Diet and population trends of warthog in the Addo Elephant National Park

By

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CONTENTS

ABSTRACT

The common warthog (*Phacochoerus africanus)* has recently been recognised as an alien invasive species in the Eastern Cape and their population is increasing rapidly within the region. This then raises a concern as it is recorded that invasive species have negative impacts on both economic and ecological aspects of biodiversity in the receiving community. There are few studies that have documented the impacts of this species in the Eastern Cape. This study therefore seeks to determine the diet and population trends of this species in the Addo Elephant National Park (AENP) Main Camp and the results obtained can be correlated with previous studies and used to quantify the impacts of this species in the Eastern Cape. Warthogs are specialized grazers, it was therefore hypothesized that they will have potential impacts on grazing resources in the AENP Main Camp. The diet of common warthogs in the AENP Main Camp was determined through microhistological analysis of faecal material of samples collected seasonally. Population trends of common warthogs were determined in relation to the effects of predation on the population growth and population age structure of these animals within the AENP Main Camp. The results were compared with the findings for common warthog population growth and population age structure of Great Fish River Nature Reserve (GFRNR), a predator free population. It was hypothesized that the population growth rate of common warthogs in the AENP Main Camp before the introduction of lions and hyaenas in the AENP would not differ from the population growth rate of common warthogs in GFRNR. Secondly, the post-lion/hyaena common warthog population in the AENP Main Camp would differ from both the AENP Main Camp pre-lion/hyaena and GFRNR common warthog populations due to the presence of large predators in the AENP Main Camp. For population age structure it was hypothesized that the two populations, AENP Main Camp and GFRNR would differ because of predators increasing mortality. The diet of common warthogs was dominated by grass (87.4%), with *Cynodon dactylon* being the dominant grass species. Common warthogs in the AENP Main Camp should be properly managed because they have potential impact on grasses. The population growth of common warthogs in the AENP Main Camp showed no effect of predation, with population growth not differing from that of GFRNR. Predation had an effect on common warthog population age structure with AENP Main Camp and GFRNR populations differing, particularly in terms of adult structure. Thus, population growth of common warthogs in the AENP Main Camp is not determined by the presence of predators. These findings highlight the status of common warthog as an invasive species in the AENP Main Camp and potentially impacting on grass species and show little effects of top-down population regulation. These results show a need of monitoring common warthog population as well as their potential impacts in the area.

Key words: *Addo Elephant National Park Main Camp, common warthog, Great Fish River Nature Reserve, invasive species*, *microhistological faecal analysis, population growth, population age structure, and predation.*

CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

Invasive alien warthog as a problem in a conservation area

The impact and population increase of the introduced common warthog (*Phacochoerus africanus*) in the Eastern Cape has led to this species being regarded as an invasive species in this region (Skead 2007; Nyafu 2009). The major concern is that common warthog numbers are increasing rapidly despite initiatives to manage or reduce them (Skead 2007; Nyafu 2009). These animals are perceived as a threat to both conservation areas and commercial landowners in the Eastern Cape, causing impacts on grass cover, soil and fences (Somers 1992; Somers *et al*. 1994; Nyafu 2009). This then raises the prospect that the impacts of these animals will indirectly affect other herbivores through resource depletion or competition, and also affect other ecosystem processes, and the rural economy.

Invasive species are capable of changing fundamental ecological properties in the receiving community, these include affecting the abundance of dominant species, an ecosystem's physical features, nutrient cycling and plant productivity (Mack *et al*. 2000). It may therefore be predicted that preferred plant species are at risk through invasive species use. The mechanism of these impacts is a function of animals' physical and behavioural adaptations. Warthogs are classified as specialized grazers with the greatest proportion of their diet consisting of grasses (Ewer 1958; Cumming 1975; Mason 1982; Smithers 1983; Rodgers 1984; Somers 1992; Vercammen & Mason 1993; Boomker & Booyse 2003; Treydte 2004; Treydte *et al.* 2006; Nyafu 2009). They have a specialised multi-cusped hypsodont third molar and reduced premolars which makes them well-adapted to grazing (Ewer 1958; Mendoza & Palmqvist 2007). These structures are strong enough to withstand the silica (Lucas *et al*. 2000) secreted by grasses which serves as an anti-herbivore defence (Gali-Muhtasib & Smith 1992). Nyafu (2009) hypothesised that the presence of functional incisors in the common warthog may explain the success of this invasive species in the Eastern Cape, whereas the now locally extinct Cape warthog (*P. aethiopicus*) lacked the incisors (Grubb 1993).

Invasive species are recognized as one of the leading threats to natural ecosystems and biodiversity, as well as on human health (Mack *et al*. 2000; McNeely *et al*. 2001; Wittenberg & Cock 2001). Introduced species frequently consume native ones, overgrow them, transmit diseases to them, compete with them, attack them or hybridise with them (Wittenberg & Cock 2001). Thus, common warthogs in the Eastern Cape consume grasses (Somers 1992; Nyafu 2009) and potentially compete with native grazing herbivores that co-exist with them.

Grasses are not only important in warthog diets but to other grazers occurring in areas of the Eastern Cape invaded by common warthog (i.e. Cape buffalo, *Syncerus caffer* and Zebra, *Equus burchelli*; Landman & Kerley 2001). This emphasises the importance of understanding the diet of common warthogs so as to assess their potential impacts on grazing resources before their impacts can severely affect other herbivores. Though the impacts of common warthogs on biodiversity and resources vary, with these animals having impacts on plants and soil (Somers 1992; Somers *et al*. 1994; Nyafu 2009), information on diet preferences may provide a useful guide for predicting their impacts (Forsyth *et al*. 2002). Understanding the diet of these animals will provide an important step towards the management of their impacts (Forsyth *et al*. 2002).

Invasive species typically have high population growth rates and their effects on receiving ecosystems are typically a function of high numbers on the landscape (Mack *et al*. 2000). Warthogs have a high reproductive capacity and rapid population growth rate (Child *et al.* 1968; Cumming 1975; Boshe 1981; Mason 1982; Rodgers 1984; Somers & Penzhorn 1992). Despite their high reproductive rate, there are a number of factors that affect their population dynamics and these include predation, climate factors, diseases and food availability (Cumming 1975; Boshe 1981; Mason 1982; Mason 1990; Vercammen & Mason 1993). These factors may vary independently and in an area-specific fashion. It is worth noting that common warthog numbers are increasing rapidly in the Eastern Cape, such that the population is now considered to be in the rapid population growth phase (Nyafu 2009). The increase of common warthogs in different areas in the Eastern Cape and their potential impacts raises the need to understand the response of these populations to population-regulating factors in this region. Understanding their response to such extrinsic factors is important especially in areas like Addo Elephant National Park where they are confined in one area with large predators like lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). Previous studies in other parts of Africa reported lion predation on warthogs but their populations seemed not to be significantly affected (Druce *et al*. 2004; Rapson & Bernard 2007). This could probably reflect their high reproductive capacity which allows them to recover quickly after environmental disturbances (Vercammen & Mason 1993). In order to understand the response of warthogs to environmental disturbances, it is important to compare populations from different areas with different environmental factors. This study therefore seeks to develop an understanding of common warthog population drivers and resource use in the Eastern Cape by describing and comparing population trends and diet in the AENP Main Camp and Great Fish River Nature Reserve.

1.2 Background to Cape and Common warthogs

Extinction of the Cape warthog and introduction of the alien Common warthog in the Eastern Cape

Two species of warthogs occur in Africa (d'Huart & Grubb 2001). These are the Cape warthog (*P. aethiopicus*) and the common warthog (*P. africanus*) (Grubb

1993; d’Huart & Grubb 2001). These two species are distinguished largely through the presence and absence of functional incisors (Grubb 1993) and external appearance (d’Huart & Grubb 2005).

Records of the historical occurrence of warthogs in the Eastern Cape are limited (du Plessis 1969; Skead 2007). Warthogs are not referred to in any of the extensive journals kept by some of the 1820 settlers. There were a few records of warthogs (Figure 1.1), in other texts from the same period (Skead 2007). The paucity of these records is strange considering the species’ clear distinctive features i.e. its diurnal activity pattern, distinctive appearance, and its characteristic habit of keeping its tail erect when running, and of backing down into its burrow (Skead 2007). Another problem with the early literature is that the original observers did not always provide enough identifying features to enable a reliable distinction between warthog and bushpig records (Skead 2007). This has led to these records being treated with caution, as warthog and bushpig were often confused. Despite the scarcity of historical records of warthogs, the evidence of the occurrence of Cape warthog (*P. aethiopicus*) in the broader Eastern Cape is provided by the archaeological records (Plug & Badenhorst 2001). These records comprised of identifiable remains coming from at least as long ago as 30 000-25 000 years BP (Before Present) and as recently as 500 years BP (Plug & Badenhorst 2001). The presence of warthogs in the Eastern Cape is further supported by the recently discovered bone and tooth material (last 150 years) (Skead 2007).

The Cape warthog was first described from a specimen brought to Holland in 1765 (d’Huart & Grubb 2001). Later, Grubb (1993) classified the Cape warthog into two subspecies, one extant (*P. a. delamerei*) and one extinct (*P. a. aethiopicus*). The Cape warthog occurred in South Africa (Grubb 1993; Vercammen & Mason 1993; d’Huart & Grubb 2001; Skead 2007). It has been postulated that the Cape warthog was driven to extinction by heavy human hunting, but there is no evidence to support this given the technological limitation of the early hunters (Skead 2007; Nyafu 2009). An alternative explanation of this could be climate change which is known to have a profound effect on plant and animal species and communities (Skead 2007). The full extent of the historical distribution of Cape warthog was never properly identified, therefore it remains unknown (Grubb 1993; Randi *et al*. 2002; Skead 2007). This species is currently limited to areas of Somalia, where it is represented by the *P. a. delamerei* subspecies (Grubb 1993).

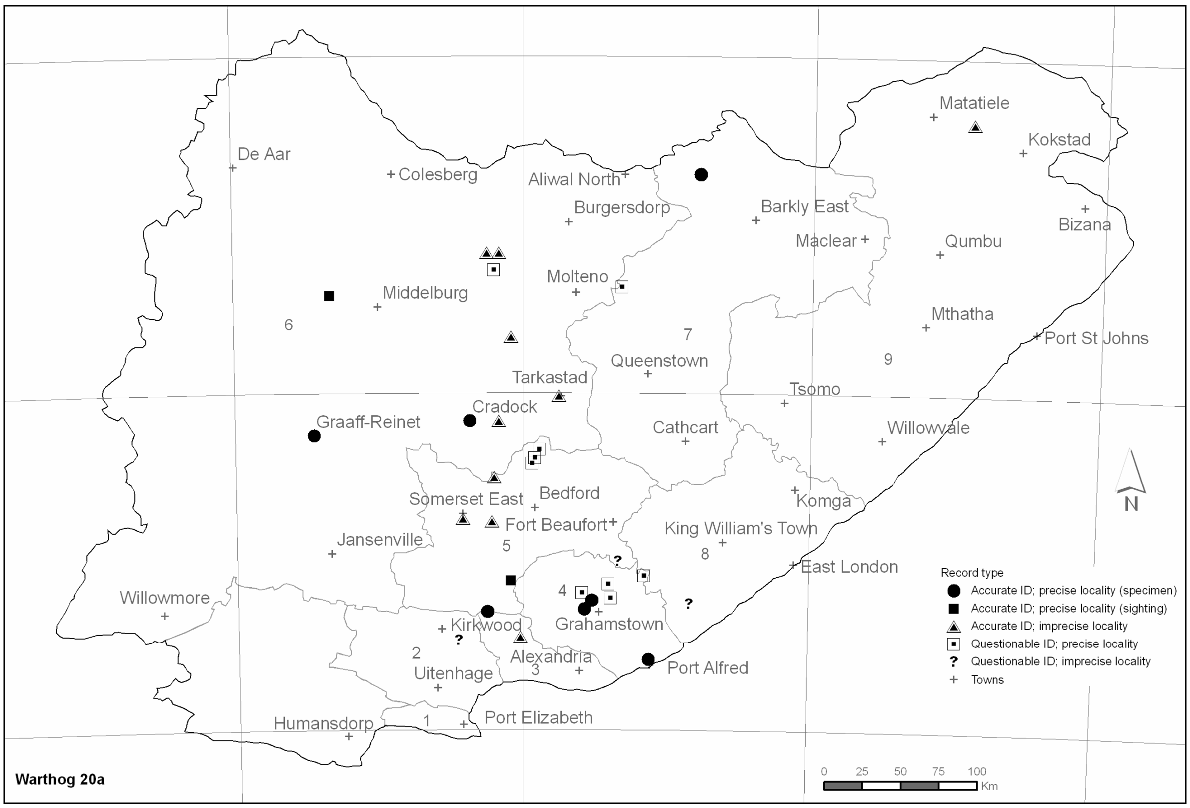


Figure 1.1 Historical records of warthog (*P. aethiopicus*) in the Eastern Cape (Skead 2007).

The common warthog was first described in 1766 by Buffon (Vercammen & Mason 1993). Grubb (1993) later described four subspecies of common warthog, and provided their geographic distribution. The distribution of common warthog extends from sub-Saharan countries, central and northern Ethiopia, eastern and central Africa to the northern parts of the southern African sub-region (Figure 1.2)

(Vercammen & Mason 1993; Skinner & Chimimba 2005). In South Africa, common warthog occur throughout the North West Province, Northern Cape and in KwaZulu-Natal (Vercammen & Mason 1993). This species has been introduced into the Eastern Cape and it is now spreading within the region (Somers & Penzhorn 1992; Somers & Fike 1993; Vercammen & Mason 1993; Skinner & Chimimba 2005; Nyafu 2009).

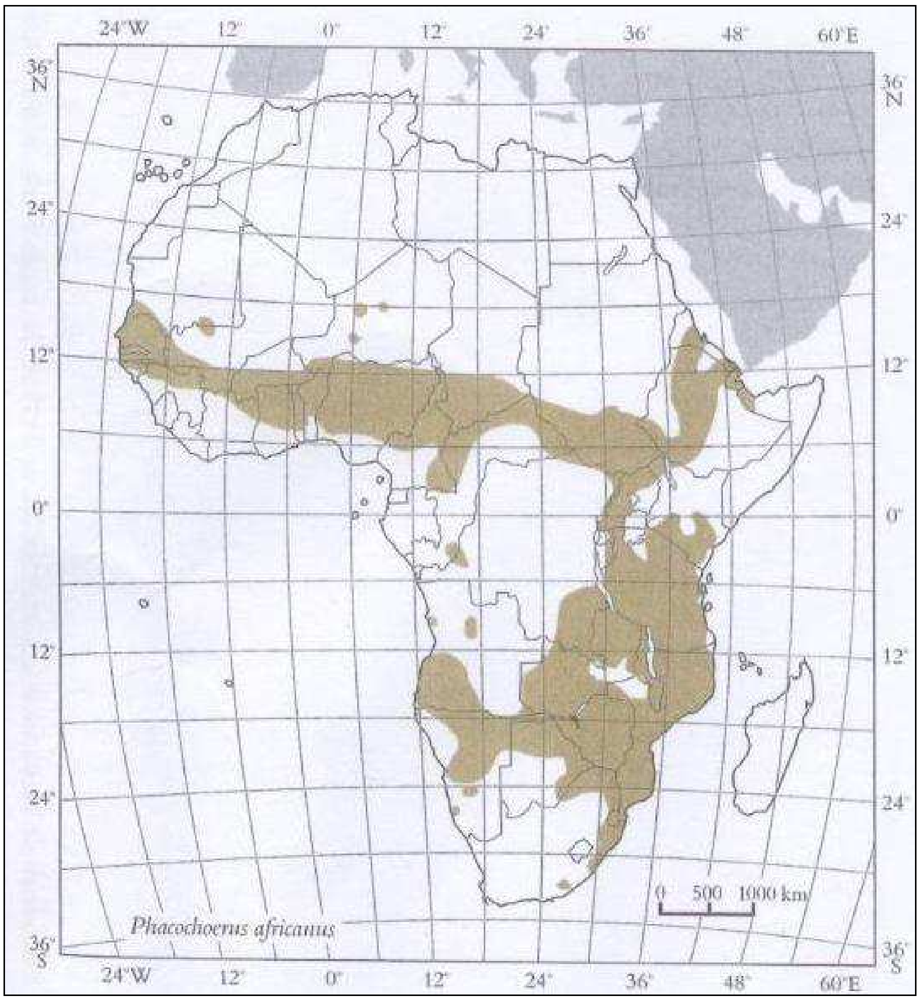


Figure 1.2 Distribution of Common warthog (*P. africanus*) in Africa (Skinner & Chimimba 2005).

When this species was introduced into the Eastern Cape in the early 1970's (Somers & Penzhorn 1992; Somers & Fike 1993), the introduction was based on the understanding that it had historically occurred in this region and it was only later recognised that it was a separate species (*P. africanus*) (Grubb 1993), not the historically occurring species (*P. aethiopicus*). When common warthog was described by Grubb (1993) as a separate species from the historically-occurring species in the Eastern Cape, common warthogs had already increased significantly in numbers at an estimated rate of 45% pa from 1976-1987 (Somers & Penzhorn 1992; Somers & Fike 1993) and had expanded their range, particularly within the Fish and Sundays River Valleys of the Eastern Cape.

Prior to their description as a separate species and being recognized as an invasive species in the Eastern Cape region, these animals had already shown some impacts in the Great Fish River Nature Reserve (Somers 1992; Somers *et al*. 1994). Common warthogs had been identified as degrading grazing resources and opening up fences, which led to increased movement of the blacked-backed jackals *Canis mesomelas*, causing problems for many local farmers (Somers *et al*. 1994). Few studies however have documented the impacts of this species on grazing resources and on other ecological aspects in the Eastern Cape (Somers 1992; Nyafu 2009). This calls for further investigations to be done on this species in the area.

1.3 Rational & Research approach

The introduction of common warthogs into the Addo Elephant National Park (AENP) occurred in 1995 (unpublished AENP records). This was prior to the general recognition of common warthogs as being an alien species in the Eastern Cape, or that they may serve as an invasive species. The AENP provides an interesting opportunity to explore the interactions between invasive species and predators. When this species was introduced into the AENP, there were no large predators. In 2003, lions and spotted hyaenas were re-introduced into the AENP (Hayward *et al*. 2007). It has been confirmed that common warthogs are preyed upon by lions and spotted hyaenas in AENP (Ravnsborg 2004; Franklin 2005; Tambling *et al*. 2009). Understanding the role of predation on this common warthog population will provide insight about their population growth and whether predation may influence population trends.

This is of particular value in understanding and predicting the population response of this invasive species.

The introduction of common warthog in 1976 into the Andries Vosloo Kudu Reserve (AVKR) which now forms part of Great Fish River Nature Reserve (GFRNR) was successful and the population has expanded their range and increased in numbers significantly by 45% pa in the GFRNR (Somers & Penzhorn 1992; Somers & Fike 1993). Common warthog introduction into the AENP was also successful, with common warthog numbers increasing rapidly (unpublished AENP records). In the AVKR, common warthogs did not have to deal with large predators like lions, the only predators that could have probably preyed on common warthogs were caracal (*Caracal caracal*), leopard (*Panthera pardus*), brown hyaena (*Parahyaena brunnea)* and black-backed jackal (*Canis mesomelas)* (Somers & Penzhorn 1992; Somers & Fike 1993). In contrast, common warthogs in the AENP were exposed to large predators like lions and spotted hyaenas. In AVKR, Somers (1992) considered predation to be a minor factor causing mortality during his study period, and hypothesised that the absence of predators could explain the observed rapid population growth in the GFRNR.

The aim of this study was to determine the possible effects of predation on common warthogs in the Addo Elephant National Park Main Camp. The potential impact of common warthogs on grazing resources in the AENP Main Camp through a description of diet was also investigated. The research approach was to describe the diet of common warthogs in the AENP Main Camp and compare the population trends of common warthogs in the AENP Main Camp before and after the introduction of large predators, as well as with that of GFRNR.

1.5 Hypotheses

The present study therefore addressed the following hypotheses:

- The introduction of large predators reduced common warthog population growth in the AENP Main Camp. Thus it was predicted that post-predator introduction common warthog population growth would be slower than that in the AENP Main Camp pre-predator introduction, and that in the GFRNR. This was addressed by comparing the population growth and structure of the two populations, AENP Main Camp (pre- and post-predators) and GFRNR, in order to assess the possible effect of predation on common warthogs.
- Warthogs are specialized grazers, and will therefore potentially have a significant impact on grasses and grazing resources in the AENP Main Camp. This was addressed through a description of diet.

