FEEDING ECOLOGY AND CARRYING CAPACITY OF A REINTRODUCED PACK OF AFRICAN WILD DOGS IN A RELATIVELY SMALL, FENCED RESERVE

by

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As the candidate's supervisor I have approved this thesis/dissertation for submission

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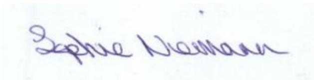
ABSTRACT

Reintroduction has been used successfully as a tool to restore declining populations of many threatened species. However, the lack of detailed evaluations of past reintroduction attempts has hindered *a priori* planning of management actions to achieve conservation goals. The metapopulation approach resulted in the most extensive and successful reintroduction efforts of the African wild dog (*Lycaon pictus*) in South Africa, but the approach was only recently evaluated by Gusset et al. (2008). For future reintroduction attempts to be successful on relatively small reserves, extensive evaluations are needed. Particular focus on feeding behaviour and impact on prey populations is essential to predict sustainability and carrying capacities in these areas for the African wild dog. A small reintroduced population of African wild dogs (pack number varying from 3 to 13 during the study period) were studied in the Karongwe Game reserve (79 km^2) between January 2002 and January 2004. Fourteen prey species were identified: impala (*Aepyceros melampus*, 60 %) was the most dominant prey followed in descending order by bushbuck (*Tragelaphus scriptus*, 7.4 %), waterbuck (*Kobus ellipsiprymnus*, 4.9 %), warthog (*Phacochoerus aethiopicus*, 4.7 %), kudu (*Tragelaphus strepsiceros*, 4.4 %), and grey duiker (*Sylvicapra grimmia*, 4.4 %). Generally, prey were included in the diet in relation to abundance, and the dogs were not rate maximizing foragers but, unlike the findings of previous studies, were opportunistic feeders. The fences and angles in the fence, were used to assist hunting, but only for medium sized prey, impala and bushbuck, which were killed significantly more than expected along the fence line. A predictive prey preference model was then tested, but the model did not account for possible differences in feeding behaviours and prey preferences found in this, nor another study from the small Shambala Game Reserve. The model had limited accuracy as a predictive tool for proposed reintroductions into relatively small reserves. Models which can predict carrying capacity and minimum area requirements were also tested. Large variation and low numbers were predicted, which conflicted with social requirements needed for the survival of the population; further the models did not account for interspecific competition nor simultaneous depletion of prey by other guild predator. If the metapopulation approach is to continue to be successful and sustainable, more detailed evaluations of reintroductions of African wild dog on relatively small, fenced reserves are needed to determine the impact of these dogs on prey populations, and to determine if African wild dog feeding behaviour does differ for these areas in comparison to previously described open systems. With this information, more appropriate protocols regarding reintroduction and management can then be developed, thereby meeting one goal of management and conservation for the African wild dogs and their coexisting prey populations, and which can be used as a model for managing other large predators.

PREFACE

The experimental work described in this dissertation was carried out on the Karongwe Conservancy from January 2002 to January 2004, under the supervision of Prof. Robert Slotow (University of KwaZulu-Natal).

These studies represent original work by the author and have not otherwise been submitted to any tertiary institution in any form for a degree or diploma or any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

Signature:  **Date**: 07/12/09

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1

NIEMANN, S., OWEN, C., AND SLOTOW, R. Diet, capture success, and the use of boundary fences by hunting African wild dogs on a small, fenced reserve: a case study

Author contributions:

SN conceived and designed paper, collected and analyzed data, and wrote paper. CO assisted in field collection of data. CO and RS contributed valuable comments to the manuscript

Publication 2

NIEMANN, S., OWEN, C., AND SLOTOW, R. Predicting carrying capacities and prey of the African wild dog reintroduced onto a small, fenced reserve: a case study

Author contributions:

SN conceived and designed paper, collected and analyzed data, and wrote paper. CO assisted in field collection of data. CO and RS contributed valuable comments to the manuscript.

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CHAPTER 1

General Introduction

Human population growth and associated habitat loss, degradation and fragmentation are the main causes of many species declines and extinctions (IUCN 2007). In particular, large carnivores, due to their size and trophic position, have been eliminated disproportionately to other species, and are important components of the ecosystem as top-down regulators (Hilberbrand et al. 1999). Large carnivores have shown a drastic decline in population size and geographic range due to habitat loss, depletion of prey, hunting, and direct persecution from humans (Clark 2009). In the past century alone four distinct subspecies of tiger (*Panthera tigris*) have become extinct (Johnsingh & Madhusudan 2009), as have the brown bear (*Ursus arctos*), wolf (*Canis lupus*) and lynx (*lynx* spp.) in Europe (Breitenmoser 1998).

As a consequence of this decline, conservation and management of small fragmented populations of large carnivores has become unavoidable, with reintroduction and translocation being used as important conservation tools to aid population recovery (Davies-Mostert et al. 2009). Before interventions such as reintroduction are carried out, careful consideration is needed to determine whether a release site is suitable for a particular large carnivore (Clarke 2009, Mills et al. 1998). In particular, habitat evaluation is essential as a reintroduction is unlikely to be successful if the habitat is unsuitable (Clarke 2009), and the single most critical habitat component for most large carnivores is food (Clarke 2009). Predator numbers will decline if prey numbers decline, through a bottom up limitation (Hayward 2009). Encouragingly, most large carnivores have been well studied, resulting in an in depth knowledge of their behavioural and evolutionary ecology (Somers & Gusset 2009), thus allowing the development and implementation of appropriate management actions, such as reintroduction (e.g. Gusset et al. 2008, Slotow & Hunter 2009). Although globally past reintroductions have been poorly documented (Davies-Mostert et al. 2009), important information from past reintroductions of large carnivores within South Africa has delivered important information with regard to the methods of reintroduction of large carnivores (e.g. Gusset et al. 2008, Slotow & Hunter 2009).This information has also highlighted the information deficiencies essential in making successful and satisfactory management decisions (Hayward 2009). Knowledge and a holistic consideration of a variety of factors and behaviours of large carnivores are essential, as these could effect the survival and success of a reintroduction. Such factors include feeding ecology (Hayward 2009), genetic considerations (Frankham 2009), social systems and life history requirements (Somers & Gusset 2009).

The IUCN (1998) guidelines for reintroductions details the evaluation of possible reintroduction sites. These points stipulate that the site must be within the species' former natural habitat and range, that the population must be able to be sustained for the foreseeable future, and that there should be sufficient carrying capacity of the location to sustain growth of the reintroduced populations (IUCN 1988). In order for any reintroduced population to be sustained, there must be enough resources to support a growing population. In the case of large carnivores, this means ungulate prey. Successful growth of large carnivore populations can potentially impact negatively on the underlying prey base, and many reintroductions have failed as a result of reintroduced predators having severe unforeseen effects on prey populations (Hayward et al. 2007a, Armstrong & Seddon 2007). Lion (*Panthera leo*) in Madjuma Game Reserve and cheetah (*Acinonyx jubatus*) in Suikersbosrand Nature Reserve were removed from those reserves, because the prey populations were insufficient to sustain the reintroduced carnivores (Hayward et al. 2007b). In other reintroduction sites, such as Pilanesberg National Park, Madikwe Game Reserve and Welgevonden Game Reserve, large, expensive prey supplementations are currently being undertaken in a range of reserves to supplement a declining prey population (Slotow, 2008, pers. comm.). Knowledge on the feeding strategies of the large carnivore that is due to be reintroduced is thus important to predetermine the possible diet (species and numbers of prey killed), and what the overall impact on the prey population would tend to be (Hayward 2009). These data can be used to predict the number of predators and area can sustain, a value know as carrying capacity (Hayward 2009). The feeding strategies of large carnivores differ as the evolutionary arms race between predators and their prey has lead to morphological and behavioural features that increase success, and reduce energy expended in catching, killing and consuming prey As a consequence, most African large carnivores adapt to feed preferentially on specific species of prey (Hayward 2009) and in particular habitats (Balme et al. 2007), often with preferences that increases their overall net energy gains (Hayward & Kerley 2005), according to optimal foraging theory (Krebs 1978, Stephens 2008). Depending on the hunting strategies employed by the predator, a choice of a predator's feeding habitat can be motivated either by where it is easier to catch prey (landscape attributes) or simply where the prey is most abundant (Balme et al. 2007). The alternative to an optimal foraging strategy is having an opportunistic foraging strategy, where large carnivores are found to be unselective in their prey preference (Hayward 2009). For example, spotted hyena (*Crocuta crocuta*), based on diet preferences from 15 studies, were opportunistic, feeding on the most abundant prey (Hayward 2009). Predators vary in their foraging strategies, so any additional knowledge of the feeding behaviour of reintroduced species should enable conservation managers to more accurately predict diet and carrying capacity (based on diet alone) of large predators at reintroduction sites. This is critical to the success of reintroductions, as it enables managers to ensure an adequate prey base is present to support the reintroduced population, and to identify management actions needed to avoid over population (Hayward 2009). Even for opportunistic carnivore species , managers, with this knowledge, can expect the reintroduced population to kill prey in relation to abundance, and can manipulate game numbers to ensure threatened or expensive game are not negatively effected, by altering the relative abundance of one prey species to provide a buffer for a rare prey species (Hayward et al. 2007b).

Another important factor that needs to be taken into account prior to reintroduction is the genetic considerations, such as avoiding inbreeding and loss of genetic diversity (Frankman 2009), to ensure both the initial survival and long term viability of a population. Inbreeding and loss of genetic diversity are major concerns, and unavoidable in closed systems, unless unrelated individuals are introduced at regular intervals (e.g. Trinkel et al. 2008). Usually the reintroduced population is small and within a few generations a high degree of inbreeding is likely so active management needs to be integrated into the reintroduction management plan to augment or replace with individuals from other populations (Kettles & Slotow 2009). Another factor to be considered is the social behaviour of the large carnivore and this is often disregarded by wildlife managers (Somers & Gusset 2009). Without group cohesion and mate selection prior to release, the animals are less likely to become successful breeders after release (Somers & Gusset 2009). This was demonstrated with the African wild dog (*Lycaon pictus*) where management manipulation of social relationships was used to successfully promote pack bonding (Graf et al. 2006). In addition, post release factors of a reintroduction such as critical group size have to be considered to avoid an Allee effect. Allee effect is defined as the reduction in individual fitness with decreasing size of aggregation unit considered (Courchamp et al. 1999, Somers et al. 2008). For example obligate cooperative breeders, such as the African wild dog, would suffer inverse density dependence due to their need of helpers within the pack to ensure survival and reproduction, as helpers are imperative for pup guarding and feeding, cooperative hunting and defense of kills (Courchamp et al. 2000). Thus, for an obligate cooperator such as African wild dog, a critical number within a group is needed to ensure the survival of the population (Courchamp et al. 2002). This factor should not be disregarded in reintroduction plans, as often small founder populations, susceptible to Allee effects) are reintroduced.

Despite many large carnivore species having been studied extensively (Hayward & Somers 2009) more replicated monitoring is needed to assemble descriptions of the basic natural history of a threatened species in varying time and space. This knowledge is an essential requirement for successful conservation management of threatened species. For example, one of the most extensive endangered species reintroduction efforts to date was that of the African wild dog in South Africa (Davies-Mostert et al. 2009, Gusset 2009). Successful establishment of an actively managed metapopulation of the African wild dog was buffers against the declining wild dog numbers (Gusset et al. 2008). The information gleaned from this initiative from pre- and post-reintroduction monitoring has improved wild dog management practises in South Africa (Davies-Mostert et al. 2009). It is to this initiative that this study hopes to contribute, particularly with regard to additional information on reintroduction of African wild dog into relatively small reserves (< 500km^2), and which is currently poorly documented. Lessons learnt during the metapopulation initiative could benefit similar schemes in Africa and highlights the need for more information regarding the reintroduction of other large carnivores.

The conservation status of the African wild dog is stated as an endangered species in the IUCN red list (IUCN 2007), and has shown a dramatic decline in numbers over the last 50 years, with population estimates of only 3000 to 5500 in Africa (Woodroffe & Ginsberg 1997a). In the past, the African wild dog was widespread across Africa, and was recorded in 34 countries (Smithers & Chimimba 2005). However, more recently populations have become extinct in 19 of these countries, and viable populations exist only in six (McNutt et al. 2008). The main causes of death have been identified as human activities and infectious diseases (Fuller & Kat 1990, Creel & Creel 1996), which have been compounded by habitat fragmentation (IUCN 1997, Woodroffe & Ginsberg 1998). Negative perceptions and persecution of African wild dog have persisted through the centuries and are still present today. For many, the African wild dog has a negative association; rural farmers surrounding reserves and national parks persecuted them in the past to protect their domestic stock, and as recently as the 1960's predator control programmes were enforced against them in Kruger National Park (KNP, South Africa), and in 1975 within in parks of Zimbabwe (Childes 1988, IUCN 1997), decimating their numbers. There is a conflict of human interest today toward the African wild dog. Recent studies showing negative attitudes and persecution of African wild dogs still persist in the rural population due to the threats to their livestock, however tourists had a overwhelmingly positive attitude (Gusset et al. 2008).

Infectious diseases such as canine distemper, rabies virus and canine parvovirus have been suggested to play a combined role in the decline of some populations (Creel & Creel 2002), while some authors regard disease as one of the main cause of the decline of African wild dog across the continent (Kat et al. 1995). The reduction and fragmentation of the African wild dog habitat by human activities is a major contributing factor in their decline (Woodroffe & Ginsberg 1997a, Creel & Creel 2002). The combined effects of persecution, conflicting farming practices, and unsustainable yields of prey around the borders of reserves, have lead to a substantial edge effect around all but the largest reserves (Woodroffe & Ginsberg 1998). While habitat loss and disease are crucial factors limiting African wild dogs on a continental scale, locally within ecosystems other factors are limiting populations, such as interspecific competition (Creel & Creel 2002), particularly with lion and spotted hyena

(Creel & Creel 2002). Lion limit African wild dog numbers through both competitive exclusion and direct predation (Mills & Biggs 1993, Creel & Creel 2002, Van Dyk & Slotow 2003). In KNP, 43 % of natural deaths recorded were due to lions, and African wild dog were found to avoid areas with high impala (*Aepyceros melampus*) densities due to the high densities of lion in those areas (Mills & Gorman 1997). Kleptoparasitism and dietary overlap with hyena have led to exploitation competition, reducing feeding performance in small packs of African wild dogs (Carbone et al. 1997, Carbone et al. 2005), as they are vulnerable to even low levels of food theft, which may have a large impact on the time that a dog must hunt to achieve energy balance (Gorman et al. 1998). This has led to low populations of wild dog where kleptoparasitism is high (Carbone et al. 1997, Gorman et al. 1998), as found in the Selous Game Reserve, Tanzania where there was a negative correlation of African wild dog with hyena. Collectively, all these elements result in seemingly large conservation areas only being able to support only a small and often unviable population of African wild dogs, putting pressures on an already declining population (Woodroffe & Ginsberg 1997a, Creel & Creel 2002).

Past opinion was that African wild dog populations should not be maintained in protected areas smaller than 1000 km^2, and reintroduction into areas any smaller were believed to have limited value for conservation (Woodroffe & Ginsberg 1997b). African wild dog have been shown to occupy large home ranges ranging from 218 to 3800 km^2 (Fuller et al. 1992, Andreka et al. 1999) with an average of 537 km^2 (Mills & Gorman 1997). Despite this, the successful expansion of African wild dog distribution in South Africa has been largely dependent on reintroductions into privately owned reserves smaller than 1000 km^2, and many of which are smaller than African wild dog home ranges (Krűger et al. 1999, Van Dyk & Slotow 2003, Lindsey et al. 2004, Rhodes & Rhodes 2004).

