The ecology and potential factors limiting the success of sable antelope in southeastern Zimbabwe: Implications for conservation

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Declaration

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Abstract

The decline of sable antelope through much of the lowveld region of Zimbabwe and South Africa has become an issue of concern for wildlife managers. On Malilangwe Wildlife Reserve (MWR) alone, sable numbers crashed from 237 animals in 1994 to only 62 by 2005. The purpose of this study was to determine the cause of the decline and the continued lack of success in the sable population. The study had three specific aims: 1) to assess the current viability of the sable population at MWR and understand the sensitivity of the population to environmental changes, 2) to gain an understanding of the space-use and habitat selection of sable at the landscape scale, and 3) to speculate on the possible causes of the decline in sable antelope numbers at MWR.

GPS collars were fitted to four sable herds at MWR and a fifth herd was monitored opportunistically over the study period. From these, life history data were collected and fed into a VORTEX population viability model to assess the current viability of the sable population at MWR. Vital rates input into the model were then manipulated, simulating the effect of natural pressures placed on the population. A sensitivity analysis was used to determine the sensitivity of the population to these natural pressures, using the long term growth rate as a relative measure of overall fitness. The results suggest the current population will remain extant but that natural pressure placed on the adult female segment of the population could have a drastic impact on the success of the sable population. The evidence indicates that the decline in sable numbers at MWR must have been driven by an increase in mortality in the adult segment of the population.

The GPS collars gave regular fixes enabling the development of a spatial pattern of home-range and habitat use over time. LoCoH was used to develop seasonal home ranges and utilization distributions for the sable herds at MWR. A multiscale approach was used to investigate habitat selection by sable over time at MWR, using a Bonferonni Z-statistic, time series graphs and Maximum Entropy modeling. Sable used much larger ranges during the early wet season than during any other season at MWR and were highly selective at the broad scale spending more than 92% of their time foraging on the nutrient rich basalt derived soils. At the finer scale sable generally chose for areas characterized by a well developed grass layer on shallow calcareous soils moving onto areas of deeper clay rich soils during the dry season and consistently made use of areas further than average from water.

Data from the collars were then used to conduct bi-monthly tick drags along the sable foraging paths to assess the level of tick challenge faced by each herd over time and this was related back to the survival rate of calves within each herd using linear regressions. The effects of predation were assessed again using the GPS collar data and a novel method of determining predation risk using motion sensor camera traps. The level of predation risk was then related back to the survival rate of each age class in the sable population. The long term effects of predation on the sable population was investigated using historical data on sable carcasses discovered and the annual rate of population decline. These were regressed against lion population numbers to determine whether any relationship existed between lion population numbers and the rate of population decline. Tick challenge had no effect on the survival of sable calves and the overall tick challenge at MWR was extremely low during the study period. Predators however seemed to have an impact on the sable population in a number of ways. Hyaena's seemed to have a major impact on the survival of sable calves, particularly during the first few weeks

of life and lion numbers showed a strong relationship with the overall rate of population decline.

Sable antelope are highly susceptible to predators and lions seem primarily to blame for driving the decline in the species at MWR. The relationship is however not entirely clear and evidence suggests that a number of variables including vegetation cover and water distribution play a role in determining the impact that predators have on sable populations.

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"Humankind has not woven the web of life. We are but one thread within it. Whatever we do to the web, we do to ourselves. All things are bound together. All things connect." Chief Seattle.

Dedication

This thesis is dedicated to three people that left this life too early. All played a unique but large part in my life and will forever live in my memories.

My Father – Phillip Johnson Capon – 14 October 1946 – 28 October 1995 My Friend – Karl Brian Stewart - 24 September 1983 - 06 May 2010 My Nephew – Kieran James O'Brien – 09 November 2007 – 27 March 2010

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1. CHAPTER 1 General Introduction

1.1 Introduction

1.1.1 Aims and objectives

The main aim of the project was to investigate the possible factors leading to the continued decline of sable antelope on Malilangwe Wildlife Reserve (MWR).

The main objectives of the study were:

- 1. To understand the population dynamics of sable antelope at MWR and assess the risk of local extinction thereof.
- 2. To investigate habitat and resource selection by sable antelope at MWR and understand how this changed over time.
- 3. To investigate the possible causes of the decline in sable antelope at MWR and provide management recommendations that would encourage growth and recovery of the sable population.

The study was taken on under request from managers at MWR who were concerned about the current trends observed in their sable population. The project formed a collaboration between the Department of Conservation Ecology and Entomology at the University of Stellenbosch and the Research and Ecology Department at MWR. The study was designed according to the anticipated outcomes requested by managers at MWR and the limitations set out by them.

1.2 Motivation for the study

Zimbabwe was once considered to be a world leader in conservation and was stated to have some of the most progressive wildlife management policies in Africa (Pinchin, 1993). Some 13.1% of its land surface had been set aside as National Parks or Protected Areas and with the addition of private conservancies this figure amounted to over 30% (Pinchin, 1993). Zimbabwe's landscape is generally characterized by wooded savannas composed of miombo woodland at higher altitudes and drier mopane and acacia woodland at lower altitudes (Child, 1995). The country boasts, taking into account its size, some of the richest diversity in Africa in terms of both flora and fauna (Child, 1995). In recent years, however, the take over of several private conservancies as a result of the government sanctioned land invasions has put enormous pressure on existing wildlife populations and marked increases in poaching have been seen throughout the country. Economic pressures, political unrest, unemployment and periods of drought have resulted in much of the population living below the poverty line, further exacerbating the pressure being placed on the remaining wildlife reserves. Problems such as these are not unique to Zimbabwe and similar patterns have been seen in other areas of Africa, where expanding human populations and competition for scarce resources has led to the destruction of habitats essential for the preservation of wildlife populations.

Zimbabwe has an especially rich diversity of megafauna (Child, 1995) and much work has been done to conserve rare species that have otherwise been declining elsewhere in Africa. These projects have largely been successful, an example being the several rhino conservancies established across the country. Despite this however, some species continue to decline notwithstanding efforts to curb the trend. Sable Antelope (*Hippotragus niger*) have been one such species, showing marked declines in numbers throughout much of its range, particularly in the lowveld regions of Zimbabwe and South Africa (Grant & van der Walt, 2000; Magome *et al.*, 2008; Goodman, 2009).

On the MWR, Booth (1980) estimated the population to be well over 200 but following the severe drought of 1991-1992, the population declined to only 40 animals (Saunders, 2009). In 1994, after the establishment of the Malilangwe Trust, some 197 sable were introduced but by 2005, numbers once again declined dramatically to only 62 individuals (Fig. 1.1) (Goodman, 2009). This trend is not unique to MWR and has been well observed and investigated in the Kruger National Park (KNP), South

Africa. Grant & Van der Walt (2000) report that there were some 2240 sable in the KNP in 1986 but numbers had declined to just over 300 individuals by 2006 (Le Roux, 2010).

Although sable remain one of Africa's best known antelope (Verster, 1992), the actual mechanisms behind the decline of the species remain a mystery. Many of the potential factors leading to the decline are confounded and Owen-smith *et al.* (2005) suggest that a number of different factors may in fact interact, resulting in the observed trends. Several hypotheses have been proposed in an attempt to explain the decline of sable antelope in Southern Africa, including competition with other grazers (Harrington *et al.*, 1999), increased predation (Grant & van der Walt, 2000; Owen-Smith *et al.*, 2005), rainfall variation (Owen-Smith *et al.*, 2005), disease (Nijhof *et al.*, 2005; Oosthuizen *et al.*, 2008) and habitat loss (Grant & van der Walt, 2000).



Figure 1.1 Shows the population trend of sable antelope on Malilangwe Wildlife Reserve between 2000 and 2010 (Malilangwe Wildlife Management Database).

1.3 Literature Review

1.3.1 Study species

The sable antelope, *Hippotragus n. niger*, was formerly widely found throughout the woody savannas of eastern and southern Africa, with an isolated population in central Angola (IUCN, 2008). Sable numbers have however shown alarming declines in the past decades (Nijhof *et al.*, 2005; Grant & van der Walt, 2000) and have been eliminated totally from many areas within their previous range, due to meat hunting, habitat loss, disease and expanding human populations (East, 1999). There are four recognized subspecies of sable antelope, namely the eastern (*Hippotragus n. roosevelti*), Zambian (*Hippotragus n. kirkii*), common or southern (*Hippotragus n. niger*) and giant or Angolan (*Hippotragus n. variani*) sable (Ansell, 1971).

In this study, the ecology and habitat selection of the common sable antelope (*Hippotragus n. niger*) was investigated including an examination into the possible factors playing a role in the decline of the subspecies at MWR. Although the study was restricted to a relatively small reserve in south-eastern Zimbabwe, it was hoped that information emanating from the project would contribute to the bigger picture relating to the decline of sable antelope in Southern Africa.

1.3.2 Population dynamics and social ecology of sable

Understanding the dynamics of populations is a crucial tool in the conservation of declining species. Studying these dynamics can provide insights into the vulnerability of different age classes within a population and provide estimates of survival and mortality rates critical to performing useful studies of population viability (Wittmer *et al.*, 2005). Studies that identify which age class survival and mortality rates are more variable and how these are likely to influence overall population size are particularly useful in understanding ungulate population dynamics (Tuljapurkar & Caswell, 1997; Gaillard *et al.*, 1998) Population Viability Analysis (PVA) is a useful tool in this regard. PVA makes use of real life history data to predict the probability of extinction of a population by projecting the population forward stochastically using a computer simulation (Brook *et al.*, 2000). PVA enables managers to simulate the effect of different scenarios on population persistence and understand the potential consequences of different management decisions (Brook *et al.*, 2000; Cancino *et al.*, 2010). Insights into the dynamics

of the sable population on MWR may therefore be the key to understanding the possible causes of decline and assessing the risk of local extinction on the reserve.

Sable antelope are a gregarious species, typically occurring in herds of 20-25 individuals (Wilson & Hirst, 1977; Skinner & Chimimba, 2005). The herds are normally composed of a dominant adult bull, adult cows, sub adult and juvenile females, young bulls (normally younger than 24 months) and calves (Bothma & van Rooyen, 2005). Sable herds display a strong social order and within each breeding herd there is an alpha or dominant female who leads the herd to feed or to water (Wilson & Hirst, 1977; Skinner & Chimimba, 2005). Territorial sable antelope bulls are aggressive and will fight with any other adult bulls that enter his territory. The territorial bull will also evict young bulls from the breeding herd when they reach about 24 months of age (Skinner & Chimimba, 2005; Bothma & van Rooyen, 2005). These young bulls then move off to form small bachelor herds until they are old enough to establish their own territory (Grobler, 1974). Parrini (2006) found that sable bulls within the Kgwasane Mountain Reserve (KMR) tended to stay with the breeding herd never leaving to form bachelor herds. Sable are a long-term polygynous species, with dominant territorial males monopolizing breeding rights over a herd of females (Wilson & Hirst, 1977; Grobler, 1980; Skinner & Chimimba, 2005). Therefore age of first reproduction in male and female sable differs markedly. Both male and female sable become sexually mature at about 2 years of age, however young bulls are prevented from breeding by territorial bulls until they are about six years of age and have managed to establish their own territory (Grobler, 1980). Sable females commonly conceive at the age of 2 years and generally calve for the first time in their third year of life (Wilson & Hirst, 1977; Grobler, 1980). Sable antelope have been reported as still being able to reproduce at over 10 years of age in the wild (Grobler, 1980).

In a sable herd it is not uncommon for each adult cow to become pregnant in the breeding season and natural population growth can be up to 20% (Bothma, 2002). In areas where conditions are suitable, sable populations have been recorded as increasing at 13% per annum (Sekulic, 1981; Parrini, 2006). Grobler (1980) recorded a conception rate of 97% for sable in the Rhodes Matopos National Park and states that conception rates for sable cows during the study period (1971-1978) were consistently high but that calf survival to 6 months was extremely variable. In February 1978, Grobler (1981) states that 18 out of 19 sable cows from one herd were expected to give birth but by March 1978 there were only 7 surviving calves. This indicates a calf mortality rate of 61%. Bothma (2002) mentions that mortality in sable calves younger than one year can be as high as 64%, suggesting that calf mortality may be a

key factor in explaining the decline of the species. In the Kruger National Park, sable numbers have been on the decline since the early 1980's and Nicholls *et al.* (1996) reports a negative growth rate of - 5.4% for sable between 1983 and 1992. They state that the sable population within the KNP is under serious risk of local extinction within the next 100 years.

MWR currently has a total of 77 sable antelope, a drastic decrease from the 197 that were introduced to the existing population of 40 between 1994 and 1997 (Goodman, 2009). There are five herds on the reserve ranging in size from 11-18 animals. Although herd numbers on MWR do fall below the typical herd size of 20-30 individuals, as stated in many mammal guides, they do fall within and around the average of 15.2 suggested by Du Toit (1992), which he suggests represents the minimum viable herd size. The author further suggests that a minimum population of 50 breeding individuals is needed to prevent an inbreeding depression. In KMR, where sable populations are reportedly doing well, the two herds studied numbered 70 individuals in total (Parrini, 2006), suggesting herds there are much larger than those on MWR.

1.3.3 Ecology and habitat selection

Sable Antelope can be described as an ecotonal species, making use of the woodland-grassland ecotone and are highly selective (Bothma, 2002; Estes & Estes, 1974). They are generally found in fairly sparse open woodland and are selective of dense medium – tall grass swards, generally avoiding areas of heavy grazing pressure (Bothma, 2002; Traill, 2003). Sable generally select leafy, palatable grasses with the most important species reported as being *Chrysopogon serrulatus*, *Panicum maximum*, *Heteropogon contortus* and *Themeda triandra* (Magome *et al.*, 2008). Parrini (2006) suggests that, during the dry season, wetland areas form a key resource but notes that sable also fed on hill slopes and plateaus, provided these retained green grass during this period. Many studies have noted a shift in range of sable during the late dry season (Parrini, 2006), often grazing further away from water sources than other grazers (Traill, 2003; Rahimi & Owen-Smith, 2007). This could be to reduce competition from other grazers and take advantage of isolated resource patches. Sable generally select for a high crude protein and low fibre diet, often making use of recently burnt patches with new grass growth, particularly during the dry season (Parrini, 2006; Magome *et al.*, 2008). Magome *et al.* (2008) noted that feacal protein levels remained high in sable in the Pilanesburg Game Reserve even through the dry season, never dropping below 6.6%. In Kgwasane Mountain Reserve fecal protein levels in sable were

7.4% when feeding on unburnt areas and as high as 11.6% when utilizing green regrowth from burns (Parrini, 2006).

There have been conflicting reports on the dependence of sable on permanent water sources. Many field guides and older scientific studies suggest that sable antelope are highly water dependent, relying on water every day and never moving further than 2,5km from a permanent water source (Skinner & Chimimba, 2005; du Toit, 1992). However, more recent studies on habitat selection and range studies utilizing GPS collars have suggested that herds in the Kruger National Park may only drink every 2-3 days and may move up to 7km from water sources, particularly during the dry season (Rahimi & Owen-Smith, 2007).

Wilson and Hirst (1977) noted that sable home ranges are heavily influenced by a number of factors including the local terrain, vegetation types, the availability of water as well as intra-specific factors. Estimated home range sizes for sable herds range from 2.8 km² (Grobler, 1974) in the Matopos National Park, Zimbabwe to 27.3 km² (Magome, 1991) in the Pilanesberg National Park, South Africa. The variation in home range sizes published for Sable again could be due to a number of factors including advancements in technology, use of different home range estimation techniques and differing environmental conditions.

1.3.4 Possible causes of decline

PREDATION

A number of studies have been undertaken on the prey preference of various large predators in Africa, however many of the studies have been conducted in areas with either very few or no sable. It is therefore difficult to quantify the role that predation may play in the decline of the species. Coupled with this, prey preference studies have many downfalls in that they often assume a uniform distribution of both predator and prey species, which in nature is not realistic. Hayward and Kerley (2005) suggest lions neither selected nor avoided sable but that they preyed on sable relative to their abundance in the environment. Studies indicate that, based on Jacob's index values, leopard and hyaena avoided sable as prey and suggest that both predators may only opportunistically prey on young sable (Hayward *et al.*, 2006; Hayward, 2006). Many studies have speculated that predation may be a key factor in explaining the decline of the species in the Kruger National Park (Grant & van der Walt, 2000; Owen-Smith *et al.*,

2005). This goes against suggestions made by Wilson and Hirst (1977), who said that they found no evidence to suggest predation is a limiting factor in the success of sable populations. Owen-smith *et al.* (2005) suggest that the provision of artificial water points led to an increase of prey species within the range of sable, subsequently causing an increase in the number of lions in the area and thus an elevated predation risk.

Several studies have documented the effects that predators can have on prey numbers, particularly in limiting populations of low-density ungulates (Harrington *et al.*, 1999). High-density prey species on the other hand seem to be regulated more by food abundance and not by predation as demonstrated by Sinclair *et al.* (1985) in the Serengeti system. The level of predation risk faced by a species is determined by a suite of factors including the density of different predator species, the average body size of the prey species concerned, average herd size, habitat selection and its relative abundance in relation to other prey species (Hayward & Kerley, 2005; Hayward *et al.*, 2006).

The use of predation refuges forms an important part of any natural system allowing a species to effectively reduce the risk of being preyed upon (Sih, 1987). Refuges can be spatial, temporal or relating to behavioral adjustments or strategies employed by a particular prey species in order to avoid being killed. Manipulation of natural systems such as provision of artificial water-points, careless burning regimes and culling of populations can alter refuge use and availability, potentially causing an imbalance in the complex predator-prey relationships. These imbalances could be manifested in the form of a loss of biodiversity, declines in either predator or prey numbers or massive increases in predator or prey numbers and a suite of knock-on effects.