CHAPTER 2

GENERAL DESCRIPTION OF STUDY ANIMAL AND STUDY AREA

2.1 STUDY ANIMAL: COMMON WARTHOG *(Phacochoerus africanus)*

2.1.1 Taxonomy

There are two species of warthogs, the common warthog (*P. africanus*) and the Cape or the desert warthog (*P. aethiopicus*) (Grubb 1993). The former has four subspecies and the latter two subspecies, with one living and one extinct (Grubb 1993; Vercammen & Mason 1993). The current study focuses on the former species.

2.1.2 Physical characteristics

Common warthogs are medium-sized animals and adult males usually weigh up to about 100 kg, whilst females weigh around 70 kg (Treydte *et al.* 2006; Smithers 1983). Their bodies are grey in colour (Smithers 1983), and sparsely covered with coarse bristles about 40 cm long (Smithers 1983). There are long black, brown or yellowish erectile hairs along the mid-back from the ears to the base of the tail (Skinner & Chimimba 2005). The tip of their tails has a small clump of black hair (Smithers 1983). Warthogs are short-sighted and short-legged, as a result they are quick to respond to the warning calls of other mammals or birds (Smithers 1983). They are characterized by a broad snout, long curved tusks and warts on the sides of the face (Child *et al*. 1968; Ewer 1958; d'Huart & Grubb 2005). Males are bigger than females and their tusks are longer compared to females (Mason 1982; Smithers 1983). The upper tusks of old adult females tend to curl over the top of the snout more than those of males (Ewer 1958; Smithers 1983). Common warthogs are distinguished from desert warthogs by the presence of two upper and six lower functional incisors (Grubb 1993). They have cone-shaped warts under the eye, their ear tips are erect and the head is slightly diabolo-shaped when viewed from the front, whereas the desert warthog has hooked warts, bent ear tips and the head is more egg shaped (d'Huart & Grubb 2005).

2.1.3 Distribution

The common warthog is the most widespread wild pig species in Africa (Grubb 1993; Vercammen & Mason 1993; Randi *et al*. 2002; Muwanika *et al.* 2003). The distribution of common warthog is provided in Chapter 1. Recently, common warthogs have been spreading in the Eastern Cape due to the stocking of private and government reserves (Vercammen & Mason 1993). Their spread in this area has been augumented through natural dispersal (Nyafu 2009).

2.1.4 Habitat

Warthogs prefer open woodland and bushland habitats with shorter grassland and water (Vercammen & Mason 1993; Skinner & Chimimba 2005). Although warthogs prefer areas close to water, they also occur in dry areas where water may only be available seasonally and survive by rooting for fresh rhizomes (Cumming 1975; Mason 1982). Estes (1991) reported that warthogs are the only pig species adapted to graze and survive in savanna habitats.

2.1.5 Behaviour

Warthogs are social animals that live in small groups, together with their family members which comprise of one to three adult females and their young (Smithers 1983; Vercammen & Mason 1993; Somers *et al*. 1995). Warthog adult males are not territorial, but they fight among themselves for access to females (Vercammen & Mason 1993). They are diurnal (Cumming 1975; Mason 1982; Somers 1992; Vercammen & Mason 1993) and feed during the day and at night retreat to burrows (Smithers 1983). Burrows are very important in their lives, they use them for protection against predators and for thermoregulation (Mason 1982; Smithers 1983; Somers 1992; Vercammen & Mason 1993). The use of each burrow is based on a first-come, first-served basis (Estes 1991). One of the most characteristic behaviours of warthogs is to keep their tails erect and their heads lifted slightly when running (Somers 1992; Skead 2007).

2.1.6 Foraging ecology and diet

Common warthogs are grazers, foraging on a wide range of food resources with high nutrient levels, specifically grasses (Ewer 1958; Cumming 1975; Mason 1982; Smithers 1983; Rodgers 1984; Somers 1992; Vercammen & Mason 1993; Boomker & Booyse 2003; Treydte 2004; Treydte *et al.* 2006; Nyafu 2009). The diet of these animals consists of grasses, sedges, fallen fruits and forbs (Ewer 1958; Vercammen & Mason 1993; Nyafu 2009). Warthogs can also dig out roots using their tusks and rhinarium, depending on the abundance of food resources available (Ewer 1958). They prefer to feed in damp areas, with fresh and green grass (Somers 1992; Vercammen & Mason 1993). Nyafu (2009) showed that in the Eastern Cape they may increase browse intake, particularly in winter.

2.1.7 Reproductive biology

Common warthogs are seasonal breeders with the mating season occurring in May and June (Skinner & Smithers 1990; Somers *et al*. 1995). The mating system of warthogs is promiscuous, with males mating with numerous females and the females mating with more than one male (Somers *et al*. 1995). Their gestation period is approximately 170 days, and the average litter size is 3 with a range of 1-8 (Child *et al.* 1968; Mason 1982; Somers & Penzhorn 1992). Adult female warthogs (between three and five years) have a high reproductive capacity (Boshe 1981), as compared to older and young ones. Warthogs can live up to the age of about 17 years (Mason 1982).

2.1.8 Economic value

Warthog provide a high proportion of lean meat (Somers & Penzhorn 1992) and a large carcass; as a result in many countries they are highly valued for local consumption (Vercammen & Mason 1993). Warthogs are considered to have an economic value for both meat and ecotourism (Somers & Fike 1993; Nyafu 2009).

2.1.9 Threats to warthog

The major threats to warthogs include overhunting, adverse climatic conditions, disease and predation. Humans are a threat through overhunting for meat and are probably the most important threats to *P. africanus* (Vercammen & Mason 1993). Human overhunting is allegedly the main factor that contributed to the early extinction of the Cape warthog *P. aethiopicus* (Vercammen & Mason 1993) although the evidence for this is limited (Skead 2007). Vercammen & Mason (1993) noted that warthogs are highly susceptible to a range of diseases that could seriously affect local populations i.e. African Swine Virus (Dixon & Wilkinson 1988). They are also susceptible to low temperatures such that high mortalities occur during extreme cold weather conditions (Vercammen & Mason 1993). This could probably be caused by their lack of insulation (Smithers 1983; Vercammen & Mason 1993). Warthogs are preyed upon by lions, leopard and spotted hyaena (Cumming 1975; Ruggiero 1991; Somers & Penzhorn 1992; Vercammen & Mason 1993; Druce *et al*. 2004; Hayward & Kerley 2005; Bauer *et al*. 2006; Rapson & Bernard 2007; Tambling *et al*. 2009). Lions are the top predators preying on warthogs, probably followed by leopards (Vercammen & Mason 1993). Other possible predators of warthogs include Caracal, brown hyaena and black-backed jackal (Somers & Penzhorn 1992; Somers & Fike 1993). Warthogs can sometimes defend themselves against predation by cheetahs and wild dogs (Mason 1982). Sometimes warthogs are taken out of their burrows by lions (Schaller 1972; Smithers 1983).

2.2 STUDY AREA: ADDO ELEPHANT NATIONAL PARK

2.2.1 Location

The study was undertaken in the Addo Elephant National Park Main Camp ($33^{o}31`S$, $25^{o}45`E$), approximately 60 km north east of Port Elizabeth in the Eastern Cape Province, South Africa. The park covers a much larger area (1680 km^2; I. Welgemoed, SANParks *Pers. comm*.) but this study was limited to the Main Camp, hereafter referred to as AENP. The Main Camp covers an area of about 103 km^2 (De Klerk 2009).

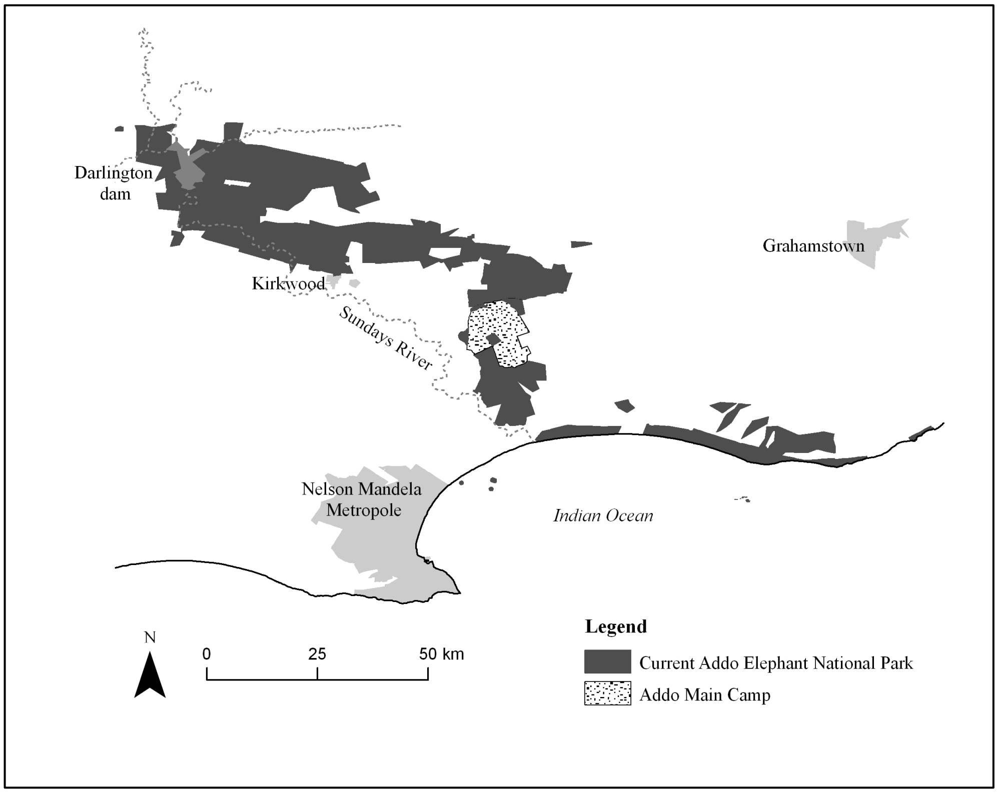


Figure 2.1 Study area map, showing the AENP Main Camp.

2.2.2 Climate

The AENP falls within the semi-arid region, with mean daily temperatures ranging from 32-40℃ in summer and 13℃ in winter (Stuart- Hill 1992). Rainfall occurs throughout the year with peak rain periods in late summer (February-March) and spring (October-November) (Stuart-Hill 1992). The mean annual rainfall recorded in the AENP during the period 1959 to 2008 was 394 mm (SA Weather Service 2008).

2.2.3 Vegetation

The AENP is located in the endemic-rich succulent thicket of the Albany Centre (Johnson *et al.* 1999). Four plant communities have been identified within the AENP Main Camp. These include Sundays Thicket, dominated by *Portulacaria afra* which covers more than 66% of the AENP Main Camp (Figure 2.2), Coega Bontveld, Albany Coastal Belt, and Albany Alluvial Vegetation (Mucina & Rutherford 2006). The vegetation largely comprises of evergreen shrubs, woody lianas, herbs, geophytes, succulents and grasses (Vlok *et al.* 2003). Shrubs and trees dominating in the AENP Main Camp include *Azima tetracantha, Capparis sepiaria, Carrisa haematocarpa, Gymnosporia spp., Rhus spp., Euclea undulata* and *Schotia afra* (Landman *et al.* 2008). However, the vegetation in the AENP Main Camp is not uniform due to varying historical land uses (Paley & Kerley 1998). AENP Main Camp is a thicket dominated area, with some sections comprise of large grasslands that were previously cleared for agriculture areas with a high incidence of *Cynodon dactylon* and *Platythyra haeckeliana* (Paley & Kerley 1998; Landman *et al*. 2008).

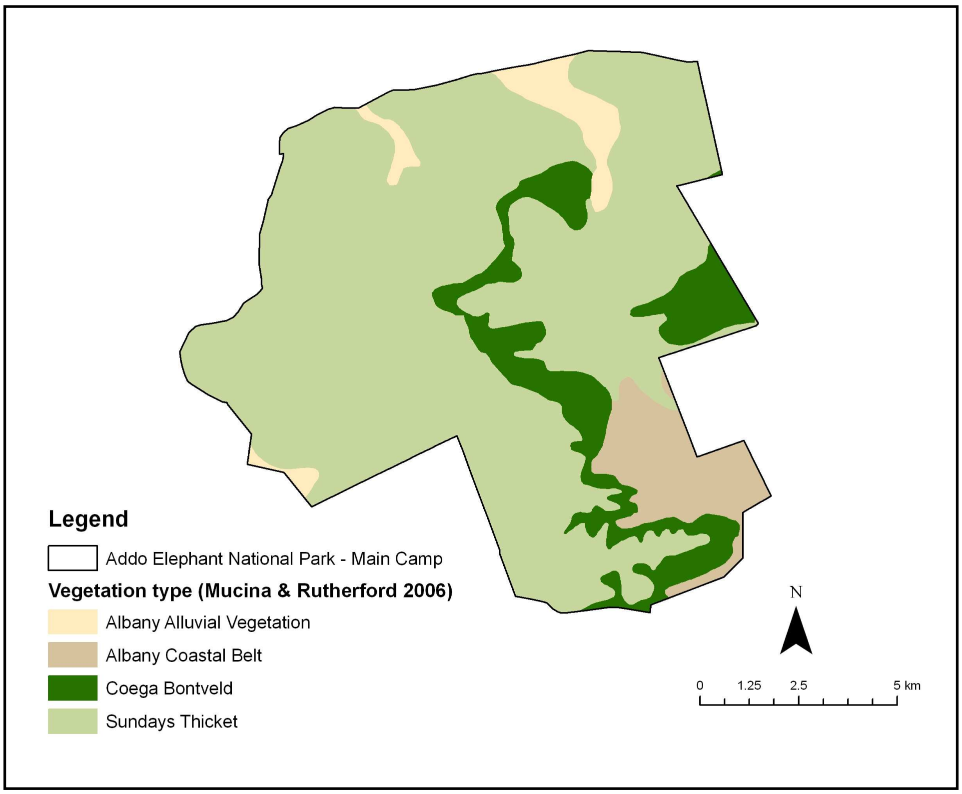


Figure 2.2 Vegetation map of the AENP Main Camp, study area (from Mucina & Rutherford 2006).

2.2.4 Topography, geology and soils

The AENP Main Camp is characterized by a series of low undulating hills, which rise from 71-354 m.a.s.l. (Paley & Kerley 1998). It is also characterized by red clay loam soils (approximately 1 m deep). There are a number of artificial water holes and dams throughout the AENP Main Camp, with ephemeral water bodies occurring after substantial rains.

2.2.5 Ungulates in the AENP

AENP Main Camp is rich in flora and fauna, with flora described above and the fauna comprise a number of ungulates which include African elephant (*Loxodonta africana*), black rhinoceros (*Diceros biconis*), Burchell's zebra (*Equus burchelli*), bushpig (*Potamochoerus porcus*), common warthog, red hartebeest (*Alcelaphus buselaphus*), blue duiker (*Cephalophus monticola*), common duiker (*Sylvicapra grimmia*), grysbok (*Raphicerus melanotis*), Cape buffalo (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus scriptus*) and eland (*Tragelaphus oryx*) (Boshoff *et al*. 2002). Of these, zebra, buffalo and red hartebeest are considered to be predominately grazers (Landman & Kerley 2001; Schlebusch 2004), whereas elephants tend to use grass seasonally (Landman *et al*. 2008).

2.2.6 Predators in the AENP

Predators present in the AENP Main Camp include black-backed jackal (*Canis mesomelas*), leopard (*Panthera pardus*), caracal (*Caracal caracal*), spotted hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) (Boshoff *et al*. 2002; Hayward *et al*. 2007).

CHAPTER 3

ASSESSING EFFECTS OF PREDATION ON INTRODUCED WARTHOG POPULATIONS

3.1 Introduction

The effects of predation are complex and operate at a variety of levels (Schaller 1972; Hunter 1998; Eloff 2002). A possible explanation of this could be the typically large numbers of prey species and predators involved (Mills & Shenk 1992). There are numerous parameters that need to be considered when measuring the effects of predation. These include numbers of predators and prey species in the area, how predators select their prey items with respect to species, sex, age and condition, how often the predators kill, and the fecundity and the survival rates of the prey species (Schaller 1972; Mills 1990; Mills & Shenk 1992). Predation might have a marked negative influence on certain prey species when both predator and prey species are confined to an area (Smuts 1978; Taylor 1984). It is thus important to study predator-prey interaction within a particular area so as to better understand predator and prey behaviour and ecology (Lima 2002). Altendorf *et al*. (2001) pointed out that predation results in changes in the behaviour of prey species, for example reduction in prey activity times, alteration of habitat use, increased group size and changed vigilance levels. The presence of predators in a particular area is important as they might keep non-native species from becoming invasive or from succeeding in becoming established (Juliano & Lounibos 2005). Heithaus & Dill (2002) noted that many prey species change their habitat use in response to predation risk and this results in reduction of forage quality or quantity available for use by the prey. Apart from the direct effects of predation, the behavioural responses of prey species to predation risk reduces animal fitness which may eventually result in a reduction in prey numbers (Schmitz *et al*. 1997; Creel *et al*. 2005).

The effects of predation in the current study were investigated on an invasive species, the common warthog. Juliano & Lounibos (2005) defined invasive species as species that have been introduced, increased, spread and created potential impacts on native species and ecosystem, or on human activities (i.e. agriculture, conservation). The population increase of an introduced species typically follows a certain growth pattern, which involves a number of stages including the lag phase, rapid growth phase and carrying capacity or asymptote (Figure 3.1) (Andow *et al*. 1990; Mack *et al*. 2000). The success and impacts of alien species depends on their biological attributes, the environmental characteristics of the receiving ecosystem and the biotic interactions with the community (Vilá & Weiner 2004).

Biological invasion begins when organisms are transported from their native ranges to new regions (Mack *et al*. 2000). Despite the risks encountered by organisms either in transportation or soon after arrival, they occasionally survive to reproduce and become established (Mack *et al*. 2000). Among these species that establish, a few will go on to become invaders (Mack *et al*. 2000). The progression from immigrant to invader often includes a delay or lag phase, followed by a phase of rapid exponential increase (Mack *et al*. 2000). The lag phase is the interval between the initial colonization (Figure 3.1) and the initiation of rapid population growth and range expansion of invasive species (Mack *et al*. 2000). The duration of the lag phase varies, depending on the species and environmental conditions (Mack *et al*. 2000). The establishment or lag phase (Figure 3.1) is thus characterised by a viable self-sustaining and expanding population (Sakai *et al*. 2001; With 2002; Theoharides & Dukes 2007). The establishment and interaction of an invasive species with other species in the new invaded environment determines the period in which the non-native species will remain in the lag phase (Theoharides & Dukes 2007). Mack *et al*. (2000) noted that a population of an invasive species eventually proceeds into a phase of rapid and accelerating growth, both in numbers and areal spread. This population increase often occurs at a fast rate and there are numerous accounts of invasion that proceeded through this phase, despite the effects of predators or disease (Mack *et al*. 2000). After this the invading population typically reaches the environmental and geographic limits (carrying capacity or asymptote; Figure 3.1) of the new environment and at this stage the populations persist but do not expand (Mack *et al*. 2000) as the populations are limited by top-down and or bottom-up effects. All these phases are potentially influenced by predation which may prevent establishment, extend the lag phase, slow down the growth phase and depress the asymptote (Juliano & Lounibos 2005). Predation is therefore a potentially key factor on species invasions but is not well studied.

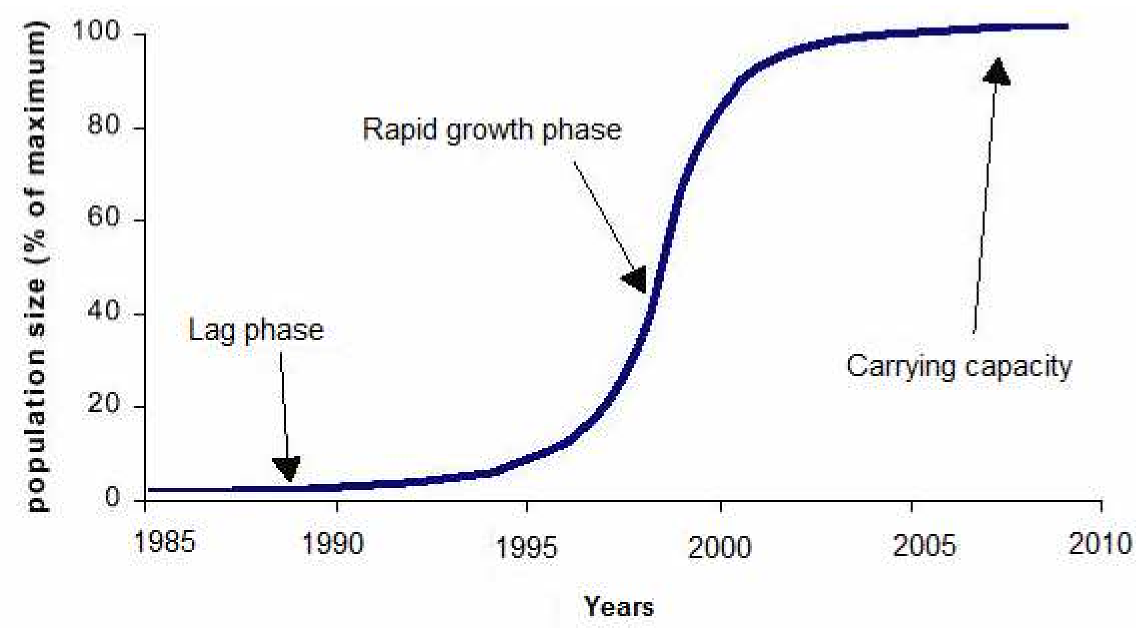


Figure 3.1 Population growth pattern of an introduced species (Mack *et al.* 2000).