Many private reserves in South Africa have moved away from historical patterns of land use, such as livestock farming, in preference to conservation, game ranching, and ecotourism (Bissett 2004, Hunter et al. 2007). Ecotourism has fuelled the current trend of the establishment of conservancies, where landowners collaborate to remove fences and form potentially larger wildlife areas which are respectively more suitable reintroduction sites for African wild dog (Bissett 2004, Lindsey et al. 2004). As a consequence, these reserves now offer predator-proof fencing and limited edge effects from human activities (Lindsey et al. 2004), assisting the conservation efforts to reduce the decline of this and other endangered carnivores through reintroduction (Gusset et al. 2008). As mentioned previously, reintroduction and confinement of large predators in small reserves does not come without its own problems as the populations are isolated, and appropriate management plans have to be put in place which consider all the issues (Gusset et al. 2008, Kettles & Slotow 2009). Such problems that need addressing include social needs, inbreeding, negative impact on prey populations, lack of refuges from other predators, disease, and often intense competition with other large predators (Woodroffe & Ginsberg 1997a, Gusset et al. 2008). To alleviate some of these issues, an extensive metapopulation approach was adopted in a number of reserves in South Africa, linking populations through management (Mills et al. 1998): including Hluhluwe-Umfolozi Park (960 km^2); Madikwe Game Reserve (750 km^2); Marakele National Park (900 km^2); Pilanesberg National Park (550 km^2); and Venetia Limpopo Game Reserve (370 km^2). The concept was to release African wild dogs of the local genotype into a network of small fenced reserves. One, or a few, packs were released on each reserve, and then collectively and intensively managed with regard to fencing, disease control, and artificial genetic and demographic exchange between reserves to maintain genetic diversity (Gusset et al. 2008). Overall, this approach has had excellent success, resulting in high survival rates of reintroduced dogs and offspring, and ensuring long-term persistence of reintroduced populations in small, enclosed reserves (Gusset et al. 2008). Even though a number of reintroductions have been successful, a predictive framework is still needed to detail the most effective methods of reintroduction of many species (Gusset et al. 2008), including African wild dog. There is a lack of evaluations of past reintroduction attempts and thus gaps in knowledge (IUCN 1998)to determine which factors affect survival of, or limit, the reintroduced population (Gusset et al. 2008). Studies need to focus on the ecological, behavioural, socio-political and management related limitations of reintroductions (Gusset et al. 2008). One area, specifically identified by the IUCN (1997) as being one of the current gaps in knowledge of African wild dog reintroduction, was to more accurately investigate and monitor the impact and sustainability of reintroduced populations on small reserves. In order for any reintroduced large predator population to be sustained, there must be enough resources to support a growing population for the foreseeable future (Hayward et al. 2006). Prior knowledge on resource availability and their feeding ecology, specifically prey preference, is essential to make *a priori* estimates of carrying capacities of an area (Morgan et al. 2009) and to develop appropriate management plans. Current insight into behavioural and feeding ecology of reintroduced populations of the African wild dog in general is limited for relatively small fenced reserves (Krűger et al. 1999, Van Dyk & Slotow 2003, Rhodes & Rhodes 2004). As the majority of studies of African wild dog are in open systems such as Serengeti National Park, (Frame et al. 1979), Selous National Park, Tanzania (Creel & Creel 1991, 1995, 1996), Kenya (Fuller & Kat 1990, Fuller et al. 1992, 1995) and KNP (Mills 1992, Mills & Biggs 1993, Mills & Gorman 1997). Generally, African wild dog are regarded as size selective, social predators with small (<25 kg) to medium (40-90kg) ungulates forming the most important component of the diet (Fuller & Kat 1990, Creel & Creel 1995, Krűger et al. 1999). Larger prey species have been documented in the diet of African wild dog, but are mainly kills of the young of larger prey species such as kudu (*Tragelaphus strepsiceros*,) waterbuck (*Kobus ellipsiprymnus),* wildebeest (*Connochaetes taurinus),* hartebeest (*Alcelaphus buselaphus)* and zebra (*Equus grevyi*, *Equus burchelli*) (Schaller 1972, Fuller & Kat 1990). The only studies that mentioned a substantial use of adults of larger prey species are from one study in the Serengeti National Park, where the pack specialized on zebra (Malcolm & Van Lawick 1975) and in KNP (Pienaar 1969, Mills & Biggs 1993). In contrast recent studies on relatively small, fenced reserves such as Pilanesberg National Park and Shambala Game Reserve found a strong shift in prey preference towards larger prey items, including adult kudu and waterbuck (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004). The cause of which has been attributed to the use of electric fence lines to assist in prey capture of these larger species (e.g. Van Dyk & Slotow 2003). Additional studies are needed to document whether this preference of large prey and fence use is common to reintroduced populations of African wild dog into relatively small reserves. Managers need to be able to plan for potential impact on the prey populations after release, otherwise this could undermine the success of a reintroduction due to the unexpected economic loss of larger, more expensive prey being selected, and unsustainable impact on the preferred prey population.

Past reintroductions of large carnivores carried out in South Africa have yielded important information on methods for successful reintroductions, with a particular focus on predicting prey and impact on prey populations. An in depth assessment of African wild dog prey preference was calculated by Hayward et al. (2006), from the results of 18 past studies on the African wild dog. It was investigated which prey species African wild dogs in general select more frequently than expected, based on abundance, using the Jacobs Index (Jacobs 1974). Overall African wild dog have a specific prey preference for kudu, Thomson gazelle (*Gazella thomsonii*), impala, and bushbuck (*Tragelaphus scriptus)* (Hayward et al. 2006). The implication for management of any preference is that if the preferred species is not available in sufficient numbers within a reserve, it will be unable to sustain the African wild dog population, and they may then select larger, more expensive (e.g. Van Dyk & Slotow 2003), or rare species as an alternative (Hayward et al. 2007a). Thus, it is important to ensure that preferred resources are available over the long term, to make reintroduction a viable and sustainable option for management.

African wild dogs are also said to be rate maximizing foragers, following the prey model which assumes that the forager select prey to maximize their long-term rate of energy intake (Schoener 1987, Krűger et al. 1999). The theory predicts that an animals will maximise their rate of energy intake by ranking prey types and including them in the diet in relation to their profitability, where profitability (p) is a measure of prey energy (E) and handling time (h) so that ($p_i = E_i/h_i$) (Stephens & Krebs 1986, Krűger et al. 1999, Stephens 2008). Larger prey have great potential energetic gains, but the cost of chasing, capturing, and killing, and the potential for injury, ranks larger prey low on the profitably list of prey (Creel & Creel

2002). So it is expected that larger prey would not be selected in the diet (Krűger et al. 1999, Creel & Creel 2002). However, as previously mentioned the shift in preference to larger prey in small fenced reserves, facilitated by using the fence as a hunting aid, may be a consequence of reduced handling time of larger prey. This reduction in handling time would increase the net gains from previously unselected larger prey species (Rhodes & Rhodes 2004). The economic implication of larger, more expensive, prey being selected will have substantial management implications (Lindsey et al. 2005). If prior knowledge of this feeding preference is not accounted for in the evaluation of reintroduction sites and management of the population, this may hamper conservation efforts, and reintroduction may be a less viable option for relatively small reserves.

To plan future conservation management of a reintroduced population, evidenced based decisions need to be made with reference to suitable population sizes, possible impact on prey, and measurement of future conservation success (Morgan et al. 2009). For this reason, more studies focusing specifically on reintroduced packs on small fenced reserves are needed to determine these factors, and any other that may threaten survival, or the success of a reintroduction. Models have recently been developed to assist in the prediction of appropriate carrying capacities and area requirements of large carnivores. Hayward et al. (2007b) showed relationships between the preferred prey of African large predator guild, including African wild dog, and their population densities, to predict the carrying capacity of large carnivores in South African conservation areas. The only carnivores used to test the predictions to date are lions, which when tested were shown to be accurate for 9 out of 13 test locations (Hayward et al. 2007a). Another model is the minimum area requirement model developed by Lindsey et al. (2004), and it is based on the area needed to sustain an adequate population of the most important prey species in the diet of African wild dog. The area requirements for a pack of five African wild dog was predicted to be 147 km^2 for north-eastern South Africa (Lindsey et al. 2004), based on the prey profiles recorded in the southern KNP (Mills & Gorman 1997). Unlike other regional predictions, this method predicted area requirements that exceeded the size of the reserve. Pilanesberg National Park (500 km^2) and the different prey profile of this population when compared to those described in more open systems (Frame et al. 1979, Creel & Creel 1991, 1995, 1996, Fuller & Kat 1990, Fuller et al. 1992, 1995, Mills 1992, Mills & Biggs 1993, Mills & Gorman 1997) may have resulted in a general prediction of elevated area requirements (Lindsey et al. 2004). The suitability of this and other models needs to be addressed to ensure the predictions are appropriate for the planning and management of reintroduced populations that show new patterns in feeding behaviour within small areas.

Research purpose

Long-term monitoring of reintroduced packs of African wild dog onto small reserves is crucial to determine not only the success of a reintroduction, but also the feeding behaviour of packs in these areas, and the extent of deviation of packs from the previously described studies on diet (Frame et al. 1979, Creel & Creel 1991, 1995, 1996, Fuller & Kat 1990, Fuller et al. 1992, 1995, Mills 1992, Mills & Biggs 1993, Mills & Gorman 1997) .This was the motivation for this study on the 79 km^2 ,Karongwe Game Reserve (KGR), Limpopo province, South Africa. For the wild-dog metapopulation programme, this reserve was the smallest, and it has successfully exported 10 dogs to found/supplement other population. This study was unique in its time-scale and intensity, being a two year continuous study of a reintroduced pack on a small reserve, although only a single pack was studied. In relation to reserve size, the most comparable studies with this one are those done in Hlhuhlwe Umfolozi Park (HUP, 22 adults were reintroduced 1981, with only 10-13 individuals present at time of study, Krűger et al. 1999), Pilanesberg National Park (nine dogs were reintroduced in September 1998, three adults and five pups, the pack denned twice and at the end of the study in May 2001, the pack consisted of 12 individuals , Van Dyk & Slotow 2003), and Shambala Game Reserve (7 dogs were reintroduced in April 2002, the pack denned once with 10 pups and at the end of the study the pack consisted of 12 dogs in January 2003, Rhodes & Rhodes 2004). All of these reserves have reintroduced populations on relatively small, fenced reserves (See Chapter 2: Table 7 for summary of data).

Given the previously documented behaviour of African wild dog, we expect the pack to be rate maximizers, and to show preference for large prey species through the use of the fence to facilitate hunts. The study aims were thus to determine whether the feeding behaviour of this case study pack of African wild dog was similar to recent studies on packs reintroduced into relatively small reserves, and to discuss the management implications of the findings. The study then aimed to test various models which predict the carrying capacities and minimum area requirements of carnivores, to compare results, and to assess the suitability of predictive tools for reintroduced packs on relatively small fenced reserves

The main objectives of this study were to determine (1) diet composition, (2) prey preference, (3) whether the pack was rate maximizing and (4) the use of the fence as a hunting tool. Then using these results, (5) to calculate the minimum area requirement to support the pack, (6) to determine the maximum sustainable offtake for each key prey species for KGR and therefore predict the carrying capacity of this area, (7) to predict carry capacities of African wild dog using various measures of prey biomass, using the model of Hayward et al. (2007b), and (8) to test predictions of diet against actual diet as recorded in this study. Then a conclusion was reached about the value of such models for the conservation management of reintroduced predator populations in relatively small reserves.

The thesis is divided into four chapters and the aims of the two data chapters are as follows.

Chapter 2: This chapter contains an analysis of the feeding ecology of a reintroduced African wild dog population on a small fenced reserve as a case study, with the aim to further the knowledge in the feeding behaviour of African wild dogs within these relatively small enclosed areas. The diet composition, prey preference, and foraging strategies were examined, as well as the use of fences and fence angles as hunting tools.

Chapter 3: This chapter contains an analysis of the current models that predict carrying capacities of small reserves for African wild dog and their minimum area requirements. The suitability of these small reserves is also discussed. Using feeding data collected and presented in Chapter 2, the prey preference model was also tested, and its use as a management tool discussed.

In each chapter, the conservation management implications for African wild dog are discussed. In the final chapter, the results from the two data chapters are linked together, highlighting the importance of further evaluation, and indicating gaps in knowledge and directions for further research.

Overall, on a management level, this study aimed to unravel the conflicting opinions regarding African wild dog management by substantiating previous claims of feeding behaviour of African wild dogs on relatively small reserves. Accurate prior knowledge of African wild dog prey preferences should lead to appropriate prediction of carrying capacities. This will allow managers to plan in advance rather than respond to crises, and to accurately assess the viability and success of future reintroductions based on current prey species and numbers. This should lead to the implementation of more accurate and informed management strategies and reintroduction protocols, and increase the success rate of reintroductions thereby providing a model for other large carnivore species.

The two data Chapters (2, 3) are written in scientific manuscript format. Therefore, there may be some repetition. Each chapter has its own reference list. I plan to submit these chapters to scientific peer-reviewed journals to be published as independent papers.

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CHAPTER 2

Diet, capture success, and the use of boundary fences by hunting African wild dogs on a relatively small fenced reserve: a case study

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Abstract

The success and survival of endangered large predators is dependent on foraging data being used for proper planning for reintroductions and management. Investigations into feeding ecology are essential to determine the foraging behaviour and sustainability of African wild dog (*Lycaon pictus*) on small reserves. A small reintroduced population of African wild dogs (pack size ranging from 3 to 13 during the study) were studied in Karongwe Game Reserve (79 km^2) between January 2002 and January 2004. Fourteen prey species were identified as having been killed: impala (*Aepyceros melampus*, 60 %) was the most dominant prey, followed by bushbuck (*Tragelaphus scriptus,* 7.4 %), waterbuck (*Kobus ellipsiprymnus,* 4.9 %), warthog (*Phacochoerus aethiopicus,* 4.7 %), kudu (*Tragelaphus strepsiceros*, 4.4 %), and grey duiker (*Sylvicapra grimmia* 4.4 %). Generally, prey were included in the diet in relation to abundance and the dogs were found not to be rate maximizing foragers, but opportunistic. Between 1.9 and 2.8 % of the available edible biomass was killed annually, with each adult African wild dog feeding unit (WFU) consuming between 2.9 and 3.4 kg daily. The average ± (SE) interval between kills was 1.5 ± 0.05 days (n = 470 days of observation/kills). There was no correlation between kill interval, or size of prey, and pack size. Overall, prey capture success was 54.9 %, with bushbuck and impala hunts being the most successful. Impala, bushbuck and warthog were killed more often than expected along the fence line relative to abundance and angles in the fence were also found to facilitate kills being made. Although this pack did include some larger species in its diet, it did not conform with previous studies where large prey were killed in higher proportions than available abundance. More studies are needed in relatively small reserves to determine if the behaviour of these populations does differ to those previously described in open systems. Managers will then have more reliable information regarding the possible

impact of the reintroduced population, and to plan to avoid possible problems regarding sustainability. This will lead to more appropriate metapopulation management of this endangered species.

Key words: *foraging, profitability, barriers, fence, Aepyceros melampus, Tragelaphus scriptus, Kobus ellipsiprymnus, prey preference, Jacobs Index.*

Introduction

Human population expansion and subsequent habitat fragmentation are the primary causes of the decline and extinction of large carnivore populations over the past century (IUCN 2007). As a consequence conservation and management of small fragmented populations of large carnivores has become a necessity, with reintroduction and translocation methods being used as an important conservation tool to aid population recovery (Davies-Mostert et al. 2009). Large carnivores are important components of an ecosystem, and are known to shape the behaviour, distribution and abundance of their prey (Berger et al. 2001). Thus careful consideration is needed to determine whether a release site is suitable for a particular large carnivore prior to reintroduction (Clarke 2009, Mills et al. 1998). Evaluation of the habitat is essential and the single most critical habitat component for large carnivores is food, as their numbers will decline if prey numbers decline through a bottom up limitation (Hayward et al. 2007a). Successful growth of large carnivore populations can potentially impact negatively on the underlying prey base, and many reintroductions have failed as a result of reintroduced predators having severe unforeseen effects on prey populations ((Hayward et al. 2007a, Hayward et al. 2007b, Armstrong & Seddon 2007). In order for informed and successful conservation strategies to be put in place by managers, prior to reintroduction of large carnivores, there are some key questions that need to be asked such as: What will the reintroduced population feed on, what will their impact be on the prey population and ultimately what numbers of predators can the area sustain (the carrying capacity of the reserve (Hayward 2009)? Such questions can only be answers through monitoring and evaluation of previous reintroduction attempts.