Тіскз

Currently, very little work has been undertaken investigating the potential effects of diseases and parasites on sable (Meltzer, 1992; Verster, 1992). Some 60 parasites have been recorded from Sable, however little information exists on the effects of these parasites (Verster, 1992). For the purposes of this study we will focus on the role that ticks may play in the decline of Sable on MWR. Sable Antelope are susceptible to tick borne parasites such as *Theileria*, *Babesia* and *Anaplasma* (Grobler, 1981; Nijhof *et al.*, 2005; Oosthuizen *et al.*, 2008) but it is suggested that they often become subclinically infected as calves and recover to become immune carriers (Meltzer, 1992; Fivaz, 2009). This being said, there is evidence that some individuals may become infected with potentially lethal strains of *Theirelia* as calves, leading to mortality at a young age (Wilson *et al.*, 1974; Meltzer, 1992; Fivaz,

2009). This has been suggested as possibly one of the main contributors to the decline of the species in Southern Africa (Nijhof et al., 2005), suggesting that calf mortality could be a 'key factor' in explaining the decline of the species over the past two decades. Wilson et al. (1974) recorded a mortality rate of 44% in Sable Antelope in the Percy Fyfe Nature Reserve in South Africa, with 62% of these mortalities recorded in animals less than 12 weeks of age. Coupled with this, Norval (1977) proposes that confining animals within relatively small wildlife reserves can lead to a build up of large tick populations, which in turn would increase the potential of infection of young calves by *Theileria*infected ticks as well as exposing animals to tick toxicosis. Nijhof et al. (2005) also suggest that other Bovidae species have the potential to form a natural reservoir of Theileria sp. (sable), thereby potentially limiting the success of sable antelope found confined within the same areas. Ticks and tick borne diseases has been relatively overlooked thus far as playing a key role in the decline of sable and many studies suggest that stress may play an integral part in the relationship between ticks, tick-borne diseases and mortality events. Grobler (1981) found that parasitism (both internal and external) was indicated as the main cause of mortality in sable antelope in Matopos and goes on to state that ticks undoubtedly played a major role in the mortality of sable within his study area. He suggests that tick infestations often resulted in extreme anemia leading to mortalities in the early wet season due to poor physical condition following the food shortages in the dry season and the increase in ticks brought on by optimal conditions. Grobler (1981) suggests that tick infestation was the most likely cause of the extremely high neonatal mortality. He also found a negative correlation between calf survival and the preceding annual precipitation, which one could speculate may be due to the high parasite load associated with the subsequent optimal conditions.

1.4 Study Area

The study site is located on the MWR in south-eastern Zimbabwe. The reserve is owned and run by The Malilangwe Trust. This section describes the location and physical geography of the area, as well as its climate and management history.

1.4.1 Location

The MWR stretches some 39 378 ha in extent and is located in the south-eastern lowveld of Zimbabwe. The reserve is bound on the west by the Chipimbi, Chiredzi and Runde Rivers respectively. The East and South of the reserve are bordered by the Chizvirizvi Communal Land and Gonarezhou National Park and by resettlement land to the north (Figure 2.1).

The entire property is fenced with a 2.1m high electrified fence except for the western portion of the property along the Chiredzi River which opens into the Hippo Valley Game Section. Along the southern portion of the property bordering the Gonarezhou National Park the fence has been poorly maintained, thereby allowing some movement of game between the reserve and the National Park. However these movements are carefully monitored by the Malilangwe Scout Force on their daily boundary patrols.



Figure 1.2 Map showing the location of Malilangwe Wildlife Reserve.

1.4.2 History & Management

A large portion of the current MWR is made up of the Lone Star Ranch, a property pioneered in 1949 by Mr. Ray Sparrow. The ranch was stocked with cattle and remained this way until 1985. After 1985, hunting safaris, small-scale agriculture, live game sales and photographic safaris became the dominant forms of land use.

In 1994, Lone Star Ranch and the neighboring Maranatha Ranch were purchased by the Malilangwe Trust, a donor-funded, non-profit organization aiming to conserve biological diversity and improve

social welfare through community development and employment. This paved the way for the creation of the MWR. Today the sole form of land-use on the reserve is ecotourism.

In line with the principles of the trust, several species that had either become locally extinct or had declined to critical levels were re-introduced to the reserve including black and white rhino, lichtenstein's hartebeest, sable and roan antelope. Since 1994 most species have experienced continued success, however some species including sable and roan antelope have been a cause for concern.

Since the 1950's, fire had been completely excluded from the landscape and was only reinstated as a management tool post the creation of the MWR in 1994. Today, a portion of the property is burnt annually using semi-controlled burns, the portion chosen being determined by a combination of factors including time since last burn, rainfall and state of the vegetation.

As a result of previous land practices on Lone Star and Maranatha, several artificial water points had been created over the property. Many of these water points have since been closed and the average distance from water during the height of the dry season is currently about 2 km.

1.4.3 Climate

RAINFALL

The estimated annual average, measured at the MWR Head Quarters from July to June over a 58 year period (1951-2009), was 562mm. The rain follows a distinctive seasonal pattern with approximately 88% falling in the summer months, between October and March (Figure 2.2). Periods of drizzle and overcast skies, however, are not uncommon during the winter.

A clear rainfall gradient exists over the property running from north-east to south-west. The northeastern side of the property receives an annual average estimate of 590 mm, with the south-western side only receiving approximately 530 mm. There is also high inter-annual variation in rainfall with a coefficient of variance of 35%. Severe droughts have consistently had an impact on the area and occur in a roughly decadal cycle (1972, 1982, 1986, 1991, 2001 & 2009).



Figure 1.3 Chart showing mean monthly rainfall calculated from a 59 year record (1951-2010), at Malilangwe Head Quarters.

TEMPERATURE

The climate is characterized by three semi-distinct seasons, a hot-wet season from November to March, a cool-dry season from April to August and a hot-dry season from September to October. The average monthly maximum ranges from 33.9°C in summer (November) to 24.3°C in winter (June), with the average monthly minimums ranging from 23.5°C in summer (December) to 13.0°C in winter (July). Summers are therefore extremely hot with winters remaining relatively dry and mild (Figure 2.3).



Figure 1.4 Average monthly minimum and maximum temperatures for MWR, calculated over a 9 year period (2001-2010).

1.4.4 Geology & Soils

The reserve has seven geological types, namely acid and basic gneiss, dolerite, shales and mudstone, grit, alluvium, stormberg sandstone and Jurassic Basalt (Figure 2.4). The most prominent feature of MWR's topography is the range of stormberg sandstone hills running from east to west across the northern portion of the property.

North of the Malilangwe Range the geology is dominated by acid and basic gneiss dotted with several dolerite dykes. The area is characterized by a gently undulating topology with coarse grained, well drained sandy soils. Immediately south of the Malilangwe Range, soils are dominated by deep, well drained sands, derived from the stormberg sandstone. Further south, the area is characterized by a flat topology dominated by Jurassic Basalt derived from the Upper Karroo system (Clegg, 2010). The soils on the basalt flats range from deep heavy clays to fairly shallow sandy loams. The basalt derived soils are generally fertile but water is held strongly by the clays and resists uptake by plants, resulting in reduced woody plant growth and a good grass cover (Chawanji, 2000).

To the west of the Malilangwe Range, the area is dominated by a mosaic of grits, dolerite, shales and mudstone. Along the Chiredzi and Runde Rivers to the west and the Nyamasikana River in the North, the geology is dominated by alluvial deposits. The alluviums provide ample moisture and nutrients, enabling good woody plant growth and limited grass cover.



Figure 1.5 Geological map of MWR (Clegg, 2010).

1.4.5 Relief & Drainage

There is a general sloping from north-east to south-west across the property, ranging from 510 m above mean sea level (amsl) on Hunyugwe in the Malilangwe Range down to 300 m amsl at the Chiredzi-Runde confluence.

The north, west and central areas of the reserve are drained by the Chipimbi, Gananda and Nyamasikana Rivers, which all flow into the Chiredzi River. The southern and eastern areas of the reserve are drained by the Nyamsaan, Mulovele, Mahande and Chiloveka Rivers, all draining into the Runde River. These tributaries are predominantly ephemeral with the Chiredzi and Runde Rivers being the only rivers with a permanent supply of surface water all year round.

1.4.6 Vegetation

MWR is generally characterized by open savanna woodland dominated by *Colophospermum mopane*. The Malilangwe Range is dominated by *Brachystegia glaucescens* and *Julbernardia globiflora* with the sandstone derived flats being characterized by mixed broadleaf woodland made up by species such as *Pteleopsis myrtifolia*, *Albizia petersiana* and *Lannea schweinfurthii*. The grass layer on MWR is mostly dominated by species such as *Urochloa mossambicensis*, *Digitaria eriantha*, *Aristidia spp.* and *Heteropogon contortus*. Thirty eight distinct vegetation types have been identified by Clegg (2010) in his description of the vegetation units on MWR (Figure 2.5). The classification took into account the composition of both the woody and herbaceous layers, the structure of the woody component and the topo-edaphic factors influencing the plant communities. For a detailed description of MWR's vegetation and its classification see Clegg (2010).



Figure 1.6 Vegetation map showing the 39 vegetation types found on MWR (Clegg, 2010).

1.5 Study Design & Thesis Structure

The study was conducted over a period of one year from June 2009 until the end of May 2010. Although the actual study period only began in June 2009, the herds were under observation from March 2009 thus allowing for the inclusion of population data from two calving seasons.

An adult female sable from four of the five herds on MWR was fitted with a GPS/VHF collar (Telemetry Solutions, California) in March 2009. Each individual was immobilized from the air by helicopter and blood and tick samples taken before the collar was fitted and an antidote was administered. The collars ensured that animals could be located at any time for observation using the VHF signal emitted form the collar. The collars were also programmed to take a GPS position every 2 hours day and night for the duration of the study.

The four collared herds all inhabited the extreme eastern and southern regions of the property. The Manyoka herd occupied a woodland habitat in the north-eastern part of MWR close to the start of the Malilangwe range. The Benzi herd inhabited a more open woodland habitat along the eastern boundary of the property and often ventured northwards close to the range of the Manyoka herd. The Chavagwiza herd dominated in the southern portion of the property bordering the Gonarezhou National Park. The area is characterized by a drier woodland habitat interspersed with several small drainage lines. The Chivoko herd inhabited an area fairly close to the Chiredzi River, venturing eastwards along the Mahande drainage line reaching as far north as the Mulovele stream. The area is generally dominated by open woodland habitat interspersed with drainage lines and contains some riverine habitat along the Chiredzi River.

During observations, herds were studied from a parked vehicle or on foot using 10 x 42 binoculars. Downloads from the collars were conducted during observation times every 15 days via a wireless signal using a Hewlett Packard personal digital assistant (PDA). The study design was developed using GIS software.

Chapter 2 of the thesis covers the population ecology of the sable at MWR as well as predicting future trends and persistence of the population under different scenarios. The viability of the sable population on MWR was modeled using VORTEX 9.99b software (Lacy *et al.*, 2009) developed by the

Chicago Zoological Society. Data for the model were developed from observations of the sable population between 2009 and 2010 and from historical datasets available at MWR. The models were calibrated and tested against the sable population trend before projecting the population forward under a number of hypothetical scenarios.

Chapter 3 studies space use and habitat selection of sable on MWR at the landscape scale using the local nearest-neighbor convex-hull method described by Getz and Wilmers (2004) to construct home ranges for each herd over time, analyzing how seasonal changes influenced their ranges and area. An IDRISI GIS (Eastman, 2001) was used to study habitat selection by sable, quantifying sable's use of resources in relation to their availability in the landscape. Selection was analyzed at a broad scale using the Neu method (Neu *et al.*, 1974) before focusing on selection at a finer scale. Finally, Maximum Entropy modeling (Phillips *et al.*, 2006) was used to show the importance of each environmental variable and how they contributed to predicted habitat suitability for sable.

Chapter 4 investigates the possible causes of the decline of sable at MWR. Predation and tick challenge were theorized to be the possible causes of the decline and the study looked to unravel these two factors. Tick drags were conducted every 15 days following foraging paths developed from data downloaded off the GPS collars. This gave us an idea of the potential tick challenge faced by each herd over time. Historic data on population trends, predator densities and predation risk were used to establish whether there was any evidence to suggest that predators may be to blame. A predator survey was also conducted in order to predict the potential risk of predation spatially over Malilangwe. These factors were then related back to the survival rates observed for each herd.

Chapter 5, the final chapter in the thesis, draws on the discussions from each of the previous chapters in order to develop ideas as to what factors may be limiting the success of sable at MWR. The chapter contains proposed management recommendations for the species and covers future potential avenues for research. The potential shortfalls of the study are also discussed and where possible, solutions or alternatives are suggested that may help with similar future studies.

The thesis has been prepared in such a way that each chapter represents a draft manuscript. This design allowed for a clear and concise presentation of the study as a whole.

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2. CHAPTER 2 Population ecology & persistence of sable antelope (*Hippotragus niger*) on Malilangwe Wildlife Reserve, Zimbabwe

2.1 Introduction

Crisis management is a common element of conservation biology (Begon *et al.*, 1996) because small or declining populations often require urgent action to prevent extinctions. Small or declining populations are particularly vulnerable to extirpation because they are governed by a high level of insecurity due to demographic and environmental stochasticity and spatial uncertainty (Begon *et al.*, 1996). Grant and van der Walt (2000) explain that at low densities populations are particularly at risk of extinction and any mortality in the population can be disastrous. Further, it has been shown that at low densities, stochastic events can wipe out small and declining populations altogether (Ginsberg *et al.*, 1995).

Past studies have focused on identifying factors that influence population abundance but less effort has focused on determining how age class survival rates may affect population dynamics (Gaillard et al., 1998). Studies of population dynamics can often give insights into the possible causes of decline by identifying areas of breakdown in recruitment. They can also provide a better understanding of population trends and provide vital rates crucial to accurate viability analyses. Population viability analysis (PVA) is a very useful tool in predicting future population sizes and assessing viability under a range of management scenarios (Brook et al., 2000). PVA makes use of real life-history data of a species or population to train the model and project the future population utilizing stochastic variation in demography (Boyce, 1992; Brook et al., 2000). Due to their long generation time, large mammals were often excluded from population ecology studies. Gaillard et al. (1998) suggest however that large mammals make ideal subjects for population studies because they can readily be distinguished into discrete age classes. This allows for accurate estimation of age-specific vital rates, an important component of any PVA. The low density of occurrence and strict seasonality of reproduction in sable antelope (Hippotragus niger) makes them ideal subjects for population studies and PVA may be a very useful tool in assessing the viability of isolated populations such as that on Malilangwe Wildlife Reserve (MWR). Sable antelope are a long-term polygynous species, with dominant territorial males monopolizing breeding rights over a herd of females within his territory (Wilson & Hirst, 1977;
Grobler, 1980b; Skinner & Chimimba, 2005). Consequently age of first reproduction in male and female sable differs markedly. Both male and female sable become sexually mature at about 2 years of age, however young bulls are prevented from breeding until they are able to establish a territory of their own, usually at about six years of age (Grobler, 1980b). Sable females commonly conceive at the age of 2 years and generally calve down for the first time in their third year of life (Wilson & Hirst, 1977; Grobler, 1980b). Sable antelope have been reported as still being able to reproduce at over 10 years old in the wild (Grobler, 1980b).

The population of sable antelope on MWR in the south-eastern lowveld of Zimbabwe declined from over 200 animals in 1994 to only 62 by 2005. This was followed by a period of relative recovery where the population increased to 77 by 2010. This trend is not unique to Malilangwe and is similar to that reported for sable in the Kruger National Park (KNP), South Africa. Grant and Van der Walt (2000) note that the sable population in the KNP declined from 2240 in 1986 to only 505 by 1999. A number of hypotheses have been put forward to explain the decline including competition with other herbivores (Harrington *et al.*, 1999), increased predation (Grant & van der Walt, 2000; Owen-Smith *et al.*, 2005), rainfall variation (Owen-Smith *et al.*, 2005), disease (Nijhof *et al.*, 2005; Oosthuizen *et al.*, 2008) and habitat loss (Grant & van der Walt, 2000). An understanding of the population dynamics of sable on MWR may give insights into the factors responsible for the decline and could in turn, help to formulate a mitigating management strategy.

The objectives of this chapter were: i) to understand the dynamics of the sable population on MWR and ii) to assess its future viability. By gaining an understanding of the population's dynamics, it may be possible to identify areas of breakdown in recruitment and the effect these had on overall growth. A PVA was used to model the viability of the current population under a number of management scenarios and the PVA was further applied to a sensitivity analysis of the overall long-term population growth to determine variability in age-class survival.

2.2 Methods

2.2.1 Study Site

The MWR (39 378 ha) is located in the south-eastern lowveld of Zimbabwe. The reserve in bordered by the Gonarezhou National Park to the south, the Hippo Valley Game Section to the west and by communal land to the north and east (Fig. 2.1). The area has three distinct seasons: a hot wet season from November to March, a cool dry season from May to August and a hot dry season from September to October. The long-term average annual rainfall for the area is 562 mm measured at Malilangwe Headquarters from 1951 to 2009. During the 2009 to 2010 season, MWR received 552 mm of rainfall and the average monthly maximum and minimum temperatures recorded were 33.9°C in November and 13°C in July, respectively. Much of the reserve is dominated by a variety of open *Cholophospermum mopane* woodland with the Malilangwe sandstone range being characterized mostly by *Brachystegia* woodlands. The property has been classified into 38 vegetation types based on the species composition of both the woody and herbaceous layers, the structure of the woody component and the ecological factors that influence the plant communities (Clegg, 2010a).



Figure 2.1 Map showing the location of MWR.

2.2.2 Field Data Collection

Data on the population structure of sable antelope at MWR were collected between March 2009 and January 2011. To facilitate this, an adult female from four of the sable herds at MWR was immobilized and fitted with a GPS/VHF collar (Telemetry Solutions, California). A fifth herd, the only remaining herd on MWR, was monitored opportunistically over the study period, allowing us to ensure all sable individuals except for itinerant males were accounted for. The VHF signal emitted by the collars was used to locate each herd every three days. On locating a herd, a total count was made, followed where possible, by an age-sex specific count. Individuals were assigned to either male adult (6+ years), female adult (3+ years), sub-adult (2-3 years), yearling (1-2 years) and juvenile (0-1 year) age classes, according to Grobler (1980a) who suggests the use of a combination of horn characteristics and physical appearance for classification. By combining data from the counts of each herd, changes in the number of animals in each age class were recorded over the study period. In most cases, all four collared herds were seen in one day and the fifth herd was encountered at least once every fortnight. For all the female age-classes and the male juvenile and yearling age-classes, if an individual disappeared for more than a month it was assumed dead. If the individual later returned to the herd, the assumed mortality was reversed and the animal was placed back into the population records. It was not considered entirely necessary to recognize each individual sable since the entire population was being monitored over the study period. During the wet season sable herds often split up into smaller units but in nearly all cases reliable counts were achieved at least twice per month. This provided a continuous data set for the entire study period, March 2009 to January 2011, covering two calving seasons. These demographic data were then used to estimate vital rates (see below) and develop a baseline for the PVA.

