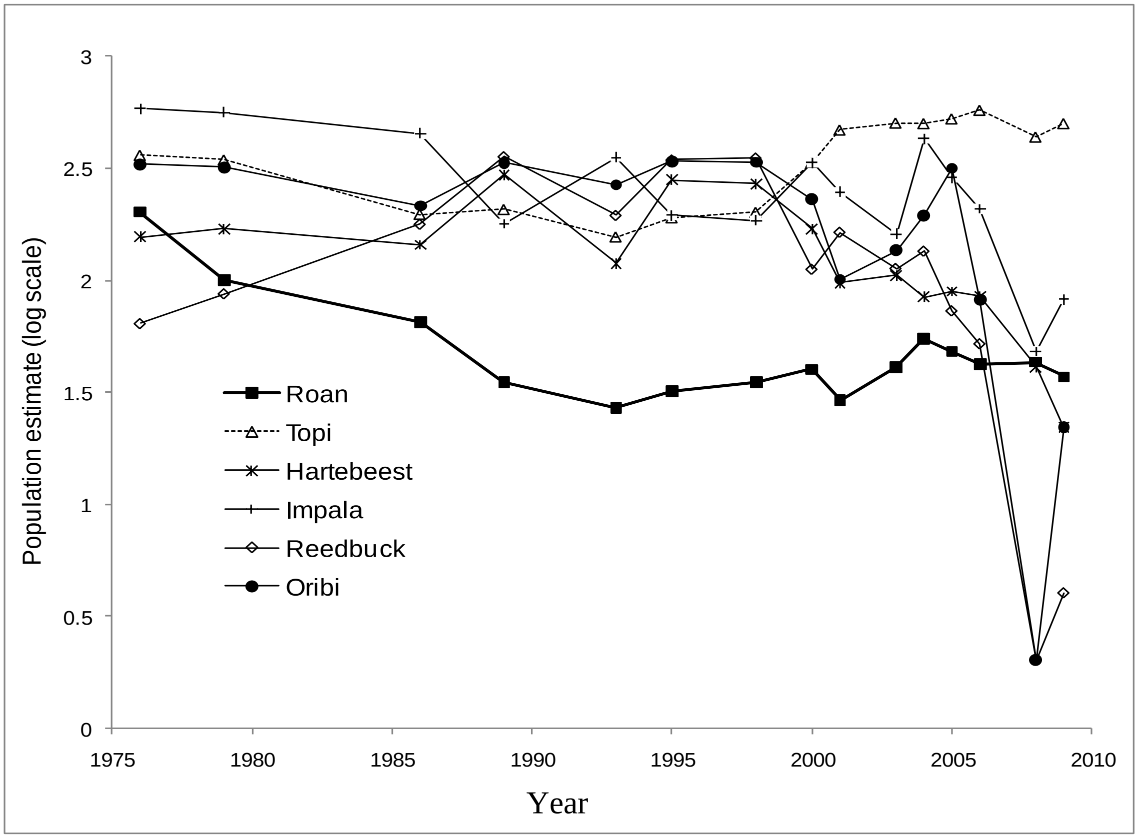


Figure 2.9: The changes in population (log scale) of roan, topi, impala, reedbuck, hartebeest and oribi in RNP

2.3.2.4 Roan population age and sex structure

All the roan age groups and sexes declined from 1976 to 2008 as shown in Figure 2.10. There was a significant decrease in roan juveniles (R^2 = 0.561, p = 0.010), sub-adults (R^2 = 0.577, p = 0.013) and adult males (R^2 = 0.202, p = 0.040) but an insignificant decrease in adult females and total adults. However, the regression results for decrease in adult females ($R^2 = 0.434$, $p = 0.075$) and total adults ($R^2 = 0.388$, $p = 0.061$) were almost significant. There was also an insignificant overall decrease in the roan calf:cow ratio. A critical look at the calf:cow ratio revealed that it only seriously declined in 1986 and 2004 but was very high between 1993 and 1998, a period when the total roan population was the lowest (Figure 2.11).

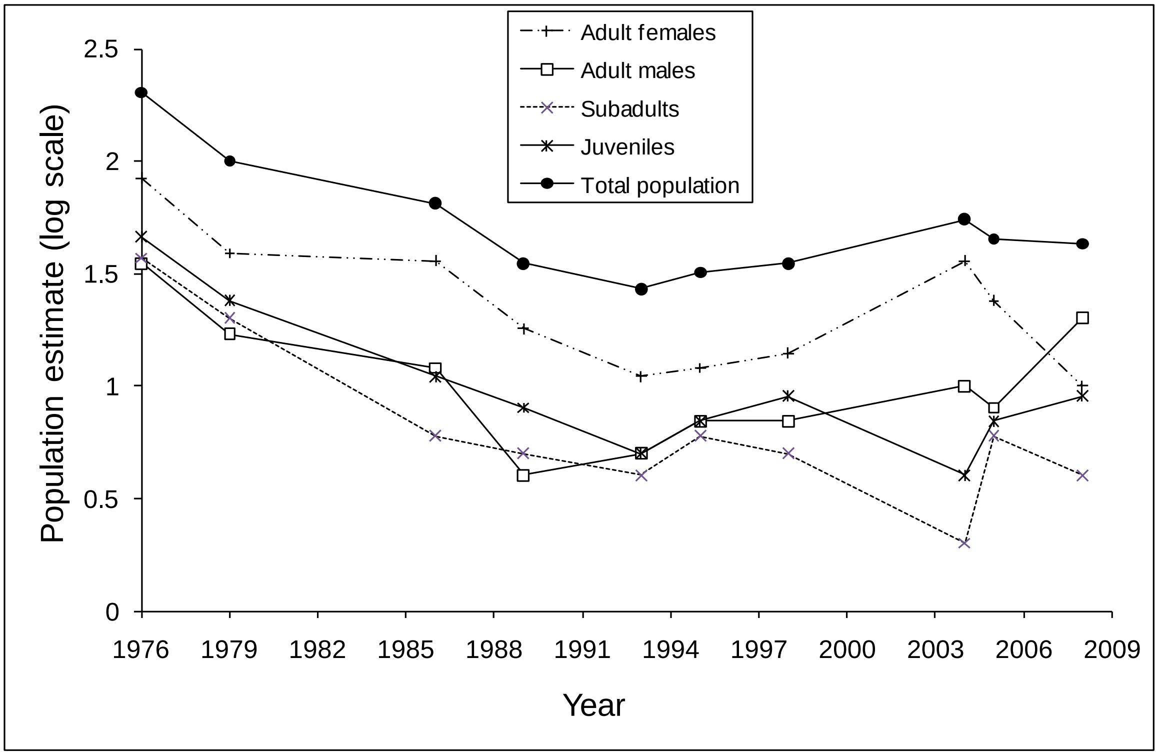


Figure 2.10: Changes in roan population of different age and sex groups from 1976 to 2008 in RNP

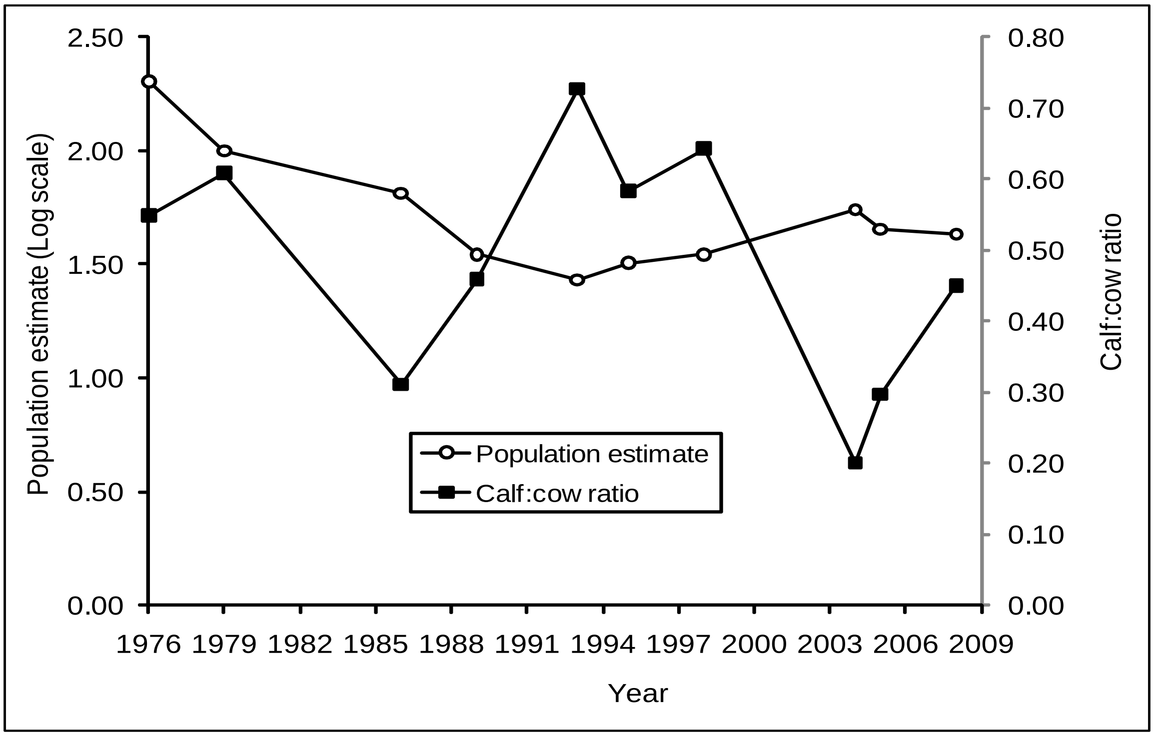


Figure 2.11: Comparison of changes in the roan population (log scale) and calf:cow ratios between 1976 and 2008 in RNP

2.3.3 Diagnosing the causes of herbivore population decline in RNP

Principal component analysis (PCA) showed that the first and second principal components explained a total of 84% of the variation in the herbivore populations in RNP from 1976 to 2005. A PCA correlation biplot showed that topi are closely associated with impala (Figure 2.12). The roan is also slightly associated with the topi and impala. The PCA1 had strong positive loadings from impala, topi and roan, and strong negative loadings from reedbuck and hartebeest. The PCA2 had strong positive loadings from Oribi, roan and hartebeest.

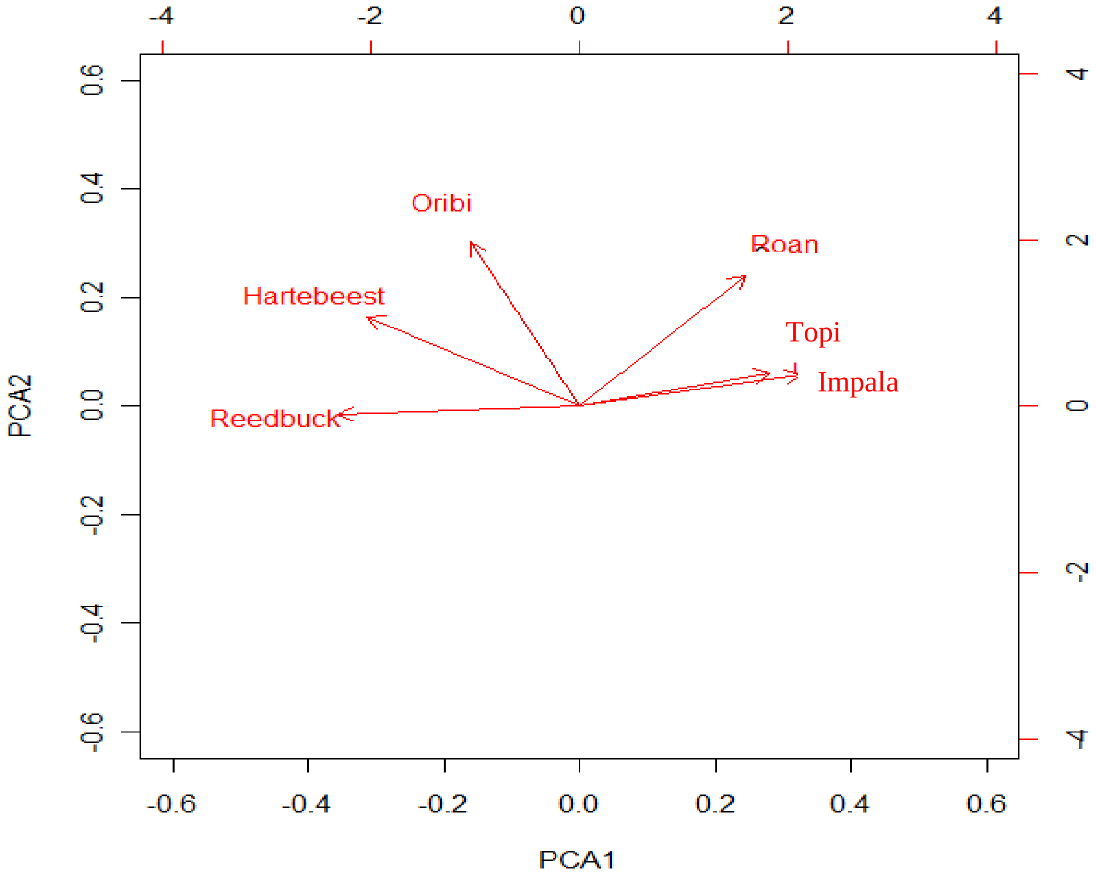


Figure 2.12: PCA correlation biplot of antelope population fluctuations in RNP from 1976 to 2005 showing factor loadings plotted along the first 2 principal component axes.

Constrained ordination redundancy analysis (RDA) performed using all the six antelopes and seven environmental variables showed that three variables are significantly important in explaining the fluctuations in the population of the six antelope species (roan, Impala, Topi, Reedbuck, Hartebeest and Oribi). The significant variables include annual rainfall (ANR) (r^2 = 0.605, n=15, p=0.032), prior accumulated rainfall for the past 5 years (PA5YRS) (r^2 = 0.745, n=15, p=0.004), and habitat (HAB) (r^2 = 0.782, n=15, p=0.015). Three more variables – long wet (WET 1), short wet (WET 2) and long dry (DRY 2) season rainfalls, seemed important but their effects were all insignificant ($p > 0.05$). Figure 2.13 presents all the seven environmental variables that were included in the constrained redundancy analysis. It is clear from the RDA triplot that topi prefers drier areas than the other antelopes and oribi population is not influenced much by the variables considered in this study. This is because the topi appears in the quadrant that is far from and opposite to arrows indicating the importance of rainfall whilst the oribi is located near the origin of the triplot. The hartebeest and reedbuck populations were more influenced by rainfall decline and they preferred wet areas. The fluctuations in roan and impala populations were more influenced by changes in the habitat. Also, the results showed that the hartebeest and reedbuck are more closely associated together.

Constrained ordination redundancy analysis (RDA) performed using all four age-sex roan groups (adult females, adult males, sub-adults and juveniles) and seven environmental variables showed that no variable was significantly important in explaining the fluctuations in the population of these age-sex groups.

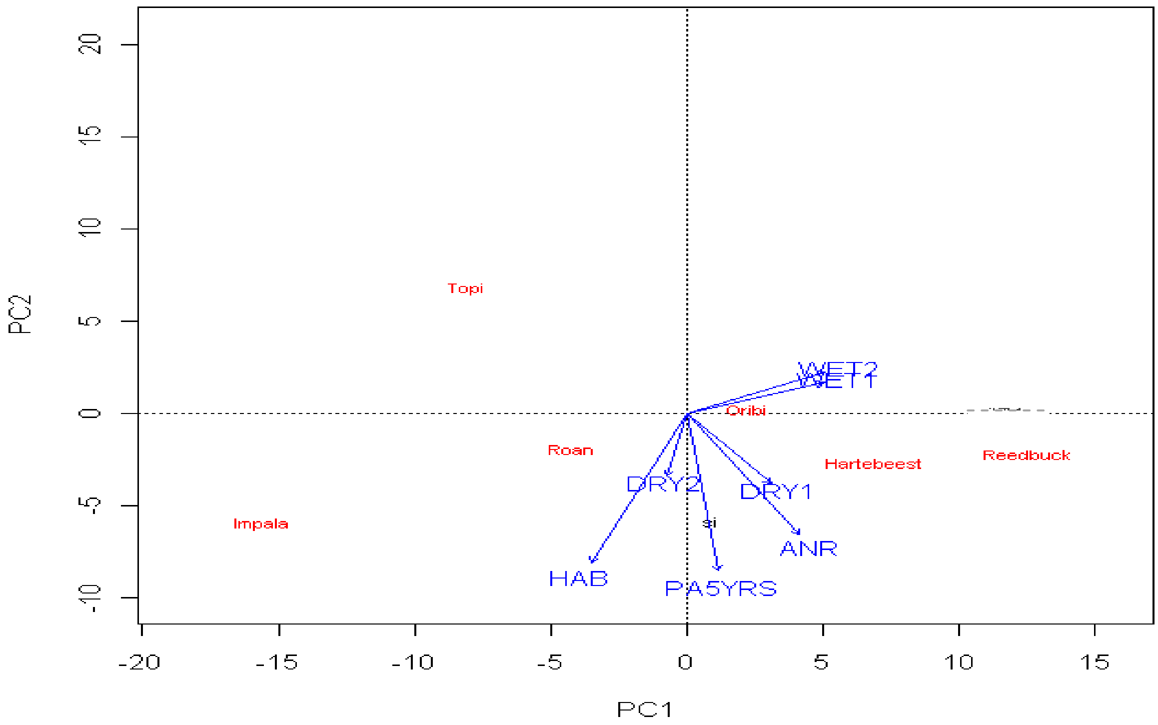


Figure 2.13: Variable loadings plotted along the first 2 ordination axes generated from a constrained redundancy analysis of population of six antelopes against rainfall and habitat variables. The abbreviations are ANR = Annual rainfall (Mar-Feb), WET 1 = long wet season rainfall (Mar-Jun), WET 2 = short wet season rainfall (Sept-Nov), DRY 1 = short dry season (Jul-Aug), PA5YRS = prior accumulated rainfall for the past 5 years, HAB = grassland habitats.

2.3.4Herbivore population models

Negative binomial regression showed that the population decline of different antelope species was attributed to different factors except the Oribi whose decline could not be explained by any of the factors considered in this study. For some species the best model did not have adequate support or relative likelihood for it to be reliably considered alone for model inference. Due to model selection uncertainty, the best model plus a couple of other models with AICc differences less than 7 (ΔAICc < 7) were considered as valid models for such species as shown in Table 2.3. Below is a presentation of how the abundance of each antelope species was influenced by changes in various rainfall components and the habitat.

The fluctuation in the abundance of impalas was attributed to significant changes in rainfall and habitat as indicated by two competing plausible models in Table 2.3. Details of the predictor coefficients and associated significant values for all the plausible models for the impala as well as other antelope species are presented in Table 2.4. The Impala abundance was significantly correlated negatively with the long wet season (WET 1), short wet season (WET 2) and annual (ANR) rainfalls, which was against the expectation that high rainfall will boost the population. However, this negative effect of wet season and annual rainfalls suggests that excessive rains may have caused death of newly born impala through flooding. Also decrease in habitat (open and wooded grasslands) negatively influenced the abundance of impalas in the park as expected.

The abundance of topi was significantly positively correlated with the changes in the habitat but negatively correlated with both the prior accumulated and annual rainfalls, suggesting that this species prefers dry habitats with little rainfall. On the other hand, fluctuations in reedbuck population were significantly positively correlated with both the prior accumulated and annual rainfalls but negatively correlated with habitat change. This implies that rainfall fluctuations are more important for reedbucks than habitat, as the rainfall can influence changes in the habitat. Similarly, the fluctuations in hartebeest population were significantly positively correlated with the annual rainfall, long wet and short dry season rainfalls.

The abundance of roan was correlated positively with changes in habitat and negatively with annual rainfall and prior accumulated rainfall (Table 2.3). This may suggest that high annual or accumulated rainfall may have been detrimental to roan calves through flooding. Analysis of declines in different roan age-sex groups showed few differences in the importance of variables influencing the population fluctuations. The roan total population, adult population, adult males and females had similar results with a common model selected as the best. This best model showed that these four age-sex groups were significantly positively correlated with habitat and negatively correlated with prior accumulated rainfall. However, the roan sub-adults and juveniles were only significantly positively correlated with habitat. Also, the roan sub-adults and juveniles seemed to be more adversely affected by decline in habitat than the adults as indicated by the high coefficients of determination (R^2) (Table 2.3) and high regression coefficients (Table 2.4), when comparing results of the model with habitat as the only variable. With reference to the same model, adult males were more affected by habitat change than their female counterparts (model not shown for adult females).

Table 2.3: Model selection statistics for the population dynamics of six antelope species in RNP (n = 15). Notice that no variable could explain fluctuations in oribi population. For roan antelopes several age-sex groups were considered. Models considered to be the overall best models are written in bold. Model parameter abbreviations are presented in figure 2.13.

Species	Model	R^2	AIC	ΔAIC	Relative likelihood
Impala	**HAB - ANR**	**0.53**	**116.18**	**0.000**	**0.492**
	-WET1	0.34	117.25	1.070	0.288
	-WET2	0.30	117.79	1.610	0.220
Topi	**HAB - PA5YRS**	**0.70**	**104.64**	**0.000**	**0.776**
	-PA5YRS	0.51	107.12	2.480	0.224
Reedbuck	**ANR - HAB**	**0.62**	**108.71**	**0.000**	**0.788**
	PA5YRS - HAB	0.26	114.61	5.900	0.041
	ANR	0.33	111.77	3.060	0.171
Hartebeest	ATR	0.42	103.91	5.680	0.055
	WET1 + DRY1	**0.53**	**98.23**	**0.000**	**0.945**
Oribi	-	-	-	-	
Roan	HAB	0.54	89.28	5.530	0.053
(All individuals)	HAB - ANR	0.68	87.99	4.240	0.101
	HAB - PA5YRS	**0.80**	**83.75**	**0.000**	**0.845**
Roan (Adults)	HAB	0.40	83.34	6.630	0.035
	HAB - PA5YRS	**0.77**	**76.71**	**0.000**	**0.965**
Roan (Subadults)	**HAB**	**0.67**	**55.81**	**0.000**	**1.000**
Roan (Juveniles)	**HAB**	**0.73**	**58.26**	**0.000**	**1.000**
Roan (Adults females)	**HAB - PA5YRS**	**0.77**	**70.92**	**0.000**	**1.000**
Roan (Adult males)	HAB	0.49	59.55	2.700	0.137
	HAB - ANR	0.66	57.77	0.920	0.334
	HAB - PA5YRS	**0.70**	**56.85**	**0.000**	**0.529**

Table 2.4: The parameter coefficients and standard errors for the best models and other plausible models with ΔAICc < 7 for relating the abundance of five antelopes with changes in rainfall components, abundance of other competing grazers and habitat in RNP. Model parameter abbreviations are presented in figure 2.14.

	Model parameters																	
	HAB			ANR			WET1			WET2			DRY1			PA5YRS		
Species	Coefficient	SE	p	Coefficient	SE	p	Coefficient	SE	p	Coefficient	SE	p	Coefficient	SE	p	Coefficient	SE	p
Impala	0.0005	0.0002	0.0037	-0.001	0.0004	0.0202												
							-0.0015	0.0006	0.021									
										-0.0029	0.0014	0.0352						
Topi																-0.0024	0.0008	0.0028
	0.0003	0.0001	0.0215													-0.0035	0.0008	<0.0001
Reedbuck				0.0014	0.0007	0.0274												
	-0.0006	0.0002	0.0048	0.0021	0.0006	0.0002												
	-0.0006	0.0003	0.0506													0.0041	0.0021	0.0482
Hartebeest				0.0011	0.0004	0.0094												
							0.0014	0.0006	0.0142				0.0023	0.0009	0.0149			
Roan (All individuals)	0.0006	0.0002	0.0042															
	0.0008	0.0002	<0.0001	-0.0012	0.0006	0.0383												
	0.001	0.0002	<0.0001													-0.0042	0.0013	0.0012
Roan (Adults)	0.0005	0.0002	0.0348															
	0.001	0.0002	<0.0001													-0.0051	0.0014	0.0004
Roan (Subadults)	0.0011	0.0003	0.0001															
Roan (Juveniles)	0.001	0.0002	<0.0001															
Roan (Adults females)	0.0011	0.0002	<0.0001													-0.0057	0.0015	0.0002
Roan (Adult males)	0.0006	0.0002	0.0067															
	0.0011	0.0003	<0.0001													-0.0044	0.002	0.0252
	0.0009	0.0002	<0.0001	-0.0014	0.0007	0.0326												

2.3.5 Model assessment

The precision of the coefficients of all the variables in the best models was assessed by comparing the coefficients of the original model with that of bootstrap models. This was necessary to validate the model results. For all the models the coefficients of the original model were similar to those of bootstrap models (Table 2.5). The use of 95% confidence intervals confirmed that every predictor that was identified as significant by the original model was also significant in the corresponding bootstrap models for all the five antelope species. Model performance was also assessed using the r^2 statistic, AICc and relative likelihood values (Table 2.3). Most of the best models had r^2 greater than 40% some had high r^2 values greater than 70%. This implied that the models explained a substantial amount of variation in the data. For species with several plausible models only those with an AICc difference (ΔAICc) less than 7 were considered for model inference as these are considered to have substantial empirical support. This implies that if the analyses are repeated with different data sets these models will still be selected among the best models.

Table 2.5: Population dynamics models (original and bootstrap) estimated using negative binomial regression to identify factors influencing the population decline of four antelope species in RNP

		Best model				Bootstrap Models			
Species	Predictors	Parameter estimate	Standard error	Lower 95%CI	Upper 95%CI	Parameter estimate	Standard error	Lower 95%CI	Upper 95%CI
Impala	HAB	0.0005	0.0002	0.0001	0.0009	0.0005	0.0000	0.0005	0.0005
	ANR	-0.001	0.0004	-0.0018	-0.0002	-0.0011	0.0000	-0.0011	-0.0010
Topi	HAB	0.0003	0.0001	0.0001	0.0005	0.0003	0.0000	0.0003	0.0003
	PA5YRS	-0.0035	0.0008	-0.0051	-0.0019	-0.0039	0.0001	-0.0041	-0.0038
Reedbuck	ANR	0.0021	0.0006	0.0009	0.0033	0.0021	0.0000	0.0021	0.0022
	HAB	-0.0006	0.0002	-0.0010	-0.0002	-0.0006	0.0000	-0.0007	-0.0006
Hartebeest	WET1	0.0014	0.0006	0.0003	0.0025	0.0013	0.0000	0.0012	0.0014
	DRY1	0.0023	0.0009	0.0004	0.0041	0.0025	0.0000	0.0024	0.0026
Roan (All individuals)	HAB	0.0010	0.0002	0.0006	0.0014	0.0011	0.0000	0.0011	0.0011
	PA5YRS	-0.0042	0.0013	-0.0067	-0.0017	-0.0048	0.0001	-0.0050	-0.0046
Roan (Adults)	HAB	0.0010	0.0002	0.0006	0.0014	0.0011	0.0000	0.0010	0.0011
	PA5YRS	-0.0051	0.0014	-0.0078	-0.0024	-0.0056	0.0001	-0.0058	-0.0054
Roan (Subadults)	HAB	0.0010	0.0003	0.0003	0.0017	0.0011	0.0000	0.0010	0.0012
Roan (Juveniles)	HAB	0.0011	0.0002	0.0007	0.0016	0.0010	0.0000	0.0009	0.0011
Roan (Adult females)	HAB	0.0011	0.0000	0.0011	0.0012	0.0011	0.0000	0.0011	0.0012
	PA5YRS	-0.0057	0.0015	-0.0086	-0.0028	-0.0063	0.0001	-0.0065	-0.0060
Roan (Adult males)	HAB	0.0011	0.0003	0.0005	0.0017	0.0011	0.0000	0.0011	0.0011
	PA5YRS	-0.0044	0.002	-0.0083	-0.0005	-0.0049	0.0001	-0.0051	-0.0047

2.4 Discussion

2.4.1 Herbivore population changes

Out of the six antelope species studied, only topi population showed a slight overall increase, whereas all the rest showed overall population decline for the past 30 years. Roan and impala populations declined significantly. Oribi, reedbuck and hartebeest showed overall insignificant declines. There is need to disentangle the causes of decline for each affected species and take intervention measures to avert further population decline, promote population recovery, and ensure a continued existence of viable populations of each species in the park. This is essential to achieve one of the park's main objectives of maintaining high biological diversity. The task is made challenging by data deficiency. For example, herbivore populations were counted consistently only at one time of the year, and hence no information is available on population numbers or structure at any other time of the year. Also, only five antelope species had population counts for the years matching those of roans. Consistent population counts for other potential competing grazers such as waterbucks, bushbuck, duiker and buffalo were not available. Below is a discussion of the causes of population decline or fluctuation of the six antelopes in RNP.

2.4.1.1 Topi

The continued existence of high numbers of topi in the park over the past 30 years shows that the park as well as the changes in rainfall, habitat and population of other grazers provides a very suitable environment for this species. The findings of this study concur with earlier studies that have shown that topi prefers drier savannah habitat (Ogutu et al., 2008; Murray and Brown, 1993) than other antelopes. Therefore, low rainfall scenario in the park may have enabled the topi to out-compete the other antelope species, and consequently increase in number at the expense of the other species. The negative correlation of topi population with both prior accumulated and annual rainfalls suggests that increased rainfall and consequent flooding may have caused deaths of topi individuals especially the newly born young. Results support this hypothesis as there was a very marked increase in annual rainfall between 1988 and 1990 as well as long wet season rainfall in 1994 - 1995 that was followed by a noticeable decline in the topi population in 1989 and 1995, respectively. However, although flooding in RNP may occur occasionally due to its location in a valley sandwiched between hills, this did not seem to cause a significant overall decrease in the topi population. Therefore, the topi population may not be adversely affected like other species by the continuing local and global climate change.

A couple of other factors may have made the topi population to remain stable in RNP. Firstly, they are able to dwell in various habitats including flood plains, dry areas of open savannah and open woodlands (AWF, 2009), which were readily available in the park. Secondly, topis are not only flexible in habitat requirements but also very flexible in reproduction and behaviour, which enable them to quickly adapt to changing environment). For instance, (i) when food supplies are good they conceive at different times of the year with shorter intervals between calves; and (ii) they are able to stall birth process if they sense immediate danger (AWF, 2009). Thirdly, they have precocial young that are able to follow the herd soon after birth without requiring conducive habitat cover for hiding them from predators (Sinclair et al., 2000). Therefore, decline in habitat could not cause decline in young topi population. Last but not least, topi synchronize their births with periods of plentiful food availability (Sinclair et al., 2000). When births occur synchronously then predators become satiated and survival of the remaining newborn animals increases according to the predator ‘satiation’ hypothesis (Rutberg, 1987).

2.4.1.2 Impala

The significant decline of impala population can be attributed to combined effects of rainfall and declining habitat. The decline in grassland habitat had a significant effect on the population decline. This is a bit contrary to expectation because impalas are mixed feeders (Murray and Brown, 1993) and therefore the effect of decline in grasses should be counteracted by utilizing more browsing material. Hence, the decline in grassland habitat is likely to have caused greater decline in the young impalas compared to the other age groups, due to exposure to predators. Impalas have non-precocial young (Sinclair et al., 2000), which need to be secluded for more than a week after birth in conducive tall grasslands against predators (AWF, 2009). Therefore, the survival of newly born young depends on availability of conducive tall grasslands for hiding them from predators. This is consistent with the predator ‘avoidance’ hypothesis (Ims, 1990). The significant decline in grassland habitats coupled with frequent occurrences of unpredictable fires throughout the park especially during the dry season may have contributed greatly to mortality of young impalas due to predation by hyenas in the park and consequently led to impala population decline. However, more research focussing on age-specific survival is needed to yield more confirmatory conclusions.

Impala population decline was also attributed to high wet season rains. Although impalas breed all year round, they have less synchronized births with the birth peaks coinciding with the wet rainfall seasons (Sinclair et al., 2000). This coincidence can be seen as beneficial because it ensures adequate food supplies for the young. However, when the rains are too high leading to flooding, this becomes disastrous for the young impala. A long term study by Ogutu et al., (2008) in Masai Mara National Reserve found out that young impalas drown to death during floods. The modelling results of this study, which shows significant negative correlations between impala population decline and wet season rains, concur with the findings of the earlier study.

2.4.1.3 Hartebeest

The hartebeest population did not decline significantly, which may suggest that they are better suited than other antelopes in this park. The hartebeest is a pure grazer that is not selective and quite tolerant of poor quality food as well as more tolerant of tall grass and woods than other plains antelopes (AWF, 2009). This makes them able to cope with the dry season, which is a very critical period for the survival of many grazers. In RNP there is low grazing pressure that allows a lot of grasses to grow tall, mature and dry out in the dry season. To utilize these dry season coarse grasses needs a special adaptation. Fortunately, the hartebeests have better skull morphological capability that enable them to utilize more coarse grasses than other antelopes during the dry season when forage availability is lowest (Schuette et al., 1998). Although hartebeests bear young throughout the year, their conception and breeding peaks are influenced by food availability (AWF, 2009; Sinclair et al., 2000), which ensures that many young are born when food is plentiful and hence their survival is enhanced. Since food availability is mainly influenced by rainfall, the modelling results showed that the hartebeest population was positively correlated with rainfall. Their newly born young are precocial (Sinclair et al., 2000) and thus able to follow their mothers without needing conducive breeding habitat for seclusion. Therefore, they employ the predator ‘satiation’ antipredatory behaviour (Rutberg, 1987) in protecting their newly born young.

2.4.1.4 Reedbuck

Although regression analysis showed insignificant overall decrease in reedbuck population from 1976 to 2008, the graphical illustrations demonstrate that its population declined precipitously from over 300 animals in 1998 to less than 10 in 2008. Clearly, this indicates that the reedbuck is faced with imminent local extinction in this park, unless urgent interventions are implemented. Failure to detect significant decline in reedbuck population may have been caused by the low population estimates in 1976, which might have been underestimates. Presumably, if the maximum population within the survey period (e.g. 1989 estimate) was used as a baseline, significant population decline of reedbuck will have been found. However, this was not investigated because this would have reduced the sample size to a level where the findings would be questionable. Modelling showed that they are negatively affected by decrease in both annual rainfall and prior accumulated rainfall. Reduced rainfall and occurrence of droughts will cause drying out of wetlands that are the preferred habitats for this species. The natural habitat for reedbucks is wet grasslands or reeds near water bodies (Wildlife Safari, 2010). Monitoring in Kruger National Park has shown that shrinking of these habitats has caused subsequent reduction in the number of reedbucks (Kruger National Park, 2010). Other two factors that could be playing a key role in reedbuck reduction in RNP are uncontrolled burning and poaching via snares. Burning removes the suitable vegetation cover for hiding the secluded non-precocial newly born young, which exposes them to high levels of predation by hyena.

2.4.1.5 Oribi

Although regression analysis showed an overall decline in oribi population, its population had remained steady from 1976 to 2005 and only showed decline in 2008. However, the decline could not be explained by rainfall fluctuations or habitat change. This implies that other factors, not considered in this study, might have been more important in explaining the overall decline in oribi population. Alternatively, the recorded small oribi population in 2008 may be an underestimate. The census method used in RNP of total counts in blocks was found to yield underestimates for small antelopes in Serengeti National Park, because they are small, secretive and can easily hide in tall grassland (Mduma, 1995). Therefore, the observed steady oribi population for 30 years (1976-2005) could imply that RNP provides a suitable habitat for this species, despite the habitat change and alteration. Studies of habitat preference in South Africa and Tanzania indicated that oribi preferred recently burned areas (Mduma and Sinclair, 1994; Rowe-Rowe, 1982). Therefore, the uncontrolled burning in RNP may be beneficial to this species.

2.4.1.6 Roan

Since only the roan and impala populations declined significantly in RNP over the past 30 years, it implies that management interventions should be directed towards population recovery of these two species. However, there are several sufficiently viable populations of impalas in many well protected national parks and reserves in Kenya. Therefore, the roan is the only herbivore population that needs urgent intervention because this species is only found in RNP in Kenya. The matter is made more grievous by the fact that the species used to occur in three more conservation areas in Kenya in 1970s where it eventually became locally extinct. Therefore, the rest of the discussion in this chapter deals with more detailed analysis of causes of roan population decline. Specifically, the section tries to disentangle (1) resource competition between roan and other antelopes; (2) the effects of low rainfall on vegetation and hence food resources for roan; (3) effects of habitat decline and fragmentation on the roan population and distribution; and (4) the key age-sex groups contributing majorly to roan population decline.

Roan competition with other grazers

Correlation analysis indicated that the abundance of roans is negatively associated with the abundance of reedbuck and hartebeest populations. Although such associations were not significant, probably due to the effect of a small sample size (n=15), the decline in roan population seems to be closely association with the increase in both reedbuck and hartebeest populations in the park. From 1976 to 1989 when the roan population was declining precipitously, the populations of reedbuck and hartebeest were increasing to their peak numbers. Also, between 1998 and 2008 when the two populations of reedbuck and hartebeest were decreasing, the roan population was increasing. The two competing grazers seem to create a grazing pressure on the limited food resources in the park, especially in the dry season. Schuette et al (1998) found out that hartebeests have better skull morphological capability that enable them to utilize more coarse grasses than roans during the dry season when forage availability is lowest. Microhistological studies by Schuette et al (1998), revealed that roans shift their diet in dry season from predominantly grazers (>95 grass) to mixed feeders (<50% grass) during the dry season when browse materials are more plentiful than drying re-growth of perennial grasses.

Although some authors (Saleni et al., 2007; Sale, 1974; Colwell and Futuyma, 1971) postulate that such seasonal dietary divergence during periods of limited food resources foster coexistence and minimize competition, other studies have shown the opposite (Jenkins and Wright, 1987; Schoener, 1982). This dietary shift by roans is dependent on availability of unlimited browse material, the absence of which may make roans reluctant in shifting to mixed feeding. Shifting to mixed feeding may also place roans at a disadvantage in respect to mixed feeders in the park, which are more adapted in utilizing browse food materials. This implies that if browse materials are not readily available during the dry season roans may either (1) avoid shifting their diet to mixed feeding and hence interspecific competition will occur between hartebeest and roans for the limited grasses; or (2) shift to mixed feeding and enter into competition with mixed feeders for the limited browse materials. Therefore, both way the roans are disadvantaged and their survival is critically affected during periods of dry season. For this study, interspecific competition can only be implied in RNP where increases in hartebeest and reedbuck populations have been associated with decline in roan population. Although competition can be best studied by subjecting small mammals to experimental conditions (Neill, 1975; Park, 1962), past studies have documented competition for food among ungulates in natural conditions (Sinclair, 1985; Singer, 1979; Hudson, 1976).

Resource competition could adversely affect the nutritional status of the roans. Malnutrition has been shown to cause high juvenile than adult mortality in Kudu (Owen-Smith, 1990). This implies that if malnutrition was the major cause of total roan population decline there should be more deaths in juveniles than adult roans during the period of decline. However, graphical illustrations show that the initial roan precipitous decline from 1976 to 1993 was associated with similar declines in juveniles and adult roans. Therefore, malnutrition can only be seen as one of the factors but not the main or sole demise factor. Furthermore, there was an inverse relationship between total roan population decline and recruitment rate. This suggests that malnutrition did not have much effect on reproduction rate and therefore other factors must have played a bigger role in triggering the decline in roan population.

Effects of habitat change on roan population decline

Modelling showed that the overall roan population decline in RNP for the past 30 years was attributed to overall reduction in grassland habitat. The habitat is necessary for providing food, shelter from adverse weather conditions, breeding sites and cover from predators for the newly born young. However, it is apparent that decrease in grassland habitat was not the initial cause of roan decline. For instance, during the period of initial severe roan population decline from 1976 to 1989 by 83%, the decrease in the habitat was only 9%. The reduction in the grassland habitat has been caused mainly by bush encroachment (Muriuki et al., 2005). Progressive growth of bush cover has been shown to cause reduction in herbaceous vegetation and decline in range condition (Oba et al, 2000). Therefore, bush encroachment not only reduces grasslands but also eliminates herbs, which are a preferred alternative diet for roans during extreme dry season periods.

Bush encroachment in RNP is promoted by lack of prescribed burning, low numbers of browsing wildlife populations, high numbers of grazers, and bushy re-growth from former farms that were abandoned after establishment of the park in 1983 (Muriuki et al., 2005). The mechanism involves reduction of fire frequency and intensity as a result of grazing pressure on the grass layer, which causes the tall grasses to become largely replaced by shorter grasses (Owen-Smith, 2007). Grass growth, and hence the fuel materials for fire, are also reduced during periods of low rainfall. Once the bush cover develops, it tends to persist because the sparse grass cover no longer supports hot fires.

Bush encroachment has caused habitat fragmentation and creation of smaller habitat patches within the park that are consequently thought to have impacted negatively on the roan population. This may have either (1) caused separation of roan herds into smaller non-viable populations which got locally extinct as a result of amplified stochastic processes and demographic variability or (2) confined all roan groups within the largest contiguous habitat patch, which was obviously smaller than the previously connected whole park habitat, thus limiting the increase of the roan population due to limited food and water resources. This main separation of the roan habitat is caused by the elongated expansion of the Olambwe river forest thicket. Allsopps (1979) documented the distribution of roan groups on both sides of the river in 1970s when the roan habitat was not separated and fragmented by the increasing bush encroachment in the park (see illustrations in chapter 5 section 5.4.4). However, today roans only occupy one side of the river probably because the riverine forest thicket has blocked their movement. Bush encroachment adversely affects all grazers in the park. Van Wijngaarden (1985) showed that an increase in bush cover by 10% reduces grazing by 7%, and an increase of 90% bush cover eliminates grazing completely in East African savannahs.

Modelling indicated that decline in grassland habitat affected juveniles and sub-adults more than adult roans. Also adult males were more affected by habitat change than their female counterparts. The juveniles and sub-adults are less adapted and hence more vulnerable to effects of habitat change than the adults. Past studies have shown that juvenile survival is more affected by annual variability in resources or weather conditions (Owen-Smith and Mason, 2005) and effects of malnutrition seem to affect juveniles than adults (Owen-Smith, 1990). Pienaar (1969) showed that male ungulates are more vulnerable to predation than their female counterparts. Since roans portray territorial behaviour, a reduction in suitable habitat (making it a limiting factor) will force lone male adults to occupy marginal habitats whilst the female groups utilize the optimal habitat.

Rainfall effects on roan population decline

Modelling showed that annual and accumulated rainfalls had negative effect on the roan population. Although most rainfall components showed insignificant decrease over the 30-year period of this study, graphical illustrations demonstrate that there were years of extreme low rainfall (droughts) and high rainfall (floods). Periodic occurrence of droughts and floods could have contributed to decline of the roan population. The roans are severely affected by drought and move a lot during such periods in search of water and food (Dorst and Dandelot, 1990). With the RNP fenced in most areas the roans are confined in a limited area during such adverse periods. Furthermore, dispersal of the roans outside the park is not an option because of the surrounding dense human settlements and farming activities. Floods could cause death of newly born young and weak or sick roans via drowning. A rigorous study by

Ogutu et al (2008) confirmed that floods arising from high wet season rains led to decrease in numbers of juvenile impalas in Masai Mara ecosystem in Kenya.

2.4.2 Conclusions

Apart from topi all the other antelopes declined significantly (roan and impala) or insignificantly (reedbuck, hartebeest, oribi). Therefore, there is need to implement management interventions to halt further population decline and prevent possible local extinction of vast number of herbivores in the park. The two most important factors influencing antelope population dynamics in RNP are rainfall fluctuations and habitat change. Rainfall affected roan, impala, topi, reedbuck and hartebeest whereas habitat change had impact on roan, impala and topi. Although, roans were significantly affected by both habitat change and rainfall just like impala and topi, they showed the greatest population decline. This could be because they have specialised habitat requirements and extreme sensitivity to habitat deterioration (Schuette et al., 1998). Alternatively, this may imply that other factors were responsible for triggering roan decline, and then consequences of small isolated population prevented the population from increasing. Further analysis of potential factors driving the roan population decline in RNP is dealt with in chapter 6 using population viability analysis.

2.4.3 Limitations and constraints

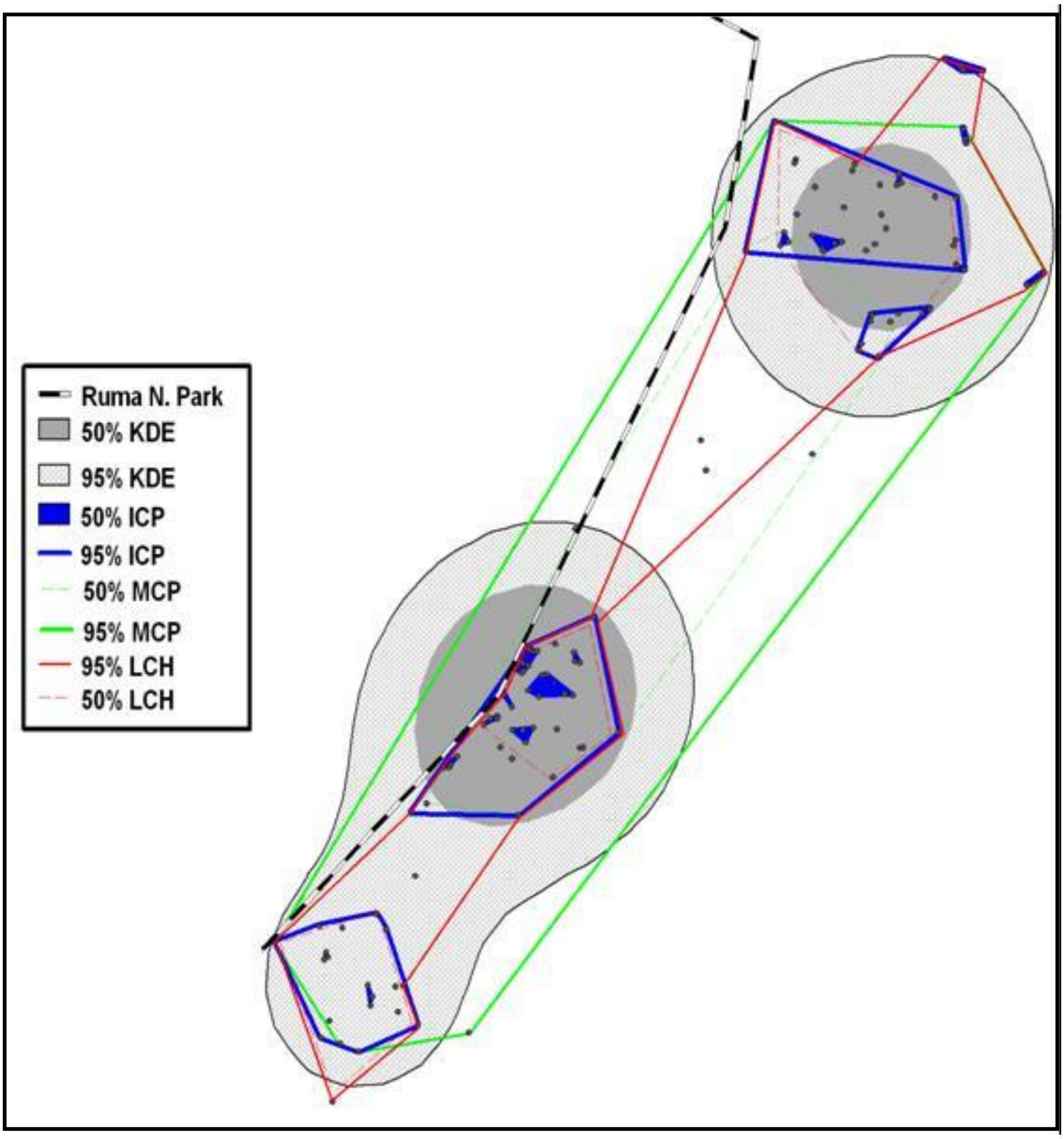
- The limited sample size (n = 15) may make it harder to partial out residual variation (error) from the analyses of the data. However, the use of different analytical methods (that is, multivariate techniques and generalized linear models) that produced similar results indicates that the small sample size did not cause bias that may invalidate the findings. Error structures resultant from the models were robust.
- Only a limited number of other grazing species had adequate population estimates for analysis that could be compared to roan population decline. Better understanding of herbivore population dynamics could have been achieved if data were available for all grazers in the park.
- The collection of roan population estimates and age structure by different persons from 1976 to 2009 may include errors. However, it is assumed that the resident

research scientist in RNP coordinated and supervised the census process to minimize errors that may occur.

- Current method used in RNP of counting animals using total counts in census blocks appears to be inadequate, since flaws were detected on population estimates for some years. This census method was found to yield underestimates for small antelopes in Serengeti National Park (Mduma, 1995). Two other methods: (i) total counts of known individuals and (ii) sample counts by ground line-transects, that are more reliable and less biased in counting the population of antelopes (Mduma, 1995), need to be used to complement or replace the existing method.
- The use of calf : cow ratio does not provide a reliable proxy of recruitment rate. However, this ratio is widely used to monitor population levels in the field (Smart et al., 2004) and could be the only information available in some cases. Reliable estimates of survival and pregnancy rates obtained from marked animals and foetus sampling are more accurate (Bonenfant et al., 2005).
- It is recognised that use of an arbitrary cut-off point for the wet and dry season could bias the findings on effect of rainfall on the population dynamics of the studied antelopes. Any such bias was, however, minimized by the use of long-term seasonal rainfall data (1976-2005) and literature on the weather patterns of the study area.
- The assessment of temporal vegetation change using Landsat images from different sensors with different resolution might introduce errors. However, it is assumed that the atmospheric corrections done on the images during pre-processing stage prevented these errors.
- Ground truthing using estimation of vegetation canopy cover instead of actual measurement may introduce bias. This error was minimized by using only two researchers in vegetation survey; training on how to estimate canopy cover was also achieved using a forest densiometer.
- Model assessment without independent data is not robust. However, the validity of models was increased by assessing model accuracy using several techniques: bootstrapping, AIC, and r2 statistic, which all produced similar results.

CHAPTER 3

HOME RANGE ANALYSIS FOR ROAN ANTELOPES IN RNP



Differences in home range sizes, shapes and structure as produced by 4 home range estimators for one roan group in RNP

CHAPTER 3: Home range analysis for roan antelopes in RNP

3.1 Introduction

Objective estimation of the size, shape and structure of the home range of a species is vital to understand that species' behavioural ecology and management requirements (Kenward, 2001; Swihart and Slade, 1985a). A home range can be defined as an area repeatedly occupied by an animal during a specified time period (Katajisto and Moilanen, 2006; Kenward, 2001; White and Garrot, 1990). Estimation of home range size is vital to estimate the minimum viable area for a roan sanctuary. Home range shape is important to understand how the roan home range is spatially placed in the park in relation to vital resources and infrastructure as well as how home ranges for different breeding roan groups fit together with those of lone males and bachelor herds. Study of home range structure can be used to predict the likelihood of encounter during population census (Kenward, 2001) or to reveal details of how roan individuals intensively use different parts of their home range.

Many techniques have been developed to estimate an animal's home range based on data collected using radio-tracking techniques or field observations (Katajisto and Moilanen, 2006; Kernohan et al., 2001). Critical reviews of the existing techniques for home range analysis have been carried out by Worton (1987), Harris et al (1990), White and Garrott (1990), Kenward (2001), and Laver and Kelly (2008). However, there is still no consensus on the best home range estimators and no single best method for estimating all home range characteristics. As a result many authors recommend the use of more than one home range estimator in any single study (Huck et al., 2008; Wauters et al., 2007; Hemson et al., 2005).

The selection of an appropriate method for home range analysis depends on four main factors (Getz and Wilmers, 2004; Kenward, 2001). Firstly, the biological questions being asked and hence the particular home range indices required. For example, some estimators are good at estimating the home range size and shape whilst others give more details on the home range structure. Secondly, the choice is dependent on behavioural characteristics of the species being studied, that is, how the animals move in relation to resources. For example, if animals are foraging in habitats with abrupt boundaries, polygon methods may be the best (Kenward, 2001). Thirdly, the sample size of collected data determines which estimator is valid. Some estimators such as ellipses can produce stable home ranges with less than 15 animal locations while others such as grid cells need at least 100 locations (Kenward, 2001). Fourthly, the choice is also determined by the accuracy and detail required by the research. In practice a balance must be struck between the level of accuracy and the scope of details to be revealed by home range analysis. To achieve both high accuracy and greater detail requires large number of locations that may not always be available or maybe too costly to collect.

Another important factor that affects the results of home range analysis is the choice of a computer software package for carrying out the selected estimators. Not all estimators are implemented in each and every available software package. The starting point for a beginner ecologist is to select the software in which the required techniques are implemented. Past research on home range estimation techniques has dealt mainly with identification of the right technique for various biological questions and animal species, and developing of more sophisticated methods. Although further research is still needed in this area (Huck et al., 2008; Hemson et al., 2005), very little has been done to show how home range estimates differ across software packages. It has already been noted that a particular home range estimation technique implemented in different software can produce different results (Lawson and Rodgers, 1997; Larkin and Halkin, 1994). However, no solution to this problem has been sought by software developers as each seems to operate independently. This presents a serious issue of concern to ecologists who have no prior knowledge on these differences and seeks to use the default functionalities in available software to solve biological problems. It becomes even more complicated when comparing home ranges from different studies where the authors fail to state which software was used. Further investigations need to be carried out to test how home range estimates calculated using newly developed software packages differ from those computed using already established packages.

Regardless of the home range estimator used, the sampling protocol influences the results obtained in home range analysis. Two factors need to be considered when designing a sampling protocol for home range estimation (Huck et al., 2008; Laver and Kelly, 2008; Kenward, 2001; Kernohan et al., 2001): (i) one needs to decide whether to use the continuous sampling or the point location sampling methods and (ii) the sampling time intervals between successive observations should be selected with consideration of the effect of autocorrelation. Point sampling is better than continuous sampling because it yields independent location records (Kenward, 2001). Some approaches (e.g. the Brownian bridge approach) and some biological questions (e.g. analysis of movement trajectories) specifically require autocorrelated data, in which case continuous sampling is necessary (Davison et al., 2009; Huck et al., 2008). Also, non-statistical techniques (such as polygon measures) can analyze autocorrelated home range data without bias (Swihart and Slade, 1985a).

On the other hand, for results to be valid statistical analyses on home ranges require statistical independence between successive animal observations (Kenward, 1992; White and Garrot, 1990; Swihart and Slade, 1985b). Lack of independence between observations inflates the degrees of freedom and hence increases the type I error (Crawley, 2007; Legendre, 1993). Autocorrelation has also been shown to cause underestimation of home ranges (Cresswell and Smith, 1992). Swihart and Slade (1985b) developed a test of Time to Independence using Schoener's (1981) index. To eliminate autocorrelation the index value should be at least 2 (Swihart and Slade, 1985b). Using this index, ecologists can sub-sample their data until all the remaining observations are statistically independent (Kenward, 1992). Alternatively, ecologists can do a pilot study to establish the most efficient sampling protocol based on the optimal interval time between successive observations that confers independence (Kenward, 2001; De Solla et al., 1999). Unfortunately, this may impose a long interval time that implies a very long period of data collection, which maybe too expensive or may delay achieving results especially when dealing with urgent cases involving endangered species.

However, strict adherence to autocorrelation analysis can also cause counteractive problems in home range analysis. De Solla, et al. (1999) found out that eliminating autocorrelation via sub-sampling reduces the sample size such that home ranges are underestimates. Therefore, dealing with the problem of autocorrelation in home range analysis needs more careful thought. Kenward (2001) investigated the Schoener's index and found that autocorrelation only brings severe effects to home range estimation when the index value was below 1. He therefore concluded that a sampling protocol where the index value is at least 1 is more efficient and practical than that which eliminates autocorrelation. Apart from autocorrelation, one needs to account for an animal's timetabling to avoid collecting biased observations (Kenward, 2001). For instance, if data is collected once per day (to allow for independence) and that time coincides with an hour when an animal is always resting at a particular habitat, the data will be severely biased.

Since the roan antelopes in RNP have not been studied in the past using objective methods, four commonly used home range estimators were used to obtain home range size, shape and structure for comparisons and also to form baseline information for future studies. The selected estimators were: (1) minimum convex polygon (MCP), (2) incremental cluster analysis polygon (ICP), (3) kernel density (KDE) and (4) local convex hull (LCH). This was necessary because there is no single best estimator and many authors recommend the use of more than one in any single study (Huck et al., 2008; Wauters et al., 2007; Hemson et al., 2005). Selection of these three estimators provided adequate variety of methods needed for analyzing the diverse nature of the available roan antelope data and answering various biological questions. The four selected home range estimators have particular advantages over other methods that make them more suitable for this study as discussed below.