One of the most extensive and well documented endangered species reintroduction efforts to date was that of the African wild dog in South Africa (Davies-Mostert et al. 2009, Gusset 2009). Here the establishment of an actively managed metapopulation of the African wild dog was implemented in an attempt to restore the declining wild dog numbers. The information gleaned from this initiative has improved wild dog management practises in South Africa (Davies-Mostert et al. 2009) and is to which this study hopes to make a contribution with regard to additional information of reintroductions of African wild dog onto relatively small reserves. The detailed information that has been documented during the reintroduction and metapopulation management of these African wild dog could benefit similar schemes in Africa, through the lessons learnt and shows the importance of additional monitoring of all large carnivores.

The African wild dog (*Lycaon pictus*) are in danger of extinction if nothing is done to halt the populations' decline (Creel & Creel 2002, Gusset 2007). Currently, the few remaining populations are scattered and fragmented, and numbers are declining. Past opinion indicated that African wild dog should not be maintained in areas smaller than 1000 km^2, and that such areas had limited value for conservation (Woodroffe & Ginsberg 1997). Recently, however, within South Africa there has been a swift increase in the number of relatively small reserves (< 1000 km^2) and African wild dog have been successfully reintroduced in a number of these (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004, Gusset et al. 2008a) including several smaller than 100 km^2. The majority of these populations are linked by management using a metapopulation approach (Mills et al. 1998, Gusset et al. 2008a). The success and survival of these metapopulations are critical for African wild dog conservation in South Africa and investigations into feeding ecology are essential to determine the true impact, and thus sustainability, of African wild dog on such small reserves. Any selection of expensive, larger prey species, more productive females, or more huntable trophy males (e.g Van Dyk & Slotow 2003) may have an impact on and affect the sustainability of reserves, and make reintroduction of African wild dog a relatively less viable option.

Generally, African wild dogs are regarded as being size selective, social predators with small (< 25 kg) to medium (40 kg to 90 kg) ungulates forming the most important component of the diet (Fuller & Kat 1990, Creel & Creel 1995, Krűger et al. 1999). Of the few studies carried out in relatively small, fenced reserves, results showed that African wild dog prey preference shifted towards larger prey, including adult kudu (*Tragelaphus strepsiceros*) and waterbuck (*Kobus ellipsiprymnus*) (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004), through the use of electric fence lines to assist in prey capture of these species (e.g. Van Dyk & Slotow 2003). Angles along the fence have been suggested as a factor which further enhances the African wild dogs' hunting success, as the pack uses acute angles as a type of a funnel, trapping the quarry between two sides of a fence (Rhodes & Rhodes 2004).

Prey preferences can be a threat to a reintroduced predator's survival (Hayward et al. 2007b), because, if sufficient prey species are not present at a particular release site, then the predator is unlikely to survive (Hayward et al. 2007a). Prey preference can also curtail, or reduce, possible reintroductions, if preferred prey are not available in sufficient numbers to sustain a pack (Hayward et al. 2007a). b). As a consequence, if the pack then selects expensive or rare game species as an alternative, this can become unviable for a reserve to sustain. The more information and understanding one has of the feeding ecology of relocated African wild dogs the more accurately one can predict or plan for a pack's possible impact prior to release . This should improve survival and success rate of releases and allow appropriate management plans to be put in place from the onset rather than only when problems arise (Hayward et al. 2007a).

One test to determine the preferences of carnivores it to use the Jacobs Index (Jacobs 1974) which investigates whether a predator selects prey more frequently than expected based on its abundance. Hayward et al. (2006), using data from 18 studies, found that generally African wild dog prefer to prey on Thomson gazelle (*Gazella thomsonii*), kudu, impala (*Aepyceros melampus*) and bushbuck (*Tragelaphus scriptus*). This method, however, is too simple because it reflects only the preference and ease with which a prey animal is captured. Another model analyses in more detail the energetics of feeding behaviour and decision making, testing whether a predator is rate maximizing or opportunistic (Stephens 2008). Rate maximizers' feeding decisions should be based on the net energy gains after expending energy to capture, kill and consume a specific prey, not simply on relative abundance. African wild dog are said to be rate maximizers (Creel & Creel 2002, Krűger et al. 1999, Rhodes & Rhodes 2004, Hayward et al. 2006), because their prey preferences reflect this model and they select prey which optimizes their net energy gains. However, neither test has been used to specifically determine the preference of relocated dogs on relatively small reserves. The shift in preference for larger prey and the use of fences as a hunting aid may assist in reducing the handling time of larger prey previously unselected for, thereby increasing the net gains of selecting larger prey species (Rhodes & Rhodes 2004), thus changing the foraging strategy.

Long-term monitoring and research is imperative to gain more insight into the feeding behaviour of packs in these areas. Although this only a case study of one pack (n=1) on a relatively small reserve, it is unique in its time-scale and intensity, being a two-year continuous study of a relocated pack on a 79 km^2 reserve, Karongwe Game Reserve (KGR). On a theoretical level, the study aimed to test whether the prey preference of the pack was similar to those found in previous studies, and to determine whether the dogs were rate maximizing foragers or opportunistic. On a management level, the study aimed to unravel the discrepancies regarding African wild dog management, by substantiating previous patterns of feeding behaviour of African wild dog on relatively small reserves. Prior knowledge of diet will allow managers to plan in advance for all possible feeding behaviours reported in the field, rather than responding when unsustainable prey offtake occurs. This is possible whether the population shows preferences or feeds opportunistically (relative to abundance) and can assist in more accurately assessing the viability of future reintroductions of African wild dog based on current prey species and numbers. Even if wild dogs are found to be opportunistic, managers with this knowledge can expect the reintroduced population to kill prey in relation to abundance and manipulate game numbers to ensure threatened or expensive game are not negatively effected, by altering the relative abundance of one prey species to provide a buffer for a rarer prey species (Hayward et al. 2007a). This increased knowledge should lead to the implementation of more relevant and informed management strategies of both predator and prey than presently occurs. This should increase the success rate of releases and survival of the African wild dog as a whole.

Methods

This study was undertaken at KGR, Limpopo Province, South Africa (24°25'S, 30°61'E) between 12 January 2002 and 12 January 2004. KGR is situated on the savanna lowveld plain, 300 to 500 m a.s.l., with a combination of undulating terrain and rocky outcrops. The vegetation type is described as Granite Lowveld (SVI3) in the savannah biome of the Lowveld bioregion (Mucina & Rutherford 2006). These areas are characterised by dense thicket to open savanna which is dominated with *Acacia nigrescens*, *Dictrostachys cinerea* and *Grewia discolor* in the woody layer and a dense herbaceous layer dominated by *Digitaria eriantha, Panicum maximum* and *Aristida congesta*. The vegetation map developed for KGR using Orthorectified Landsat Enhanced Thematic Mapper (ETM+) image mosaics (https://zulu.ssc.nasa.gov/mrsid/, see Appendix D for procedures), detailed the dominant vegetation types are mixed woodland (54 %), *Acacia-Combretum* woodland (20 %) and mixed *Acacia* woodland (15 %). Riparian vegetation is represented as 5.5 % on the reserve.

This area has a mean annual rainfall of 450 mm p.a. falling in the summer, between October and March. Winters are dry with mean monthly maximum and minimum temperatures reaching 38.0 °C and 3.7 °C for January and July respectively (Mucina & Rutherford 2006). Artificial water points have been created in the conservancy, some of which are supplied with borehole water, especially during the dry winter months.

The 79 km^2 KGR was founded in 1998 by adjacent farms removing fences, and is surrounded by a 65 km electrified boundary fence that effectively prevents outward movement of all large mammal species, excepting leopard (*Panthera pardus*), from the reserve. In 1999, a free-roaming pack of four male African wild dogs entered through the perimeter fence and became resident. In April 2000, as part of the African wild dog metapopulation management plan, two males where relocated to Madikwe Game Reserve, and the two of these remaining males (WM2 & WM3), with estimated ages of 3 to 4 years, were captured and held in a holding facility (boma) on KGR during previous unsuccessful bonding and reintroduction attempts, over a 14 month period. In November 2001, they were bonded with a 1.5 year-old captive female (WF1) from De Wildt Cheetah Breeding Centre, Brits, South Africa, for approximately two months prior to their release on 12 January 2002. The female first denned on 9 May 2002 with three female and three male pups. One male pup was killed by an unknown predator on 14 April 2003. In May 2003 the three female yearlings were relocated to Shamwari Game Reserve. The alpha female denned for the second time on 22 June 2003, resulting in five female and three male pups. One female and two male pups died before reaching 3 months, one death being due to lions (*Panthera leo*) and the others unknown. At the end of the study in January 2004, five pups had survived to make up a pack of ten, with the original adults and two sub-adults from first litter.

The pack which remained together, was located on consecutive days, twice daily over the two year study period (located on 702 days of the 734 day study period) throughout the different seasons, using a TR4 receiver and hand held Yagi antennae (Telonics, Arizona). While in captivity one male was fitted with a radio collar (SB2 radio transmitter with D-Cell battery with a 148-152 MHz frequency range), and the pack was followed by a 4X4 vehicle for short duration direct observations of between 2 - 15 h, as carried out in other predator studies (Schaller 1972, Mills 1992, Hunter 1998, Funston et al. 2001). The African wild dogs at KGR had a bimodal pattern of activity (Niemann 2008, pers. obs., unpublished data, see also Estes & Goddard 1967, Fuller & Kat 1990, Creel & Creel 1995, Rhodes & Rhodes 2004), and monitoring was designed around these times. To test if the pack was active at night, we located the pack between 20:00 and 02:00, and the African wild dog were inactive on 25 out of 29 (86.2 %) randomly selected nights. Consequently we located the pack approximately 30 min before sunrise and followed them until they settled (the whole pack resting, heads down sleeping, for longer than 30 min), usually 3 h after initial daily movement. We located and followed them again in the early afternoon (from about 15:30) up until they settled again, even if this was after dark. We followed the pack at a distance of 10 to 100 m for the duration of their active period. KGR has a comprehensive road network which the pack frequently used and which made observations easier. On occasions when the pack moved quickly through thick vegetation, we anticipated where they would emerge, and located them with radio-telemetry. If the pack did not appear within 10 min, we tracked them off-road. Activities were recorded chronologically, including behaviour, spatial movement, prey encounters, group composition, hunting behaviour, kill information (species, sex, and estimated age of prey), and interactions with other predators.

Data from direct observations (n = 472 kills from 796 attempted hunts, 59.3 % success) provided a reliable record of prey species, age, and sex of kills during the study. We were able to investigate all known kills, and when in dense bush we either approached the habituated pack on foot to within 15 m, or returned to the carcass when the pack had moved off. We identified the carcass in the field where possible or we collected unidentifiable remains for later identification by tracker experts. Smaller prey (< 10 kg) may have been missed due to the quick handling time and limitations for researchers navigating in dense vegetation (Rhodes & Rhodes 2004). Of the total of 472 kills recorded, 427 (90.5 %) of the prey species were identified from direct observation of the carcasses, and 45 (9.5 %) were recorded as being unidentified, i.e. if the prey species could not be identified from the carcass, if the pack members had blood on their faces but no carcass was evident, and/or if there was an increase in the belly score to indicate a kill had been made in our absence (Bertram 1975, Ginsberg et al. 1997). Established sex and aging criteria were used (Bothma 1996) and carcasses were categorised as adults (> 2 years), sub-adults (1 to 2 years) and juveniles (0 to 1 year). We grouped species into general size classes: small (< 30 kg: grey duiker (*Sylvicapra grimmia)*, steenbok (*Raphicerius campestris)*, and juvenile impala and bushbuck); medium (30 – 60 kg: adult bushbuck, impala, nyala (*Tragelaphus angasii*), and juvenile kudu, waterbuck, blue wildebeest (*Connochaetes taurinus)*, red hartebeest (*Alcelaphus buselaphus))*; and large (> 60 kg: adult kudu, waterbuck, red hartebeest, blue wildebeest). Carcasses not fed on (n = 2) were excluded from all further analyse.

Studies in Pilanesberg National Park showed that there was a variation in prey composition in relation to breeding cycle (Van Dyk & Slotow 2003). Waterbuck were found to be important prey component during denning and when young pups were first on the move, and impala less important than during the balance of the cycle. The breeding cycle period (developmental stage) was used in this study to investigate any feeding preference in the KGR pack during this period, and was identified as period of approximately 3 months (DS2), when pups were too young to follow the adults during long trips and when the pack showed refuging rather than nomadic life styles. To investigate if the KGR pack showed any similarities in feeding behaviour during this time, and during subsequent pup development stages, similar time periods of 3 months for each subsequent stage were used in the analysis until they reach a year old (DS3= 3 to 6 months, DS4 = 6 to 9 months, DS5= 9 to 12 months). At an age of approximately one year old the off-spring were active members of the hunting pack and a similar size to the adults, so were considered to be equal to 'adults' in their feeding requirements, and although not experienced hunters their presence in the pack contributes to foraging success (Courchamp et al. 2002). The data were separated into periods when there were only adults and yearlings only on the reserve (DS1 = all individuals >12 months). The pack successfully denned on two occasions during the study, the first litter born on the 9 May 2002 and the second litter on 22 June 2003). Sex and size class of prey was compared between litter periods (litter 1, 13th Jan 2002 to 4th May 2003 and litter 2, 5th May 2003 to 6th January 2004) and between developmental stages of the pups. Litter periods also served for an analysis of pack size and diet, as the diet was compared between litter 1, (average pack size 5.65) and litter 2 (average pack size 7.17).

Aerial census counts of game were carried out annually on KGR during the drier months of September 2002 and 2003 when visibility was at its best. A helicopter with four observers (including the pilot and one data capturer), flew transects in an east/west or west/east direction counting individuals 150 m either side of the helicopter; counts were completed within a day. Methods such as this may be biased towards species that are more easily observed from the air. A correction factor (Owen-Smith & Mills 2008) was used to provide a more representative number of the true abundance of species. The corrected aerial game counts were used to determine the relative abundance of the six most common prey species in the pack's diet.

Relative prey preference was calculated following the method of Hayward et al. (2006), using the Jacobs Index *(*Jacobs 1974*)* where selection (D) is:

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$$D = \frac{r - p}{r + p - 2rp}$$

and r is the relative proportion of kills, and p is the relative abundance of the prey of the total prey population. We calculated selection, ranging from -1 (maximum avoidance) to +1 (maximum preference), for each prey species. We tested preference in relation to abundance using a Chi Squared test (χ^2) for years separately, by contrasting the observed proportion of kills versus the expected proportion based on abundance. We also contrasted the number of kills of each species averaged across years (observed) against the average abundance for the 2002 and 2003 game counts (expected).

The theory of optimal diet predicts that a predator, in order to maximize the rate of energy intake, ranks prey types by profitability, where profitability (ρ) is a combined measure of prey energy (*E*), and handling time (*h*), so that ($\rho = E_i / h_i$) (Krűger et al. 1999). The predator adds different species to the diet in the order of ranking, on condition that the profitability exceeds the cost of ignoring the prey and searching for other opportunities. The expected diet choice of the pack was determined by adding the prey species to the diet in an order of decreasing profitability until the relationship below was satisfied, when the first *K* prey types were included in the diet and the rest were excluded. If the pack is seen to adopt a feeding strategy similar to the model they are then described as rate maximizers (Krűger et al. 1999), or if not, then as opportunistic.

$$(E/T)_{k+1} < \sum^{k} \lambda_i E_i \,/\, (1 + \sum^{k} \lambda_i h_i)$$

Energy (E) was taken to be the edible body mass (kg) of the prey, and live body mass of prey species was taken to be that given by the literature (Bothma 1996), and for warthog (*Phacochoerus aethiopicus*) carcasses that given by Mason (1985). The mass of the edible percentages of carcass consumed was estimated to be 60 % of the prey body mass (Estes &

Goddard 1967, Bothma 1996) and the inedible portion was subtracted. Prey handling costs (*h*) of African wild dog, was the sum of the time (t) taken to pursue, capture, and ingest prey. In this study, observations of successful African wild dog hunts (n = 43) were used to estimate pursuit, capture, and ingestion for each species (Table 3), where no data were available in this study for some species, the handling times detailed in Krűger et al. (1999) were used.