Age class mortality rates :

Age-specific mortality rates for sable were calculated for each annual cycle of the study period using population data gathered during the fieldwork phase of the study, as described above. The start and end of the annual cycle was taken as April and January respectively because February to March is the calving season for sable at MWR. This meant that by April a new crop of calves would emerge pushing existing animals into the next age-class. Data derived from life tables were used to calculate age-class mortality rates using the formula developed from methods described in Caughley (1966):

$$Qc = [\{N_{\chi} - N_{\chi+1}\} / N_{\chi} * 100]$$

Where Qc is the mortality rate of age class c, N_{χ} is the number of individuals in age class c at time χ and $N_{\chi+1}$ is the number of individuals still alive in age class c at time χ_{+1} . This method of deriving mortality rates was employed for all but the juvenile age-class. The mortality rate for the juvenile ageclass was calculated by dividing the number of calves alive at the end of the annual cycle by 0.96 times the number of adult females in the herd at the beginning of the cycle and subtracting this value from one. This figure was then multiplied by 100 to convert the mortality rate into a percentage. The value of 0.96 was derived from observations made from sable antelope at MWR during the 2009 and 2010 breeding seasons, where 96% of adult females fell pregnant and were assumed to give birth to a healthy calf. Pregnancy was estimated somewhat subjectively following Grobler (1980b), who used the shape of the stomach and presence of a bulging udder to determine pregnancy. In all but the adult age-class, no distinction in mortality rate was made between male and female sable. At the younger stages it was not considered necessary as both males and females stay within the herd and in theory face the same risk of mortality. Determining a mortality rate for sub-adult males was more difficult because they often leave the herd making it impossible to monitor them regularly. The same mortality estimates developed for sub-adult female sable were therefore used for sub-adult males, possibly a rather conservative estimate for the part of sub-adult males.

2.2.4 The PVA Model

For the analysis and simulation of the PVA, VORTEX version 9.99b was used. (Lacy *et al.*, 2009). The model was developed to stochastically simulate the risk of extinction faced by a species. The VORTEX model takes into account a description of the species reproduction system and reproductive rates, a specified age structure, age specific mortality rates, catastrophic events, demographic and environmental stochasticity, density dependence and options for the harvest and augmentation of the population.

Assessing the viability of the sable population at MWR using VORTEX involved a stepwise process. The first stage entailed calibrating the model and replicating the historical trend of the population. An analysis of the historical population trend revealed two distinct periods. The first was the declining period between 2000 and 2005 and the second, the increasing period between 2005 and 2010. Accordingly, the calibration of the population model was divided into these two distinct periods. The second stage of the process involved projecting the population forward under a number of different

scenarios using data developed during the calibration of the model. Baseline settings used in the model were as follows:

Scenario Settings:

Although five separate sable herds exist on MWR, the reserve is essentially a closed system and therefore MWR's sable were described as a single population. During the calibration process, the PVA was simulated 500 times over two five year periods, from 2000 to 2005 and from 2005 to 2010. Following calibration, the model was again simulated 500 times for a period of 100 years in each of the subsequent scenarios. This enabled predictions of the future trends in the sable population under a number of theoretical circumstances.

REPRODUCTION SYSTEM, AGE OF FIRST REPRODUCTION AND LONGEVITY:

Age of first reproduction in the VORTEX model was set at three and six years old for females and males respectively. Although both male and female sable become sexually mature at about 2 years of age, young bulls are prevented from breeding by territorial bulls until they are about six years of age and have managed to establish their own territory (Grobler, 1980). Sable females commonly conceive at the age of 2 years and generally calve for the first time in their third year of life (Wilson & Hirst, 1977; Grobler, 1980). Based on personal observations at MWR and discussions with captive breeders, under natural conditions of predation, disease and environmental variability, the maximum age of reproduction in sable was set at 12 years of age..

REPRODUCTION RATE:

In the study, it was assumed from field observations, that 96% of the adult females in the population would fall pregnant each year and each would produce a single calf. From observations made over two calving seasons at MWR, the calf sex ratio at birth was estimated at 1:1.

CATASTROPHIC EVENTS:

Catastrophic events were not included in this PVA.

INITIAL POPULATION:

Data on the size of the sable population (Fig. 2.2) in 2000 and 2005 on MWR used in calibrating the model were taken from the annual aerial census data conducted by helicopter between 2000 and 2010 (Goodman, 2009). As the age specific population structure was unknown in both 2000 and 2005, the

model was run using a stable age distribution in both scenarios to test the baseline data and calibrate the model. Once calibrated, the model was simulated using the age specific population structure (Appendix I) determined at the beginning of the study period in March 2009. The age of each individual was determined subjectively following guidelines set out by Grobler (1980a). On encountering each herd, photos were taken of the group allowing us time to scrutinise each individual and divide the population into distinct yearly age classes based on body size, horn shape and size, secondary growth and the number of annulations.

CARRYING CAPACITY (K):

A value of 200 was used in the PVA as a measure of carrying capacity (K) on MWR and was taken from historical population estimates made by Booth (1980). It was not considered essential to use an entirely precise figure for K as the purpose of this study was to assess the risk of extinction of the current population and to assess the trend of the population under a number of different scenarios, rather than being concerned with actual figures for final population size after 100 years.

SUPPLEMENTATION AND HARVEST:

An introduction of a further 30 sable is planned for 2011, the first supplementation of the population since 1994. The population model was run using current population estimates as well as testing the effect of boosting the population with a further 30 individuals (10 adult females; 5 sub-adult males; 5 sub-adult females; 5 juvenile males and 5 juvenile females). No harvest of the sable population was included in the PVA.

In the VORTEX model, standard deviation in vital rates or carrying capacity due to environmental variance was stated as zero in all cases. Although it was recognized that environmental variation may well cause year to year variation in survival, no data were available on the actual effect of this variation. It was therefore decided not to include this effect, but rather to work with a relatively simplified version of the model. Table 2.1 below shows a summary of those baseline data input for each scenario of the VORTEX model.

2.2.5 Model Scenarios

Vital rates used in the VORTEX model were manipulated to simulate the effect that long-term changes in survival of different age classes could have on the population trend. The VORTEX PVA model simulated a number of environmental conditions. In scenario 1, the current conditions using vital

rates recorded over the study period were simulated and these were tested against the trend observed between 2005 and 2010. Historical data from scout patrol reports on sable carcasses were then used to estimate a factoring for the adjustment of current mortality estimates for the second scenario. Five times as many sable carcasses were found by scouts on patrol during the period 2000 to 2005 than during 2005 to 2010, despite an even patrol effort between years. Of the carcasses discovered, 88% were from the adult and sub-adult age classes, hence mortality rates for only the adult and sub-adult age classes were increased by a factor of 5. It was impossible to estimate a factoring for the juvenile age class as juvenile carcasses are notoriously difficult to find often being completely eaten leaving no trace (Owen-Smith & Mills, 2008). The new vital rates developed from the factoring process were then tested in the model against the observed trend between 2000 and 2005. In Scenarios 3 and 4, the population was projected forward by 100 years using the vital rates derived for scenarios 1 and 2. Additionally, in scenarios 3 and 4, the effect of augmenting the sable population with 30 individuals was simulated. In the final scenarios, adult and juvenile survival rates were each reduced by 5% and 10% in turn. This simulated the effect that an increase in mortality in each age class would have on the overall population trend.

2.2.6 Sensitivity Analysis

In the sensitivity analysis, the VORTEX model was run varying survival of each age class in turn whilst keeping all others at their average value. The percentage change in survival rate for each age class was plotted against the VORTEX output value of mean long-term population growth rate (r). This allowed the determination of the sensitivity of the population growth to changes in survival of each age class.

Table 2.1 Summary of baseline data used in the VORTEX model under various sce	enarios
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PARAMETER	Scenario 1: Calibration 2005-2010	Scenario 2: Calibration 2000-2005	Scenario 3	Scenario 4	Scenario 5	Scenario 6
Number of iterations	500	500	500	500	500	500
Number of years	5	5	100	100	100	100
Age of first offspring - F (years)	3	3	3	3	3	3
Age of first offspring - M (years)	6	6	6	6	6	6
Maximum age of reproduction (years)	12	12	12	12	12	12
Maximum broods per year	1	1	1	1	1	1
Offspring per brood	1	1	1	1	1	1
% Adult females breeding	96	96	96	96	96	96
% Adult males breeding	29	29	29	29	29	29
Female mortality from age 0 - 1 years	57	57	57	57	57	60.1 ; 62.2
Female mortality from age 1 - 2 years	6	6	6	6	6	6
Female mortality from age 2 - 3 years	8	40	8	40	8	8
Mortality of females older than 3 years	4	20	4	20	8.8;13.6	4
Male mortality from age 0 - 1 years	57	57	57	57	57	60.1 ; 62.2
Male mortality from age 1 - 2 years	6	6	6	6	6	6
Male mortality from age 2 - 3 years	8	40	8	40	8	8
Mortality of males older than 3 years	9	45	9	45	13.5 ; 18.1	9
Initial Population Size	62	110	77	77	77	77
Carrying Capacity (K)	200	200	200	200	200	200
Supplementation	0	0	$0^{a}; 30^{b}$	$0^{a}; 30^{b}$	0	0

^a No augmentation of the population.

^b Augmentation of the population by 30 individuals (10 Adult Females, 5 Sub-adult females, 5 Sub-adult Males, 5 Juvenile Females & 5 Juvenile Males).

2.3 Results

DEMOGRAPHIC PARAMETER ESTIMATION, POPULATION SIZE AND REPRODUCTIVE RATE:

Demographic parameters were calculated from the field data collected over the entire study period (Table 1). In general, mortality rates (MR) were considered low for all but the juvenile age class (MR = 57%). Adult female sable had the lowest mortality rate of all the age classes (MR = 4%) followed by the yearling age class (MR = 6%). Adult male mortality rate was more than double that of adult females at 9% and this was reflected in the sable population structure at MWR. The historical trend in the sable population at MWR revealed a period of sharp decline between 2000 and 2005, followed by a recovery between 2005 and 2010 (Figure 2.2). Between 2000 and 2005, the sable population declined from 110 individuals to only 62. The population then began to stabilise and had grown to 77 individuals by 2010. During the 2009-2010 breeding season, 21 out of 22 adult females were pregnant and due to give birth in March 2010. By April 2010 there were only nine surviving calves. A further three calves, all from the same herd, were seen soon after birth and all seemed healthy. This particular herd had no calves accompanying the adults by May 2010 suggesting that many more calves may have been born healthy but perished during the calf hiding phase.



Figure 2.2 The historical trend in the sable population at MWR between 2000 and 2010. Evident are two distinct trends in the population between 2000 and 2005 and between 2005 and 2010.

REPLICATING THE HISTORICAL POPULATION TREND:

Results from the overall training and testing of the model proved highly comparable with that of the observed population trend (Figure 2.3). During the 5 year period, 2000 to 2005, the modelled population declined from a total of 110 individuals down to only 61 by 2005. This was very similar to observed trends which showed a decline from the same initial population to only 62 individuals over the same period. VORTEX predicted a growth rate of -0.1209 (SD = 0.0777) and a probability of extinction within the 5 years of 0.



Figure 2.3 Modelled versus observed sable population trend between 2000 and 2005. Error bars represent 95% confidence limits set out by the modelled population.

The modelled population projected between 2005 and 2010 tracked the observed trend closely (Fig. 2.4). The modelled population increased from an initial population of 62 individuals to 79 by 2010. Similarly the observed population increased from 62 to 77 over the same period, falling well within the 95% confidence limits set by the modelled population. The modelled and observed populations increased at average rates of 4.8% (SD = 5.02) and 4.95% per year respectively.



Figure 2.4 Modelled versus observed sable population trend between 2005 and 2010. Error bars represent 95% confidence limits set out by the modelled population.

FUTURE POPULATION VIABILITY:

Using the vital rates estimated for the period 2000 to 2005, the modelled population is predicted to decline sharply at an overall rate of 16.7% (Figure 2.5), with extinction predicted after just 18 years. Augmenting the population with a further 30 sable does not curb this trend and the sable population is predicted to remain extant on MWR for only the next 22 years. The addition of 30 sable to the population slows the decline slightly to 16.1% but there remains no chance of recovery for the population under these circumstances.

Under the current circumstances, using vital rates estimated for the period 2005 to 2010, the sable population is predicted to increase steadily at a rate of 4.9% per year, quickly stabilizing at carrying capacity (K) (Figure 2.5). In this case the population reaches K after only 30 years and the model predicts no chance of extinction within 100 years. Under these conditions, supplementation of the population with a further 30 sable causes the population to increase again at a rate of 4.9%, stabilizing around K after just 20 years. Again, the model forecasts no chance of extinction within the 100 year period.



Figure 2.5 Mean sable population trend over 100 years modelled using estimates of vital rates taken from 2000 to 2005 and 2005 to 2010. Also shown are the effects of augmenting the population in both instances with 30 sable.

In the final scenarios, adult and juvenile mortality rates were varied in turn, examining the effect of each on the population trend (Figure 2.6). In the first instance, adult survival was reduced by 5%, simulating a small increase in predation by lions on the adult segment of the population. In this scenario, the population continued to grow (GR = 0.021), albeit slowly, with no predicted chance of extinction (P(E) = 0). A further reduction in adult survival, this time by 10%, caused the population to decline at a rate of -0.01. In this case, the probability of extinction within 100 years increased to 0.14 and of the 500 runs, 70 were predicted to go extinct. In the last scenario, a reduction of juvenile survival by both 5% and 10% had little effect on the overall trend of the population. The population continued to increase at rates of 0.044 and 0.036 respectively and the model predicted no chance of extinction within 100 years. In both cases the population grew sharply stabilizing around K after 40 years.



Figure 2.6 Mean sable population trends modelled for 100 years at increased estimates for adult female and juvenile mortality rates.

POPULATION SENSITIVITY:

The sensitivity of the population growth rate to changes in survival of the different age classes is shown in Figure 2.7. From the analysis it is clear that proportional changes to adult female survival had the greatest effect on the average long-term population growth rate. As little as a 10% reduction in survival of adult females led to a negative growth rate (r = -0.007) in the population. Comparatively, a reduction of as much as 25% in the survival rate of the other age classes still led to positive growth in the overall population. Though marginally so, sub-adult survival had the next greatest effect on overall population growth, with a 25% reduction in survival reducing population growth to just 0.006 per year. Adult male survival had the least impact, if any, on the overall growth rate of the population.



Figure 2.7 Sensitivity of the population growth rate to changes in survival rate of different age classes. The truncation of the adult male and female, sub-adult and yearling lines to the right is because increases of 5-10% in survival rate results in 100% survival in these classes.

2.4 Discussion

There have been heated debates in the literature regarding the value and accuracy of PVA models for predicting future population trends. In spite of this, PVA has been employed widely as a tool for assessing the vulnerability of threatened populations and for evaluating possible options for their recovery (Brook et al., 2000; Kelly & Durant, 2000; Cancino et al., 2010). The usefulness of a PVA model, however, depends entirely on the quality and accuracy of the baseline data (Coulson et al., 2001). The probability of extinction of a population is influenced by both uncertainty in the natural environment as well as uncertainty in the estimation of parameters used in the model (Taylor, 1995). Although environmental variation plays a role in varying the predictions of the model, uncertainty in the estimation of input parameters had a much greater effect on the overall output (Taylor, 1995). McLoughlin and Owen-Smith (2003) state that models that ignore predation pressure and take into account only demographic and environmental stochasticity may greatly underestimate extinction risk. In this study, the data used was collected intensively over a two year period to derive vital rates for the population. These rates were tested by comparing the modelled trend to the observed trend in the population over the past 5 years. The observed population fluctuated above and below the modelled population which showed a steady increase between 2005 and 2010, a result of taking an average of 500 iterations. The relatively short duration of the study meant that the effect of environmental stochasticity was essentially excluded from the model. However, testing of the output against historical data lent strong support to the model parameters despite the limited period of observation.

Replicating the declining trend of the sable population between 2000 and 2005 proved more challenging as it was clear that under current conditions, the sable population on MWR was predicted to increase. Historical data on the number of sable carcasses found by scouts on patrol clearly indicated a period of considerably higher mortality in sable between 2000 and 2005 (Appendix II), particularly among the older age classes. This period coincides with a period of markedly higher lion numbers at MWR (Clegg, 2010b) (Appendix III). Of the total number of sable carcasses found between 2000 and 2005, 77% were attributed to lion predation. Lions show a clear preference for medium- to large-bodied prey (Hayward & Kerley, 2005) and this was evident in the fact that 88% of sable killed by lions between 2000 and 2010 fell into the adult and sub-adult age classes. This fact further justified the factoring of the vital rates for the 2000 to 2005 period. The output from the model followed the observed trend well, again lending support for the estimates of the vital rates for the period 2000 to

2005. The long-term rate of decline over this period was -0.1209 (SD=0.0777), markedly higher than that reported by Nicholls *et al.* (1996) for the KNP between 1983 and 1992.

Under the current conditions the sable population on MWR is predicted to remain viable, steadily increasing to carrying capacity over the next 30 years. The sensitivity analysis shows, however, that even a small change in adult female survival (10%) could have disastrous effects. Even more alarming is that a 10% reduction in survival of adult females equates to a total loss of only 4 adult female sable per year. This means that the sable population on MWR, although currently stable, remains highly vulnerable to changes in predation pressure, environmental and demographic stochasticity and management interventions. Similarly, sable antelope in the KNP are at serious risk of extinction within the next 100 years (Nicholls *et al.*, 1996) and Owen-smith *et al.* (2005) attribute the decline of the species there to increased predation by lions. On MWR evidence points to a similar pattern where increased lion numbers were primarily driving the decline of the species until 2005. In 2005, emigration of two lion prides at MWR effectively halved our lion population (Clegg, 2010b), following a outbreak of anthrax that devastated prey populations in 2004 (Clegg *et al.*, 2007). Since then, the relatively high rate of juvenile mortality has prevented the sable population from growing at its full potential.

The long-term growth rate of a population can be used as a direct measure of the fitness of the population (Ranta *et al.*, 2006) and as such changes in the demographic components within the population can have direct impacts on its overall viability. Sensitivity analyses can determine which vital rates have the greatest impact on overall population growth and thus fitness. Examining the results from the sensitivity analysis allows one not only to determine which demographic parameters have the greatest impact on overall population growth but to assess the effect of variability or uncertainty in these parameters. The finding that a change in adult female survival has the greatest effect on overall population growth rate is not unusual and has been documented for other taxa (Gaillard *et al.*, 2000; Saether & Bakke, 2000). The extent of this sensitivity in relation to that of other age classes indicates that the historic decline of the species on MWR must have been caused by, inter alia, an increase in mortality in the adult female age class. This observation again lends support to the theory that increased predation, particularly by lions, was responsible for the decline of the species. In general, Gaillard *et al.* (1998) state that adult survival amongst large ungulates is always less variable than juvenile mortality and attribute this to the fact that recruitment is often the foremost target of limiting factors, both density-dependent and independent. Highly variable juvenile mortality has been linked to population

declines (Gaillard *et al.*, 1998) and Owen-Smith and Mason (2005) state that variations in juvenile survival could be a key factor responsible for fluctuations in population numbers. On MWR it seems unlikely that juvenile mortality alone could be responsible for the decline of the species between 2000 and 2005 based on the fact that a reduction in juvenile survival of as much as 25% still led to an overall positive growth rate in the population. It is possible to suggest however, that variable juvenile mortality potentially causes short-term fluctuations in the population and increased mortality targeting the adult segment of the population is the driving factor in long-term sharp declines.