3.1.1Minimum Convex Polygon (MCP)

A minimum convex polygon (MCP) is formed by drawing a line round the outermost animal locations. The MCP method still remains the most widely used technique for estimation of home range size and shape and for comparison of home ranges analysis between studies (Huck et al., 2008; Simcharoen et al., 2008; Wauters et al., 2007;

Franzreb, 2006; Harris et al., 1990; White and Garrot, 1990). The MCP method is easily understood and can be computed using all available home range analysis computer software. Although the MCP method has been shown by many authors to yield overestimated home ranges (Katajisto and Moilanen, 2006; Ryan et al., 2006; Burgman and Fox, 2003), it has also been shown to produce more realistic home range estimates when sample size is relatively small (Wauters et al., 2007). The home range size and shape of MCP is greatly affected by outlying locations, which makes it yield overestimated home ranges covering large unused areas. However, these outliers can be excluded effectively before computing the home ranges using several techniques: (1) excluding 5% of all the outer locations in a home range (Ackerman et al., 1990); (2) testing for discontinuity in frequency of locations in grid cells (Samuel and Green, 1988; Samuel et al., 1985); (3) use of statistical outlier exclusion methods (Hodder et al., 1998; Ackerman et al., 1990), and (4) using utilization plots from incremental cluster analysis (Kenward, 2001; Hodder et al., 1998; Clutton-Brock et al., 1982). The first method is the most widely used technique for eliminating outliers (Franzreb, 2006; Kenward, 2001; Hanski et al., 2000). This is probably because it is easily understood, easily repeatable for comparison of studies and it corresponds to the conventionally accepted statistical alpha error of 5% (α = 0.05). The second method requires large numbers of locations for significant results to be obtained. Most of the statistical techniques used are complex and are not readily available in the common computer software packages used in home range analysis.

3.1.2 Incremental Cluster Analysis Polygons (ICP)

An incremental cluster polygon (ICP) is formed in such a way that the first three locations with minimum sum of nearest-neighbour distance form the first cluster. Another location is then added if its distance is smaller than the mean nearest-neighbour distance in the next potential cluster, and so on. Utilization plots in Incremental Cluster Analysis constructed by plotting the percentage of animal locations against the percentage of home range area are used to exclude outliers. These are locations beyond the point where there is a clearly defined discontinuity in the curve (that is, beyond the inflection point on the curve). A single inflection point indicates a mononuclear home range whereas more than one inflection point indicates multinuclear home range (that is, the one with more than one core area) (Wauters et al., 2007; Kenward, 2001). Apart from eliminating outliers cluster analysis is particularly good for separating multinuclear range cores without the tendency of contours expanding into unused areas (Kenward, 2001). This can identify patchiness in range use by the roan antelopes. Cluster analysis is said to be more stable than kernel contours (Hansteen et al., 1997) but with low number of locations it is the least stable technique for home range analysis (Robertson et al., 1998) and hence it requires more than 30 locations (Kenward, 2001).

3.1.3Kernel density (KDE) methods

The kernel method defines a probability density function (kernel) over each data point by adding *n* components such that where there is a concentration of points the kernel estimate has a higher density than where there are few points. Kernel methods are mathematically robust, less-matrix-dependent, produce consistent results and are very good in highlighting areas of concentrated activity (Worton, 1987). Worton (1989) also noted that the kernel methods are often sufficient to make all the useful interpretations of an animal’s movements from the home range data and that they have an intuitive appeal to biologists. (Kenward, 2001) found out that kernel methods with relatively low smoothing can obtain stable home range sizes with 15-20 locations but they are more sensitive to outlying locations than harmonic mean contouring. Similar results have been obtained by Powel et al., (1997) and Seaman et al., (1999), who recommend the use of at least 20 or 30 locations, respectively, to estimate stable fixed kernel home range sizes.

There are different types of kernel functions. Faucher et al (2001) studied the sampling properties of quantile estimators based on different kernels and concluded that Gaussian (bivariate normal), Epanechnikov, biweight and EVI kernels yield similar results, while Cauchy and rectangular kernels yield poor results. Faucher et al., (2001) further demonstrated that the Epanechnikov kernel is better than all the other kernels as it minimizes the mean integrated square error (MISE), that is, the difference in volume between the true utilization distribution (UD) and the estimated UD. Kernel methods can be divided into two types (fixed and adaptive kernel estimators) depending on the characteristics of the smoothing parameters *h* used (the smoothing parameter is conventionally denoted by a letter *h*). For fixed kernel estimators the smoothing parameters are of fixed value over the plane. Adaptive kernel methods are more sophisticated and they vary the smoothing parameter so that areas with a low concentration of points have higher *h* values than areas with a high concentration of points, and are thus smoothed more. The fixed kernels have been found to yield better results than the adaptive kernels (Seaman and Powell, 1996; Worton, 1989) when the appropriate reference smoothing parameter is chosen. This is because the estimation of the smoothing parameter in adaptive kernels requires in-depth skills and experience. The estimation is also somewhat subjective (Katajisto and Moilanen, 2006) when estimated by different researchers. Therefore, home ranges estimated using adaptive kernels may not be valid for comparison in different studies.

A lot of research has been done on the kernel methods and different formulas have been advanced to estimate the smoothing parameters: optimum or ad hoc *h*ref (Worton, 1995; 1989); reference bandwidth (*h*ref) (Seaman and Powell, 1996); least-squares cross validation (LSCV) (Silverman, 1986); Epanechnikov's *h*ref (Silverman, 1986) and user defined *h* (Calenge, 2006; Worton, 1989). The user defined *h* yields best results when used by experienced researchers (Calenge, 2006) and thus not suitable for comparison of studies. The Epanechnikov's *h*ref is computed as Worton's ad hoc *h*ref multiplied by a constant value of 1.77 (Calenge, 2006). The LSCV has been shown to produce more reliable estimates of home range when compared with *h*ref smoothing parameters (Hemson et al., 2005) and is said to be one of the best bandwidth estimation method . The estimated value of LSCV minimizes the mean integrated square error (MISE). The disadvantage of LSCV is its high variability at small sample sizes and frequent failure to converge to the true utilization distribution (UD) at large sample sizes, which is related to biologically relevant patterns of space use, such as intensive use of core areas and territorial behaviour (Hemson et al., 2005). This makes the method limited in comparing home range estimation results in different studies. Faucher et al (2001) also pointed out that LSCV is not appropriate for discrete data (that is data sets containing observations with identical values) or samples divided into clusters.

3.1.4 Local convex hull (LCH) method

The local convex hull (LCH) (Getz et al., 2007; Getz and Wilmers, 2004) is a generalization of the minimum convex polygon (MCP) method and is also essentially a nonparametric kernel method. The LCH produces a utilization distribution by constructing a set of local convex polygons for each data point, using a given number of nearest neighbours. Getz et al., (2007) presents three ways of computing the LCH: (i) fixed number of points, *k*, where all kernels are constructed from *k*-1 nearest neighbours of root points; (ii) fixed sphere of influence, *r*, in which kernels are constructed from all points within a fixed radius *r* of each reference point; and (iii) adaptive sphere of influence, *a*, where kernels are constructed from all points within a radius *a* such that the sum of the distances of all points within the radius to the reference point is less than or equal to *a*. Overall, the a-LCH yields better results than *k*- and *r*-LCH (Getz et al., 2007). The LCH has been shown to construct more appropriate and realistic home ranges and utilization distributions than the parametric kernel methods, because of its ability to identify hard boundaries (such as park fence lines, rivers and cliffs) and irregular structures (such as rocky outcrops), its convergence to the true distribution as sample size increases, and capability to analyze sample data with replicates. The LCH method is relatively new and needs to be evaluated to ascertain its usefulness in comparison to the other established home range estimators.

3.1.5 Objectives

This chapter aimed at achieving the following objectives:

- To investigate the effect of software packages in home range estimation.
- To determine the most cost-effective sampling protocols for collecting roan movement and distribution data.
- To identify the most accurate and efficient home range estimators for analyzing roan movement data.

- To investigate the differences and interactions of the home ranges of roan groups and lone males in RNP.

3.1.6 Hypotheses and predictions

This chapter had the following hypotheses:

- Different software packages yield different roan home range estimates. It was predicted that the home ranges estimated using the new adehabitat package would differ from those of the more established RANGES package, as it has previously been noted between RANGES and other packages.

- Different sampling protocols for collecting roan movement and distribution data are likely to differ in both cost and effectiveness. It was predicted that (i) sampling protocols involving random sampling at longer time intervals would be cheaper than systematic sampling at shorter time intervals; and (ii) random and systematic sampling protocols would yield different results.

- Home range estimators for analyzing roan movement data differ in accuracy and performance. It was predicted that there would be varying accuracy and performance among the 4 home range estimators used: local convex hull (LCH, kernel density (KDE), incremental cluster analysis polygon (ICP) and minimum convex polygon (MCP).

- Roan groups and lone males differ in their home range characteristics in different seasons. It was predicted that (i) roan groups would occupy larger home ranges as they require more resources than the individual lone males; (ii) the roan group home ranges would not overlap each other but that the lone males would track the roan groups in pursuit of females or with attempt to overthrow the dominant male; and (iii) the roan groups would be larger, spread less and travel longer distances at greater speed in the dry season than in the wet season, due to constraints of limited resources in the dry season.

3.2 Methods and Data analysis

3.2.1 Collection of roan movement and distribution data

Data on roan movement and distribution in RNP was collected using both continuous monitoring and point location sampling methods as described by Kenward (2001). The continuous monitoring method was only used in a pilot study to aid in the implementation of the point location sampling method. The pilot study lasted for two weeks and data was collected for 6 full days, 3 days each for a different roan group. During the pilot study a roan group was tracked and monitored continuously but data on animal locations was recorded at intervals of 10 minutes throughout the day from 0700 to 1900 hours.

Autocorrelation analysis was done on the pilot study data using Schoener's index (Swihart and Slade, 1985b; Schoener, 1981) to test for statistical independence between successive locations. Autocorrelation among roan locations declined as the time interval between observations increased, until statistical independence was reached at an interval of 7½ hours when the Schoener Index was 2.0±0.01 (Figure 3.1). This meant that eliminating autocorrelation from the roan movement data would remove over 65% of the data. The Schoener's index results were combined with observed roan timetabling to decide on the optimal time interval for the point sampling method. Based on Kenward's (2001) recommendation, it was decided that roan movement data for the point location sampling method be collected at a regular time interval of 2 hours that corresponded to an index value of 1.1±0.07. This time interval yielded 6 locations per day (that is, at 0800, 1000, 1200, 1400, 1600 and 1800 hours) for roan groups. However, due to difficulties of locating and tracking lone males, these were observed only once per day.

For each target roan individual, the following information was recorded: XY location coordinates of observer using a GPS, estimated distance to the animal, angle direction of the animal using a pair of binoculars with in-built compass, activity, sex, age and habitat. In addition, for each group, the number, age structure and spread of the group were recorded. Data were collected for 3 groups, 5 lone males, and 1 bachelor herd. For each target roan animal, data was collected once per week for 6 months (February to July 2008). In total, there were 22 days of data for groups 1 and 2 each, and 7 days for group 3, which translated into 132 animal locations for group 1 and 2 each, and 42 locations for group 3. The third group had fewer locations because it was formed by females that split from group 1, midway through the fieldwork period. Only 3 lone males had substantial amount of data that could be analyzed. The 3 males had 20, 15, and 14 samples sizes, respectively. The other two lone males and the bachelor herd were only observed twice during the study period and thus their data were not included in home range analysis.

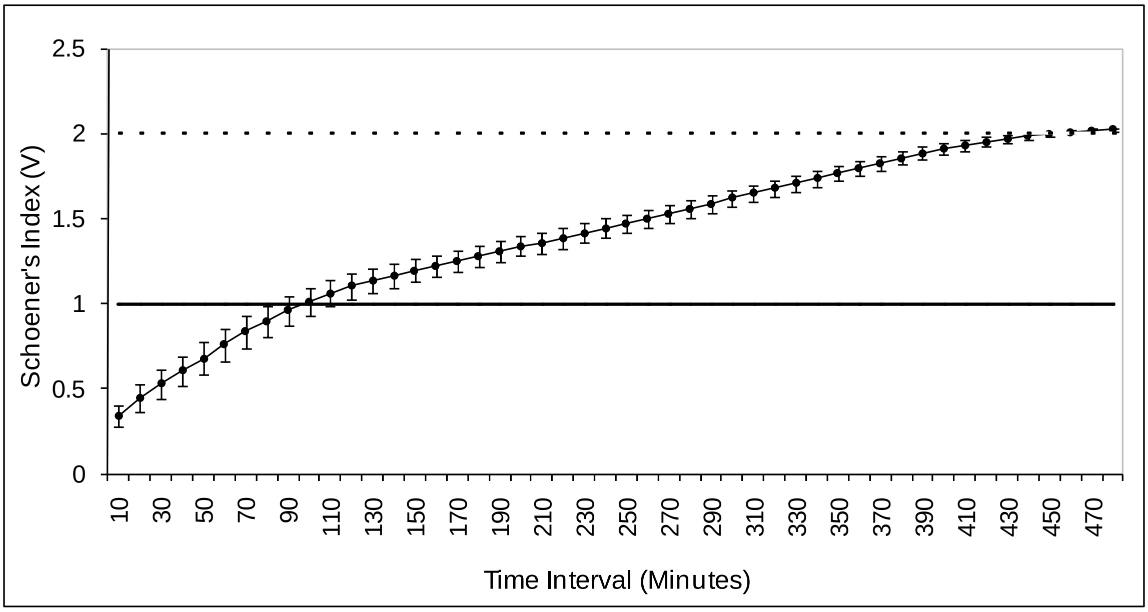


Figure 3.1: Testing time to independence using the Schoener's index (V ± SE) at different time intervals. The horizontal dashed line depicts the expected value of V when animal locations are statistically independent whilst the horizontal solid line indicates a more practical index value beyond which autocorrelation does not have significant effect on home range estimates.

3.2.2 Data analysis

Roan home range analyses were divided into two categories: (a) analysis of sub-sampled data to achieve objectives 1 to 3, and (b) analysis of the original data to achieve objective 4. Sub-sampling was necessary to increase the sample sizes for comparative analysis on different home range estimators and software packages. Sub-sampling has been used successfully to study the influence of sample size and sampling protocols on home range estimation of snapping turtles and antler flies (De Solla et al., 1999) and red squirrels (Wauters et al., 2007). Sub-sampling was done on the two roan groups, which had sufficiently large number of locations (n=132). This is because incremental area analysis showed that area-observation curve (plot of estimated home range size with MCP against the percentage number of locations used to generate the estimate, Kenward et al, 2008) reached an asymptote for the two roan groups at mean ± SE of 116 ± 3 locations or 87.5 5 ± 2.5% of total locations. Therefore, the data were sufficient to describe adequately the roans' home ranges.

Each of the two roan groups was sub-sampled using two procedures: random and systematic. For the random sub-sampling, locations were drawn randomly with replacement, producing six subsamples (which was the maximum number of replicates for the smallest sample size of 22 locations) for each of the following percentages of total sample size: 16.66, 33.33, 50, 66.66, and 83.66% of 132 locations, hereafter referred to as trials. These percentages corresponded to 22, 44, 66, 88, and 110 locations, respectively. This produced 30 subsamples per roan group, making up a total of 60 subsamples. For the systematic sub-sampling procedure, locations were drawn without replacement that yielded subsamples of sizes 22, 44, 66, 88, and 110, with 6 trials, 5 trials, 4 trials, 3 trials, and 2 trials, respectively. This produced 20 subsamples per roan group, making up a total of 40 subsamples. For studying the effect of sampling time intervals, subsamples of 44 animal locations each were drawn without replacement with 5 trials, 4 trials, 3 trials, 2 trials and 1 trial that corresponded to 2, 4, 6, 8 and 10 hour intervals, respectively.

3.2.2.1 Comparison of the effects of software packages, home range estimators and sampling protocols in home range estimation

The effect of software packages in estimation of home ranges was investigated using two packages that have the potential to dominate home range analysis: the RANGES software package (Kenward et al., 2009) and the Adehabitat software package (Calenge, 2006). The RANGES software is costly and was developed in the 1980s for home range analysis and has since dominated the field as evidenced by the great number of papers published using the software (Anatrack, 2010). The Adehabitat package was developed in 2006 and has the following advantages: (i) it is free and open source software, (ii) it has more home range estimation functionalities including the newly developed techniques such as the Brownian bridge approach (Horne et al., 2007) and local convex hull (Getz et al., 2007), and (iii) it is a package implemented in a larger software – the R software for statistical computing (R Core Team Development, 2007), which contains other diverse packages and tools for further data analysis including ecological modelling. Therefore, the future of the Adehabitat package seems to be bright especially because of its free availability in a world battling global economic crisis. Therefore, there is an urgent need of a review of the new Adehabitat software before it dominates the field. Past studies have compared the RANGES software with other home range analysis software other than Adehabitat (Lawson and Rodgers, 1997; Larkin and Halkin, 1994).

This study compares three commonly used home range estimators that are used as default functionalities in both RANGES 8 and Adehabitat 1.8.1. These include minimum convex polygons (MCP), fixed kernel density (KDE), and incremental cluster analysis polygons (ICP). The performance of these three estimators was assessed using percentage coefficient of variation (%CV). Estimators with best performance are those which produce similar home range estimates over different subsamples taken from the same animal (Wauters et al., 2007). That is, the lower the %CV, the higher the performance and *vice versa*. Correlation analysis was carried out between sample size and home range size, and sample size and coefficient of variation to investigate how the performance and home ranges varied with sample size.

To establish an appropriate future sampling protocol for the endangered roan antelope that is accurate, efficient and cost-effective, the sub-sampled roan location data was analyzed using different (1) sample sizes, (2) sampling intervals between successive locations, (3) times of the day and (4) sampling procedures (that is, systematic and random). The analyses of sub-sampled data tested the effect of each of these factors on the roan antelope's home range and core area estimates. For all home range analysis, 95% and 50% of the locations were used to represent home range and core area estimates, respectively, as these cut-off points are commonly used in past studies (Franzreb, 2006; Cimino and Lovari, 2003; Walters et al., 2002; Doster and James, 1998), and therefore relevant for comparison of studies.

The time of the day was sub-divided into three sessions: morning (0800-1000), mid-day (1200-1400) and afternoon (1600-1800). The two sampling procedures were investigated by sub-sampling the data systematically with constant time intervals (of 2, 4, 6, 8 or 10 hours) and at random with a mix of different time intervals. For example, for the systematic sampling five locations per day (0800-1800) can only be recorded in 2 ways: 0800, 1000, 1200, 1400, and 1600 or at 1000, 1200, 1400, 1600 and 1800. However, the five locations per day for the random sampling can be recorded in these two ways plus 4 more different combinations: 0800, 1000, 1200, 1400, and 1800, or 0800, 1000, 1200, 1600, and 1800, or 0800, 1000, 1200, 1600, and 1800, or 0800, 1000, 1400, 1600, and 1800 or 0800, 1200, 1400, 1600, and 1800. For the purpose of making direct comparisons for the systematic and random sampling procedures, the sample sizes were the same (that is, 22, 44, 66, 88, 110 and 132 animal locations).

3.2.2.2 Comparison of home range characteristics for roan groups and lone males

Home range analysis based on original data for roan groups and lone males was carried out in RANGES software using three estimators (KDE, MCP, and ICP) and in Adehabitat package using the local convex hull (LCH) method. Home range sizes, shapes and overlap were compared for the roan groups and lone males. For the 3 roan groups, five home range indices were computed for the wet, dry and combined seasons. The five indices were: home range size using LCH method, distance travelled per day, speed of movement, spread of the group and herd size.

3.2.2.3 Home range estimators explored

Before home range analysis using the three estimators, described in section 3.2.2.1 and 3.2.2.2, an exploratory data analysis was carried out during which several techniques of home range estimation were explored using the available data of the roan antelopes. The Brownian Bridge (BB) approach produced very large home range sizes in an order of magnitude more than those estimated using the MCP and Kernel density (KDE) methods. Such huge differences are unrealistic and contrary to existing literature**.** Huck et al (2008) also reported obtaining extraordinary home range overestimates when using the BB approach. These authors also found that the BB approach is unsuitable for species in which range size is small compared to average travel speed. The BB approach is said to be suitable for estimating a more ecologically meaningful home range (Horne et al., 2007) and for identifying important characteristics of migration routes, such as stopover sites (Mehlman et al., 2005), movement corridors (Berger, 2004), and migratory landscape and habitat features (Skagen et al., 2005). However, this method is dependent on several factors: distance between observed locations both in space and time, the error associated with each observed location, and the animal's mobility (Horne et al., 2007). This may limit the validity of the results of this method in cases where the error associated with each observed location was not accurately determined during data collection period. Based on preliminary results the BB approach was found to be unsuitable for this study and therefore was not pursued further.

Different smoothing parameters for the kernel density method were explored. The Epanechnikov's *h* smoothing parameter produced larger home ranges areas than the reference h_{ref} and twice as large as the MCP home ranges. These estimates are contrary to past studies that have found that MCP estimates are usually larger than other methods (Laver and Kelly, 2008; Kenward, 2001; Harris et al., 1990). The Least Squares Cross Validation (LSCV) failed to compute roan home ranges in all the cases due to failure to converge to true utilization distribution. The reason for this failure may be due to the discretization of the roan data, that is, the data had identical values due to animals resting for more than two hours (interval time between observed animal locations) in the same place. This problem has been noted by other users but no solution has been found to fix it (Hemson et al., 2005; Silverman, 1986). Therefore, the analysis in this study was carried out using fixed kernel density with the *h*ref smoothing parameter (KDE_{href}).

3.3 Results

3.3.1 The effect of software packages in home range estimation

A comparison of home range and core area estimates between Adehabitat and RANGES software showed similar results for MCP and ICP methods but different estimates for KDE_{href} method (Figure 3.2). Paired t-test indicated that KDE_{href} estimates computed using Adehabitat software were significantly greater than KDE_{href} estimates computed using RANGES software for both home range (t=12.443, df=60, p<0.0001) and core area (t=11.471, df=60, p<0.0001). Also, the KDE_{href} estimates computed using Adehabitat software had greater variation than the other estimates.

A comparison of home range sizes within each software showed that the three estimators produced different estimates. For the Adehabitat software, the ICP estimates were significantly smaller than MCP (t = -14.276, df = 60, p<0.0001) and KDE (t = -15.110, df = 60, p<0.0001) estimates. Similarly, for the RANGES software, the ICP estimates were significantly smaller than MCP (t = -17.253, df = 60, p<0.0001) and KDE (t = -23.903, df = 60, p<0.0001) estimates. Also, for the Adehabitat software the KDE estimates were significantly larger than the MCP estimates (t = 12.207, df = 60, p<0.0001). Comparison of core areas yielded the same results. In both software packages the 95% ICP home range estimates were so small that they were similar to the core areas of 50% MCP and 50% KDE estimators.

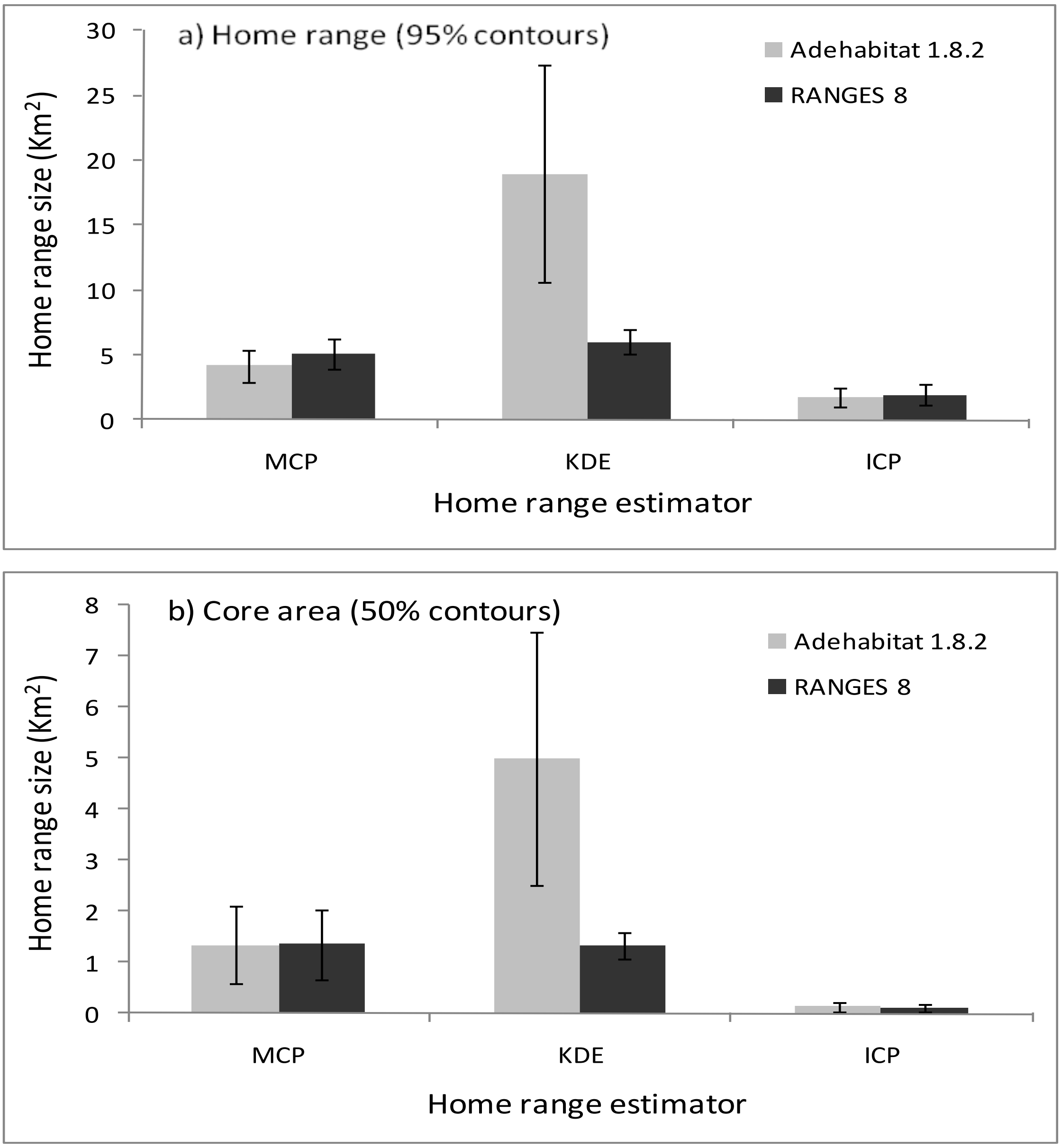


Figure 3.2: Assessing the effect of software package in estimation of a) home range sizes and b) core areas for roan antelopes using incremental cluster analysis polygons (ICP), fixed kernel density (KDE) and minimum convex polygon (MCP) estimators. The bars represent mean ± SD of estimates.

3.3.2 Comparison of performance of three home range estimators

Assessment of performance of home range estimators using percentage coefficient of variation (%CV) showed large differences (Table 3.1). The mean ± SD of %CV showed that the MCP (11.92 ± 6.65) and KDE (12.04 ± 6.60) had similar and best performance for estimating home ranges as compared to ICP (29.90±3.82) method. The KDE (15.48 ± 10.97) had the best performance for estimating core areas followed by MCP (18.88 ± 12.88) whereas ICP had the poorest performance (49.23±6.77) for core area estimation.

All %CV decreased with increase in sample size for all three estimators for both home range and core area estimates, that is, performance was best at high sample sizes for all estimators for home range and core area estimation (Table 3.1; Figure 3.3). For KDE method the %CV decreased significantly with increase in sample size for both home range and core area estimates. However, for MCP the %CV decreased significantly for home range estimation but decreased insignificantly for core area estimation with increase in sample size. The opposite was true for ICP estimator in which the %CV decreased insignificantly for home ranges but significantly for core areas with increase in sample size.

Table 3.1: Percentage coefficient of variation (%CV) for home range (95% contours) and core area (50% contours) estimators using sub-sampled data of two groups of roans. Over all subsamples, the number of animal locations (sample size) varied between 22 and 110 (mean ± SD = 66 ± 31). Spearman's r for correlations between sample size (n, number of animal locations) and the various range-size estimators; NS, not significant ($p>0.05$), *$p<0.05$, **$p<0.01$

Parameter	KDEhref	MCP	Cluster
Coefficient of variation (%CV) for home ranges: mean ± SD	12.04 ± 6.6	11.92 ± 6.65	29.91 ± 12.07
Coefficient of variation (%CV) for Core areas: mean ± SD	15.48 ± 10.97	18.88 ± 12.88	49.23 ± 21.40
Correlation coefficients, r			
n, home range size	- 0.34 NS	+ 0.95**	+ 0.14 NS
n, core area size	+ 0.11NS	+ 0.87*	- 0.84*
n, %CV home ranges	- 0.89*	- 0.96**	- 0.37 NS
n, %CV core areas	- 0.90*	- 0.43 NS	- 0.90*

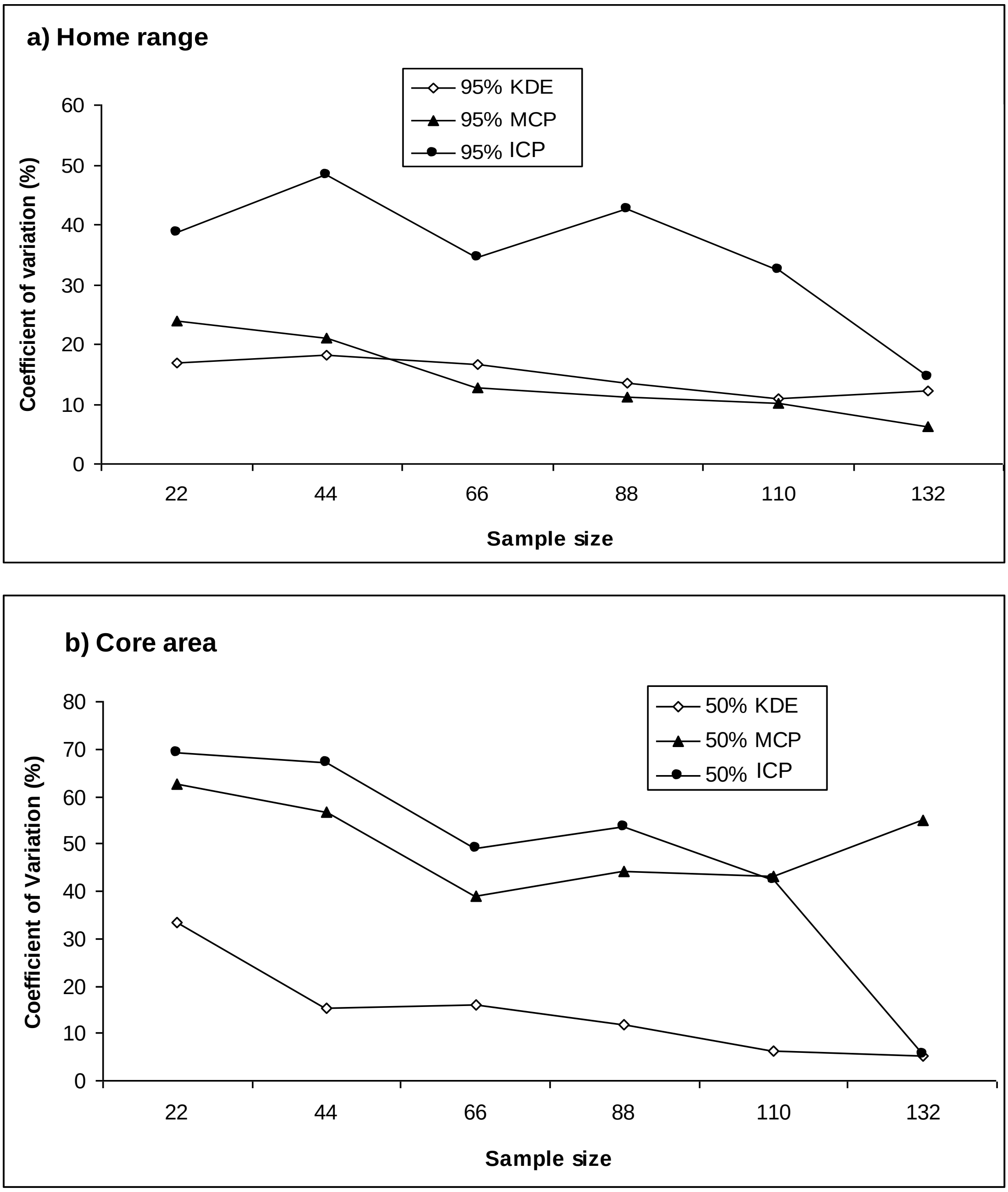


Figure 3.3: Coefficient of variation in (a) home range and (b) core area against sample size, for each of the three estimators. Coefficient of variation is a measure of performance of an estimator.

3.3.3 Influence of sample size and sampling procedure (random and systematic) on home range estimation

There was no significant difference between the home range and core area estimates for data sub-sampled randomly or systematically in all the three estimators (Figure 3.4). However, the home range and core area estimates increased and decreased with increasing sample size for MCP and KDE, respectively. The MCP estimates significantly increased with sample size for both home ranges ($r = 0.99$, $n = 12$, $p = 0.003$) and core areas ($r = 0.99$, $n = 12$, $p = 0.02$). The correlation of KDE home range and core area estimates with sample size was insignificant. The ICP estimator indicated an insignificant positive and significant negative correlation ($r = -0.84$, $n = 12$, $p = 0.04$) with sample size for home range and core area estimates, respectively. Therefore, MCP estimator was more sensitive to sample size than KDE and ICP methods. This implies that at small sample sizes the MCP will produce underestimates for home ranges and core areas.

Figure 3.4 shows that at sample sizes of about 40 locations for core areas and 100 locations for home ranges, the KDE and MCP produced the same estimates for both the systematic and random sampling protocols. This illustration suggests that an average of the KDE and MCP estimates can be a good measure of core areas and home ranges for the roan antelopes at varying sample sizes. Based on this KDE-MCP average, further analysis were carried out to investigate whether small-sized datasets collected once daily using either systematic or random sampling protocols differed with the large-sized data collected 6 times a day. Results showed no significant difference between estimates computed using data of 32 samples (collected at a frequency of 1 location per day for 32 days) and 132 samples (collected at a frequency of 6 locations per day for 22 days) (Figure 3.5). Calculations based on past field data collection costs in Kenya indicated that using the data of 32 samples instead of the 132 samples could save up to 60% of the total cost (Table 3.2). The costs can even be lower if data were collected randomly as opposed to systematic sampling. Random collection of roan location data can be combined with routine schedules of security patrol, research or management duties to lower the cost.

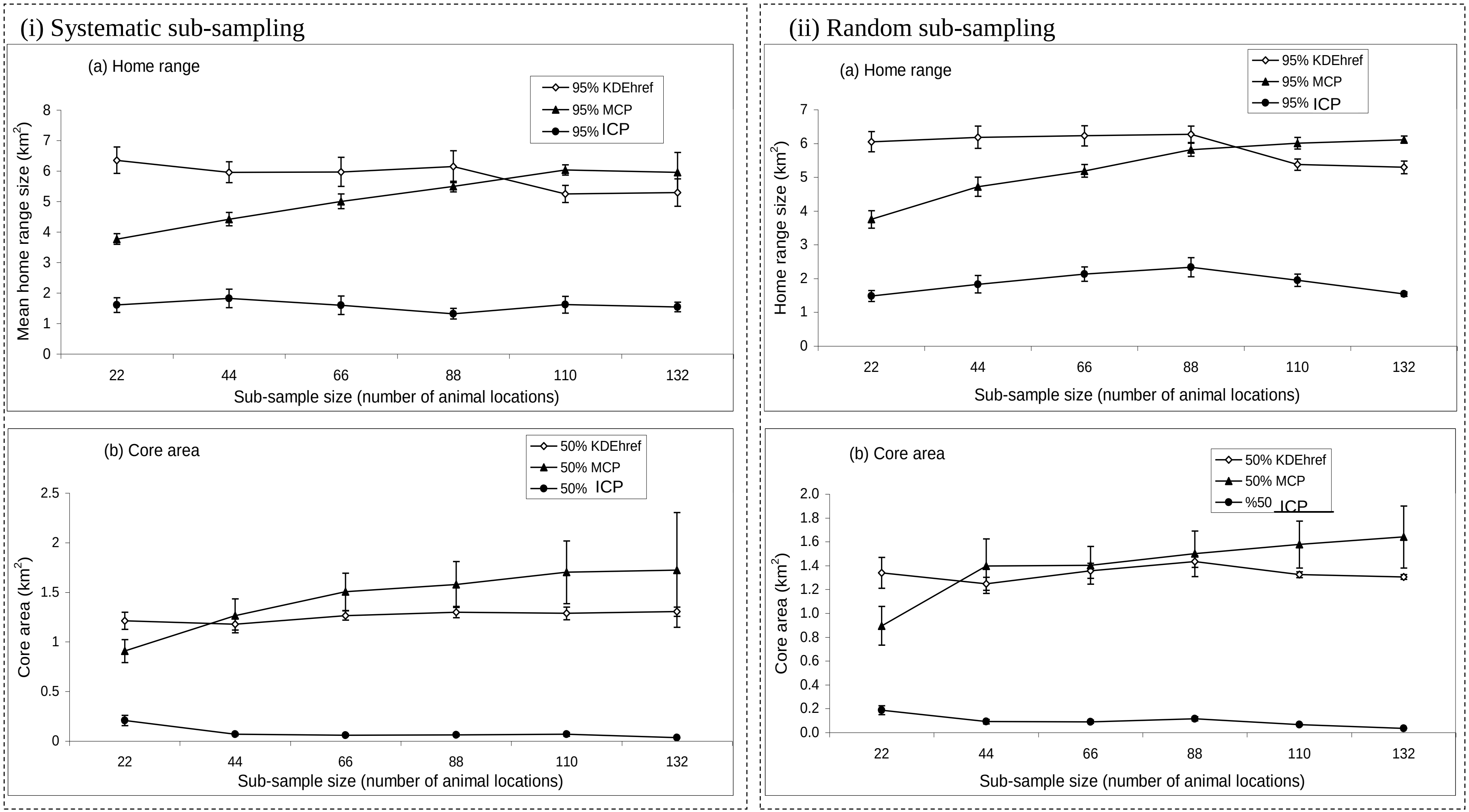


Figure 3.4: Comparison of change in (a) home range size and (b) core area produced by three estimators against sample size using animal locations of two roan groups sub-sampled using (i) systematic and (ii) random sampling procedures. Points are mean ± SE.

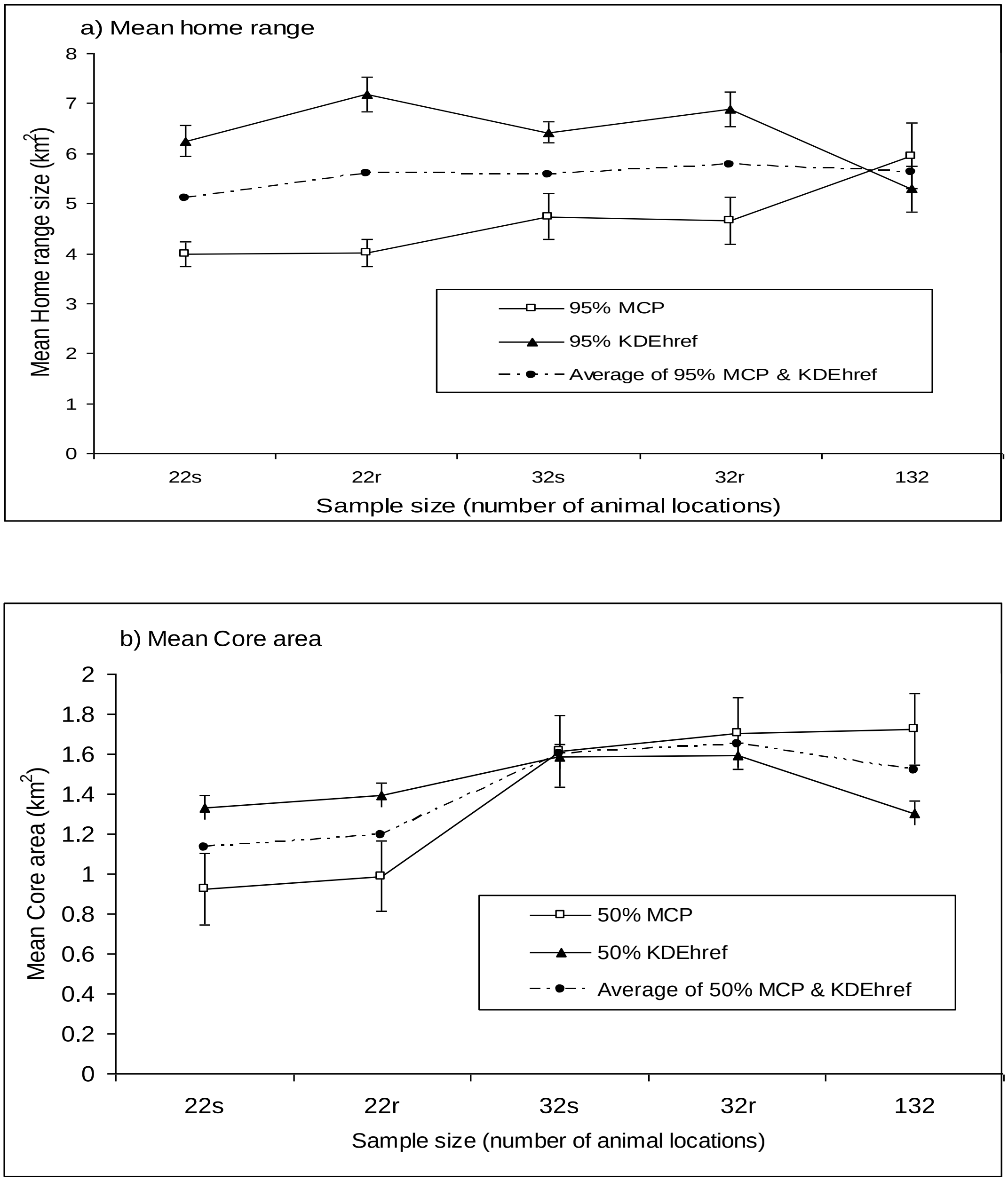


Figure 3.5: Comparison of (a) mean home range size and (b) core area of subsamples with original sample (n=132; 6 locations per day) of two groups of roans using two home range estimators. The points are mean ± SE; sub-samples were sampled using random procedure (r) and systematic procedure (s) with 1 location per day.

Table 3.2: Estimated cost of collection of data with varying sample sizes. The cost per full day is a rough estimate based on the actual amount of money spent during data collection in Ruma National Park, Kenya

Sample size	Cost per full day	No.of days	Length of day	Total cost
22 locations (22 quarter days * 1 location per day)	Ksh. 5,000	22	Quarter	Ksh.27,500
32 locations (32 quarter days * 1 location per day)	Ksh.5,000	32	Quarter	Ksh.40,000
132 locatios (22 full days * 6 locations per day)	Ksh. 5,000	22	Full	Ksh.110,000

3.3.4Influence of sampling interval on home range estimation

Comparison of home ranges and core areas calculated using data (n = 44 animal locations) collected at sampling intervals of 2, 4, 6, 8 and 10 hours between successive animal locations did not show any significant differences in the three home range estimators (MCP, KDE and ICP) (Figure 3.6). All sampling intervals yielded similar estimates, implying that the time intervals considered did not have any effect on the home range and core area estimation. However, the precision and accuracy of home range and core area estimates was higher at shorter time intervals, as shown by smaller standard errors.

3.3.5Effect of time of the day on home range estimation

Comparisons showed that home range and core area estimates for the mid-day session (12 noon -2 pm) were smaller than those of the morning (8 – 10 am) and afternoon (4 – 6 pm) sessions for the MCP and KDE estimators (Figure 3.7). This is probably because the roans were always resting in particular areas during the hot mid-day session, especially in areas next to water points as the roans drink mostly during the hot session of the day. However, none of these differences were significant.

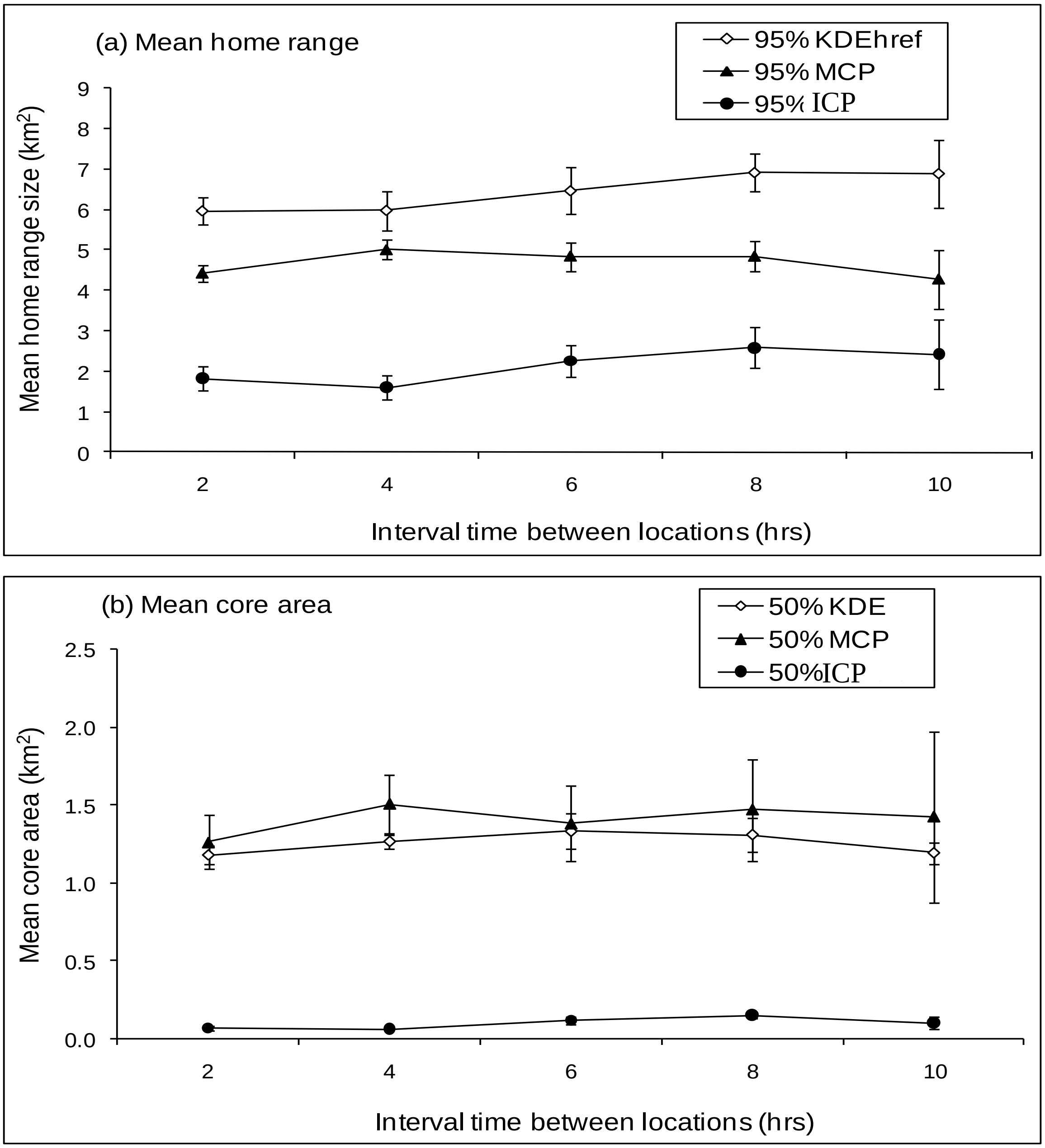
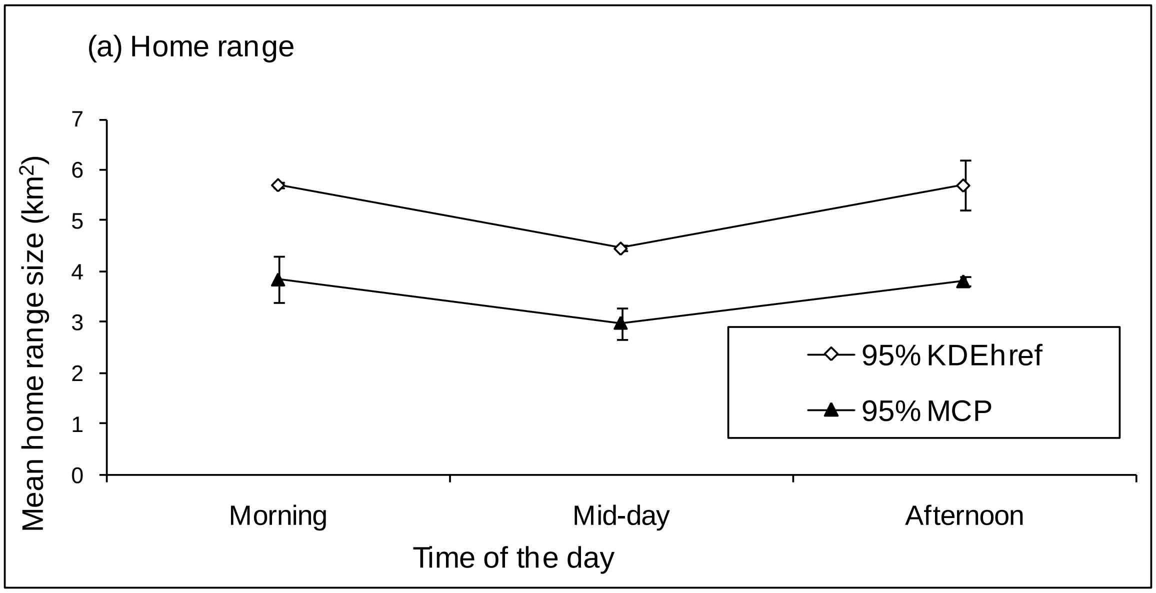


Figure 3.6: Comparison of change in (a) home range size and (b) core area produced by three estimators against sampling interval time between animal locations of two roan groups using data sub-sampled systematically with subsamples of 44 locations. Points are mean ± SE.


(a) Home range

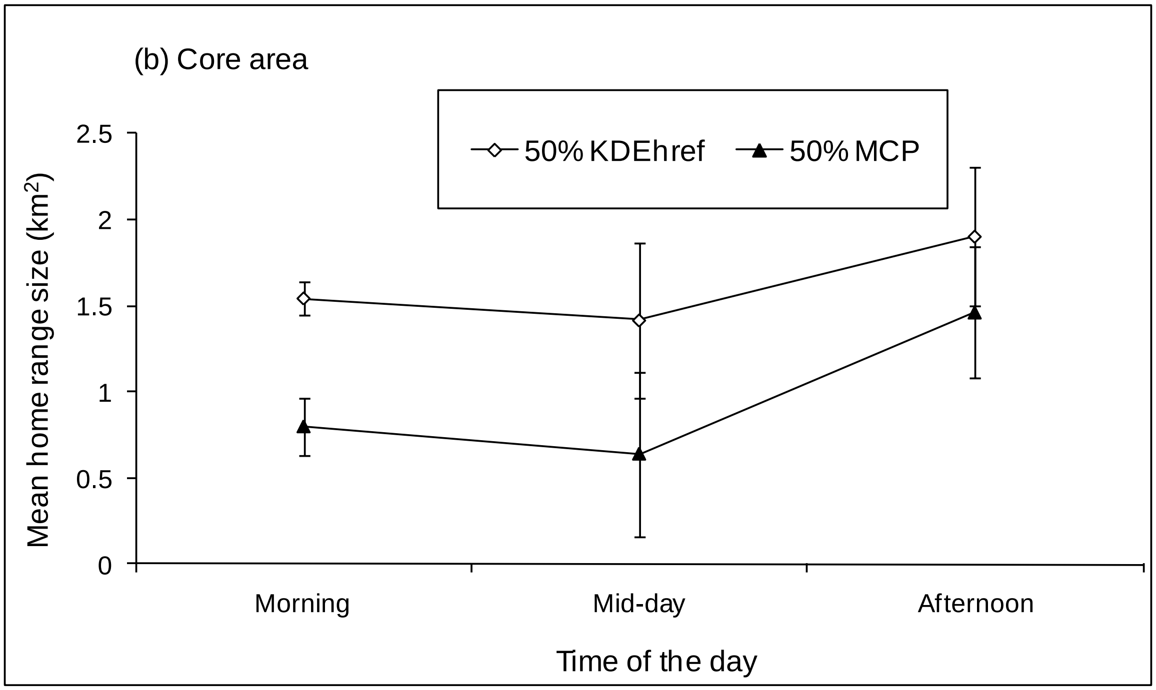

(b) Core area

Figure 3.7: Comparison of change in (a) home range size and (b) core area produced by two estimators against time of the day using sub-sampled animal locations of two roan groups. Points are mean ± SE.

3.3.6Comparison of home range characteristics for roan groups and lone males

Estimation of home ranges for roan groups using three estimators (KDE, MCP and LCH) yielded insignificantly different estimates (Figure 3.8). The MCP estimator had the largest estimates followed closely by KDE whilst the LCH estimates were the smallest. On the other hand, the largest estimates for lone males were produced by KDE whilst MCP and LCH yielded similar estimates. However, considering the home range shape, LCH estimates were more realistic and more accurate as they aligned well with sharp features like park fence that delineates the actual roan home ranges in RNP (Figure 3.9). Also, the core areas computed by LCH method represented the animals' locations more accurately than the other two methods. The LCH had 3 core areas; KDE had two core areas whereas MCP had a single mononuclear core area, which poorly represented the animals' locations. The home range and core area estimates computed by KDE and MCP spilled over the RNP boundary, implying that they were overestimates. Comparison of home ranges between roan groups and lone males showed no significant differences for all three estimators.

For both the roan groups and lone males the three estimators showed that the combined season estimates were the largest whilst the dry season estimates were the smallest. However, all the three methods indicated that these seasonal differences in home ranges of roan groups and lone males were insignificant. Analysis of seasonal variation in other home range characteristics for the roan groups in RNP indicated no significant difference in the distance travelled daily and average speed of movement (Table 3.3). However, during the dry season roan groups significantly spread less (t = 4.399, df = 57, $p < 0.0001$) and had larger herd sizes (t = 5.073, df = 65, $p < 0.0001$) than in the wet season.

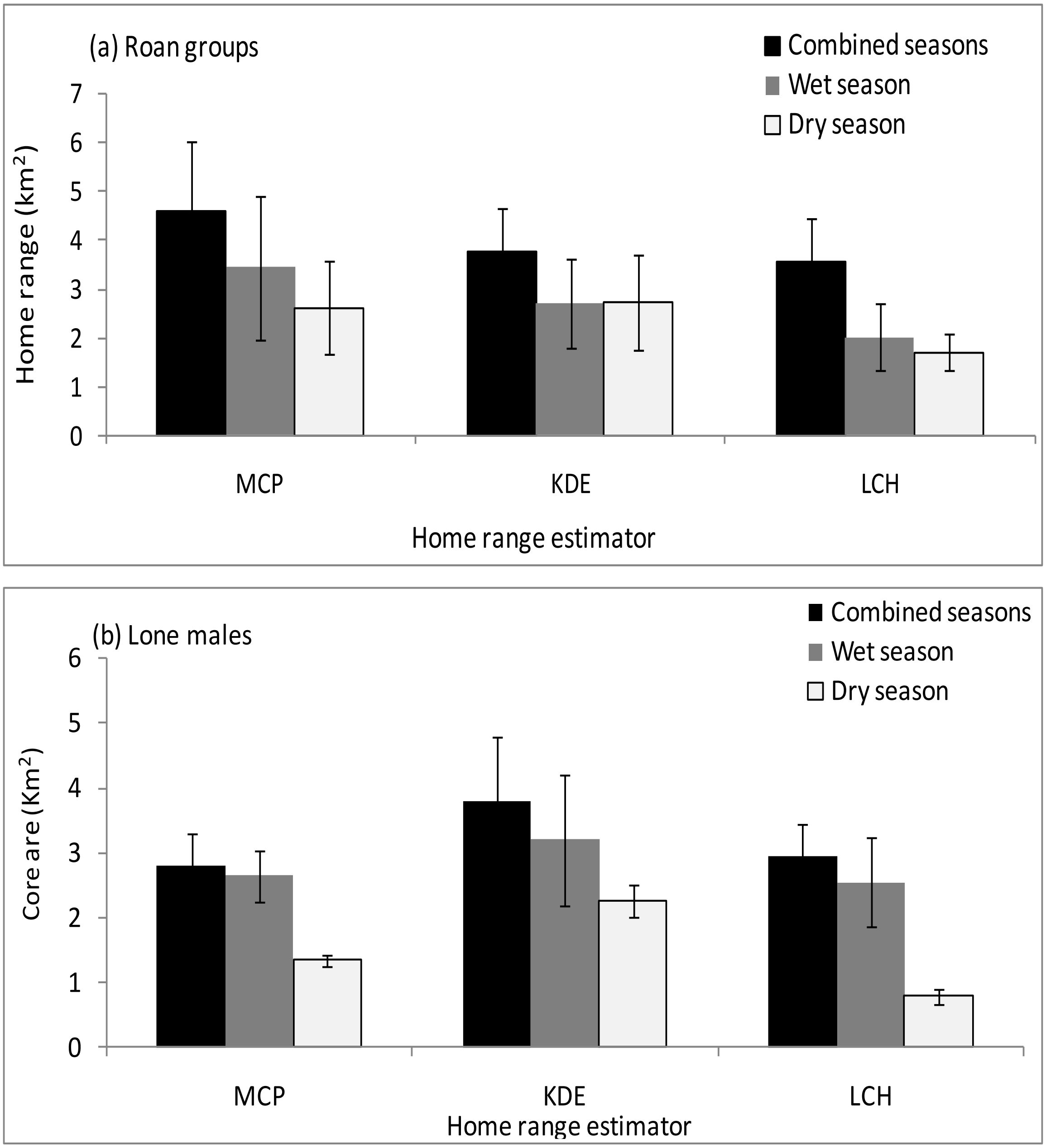


Figure 3.8: comparison of home ranges estimates of (a) 3 roan groups and (b) 3 lone males in RNP in different seasons using 3 estimators.