Prey encounter rates (λ) were obtained from road transect encounters of prey (census method following Hirst (1975) for wild ungulates in African woodland). We drove two counting routes of 31 km and 49 km, which covered most of KGR and all habitats, at 15 to 20 $km.h^{-1}$ simultaneously starting at sunrise, five times on consecutive days (starting and end point alternated each day). There were 4 observers per vehicle, and we noted location, species, number of individuals, and time of day. We repeated these counts three times per year in March, August, and November. We calculated prey encounter rate (λ) by dividing the total time taken to conduct all transects in a particular season by the number of encountered of a particular species (Krűger et al. 1999) and then multiplied the result by the coursing speed of African wild dogs, estimated as 10 $km.h^{-1}$ along roads (Creel & Creel 1995). We compared the observed diet choice with the expected diet choice using a Spearman's Rank Correlation Coefficient, to determine if the pack was indeed following the predicted prey rankings in their decision making.

The carcass weight listed by Bothma (1996) for herbivores and Mason (1985) for warthog were used in the biomass calculations. Unknown carcasses were assigned a weight based on the following assumption: the relative proportion of unidentified species killed would be similar to the proportion of known kills in the diet. So the total biomass of the diet was divided by the total number of kills to get a weight value for unidentified carcasses. The mass of the assimilable percentages of carcasses that were consumed was estimated as 60 % of the average prey body mass (Bothma 1996).

The body mass of each prey species was then multiplied by the number of individuals killed by the African wild dog and totalled in order to calculate the biomass removed by the pack in individual years. We calculated the biomass killed per African wild dog per year by dividing the biomass killed each year by the average number of WFU in the population for that year, assuming all carcasses were divided equally among them. An adult African wild dog (>12 months) was considered to have a WFU of 1, pups were considered to be a proportion of WFU depending on their age (0 to 3 months = 0.25, 3 to 6 months = 0.5 and 6 to 12 months = 0.75 of a WFU), to give a more accurate calculation of the amount of assimilable biomass a growing pup consumes. Daily biomass consumed per WFU was calculated by dividing the annual consumption by 365 days.

We determined the African wild dog kill interval by calculating the time interval between each kill, and dividing it by the total number of kills to give the mean interval between kills for the study period. Outliers were removed where gaps in data indicated an interval of > 6 days between kills, as African wild dog need to eat more frequently than this (Van Dyk & Slotow 2003). We tested for effects of prey species or size class of kill on the interval between kills with one-way analysis of variance (ANOVA), followed by a least significant difference *post hoc* test.

We recorded African wild dog capture success from direct observations of successful and unsuccessful hunting attempts, and calculated a percentage of successful pursuits by the entire pack, or most of the pack, for each species (Fanshawe & Fitzgibbon 1993). We defined 'hunting' to be the dog alert while walking, or trotting purposefully (Krűger et al. 1999), and 'pursuits' to be an increase in speed towards the prey. If the pack was found on a kill at the beginning of any observation session this was not included as a successful hunt, so as to reduce any bias towards success..

To investigate if the KGR pack made use of the perimeter fence to their advantage when hunting, the location points of all kills were examined in relation to the boundary fence using Arcview 3.2 (www.esri.com). We created a 200 m buffer area along the inside of the fence line boundary using the Geoprocessing Wizard. This distance from the fence was used to include all kills made directly on the fence, as well as including any injured quarry being actively chased into the fence and injured before being captured some way from the fence, which was observed in the field (Niemann per. obs). The proportions of all kills of different species killed by the pack within the buffer were calculated. This proportion was then compared, using a Chi-square test, with the proportion of the total herbivore population available on the reserve. Game numbers were based on the average of the game counts for the two study years conducted on KGR. Landscape attributes have been shown to be one of the factors of resource selection in carnivores (Stephen & Krebs 1986). Leopards in Phinda Resource Reserve were found to hunt in habitats that were easier to capture prey (Balme et al. 2007) rather than where the prey was most abundant. So it is important that the landscape is also investigated to determine if there was a habitat effect on kills made rather than the effect of the fence. To analyse this, all kills made in different vegetation types were determined by clipping the kills data to the KGR vegetation map shape file. The percentage vegetation type available within the buffer was compared with the vegetation type available on the rest of the reserve, using a Chi-squared test, and then proportion of kills made within each habitat type was compared.

We tested whether there was an unequal spread of African wild dog kills along the fence in sections with notable angles (acute:15^{o} to 165^{o}, and obtuse:195^{o} to 345^{o}). We divided the 200 m wide buffer area along the fence line into 500 m sections (area of each block equalled 10 ha), and identified sections with a fence angle within this range. We tested the number of kills made in these sections which were then tested against the expected using a

Chi Squared test. Firstly, we calculated the number of each prey species killed and size class killed in sections with no notable angles divided by the total area calculated for those sections. Expected values were then generated according to the area of those sections which had notable angles.

Results

The African wild dog were recorded as having killed a total of 472 prey over the 24 month study, representing 14 species on KGR: Impala, bushbuck, waterbuck, grey duiker, kudu, warthog , steenbok , bushpig (*Potamochoerus porcus*), red hartebeest, blue wildebeest , leopard tortoise (*Geochelone pardalis pardalis*), helmeted guinea fowl (*Numida meleagris*), Egyptian goose (*Alopochen aegyptiacus*), and unidentified small rodent species. Two black-backed jackals (*Canis mesomelas*) were killed but not fed upon, so this species was discounted from further analyses.

Overall, impala was the most dominant prey species whether expressed as percentage of diet (60.6 %) or as a percentage of biomass (56.1 %). Bushbuck, waterbuck, warthog, duiker and kudu formed a significant proportion (25.8 %) of the remaining diet (Table 1), and the rest of the analyses considered only these six ungulate species.

In terms of age of prey of African wild dog, significantly, more adults (75 %) than juveniles (13.1 %) or sub-adults (13.4 %) were killed over 24 months ($\chi^2_1 = 50.27, 49.87$, $P < 0.05$). Over the 2 year study period, more warthog (45.5 %) and kudu (57.1 %) juveniles were killed than in other age classes, while more adults of impala (82.2 %), bushbuck (61.8 %), waterbuck (71.4 %), and duiker (85.7 %) were killed than other age classes. There was a significant difference between the sexes killed ($P < 0.05$) across all species except warthog. Impala provided more males than females in the African wild dog diet ($\chi^2_1 = 55.14$, $P < 0.05$), while in all other important species more females than males were killed.

The overall number of kills made by African wild dog in all seasons differed significantly from each other ($P < 0.05$), with the exception of summer and spring ($n = 136$, $n= 146$). The diet composition in the winter differed significantly from all other seasons ($P < 0.001$ for all comparisons). The main differences in the winter season were due to the lack of bushbuck in the diet, less waterbuck compared to autumn and more duiker compared with spring. Both denning (DS2) periods occurred in winter months which could account for the prey difference during this time, as the pack were localised in the south of the reserve (Figure 2).

No significant difference was found in the size class of prey of African wild dog selected over the seasons. However, when all seasons were combined, the pack killed more medium sized prey (69.1 %) compared with small (25.5 %) or large (5.6 %) sized classes of prey. There were significantly more males (54 %) preyed on in winter compared with other seasons (all season > 64 % females) ($P < 0.001$ for all). In terms of prey preference of African wild dog, there was no significant selection or avoidance of prey for all years combined (χ^2_5 = 2.74, $P > 0.05$), but in the second year, bushbuck (χ^2_1 = 10.34, $P < 0.05$) were selected and warthog avoided (χ^2_1 = 5.46, $P > 0.05$ (Figure 1). When looking at the distribution of kills across the reserve during the different seasons (Figure 2), the kills appear non-random in general, with a concentration of kills made at the angles and eastern fence line of the reserve during spring and summer, compared to autumn and winter. In autumn and winter, the fence seems to be used less as a hunting tool.

Based on profitability and after uncommonly fed on animals (outliers) were omitted, the rate maximizing model predicted that the African wild dogs on KGR would include waterbuck and kudu in the diet. The pack did not rank their prey in the diet in relation to profitability (Spearman's rank r_{s-} = 0.14, n = 6, P = 0.797*).* A significant positive correlation that was found between the observed preference of species and encounter rate of herds (r_{s-} = 0.88, P = 0.0016) suggested the pack made opportunistic hunting decisions based on the encounter rate rather than profitability.

The available biomass removed from the reserve was 1.9 % in 2002 and 2.87 % in 2003. The biomass consumed per WFU was 1239 kg $annum^{-1}$ (3.38 $kg.day^{-1}$) in the first study year and 1543 kg $annum^{-1}$ (2.89 kg day^{-1}) in the second. There was no significant correlation between pack size and the biomass consumed per adult per day (r_s= 0.613, P = 0.07)

When prey size class, sex and species composition in the diet were compared between the two different African wild dog litter periods, only size class of prey was found to be significantly different ($G_{0.05,2}$= 21.96, $P < 0.001$), as more larger prey were eaten during litter 2 than litter 1, probably due to larger pack size in the second litter (average pack size of 7.17 in litter 2 compared to 5.65 in litter 1). Similarities between corresponding developmental stages (DS) in the two litters were tested with respect to the prey size, sex and species of kills made, but no specific pattern could be identified. DS1 (adults only) and DS2 (0 to 3 months) showed similarities with respect to species ($G_{0.05,4}$ = 4.002, 8.184, $P > 0.05$) , DS4 (6 to 9 months) with respect to sex ($G_{0.05,2,}$ =5.425, $P > 0.05$) and corresponding DS1 and DS3 (3 to 6 months) with respect to size class of kills made ($G_{0.05,2,}$ = 3.59, $P > 0.1$, 1.403, $P > 0.25$). As previously found (Van Dyk & Slotow 2003) the period when the pups were in the den and first starting to move (DS2) show similarities with regard to prey composition but not size class of kills ($G_{0.05, 6}$ = 12.49, $P < 0.05$). The corresponding periods of the two litter periods showed similarities with regard to the proportions of impala, waterbuck and duiker in the diet, but in DS2 (litter 2), kudu not warthog were killed accounting for the differences in size class of prey taken in DS2. Waterbuck proportions in DS2 were not elevated during this period when compared to other developmental stages of the pups, and the proportions were actually lower than found when only adults were within the population (DS1).

The average ± (SE) interval between kills (observed and unidentified) over the two years was 1.5 ± 0.05 days (n = 470 days of obs/kill). The number of days between kills ranged from the same day to 6.0 days between kill events. No significant correlation was found between kill interval when tested against the size of prey or against pack size.

The capture success of African wild dog for all ungulate species was 54.9 % (n = 334 of 608 pursuits with known outcome) and 59.9 % for important species (n = 325 of 548) (Table 3), with hunts of bushbuck (78.6 %) being the most successful and warthog being the least (32.2 %).

When the proportion of kills made along the fence line was investigated, more bushbuck, impala and warthog (χ^2_1 = 5.388, 6.05, 5.625, $P < 0.05$), and less wildebeest (χ^2_1 = 13.140, $P < 0.5$), were found to be killed along the fence line in relation to available abundance. However, no significant difference of large species, such as kudu and waterbuck were found to be made along the fence. When proportion of habitat available within the buffer was compared to those on rest of the reserve no significant difference was found for all, except more bare soil surface (roads) habitat type and less mixed *Combretum* woodland (χ^2_1 = 17.680, 5.069 $P < 0.05$) was available within the buffer. The proportion of kills were only found to be made significantly more frequently in the bare soil (road) and riparian habitats within the fence buffer (χ^2_1 = 9.064, 23.937, $P < 0.5$). However, no significant difference of the proportion of kills made in the bare soil (road) habitat type in the area away from fence was found, suggesting a fence effect rather than vegetation effect along the fence. Away from the fence, significantly more kills were made in old lands and riparian habitats (χ^2_1 = 8.204, 6.337, $P < 0.05$) and fewer kills made in mixed *Combretum* woodland and *Acacia-Combretum* woodland (χ^2_1 = 8.063, 5.487, $P < 0.05$) in relation to available habitat.

There were significantly more kills by African wild dog made at the notable angles (acute: 15^{o} to 165^{o} and obtuse: 195^{o} to 345^{o}) along the fence line (χ^2_5 = 265.59, $P < 0.001$), compared with areas within the 200m fence line buffer with no angles. Significantly more impala, bushbuck and waterbuck were killed at notable angles than at other flat sections of the fence line (χ^2_1 = 67.48, 29.94, 167.24 respectively, $P < 0.05$).

Table 1: *The percentage contribution of various prey species to the diet of the KGR pack of African wild dogs, in different seasons and overall. Prey falling into 'Other' category includes all non-herbivore, infrequent (hartebeest (Alcelaphus busclaphus), steenbok (Raphicerus campestris), bush pig (Potamochoerus porcus), wildebeest (Connochaetes taurinus), avian and rodent species) killed.*

Prey Species	Jan - Feb 2002 Summer (%)	Mar - Apr 2002 Autumn (%)	May - Jul 2002 Winter (%)	Aug - Oct 2002 Spring (%)	Nov - Feb 2003 Summer (%)	Mar - Apr 2003 Autumn (%)	May - Jul 2003 Winter (%)	Aug - Oct 2003 Spring (%)	Nov - Jan 2004 Summer (%)	Overall (%)
Impala	53	39	70	62	69	60	66	57	50	61
Bushbuck	6	7	0	1	7	6	0	26	16	7
Waterbuck	6	7	2	1	0	11	4	7	19	5
Warthog	6	2	13	8	7	0	0	0	0	5
Duiker	0	2	2	11	4	11	2	2	0	4
Kudu	6	7	0	6	4	4	10	2	3	4
Wildebeest	6	0	0	0	1	0	0	0	3	1
Unknown	18	29	9	8	0	9	18	7	3	10
Other	0	5	5	2	8	0	0	0	6	3
Total No.	**17**	**41**	**56**	**85**	**83**	**47**	**50**	**61**	**32**	**472**

Table 2: *The African wild dog pack prey selection (following Krűger et al. 1999) in KGR (2002-2004). Comparison of ranked observed and expected African wild dog diet choice based on profitability (E/h) of prey. Handling time (h) is the sum of pursuit time +capture success + ingestion time, estimated from our observations and from Krűger et al. (1999). Energy values (E) are given as kg, and encounter rate (λ, encounters per hour) of potential prey species are estimated from road counts (see text). Entries in bold signify that the prey model predicts the African wild dogs would take only these species in that order of preference and other species would be avoided.*

Prey Species	*H*	*E*	Λ	*E/h*	*E/T*	Prey ranking Observed	Expected
Waterbuck	**0.48**	**122.8**	**0.46**	**254**	**46.3**	**3**	**1**
Kudu	**0.80**	**81.8**	**0.39**	**102**	**58.6**	**5**	**2**
Bushbuck	0.60	17.7	0.43	30	60.6	2	3
Warthog	0.72	17.4	0.61	24	54.6	4	4
Impala	1.23	24.5	0.94	20	44.1	1	5
Duiker	0.36	6.0	0.24	17	43.4	6	6

Table 3: *Capture success expressed as a percentage of pursuits with known outcomes for prey species pursued by the African wild dog pack on KGR (2002-2004). Entries in bold signify the key species in the diet.*

Prey species	Unsuccessful hunts	Successful hunts	Total hunts	Capture success (%)
Impala	**123**	**222**	**345**	**64.3**
Bushbuck	**9**	**33**	**42**	**78.6**
Waterbuck	**22**	**17**	**39**	**43.6**
Warthog	**40**	**19**	**59**	**32.2**
Duiker	**14**	**16**	**30**	**53.3**
Kudu	**15**	**18**	**33**	**54.5**
Steenbok	3	5	8	62.5
Wildebeest	28	2	30	6.7
Hartebeest	0	2	2	100
Eland	3	0	3	0
Zebra	14	0	14	0
Giraffe	1	0	1	0
Nyala	2	0	2	0
Total	**274**	**334**	**608**	**54.9**