Using baseline data designed to simulate conditions observed between 2000 and 2005, the PVA model predicted a local extinction of the sable population on MWR within the next 20 years. The augmentation of the population under these circumstances does little to curb the trend and management would need to look at ways of reducing the rate of mortality in the older age classes. This is similarly the case with roan antelope (*Hippotragus equinus*) in the Kruger National Park, where predation risk remains high for adult roan and augmentation of the free range population is seen as being a wasteful option at this stage (McLoughlin & Owen-Smith, 2003). In the long-term, manipulation of water points on MWR to reduce the density of other herbivores and thus predators within the range of the sable herds may be a feasible option. However, managers within the Kruger National Park have attempted this with limited success (McLoughlin & Owen-Smith, 2003). McLoughlin and Owen-smith (2003) suggest this could be due to only a partial emigration by predators from these areas. The authors warn that reducing the density of other herbivores in these areas may leave predators more reliant on the low density ungulates, with devastating consequences. A further complication arises because water points are an important resource for many other species as well as being a focus of game drives on MWR. Therefore, with the limited number of alternatives, some control of predators, particularly lions, may be necessary to reduce the predation risk faced by the sable population

2.5 Conclusion

Although the training and testing of the model proved accurate when compared with the observed trend, one must take note of the fact that the study was conducted over a relatively short period of time. Consequently any yearly variability in vital rates may have been missed and it is recommended that future studies be conducted over a longer period of time using similar methods. Whilst the potential shortcomings of this study are recognized, the accuracy in the training and calibration of the model offers good credibility to the PVA and provides a robust backing to the results and trends presented here. The results echo those presented elsewhere, showing that sable antelope populations in the lowveld regions of Zimbabwe and South Africa remain highly vulnerable to predation pressure, particularly by lions (Grant & van der Walt, 2000; Owen-Smith *et al.*, 2005).

2.6 References

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3. CHAPTER 3 Home Range and Habitat selection by sable antelope (*Hippotragus niger*) on Malilangwe Wildlife Reserve, Zimbabwe

3.1 Introduction

How an animal uses its environment is central to understanding its ecology (Johnson, 1980). This knowledge is essential if habitats are to be managed to encourage species survival. Understanding the habitat selection process involves quantifying the animal's use of resources in relation to their availability in the landscape (Johnson, 1980; Manly et al., 2002). Resource selection by animals operates at a number of different scales, ultimately determining where an animal lives. Senft et al. (1987) state that scale is an important component in determining the selection criteria of herbivores. They state that at different scales a variety of factors play a role in determining whether an animal chooses a specific area or not. The distribution of ungulates is influenced by both abiotic and biotic factors (Senft et al., 1987; Bailey et al., 1996). Abiotic factors generally form the overarching feature in large-scale distribution patterns and within this constraint, biotic factors interact at a finer scale ultimately determining the selection of a niche within the landscape (Bailey et al., 1996). At the regional scale, abiotic factors such as geomorphology, regional climate, physical barriers and water all play a role (Senft et al., 1987), whereas at the landscape scale topography, distance from water, geology, vegetation type and general microclimate are important (Senft et al., 1987). At an even finer scale, the micropatch/feeding station, ungulates select plants on the basis of morphology, nutritive quality and ease of harvest (Senft et al., 1987).

Habitat selection studies at the landscape scale essentially take a two pronged approach, firstly looking at how animals interact with environmental resources in space and secondly how these interactions change over time (Clegg, 2010). Temporal changes in the spatial distribution of discrete units/herds of ungulates has been repeatedly demonstrated (Fryxell & Sinclair, 1988; Parrini, 2006). This reflects seasonal changes in the abiotic and biotic components of the environment (Manly *et al.*, 2002). Response to seasonal variation in these components could manifest as relatively small changes in home-range within a small confined park (Harrington *et al.*, 1999; Parrini, 2006) or large distributional changes such as those observed with wildebeest in the Serengeti-Mara system of east Africa. Many habitat selection studies have failed to take account of seasonal changes in resource

availability, focusing mostly on the dry season (Parrini, 2006; Chirima, 2009) and hence their merits may be limited. Multi-scale approaches that incorporate a temporal theme may provide a more comprehensive and therefore more useful analysis of resource selection by ungulates.

Identifying which factors play a primary role in habitat selection by herbivores over time is not straight forward. In theory, herbivores should select areas with optimal food quantity and quality (Manly *et al.*, 2002). However, in practice, herbivores are influenced at various scales by the availability of surface water, prevailing climatic conditions, predation and other factors which modify their selection criteria (Morin, 2011). Selection by animals is also influenced by what resources are available and in some cases animals may utilize less favoured resources because better resources are too limited in extent in the environment (Manly *et al.*, 2002). Consequently, Manly *et al.* (2002) state that researchers should interpret results from habitat selection studies cautiously, taking into account influences of scale, resource availability and abiotic factors.

Sable antelope on Malilangwe Wildlife Reserve (MWR) exhibit a restricted distribution, making them ideal for the study of habitat selection. The species more commonly occurs in the wetter regions of Africa (Skinner & Chimimba, 2005) and MWR falls near the southern edge of their range. Sable have shown alarming declines through much of their range, particularly in southern Africa (Grant & van der Walt, 2000; Magome *et al.*, 2008), making them a priority species for conservation. On MWR, the sable population declined from 197 individuals in 1994 to only 62 by 2005. A similar trend has been reported for the Kruger National Park (KNP), South Africa, where Grant and van de Walt (2000) note a decline from 2240 animals in 1986 to only 505 by 1999. Understanding the spatio-temporal ecology of sable on MWR and elsewhere may be key to controlling the decline of the species and managing the landscape to enhance recovery.

In this chapter home range use and habitat selection by sable antelope was investigated on MWR at the landscape scale. Seasonal changes in home range and habitat use and the factors that influenced these changes were examined. We hypothesized that sable should 1) utilize larger areas during the hot dry season; 2) select for vegetation types characterized by open canopies with dense grass layers; 3) optimize energy expenditure and water budgets by ranging closer to water during the dry season; 4) utilize areas with the greenest grass available; and 5) show a general movement into the bottomlands during the dry season.

3.2 Methods

3.2.1 Study Site

The 39 378 ha Malilangwe Wildlife Reserve is located in the south-eastern lowveld of Zimbabwe. The reserve in bordered by the Gonarezhou National Park to the south, the Hippo Valley Game Section to the west and by communal land to the north and east (Fig. 3.1).



Figure 3.1 Map showing the location of Malilangwe Wildlife Reserve.

The MWR has a typical savanna climate with hot wet summers and cool dry winters. The study period was divided into 4 distinct seasons based on daily rainfall and temperature. The seasons were defined as, the cool dry season from the 25 May to 28 August 2009, the hot dry season from the 29 August to 16 November 2009, the early wet season from the 17 November 2009 to 17 February 2010 and the late wet season from the 18 February to 24 May 2010 (Fig. 3.2). The long-term average annual rainfall for the area is 562 mm measured from 1951-2009. During the 2009-2010 season, Malilangwe

received 552 mm of rainfall and the average monthly maximum and minimum temperatures recorded were 33.9°C in November and 13°C in July respectively. Seven geological types are present, the major ones being acid and basic gneiss which dominates the northern portion of the property, alluvium which occurs along most of the major drainage lines, forest sandstone found in association with the Malilangwe range and Jurassic basalt which is primarily found in the southern and eastern parts of MWR. Much of the reserve is dominated by various types of open *Cholophospermum mopane* woodland with the Malilangwe sandstone range being characterized by *Brachystegia* woodland. The property has been classified into 38 vegetation types based on the composition of both the woody and herbaceous layers, the structure of the woody component and the topo-edaphic factors that influence the plant communities (Clegg, 2010).



Figure 3.2 MWR average rainfall (a) and temperature (b) for 2009-2010, showing seasonal divisions.

3.2.2 Field Data Collection

An adult female sable from four of the five herds on Malilangwe was immobilized and fitted with a GPS/VHF collar (Telemetry Solutions, California). Each collar was programmed to record a position every two hours, day and night. Positional data were stored on the collar until downloaded wirelessly via a Hewlett Packard Personal Digital Assistant (PDA). Downloads were performed bi-monthly, at the beginning and middle of each month, by tracking the herds using the VHF signal emitted from the collar. When the herd was encountered, a wireless connection was established between the collar and the PDA and data from the required period was downloaded. Collar failure resulted in missing data for certain periods. When a collar failed, it was replaced as soon as was possible. In one instance, a collar manufactured by Televilt, Sweden was used as a replacement.

GPS TELEMETRY DATA

To construct each herd's home range we randomly selected 6 GPS positions per day for each herd in each season. Within a season, the same number of points was used for each herd but the number varied between seasons due to variation in season length. Pearson's Correlation was used to test the effect of different sample sizes on home range estimation. This was to ensure that varying seasonal length did not introduce a bias into the home range estimates.

3.2.3 Home-Range Analysis

To construct home ranges and utilization distributions for each herd, we used the *k*-nearest neighbour convex hull method (Getz & Wilmers, 2004). The method, which was applied using the LoCoH extension for ArcGIS 9x (ESRI, 2009), constructs local hulls around a user-specified number of nearest neighbours (the parameter k). The method then merges these local hulls, essentially a number of polygons, and creates isopleths of utilization starting with the smallest and ending with the largest. LoCoH is a useful method of home-range estimation because it can identify unused areas within a species range as well as converging on the species' true distribution even with the addition of data points (Getz & Wilmers, 2004). The method used in the LoCoH extension for ArccGIS 9x differs slightly from that described by Getz and Wilmers (2004) in that *k*-nearest neighbours are used in hull construction instead of k - 1 nearest neighbours as originally described by them. To construct accurate estimates of the sable home ranges we ran the method in ArcMap 9x ((ESRI, 2009) for k values from 5 to 75 at intervals of 5. We then plotted a scatter plot of area vs k to find the plateau that represents a

stable-area value, i.e. where the area of the home range remains constant over a range of k values (Fig. 3.3). The value of k in all cases was taken as the first point where the following two data points created a stable-area value on the graph. In two cases more than one plateau was present representing two stable-area values for k. Our method of selecting the first point in a series of at least three stable area values indirectly incorporated a trade-off between type I (excluding areas where the species occurred) and type II (including areas where the species did not occur) errors in home range estimation.



Figure 3.3 An example of a home range area versus *k*-value graph for sable showing method for choosing *k*.

3.2.4 Broad-Scale Habitat Selection

Habitat selection was investigated at the broad scale by comparing observed use of geology and vegetation type with expected use given a random distribution. Clegg (2010) describes the geological and vegetation divisions used. Positions collected by the GPS collars were used as presence data. To reduce the effects of spatial auto correlation and to standardise the number of positions per herd, seasonal datasets were constructed by randomly selecting a single position from each day during the peak feeding time, which was taken as 08.00 hrs and 16.00 hrs (Grobler, 1981). An IDRISI 32 (Eastman, 2001) GIS was used to extract the geology and vegetation type for each position within the seasonal datasets. To compare the observed selection of geology and vegetation type with availability,

the same number of points used for each season were randomly placed over MWR using the Hawths Tools extension in ArcGIS 9x. IDRISI 32 was then used to extract the geology and vegetation type for these random points, which represented the expected use of each variable.

Selection for geological type and vegetation type was tested using the Neu method (Neu *et al.*, 1974), a simple chi-square that tested the null hypothesis that use of each category was no different from that expected by a random distribution. The Bonferroni *Z*-statistic was used to calculate confidence intervals to determine whether a specific category was used more or less frequently than expected (Neu *et al.*, 1974; Alldredge & Ratti, 1992). The confidence intervals were calculated using the formula (Neu *et al.*, 1974):

$$\overline{p_i} - Z_{(1 - a/2k)} \sqrt{p_i} (1 - \overline{p_i})/n \leq p_i \leq \overline{p_i} + Z_{(1 - a/2k)} \sqrt{p_i} (1 - \overline{p_i})/n$$

Where $\overline{p_i}$ is the proportion of sable in the *i*th category and *Z* is the Bonferroni *Z*-value at 1-*a*/2*k*. The variable *a* is the significance level and *k* represents the number of categories.

3.2.5 Landscape-Scale Habitat Selection

To assess habitat selection by sable at the landscape scale, time series graphs were used to compare the average use of a resource to the average availability of that resource in the landscape. The advantage of this simple yet effective method was that it not only allowed us to compare the use of a resource in relation to its availability but also enabled us to determine how the use of each resource changed over time. The study period was divided into 32-day intervals to match the remotely sensed vegetation data. 25 GPS presence points were randomly selected for each herd during each period, again from the peak feeding times as determined by Grobler (1981). The presence points for all of the herds were combined and were used in an IDRISI 32 (Eastman, 2001) GIS to extract the average value for each environmental variable for each 32-day period. The environmental variables were input into the IDRISI 32 (Eastman, 2001) GIS as raster files. Six environmental variables which revealed the most about the environmental niche being utilized by sable at MWR were used. The six variables were distance from water, grass enhanced vegetation index (EVI), woody EVI, soil depth, clay content and grass cover. The average value extracted for each variable over the 32-day periods was plotted against the study site average, giving a time series comparison of use versus availability for each variable. A 95% confidence interval was calculated for each point, giving a visual statistical comparison of use versus availability.

ENVIRONMENTAL VARIABLES

Distance from Water - 382 pans, dams and springs on MWR were monitored over the study period. Each water source was visited every two weeks and its percentage full estimated using a 7 point scale (0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95% and 96-100%). If a pan was predicted to dry up before the next visit, the date on which it would dry up was estimated. These data were then plotted on graphs, with percentage full on the x-axis and time on the y-axis, for each water source using KyPlot 4.0 (KyensLab Inc., 2002). By interpolating between points using a smoothing spline regression, daily estimates of percentage full were estimated for each source over the study period. These data for each point extracted from KyPlot 4.0 (KyensLab Inc., 2002) and were used in an IDRISI 32 (Eastman, 2001) GIS to plot daily maps of water distribution on MWR. This was done by assigning each water point a daily value representing its percentage full, resulting in 365 maps showing water availability over the year. The value assigned to each water source was then scaled to a 0-1 map by assigning any water point that was less than 5 % full a value of zero and any water point greater than 5 % full a value of 1. From this, we used the distance function in IDRISI 32 (Eastman, 2001) to create daily maps, showing the distance from water sources at MWR. These daily maps were then averaged out over the 32 day periods used in the habitat selection analyses.

EVI data – We used the 16-day Moderate Resolution Imaging Spectroradiometer (MODIS) enhanced vegetation index (EVI) images from the period 25 May 2009 – 24 May 2010 to quantify change in vegetation structure and greenness over time. We clipped the images in ArcGIS 9x to match the spatial extent of our study area and modified the resolution of the image from 250 x 250 meter pixels down to 25 x 25 meter pixels. EVI images incorporate both the reflectance of the woody layer as well as the canopy background, essentially the herbaceous layer (Huete *et al.*, 2002). This makes it difficult to make sound conclusions as to how animals react to temporal changes in the characteristics of the vegetation. We therefore divided EVI for each vegetation type at MWR into Woody and Grass EVI following the methods described by Archibald and Scholes (2007). The time taken for trees to reach their full "greenness" from the onset of greening up is relatively fixed from year to year (Archibald & Scholes, 2007). Green up times for the woody layer in each vegetation type at MWR

were calculated by Clegg (2010) and used in this study to separate the elements contributing to total EVI. An intra-season drought in the early wet season of 2010, by chance, allowed us to determine a value of woody maximum EVI. Grass cover during this period was assumed to be completely dry, meaning that the EVI value at that time was contributed solely by the woody layer. This assumption is not entirely accurate due to the nature of the 16-day EVI image and the difference between vegetation types but it was considered more accurate and meaningful than utilising the combined EVI image. Grasses consistently dried up before the woody layer (Archibald & Scholes, 2007) allowing us to create a curve representing woody EVI for each vegetation type at MWR. This was then subtracted from total EVI thereby separating out the contribution of both the woody and grass layer to total EVI. Each 16-day image representing woody and grass EVI was then averaged out to 32-days by adding the images and dividing by two. These 32-day images were then used in our analysis of habitat selection by sable.

Soil Depth & Clay Content –Depth and clay content of the soil were taken from existing data at MWR. A description of the methods used to collect data on soil depth and clay content are described in Clegg (2010).

Perennial Grass Cover – Data on the aerial cover of grass species in each vegetation type at MWR were taken from Clegg (2010). Total cover of perennial grasses for each vegetation type was calculated and a map depicting perennial grass cover was constructed for the study area by assigning the calculated cover estimates to their respective vegetation types using IDRISI 32 (Eastman, 2001).

3.2.6 Habitat Suitability Modelling

To model suitability of habitats for sable at MWR we used MAXENT version 3.3.3 (Phillips *et al.*, 2006). MAXENT predicts the probability distribution of a species, using "presence only" data, by determining its distribution of maximum entropy (i.e. the most evenly spread) whilst being constrained by a suite of environmental variables (i.e. explanatory variables for the "presence only"/response variable data) (Phillips *et al.*, 2006). MAXENT provides a map output of the probability distribution of the study species, essentially a predicted habitat suitability map. The program also provides an output of the contribution of each variable to the model, essentially ranking the importance of each to the suitability of habitats for sable, and in turn predicts the response of the sable to each environmental

variable. The model allows the user to select a number of input and output features, based on the requirements of the user. In order to simplify the output of the model we used only linear and quadratic fitting of the response variables. We used a regularisation multiplier of 5 to reduce over-fitting of the model due to the assumed autocorrelation of the GPS data (Phillips, 2010) and used independent test data to test the output of the model. All other features of the model were left in their default state. Evaluation of the MAXENT output was done using two methods, firstly by using independent test data and secondly using the built in area under (AUC) the receiver operating curve (ROC) function. Values of 0.5-0.7 indicate poor accuracy of the model, values of 0.7-0.9 indicate useful models and values >0.9 indicate highly accurate models (Swets, 1988).