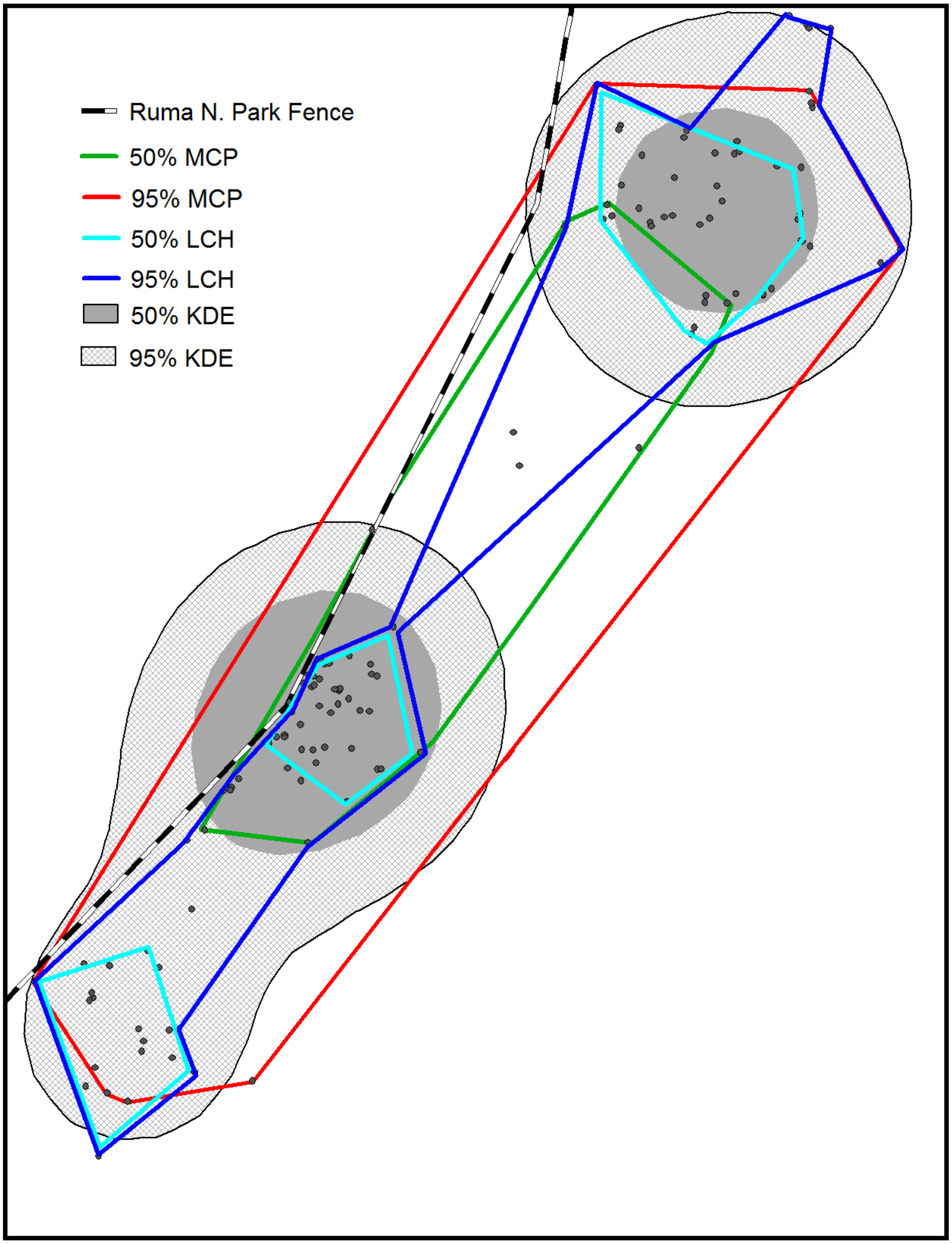


Figure 3.9: Comparison of home range and core area shapes of one roan group in RNP using three estimators. The black dots represent animal locations.

Table 3.3: Comparison of mean ± SE of range indices in wet, dry and combined seasons for 3 roan groups in RNP. Note: * indicates statistical significance at p=0.05 for differences between wet and dry seasons; and n is sample size.

Home range Index	Combined seasons	n	Wet seasons	n	Dry seasons	n
Home range size (km^2)[a]	3.57±0.88	3	2.02±0.67	3	1.71±0.36	3
Distance travelled per day (km)	1.43±0.08	49	1.41±0.10	28	1.44±0.12	21
Speed (m/min)	2.38±0.13	50	2.35±0.17	30	2.41±0.19	20
Spread of roan group (m)*	80.91±6.38	59	147±19.50	33	59.37±4.16	26
Herd size (nos./group)*	10.56±0.53	67	8.59±0.59	41	13.96±0.53	26

Nb: [a] the home range estimates were based on the Local Convex Hull (LCH) technique.

The KDE estimator was used to assess home range overlap because it was shown to be less sensitive to sample size variation and Kenward (2001) demonstrated that this method can yield stable estimates with small sample sizes. Mapping of home ranges showed more percentage overlap between roan groups and lone males' home ranges than within roan groups or lone males' home ranges (Figure 3.10). Only the home ranges of 2 roan groups overlapped slightly by 1% between each other whilst the home ranges of all the 3 lone males did not overlap between each other at all (Figure 3.11). However, the home ranges of all the 3 lone males overlapped substantially with those of their corresponding 3 roan groups. In particular, male 1 overlapped with group 1 by 46%, male 2 overlapped with group 2 by 67%, and male 3 overlapped with group 3 by 47%.

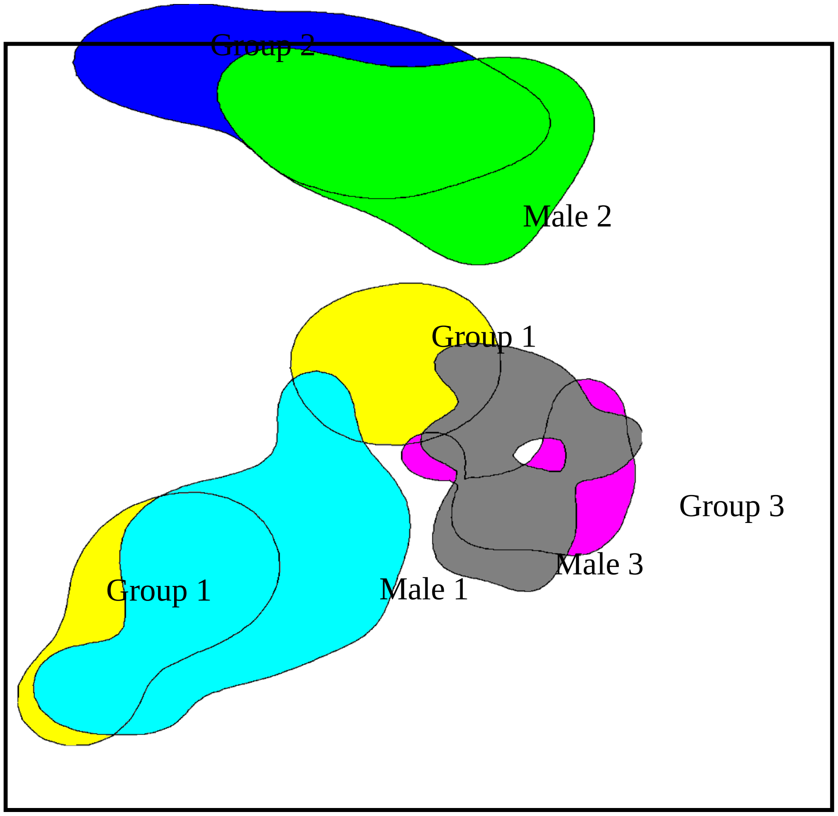


Figure 3.10: Overlap between home ranges for 3 roan groups and 3 lone males in RNP estimated using fixed kernel density (KDE).

	Group 1	Group 2	Group 3	Male 1	Male 2	Male 3
Group 1						
Group 2	0%					
Group 3	1%	0%				
Male 1	46%	0%	0%			
Male 2	0%	67%	0%	0%		
Male 3	12%	0%	47%	0%	0%	

Figure 3.11: Percentage overlap between and within home ranges of 3 roan groups and 3 lone males in RNP.

3.4 Discussion

3.4.1The effect of software packages in home range estimation

The results showed that the RANGES 8 and Adehabitat 1.8.2 software packages produce different home range estimates. This concurs with findings by Lawson and Rodgers (1997), who found out that home range estimates calculated using RANGES, HOME RANGE, CALHOME, AND TRACKER software packages were all different. Although, home range estimates differed between RANGES and Adehabitat packages for ICP and MCP estimators, significant differences occurred only for the KDE estimator. In general, differences in home range estimates in KDE methods arise due to four main reasons (Lawson and Rodgers, 1997): (i) the kernel function used (such as bivariate normal, Epanechnikov, Cauchy, and bi-weight), (ii) the smoothing parameter used (that is, h_{ref}, LSCV and user defined), (iii) the number of grid cells used for the estimation, and (iv) the method used in computing the limits of the home range from the utilization distribution (UD). In this study, the kernel function (bivariate normal), smoothing parameter (h_{ref}) and number of grid cells (40 * 40) were all the same for both Adehabitat and RANGES software packages. Therefore, the differences between Adehabitat and RANGES fixed kernel density (h_{ref}) estimates were caused by the use of different (1) methods for computing the limits of the home range from the UD and (2) formulas for calculating the reference smoothing parameter. RANGES software uses Seaman and Powell's (1996) reference smoothing parameter whereas Adehabitat uses the Worton's (1995) reference smoothing parameter. The latter parameter is said to over-smooth the kernel density especially when the UD is multimodal (Kenward et al., 2009). Cluster analysis already confirmed that the roan locations are multimodal.

These findings suggest that the RANGES software performs better than the Adehabitat software in home range analysis. This is because MCP and KDE home range estimates produced by RANGES are similar but those of Adehabitat are significantly different. The Adehabitat KDE estimates were more than 3 times higher than MCP estimates, which is contrary to past studies. Past research studies on home range analysis (Burgman and Fox, 2003; Kenward, 2001) show that MCP estimates should either be larger than or at least similar to KDE estimates. In many instances, the MCP estimates are far larger than all other estimators because they include large areas that are never used by the studied animal. In order to improve the performance of the Adehabitat software, it could implement a parallel bivariate normal fixed kernel density estimator using the Seaman and Powell's (1996) reference smoothing parameter, which is not affected by multimodal distribution of animal location data. This will provide an alternative to the Worton's (1995) smoothing parameter that is already implemented in Adehabitat software.

Based on the differences noted in this study and past studies, comparisons of home range size and habitat use of a particular species between different studies could be very misleading. Problems occur if the different studies fail to report the software package used in home range analysis, home range estimator used, user-selected options for calculating the estimator, and the input values of parameters (Lawson and Rodgers, 1997). There is increasing concern that valid comparisons among home range studies may not be possible with the on-going proliferation of computer software packages to meet specific objectives of individual research projects. There is currently no agreement upon software for home range analysis. As recommended by Larkin and Halkin (Larkin and Halkin, 1994) and Lawson and Rodgers (1997) there is a need to develop a comprehensive analysis software to provide common standards and be capable of computing all home range characteristics of animal movement.

3.4.2 Comparison of home range estimators

Comparison of the 4 home range analysis estimators demonstrated that there is no single method suitable for computing all home range characteristics. The incremental cluster analysis polygon (ICP) home range estimates were significantly smaller than all other methods; its 95% home range was as small as 50% core areas of the other methods. Therefore, the ICP method is suitable for estimating multinuclear core areas as opposed to home ranges, as earlier concluded by past studies (Wauters et al., 2007; Kenward, 2001; Kenward, 1992). The fixed kernel density (KDE) is more reliable for estimating core areas as well as home range sizes. However, the minimum convex polygon (MCP) is only suitable for estimating home ranges sizes and not core areas. If used for estimating core areas, the MCP produces overestimated mononuclear core area that includes areas not utilized by the animals (Kenward, 2001; Kenward and Hodder, 1996).

The KDE and MCP produced similar home range and core area estimates. In most cases the MCP estimates were slightly larger than those of KDE estimator. The KDE estimator was less sensitive to changes in sample size than the MCP. The KDE estimator requires fewer animal locations to produce stable home ranges than the MCP (Kenward, 2001). Therefore, in this study KDE performed better in estimating both roan home ranges and core areas. Many past studies (Laver and Kelly, 2008; Kernohan et al., 2001; Worton, 1995) agree that KDE is a better estimator than MCP especially when the right smoothing parameter is used. However, KDE has also been shown to produce underestimated or overestimated home ranges in some instances (Getz and Wilmers, 2004). Although, some authors (Laver and Kelly, 2008; Borger et al., 2006) advocate against the use of MCP as a home range estimator, other authors (Huck et al., 2008; Wauters et al., 2007) argue that MCP is important in certain circumstances. For example, MCP could be useful in estimating absolute size of the area covered by an animal or population, regardless of the internal structure (Huck et al., 2008). Estimation of such an area could be important for management of a protected species by ensuring that the estimated range contains adequate resources. Overall, MCP is the oldest method and still remains the most widely used for home range estimation and comparison between studies (Huck et al., 2008; Harris et al., 1990).

3.4.3 Comparison of sampling protocols for roan movement data

Results showed that 6 factors need to be considered when designing a sampling protocol for collection of roan movement data: sample size, sampling procedure (random or systematic), sampling frequency (continuous or point location sampling), sampling time interval between successive animal locations, autocorrelation of animal locations, and timetabling (time partitioning during the day). Roan movement data can be collected cost-effectively at random using the point location sampling at longer time intervals such as one animal location per day. The results of this study showed that there are no differences in the home ranges estimated using either random or systematic sampling procedures. Past research recommends the use of systematically sampled data to minimize the effect of autocorrelation and increase the accuracy in home range estimation (De Solla et al., 1999). However, considering the cost of field data collection in a National Park, the random sampling procedure is preferable because data can be collected by security rangers on routine patrols, researchers on routine research schedules and managers on routine management duties instead of allocating a particular vehicle, staff and other resources specifically for data collection. Results also showed that the home ranges estimated using a smaller sample size (n=32) sampled once daily were not significantly different from those estimated using a larger sample size (n=132) sampled 6 times per day. This emphasizes that data collection costs can be reduced by collecting fewer samples at longer time intervals provided that time available for the research is not limited. This sampling design is suitable for long term monitoring of roan movement and distribution. However, in cases where research results are needed urgently such as this study, data should be collected at shorter time intervals for a short period.

Autocorrelation still remains controversial but needs to be addressed when designing sampling protocols for collecting roan movement data because it affects home range estimation. The risk of autocorrelation in the randomly sampled data can be reduced by sub-sampling it until the right sampling time interval is reached. Such a time interval should be lower than that required for statistical independence between successive animal locations. For statistical independence the Schoener's (1981) index should be at least 2 (Swihart and Slade, 1985b). However, the correct time interval should be the one that yields a Schoener's index of at least 1 (Kenward, 2001). For the roan antelope a time interval of 2 hours was adequate to attain a Schoener's index of 1 whilst an interval of about 8 hours was required to yield a Schoener's index of 2 (Figure 3.1). Further analysis of roan movement data using 2, 4, 6, 8, and 10 hour time intervals supported Kenward's (2001) hypothesis that home range estimation is not significantly affected by autocorrelated observations when the Schoener's (1981) index is at least 1. The results showed that home ranges estimated using autocorrelated data sampled at 2 to 6 hour intervals were not significantly different from those estimated using statistically independent data sampled at 8 to 10 hour intervals (Figure 3.6). If autocorrelation had an effect, the home range size would have increased with time interval until autocorrelation is removed as demonstrated by De Solla et al, (1999). However, elimination of autocorrelation has been shown to reduce the biological relevance of home range estimates and yield underestimates (De Solla et al., 1999). Moreover, autocorrelated data has been shown to be useful in producing more accurate and precise estimate parameters of home range size, time partitioning and distance moved (De Solla et al., 1999). However, tests of statistical independence should not be ignored but instead autocorrelation should be included in valid statistical models such as the generalized linear mixed models (GLMM) (Legendre, 1993).

Time partitioning needs to be considered when designing sampling protocols for roan movement studies. If it is ignored, it can lead to biases depending on the sampling design used. Although there was no significant difference between home ranges computed using data collected at different times of the day, the results showed that home ranges of mid-day (1200 – 1400hrs) data were consistently smaller than those of other sessions of the day. This is probably because during this period the temperatures were too high and the roans spent most of the time resting in particular habitats (see chapter 4 section 4.3.3) especially those near water sources. Field observations in RNP indicated that roans mostly drink water during this period and Joubert (1974) noted that after drinking the roans do not move more than 1 km away from water sources during the hot periods of the day. This roan timetabling implies that if movement data are to be collected only once per day, it should not be collected during the mid-day period but instead it should be collected either in the morning (8 - 10 am) or afternoon (4 – 6 pm) periods.

3.4.4Comparison of home range characteristics for roan groups and lone males

All the four home range estimators proved to be useful in characterizing different aspects of the roan home range, but overall the local convex hulls (LCH) method produced the most realistic home range and core area estimates. This is because the LCH home range estimates aligned well with sharp features in the RNP such as the park fence that marks the true roan home range boundary. The LCH method produced three core areas that accurately represent the three suitable patchy habitats near mineral salt lick, water dams and unburned breeding habitat for roan antelopes, respectively. The fixed kernel density (KDE) method produced a home range consisting of two separate portions that accurately represented the roan main habitat utilized most of the time and the breeding habitat. However, the LCH method yielded even a better home range by producing the two portions connected by a narrow corridor that indicates the route used by the roans to migrate to the breeding habitat. The only shortcoming of the LCH method is that its estimates were consistently smaller than those of other methods. This concurs with Getz et al, (2004) findings that LCH yields underestimated home ranges. Therefore, to estimate the total range size of roans, it is better to combine LCH with other methods as recommended by Huck et al (2008).

Assessment of seasonal variation in various roan home range characteristics showed significant differences in only two of them: group herd size and spread. All the other range characteristics (home range size, daily travel distance, and speed) were not statistically significant, probably due to the small sample size, the short period of data collection, and the use of data for only one year. Also, the roan daily behaviour (such as travel distance and speed) may have been altered by the occurrence of births in two roan groups during the wet season. The larger herd sizes that are spread less in the dry season imply the importance of group living in a harsh environment with limited resources. Dorst and Dandelot (1990) found that during the dry season many roan herds merge together into large groups as a result of food and water shortage. During the wet season there is no limitation of food and water and therefore the individual roans can afford to spread out and groups can split up. Wilson and Hirst (1977) noted that roans could be sedentary and occupy the same home range during the wet and dry season if there is plenty of food and water throughout the year.

Although further investigations are needed, these differences in home range characteristics suggest that in the dry season, the roans' habitat was limited by availability of water. Roans are highly water-dependent and are always found near water sources (Dorst and Dandelot, 1990). They have been shown to be severely affected by droughts and to move a lot in search of water (Schuette et al., 1998). However, roans in RNP cannot move far due to restrictions of the park fence and the surrounding farming communities. A combination of these factors may suggest that the roan population in RNP is suffering from the effects of stress. While this needs further research, an urgent solution to boost recovery of the declining roan population in RNP is to ensure adequate supply of water especially during the dry season and periods of drought.

The lack of home range overlap between different roan groups demonstrates that dominant roan bulls defend an area around their herds from intrusion by neighbouring bulls. This is what Joubert (1974) termed the intolerance zone, which differs from a true territory by lack of fixed boundaries. The lone male home ranges managed to overlap with the roan group home ranges by almost 50% because the defended area is not fixed and the lone males keep on tracking the roan groups at a far distance with the aim of accessing females or overthrowing the dominant bull. Joubert (1974) noted that the intruding lone males are not persecuted by the dominant bull as long as they keep a distance of at least 500m away from the roan herd. Although, there is no evidence of the lone males occupying marginal habitats, in cases where resources are very limited, it is likely that the lone males will be forced by the dominant bulls to occupy marginal habitats most of the time.

3.4.5 Limitations and constraints

- Data on roan movement patterns were collected only for 6 months. Although the sample size was adequate for the home range estimators used, better results would have been obtained if data were collected for a longer period or by use of long-term data covering several years and seasons.
- The use of ground-tracking led to collection of only diurnal movement data. Further roan movement data needs to be collected, probably through radio-tracking, to cover day and night. This would provide more insight into roan movement patterns and habitat use in the park.
- Some home range estimators were only implemented in one software package e.g. LCH in Adehabitat package, and therefore in such cases no comparisons could be done.
- Location data for lone males were collected once per day whereas for the roan groups locations were recorded 6 times a day. This could have bias implications when comparing home range characteristics of these two categories. Use of radio collars could effectively avoid this unwanted scenario.
- Some calves were born during the wet season, which may have affected the comparison of home range characteristics between dry and wet seasons. The use of long-term roan movement data including several seasons could have improved the findings.

CHAPTER 4

ANALYSIS OF HABITAT SELECTION BY ROAN ANTELOPES IN RNP USING COMPOSITIONAL ANALYSIS

Different habitat features in RNP

CHAPTER 4: Analysis of habitat selection by roan antelopes in RNP using compositional analysis

4.1 Introduction

4.1.1 Resource selection analysis

Resource selection is a common and important aspect of wildlife science (Alldredge and Ratti, 1986). Information on resource selection allows wildlife managers to make informed decisions on which priority habitats or resources to conserve (McDonald and McDonald, 2002), identify geographical ranges of animals (Millspaugh et al., 2006), and map the potential distribution of animals based on model predictions (Fielding and Bell, 1997). The selected habitats or resources (that is, used disproportionately to their availability) are generally assumed to improve the animal's fitness, reproduction or survival (Thomas and Taylor, 2006) and therefore need to be accurately identified using the available technological and analytical tools.

A vast number of analytical methods have been developed to analyse the diverse hypotheses associated with the concept of resource selection (Pendleton et al., 1998). The high number of methods has been prompted by the lack of agreed upon definition of habitat selection (McClean et al., 1998). Resource selection analysis methods include selection indices, hypothesis tests and confidence interval procedures (Manly et al., 2002). Selection indices are less powerful when compared with other methods. One of the simplest selection index methods is the Ivlev's index (Ivlev, 1961) that does not perform a statistical test but only provides a ratio of habitat use to habitat availability. Common statistical hypothesis testing methods in wildlife habitat studies include the chi-square goodness-of-fit test, Johnson's (1980) technique, and compositional analysis (Aebischer et al., 1993). More advanced tests include regression approaches such as logistic regression, log-linear models, generalized linear models (Manly et al., 2002) and the recently developed information-theoretic approaches (Burnham and Anderson, 2002).

Comparisons of many available habitat selection techniques have been carried out by Alldredge and Ratti (1992; 1986), Alldredge et al, (1998), McClean et al, (1998), Alldredge and Griswold (2006), and Thomas and Taylor (2006; 1990). These studies concluded that there is no single best method and that they are based on various assumptions, which are summarized by Manly et al (2002). These authors noted that not all methods require every assumption to be met and concluded that consideration of the validity of assumptions should guide the selection of a method of analysis.

The choice of a method of statistical analysis of habitat selection is complex and needs consideration of several factors (Manly et al., 2002). The choice of the right method is primarily dependent on the study design selected (Thomas and Taylor, 2006). Study design involves 3 choices: (1) level at which data will be collected – individual animals or population level (Thomas and Taylor, 1990); (2) scales of selection to be studied (Johnson, 1980); and (3) how use and availability (or non-use) data are defined and measured (Buskirk and Millspaugh, 2006). Thomas and Taylor (2006) present a summarized account of 4 study designs used in resource selection studies based on the level at which habitat availability and use are measured – designs I-III originally described by Thomas and Taylor (1990) and design IV by Erickson et al (1998). In design I, use and availability data are measured at the population level; individual animals are not identified. In design II, individual animals are identified and the use of resources is measured for each, but availability is measured at the population level. With design III, individual animals are identified and data on use and availability (or non-use) are measured for each animal. In design IV, resource use (e.g. burrows, roosts, nests, relocations or feeding bouts) is measured multiple times for each animal, and availability (or non-use) is measured for each use site.

Scale is crucial in habitat selection studies as it affects interpretation of results (Ciarniello et al., 2007; Johnson, 1980). This is because different biological processes may operate at multiple spatial scales, and what may appear important at one scale may not be relevant at another (Guisan and Thuiller, 2005). Many authors agree that habitat selection is scale-dependent (Ciarniello et al., 2007; Boyce, 2006; Addicott et al., 1987; Johnson, 1980). Therefore analysis should be done at multi-spatial scales because conclusions from habitat selection studies are valid only within the spatial scale examined (Ciarniello et al., 2007; Lord and Norton, 1990). This means that findings of habitat selection carried out at a finer scale cannot be extrapolated to large scales and conversely, conclusions of large scale cannot be extended to cover the finer scale.

Johnson (1980) proposed four hierarchical orders of habitat selection: the geographic range of a species (first order), selection of a home range within a study area (second order), selection of patches of resources within the home range (third order) and selection of food items within the patch (fourth order). These habitat selection orders or scales of selection are related to Thomas and Taylor's (1990) sampling designs for habitat selection studies. Study design I and design II typically define availability as the study area, which is usually determined by researchers based on a political boundary e.g. a national park. In design III, availability is commonly defined as a home range or a feeding site whilst in design IV availability is defined as an area surrounding a use site. Measuring availability for each use site in design IV distinguishes it from design III where availability is measured for each animal (Thomas and Taylor, 2006). Combining Thomas and Taylor's (1990) study designs with Johnson's (1980) selection orders can enable asking of more broad questions about habitat selection. For example, if design I is combined with the second order selection, one can ask "where are the animals located on the landscape?" (Ciarniello et al., 2007).

The selection of study design and analysis is mainly based on the sampling unit used to assess habitat selection (Thomas and Taylor, 2006). With designs II, III, and IV that usually record animal relocations over time, either an animal or relocation can be used as the sampling unit. However, when relocations are used as the sampling unit and data combined for different animals, extra measures should be taken to assess temporal dependency among relocations and to test the effect of variability in number of relocations per animal (Thomas and Taylor, 2006). Ignoring these measures may yield spurious results because of pseudo replication arising from temporal dependency (Crawley, 2007) and effects of variability among individual animals (Garshelis, 2000). The best recommended sampling unit in habitat selection studies is the use of animals rather than relocations (Thomas and Taylor, 2006; Alldredge et al., 1998; Pendleton et al., 1998; Aebischer et al., 1993). Nonetheless, pooling of relocation data across animals is commonly used to analyze categorical resource use-availability data using chi-square goodness-of-fit test as well as analyzing site-attribute data in logistic regression (Alldredge et al., 1998). Logistic regression has been shown to be suitable for assessing habitat selection in 3 sampling designs (Thomas and Taylor, 2006; Keating and Cherry, 2004; Manly et al., 2002): 1) when each sampling unit in a random sample of units is classified as used or not, 2) when independent random samples of used and non-used units (case-control) are collected, and 3) in Thomas and Taylor's (1990) design I, where individual animals are not identified.

The use of animals as sampling units rather than relocations in habitat selection studies has not gone without criticism. Since the use of animals as sampling unit allows assessment of habitat selection for a group of animals but fails to consider variability in habitat selection among individual animals, Mysterud and Ims (1998) warn that the individual variability in habitat selection should not be ignored. Hence, the K-select analysis method has been developed to identify habitat variables that are selected by individual animals (Calenge et al., 2005). The advantages of this technique are that: 1) a large number of variables can be analyzed simultaneously, 2) it takes into account individual variability in habitat selection, 3) it lacks strict underlying assumptions and 4) its results are displayed graphically, which is a very attractive feature to biologists (Calenge et al., 2005). Its shortcomings are that: 1) it is not a statistical test, 2) it is only suitable for exploratory data analysis and needs further analysis for confirmatory results, 3) its performance has not been rigorously evaluated, and 4) methods such as generalized linear mixed models (glmm) can incorporate individual variability of habitat selection as random effects.

Since there is no single best method for analyzing habitat selection (Thomas and Taylor, 2006; Alldredge et al., 1998; McClean et al., 1998; Alldredge and Ratti, 1992), three techniques were used in this study: compositional analysis, logistic regression and information-theoretic approaches. Compositional analysis is used in this chapter whilst the other two methods are applied in chapter five. Compositional analysis is applied on a regular basis in literature (Manly et al., 2002). It accommodates the potential problems of habitat selection analysis that can arise from: (1) inappropriate sampling level, (2) the unit-sum constraint, (3) differential use of resources by different groups of animals, and (4) arbitrary definition of availability (Pendleton et al., 1998; Aebischer et al., 1993). Compositional analysis counters these problems by: (1) using animals rather than individual animal locations as the sample units; (2) testing for overall departure from random habitat use and determining habitat types used more or less than expected by chance; (3) allowing habitat selection to be grouped into distinct categories (e.g. age, sex, season of observation); and (4) analysing habitat selection at different geographic scales such as study area and home range (Pendleton et al., 1998; Aebischer et al., 1993). Compositional analysis is appropriate for Thomas and Taylor’s (1990) study design II and III and Johnson’s (1980) habitat selection orders 2 and 3. Therefore, analyses were done for both the second – and third – order selection to determine the habitat selection by roan antelopes in different seasons and periods of the day.

4.1.2 Objectives

This chapter aimed at achieving the following objectives:

- To identify the preferred habitats by roan antelopes in RNP.

- To determine how habitat selection by roan antelopes in RNP varies with seasons and times of the day.
- To investigate how roan antelopes allocate time for different activities at different times of the day.

4.1.3 Hypotheses and predictions

This chapter had the following hypotheses:

- Roans prefer certain habitats over others based on distribution of habitat features. It was predicted that (i) roans would prefer habitats that provide adequate resources for forage, water, cover from predators and areas that minimize energy expenditure during normal foraging periods such as low slopes and elevation; and (ii) roans would avoid areas that have high risk of poaching such as near public roads, snare hotspots, unfenced park boundary, and away from security outposts and gates.
- The preferred habitat by roans varies with season and time of the day. It was predicted that (i) during the breeding season roans would prefer unburned vegetation that has conducive habitat cover from predation for calves; (ii) habitats near water are more preferred by roans in the dry season whereas limited habitat selection occur in the wet season; and (iii) roans select habitats with best forage in the morning and evening when feeding activity is expected to be highest whilst habitats with best shelter and near water points are selected during the hot afternoon session when resting and drinking activities are expected to be highest.
- Roans allocate varying amounts of time to different activities at different times of the day. It was predicted first that roans would spend more time feeding than other activities such as resting and movement; and second roans would feed primarily morning and evening in contrast to resting and regurgitating in the hot afternoon.

4.2 Methods

4.2.1Roan data collection: Use data

Habitat selection use data was obtained from 6 roan individuals. The 6 individuals represented individuals within 3 roan groups and 3 lone roan males. The 3 roan groups had different numbers of animal locations (group1 = 132, group2 = 132, and group3 = 42) that were collected at a rate of 6 animal locations per day. For each roan group, it was the dominant male that was tracked because it was easy to recognize and identify in the field. The 3 lone roan males also had varying number of locations (male1 = 20, male2 = 15 and male3 = 14) that were collected at a rate of one animal location per day. The differences were necessitated by the fact that animal locations were collected by tracking the animals on the ground and sometimes it was difficult to trace the animals and especially the lone ones. To ensure an overall consistency in the sampling procedure as recommended by Aebischer et al (1993), a single random animal location per day was selected from the roan groups so as to match the sampling protocol of the lone males. Detailed description of the methodology used in collecting the animal locations in the field is presented in chapter 3 section 3.2.1.

4.2.2Potential variables and preparation of GIS maps: Availability data

The following 12 habitat variables were considered in analysing habitat selection by roan antelopes in Ruma National Park – vegetation, vegetation burned status, slope, soil, distances from surface water points, thick vegetation, snare hotspots, salt licks, roads, security gates / outposts, park fence and unfenced park boundary. Details on the justification for inclusion of these variables in habitat selection are described in chapter 5 section 5.2.2. The methods used in preparation of the vegetation map for RNP is described in detail in chapter 2 section 2.2.1.2. Based on the animal locations, 7 out of the 10 vegetation classes were utilized by the roan antelopes in Ruma

National Park, that is, grassland (GL), dwarf shrub grassland (DSGL), sparsely shrub grassland (SSGL), shrub grassland (SGL), thin-wooded grassland (TWGL), wooded grassland (WGL) and sparsely wooded grassland (SWGL). However, these 7 vegetation classes were too many for inclusion in compositional analysis given the number of roan animals for which habitat use data was collected. Habitat use data was only collected for 6 roans, which is also the minimum number of individuals needed for compositional analysis (Aebischer et al., 1993). Therefore, the 7 vegetation classes were reclassified and reduced to 4 classes by combining 4 most similar classes (GL, SWGL, SSGL, and DSGL) into one broad class – the open grassland (OGL). The 4 vegetation classes were justifiably combined together because they all had high grass percentage cover of greater than 60% and low tree or shrub canopy cover of less than 10% as shown in Table 2.2 (see chapter 2 section 2.2.1.2.2). Therefore, the 4 vegetation classes included in compositional analysis were OGL, SGL, TWGL and WGL.

Apart from the vegetation burned status, all the GIS maps for the other habitat variables were subdivided into three classes each. The vegetation burned status map was only divided into two classes: burned and unburned vegetation. The slope map in degrees was divided into flat slope with less than 5 degrees, moderate slope with 5 to 10 degrees, and steep slope with more than 10 degrees. The soil map was divided into cambisols, solonetz, and other soils, because the first two soil classes were the ones utilized by the roans. All the distance maps were sliced into 3 distance classes: near (< 0.5 km), medium (0.5 – 1.5 km), and far (> 1.5 km). The cut off distance of 1.5 km was used because it is the mean daily distance travelled by roans in RNP as shown in chapter 3 section 3.3.7.

4.2.3 Data analysis

Habitat selection was performed using compositional analysis technique (Aebischer et al., 1993; Aitchison, 1986) via RANGES 8 (Kenward et al., 2009) and the Smith's (2003) Compos Analysis. Compositional analysis is a technique that uses MANOVA to analyse two sets of habitat data in which variables are represented as proportions. It is used to determine the statistical significance of differences and the rank order of differences between the variables.

Before compositional analysis was done, data were tested for normality. In many cases the proportions data were not normally distributed. Since this invalidated the use of the t-test in testing for random habitat use (Aebischer et al., 1993), the randomization test (λ) results were used rather than those of the parametric t-test. Fortunately, the Smith's (2003) compositional analysis tool that was used in this study automatically performs the two tests: the t-test and the randomization test. The compositional analysis was run with 5000 iterations. Manly (1997) recommends that a minimum of 1000 iterations but this was not adequate as it showed variations in the results.

During compositional analysis, two corrective measures were undertaken. First, the habitat types that were available but not utilized by an animal (0% in the utilized habitat composition) were assigned a value of 0.01% or any other appropriate value that was an order of magnitude less than the smallest nonzero value as recommended by Aebischer et al (1993). Second, weighting of cases was applied to compensate for the differences in sampling intensity (differences in the number of locations per animal). The compositional analysis assumes that compositions from different animals are equally accurate but this is not true if numbers of animal locations vary widely from animal to animal (Aebischer et al., 1993). Without applying weighting of cases, calculation of means and variances in compositional analysis still uses an implicit weighting of 1/ (number of animals) (Snedecor and Cochran, 1980) that is the same for each animal. The weighted analysis replaces these equal values with ones that vary from animal to animal and are constructed as (individual weight)/(sum of weights) (Smith, 2004). In this study the weight applied was the square root of the sample size (n) of each animal. Hence, the square root of n was then used to weight the log-ratio differences during the analysis as recommended by Aebischer et al (1993).

Habitat selection was considered at two levels: selection of a home range from the whole study area (the park) and habitat use within the home range. The former level is termed the second-order selection and the latter is termed third-order selection by Johnson (1980). The second-order selection gives a broad view of the roans' requirements by comparing the home range composition with the total study area. The third-order selection presents a detailed view of resource use by the roans by comparing proportional habitat use based on animal locations within the home range composition. For the second-order selection the home range for each animal was computed using the Minimum Convex Polygon (MCP) estimator. This allowed the estimation of the largest possible home range from the relatively small number of locations per animal, available for this study.

The second- and third-order habitat selection were performed separately for different categories of habitat use based on: (1) seasons (wet, dry, breeding and combined); (2) times of the day (morning, mid-day, and afternoon); and (3) animal activities (resting, feeding, and moving). However, these categories were only used for analyzing selection of vegetation types, vegetation burned status and distance to drinking water. All the other variables were analyzed using the combined season data. In addition to habitat selection, diurnal time-activity budget for the roan antelopes was analyzed.

4.3 Results

4.3.1Selection of vegetation types

Evaluating second order selection (study area vs. MCP), roans showed significant habitat selection for combined ($\lambda = 0.019$, $p<0.035$), dry ($\lambda = 0.141$, $p = 0.032$), wet ($\lambda = 0.053$, $p = 0.040$) and breeding ($\lambda = 0.098$, $p = 0.045$) seasons. In all these seasons, the OGL and TWGL habitats were ranked first and last respectively, except for the breeding period in which the TWGL was not utilized. For the combined, dry and wet seasons the TWGL was selected significantly less than the other habitats

(Table 4.1) whereas for the breeding season the difference between rankings of each habitat was not significant. At third order habitat selection vegetation types were selected significantly differently from random for combined (λ = 0.127, p = 0.030), dry (λ = 0.153, p = 0.029) and breeding (λ = 0.313, p = 0.028) seasons. In all the cases, WGL and OGL were selected significantly more than SGL whereas the TWGL was mostly totally avoided except for combined season (Table 4.1). There was no significant difference between WGL and OGL and therefore the rankings of these two habitats are interchangeable.

Results on second order habitat selection by roans during different times of the day indicated that vegetation types were selected significantly non-randomly in the morning (λ = 0.014, p=0.035), mid-day (λ = 0.173, p=0.039) and afternoon (λ = 0.003, p=0.037). In all cases, OGL was ranked first and the TWGL was ranked last (Table 4.1). However, in the morning section the roans selected significantly the OGL more than the other habitats whereas in the afternoon TWGL was significantly less selected than the other three habitats. The difference between rankings of each habitat type was not significant in the mid-day period. At the third order level only the mid-day period showed non-random habitat selection (λ = 0.103, p=0.030) but rankings between each habitat were not significantly different (Table 4.1).

Roans showed non-random habitat selection for feeding (λ = 0.028, p=0.037) and resting (λ = 0.141, p=0.041) activities but random habitat selection for moving activity (p>0.05). For the two activities the habitat rankings were the same with the OGL being ranked first and the TWGL being selected significantly less than all the other three habitats (Table 4.1). At the third order level only the resting activity showed a non-random habitat selection (λ = 0.070, p=0.048) but rankings between each habitat were not significantly different (Table 4.1).

Table 4.1: Compositional analysis results of roan habitat selection of 4 vegetation types for different seasons, time of the day and activities. The habitats are: open grassland (OGL), wooded grassland (WGL), thin-wooded grassland (TWGL) and shrub grassland (SGL). >>> shows significant difference at p = 0.05.

Season / Time period / Activity	Selection order	Lambda, λ	p	Habitat type ranking
1 Seasons				
a) All seasons combined	2nd	0.019	0.035	OGL>WGL>SGL>>>TWGL
	3rd	0.127	0.030	WGL>OGL>>>TWGL>SGL
b) Dry season	2nd	0.141	0.032	OGL>WGL>>>SGL>>>TWGL
	3rd	0.153	0.029	WGL>OGL>>>SGL
c) Wet season	2nd	0.053	0.040	OGL>>>SGL>WGL>TWGL
	3rd	0.142	0.116	-
d) Breeding period	2nd	0.098	0.045	OGL>WGL>SGL
	3rd	0.313	0.028	WGL>OGL>>>SGL
2 Time of the day				
a) Morning	2nd	0.014	0.035	OGL>>>SGL>WGL>TWGL
	3rd	0.221	0.145	-
b) Mid-day	2nd	0.173	0.037	OGL>SGL>WGL>TWGL
	3rd	0.103	0.030	OGL>WGL>SGL
c) Afternoon	2nd	0.003	0.037	OGL>WGL>SGL>>>TWGL
	3rd	0.135	0.379	-
3 Activities				
a) Feeding	2nd	0.028	0.037	OGL>WGL>SGL>>>TWGL
	3rd	0.236	0.184	-
b) Resting	2nd	0.141	0.041	OGL>WGL>SGL>>>TWGL
	3rd	0.070	0.048	OGL>WGL>SGL
c) Moving	2nd	0.137	0.087	-
	3rd	0.100	0.133	-

To investigate the effect of burning on habitat selection by roans, 2 habitats were derived from the most preferred habitats (lightly wooded grassland and wooded grassland): burned grassland (GL_B) and unburned grassland (GL_UB). Second order selection indicated that roans selected burned and unburned habitats non-randomly during the breeding season (λ = 0.001, p = 0.025) but at random for the combined, wet and dry seasons (p>0.05) (Table 4.2). The unburned grassland (GL _UB) habitat was ranked first for the breeding period but it was not significantly different from the burned grassland (GL_B) habitat. At the third order level the burned and unburned grassland habitats were selected randomly for all the seasons.

Table 4.2: Compositional analysis results of roan habitat selection of 2 vegetation types at different seasons. The habitats are: burned grasslands (GL_B) and unburned grasslands (GL_UB).

Season	Selection order	Lambda, λ	p	Habitat type ranking
All seasons combined	2nd	0.004	0.106	
	3rd	0.005	0.129	
Breeding period	2nd	0.000	0.046	GL_UB>GL_B
	3rd	0.005	0.301	
Dry season	2nd	0.029	0.413	
	3rd	0.008	0.350	
Wet season	2nd	0.005	0.080	
	3rd	0.039	0.191	

4.3.2 Selection of eco-geographical variables

Investigation of habitat selection by roans showed that a few eco-geographical variables are utilized at random whilst many are selected non-randomly (Table 4.3). Evaluating second and third order habitat selection using combined seasons data showed that there was no significant difference between proportions of selected and available soil types, distances from public roads and foot paths, saltlicks and park fence. However, at the second order selection level, distance to drinking water was selected significantly non-randomly for combined ($\lambda = 0.262$, $p = 0.018$) and dry ($\lambda = 0.107$, $p = 0.024$) seasons but randomly for the wet season ($p>0.05$). For the combined and dry seasons, the nearest distance to water was ranked first followed by medium and far distances to water. Also, for the combined and dry seasons, the farthest distance to water was selected significantly less than near and medium distances to water but there was no significant difference between the near and medium distances for the combined season, implying that the ranking meant little and that the class rankings could be interchanged. Third order selection indicated that roans selected distances to water for combined and wet seasons at random (p>0.05) and non-randomly for the dry season (λ = 0.215, p = 0.044). The medium distance to water was ranked first followed by near and far distances but the difference between rankings of each water distance class was not significant.

Table 4.3: Compositional analysis results of roan habitat selection of various eco-geographical variables using combined season data. All distance variables were sliced into 3 classes: near (0.5 km), medium (0.5 - 1.5 km) and far (>1.5 km). >>> shows significant difference at p = 0.05

Eco-geographical variable	Selection order	Lambda, λ	p	Habitat type ranking
Distance to surface water				
a) All seasons combined	2nd	0.262	0.018	Near>Medium>>>Far
	3rd	0.872	0.904	-
b) Dry season	2nd	0.107	0.024	Near>>>Medium>>>Far
	3rd	0.215	0.044	Medium>Near>Far
c) Wet season	2nd	0.322	0.068	-
	3rd	0.752	1.000	-
d) Breeding season	2nd	0.046	0.028	Near>>>Medium>>>Far
	3rd	0.856	0.936	-
Slope type	2nd	0.069	0.039	Flat>Moderate>>>Steep
(Flat<5 ^{0}C, moderate = 5 - 10 ^{0}C, steep >10^{0}C)	3rd	0.022	0.031	Flat>>>Moderate>Steep
Distance to thick vegetation	2nd	0.036	0.031	Far>Medium>>>Near
	3rd	0.120	0.020	Far>Medium>Near
Soil type	2nd	0.878	0.476	-
(Cambisols, Solonetz, other soils)	3rd	0.938	0.725	-
Distance to Saltlicks	2nd	0.929	0.878	-
	3rd	0.541	1.000	-
Distance to Security	2nd	0.364	0.048	Near>Far>Medium
	3rd	0.183	0.133	-
Distance to unfenced park boundary	2nd	0.054	0.046	Medium>Far>Near
	3rd	0.673	0.545	-
Distance to park fence	2nd	0.139	0.401	-
	3rd	0.730	0.851	-
Distance to public roads and foot paths	2nd	0.633	0.387	-
	3rd	0.588	0.711	-
Distance to snares hotspots	2nd	0.209	0.039	Far>>>Medium>Near
	3rd	0.141	0.375	-

Slope types were selected significantly differently from random at the second order ($\lambda = 0.069$, $p = 0.039$) and third order ($\lambda = 0.022$, $p = 0.031$) habitat selection levels (Table 4.3). In all cases, flat areas were ranked first followed by medium and steep. At the second order level, the steep slopes were selected significantly less than the flat and moderate slopes whereas at the third order level the flat areas were selected significantly more than the moderate and steep slopes. Similarly, distances from thick vegetation were selected significantly differently from random at second ($\lambda = 0.036$, $p = 0.031$) and third ($\lambda = 0.120$, $p = 0.020$) order levels (Table 4.3). In both selection orders, far distances were ranked first followed by medium and near distances. At the second order selection, the near distance class was selected significantly less than medium and far distances whilst at the third order the difference between rankings of each distance class was insignificant.

At second order level roans showed non-random selection of distances from security gates / outposts ($\lambda = 0.364$, $p = 0.048$), unfenced park boundary ($\lambda = 0.054$, $p = 0.046$) and snare hot spots ($\lambda = 0.209$, $p = 0.039$). The areas near the security were ranked first followed by far and medium distances whilst rankings for distances from unfenced park boundary were exactly opposite. However, in these two eco-geographical variables the difference between rankings of each distance class was not significant. The distances far away from snare hot spots were selected significantly more than near and medium distances. At the third order level, all the three eco-geographical variables were selected at random ($p>0.05$) (Table 4.3).

4.3.3 Diurnal time-activity budget for roan antelopes

There were differences in the time spent by roans for different activities at different periods of the day (Figure 4.1). The overall time spent on daily movements was significantly lower than that spent on either feeding or resting ($\chi^2 = 32.274$, df = 2, $p < 0.0001$). The time spent on the three main activities (feeding, resting and movement) differed significantly for the mid-day ($\chi^2 = 46.043$, df = 2, $p < 0.0001$) and afternoon ($\chi^2 = 36.602$, df = 2, $p < 0.0001$) periods. The time spent on feeding was significantly lower during mid-day than morning or afternoon periods (χ^2 = 25.346, df = 2, p < 0.0001). In contrast, the time spent on resting was significantly higher during the mid-day than the morning or the afternoon periods (χ^2 = 17.836, df = 2, p = 0.0001). Also time for movement was significantly lower in the afternoon (χ^2 = 7.685, df = 2, p = 0.021) than the morning and afternoon periods.

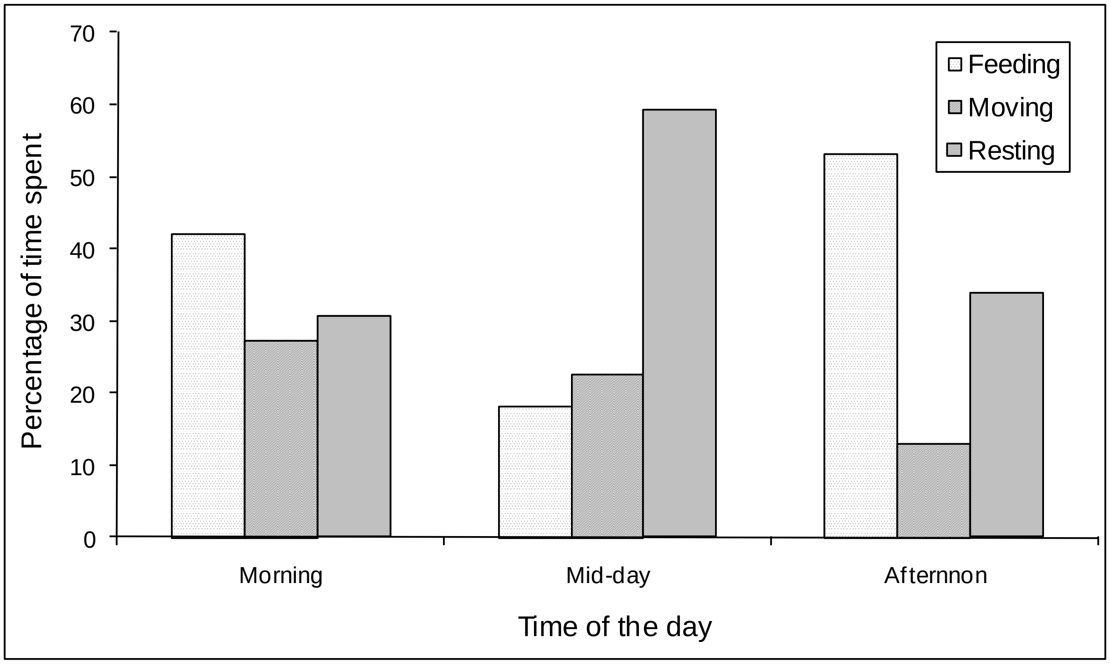


Figure 4.1: Diurnal time-activity budget of roan antelopes using 6-months combined data for both dry and wet season. The time of the day was divided into 3 periods: 0800-1000 (morning), 1200-1400 (mid-day), and 1400-1600 (afternoon).

4.4 Discussion

The most preferred habitats for most seasons, times of the day and various activities were the open grassland (OGL) and wooded grassland (WGL). This concurs with findings of previous studies that roans prefer lightly wooded savannah with open areas of medium to tall grasses (Schuette et al., 1998; Smithers, 1983). These habitats are suitable for roans as they offer foraging grasses, shelter from adverse weather and cover from predators. Park management needs to put measures in place to ensure continued availability of such preferred habitats.

The least preferred habitats for most seasons, times of the day and various activities were the shrub grassland (SGL) and the thin-wooded grassland (TWGL); the TWGL was avoided most of the time. The least preference of the SGL habitat is in accordance with past research where roans have been noted to avoid thick closed stands of bush (Joubert, 1976). This may be associated with the fear of being trapped by poaching snares that are usually set up in the shrubs. The avoidance of TWGL habitat maybe also associated with the fear of poachers. During fieldwork in RNP, it was observed that when roans were found in the TWGL habitat they were very scared and quickly ran away but the same group of roans appeared very calm when encountered in open or lightly wooded grasslands. Results showed that roans avoided the TWGL whereas they preferred the WGL habitat that had similar habitat composition, which suggests that the difference was due to the effect of fire in the TWGL habitat. The unique thin-wooded grassland (TWGL) has developed as a result of repeated burning in some areas of the park, especially those next to the communal land. This vegetation comprises grassland with scattered black-stemmed thin Acacia trees that have survived burning for many years. (Smithers, 1983) noted that roans spend little time on burned areas even when a green flush occurs. Observations by the Ruma N. Park warden confirmed that poachers mainly lay snares in this TWGL habitat in the early wet season after the sprouting of fresh grass that attracts a diverse number of wildlife species. However, a more detailed statistical analysis of the factors influencing the snare-poaching in RNP is presented in Chapter 7.

Unburned grasslands were most preferred during the breeding season. This was probably because the unburned grasslands form several layers of thick grass that provide a very conducive habitat cover for hiding the newly born young from predators. This concealing habitat is vital because the roans usually leave the newly born young alone for many hours and thus the major protection from predators is the habitat cover (Starfield and Bleloch, 1986; Joubert, 1976). However, more research is needed on the relationship between calf mortality and habitat type to ascertain the reason for preference of unburned grasslands.

The selection of habitats by roans based on burned vegetation status implies that fire management is crucial for the park. There is a need for long-term prescribed burning to ensure continued availability of open and wooded grasslands throughout the year. This will also prevent over burning of the park vegetation as a result of accidental fires that might destroy the breeding habitat. Also, if prescribed burning is not done, uncontrolled burning will continue as it has been happening year after year. Park records indicate that every year during the dry season over 50% of the park area is burned by fire outbreaks mainly started by the surrounding communities either as a poaching tool or in retaliation to unresolved conflicts with the park management. In many cases the fires act as a poaching tool when they burn old grass especially just before the rainfall season so that fresh grass that sprout after the rains will attract wildlife grazers. The poachers then either set up snares or ambush the unsuspecting animals with bows and arrows in these areas. The fires also have been set for purely political reasons. For instance, during the 2008 post-election violence in Kenya, the surrounding communities set fires in the park in a bid to flush out people of other communities who sought refuge inside the park. Establishing a fire break road along the park boundary can protect the park from fire outbreaks from the surrounding community, since the fires are started in the community land and then spread over to the park. Also, the relationship between the surrounding community and the park authorities needs to be enhanced and strengthened as a long-term solution to the deliberate setting of fires.

Apart from vegetation, 4 more eco-geographical factors were significantly selected by the roan antelopes: surface water, slope, and distances to thick vegetation and snare hotspots. Roan home ranges were significantly located near surface water (less than 500m) during the dry and breeding seasons but near to medium distances (≤ 1.0 km) for the combined season data. Since roans are highly water dependant and need to drink daily they need to dwell near water (Smithers, 1983; Joubert, 1976) especially during the critical periods of dry and breeding seasons. However, water was irrelevant during the wet season, because roans could access sufficient water from rainfall-fed temporary pools throughout their home ranges.

Similarly, roan home ranges were significantly located at flat to moderate slopes (0^0 - 10^0C), moderate to far from thick vegetation habitats (1.0 – 1.5 km), and far from snare hotspots (greater than 1.5 km). Flat areas enable the roans to minimize energy expenditure during foraging and other essential activities; also most parts of the park consist of steep cliffs and hills that cannot be accessed by antelopes. The avoidance of thick vegetation and areas of high snares was mainly to avoid being trapped by snares. Joubert (1976) observed similar avoidance of thick vegetation by roans in Kruger National Park.

The scale of habitat selection analysis is important for roan antelopes, as some factors were only significant at the study area level but not at the home range level. This implies that once a home range has been established with reference to important factors, the individual roans could access these resources within the borders of the home range and hence habitat selection within the home range is dependent on other more important factors at that scale. For example, once a home range has been established near water during the breeding season, all the animals can access the water from any part of the home range. These findings concur with earlier studies that found out that habitat selection is scale dependant (Ciarniello et al., 2007; Thomas and Taylor, 2006; Johnson, 1980). Due to this dependency on scale, habitat selection at lower scale cannot be extrapolated to a finer scale and vice versa (Ciarniello et al., 2007). Therefore, for accurate conclusions to be drawn from habitat selection it is necessary to carry out multi-scale analysis.