Table 4: *Chi-squared results of observed prey selection by African wild dog along the fence line compared to expected number of kills based on proportion of prey species available.*

Prey species	Observed no. of kills	Expected no. of kills	Chi Squared Value
Impala	99	78	5.388 *
Bushbuck	11	5	6.050 *
Waterbuck	10	0.67	0.025 NS
Warthog	3	1.06	5.625 *
Wildebeest	2	16	13.141 *
Kudu	4	0.95	1.750 NS
Prey size class	**Observed no. of kills**	**Expected no. of kills**	**Chi Squared Value**
Small	33	36	0.356 NS
Medium	97	86	1.134 NS
Large	11	7	1.393 NS

* $P < 0.05$

d.f. = 1

Table 5: *Chi-squared results of the proportion of each vegetation type found within the buffer as compared to the available proportion out of the buffer area.*

Vegetation type	Proportion in Buffer area (%)	Proportion out of buffer area (%)	X^2
Acacia-Combretum woodland	16.64	20.22	0.822 NS
Bare soil surface	5.36	0.89	17.609 *
Mixed *Acacia* Woodland	0.01	0.01	0.002 NS
Mixed *Combretum* woodland	7.27	15.68	5.069 *
Mixed woodland	61.01	52.79	1.130 NS
Mopane	0.95	0.95	0.265 NS
Old Lands	4.39	3.64	0.017 NS
Riverine	4.26	5.65	0.631 NS
Water body	0.10	0.16	1.989 NS

* $P < 0.05$

d.f. = 1

Table 6: *Chi Squared results to determine whether kills were made in proportion to available vegetation type of KGR.*

Vegetation type	Proportion of kills (%)	Proportion of available habitat (%)	X^2
Acacia-*Combretum* woodland	10.19	20.22	5.487 *
Bare soil surface	2.16	0.89	0.655 NS
Mixed *Acacia* Woodland	0.00	0.01	0.008 NS
Mixed *Combretum* woodland	4.94	15.68	8.063 *
Mixed woodland	59.57	52.79	0.747 NS
Mopane	0.93	0.95	0.289 NS
Old Lands	8.95	3.64	6.337 *
Riverine	12.96	5.65	8.204 *
Water body	0.31	0.16	0.772 NS

* $P < 0.05$

d.f. = 1

Table 7: *Summary of the findings of other studies regarding the diet of African wild dog, as a comparison to the study at the KGR.*

Reference	Reserve	Area	Dominant Species in diet	Consumption rate (kg.prey.dog^{-1}day^{-1})	Capture success (%)
Rhodes & Rhodes (2004)	Shambala Game Reserve, SA	83.5km^2	Kudu (60%), wildebeest (5%), waterbuck (5%)	-	-
Van Dyk & Slotow (2003)	Pilanesberg National Park, SA	500km^2	Kudu (49.6%), impala (30.7%), and waterbuck (15%)	9	-
Kruger et al. ((1999)	Hluhluwe Umfolozi Park, SA	960 km^2	Nyala and impala (77%)	-	48
Hayward et al. (2006)	18 studies	83.5->1000km^2	50kg prefered wieght range, bimodal peaks at 16-32kg, and 120-140kg	-	-
Creel & Creel (1995)	Selous National Park, Tanzania	>1000km^2	Impala (54%), wildebeest (28%, mean mass 92.7kg), warthog (31%)	2-2.5	47 (44 pooled data)
Estes & Goddard (1967)	Ngorogoro crater, Tanzania	>1000km^2	Thompon Gazelle (54%), wildebeest (36% calves), Grant's gazelle (8%)	2 (12-21 dogs), 4.1 (6-7 dogs)	-
Fuller et al. (1995)	Masi Mara National Reserve, Kenya	>1000km^2	Thompson Gazelle (60-92%), impala (0-8%), wildebeest (40-18% all calves)	0.08 - 0.20	27-69
Fuller & Kat (1990)	Masai Group ranch, Kenya	>1000km^2	Thompson Gazelle (67%), impala (17%), and wildebeest (8% (4 of 5 calves))	1.7 (pooled data) 1.2-5.9 average of 3.16 (+/-0.05)	-
Mills & Biggs (1993)	Kruger National Park, SA	>1000km^2	Impala (69.2%), kudu (15.38% calves only), and reedbuck (15.38%)	-	-
Mills & Gorman (1997)	Kruger National Park, SA	>1000km^2	Impala (73.2%), kudu (5.4%), duiker, and steenbok (8.9%)	-	-
Pienaar (1969)	Kruger National Park, SA	>1000km^2	Impala (87%), kudu (4.6%), and waterbuck (2.6%)	-	-

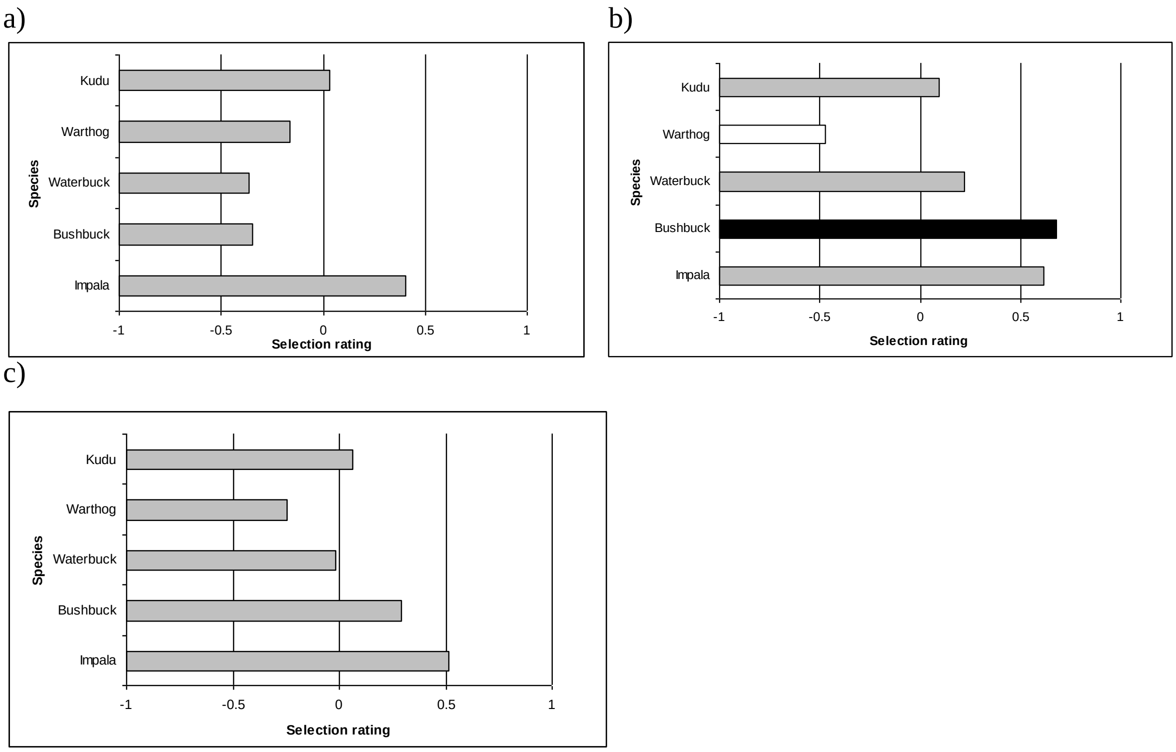
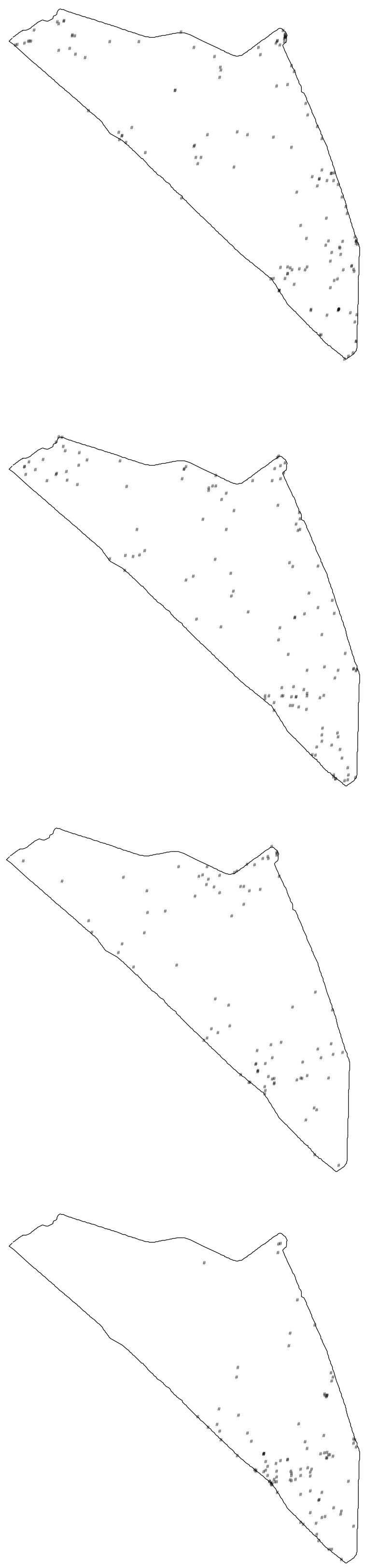


Figure 1: *Dietary preference of the African wild dog pack for the six most common prey species. Presented are Jacobs Index for (a) 2002, (b) 2003, and (c) the average for the two years. Black bars represent the species preyed upon significantly more than expected, based on the proportion of observed number of kills in the diet versus the proportion of their abundance; grey bars indicate species preyed upon in accordance to their abundance, or not significantly preferred, or avoided; unfilled bars show the species which were killed significantly less frequently than expected based on their abundance.*



a)

b)

c)

d)

Figure 2*: Kill positions plotted on KGR during each of the seasons a) spring, b) summer, c) autumn, d) winter.*

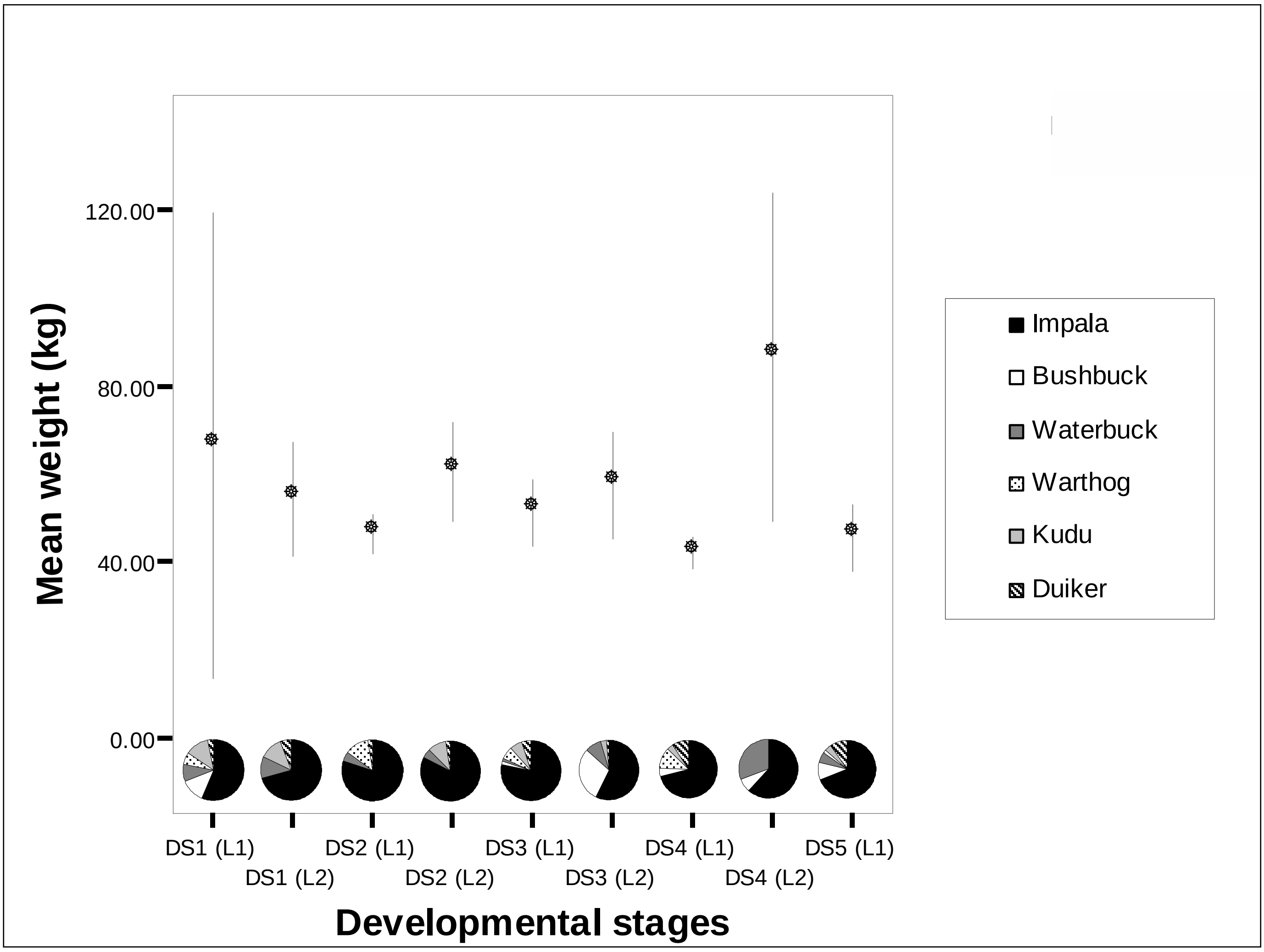


Figure 3 *The mean prey body mass (± SE) and proportion of different prey in diet taken during the different developmental stages of the pack of African wild dog (DS1 = adults only, DS2 = 0 to 3 months, DS3 = 3 to 6 months, DS4 = 6 to 9 months, DS5= 9 months) in different litter periods: L1 = litter 1 (2002), L2 = litter 2 (2003).*

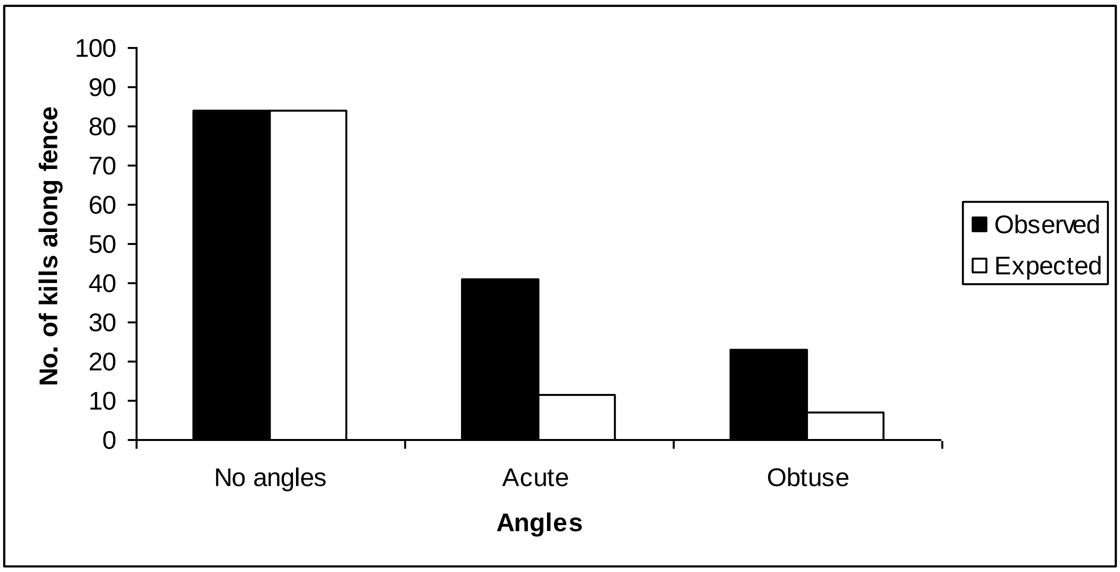


Figure 4: *The effect of fence angles on hunting success of a pack of African wild dogs on the KGR (2002-2004). The number of observed and expected kills made along the fence line (200m buffer) for no angles, for acute and for obtuse angles are shown.*

Discussion

Over the two year study period, the African wild dog pack's diet consisted mainly of small to medium sized prey species (< 50 kg), impala and bushbuck, as was found in previous studies (Estes & Goddard (1967), Pienaar (1969), Mills & Biggs (1993), Fuller & Kat (1990), Creel & Creel (1995), Fuller et al. (1995), Mills & Gorman (1997), Krűger et al. (1999), Van Dyk & Slotow (2003), Rhodes & Rhodes (2004), Hayward et al. (2006); Table 7). Although some larger prey species were included in the diet, including kudu and waterbuck adults, contrary to expectations the proportion of kudu in the diet was not as high as that seen in studies within other small reserves such as in Pilanesberg National Park (Van Dyk & Slotow 2003) and Shambala Game Reserve (Rhodes & Rhodes 2004). The pack did use the fence line as an effective barrier to enable them to capture higher proportions of prey than expected relative to abundance. However, this was only evident with medium sized prey, not large prey as seen in previous studies. It is unknown whether using fence lines is a conscious hunting strategy to enable the dogs to kill more prey, or whether using the fence lines is the result of the small size of the reserve that increases the chances of quarry meeting a fence during a pursuit. It should be considered that both studies in Shambala Game Reserve and Pilanesberg National Park did, however, suggest that these elevated levels of kills of large prey killed along the fence may be due to a measure of bias in the data, from increased effort in data collection long the fence line. No such biases were present in our study, and perhaps the data presented here are therefore relatively more representative of the feeding behaviour of packs on relatively small reserves. The fence may not have a mutually exclusive effect and other factors including habitat may have a combined effect on hunting preferences, and needs to be investigated further. More relatively small reserves with African wild dog packs need to be studied to increase the sample size for more accurate analysis and to determine if any pattern is emerging for these populations, and more detailed investigations need to be made into possible variables that may influence foraging behaviour.