The MAXENT model was run for each pre-defined season at Malilangwe using the same GPS presence data used in the broad scale habitat selection analysis. The same suite of environmental variables were used in the landscape scale analysis, averaging each 32-day image out to match the defined seasons. Care was taken to exclude any variables that were highly correlated as well as to keep the base scale of each variable constant. This was to reduce the ambiguity of results caused by using highly correlated variables or by using a multi-scale approach. The independent test data used in each model was taken from GPS sighting reports of sable made by the MWR scouts on their daily patrols. Sighting data were extracted from the Malilangwe Wildlife Population Management database for each seasonal period and included as "test points" in the model.

3.3 Results

3.3.1 Home-Range Analysis

Sable at MWR had an average seasonal range of 28.7 km² \pm 7.39 km² (mean \pm SE), ranging from 18.7 km² \pm 4.46 km² (mean \pm 95% CI) in the cool dry season to 50.5 km² \pm 21.9 km² (mean \pm 95% CI) in the early wet season. The sable's home range was largest during the early wet season (50.5 km²), being more than double that of the hot dry season (25.4 km²). Both the 90% utilisation distribution (UD) isopleth and 50% core UD showed similar patterns peaking in the early wet season (Fig 3.4).



Figure 3.4 Seasonal home range and utilisation distribution extents for sable at MWR. Data shown are an average of four individual herds. Shown are error bars representing 95 % confidence intervals of each mean.

Individual herd home ranges all followed a similar trend with a peak of home range extent in the early wet season (Table 1). A Pearson's Correlation was run in excel to test whether the varying sample sizes used between seasons was introducing bias in the home range analysis. Results showed that no relationship existed between sample size and home range extent in the analysis (R = -0.03146; p=0.915). In addition, herd size seemed to have no influence on range extent at MWR (R = -0.254; p = 0.745).

		Cool Dr	γ		Hot Dr	v		Early Wo	et		Late We	et
Herd ID	No. of Points	k - Value	Range Extent (km ²)	No. of Points	k - Value	Range Extent (km²)	No. of Points	k - Value	Range Extent (km ²)	No. of Points	k - Value	Range Extent (km ²)
BNZ				480	30	24.46	558	40	62	576	45	20.57
CVG	576	30	15.09	480	55	19.05	558	40	28.14	576	50	13.95
СVК	576	45	17.98	480	35	26.71				576	55	18.91
MNY	576	55	22.89	480	40	31.52	558	45	61.38	576	35	28.15

Table 3.1 Seasonal home range extent for each sable herd on MWR. Grey shading represents seasons where complete data were unavailable for a particular herd due to collar failures.

3.3.2 Broad-scale Habitat Selection

The chi-square test analysis for selection of geological type at MWR was significant ($\chi^2 = -4.51$; p < 0.0001) for all seasons and the null hypothesis, that sable used geological types in proportion to their availability in the landscape, was rejected. Bonferroni-corrected confidence intervals (95% CI) showed that sable select almost exclusively for Jurassic Basalt, essentially avoiding all other geological types at MWR (Table 3.2).

Similarly, the chi-square analysis of selection of vegetation type at MWR was significant for all seasons ($\chi^2 = -7.88$; p < 0.0001) and sable at MWR did not utilise vegetation types in proportion to their availability in the landscape. Sable only positively selected for seven of the 38 vegetation types at MWR and only four of these were utilized consistently throughout the year (Table 3.3). Bonferroni-corrected confidence intervals (95% CI) also revealed that a further 11 vegetation types were utilised in proportion to their availability in the landscape and the remaining 20 vegetation types were almost completely avoided by sable. A detailed description of the vegetation types at MWR can be found in Clegg (2010).

Table 3.2 Seasonal selection of geological type by sable antelope at MWR.

			Cool Dr	y Season		Hot Dry Season							
Geological Type	No. of GPS No. of GPS Expected Observed Fixes Fixes Use Use Observed Expected				Confidence interval on No. of observed use (95% level Fixe of confidence) Obser			No. of GPS No. of GPS Fixes Fixes Observed Expected		Observed Use	Confidence interval on observed use (95% level of confidence)		
Stormberg Sandstone	4	57	0.1979	0.0139	$0.0000 \le p_{i} \le 0.0322$	-	10	60	0.1905	0.0317	$0.0055 \le p_i \le 0.0579$	-	
Alluvium	3	30	0.1025	0.0104	$0.0000 \le p_{i} \le 0.0263$	-	14	34	0.1079	0.0444	$0.0137 \le p_{\pm} \le 0.0752$	-	
Jurassic Basalt	279	142	0.4947	0.9688	$0.9416 \le p_{i} \le 0.9959$	+	291	152	0.4825	0.9238	$0.8842 \le p_{\gamma} \le 0.9635$	+	
Grit	2	10	0.0353	0.0069	$0.0000 \le p_{i} \le 0.0199$	-	0	8	0.0254	0	$0.0000 \le p_i \le 0.0000$	-	
Shales & Mudstones	0	2	0.0071	0	$0.0000 \le p_{i} \le 0.0000$	-	0	5	0.0159	0	$0.0000 \le p_{i} \le 0.0000$	-	
Dolerite	0	11	0.0389	0	$0.0000 \le p_{i} \le 0.0000$	-	0	18	0.0571	0	$0.0000 \le p_{i} \le 0.0000$	-	
Acid & Basic Gneiss	0	36	0.1237	0	$0.0000 \le p_i \le 0.0000$	-	0	38	0.1206	0	$0.0000 \le p_{i} \le 0.0000$	-	
	288	288					315	315					

			Early W	Late Wet Season								
Geological Type	No. of GPS Fixes Observed	No. of GPS Fixes Expected	Expected Use	Observed Use	Confidence interval on observed use (95% level of confidence)		No. of GPS Fixes Observed	No. of GPS Fixes Expected	Expected Use	Observed Use	Confidence interval on observed use (95% level of confidence)	
Stormberg Sandstone	35	56	0.2022	0.1268	$0.0737 \le p_{i} \le 0.1799$	-	10	58	0.1512	0.0262	$0.0045 \le p_{i} \le 0.0480$	-
Alluvium	2	26	0.0939	0.0072	$0.0000 \le p_{i} \le 0.0208$	-	4	46	0.1220	0.0105	$0.0000 \le p_{i} \le 0.0243$	-
Jurassic Basalt	239	138	0.4982	0.8659	$0.8116 \le p_i \le 0.9203$	+	366	180	0.4721	0.9606	$0.9342 \le p_{\gamma} \le 0.9871$	+
Grit	0	5	0.0181	0	$0.0000 \le p_i \le 0.0000$	-	0	17	0.0451	0.0000	$0.0000 \le p_i \le 0.0000$	-
Shales & Mudstones	0	3	0.0108	0	$0.0000 \le p_i \le 0.0000$	-	0	5	0.0133	0	$0.0000 \le p_i \le 0.0000$	-
Dolerite	0	10	0.0361	0	$0.0000 \le p_i \le 0.0000$	-	0	18	0.0477	0	$0.0000 \le p_i \le 0.0000$	-
Acid & Basic Gneiss	0	39	0.1408	0	$0.0000 \le p_i \le 0.0000$	1	1	57	0.1485	0.0026	$0.0000 \le p_i \le 0.0096$	1
	276	276					381	381				

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Table 3.3 Seasonal selection of vegetation type by sable at MWR (Pale yellow highlights indicate positive selection for a specific vegetation type)

			Cool [Dry Season		Hot Dry Season								
Veg. Type	No. of Sable Observed	No. of Sable Expected	Expected Use	Observed Use	Confidence interval on observed use (95% level of confidence)		No. of Sable Observed	No. of Sable Expected	Expected Use	Observed Use	Confidence interval on observed use (95% level o confidence)	of		
1	0	3	0.0106	0	$0 \le p_j \le 0$	-	0	3	0.0095	0	$0 \le p_j \le 0$			
2	1	16	0.0563	0.0035	$0.0000 \le p_{\perp} \le 0.0103$	-	0	14	0.0442	0	$0 \leq p_{\perp} \leq 0$	-		
3	3	9	0.0317	0.0104	$0.0000 \le p_{i} \le 0.0221$	-	5	14	0.0442	0.0159	$0.0021 \le p_{\perp} \le 0.0297$	-		
4	0	19	0.0669	0	$0 \le p_{\perp} \le 0$	-	5	14	0.0442	0.0159	$0.0021 \le p_{\perp} \le 0.0297$	_		
5	0	0	0	0			0	4	0.0126	0	$0 \le p_{i} \le 0$	-		
6	0	1	0.0035	0	$0 \le p_{i} \le 0$	-	0	2	0.0063	0	$0 \le p_{i} \le 0$	-		
7	0	4	0.0141	0	$0 \le p_{i} \le 0$	-	0	4	0.0126	0	$0 \le p_{+} \le 0$	-		
8	0	3	0.0106	0	$0 \le p_{i} \le 0$	-	2	1	0.0032	0.0063	$0.0000 \le p_{\perp} \le 0.0151$	ns		
9	1	4	0.0141	0.0035	$0.0000 \le p_{i} \le 0.0103$		0	10	0.0315	0	$0 \le p_{i} \le 0$			
10	0	3	0.0106	0	$0 \le p_{i} \le 0$	-	0	1	0.0032	0	$0 \le p_{i} \le 0$	-		
11	0	4	0.0141	0	$0 \le p_{i} \le 0$	-	0	1	0.0032	0	$0 \le p_{ij} \le 0$	-		
12	9	2	0.0070	0.0313	0.0111 ≤ <i>p</i> _i ≤ 0.0513	+	1	2	0.0063	0.0032	$0.0000 \le p_{i} \le 0.0094$	ns		
13	0	1	0.0035	0	$0 \le p_{i} \le 0$	-	0	0	0	0				
14	0	4	0.0141	0	$0 \le p_{i} \le 0$	-	0	3	0.0095	0	$0 \le p_{i} \le 0$	-		
15	0	1	0.0035	0	$0 \le p_{i} \le 0$	-	0	0	0	0				
16	0	2	0.0070	0	$0 \le p_{i} \le 0$	-	0	5	0.0158	0	$0 \le p_{i} \le 0$			
17	2	6	0.0211	0.0069	$0.0000 \le p_{i} \le 0.0165$	-	0	5	0.0158	0	$0 \le p_{+} \le 0$	-		
18	2	13	0.0458	0.0069	$0.0000 \le p_{i} \le 0.0165$	-	12	21	0.0662	0.0381	0.0170 ≤ p _/ ≤ 0.0592	-		
19	0	1	0.0035	0	$0 \le p_{i} \le 0$	-	0	4	0.0126	0	$0 \le p_{i} \le 0$	-		
20	0	11	0.0387	0	$0 \le p_{i} \le 0$	-	0	18	0.0568	0	$0 \le p_{i} \le 0$	-		
21	0	18	0.0634	0	0 ≤ p ; ≤ 0	-	0	17	0.0536	0	$0 \le p_{i} \le 0$	-		
22	29	12	0.0423	0.1007	0.0659 ≤ p _i ≤ 0.1354	+	24	9	0.0284	0.0762	0.0469 ≤ p _/ ≤ 0.1055	+		
23	84	42	0.1444	0.2917	0.2392 ≤ p _i ≤ 0.3442	+	106	51	0.1609	0.3365	0.2843 ≤ p _i ≤ 0.3887	+		
24	15	10	0.0352	0.0521	0.0264 ≤ p _i ≤ 0.0777	ns	18	8	0.0252	0.0571	0.0315 ≤ p _/ ≤ 0.0828	+		
25	2	8	0.0282	0.0069	$0.0000 \le p_i \le 0.0165$	-	16	9	0.0284	0.0508	0.0265 ≤ p _i ≤ 0.0750	ns		
26	0	3	0.0106	0	$0 \le p_i \le 0$	-	0	0	0	0				
27	0	14	0.0493	0	$0 \le p_{i} \le 0$	-	0	19	0.0599	0	$0 \le p_{\perp} \le 0$	-		
28	1	2	0.0070	0.0035	$0.0000 \le p_i \le 0.0103$	ns	5	5	0.0158	0.0159	$0.0021 \le p_{\perp} \le 0.0297$	ns		
29	0	0	0	0			0	2	0.0063	0	$0 \le p_{i} \le 0$	-		
30	3	11	0.0387	0.0104	$0.0000 \le p_{i} \le 0.0221$	-	5	3	0.0095	0.0159	$0.0021 \le p_{\perp} \le 0.0297$	ns		
31	0	2	0.0070	0	$0 \le p_{i} \le 0$	-	0	0	0	0				
32	52	7	0.0246	0.1806	$0.1361 \le p_i \le 0.2250$	+	47	11	0.0347	0.1492	$0.1099 \le p_{i} \le 0.1886$	+		
33	6	4	0.0141	0.0208	$0.0043 \le p_{i} \le 0.0373$	ns	7	12	0.0379	0.0222	$0.0059 \le p_{\perp} \le 0.0385$	ns		
34	1	9	0.0317	0.0035	$0.0000 \le p_{i} \le 0.0103$	-	0	10	0.0315	0	$0 \le p_{\perp} \le 0$	-		
35	0	1	0.0035	0	$0 \le p_{i} \le 0$	-	0	1	0.0032	0	0 ≤ p _i ≤ 0	-		
36	18	10	0.0352	0.0625	$0.0345 \le p_{i} \le 0.0905$	ns	17	7	0.0221	0.0540	$0.0290 \le p_{i} \le 0.0789$	+		
37	9	6	0.0211	0.0313	$0.0112 \le p_{i} \le 0.0513$	ns	5	4	0.0126	0.0159	0.0021 ≤ p _i ≤ 0.0297	ns		
38	50	18	0.0634	0.1736	0.1299 ≤ p _i ≤ 0.2174	+	40	21	0.0662	0.1270	0.0902 ≤ <i>p</i> _i ≤ 0.1638	+		

			Early V	Vet Season			Late Wet Season								
Veg. Type	No. of Sable Observed	No. of Sable Expected	Expected Use	Observed Use	Confidence interval on observed use (95% level o confidence)	f	No. of Sable Observed	No. of Sable Expected	Expected Use	Observed Use	Confidence interval on observed use (95% level o confidence)	of			
1	0	3	0.0108	0	$0 \le p_i \le 0$		0	2	0.0053	0	$0 \le p_{i} \le 0$				
2	2	16	0.0578	0.0072	$0.0000 \le p_{\perp} \le 0.0173$	\sim	0	19	0.0501	0	$0 \le p_{\perp} \le 0$	(L2)			
3	15	7	0.0253	0.0543	$0.0276 \le p_{\perp} \le 0.0811$	+	7	7	0.0185	0.0184	$0.0049 \le p_{\perp} \le 0.0319$	ns			
4	15	16	0.0578	0.0543	0.0276 ≤ p _i ≤ 0.0811	ns	2	16	0.0422	0.0052	$0.0000 \le p_{i} \le 0.0125$	-			
5	0	4	0.0144	0	$0 \le p_i \le 0$	(7)	0	2	0.0053	0	$0 \le p_{i} \le 0$	570			
6	0	1	0.0036	0	$0 \le p_i \le 0$	-	0	2	0.0053	0	$0 \le p_{i} \le 0$	(23)			
7	1	1	0.0036	0.0036	$0.0000 \le p_{i} \le 0.0107$	ns	1	2	0.0053	0.0026	$0.0000 \le p_{\perp} \le 0.0078$	ns			
8	0	2	0.0072	0	$0 \le p_i \le 0$	-	0	3	0.0079	0	$0 \le p_{i} \le 0$				
9	1	3	0.0108	0.0036	$0.0000 \le p_i \le 0.0107$		1	10	0.0264	0.0026	$0.0000 \le p_{i} \le 0.0078$	170			
10	0	4	0.0144	0	$0 \le p_i \le 0$	-	1	4	0.0106	0.0026	$0.0000 \le p_{i} \le 0.0078$	<u> </u>			
11	0	1	0.0036	0	$0 \le p_i \le 0$	-	0	8	0.0211	0	$0 \le p_{i} \le 0$	-			
12	6	1	0.0036	0.0217	0.0045 ≤ <i>p</i> _i ≤ 0.0389	+	4	4	0.0106	0.0105	$0.0003 \le p_{i} \le 0.0207$	ns			
13	0	2	0.0072	0	0 ≤ <i>p</i> _i ≤ 0		0	0	0	0					
14	0	4	0.0144	0	$0 \le p_i \le 0$	-	0	10	0.0264	0	$0 \le p_i \le 0$	(23)			
15	0	1	0.0036	0	$0 \le p_i \le 0$	-	0	4	0.0106	0	$0 \le p_i \le 0$				
16	0	3	0.0108	0	$0 \le p_i \le 0$	-	0	5	0.0132	0	$0 \le p_i \le 0$	-			
17	0	1	0.0036	0	$0 \le p_i \le 0$	\odot	0	7	0.0185	0	$0 \le p_{i} \le 0$	170			
18	1	13	0.0469	0.0036	$0.0000 \le p_i \le 0.0107$	\sim	2	17	0.0449	0.0052	$0.0000 \le p_i \le 0.0125$	(<u>1</u>)			
19	2	4	0.0144	0.0072	$0.0000 \le p_i \le 0.0173$	ns	0	3	0.0079	0	$0 \le p_i \le 0$	-			
20	0	10	0.0361	0	$0 \le p_i \le 0$	-	0	18	0.0475	0	$0 \le p_i \le 0$	-			
21	0	16	0.0578	0	$0 \le p_i \le 0$	0.770	0	25	0.0660	0	$0 \le p_i \le 0$	8 7 87			
22	30	10	0.0361	0.1087	0.0720 ≤ <i>p</i> _i ≤ 0.1454	+	43	8	0.0211	0.1129	$0.0811 \le p_{\pm} \le 0.1446$	+			
23	84	46	0.1661	0.3043	$0.2501 \le p_i \le 0.3586$	+	131	56	0.1478	0.3438	$0.2961 \le p_{i} \le 0.3915$	+			
24	7	8	0.0289	0.0254	$0.0068 \le p_i \le 0.0439$	ns	10	4	0.0106	0.0262	$0.0102 \le p_{i} \le 0.0423$	ns			
25	7	13	0.0469	0.0254	$0.0068 \le p_{i} \le 0.0439$	-	24	17	0.0449	0.0630	0.0386 ≤ p _/ ≤ 0.0874	ns			
26	0	2	0.0072	0	$0 \le p_i \le 0$	-	0	2	0.0053	0	$0 \le p_{i} \le 0$	-			
27	0	20	0.0722	0	$0 \le p_i \le 0$	-	0	27	0.0712	0	$0 \le p_{i} \le 0$	-			
28	7	6	0.0217	0.0254	$0.0068 \le p_{i} \le 0.0439$	ns	10	6	0.0158	0.0262	$0.0102 \le p_{\perp} \le 0.0423$	ns			
29	0	1	0.0036	0	$0 \le p_i \le 0$	-	1	2	0.0053	0.0026	0.0000 ≤ p _i ≤ 0.0078	ns			
30	7	4	0.0144	0.0254	$0.0068 \le p_{i} \le 0.0439$	ns	7	4	0.0106	0.0184	$0.0049 \le p_{\perp} \le 0.0319$	ns			
31	0	1	0.0036	0	0 ≤ p _i ≤ 0	-	0	0	0	0					
32	31	4	0.0144	0.1123	0.0751 ≤ p _i ≤ 0.1496	+	40	17	0.0449	0.1050	0.0742 ≤ p _i ≤ 0.1358	+			
33	3	5	0.0181	0.0109	$0.0000 \le p_i \le 0.0231$	ns	21	17	0.0449	0.0551	0.0322 ≤ p _i ≤ 0.0780	ns			
34	2	10	0.0361	0.0072	$0.0000 \le p_i \le 0.0173$	-	5	10	0.0264	0.0131	0.0017 ≤ p _i ≤ 0.0246	-			
35	0	3	0.0108	0	$0 \le p_{i} \le 0$	-	0	4	0.0106	0	$0 \le p_{i} \le 0$	-			
36	9	6	0.0217	0.0326	$0.0117 \le p_{i} \le 0.0536$	ns	13	12	0.0317	0.0341	$0.0159 \le p_{i} \le 0.0523$	ns			
37	9	4	0.0144	0.0326	$0.0117 \le p_{i} \le 0.0536$	ns	7	7	0.0185	0.0184	0.0049 ≤ <i>p</i> _i ≤ 0.0319	ns			
38	37	21	0.0758	0.1341	0.0939 ≤ p _i ≤ 0.1743	+	51	16	0.0422	0.1339	0.0997 ≤ p _i ≤ 0.1680	+			
3.3.3 Landscape-scale Habitat Selection

DISTANCE FROM WATER

Sable at MWR consistently chose to forage in areas further than the average from water sources, 2.6 km \pm 0.26 km (Sable Average Dist. \pm 95% CI), particularly during the hot dry season (Fig. 3.5a). Sable travelled as far as 5.3 km from the nearest water point at the peak of the dry season.