<u>3.2 Predator-prey interaction: lions and spotted hyaenas</u>

Predation is one of the key factors that govern patterns in natural systems (Sih *et al*. 1998). Hayward & Kerley (2005) noted that predation takes place when a predator encounters a prey, and the rate of predation may be affected by the type of habitat. Common warthogs in the AENP are preyed upon by lions and spotted hyaenas (Ravnsborg 2004; Franklin 2005; Tambling *et al*. 2009). A brief description of these two predators in terms of prey preferences and hunting success is therefore appropriate.

Lions prefer to prey on species that are within a weight range of 190 to 550 kg, thus warthogs are below the preferred weight range for lions (Hayward & Kerley 2005). Regardless of this, lions do prey upon warthogs and they take them in accordance with their abundance (Hayward & Kerley 2005). Funston *et al.* (2001) documented that grass and shrub cover are the most important parameters for the hunting success of lions, whilst Smithers (1983) noted that grasslands are suitable areas for warthogs. The occurrence of warthogs in open areas and their foraging on grasses may increase their vulnerability to lion predation. Druce *et al*. (2004) noted that the susceptibility of warthogs to drought conditions makes them lose condition, and this results in them becoming easy targets for predators. Their short height and lack of speed also makes them highly susceptible to lion predation (Schaller 1972).

Spotted hyaenas are non-selective hunters but they do show preferences when it comes to weight of a prey item (Hayward 2006). Their preferred weight range of prey items is between 56-182 kg (Hayward 2006). Warthogs are within the preferred weight range of spotted hyaenas, and this makes them susceptible to predation by spotted hyaenas. Spotted hyaenas usually hunt in groups, allowing them to overcome large prey species (Mills 1990; Eloff 2002). There is a dietary overlap between lions and hyaenas (Mills 1990; Franklin 2005). Given that warthogs are diurnal (Cumming 1975; Mason 1982; Somers 1992; Vercammen & Mason 1993), while spotted hyaenas tend to hunt nocturnally (Di Silvestre *et al*. 2000) there is some degree of temporal separation of these two species, which will influence predator or prey interaction between the two species. Because of their temporal separation warthogs may be excavated from their holes at night by spotted hyaenas (Di Silvestre *et al*. 2000).

Other possible predators of common warthogs in the AENP Main Camp include black-backed jackal (*Canis mesomelas*), Caracal (*Caracal caracal*) and leopard

(*Panthera pardus*), but de Klerk (2005) found no evidence of common warthogs in the diet of jackal. Leopards are non-selective hunters and they prefer prey items within a weight range of 10-40 kg with an optimal weight range of 23 kg (Hayward *et al*. 2006). Warthogs are within the preferred weight range of leopard and this makes them susceptible to leopard predation. No study has investigated the diet of leopard in the AENP, therefore the level of predation of common warthogs by leopard in the AENP remains unknown.

Previous studies in other parts of Africa showed that warthogs are preyed upon by lions (Cumming 1975; Mason 1982; Ruggiero 1991; Druce *et al*. 2004; Hayward & Kerley 2005; Bauer *et al*. 2006; Rapson & Bernard 2007). However, Smuts (1978) and Eloff (1984) pointed out that the impacts of predation need not be generalized since these impacts vary temporally in different areas. Effects of predation may limit population growth of a particular prey species in a particular area, whereas these effects may not be the same in another area (Smuts 1978; Eloff 1984). This can be illustrated by examples from previous studies, Rapson & Bernard (2007) recorded lion predation on common warthogs with no significant effect on the common warthog population in Shamwari Private Game Reserve, whereas Cumming (1975) recorded a warthog population decline in the Sengwa Wildlife Research Area and lion predation was allegedly the main factor of this decline, as this decline coincided with increased lion numbers.

3.3 Warthog, lion and hyaena populations in the AENP

Common warthogs were introduced in the AENP in 1995 (unpublished AENP records). Based on historical records of warthogs in the Sundays River Valley (Skead 2007), this was considered a reintroduction of this species into the AENP. This introduction was highly successful, and the population has expanded significantly within the AENP (unpublished AENP records).

Lions and spotted hyaenas were re-introduced into the AENP (Hayward *et al*. 2007) after their absence in the Eastern Cape for approximately two centuries.

This re-introduction comprised of six lions, which were re-introduced within the AENP in 2003 (Hayward *et al.* 2007). Four hyaenas were reintroduced two weeks after the lions, and a further four hyaenas were re-introduced in 2004 (Hayward *et al*. 2007).

In contrast to the situation in AENP, common warthogs in the GFRNR have not been exposed to predators such as lions and spotted hyaenas. Potential predators such as leopards are rare (Somers 1992). These two populations therefore provide an opportunity to investigate the effects of predation on the population of an invasive alien species, the common warthog. This was addressed by comparing the population growth rates and population age structures of common warthogs in the AENP Main Camp (before and after predator re-introduction) and GFRNR.

The aim of this chapter was therefore to determine the effects of predation on the population trends and population age structure of common warthogs in the AENP Main Camp (before and after predator re-introduction) and how this population differs from the common warthog population in GFRNR, which is a predator free population.

3.4 Hypotheses

Based on the predator differences and similarities it was hypothesized that:

- The pre-lion/hyaena common warthog population growth rate in the AENP Main Camp is similar to the population growth rate of common warthogs in the GFRNR, given that both populations were in similar habitats and not exposed to large predators. The specific prediction is that the growth rates would not differ.
- The population growth rate of common warthogs after the introduction of predators in the AENP Main Camp is slower than both the AENP Main Camp pre-lion/hyaena and GFRNR populations, due to the presence of predators in the AENP Main Camp.

These two hypotheses address Somers (1992) hypothesis that the reason for the rapid common warthog population growth in the Eastern Cape was the absence of predators.

- The population age structure of common warthogs in the AENP Main Camp with lion/hyaena is not the same as the population age structure of common warthogs in the GFRNR. As lions and hyaenas are known to have a preferred weight range and juvenile warthogs were well below this for both predators it was therefore predicted that adult common warthogs are likely to be preyed upon by both predators. Thus adult common warthogs are more likely to be affected than juveniles. This would therefore be exposed as a relative decline in the proportion of adults in the populations.

This study effectively compared population growth rates and population age structures of common warthogs in AENP Main Camp with that of published and unpublished data for GFRNR.

3.5 MATERIALS AND METHODS

3.5.1 Predation on warthogs in AENP

The available literature on predation in AENP (Ravnsborg 2004), (Franklin 2005) and (Tambling *et al*. 2009) was summarized to quantify the extent of predation on common warthogs by lions and spotted hyaenas.

3.5.2 Population growth

Common warthog census data were obtained from the AENP (Unpublished AENP records). The data used in the current study for common warthogs were counts since common warthog introduction into the AENP in 1995, until 2009. The data collection was based on aerial counts conducted for all large animals within the AENP. These data were separated into two parts, data obtained before and after the introductions of lions and hyaenas into the AENP. Another data set was obtained from unpublished and published records in the Andries Vosloo Kudu Reserve section of the GFRNR (GFRNR unpublished records; Somers & Penzhorn 1992).

3.5.3 Population age structure

The effect of predation on common warthog population age structure was based on aging animals through the measurement of lower jaws from culled individuals within the AENP Main Camp. One hundred and ten common warthogs culled during 2008 were obtained from the AENP Main Camp. Culling was random, it was therefore assumed that the culled individuals represent the actual common warthog population age structure in the AENP Main Camp. Following a method modified by Hopkins (1992) from Mason (1982), common warthogs were grouped into four different age classes (Table 3.1). These groups comprised of juveniles, yearlings, subadults and adults. Juveniles were classified as those that had elements of deciduous dentition. The yearling class comprised of those showing the eruption of the permanent premolar, the permanent incisors and length of the third molar teeth ranges between 0-15 mm; subadults were those that have completed the eruption of the third molar which ranges between 16-30 mm in length and those that their third molar exceeded 30 mm in length were considered as adults (Table 3.1). Hopkins (1992) did the same for the AVKR section of GFRNR common warthog population structure and the results obtained from the current study were compared with the results found by Hopkins (1992).

Table 3.1 Common warthog age classes and age estimation method, modified by Hopkins (1992) from Mason (1982).

Age class	Observed range (length)
Juveniles (0-12 months)	Deciduous teeth only
Yearlings (12-24 months)	Permanent premolar & incisors erupting , M3 (0-15 mm)
Sub-adults (24-36 months)	M3 (16-30 mm)
Adults (> 36 months)	M3 (> 30 mm)

3.5.4 Data analysis

Population growth

A variety of population growth models including exponential, linear and power models were tested on the data. The exponential model was used further to test the difference between the entire population growth rates of common warthogs in the AENP Main Camp and GFRNR. Regression analysis in Graph pad PRISM (version 4) was used to determine whether there were significant differences in the growth rate of common warthogs before and after lion/hyaena introductions in the AENP Main Camp. The results of the above analysis were further compared to the growth rate of common warthogs in the GFRNR. The population growth rate of common warthogs in GFRNR was calculated in the current study from the data obtained in the GFRNR (GFRNR unpublished records; Somers & Penzhorn 1992).

Population age structure

The number of common warthogs obtained from each age group was compared with the findings of GFRNR (Hopkins 1992) using the Chi-square test in order to assess the difference between the population structures of AENP Main Camp and GFRNR common warthog populations.

3.6 Results

3.6.1 Predation on warthogs in AENP

Available data indicated that common warthogs contributed in the diet of lions and spotted hyaenas in the AENP Main Camp as follows - lion diet: 5.8% (Ravnsborg 2004), hyaena diet: 1.7% (Franklin 2005), lion diet: *c*. 14%, hyaena diet: *c*.19% (Tambling *et al*. 2009) when using similar methods of diet estimation, faecal analysis.

3.6.2 Population growth

The models show a clear population growth pattern characteristic of an invasive species, with a lag phase and a period of rapid growth phase (Mack *et al*. 2000).

Of the three models tested, the simple exponential model was the best fit. The exponential graphic analysis of the entire common warthog population growth revealed that common warthog populations in the AENP Main Camp grew at a higher rate than GFRNR (Figure 3.2). Despite the difference in their growth rate, these populations are both in the rapid population growth phase according to the population growth pattern of the introduced species. The GFRNR common warthog population multiplied rapidly, moving quickly from the lag phase to rapid population growth phase after about six years (Figure 3.2a), whilst the AENP Main Camp common warthog populations occurred at low densities for about eight years after their introduction (Figure 3.2b).

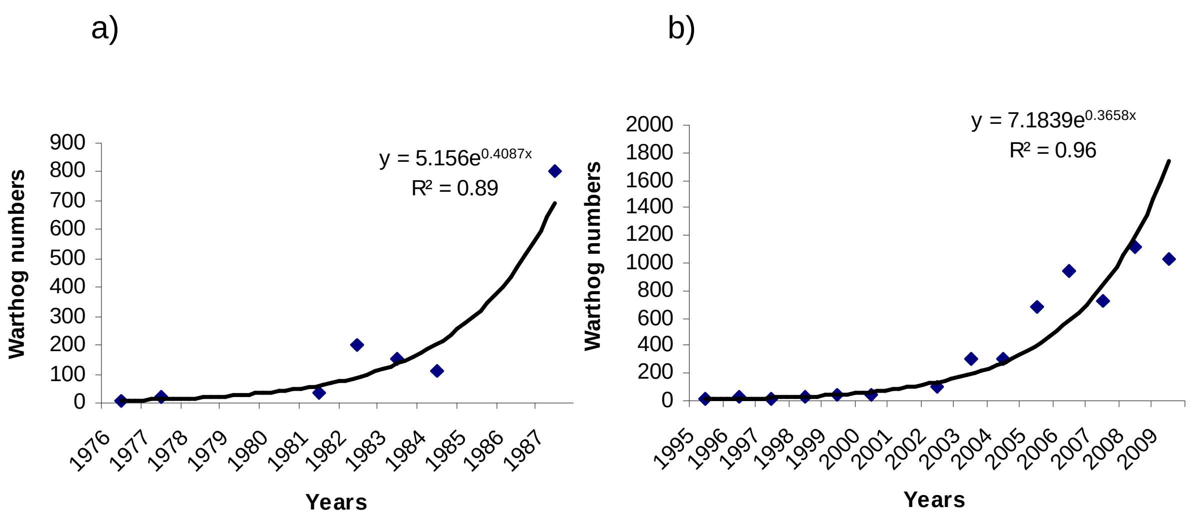


Figure 3.2 Overall population growth rates of common warthogs in (a) GFRNR & (b) AENP Main Camp, (solid symbols) - common warthog census data and (bold line) - exponential curve. Note that in GFRNR there are some missing data points (no census data during these periods, and for AENP Main Camp 2001 data is also missing).

The linear regression analysis revealed that AENP Main Camp pre-lion/hyaena and GFRNR common warthog population growth rates were not significantly different ($F = 2.52$, $df = 11$, $p = 0.14$). Similarly, AENP Main Camp post-lion/hyaena and GFRNR common warthog population growth rates showed no significant differences ($F = 4.53$, $df = 11$, $p = 0.06$). AENP Main Camp pre- and post-lion/hyaena common warthog population growth rate showed significant differences (F = 19.63, df = 11, $p < 0.05$), with AENP Main Camp post-lion/hyaena common warthog population growing faster than pre-lion/hyaena common warthog populations (Table 3. 2 & Figure 3. 3 a, b & c). Thus, common warthog population growth rate in the GFRNR were not significantly different from the population growth rate of common warthogs in the AENP Main Camp before and after the introduction of lions and hyaenas into the AENP Main Camp.

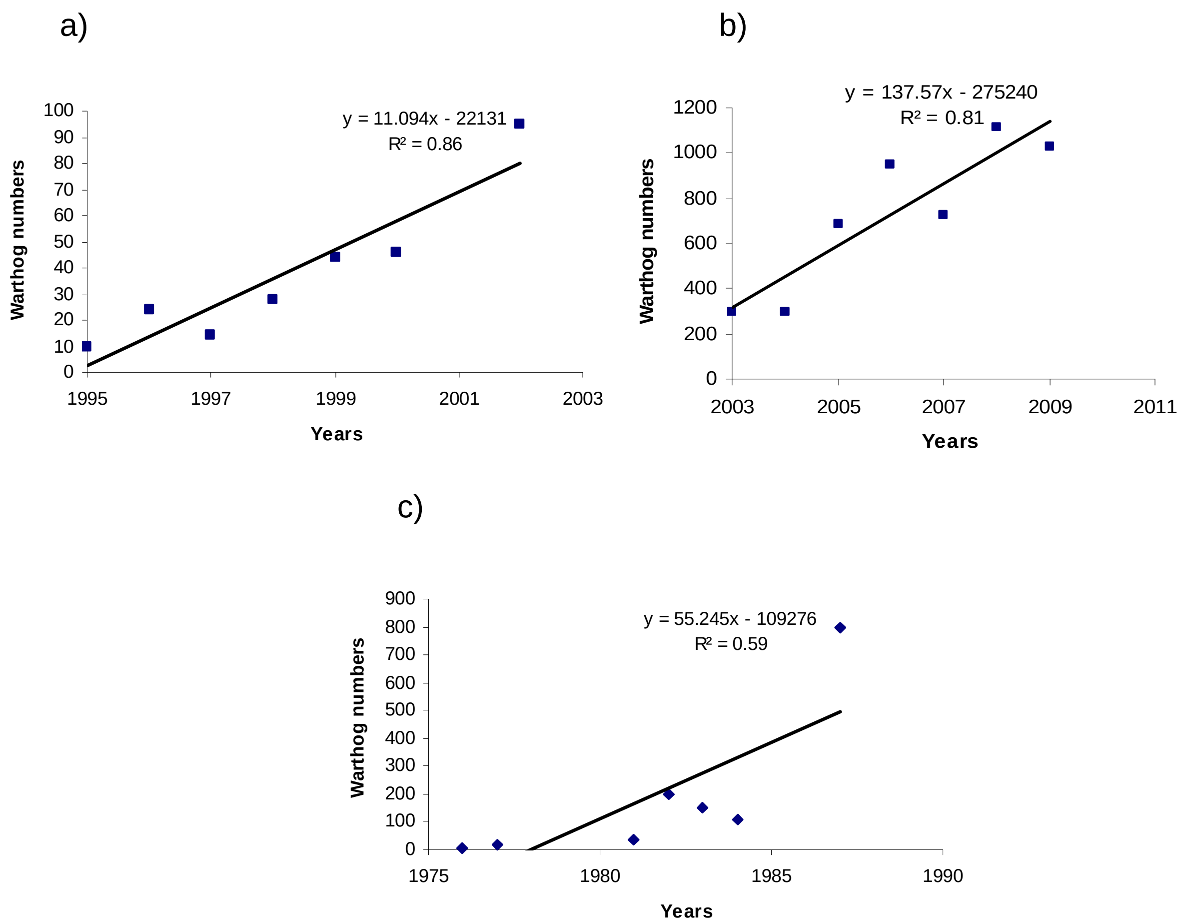


Figure 3.3 Population growth rate of common warthogs; a) - AENP Main Camp pre-lion/hyaenas, b) - AENP Main Camp post-lion/hyaenas, c) - in GFRNR.

Table 3.2 The slopes, confidence intervals, R^2 values and probability estimates of three population growth rates; GFRNR, AENP Main Camp pre-lion/hyaenas and AENP Main Camp post-lion/hyaenas.

Statistical parameters	GFRNR	AENP-PRE	AENP-POST
Slope	55.25	11.09	137.6
CI	1.864 to 108.6	5.901 to 16.29	60.50 to 214.6
R^2	0.5861	0.8578	0.81
P	0.0448	0.0027	0.01

3.6.3 Population age structure

The AENP Main Camp common warthog population was dominated by adults (Table 3.3). Chi-square results (χ^2 = 69.65; df = 3 and p < 0.001) showed significant differences between AENP Main Camp and GFRNR population age structures. The highest within-age group χ^2 observed was between adults (Table 3.3). Suggesting that this group may contribute most to the significant differences between the two populations.

Table 3.3 The percentage population age structure of common warthogs in the AENP Main Camp and GFRNR (Hopkins 1992).

AREA	Juveniles (%)	Yearlings (%)	Sub-adults (%)	Adults (%)
AENP	8.2	22.7	22.7	46.4
GFRNR	12.2	12.2	17.0	58.5
Individual χ^2values	12.9	0.3	5.0	51.4

3.7 Discussion

The available data revealed that lions and spotted hyaenas do prey on common warthogs in the AENP Main Camp, with their predation rate apparently increasing over time (i.e. lion 5.8→ *c*.14% and hyaena 1.7→ *c*.19%). The increase in predation rate could be caused by the increase of common warthog numbers in the AENP Main Camp. Another possible explanation could be that lion preferred prey items (i.e. buffalo, kudu and red hartebeest) in the AENP are slightly declining in numbers (Tambling *et al*. 2009). This could result in these predators consuming common warthogs to compensate for their nutritional requirements. This could be supported by the fact that currently common warthogs in the AENP Main Camp are among the top prey species preyed upon by lions based on direct observation of lion and hyaena diet (Tambling *et al.* 2009). The findings of lion predation on common warthogs in the AENP Main Camp (Tambling *et al*. 2009) are consistent with those of Druce *et al*. (2004), who observed that common warthogs are among the top prey species preyed upon by lions in the Great Makalali Conservancy. More data on these possible trends are needed to explain these observations.