The African wild dog pack showed no preference for any species over the two years combined, and they fed in relation to the abundance of prey, and in general did not select any prey on any other merit. Preference was evident only in the second study year for bushbuck and avoidance of warthog. This was probably due to increased pack size enabling it to select prey, and show avoidance of warthog which is know to have a high injury threat (Hayward et al. 2006) for relatively little energetic gain. Rhodes and Rhodes (2004) found dogs had a strong preference for kudu but no other species. Our results contrast with the findings of the in-depth study by Hayward et al. (2006), who, using the Jacobs Index across 18 different studies, showed that bushbuck, impala, and kudu were preferred prey species. One reason for this difference could be due to the small sample size of this study, as it should be highlighted that although the intensity of data collection was high, the results of this study only represent one pack. In addition, the majority of the study sites used previously, were in open systems, with only five used in Hayward et al.(2006) analysis represented reintroduced populations of African wild dog in fenced reserves, and only one representing reserves of < 250 km^2. So preferences in relatively small reserves were not well represented, and thus needs to be investigated further. Another explanation could be that the pack size of the KGR population (n = 3 to 13, average 6.3 WFU) varied through management intervention but in general was much lower than the pack sizes of the comparative studies on other relatively small reserves (Hlhuhlwe Umfolozi Park, n = 10 to 13, Pilanesberg National Park, n = 9 to 12, and Shambala Game Reserve, n = 7 to 12), as well as those in open systems. Foraging behaviour of African wild dog is more efficient with the cooperation of helpers (Creel & Creel 1995, Courchamp & Macdonald 2001), usually yearlings and older. As pack size increases so does hunting success and mass of prey killed, while distance chased per hunt decreases (Creel & Creel 1995). In the second litter when the pack size had increased (average 7.17 WFU with 5 adults) we saw some preferences emerging and larger size of prey being killed. Perhaps the reason for the difference found in this study, was due to the low pack size and the lack of experienced helpers in the pack, particularly in the first litter period (average 5.65 WFU with 3 adults).

We should also consider the differences seen in this study could be due to effect of the presence that other competitive species might have on prey selection. Competition from lion excluded wild dog from areas of high prey density (Mills & Biggs 1993) and subordinate predators (African wild dog and cheetah) use refuge habitat to avoid competitive interactions (Hayward et al. 2007c). The absence or presence of competing dominant carnivores (lion and spotted hyena, *Crocuta crocuta*) could have had a profound effect on the actual available prey in relation to their spatial movements of the pack (Hayward 2009). More accurate prey availability taking into account movement shifts from intraguild competition, should be used in the analysis of prey selection by subordinate large carnivores.

Likewise, when using the rate maximizing model to test preferences in relation to net energy gains, we found the African wild dog pack to be opportunistic and not rate maximizing foragers. Previous studies have found African wild dogs to be rate maximizers (Krűger et al. 1999, Creel & Creel 2002, Rhodes & Rhodes 2004), with a diet based on profitability as the model predicted (Stephens & Krebs 1986, Stephens 2008). Furthermore in contrast to our findings, only larger packs (> 8) are found to be less selective (Creel & Creel 2002) and kill most species in proportion to abundance as they are relatively more efficient hunters of a larger range of prey when compared to smaller packs. Our unexpected result suggests that either this small pack is unusual in its feeding preferences, or that the model may simply be unsuitable to the diet profile of packs in small reserves. Creel & Creel (2002) suggest that communal hunting behaviour of African wild dog does not fit the model as well as solitary hunting, because prey size is correlated to hunting group size which increased the number of larger species included in the diet. This leads to profitability becoming inflated due to decreased handling time, thus skewing the predictions of the model towards larger prey. The tendency of packs to use fence lines as a barrier to catch prey more easily was suggested to reduce handling time (Rhodes & Rhodes 2004) having a similar effect on the model. To support this theory the handling time of larger prey, in particular waterbuck and kudu, was found to be considerably lower in KGR than that detailed in Krűger et al. (1999). Another consideration regarding the unsuitability of the model is that the net profitably was elevated for larger species as the mass of the population (which included adults) was used in the calculation, rather than the calf mass as was detailed in Krűger et al. (1999). As seen to varying degrees, adults of large prey species are typically included in the diet of African wild dogs in relatively small reserves (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004). In Shambala Game Reserve, although the specific model was not tested, it was concluded that the pack was rate maximizing due to the strong preference for kudu (60 %), and the use of the fence line aided in killing this more profitable prey. In our study, although an increase was found of some prey species along the fences, particularly at angles, overall this increase was not to the degree that the rate maximizing model predicted and kudu were in fact found to be avoided. Further investigations are needed to determine whether, in general, on small reserves dogs are rate maximizing foragers and if this pack is simply an exception. If similar results are found on other small reserves, then the model needs to be modified for analysis for these specific populations and then one needs to determine what other factors affect the foraging strategies of these packs.

Previous studies of African wild dog have documented a large range of consumption rates but only a few mentioned kill interval or commented on kill frequency. East African studies (reviewed in Fuller & Kat 1990) ranged between 1.2 to 5.9 $kg.dog^{-1}.day^{-1}$ and only two studies mentioned that two kills or more were made per day (Estes & Goddard 1967, Creel & Creel 2002). The mean consumption rate of these latter two studies (3.16 $kg.dog^{-1}.day^{-1}$) was almost identical to the mean results found in our study (3.14 $kg.dog^{-1}.day^{-1}$), but we observed a longer kill interval of 1.53 days between kills. Elevated consumption rates were seen in the pack in Pilanesberg National Park (Van Dyk & Slotow 2003) where a high consumption rate value of 9 kg dog^{-1} day^{-1} and a kill interval estimated as occurring every two days was documented. This was said to be due to the relatively large size of prey being taken thus increasing the biomass consumed and also due to possible biases in data collection (Van Dyk & Slotow 2003). We expected the KGR pack followed similar patterns documented on other relatively small reserves. In contrast, no a strong tendency was found for the KGR pack to take larger prey species in their diet, so the consumption rate was more in line with studies in more open systems.

As a rule, consumption rates of African wild dog are used as a measure of foraging success, and increase as pack sizes increase (Creel & creel 1995). However, Creel and Creel (1995) also noted that initially as pack size increased the consumption rate (kg dog^{-1} day^{-1}) decreased reaching a minimum when 8 to 9 adults were in the pack, before subsequent increase. This is due to costs of competition for food versus the benefits related to an increase in foraging success of increased pack size. They even suggested that, because of this ,packs between 7 and 11 adults should be avoided, which the KGR pack size reached on occasions during the study, with range of between 3 and 8.8 WFU (mean 6.2) over the study period. Despite some larger prey in the diet and the use of the fence line as an effective hunting tool, the consumption rate was lower than expected based on the findings on other relatively small reserves, and is probably due to the less large prey species in the diet, small pack size and the longer kill interval. However, the high capture success of the pack maintained the consumption rate to a level similar to studies with larger pack sizes.

Overall, the annual biomass consumed by the pack of African wild dog represents only a small proportion of the available biomass in this relatively small reserve. If we used this figure as a benchmark to determine if a reserve could sustain large carnivores in the long term, as some studies have (Druce et al. 2004, Hayward et al. 2007b, Power 2002), then it is fair to assume the pack is sustainable in the short term as long as it continues to forage opportunistically and the pack size is managed to a similar level. However, if a pack is observed to select specific animals this may impact on and affect the sustainability of reserves, particularly if the animals are expensive, rare, more productive females or more huntable trophy males (e.g Van Dyk & Slotow 2003). This would make reintroductions of African wild dog a less viable option for management.

To ensure sustainability of relocated African wild dog packs, detailed assessments of carrying capacity (Hayward et al. 2007a,b), and minimum area requirements (Lindsey et al. 2004) on relatively small reserves are needed. This is investigated in Chapter 3 using data presented here.

Communal hunting and increased pack size of African wild dog can improve capture success (Creel & Creel 2002). Even though the pack sizes on KGR are relatively small, the capture success rate of 54.9 % is higher than previously reported average rates of 35 % (20 to 44 %), in other dense habitats (Creel & Creel 1995, Reich 1981). East African studies showed a pooled average of 44% capture success (Creel & Creel 1995). Higher values of up to 69% were found in some packs in Kenya (Fuller et al. 1995) and with a 64 % average in other studies in East African (Krűger et al. 1999). The lack of visibility in more dense habitats has been found not to reduce capture success, because hunting techniques such as ambushing and short chases are used by the packs (Krűger et al. 1999, Creel & Creel 1995). These techniques seem to be relatively as successful. In fact, packs in KNP were found to avoid open areas and hunted successfully in denser habitat types (Mills & Biggs 1993). To determine why the capture success was at the upper end of the documented range, and considering the small pack size, more investigations are needed. However, the use of the fence line as a hunting tool could have contributed to the relatively high success rate. Although not investigated in this study specifically, other factors need to be investigated to establish their influence on capture success, these include the effect encounter rate has on capture success on well stocked reserve, condition of prey and vigilance of prey (Hunter & Skinner 1998). Lack of vigilance behaviour by predator-naive ungulates to a newly reintroduced wild dog foraging may make them more vulnerable, thereby increasing success rate.

Conclusion

Previous studies on relatively small reserves, have shown that a pattern is emerging and African wild dog are showing a preference for larger prey and are increasing capture success through the used of effective barriers, when compared to more open systems , (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004). The results in this study do not replicate these patterns regarding larger prey, and the pack was opportunistic, although using the fence as a hunting tool for certain species of medium sized prey. Management plans for African wild dogs are currently based on the feeding behaviour of African wild dogs in open systems, and from which estimates of specific carrying capacities and sustainability are based. If, after more detailed studies on relatively small reserves it is found that feeding behaviour differs from previous studies with regard to proportion of larger prey in the diet, preferences, foraging strategies, and use of fences, or a combination of these, then it can lead to unexpected economic and ecological effects on the reserve. This could potentially jeopardise the success of a reintroduction of African wild dog in terms of the negative effect on population dynamics, the economics of sustainable offtake of rare and expensive game, and increase the risk of break-out of African wild dog or other species due to fence damage. Economically the loss of expensive or rare game because of African wild dog predation, due to preferences or opportunistic kills on high densities of these species, has serious cost and management implications, particularly if restocking is necessary to maintain a healthy population. Large, expensive, prey supplementations are currently being undertaken in a range of reserves such as Pilanesberg National Park, Madikwe Game Reserve, and Welgevonden Private Game Reserve (Slotow 2008, pers. comm.) as a result of large carnivore prey preference. Fence maintenance and monitoring due to damage made during hunts also has its associated costs and risk if break-outs occur. Break-outs could jeopardise the survival of African wild dog, as once out of the protection of a reserve they are at risk of human persecution (Gusset et al. 2007). Also, break-outs can result in inevitable livestock loss which could entrench negative attitudes of local stakeholders towards African wild dogs (Gusset et al. 2008b), possibly obstructing future conservation efforts in the area, or the survival of any free-roaming packs. Future studies on small reserves are necessary to ascertain whether any patterns are emerging and common to the majority of packs in these areas or whether in fact the biases found in the studies in Pilanesberg National Park and Shambala Game Reserve skewed interpretation. Studies are needed to investigate the effect that pack size has on foraging behaviour, and to determine more precisely what the hunting strategy of the African wild dog is in general within these areas. Only then can managers be informed of the management implications of reintroduction prior to release, leading to the development of effective management strategies and ensuring the success of the reintroduction. Failed reintroductions of other carnivores have occurred in the past due to lack of information regarding feeding preferences prior to reintroduction onto small reserves. Lion in Majuma Game Reserve (15km^2) and cheetah in Suikerbosrand Nature reserve (130km^2) due to unforeseen effects on prey populations (Hayward et al. 2007a). Globally this is a problem as reintroductions of large carnivores have been poorly documented (Davies-Mostert et al. 2009), and even less information is available for reintroductions on relatively small reserves. Similar focus should be applied to other reintroduced large carnivore species onto small reserves, in particular to other cursorial hunters, such as hyena and endangered species. More detailed monitoring may also highlight some contrasting behaviours in these populations as compared to those in open systems. With increased knowledge, an improved predictive framework could be developed specifically for the reintroduction of large carnivores onto small, fenced reserves. This would ensure future reintroductions were more successful and the conservation goals for large carnivores achieved

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CHAPTER 3

Predicting carrying capacities and prey of African wild dog reintroduced in a relatively small, fenced reserve: a case study

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Abstract

The success and survival of endangered large predators is dependent on foraging data being used for proper planning for reintroductions and management. Until recently, no accurate tools were available for conservation managers to predict sustainable densities of predators and their expected impact on an area. Here we test the models which predict carry capacities, minimum area requirements, and diet of the African wild dog (*Lycaon pictus*), using independent data collected from a reintroduced population on Karongwe game reserve (KGR). The carrying capacity models showed much variation and the prey preference was not accurate for this case study, as a number of factors were not accounted for including: differences in feeding behaviours and prey preferences of populations on relatively small reserves in relation to previous studies in open systems, variations in prey availability over time, the Allee effect, interspecific competition and interference; and the simultaneous depletion of prey by other predator guild species. These predictive tools need to be modified to account for the limiting factors before they can accurately be used to predict sustainable carrying capacities of African wild dog on relatively small, fenced reintroduction sites. Then they could become essential tools in metapopulation planning and management or more appropriate alternatives can be developed.

Keywords: Carnivora, habitat, *Lycaon pictus*, predator-prey relations, Jacobs Index, optimal foraging, predation preference, testing predictions.