GRASS EVI

For the most part, sable selected for areas with significantly lower grass EVI levels than the average at MWR. During the late wet season however, sable chose for significantly higher grass EVI levels than average, indicating selection for greener and denser grass swards later in the wet season (Fig. 3.5b).

WOODY EVI

In general sable utilised areas of below average woody EVI except in the hot dry season where there seemed to be a shift towards areas with average to slightly above average woody EVI levels. During the late wet season sable chose areas with significantly lower woody EVI levels than the average available at MWR (Fig. 3.5c).

Soil Depth

Sable antelope spent the majority of their time foraging on shallower soils that the average available at MWR (Fig. 3.5d). They tended to move onto deeper soils as the dry season progressed, returning to shallow soils at the onset of the rains.



Figure 3.5 Time series graphs comparing the average use of each environmental resource by sable with the average available at MWR. Error bars represent 95% confidence intervals.

CLAY CONTENT

Sable chose soils with a higher clay content than average. Choice of clay content, as with soil depth, followed a seasonal trend, whereby sable chose soils with a significantly higher clay content during the dry season, moving into areas with a lower clay content during the early wet season (Fig. 3.5e).

PERENNIAL GRASS COVER

Sable tended to forage in areas with higher perennial grass species cover than the average available at MWR (Fig. 3.5f). There was no seasonal pattern of selection but slight peaks did exist in the early wet season and in the cool dry season.

3.3.4 MAXENT Model

MODEL EVALUATION

All outputs from the seasonal MAXENT models were considered useful, with AUC values ranging from 0.73 to 0.77. In general, all test data supported each seasonal model well, themselves producing useful fits to the models (AUC - 0.65 to 0.72), further strengthening the accuracy and usefulness of each.

VARIABLE CONTRIBUTION & PREDICTED RESPONSES

The contributions of each environmental variable for each season are given in Fig. 3.6. During the cool and hot dry seasons, clay content, soil depth and distance from water contributed the most to the MAXENT model. The general response of sable towards these variables seemed to be a selection for areas of higher clay content, shallow soils and longer distances to water. The model indicates that in the hot dry season clay content of the soil and distance from water were particularly important. During this period the predicted probability of finding sable in an area increased as clay content and the distance from water increased. During the early wet season, grass EVI contributed most to the development of the model (>60%).



Figure 3.6 Seasonal contribution of each environmental variable to the construction of the MAXENT model.

The predicted probability of finding sable decreased sharply as grass EVI increased, suggesting sable selected for areas with a lower cover of green grass during this period. Perennial grass cover and distance from water also contributed significantly to the model during this period and the predicted probability of presence increased as perennial grass cover and distance from water increased. In the late wet season, distance from water and woody EVI contributed most to the model and again the predicted probability of finding sable increased with increasing distance from water. Predicted probability of presence increased at intermediate woody EVI values and shallower soil depths. Response curves for environmental variables that contributed at least 10% to each seasonal model are shown in Fig. 3.7.



Figure 3.7 Response curves illustrating the relationship of the probability of sable presence to environmental variables over the seasons at MWR.

3.4 Discussion

These results supported hypotheses 2 and 5, which suggested sable should utilise vegetation types characterised by open canopies and well developed grass layers and that there should be a general movement of sable down the catena into the bottomlands during the dry season. However, the idea that sable should utilise larger areas during the dry season (hypothesis 1) was refuted by these results, which showed a major increase in range use by sable during the early wet season. This goes against the findings of Wilson and Hirst (1977), Parrini (2006) and Dabengwa (2009) who found that sable occupied larger areas during the dry season. The differing lengths of season used in the study were recognised as a possible source of bias but results from a Pearson's correlation analysis showed that no relationship existed between sample size and home range extent in our analysis (R = -0.03146; p=0.915). The LoCoH method of home range estimation has been shown to resist a point-number bias in range extent, converging on an area with further addition of points (Getz & Wilmers, 2004; Ryan et al., 2006). This evidence suggests that the spatial use pattern observed is ecological in character rather than the result of sampling or estimation bias. Hypotheses 3 and 4, stating that sable should range closer to water in the dry season and should choose for areas with the greenest grass, were also disproved by our results. Sable were found to be selecting areas further than the average from water sources at MWR, particularly during the hot dry season. This supported the findings of Rahimi and Owen-Smith (2007) who found that sable in the Kruger National Park spent time further from water during the dry season, only drinking every 3-4 days. Sable did not utilise areas with the greenest grass available at MWR until late in the wet season. This is contradictory to the findings of Parrini (2006) and Magome et al. (2008) who state that sable tend to select for areas with the greenest grass, even shifting range to make use of recently burnt, green flushes of grass. Gureja and Owen-Smith (2001) however found that sable were not attracted by greener, recently burnt areas and instead fed mostly on the unburnt areas at Madrid Game Ranch.

SEASONAL RANGE USE

Overall, average annual range use by sable antelope at MWR compared well with those reported for sable in the Kruger National Park by Rahimi and Owen-Smith (2007). However, the seasonal variation in spatial range use and extent at MWR indicates that sable antelope are sensitive to changes in prevailing climatic and environmental conditions. Temporal changes in range use and extent reflect changes in resource availability in the landscape. The seasonal range extent and the 90% and 50%

utilisation distributions of sable during the early wet season at MWR were significantly larger than those of any other season. This seems contrary to expectation, where studies have shown that during the critical resource limiting period, the dry season, herbivores tend to range further in search of sustenance (Wilson & Hirst, 1977; Ryan *et al.*, 2006). Results from this study suggest an environmental influence in the extension of range during the early wet season. Sable may very well select for small patches of high quality resources during the late wet and the cool and hot dry seasons restricting their range. During the early wet season, however, an abundance of high quality resources means that sable are not bound by resource availability and may range over much larger areas. An intra-season drought is also suspected as possibly playing a role in the results but since the study was conducted over only one annual cycle we were unable to verify the impacts of this drier period.

HABITAT SELECTION

The MWR is a diverse savanna ecosystem, divided into 7 geological types and 38 vegetation types. Despite this, sable tend to be selective in terms of both geology and vegetation type. Sable at MWR utilised the nutrient rich basalt derived soils almost exclusively, avoiding all other geological types (Table 3.2). Similarly, in the Matetsi Complex in western Zimbabwe, sable were also found on rough, gravely soils derived from basalt (Wilson & Hirst, 1977). This is in contrast to observations made by Chirima (2009) who found that sable in the Kruger National Park were found mostly on the nutrient poor granite and sandstone derived soils. By the nature of the geology, sable generally selected shallow, loamy soils, particularly during the wet season, often at the ecotone between woodland and grassland and along the transitional area from slope to bottomland (*pers. obs.*). This was similar to findings in previous studies which document the use of ecotonal areas by sable during the wet season (Jarman, 1972; Estes & Estes, 1974).

Sable at MWR made use of only about half the vegetation types potentially available to them. Of the 38 vegetation types found on the reserve, sable only positively selected for a total of seven over the year. A further 11 were utilised in proportion to their availability in the landscape and the remaining 20 were avoided almost entirely. Sable at MWR therefore seem highly selective in terms of vegetation type at the broad scale spending about 70% of their time foraging on four main vegetation types (1. *Colophospermum mopane – Heteropogon contortus* open woodland; 2. *C. mopane – Enneapogon scoparius* open woodland; 3. *Acacia nigrescens – Grewia villosa* open woodland; 4. *C. mopane – Endostemon tenuiflorus* open woodland) covering about 28% of the property. These four vegetation types are utilised throughout the year and are generally characterised by shallow, loamy soils

dominated by open woodland and a well developed grass layer. A further three of the 38 vegetation types at MWR were selected seasonally by sable. These were Combretum imberbe - Sporobolus consimilis open woodland on deep sandy clay loams. This vegetation type was strongly selected during the cool dry season and generally used in proportion to its availability during the other seasons. C. mopane – Panicum maximum dense shrub woodland and C. mopane – Bracharia eruciformis open woodland, both found on deep clay soils, were positively selected by sable during the hot dry season but again were utilised in proportion to their availability during the other seasons. These changes in selection of vegetation type indicated a general movement down the catena to deeper more clay rich soils in the dry season, which was further supported by our fine-scale analysis. At the finer scale, sable at MWR tended to move into deeper soils, choosing areas with higher clay content during the dry season. Similarly, both Parrini (2006) and Magome et al. (2008) documented a general movement of sable into the bottomlands during the dry season. Bottomland areas often retain moisture into the dry season, supporting green patches of grass which possibly represent key resource areas for sable. The results from our MAXENT model showed that soil depth and clay content became important factors in the suitability of habitats for sable during the dry season. The model predicted that habitat suitability for sable increased on shallower clay rich soils, which supported our habitat selection analyses.

MWR is generally well supplied with water points, with less than 2% of the area being more than 5 km from water during the height of the dry season. Water points consist of both linear and point sources, both naturally and artificially supplied. In the past literature, there have been mixed reports on the dependency of sable to permanent water. It has been reported in a number of studies that sable are a highly water dependent species, rarely venturing further than 2 km from water sources (Wilson & Hirst, 1977; Skinner & Chimimba, 2005). More recently however, Rahimi and Owen-Smith (2007) have documented more water independent behaviour in sable in the Kruger National Park. They suggest sable may be more water independent, drinking only every 3-4 days and travelling up to 7 km from water sources. Similar observations were made at MWR, where sable consistently foraged further than average from water sources, particularly during the dry season. Our MAXENT model also showed that distance from water was an important factor in determining the suitability of sable habitats, showing that habitat suitability increased with increasing distance from water. These results suggest that sable may be more water independent than previously thought, enabling the species to separate out from other more water dependent bulk grazers. This spatial separation resulting from water independence would thereby reduce interspecies competition for food as well as indirectly reducing predation risk (de Boer et al., 2010). Grazing ungulates are generally more water dependent than those

that browse (Redfern *et al.*, 2003). Sable antelope at MWR were often found browsing in the late dry season utilising a variety of woody species. This behaviour may provide a means of reducing their dependency on water during the dry season. Browsing during the dry season has been reported for sable previously in the Matetsi Safari Area in western Zimbabwe but was not documented for any reserves in the Transvaal region of South Africa (Wilson & Hirst, 1977).

Sable are classified as selective feeders (Estes, 1995), choosing areas retaining greenest grasses into the dry season (Parrini, 2006; Chirima, 2009). Conversely, it was found in this study that sable at MWR utilised areas with lower grass EVI values than the average available, particularly during the early wet season. During the late wet season however, sable selected for areas with a significantly higher grass EVI than the average available. We suggest that sable antelope, being selective, are able to select at the level of plant parts, negating the need to utilise uniform areas of dense, green grass swards. This type of selection would be at a scale finer than that detectable by EVI data, hence the conflict of results. It was however also evident from the grass EVI raster maps that areas on other geological types flushed before the basalt derived soils, suggesting that nutrients derived from the basalt soils may be more important than the absolute greenness of the grass sward. The selection of greener areas late in the wet season could be linked to the calving period, when sable require cover to hide calves during the lying-out phase. This is supported by the fact that sable used areas of open woodland, as evidenced by vegetation type and woody EVI, with well established shrub and grass layers during this period.

MAXENT MODEL

In general, the response outputs of our seasonal MAXENT models supported those of our habitat selection analyses. The main benefit of including the MAXENT analysis in the study, however, was to provide us with an idea of the relative importance of environmental variables towards the suitability of habitats for sable. The problem is that it is usually difficult to determine with modelling because the results are influenced by the correlation of the environmental predictors (Edren *et al.*, 2010). To avoid this problem, variables were pre-selected so as to avoid colinearity between predictors by excluding any environmental variables that were highly correlated. Although the models proved useful with AUC values between 0.73 and 0.77, other studies have shown much higher values (Phillips *et al.*, 2006; Kuemmerle *et al.*, 2010). This is not an indication that the models were not good but is rather a product of scale. In studies where presence only data is used, high AUC values can be obtained by utilising a large study area (Regional or sub-continental) in which the program can test absences (Wisz *et al.*, 2008).

3.5 Conclusion

The combination of using MAXENT and the habitat selection analysis proved useful in clearly showing how habitat selection by sable changed over time. This study revealed several unexpected responses of sable to seasonal changes in the landscape. Geological type at MWR seemed to form an overarching influence on habitat selection by sable and within this bound, sable selected for environmental features based on habitat structure, distance from water and species composition of the vegetation. These data suggest that sable may indirectly be sensitive to manipulations of water distribution through the associated increase in inter-specific competition and ensuing increase in predation risk. Unfortunately this study was unable to conclusively test the influence of predation pressure on habitat selection by sable because a continuous spatial distribution of predators is almost impossible to obtain. However the MAXENT model was run incorporating a 'static' estimate of predation pressure and found that predation pressure did not contribute much to the habitat selection model. For the purposes of continuity through the study, these results were however not included here. It is therefore suggested that where possible, the effect of predation pressure be included in habitat selection analyses, as it has been shown that predation pressure can have a major influence on the distribution of ungulate species.

3.6 References

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4. CHAPTER 4 The possible causes of the decline of sable antelope (*Hippotragus niger*) in south-eastern Zimbabwe.

4.1 Introduction

On the Malilangwe Wildlife Reserve (MWR), formerly Lonestar Ranch, Booth (1980) estimated the sable population to be in excess of 200 individuals but following the severe drought of 1991-1992, the population declined to only 40 animals (Saunders, 2009). In 1994, after the establishment of the Malilangwe Trust, 197 sable were introduced from the Matetsi safari area in western Zimbabwe in the hope of boosting the existing population. However, the population failed to recover and numbers had again declined dramatically to only 62 individuals by 2005 (Fig. 1.1) (Goodman, 2009). This unfortunate trend has been witnessed in several protected areas in Southern Africa, most notably in the Kruger National Park (KNP) which is one of Africa's largest and most carefully managed parks. Grant and van der Walt (2000) state that in 1986 there were some 2240 sable in the KNP but by 1999 these had declined to only about 505. This is not a new phenomenon, with Wilson and Hirst (1977) reporting declines in sable throughout southern Africa in the 1970's. A number of hypotheses have been put forward to explain the decline including competition with other herbivores (Harrington et al., 1999), increased predation (Grant & van der Walt, 2000; Owen-Smith et al., 2005), rainfall variation (Owen-Smith et al., 2005), disease (Nijhof et al., 2005; Oosthuizen et al., 2008) and habitat loss (Grant & van der Walt, 2000). The common basis of many of these hypotheses stems from the provision of artificial water and the effects thereof. As a result, the factors leading to the decline of the species are confounded making solving of the problem difficult.

In the KNP, Owen-smith *et al.* (2005) suggest that elevated predation pressure, as a result of the influx of zebra and wildebeest into the sable ranges, has precipitated the decline. They speculate that the provision of artificial water points in these areas has attracted high density, water dependent herbivores to the area leading to an increase in lion numbers and subsequently increased predation pressure. Similarly, Owen-Smith & Mason (2005) propose that the decline can be attributed to elevated predation-related mortality, specifically on the adult segment of the sable population. An alternative theory could be that an increase in the density of other herbivores may cause a significant increase in the tick challenge faced by sable over time. This could result in significantly higher tick loads and the

transmission of potentially lethal tick borne diseases to the sable. It has been repeatedly shown that ticks and tick borne diseases have the capacity to cause mortalities in sable and particularly in the juvenile age-class (Wilson *et al.*, 1974; Grobler, 1981; Meltzer, 1992).

4.1.1 Predation as a threat

The top-down impacts of predators on prey populations have been well documented. Impacts are particularly limiting when populations are small, such as the roan antelope population in the Kruger National Park (Harrington *et al.*, 1999; McLoughlin & Owen-Smith, 2003). It has been shown that predation undoubtedly plays a major role in preventing the growth of plains game populations in the Etosha National Park, Namibia (Gasaway *et al.*, 1996) and Festa-Bianchet *et al.* (2006) demonstrate that stochastic predation events have a detrimental impact on the persistence of bighorn sheep in North America. The susceptibility of a prey species to predation is governed by a number of factors including the density of different predator species, the average body size of the prey species concerned, average herd size, habitat selection, its relative abundance and anti-predatory tactics (Hayward & Kerley, 2005; Hayward *et al.*, 2006). Through the manipulation of the environment, man indirectly alters the predator-prey balance, rendering some species more susceptible to predation. Sih (1987) explains that prey refuges, whether behavioural, spatial or temporal, form an important part of the stability of predator-prey relationships. Changes in habitat structure, abundance of prey species, availability of resources and animal behaviour associated with the provision of artificial water points can therefore upset the delicate balance.