The exponential growth curves for both AENP Main Camp and GFRNR common warthog population growth resemble that of an invasive species, with these two populations currently in the rapid growth phase based on the data obtained in the AENP Main Camp and older data for GFRNR. Both populations were successfully introduced, they managed to establish very well within their introduced areas and they remained at low densities before they started to increase within their introduced and surrounding areas. The difference in the duration of lag phase in the AENP Main Camp (about 8 years) and GFRNR (about 5-6 years) common warthog population growth patterns could be explained by the difference in the number of animals introduced within these areas. In GFRNR (AVKR) there were five common warthogs introduced in 1976 and fifteen common warthogs were added in 1977 (Unpublished GFRNR records), whilst in the AENP Main Camp ten common warthogs were introduced (Unpublished AENP records). Thus the GFRNR founder population was approximately double that of AENP Main Camp. An alternative explanation could be the differences in the sex ratios (Caughley 1994) of the introduced animals in these areas and the difference in the types of habitat that these animals were introduced.

The rapid population growth phase of common warthogs in the Eastern Cape was noted by Nyafu (2009) and this corresponds with the findings obtained for common warthog population growth in the AENP Main Camp and GFRNR. Common warthogs in the Eastern Cape have high rates of population growth and range expansion, with these animals moving quickly from one area to another without any human assistance (Somers & Penzhorn 1992; Nyafu 2009). The increase of these animals in the Eastern Cape seems not to be affected by the environmental factors or predation, while in other parts of Africa population declines have been reported due to predation (Cumming 1975; Mason 1982; Hunter 1998). This point reflects that the impacts of predation vary temporarily or spatially, with some species more preyed upon in one area than others (Smuts 1978; Eloff 1984). In the AENP Main Camp, common warthog population growth seemed unaffected by predation, but this might change depending on the abundance of prey in the future as this would lead to shifts in predation pattern (Hayward *et al*. 2007).

The results of the linear regression revealed that common warthogs in the AENP Main Camp prior to lion/hyaena introductions and common warthogs in GFRNR grew at a similar rate. The non-significant differences obtained between these two populations could be explained by the fact that both populations were in similar habitats and not exposed to large predators. These results support our prediction that the growth rate of the two populations would not differ due to the above mentioned facts. The non-significant differences in the AENP Main Camp and GFRNR population growth rates reflect that predators do not have significant effect in the growth rate of common warthogs in the AENP Main Camp, these rates remaining high. The significant increase in population growth rate between the two populations namely, AENP Main Camp pre- and post-lion/hyaenas disagree with the hypothesis that the rapid common warthog population growth in the Eastern Cape is caused by the absence of predators (Somers 1992). The common warthog population growth rate was expected to decline within the AENP Main Camp after the introduction of predators, considering the direct and indirect effects of predators (Schmitz *et al*. 1997; Creel *et al*. 2005), and habits of predators feeding on the most abundant prey species (Schaller 1972; Hayward & Kerley 2005). The predation rate on common warthogs within the AENP Main Camp is lower compared to other prey species, like kudu, buffalo and red hartebeest (Franklin 2005; Tambling *et al*. 2009). The possible explanation to this could be that by the time the large predators were re-introduced into the AENP Main Camp, the common warthog population had already entered into a rapid growth phase, and the levels of predation were not sufficient to suppress them. This idea is supported by the relatively low levels of common warthog predation initially observed in the AENP Main Camp (Ravnsborg 2004; Franklin 2005).

The findings of this study suggest that predation may have an influence on the population age structure of common warthogs in the AENP Main Camp, by selecting certain age groups among the individuals within the AENP Main Camp. The difference obtained between population structures, specifically in the adult age group of AENP Main Camp and GFRNR populations may reflect the fact that lions and hyaenas select adult common warthogs and ignores juveniles because of the preferred weight range of lions (Hayward & Kerley 2005) and hyaenas (Hayward 2006) are closer to that of adult warthogs. This supports the prediction of the impact of predators being largely on the adults.

The findings of this study therefore led us to conclude that predation in the AENP Main Camp only affects population age structure of common warthogs not population growth. This then suggest that this invasive species in the Eastern Cape is not controlled by the predators, it is therefore important to devise other management plans to control or manage this species in the region.

CHAPTER 4

DIET OF COMMON WARTHOG IN THE AENP

4.1 Introduction

Common warthogs are predominantly grazers and forage mostly on high quality food items (Ewer 1958; Cumming 1975; Mason 1982; Smithers 1983; Rodgers 1984; Somers 1992; Vercammen & Mason 1993; Boomker & Booyse 2003; Treydte 2004; Treydte *et al.* 2006; Nyafu 2009). They also include some browse in their diet, including forbs, fallen fruits and woody shrubs (Ewer 1958; Cumming 1975; Mason 1982; Smithers 1983; Rodgers 1984; Somers 1992; Vercammen & Mason 1993; Boomker & Booyse 2003; Treydte 2004; Treydte *et al.* 2006; Nyafu 2009). Given that grass forms the greatest part of their diet, warthogs are expected to compete for forage with other grazers that coexist with them. Mason (1982) noted that white rhino (*Ceratotherium simum*) and blue wildebeest (*Connochaetes taurinus*) could be potential food competitors of warthogs as they also prefer the short grass eaten by warthogs. In the Addo Elephant National Park, the potential competitors of common warthogs could be Cape buffalo, zebra (Landman & Kerley 2001) and possibly elephant, eland and red hartebeest. Previous studies conducted in the AENP showed that Cape buffalo, zebra and red hartebeest are largely grazers (Landman & Kerley 2001; Schlebusch 2002). This reflects possible opportunities of competition among these herbivores. It is therefore important to study the diet of common warthogs in order to understand their resource requirements and potential impact they might have on native species, through competition.

In some areas, changes in vegetation structure and ecosystem functioning have been observed due to high densities of herbivores (Augustine & McNaughton 1998; Treydte 2004; Kerley & Landman 2006). One of the ways in which herbivores can affect the vegetation structure and ecosystem functioning is the direct consumption of entire plants or plant parts (Davis 2004; Landman *et al*.

2008), and possibly digging and seed dispersal (Vavra *et al*. 2007). Solanki & Naik (1998) noted that different ungulates may exploit their natural environment differently, depending on their feeding behaviour. The warthog behaviour of kneeling and digging while feeding (Mason 1982) results in bare ground because when digging they exhume everything in the ground using their tough snout, even in hard ground (Ewer 1958).

Since the establishment and spread of common warthogs in the Eastern Cape their impact on vegetation structure has become a cause of concern (Nyafu 2009). In the AENP, the main cause of concern regarding impact on vegetation is elephant herbivory (Kerley & Landman 2006), elephant have been reported to feed on 146 plant species in the AENP (Kerley & Landman 2006). There is however no literature available about the impacts of common warthog in the AENP. The current study will therefore determine which plant species are available and selected by common warthogs and which therefore are at risk through their herbivory.

Herbivore diets have been determined by a variety of techniques including direct observation of the animal (Field 1970; Viljoen 1983; Somers 1992; Henley *et al*. 2001), oesophageal fistulation (Van Dyne & Heady 1964; Henley *et al*. 2001), stomach analysis (Smith & Shandruk 1979; Kerley 1992), stable carbon isotopes (Codron *et al*. 2006; Nyafu 2009), DNA-based analyses (Bradley *et al*. 2007; Valentini *et al*. 2009) and microhistological faecal analysis (Sparks & Malechek 1968). This study used the microhistological analysis. This technique has become the most frequently used (Holechek 1982) and is the best for dietary analysis since it can provide valid information about the diet of an animal (Treydte *et al.* 2006). It is cheap and specific and does not involve the killing of animals (Holechek *et al*. 1982). It can be used for endangered wild herbivores and it also allows sampling for a large number of animals under natural conditions and without disturbing them (Holechek *et al*. 1982). This technique has been successfully used in previous studies to determine the diet composition of a range of herbivores (van Teylingen 1992; Landman & Kerley 2001; Davis 2004; Treydte *et al*. 2006; Cooper 2008; De Beer 2008; Landman *et al*. 2008; Milne 2008) including common warthog (Nyafu 2009). Holechek *et al*. (1982) summarized both the advantages and disadvantages of this technique.

The aim of this chapter was to describe the diet of common warthogs in the AENP Main Camp in order to identify plants potentially at risk from common warthog herbivory, and how it overlaps with the diet of other herbivores in the AENP, by looking at the existing literature on the diet of herbivores that coexist with common warthogs in the AENP.

4.2 MATERIALS AND METHODS

4.2.1 Microhistological dietary determination

The diet composition of common warthog was determined by microhistological faecal analysis, a technique that involves the identification of plant epidermal fragments occurring in faecal material (Sparks & Malechek 1968).

4.2.2 Dietary composition

Fifteen fresh faecal samples were collected seasonally; spring (October) 2008, and summer (January), autumn (May) and winter (July) 2009 in the Addo Elephant National Park Main Camp. The samples were oven-dried at 50^{o}C for a week, ground through a 2 mm mesh screen and stored until analysis. The technique modified by Landman *et al*. (2008) was followed for digestion of faecal samples. Five grams of the dung samples were boiled in 20 ml of 55% nitric acid for two minutes. Then 100 ml of water was added and samples were boiled for a further 5 minutes. After the completion of the boiling process samples were rinsed through a 250 µm sieve (Macleod *et al*. 1996) and stored in formalin acetic acid (25% water, 60% alcohol, 10% formalin & 5% glacial acetic acid) until analysis.

A small amount of the prepared sample was placed on a gridded microscope slide and one hundred epidermal fragments drawn from two subsamples were identified using the Centre for African Conservation Ecology (ACE) plant epidermal reference collection (Landman *et al*. 2008). The fragments were viewed under a compound microscope, at 400X magnification and compared to reference photos of plant species.

Additional reference collection samples were prepared from all the plant species collected in 2009 in the AENP Main Camp but absent from the ACE reference collection. Plant species were identified using NMMU herbarium. Preparation for inclusion in the ACE reference collection followed the method used by Macleod *et al.* (1996). The leaves of collected plants were cut into small squares and boiled in 10% nitric acid until the mesophyll and epidermis separated. After the completion of the boiling process (approximately 5 minutes), the epidermis was rinsed under tap water and the remaining mesophyll, if it is not completely removed, was removed gently with a scalpel. The epidermis was then placed on a microscope slide, stained with Ruthenium Red and mounted with DPX once it had dried out completely. For each plant species, photographs were taken for both abaxial and adaxial surfaces where possible. These photographs (Appendix 1) were taken at different magnifications i.e. 100x or 400x depending on the clarity of each photo (Gaylard & Kerley 1995; De Boer *et al*. 2000).

4.2.3 Forage Availability

The relative availability of forage species for common warthog was determined in different habitats of AENP Main Camp. This was based on the point intercept method (Mueller-Dembois & Ellenberg 1974) which involved the measurements of plant species recorded at 20 cm intervals along 15 X 50m transects for each period. Only plant species within the foraging height of common warthog were recorded and maximum foraging height of warthog of 50 cm is noted by Cumming (1970) and Mason (1982). Plants above 50 cm were excluded. The data for forage availability were collected twice, in May and July 2009. These data were used to estimate forage availability and hence selectivity by comparison with the diet for these periods.

4.2.4 Data analysis

Species accumulation curves (50 randomised iterations) were plotted using *EstimateS* Ver. 7.5 (Colwell 2005) to show the number of plant species recorded per common warthog faecal sample for each season. The incidence-based coverage estimator (ICE) was used to estimate the number of species missed during plant species identification. ICE estimates the total species richness based on the relative proportions of common, infrequent, and unique species (Foggo *et al*. 2003). This was done in order to investigate the adequacy of the number of faecal samples, and to estimate the number of plant species consumed. Plant species identified in the diet of common warthog were grouped into growth forms and their proportions were calculated. A Multidimensional Scaling (1000 permutations) ordination in Primer 6 was used to visually assess seasonal variation in the diet eaten by common warthogs. The plots of MDS were based on Bray-Curtis similarity matrices with square root transformed data (Bray & Curtis 1957). A stress value of < 0.2 was considered in the current study as it provides potentially useful 2-d plots (Clarke *&* Warwick 2001; Quinn & Keough 2002). For further analysis, One-Way Analysis of Similarity (5000 permutations) was used to determine significant differences in the diet between seasons. ANOSIM compares variation both between and within groups (Clarke *&* Warwick 2001; Quinn & Keough 2002). The difference between and within groups would be suggested by R values, ranging between + 1 and 0. R values of zero indicate that there is no difference and R values close to one indicate that replicates are more dissimilar between groups than within groups (Clarke *&* Warwick 2001; Quinn & Keough 2002). Petrides (1975) defined principal dietary items as those that are eaten in the greatest quantities and in this study they were defined as those that contributed more than 2% to the diet of an animal (Landman *et al*. 2008).

To determine preferences for plant species by common warthog, Jacob's index was used (Jacobs 1974). Jacob's index was calculated as follows:

$$D = (u-a) \cdot (u+a-2ua)^{-1}$$

The variable *u* is the proportional utilization and *a* is the proportional availability of food items. The index, *D* ranges from +1 (maximum preferred) to -1 (maximum avoidance) (Jacobs 1974). Dietary items were considered to be significant preferred/avoided if the confidence interval of utilization did not overlap with the mean relative availability (Neu *et al*. 1975). Statistica version 8 was used to calculate 95% confidence interval and the data were arcsine transformed to conform to normality. A Chi-square test was used to test if the plants available were utilized in proportion to their relative availability.

4.3 Results

4.3.1 Food Availability

Ninety-five plant species which were considered potentially accessible to common warthogs were found in the AENP Main Camp during the study period. These plants were dominated by woody shrubs (42 spp.) and forbs (28 spp.).

4.3.2 Dietary composition of common warthog

The cumulative species sampling curves for all seasons clearly approached the asymptotes (Figure 4.1). Only a single plant species was estimated as being missed by the ICE estimator for each season (Table 4.1). Forty-two plant species were identified in the diet of common warthog over all sampling periods, and these comprised of grasses (19 spp.), forbs (16 spp.), woody shrubs (6 spp.) and a single succulent species. However, ten of the forty-two plants could not be identified to species and genus levels and were only identified to growth form level. The number of plant species identified varies across the seasons, with the total number ranging between 27 (spring) and 33 (autumn) species.

The MDS plots (Figure 4.2) showed a relatively high stress value (0.23) and consequently does not show clear distinction between seasons. The ANOSIM results were significant ($p < 0.001$ and $R = 0.421$), showing significant differences in the diet of common warthogs between seasons. The highest difference was observed between spring and autumn ($R = 0.655$), followed by summer and autumn ($R = 0.511$), summer and spring ($R = 0.459$), summer and winter ($R = 0.367$), spring and winter ($R = 0.349$) and finally autumn and winter ($R = 0.236$).

SIMPER however showed a high percentage similarity of samples between seasons and summer samples showed the highest percentage of similarity (70.2%), spring (65.1%), autumn (65.6%) and winter (60.6%). These similarities are reflected in the MDS plot (Figure 4.2), where summer, spring and autumn samples are closely grouped in the MDS space, whereas winter samples are dispersed.

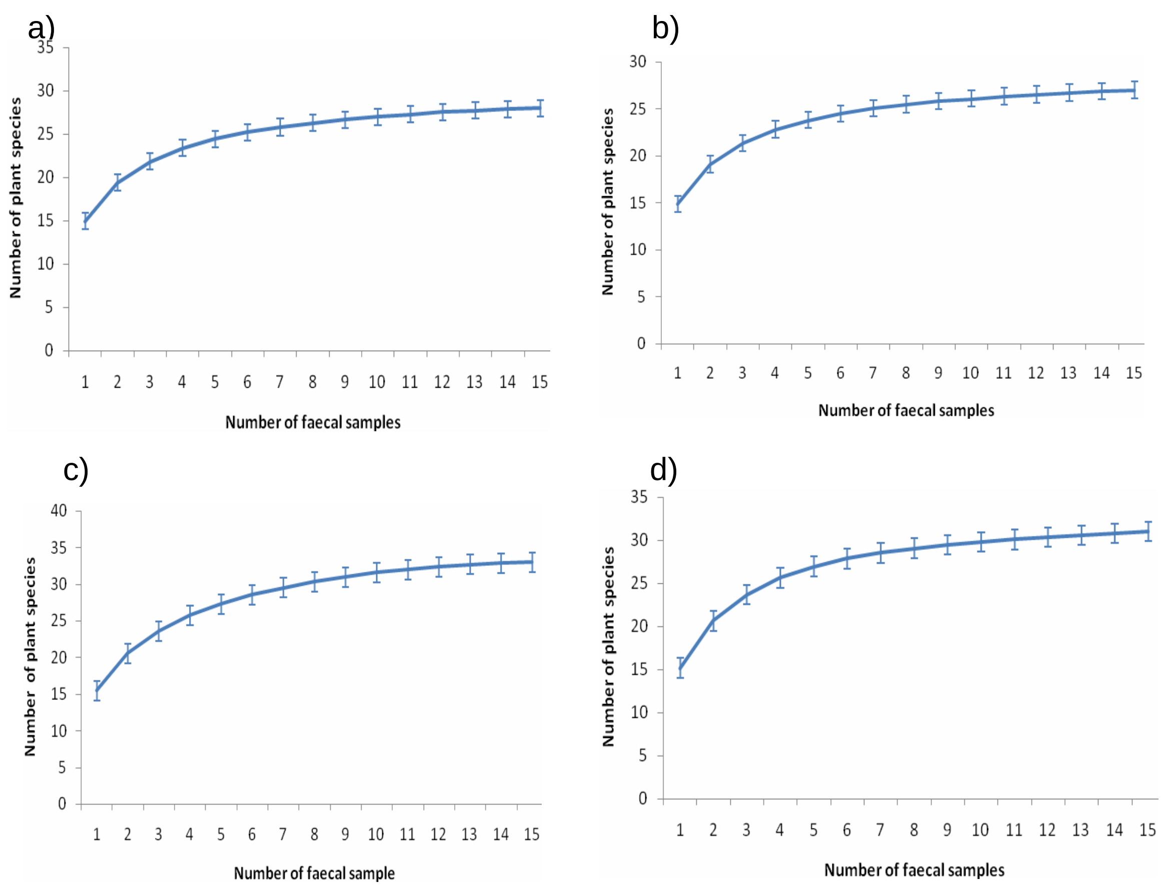


Figure 4.1 Cumulative curves (mean ± 1 SD; 50 randomised iterations) of plant species recorded per common warthog faecal samples for all four seasons in the AENP Main Camp. a – summer, b – spring, c – autumn and d – winter.

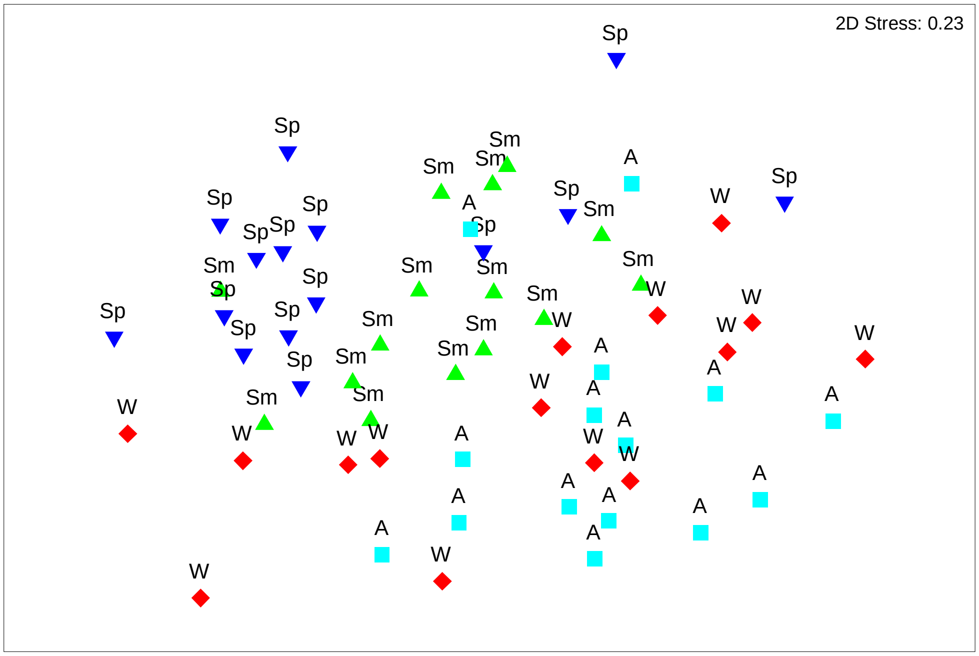


Figure 4.2 n-Multidimensional scaling ordination (1000 permutations) of common warthog diet, for four seasons; Sm = summer, Sp = spring, A = autumn and W = winter.