Understanding of the proportions of time spent in different periods of the day is important for designing effective and efficient sampling protocols for monitoring of roan movement. Since all activities occur uniformly in the morning period of the day

(0800 – 1000), it implies that this is the right period to collect roan location data for assessing habitat use, especially when only one location is collected per day. If one animal location per day is collected in other periods of the day it may lead to biased data. For example, if one location per day is collected in the mid-day period (1200 – 1400), it may coincide with a time when the animals are always resting as this was the major activity during this period. Kenward (2001) emphasizes that timetabling should be considered when designing animal movement sampling protocols to avoid bias and poor data that leads to underestimated home ranges.

Analysis of proportion of time spent by roans for different activities could help in understanding of roan ecology. The roans spent more time during the day on feeding and resting and little time in movements. The occurrence of highest feeding time in the afternoon (1600 – 1800) suggests that feeding may be continuing into the night. Also, the large portion of time used on resting during the day when the tropical sun is too hot may be compensated for by feeding in the night. Nocturnal studies through radio tagging of roans are needed to confirm this hypothesis.

The findings from compositional analysis might have been affected by high Type I and Type II errors due to (i) the small number of locations per animal and (ii) the small sample size of 6 animals, which is the minimum number of individuals required for compositional analysis (Aebischer et al., 1993). A Type I error is committed when a significant difference in proportional selection is proclaimed when, in fact, habitats are selected according to their availability. A Type II error is committed when a difference in proportional habitat selection is not detected when, in fact, it should. Alldredge and Ratti (1986) found out that the occurrence of Type II errors in most techniques for analysis of habitat selection is increased by high number of habitats, low number of animals, and low number of observations per animal. Preliminary analysis for roan habitat selection using 6 animals and 6 habitats showed that no proportional habitat selection could be detected, whilst reducing the habitats to 4 detected proportional habitat selection. Due to the possibility of the findings of compositional analysis being biased, the habitat selection analysis of this chapter is repeated with alternative techniques – the stepwise logistic regression and the information-theoretic techniques, in chapter 5. Comparisons of findings on roan habitat selection from these three techniques are discussed in chapter 8.

4.4.1 Limitations and constraints

- The use of a sample size of 6 animals, which is the least number of individuals required for compositional analysis (Aebischer et al., 1993), may have caused inflation of type II error. The habitat selection results could have been improved by increasing the sample size.
- The use of the burned vegetation status observed within a period of 6 months could be unreliable. However, in this study such bias was minimized by using past records on burned vegetation status of the park.
- Only diurnal time activity budget for the roans was done, due to lack of nocturnal data. Collection of both diurnal and nocturnal data using radio-collars can greatly improve the understanding of the roan time activity budget and habitat selection.
- Whilst the analysis of habitat selection at the study area (national park) level may be considered as arbitrary, it was nevertheless appropriate because habitat management is done at the park level.
- The compositional analysis technique is limited by the difficulty caused by zero records in either the use or the availability data for one or more animals. However, the similarity of its results to those of stepwise regression analysis and information theoretic approach, demonstrated its usefulness in habitat selection analysis.

CHAPTER 5

HABITAT SUITABILITY MODELLING OF ROAN ANTELOPES IN RNP USING STEPWISE LOGISTIC REGRESSION AND INFORMATION-THEORETIC APPROACH

Different habitat features in the wet and dry seasons in RNP

CHAPTER 5: Habitat suitability modelling of roan antelopes in RNP using stepwise logistic regression and information-theoretic approach

5.1 Introduction

5.1.1Statistical modelling

Effective conservation and management of endangered wildlife species is dependent on knowledge of the species' range of occurrence and understanding the factors influencing their distribution as well as those causing endangerment. Knowledge of species distribution and important habitat resources coupled with spatial representation of this information can be used to implement population decline mitigation measures, establish protection sanctuaries or ecological reserves, initiate reintroductions in known ranges, and in planning further research (Johnson et al., 2004; Rushton et al., 2004). Ideally, the distribution and habitat for large animals in small areas can be documented via field surveys. However, this is slow, time consuming, expensive and only limited to small areas and few species that are conspicuous and less mobile.

Modelling offers a powerful tool for understanding the species – habitat relationships and distributions (Rushton et al., 2004). This allows diverse data on the species and habitat variables to be acquired using various methods. The widely used methods for collecting species data for modelling include: field surveys (e.g. (Ambrosini et al., 2002; Manel et al., 2001), aerial surveys (Erickson et al., 1998), radio-tracking (Johnson et al., 2004; Schadt et al., 2002), and questionnaires (Vaughan et al., 2003). Habitat variable data for modelling purpose are mainly obtained via remote sensed images (Collingham and Huntley, 2000) mapped habitat data using geographical information systems (GIS) (Cabeza et al., 2010), and field surveys (Frair et al., 2004). In many cases, studies employ a combination of these techniques in collecting the species and habitat variable data. The wide availability of remotely sensed images and advancement in geographical information systems has made it feasible to conduct species-habitat modelling on large areas within a very short time while yielding accurate biological and management conclusions (Rushton et al., 2004).

One common problem in species-habitat modelling, which still remains a challenge, is to determine the appropriate sampling unit that corresponds to the scale at which the focal animal is selecting the habitat (Whittingham et al., 2005; Rushton et al., 2004). Animals select habitat at different scales. In determining the correct scale, reference should be made to the species' biology. For instance, habitat selection of a territorial species is different from a non-territorial species (Johnson, 1980). In cases where the information on the right scale is not known, researchers can study habitat selection at different scales to identify the appropriate one (Manly et al., 2002). Erickson et al (1998) studied habitat selection for moose at different spatial scales and concluded that habitat selection models changed as a function of the scale. Such studies are usually made feasible by the use of geographic information systems. Whittingham et al (2005) studied habitat selection by yellowhammers at the territory and boundary scales and concluded that the boundary occupancy was more closely correlated with regional habitat selection whereas territory occupancy indicated more detailed habitat selection. Collingham et al (2000) did species distribution modelling of weed species at the regional and national level and concluded that scaling down from coarse to fine resolutions led to poorer models.

Another problem associated with habitat modelling is the use of different data types; binary (presence versus absence), discrete, categorical, proportions and continuous. Basic statistics cannot handle such complex data without bias. However, advanced statistical methods such as logistic regression are robust enough to handle binary response (non-normal data) and mixed data sets of categorical, discrete and continuous predictor variables (Manly et al., 2002; McGarigal et al., 2000). Logistic regression analysis is the widely used generalized linear model (GLM) techniques in species distribution modelling. A GLM consists of three components: a random response variable that assumes a probability distribution appropriate for the response variable, for example normal, binomial or Poisson; a linear predictor of explanatory variables; and a link function that relates the mean of the response variable to the linear predictor.

Data from observational studies are often faced with additional problems of random effects, which when ignored cause pseudo-replication (Legendre and Legendre, 1998). Random effects in observational studies arise out of variation in space and time or among individuals (Crawley, 2007). Recent studies in ecology have emphasized the importance of estimating these random variations (Melbourne and Hastings, 2008; Chesson, 2000). Quantifying these random variations enables ecologists to validly extrapolate statistical modelling results beyond their study area (Bolker et al., 2009). The best method to deal with the problem of random effects is to use generalized linear mixed models (GLMMs) that are capable of incorporating random effects and handling non-normal data by using link functions and exponential family distributions such as Poisson and binomial (Bolker et al., 2009; Agresti, 2007). GLMs and GLMMs allows researchers to draw statistical and biological conclusions from data by examining parameter estimates and their confidence intervals, testing hypotheses, selecting the best model (s) and evaluating differences in goodness of fit among models. Bolker et al, (2009) give a detailed review of the various options available for GLMM parameter estimation and statistical inference. They discuss the top-of-the-range GLMM parameter estimation techniques including pseudo-and penalized quasi-likelihood (PQL), Laplace approximations, Gauss-Hermite quadrature (GHQ), and Markov chain Monte Carlo (MCMC) algorithms. GLMMs help in solving the problem of overdispersion, which is the occurrence of more variance in data than predicted by a statistical model (Bolker et al., 2009). Overdispersion may occur due to the use of a wrong error structure or failure to include key predictor variables in a model (Rushton et al., 2004) resulting in too much unexplained error in the model.

Last but not least, use of conventional statistical methods such as stepwise regression in analysing species-habitat relationships have been heavily criticised in the recent past. The main shortcomings of these methods are (1) the use of arbitrary significance levels (such as p = 0.05), which have no theoretical basis (Anderson et al., 2000; Royall, 1997); (2) the testing of uninformative null hypotheses that do not add any new knowledge to science (Anderson et al., 2001; Anderson et al., 2000); (3) lack of proper scientific thought in formulating null hypotheses and their single alternatives (Anderson and Burnham, 2002; Johnson, 1999; Yoccoz, 1991); (4) confusion and contradiction arising due to the use of different significance levels such as p = 0.05, 0.01, 0.1or 0.15 without proper reporting (Anderson et al., 2000; Johnson, 1999); (5) over-dependence on sample size such that at large sample sizes the null hypothesis is always rejected (Anderson et al., 2000); and (6) model selection and parameter estimation are done concurrently, which can lead to biases in model parameters, overfitting and incorrect significance tests (Whittingham et al., 2005). However, despite of these limitations, these methods continue being used in statistical modelling.

Burnham and Anderson (2002) have strongly advocated for a paradigm shift in statistical modelling from the traditional null hypothesis testing to the new information theoretic approaches. The new approaches have superior scientific qualities as compared to the former. Information theoretic approaches use the concept of multiple working hypotheses that encourages better science questions (Anderson and Burnham, 2002). The strength of these approaches hinges on (1) the use of the principle of parsimony as the basis for model selection, (2) estimation of Kullback-Leibler information based on deep theory, and (3) the use of Akaike's information criteria (AIC) to estimate the expected, relative Kullback-Leibler information. The principle of parsimony involves the search for model(s) that best approximates the information in the data at hand, while keeping the structure as simple as possible and using the smallest possible number of parameters. It does not assume that a true model exists but tries to find a model that minimizes that probability of over-fitting or under-fitting the data. The information lost when a model is used to approximate the truth is called the Kullback-Leibler information (Burnham and Anderson, 2002). Establishment of a formal relationship between Kullback-Leibler information and maximum likelihood led to an estimate known as the Akaike's information criterion (AIC) (Anderson et al., 2000). AIC has been used widely in model selection as the basis for comparing a set of competing models. AIC is used to compute Akaike weights for each model, which are weights of evidence in favour of each model in reference to consideration of all models in the set. These Akaike weights are useful in ranking models with top best ranked models having the highest scores. If a single predictive model is desired, these approaches use model averaging to yield a final best model that includes aspects of a number of top ranked models. This has the advantage of allowing model inference to be based on a set of the best top ranked models instead of using only one single best model and ignoring other competing models which are equally good. The use of this multi-model inference is necessary so as to incorporate model selection uncertainty. Information theoretic approach also allows computation of Akaike weights for each predictor used in a model that enables assessment of relative importance of the predictor variables (Burnham and Anderson, 2002). The use of Akaike weights for each predictor and model coupled with parameter coefficients, confidence intervals and/or standard errors give a deeper understanding of the process being modelled (Greaves et al., 2006).

However, one of the challenges of the information theoretic approach is that its model results are dependent on the depth of understanding of the system or process being modelled and hence the quality of predictors used (Johnson and Omland, 2004). In essence, if poor models are developed, the AIC will only select the best model out of the poor set. Burnham and Anderson (2002) emphasize the need to select a small set of predictors based on logic and biological importance so as to avoid use of too many predictors that yield poor models with little biological significance. Eberhardt (2003) recommends that model selection using AIC should be complemented by concurrent assessment using other criteria such as the r^2

statistic that indicates how much of the variation in the data is explained by the model.

5.1.2 Objectives

This chapter was written with the aim of achieving the following objectives:

- To determine the factors that constitutes a suitable habitat for roan antelopes in different seasons in Ruma N. Park.
- To prepare habitat suitability maps for roan antelopes in different seasons in RNP
- To determine whether the factors that constitute potential roan suitable habitat in the whole park are the same as those that constitute suitable habitat within the roan home range level.
- To investigate whether roan habitat suitability model results change as a function of the spatial scale of sampling.
- To collate the statistical methods used in habitat suitability modelling for the roan antelopes.
- To recommend appropriate habitat management strategies for the roan antelope in order to aid population recovery.

5.1.3 Hypotheses and predictions

This chapter had the following hypotheses:

- Roans prefer certain habitats over others based on distribution of habitat features. It was predicted that (i) roans would prefer habitats that provide adequate resources for forage, water, cover from predators and areas that minimize energy expenditure during normal foraging periods such as low slopes and elevation; and (ii) roans would avoid areas that have high risk of poaching such as near public roads, snare hotspots, unfenced park boundary, and away from security outposts and gates.

- Roan antelopes prefer different habitats in different seasons in RNP. It was predicted that (i) during the breeding season roans would prefer unburned, secluded vegetation to provide habitat cover for new-born calves; (ii) habitats near water would be more preferred by roans in the dry season in contrast to more limited habitat selection in the wet season.

- Habitat selection in roan antelopes is spatially scale dependent. It was predicted that (i) habitat selection by roans at the park level is determined by the most important factors such as water and forage whilst habitat selection within the home range is determined by other factors of lower importance at this scale such as geographical features and park infrastructure; (ii) the predictive power of habitat suitability models would vary with the spatial scale of sampling used, such that the best model (s) is attained at a scale that corresponds to the scale at which data for most predictors were collected or at a scale that corresponds to the biology of the roan antelope.
- Different statistical methods of habitat suitability yield different results for roans. It was predicted that the new information-theoretic approach would produce different roan habitat selection results from the conventional stepwise logistic regression.

5.2 Methods

5.2.1 Roan location data collection

Data on roan locations were collected via ground-tracking three groups of roans for six months (February to July) in 2008 in Ruma National Park, Kenya. A total of 306 locations were recorded across various vegetation types in the park and these are taken to be the locations where roans were present. To enable analysis of the roan distribution data using logistic regression, an equal number of random points were generated within the same area using ILWIS Academic GIS software package (ILWIS, 2009). These formed the locations where roans were absent.

5.2.2 Potential variables and variable selection

A combination of literature search, remote sensing techniques and field work identified 18 factors that could influence the distribution of roans in Ruma N. Park. These factors can be classified into five major groups: vegetation (6), water (2), soil (2), threat of poaching (6) and geographical features (2). The output of models is dependent on the variables selected as predictors (Johnson and Omland, 2004). It is important to select only variables that are of biological importance to the species being studied and that are most relevant in answering the research question being investigated (Anderson and Burnham, 2002). Based on this consideration and coupled with the results of initial analyses described below, the predictor variables were reduced to 11: open grassland, wooded grassland, vegetation burned status, water points, streams and river, soil type, distance to fenced park boundary, distance to unfenced park boundary, distance to park gates and outposts, distance to snare hot spots and slope. Table 5.1 presents the 11 factors and the reasons why they were considered as important factors in predicting the distribution of roans in RNP. Each variable was prepared using ILWIS package as a GIS map with a given spatial resolution. Different sets of spatial scales were used for comparison and these are discussed in detail in section 5.2.5. Figure 5.1 presents maps of these 11 variables ready for inclusion in habitat suitability modelling.

Table 5.1: List of potential predictor variables of roan habitat suitability in Ruma National Park

Predictor name / definition	Abbreviation	The importance of the predictor / reason for inclusion
Distance to park fence	Dfe	Roans are likely to prefer habitats near fences for security reasons or as an indication that the fence acts as a barrier of a once contiguous suitable habitat.
Distance to unfenced park boundary	Dun	Unfenced boundary allow roans to come out of the park and risk poaching by surrounding local people. Roans are likely to refrain from these areas as a result of prior encounters with poachers.
Distance to park security gates and outposts	Dse	Field observations indicated that roan presence is associated with park gates/outposts, which offer security from poachers. This hypothesis needs to be tested.
Distance to snare hot spots within the park	Dsn	Poaching using snares is a major problem in RNP (YFC, 2006). It can be hypothesized that roan suitable habitats are located away from snare hot spots.
Distance to streams and/or river Olambwe	Dsr	River Olambwe is located in the midst of a riverine forest and the streams occur on steep slope areas. Roans are never found in the thick vegetation like forests (Schuette et al., 1998). Due to these, limitations it can be hypothesized that roans never access the river and streams for water.
Distance to water points (dams & water toughs)	Dwa	Roans are water dependent (Kingdon, 1984) and are mainly found in close proximity to water (Joubert, 1974). Water points are the nearest water sources for roans in RNP. It is expected that during the dry season roans will prefer habitats that are close to permanent water sources.
Slope in degrees	Slope	Field observations indicated that roans occupied flat areas and were never found on steep areas. This hypothesis needs to be tested.
Open grassland	OGL	Vegetation is the main factor for determining the suitable habitat for roan antelopes as it provides forage, shelter and cover. Roans prefer lightly to moderately wooded grasslands (Schuette et al., 1998).
Wooded grassland	WGL	
Vegetation burned status was included as 1 factor with 2 levels: Burned and unburned	BS	RNP had areas that were burned recently and those that had not been burned for more than 1 year. Roans generally avoid areas that have been recently burned (Joubert, 1974) and during the breeding season they need unburned grasslands for concealment of calves (Starfield and Bleloch, 1986).
Soil was considered as 1 factor with two levels: Cambisols and Solonetz	Soil	The areas where roans occur in RNP have 2 types of soil (Cambisols and Solonetz). Solonetz have more minerals and higher water holding capacity than the Cambisols (FAO, 2009). Roans may select soils that are rich in minerals and those capable of holding rain water for a longer period.

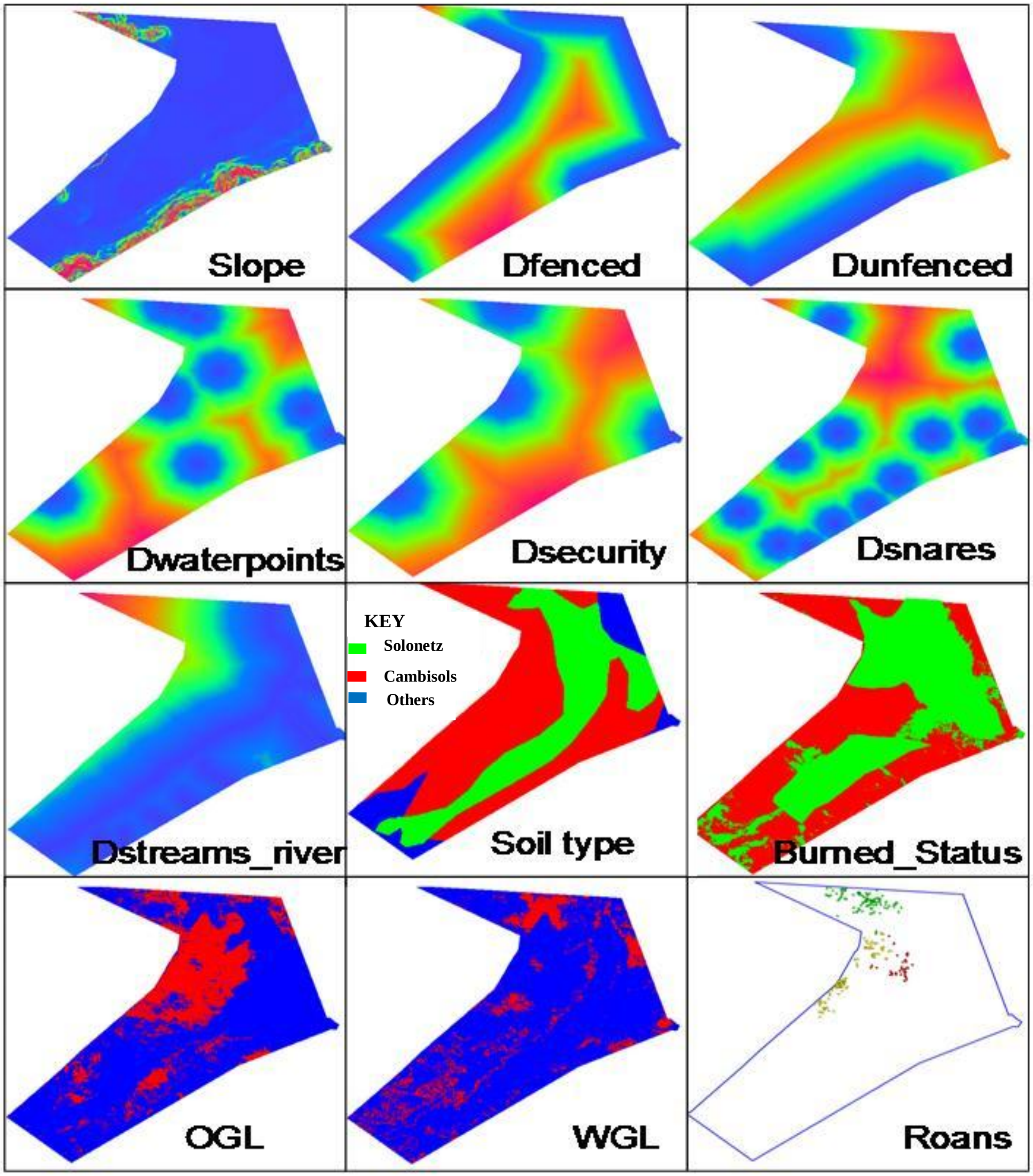


Figure 5.1: GIS maps of the distribution of roans in RNP and 11 predictor variables used to extract data for roan habitat suitability modelling. The variables studied are slope, distances to park fence (Dfenced), unfenced park boundary (Dunfenced), water points (Dwaterpoints), park outposts/gates (Dsecurity), snare hot spots (Dsnares), streams and the Olambwe river (Dstreams_river), soil type, vegetation burned status (Burned_status), and vegetation types – open grasslands (OGL) and wooded grasslands (WGL). The first 7 maps are continuous variables with values decreasing from blue to red whereas the 4 penultimate maps are categorical maps with blue colour showing areas that are not relevant. The last map presents the animal locations for 3 roan groups used in this study.

Vegetation

Under the vegetation category there were five potential predictors based on vegetation type: wooded grassland (WGL), sparsely wooded grassland (SWGL), sparsely shrub grassland (SSGL), dwarf shrub grassland (DSGL), grassland (GL) and one predictor on burned status of the vegetation (Burned_veg). Correlation analysis indicated that four of these vegetation types (GL, DSGL, SSGL and SWGL) were highly positively correlated (all $r > 0.8$, $p < 0.05$). Zar (2010) recommends deleting or combining of highly correlated variables to solve the problem of multi-collinearity. Hence, these 4 vegetation types were combined into one vegetation type – the open grassland (OGL), based on the positive correlations and the fact that all of them had a vegetation canopy cover greater than 50% and a similar vegetation composition. Therefore, the initial 6 vegetation factors were reduced until only 3 most important remained for inclusion in habitat suitability modelling: open grassland, wooded grassland and vegetation burned status. The vegetation burned status was considered as one factor with two levels: burned and unburned. The unburned category comprised of vegetation that had not been burned for at least one year.

Water

Availability of surface drinking water is a vital resource for the roan antelopes because they are highly water dependent and they usually drink daily (Schuette et al., 1998). Literature shows that the species existed in most African savannah where water was abundant (Kingdon, 1984). In Ruma N. Park there are two permanent sources of water for animals: (1) man-made dams and water troughs and (2) natural streams and the Olambwe River. The dams and water troughs (hereafter referred as water points in this study) are located very close (0.8 ± 0.04 km) to the roan home range region whereas the streams and the Olambwe river are located far away (3.6 ± 0.06 km) from the roan presence region. In addition, the streams are located in very steep and hilly areas whereas the Olambwe River is in the middle of a riverine forest, which may make them inaccessible to the roans. Analysis on roan movements showed that their mean daily travelling distance is 1.43 ± 0.08 km and their average home range size is 3.57 ± 0.88 km2, which suggests that the roans may not be utilizing the water from streams and the river unless in very severe drought periods when water is very scarce. In order to investigate whether the roans utilize the two sources of water, the available water to roans was divided into two variables: water points, and streams and river.

Soil

There were two variables in this category: soil type and saltlicks. The saltlicks variable was dropped because it was thought to be a subset of the soil type variable and hence it measures the same habitat characteristic as the soil type. Inclusion of two variables measuring the same habitat characteristic has been shown to cause the problems of collinearity (Legendre and Legendre, 1998). Soil type is important for provision of minerals and salt licks to the roans, which is essential because wild animals in Kenya parks are not provided with artificial mineral supplements. Soils with high clay content are capable of holding rain water in natural pools for a longer period. The type of soil also determines the distribution of grass and other plant species in the park. There are five soil types in RNP but roans occurred only in areas with two soil types: cambisols and solonetz. The solonetz soils have more clay content of about 70%, deep profile, more minerals and are poorly drained, with a base saturation of more than 80% in most horizons (Omoto, 1994). The Solonetz soils occur on the flat valley bottom plains in the park and are seasonally waterlogged, which provides stagnant pools of water for animals. The cambisols occur at the foot slopes and are relatively young with significant quantity of weatherable primary minerals and a base saturation of about 50% (FAO, 2009). Based on these soil properties it can be hypothesized that the roans will select areas with solonetz soils as opposed to the cambisols. For purpose of modelling the soil type was taken as one factor with two levels. The soil data was obtained from a soil map of Ruma N. Park at a scale of 1:50 000 (Omoto, 1994).

Threat of poaching

Variables in this category were extracted from the infrastructural and vegetation maps of RNP using ILWIS Academic GIS software package (ILWIS, 2009). There were 6 variables that were potential indicators of areas where roans had the highest threat of poaching by surrounding community or passersby: distance to public roads and foot paths inside the park, distance to fenced park boundary, distance to unfenced park boundary, distance to thick vegetation (forest and bushland), distance to snare hot spots, and distance to park gates and outposts. Poaching has been identified as one of the causes of wildlife population decline in RNP (Kones, 2005; Waweru et al., 1995) and hence it is vital for a poaching element to be incorporated in modelling of roan distribution and habitat suitability. However, the importance of the poaching element in modelling is mainly for management purposes as opposed to the other aforementioned factors that are of biological significance to the roan. The public roads and paths variable was deleted because it was strongly positively correlated ($r = 0.736$, $df = 426$, $p < 0.001$) with unfenced park boundary indicating that many public roads and foot paths in RNP are located in areas that are not fenced; hence these two variables measured the same habitat characteristic. The distance to thick vegetation was also deleted because it was measuring the same habitat characteristic as the vegetation types and snare hot spots. The distance to thick vegetation was also positively correlated with snare hot spots ($r = 0.437$, $df = 426$, $p < 0.001$) indicating that most snare hot spots were located in thick vegetation that was far away from the roan home range region. Snares were considered to be of more direct effect on roan distribution than the distance to thick vegetation. After these deletions only 4 variables remained in this category: distance to fenced park boundary, distance to unfenced park boundary, distance to park gates and outposts and distance to snare hotspots. During the habitat suitability modelling, two variables concerning the effect of snares were tested separately to ascertain the best predictor for roan occurrence: distance to snare hotspots and density of snares (obtained from chapter 7). Field observations on roan movement indicated that the roans select areas that are close to park fences and park gates and outposts while they avoided areas near unfenced park boundaries. It was thus important to test whether the field observations were statistically significant.

Geographical features

There were two variables in this category: slopes and elevation. Elevation is more important when considering the geographical distribution of roans at a national or even higher level. It was therefore not considered as an important factor in impacting directly on roan habitat selection at the park level. Elevation was also strongly positively correlated with slopes ($r = 0.740$, $df = 426$, $p < 0.001$). Hence based on these considerations, elevation was not included in the modelling because it is important to use only the direct causal factors as variables (Johnson and Omland, 2004). Slopes were left for inclusion in modelling because they can impact directly on roan habitat selection at the park level with animals probably selecting low slope areas which minimize energy expenditure.

5.2.3Number of predictors versus sample size

Initially statistical modelling was carried out using all the 11 variables already identified as potential explanatory predictors for the distribution of roan antelopes in RNP. This yielded a total of 2047 models without counting the null model, as the number of models (R) is given by the formula, $R = 2^p - 1$, where p is the number of predictors considered.

Burnham and Anderson (2002) point out that analysis is considered as exploratory rather than confirmatory when the number of models greatly exceeds the sample size. Hence, this initial analysis which had 2047 models and a sample size to predictor ratio of 39 was taken to be exploratory analysis. It needed further analysis with fewer predictors in order to yield models that can be considered confirmatory. Therefore, the number of predictors were reduced to 8 based on literature and understanding of the roan antelope biology. Alternatively, the top 8 predictors with the highest predictor weights from the exploratory analysis could have been selected but this procedure is not recommended; instead modellers advocate reduction of the number of variables based on theory and/or logic (Burnham and Anderson, 2002). However, the 255 models obtained using the 8 predictors were not better than those obtained using the initial 11 predictors. In a bid to obtain the best set of models that can be relied upon with greater certainty in explaining habitat selection for the roans in RNP, the number of predictors were finally reduced to 5 most important ones and analysis repeated. This final reduction of number of predictors was still based on literature and roan biology. However, the consideration of models constructed using the 5 and 8 set of predictors does not diminish the validity of those generated using 11 predictors. Literature shows that model results based on lower sample size to predictor ratios (n/K) have been used reliably in modelling. For instance, Whittingham et al, (2005) modelled habitat selection by yellowhammers using n/K ratio of 32.8 while Greaves et al, (Greaves et al., 2006) modelled the dormouse distribution using a ratio of 38.

5.2.4Levels of habitat suitability analyses

From a biological viewpoint, an animal's use of the available habitat is taken to be the result of choices at different levels (Johnson, 1980). The first level is habitat selection within an arbitrarily defined study area and the second level is the habitat selection within an animal's home range. Different factors may be responsible for habitat selection at each level and therefore analyses should be performed in stages to identify the specific factors (Aebischer et al., 1993). This study considered habitat selection at three levels: (1) selection within the whole park (hereafter referred as the 'Whole Park'); (2) selection within the roan home range region defined as the minimum convex polygon of locations from all roan groups combined together (hereafter referred as the 'Roan home range region') and (3) selection within individual roan home ranges defined as the minimum convex polygon of locations of each roan group separately (hereafter referred as the 'Individual roan home ranges'). Clear illustrations of these three levels are presented in Figure 5.2.

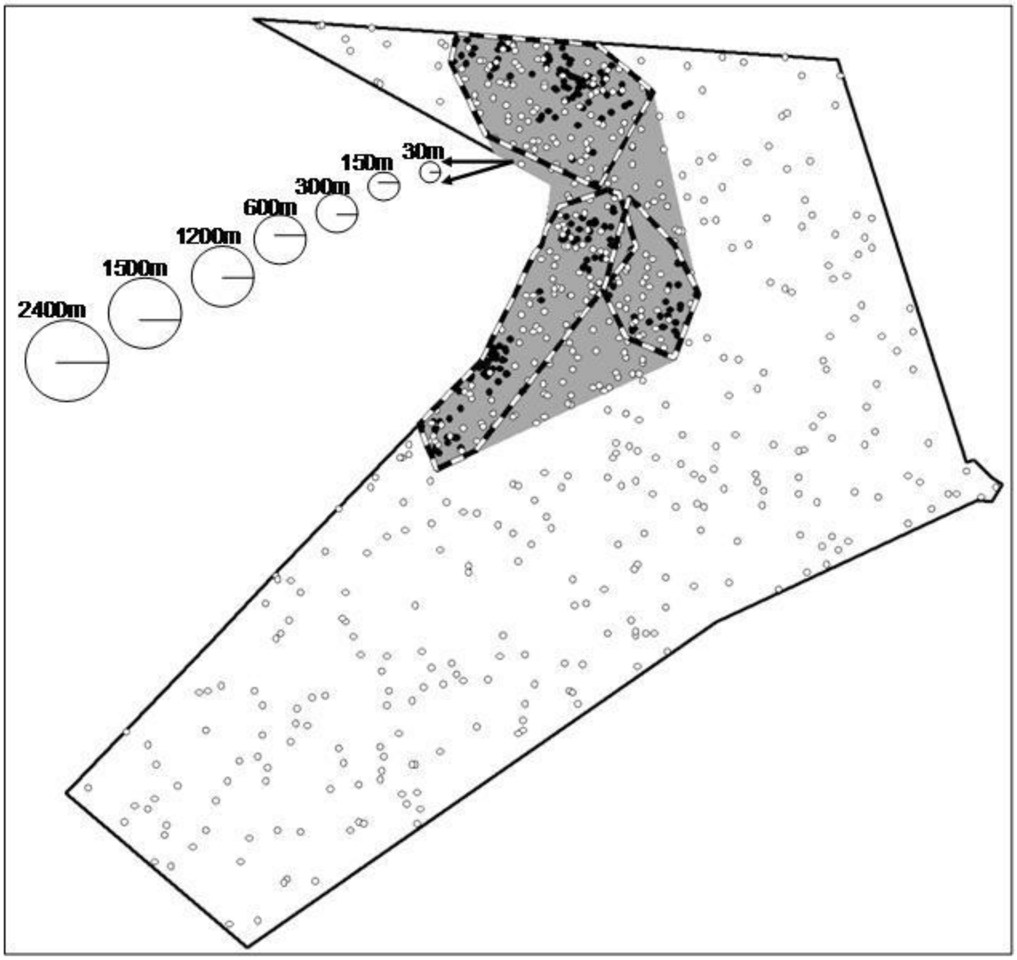


Figure 5.2: The roan presence points (black circles) and absence or random points (white circles) of roans in RNP in 3 nested levels: whole park (black line), roan home range region (shaded in grey), and individual roan home ranges (black and white blocked line). The top left concentric circles indicate the 7 different spatial scales representing buffer radii of 30m, 150m, 300m, 600m, 1200m, 1500m, and 2400m, at which data was extracted around each point.

5.2.5Spatial scales of habitat suitability analyses

The variables for this study were collected at different spatial scales but were all converted to a spatial resolution of 30m because most of the variables were obtained at 30m scale such as the vegetation types, geographical features and variables measuring threat of poaching. Maurer (2002) showed the importance of ensuring that the scale of measurement of predictors matches the scale of the ecological process being studied. Determining the appropriate scale of sampling unit in species distribution modelling still remains a problem (Whittingham et al., 2005; Rushton et al., 2004). These authors emphasize the importance of understanding the biology of the species being studied in defining habitat predictors at the right scale. In cases where the correct scale is not known based on the species biology, the appropriate scale can be investigated by varying the sampling unit and repeating the analysis to assess whether the habitat selection results change as a function of the sampling unit and hence determine the optimal scale for the species in question. However, this flexibility is only possible if GIS data is the basis for the models. Erickson et al (1998) investigated the dependency of habitat selection model results on the scale of the sampling unit by using varying buffer sizes. They concluded that more research needs to be done to address the scale issue in habitat selection modelling but the initial sampling unit should be based on the knowledge of the species being studied.

In this study, the effect of the spatial scale on the habitat selection by roan antelopes was investigated by using 7 spatial scales. The scales were practically implemented via ILWIS Academic GIS software package by using buffers with 7 different radii as the sampling units around each presence and absence roan location: 30m, 150m, 300m, 600m, 1200m, 1500m and 2400m. A schematic diagram illustrating the buffers is given in figure 5.2. Buffers were used because they are more robust than single pixels in the sense that small errors in animal locations will have relatively little effect (Erickson et al., 1998). The initial buffer radius of 30m was used because it matched with the scale of measurement of all predictor variables as aforementioned. The third radius of 300m is based on the average distance travelled by roan groups in two hours (the sampling time interval between consecutive roan locations), which is 288 ± 80m. The sixth radius of 1500m is based on the average daily travel distance by roans, which is 1430 ± 80m. The other four radii are all arbitrary values for the purpose of comparison.

5.3 Statistical methods

Generalized linear models (GLM), which can handle non-normal response variables such as roan presence or absence, were used to study the relationship between roan probability of occurrence and habitat. In particular, a special case of a GLM known as the binary logistic regression, which has a binomial error distribution and logit link function, was used. Logistic regression is a robust technique when using mixed data sets of continuous, discrete and categorical predictor variables (McGarigal et al., 2000), which is the case for this study. All the statistical analyses were carried out using the open source R software package for statistical computing (R Core Team Development, 2007). Data analysis and inference was done using both the conventional stepwise regression and the new information theoretic approach for the purpose of making comparisons.

5.3.1Stepwise regression

Stepwise logistic regression analysis was performed to ensure the predictor variables that remain in the final best model were statistically significant at the stated p-value. Two p-values were used in this analysis as the cut off point of significance level: $p = 0.05$ and $p = 0.15$. The $p = 0.05$ is the widely used and conventionally accepted level of significance by statisticians but the $p = 0.15$ is recommended as the selection criterion in modelling applications as it yields better results (Greaves et al., 2006; Anderson et al., 2000). The two selection criteria were used in habitat suitability modelling of the endangered roan antelope to assess whether their performance was different.

5.3.2Information-theoretic approach

The information-theoretic approach described by Burnham and Anderson (2002) was used to come up with a set of models. The approach uses Akaike's information criterion (AIC) in model selection. The AIC was calculated based on the maximized likelihood estimation using the formula,

$$AIC = -2LL+2K,$$

where LL is the value of the maximized log-likelihood and K is the number of predictors in the model plus one for the regression intercept. AIC was calculated for each of the models in the set and the best model is the one with the smallest AIC value (denoted as AIC_{min}). In order to rank the candidate models on how closely they approximate reality, AIC differences (Δ) were calculated relative to the AIC_{min}, such that for a model i the AIC difference (Δ_i) is given by the formula,

$$\Delta_i = AIC_i - AIC_{min}$$

The absolute size of the AIC is not important but the AIC differences are very useful in estimating the relative expected Kullback-Leibler differences between each candidate model and the reality (Burnham and Anderson, 2002).

If the sample size (n) is small relative to the number of predictors (p) used in the modelling (that is, $n/p < 40$), a corrected AIC_c with an additional bias-correction term is calculated as,

$$AIC_c = -2LL + 2K + 2K(K+1)/(n-K-1)$$

The AIC_c was used in this study because for the largest number of predictors (11) used in the initial modelling, the n/p ratio was 38.9. For other numbers of predictors (5 and 8) used in further statistical modelling the ratios were more than 40, but Burnham and Anderson (2002) recommend choosing either AIC or AIC_c and using it consistently in a given analysis, rather than mixing the two criteria.

5.3.3Multi-model inference (MMI) and model averaging

Multi-model inference (MMI) refers to the formal inference from more than one model. As part of MMI the fitted models were ranked from best to worst, based on the Δ_i values and then scaled to obtain the relative plausibility of each fitted model by a weight of evidence (w_i) relative to the selected best model (Burnham and Anderson, 2002). The Akaike weight of model i (w_i) was calculated using the formula,

$$w_i = \frac{\exp(-\Delta_i / 2)}{\sum_{r=1}^{R} \exp(-\Delta_i / 2)}$$

where R is the number of all possible models as determined by the number of predictors included in the modelling.

The sum of Akaike weights (w_i) for all R models equals 1. The weights have a probabilistic meaning such that, w_i is the probability that model i would be selected as the best fitting model if the data were collected again under the same underlying process (Whittingham et al, 2005). If the model ranked as number one has a $w_i > 0.90$, it can be considered to be the final best model and inference be done based on only this one model (Anderson et al, 2001; (Burnham and Anderson, 2002). Otherwise a set of top best models should be selected using a certain criterion and model averaging carried out on these models to come up with the final best model. Burnham and Anderson (2002) present different criteria that can be used to select the top best models for averaging but only two are considered in this study as they are easily understood and have received wide acceptance among modellers: (1) using Akaike weights as approximate probabilities of each model being the actual best model for a given data set and (2) setting a cut-off for AIC differences (Δ_i) based on the level of empirical support of the Δ_i. The first approach involves summing up the Akaike weights of the fitted models from largest to smallest until the sum is ≥ 0.95 or ≥ 0.99 (Burnham and Anderson, 2002); the corresponding subset of models is a type of confidence set on the Kullback-Leibler best model. For the second approach, Monte Carlo studies on the sampling distribution of the Δ_i have been used to establish a rule of thumb such that models within a Δ_i of (a) 0-2 have substantial empirical support, (b) 4-7 have considerably less support and (c) > 10 have essentially no support, of being the Kullback-Leibler best model (Burnham and Anderson, 2002; 2001).

All the above criteria were used in this study to compare their performance and to aid in selecting the best set of models for averaging. Model averaging uses the average of parameter coefficients from each model in the selected set of best models, weighted by its Akaike weight. A weighted average was calculated for the coefficient of each parameter in the selected set of best models using Burnham and Anderson's (2002) formula,

$$\overline{\beta}_j = \frac{\sum_{i=1}^{R} w_i \hat{\beta}_{j,i}^{+}}{\sum_{i=1}^{R} w_i}$$

where w_i is the Akaike weight of model i and $\hat{\beta}_{j,i}^{+}$ is the estimate of regression coefficient associated with predictor j if the predictor is included in model i, or is zero otherwise. Model averaging enabled inference to be made on a large number of selected top best models instead of using a single best model. Model averaging therefore provides a more stabilized inference with reduced model selection bias effects on regression coefficient estimates (Burnham and Anderson, 2002).

5.3.4Model assessment

It is generally recommended that model performance be tested using an independent data set (Pearce and Ferrier, 2000; Fielding and Bell, 1997). To achieve this, the original data set of 306 locations was split into two data sets: a training set and a testing set. The formula advocated by Huberty (1994) was used in deciding how many locations should be set aside as a testing data set, that is,

Percentage of testing data = $\{[1 + (p-1)^{1/2}]^{-1}\}*100$, where p is the number of predictors.

Based on this equation, 30% of the original data was set apart as testing data set (that is, 92 locations) and the rest used as the training data set. A bootstrapping technique described by Manly (2007) was used to validate the model results from the training data set. The technique was carried out by resampling (with replacement) the training data to construct bootstrap samples, which were used to compute coefficients to assess the variability and bias in the original coefficients estimated using the training data set. The bootstrap model was run 999 times each time selecting at random 100 presences and 100 absences. The

Bootstrap technique was done using automated stepwise regression at two significance levels, that is, p = 0.05 and p = 0.15.

5.3.5ROC plots

It is important to assess the model fit using another criterion other than AIC (Eberhardt, 2003). This is because AIC is used to rank models and select the most parsimonious model from the set of models already developed (Burnham and Anderson, 2002). However, if the whole set of models do not fit the data well, then AIC can only select the best model from a poor set.

There are many measures that have been developed for assessing the prediction success of presence/absence models. These measures compare observed presences and absences with those predicted by the model (Fielding and Bell, 1997). The computations can be presented in a confusion matrix like the one shown in Figure 5.3. However, most of the measures have been found to exhibit 3 shortcomings. Firstly, they fail to make full use of the information contained in the confusion matrix (Fielding and Bell, 1997). Secondly, they depend upon a selected critical threshold probability, which varies according to the use of the model. The threshold is usually set at 0.5 and any probabilities above it are taken to be 1 (presences) and those below as 0 (absences) (Fielding and Bell, 1997). Thirdly, they fail to distinguish whether correct predictions are true positives or true negatives (Greaves et al., 2006).

Due to these problems, the receiver operating characteristic (ROC) plots were used to assess model fit in this study. ROC plots are threshold independent and have been shown to yield better results than most of the other methods (Fielding and Bell, 1997). A ROC plot is constructed by plotting the true positives (presences predicted correctly) against their corresponding false positives (absences predicted incorrectly as presences) for all thresholds between 0 and 1. The area under the curve (AUC) of a ROC plot is a measure of the overall performance or accuracy of a model and its values range from 0.5 to 1.0. The ROC plot of a good model will rise steeply at the origin, and then level off at a value near the maximum of 1, because it will achieve a high true positive rate while the false positive rate is still small. The ROC plot for a poor model (whose predictive ability is the equivalent of random assignment) will lie near the diagonal, where the true positive rate equals the false positive rate for all thresholds. Good models have an AUC close to 1, while poor models have an AUC close to 0.5.

		Observed	
		+	-
Predicted	+	*a*	*b*
	-	*c*	*d*

Figure 5.3: A confusion matrix showing the two possible prediction errors in presence/absence models. The plus (+) denotes presence and minus (-) denotes absence. The letters: a is the number of observed presences that the model correctly predicts; b is the number of absences the model incorrectly predicts to be presences; c is the number of presences the model incorrectly predicts as absences; and d is the number of absences the model correctly predicts (modified from Fielding and Bell (1997)).

5.3.6Set of models explored

Data from observational studies is often faced with the problem of random effects, which when ignored cause pseudo-replication (Bolker et al., 2009). For this study, random effects were suspected to arise out of collection of repeated observations from the same roan group at different times of the day. Two random effects were investigated: group and time. Variations between roan groups could occur due to differences in age structure and group size. Also, differences in time periods can be caused by preference of different resources (such as water, shelter, cover and forage) at different times of the day. The two random effects were investigated using two statistical methods. First, a variable coding for roan group and another for time period were included as random effects in Generalized Linear Mixed Models (GLMM) and model inference done using the Gauss-Hermite quadrature (GHQ), which is the best for handling binary data (Bolker et al., 2009). Secondly, the same variable codes for roan group and time period were included as fixed effects in Generalized

Linear Models (GLM). Results from both analyses showed no quantitative difference and led to the same conclusion concerning important variables for predicting habitat suitability for roan antelopes. The two analyses showed that the roan group and time period were not significant factors and deleting them did not affect the results on roan habitat suitability and thus they were omitted for the rest of the modelling process in this study.

Three classes of models were computed as a result of various combinations of predictor variables. The three types were (i) vegetation only models – based on only vegetation types as the predictor variables; (ii) environment only models – based on environmental variables only and (iii) combined variable models – based on a combination of all vegetation types and environmental variables. Results showed that the combined models performed better than the other two model classes (Table 5.2), although all three model classes had good overall accuracy far higher than chance (AUC > 0.8). The combined model explained more deviance (r^2 =0.62) and was more parsimonious than the others (AIC = 188.77). The findings imply that modelling using either vegetation only or environment only variables omits important variables for predicting habitat suitability for roan antelopes. Therefore, the rest of habitat suitability modelling in this study was based on the combined variable models.

To ascertain the best snare variable for prediction of roan occurrence in RNP, models were built using two contrasting snare variables: snare density obtained from Chapter 7 and distance to snare hotspots. For the 3 levels of analysis (whole park, home range region and individual home ranges), the snare density was insignificant whereas the distance to snare hotspots was significant at the home range region level only. A comparison of the two models at the home range region revealed that the snare distance model was better than the snare density model (Table 5.3). It was more accurate, explained more variation of the data, fitted well to the data and was more parsimonious.

Table 5.2: Comparison of the performance of different logistic models based on various combinations of predictor variables

Predictor variables	AIC	r^2	Overall accuracy (AUC)
Vegetation type variables only	245.75	0.56	0.81
Environmental variables only	254.65	0.56	0.92
Vegetation and environmental variables	188.77	0.62	0.93

Table 5.3: Comparison of models using snare density and distance to nearest distance at the home range region level

	AIC	r^2	AUC
Snare Density model	538.73	0.14	0.62
Snare Distance model	532.96	0.16	0.69

5.4 Results

5.4.1Stepwise regression

5.4.1.1 Comparing models build using a significance level of p=0.05 vs. p=0.15

Stepwise regression models built using a significance level of p = 0.15 were different and slightly better than those built using p = 0.05. Comparing models constructed for the whole park and home range levels at varying spatial scales consistently showed that the AIC scores for p = 0.15 models were either less than or equal to and never greater than those of p = 0.05 models (Figure 5.4). Similarly, the area under the curve (AUC) of ROC plots for p = 0.15 models were higher than or equal to and never smaller than those of p = 0.05 models. The AUC were 0.9305 versus 0.9341 for the whole park, 0.7279 versus 0.6881 for the roan home range region and 0.6554 versus 0.6554 for the individual roan home ranges, for the p = 0.15 versus p = 0.05 models, respectively (Figure 5.5). The best models obtained using p

= 0.15 had more variables than those obtained using the p = 0.05. The number of variables for the best model was 6 versus 5 for the whole park, 7 versus 5 for the home range region and 6 versus 5 for the individual roan home ranges, for the p = 0.15 versus p = 0.05 models, respectively (Table 5.4). The precision of the coefficients of all the variables in the models was assessed by comparing the coefficients of the original model with that of bootstrap models. For all the models the coefficients of the original model were similar to those of bootstrap models (Table 5.4).

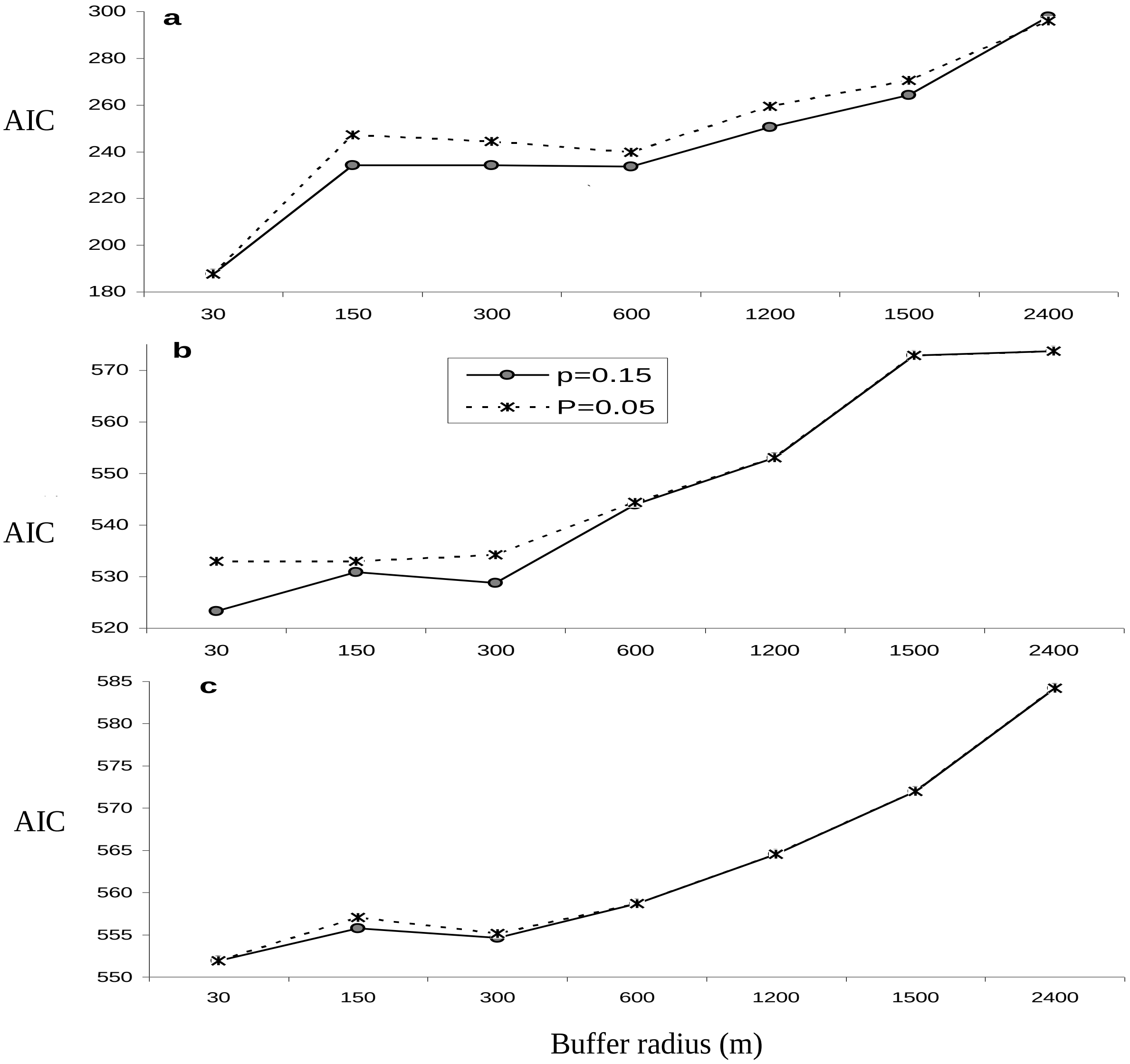
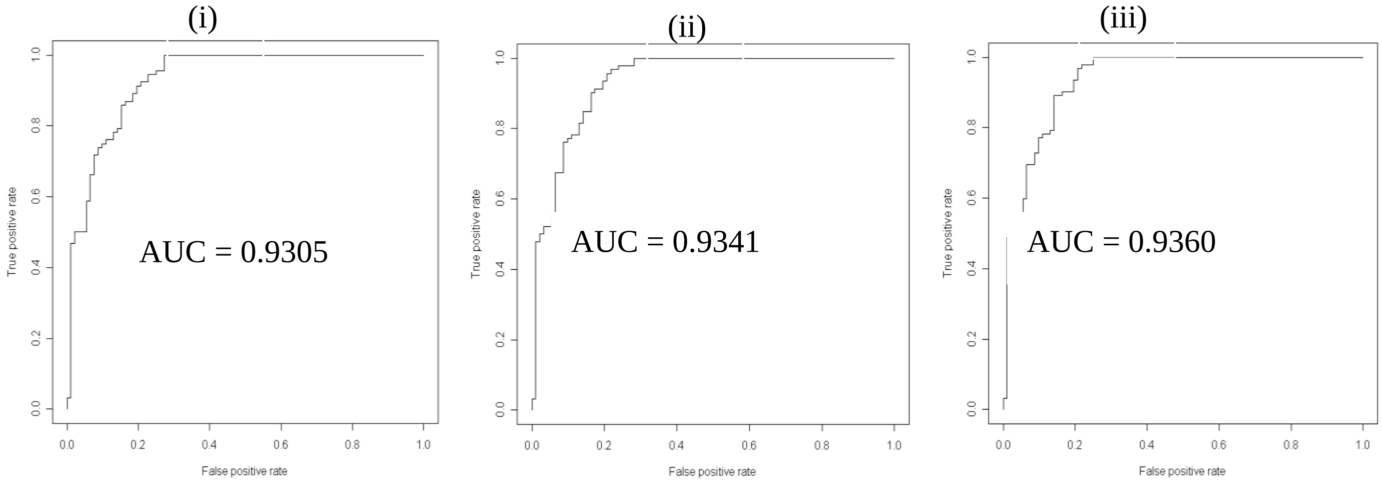
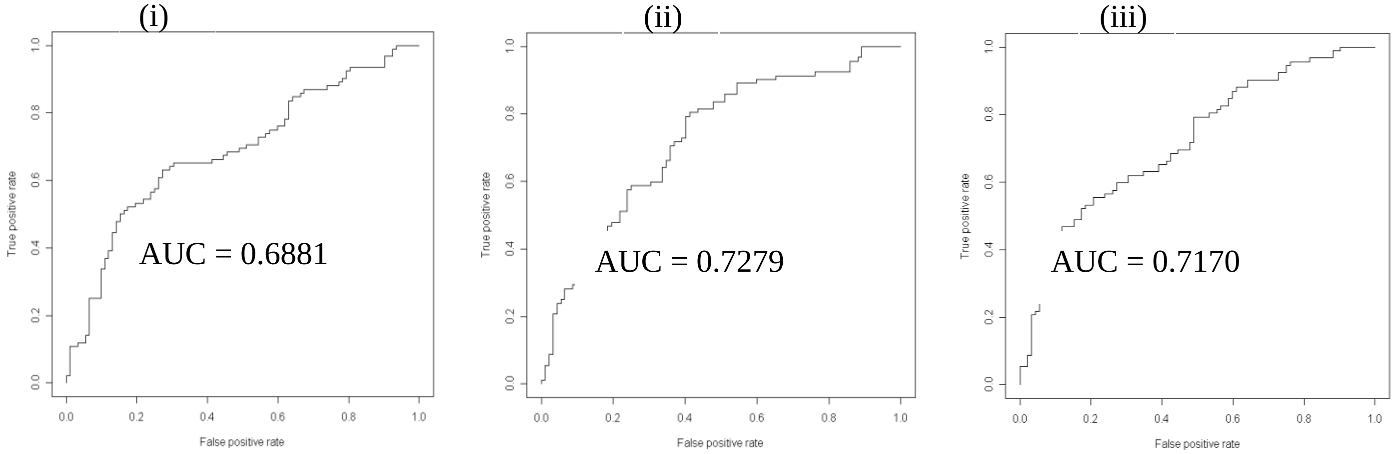


Figure 5.4: Assessing the effect of buffer radius and significance level (p = 0.05 & p = 0.15) on the habitat suitability models estimated using stepwise regression for the a) whole park, b) roan home range region and c) individual roan home ranges.

a) Whole park


(i) (ii) (iii)

b) Roan home range region


(i) (ii) (iii)

c) Individual roan home ranges

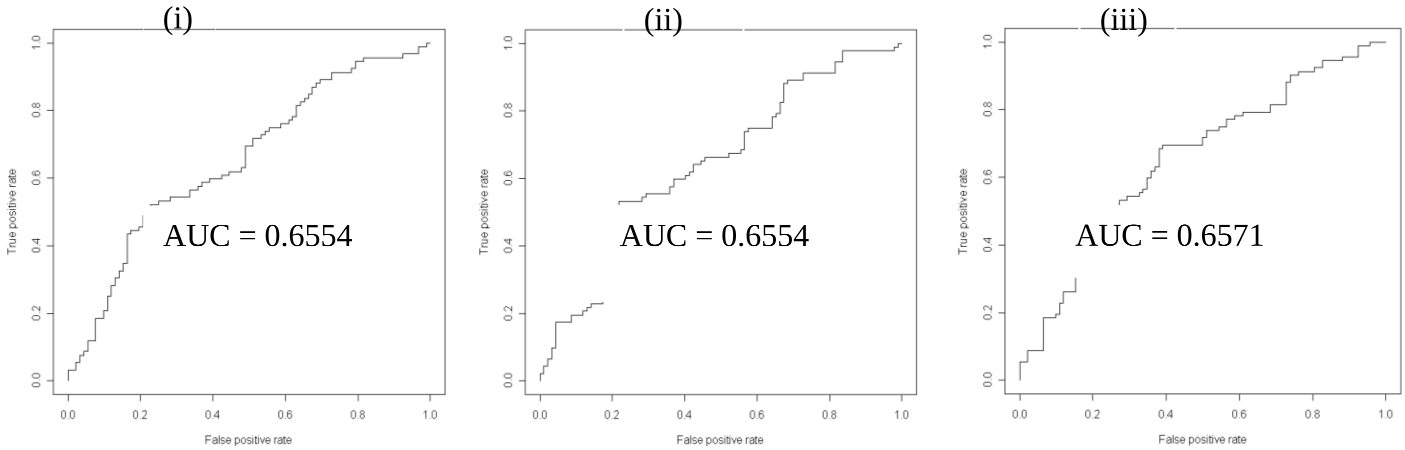

(i) (ii) (iii)

Figure 5.5: ROC plots for final models from stepwise selection with a significance level of (i) $p = 0.05$, (ii)$p = 0.15$, and (iii) information-theoretic approach based on AIC_c model average for the (a) the whole RNP, (b) roan home range region and (c) individual home ranges

Table 5.4: Habitat suitability models (original and bootstrap) estimated for roan antelopes using stepwise selection with significance level of p = 0.05 and p = 0.15 for the (a) whole RNP, (b) roan home range region and (c) individual roan home ranges

a) Whole park

	P = 0.05				P = 0.15			
	Best model		Bootstrap Models		Best model		Bootstrap Models	
Predictor	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error
Intercept	-6.28316	1.19875	-12.46550	2.76958	-5.54461	1.26830	-9.67958	2.46352
Dsecurity					-0.00029	0.00020	-0.00032	0.00001
Dstreams_river	0.00077	0.00017	0.00087	0.00001	0.00068	0.00018	0.00078	0.00001
Dwaterpoints	-0.00145	0.00034	-0.00151	0.00002	-0.00135	0.00035	-0.00141	0.00002
Slope	0.16751	0.05346	0.20527	0.01438	0.17642	0.05456	0.21907	0.03295
OGL	7.45774	0.96432	13.56425	2.80094	7.48905	0.96682	11.59723	2.46135
WGL	7.40752	0.93867	13.46918	2.79949	7.40451	0.94217	11.44913	2.45165

b) Roan home range region

	P = 0.05				P = 0.15			
	Best model		Bootstrap Models		Best model		Bootstrap Models	
Predictor	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error
Intercept	3.08059	0.45635	3.12224	0.01686	-2.31262	1.55545	-2.40328	0.07929
Dfenced	-0.00057	0.00016	-0.00059	0.00001	-0.00050	0.00017	-0.00052	0.00001
Dsnares	-0.00034	0.00012	-0.00034	0.00000	-0.00033	0.00013	-0.00034	0.00001
Dwaterpoints	-0.00102	0.00019	-0.00103	0.00001	-0.00104	0.00020	-0.00108	0.00001
Slopes	-0.16618	0.06651	-0.17178	0.00190	-0.16522	0.06991	-0.17449	0.00306
Soiltype	-0.75884	0.25572	-0.78134	0.00900	-1.12057	0.28381	-1.16947	0.01457
Dstreams_river					0.00098	0.00028	0.00102	0.00001
Dunfenced					0.00059	0.00018	0.00061	0.00001

b) Individual roan home ranges

	P = 0.05				P = 0.15			
	Best model		Bootstrap Models		Best model		Bootstrap Models	
Predictor	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error
Intercept	0.72510	0.36930	0.75593	0.01259	0.65190	0.37390	0.69161	0.01280
Dfenced	-0.00040	0.00016	-0.00042	0.00001	-0.00046	0.00017	-0.00048	0.00001
Dunfenced	0.00030	0.00008	0.00031	0.00000	0.00029	0.00008	0.00030	0.00000
Dwaterpoints	-0.00056	0.00020	-0.00058	0.00001	-0.00061	0.00020	-0.00063	0.00001
Slopes	-0.17400	0.06476	-0.20008	0.00255	-0.17710	0.06456	-0.19574	0.00242
Soiltype	-0.87600	0.26060	-0.88616	0.00921	-0.82900	0.26320	-0.85077	0.00952
OGL					0.36880	0.23280	0.38037	0.00825

5.4.1.2 Effect of spatial scale of sampling on habitat suitability modelling

The performance of habitat suitability models from stepwise regression changed as a function of the spatial scale of sampling. The best models based on AIC scores were obtained at the smallest spatial scale and model performance decreased consistently as the spatial scale increased such that the poorest models were obtained at the largest spatial scale used. The best spatial scale was 30m for the whole park and between 30m and 300m for the home range levels of analysis (Figure 5.4). The spatial scale of 30m was equal to the spatial scale of sampling of vegetation in the field and the spatial resolution of the Landsat image from which various continuous variables were extracted. Also, the spatial scale of 300m was equal to the mean distance travelled by roans in 2 hours, which was the sampling time interval between 2 consecutive animal locations. The performance seemed to change systematically with increase in spatial scale until a threshold is reached beyond which the system breaks down and suddenly the model performance becomes very poor for the rest of the consecutively larger spatial scales. The threshold was 600m for the whole Park and 300m for the home range levels of analysis (Figure 5.4).