4.1.2 Ticks as a threat

The possible role that ticks and tick-borne diseases may play in the decline of sable antelope has been relatively overlooked in the literature thus far. It has, however, been repeatedly demonstrated that ticks can have significant impacts on wildlife through reduced fecundity, poor overall condition and disease related mortalities (Grobler, 1981; Lightfoot & Norval, 1981; Oosthuizen *et al.*, 2008). The effects ticks have on ungulates can be generally divided into five categories, namely: tick-borne diseases, tick worry, metabolic debilitation, tick toxicoses and secondary infections (Lightfoot & Norval, 1981). Grobler (1981) states that ticks played a major role in the mortalities of sable in the Rhodes Matopos National Park and describes cases of metabolic debilitation, secondary infections, tick-borne diseases

and tick toxicosis. Lightfoot & Norval (1981) suggest that sable are highly susceptible to ticks and many previous studies describe cases of sable in poor condition carrying massive tick loads and possessing *Theilleria*-like piroplasms in blood smears (Wilson *et al.*, 1974; Grobler, 1981; Oosthuizen *et al.*, 2008). The potential impact that ticks may have on a species is determined, inter alia by the level of tick challenge faced over time. In general, tick abundance is determined by a suite of factors such as rainfall, grass cover, humidity, temperature and stocking rate (Walker *et al.*, 2003). Increased zebra and wildebeest abundance around artificial water holes therefore could, in theory, have the potential of causing increased tick densities, negatively affecting other animals inhabiting these areas.

Both predation and ticks could potentially be key factors contributing to the decline of the species at MWR. Further, the effects of predation and ticks on sable populations may be confounded due to the reduced fitness associated with tick infestation and the subsequent capture of weaker, more vulnerable animals by predators. This paper speculates on the possible role of each of the two hypotheses in the decline of the species and looks at what measures may be taken to stabilize and promote recovery of the sable population at MWR.

4.2 Methods

4.2.1 Study Site

The MWR is located in the south-eastern lowveld of Zimbabwe and stretches some 39 378 ha in extent. The reserve in bordered by the Gonarezhou National Park to the south, the Hippo Valley Game Section to the west and by communal land to the north and east (Fig. 4.1).



Figure 4.1 Map showing the location of MWR.

The MWR falls under a typical savanna climatic regime with hot wet summers and cool dry winters. The long-term average annual rainfall for the area is 562mm measured from 1951-2009. During the 2009-2010 season, MWR received 552mm of rainfall and the average monthly maximum and minimum temperatures recorded were 33.9°C in November and 13°C in July, respectively. Much of the reserve is dominated by various types of open *Cholophospermum mopane* woodland with the Malilangwe sandstone range being characterized by *Brachystegia* woodland. The property has been classified into 38 vegetation types based on the composition of both the woody and herbaceous layers,

the structure of the woody component and the topo-edaphic factors that influence the plant communities (Clegg, 2010a).

4.2.2 Data Collection

An adult female from four of the five herds at MWR was fitted with a GPS/VHF collar (Telemetry Solutions, California). Each collar was programmed to take a GPS position every two hours, night and day. These data were then stored on the collar until downloaded via a wireless signal to a Hewlett Packard IPAQ personal digital assistant (PDA). Downloads from the collared female in each herd were performed from a stationary vehicle parked 30-50 meters from the collared female. Data were downloaded bi-monthly on the 1st and 16th of every month and these data were then used in the study design and analysis of both theories mentioned above. Several collar failures were experienced during the study period, but in all cases collars were replaced as soon as was possible. Collar failures had no effect on the analysis of predation data but failures did hamper our efforts to perform tick drags for some herds during the study period.

PREDATION RISK

To predict the risk of predation by lion, leopard and hyaena spatially, data emanating from a leopard census conducted over the sable study period were used. The method employed for the leopard census was devised by Dusty Joubert of Sango Wildlife Ranch (SWR), who was conducting the same study concurrently. He was looking at the effects of hunting on leopard populations at SWR and using MWR as a comparison. Essentially the method involved a strategy of "mark and recapture" to estimate the total number of leopards at MWR. The distribution of large predators over the property was estimated as a by-product of the leopard study and this was developed into a spatial representation of the predation risk posed by each species.

The "mark and recapture" study was conducted over two phases, spanning the 2009 and 2010 dry seasons. During the first phase, the reserve was divided into squares using a 4 x 4 km grid. Within each grid square, 3 bait sites were chosen, commonly at the intersection of roads or paths. Predators often use roads when moving from one area to another and as a result the probability of a bait being taken is increased. To further enhance the probability of predators finding the baits, intestines soaked in blood and stomach contents were dragged along the road for the last 300 m of the route to the bait sites. At each bait site, an impala carcass with its skin removed was hung in a suitable tree. The carcass was

positioned at least 1.8 m above the ground and was securely fastened to the tree. A forked leading pole was placed against the bait tree to provide an access route for predators to the bait. Baits were covered with leafy branches to camouflage them from vultures so as to prolong the life of the bait. A Moultrie infrared camera (Global Point Products, New York) with a built-in motion sensor was positioned on a suitable tree 2 - 4 m to the right side of each bait, with its line of sight at 90° to the leading pole. When a predator or any other animal climbed up the leading pole or approached the bait, the motion sensor triggered the camera. The minimum interval between photographs was set to 1 minute. Due to its position to the right of the leading pole the camera always took a picture of the right side profile of the animal.

Baits were hung in batches of 9 (limited by the number of cameras) at a total of 76 sites (Fig. 4.2), working from west to east, and starting in the north and moving to the south of the reserve. Photographs stored on the cameras were downloaded at 3 day intervals to a laptop computer, allowing us to identify if any animals had visited each site. Each bait was monitored for a maximum of 14 days, after which it was removed. Leopards captured in pictures at each bait site were identified by their spot patterns and records of each were stored as an identikit.

Phase two of the "mark and recapture" study entailed the setup of a further 26 baits over the reserve. This was done using a stratified random sampling method with Hawth's tools, an extension in ArcGIS 9x (ESRI, 2009). This phase formed the "recapture" phase of the census and allowed us to estimate the total population of leopards on the property by counting the number of "marked" and "unmarked" leopards captured. The total number of leopard on the reserve was estimated using the Peterson method (Greenwood, 1996) which estimates the population size (N) as

$$N = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1) - 1}$$

where: n_1 = the number of leopards identified during the marking phase; n_2 = the total number of leopards captured during the recapture phase, and m_2 = the number of leopards recaptured that had already been identified during the marking phase.



Figure 4.2 Shows the location of bait sites used in the predator study at MWR between April 2009 and August 2010.

Photos derived from each bait site were analysed and the presence of a large predator species was noted. For leopards, each individual that visited a bait was identified by its spot patterns and the actual number of leopards visiting each bait was used as a weighting for that site. For lion and hyaena, which are impossible to identify from a distance, a novel method of determining predator density was developed. Each bait site was weighted according to the time it took for a predator to take the bait. If a predator took the bait within three days of it being put up, the bait was assigned a weight of 3 for that specific predator. If it took between four and seven days for the predator to strike, the bait was assigned a weight of 2 and if the bait was taken between eight and 14 days after being put up it was assigned a value of 1. If no predators were discovered at a bait site, the site was assigned a value of zero.

The presence of a large predator species at each bait site was then plotted on a map of MWR using ArcGIS 9x (ESRI, 2009) software and assigned the corresponding weighted value according to the time it took for the animal to discover the bait, or in the case of leopard, the number of individual leopards visiting the bait site. An inverse distance weighted technique (IDW) was used in ArcGIS 9x (ESRI, 2009) to interpolate between the points, essentially creating a density surface for each predator species at MWR. These density surfaces were then exported to IDRISI 32 (Eastman, 2001) GIS software, where a utilization distribution (UD) was created by making the total value of all the pixels on the map add up to one. The UD maps for each predator species were then multiplied by their respective population estimates at MWR, giving an estimate of the potential predation risk posed by each predator species was assumed uniform. This was due to the fact that the juvenile and sub-adult stages of the sables' life cycle fall well within the prey size ranges of both leopard and hyaena (Hayward, 2006; Hayward *et al.*, 2006) and adult sable fall within the range of prey size preferred by lions (Radloff & du Toit, 2004).

TICK CHALLENGE

To estimate the potential tick challenge faced by sable over the study period an intensive method of drag sampling over vegetation within the range of each sable herd was employed. On the 1st and 16th of each month GPS data were downloaded from each herd's collar and imported into ArcGIS 9x (ESRI, 2009). The GPS positions downloaded for each herd were sequentially joined using the Hawth's tools extension in ArcGIS 9x, essentially creating a foraging path for each herd over the 15 day period. Again, using the Hawth's tools extension, sample points were placed every five kilometres along the foraging path and these points were used as the starting position of each tick drag. Tick drags were performed using ten 1 000 mm x 100 mm flannel strips, with an 80 mm x 4 mm diameter metal rod sewn into their loose ends as a weight. These were attached adjacent to one another on a 1 200 mm-long wooden spar by means of Velcro tape. The flannel strips were dragged at normal walking pace, by means of a harness attached to the ends of the wooden spar, over the vegetation in a circle for a distance of 100m, finishing at or as close to the starting point as possible. After each drag, the wooden spar with the flannel strips attached was suspended between two trees 1.5 m off the ground. Each flannel strip was then removed from the spar, always working from left to right, and ticks were picked off using forceps. Tick samples taken off each strip were then placed in vials of 70% ethanol, with labels recording the date and time of the drag, the GPS point at the start of the drag and which herd's range the drag was performed in. Once the ticks had been removed from each strip, the strip was reattached to the spar in readiness for the next drag. At each drag point the date and time of the drag, the vegetation type, the density of the grass cover and the number of ticks collected were recorded on a data sheet. This provided an estimate of the potential tick challenge faced by each sable herd over time and allowed us to compare the tick challenge faced by sable at MWR with data from elsewhere. Collar failures proved to be a major problem during the field work phase of the study and as a result it was impossible to conduct tick drags for all herds consistently over the study period.

4.2.3 Data Analysis

PREDATION DATA

Adult and sub-adult survival of sable at MWR was good (96%) for all herds during the study period and it was therefore not meaningful to include these data in the analysis of the effects of predation risk on ageclass survival. Therefore, linear regressions were used to test the relationship between only juvenile survival and predation risk during the period between February and May 2010. It was recognised during the study that sable calves seem most vulnerable in the first few months of life, hence our focus on the calving and post-calving period between February and May 2010. The risk of predation was regressed in KyPlot (KyensLab Inc., 2002) against the rate of juvenile survival of sable for each large predator species at MWR. Juvenile survival rates for sable were determined by working out the ratio of juveniles present in each herd at the beginning of May 2010 with the number of adult females in the herd. It was considered fair to assume that each adult female in each herd fell pregnant every year, as it has been widely stated that sable females are highly fecund and that conception rates are consistently high (Wilson & Hirst, 1977; Grobler, 1980). At MWR alone 96% of the adult females were observed to be pregnant in the 2009 to 2010 breeding season (*Pers. Obs.*).

Predation risk was determined by extracting the average risk of predation from the utilisation distribution surfaces for each predator species between February and May 2010 in IDRISI 32 (Eastman, 2001), using presence data downloaded from the sable GPS collars. Using only four data points in the regression representing the four collared herds at MWR was not considered adequate. Therefore, a fifth data point was developed for each regression by using data collected opportunistically from the fifth sable herd at MWR. This herd was encountered relatively frequently during the fieldwork phase of the study and during each encounter the demographic breakdown of the herd and the GPS position were recorded. These GPS data collected between February and May 2010 (nine positions) were used to extract the average

predation risk faced by this herd from each predator species. Data on juvenile survival to May 2010 were also derived from these opportunistic sightings and included in the regression.

The long-term effect of predation on the sable population was tested using historic data extracted from the MWR report database. Data on the number of sable carcasses reported between 2000 and 2010 were extracted from the database, along with information on the date and time of each report, their spatial position, the sex and age of the animal and the cause of death. These data were recorded by the MWR scout force on their daily patrols. Patrol effort by each patrol group is constantly monitored at MWR using coverage reports and effort between years is relatively consistent. Sable mortality data extracted from the database were compared using a bar graph to show the causes of mortality in the sable population at MWR between 2000 and 2010. The percentage of sable mortalities attributed to predation was compared with other causes and the contribution of each predator to the total number of sable mortalities between 2000 and 2010 was estimated. Linear regressions were used to determine the relationship between the annual rate of population decline in sable between 2000 and 2010 and the number of lion at MWR during the same period. Lion population numbers at MWR between 2000 and 2010 were estimated using a number of different methods including spore counts, call-up surveys and known pride numbers. Estimates were also not conducted at the same time every year and no consistent data were present on the demographic structure of the population. To reduce the uncertainty associated with this, a two-point moving average of the lion population estimate was used for each year in these linear regressions. Similarly, for ungulates at MWR, the annual census is conducted in September or October each year meaning that losses of sable may be incorrectly associated with lion population estimates for each year. Therefore a two-point moving average of the sable population estimates was also used to derive the annual rate of decline in sable numbers. The annual rate of decline was estimated by subtracting the size of the sable population in year x (N_x) from the population size in year x+1 (N_{x+1}) and dividing by N_x (Scott Mills, 2007).

TICK DRAG DATA

The total number of ticks, the number of drags and the average number of ticks collected during each drag were determined from data recorded during the study period. The seasonal abundance of ticks was analysed by plotting a time series graph of the \log_{10} transformed average number of ticks collected per drag during each 15-day period over the year. Tick abundance data were \log_{10} transformed to reduce the effects of over dispersion of these data (Horak *et al.*, 2006). A B-spline fit was fitted to the data in KyPlot (KyensLab Inc., 2002) to smooth the data and reveal the trend. Mortalities caused by tick infestation or

disease most often occurs in juveniles or neonates of species, with adults generally being resistant to tick toxicosis and tick borne diseases (Grobler, 1981). Therefore, for each sable herd at MWR, the \log_{10} transformed average number of ticks collected per drag between February and May 2010 was regressed against juvenile survival to test whether the potential tick challenge had any influence on calf survival during the first few months of life.

4.3 Results

EFFECT OF PREDATION

Predation risk was not uniform over MWR and although some overlap between areas of high predation risk existed, the distributions of risk from each large predator species were markedly different (Appendix V). As such, a distinction could be made between the potential effects of each predator species. Juvenile survival was negatively correlated (R = -0.795; $R^2 = 0.632$) with hyaena predation risk (Fig. 4.3) but was not significant at the 95% level (p = 0.108). The results suggest that hyaena may play a role in the poor survival rates observed for sable neonates at MWR. As the risk of predation by hyaena increased, juvenile survival declined.



Figure 4.3 Linear plot showing the relationship between juvenile survival and predation risk by hyaena. The red data point represents the fifth sable herd at MWR.

Conversely, juvenile survival was positively correlated with both leopard and lion predation risk. The relationship between leopard predation risk and juvenile survival (Fig. 4.4) was weak (R = 0.564; $R^2 = 0.3178$) and results suggested that leopard predation had little effect, if any, on the survival of juvenile sable during their first few months of life.



Figure 4.4 Linear plot showing the relationship between the risk of predation by leopard and survival of juvenile sable at MWR. The red data point represents the fifth sable herd at MWR.

Juvenile survival however showed a stronger positive relationship towards increasing lion predation risk (R = 0.833; $R^2 = 0.693$), indicating that as lion predation risk increased, the chances of survival for juvenile sable improved (Fig. 4.5).



Figure 4.5 Linear plot showing the relationship between juvenile survival and predation risk by lions. The red data point represents the fifth herd at MWR.

Historic data on sable mortalities at MWR between 2000 and 2010 show that predator related mortality is the primary cause of death in sable antelope (Fig. 4.6). Predators accounted for 76% (n = 38) of all sable mortalities between 2000 and 2010. Two further mortalities are explained by the 2004 anthrax outbreak, which devastated populations of many herbivore species at MWR (Clegg *et al.*, 2007). The

majority of carcasses discovered, 87%, were from the adult and sub-adult age classes with only 5 of the 38 mortalities discovered between 2000 and 2010 being from the juvenile age class.



Figure 4.6 Bar graph showing the cause of recorded mortalities in sable antelope at MWR between 2000 and 2010.

Predation accounted for most of the mortalities recorded thus far for sable at MWR, and of these predator related mortalities, more than 86% were attributed to lion predation. Results of a linear regression investigating the relationship between lion numbers and the rate of annual decline in the sable population between 2000 and 2010 (Fig. 4.7) suggest that lions play a major role in limiting the success of sable at MWR (R = 0.811; $R^2 = 0.659$; p < 0.01). As lion numbers increased, sable numbers declined.



Figure 4.7 Linear plot showing the relationship between lion population size and the rate of annual population decline.

EFFECT OF TICK CHALLENGE

We conducted a total of 773 tick drags over the study period collecting a total of 12 640 ticks. The number of ticks collected between drags was highly variable, even when points were very close together. Individual herd size seemed to have no relationship with the average number of ticks per drag for each herd, suggesting that tick abundance on the vegetation during the study period had no effect on herd numbers. Fig. 4.8 shows the log_{10} of the combined average number of ticks collected per drag over the entire study period at MWR. The smoothing curve reveals a somewhat cyclic trend in tick abundance on the vegetation during the study period by drags, seemed to be highest during the dry season and lowest during the early wet season (Fig. 4.8).



Figure 4.8 Log_{10} of the combined average number of ticks picked up per drag over the study period at MWR. A smoothing curve was fitted to these data to reveal the trend.

Tick challenge determined by dragging seemed to have no influence on juvenile survival (R = -0.120; $R^2 = 0.014$) at MWR (Fig. 4.9). The Manyoka herd had a 75% survival rate of calves to four months, the highest of any herd at MWR, and showed the highest level of tick challenge between February and May 2010. The second highest level of tick challenge was found in the Chavagwiza area and conversely, the Chavagwiza herd had no calves survive to four months of age. The remaining herds had extremely low tick challenges, as revealed by dragging, and calf survival to four months was 50% for each.



Figure 4.9 Linear plot showing the relationship between juvenile survival and tick abundance between February and May 2010.