Grasses formed the largest percentage of common warthog diet (Table 4.2), with *Cynodon dactylon* contributing the greatest percentage of grasses throughout the seasons. Forbs contributed a small amount to the diet of common warthog followed by woody shrubs and finally succulents. No geophytes were identified in the diet of common warthogs during the study period. There were no significant differences in the contribution of growth forms between seasons except that autumn showed a slight decline of grass intake, which was compensated for by higher intake of browse. The contribution of browse to the diet of common warthog was high in autumn compared to other seasons, followed by winter. Fifteen of these plant species were identified as principal dietary items (Table 4.3), and together these contributed 89.4% to the total diet of common warthog in the AENP Main Camp. Principal dietary items show slight variation seasonally with the total number of PDI's increasing from eight in summer to twelve in autumn.

Table 4.1 Total number of plant species observed in the diet of common warthog in AENP Main Camp for four seasons and the incidence-based estimator (ICE).

Seasons	Observed spp.	ICE (spp. richness estimator)	Estimated no. of missed spp.
Summer	28	29	1
Spring	27	28	1
Autumn	33	34	1
Winter	31	32	1

Table 4.2 Overall percentage contribution of growth forms to the diet of common warthog in the AENP Main Camp.

Growth form	Diet (%)	Number of spp.
Grasses	87.4	19
Forbs	8.2	16
Woody shrubs	2.5	6
Succulents	1.9	1

4.3.3 Forage preference

Growth forms and all PDI's were not utilized in proportion to their relative availability for both the May (Growth forms; χ^2 = 100.18; $p < 0.05$; PDI's; χ^2 = 60.55; $p < 0.05$) and July periods (Growth forms; χ^2 = 148.1; $p < 0.05$; PDI's; χ^2 = 51.89; $p < 0.05$) (Figure 4.3). Grasses were highly preferred during both periods, May (D = 0.81) and July (D = 0.93), whilst woody shrubs were significantly avoided (May; D = -0.67 & July; D = -73). All principal dietary items were preferred, (Figure 4.3) except for *P. afra* which was significantly avoided in May but not significantly so in July.

Table 4.3 Percentage contribution (mean ± SD) of principal dietary items to the diet of common warthog in the AENP Main Camp for four seasons. Dashes indicate the species that were found in the diet of common warthogs in that season but not as a principal dietary item. Sm = summer, Sp = spring, Aut = autumn, Win = winter.

Growth forms	Species	Sm (%)	SD	Sp (%)	SD	Aut (%)	SD	Win (%)	SD
Grass	*Cynodon dactylon*	28.1	8.4	20.6	16.2	24.7	7.6	28.9	13.3
Grass	*Eragrostis obtusa*	16.5	4.6	11.7	5.4	12.0	4.1	13.9	6.2
Grass	*Panicum deustum*	11.6	6.4	15.0	6.9	10.5	5.0	13.9	9.2
Grass	*Aristida diffusa*	7.5	4.9	11.1	9.2	3.3	4.6	4.1	6.9
Grass	*Eragrostis curvula*	7.3	3.5	6.3	2.8	8.5	4.9	5.3	3.8
Grass	*Panicum maximum*	7.1	6.2	7.1	4.4	4.9	3.4	4.3	3.6
Grass	*Eustachys paspaloides*	4.5	2.5	4.2	3.3	3.1	3.6	2.1	2.6
Grass	Unidentified 1	2.9	2.4	2.7	1.8	6.3	3.5	4.7	2.9
Grass	*Ehrharta calycina*	-	-	3.3	4.3	-	-	2.1	3.0
Succulent	*Portulacaria afra*	-	-	-	-	3.9	3.1	2.9	3.9
Grass	Unidentified 4	-	-	-	-	2.6	3.0	4.3	4.0
Woody shrub	Unidentified 3	-	-	-	-	5.4	3.0	-	-
Grass	*Eragrostis spp.*	-	-	3.0	2.5	-	-	-	-
Forb	*Senecio spp.*	-	-	-	-	2.6	2.1	-	-
Grass	Unidentified 8	-	-	2.1	2.4	-	-	-	-

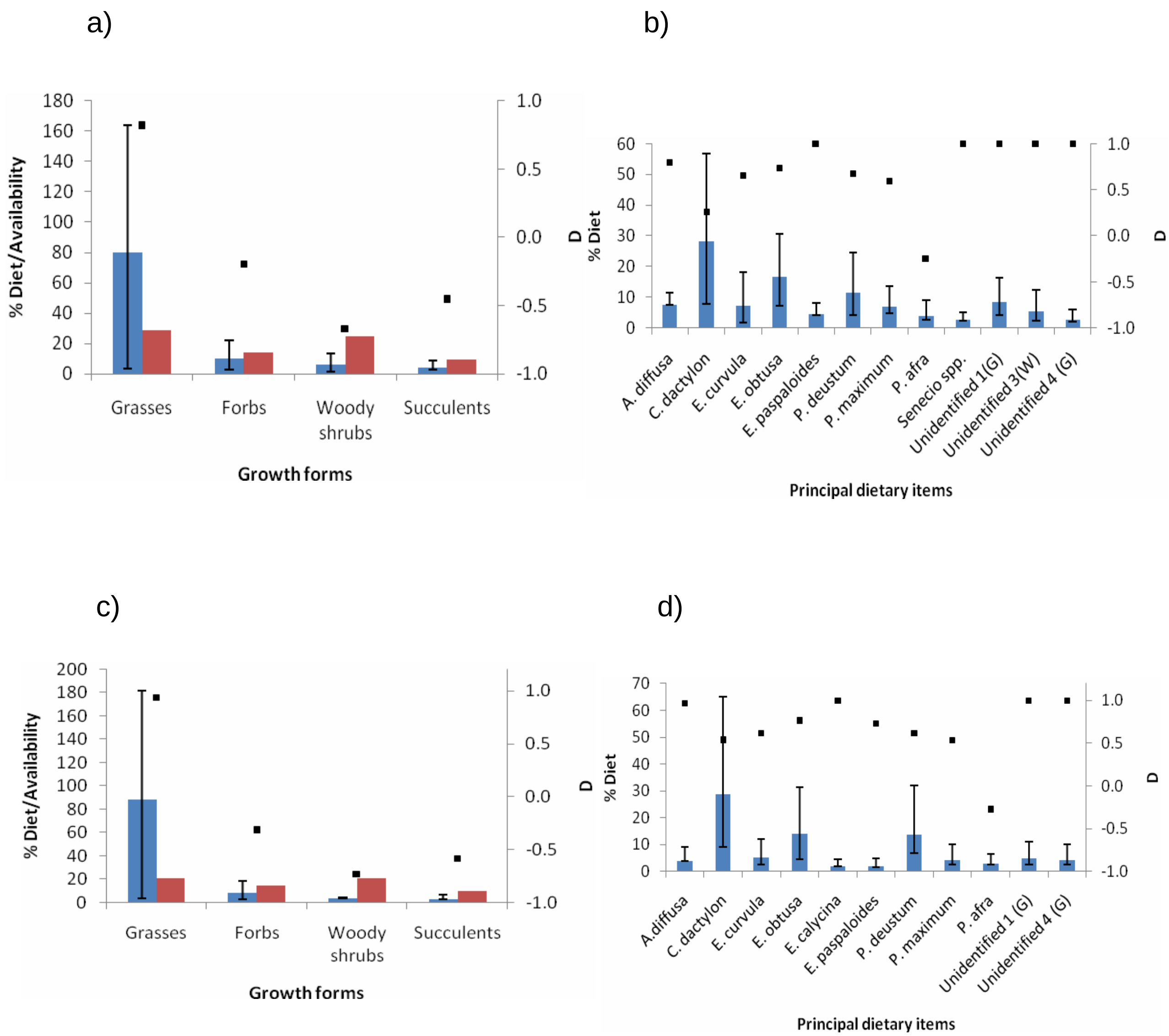


Figure 4.3 Utilization (mean ± 95% confidence interval; blue bars) and mean relative availability (red bars) of plant growth forms and PDI's identified in the diet of common warthog. Jacobs' index (black bars) indicate preference (D > 0) or avoidance (D < 0). a & b (growth forms and PDI's - May) and c & d (growth forms and PDI's - July). (Note G - refers to grass and W - woody shrub).

4.4 Discussion

The cumulative species sampling curves clearly approached the asymptote, with the ICE estimator showing one species missed in the diet of common warthogs during plant species identification for each season. This shows that fifteen faecal samples per season were adequate to describe the diet of common warthogs in the AENP Main Camp. This is supported by the results found by Nyafu (2009) for common warthog in the GFRNR and Milne (2008) for Angora goat (*Capra hircus*) in Blaaukrantz farm, Eastern Cape who also used fifteen faecal samples. Moreover, Davis (2004) used 13-14 faecal samples to confidently describe the diet of elephants.

Although the food available for common warthogs in the study area was mainly dominated by woody shrubs and forbs, the diet of common warthogs was dominated by grasses. Common warthogs in the AENP Main Camp consumed a variety of plant species with some not encountered in any of the transects during measurement of forage availability. Certain grass species occurred in greater quantities in the diet of common warthogs as they were recorded as principal dietary items in the current study (Table 4.3). The high level of grass intake by common warthogs throughout the four seasons in the current study and previous studies in other parts of Africa (Ewer 1958; Cumming 1975; Mason 1982; Smithers 1983; Rodgers 1984; Somers 1992; Vercammen & Mason 1993; Boomker & Booyse 2003; Treydte 2004; Treydte *et al.* 2006; Nyafu 2009) confirms that common warthogs are specialized grazers across their range.

The present study confirmed that common warthogs in the AENP Main Camp are essentially grazers, feeding consistently on grasses which made about 87.4% of their diet. Although common warthogs fed mainly on grasses throughout the seasons, their diet varied by season with more browse utilized in autumn compared to other seasons. This seasonal variation could be measured by the increase in the number of plant species consumed by common warthogs in different seasons, with the number of plant species increased from 27 spp. in spring to 33 spp. in autumn. There is a decline in the relative availability and nutritive value of grass during dry seasons (Sinclair 1975). This decline could be caused by low rainfall and temperatures during these periods. Sinclair (1975) found that ungulates require an average value of 4-5% crude protein to maintain their body weight, but due to decline in the quantity and quality of food during dry periods, the animals could only achieve this by actively selecting for small quantities of green material. This could explain why common warthogs increased browse intake and the number of plant species eaten during these periods. These results are consistent with the results found by Nyafu (2009) for common warthog diet in the GFRNR. The increase of browse intake and number of plant species eaten by common warthog during dry seasons has been found for other herbivores as well from previous studies including, Angora goat (Milne 2008), and fallow deer (*Dama dama dama*) (Cooper 2008).

Although the impacts of common warthogs in the AENP Main Camp were only investigated through diet description, the information obtained from this study on the diet of common warthogs in the AENP Main Camp is a useful guide for predicting their impacts in the AENP Main Camp. Understanding what is available to common warthogs and what they prefer in the AENP Main Camp provided worthwhile information about the possible impacts they might have. Common warthogs selected certain grass species and took them at greater quantities than others and these species can be used as indicators to monitor the impacts of common warthogs.

The PDI's were all preferred except for *P. afra*, and these PDI's were dominated by grasses. Of the nineteen grass species recorded in the diet of common warthogs in the current study, twelve of them were PDI's. The remaining seven grass species were also eaten, but not in large quantities. The possible explanation to this could be the low availability of these grasses in the AENP Main Camp, as some were recorded infrequently and others were not recorded during collection of food availability data (Appendix 2 for grass species not recorded during collection of forage availability data). During summer and spring all PDI's were grasses, whereas PDI's in autumn and winter include some browse species. Nyafu (2009) also recorded more browse PDI's in dry seasons (autumn & winter) than wet seasons (spring & summer). Cooper (2009) also noted the increase in the number of PDI's in the diet of fallow deer, from ten PDI's during summer to twelve PDI's in winter. The increase in the number of PDI's during the dry season may simply indicate that the preferred dietary items were limited (Owen-Smith & Novellie 1982).

Newman *et al*. (1995) documented that constant selection of dietary items by large grazing mammals may lead to local extinction of preferred plant species. This then shows that plant populations, specifically grasses are at risk of extinction through common warthog diet selection in the AENP Main Camp. Milne (2008) noted that *P. afra* was a preferred plant species and a PDI of Angora goat, however the availability of this plant species was very low in the transformed treatment in Blaaukrantz farm. The consistent feeding of goats to *P. afra* has led the goats to be blamed for this decline (Stuart-Hill 1992; Moolman & Cowling 1994; Milne 2008). Similarly, the constant feeding of common warthogs on grasses in the AENP Main Camp, especially *C. dactylon,* would lead to the conclusions that common warthog may alter grass dynamics in the AENP Main Camp.

Resource overlap

The results of this study have shown that the diet of common warthogs overlap with the diet of other herbivores occurring in the AENP Main Camp and in other parts of Africa. Grasses form a significant proportion of the diet of elephants with *C. dactylon* being the dominant grass species in elephant diet (Paley & Kerley 1998; Davis 2004; Landman *et al*. 2008). During autumn and winter, common warthog showed a high consumption of *P. afra* in the AENP Main Camp; it was then recorded as a principal dietary item during these seasons. This plant species has been recorded as one of the elephant principal dietary items

(Landman *et al*. 2008). This resource overlap shows the possible opportunities for competition between elephants and common warthogs. Despite that, common warthogs may also benefit from elephant impact because elephants creating new areas of grasslands through their overgrazing thicket (Kerley & Landman 2006). During drought periods it is however likely that elephants and common warthogs may compete directly for grass resources.

Landman & Kerley (2001) documented that grasses contributed 91% of the diet of zebra and 71.9% of the diet of buffalo (with *E. curvula* being the dominant food item for both species) in the AENP. Schlebusch (2002) noted that red hartebeest is a specialized grazer with its diet dominated mainly by grasses (82.5%) whilst eland proved to be a browser with small proportion of grass (36.5%) in their diet compared to red hartebeest (Table 4.4). Schlebusch (2002) showed that *C. dactylon* was the dominant food item in the diet of red hartebeest, whilst *P. deustum* was the dominant grass species in the diet of eland. All three grass species (*C. dactylon*, *E. curvula. & P. deustum*) were also dominant in the diet of common warthogs in the AENP Main Camp during the study period. Schoener (1982) noted that similarities in the diet of animal species show opportunities for competition for resources especially if such animals co-exist and the availability of the food item is limited. This therefore highlights the possible role of common warthogs as a competitor for these indigenous species.

The availability of grass species might change, depending on the environmental conditions. Previous studies in other parts of Africa (Sinclair 1975; Bakker *et al*. 1983; Armstrong *et al*. 1997) noted that the availability of grass varies, with both quantity and quality of grass declining during dry seasons and drought periods. Stuart-Hill & Aucamp (1992) documented a collapse in grazing resources in thicket near Addo during a drought. It is thus predicted that the scarcity of grass in the AENP Main Camp during drought will increase chances of competition among species, especially those predominately feeding on *C. dactylon*. Though it might be the case, warthogs have advantages over other grazing herbivores because they are capable of feeding in areas inaccessible to other grazers and cropping grasses shorter (Ewer 1958). Warthogs also have an advantage because they are hindgut fermenters (Treydte *et al*. 2006) and they have high rates of passage of digestion. In addition, the high fecundity of warthog (Child *et al.* 1968; Cumming 1975; Boshe 1981; Mason 1982; Rodgers 1984; Somers & Penzhorn 1992) allows them to respond demographically very rapidly to available grazing resources.

Table 4.4 Percentage contribution of grass to the diet of herbivores in the AENP.G spp. = (Grass species).

Species	% diet (grass)	Dominant G spp.	Reference
Zebra	91	*E. curvula*	Landman & Kerley (2001)
Common warthog	87.4	*C. dactylon*	Current study
Red hartebeest	82.5	*C. dactylon*	Schlebusch (2002)
Buffalo	71.9	*E. curvula*	Landman & Kerley (2001)
Eland	36.5	*P. deustum*	Schlebusch (2002)
Elephant	36.4/ 26.6/ 34.1	*C. dactylon*	Paley & Kerley 1998; Davis 2004; Landman *et al*. 2008
Black rhino	20.8	*C. dactylon*	Landman (In prep)

CHAPTER 5

CONCLUDING DISCUSSION

5.1 Introduction

This dissertation set out to test hypotheses regarding population responses of common warthogs and to describe their diet in the AENP Main Camp, in order to contribute to the understanding of their population dynamics and potential impacts in the Eastern Cape. These objectives have been fulfilled, with results showing that common warthogs show the first phases (slow establishment followed by rapid growth) of a sigmoid-population growth curve after establishment, with no discernable effects of the levels of predation experienced in the AENP Main Camp. This calls into doubt Somers (1992) original hypothesis of the role of the absence of predation in the observed rapid population growth in the GFRNR. Furthermore, the diet data confirm that common warthogs are largely grazers, showing high preference for specific grasses. These identified dietary species may be useful in monitoring the impacts of common warthog in the Eastern Cape. The implications of these findings are further expanded upon below.

5.2 Population trends and age structure of common warthog

The observed common warthog population growth in the AENP Main Camp was not in agreement with our prediction that the common warthog population growth is slower into the presence of predators. Instead, the high rate of increase of common warthog population within the AENP Main Camp illustrates that common warthog population growth is not determined by the presence of predators (at least at these levels of predation). This observation also disagrees with Somers (1992) hypothesis of the rapid common warthog population growth being due to the absence of predators in the GFRNR. This suggests that common warthog populations in the Eastern Cape should be carefully monitored and investigated in order to identify their population-regulating factors, so that alternative approaches can be developed to manage their populations. Although there is some culling already taking place in the AENP Main Camp, but it is not effective in producing a discernable decline in the rate of increase of this population. If population regulation is attempted through culling, the levels of offtake will have to be aligned with the reproductive rate of this species.

The population growth rate of common warthogs in the AENP Main Camp shows the first phases of a typical S-shaped or sigmoid curve with this population apparently currently not influenced by predation (at least in comparison with available data from the GFRNR). The available older data for the population of common warthogs for GFRNR includes data up to well into the rapid growth phase, confirming that they have not yet reached the carrying capacity. Based on the population growth pattern of an introduced species (Mack *et al*. 2000) it might be expected that the population growth pattern of the future common warthog in these areas might stabilize around some asymptote. This population stabilization will only take place when these populations have reached their environmental limits (so-called carrying capacity). Mack *et al*. (2000) noted that once a species reached the carrying capacity, the populations persist but do not expand.

Due to the high population growth rate of common warthogs in the GFRNR a reduction program (harvesting) was initiated to manage this population. However, it was noted that this reduction program continued without considering the long term effect it might have on the common warthog population (Somers & Fike 1993). This led to further investigations by Somers (1997), who discovered that the reduction program might eventually lead to population extinction. Therefore to ensure proper scientifically based management Somers (1997) recommended that common warthog population monitoring program and simulations should be put in place. However this was prior the general recognition of common warthog as an invasive species in the Eastern Cape. From this perspective, it may have been more appropriate for Somers (1997) to recommend the management goal of extinction.

The older data obtained from the study of Somers (1992) on the common warthog population in the GFRNR only shows the common warthog population in its rapid growth phase, and this was before the attempt of the population reduction in this area. This could suggest that the common warthog numbers might have declined or stabilise since the Somers (1992) study in the GFRNR. More data is therefore needed to quantify the role of the reduction program on warthog population in the area.

Warthog population increases are supported by their high reproductive rates (Child *et al*. 1968; Cumming 1975; Boshe 1981; Mason 1982; Rodgers 1984; Somers & Penzhorn 1992). Their population growth has been augumented through allomothering, a social interaction of females which are not the mother helping raise piglets, which contributes to high juvenile survival rate even if the mother died (Somers 1992). Despite the fact that some predators select adult warthogs because they are close to their preferred weight range (lions - Hayward & Kerley 2005; spotted hyaena - Hayward 2006; leopard - Hayward *et al*. 2006), the social interaction of warthogs taking care of one another brings more stability to the population (Somers 1992). This then decreases the efficiency of population reduction programs where whole groups are not killed (Somers 1992). These ideas suggest that warthog population regulation through predation or culling cannot simply be based on numbers killed, but needs to take social factors into account.

The differences in the adult age structure of AENP Main Camp and GFRNR common warthog population agreed with our prediction. The effect of predation in the AENP Main Camp only affected population age structure, but not population growth. In other parts of Africa, predation affected population growth, resulting in common warthog populations decline (Cumming 1975; Mason 1982; Hunter 1998). These findings are contrary to the findings of the present study, but what factors influence these are not known. Despite the fact that these studies did not assess the effect of predation on common warthog population age structure, given the preferred prey weight range of lions (Hayward & Kerley 2005), it reflects that adults were the most preferred prey item, rather than the piglets. The present study has therefore contributed to our understanding of the role of predation in common warthog demographics, but has actually raised a series of questions as to what levels of predation are required for top-down regulation of common warthog, and what other factors can play a role in this process.