The number and types of important variables selected by the best models from stepwise regression changed as a function of the spatial scale of sampling. Generally, the number of important variables was highest at the best spatial scales and it decreased beyond the threshold point with the largest spatial scale having the smallest number of important variables. Considering spatial scales occurring before the threshold point is reached the number of variables selected by different best models ranged from 6 to 7 for the whole park, 7 to 8 for the roan home range region and 4 to 6 for the individual roan home ranges (Table 5.5). The best model for the whole park at the best spatial scale of 30m contained only 6 variables (wooded grassland, open grassland, streams and river, water points, slope and security). However, the best models at the second and third best spatial scales of 600m and 150m, respectively, included two more significant variables (unfenced park boundary and snare hotspots) as important for predicting roan habitat suitability. Similarly, for the roan home range region the best model at 30m contained 7 variables (streams and river, water points, slope, park fence, unfenced park boundary, snare hotspots and soil type). However, the best models at the second and third best spatial scales of 300m and 150m, respectively, added two more important variables (wooded grassland, open grassland). For the individual roan home ranges, the best model at 30m contained 6 important variables (open grassland, water points, slope, park fence, and unfenced park boundary and soil type). However, the best models at the second and third best spatial scales of 300m and 150m, respectively, did not include water points, park fence and unfenced park boundary but added two more important variables (wooded grassland and vegetation burned status). Therefore, considering several relevant spatial scales of sampling (that is, before the threshold is reached) and the 3 levels of analysis, all the 11 variables presented in table 1 are important variables for predicting the suitable habitat for roan antelopes in Ruma N. Park.

Table 5.5: Predictor variables selected for each final model estimated using stepwise selection at p = 0.15 across 7 different spatial scales (30m, 150m, 300m, 600m, 1200m, 1500m, and 2400m) with a sample size of 428 locations for the (a) whole RNP, (b) roan home range region and (c) individual roan home ranges

a) Whole park

Buffer radius (m)	Habitat selection function	AIC
30	exp(7.4045WGL + 7.4578OGL + 0.0008Dsr - 0.0015Dw + 0.1675Slop)	188.77
150	exp(2.7089WGL + 3.3414OGL + 0.0010Dsr - 0.0016Dw - 0.0005Dse+0.0006Dun+0.0005Dsn)	243.65
300	exp(3.4725WGL + 3.929OGL + 0.0009Dsr - 0.0015Dw - 0.0005Dse+0.0005Dun+0.0005Dsn)	243.11
600	exp(6.2991WGL + 6.8771OGL + 0.0009Dsr - 0.0014Dw +0.0004Dun+0.3766Slop)	243.94
1200	exp(7.3480WGL + 10.8828OGL + 0.0008Dsr - 0.0017Dw - 0.0006Dse+0.0005Dsn+1.1611Slop-1.3324Soil+2.0060Bveg)	250.7
1500	exp(5.8568WGL + 7.1932OGL + 0.0007Dsr - 0.0025Dw - 0.8119Soil+1.7873Bveg)	272.54
2400	exp(11.3890WGL + 3.1571OGL - 0.0010Dse + 0.0008Dsn)	288.2

b) Roan home range region

Buffer radius (m)	Habitat selection function	AIC
30	exp(0.0010Dsr - 0.0010Dw + 0.0006Dun - 1.1206Soil - 0.0005Dfe - 0.1652Slop - 0.0003Dsn)	523.28
150	exp(0.0011Dsr - 0.0012Dw + 0.0007Dun - 1.1612Soil - 0.0006Dfe + 1.6486WGL+ 1.4862OGL - 0.0004Dsn)	530.85
300	exp(0.0010Dsr - 0.0010Dw + 0.0006Dun - 1.2797Soil - 0.0005Dfe + 2.2341WGL+ 2.3444OGL + 0.6220Slop)	528.75
600	exp(0.0011Dsr - 0.0008Dw + 0.0009Dun - 1.4279Soil - 0.0007Dfe + 0.2317Slop)	543.94
1200	exp(0.0003Dsr - 1.3975Soil + 3.1321WGL+ 5.1229OGL + 1.7132Slop - 0.0005Dse)	552.98
1500	exp(0.0009Dsr + 0.0005Dun - 0.9573Soil - 1.4657OGL)	572.78
2400	exp(0.0004Dsr + 0.0029Dfe - 1.8606LWGL + 0.6316Bveg)	573.66

c) Individual roan home ranges

Buffer radius (m)	Habitat selection function	AIC
30	exp(-0.8290Soil - 0.1771Slop + 0.3688OGL - 0.0005Dfe + 0.0003Dun)	554.6
150	exp(-0.8667Soil + 0.9523Bveg - 0.0799Slop + 2.429WGL + 3.1808OGL)	555.77
300	exp(-0.9350Soil + 1.1712Bveg + 2.9204WGL+ 3.9043OGL)	551.89
600	exp(-1.0228Soil + 1.2035Bveg + 2.3726WGL+ 3.3672OGL)	558.67
1200	exp(-1.3533Soil + 0.5290Bveg)	564.54
1500	exp(-1.2971Soil + 0.6496Bveg)	571.98
2400	exp(-0.7109Bveg - 3.4731OGL + 0.0038Dfe)	584.19

5.4.2 Information theoretic approach

5.4.2.1 Model selection and multi-model inference

Considering the whole park, the AIC_c top ranked model contained 6 variables (wooded grassland, lightly wooded grassland, streams and river, water points, slope and security) but it had an Akaike weight of only 0.054. Due to model selection uncertainty, this model could not be considered as the final best model. The top 12 models had $\Delta_i < 2$ (Table 5.6a) and therefore were considered to be the most parsimonious models according to Burnham and Anderson (2001). The best final model based on Multi-model inference (MMI) using cumulative Akaike weights ≥ 0.95 as the criterion for model selection, showed that all the 11 initial variables needed to be included in the 95% certainty model average to define the suitable habitat for the roans in the whole park (Table 5.7a). Model selection indicated that 92 models could be considered as valid models (that is, a 95% confidence set of models) for roan habitat suitability. All these models included wooded grassland, lightly wooded grassland, streams and river and water points. The Akaike weights of these 4 variables were very high (> 0.99), indicating high level of support. This suggested that these 4 variables were very important as predictors and hence were necessary for a model to be plausible. However, a model consisting of only these 4 most important variables had an Akaike weight of 0.012 and was ranked as number 16 out of the 2047 models. Six of the other variables, park fence, unfenced park boundary, snare hotspots, soil type, security and vegetation burned status had low Akaike weights (< 0.5), indicating weak support and hence less important as predictors. The last variable, slope, had moderate support with Akaike weight of 0.821.

The coefficients for the predictors of the MMI averaged model and the AIC top ranked model are given in Table 5.6a. The coefficients of the two models were very similar except that the MMI averaged model had 7 more variables; slope, park fence, unfenced park boundary, snare hotspots, soil type, security and vegetation burned status. The ranking of the coefficients of the 4 variables with strongest support (> 0.99), was open grassland > wooded grassland > water points > streams and river.

Table 5.6: Information-theoretic statistics for all top habitat suitability models for roans in RNP, with substantial support (AIC Δi < 2) presented in rank order (from high to low Akaike weights) at 3 levels of analysis. The table indicates the variables included in the model, the maximized log-likelihood value (LogLik), the AICc, AICc differences (AICc Δi), and the model Akaike weight (wi). The wi values are also computed for each predictor across all models by summing all wi scores for all possible models in which the predictor was included.

a) Whole park

Model												R^2	LogLik	K_i	AICc	ΔAICc	W_i
1	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL			Dsecurity		0.6	-87.32	7	188.90	0.00	0.054
2	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL					0.6	-88.39	6	188.97	0.07	0.052
3	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced				0.6	-87.57	7	189.40	0.50	0.042
4	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL		Dunfenced			0.6	-87.77	7	189.80	0.90	0.034
5	Slopes		Dsnares	Dstreams_river	Dwaterpoints	WGL	OGL			Dsecurity		0.6	-86.79	8	189.92	1.02	0.032
6	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL		Dunfenced	Dsecurity		0.6	-86.88	8	190.10	1.20	0.030
7	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced	Dunfenced			0.6	-86.92	8	190.18	1.28	0.029
8	Slopes	Soiltype		Dstreams_river	Dwaterpoints	WGL	OGL			Dsecurity		0.6	-86.94	8	190.22	1.33	0.028
9	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced		Dsecurity		0.6	-87.22	8	190.77	1.88	0.021
10	Slopes	Soiltype		Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced				0.6	-87.22	8	190.78	1.88	0.021
11	Slopes	Soiltype		Dstreams_river	Dwaterpoints	WGL	OGL					0.6	-88.30	7	190.86	1.96	0.020
12	Slopes			Dstreams_river	Dwaterpoints	WGL	OGL				Burned_Veg	0.6	-88.31	7	190.88	1.98	0.020
Akaike weight	0.821	0.332	0.307	0.994	0.998	>0.999	>0.999	0.396	0.371	0.464	0.274						

b) Roan home range region

Model												R^2	LogLik	K_i	AICc	ΔAICc	W_i
1	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints			Dfenced	Dunfenced	Dsecurity		0.2	-251.92	9	522.26	0.000	0.122
2	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints			Dfenced	Dunfenced	Dsecurity	Burned_Veg	0.2	-251.01	10	522.54	0.278	0.106
3	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints		OGL	Dfenced	Dunfenced	Dsecurity		0.2	-251.23	10	522.98	0.721	0.085
4	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints			Dfenced	Dunfenced			0.2	-253.64	8	523.62	1.362	0.062
5	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced	Dunfenced	Dsecurity		0.2	-250.51	11	523.66	1.398	0.061
6	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints	WGL		Dfenced	Dunfenced	Dsecurity		0.2	-251.69	10	523.90	1.643	0.054
7	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints		OGL	Dfenced	Dunfenced	Dsecurity	Burned_Veg	0.2	-250.70	11	524.03	1.774	0.050
Akaike weight	0.981	0.999	0.832	0.996	>0.999	0.341	0.419	0.975	0.990	0.624	0.451						

Table 5.6: Continued

c) Individual roan home ranges

	Model											R^2	LogLik	K_i	AICc	ΔAICc	Wi
1	Slopes	Soiltype			Dwaterpoints	WGL	OGL	Dfenced	Dunfenced		Burned_Veg	0.12	-268.16	9	554.75	0.00	0.025
2	Slopes	Soiltype			Dwaterpoints		OGL	Dfenced	Dunfenced			0.12	-270.30	7	554.86	0.12	0.023
3	Slopes	Soiltype			Dwaterpoints		OGL	Dfenced	Dunfenced		Burned_Veg	0.12	-269.34	8	555.03	0.29	0.021
4	Slopes	Soiltype		Dstreams_river	Dwaterpoints			Dfenced	Dunfenced			0.12	-270.42	7	555.12	0.37	0.020
5	Slopes	Soiltype			Dwaterpoints	WGL	OGL	Dfenced	Dunfenced			0.12	-269.39	8	555.13	0.38	0.020
6	Slopes	Soiltype		Dstreams_river	Dwaterpoints		OGL	Dfenced	Dunfenced			0.12	-269.39	8	555.13	0.39	0.020
7	Slopes	Soiltype		Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced	Dunfenced		Burned_Veg	0.12	-267.39	10	555.31	0.57	0.019
8	Slopes	Soiltype			Dwaterpoints			Dfenced	Dunfenced			0.12	-271.56	6	555.32	0.57	0.019
9	Slopes	Soiltype			Dwaterpoints	WGL	OGL	Dfenced	Dunfenced	Dsecurity		0.12	-268.49	9	555.41	0.66	0.018
10	Slopes	Soiltype		Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced	Dunfenced			0.12	-268.50	9	555.43	0.68	0.018
11	Slopes	Soiltype			Dwaterpoints		OGL	Dfenced	Dunfenced	Dsecurity		0.12	-269.55	8	555.45	0.70	0.017
12	Slopes	Soiltype			Dwaterpoints	WGL	OGL		Dunfenced	Dsecurity	Burned_Veg	0.12	-268.51	9	555.46	0.71	0.017
13	Slopes	Soiltype		Dstreams_river	Dwaterpoints		OGL	Dfenced	Dunfenced		Burned_Veg	0.12	-268.55	9	555.52	0.78	0.017
14	Slopes	Soiltype			Dwaterpoints	WGL	OGL		Dunfenced	Dsecurity		0.12	-269.68	8	555.70	0.96	0.015
15	Slopes	Soiltype			Dwaterpoints	WGL	OGL	Dfenced	Dunfenced	Dsecurity	Burned_Veg	0.13	-267.61	10	555.76	1.01	0.015
16	Slopes	Soiltype	Dsnares		Dwaterpoints	WGL	OGL	Dfenced	Dunfenced			0.12	-268.77	9	555.96	1.22	0.013
17	Slopes	Soiltype	Dsnares		Dwaterpoints		OGL	Dfenced	Dunfenced			0.12	-269.85	8	556.05	1.31	0.013
18	Slopes	Soiltype			Dwaterpoints			Dfenced	Dunfenced	Dsecurity		0.11	-270.95	7	556.17	1.42	0.012
19	Slopes	Soiltype			Dwaterpoints		OGL	Dfenced	Dunfenced	Dsecurity	Burned_Veg	0.12	-268.89	9	556.22	1.47	0.012
20	Slopes	Soiltype				WGL	OGL		Dunfenced	Dsecurity	Burned_Veg	0.12	-269.95	8	556.25	1.51	0.012
21	Slopes	Soiltype			Dwaterpoints				Dunfenced	Dsecurity		0.11	-272.11	6	556.43	1.68	0.011
22	Slopes	Soiltype			Dwaterpoints		OGL		Dunfenced	Dsecurity		0.11	-271.10	7	556.47	1.72	0.010
23	Slopes	Soiltype		Dstreams_river	Dwaterpoints		OGL	Dfenced	Dunfenced	Dsecurity		0.12	-269.04	9	556.50	1.76	0.010
24	Slopes	Soiltype		Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced	Dunfenced	Dsecurity		0.13	-268.02	10	556.57	1.83	0.010
25	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints	WGL	OGL	Dfenced	Dunfenced			0.13	-268.03	10	556.58	1.83	0.010
26	Slopes	Soiltype	Dsnares	Dstreams_river	Dwaterpoints		OGL	Dfenced	Dunfenced			0.12	-269.08	9	556.59	1.84	0.010
27	Slopes	Soiltype	Dsnares		Dwaterpoints	WGL	OGL	Dfenced	Dunfenced		Burned_Veg	0.13	-268.04	10	556.60	1.85	0.010
28	Slopes	Soiltype			Dwaterpoints		OGL		Dunfenced	Dsecurity	Burned_Veg	0.12	-270.18	8	556.71	1.96	0.009
29	Slopes	Soiltype		Dstreams_river	Dwaterpoints			Dfenced	Dunfenced	Dsecurity		0.12	-270.19	8	556.73	1.99	0.009
Akaike weight	0.996	0.98	0.296	0.434	0.837	0.51	0.7	0.653	0.935	0.486	0.471						

Table 5.7: The coefficients and standard errors for AICc top ranked model and AICc ≥ 0.95 certainty model average for predicting roan habitat suitability for the (a) whole park, (b) roan home range region and (c) individual roan home ranges

a) Whole park

	AICc top ranked model		AICc > 95% certainty model average	
	Coefficient	S.E.	Coefficient	S.E.
Burned_Veg			0.0278	0.2135
Dfenced			-0.0001	0.0001
Dsecurity	-0.0003	0.0002	-0.0001	0.0001
Dsnares			0.0000	0.0001
Dstreams_river	0.0007	0.0002	0.0007	0.0001
Dunfenced			0.0001	0.0001
Dwaterpoint	-0.0013	0.0004	-0.0013	0.0002
OGL	7.4891	0.9668	6.7746	0.4597
Slope	0.1764	0.0546	0.1478	0.0265
Solonetz			0.1797	0.2410
WGL	7.4045	0.9422	6.7438	0.4442
Intercept	-5.5446	1.2683	-5.9797	0.6991

b) Roan home range region

	AICc top ranked model		AICc > 95% certainty model average	
	Coefficient	S.E.	Coefficient	S.E.
Burned_Veg			0.1800	0.1283
Dfenced	-0.0007	0.0002	-0.0006	0.0001
Dsecurity	0.0003	0.0002	0.0002	0.0001
Dsnares	-0.0005	0.0002	-0.0003	0.0001
Dstreams_river	0.0011	0.0003	0.0011	0.0001
Dunfenced	0.0006	0.0002	0.0006	0.0001
Dwaterpoint	-0.0012	0.0002	-0.0011	0.0001
OGL			-0.2301	0.2095
Slope	-0.1730	0.0695	-0.1709	0.0342
Solonetz	-1.0907	0.2845	1.1099	0.1305
WGL			-0.0991	0.2212
Intercept	-2.8143	1.5978	-4.0714	0.7441

c) Individual roan home ranges

	AICc top ranked model		AICc > 95% certainty model average	
	Coefficient	S.E.	Coefficient	S.E.
Burned_Veg	0.1452	0.4068	0.1462	0.1180
Dfenced	-0.0004	0.0003	-0.0002	0.0001
Dsecurity			-0.0001	0.0001
Dsnares			-0.0001	0.0001
Dstreams_river			0.0001	0.0001
Dunfenced	0.0002	0.0001	0.0003	0.0001
Dwaterpoint	-0.0002	0.0004	-0.0004	0.0001
OGL	8.2927	0.7925	0.5851	0.1888
Slope	-0.1816	0.0847	-0.1645	0.0292
Solonetz	-0.8292	0.4649	0.8762	0.1228
WGL	8.5768	0.7950	0.3086	0.2066
Intercept	-5.6456	0.9546	-1.3128	0.4199

Models based on the roan home range region yielded different results from those of the whole park. The AIC_c top ranked model with an Akaike weight of 0.1219 contained 8 variables while the 7 top ranked models with $\Delta_i < 2$, were considered to be the most parsimonious models (Table 5.6b). Model averaging and multi-model inference based on 34 plausible models (with 95% confidence intervals) showed that there was strong support for 6 variables (in order of decreasing magnitude of coefficients); soil type, slope, water points, streams and river, fenced park boundary and unfenced park boundary (Table 5.7b). All these variables had high Akaike weights > 0.97. All these variables, except fenced park boundary, were present in all the 34 top ranked models, indicating that they were required for a model to be plausible. There was moderate support for snare hot spots and security, whose Akaike weights were 0.832 and 0.624, respectively.

Model results for the individual roan home ranges were different from those of the whole park and roan home range region. The AIC_c top ranked model with an Akaike weight of 0.0247 contained 8 variables while the 29 top ranked models with $\Delta_i < 2$, were considered to be the most parsimonious models (Table 5.6c). Multi-model inference indicated strong support for 3 variables (in order of decreasing magnitude of coefficients); soil type, slope, and unfenced park boundary (Table 5.7c). These 3 variables had high Akaike weights > 0.93. However, only slope was present in all the 250 models used for model averaging. Three other variables, water points, open grassland and park fence, had moderate support with Akaike weights of 0.837, 0.718 and 0.653, respectively. The other 5 variables had Akaike weights lower than 0.52 and hence they were not considered as important variables.

Considering the variables that had strongest support (Akaike weight > 0.93) at least in one of the 3 levels of analysis, 8 variables (wooded grassland, open grassland, streams and river, water points, soil type, slope, park fence and unfenced park boundary) could be considered as the main drivers of roan habitat suitability (Table 5.6). However, none of these variables had strong support throughout all the three levels of analysis. Three variables, security, snares, and vegetation burned status had less support throughout all the 3 levels. When the mean Akaike weight was calculated for each variable across the 3 levels of analysis, the 11 variables can be ranked (from highest to lowest support) as follows: water points, slope, streams and river, soil type, unfenced park boundary, open grassland, fenced park boundary, wooded grassland, security, snares, and vegetation burned status (Figure 5.6). However, only two variables (water points and slope) had a high mean Akaike weight (> 0.93), which can be considered to be important drivers of roan habitat suitability across the 3 levels of analysis.

Overall, the whole park averaged models performed better than the home range level models, as they explained higher total deviance and had higher overall accuracy. The top ranked models for the whole park had relatively high R^2 of 62% and the best averaged model had high overall accuracy of AUC = 0.936 (Table 5.6a and Figure 5.5a). The top ranked models for roan home range region and individual home ranges had low R^2 = 18-19% and R^2 = 11-13%, respectively (Table 5.6b and Table 5.6c). Similarly, the overall accuracy for roan home range region and individual home ranges was low with AUC = 0.717 and AUC = 0.657, respectively (Figure 5.5b and Figure 5.5c)

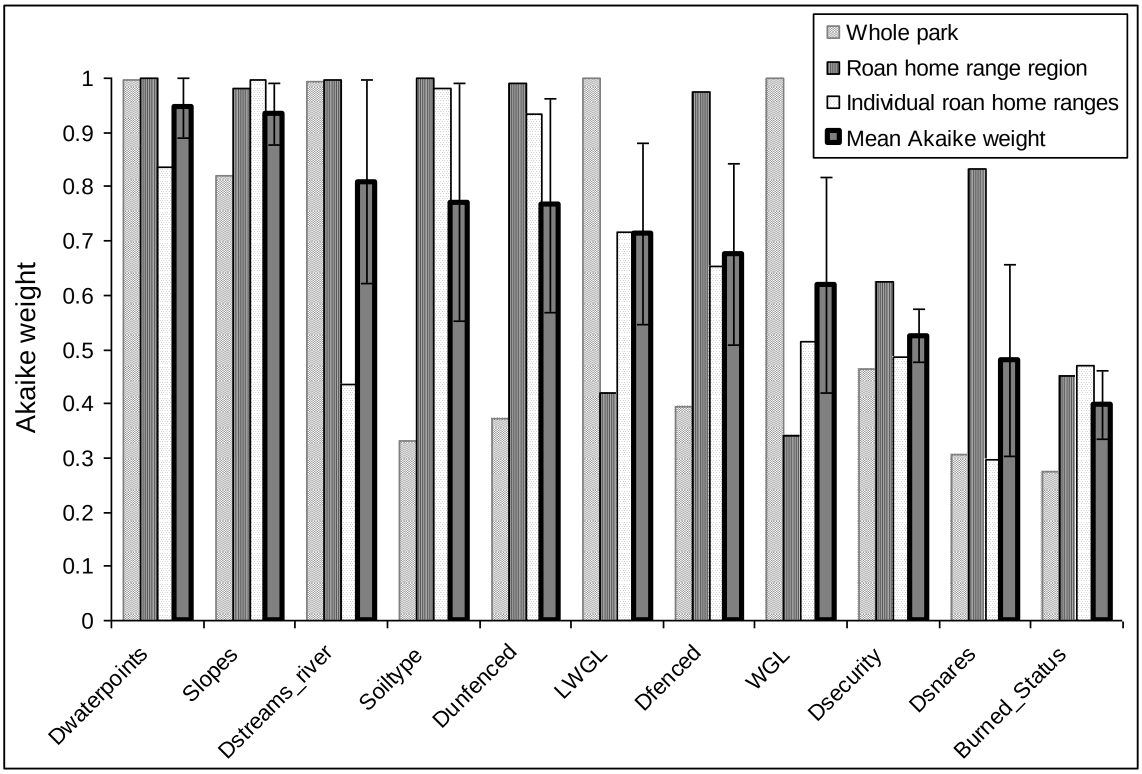


Figure 5.6: Relative importance of predictor variables across three levels of analysis. Error bars are standard errors of mean Akaike weights.

5.4.2.2 Effect of model selection techniques on multi-model inference (MMI)

Statistical analysis did not support the hypothesis that MMI results are dependent on the model selection technique used. MMI model selection using 4 criteria; AIC_c Differences (Δ_i) < 2, $\Delta_i < 7$, Cumulative Akaike weights ($\sum w_i$) ≥ 0.95, and $\sum w_i \geq 0.99$, yielded similar results. All the averaged models, regardless of the selection technique, led to the same conclusion; that all the 11 variables needed to be included in the final best model to define the suitable habitat for the roans in the whole park or home range levels (Table 5.8). Likewise, the overall accuracy of all the averaged models was relatively similar. The only difference was in the number of models included in the averaged models. The AIC_c differences (Δ_i) < 2 criterion had the smallest number of models while the Cumulative Akaike weights ($\sum w_i$) ≥ 0.99 had the largest number. The other two criteria had intermediate number of models in their averaged models. These results suggest that modellers can choose to use any of these model selection techniques according to their preference. For this study, the entire model averaging was based on the Cumulative Akaike weights ($\sum w_i$) ≥ 0.95. This criterion has been frequently used by r8cent modellers (Greaves et al., 2006; Whittingham et al., 2005) and it corresponds to the 95% confidence intervals widely used in statistical null hypothesis testing, and thus they are easily understood.

Table 5.8: Comparison of different MMI model selection techniques and their performance using area under the curve (AUC) of ROC plots. The number of predictors represents the variables contained in the averaged model and the number of models indicates the total number of models averaged by the model selection technique

	Park			Roan region			Individual roan home range		
Best model selection criteria	ROC AUC	No. of predictors	No. of models	ROC AUC	No. of predictors	No. of models	ROC AUC	No. of predictors	No. of models
ΔAIC < 2	0.935	11	12	0.717	11	7	0.652	11	29
ΔAIC < 7	0.935	11	101	0.717	11	29	0.657	11	202
Cumulative Akaike weight ($\sum w_i$) ≥ 0.95	0.936	11	92	0.717	11	34	0.657	11	250
Cumulative Akaike weight ($\sum w_i$) ≥ 0.99	0.936	11	123	0.717	11	87	0.658	11	452

5.4.3Relative importance of predictor variables

Different variables were relatively more important at some spatial scales than others. The importance of variables differed across different spatial scales, and their change as measured by Akaike weights, showed a consistent trend from the best spatial scale for the model up to a spatial scale threshold beyond which the pattern of change became haphazard (Figure 5.7). Different variables were important at different spatial scales, which corresponded to their scale of sampling. Considering the whole park at the best spatial scale of 30m there were 4 most relatively important variables (open grassland, wooded grassland, water points and streams and river) for determining roan habitat suitability, which had Akaike weights > 0.99 (Figure 5.7). The Akaike weights of these variables remained constantly high throughout all relevant spatial scales until they reached a threshold at 1500m, which corresponds to the mean (± SE) daily distance travelled by roans (1430 ± 80m). For the slope, the valid highest Akaike weight > 0.80 was only at 30m and its pattern of change (decrease) became haphazard at 300m. For the security, snare hot spots and unfenced park boundary, their highest Akaike weight was at their threshold of 150m. For soil type and vegetation burned status, the Akaike weights were highest at 600m to 1200m and lowest at 30m to 300m. The Akaike weight for fenced park boundary remained low in all spatial scales.

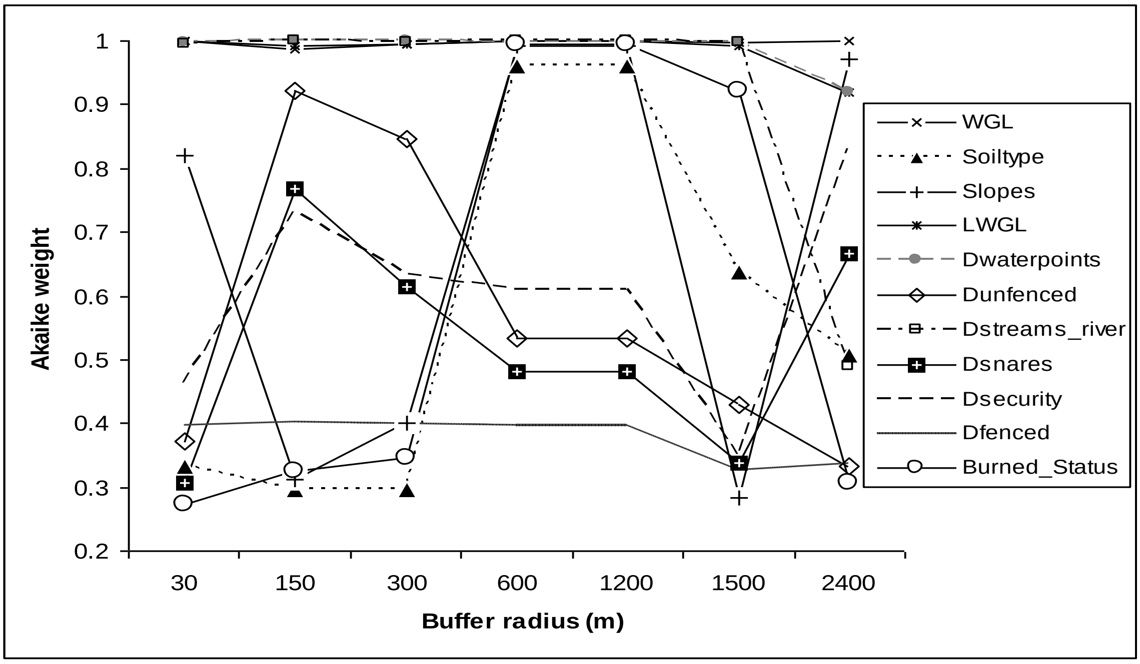


Figure 5.7: The relative importance of predictor variables in predicting roan habitat suitability across 7 different spatial scales in RNP

5.4.4Roan habitat suitability in different seasons

Analysis of habitat suitability of roans in the whole park for 3 different seasons (wet, dry and breeding seasons) yielded different models. Data were analyzed for each season separately and for all seasons combined. The results from the 3 seasons analyzed separately did not yield a single model that could be considered convincingly better than other alternative models since all models had very low selection probabilities. Figure 5.8 presents a plot of cumulative probability of models against their model rank, based on AIC scores from lowest to highest for different seasons. The 3 seasons needed 22, 22, and 124 models to reach a cumulative probability of 0.95 for the wet, dry and breeding seasons, respectively. This makes it clear that if inference was made based on only one model, it will be misleading because of the model selection uncertainty.

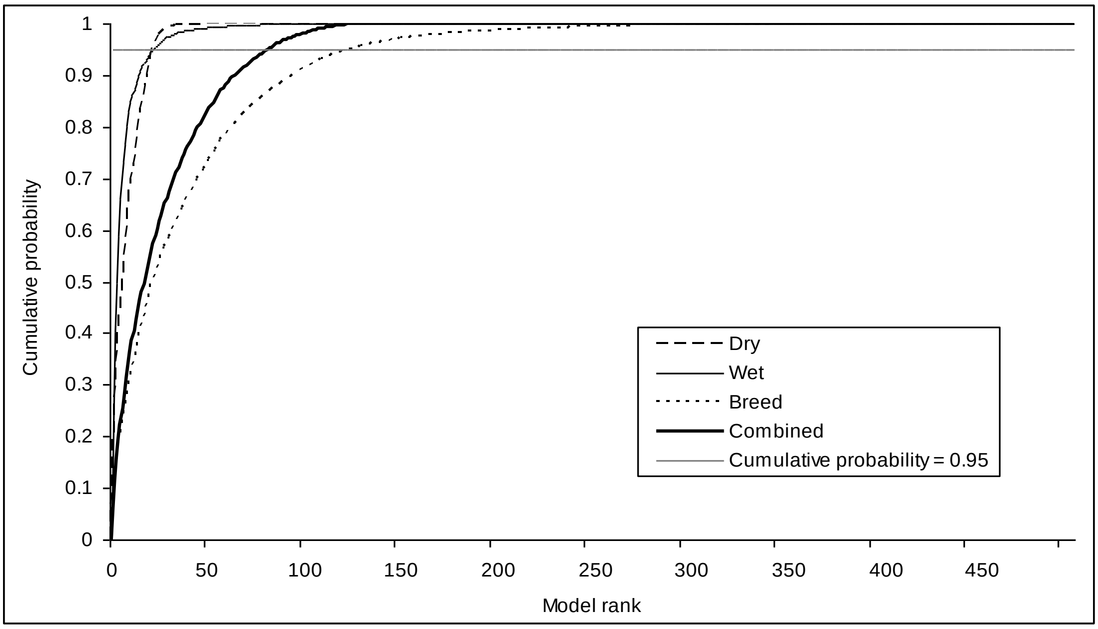


Figure 5.8: Cumulative probability curves for models fitted to data on roan habitat suitability in different seasons ranked from lowest to highest AIC scores

The variables selected by the AIC best models in the different seasons were highly varied, with only two variables (open grassland, and streams and river) commonly selected for all the seasons (Table 5.9). These two variables had high selection probabilities (>0.75) for all seasons. This highlighted that the most important driver of roan habitat suitability is the vegetation type, with the most preferred for all seasons being the open grassland. The open grassland was the only predictor with a highest Akaike weight of greater than 0.97 (Table 5.9) and highest regression coefficients for all seasons (Table 5.10). It also showed that roans did not utilize water from streams and the Olambwe River. This is probably because (i) both water sources are far away from the roan home range region, (ii) the streams are located in steep slopes and (iii) the Olambwe river is in the midst of a riverine forest, which makes it difficult for the roans to access them. Figure 5.9 illustrates the distribution of roans in relation to these landscape features.

The models based on wet, dry and breeding seasons indicated that different variables are important in predicting roan habitat suitability in different seasons. The relative importance of predictors of roan habitat suitability for different seasons, as discussed below, was assessed using two methods: (1) the predictor selection probability (Akaike weights) that indicates the probability that a given predictor will appear in the AIC-best model, if the analysis were repeated with a different set of data (Table 5.9); and (2) the regression coefficients that give the magnitude of the contribution of each predictor towards the variation in the roan habitat suitability index (Table 5.10).

In the wet season, there was strong support for (in order of decreasing coefficients) the effects of open grassland, wooded grassland, soil type, burned vegetation status, security, streams and river, park fence and snares, as indicated by high (>0.95) selection probabilities (Table 5.9). Slopes had a relatively high coefficient (0.2489) (Table 5.10) but its selection probability was relatively low (0.544) (Table 5.9). It is worth noting that water points had very little support (0.333) in the wet season despite it having very high support (>0.99) for the dry and breeding seasons (Table 5.9). In the dry season, 5 variables had strong support (>0.99) and their coefficients can be ranked as follows: open grassland > wooded grassland > water points > park fence > streams and river (Table 5.10). As expected, water was the most important variable after vegetation. There was also equivocal support (selection probabilities of 0.763 and 0.728, respectively) for the effects of unfenced park boundary and snares (Table 5.9). Finally, in the breeding season, there was strong support (in order of decreasing coefficients) for the effects of open grassland, snares, water points and security, as indicated by high (>0.97) selection probabilities (Table 5.9 and 5.10). Also, there was a relatively high support (selection probability of 0.758) for the effects of streams and river (Table 5.9).

Table 5.9: Information-theoretic statistics for all top habitat suitability models for roans in RNP, with substantial support (AIC $\Delta_i < 2$) presented in rank order (from low to high Akaike weights) for different seasons. The table indicates the variables included in the model, the AIC_c, AIC_c differences (AIC_c Δ_i), the model Akaike weight (w_i), and selection probability for each predictor.

	Predictors											AICc	ΔAICc	w_i
(a) Models for wet season														
AIC best	Slopes	WGL	OGL	Dstreams_river		Soiltype	Dsnares	Dfenced	Burned_Veg	Dsecurity		154.00	0.00	0.24
		WGL	OGL	Dstreams_river		Soiltype	Dsnares	Dfenced	Burned_Veg	Dsecurity		154.38	0.38	0.20
	Slopes	WGL	OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares	Dfenced	Burned_Veg	Dsecurity		155.32	1.31	0.12
		WGL	OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares	Dfenced	Burned_Veg	Dsecurity		155.73	1.73	0.10
	Slopes	WGL	OGL	Dstreams_river		Soiltype	Dsnares	Dfenced	Burned_Veg	Dsecurity	Dunfenced	155.98	1.98	0.09
Selection probability	0.544	1.000	1.000	1.000	0.333	0.999	0.953	0.980	0.952	1.000	0.272			
(b) Models for dry season														
AIC best	Slopes	WGL	OGL	Dstreams_river	Dwaterpoints		Dsnares	Dfenced		Dsecurity	Dunfenced	95.18	0.00	0.18
		WGL	OGL	Dstreams_river	Dwaterpoints		Dsnares	Dfenced		Dsecurity	Dunfenced	96.82	1.63	0.08
	Slopes	WGL	OGL	Dstreams_river	Dwaterpoints			Dfenced		Dsecurity	Dunfenced	97.05	1.86	0.07
Selection probability	0.5991	1.000	1.000	0.995	1.000		0.728	1.000		0.999	0.763			
(c) Models for breeding season														
AIC best			OGL	Dstreams_river	Dwaterpoints		Dsnares			Dsecurity		93.38	0.00	0.04
			OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares	Dfenced		Dsecurity		93.45	0.07	0.04
			OGL	Dstreams_river	Dwaterpoints		Dsnares	Dfenced		Dsecurity		93.45	0.07	0.04
			OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares			Dsecurity		93.95	0.57	0.03
		WGL	OGL	Dstreams_river	Dwaterpoints		Dsnares			Dsecurity		94.11	0.73	0.03
		WGL	OGL	Dstreams_river	Dwaterpoints		Dsnares	Dfenced		Dsecurity		94.74	1.36	0.02
		WGL	OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares			Dsecurity		94.79	1.41	0.02
			OGL	Dstreams_river	Dwaterpoints		Dsnares		Burned_Veg	Dsecurity		94.80	1.42	0.02
		WGL	OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares	Dfenced		Dsecurity		94.81	1.43	0.02
			OGL	Dstreams_river	Dwaterpoints		Dsnares	Dfenced	Burned_Veg	Dsecurity		94.81	1.44	0.02
			OGL	Dstreams_river	Dwaterpoints		Dsnares			Dsecurity	Dunfenced	94.96	1.58	0.02
	Slopes		OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares	Dfenced		Dsecurity		94.97	1.59	0.02
	Slopes		OGL	Dstreams_river	Dwaterpoints		Dsnares			Dsecurity		95.00	1.62	0.02
			OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares	Dfenced	Burned_Veg	Dsecurity		95.07	1.70	0.02
	Slopes		OGL	Dstreams_river	Dwaterpoints		Dsnares	Dfenced		Dsecurity		95.26	1.88	0.02
	Slopes		OGL	Dstreams_river	Dwaterpoints	Soiltype	Dsnares			Dsecurity		95.30	1.92	0.02
Selection probability	0.285	0.384	0.975	0.758	0.996	0.553	1.000	0.463	0.283	0.978	0.312			

Table 5.10: The coefficients and standard errors for the $\text{AIC}_c \geq 0.95$ certainty average models for predicting roan habitat suitability in RNP for different seasons

	Combined seasons		Wet season		Dry season		Breeding season	
Predictor	Coefficient	S.E.	Coefficient	S.E.	Coefficient	S.E.	Coefficient	S.E.
Burned_Veg	-0.0453	0.1928	-1.8665	0.2867	0.0413	0.2792	-0.1493	0.2420
Dfenced	-0.0001	0.0001	0.0011	0.0002	-0.0021	0.0002	0.0003	0.0002
Dsecurity	-0.0002	0.0001	-0.0020	0.0002	0.0022	0.0002	-0.0015	0.0002
Dsnares	0.0000	0.0001	-0.0010	0.0002	0.0005	0.0001	0.0025	0.0002
Dstreams_river	0.0009	0.0001	0.0014	0.0001	0.0014	0.0002	0.0006	0.0001
Dunfenced	0.0004	0.0001	0.0000	0.0001	0.0005	0.0001	0.0000	0.0001
Dwaterpoints	-0.0013	0.0002	0.0001	0.0002	-0.0041	0.0003	-0.0022	0.0002
OGL	4.5816	0.4010	7.4600	0.5266	6.0934	0.5560	2.6736	0.3307
Slopes	0.0263	0.0403	-0.2489	0.1364	0.1203	0.0371	-0.0195	0.0494
Solonetz	0.1746	0.2122	2.4416	0.2811	-0.1891	0.2795	-0.4184	0.2527
WGL	4.6968	0.3933	7.1883	0.5088	6.0214	0.5106	0.4521	0.4133
Intercept	-5.6045	0.7218	-4.2411	0.6919	-9.9546	1.0665	-2.8672	0.6957

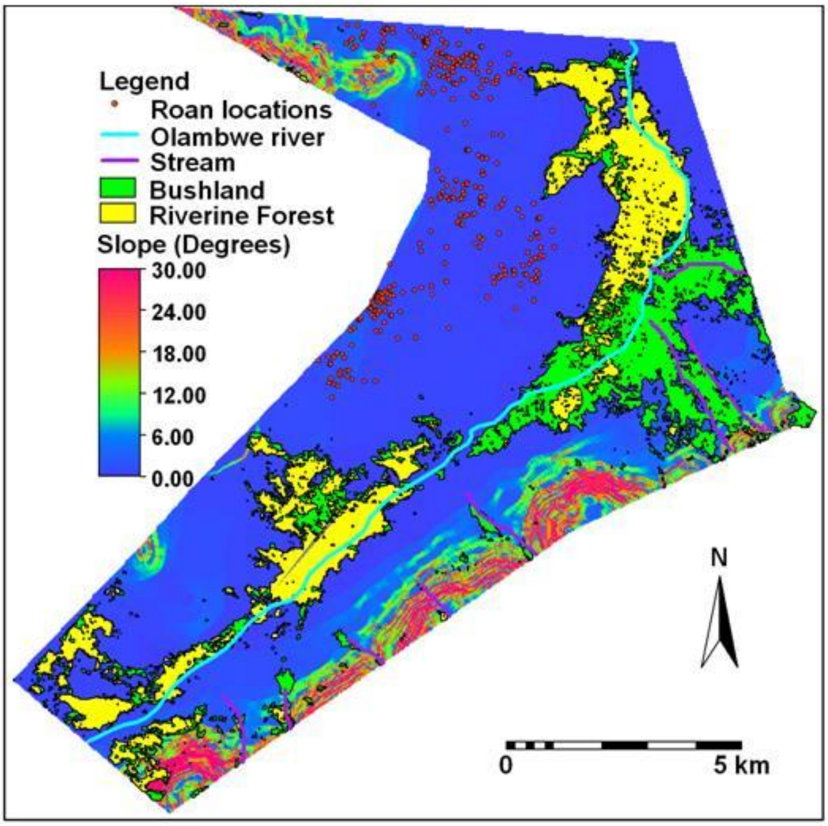


Figure 5.9: The roan distribution in relation to Olambwe river and streams in RNP. Note that the streams are located in steep slopes and the river is in the midst of a riverine forest and bushland

Roan habitat suitability maps generated using the 95% certainty MMI average models showed differences in areas predicted as suitable during different seasons (Figure 5.10). The most interesting finding was that about 50% of the park is suitable for roans during the wet season when water is not a limiting factor. The smallest suitable areas were predicted during the breeding season (9% of the park), implying that roans require particular unique habitat areas for breeding purposes. Most of the suitable areas were located in the North-West part of the park, which implies a protected sanctuary can be established in the region with a great certainty of being conducive for promoting sustainable conservation and management of roan antelopes.

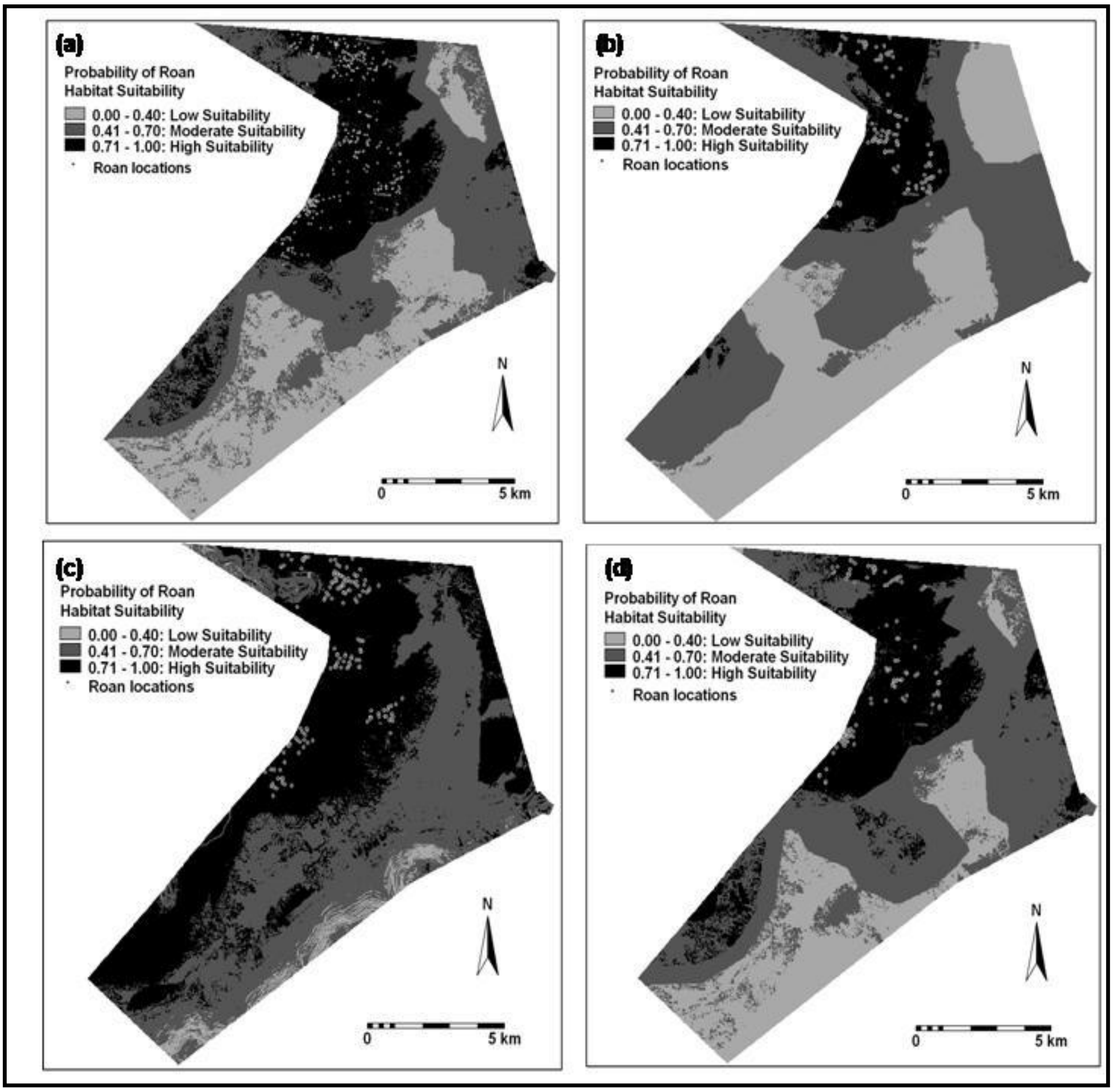


Figure 5.10: Habitat suitability maps for roans antelopes in Ruma N. Park for different seasons: (a) all seasons combined, (b) breeding season, (c) wet season and (d) dry season. Maps were prepared using the 95% certainty MMI average models computed using information-theoretic approaches.

5.4.5Comparison of number of predictors versus sample size

The initial analysis was based on 11 predictors against a sample size of 428. This is viewed by some authors as exploratory rather than confirmatory analysis (Burnham and Anderson, 2002). To obtain confirmatory results the predictors were reduced to 8 most important ones based on the roan biology literature. The chosen variables were: open grassland, wooded grassland, water points, streams and river, soil type, slope, fenced park boundary and snare hot spots. Results on models constructed using information-theoretic technique with the 8 predictors did not differ much from those obtained using 11 predictors. In both cases no single model was adequate alone to base inference concerning roan habitat suitability. However, the 8 predictors yielded a fewer number of plausible models as compare to the 11 predictors. To yield a cumulative probability of 0.95 using the 8 predictors required 13, 19 and 46 models for the whole Park, roan home range region and individual home ranges, respectively. Similarly, using 11 predictors required 92, 34, and 250 models for the 3 levels of analysis to achieve the 95% confidence set of models. Across the 3 levels of analysis, only water points had high support as a predictor with Akaike weight greater than 0.92 in each level.

Since the results based on 8 predictors did not show great improvement from those based on 11 predictors, the number of predictors was further reduced to 5 on the basis of literature and roan biology. The five most important predictors were: open grassland, wooded grassland, water points, streams and river, and soil type. The results showed no single model was adequate alone. However, the number of plausible models required to achieve a 95% confidence set of models was greatly reduced. For instance, only 2 models were required for the whole park, while the roan home range region and individual roan home ranges level required 7 and 11 models, respectively, to yield a 95% confidence set of models. Just like the 8-predictors models, only water points had high support as a predictor with Akaike weight greater than 0.93 in each of the 3 levels of analysis. Figure 5.11 presents a plot of cumulative Akaike weights and model rank for models constructed using a set of 11, 8 and 5 predictors for the three levels of analysis; whole park, roan home range region and individual roan home ranges. Generally, the number of plausible models required to yield a 95% confidence set of models decreased with reduction in the number of predictors and with increase in the spatial scale of analysis. For instance, the coarser scale (park level) required the least number of models as compared to the finer scale (home range level). Similarly, of the 3 sets, 5-predictors models required the least number of plausible models.

5.4.6Model assessment using ROC plots

The area under the curve (AUC) in a ROC plot is a measure of the overall accuracy of a model. As shown in Figure 5.5, all the models from both the stepwise regression and information-theoretic approaches were better than chance (all AUC > 0.65). However, the models produced by model averaging were slightly better than those produced by stepwise regression. Regardless of the technique used, the models constructed for the habitat suitability at the whole park level were far much better than those for the home range levels. The area under the curve (AUC) for the whole park models was greater than 0.93 while the AUC of home range models ranged from 0.65 to 0.73.