Introduction

Many carnivores are threatened with extinction due to habitat loss, disease, and human persecution (Purvis et al. 2000, Woodroffe & Ginsberg 1998). This has lead to conservation and management of small fragmented populations of large carnivores, and, as an aid to population recovery, reintroduction and translocation methods have been used (Davies-Mostert et al. 2009). Prior to reintroduction, a detailed assessment of the release site is needed to ensure it is suitable for a particular large carnivore. The IUCN (1998) guidelines for reintroductions, detail the evaluation of possible reintroduction sites, stipulating that the site must be within the species' former natural habitat and range, that the population must be able to be sustained for the foreseeable future, and that there should be sufficient carrying capacity of the location to sustain growth of the reintroduced populations. With regard to sustainability of large carnivores, the most critical component to support a population is sufficient ungulate prey (Hayward et al. 2007a). Successful growth of large carnivore populations can potentially impact negatively on the underlying prey base, and many reintroductions have failed as a result of reintroduced predators having severe unforeseen effects on prey populations (Hayward et al. 2007a, Hayward et al. 2007b, Armstrong & Seddon 2007). Prior to release it is essential to have a sound knowledge of the large carnivore's expected diet, and what their overall probable impact will be on the prey population. From this, the carrying capacity, or the number of predators an area can sustain, can be predicted more accurately (Hayward et al. 2009). Any additional knowledge of the feeding behaviour of carnivores which enables conservation managers to more accurately predict the diet and carrying capacity of large predators at reintroduction sites, is vital to the success of reintroductions. This enables managers to ensure an adequate prey base is present to support the reintroduced population, and to highlight when management actions need to take place to avoid over population (Hayward et al. 2009).

One of the most extensive endangered species reintroduction efforts to date was that of the African wild dog in South Africa, through the establishment of an actively managed metapopulation (Davies-Mostert et al. 2009, Gusset 2009). The success of reintroduction programmes like the metapopulation initiative can only be enhanced with predictive models which improve the success these conservation efforts for large carnivores.

Over the past 50 years the African wild dog population has declined dramatically, with current estimates being between 3500 to 5500, mostly in southern and eastern Africa (Fanshawe et al. 1997, Woodroffe & Ginsberg 1997). They occur in lower densities than other competing large carnivores, with, for example, about 16.7 dogs.1000 km^{-2} in Kruger National Park (KNP), compared to around 100 individuals 1000 km^{-2} for lion (*Panthera leo*) and hyena (*Crocuta crocuta*) (Mills & Gorman 1997). Past opinion held that African wild dog could not be maintained in areas smaller than 1000 km^2, thus smaller areas had limited value for their conservation (Woodroffe & Ginsberg 1997). However, successful expansion of African wild dog distribution in South Africa has been largely dependent on reintroductions based on metapopulation approach (Gusset et al. 2008). Furthermore high survival rates of reintroduced adults and offspring were seen even in some reserves smaller than 100 km^2 (Gusset et al. 2008). Electric fences around reserves have been one major factor in the success of these reintroductions, because they offer an effective barrier to reduce predator escapes and limit edge effects from human activities, promoting success (Gusset et al. 2008, Lindsey et al. 2004).

Predictions of carrying capacity of large predators are needed but has limitation as there are many factors that need to be considered to accurately determine what numbers of large predators a reserve can sustain (Somers & Gusset 2009). Such factors to be considered are feeding behaviour and preferences of the predator, prey requirements (Hayward et al. 2009) interspecific competition (Carbone et al. 2005), social system and life history constraints (Somers & Gusset 2009). However, no models are available to conservation managers which incorporate all these factors in their predictions. Models which determine sustainable carrying capacities and minimum area requirements, and predict a carnivores' prey based on prey abundance data, are the only models recently published (Lindsey et al. 2004, Hayward et al. 2007a,b). Hayward et al. (2006) derived relationships between the preferred prey of African large predator guild, including African wild dog, and their population densities, to predict the carrying capacity of South African conservation areas. The lion is the only large carnivore for which the predictions have been tested on to date, and the model was found to be correct for 9 out of 13 test locations (Hayward et al. 2007a*)*. Lindsey et al. (2004) estimated the minimum reserve size required for reintroduction of a pack, based on the area that is needed to sustain an adequate population of the most important prey species in the diet of these dogs, predicting area requirements for a pack of 5 dogs in the north eastern areas of South Africa, of 147 km^2 (Lindsey et al. 2004).

Improved understanding of the feeding ecology of African wild dog on relatively small, fenced reserves is required to enable successful establishment of metapopulations. Contribution to this larger understanding of feeding ecology of African wild dog in relatively small reserves was the motivation for this study on Karongwe Game Reserve (KGR). This is currently the smallest reserve within the present African wild dog metapopulation, which successfully exported 10 dogs to found/supplement other populations. Our aim was to establish whether we could use models to predict the carrying capacities and minimum area requirement for a reintroduced pack on a relatively small reserve. The objectives were therefore (1) to obtain a reliable record of the diet of the pack, (2) to then use these data in calculating the predicted minimum area requirement (Lindsey et al. 2004) to support the pack, (3) to determine the maximum sustainable offtake for each key prey species for KGR and discuss the predicted carrying capacity of this area, and shortfalls of models, (4) predict and discuss the sustainable dog density using various measures of prey biomass using the model of Hayward et al. (2007b), and (5) to test predictions in diet against actual diet as recorded in this study . Then we drew conclusions about the value of such models for conservation management of reintroduced African wild dog populations in relatively small reserves, and the shortcomings of such predictions.

Methods

This study was undertaken at KGR, Limpopo Province, South Africa (24°25’S, 30°61’E) between 12 January 2002 and 12 January 2004. KGR is situated on the savanna lowveld plain, 300 to 500 m a.s.l., with a combination of undulating terrain and rocky outcrops. The Vegetation type is described as Granite Lowveld (SVI3) in the savannah biome of the Lowveld bioregion (Mucina & Rutherford 2006). These areas are characterised by dense thicket to open savanna which is dominated with *Acacia nigrescens*, *Dictrostachys cinerea* and *Grewia discolor* in the woody layer and a dense herbaceous layer dominated by *Digitaria eriantha, Panicum maximum* and *Aristida congesta*. The KGR vegetation map, detailed the dominant vegetation types as mixed woodland (54 %), *Acacia-Combretum* woodland (20 %) and mixed *Acacia* woodland (15 %). Riparian vegetation is represented as 5.5 % on the reserve. This area has a mean annual rainfall of 450 mm p.a. falling in the summer, between October and March. Winters are dry with mean monthly maximum and minimum temperatures reaching 38.0 °C and 3.7 °C for January and July respectively (Mucina & Rutherford 2006.) Artificial water points have been created in the conservancy, some of which are supplied with borehole water, especially during the dry winter months. The 79 km^2 KGR was founded in 1998 by adjacent farms removing fences, and is surrounded by a 65 km electrified boundary fence that effectively prevents outward movement of all large mammal species, excepting leopard (*Panthera pardus*), from the reserve.

In 1999, a free-roaming pack of four male African wild dogs entered through the perimeter fence and became resident. In April 2000, as part of the African wild dog metapopulation management plan, two males where relocated to Madikwe Game Reserve, and the two of these remaining males (WM2 & WM3), with estimated ages of 3 to 4 years, were captured and held in a holding facility (boma) on KGR during previous unsuccessful bonding and reintroduction attempts, over a 14 month period. In November 2001, they were bonded with a 1.5 year-old captive female (WF1) from De Wildt Cheetah Breeding Centre, Brits, South

Africa, prior to their release on 12 January 2002. The female first denned on 9 May 2002 with three female and three male pups. One male pup was killed by an unknown predator on 14 April 2003. In May 2003 the three female yearlings were relocated to Shamwari Game Reserve. The alpha female denned for the second time on 22 June 2003, resulting in five female and three male pups. One female and two male pups died before reaching 3 months, one death being due to lions and the others unknown. At the end of the study in January 2004, five pups had survived to make up a pack of ten, with the original adults and two sub-adults from first litter. It should be noted that the alpha pair and four females from the second litter, were removed shortly after the study, in March 2004, and the remaining pack, consisting of four males. Ultimately the KGR pack was removed from the reserve due to negative perceptions of landowners, due the perceived impact of wild dog on the prey populations of the reserve as found with other populations (Davies-Mostert et al. 2009). There was a concern of depleting prey numbers on KGR, as a consequence of a high density of large predators, to which the wild dog predation did contribute. As a consequence of ecotourism pressure the African wild dog were removed., although based on no direct evidence to suggest they had a disproportional impact on the prey population when compared to the other more charismatic carnivore species such as the lion or cheetah.

During the study the pack was located twice daily, which remained together, using a TR4 receiver and hand held Yagi antennae (Telonics, Arizona). While in captivity one male was fitted with a radio collar (SB2 radio transmitter with D-Cell battery with a 148-152 MHz frequency range), and the pack was followed by a 4X4 vehicle using standard methods, short duration direct observations of between 2 - 15 h, as carried out in of other predator studies (Schaller 1972, Mills 1992, Funston et al. 2001). The African wild dogs at KGR had a bimodal pattern of activity (Niemann 2008, pers. obs., unpublished data, see also Estes & Goddard 1967, Fuller & Kat 1990, Creel & Creel 1995, Rhodes & Rhodes 2004), and monitoring was designed around these times. To test if the pack was active at night, we located the pack between 20:00 and 02:00, and the African wild dogs were inactive on 25 out of 29 (86.2 %) randomly selected nights. Consequently we located the pack approximately 30 min before sunrise and followed them until they settled (the whole pack resting, heads down sleeping, for longer than 30 min), usually 3 h after initial daily movement. We located and followed them again in the early afternoon (from about 15:30) up until they settled again, even if this was after dark. We followed the pack at a distance of 10 to 100 m for the duration of their active period. KGR has a comprehensive road network which the pack frequently used and which made observations easier. On occasions when the pack moved quickly through thick vegetation, we anticipated where they would emerge, and located them with radio-telemetry. If the pack did not appear within 10 min, we tracked them off-road. Activities were recorded chronologically, including behaviour, spatial movement, prey encounters, group composition, hunting behaviour, kill information (species, sex, and estimated age of prey), and interactions with other predators. Data from direct observations (n = 472 kills from 796 attempted hunts, 59.3 % success) provided a reliable record of prey species, age, and sex of kills during the study. We were able to investigate all kills, and when in dense bush we either approached the habituated pack on foot to within 15 m, or returned to the carcass when the pack had moved off. We identified the carcass in the field where possible or we collected unidentifiable remains for later identification by tracker experts. Smaller prey (< 10 kg) may have been missed due to the quick handling time and limitations of navigating in dense vegetation (Rhodes & Rhodes 2004). Of the total of 472 kills recorded, 427 (90.5 %) of the prey species were identified from direct observation of the carcasses. The balance (n = 45, 9.5 %) we noted as being unidentified kills as (1) the prey species could not be identified from the carcass, (2) the pack members had blood on faces and/or an increase in the belly score (Bertram 1975, Ginsberg et al. 1997) but we did not see the remains of the carcass.

Aerial census counts of game were carried out annually on KGR during the drier months of September 2002 and 2003, when visibility was at its optimum. A helicopter with four observers (including the pilot and one data capturer), flew transects in an east/west or west/east direction counting individuals 150 m either side of the helicopter; counts were completed within a day. Estimates of wildlife densities using this method are known to be biased towards species that are more easily observed from the air (Lindsey et al. 2004). Correction factors have been developed to account for these inaccuracies for such species (Owen Smith & Mills 2008). Analysis used both uncorrected (raw) and corrected data to compare the effect it had on the predictions while still remaining comparable with the methods of Hayward et al. (2007a,b) and Lindsey et al. (2004), which used only uncorrected abundance figures (Table 1).

The following method (Lindsey et al. 2004) was used to calculate minimum area requirements of African wild dog, and evaluate whether the current pack on KGR was sustainable within the 79 km^2 reserve. Firstly we calculated minimum sustainable yield (Caughley 1977) as :

$$\mathbf{MSY = (r_m . K/4)}$$

Where MSY is equivalent to N_{prey} (the number of individuals of a prey species killed per year by a pack of dogs) and K is equivalent to N_{min}, the minimum population size required to support the predation by a pack of African wild dog of a given size per year. Therefore (following Lindsey et al. 2004):

$$\mathbf{N_{min} = \frac{4\ N_{prey}}{r_m}}$$

Where $\mathbf{r}_m$ is the intrinsic growth rate calculated using the following equation and using the body mass of each species as 3/4 of adult female body mass of each species based on body mass given in Hayward et al. (2007a):

$$\mathbf{r_m = 1.5\ M^{-0.36}}$$

To then determine the minimum area required to support N_{min} for a given prey species, the prey density for that area was divided by N_{min} (Lindsey et al. 2004):

$$\textbf{Minimum Area (km}^{2)}\ = \frac{\mathbf{N_{min}}}{\textbf{Prey density/ km}^2}$$

As the area of the reserve (79 km^2) is known, it is possible to determine the maximum N_{prey}, sustainable offtake for prey species on KGR and thus the carrying capacity for the reserve. The equation was transformed as:

$$\mathbf{N_{prey} = \frac{(\text{Minimum area x Prey density x } r_{m})}{4}}$$

Prey density was calculated using the average prey abundances for the two study years. Once N_{prey} for each species was determined, the sustainable biomass available was calculated (kg $annum^{-1}$) by multiplying N_{prey} by the edible body mass of each species. Body mass of each species was calculated, in all analyses that follow, as being 3/4 of adult female body mass of each species based on body mass given in Hayward et al. (2007a). The edible biomass was calculated as being 60 % of the total mass (Bothma 1996). The carrying capacity of KGR for African wild dog was calculated by dividing the edible biomass by the mean annual consumption rate per wild dog feeding unit (WFU) for the two study years (Chapter 2) totalling 1144 kg p.a.

The second method used to determine the carrying capacity of KGR predicts African wild dog densities (Log-transformed densities) using (a) the total biomass of the preferred species (Hayward et al. 2007a) and (b) the biomass of the preferred species' weight range (16 - 32 kg and 120 - 140 kg) in the analysis (Hayward et al. 2007a). Carrying capacities were calculated as in Hayward et al. 2007a:

(a) Log10 y = -2.780 + 0.470 Log x (using preferred species total biomass)
(b) Log10 y = -3.012 + 0.494 Log x (using biomass of prey in preferred weight range)

Note that the text associated with Table 4 of Hayward et al. (2007a) was found to be incorrect and should be interpreted as: x representing the various measures of prey biomass/km^2 , not y. The available prey biomass (kg km^{-2}) was calculated by multiplying the prey densities by the mass of each preferred species (as detailed by Hayward et al. 2006). The total biomass for the preferred prey or the preferred weight ranges was put into the regression equations above to calculate the predicted African wild dog densities. Predictions were calculated for each study year separately.

To test the predictions of the prey of the pack on KGR we calculated the Jacobs Index (Jacobs 1974) for each species using the preference indices calculated in Hayward et al. (2006) and the prey abundance data from KGR for the two separate study years. The predicted number of kills was solved as (Hayward et al. 2007a):

$$\mathbf{R_i = (\boldsymbol{D_i p_i} + \boldsymbol{p_i})/\ (1\text{-}\ \boldsymbol{D_i} + \boldsymbol{2D_i\, p_i})\ \ x\ \ \sum \boldsymbol{K}}$$

Where R_i is the predicted number of kills of a species 'i' when we observe a total of $\sum k$ kills, D_i is the Jacobs Index value of species 'i' calculated by Hayward et al. (2006) using data from 18 studies other than on KGR, and p_i represents the proportional abundance of prey species 'i' at a site. $\sum k$ is used as a constant and is the total observed kills at a site. The predicted diet was then compared with the observed kills using the G-test (Zar 1996).

To verify the generality of this approach for African wild dog in a relatively small fenced reserve, we repeated the analysis using published data from Shambala Game Reserve (Rhodes & Rhodes 2004). In April 2002, seven African wild dogs were released onto this 83.6 km^2 reserve. In May 2002, ten pups were born, of which five survived to the end of their study in January 2003 (Rhodes & Rhodes 2004).