5.3 Impacts of introduced common warthog

The impacts of alien invasive species on biodiversity might be difficult to quantify (Castley *et al*. 2001; Spear & Chown 2009). It is thus important to understand the structure and functioning of biodiversity of the receiving community to quantify these impacts (Duelli & Obrist 2003). Noss (1990) noted three phases of biodiversity and these are composition, structure and function. These three phases are defined below: Composition is referred to as the identity and variety of elements in a system (i.e. number of species), structure is a physical organization of a system (i.e. habitat complexity) and lastly, function which is referred to as ecological and evolutionary processes (i.e. gene flow and disturbances) (Noss 1990). In addition, Traveset & Richardson (2006) noted that the impacts of alien invasive species often affect more than one aspect of this system.

In the current study, common warthogs in the AENP Main Camp have shown that they have the potential to affect compositional diversity of plants as they grazed largely on grasses and a few other plant species. They have also shown resource overlap with other herbivores co-existing with them. This could result in common warthogs having impacts on other herbivores through resource competition. Common warthog impacts on structural diversity has been recorded in the GFRNR and more broadly in the western Eastern Cape, where they were reported to have impacts on grass cover and soil (Somers 1992; Somers *et al*. 1994; Nyafu 2009). At another level, they have also been shown to influence the movement of species, such as jackal across the pastoral landscape, through damaging fences (Somers 1992; Somers *et al*. 1994; Nyafu 2009). Invaders do not always modify the entire ecosystem but they can drastically affect specific plant or animal species by feeding upon a native species to the point of its extinction (Simberloff 1996). Simberloff (1996) noted that introduced species can compete with the native ones and possible chances of competition among grazing herbivores in the AENP Main Camp have been identified in this study.

Common warthogs in the Eastern Cape have shown that they have the potential to threaten a number of grass species (Somers 1992; Nyafu 2009; current study). Their feeding specific manners of rooting and digging (Cumming 1975; Mason 1982) can alter the ecosystem processes of this region (Nyafu 2009). Nyafu (2009) noted that the potential impacts of common warthogs in the Eastern Cape are not only in conservation areas but in surrounding areas as well, such as commercial farms. This suggests that initiatives need to be taken in order to manage this species before it impacts the ecological processes of this region. This will need to be based on a better understanding about the impacts of this species in these areas so that they can be properly managed.

At a finer scale, it is clear from the results of this study and previous studies (Somers 1992; Nyafu 2009) that common warthogs are invasive species in the Eastern Cape. Given the core function of conservation areas to exclude threats to biodiversity and the fact that invasive species have been shown to play a major role in species extinctions (Caughley 1994) it is recommended that active eradication of common warthogs in Eastern Cape conservation areas, including AENP, should take place.

5.4 Future research

The current study has shown that predators in the AENP Main Camp do not have significant impacts on the population growth of common warthogs. However population trends of common warthogs in the presence of their potential predators, like lions need further research in order to understand the ecology and behaviour of common warthogs and predators (and their interactions with each other) over the long term. In addition, a common warthog population model needs to be developed, to predict predator-prey interactions within the AENP Main Camp.

The common warthog population data obtained was not complete, with some data missing, although it did not affect the analysis and the results of the present study. It is therefore suggested that a dedicated monitoring strategy be put in place to keep track of the common warthog populations, especially in conservation areas. This is particularly important where culling is applied to these populations. The outcome of this culling should be evaluated. The increase of common warthogs in different areas in the Eastern Cape also needs further investigation, as these animals seem to be increasing at a high rate in the AENP Main Camp. This could also apply to other areas in the Eastern Cape and this could be exacerbated in areas where grass resources are high and management input is low, such as the eastern Eastern Cape.

Nyafu (2009) noted the killing of common warthogs by local farmers, and the present study focused on predation in the AENP Main Camp. Neither of these seems to be working towards controlling common warthogs, there is therefore a need to develop another management strategy to control common warthogs in the Eastern Cape. This may require increased management effort and the application of multiple approaches, based on more extensive research on common warthog population regulation.

The high density of elephants and their impacts on the thicket habitat of AENP such as feeding and trampling leads to more open grassland areas (Kerley & Landman 2006). It can be hypothesized that this therefore makes way for increased resources for grazing herbivores such as common warthogs. Future research is therefore needed in order to investigate the extent to which elephants contribute towards the common warthog population increase in the AENP Main Camp (through the provision of open habitat), and the implications for the interactions between elephant and common warthog on vegetation in the AENP.

The current study and previous studies conducted in the Eastern Cape confirm that common warthogs are specialized grazers, with potential impacts on a number of grasses. Grasses eaten by common warthogs in the Eastern Cape can be used as indicators to monitor the impacts of the species in the Eastern Cape. The hypothesis developed in Chapter 4 in which specific grass species vulnerable to common warthog have been identified needs to be tested.

Digging by common warthog in search of forage resources may result in bare ground creation, which has been reported in other parts of Africa by Ewer (1958). This subsequently increases the likelihood of nutrient loss and run-off through soil erosion. Thus, common warthog impacts on soil and plant dynamics needs to be investigated not only in the AENP Main Camp but in the broader Eastern Cape as well.

Lastly, it is further suggested that density and carrying capacity of these animals needs to be investigated to develop a population model which reflects population regulation factors and quantify their impacts on the landscape. Such a broader approach can be used to evaluate and prioritize impacts and develop a landscape level management approach for this invasive species.

REFERENCES

ALTENDORF, K.B., LAUNDRÉ, J.W., LÓPEZ GONZÁLEZ, C.A. & BROWN, J.S. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* **82(2):** 430-439.

ANDOW, D.A., KARIEVA, P.M., LEVIN, S.A. & OKUBO, A. 1990. Spread of invading organisms. *Landscape Ecology* **4(2/3):** 177-188.

ARMSTRONG, H.M., GORDON, I.J., GRANT, S.A., HUTCHINGS, N.J., MILNE, J.A. & SIBBALD, A.R. 1997. A model of the grazing of hill vegetation by sheep in the UK. I. the prediction of vegetation biomass. *Journal of Applied Ecology* **34:** 166-185.

AUGUSTINE, D.J. & McNAUGHTON, S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* **62(4):** 1165-1183.

BAKKER, J.P., DE BIE, S., DALLINGA, J.H., TJADEN, P. & DE VRIES, Y. 1983. Sheep-grazing as a management tool for heathland conservation and regeneration in the Netherlands. *Journal of Applied Ecology* **20:** 541-560.

BAUER, H., VANHERLE, N., DI SILVESTRE, I. & DE IONGH, H.H. 2006. Lion-prey relations in West and Central Africa. *Mammalian Biology* **73(1):** 70-73.

BOOMKER, E.A. & BOOYSE, D.G. 2003. Digestive tract parameters of the warthog, *Phacochoerus aethiopicus. Tropical & Subtropical Agroecosystems* **3:** 15-18.

BOSHE, J.I. 1981. Reproductive ecology of the warthog *Phacochoerus aethiopicus* and its significance for management in the Eastern Selous Game Reserve, Tanzania. *Biological Conservation* **20:** 37-44.

BOSHOFF, A.F., KERLEY, G.I.H., COWLING, R.M. & WILSON, S.L. 2002. The potential distributions, and estimated spatial requirements and population sizes, of the medium to large-sized mammals in the planning domain of the Greater Addo Elephant National Park project. *Koedoe* **45(2):** 85-116.

BRADLEY, B.J., STILLER, M., DORAN-SHEEHY, D.M., HARRIS, T., CHAPMAN, C.A., VIGILANT, L. & POINAR, H. 2007. Plant DNA Sequences from Feces: potential means for assessing diets of wild primates. *American Journal of Primatology* **69:** 1-7.

BRAY, J.R. & CURTIS, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27:** 325-349.

CASTLEY, J.G., BOSHOFF, A.F. & KERLEY, G.I.H. 2001. Compromising South Africa's natural biodiversity – inappropriate herbivore introductions. *South African Journal of Science* **97:** 344-348.

CAUGHLEY, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* **63:** 215-244.

CHILD, G., ROTH, H.H. & KERR, M. 1968. Reproduction and recruitment patterns in warthog (*Phacochoerus aethiopicus*) populations. *Mammalia* **32:** 6 - 29.

CLARKE, K.R. & WARWICK, R.M. 2001*. Change in marine communities: an approach to statistical analysis and interpretation*, 2nd Edition. Primer-E Ltd: Plymouth Marine Laboratory. UK.

CODRON, J., LEE-THORP, J. A., SPONHEIMER, M., CODRON, D., GRANT, R.C. & DE RUITER, D.J. 2006. Elephant (*Loxodonta africana*) diets in Kruger National Park, South Africa: spatial and landscape differences. *Journal of Mammalogy* **87(1):** 27-34.

COLWELL, R.K. 2005. *EstimateS: statistical estimation of species richness and shared species from samples.* Version 7.5. Storrs, CT: University of Connecticut.

COOPER, R. 2008. *Plants at risk to the alien invasive Fallow Deer* (Dama dama dama L.). Hons. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

CREEL, S., WINNIE, J., MAXWELL, B., HAMLIN, K. & CREEL, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86(12):** 3387-3397.

CUMMING, D.H.M. 1970. *A contribution to the biology of warthog* (Phacochoerus africanus, Gmelin) *in the Sengwa region of Rhodesia*. PhD. thesis, Rhodes University, Grahamstown.

CUMMING, D.H.M. 1975. *A field study of the ecology and behaviour of warthog.* Museum memoir No 7. National Museums and Monuments of Rhodesia, Salisbury.

DAVIS, S. 2004*. Diet of elephants in the Nyati Concession Area, Addo Elephant National Park*. Hons. thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

DE BEER, S. 2008. *How do small herbivores deal with resources changes? dietary response of Cape Grysbok* (Raphicerus melanotis) *to clearing alien Acacias*. Hons. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

DE BOER, W.F., NTUMI, C.P., CORREIA, A.U. & MAFUCA, J.M. 2000. Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology* **38:** 188-201.

DE KLERK, C. 2005. *The diet of black-backed jackal* (Canis mesomelas) *in the Addo Elephant National Park, Eastern Cape Province*. Hons. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

DE KLERK, C. 2009. *Detecting changes in elephant body condition in relation to resource quality*. MSc. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

D'HUART, J.P. & GRUBB, P. 2001. Distribution of the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) in the horn of Africa. *African Journal of Ecology* **39(2):** 156-169.

D'HUART, J.P. & GRUBB, P. 2005. A photographic guide to the differences between the Common Warthog. In: *Suiform Soundings, IUCN/SSC Pigs, Peccaries, and Hippos Specialist Newsletter* **5:** 4-8.

DI SILVESTRE, I., NOVELLI, O. & BOGLIANI, G. 2000. Feeding habits of the spotted hyaena in the Niokolo Koba National Park, Senegal. *African Journal of Ecology* **38(2):** 102-107.

DIXON, L.K. & WILKINSON, P.J. 1988. Genetic diversity of African Swine Fever Virus isolates from soft ticks (*Ornithodoros moubata*) inhabiting warthog burrows in Zambia. *Journal of Genetic Virology* **69:** 2981-2993.

DRUCE, D., GENIS, H., BRAAK, J., GREATWOOD, S., DELSINK, A., KETTLES, R., HUNTER, L. & SLOTOW, R. 2004. Prey selection by a reintroduced lion population in the Great Makalali Conservancy, South Africa. *African Zoology* **39(2):** 273-284.

DUELLI, P. & OBRIST, M.K. 2003. Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystem & Environment* **98:** 87-98.

DU PLESSIS, S.F. 1969. *The past and present geographical distribution of the Perissodactyla and Artiodactyla in southern Africa*. MSc thesis, University of Pretoria, Pretoria, South Africa.

ELOFF, F.C. 1984. Food ecology of the Kalahari lion *Panthera leo vernayi. Supplement to Koedoe* **27(1):** 249-258.

ELOFF, F.C. 2002. *Hunters of the dunes: the story of the Kalahari lion*. Sunbird Publishing, Cape Town.

ESTES, R.D. 1991. *The behaviour guide to African mammals*. Berkeley: University of California Press.

EWER, R.F. 1958. Adaptive features in the skulls of African Suidae. *Proceedings of the Zoological Society of London* **131:** 135 – 155.

FIELD, C.R. 1970. Observations on the food habits of tame warthog and antelope in Uganda. *African Journal of Ecology* **8:** 1-17.

FOGGO, A., ATTRILL, M.J., FROST, M.T. & ROWDEN, A.A. 2003. Estimating marine species richness: an evaluation of six extrapolative techniques. *Marine Ecology Progress Series* **248:** 15-26.

FORSYTH, D.M., COOMES, D.A., NUGENT, G. & HALL, G.M.J. 2002. Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. *New Zealand Journal of Zoology* **29:** 323-343.

FRANKLIN, D.E. 2005. *Diet of spotted hyaena and lion in the Addo Elephant National Park*. Hons. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

FUNSTON, P.J., MILLS, M.G.L. & BIGGS, H.C. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology London* **253(4):** 419-431.

GALI-MUHTASIB, H.U. & SMITH, C.C. 1992. The effect of silica in grasses on the feeding behavior of the prairie vole (*Microtus ochrogaster*). *Ecology* **73(5):** 1724-1729.

GAYLARD, A. & KERLEY, G.I.H. 1995. The use of interactive identification keys in ecological studies. *South African Journal of Wildlife Research* **25(2):** 35-40.

GRUBB, P. 1993. The Afrotropical suids *Potamochoerus, Hylochoerus* and *Phacochoerus*. In Pigs, *Peccaries and Hippos. Status Survey and Conservation Action Plan,* (eds). W.L.R. Oliver. IUCN/SSC Pigs and Peccaries Specialist Group and IUCN/SSC Hippo Specialist Group. IUCN, Gland, Switzerland.

HAYWARD, M.W. & KERLEY, G.I.H. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology London* **267:** 309-322.

HAYWARD, M.W. 2006. Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with lion (*Panthera leo*). *Journal of Zoology* **270:** 606-614.

HAYWARD, M.W., HENSCHEL, P., O'BRIEN, J., HOFMEYR, M., BALME, G. & KERLEY, G.I.H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* **270:** 298-313.

HAYWARD, M.W., ADENDORFF, J., O'BRIEN, J., SHOLTO-DOUGLAS, A., BISSETT, C., MOOLMAN, L.C., BEAN, P., FOGARTY, A., HOWARTH, D., SLATER, R. & KERLEY, G.I.H. 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* **41(2):** 205-214.

HEITHAUS, M.R. & DILL, L.M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* **83(2):** 480-491.

HENLEY, S.R., SMITH, D.G. & RAATS, J.G. 2001. Evaluation of 3 techniques for determining diet composition. *Journal of Range Management* **54:** 582-588.

HOLECHEK, J.L. 1982. Sample preparation techniques for microhistological analysis. *Journal of Range Management* **35(2):** 267-268.

HOLECHEK, J.L., VAVRA, M. & PIEPER, R.D. 1982. Botanical composition determination of range herbivore diets: a review. *Journal of Range Management* **35(3):** 309-315.

HOPKINS, G. 1992. *The age and sex structure of the warthog* (Phacochoerus aethiopicus sundevalli, Lonnberg, 1908) *population in the Andries Vosloo Kudu Reserve, using teeth and jaw measurements as the determining criteria*. Hons. thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

HUNTER, L.T.B. 1998. *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa*. PhD. thesis, University of Pretoria, Pretoria, South Africa.

JACOBS, J. 1974. Quantitative measurement of food selection. *Oecologia* **14:** 413-417.

JOHNSON, C.F., COWLING, R.M. & PHILLIPSON, P.B. 1999. The flora of the Addo Elephant National Park, South Africa: are threatened species vulnerable to elephant damage? *Biodiversity and Conservation* **8(11):** 1447-1456.

JULIANO, S.A. & LOUNIBOS, L.P. 2005. Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecology Letters* **8(5):** 558-574.

KERLEY, G.I.H. 1992. Trophic status of small mammals in the semi-arid Karoo, South Africa. *Journal of Zoology London* **226:** 563-572.

KERLEY, G.I.H. & LANDMAN, M. 2006. The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets. *South African Journal of Science* **102:** 395-402.

LANDMAN, M. & KERLEY, G.I.H. 2001. Dietary shifts: do grazers become browsers in the thicket biome? *Koedoe* **44(1):** 31-36.

LANDMAN, M., KERLEY, G.I.H. & SCHOEMAN, D.S. 2008. Relevance of elephant herbivory as a threat to important plants in the Addo Elephant National Park, South Africa. *Journal of Zoology* **274:** 51-58.

LANDMAN, M. In prep. *Foraging ecology of the black rhinoceros in the Eastern Cape.* PhD thesis, Nelson Mandela Metropolitan University. Port Elizabeth, South Africa.

LIMA, S.L. 2002. Putting predators back into behavioural predator-prey interactions. *Trends in Ecology and Evolution* **17(2):** 70-75.

LUCAS, P.W., TURNER, I.M., DOMINY, N.J. & YAMASHITA, N. 2000. Mechanical defences to herbivory. *Annals of Botany* **86:** 913-920.

MACK, R.N., SIMBERLOFF, C.D., LONSDALE, W.M., EVANS, H., CLOUT, M. & BAZZAZ, F. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Issues in Ecology* **5:** 1-20.

MACLEOD, S.B., KERLEY, G.I.H. & GAYLARD, A. 1996. Habitat and diet of bushbuck *Tragegelaphus scriptus* in the Woody Cape Nature Reserve: observations from faecal analysis. *South African Journal of Wildlife Research* **26:** 19-25.

MASON, D.R. 1982. *Studies on the biology and ecology of the warthog* Phacochoerus aethiopicus sundevalli *Lönnberg, 1908 in Zululand*. D.Sc (Wildlife Management) dissertation, University of Pretoria, Pretoria, South Africa.

MASON, D.R. 1990. Juvenile survival and population structure of blue wildebeest and warthogs in the Central Region of the Kruger National Park during the mid-summer drought of 1988/89. *Koedoe* **33:** 29-45.

McNEELY, J.A., MOONEY, H.A., NEVILLE, L.E., SCHEI, P.J. & WAAGE, J. K. (eds). 2001. *A global strategy on invasive alien species*. IUCN Gland, Switzerland & Cambridge UK. x + 50 pp.

MENDOZA, M. & PALMQVIST, P. 2007. Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? *Journal of Zoology* **274:** 134-142.

MILLS, M.G.L. 1990. *Kalahari hyaenas: comparative behavioural ecology of two species*. Unwin Hyman Ltd, London.

MILLS, M.G.L. & SHENK, T.M. 1992. Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* **61:** 693-702.

MILNE, T.A. 2008. *The effects of thicket transformation on the diet and body condition of Angora Goats*. MSc. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

MOOLMAN, H. J. & COWLING, R. M. 1994. The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. *Biological Conservation* **68:** 53-61.

MUCINA, L. & RUTHERFORD, M.C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, New York.

MUWANIKA, V.B., NYAKAANA, S., SIEGISMUND, H.R. & ARCTANDER, P. 2003. Phylogeography and population structure of the common warthog (*Phacochoerus africanus*) inferred from variation in mitochondrial DNA sequences and microsatellite loci. *Heredity* **91:** 361-372.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for Analysis of utilization-availability data. *The Journal of Wildlife Management* **38(3):** 541-545.

NEWMAN, J.A., PARSONS, A.J., THORNLEY, J.H.M., PENNING, P.D. & KREBS, J.R. 1995. Optimal diet selection by a generalist grazing herbivore. *Functional Ecology* **9:** 255-268.

NOSS, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4(4):** 355-364.

NYAFU, K. 2009. *Warthog as an introduced species in the Eastern Cape*. MSc. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

OWEN-SMITH, N. & NOVELLIE, P. 1982. What should a clever ungulate eat? *The American Naturalist* **119(2):** 151-178.

PALEY, R.G.T. & KERLEY, G.I.H. 1998. The winter diet of elephant in Eastern Cape Subtropical Thicket, Addo Elephant National Park. *Koedoe* **41:** 37-45.

PETRIDES, G.A. 1975. Principal foods versus preferred foods and their relations to stocking rate and range condition. *Biological Conservation* **7:** 161-168.

PLUG, I. & BADENHORST, S. 2001. *The distribution of macromammals in southern Africa over the past 30 000 years as reflected in animal remains from archaeological sites*. Transvaal Museum Monograph 12, Pretoria.