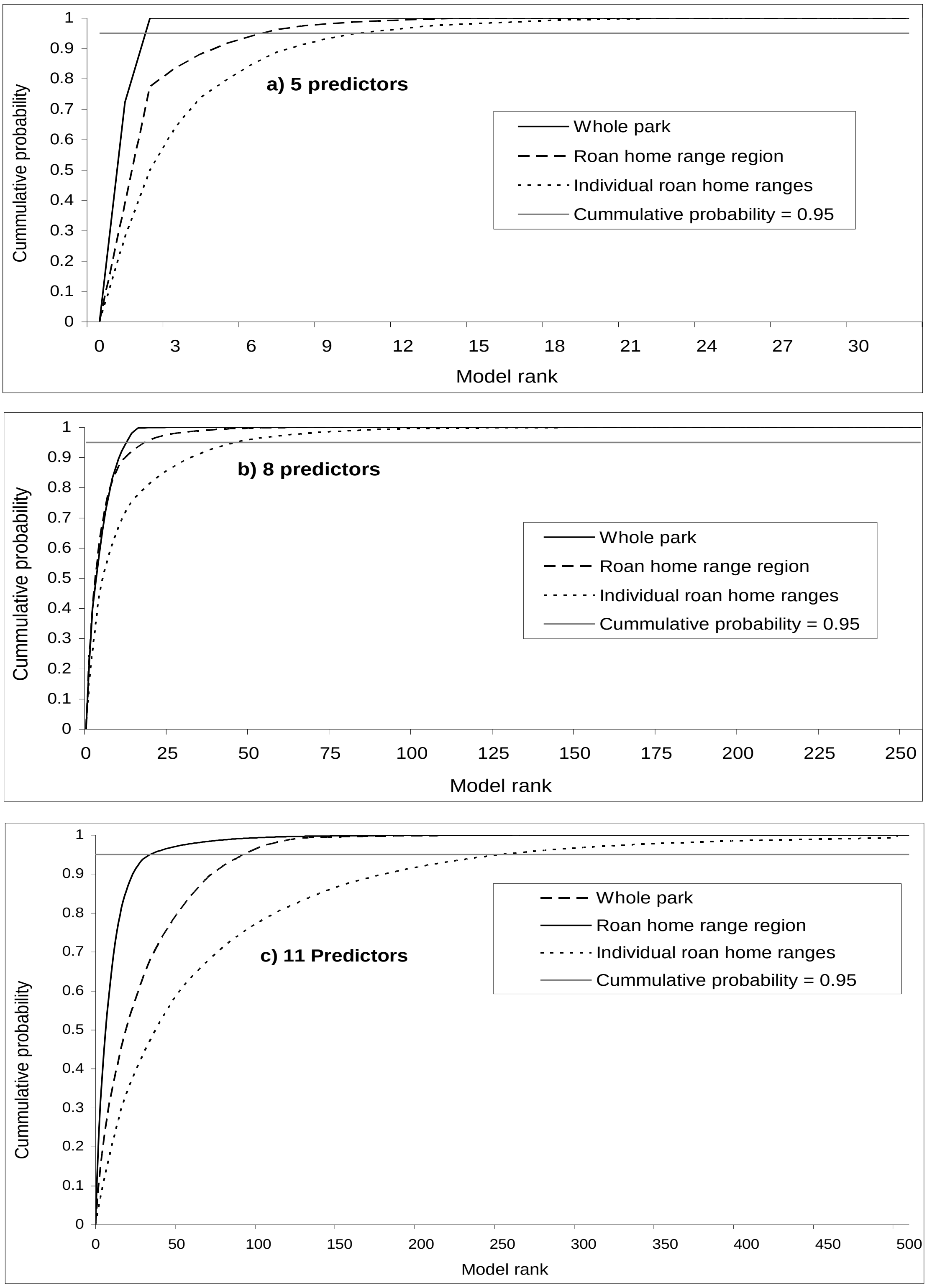


Figure 5.11: Cumulative probability curves for models fitted to data on habitat suitability of roan antelopes at 3 spatial scales using 3 sets of predictors. The curves show the summed Akaike weights for models ranked from lowest to highest AIC score.

5.5 Discussion

5.5.1Predicting the suitable habitat for roans in RNP

The logistic regression analysis strongly indicated that habitat suitability for roan antelopes in RNP for all seasons is predominantly determined by the vegetation type and water availability. The variables in these categories had the highest Akaike predictor weights. Roans preferred habitats dominated by open grasslands and wooded grasslands. The parameter coefficients of these two variables were orders of magnitude higher than the other variables. This conforms to records in literature on preferred habitats by roans antelopes (Schuette et al., 1998; Starfield and Bleloch, 1986; Smithers, 1983). The probability of roan occurrence was strongly negatively correlated with the distance to water points (dams and water troughs), implying that roans prefer habitats near permanent water sources. The mean (± SE) distance of water points from the roan locations was 0.78 ± 0.04 km. Since the mean (± SE) daily travel distance by the roans was 1.43 ± 0.08 km, the roans could not access any water resources that were further than that distance. As a result of this, the probability of roan occurrence was strongly positively correlated with the distance to streams and the Olambwe river. This supported the hypothesis that the roans never utilize the water in Olambwe river and streams. The main reasons for roans not accessing these water resources are that (1) they are far away from the roan home range, that is, 3.59 ± 0.06 km, (2) the Olambwe river is located in the midst of a riverine forest and roans never utilize thick vegetation habitats (Schuette et al., 1998) and (3) the streams are located in very steep slope areas. The roans significantly preferred habitats that are at low slopes ($t = 4.28$, $df = 213$, $p<0.001$). The slope variable had relatively high Akaike weights. These findings highlight an important point in wildlife management that the presence of water in a protected area does not automatically mean sufficient water availability to all wildlife species. It is therefore, vital for the park authorities to ensure availability of permanent water supply for the roans via construction of more dams and water toughs within the roan home range region.

Findings indicated that different predictor variables are important in predicting the suitable habitats for roans in different seasons. In the wet season, availability of surface water was not a significant factor but instead the roans preferred habitats located in Solonetz soil type. This soil type has capability of holding rain water for longer periods in temporary pools (FAO, 2009). Therefore, water supply is abundant and not a limiting factor during the wet season. Another interesting finding during the wet season is that the roan home range was located in areas relatively near snare hotspots. This is strange and contrary to the expectation that roans will stay away from areas heavily infested with snares. However, it may imply that poachers track the roans and lay snares deliberately in their home ranges. This is likely to happen due to the high intensity of poaching with snares in the park (YFC, 2006). It is disheartening to note that although the roan wet home range was significantly near security park gates and outposts, this could not deter the poachers from laying snares next to the roan locations. It implies that security efforts need to be increased in the park to stamp out poaching. Also, in the wet season the roans preferred habitats with unburned vegetation. This concurs with observations by Schuette et al (1998) that roans avoid areas that have been recently burned. Although about 50% of the park was burned one month prior to the start of this research, the roans still preferred the remaining unburned habitat. Uncontrolled burning has been an historical feature in RNP and it may be the main cause of habitat deterioration for the roans.

In the dry season, unlike the wet season, proximity of water points was strongly associated with roan occurrence whereas soil type was not a significant factor. This confirms that roan distribution in the dry season is dependent on availability of permanent water resources which are within reach. During the dry season all temporary water pools are usually dried up and thus soil type has no effect on the distribution of roans. The roan dry season home range was significantly near park fence and away from unfenced park boundary. This provided security against poachers. The unfenced park boundary was positively correlated with presence of public roads and foot paths within the park ($r=0.71$, $p<0.001$). It is therefore necessary to ensure that the whole park is fenced and public roads and foot paths passing through the park are closed and diverted outside the park as soon as possible as a measure of curbing poaching.

During the breeding season (the period when the young are born), apart from vegetation type and water availability, a few other factors were equally important in predicting roan habitat suitability. One key factor was the selection of habitats with unique unburned vegetation. One breeding roan group actually temporary migrated during the breeding period in search of such unburned habitat. The preferred unburned vegetation, which had several layers of grasses and herbs, provided conducive habitat for protection of the newly born young from predators especially in their early stage of life when they are left alone in seclusion. Starfield and Bleloch (1986) found out that roan calves are concealed for the first six weeks after birth. During this period the calf relies on vegetation cover as it remains motionless for its survival. Uncontrolled burning that removes or destroys such vegetation cover exposes the vulnerable calves to predation especially by Hyaena (Waweru et al., 1995).

Overall, the most important factors in predicting the habitat suitability for the roans are those concerning habitat features as opposed to management issues (Table 5.10). There was strong support for 4 habitat features – open grassland, wooded grassland, water points, and streams and river, as indicated by high predictor selection probabilities (>0.99). The variables on management issues – distances to snare hotspots, park fence, unfenced park boundary, and security gates, had weaker support with low selection probabilities (<0.50). Therefore, to ensure sustainable conservation of roans in RNP, there needs to be long term protection of habitat features and short-term urgent solution to the management issues such as control of poaching, maintaining a complete functional park fence, and increasing security outposts and personnel.

5.5.2Comparing stepwise regression and information – theoretic approach

The stepwise selection method produced models with a few similarities but many differences from those of information theoretic techniques. The final best model from stepwise selection using a significance level of 0.15 was the same as the AIC top ranked model for the whole park. These models selected six variables as the most significant in predicting the suitable habitat for roans in RNP, that is, open grassland, wooded grassland, water points, streams and river, slope and security. However, using the conventional significance level of 0.05 yielded a model with one fewer variable; it omitted security. This model was ranked as the second best by the AIC model rankings. This finding supports the hypothesis that the use of a p-value of 0.15 instead of 0.05 in stepwise variable selection procedures yields better models (Greaves et al., 2006; Anderson et al., 2000).

The low Akaike weights of the AIC top ranked model and the stepwise selection models showed that there was so much model selection uncertainty for any of these models to be considered as the best model. To obtain a model upon which inference can be made with greater certainty required model averaging. This is the advantage of the information theoretic approaches over the stepwise regression. To obtain a >95% certainty, the top 92 models were required to be included in the model average. This model identified 11 variables as important predictors of roan habitat suitability. Comparison of the >95% certainty model and the AIC top ranked model showed that the coefficients were very similar for most variables but slightly different for a few variables. When the importance of variables based on Akaike weights was considered it was clear that the 6 variables in the top ranked model were more important that the other 5 variables, which were included only in the model average. Similar results were obtained by Greaves et al (2006) in modelling the probability of occurrence of dormice. Since the AIC top ranked model was similar to the stepwise selection models, it can be concluded that the stepwise selection methods are adequate for identifying the most important predictors in modelling the probability of occurrence. Their inadequacy and limitation becomes important when the objective of modelling is to produce the best predictive model (Whittingham et al., 2006), which can only be achieved with greater certainty using the multi-model inference and model averaging. For this study it was necessary to use model averaging so as to yield the best predictive model and use it in preparing a GIS map of suitable habitat for roan antelopes in RNP.

The assessment of the predictive power of models generated by the two modelling approaches was done using an independent testing data set, consisting of 30% of the original data set, as recommended by Fielding and Bell (1997). However, better model prediction with wider application could be achieved using an independent data set collected in the field after model construction. The models from the two approaches had an area under the curve (AUC) greater than 0.93, which indicated that their predictive capability was far higher than chance and that the models fitted the data well. The information theoretic approach yielded models that had a slightly higher AUC than the stepwise regression. Therefore, these models can reliably be used for predicting the habitat suitability of roan antelopes in Ruma N. Park.

The findings in this study showed that the information – theoretic approach has more advantages over the conventional stepwise modelling approach. One of the disadvantages of stepwise regression is the lack of consideration of all possible combinations of models (Greaves et al., 2006). A different model may be produced from the same data set depending on the order that variables are added or removed from a model (Kleinbaum et al., 1988). However, Zar (2010) found out that this problem is magnified when there is multi-collinearity among predictors and with the use of 'step-up' forward selection procedure. Zar (2010) recommends the use of 'step-down' backward procedure that does not produce spurious results and is less labour intensive. Model inference for information-theoretic approach is based on all plausible models unlike the stepwise approach, which uses only the final best model and leaves out all the other models that are equally good (Burnham and Anderson, 2002). Another advantage of the information-theoretic approach is the measurement of the importance of each model and parameter used in the modelling process. Computation of Akaike weights of parameters and models coupled with parameter coefficients and 95% confidence intervals and/or standard errors give a more in-depth understanding of the process being modelled (Greaves et al., 2006).

To make valid comparisons of models from the two approaches the same initial number of predictor variables was used. Since model results are dependent on the variables used and the principle of parsimony requires the use of a few most significant variables, only 11 variables were included in modelling, although initially the available data set contained 18 possible predictors. The 11 variables that had biological and management importance were selected based on the roan antelope ecology and past studies reported in literature. Burnham and Anderson (Burnham and Anderson, 2002) emphasize the need to select a small set of predictors based on logic and biological importance.

5.5.3 Effect of spatial scale on habitat suitability modelling

The findings of this study clearly demonstrate that model results change as a function of the spatial scale at which variable data is obtained and analysed. Advancement in GIS techniques and computer software packages has made it possible to vary the spatial scales and assess their effect on modelling results. Different spatial scales produced different models. Therefore, it is important to determine the appropriate scale (that is, the scale producing the most accurate results) for habitat suitability modelling because the use of wrong scale will lead to misleading model results. The appropriate spatial scale of analysis was 30m and this corresponds to the spatial scale of measurement of most variables. The vegetation and environmental variables were derived from a Landsat image having a spatial resolution of 30m. The slope was derived from a digital elevation model with spatial a spatial resolution of 30m. Only soil type and vegetation burned status were obtained at a different spatial scale than 30m. These two variables were obtained at a spatial scale of 500m. This may be the reason why they were not identified as significant variables in the modelling results analysed at 30m. The second best spatial scale of analysis was 600m, which closely corresponds to the spatial scale of soil type and vegetation burned status. The results indicate that in cases where comparisons cannot be done to identify the appropriate spatial scale (especially where GIS techniques are not being used), analysis should always be done using the scale at which most of the variables were obtained. Erickson et al (1998) arrived at the same conclusion but recommended more research on the issue of spatial scale in modelling.

Alternatively, if variables were obtained at diverse multiple scales, the selection of appropriate scale of analysis should be based on the ecology of the species concerned. The use of multiple scales is a common phenomenon in species distribution models (Greaves et al., 2006), because data on variables are obtained from different sources, with initial purpose of measuring the data being different from modelling. In an ideal situation, proper data for modelling purposes should be collected using the same spatial scale that is commensurate to the research question being investigated. However, achievement of this is usually hampered by lack of resources and time. The appropriate scale is objective-dependant (Johnson et al., 2002) and is a trade off between vast quantities of less detailed information against few amounts of more detailed information (Maurer, 2002). Many authors recognize the fact that identifying the appropriate scale in species distribution modelling is still a challenging task (Greaves et al., 2006; Whittingham et al., 2005; Rushton et al., 2004).

The habitat suitability models for the whole park were better than those of the home range levels. The reason for this was due to the level of detail at which variable data was collected. Most of the data was collected at the park level, involving general observation of vegetation types and distribution of water resources and landscape features in the whole park. Hence these data could not fit analysis at a finer scale like the home range level which is more detailed. Such a fine level would have needed collection of detailed data such as measurements of specific grass or plant species fed on by the roans and mineral contents of such species. However, the park level used in this study satisfied the goal of the study to predict roan habitat suitability in the whole park, and make recommendations on habitat management and other appropriate interventions at the park level.

5.5.4Implications for conservation of roans

The results of this study showed that the most preferred habitats by the roans are characterized by presence of open and wooded grasslands and availability of permanent water resources. Proper habitat management geared towards sustainable conservation of this species must include strategies that promote the provision of these habitat features. Two effective strategies are: (1) construction of more dams and water troughs and (2) prescribed or controlled burning. It is necessary to increase the number of dams and water troughs in the roan home range region. However, it is crucial to only provide sufficient water which is well distributed within the whole park. Overconcentration of water points in a few localities have been shown to cause problems. Harrington et al (1999) found out that increase of artificial water points in the roan's range in Kruger National Park led to a decline in roan population. This was because the water points attracted high numbers of Zebra and wildebeest into these areas, which caused an increase in competition between these grazers and the roans. It also increased predation of roans by lions that migrated to the roan range in response to the zebra and wildebeest influx. Similar detrimental effects of overconcentration of water points were observed by De Leeuw et al (2001). They noted that provision of artificial water points to livestock in arid lands in Northern Kenya led to severe degradation of the areas in close proximity to the water points.

Prescribed burning can be used to maintain large areas with the required open and wooded grasslands and to prevent bush encroachment which is a form of habitat degradation for the roans. It will also reduce the probability of spread of fire to the park from surrounding communities and avoid the burning of unintended areas. Prescribed burning will ensure continued availability of burned and unburned vegetation patches for use in different seasons by the roan. Our results showed that the roans prefer the unburned vegetation for concealment of the newly born roan after birth. The loss of most young roans in Ruma National Park can be attributed to exposure to hyaena predation due to lack of enough unburned vegetation (Waweru et al., 1995). This is because currently there is no burning program in the park and the surrounding community seem to take advantage of this scenario to set fires that spread uncontrollably and spread extensively in the park every year.

Illegal hunting through snares is a grave problem in RNP. It is essential to put measures in place to curb this illegal practise. Apart from boosting security for the roans via increased intensity and frequency of routine security patrols, there is need to establish more security outposts in snare prone areas. Park records indicated that in years when more efforts were put in providing security, the roan population increased accordingly (Asila, 2004). Also, the same records show that there used to be some roans near the Kor Lang security outpost. However, after this outpost was closed down these roans either migrated to safer areas or became victims of illegal hunting.

The two main problems, illegal hunting and uncontrolled burning, facing wildlife conservation and management in RNP are caused by the surrounding communities. Community involvement in conservation activities can be a long term solution to the park problems and ensure sustainable conservation and management. Community involvement has proved to be successful in promoting sustainable conservation of biodiversity in many African countries. Good examples of community projects include the Botswana's 1975 Wildlife Management Areas (WMA) (DHV, 1980), Zimbabwe's 1989 Communal Area Management Programme For Indigenous Resources (CAMPFIRE) (Hill, 1996), the Namibia’s 1996 Nature Conservancies (Mendelssohn and Roberts, 1997), the Zambia's 1988 Administrative Management Design for Game Management (ADMADE) (Gibson and Marks, 1995) and the Tanzania’s 1994 Community based Wildlife Management (CWM) (Songorwa, 1999). Involving the local communities surrounding the RNP will help in resolving conflicts with the park authorities and give the communities more sense of responsibility in maintaining the roan habitat and in conservation and management of biodiversity in the park.

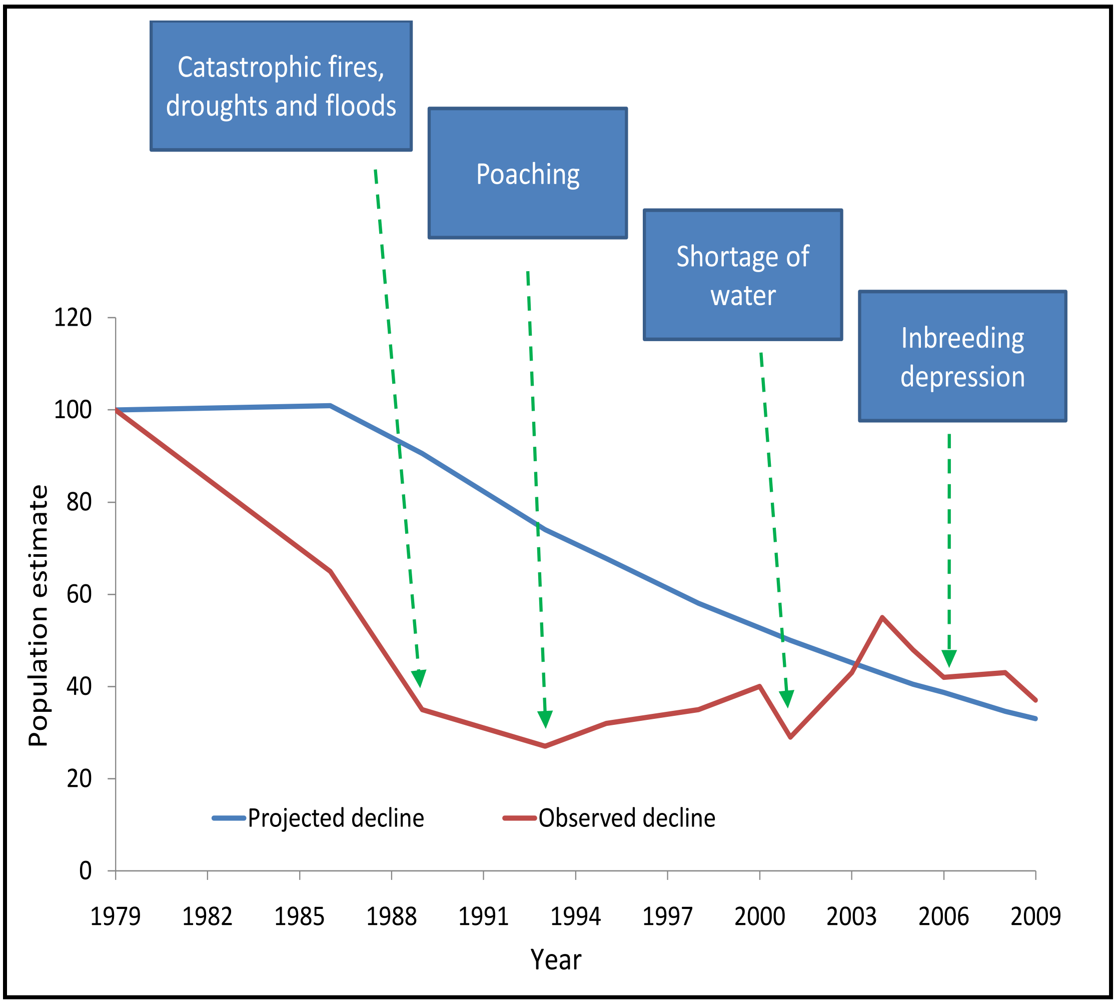
5.5.5 Limitations and constraints

- The use of random points as absence data points is a conservative procedure that may yield biased results. However, comparison of results with other methods as compositional analysis yielded similar conclusions. Since it was beyond the scope of this study to compare all possible techniques, it is recommended that before the models are implemented the data could be re-analyzed using other methods such a ecological niche factor analysis (ENFA), which uses presence only data (Hirzel et al., 2002).

- The use of many predictors with a small sample size could yield biased results. This was minimized by using a corrected AICc with an additional bias-correction term. Also a re-analysis of the habitat selection with fewer predictors yielded similar results.
- ROC plots have been criticized for being a poor method for validation of habitat suitability models (Cianfrani et al., 2010). However, the assessment of the models using alternative techniques such as bootstrapping, AICc and the r2 statistic, all produced similar results, which confirmed that the ROC plots were robust in this case.
- Data from observational studies are often affected by spatial and temporal autocorrelation. This was investigated by incorporating ‘group’ and ‘time’ random effect factors in a GLMM model. However, the two factors were insignificant and hence no indication of autocorrelation.
- Analyzing habitat selection using inappropriate sampling spatial scale could yield wrong conclusions. Since the correct scale for the roan antelope was not known, habitat selection was analyzed at varying spatial scales to identify the appropriate one before model inference.

CHAPTER 6

POPULATION VIABILITY ANALYSIS FOR ROAN ANTELOPES IN RNP AND IMPLICATIONS FOR MANAGEMENT



Comparison of observed and PVA projected roan population decline in RNP and the potential factors driving the population decline

CHAPTER 6: Population viability analysis for roan antelopes in RNP and implications for management

6.1 Introduction

The current roan population decline in RNP is of serious concern to the Park management because a population of less than 50 roan antelopes is not considered viable according to population genetic criteria (Soule, 1980). The park authorities need to act fast to halt further decline, and promote population recovery back to healthy levels. Without any interventions, the roan population in RNP will eventually go extinct just as it happened in the other Kenyan protected areas in the past. In fact, the question to ask now is not if but when the extinction will occur. The process of population viability analysis (PVA) can be used to adequately answer this question.

Population viability analysis is a set of modelling techniques that estimates the future size and risk of population extinction (Gilpin and Soule, 1986). PVA utilizes life-history or population growth rate parameters such as survival and fecundity rates as input variables to project dynamics and estimate risk of population extinction (Ludwig, 1999). PVA can be used to: (1) estimate the probability of extinction (Gilpin and Soule, 1986; Shaffer, 1981); (2) predict the future population size (Brook et al., 2000; Lacy, 1993); and (3) assess risks and benefits of alternative interventions for population recovery (Beissinger and McCullough, 2002; Lindenmayer and Possingham, 1996).

Although PVA has been shown to be good at predicting the future dynamics of populations (Brook et al., 2000), their accuracy and validity is dependent on two important conditions (Coulson et al., 2001). First, data have to be of high quality so that estimates of the distribution of vital rates or population growth rate are accurate. Second, the future mean and variation of vital rates or population growth rate will have to be similar to those observed during the period of data collection. These conditions can be met by looking for systematic variation in the distributions of population growth rates and vital rates across species and populations using data from long-term studies (Coulson et al., 2001). The assumption for meeting the second condition is that if vital rates or population growth rates were observed to be constant in the past for a considerably long time, they can as well be assumed to be constant in the future.

However, it is possible for small and endangered populations to fail to meet the above conditions due to (1) lack of long-term data and (2) showing changed dynamics over time as a result of either environmental, anthropogenic or intrinsic processes (Coulson et al., 2001). In such cases, predictions of PVAs should be treated with extreme caution. Nevertheless, this does not render PVA useless for management of populations of endangered species. PVA can be useful for comparing the consequences of alternative management interventions, and for exploring theoretically the implications of model assumptions on extinction probabilities and population dynamics (Lindenmayer and Possingham, 1996; Possingham et al., 1993).

PVA have been used in the past to model the viability of roan antelope populations and assess consequences of alternative management options (McLoughlin and Owen-Smith, 2003; Durrant, 2000; Beudels et al., 1992). However, some of the findings from these studies are site-specific and cannot be applied generally to areas outside the study area. For instance, the main cause of roan population decline in Kruger National Park (KNP) was identified as predation by lions (McLoughlin and Owen-Smith, 2003) but in RNP there are no lions. Also, poaching has been an historical feature in RNP whereas poaching is not a factor for consideration in KNP because the park is well-patrolled and well-fenced. Further research is needed to come up with more effective management interventions for sustainable conservation and management of roan antelopes. This is necessitated by the lack of adequate measures to halt roan population declines at least in the protected areas researched in the past.

6.1.1 Objectives

This chapter aimed at achieving the following objectives:

- To estimate the future population trends and likelihood of extinction of roan antelopes under the current conditions in RNP.
- To rank the risks and benefits of management alternatives for roan population recovery.

6.1.2 Hypotheses and predictions

This chapter had the following hypotheses:

- The roan population is likely to continue to decline under existing management regimes. It was predicted that the current rate of roan population decline would lead to local extinction of this species in RNP within a few decades.
- Different management interventions have different effects on roan population recovery. It was predicted that management interventions that involve direct reduction of age-specific mortalities (e.g. poaching control) would be more effective than improvement of habitat (e.g. provision of water, prescribed burning).
- Different management interventions have different economic and environmental risks and costs. It was predicted that some effective interventions would be too costly or risky in comparison to other equally effective interventions, which requires prioritization before implementation.

6.2 Methods

6.2.1PVA package used

Several computer programs are available for PVA, such as GAPPS (Harris et al., 1986), POPDYN (Ron, 1991), RAMAS family of software (AkÃ§akaya and Ferson, 1992; Ferson, 1990; Ferson and AkÃ§akaya, 1990), ALEX (Possingham et al., 1992) and VORTEX (Lacy et al., 2005). However, VORTEX is the widely and commonly used program and therefore was used for this study. VORTEX is an individual-based model (IBM) that creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime (Miller and Lacy, 2005). VORTEX keeps track of the sex, age, and parentage of each animal. Demographic events such as birth, sex determination, mating, dispersal, and death, are modelled by determining for each animal in each year of the simulation whether any of the events occur.

6.2.2 The VORTEX model

Demographic parameters and life history attributes used for the VORTEX model were based on findings of previous studies on roan antelopes (McLoughlin and Owen-Smith, 2003; Harrington et al., 1999; Skinner and Smithers, 1990; Joubert, 1976). Complementary information about home ranges and age-specific mortality rates were derived from analysis of roan population and distribution data collected in RNP from 1979 to 2009. Detailed explanations and descriptions of these parameters are presented in the following sections.

6.2.2.1 Life history attributes of roan antelopes

The roan antelope has a polygynous breeding system with one male taking charge of a mean group size of 5 to 12 females (Skinner and Smithers, 1990). The roan groups occupy home ranges estimated at a mean ± SE of 3.57 ± 0.88 km^2. Basically all adult females are in the breeding pool but only about one third of the males are responsible for fertilizing all the females; the rest of the adult males live in bachelor herds or as lone males. Adult females first breed at three years with one young per litter (Joubert, 1976) but in a few cases two young per litter have been observed (Poche, 1974). For modelling purposes the litter sizes of 2 young were assumed to represent only 5% of the cases. Males begin to reproduce at the age of 5 years (Joubert, 1976). The roans have a gestation period of 9.5 months and each female has a potential to reproduce 6 calves in 5 years (Skinner and Smithers, 1990). However, the PVA model assumed an annual reproduction, although the roans can potentially produce more than 1 calf per year. The species has a life expectancy of 18 years and an active reproductive life of 12 years (Grzimek, 1990). The sex ratio at birth is usually 1:1 (Joubert, 1976).

6.2.2.2 Age structure, births and mortalities

The roans were classified into three age classes according to Harrington et al (1999): calves (0-1 year), sub-adults (1-2 years) and adults (>2 years). Birth rate for the roan antelopes was calculated using the method described by Beudels et al (1992) and Harrington et al (1999). The number of calves born per female per year was obtained by dividing the recorded number of calves by the number of adult females in a year. The overall annual birth rate was obtained by calculating the mean for all years with available data from 1979 to 2009 as shown in Table 6.1. The mean ± SD birth rate was 0.45 ± 0.15 calves per female per year. However, these calculations were based on the number of calves observed with their mothers. Starfield and Bleloch (1986) noted that calves start living with their mothers after at least 6 weeks of seclusion. This meant that the observed number of calves were an underestimate since some may have died during the 6 weeks. Therefore, the calculated birth rate was modified by adding an extra 10%.

Annual mortality rates were calculated using the data collected between 2000 and 2009 where data for at least two consecutive years were available as shown in Table 6.2. The adult expected values were calculated by adding the previous year's adults and sub-adults. It was assumed that all the sub-adults progressed to adults within a year. The percentage adult mortality rate was computed by subtracting the observed adults from the expected adults and dividing the difference by total expected roan population for that year. The total expected population was obtained by adding all age-specific expected values. Emigration and immigration were not incorporated in computing the expected population because the roan population in Ruma National Park is isolated and has no possibility of receiving individuals from outside or dispersing individuals to other populations. Consequently, any emigration was assumed to lead to death because the park is surrounded by human settlement and farms that cannot harbour any wildlife. The mortality rates for the sub-adults and calves were calculated using the same procedure, but their expected values were estimated using a different method. The expected sub-adults were the same as the calves for the previous year because it was assumed that all the calves became sub-adults after one year. The expected calves were calculated by multiplying the mean annual birth rate by the adult females of the previous year.

Table 6.1: Roan annual birth rates between 1979 and 2009 using park records in RNP

Year	Adult Females	Calves	Birth rate
1979	39	24	0.62
1986	35	11	0.31
1989	18	8	0.44
1993	11	8	0.73
1995	12	7	0.58
1998	14	9	0.64
2000	23	8	0.35
2001	11	7	0.64
2004	35	8	0.23
2005	23	7	0.30
2006	22	5	0.23
2008	20	9	0.45
2009	16	7	0.44

Table 6.2: Age-specific annual mortalities for roan antelopes between 2000 and 2009 in RNP

	Adults			Sub-adults			Calves			Total population
YEAR	Observed	Expected	Mortality(%)	Observed	Expected	Mortality(%)	Observed	Expected	Mortality(%)	Expected
2000	32	-	-	1	-	-	7	-	-	
2001	19	33	28	3	7	11	7	10	11	50
2004	43	-	-	4	-	-	8	-	-	
2005	35	47	18	6	8	4	5	12	14	67
2006	37	51	21	0	5	10	5	10	12	66
2008	30	-	-	4	-	-	9	-	-	
2009	24	34	18	6	10	9	7	10	9	54
Mean			21			8			11	
Standard deviation (SD)			5			3			2	

6.2.2.3 Effects of inbreeding

Inbreeding depression is the reduction in fitness commonly observed when individuals are produced by mating between genetic relatives (Miller and Lacy, 2005). Past studies have shown that inbreeding depression can cause reduction in survival, mate acquisition, fertility, fecundity, number of progeny per litter, disease resistance, stress resistance and growth rate (Lacy, 1997; Soule, 1987).
When populations become very small and isolated, inbreeding is inevitable (Guo et al., 2002). The roan population in RNP falls in this category and therefore inbreeding was incorporated in the VORTEX PVA model. Since inbreeding depression could not be measured in the park, the values obtained by Ralls et al (1988) study on 40 mammalian populations were used as the benchmark. Ralls et al (1988) found out that 3.14 lethal equivalents with 50% of that due to lethal alleles was the median value for the 40 populations.

6.2.2.4 Effects of environmental catastrophes

Catastrophes are events that cause extreme environmental variation such as fires, floods, epidemic diseases and extreme drought. Catastrophes can affect both small and large populations but the former are more susceptible. Catastrophes have been shown to precipitate the final decline of small wildlife populations to extinction (Clark, 1989; Simberloff, 1988). The small population of roans in RNP are occasionally affected by extreme droughts, floods and fires.

Past studies have identified drought as one of the main causes of drastic decline of wildlife populations on Kenyan rangelands (Kimanzi and Wishitemi, 2001; Wargute et al., 1997). Drought has been found to severely affect roan reproduction and survival (Schuette et al., 1998). Analysis of rainfall variation data in RNP for 30 years (1976-2005) showed that extreme droughts may occur after every 5 years. It was assumed that in such cases the roan reproduction and survival could be reduced as a result of drought by 10% and 15%, respectively.

Fires spread into the park from the surrounding community farms and burn 25% to 75% of the park annually (Kones, 2005). However, annual fires may not be too severe to cause a significant decline in the roan population because for fires to be severe they require high amounts of fuel materials. Such materials may take several years to accumulate before causing catastrophic fires. Therefore, it was assumed that despite of annual fire outbreaks, catastrophic fires could occur after every 5 years. Such fires may cause death of up to 25% of all newly born young as a result of burning or exposure to excessive predation when the entire habitat for secluding them is burned. Since the number of calves constitutes 20% of the entire roan population, catastrophic fires could lead to mortality of 5% of overall population. Habitat destruction by the catastrophic fires may delay reproduction due to poor health of surviving adult females; this was assumed to be 5%.

Floods have been shown to cause catastrophic decline of wildlife populations. Ogutu et al (2008) found that flooding was responsible for significant decline of the population of young Impalas in Masai Mara National Reserve. Ruma National Park is susceptible to floods because it is in the floor of the East African Great Rift Valley and it is sandwiched between escarpments. Analysis of rainfall data indicated that extremely high rainfall that could lead to floods occurred about every 10 years. Floods were assumed to cause death of up to 50% of roan calves as a result of drowning, which translates to 10% of the total population since the calves born annually constitute only 20%. Floods may also decimate a small percentage of sub-adults and adults especially the weak, old and unhealthy animals that are unable to outrun the floods; this was assumed to be 5%.

6.2.2.5 Effects of carrying capacity

Carrying capacity is the upper limit for the size of the population within a given habitat. The roan carrying capacity in RNP was estimated to be 288 ± 20 individuals. This was based on the mean roan herd size, home range size and available habitat. The typical herd size for roans ranges from 5 to 12 animals (Skinner and Smithers, 1990). Vegetation mapping in chapter 2 showed that 97.5 km^2 of grazing habitat is available for roan antelopes in RNP. Also, home range analysis (chapter 3) showed that the mean roan home range size in RNP is 4 km^2. The carrying capacity of 288 was obtained by estimating that the park can support a total of 24 herds (97.5 km^2 / 4 km^2) with a maximum of 12 individuals each. It was assumed that about 20 extra roans could be lone males outside the herds.

VORTEX allows for simulation of changes in carrying capacity that could be negative due to over-utilization or positive as a result of corrective management strategies (Miller and Lacy, 2005). The carrying capacity in RNP was assumed to change according to the changes in available habitat. Analysis of roan habitat change (chapter 2) showed a decline in available habitat from 97.5 km^2 in 1973 to 78.3 km^2 in 2005. Assuming a constant annual rate of change, the rate of decrease in habitat was calculated using the formula: R = 1 - (V/P)^1/T, where R is the annual rate of decrease, V and P are the habitat areas in 1973 and 2005, respectively, and T is the time in years from 1973 to 2005. The habitat declined at an annual rate of about 1%. Therefore, it was assumed that the carrying capacity decreased at an annual rate of 1% for 30 years during the simulation period.

6.2.2.6 Effects of density-dependence

Population growth in roan antelopes has been shown to be density-dependent (McLoughlin and Owen-Smith, 2003). At high population density near carrying capacity (K), the reproduction is expected to decrease due to limited resources (such as forage and breeding sites, space for territories, etc), intraspecific competition and stress. Density-dependence was incorporated in the VORTEX model using the formula by Miller and Lacy (2005):

$$P(N) = (P(0) - [(P(0) - P(K))(\frac{N}{K})^B])\frac{K}{N+A}$$, where

P(N) is the percent of females that breed when the population size is N;
P(K) is the percent that breed when the population is at carrying capacity;
P(0) is the percent of females breeding when the population is close to zero (in the absence of any Allee effect);
A is a constant that defines the magnitude of the Allee effect; and

B is a constant that determines the shape of the curve relating the percent breeding to population size, as the population becomes large.

Roan birth rates from 1979 to 2009 were analyzed using regression analysis as recommended by Miller and Lacy (2005) to yield the P(K) and P(0) parameters; these were set at 45% and 70%, respectively. The *A* parameter was set at a low value of 0.5 because at low population, adult females may not have a problem with finding mates. The *B* parameter was set at a value of 2 following Fowler's (1981) finding that density-dependence reproduction for many large mammals can be modelled quite well with a quadratic function, that is, B = 2.

6.2.3Scenarios modelled

The VORTEX PVA model was used to simulate the population of roan antelopes in Ruma National Park (1) to replicate the observed population decline from 1979 to 2009 and (2) to project the future population viability over a 100-year period. In each of these two categories several scenarios were modelled as described below.

6.2.3.1 Replication of the observed population decline

Simulations of the observed roan population decline from 1979 to 2009 were done to investigate the factors responsible for the decline during that period. The baseline scenario used the roan parameters as described in the above sections. A summary of the specific parameter input data used for the baseline scenario is presented in Table 6.3. All other scenarios were a modification of this baseline scenario. To investigate the effect of inbreeding depression a model was simulated without inbreeding depression component. Effects of age-specific mortalities were investigated by simulating several models using varying mortality rates of 0%, 10%, 20%, 30%, and 40%. Catastrophic effects were studied by considering infrequent severe catastrophes and frequent weak catastrophes. For the infrequent and severe catastrophes scenario, the frequency of each catastrophe in the baseline scenario was halved and the severity was doubled. Likewise, for the frequent and weak catastrophes scenario, the frequency and severity of each catastrophe in the baseline scenario was doubled and halved, respectively. Simulation runs were repeated 1000 times to obtain the most likely population trajectory for each scenario.

Table 6.3: Biological and ecological attributes of roan antelopes used as input data in the baseline scenario to the VORTEX model

Parameter	Value	Source / Reference
Breeding age females	3 years	McLoughlin & Owen-Smith (2003)
Breeding age males	5 years	Joubert (1976)
Mating system	Polygynous	Joubert (1976)
Percent of adult females in breeding pool	100%	This study (See section 6.2.2.1)
Percent of adult males in breeding pool	30%	This study (See section 6.2.2.1)
Maximum litter size	2 calves	Poche (1974)
Mean litter size	1 calf	Joubert (1976)
Inbreeding Depression		Ralls et al (1988)
Lethal equivalents	3.14	
Percent due to recessive lethal alleles	50%	
Reproduction active life	12 years	Joubert (1976)
Age classes:		Harrington et al (1999)
Calves	0 - 1 years	
Subadults	1 - 2 years	
Adults	> 2 years	
Survival rates:		This study (See Table 6.2)
Calves	0.89	
Subadult	0.92	
Adult	0.79	
Birth rate per female per year	0.45 ± 0.15	This study (See section 6.2.2.2)
Sex ratio at birth	1:1	Joubert (1976)
Carrying capacity	288 ± 20	This study (See section 6.2.2.5)
Multiplicative impact of catastrophes on:-		This study (See section 6.2.3.2)
(i) Drought (a) Frequency	20%	
(b) Reproduction	10%	
(c) Survival	15%	
(ii) Fire (a) Frequency	20%	
(a) Reproduction	5%	
(b) Survival	5%	
(iii) Floods (a) Frequency	10%	
(a) Reproduction	0%	
(b) Survival	15%	

6.2.3.2 Projection of the future population viability

The roan population was simulated to project the population viability for the next 100 years using the baseline scenario and several scenarios of alternative management interventions. One of the best uses of PVA models is to rank the risks and benefits of management alternatives using estimates of relative extinction risks (Beissinger and McCullough, 2002; Beissinger and Westphal, 1998). Eight management options were investigated: 1) controlling poaching; 2) reducing the death of calves; 3) reducing death of sub-adults; 4) reducing effects of fire; 5) reducing effects of drought; 6) combined interventions consisting of reduction of mortalities, severity of fires and drought; 7) Re-stocking with more roans; and 8) establishing an intensively management protected sanctuary. Again, simulation runs were repeated 1000 times to evaluate the population persistence probabilities for each of these options.

a. Controlling poaching

Poaching will mainly affect the adult roans and therefore the mortality rate for adults was set at 10% for this scenario. The current adult mortality of 21% is attributed to high levels of poaching in the park that have been observed for the last 30 years (Kones, 2005; Allsopp, 1979). This adult mortality can be reduced to 10% by increasing security patrols as well as establishing more security outposts in the park.

b. Reducing mortality of calves

The survival of newly born calves for roans is mainly dependent on availability of conducive habitat for secluding them from predation. The calves are normally hidden for six weeks in secluded habitats after birth (Starfield and Bleloch, 1986; Joubert, 1976). The calf mortality can be reduced by maintaining these habitats through controlled burning and controlling the number of competing grazers in the park. For this scenario the calf mortality was set at 5% per year.

c. Reducing sub-adult mortality

Sub-adult males are usually evicted from breeding groups to join other sub-adults or to live alone on marginal habitats (Joubert, 1976). This increases their chances of death as opposed to those roans living in groups on the suitable habitat. The mortality of these sub-adults can be reduced by improving the habitat within the roan home range by providing enough water supplies, controlling burning and the number of competing grazers. This was assumed to reduce the sub-adult mortality to 5%.

d. Reducing the effects of fire

As discussed earlier, catastrophic fires have been implicated in the death of young roans and even adults in severe cases. The severity and spread of fires can be reduced by implementing prescribed burning programs and increasing road fire breaks. For instance, construction of a road around the park boundary can serve as a barrier of fires from the surrounding local farms. With such interventions the frequency of catastrophic fires was assumed to reduce to 10% and its effects on reproduction and survival to 2%.

e. Reducing effects of drought

The effect of drought can be mitigated by construction of more water dams and water troughs and ensuring that water is pumped to these water points during the periods of drought. Although such interventions may not reduce frequency of drought, it was assumed to reduce its severity on reproduction and survival to 5%.

f. Combined management interventions

In reality, one management intervention will have diverse effects on roan decimation factors; it is not practical to use a management option to control only one factor and presumably hold the other factors constant. Therefore, the best method to boost roan population recovery in RNP is to apply several management interventions simultaneously. In this scenario, all the above five interventions were assumed to work simultaneously to reduce age-specific mortalities and effects of catastrophic fires and droughts.

g. Re-stocking with more roans

Past studies have shown that even if original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive it to extinction (Soule, 1987; Shaffer, 1981). To investigate the effect of initial population, the baseline model was repeated with 4, 6, 8, and 10 roan groups. Each roan group was assumed to consist of 12 individuals (1 dominant male, 7 adult females, 2 sub-adults and 2 calves). This is similar to the modelling procedure by McLoughlin and Owen-Smith (2003), who modelled roans with stable groups of 12 individuals. It is also comparable to typical roan herd sizes in wild populations that range from five to twelve (Skinner and Smithers, 1990).

h. Protected roan sanctuary

Management interventions for promoting the recovery of roan populations in a park setting that is managed with the aim of conserving a diversity of wildlife species may not fully achieve the desired results. To address the gravity of population decline issue, it may be necessary to set aside a roan protected sanctuary with intensive management strategies specifically designed to halt population decline and boost recovery of the roan population to healthy levels. Such strategies could include: (i) prescribed burning; (ii) construction of more road fire breaks; (iii) construction of more water points and ensuring water is pumped to these water points during the dry season; (iv) putting more effort in controlling poaching by increasing security patrols and establishing more security outposts; (v) limiting the number of competing grazers in the sanctuary; (vi) removal of predators from the sanctuary, (vii) improving the relationship with the surrounding local communities so that they support wildlife conservation; (viii) initiating community development projects to alleviate poverty with the aim of reducing poaching for bush meat as a livelihood; (ix) providing mineral supplements; (x) offering improved veterinary services; and (xi) ensuring the sanctuary is fenced and the fence is maintained in a functioning state.

With these interventions, it was assumed that the protected sanctuary scenario will have same parameters as the combined management scenario described in no.6 above but with a higher carrying capacity. Intensive management of roans in South Africa showed that populations can grow at a rate of 20% per year and reach a density of 20 animals per square kilometre (Dorgeloh et al., 1996). Therefore, the carrying capacity was set at 640 roans. This was arrived at by multiplying the potential highest density of $20/km^2$ with the area available for a protected sanctuary of $32km^2$ (obtained from chapter 2). Although, the suitable area for roan antelopes in RNP is higher, the area that is suitable and contiguous is $32km^2$. Simulations were run for the sanctuary scenario using the current population as well as varying numbers of roan groups (that is, 4, 6, 8, and 10 groups), to investigate the effect of initial population size on population recovery.

6.2.3.3 Sensitivity analysis

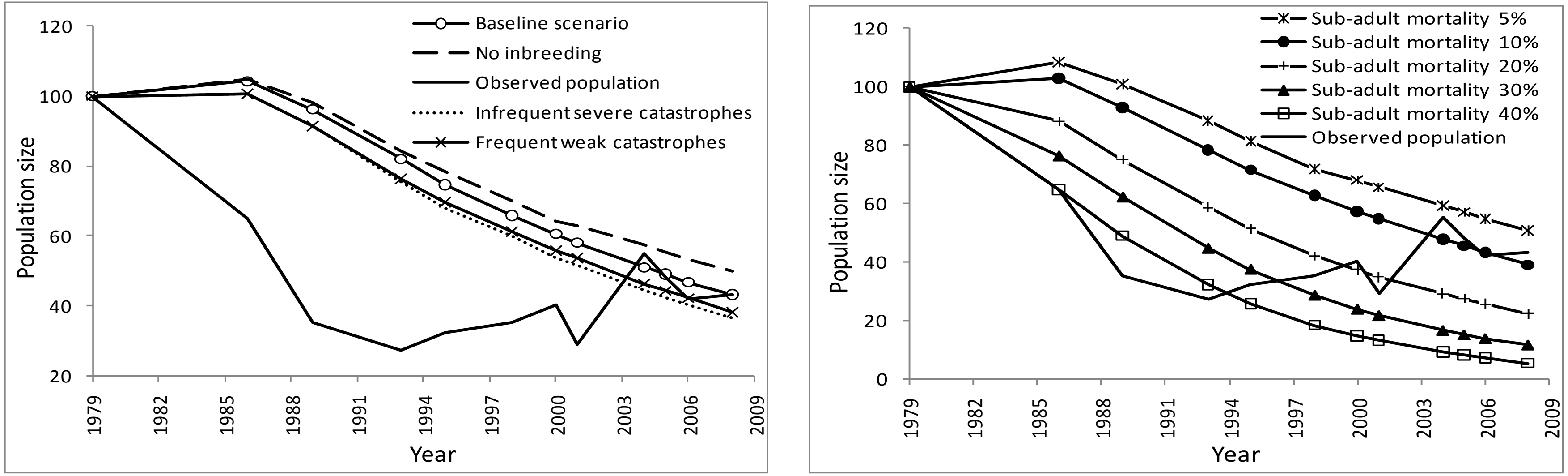
The projection of future population viability was repeated to test the sensitivity of age-specific mortalities and catastrophes. A shorter period of 30 years was used as this was considered of relevance to park management objectives at the moment. In the sensitivity analysis, the age-specific mortalities and severity of catastrophic fires and droughts were set from 0% to 40% at intervals of 5%. The population at 30 years for each of these scenarios was analyzed using a generalized linear model (GLM) to assess which parameters are most influential in the population viability analysis.

6.3 Results

6.3.1Replication of the observed population decline

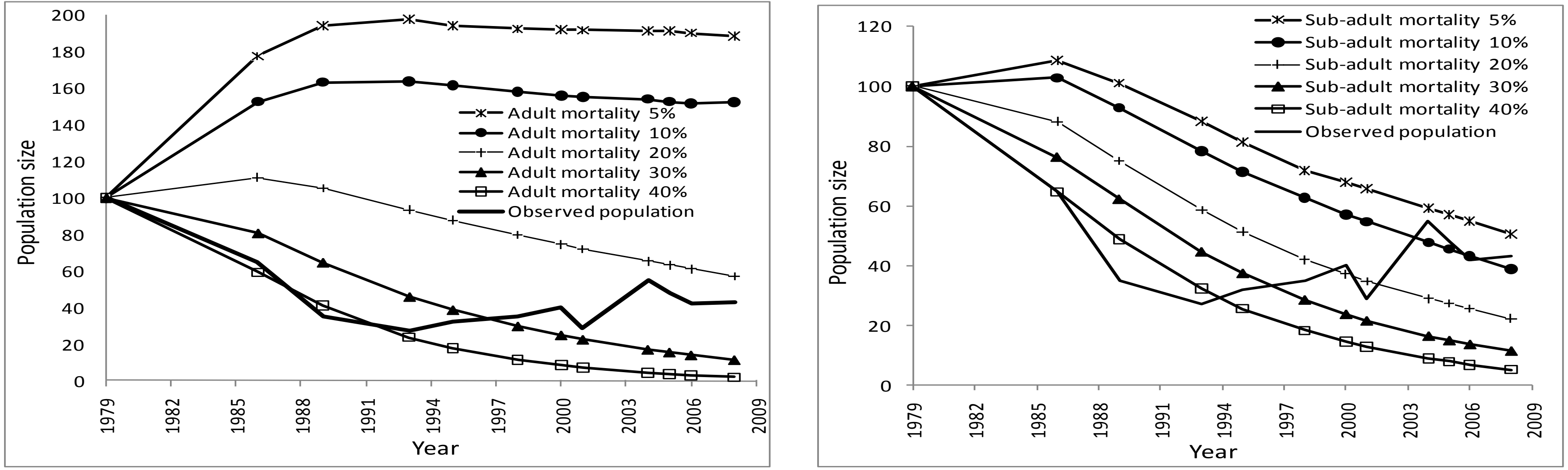
The baseline model derived from the observed roan parameters and those obtained from past studies yielded a population of 43, which is the same as the current number of roans remaining in RNP, but the model was different from the observed trend of population decline from 1979 to 2008 (Figure 6.1a). Nevertheless, it can be used as a basis for projecting future population viability.

Models that included inbreeding depression, infrequent severe catastrophes or frequent weak catastrophes were not significantly different from the baseline model (Figure 6.1a). This implies that inbreeding depression, and catastrophes were not the major causes of population decline during the past 30 years (1979-2008).



a) Catastrophes and inbreeding

c) Sub-adult mortality



b) Adult mortality

d) Calf mortality

Figure 6.1: Comparing modelled mean population size with observed roan antelope population in RNP between 1979 and 2008.

Models with varying age-specific mortality rates seemed to correspond to the observed population in a number of years. The roan population decline from 1979 to 1989 could be attributed to high mortality rates of up to 40% in adults, sub-adults or calves. Reduction of adult mortality to 10% and below caused the population to increase accordingly (Figure 6.1b). However, reduction in mortality rates of sub-adults and calves to levels as low as 5% did not halt the population decline (Figure 6.1c & d). This suggests that the observed population decline from 1979 to 2008 may have been primarily controlled by variation in adult mortalities caused by poaching of adults. This implies that years with low adult mortality could allow the population to increase and vice versa for years with high adult mortalities. For instance, population increases between 1993 and 2000 as well as between 2001 and 2004 may reflect a corresponding reduction in adult mortality.

6.3.2Future population viability

Under the current situation (as simulated by the baseline scenario), the roan population has a 100% probability of extinction before 100 years. Extinctions are estimated to begin in 32 years (Table 6.4). Re-stocking the park with more roan groups can postpone the median time to extinction up to 48 years but it does not lower the probability of extinction (Figure 6.2a, Table 6.4).

Reducing the rates of calf and sub-adult mortality to 5% did not have any significant change on the probability of extinction or time to extinction as compared to the baseline scenario (Figure 6.2 b; Table 6.4). However, reduction of fire and drought severity could reduce the probability of extinction and enable a persistence probability over 100 years of less than 1% and 3%, respectively (Table 6.4). Reduction of adult mortality to 10% changed the population growth rate from negative to positive; it caused the population to increase at a rate of 0.1% per year. Also, under this management option, the roan population showed a persistence probability of more than 86% over 100 years (Table 6.4). Combined management interventions could raise the population growth rate to 2.3% and the persistence probability to 99.8% over 100 years.

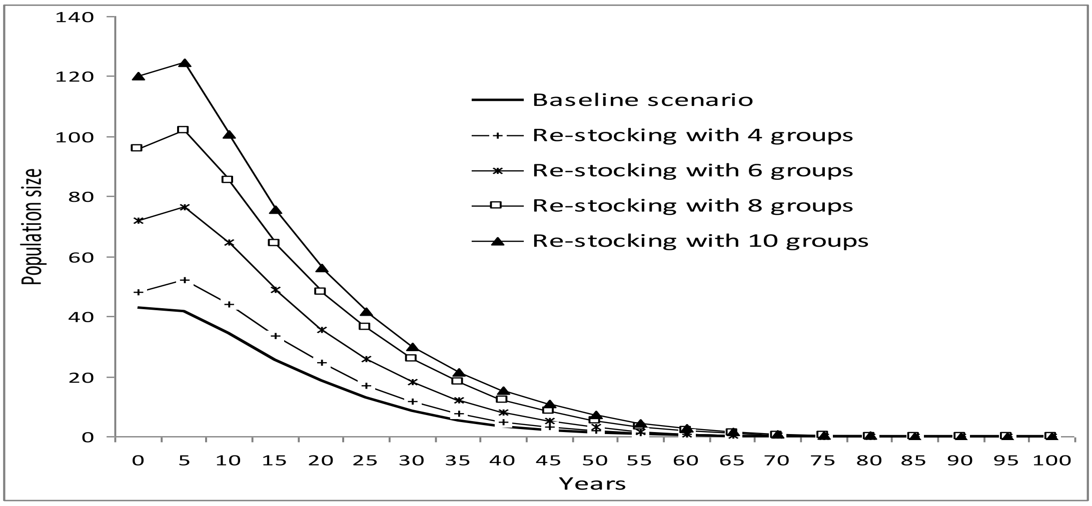
Table 6.4: Results of the VORTEX PVA model for roan antelopes simulated over 100 years under alternative management options

Management option	r	S.D.(r)	PE(%)	N	S.D.(N)	TE (years)
Baseline (no action)	-0.074	0.186	100	0	0	32
Re-stocking with 4 groups	-0.07	0.185	100	0	0	36
Re-stocking with 6 groups	-0.07	0.178	100	0.01	0	42
Re-stocking with 8 groups	-0.071	0.173	99.9	0.01	0.19	45
Re-stocking with 10 groups	-0.07	0.171	99.8	0.02	0.22	48
Reduced fire severity	-0.055	0.178	99.2	0.12	1.41	43
Reduced drought severity	-0.044	0.164	97.2	1.05	2.77	53
Calf mortality 5%	-0.061	0.183	99.9	0	0.06	38
Sub-adult mortality 5%	-0.068	0.185	99.9	0	0.06	35
Adult mortality 10%	0.001	0.134	13.7	66.37	49.27	>100
Combined interventions	0.023	0.099	0.2	248.3	31.58	>100
Protected sanctuary with current population	0.043	0.095	0	582.13	62.76	>100
Protected sanctuary with 4 groups	0.043	0.096	0	586.38	64.12	>100
Protected sanctuary with 6 groups	0.042	0.095	0	586.27	65.38	>100
Protected sanctuary with 8 groups	0.041	0.095	0	588.45	56.91	>100
Protected sanctuary with 10 groups	0.041	0.094	0	590.99	61.08	>100

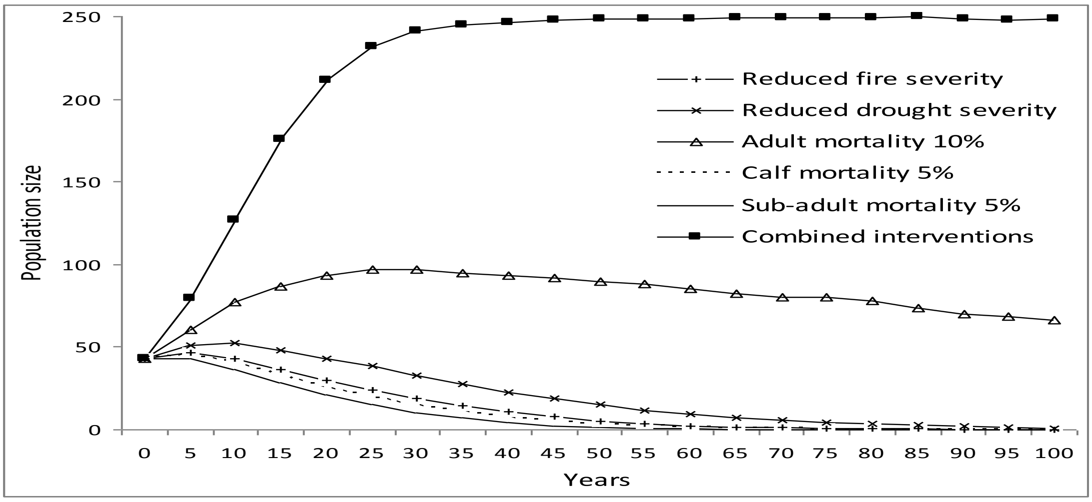
NB: r and S.D. (r) = population growth rate and its standard deviation; PE (%) = mean probability of extinction; N and S.D. (N) = mean population size and its standard deviation; TE = median time to extinction, in years.