4.4 Discussion

In theory, both predation and ticks have the potential to cause losses in the sable population at MWR (Grobler, 1981; Lightfoot & Norval, 1981; Owen-Smith & Mason, 2005). The data suggests however that predation is the main cause of mortality in sable antelope at MWR. Although the results with reference to the relationship between predation and juvenile survival may be speculative due to the limited number of data points, the indication is that hyaena predation is a key driver in the low survival rates observed for juvenile sable. Similar observations have been reported for other areas in southern Africa including the Matetsi safari area and the Okavango Delta (Fivaz, 2010; Hensman, 2011). The relationship between calf survival and hyaena predation risk, although strong, does show variance and could possibly be attributed to the level of vegetation cover available. Sable calves lie out for the first two to four weeks after birth (Estes, 1995) and rely on vegetation cover for concealment. At MWR, grass EVI, essentially a surrogate for grass cover, showed a strong relationship with calf survival. The trend showed that as the amount of grass cover declined, calf survival decreased (Appendix IV). Again the relationship showed some variance but the data suggests that vegetation cover and hyaena predation risk may interact, ultimately affecting calf survival. This interaction between vegetation cover and calf survival would be exacerbated at the marginal range for sable such as at MWR and the KNP. This is because of lower and erratic rainfall which directly influences vegetation cover. In areas of higher rainfall, where sable seem to do well (East, 1999), vegetation cover is not such a constraint and as such, juvenile survival would be better.

The trends observed for juvenile survival in relation to leopard and lion predation risk lend support to the theory that hyaena may be impacting on the survival of juvenile sable at MWR. The distribution of predator species at MWR was not uniform and although some overlap between areas of higher predation risk exist, generally, predator species showed different distributions across the reserve (Appendix V). The increased survival of sable calves in areas of higher predation risk by lions could be explained by a displacement of hyaena due to the risk of conflict with lion, as well as the fact that juvenile sable fall outside of the range of prey size preferred by lion (Hayward & Kerley, 2005). The relationship between juvenile survival and predation risk by leopard was weak and did not provide any evidence as to what impact leopard may be having on the survival of sable calves. Leopards are known to prey on juvenile sable antelope opportunistically (Grobler, 1981; Hayward *et al.*, 2006) and therefore could potentially impact on the survival of sable calves at MWR should encounters occur.

Historical evidence from MWR indicates that lion predation is responsible for the majority of sable mortalities discovered by the MWR scout force on their daily patrols between 2000 and 2010. Results from this study suggest that the higher lion numbers at MWR prior to 2005 are primarily responsible for the observed decline in the species. The decline in lion numbers post 2005 at MWR (Appendix III) was a direct result of the 2004 anthrax outbreak (Clegg, 2010b) which devastated prey populations at MWR (Clegg *et al.*, 2007). Results show that as lion numbers increased, the rate of decline in the sable population was accelerated. A similar theory was proposed to explain the decline of sable in the Kruger National Park. Owen-Smith et al. (2005) suggest that the provision of artificial water points in sable areas in the Kruger National Park attracted high density, water dependent herbivores to the area leading to an increase in lion numbers and subsequently increased predation pressure. Roan antelope in the Kruger National park have suffered the same fate and managers have closed several water points in an attempt to curb the trend (McLoughlin & Owen-Smith, 2003). The provision of artificial water in previously dry areas during the dry season allows water dependent, high density grazers to occupy areas that were historically inaccessible to them. Coupled with this, the larger area now accessible to animals allows for the establishment of more lion prides and higher lion numbers. Historically, because of limited access to water resources during the dry season, prey densities must have been lower and conflict between lion prides for food and territories must have been high. This situation would have limited lion numbers through intra-specific conflict and created prey refuges for those more water independent species, which could travel further from water sources.

Overall, tick abundance at MWR as determined by tick drags was lower than those data presented from the KNP, South Africa. Individual sable darted over the study period also showed very low tick loads when compared with those from another area in Zimbabwe (*Pers. Obs.*). In October 2009, on a game capture trip to Cawston Ranch, North of Bulawayo, several sable were found in poor condition carrying massive tick loads. One was found immobile, covered in engorged ticks, suffering from anaemia and malnutrition. The animal later died, no *theilleria*-like piroplasms were found on blood smears and it was suspected that she succumbed to tick toxicosis, a result of the massive tick load she was carrying (Fivaz, 2009). Similarly it was reported that ticks played a role in sable mortalities in the Rhodes Matopos National Park (Grobler, 1981). Results from this study indicate that tick challenge had no influence on calf survival at MWR during the study period, as determined by dragging. Dragging however, is only effective in sampling those tick species and life stages that quest for hosts on vegetation, hence limiting the spectrum of species and development stages in the sample (Horak *et al.*,

2006). Some data were collected opportunistically on the actual tick loads carried by animals when animals were darted to fit collars. These data, however, were too few to analyse and often did not coincide with periods when drags had been performed, making comparisons of actual tick loads and those collected on drags impossible. In May 2010, the fresh carcass of a young calf was discovered. Vultures had damaged the carcass to some extent and determination of the cause of mortality was impossible. The calf was sent for post-mortem and results were inconclusive (Appendix VI). It was however established from blood smears that tick borne diseases were not the causal factor, but the report speculates that malnutrition or predation may have been responsible.

4.5 Conclusion

Although speculative in places due to a lack of data points, the findings from this study provide evidence that the decline of sable antelope at MWR is being primarily driven by the top-down effects of predation. It is however also clear from past literature, and personal observations elsewhere, that ticks can potentially cause mortalities in sable. We suggest that future studies of this nature look into predator diets, through dung sampling, over the sable calving period to determine if sable calves are in fact being preyed upon. Historic data on lion numbers and population declines, as used here, may also be useful in determining the role lions play in the decline of the species. The analysis of the influence of ticks was inconclusive, due to under sampling and at times a lack of resources and it is recommended that future studies on the role of ticks be conducted over a longer period of time and use a multi-faceted approach of tick drags, tick loads carried by individual sable and lab analysis of blood samples.

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5. CHAPTER 5 Conclusions: Study findings, conservation implications and management recommendations

5.1 Conclusions

5.1.1 Overview

This study focused on determining the possible factors limiting the success of sable antelope at the Malilangwe Wildlife Reserve (MWR) in south eastern Zimbabwe. The study incorporated three key elements: (i) an analysis of the population dynamics and current viability of the sable population; (ii) a study of space-use and habitat selection by sable; and (iii) an investigation into the possible causes of the decline of the species. Although each part of the study was approached independently, the various elements combined well providing an indication of the factors driving the decline.

5.1.2 Study findings

POPULATION DYNAMICS & POPULATION VIABILITY

1. What is the future outlook on the sable population at MWR under current conditions?

Under current conditions, the sable population at MWR is predicted to increase steadily and remain viable for the next 100 years. However, this prediction is based on the conditions experienced at MWR only between 2009 and 2010. Changes in environmental variables such as rainfall, predator numbers and disease outbreaks could therefore adversely affect the sable population. The population, being small, remains vulnerable because small or declining populations are governed by a high level of insecurity due to demographic and environmental stochasticity (Begon *et al.*, 1996). Boosting the population through live introductions may well reduce the immediate risk of extinction but the ecological and social impacts of this will need to be taken into consideration.

2. What are the key areas of breakdown in the growth of the sable population?

The high neonatal mortality observed in sable at MWR was initially suspected as being the driver of the decline in the population. It was however shown in this study, that under current conditions even a 25% decrease in juvenile survival did not lead to a negative growth rate. Population growth was most sensitive to changes in adult survival and the model suggests that reduced adult survival prior to 2005 was to blame for the decline observed in the sable population. It is possible that the high neonatal mortality has restricted growth in the sable population since 2005 and under this constraint further mortalities in the adult segment of the population would lead to a population decline.

3. What effect will augmenting the population have on the overall viability of sable at MWR?

Under current conditions, augmentation of the population would provide a boost to the sable at MWR, reducing the vulnerability of the population to demographic and environmental stochasticity. The model showed however, that if measures are not taken to prevent mortalities in the adult segment of the population, augmentation will do little, if anything to ensure the continued viability of sable at MWR. Augmentation of the sable population is however not a straight forward process. Social effects of the introduction of more sable herds to MWR would have to be considered as well as determining whether there is actually enough suitable habitat to support an increased number of sable herds.

HOME RANGE USE & HABITAT SELECTION

1. Did the distribution of water during the dry season affect sable range use?

Distance from water did not seem to pose a constraint on sable at MWR during the dry season. In fact, sable foraged further than average from water, sometimes returning only every four days to drink. Similarly, distance from water in the Kruger National Park, South Africa did not restrict sable movements and herds travelled up to seven kilometres from water, only drinking every 3 to 4 days (Rahimi & Owen-Smith, 2007). The distribution of water points has been a central theme of many theories on the decline of sable antelope (Owen-Smith *et al.*, 2005) and the finding that sable are less water dependent than previously thought (Rahimi & Owen-Smith, 2007) lends weight to the hypothesis that the provision of artificial water in predator rich reserves impacts negatively on sable populations.

2. What effect did resource limitations during the dry season have on sable range use?

The dry season is considered to be the critical period for ungulates in savanna climates mostly due to the decline in forage quality and concentration of water resources. Sable at MWR did not follow the usual pattern associated with range use during the dry season. Most ungulates use larger areas during the dry season as they search for enough forage to sustain themselves throughout this resource limiting period (Ryan *et al.*, 2006). Interestingly, sable at MWR used larger ranges during the early wet season than during the resource limiting dry season. These results suggest that sable, being selective feeders, are able to make use of patches of high quality forage during the dry season, ranging further during the early wet season when the seasonal resource constraints have been lifted.

3. Which resources are key determinants in the selection of suitable habitats by sable at *MWR*?

Geology formed the overarching variable in explaining the distribution of sable at MWR. Sable foraged almost exclusively on the nutrient rich basalt derived soils which cover about 48% of the reserve. Within this constraint, sable selected for habitats characterized generally by an open woody layer and a well developed grass layer. Sable positively selected for only seven of the 38 vegetation types at MWR and made use of only four of these throughout the year. Sable seemed to utilise a niche of the environment characterised, during the wet season, by shallow calcareous soils, with underlying clay horizons, a high cover of perennial grass species and an open woody layer. During the dry season however, sable chose areas with deeper soils, a higher clay content and a more dense woody layer. These dry season areas were often found

along drainage lines, generally moisture rich areas that allow grasses to hold green leaf well into the dry season.

4. Which environmental predictors were most important in determining the suitability of sable habitats at MWR?

Distance from water, soil depth and clay content of the soil were consistently the most important predictors of habitat quality for sable. However, other predictors did become important during the wet season. Suitable habitat was generally characterised as being far from water and on shallow soils with a high percentage of clay. Grass EVI, woody EVI and perennial grass cover became important factors during the wet season with sable choosing areas with a lower grass EVI early in the wet season. Later in the wet season there was a movement into areas of higher grass cover as indicated by higher grass EVI values, lower woody cover as indicated by lower woody EVI values and areas with a high cover of perennial grass species. It is possible to speculate that the movement into areas of higher grass cover was to maximise the use of vegetation cover for calves during the hiding phase.

5. How do the ranges of the current sable herds at Malilangwe compare with the quantity of suitable habitat, i.e. is there space for more sable herds?

Results from the habitat suitability model indicate that the extent of suitable habitat at MWR is generally restricted to the basalt derived soils. The current ranges of the five sable herds at MWR occupy the major part of the basalts and hence the remaining extent of suitable habitat is limited. The successful introduction of additional sable herds at MWR may therefore be hampered by a lack of suitable habitat in which a new herd could establish a territory. It may therefore be more beneficial to manage the existing herds to encourage growth within the population, rather than through the introduction of additional herds.

POSSIBLE CAUSES OF DECLINE

1. What were the causes of mortality in the sable population between 2000 and 2010?

Historical data taken from scout patrol reports indicates that the primary cause of mortality in sable antelope between 2000 and 2010 was predation. Predators accounted for 76 % of all sable mortalities (n = 38) at MWR during this time period. A combination of factors such as poaching, disease and electrocution explain the remaining mortalities. The majority of carcasses found were from the adult age-class (87 %) and of all the sable mortalities recorded between 2000 and 2010, 87 % were recorded prior to the end of 2005.

2. How did predation affect the survival of sable during the study period?

Adult survival of sable at MWR was generally good over the study period (96 %). Only two deaths were recorded, both as a result of predation. An adult male sable was preyed upon by lions in August 2009 and in July 2010 a pack of wild dogs ambushed an adult female sable. The effect of predation on the sub-adults and yearlings was impossible to quantify because no carcasses were found for individuals in these age-classes. The survival of sable calves at MWR was low (41 %) and results indicate that predation by hyaena was a key driver. Hyaenas can consume a juvenile sable so completely that not a trace of the animal can be found (Owen-Smith & Mills, 2008) making the finding of juvenile carcasses impossible. Therefore, during the study period, it was revealed that predation had a negligible effect on the survival of the older age classes at MWR but hyaena predation impacted heavily on the survival of juvenile sable.

3. What effect did tick abundance have on the survival of sable over the study period?

Our results indicate that tick abundance at MWR was low during the study period and that ticks had no influence on the survival of sable. Although ticks have the potential to cause mortalities in sable antelope (Wilson & Hirst, 1977; Grobler, 1981; Oosthuizen *et al.*, 2008), no mortalities due to ticks were observed at MWR during the study period. Tick abundance on the vegetation at MWR was low when compared with data published for ticks in the Kruger National Park, South Africa (Horak *et al.*, 2006). Similarly, somewhat subjective observations revealed that actual tick loads carried by sable at MWR were much lower than those of sable on another ranch in Southern

Zimbabwe (*Pers. Obs.*) further suggesting that ticks at MWR had no influence on the survival of sable during the study period.

4. What is the most likely explanation for the initial decline and continued lack of growth in the sable population at MWR?

Results from this study indicate that the initial observed decline in the sable population between 2000 and 2005 at MWR was a result of increased mortality in the adult segment of the population. The results suggest that higher lion numbers were the key players in driving the decline. The continued lack of growth in the population since 2005 can be attributed to poor juvenile survival, a result of predation by hyaena and other factors. The relationship between hyaena predation and juvenile survival is not entirely clear and it is suspected that vegetation cover plays a role in mitigating the risk of predation. It is speculated that this is the reason for the lack of success of sable populations in the drought prone, marginal range for the species.

5.1.3 Conservation Implications and management recommendations

The finding that predation may be the key to explaining the decline of sable at MWR poses implications not only for the conservation of sable themselves but for the conservation of predators and other herbivore species as well. Central to the theory behind the decline of sable antelope at MWR is the age old debate about water provision. The provision of artificial water points has a number of effects on small enclosed reserves like MWR, not all of which are beneficial. The concept of the provision of artificial water points was originally initiated in an attempt to reduce the effects of a drought by ensuring a reliable supply of water (Gaylard *et al.*, 2003). The oversight was that by providing water points throughout the landscape in the dry season, areas that were previously not utilised by more water dependent species such as buffalo, zebra and wildebeest would now be accessible. This results in an artificial increase in the ecological carrying capacity of the land. Evidence suggests that the increase in herbivore numbers as a result of the provision of artificial water reduces herbivore diversity by enabling high density water dependent species and predators to expand their distributions (Smuts, 1978), this to the detriment of the rarer antelope species (Owen-Smith, 1996).

The conservation of sable at MWR is therefore not a straight forward undertaking and the mechanisms driving their decline are complex and diverse. It is expected that in order to ensure the viability of sable at MWR, some sacrifices may need to be made. The control of lion and hyaena populations may be an option but methods for controlling predator populations are not well studied and the effects of this may not be predictable. A reduction in the number of water points may be a solution but this would be a longer term solution and may impact on the high density, water dependent species found at MWR. Coupled with this, the closure of several water points in the Kruger National Park has done little to curb the trend, possibly a result of predators now being more reliant on rare antelope species following the emigration of the high density, water dependent species (McLoughlin & Owen-Smith, 2003). It may therefore be necessary to initially control predator populations, if possible, through live relocations as well as reduce the number of artificial water points at MWR.

It is recognised that there were several short-comings of this study. Firstly, the study was conducted over only one annual cycle essentially presenting data related to a "snapshot" in time. A longer study period would have gone a long way to unravelling some of the uncertainties associated with the data presented here. Many of the results presented are speculative in that trends were derived from relatively few data points. This being said, these results echo those presented elsewhere and as such provide credibility to these data. Many of the patterns observed indicated that survival in sable was influenced by an interaction of factors, a problem that could be solved through an increase in sample size and the use of multiple regressions.

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6.1 Appendices

Appendix I: Demographic structure of the sable population at MWR in March 2009.

Age (Yrs)	Females	Males
0-1	6	6
1-2	7	5
2-3	4	4
3-4	5	4
4-5	5	3
5-6	4	2
6-7	4	1
7-8	4	1
8-9	4	0
9-10	3	0
10-11	3	1
11-12	1	0
Total	50	27

Appendix II: Sable carcasses discovered by the MWR scout force on their daily patrols between 2000 and 2010.



Appendix III: Estimates of lion population at MWR between 2000 and 2010 taken from call ups, spoor counts and known pride numbers (Clegg, 2011).





Grass EVI vs. calf survival, February – May 2010.



Appendix V:Distribution of predation risk at MWR between 2009 and
2010 as determined by camera traps.



c) Lion Predation Risk



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Appendix VI: Post-mortem report performed on a sable calf found in May 2010.

DEPARTMENT OF VETERINARY SERVICES THE WILDLIFE UNIT

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Sirilie. 253100		Пага
Attn: Dr Fivaz	DATE	25/10/2010
Malilangwe Trust	Your REF	
fivaz@malilangwe.org	LAB REF	
	HISTO	W10/82
	DISK REF	01/2010

Owner:-as above.

Specimen:- Sable calf organs rec'd 10/05/2010 for histopath.

HISTORY:- poor calf survivability in the wild (and in the pens). This calf, aged about 2 months, was found dead, and mostly scavenged, in the field. Only the head was recovered.

<u>Histopath</u>

Brain – all the blood vessels were very engorged and thrombi of coagulated plasma had formed in most of them. This indicates terminal circulatory collapse.

Lymph node – lymphocyte population consisted mostly of mature cells. The macrophages were, however, prominent in the medulla.

Glandular structure – nothing significant. *Muscle* – normal.

DIAGNOSIS:- none possible but one can speculate the cause possibly being poverty as a result of premature weaning or predation.

C M FOGGIN for DIRECTOR OF VETERINARY SERVICES