QUINN, G.P. & KEOUGH, M.J. 2002. *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

RANDI, E., D'HUART, J.P., LUCCHINI, V. & AMAN, R. 2002. Evidence of two genetically deeply divergent species of warthog, *Phacochoerus africanus* and *P. aethiopicus* (Artiodactyla: Suiformes) in East Africa. *Mammalian Biology* **67(2):** 91-96.

RAPSON, J.A. & BERNARD, R.T.F. 2007. Interpreting the diet of lions (*Panthera leo*); a comparison of various methods of analysis. *South African Journal of Wildlife Research* **37(2):** 179-187.

RAVNSBORG, R. 2004. *Assessing the diet of wild lions* (Panthera leo) *in the Addo Elephant National Park, South Africa*. Hons. thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

RODGERS, W.A. 1984. Warthog ecology in south east Tanzania. *Mammalia* **48:** 327 – 350.

RUGGIERO, R.G. 1991. Prey selection of the lion (*Panthera leo* L.) in the Manovo-Gounda-St. Floris National Park, Central African Republic. *Mammalia* **55:** 23-34.

SAKAI, A.K., ALLENDORF, F.W., HOLT, J.S., LODGE, D.M., MOLOFSKY, J., WITH, K.A., BAUGHMAN, S., CABIN, R.J., COHEN, J.E., ELLSTRAND, N.C., McCAULEY, D.E., O'NEIL, P., PARKER, I.M., THOMPSON, J.N. & WELLER, S.G. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* **32:** 305–332.

SCHALLER, G.B. 1972. *The Serengeti lion: a study of predator-prey relations*. The University of Chicago Press, Chicago.

SCHLEBUSCH, Z. 2002. *Diet of Eland,* Taurotragus oryx*, and Red hartebeest,* Alcelaphus buselaphus*, in the Addo Elephant National Park: Do they utilize pasture grasses*. Hons. thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

SCHMITZ, O.J., BECKERMAN, A.P. & O'BRIEN, K.M. 1997. Behaviourally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* **78(5):** 1388-1399.

SCHOENER, T.W. 1982. The controversy over interspecific competition. *America Scientist* **70:** 586-595.

SIH, A., ENGLUND, G. & WOOSTER, D. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13(9):** 350-355.

SIMBERLOFF, D. 1996. Impacts of introduced species in the United States. *Consequences* **2(2):** 1-13.

SINCLAIR, A.R.E. 1975. The resource limitation of tropic levels in tropical grassland ecosystems. *Journal of Animal Ecology* **44 (2):** 497-520.

SKEAD, C.J. 2007. *Historical incidence of the larger land mammals in the broader Eastern Cape*, (eds) A.F. Boshoff, G.I.H. Kerley & P.H. Lloyd, Second Edition, Centre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the Southern African Subregion*. University of Pretoria, Pretoria.

SKINNER, J.D. & CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion.* Third Edition. Cambridge University Press.

SMITH, A.D. & SHANDRUK, L.J. 1979. Comparison of fecal, rumen and utilization methods for ascertaining Pronghorn diets. *Journal of Range Management* **32(4):** 275-299.

SMITHERS, R.H.N. 1983. *The mammals of the Southern African Subregion*. University of Pretoria, Pretoria.

SMUTS, G.L. 1978. Interrelations between predators, prey, and their environment. *BioScience* **28(5):** 316-320.

SOLANKI, G.S. & NAIK, R.M. 1998. Grazing interactions between wild and domestic herbivores. *Small Ruminant Research* **27(3):** 231-235.

SOMERS, M.J. 1992. *The implications of social structure for the conservation and control of a warthog* Phacochoerus aethiopicus *population in the Andries Vosloo Kudu Reserve, Eastern Cape Province.* MSc. thesis (wildlife Management). University of Pretoria, Pretoria, South Africa.

SOMERS, M.J. & PENZHORN, B.L. 1992. Reproduction in a reintroduced warthog population in the Eastern Cape Province. *South African Journal of Wildlife Research* **22(3):** 57-60.

SOMERS, M.J. & FIKE, B. 1993. Aspects of the management of warthogs in the Andries Vosloo Kudu Reserve with implications for surrounding areas. *Pelea* **12:** 63-70.

SOMERS, M.J., PENZHORN, B.L. & RASA, O.A.E. 1994. Home range size, range use and dispersal of warthogs in the eastern Cape, South Africa. *Journal of African Zoology* **108:** 361-373.

SOMERS, M.J. 1997. The sustainability of harvesting a warthog population: assessment of management options using simulation modeling. *South African Journal of Wildlife Research* **27(2):** 37-43.

SOMERS, M.J., RASA, O.A.E. & PENZHORN, B.L. 1995. Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. *Acta Theriologica* **40:** 259-281.

SOUTH AFRICAN WEATHER SERVICE 2008. www.weathersa.co.za

SPARKS, D.R. & MALECHEK, J.C. 1968. Estimating percentage dry weight in diets using a microscopic technique. *Journal of Range Management* **21:** 264-265.

SPEAR, D. & CHOWN, S.L. 2009. The extant and impacts of ungulate translocations: South Africa in a global context. *Biological Conservation* **142:** 353-363.

STUART-HILL, G.C. 1992. Effects of elephants and goats on the Kaffrarian succulent thicket of the Eastern Cape, South Africa. *Journal of Applied Ecology* **29:** 699-710.

STUART-HILL, G.C. & AUCAMP, A.J. 1993. Carrying capacity of the succulent valley bushveld of the Eastern Cape. *African Journal of Range and Forage Science* **10:** 1-10.

TAMBLING, C., HAYWARD, M., DRUCE, D. & KERLEY, G.I.H. 2009. *The buffalo of the Addo Elephant National Park following the re-introduction of large carnivores*. Centre for African Conservation Ecology Report No. C120. Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

TAYLOR, R.J. 1984. *Predation*. Chapman and Hall, New York.

THEOHARIDES, K.A. & DUKES, J.S. 2007. Plant invasion across space and time: factors affecting nonindegenous species success during four stages of invasion. *New Phytologist* **179:** 256-273.

TRAVESET, A. & RICHARDSON, D.M. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution* **21(4):** 208-216.

TREYDTE, A.C. 2004. *Ecosystem studies on the former Mkwaja Ranch and the new Saadani National Park between 2001 and 2004*. Tanzania Wildlife Discussion Paper No. 42. R. D. Baldus (Ed.).

TREYDTE, A.C., BERNASCONI, S.M., KREUZER, M. & EDWARDS, P.J. 2006. Diet of the common warthog (*Phacochoerus africanus*) on the former cattle grounds in a Tanzanian savanna. *Journal of Mammalogy* **87(5):** 889-898.

VALENTINI, A., MIQUEL, C., NAWAZ, M. A., BELLEMAIN, E., COISSAC, E., POMPANON, F., GIELLY, L., CRUAUD, C., NASCETTI, G., WINKER, P., SWENSON, J.E. & TABERLET, P. 2009. New perspectives in diet analysis based on DNA barcoding and parallel pryosequencing: the trnL approach. *Molecular Ecology Resources* **9:** 51-60.

VAN DYNE, G.M. & HEADY, H.F. 1964. Botanical composition of sheep and cattle diets on a mature annual range*. Hilgardi*a **36(13):** 465-470.

VAN TEYLINGEN, K.E. 1992. *Diet and habitat selection of Oribi in the Eastern Cape*. MSc. thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

VAVRA, M., PARKS, C.G. & WISDOM, M.J. 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology & Management* **246(1):** 66-72.

VERCAMMEN, P. & MASON, D.R. 1993. The warthog *Phocachoerus africanus* and *P. aethiopicus*. In: *Pigs, Peccaries and Hippos. Status Survey and Conservation Action Plan,* (eds). W.L.R. Oliver, pp. 75-84. IUCN-SSC Pigs, Peccaries and Hippos Specialist Group. IUCN, Gland, Switzerland.

VILÁ, M. & WEINER, J. 2004. Are invasive plant species better competitors than native plant species? - evidence from pair-wise experiments. *Oikos* **105(2):** 229-238.

VILJOEN, S. 1983. Feeding habits and comparative feeding rates of three southern African arboreal squirrels. *South African Journal of Zoology* **18(4):** 378-387.

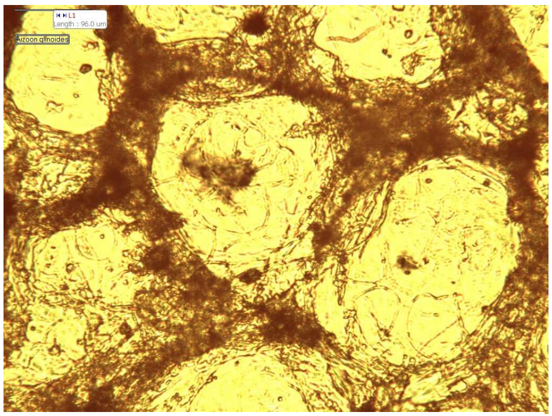
VLOK, J.H.J., EUSTON-BROWN, D.I.W. & COWLING, R.M. 2003. Acocks' Valley Bushveld 50 years on: new perspectives on the delimitation, characterisation and origin of Subtropical thicket vegetation. *South African Journal of Botany* **69:** 27-51.

WITH, K.A. 2002. The landscape ecology of invasive spread. *Conservation Biology* **16(5):** 1192-1203.

WITTERNBERG, R. & COCK, M.J.W. 2001. *Invasive alien species: A toolkit of best prevention and management practices*. CAB International, Wallingford, Oxon, UK, xvii - 228.

Appendices

Appendix 1 - Photomicrographs of the abaxial and adaxial epidermal surface of plant species potentially consumed by common warthogs in the AENP Main Camp and not previously represented in the ACE reference collection.



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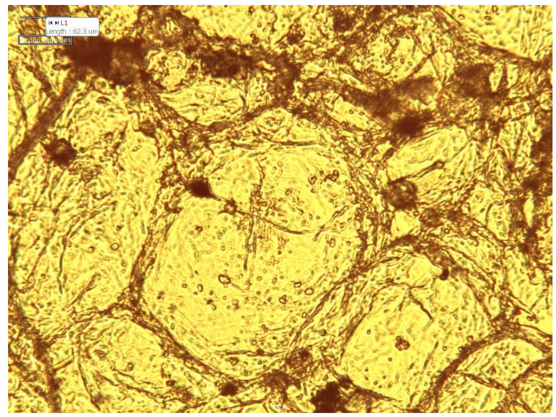

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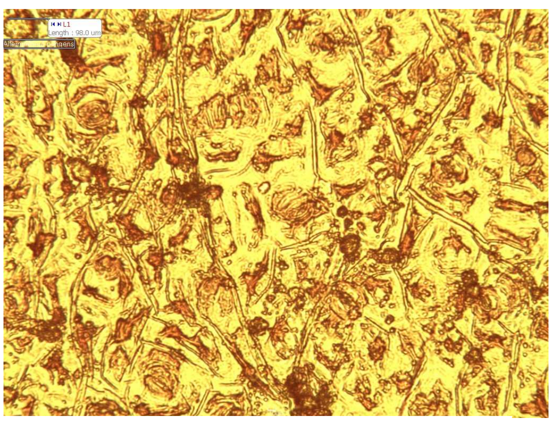

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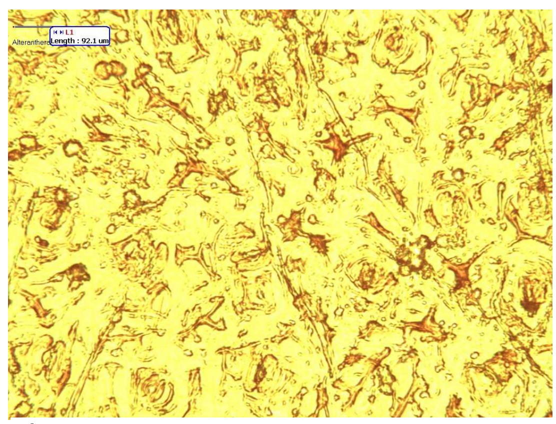

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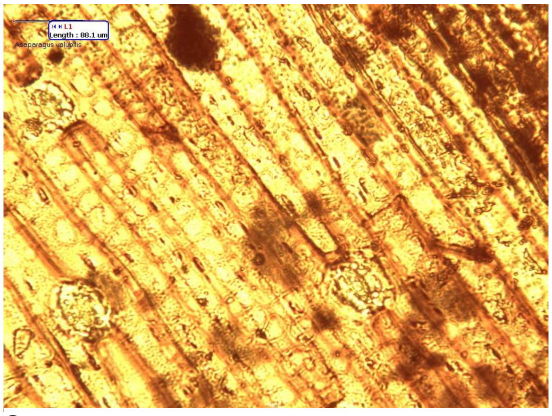
Plate1: 1 a & b: *Aizoon glinoides*; 2 a & b: *Alternanthera pungens.*



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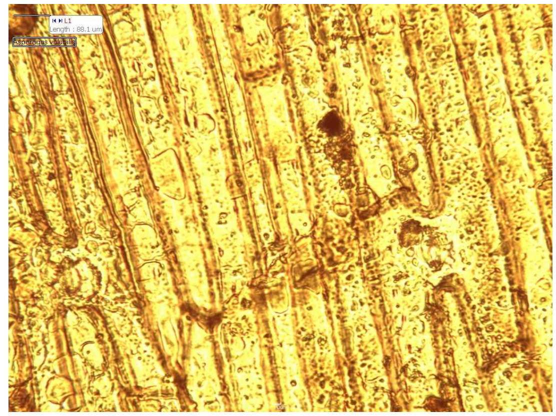

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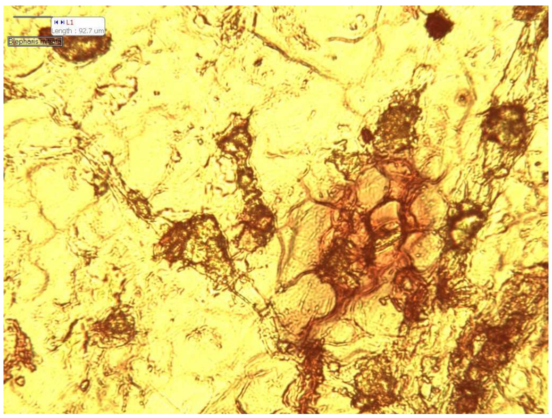

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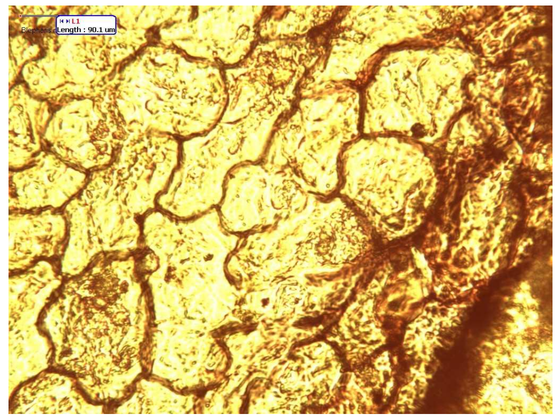

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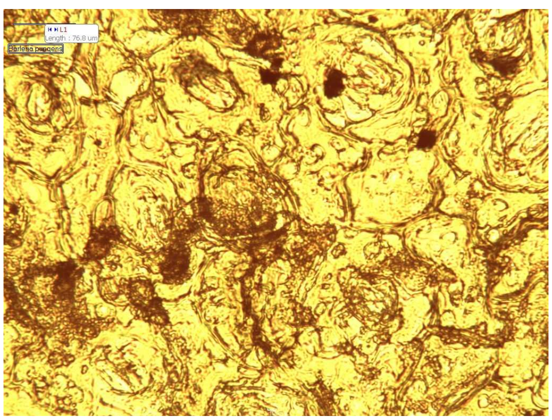

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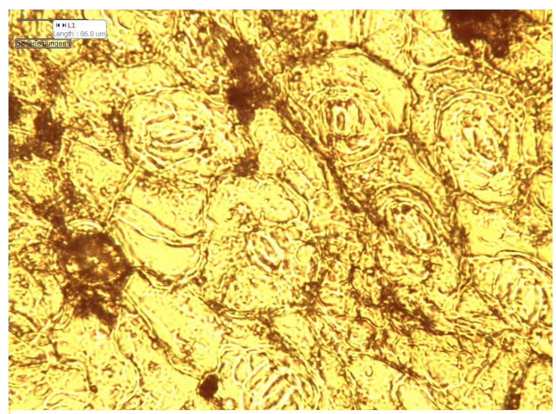

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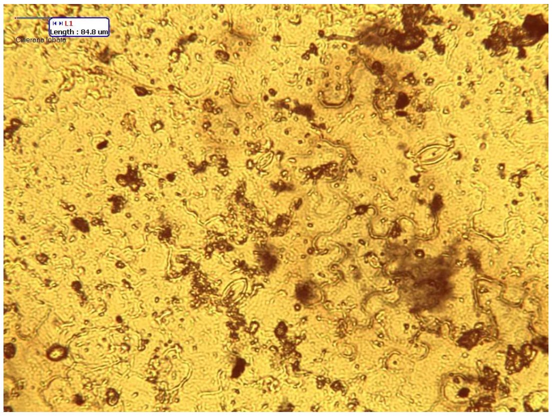
Plate 2: 3 a & b: *Asparagus volubilis*; 4 a & b: *Barleria pungens*; 5 a & b: *Blepharis mitrata*.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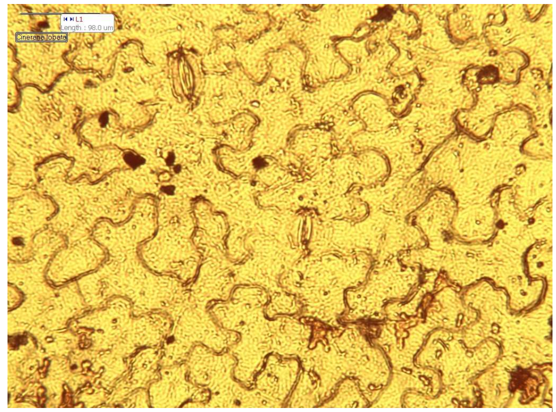
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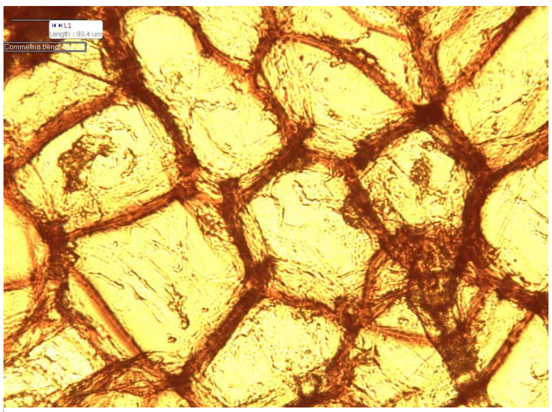
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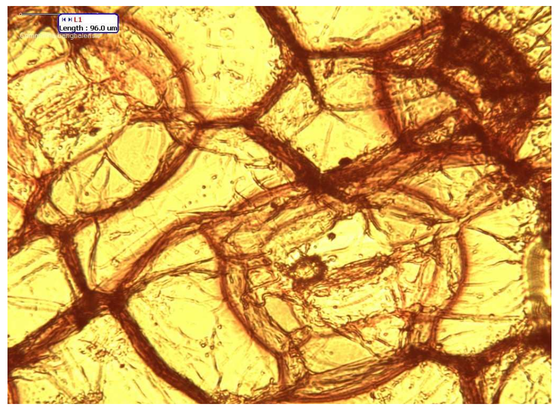
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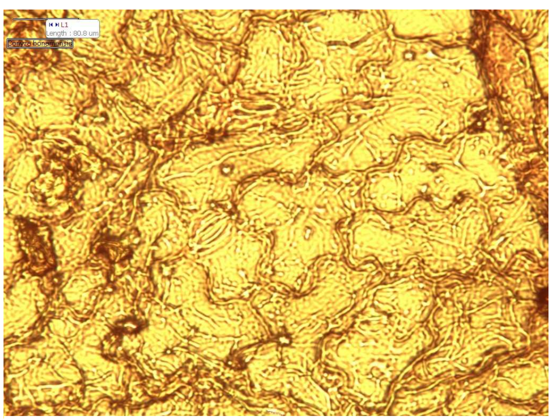
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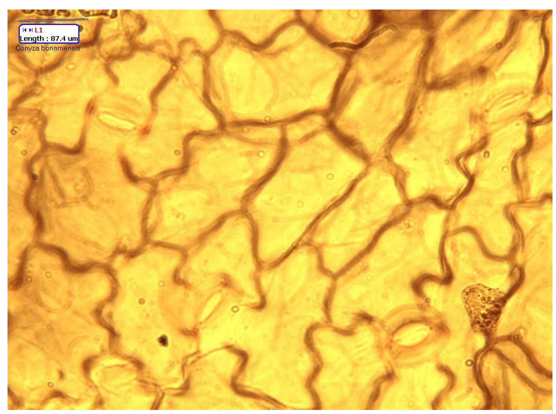
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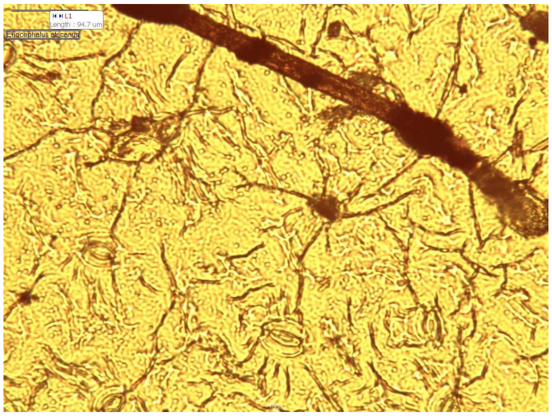
Plate 3: 6 a & b: *Cineraria lobata*; 7 a & b: *Commelina benghalensis*; 8 a & b: *Conyza bonariensis*.