Intensive management of the current roan population in a protected sanctuary could raise the population growth rate to 4.3% and allow the population to persist for 100 years with a persistence probability of 100% (Table 6.4). Under this management option, the population will reach the carrying capacity in 65 years. Re-stocking with more roan groups did not show any improvement in the overall population growth rate apart from reaching the carrying capacity slightly earlier (Figure 6.2c). However, re-stocking caused the population to reach high numbers within a short period and to reach the carrying capacity faster. For instance, at 10 years, the simulated mean population size was 130 roans for the management option with current population and 370 roans for that with an initial population of 10 roan groups. Also, using the current initial population, the simulated mean population size reached carrying capacity in 65 years whereas that with 10 groups reached the same carrying capacity about 20 years earlier.

a) Re-stocking with more roan groups



b) Age-specific mortalities and catastrophes



c) Protected sanctuary with intensive management

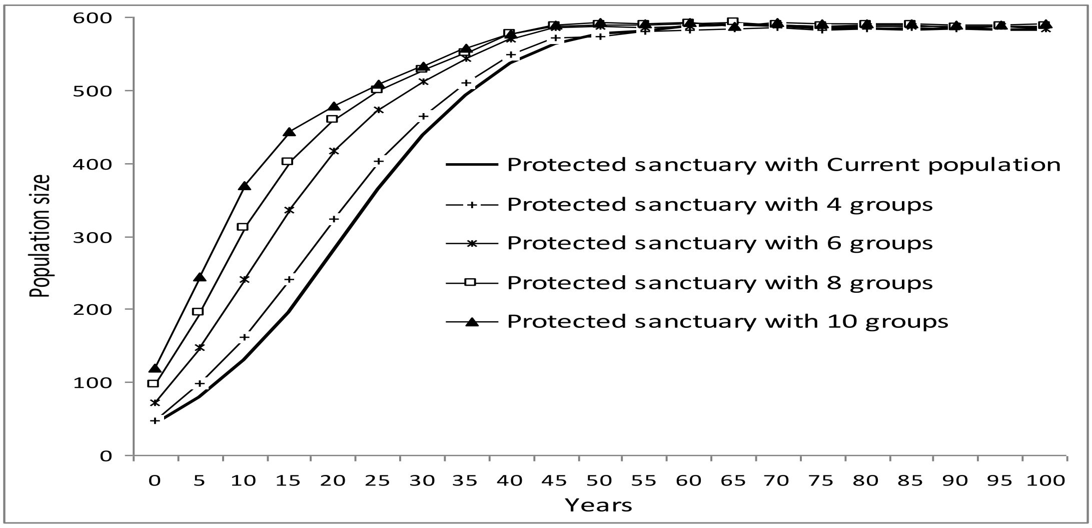


Figure 6.2: Mean population size for populations simulated over 100 years under alternative management options: (a) re-stocking, (b) reducing age-specific mortalities and catastrophes and (c) establishing a roan sanctuary with intensive management. Details on the parameters used for each management option are explained in the text (see section 2.3.2).

6.3.3 Sensitivity analysis

Sensitivity analysis was performed for the age-specific mortalities, fire and drought. Adult mortality was the most sensitive parameter and the most important in determining the change of the roan population (Figure 6.3). Maintaining adult mortality rates lower than 15% could allow the population to increase and recover. Adult mortality rates higher than 15% could cause the roan population to decrease and consequently go extinct. Maintaining the severity of catastrophic droughts at levels lower than 5% could increase the roan population at a rate lower than that caused by reduction of adult mortalities. The variation in calf and sub-adult mortalities as well as severity of fires had no substantial impact on the roan population dynamics; whether their effect is eliminated or increased the roan population will eventually decline to extinction.

Further analysis of the impact of these five parameters on roan population dynamics using generalized linear models showed that the adult mortality could account for 78% of the population decline (Table 6.5). All the other four parameters together accounted for only 18% of the decline. Examination of the regression coefficients (β) showed that drought was the second important factor responsible for roan population changes.

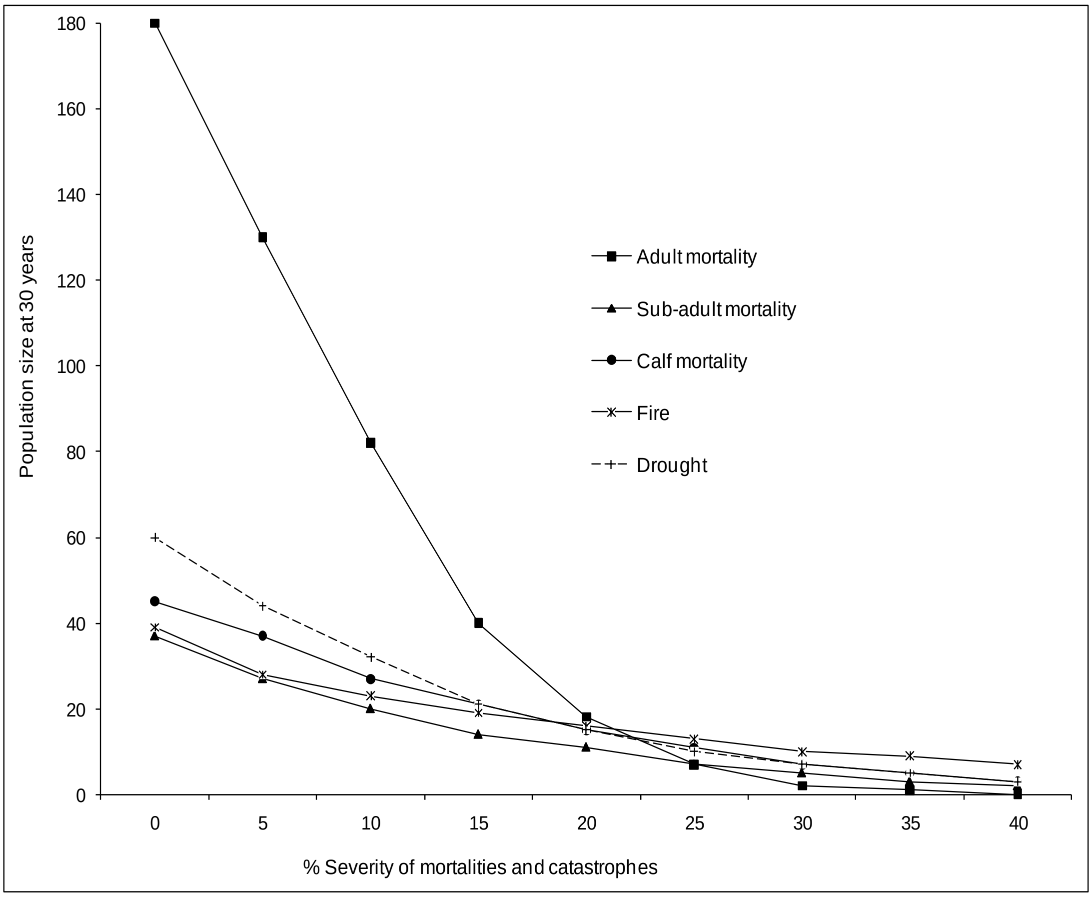


Figure 6.3: The impact of age-specific mortalities and catastrophes on roan population viability. The mean population size at 30 years was obtained by simulating a PVA model over a 30-year period with an initial population of 43 roans under varying levels of age-specific moralities and catastrophes from 0% to 40%.

Table 6.5: Relative importance of age-specific mortalities and catastrophes on roan population viability. The parameters, R^2 (coefficient of determination) and β (regression coefficient) are derived from generalized linear models (GLM)

Parameter	R^2	β
Adult mortality	78.3%	-4.096
SubAdult mortality	3.7%	-0.81
Calf mortality	3.4%	-0.925
Fire	4.8%	-0.738
Drought	6.1%	-1.257

6.4 Discussion

6.4.1 Replication of the observed population decline

Simulation to replicate the observed roan population decline helped to understand the factors responsible for the decline. Findings indicate that the most important factor is adult mortality. This confirms the fears that the main decimating factor in the park is poaching. Records show that poaching in the park was heavy as early as 1970s (Allsopp, 1979) and has continued until now (Kones, 2005). The highest rate of population decline from 1979 to 1989 coincided with a period of transition from National Reserve to National Park status (KWS, 1990). This transition may have caused escalation of poaching by the local community in retaliation to eviction from the park. In Kenya, a national reserve allows limited access of its resources to local communities but national parks are strictly managed for wildlife with total exclusion of humans. Park records also show that the slight increase in roan population observed between 2001 and 2004 was attributed to increased anti-poaching security efforts (Asila, 2004). Past studies have shown that high levels of predation especially of adults were responsible for roan population decline in Kruger National Park (McLoughlin and Owen-Smith, 2003; Harrington et al., 1999).

Other factors may have contributed to the population decline but were definitely not of major impact. Drought and the associated habitat degradation contributed to population decline but were inadequate in explaining the observed extent of roan population decline. McLoughlin and Owen-Smith (2003) obtained similar findings when modelling the effect of drought and habitat deterioration on roan population decline in South Africa.

6.4.2 Future population viability

Projections of future roan population viability based on the baseline scenario showed a high probability that at least three decades could pass before extinction eventually occurred, even if no intervention is undertaken. However, this should not send the wrong signal that interventions are not urgently needed since extinctions have been projected to happen in the near future. In Masai Mara National Reserve, a remnant roan population of 45 (±17 SE) animals in 1971 got extinct after about two and half decades (Broten and Said, 1995). Therefore, the predicted extinction of the RNP remnant roan population of 43 animals in about three decades seems realistic. Hence, this period should be used to implement management interventions.

The projections of future population viability indicated that various management interventions can halt the population decline and cause the population to recovery to healthy levels and probably to carrying capacity. These include control of poaching (in order to reduce adult mortality), combined management interventions, and establishment of an intensively managed protected roan sanctuary. Control of poaching appears to be the most crucial intervention without which the roan population is destined to go extinct in the future. The control of poaching was included as part of the combined interventions and protected sanctuary management options. The effect of poaching on adult mortality should be maintained at levels far below 15% for the recovery of the roan population to be attained**.** Studies in South Africa have found out that adult mortality rates of 15% or more severely restricts the recovery potential of roan antelopes (McLoughlin and Owen-Smith, 2003).

Unfortunately, some management interventions such as prescribed burning, construction of more water points and re-stocking under the current conditions could be a waste of time, effort and money. Although these interventions are still important and necessary they can only be effective when combined with reduction of adult mortality mainly through control of poaching.

This modelling study provides baseline findings for further research. It is also very important in guiding park authorities to make the most effective management interventions on the declining roan population in RNP. Although, as with all models, the results are said to merely reflect the assumptions made when constructing the model (McLoughlin and Owen-Smith, 2003), the parameters used in this modelling study were mainly based on the observed roan population decline from 1979 to 2009 and the environmental and climatic conditions during this period. This makes the findings more reliable especially on ranking of the benefits and risks of alternative management interventions. PVA predictions are good and reliable as long as the parameters used are derived from long term data (Coulson et al., 2001; Brook et al., 2000).

6.4.3Management and conservation implications

The next crucial stage after identification of the cause of roan population decline in RNP is to implement effective strategies that can halt the decline and propel the population to recovery. Although, increased predation by lions has been singled out as the main cause of roan population decline in South Africa (Owen-Smith, 2007; McLoughlin and Owen-Smith, 2003; Harrington et al., 1999), the management interventions taken so far have not been successful in bringing the population to recovery. The interventions were complicated because culling lions directly to reduce their numbers was futile as long as the prey base persists and an opportunity for re-colonization from surrounding regions exists. The intervention implemented involved the reduction of the abundance of zebra and wildebeest that were responsible for attracting high numbers of lions to the roan region as a result of provision of numerous artificial water points (Harrington et al., 1999). Specifically, the intervention involved closure of some water points in the roan region, so as to expel via emigration the zebra and wildebeest and the associated lions from the region. The intervention failed to cause the roan population to recover and therefore further research is needed. Investigations need to be done on how predator movements and prey selection behaviour responds to changing prey species availability (McLoughlin and Owen-Smith, 2003).

Unlike the South African case, high adult mortality rate on roan antelopes in Kenya is caused by poaching and not by predation. There are no lions in RNP and the only potential predators are hyenas, which may prey on calves and not adult roans (Waweru et al., 1995). Therefore, the best interventions in this case should include methods of controlling poaching in RNP. Such methods can involve increasing security patrols, opening more security outposts, involving the surrounding communities in management of the park, and initiating community development projects to alleviate poverty with the aim of reducing poaching for bush meat as a livelihood. More details on how to control poaching in RNP and how to prioritize security efforts is dealt with in chapter 7.

Apart from poaching, the decline in roan population was also contributed by other factors such as drought, fire, calf and sub-adult mortality. Therefore, for sustainable conservation of roans in RNP to be achieved, a combined management intervention seems to be the way forward. Such intervention could include controlling poaching, establishment of more water points to alleviate effects of drought, prescribed burning to control the effects of fires and more active manipulative management of the roan habitat. For instance, while reducing adult mortality to 10% could increase the current roan population in RNP to about 100 individuals in 30 years, employing a combined management option could propel the population to about 250 individuals over the same period.

With the current roan habitat conditions coupled with the observed habitat decline over the past 30 years, interventions in RNP under the prevailing management regime may not manage to propel the roan population to numbers that can be considered viable in isolation. Furthermore, putting all efforts of population recovery of a critically locally endangered species in one isolated population is too risky. There is need to establish other roan populations in Kenyan protected areas, where they became locally extinct in the past. Establishing an intensively managed protected sanctuary for roan antelopes in RNP can provide a ‘seed population’ that can be used to establish several other populations in the roan’s former known ranges in Kenya. This may offer a more lasting solution to the problem of roan population decline in Kenya. This concept of breeding roan antelopes in an enclosed sanctuary has already proved to be very successful in other countries. In South Africa, 7 roans were placed in a fenced enclosure within the roan range in 1994 and the population grew to 41 roans by 2001 (McLoughlin and Owen-Smith, 2003).

6.4.4 Limitations and constraints

- The use of VORTEX software leads to a relatively limited form of PVA analysis. However, VORTEX is established software with set standards. Developing one's own individual based model (IBM) may have led to complexity in interpretation of models and probably raise more questions than answers. Since this was the first comprehensive study on roan antelopes in Kenya, the VORTEX models form baseline information for further research work using advanced and complex PVA and IBM techniques.
- Most of the parameters for the catastrophic droughts, fires and floods were based on assumptions. Better results would have been found if parameters derived from field data were available.
- Information on temporal age and sex structure for roans may have been biased due to observation by different researchers over time. However, the error was minimized in PVA analysis by using the mean vital rates from long term data (1976 – 2009).

CHAPTER 7

APPLICATION OF MODELS TO PREDICT THE IMPACTS OF SNARES IN RNP

Bundles of wire snares used for poaching (Photo by Maina(2008))

CHAPTER 7: Application of models to predict the impact of snares in RNP

7.1 Introduction

Hunting of wildlife for human consumption is part of the culture of many rural people in the tropics (Barnes, 2002; Fa et al., 2002; Noss, 1995; Asibey, 1974). Meat from wild animals (known as 'bushmeat' or 'wild meat') provides an important source of protein and income to these rural people (Fa et al., 2005; Robinson and Bennett, 2000; Wilkie and Carpenter, 1999). Overhunting of wild animals for meat is currently a major threat to biodiversity conservation in the tropics (Milner-Gulland and Bennett, 2003; Fa et al., 2002). Since the tropics harbour two-thirds of earth's biodiversity (Dirzo and Raven, 2003), losses in the tropics implies significant loss in the global biodiversity. Past studies indicate that overexploitation of wildlife accounts for about one-quarter of extinctions (Rowcliffe et al., 2003; Mace and Reynolds, 2001); whilst hunting and international trade contribute to the extinction of almost one-third of the bird and mammal species listed as threatened by the World Conservation Union (IUCN) (Mace and Reynolds, 2001).

Uncontrolled bushmeat hunting in Africa is unlikely to be sustainable due to the increasing demand for meat for the rapidly increasing human population coupled with the rapid loss of wildlife habitats (Sodhi, 2008; Fitzgibbon et al., 1995). Recent studies show that the demand for wild meat in Africa is growing faster than wildlife production (Barnes, 2002; Wilkie and Carpenter, 1999). Bushmeat hunting in west and central Africa has caused significant declines and local extinctions of several wildlife populations (Robinson and Bennett, 2000). Harvest rates in west and central Africa are increasing due to human population growth, increased access to forests through improved road network, rise in hunter numbers and use of more efficient hunting methods (Fa et al., 2005).

While bushmeat hunting in west and central Africa has reached crisis level and attracted many studies (Milner-Gulland and Bennett, 2003; Fa et al., 2000; Wilkie and Carpenter, 1999; Noss, 1998), the situation is less studied in East Africa (Nielsen, 2006). However, available information shows that illegal bushmeat trade is developing fast in urban areas and therefore if it is not managed within the sustainable limits, it will eventually be a serious threat to conservation of wildlife in East Africa (Nielsen, 2006; Wato et al., 2006; Fitzgibbon et al., 1995).

In Kenya, hunting and associated forms of consumptive utilization of wildlife were banned in 1977 when they were seen as potential threats for extinction of many wildlife species (KWS, 1990). Since then Kenya has maintained a very restrictive stance on consumptive wildlife utilization with wildlife policy focused on the promotion of all non-consumptive forms of utilization such as photographic tourism (Ottichilo, 1995). Although such policy significantly slowed down poaching initially, the problem of poaching exacerbated later on due to availability of ready market for wildlife products and the resentment of local people over resource use (Cater, 1989). Kenya lacked the policy framework for ensuring that benefits from non-consumptive utilization of wildlife reached the local people living adjacent to protected areas (KWS, 1990). These locals deserved to receive such benefits as they suffered most from the problems associated with wildlife conservation such as crop herbivory, livestock predation and human death and/or injury caused by wild animals (Kimanzi and Wishitemi, 2003). The ownership of wildlife by the state, coupled with lack of benefits has led Kenyan local communities to view wildlife as a liability and consequently developed a negative attitude towards wildlife conservation. This has led them to practice illegal bushmeat hunting in retaliation in order to gain economic benefits as well as to get rid of wildlife from their private lands to create ample space for their livestock. Norton-Griffiths (1997) asserts that a farm with less wildlife is viewed as more efficient and profitable than one with abundant wildlife. The tragedy is that once wildlife is depleted from their private lands they resort to hunting in the protected areas in a quest to satisfy their demand for cheap meat and income.

Barnett (1997)argued that consumptive forms of wildlife utilization could be more appropriate to many rural areas as it would provide more benefits to communities through revenue and meat distribution. The lack of such option in Kenya may be the reason for failure of local people in participating in wildlife conservation and the current increased illegal bushmeat hunting (Kock, 1995). However, a recent study by Nielsen (2006) in Tanzania showed that incorporation of bushmeat hunting in community based wildlife management (CBWM) is not a feasible option. He found out that bushmeat hunting is caused by poverty and lack of an alternative source of protein. He recommended that for sustainability to be realized conservation efforts should be focussed on protecting wildlife against exploitation and discourage any form of consumptive use. This requires heavy monetary investment in law enforcement, which many developing countries may not afford.

Therefore, there is need to identify geographical regions inside or outside protected areas where bushmeat hunting is most severe, and direct wildlife protection efforts in these areas. More emphasis also should be given to areas where hunting is threatening to cause extinction of already endangered wildlife species. Monitoring impacts of hunting on wildlife requires measurements of wildlife stocks and hunting rates for a considerable time period (Rowcliffe et al., 2003). Review of bushmeat studies sends the message that uncertainty still exists in our ability to quantify bushmeat consumption, offtake rates and production (Rist et al., 2008; Wilkie and Carpenter, 1999). Whilst this monitoring is not easily achievable, in countries where hunting is practiced legally such as Tanzania (Barnett, 1997), tools that allow the impacts of hunting to be assessed indirectly like surveying meat in the market, could provide valuable information for management (Wato et al., 2006). However, in countries where hunting is illegally practiced, like in Kenya, monitoring the harvest rates is more complex because the hunters do not provide the information for fear of being arrested (Wato et al., 2006). To assess the impacts of hunting in such cases may require use of other indirect methods such as modelling using data on wildlife population dynamics, remote sensed Landsat images and field surveys.

Bushmeat hunting has been a historical feature in RNP since the park was established (Waweru et al., 1995; Allsopp, 1979; Allsopp, 1972). The park was mainly established to protect the endangered population of the endemic roan antelopes (*Hippotragus equinus langheldi*), which is not found anywhere else in Kenya (KWS, 2006). Therefore, any form of hunting could severely affect the small roan population. Population viability analysis of the roan antelopes in the park (see chapter six) identified poaching as the main cause of the observed roan population decline from 1979 to 2009. Poaching in this park is mainly done using wire snares. Therefore, a better understanding of the snaring patterns could help the park authorities formulate effective methods of wildlife protection by identifying snare 'hotspots' and concentrating efforts and resources on these sites to minimize wildlife loss and prevent the likely local extinction of the roan antelopes.

7.1.1 Objectives

This chapter aimed at achieving the following objectives:

- To determine how the snares in RNP are spatially distributed.
- To identify the factors influencing the distribution of snares in RNP.
- To recommend ways of curbing the poaching activities in the park so as to promote recovery of the roan population to healthy levels.

7.1.2 Hypotheses and predictions

This chapter had the following hypotheses:

- Snare locations in the park are not randomly distributed. It was predicted that (i) snares show clumped distribution in areas with essential wildlife resources such as water, mineral saltlicks and forage and (ii) that the probability of snare occurrence was influenced by the distribution of geographical features (slope, elevation), park infrastructure (roads, fence) and essential wildlife resources (water, saltlicks, forage).
- Density of snares varies with the density of wildlife in the park. It was predicted that high snare density is found in areas with high wildlife density and *vice versa*.

- The distribution of snares is associated with the distribution of roan antelopes in the park. It was predicted that most snares are set in areas within or near the roan home range, if the roans are the targeted wildlife species by the poachers.

- Density of snares is influenced by the vegetation type and its burned status. It was predicted that (i) high snare density is located in the burned vegetation as poachers are expected to lay snares in these areas to take advantage of grazers attracted by the fresh grass sprouting after fires; and (ii) high snare density is located in grasslands as opposed to non-grasslands, if grazers are the most targeted wildlife species by poachers.

7.2 Methods

7.2.1 Snare data collection

Data on snares were collected by park security rangers on routine patrols for 3 years from 2006 to 2008. The security patrols were done once per week throughout the year across the whole park but sometimes patrols were irregular due to vehicle breakdown or lack of fuel. To ensure all parts of the park were covered the vehicle patrols were combined with foot patrols. The rangers were transported by a vehicle to an area that was subsequently searched on foot. A total of 651 snares in 56 locations were recorded during the 3 years. Each location covered a circular plot with a radius of about 150m. The number of snares per location ranged from 1 to 74 snares.

7.2.2Potential variables

Eleven variables were considered for inclusion in the analysis of factors influencing distribution of snares in RNP: wildlife density, elevation, slope, vegetation type, vegetation burned status, and distances from roan home range, roads, water points, security gates, saltlicks and park boundary. Reasons for inclusion of some of these factors are partially explained in chapter 5 section 5.2.2 whilst others were considered based on field knowledge. The rationale for considering these factors is also briefly explained below.

Past studies have shown that hunters target different wildlife species depending on the main reason for hunting (subsistence or commercial), animal body size and species abundance (Fa et al., 2005; Noss, 1998). For instance, large sized animals such as buffalo are targeted for sale because of their body size (Sinclair, 1977) whilst snare hunting tends to overexploit the most common wildlife species (Noss, 1998). Therefore, the density of snares is predicted to be high in areas with high density of targeted species. Since most wildlife herbivores prefer habitats that are located at low to moderate slopes and elevation, hunters may use this knowledge to lay more snares in these areas. The local hunters also may use their indigenous knowledge about suitable habitats for targeted species when placing snares. Water and saltlicks are essential resources for many wildlife species. Therefore, snaring in areas near these resources could be more rewarding for bushmeat hunters. To avoid being caught by security rangers, hunters may lay snares away from security gates and outposts as well as relatively near the park border, where they can easily escape if they spot rangers on patrol. Investigation of how snaring patterns correlate with the park road network can help rangers to know whether vehicle patrols are effective or whether they need to be combined with foot patrols.

Each variable was prepared as a GIS map at a spatial resolution of 30m. Vegetation type and vegetation burned status were included in models as categorical variables whilst the other variables were continuous. The vegetation map layer was classified into two classes: grasslands and non-grasslands (see section 2.2.1.2.3 for more details). Investigation of snaring patterns in grasslands was the main focus because most of the animals in RNP are grazers. Vegetation burned status was also included as a single factor with two levels: burned and unburned. To compute the wildlife density, the mean wildlife estimates for 3 years (2006-2008) for each animal counting block was divided by its corresponding area. Wildlife estimates for these 3 years were used because this corresponded with the period when snares data were collected in the park by security rangers. All the other distance maps were derived from remote sensing and GIS techniques.

7.2.3 Variable selection

As is common in observational studies a number of the variables chosen as potential predictors could be correlated with each other. The highly correlated variables should not be included in modelling as this could yield biased results (Crawley, 2007). The choice of which variables to drop can be based on common sense, biological knowledge or the variance inflation factor (Zuur et al., 2010). The problem of collinearity of variables was investigated using variance inflation factor (VIF), which is a more objective tool of identifying the highly correlated variables (Zuur et al., 2010). In VIF, one explanatory variable is selected as response variable and all the others are set as explanatory variables within a linear regression (Montgomery and Peck, 1992). The VIF value for the selected variable is given by the formula:

$$\mathrm{VIF} = 1/(1-R^2),$$

where R^2 is the R-squared from a linear regression that gives the amount of variation explained by the regression model. For each analysis, a different explanatory variable is set as response variable in the regression. The VIF is calculated for every explanatory variable. A high VIF value indicates collinearity because it means that the variation in the response variable is explained well by the other variables (Zuur et al., 2007). However, for this study, all VIF values were less than 10, which implied that there were no highly correlated explanatory variables. Because there is no real cut off level for the VIF, this decision is subjective; but some statisticians suggest that values greater than 10 are too high (Montgomery and Peck, 1992).

7.2.4 Data analysis

Data analysis was done using R software (R Core Team Development, 2007). Spatial point pattern analysis was done using Ripley's K and L functions in 'Spatial' library to study the distribution of snares in RNP. Negative binomial regression was done using the 'MASS' library to predict the probability of snare occurrence in RNP.

7.2.4.1 Ripley’s K and L functions

The Ripley’s K function quantifies the spatial pattern intensity of points for various sizes of a circular search window (Fortin et al., 2002; Ripley, 1976). Points correspond to the locations of discrete events such as snares in this study. Ripley’s K function computes the overall mean number of points lying within a circular search window of radius t:

$$\widehat{K}(t) = \frac{\lambda^{-1}\sum_{i=1}^{n}\sum_{j=1}^{n} I_t(e_i,e_j)}{n}, \text{ for } i \neq j \text{ and } t > 0$$

where the point intensity, λ, is estimated as the density of snares per unit area (n/A), I_t is an indicator function that takes value 1 when e_j is within distance t of event e_i (and 0 otherwise), n is the total number of events and A is the area of the study plot. By using a circular window, Ripley’s K function is an isotropic cumulative count of all points at distances from 0 to t. The expected number of events under a complete spatial randomness (CSR) process is πt^2, the area of the search region for the points.

To linearize and stabilize the variances, the $\widehat{K}(t)$ function is modified into $\hat{L}(t)$ function (Cressie, 1993). The Ripley’s $\hat{L}(t)$ is calculated using the formula:

$$\hat{L}(t) = \sqrt{\widehat{K}(t)/\pi}$$

The expected value of $\hat{L}(t)$ under a Poisson process is 0: positive values indicate spatial clustering, while negative values indicate spatial segregation. Monte Carlo simulations of the Poisson point pattern process (i.e. CSR) are used to provide a confidence envelope of the L(t) function (Venables and Ripley, 2002). For complete spatial randomness, the plot of L(t) against distance should lie within the confidence envelope; plots above the envelope indicate aggregated pattern whilst plots below the envelope indicate regular pattern. The L(t) function, instead of K(t) was used in this study to analyze the distribution of snares in RNP, as it is more recommended (Crawley, 2007; Fortin et al., 2002; Venables and Ripley, 2002).

7.2.4.2 Generalized linear models (GLM)

The probability of snare occurrence in RNP was studied using negative binomial regression. This was used because a generalized linear model with a Poisson error distribution showed overdispersion. The effect of year of snare collection and effect of clumped distribution of snares as a random effect factors were also investigated using a generalized linear mixed model with a penalized quasi-likelihood (glmmPQL). The results showed that the occurrence of snares was not associated with the year of data collection but the clumped snare distribution was a significant factor. However, the model including the clumped snare random effect led to the same conclusion as the model without the random factor, and the former did not show significant improvement in model predictive power. The two models identified the same predictors associated with the distribution of snares in RNP. The model without the clumped snare random effect factor was preferred because it is simpler and more parsimonious according to Occam's razor principle (Crawley, 2007). Therefore, the rest of the analysis on the probability of snare occurrence in RNP was done using the negative binomial regression, which has been shown to yield good results with overdispersed data (Crawley, 2007).

7.2.4.3 Model assessment

A bootstrapping technique described by Manly (2007) was used to validate the negative binomial regression model results. The technique was performed by resampling (with replacement) the snares data to construct bootstrap samples, by leaving out 20 data values out of the 56 at a time. The bootstrap model was run 999 times and its coefficients used to assess the variability and bias in the coefficients of the original model.

7.3 Results

7.3.1Spatial distribution of snares in RNP

Analysis using Ripley's L function showed that the snares have an aggregated pattern where individuals are more clumped than random distribution at distances up to 4km because the plot of L(t) against distance lies above the lower envelope of the complete spatial randomness (CSR) line (Figure 7.1). Merging of the snares in each clump and repeating the CSR analysis using the centre of the clump confirmed that the snare clumps have a complete spatial random distribution at all distances (Figure 7.2). The distribution of these snare clumps (here after referred to as 'snare hot spots') seems to be related to the distribution of several park features. Many snare hotspots appear to be near water points, saltlicks and near the park boundary (Figure 7.3). However, these relationships are analyzed statistically in the next section.

These snare hotspots can be statistically analyzed as independent points but due to the limited number of snare hotspots (n= 15), further analysis was based on modelling snare density at the pixel scale, for the whole park, using information from pixels with snares. Therefore the number of snare locations (n = 56) rather than the snare hotspots was used as the sampling unit for further analysis in this study. The effect of spatial variation arising from the clumped distribution of snare hotspots was investigated using a generalized linear mixed model with a penalized quasi-likelihood (glmmPQL). In this GLMM model the distribution of snare hotspots was included as a random effects factor. However, this GLMM model was very similar to that obtained using negative binomial regression. Therefore, further analysis was carried out using negative binomial regression, which is a simpler model.

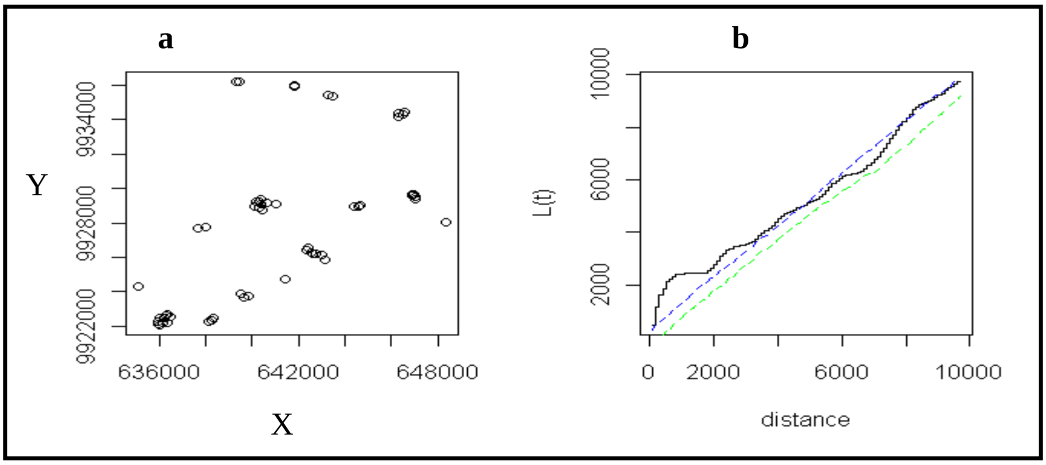


Figure 7.1: A plot of the (a) spatial distribution of snares collected by park rangers from 2006 to 2008 in RNP and (b) Ripley's L function for assessing complete spatial randomness (CSR) of the snares. The blue and green lines define a 95% confidence envelope such that plots within the confidence envelope indicate CSR, plots above the envelope indicate aggregated pattern and plots below it indicate regular pattern.

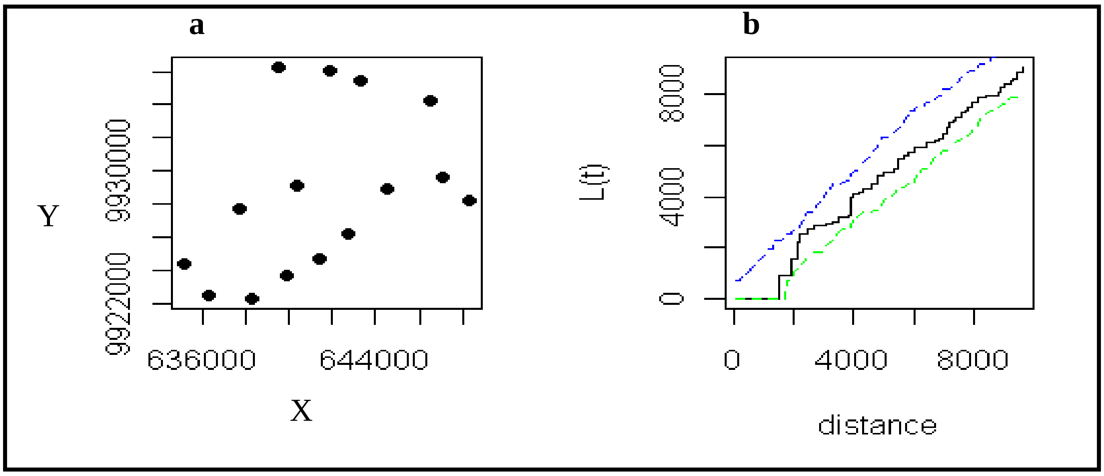


Figure 7.2: A plot of the (a) spatial distribution of snare hotspots in RNP and (b) Ripley's L function for assessing the complete spatial randomness (CSR) of these snare hotspots. The distribution of the snare hotspots indicates complete spatial randomness because the plot of L(t) against distance lies completely within the CSR confidence envelope.

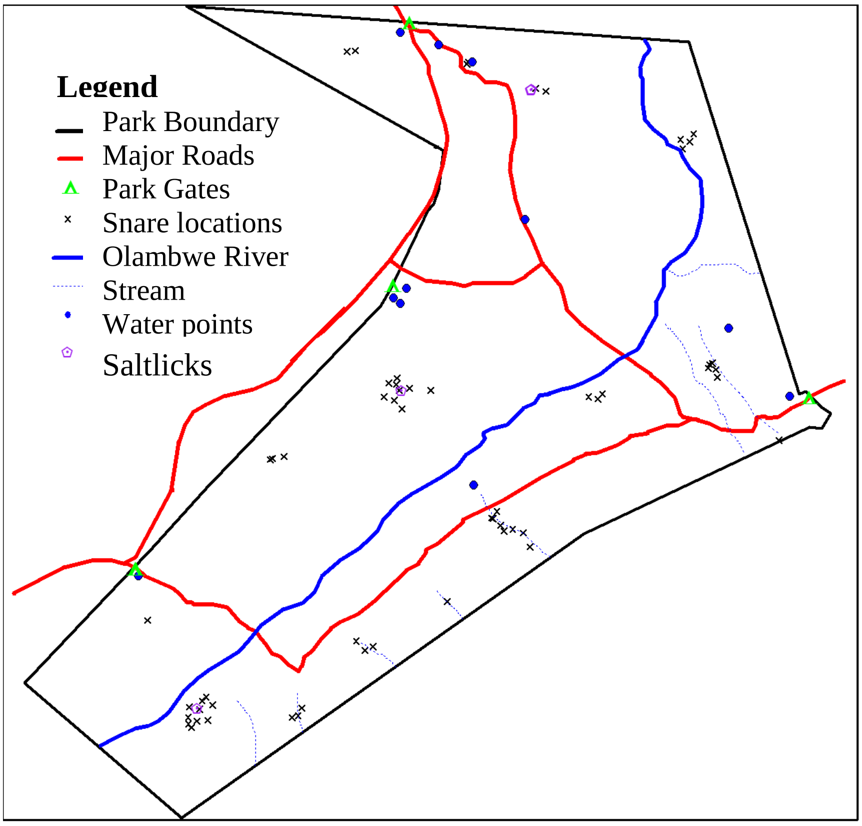


Figure 7.3: Snare distribution in relation to park infrastructure and environmental features.

7.3.2Model selection and assessment

Negative binomial regression showed one model could be considered to be the most parsimonious model in explaining snare densities in RNP. This best model had a selection probability of 0.986 and explained about two thirds ($R^2 = 0.66$) of the variation in snare densities in the park. Assessment of the best model using bootstrapping techniques showed that its parameter coefficient estimates were very similar to those of the bootstrap model (Table 7.1). The similarity of the two models implies that the same model will be identified as the best model if the analysis were repeated under similar conditions using a different set of the field data. Therefore, the model can be used reliably for predicting snare densities in the park.

Table 7.1: Predictive models (best and bootstrap) estimated using negative binomial regression for distribution of snares in Ruma National Park. The predictors are: slopes; vegetation burned status (VegBUB); wildlife density (WildDen); distances to water (Dwater); roads (Droads); mineral saltlicks (Dsaltlicks); roan home range (Droans) and park boundary (DParkBound).

Predictor	Best model		Bootstrap model	
	Parameter estimate	Standard error	Parameter estimate	Standard error
Slopes	0.26110	0.02470	0.24801	0.01089
Slopes^2	-0.00669	0.00095	-0.00588	0.00052
VegBUB	0.62300	0.10910	0.60055	0.02003
WildDen	-0.01808	0.00565	-0.01520	0.00209
Dwater	-0.00124	0.00012	0.00101	0.00009
Droads	0.00071	0.00005	0.00075	0.00002
Dsaltlicks	-0.00095	0.00005	-0.00079	0.00002
Droans	0.00020	0.00003	0.00018	0.00001
DParkBound	0.00323	0.00031	0.02043	0.00022
DParkBound^2	-0.00001	0.00000	-0.00001	0.00000

7.3.3. Factors influencing snare distribution

The results of the most parsimonious model showed that 8 factors are significant drivers of snare densities in RNP: burned status of the vegetation, wildlife density, slope, and distances to surface water resources, roads, roan home range, saltlicks, and park boundary (Table 7.1). High snare densities were set in burned vegetation, areas with low wildlife density and far away from roan home range regions and park roads. Also, high snare densities occurred in areas near water resources and mineral saltlicks. The density of snares increased with slope from 9.6 snares / km^2 at 0^0 up to a maximum density of 17.5 snares / km^2 at 11^0 and then decreased as the slopes became steeper (Figure 7.4). There were no snares at slopes steeper than 25^0. The density of snares also increased with the distance from the park boundary up to a highest density of 17.2 snares / km^2 at 1.5km and then decreased continuously beyond this threshold (Figure 7.5).

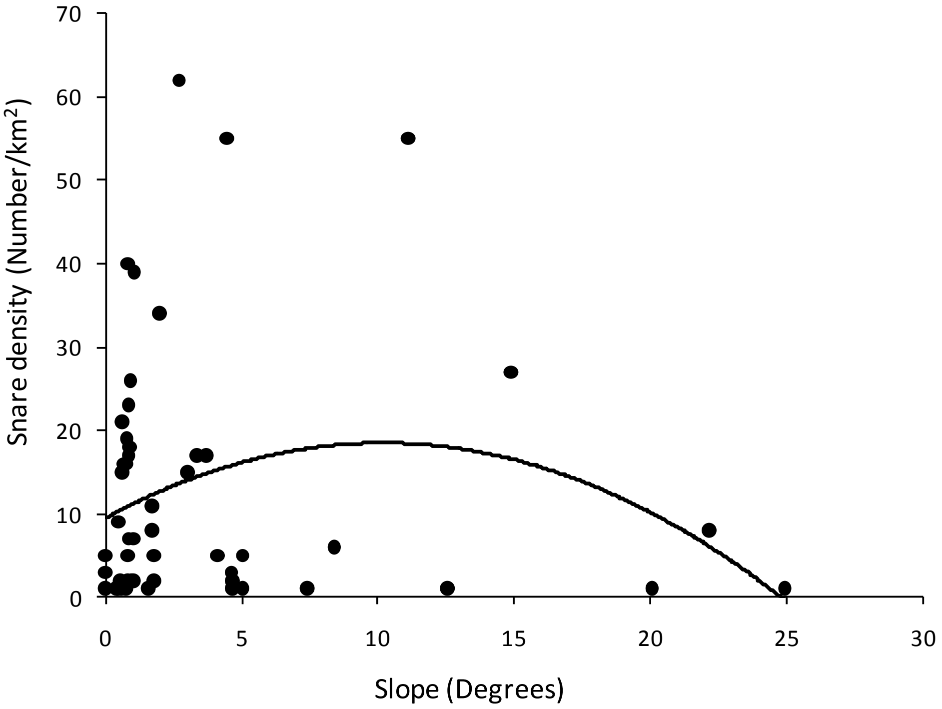


Figure 7.4: Relationship between snare densities and slope in Ruma National Park

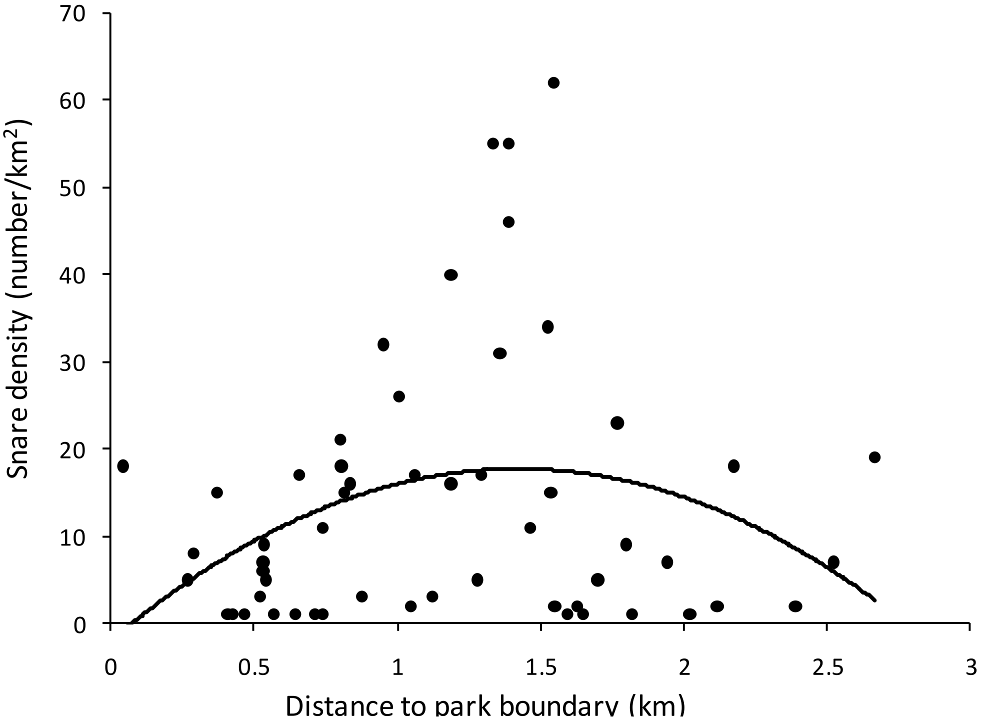


Figure 7.5: Relationship between snare densities and the Ruma National Park boundary

7.3.4Mapping the poaching risk and roan habitat suitability in RNP

A map of poaching risk prepared using the best snare distribution model, showed that 46% of the park area has a high poaching risk whereas 77% has moderate to high poaching risk (Figure 7.6). The problematic finding is that 30% of the highly suitable habitat for roan antelopes is located in the area with high poaching risk. Furthermore, 96% of the moderately to highly suitable roan habitat is located in the moderate to high poaching risk areas. However, modelling showed that distance to roan location has no significant effect on snare densities in the park. The poaching risk map also showed that most of the snare hot spots occur near water resources (Olambwe river, streams, water dams and water troughs).

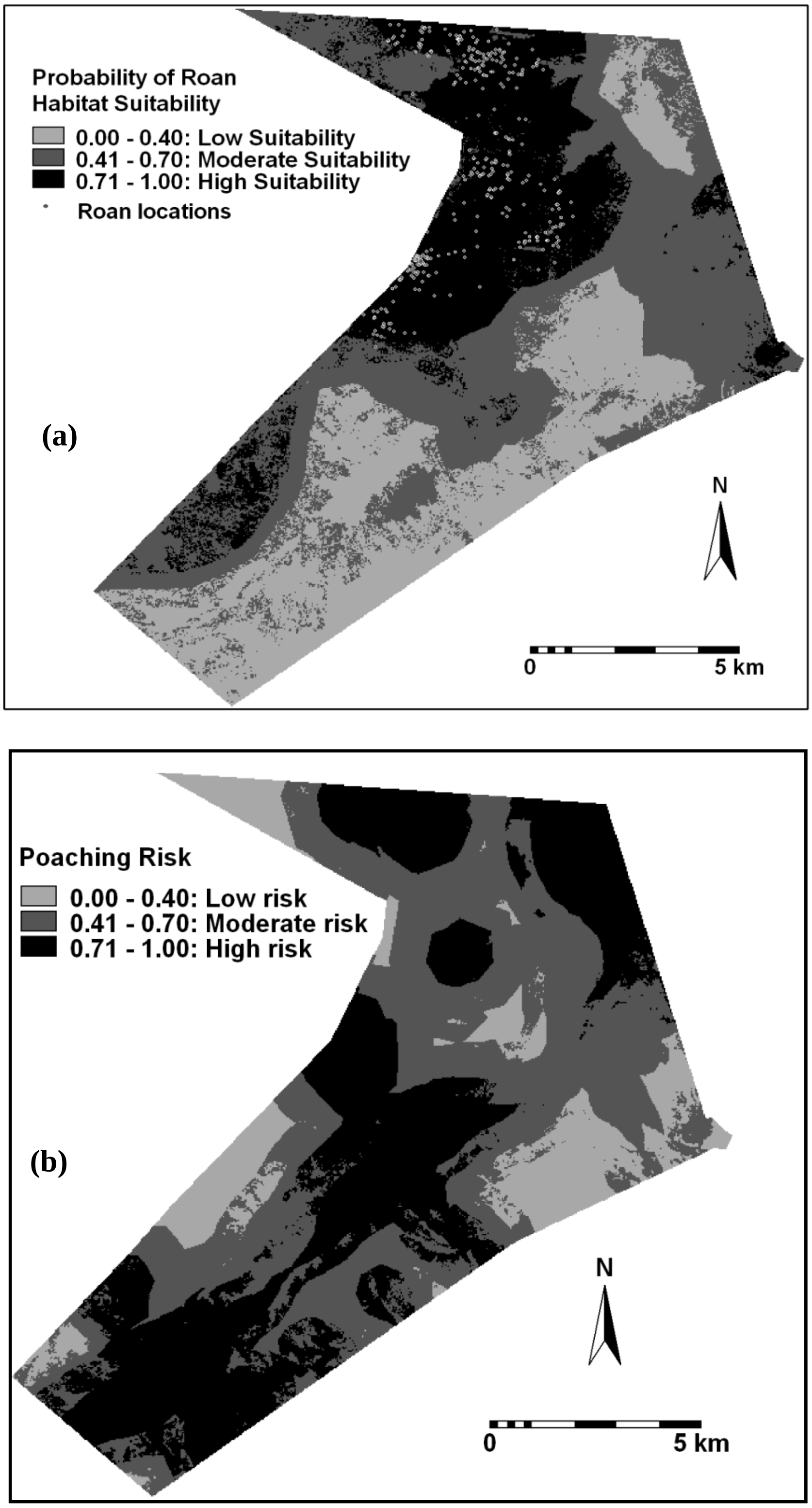


Figure 7.6: Roan habitat suitability (a) and poaching risk (b) in Ruma National Park. The maps were derived from models constructed using binary logistic and negative binomial regressions, respectively. Notice that large portions of highly suitable habitats for roans are located in areas with high poaching risk

7.4 Discussion

7.4.1 Spatial distribution of snares

The clumped snare hot spots suggest that poachers have identified particular sites with high potential of catching their intended animals, based on their past experience or knowledge on the behavioural ecology of the targeted wildlife species. Past studies have shown that poachers have a wealth of indigenous knowledge on their targeted wildlife species (Gadgil et al., 1993). This implies that if these sites are well documented and mapped, the limited park security team will be able to combat illegal hunting effectively. This will be made possible by prioritizing their patrol efforts to these few snare hot spots instead of the routine patrol on the whole park. The clumped nature of snare distribution can be used to aid identification of snares in new areas. In such areas if a snare is found it can be used as clue for the security team to search the surrounding area for snares up to a distance of 4 km away. However, this clumping distribution of snares needs to be studied in other protected areas before it is used as an anti-poaching knowledge tool.

7.4.2 Factors influencing snare distribution

An understanding of the factors driving snare distribution is a vital prerequisite to formulate anti-poaching management interventions. Modelling identified 8 factors that are significant in explaining the distribution of snares in RNP. These included: burned status of the vegetation, wildlife density, slope, and distances to roan home ranges, park boundary, water resources, mineral saltlicks and park roads. High densities of snares were located in the burned parts of the vegetation which supports Kones' (2005) hypothesis that poachers burn the park with intention of poaching the animals that are attracted by the consequent sprouting up of green grass. This might suggest that poachers target to set snares in grasslands as opposed to non-grasslands. However, there was no significant difference between snare density in grassland and non-grassland habitats (bushland and forested areas). The insignificance difference may indicate that poachers are targeting both grazers and browsers that utilize grasslands and non-grasslands. Similar results were found by Wato et al (2006). Their study in Tsavo National Park that harbours relatively equal proportions of grazers and browsers, showed no significant difference between snare density in grasslands and non-grassland vegetation. Instead, they showed that the snare sizes in different habitats were significantly different. This is expected because different snare sizes are used for different animals that dwell in different habitats.

The results showed that snare density was negatively correlated with wildlife density and distance to roan home range. Although this was against expectation, it may be an indicator that animals are deliberately avoiding snared areas. For example, during fieldwork in RNP a particular roan group behaved in a scared manner when found near thick vegetation but it was calm when encountered in open grasslands. Such difference in behaviour shows that roans are aware of areas with high poaching risk as a result of past poaching incidences and therefore may choose to avoid such areas. Joubert (1976) found that roans avoid thick vegetation habitats in Kruger National Park. Similarly, analysis of habitat selection using compositional analysis in chapter 4 showed that roans avoid habitats near thick vegetation in RNP. The insignificance correlation between snare density and wildlife density may also be an indicator that wildlife has been eliminated in areas that have experienced high poaching incidences for a long period. Wire snares can stay functional up to 2 years (Noss, 1998) and hence occurrence of high snare density in some parts of the park today may be an indicator that wildlife density used to be high in those areas but today it is low due to the hunting impact.

Although snare density was negatively correlated with roan distribution, mapping of the overall poaching risk in the park showed that some areas of high poaching risk are located in the roan home range. Population viability analysis (chapter 6) showed that roan population decline in the park was mainly attributed to poaching. Population viability analysis for roans showed that the population in the park cannot recover to healthy levels unless annual mortality rates attributed to poaching are reduced to levels below 15%. Therefore, the roans may not be the main targeted species by bushmeat hunters but they are severely negatively affected by poaching due to their small population. Edroma and Kenyi (1985) found out that various wildlife species in small protected areas in East Africa are potentially at risk of local extinction from illegal hunting. In North America overhunting is the leading cause of endangerment and extinction among mammals (Hayes, 1991). Therefore, the problem of poaching needs to be solved to enable sustainable conservation of the endangered roan antelopes in RNP.

Other significant factors influencing distribution of snares included slope, and distances to, water, roads, and saltlicks and park boundary. The highest numbers of snares were mainly set in areas with slopes ranging from 0^0 up to 20^0. This slope range seems to be the optimum for most grazers, which were the targeted species. Ruma National Park consists of a valley located between escarpments and hills. Therefore, some parts of the park have high slopes which are inaccessible by many grazers for normal foraging activities. For example, roan antelopes do not utilize steep areas. Chapter 4 showed that roans prefer areas with slopes ranging from 0^0 to 10^0.

Essential resources such as water sources and mineral saltlicks were used as snare hot spots because most animals visit them frequently. The permanent water points in the roan home range were the centres of high poaching incidences or snare hotspots. Therefore, concentrating routine security patrols on areas near water sources and mineral saltlicks can be more effective in curbing illegal hunting in the park, instead of patrolling the whole park.

Although roads can facilitate easy access by hunters to snare sites, most snares were far away from the road probably to avoid being seen by park rangers on their routine security patrols. This means that security patrols via park roads is not effective but instead patrols should be complemented by foot patrols. A study by Arcese et al (1995) confirmed that a combination of vehicle and foot patrols are more effective in combating bushmeat hunting than either the vehicle or foot patrol alone.

The last but not least factor influencing snare distribution was the distance from the park boundary that increased with snare density up to a peak at 1.5km and then decreased at longer distances. This was in agreement with findings by Wato et al (2006) who found that trap abundance increased with distance from park boundary and peaked at 4km, then decreased rapidly. The difference in the peaking distance may be explained by the differences in the geographical scale of the two studies. This study covered an area of 120km^2 whereas that of Wato et al (2006) dealt with an extensive area of 9 000km^2. This trend in snare abundance is consistent with behaviour of local bushmeat hunters in Africa. Snares normally require frequent checking to ensure that ensnared animals do not break and escape, are not eaten by other predators, or are not lost to decomposition (Wato et al., 2006). Noss (1998) estimated that a quarter of snared wild animals are lost to decomposition or scavenging, which makes trapping a very extravagant, wasteful and destructive method of utilizing wildlife. Furthermore, poachers need to carry snares and their catch back home, which makes it impractical for them to travel far from their homes to set the traps (Fitzgibbon et al., 1995). Therefore, there is a need to intensify security patrols along the park boundary and also ensure that the park is completely fenced to restrict poacher movements. Construction of a road around the park boundary can facilitate the security patrols.