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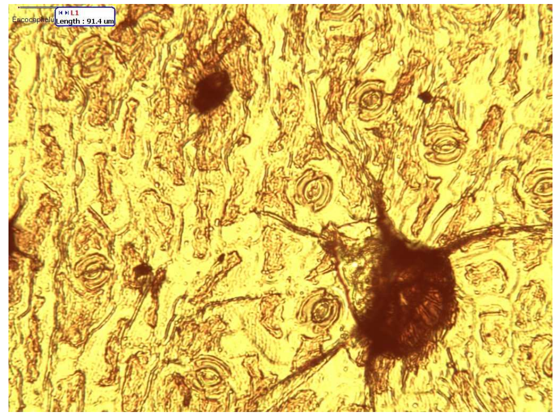

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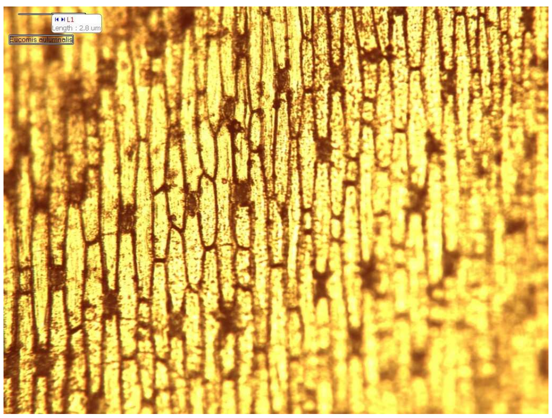

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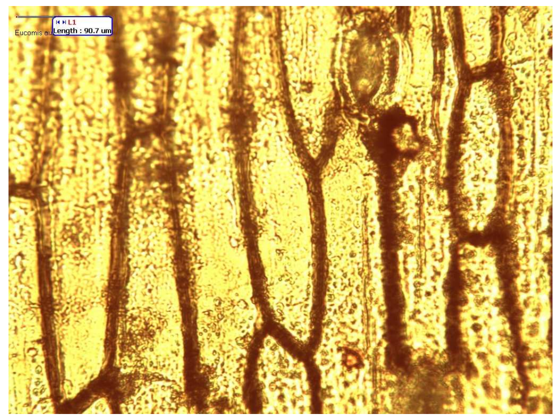

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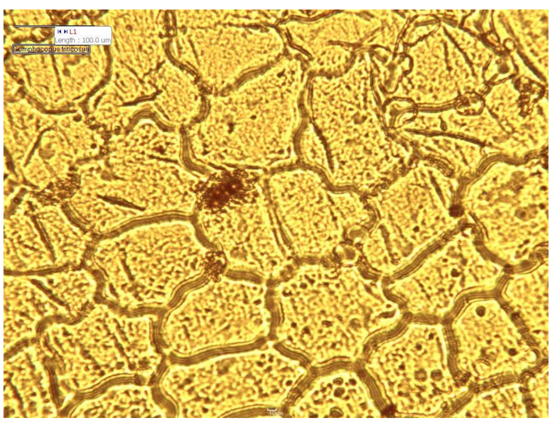

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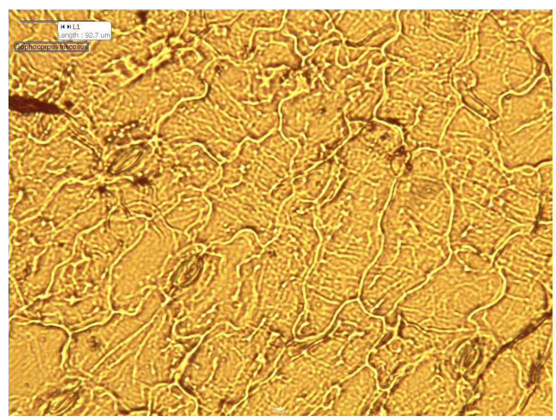

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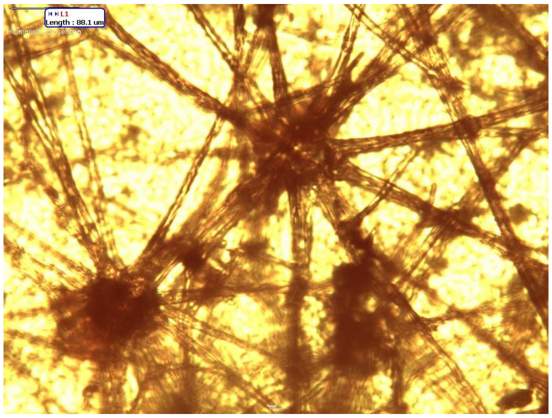
Plate 4: a & b: *Eriocephalus africanus*; 10 a & b: *Eucomis autumnalis*; 11 a & b: *Gomphocarpus fruticosus*.



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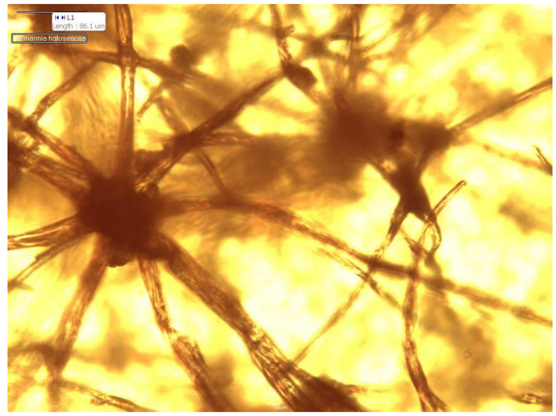

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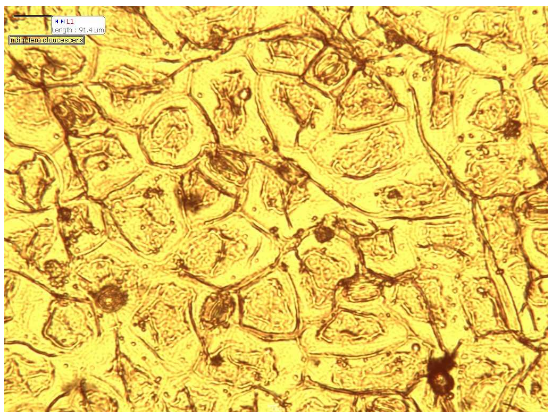

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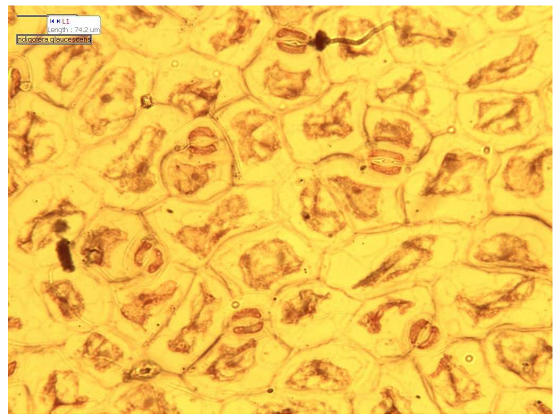

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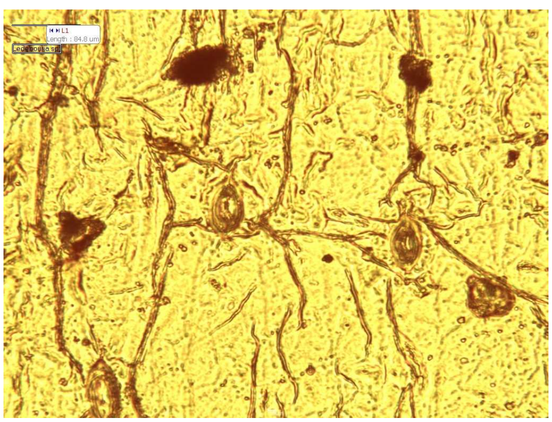

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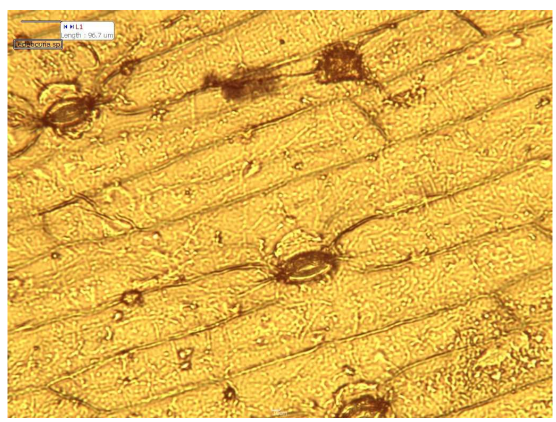
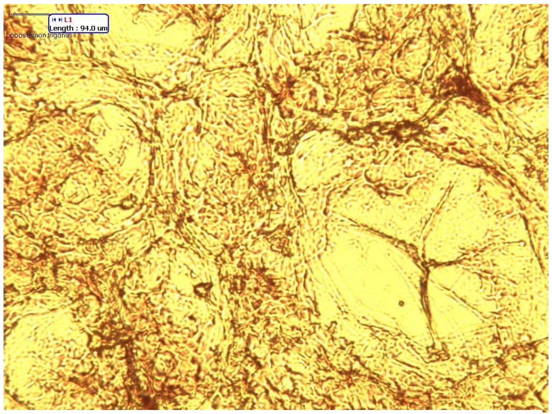


14b

Plate 5: 12 a & b: *Hermannia holosericea*; 13 a & b: *Indigofera glaucescens*; 14 a & b: *Ledebouria spp.*



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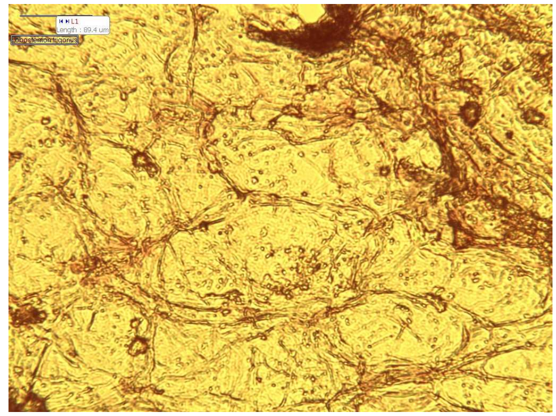

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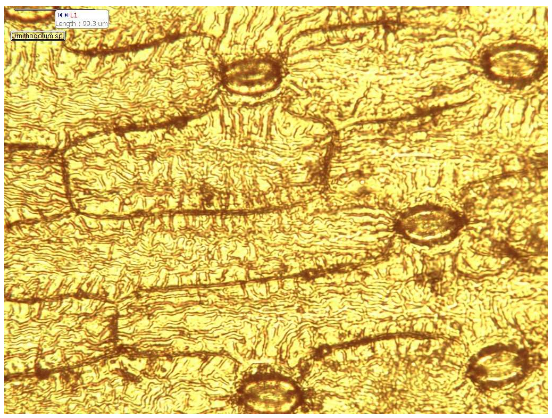

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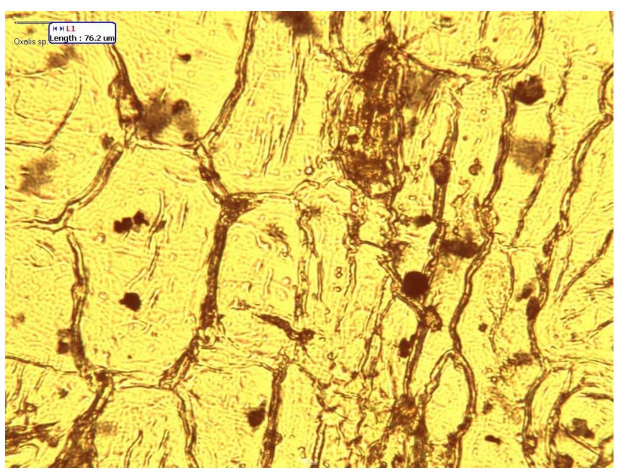
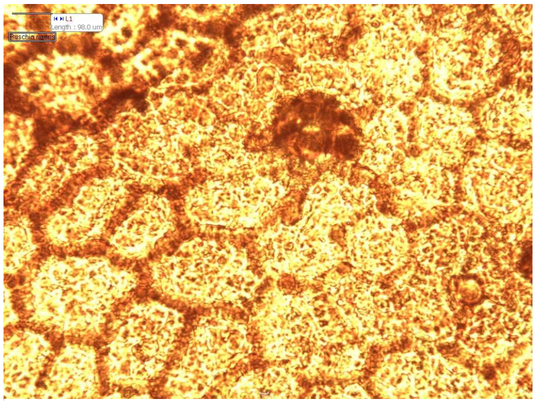


17

Plate 6: 15 a & b: *Lobostemon trigonus*; 16 a & b: *Ornithogalum spp*.; 17: *Oxalis spp.*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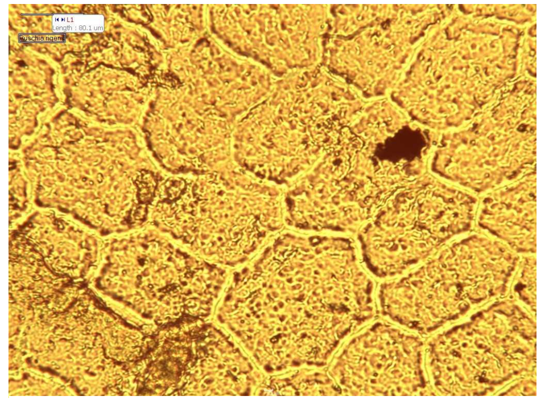
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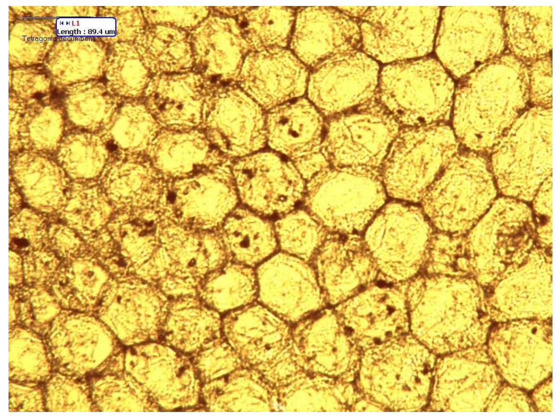
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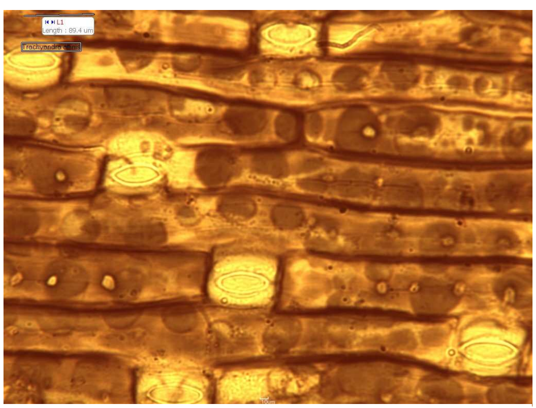
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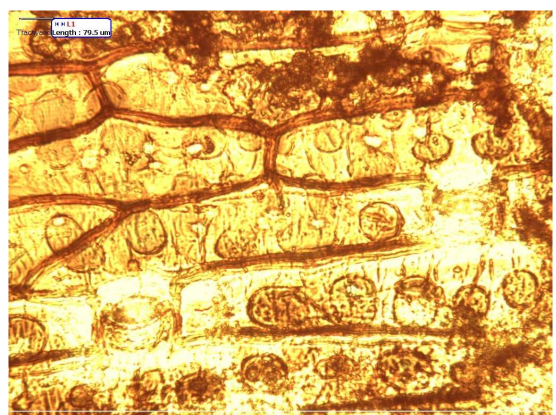
21b

Plate 7: 18 a & b: *Ruschia rigens*; 19: *Schkuhria pinnata*; 20: *Tetragonia decumbens*; 21 a & b: *Trachyandra affinis*.

Appendix 2 - Percentage contribution of plant species in the diet of common warthog in the AENP Main Camp. Species names in bold indicate grass spp. found in the diet but not in forage availability.

Family	Species	Summer	Spring	Autumn	Winter
Grass (19 spp.)					
Poaceae	*Aristida diffusa*	7.5	11.1	3.3	4.1
Poaceae	***Cymbopogon plurinodis***	0.0	0.0	0.0	0.4
Poaceae	*Cynodon dactylon*	28.1	20.6	24.7	28.9
Poaceae	***Ehrharta calycina***	1.1	3.3	0.1	2.1
Poaceae	*Eragrostis curvula*	7.3	6.3	8.5	5.3
Poaceae	*Eragrostis obtusa*	16.5	11.7	12.0	13.9
Poaceae	***Eragrostis racemosa***	0.5	0.5	0.1	0.4
Poaceae	*Eragrostis spp.*	0.5	3.0	0.7	1.2
Poaceae	*Eustachys paspaloides*	4.5	4.2	3.1	2.1
Poaceae	*Panicum deustum*	11.6	15.0	10.5	13.9
Poaceae	*Panicum maximum*	7.1	7.1	4.9	4.3
Poaceae	***Sporobolus fambriutus***	0.2	0.0	0.0	0.0
Poaceae	***Stenotaphrum secundatum***	0.1	0.0	0.5	0.7
Poaceae	*Stipa dregeana*	0.3	0.1	1.9	0.7
Poaceae	*Themeda triandra*	1.9	0.7	0.3	0.7
	Unidentified 1	2.9	2.7	6.3	4.7
	Unidentified 4	0.9	0.4	2.6	4.3
	Unidentified 5	0.8	0.8	0.0	0.3
	Unidentified 8	0.0	2.1	0.2	0.6
Forbs (16 spp.)					
Aizoceae	Aizoon rigidum	0.0	0.0	0.2	0.7
Asteraceae	*Barleria irritans*	0.1	0.0	0.0	0.3
Asteraceae	*Barleria pungens*	0.1	0.0	0.0	0.0
Asteraceae	*Blepharis capensis*	0.0	0.0	0.1	0.0
Asteraceae	*Commelina africana*	1.2	1.7	0.8	0.0
Asteraceae	*Commelina benghalensis*	1.5	1.1	1.5	1.0
Asteraceae	*Commelina spp.*	0.0	1.9	1.2	1.9
Asteraceae	*Cuspidia cernua*	0.0	0.1	0.2	0.0
Asteraceae	*Oxalis spp.*	0.0	0.0	0.0	0.8
Asteraceae	*Schkuhria pinnata*	0.0	0.0	0.1	0.1
Asteraceae	*Senecio linifolius*	0.4	0.2	1.9	0.4
Asteraceae	*Senecio spp.*	0.8	1.3	2.0	1.7
	Unidentified 2	1.2	0.0	1.2	0.9
	Unidentified 7	0.0	1.0	0.4	0.0
	Unidentified 9	0.0	0.7	0.0	0.0
	Unidentified 10	0.0	1.5	0.6	0.3

<u>Woody shrubs (6 spp.)</u>					
Asparagaceae	*Asparagus striatus*	0.3	0.0	0.3	0.0
Asparagaceae	*Asparagus suaveolens*	0.0	0.0	0.0	0.1
Asparagaceae	*Asparagus spp.*	0.0	0.0	0.3	0.0
Asteraceae	*Felicia fascicularis*	0.0	0.0	0.2	0.0
	Unidentified 3	0.7	0.0	5.4	0.4
	Unidentified 6	1.7	0.9	0.0	0.0
<u>Succulent (1 spp.)</u>					
Portulacaraceae	*Portulacaria afra*	0.5	0.1	3.9	2.9