However, differing snare trends were obtained by Fitzgibbon et al (1995) who found that snare abundance was highest along the forest reserve border and decreased with increasing distance from the forest edge. This may suggest that the abundance of the targeted species near the forest reserve boundary was sufficient to satisfy the bushmeat hunters and hence they did not need to travel far away from their homes. Alternatively, it may reflect a trade off between snaring success and probability of being arrested by forest guards. Areas near the forest reserve boundary may be suboptimal for trapping animals but safer and easier to escape from arrest. Other studies have shown that hunting effort can be uneven among populations in both space and time (Lyon and Burcham, 1998).

The problem of bushmeat hunting is widespread, complex and a real challenge to conservationists. Successful solutions to the bushmeat crisis should involve multifaceted approaches, and the full integration of the conservation of natural resources into development objectives at the local, national and international levels (Milner-Gulland and Bennett, 2003). This echoes the words of Sodhi (2008) that *"any meaningful success in tropical conservation will need active participation by the civil society, biologists, social scientists, lawyers, funding agencies, national and multinational corporations, governments and non-governmental organizations*". Effective strategies for solving the bushmeat crisis in RNP require support from other sectors of the economy, the government and international community. For instance, there are reports of cases where political intervention has been used to acquit poaching culprits, which frustrates the law enforcement efforts by the park. Harmonisation of wildlife policies and cross-border co-operation in countries sharing park borders can help curb poaching. For example, the game meat cropping schemes undertaken around various parks and reserves in Tanzania could offer ready market for bushmeat harvested in Kenya, where hunting is illegal (Wato et al., 2006).

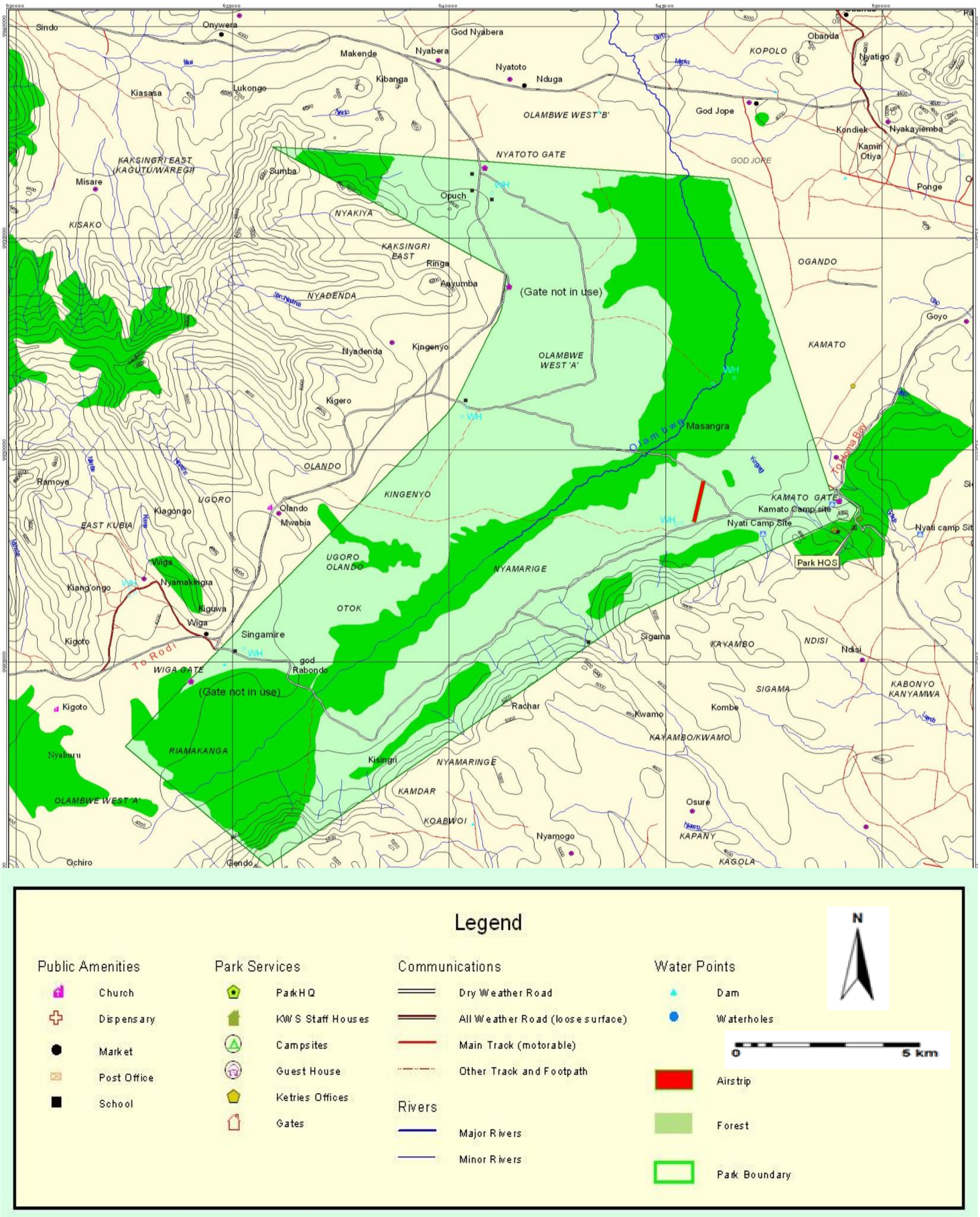
7.4.3 Limitations and constraints

- The use of snares only could not reveal all information on poaching in RNP as other methods of poaching could occur such as ambush with dogs and use of bows and arrows. Such poaching methods were rampant in the past in RNP and its environs as the traditional ways of hunting (Allsopp, 1979).
- Snare distribution data were collected by park rangers for security reasons and not for modelling or research work. Therefore, there is a possibility of some of the data being biased in times when the sampling design was not adhered to. For instance, it is possible that rangers visited more frequently the areas they had encountered snares in the past, although this was not reported. It is also likely that remote areas of the park that were difficult to access were never visited. Hence, to ascertain the reliability of the snare models, data should be collected from RNP using a systematic sampling procedure and used to validate the models.

- There was no data available on the different sizes and types of snares. Collection of snare data for the purpose of modelling can address this problem.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSION



Ruma National Park and its environs (Adopted from Kones, 2005)

CHAPTER 8: General discussion and conclusion

8.1 Introduction

The main aim of this thesis was to evaluate the roan antelope habitat and population in Ruma National Park (RNP) through accurate mapping and modelling, and to recommend scientifically-based interventions for population recovery. This has been covered in detail in Chapter 2 to 7 using comparative statistical and modelling techniques. This final chapter addresses four main issues that help to link up all the chapters together and to place this research in a wider context. It first of all, highlights the most important findings of this study, and evaluates whether the research questions asked at the start of this thesis have been answered adequately. Secondly, it collates the analytical methods used to study roan habitat selection in RNP. Thirdly, it discusses the prioritised management interventions for recovery and sustainable conservation of the roan population and its habitat. Finally, it outlines the limitations experienced during the course of the PhD research, the work that was not covered in this study due these limitations, and recommends possible topics for future research.

8.2 Mapping and modelling the roan habitat and population

Evaluation of the roan habitat and population is important for roan conservation. Mapping using GIS techniques and Landsat images is an effective method for habitat evaluation whilst modelling offers a powerful tool for understanding the species-habitat relationships and population dynamics of the roan antelope. Such an evaluation through mapping and modelling is a prerequisite for formulating effective habitat management and population recovery interventions for sustainable conservation of the endangered roan antelope in RNP.

The first step before effective interventions can be formulated for the declining roan population is to understand the extent and the cause of the decline. Many hypotheses have been put forward to explain the roan decline (Harrington et al., 1999) but these causes seem to be site-specific. Worse still, efforts to mitigate their effects have not been successful (McLoughlin and Owen-Smith, 2003). Chapter 2 modelled the relationship between changes in population of six antelope species and different components of two factors (vegetation and rainfall) identified as potential causes of population decline in RNP. The research question for Chapter 2 was “what factors are threatening roan and other antelope populations in RNP and how can these threats be mitigated?” To answer this question in more detail further analysis was done in Chapter 6, which simulated the observed roan population decline from 1979 to 2009 to identify the factors responsible for the decline.

Objective estimation of the home range of a species is required to better understand that species’ behavioural ecology and management requirements (Kenward, 2001). There is no consensus on the best home range estimator, and the choice of an appropriate method for the endangered roan antelope requires consideration of several factors. Chapter 3 compared the performance and effectiveness of 4 home range estimators (Minimum Convex Polygon (MCP), Incremental cluster polygons (ICP), Fixed kernel density (KDE), and the Local convex hull (LCH)) using Adehabitat and RANGES software packages in varying samples sizes and sampling protocols. There were three research questions in chapter 3: (i) what sampling protocols and analytical methods are cost-effective and accurate for monitoring the roan antelope’s movement and distribution patterns in RNP? (ii) Does analysis of roan movement differ significantly across software packages? (iii) How do the home ranges of the roan groups differ from and interact with those of lone males in RNP?

Results indicated that all four home range estimators are useful in characterizing different aspects of the roan home range, but overall the LCH method produced the most realistic home ranges that align well with sharply defined physical features like park fence and cliffs, and it allows analysis of repeated animal locations. However, LCH estimates were consistently smaller than those of other methods and hence to estimate the total range size of roans, it is better to combine LCH with other methods as recommended by Huck et al (2008). Therefore, the KDE and MCP home ranges estimates were better for delineating a protected sanctuary for population recovery of the endangered roan antelope that is large enough to harbour all the required resources. The ICP home range estimates were so small that they should only be considered useful in estimating the roan core areas.

Cost-effective data on roan movement and distribution can be collected using the Ranger-based method, in which rangers are trained and provided with equipment for recording data during routine security patrols. However, to reduce costs further roan locations can be efficiently collected randomly or systematically at higher interval times such as once daily. For the roan antelopes, movement data can be collected at time intervals of 2 hours, which is an optimal interval such that the autocorrelation is not eliminated but minimises its effect on home range results. Elimination of autocorrelation reduces the accuracy of home range estimates and destroys biological relevant information (De Solla et al., 1999) whilst severe autocorrelation inflates the degrees of freedom and increases the Type I error (Crawley, 2007; Legendre, 1993) and causes underestimation of home ranges (Cresswell and Smith, 1992).

The results also showed that the RANGES 8 and Adehabitat 1.8.2 software packages produce different home range estimates. The Adehabitat KDE estimates were significantly higher than the RANGES KDE estimates. This was caused by the use of the Worton (1995) reference smoothing parameter in Adehabitat software and the Seaman and Powell's (1996) reference smoothing parameter in RANGES software. To avoid misleading conclusions in comparisons of home range studies, it imperative to state the software package and version used, home range estimator used, the smoothing parameter used, user-selected options for calculating the estimator, and the input values of parameters (Lawson and Rodgers, 1997).

Habitat selection allows wildlife managers to identify target priority habitats or resources to conserve (McDonald and McDonald, 2002), improve habitat management, and to map the potential distribution of animals based on better model predictions (Fielding and Bell, 1997). A vast number of analytical methods have been developed to test the diverse hypotheses associated with the concept of habitat selection (Pendleton et al., 1998), which have arisen due to lack of an agreed definition of habitat selection (McClean et al., 1998). Chapters 4 and 5 deal with habitat selection by roan in RNP using three methods: compositional analysis, stepwise logistic regression, and information-theoretic approach. There were three research questions in these two chapters: (i) what habitat features characterize a suitable habitat for the roan antelope in different seasons, times of the day and for different activities? (ii) Is habitat selection by roan antelopes spatially scale dependent? and (iii) which are the most effective and accurate analytical methods for analyzing habitat selection by roan antelopes for management purposes.

The most important habitats for roans, identified by all analytical methods, are open grassland, wooded grassland, surface water and slope. However, habitat suitability depended on roan activity, changed over the seasons but was the same throughout the day. Feeding and resting activities were predominantly carried out in open and wooded grasslands whilst moving occurred randomly across all habitats. Surface water was significant for the dry and breeding seasons but insignificant during the wet seasons when animals could access water in readily available temporary pools. Instead in the wet season roans preferred solonetz soil that had capability of holding rain water for longer periods in temporary pools. In the breeding season the preferred habitats were far away from snare hotspots and near security gates. During this period the secluded roan calves and their solitary nursing mothers are vulnerable to predators and poachers and therefore need secure habitats (Starfield and Bleloch, 1986).

The results also demonstrated that habitat selection by roans is spatially scale dependent. Habitat selection varied in grain (spatial resolution measured) and extent (overall area of the landscape examined) as defined by Hobbs (2003). Habitat suitability model performance increased as the spatial scale decreased such that the best models were obtained at the smallest spatial scale used (see Figure 5.4). The best spatial scale was 30m, which was equal to the spatial resolution of the Landsat image from which various habitat features were derived. However, some habitat features were only significant at the study area level but not at the home range level. This implies that once a home range has been established with reference to important features, the individual roans could access these resources within the borders of the home range and hence habitat selection within the home range becomes dependent on other more important factors at that scale. Therefore, for accurate conclusions to be drawn from roan habitat selection it is necessary to carry out multi-scale analysis.

The roan population in RNP has been below 50 animals in the past 20 years and this is not considered viable according to population genetic criteria (Soule, 1980). The process of population viability analysis (PVA) can be used to estimate the probability of extinction and to prioritize potential management interventions. Chapter 6 simulated a PVA model to replicate the observed roan population decline from 1979 to 2009 in RNP and project the future population viability over a 100-year period. This chapter sought to answer 2 research questions: (i) what is the probability of persistence for the roan antelopes under the current conditions in RNP? (ii) What are the most cost-effective management interventions for roan population recovery in RNP? Results showed that under the current conditions the roan population in RNP will became locally extinct within 3 decades. Control of poaching combined with other management interventions could halt roan population decline and cause the population to recover to healthy levels.

The results of redundancy analysis, negative binomial regression, and population viability analysis showed that the main cause of roan population decline in RNP was high adult mortality attributed to poaching with snares. Other causes include habitat loss and modification due to uncontrolled fires and bush encroachment, rainfall fluctuations with its associated drought and flooding effects, and competition with other grazing antelope species. Although, other antelope species in the park are also affected by these factors, roans are the most severely affected. This could be because they have specialised habitat requirements and extreme sensitivity to habitat deterioration (Schuette et al., 1998).

The snaring patterns were analysed and mapped to help the park authorities formulate effective methods of wildlife protection. Chapter 7 carried out spatial point pattern analysis of snares using Ripley's K and L functions, and modelled the probability of snare occurrence in RNP. The chapter sought to answer one research question: what factors influence the distribution of snares in RNP and how can poaching via snares be mitigated? Results showed that snares in RNP are distributed in clumped pattern and hence identification and mapping of these clumps can help improve effectiveness of park security patrols, by concentrating on these sites instead of the whole park. These clumped snare hotspots were located mainly (i) around water sources and mineral saltlicks, (ii) at low elevation and low slopes ranging from 0^0 up to 15^0, (iii) at intermediate distances of between 1km and 2 km away from the park boundary, (iv) in grassland habitats that were unburned, and (v) far away from roads and security gates. A map of poaching risk showed that 46% of the park area has a high poaching risk and that 30% of the highly suitable habitat for roan antelopes is located in the area with high poaching risk (see Figure 7.6).

8.3 Comparison of analytical methods used in habitat selection

Since there is no single best method for analyzing habitat selection (Thomas and Taylor, 2006), three techniques were used to study habitat selection by roan antelopes in RNP: compositional analysis, stepwise logistic regression and information-theoretic approach. A comparison of results from the three methods showed that the roans mainly selected areas with wooded grassland, open grassland, near surface water and at low slopes (Table 8.1). There were a few discrepancies in the results though. Compositional analysis and stepwise regression indicated that roans also select habitat near security gates or ranger outposts. Compositional analysis also showed that habitats far away from snare hotspots and unfenced park boundary are preferred by roans. The information-theoretic technique yielded an average model that included all the eleven predictors considered in this study and gave a weighting to each predictor.

Table 8.1: Comparison of habitat selection results for roan antelopes in RNP using compositional analysis via randomisation test (λ), stepwise logistic regression, and information-theoretic approach

	Compositional Analysis		Stepwise logistic regression at p = 0.15		Information-theoretic approach (AICc > 95% certainty model average)		
Predictor	λ	p	β	S.E.	β	S.E.	Selection Probability
Burned_Veg	0.004	0.106			0.0278	0.2135	0.2735
Dfenced	0.139	0.401			-0.0001	0.0001	0.3958
Dsecurity	0.364	0.048	-0.0003	0.0002	-0.0001	0.0001	0.4643
Dsnares	0.209	0.039			0.0000	0.0001	0.3075
Dstreams_river	0.262	0.018	0.0007	0.0002	0.0007	0.0001	0.9944
Dunfenced	0.054	0.046			0.0001	0.0001	0.3707
Dwaterpoint	0.262	0.018	-0.0013	0.0004	-0.0013	0.0002	0.9977
OGL	0.019	0.035	7.4891	0.9668	6.7746	0.4597	1.0000
Slope	0.069	0.039	0.1764	0.0546	0.1478	0.0265	0.8207
Soiltype	0.878	0.476			0.1797	0.2410	0.3325
WGL	0.019	0.035	7.4045	0.9422	6.7438	0.4442	1.0000
Intercept			-5.5446	1.2683	-5.9797	0.6991	1.0000

Compositional analysis is adequate for identifying the most important habitat features for defining the suitable habitat for roan antelopes whilst the stepwise logistic regression and information-theoretic approach are capable of both identifying the most important variables and predicting the probability of roan occurrence. The information-theoretic approach has another advantage of being capable to produce the best predictive model with greater certainty by using multi-model inference and model averaging. Therefore, when the objective of the research is to produce the best predictive model, the information-theoretic approach is a more powerful tool than the other habitat selection methods. Similar conclusions were reached by Whittingham et al (2006) when analyzing habitat selection for the yellowhammer. For this study, it was necessary to use the information-theoretic approach so as to yield the best predictive model and use it in preparing a GIS map of habitat suitability for roan antelopes in RNP.

This comparison demonstrates that the three techniques are all useful in analyzing habitat selection by roan antelopes, as long as the underlying assumptions for each method are fulfilled. For example, compositional analysis requires that: (i) movement data are collected for at least 6 animals (Aebischer et al., 1993), and (ii) available habitats that are not utilized by animals are not included in the analysis to avoid inflation of the Type I error (Bingham and Brennan, 2004). Logistic regression and information-theoretic approaches are more suitable when (i) each sampling unit in a random sample of units is classified as used or not (Manly et al., 2002); (ii) independent random samples of used and non-used units (case-control) are collected (Keating and Cherry, 2004); and (iii) where individual animals are not identified as in design I of Thomas and Taylor (2006; 1990). Therefore, when location data is collected for many animals (n > 6) compositional analysis is more suitable whilst logistic regression and information-theoretic approach are better if data is only available for a few individual animals with high number of locations per individual.

Each of the three methods has advantages and disadvantages. One of the major limitations of the compositional analysis is the difficulty caused by 0's in either the use or availability data for one or more animals. Use and availability estimates of 0 are both inadmissible in log-ratio analyses that are used by compositional analysis, because they require either taking logarithms of 0 or dividing by 0, which is undefined. Pendleton et al, (1998) argue that when legitimate data values are inadmissible under a statistical model, it is an indication that the model is not completely adequate. But compositional analysis has advantages over other competing methods. It addresses 4 common problems associated with habitat selection (Aebischer et al., 1993): sample units, independence of proportions, tests among groups, and scale dependent definitions of availability. One of the best features of compositional analysis is the use of animals as the sample unit rather than each point location, which is more difficult to incorporate in logistic regression and information-theoretic approach (Manly et al., 2002) except advanced methods like generalized linear mixed models.

8.4 Recommended management interventions based on research findings

The ultimate goal of this research was to recommend scientifically-based interventions for population recovery and sustainable conservation of the roan antelopes in Kenya. Based on the research findings, recommendations are made on three main areas that are considered important to achieve the purpose of this study. These include: poaching control, habitat management, and population recovery.

8.4.1 Poaching control

Based on the lessons learned from the past studies on bushmeat hunting in Africa (Nielsen, 2006; Milner-Gulland and Bennett, 2003; Mbotiji, 2002; Wilkie and Carpenter, 1999) coupled with findings from this study, five strategies can be used to solve the bushmeat hunting problem or mitigate its impacts in RNP. These include: (1) improvement of law enforcement efforts; (2) improvement of park infrastructure; (3) improvement of community involvement in wildlife conservation and management; (4) initiating and funding community development projects with the aim of alleviating poverty; and (5) providing alternative sources of protein.

Researchers and conservationists seem to agree that one of the best ways of halting hunting that threatens to cause extinction of endangered species in a protected area is by law enforcement (Nielsen, 2006; Wilkie and Carpenter, 1999). Law enforcement and anti-poaching efforts in RNP can be improved by the following 7 strategies:

- Closing of all the public roads and footpaths passing through the park, as these facilitate the transportation of bushmeat to local markets. Figure 8.1 shows the public roads and footpaths that should be closed and the proposed road diversion outside the park. The proposed new location for the public road is feasible because it already has an operational footpath. The new road location will lead to loss of a small portion of the park, which is rocky, hilly and never utilized by wildlife.

- Deploying a special team of rangers to patrol and search all passers-by using the public roads and footpaths within the park, in case closing them is not acceptable by the community.
- Conducting frequent security patrols in areas known or predicted to be snare hotspots, as this will be more effective than patrolling the whole park.
- Developing and implementing a routine schedule for monitoring anti-poaching activities so as to ensure efficient use of the existing ranger force in RNP.
- Recruitment of more security personnel, as the current number of rangers is too small to cover all the areas affected by poaching in the park.

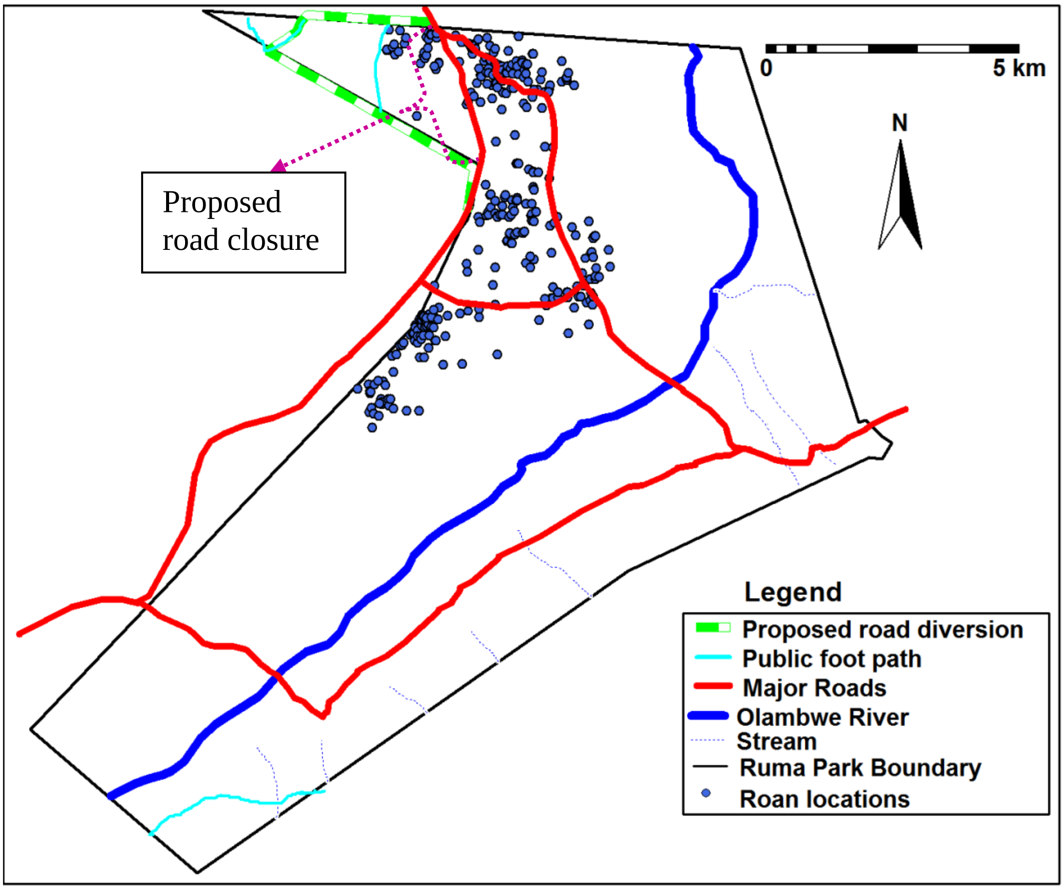


Figure 8.1: Location of existing public roads and footpaths and proposed road diversion and closure in RNP

- Soliciting for funds for purchasing, fuelling and maintaining security patrol vehicles, as availability of security vehicles and fuel has been lacking in RNP. Whilst vehicles are expensive to buy and maintain, it is imperative to have them for effective implementation of anti-poaching efforts. A study by Arcese et al (1995) indicated that vehicle patrols combined with foot patrols (in areas inaccessible by vehicles) were three to five times more successful than foot patrols alone at combating poaching in Serengeti National Park.
- Providing incentives and motivations to the security rangers to boost their morale for carrying out the risky work of combating poachers. Ranger motivation could be improved by creating and funding a special 'Anti-poaching Unit' as well as provision of specialized training and more equipment such as radios, binoculars, and wet weather gear.

The parts of the park that are severely affected by poaching are those next to water sources, mineral saltlicks and away from roads. Improvement of park infrastructure such as roads, fence, and ranger outposts can help reduce poaching incidences in these areas. Construction of more patrol roads to allow access to areas near water and saltlicks could improve security. The park roads should be upgraded to all-weather status to enable vehicle patrols during the rainy season that makes most parts impassable. Improved roads can also increase the tourist flow throughout the year and hence reduce poaching incidences. Maintaining a fully functional fence around the park can reduce access to the park by some poachers. Currently, about one-quarter of the park is not fenced and in other areas the park fence has been vandalized to supply wire for snares. Also, the unfenced parts provide a route for roans to move out into the areas of dense human settlement, which exacerbates the risk of poaching. The Kor Lang ranger outpost in Kanyamwa escarpment needs to be re-opened and three other outposts should be established in the Gendo, Ogando and Nyakiya areas (Figure 8.2). The Kor Lang and Nyakiya outposts will be next to unfenced park boundary and on higher ground to easily monitor activities in the park valley floor. The Gendo and Ogando outposts will be located in areas near water sources and saltlicks that have been identified as snare hotspots. Also, Gendo area has been identified as a suitable site for construction of a new dam.

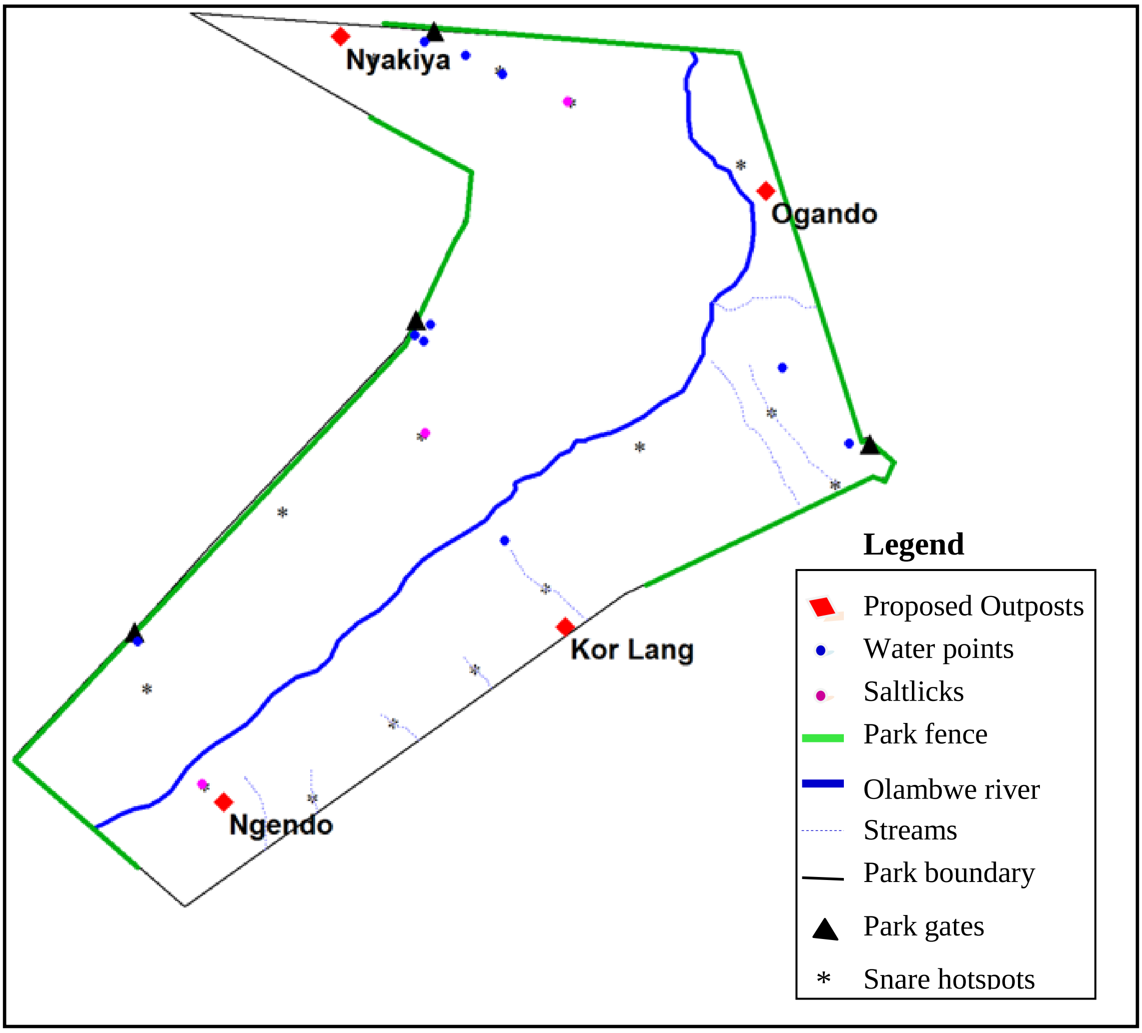


Figure 8.2: Location of proposed ranger outposts in relation to existing park infrastructure and snare distribution in RNP

The poaching in RNP is done by the local people living adjacent to the park. Therefore, involving them in wildlife conservation and management activities and decision making can help resolve conflicts and create a positive attitude towards biodiversity conservation. The park can use the following three strategies to improve community involvement:

- Employing a team of community youth security eco-guards to act as agents for reporting bushmeat hunting incidents to park authorities.
- Having frequent public meetings between park authorities and the local community to create awareness and educate the community concerning

the impacts of bushmeat hunting and the importance of wildlife conservation (e.g. following the example of Nouabale Ndoki National Park - (Elkan, 2000).

- Improving community wildlife extension services to help resolve human-wildlife conflicts and to advise the locals to undertake land use practices that are compatible with wildlife conservation.

Bushmeat hunting is practiced as a way of life by people in many rural areas due to poverty and lack of alternative means of feeding themselves and earning income (Nielsen, 2006; Noss, 1998; Dahl, 1979) and the local people around RNP are not an exception. Therefore, the problem of poaching in RNP may not be resolved unless the problem of poverty is tackled (Robinson and Bennett, 2000). It is worth noting that the local people may never support wildlife conservation unless they are benefiting from it and until their basic needs of livelihood are met. Agrawal and Redford (2006) recommends integration of poverty alleviation issues in conservation. The park should initiate and fund community development projects and social facilities to contribute towards poverty alleviation. A good example to emulate is Masai Mara National Reserve where 19% of reserve entry fee collection is used to fund community social facilities such as cattle dips, schools, hospitals and bridges (Kimanzi and Wishitemi, 2003). Other development projects could include bee keeping, harnessing solar energy, making and selling of traditional artefacts to tourists, and performing of traditional dances to tourists. However, the locals should be encouraged to identify the perceived needs and problems because every community is unique and requires unique solutions. General economic & ecological theories of dealing with rural economies and natural resource utilization should be applied with caution (Milner-Gulland and Bennett, 2003).

Long term solution to the bushmeat hunting problem could be achieved by providing alternative sources of protein to those people relying on bushmeat as the only source (Mbotiji, 2002; Noss, 1998). Two alternative sources of protein are fish and livestock. Past studies have demonstrated that high bushmeat consumption in west Africa is associated with low availability and high prices of fish and livestock in the market (Brashares et al., 2004; Milner-Gulland and Bennett, 2003). Boosting the fisheries and livestock production in the areas around RNP could reduce dependence on bushmeat. The government and the park management should fund and offer technical support to promote fish farming in the area. The Lambwe valley has a historical problem of trypanosomiasis (Cibulskis, 1992; Mihok et al., 1990; Allsopp, 1979; Robson et al., 1972) which reduces livestock production. Therefore, there is need to increase funding for the on-going trypanosomiasis control program (Muriuki et al., 2005) as well as embrace new livestock production technology and veterinary services so as to improve livestock production in the area.

8.4.2 Habitat management

Proper habitat management geared towards sustainable conservation of roan antelopes must include the following three strategies: (1) provision of sufficient well-distributed surface water, (2) prescribed or controlled burning and (3) control of stocking level of animals in the park. Sufficient water can be provided by constructing more dams and water troughs in the roan home ranges and other strategic areas of the park. Water can be pumped to water troughs during the long dry season to alleviate effects of drought. However, water points should not be concentrated in few locations as this can lead to degradation of the areas in close proximity to the water points as a result of overutilization (De Leeuw et al., 2001). Figure 8.3 indicates proposed locations of 8 new water points that cover not only the roan home range region but the whole park.

Prescribed burning can be used to maintain large areas with the preferred open and wooded grasslands and to curb the on-going bush encroachment, which is a form of habitat degradation for the roans. The current lack of a prescribed burning program in the park increases the probability of spread of fire to the park from surrounding communities due to accumulation of large amounts of fuel material for fire. Prescribed burning will ensure continued availability of burned and unburned vegetation patches for use in different seasons by the roan. Figure 8.3 also shows 15 burning blocks that can be used for prescribed burning in RNP. These blocks are marked by existing park roads, rivers, and fire break tracks. The blocks should be burned alternately such that each of the blocks is burned after every 2 years except blocks 1, 4, 5, 10 and 11. Burning every 2 years will prevent over-accumulation of fuel materials that cause fires to burn uncontrollably in unintended areas. Blocks 4 and 5 are the breeding habitats for the roan and therefore could be burned alternately after every 5 years. This will ensure that there is conducive breeding habitat every year. The location of blocks 4 and 5 will ensure that the 3 roan breeding groups have access to breeding habitat at any time. Blocks 1, 10 and 11 should never be burned because they are dominated by forest and bushland habitat and hence should be maintained for the browsers in the park.

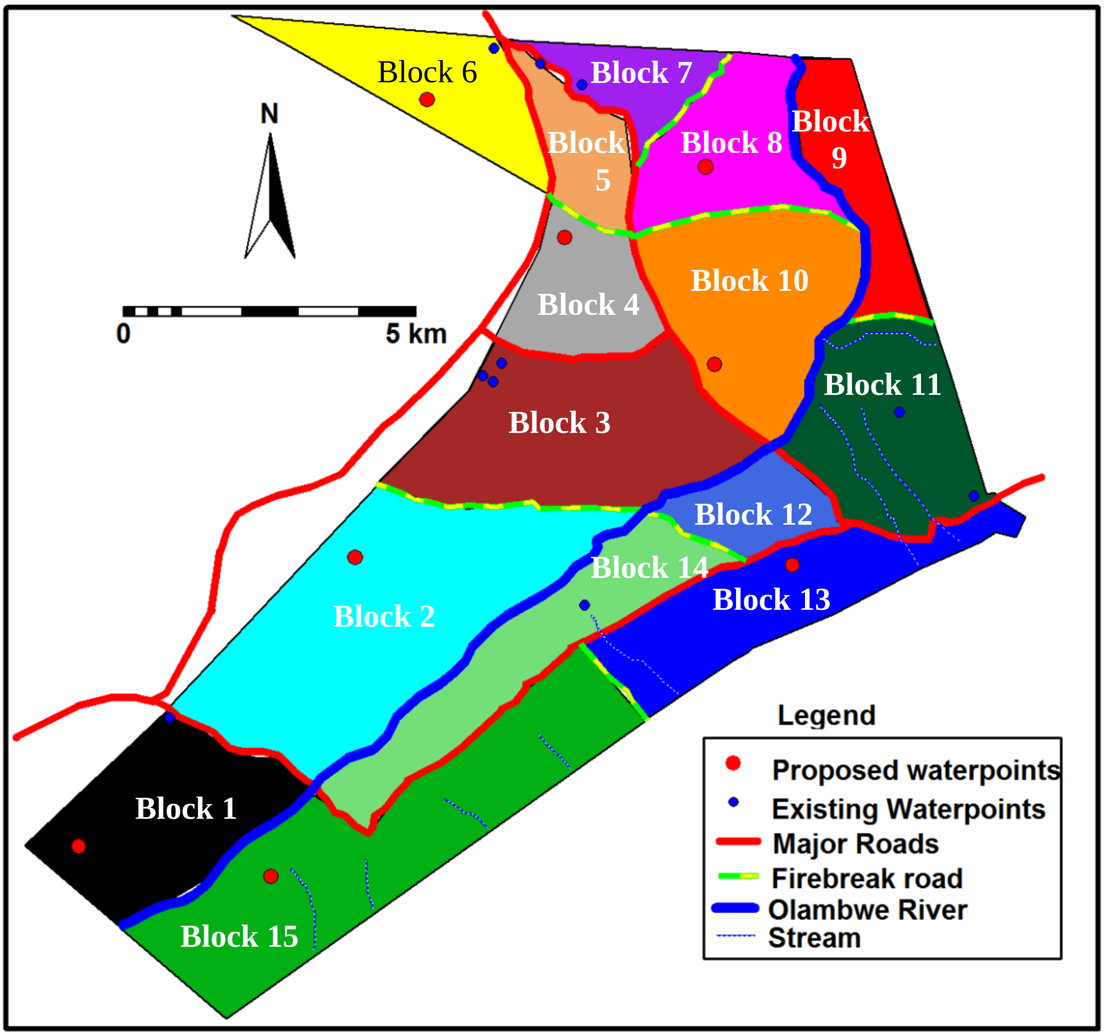


Figure 8.3: Proposed water points and prescribed burning blocks in RNP

The exact season, time and schedule of burning should be decided by the research scientist in the park after inspection of the various blocks and in consideration of the following factors as recommended by Starfield and Bleloch (1986): (i) whether there is sufficient combustible material in the block to sustain a fire; (ii) if the purpose of burning is to thin out shrubs and bushes, the fire should be as intense as possible, so burning before the first rains is necessary; (iii) burning too frequently in some soil types can be deleterious, leading to soil erosion and proliferation of those grasses and plants that thrive on disturbed soils; and (iv) fire can be used to alter the vegetation in such a way as to favour one herbivore species rather than another.

Bush encroachment is caused by high density of grazers and low density or absence of browsers coupled with uncontrolled burning (Walker et al., 1981). Therefore, control of the stocking levels of both grazers and browsers in RNP can help maintain the preferred grassland habitat and prevent the spread of the bush encroachment. Although, reducing the number of wildlife in the park may be incompatible with the general aim of maintaining high biological diversity, it is worthwhile to single out the species that should be restricted or those to be increased. For example, elephants that adversely alter the habitat structure and zebra that are the most likely ecological competitor with roans (Kingdon, 1984) should not be re-introduced in RNP. Use of the park by cattle from surrounding communities should be prevented as they have been shown to cause decline of other antelopes (Dunham et al., 2003). The proposed plans to re-introduce black rhinos to RNP (Okita-Ouma and Njue, 2006) are welcome as this will improve the roan habitat by halting bush encroachment through increased browsing intensity.

Since roans have strictly defined habitat requirements and preferences, and because the survival of their calves is so intimately dependent on optimal habitat conditions, roans are particularly susceptible to habitat degradations. This makes the species a very sensitive indicator of the health of the ecosystems of which they form an integral part. The loss of roans from such large areas of their former distribution range not only in Kenya but in the whole of Africa, serves as an important reminder of the loss of ecological qualities in those areas. Likewise putting measures to conserve roan habitat will also conserve other species with similar habitat requirements as well as generalist species.

8.4.3Population recovery

The process of roan population recovery can be boosted using the following five strategies: use of combined management interventions, reinforcing RNP roan population via re-stocking, establishment of a predator-proof sanctuary, establishment of other populations in known roan ranges in Kenya, and improving tourism development. This research's PVA simulations showed that combined management interventions are the most effective in propelling the roan population to recovery. Such interventions should include controlling poaching, establishing more water points and prescribed burning. However, for any intervention to succeed in bringing about roan population recovery in RNP, it must include a poaching control component.

The roans should be managed across the whole of RNP and their numbers increased by re-stocking from neighbouring countries such as Tanzania. However, care should be exercised to ensure that only the East African endemic roan subspecies (*Hippotragus equinus langheldi*) is translocated to Kenya. Research on roan translocations in South Africa has revealed that currently there might be no pure endemic subspecies in that country. This is because the *H. e. cottoni* subspecies from Malawi was translocated and bred with the South Africa's *H. e. equinus* subspecies (Barrie, 2009).

Another strategy is to establish a predator-proof sanctuary for conservation of the roan and its suitable habitats within the RNP. A well fenced sanctuary could keep off both human and wild predators. The sanctuary should be managed based on the combined management interventions (as described in section 6.2.3.2) coupled with control of the number of wildlife grazers within the sanctuary enclosure. The sanctuary boundary should be delineated based on (i) the roan habitat suitability map prepared using the 95% certainty best predictive model from information-theoretic approach and (ii) the connectivity of the predicted suitable habitat patches. Figure 8.4 shows the location of the proposed roan sanctuary in RNP.

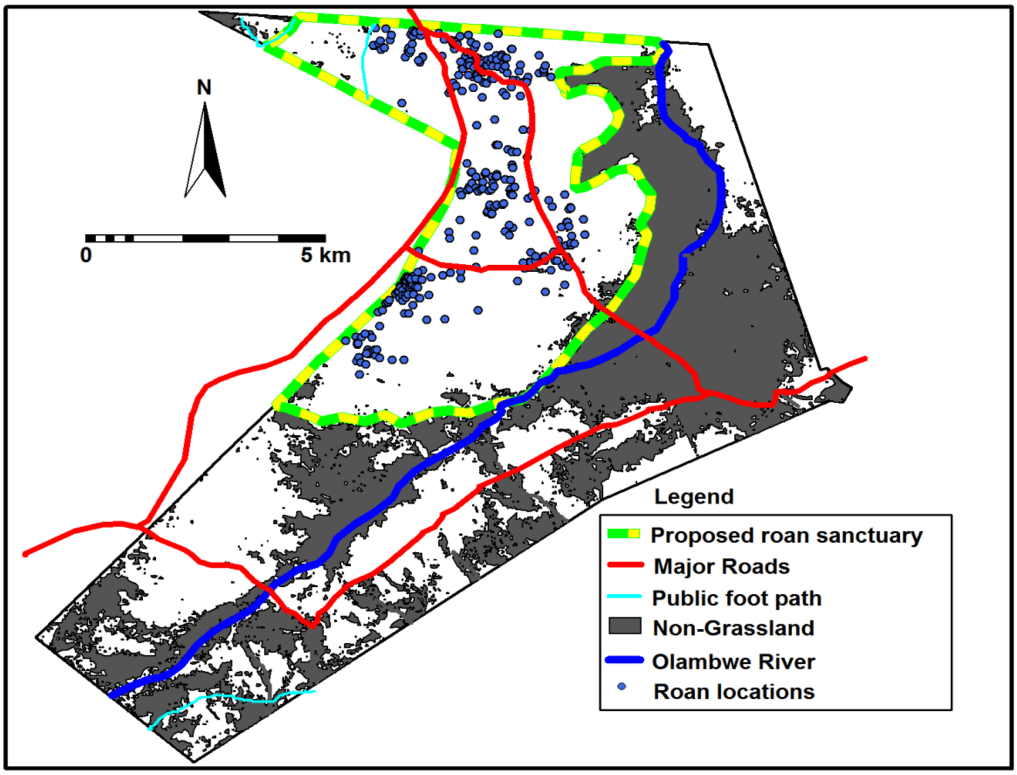


Figure 8.4: Proposed roan sanctuary in RNP

Strategy 4 proposes establishment of populations in other protected areas in known roan ranges in Kenya such as the Masai Mara National Reserve. This will avoid the reliance on one small isolated roan population and hence reduce the probability of extinction. Such re-introductions should only be carried out after detailed research on roan habitat suitability in the protected areas concerned. Past roan translocations into Kenya's Shimba Hills National Reserve in 1972 were unsuccessful (Litoroh, 1989). Since the roan population is declining all over the East African region, a regional workshop is necessary to bring its plight to the attention of the wider scientific community and wildlife authorities in order for these interventions to be implemented in all East African countries that harbour the *H. e. langheldi*.

Lastly, boosting tourism development in the RNP could provide a long-term means to alleviate poverty and win support of the local community in wildlife conservation. The park could be a highlight in the proposed tourist circuit for

Western Kenya, and a logical stopping point between the Masai Mara N. Reserve, the islands and fishing camps of Lake Victoria, Kakamega Forest Reserve and Mt. Elgon N. Park (Kock et al., 1995). The tourist circuit could be boosted by (i) advertising and campaigning for the routine increased use of the Eldoret International Airport by tourists, and (ii) improving roads within and outside the park to all-weather road status to ensure continuous flow of tourists throughout the year. Establishment of guided walking safaris and eventual development of tented camps and a tourist lodge, could provide employment for the local people as tour guides, security guards, drivers, hotel staff as well as income through sale of farm produce. The recommendation by Okita-Ouma and Njue (2006) to re-introduce black rhinos in RNP should be implemented as soon as possible to increase the touristic value of the park and consequently boost tourism.

8.5 Outline management plan for roans in RNP

This section presents a brief outline of a management plan for roan antelopes in RNP. It discusses how the management recommendations should be prioritized before their implementation in the light of their relative costs as well as their likely conservation benefits. It also outlines effective methods of monitoring and data storage in RNP.

8.5.1 Implementation of management strategies

Implementation of research findings are always limited by availability of finances, time and manpower and hence the need for prioritization. For any management intervention for roan population recovery in RNP to be successful it must include measures to control poaching and thus these measures should be the first priority. Therefore, the first priority should be given to poaching control. Coincidentally, poaching control is one of the most feasible strategies to implement in RNP because it is an on-going activity. If the steps outlined earlier in section 8.4.1 are followed, the objectives of anti-poaching efforts would be achieved effectively. Depending on the availability of resources, poaching control can be done simultaneously with habitat management interventions such as provision of water and prescribed burning. While poaching control requires a lot of funds to keep it going, provision of water would require little funds for maintenance, although it would require more initial funds to implement it. In contrast, prescribed burning would require very minimal funds for both implementation and maintenance. In fact, with a proper schedule, the anti-poaching team could handle its maintenance without extra costs.

Establishment of a roan sanctuary and re-introduction of roans in other known former ranges, are the most expensive strategies. Due to cost implications, the establishment of a predator-proof sanctuary should be the last resort. Likewise, all *in situ* measures should be thoroughly tried before considering *ex situ* interventions. Other measures such as involvement of the local community in wildlife conservation and funding of development projects are on-going and just need strengthening and improvement. These are long term interventions that need re-evaluation with time so as to meet the perceived needs of the society that are ever changing.

Apart from costs, the recommended interventions could also be prioritized based on their conservation benefits. Some strategies only benefit particular age groups within the roan population while others could provide benefits across all age groups and therefore has higher conservation value. For example, establishment of a roan sanctuary that is managed with combined interventions as discussed in section 6.2.3.2 would benefit all age groups by eliminating human and wild predators, controlling poaching, prescribed burning, provision of water, minerals and food supplements. Poaching control, which is essential for roan population recovery only aids in reduction of adult mortality (which was identified as the most likely cause of roan population decline). Prescribed burning would most likely benefit the calves as this ensures availability of a conducive habitat for cover from predators. Prescribed burning would also provide green forage that would promote the survival of all age groups. Provision of water would be beneficial to most of the age groups but least important for the new born calves as they depend on their mothers.

Miller-Gulland et al (2003) recommend that for research findings to be properly and thoroughly implemented they need to be included in a management plan for the relevant park. Fortunately, the completion of this research comes at a time when the Kenya Wildlife Service (KWS) has constituted a Roan Antelope Conservation Task Force to formulate a national conservation strategy and action plan for the roan antelopes in Kenya. Effort will be made to ensure that research findings of this study are incorporated into that strategy.

Many of the interventions are based on model results of this study whose performance were mainly assessed using bootstrapping techniques, which may not be powerful enough. Fielding and Bell (1997) recommend the use of an independent data set to test the validity and performance of ecological models. Therefore, before implementing the model-derived interventions, more thorough testing should be performed using an independent data set preferably obtained from other roan populations apart those in RNP. The testing can be done concurrently with the formulation of the conservation strategy and action plan, so that it does not delay the implementation phase. Also, further research should be done before some recommendations can be implemented especially those concerning re-introduction of roans in other known former ranges.

However, the success in the implementation of these interventions is dependent on a number of assumptions. First of all it is assumed that the Kenya Wildlife Service (KWS), which is the custodian of wildlife in Kenya, together with the Government will be willing to implement the interventions. Secondly, the prevailing political climate both locally and nationally will favour wildlife conservation as a sustainable land use practice in RNP. The adoption and implementation of the new constitution of Kenya, which was approved by the referendum on 4th August 2010, could be a great boost to wildlife conservation. The most important section of the new constitution relevant to wildlife conservation is section 69 clause 1(a) to 1(d) (Republic of Kenya, 2010), which states that: "*The state shall –*

a) *Ensure sustainable exploitation, utilization, management and conservation of the environment and natural resources, and ensure the equitable sharing of the accruing benefits;*

b) Work to achieve and maintain a tree cover of at least ten percent of the land area of Kenya;

c) Protect and enhance intellectual property in, and indigenous knowledge of biodiversity and the genetic resources of the communities;

d) Encourage public participation in the management, protection and conservation of the environment".

Thirdly, it is assumed that the local people will be willing to cooperate and work together with the park authorities and the government as well as accept responsibility in sustainable conservation of biodiversity. Investment in tourism development could be the best initial step to encourage the local community to actively participate in wildlife conservation. Lastly, funds from the government and non-Governmental organizations will be available at least to jump start the implementation process. Already, the on-going support and investment in the Roan Antelope Conservation Task Force by KWS is a sure sign of willingness and availability of funds.

8.5.2 Monitoring and data storage

One of the problems encountered in this study is lack of adequate long-term data. Ranger-based methods can be cost effective in collecting long-term research data for the roan antelope and other animals in RNP. Such methods involve training rangers and providing them with adequate equipment including field notebooks, identification field guides, pens, datasheets, binoculars and GPS enabling them to collect data during routine security patrols. This could provide cheaper long-term research data since no extra resources will be needed for data collection. However, the Ranger-based methods should be supervised and coordinated by the resident research scientist in RNP. Since the Ranger-based methods are new methods they need to be rigorously tested and compared with conventional methods to ascertain their accuracy and reliability before they are widely accepted and adopted. However, these methods have been used in a few case studies in developing countries that have found them to be cost-effective, efficient, sustainable and more relevant to the needs of wildlife managers (Brashares and Sam, 2005; Danielsen et al., 2005; Gray and Kalpers, 2005).

Yoccoz et al (2003) adds that these methods could yield reliable results as those of conventional techniques through proper training and sampling design.

Current methods being used to count animals including roan antelopes in RNP appear to be inadequate. Animals are counted using total counts in census blocks as described by Sutherland (1996). This census method was found to yield underestimates for small antelopes in Serengeti National Park, because they are small, secretive and can easily hide in tall grassland (Mduma, 1995). It also yielded flawed population estimates of antelopes for some years in RNP. For example, in some cases population estimates in September were higher or lower than those in March of the same year by more than 50%. Therefore, there is need to complement or replace this method with other better counting methods. Mduma (1995) found that two other methods were more reliable and less biased in counting the population of antelopes. These are, the total counts of known individuals and sample counts by ground line-transects as described by Buckland et al (2001). Estimation of roan antelopes is likely to be more accurate using total counts of known individuals because of the stability and permanence of roan territories, and their affinity to particular areas.

The format or system of storing data in RNP is inefficient. Research data and other information are kept raw (unsorted or unprocessed) in files that are not long lasting as evidenced by torn-out pages and missing data. This format is not easily accessible and is deemed to lead to errors and inconsistent conclusions when used by different researchers due to variability in subjective judgments when compiling the data. The best way forward is to compile the data into a permanent computer-based database that can be readily accessible in a standardized format with off-site file backups.

8.6 Recommendations for further research

This research is the first comprehensive study on the Kenyan roan antelopes and hence it will form baseline information for future studies. Due to time, data availability and financial constraints some important research topics could not be tackled by this study. These are outlined below.

The methodology for collecting roan movement and distribution data was changed from radio-tracking to ground-tracking based on recommendations from Kenya Wildlife Service (KWS). KWS argued that the use of tranquilizers and radio collars could have adverse effects on the endangered roans that may trigger the process of extinction. However, there is no scientific evidence of such claims. The use of ground-tracking for 6 months led to collection of limited diurnal movement data. During the ground-tracking fieldwork sometimes the roans could not be traced and there were claims from rangers that the roans do move out of the park into the areas of dense human settlement. Further roan movement data needs to be collected for a longer period properly through radio-tracking to cover day and night. This would provide more insight into roan movement patterns and habitat use in the park.

Habitat selection by roan antelopes was carried out at the park and home range levels. There is need for habitat selection to be carried out at a finer scale, because this study has shown that findings at these scales cannot be extrapolated to a finer scale. Further research is needed to identify particular grass and herb species preferred by the roans. This will be more useful when planning for translocation of roans to other protected areas; they must harbour sufficient amounts of the preferred plant species. The roan diet can be studied using microhistological analysis of faeces or by observational studies. Past studies on roan diet have identified several preferred plant species in West Africa (Tyowua et al., 2010; Schuette et al., 1998) and South Africa (Knoop and Owen-Smith, 2006; Perrin and Taolo, 1999; Joubert, 1976). However, most of these preferred plant species are not found in Kenya, which necessitates a diet analysis study.

The small roan population in RNP for the last two decades, coupled with the polygamous mating system of the roan antelope, is likely to have resulted in high levels of inbreeding. Guo et al (2002), asserts that when populations become very small and isolated, inbreeding is inevitable. Although, PVA simulations carried out in this study showed that inbreeding was not the cause of population decline, there is need to carry out a field-based genetic analysis to investigate thoroughly the issue of inbreeding. Levels of inbreeding and inbreeding depression in wild populations can be studied using microsatellite genetic markers that have the distinct advantage of not interfering with natural patterns of mating, dispersal and survival (Keller and Waller, 2002). Fortunately, there is an on-going study to establish the degree of inbreeding among roans in RNP by KWS in collaboration with the National Museums of Kenya.

Disease related deaths have not been reported among roans in RNP recently, but there is inadequate monitoring of roan epidemiology in RNP. A detailed study on the impact of diseases on the roan population dynamics is needed to ascertain whether or not diseases are one of the causes of the observed roan population decline in the park. The effect of diseases on roan population decline should not be ignored because a variety of diseases have been shown to cause severe population declines in African ungulates. For example, diseases such as rinderpest has caused high mortalities in buffalo and wildebeest (Owen-Smith, 2007), anthrax in roans (Pienaar, 1967), elephants and other wild ungulates (Bengis et al., 2003), and bovine tuberculosis in buffalo (Bengis et al., 2003).

Predation has been shown to be the main cause of roan population decline in Kruger National Park, South Africa (Harrington et al., 1999). Past observations in RNP have also attributed the death of roan calves to predation by hyaena and leopards (Waweru et al., 1995). The issue of predation could not be tackled by this study due to lack of data on predators. Further research is needed to investigate the role of predation on the roan population's recovery rate in RNP.

This study has identified bushmeat hunting via snares as the main cause of roan population decline. Further research should be directed towards understanding the socio-cultural, economic and political factors driving the bushmeat hunting in RNP. The roans are hunted more than other antelopes because their meat is considered a delicacy and their horns are highly valued as musical instruments and played during traditional ceremonies (KWS, 2006). Also, some unconfirmed reports from local people around RNP indicated that the roan skin is highly priced for use in traditional burial ceremonies for old people in the society.

The main problems (poaching and habitat loss and modification) facing conservation efforts in RNP are directly or indirectly caused by the surrounding local community. Past efforts by the park authorities to collaborate with the local community in wildlife conservation have not been successful. Further research is needed to understand and integrate indigenous technical knowledge into wildlife conservation and to gauge the usefulness of the perceived solutions from the local community's point of view to wildlife conservation problems.

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