Results

Given the prey profile of the KGR African wild dog pack, using the $\boldsymbol{N_{prey}}$ method with uncorrected prey abundance data, the observed average pack size of 5.08 and 7.06 WFU

(Chapter 2) for 2002 and 2003 study years respectively was unsustainable on KGR overall (Tables 2 and 3). In 2002, offtake was sustainable for all prey species except waterbuck (*Kobus ellipsiprymnus*) and kudu (*Tragelaphus scriptus*), as the preys' sustainable area requirements were greater than the reserve area of 79 km^2 (Table 1). In 2003, with an average of 7.06 WFU, all species except wildebeest (*Connochaetes taurinus)* and warthog (*Phacochoerus aethiopicus)* required larger areas to be sustained (***N_{prey}***), and bushbuck (*Tragelaphus scriptus)* showed an elevated area requirement of 323 km^2 to sustain the current offtake (Table 1). If only the two most important prey species represented in the diet (Chapter 2), impala (*Aepycerus melampus*) (proportion of 60.6 % found in the diet) and bushbuck (proportion of 7.4 %) were used in analysis (as by Lindsey et al. (2004)), the minimum area requirements were satisfied in 2002, but not in 2003. When the correction factor for counting was incorporated into the analysis, the offtake was sustainable for this size of reserve for all species in 2002 (Table 2) and all except bushbuck in 2003 (Table 3).

N_{prey} for each species for KGR was calculated, and all African wild dog offtake was higher than the sustainable level calculated with this method, except for kudu (Table 4). However, overall, the edible biomass available of N_{prey} of all species was 7255 kg per annum with no correction factor and 12065 kg per annum using the correction factor (Table 2). Using the average daily consumption rate of 3.13 kg per day (1144 kg p.a.) as calculated for the KGR pack (Chapter 2), the maximum number of WFU that KGR can sustain was found to be 6.34 based on uncorrected census data or 10.6 using the correction factor for census data.

The mean predicted density of 3.3 (SD ± 0.56) African wild dog was calculated according to the methods of Hayward et al. (2006), using preferred prey species and preferred weight range for the 79 km^2 KGR. Variation occurred between the study years with the predictions for 2002 being consistently higher than 2003 when using both methods, and the results using a correction factor showed higher carrying capacities (Table 5). Using the preferred prey species method, the maximum density predicted for KGR was 3.3 dogs (uncorrected data) and 4.3 dogs (corrected data) in 2002.

The model predicting the African wild dog diet for KGR did not accurately predict the observed number of kills for each prey species for either study year, whether using uncorrected (2002: $G_{11} = 37.08$, $P < 0.01$; 2003: $G_{11} = 34.57$, $P < 0.01$) or corrected census data (Table 1). Removing from the analysis the grey duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) , both of which are difficult to count, and the bushpig (*Potamochoerus porcus)* and red hartebeest (*Alcelaphus buselaphus*), both of which were infrequently killed, the model still did not predict the observed kills (corrected data: 2002: $G_7 = 22.22$, $P < 0.05$; 2003: $G_7 = 19.329$, $P < 0.05$; uncorrected data: 2002: $G_7 = 16.17$, $P < 0.05$; $G_7 = 25.55$, $P < 0.05$). When kudu was removed from the analysis, the model then predicted the observed prey using only 2002 uncorrected data ($G_6 = 9.44$, $P > 0.10$) and 2003 corrected data ($G_6 = 12.47$, $P > 0.05$). Kudu was observed to be killed less frequently than expected.

When the data collected by Rhodes and Rhodes (2004) in Shambala Game Reserve were tested with the same predictive model, it did not predict the observed kills ($G_{13} = 25.30$, $P < 0.05$). However, when removing kudu as an outlier, the model did predict the observed kills on Shambala Game Reserve ($G_{13} = 17.45$, $P > 0.10$) (Table 6). Kudu was observed to be killed more frequently than expected.

Table 1: *Potential prey species of African wild dog on KGR in 2002 and 2003, their Jacobs Index values (from Hayward et al. 2006), their abundances based on aerial game counts (Chapter 2), and the number killed predicted by the model (Pred.) and actually killed (Obs.) using uncorrected and corrected (Owen-Smith & Mills 2008) abundance data.*

		2002					**2003**				
		Uncorrected[b]		**Corrected** [c]			**Corrected**		**Uncorrected**		
Prey Species	**Jacobs Index**[a] **(*D*)**	**No.**[d]	**Pred.**[e]	**No.**	**Pred.**	**Obs.**[f]	**No.**	**Pred.**	**No.**	**Pred.**	**Obs.**
Impala	0.06	1782	125	2976	122	**145**	1252	124	2091	124	**141**
Bushbuck	0.27	127	14	381	24	**7**	56	16	168	9	**28**
Waterbuck	-0.35	205	7	342	7	**6**	185	9	309	9	**17**
Warthog	-0.52	266	6	665	9	**18**	119	6	298	4	**4**
Duiker	0.15	18	2	18	1	**13**	0	0	0	0	**8**
Kudu	0.35	144	19	259	20	**10**	140	28	252	26	**11**
Steenbok	-0.34	0	0	0	0	**5**	0	0	0	0	**0**
Hartebeest	-0.56	4	0	7	0	**0**	4	0	4	0	**2**
Wildebeest	-0.7	321	4	385	3	**2**	298	4	358	6	**1**
Bush pig	-1	0	0	0	0	**1**	0	0	0	0	**1**
Nyala	-0.48	27	1	54	1	**0**	30	1	60	1	**0**
Zebra	-0.88	206	1	247	1	**0**	190	1	228	1	**0**

[a] Jacobs Index values for prey species of African wild dog as recorded in Hayward et al. (2006).
[b] Using uncorrected annual game census data.
[c] Using annual game census data corrected for species detectability (see methods).
[d] Abundance based on helicopter-derived total counts.
[e] Number of kills predicted by the model.
[f] Number of kills actually observed.

Table 2: *Sustainability of the African wild dog pack on KGR.. Minimum predicted sizes of prey populations, and areas required to support predation by an average pack size of 5.08 WFU in 2002*

				Uncorrected data [a]		Corrected data [b]	
Prey species	N_{prey} [c]	r_m [d]	N_{min} [e]	**Prey density[f] km^{-2}**	**Area (km^2) [g]**	**Prey density km^{-2}**	**Area (km^2)**
Impala	145	0.44	1316	22.5	58.5	37.5	35.7
Kudu	10	0.26	156	1.8	**85.9** [h]	3.3	47.7
Waterbuck	18	0.23	316	2.6	**122.4**	4.3	73.3
Wildebeest	2	0.26	31	4.1	7.7	4.9	6.4
Warthog	18	0.38	189	3.4	56.4	8.4	22.5
Bushbuck	7	0.49	57	1.6	35.8	4.8	11.9

[a] Using uncorrected annual game census data.
[b] Using annual game census data corrected for species detectability (see methods).
[c] Estimated number of individuals of a prey species killed p.a. by the KGR pack.
[d] Estimated intrinsic growth rate of the prey population.
[e] Estimated minimum size of prey population required to support predation by a pack p.a.
[f] Actual prey density on KGR calculated from corrected aerial count data
[g] Predicted area of reserve that would be required for that prey species to be sustained under offtake from the African wild dog pack.
[h] Area requirements exceeding the reserve's area (79 km^2), shown in bold.

Table 3: *Sustainability of the African wild dog pack on KGR.. Minimum predicted sizes of prey populations, and areas required to support predation by an average pack size of 7.06 WFU in 2003*

				Uncorrected [a] data		Corrected data [b]	
Prey species	N_{prey} [c]	r_m [d]	N_{min} [e]	**Prey density** [f] **km^{-2}**	**Area** [g] **(km^2)**	**Prey density km^{-2}**	**Area (km^2)**
Impala	141	0.44	1282	15.8	**81.1** [h]	26.4	48.6
Kudu	11	0.26	172	1.8	**97.5**	3.2	54
Waterbuck	17	0.23	299	2.3	**128.2**	3.9	76.7
Wildebeest	1	0.26	16	3.8	4.2	4.5	3.5
Warthog	4	0.38	42	1.5	28	3.8	11.2
Bushbuck	28	0.49	229	0.7	**322.6**	2.1	**108.2**

[a] Using uncorrected annual game census data.
[b] Using annual game census data corrected for species detectability (see methods).
[c] Estimated number of individuals of a prey species killed per year by KGR pack.
[d] Estimated intrinsic growth rate of the prey population.
[e] Estimated minimum size of prey population required to support predation by a pack p.a
[f] Actual prey density on KGR calculated from corrected aerial count data.
[g] Predicted area of reserve that would be required for that prey species to be sustained under offtake from the African wild dog pack.
[h] Area requirements exceeding the reserve's area (79 km^2), shown in bold.

Table 4: *Maximum sustainable offtake (*N_{prey}*) and sustainable edible biomass of African wild dog in KGR (79 km*^{2}*) using uncorrected and corrected prey abundance data. (see Table 2 for explanation of columns)*

		Uncorrected data			Corrected data		
Prey species	**Biomass**	**Prey density km^{-2}**	**N_{prey}[a]**	**Edible Biomass[b] (kg)**	**Prey density km^{-2}**	**N_{prey}**	**Edible Biomass (kg)**
Impala	30	19.1	167	3011	31.9	279	5026
Kudu	135	1.8	9	737	3.2	16	1327
Waterbuck	188	2.5	11	1252	4.1	19	2091
Wildebeest	135	3.9	20	1607	4.7	24	1929
Warthog	45	2.4	18	495	6.1	46	1237
Bushbuck	23	1.2	11	151	3.5	34	453
Total				**7255**			**12065**

[a] Estimated number of individuals of a prey species that can be sustainably killed p.a.

[b] Estimated edible biomass of a prey species that can be sustainably removed p.a.

Table 5: *Carrying capacity predictions for African wild dog in KGR using uncorrected and corrected prey abundances in the analyses*

	Preferred prey species method [a]			Preferred weight range method [b]		
Study year	**Correction factor** [c]	**Density** [d] **(Dogs. km^{-2})**	**WFU KGR** [e]	**Correction factor**	**Density (Dogs. km^{-2})**	**WFU KGR**
2002	No	0.042	3.31	No	0.036	2.86
	Yes	0.054	4.31	Yes	0.045	3.56
2003	No	0.037	2.91	No	0.033	2.6
	Yes	0.048	3.78	Yes	0.04	3.19

[a] Measure of prey biomass using preferred species as detailed by Hayward et al. (2006).
[b] Measure of prey biomass using preferred weight range as detailed by Hayward et al. (2006).
[c] Indication of use of the a correction factor which corrects annual game count census data depending on species delectability (see methods).
[d] Predicted sustainable density of African wild dog per km^2.
[e] Predicted sustainable WFU for the KGR (79 km^2).

Table 6: *Potential prey species of African wild dog on Shambala Game Reserve, their Jacobs Index values (from Hayward et al. 2006), their abundances based on aerial game counts (from Rhodes & Rhodes 2004). (See Table 1 for explanation of headings)*

Prey Species	Jacobs Index (*D*)	No.	Pred.	Obs.
Impala	0.06	540	21	7
Bushbuck	0.36	2	0	0
Waterbuck	-0.35	50	1	3
Warthog	-0.52	120	1	6
Duiker	0.15	11	1	0
Kudu	0.35	225	14	34
Steenbok	-0.34	6	0	0
Wildebeest	-0.7	221	2	3
Nyala	-0.48	15	0	1
Zebra	-0.88	235	1	0
Blesbok	-0.55	50	1	2
Bush pig	-1	15	0	0
Duiker	0.15	11	1	0
Eland	-0.71	77	0	0
Hartebeest	-0.56	8	0	0

Discussion

The predicted carrying capacities of KGR for African wild dog varied considerably between methods, and also within methods, depending on whether the abundance data had been corrected using the correction factor of Owen-Smith & Mills (2008). The method of Lindsey et al. (2004) predicted almost double the carrying capacity as that predicted by the method of Hayward et al.(2007b). Such contrasts highlight the need for more research and the caution needed when predicting carrying capacities of populations on relatively small reserves. Also, the prey preference model Hayward et al. (2007a), did not predict the observed number of kills on either KGR or Shambala Game Reserve by African wild dog. However it should be noted that the impact of individual differences in behaviour and selectivity, particularly for a highly social species may have had a profound effect on the results as would the small sample size is used. Individuals can substantially bias the decisions of the pack and due to the variation amongst individuals, it can result in substantial bias in interpretations. In contrast to behaviour as described in the literature, the KGR dogs were found to be opportunistic feeders, with limited prey preference and did not use rate maximizing strategies (Chapter 2). In this case study, the higher carrying capacity predicted in the method of Lindsey's et al. (2004), may give a more representative carrying capacity for the KGR, and other reserves with packs which may have similar feeding behaviour. This first method does not incorporate the pack's prey preference, and assumes prey were killed in proportion to their relative abundance, as was found in this study (Chapter 2). However, this method would be less appropriate for packs which are found to be rate maximisers (Creel & Creel 2002, Krűger et al. 1999), or which exhibit strong preferences for certain species (Hayward et al. 2006), as any preference elevates minimum area requirements predictions (Lindsey et al 2004). This effect was apparent in this study in 2003, when for the first time the KGR pack showed a significant preference for bushbuck (Jacobs Index 0.68, Chapter 2), which elevated the minimum area requirement to 323 km^2 (18.2 km^2 using correction factor) for an average pack size of 7.06 WFU. So according to this method the founder pack of 3 adults was a sustainable number of individuals for KGR for reintroduction and management intervention would be needed to prevent the pack size going higher than ten individuals or supplementation of prey would be needed to sustain the population. In March 2004, the alpha male and female plus 4 female pups were relocated due to perceived over-utilization of the prey by the predators on KGR. So the remaining four males would have been sustainable according to both models, as a single sex group the population would have remained constant. However, this group structure would have contributed little to the conservation of wild dogs, except for stimulating ecotourism and awareness, and thus were removed.

The method by Hayward et al. (2006) was developed to determine the prey preference of African wild dog, this is a comprehensive evaluation of 24 assessments of African wild dog prey preference (Jacobs Index), from 18 studies from throughout the African wild dog distributional range (Hayward et al. 2006) However, most of the data were obtained from open systems. Only five of the studies: Hluhluwe – Umfolozi (960km^2), Madikwe (750km^2), Pilanesberg National Park (500 km^2), Shamwari Game Reserve (250km^2), and Shambala Game Reserve (87.2 km^2) involved reintroduced populations of African wild dog into fenced reserves, and only one of the five represented a reserves of < 250 km^2 . As the KGR pack showed no preferences overall and killed opportunistically, we suggest this model should be avoided as an estimation of carry capacity for this reserve. A revised mean Jacobs Index for small reserves displaying different feeding behaviours needs to be calculated and incorporated into the model to develop a more robust tool than one used at present to predict prey numbers more accurately. Both methods show some common limitations as their prediction of carrying capacities of African wild dog is based on prey availabilities. Firstly that the prey availabilities incorporated into the calculations are taken at the end of the dry season, and for two particular years. The prey population size can vary as environmental conditions change, which will alter the carrying capacities (Lindsey et al. 2004). Number of prey will decrease during times of drought, and their poor condition improves hunting, such that African wild dog numbers often increase (Mills 1995). African wild dog generally select impala in poor condition (Pole et al. 2004), and if certain species are relatively more susceptible to loosing condition in times of drought, African wild dog preferences may change accordingly. Therefore, predicted carrying capacities based on a single year's prey counts, or multiple years' during good conditions, should be interpreted cautiously. Historical trends of prey numbers and rainfall need to be incorporated into the calculations of available prey, to give a relatively more accurate assessment of the sustainable carrying capacities. It should be noted that prey population trends and dogs' preferences need to be monitored after a reintroduction to continuously assess the pack's sustainability, and to manage the pack and its prey appropriately, in line with management objectives (see Gusset et al. 2008). If management had not decided to remove the KGR pack it would have been interesting to monitor the feeding behaviour of the pack beyond the study period, to determine if the pack developed preference or altered their feeding strategies. As results in this study may well change over time as prey populations fluctuated and pack size varies.

Another point to highlight is that the use of both corrected and uncorrected prey abundances (Owen-Smith & Mills 2008) in the analysis delivered contrasting results in all methods. The correction factor elevated abundance value for prey species that are less easily counted from the air, increased values of available biomass, and predicted carrying capacities for African wild dog. Using the correction factor gave a more accurate abundance value, and where the correction factor is not used, predictions underestimate the carrying capacity for these dogs.

The ability to predict diet and carrying capacity of predators at reintroduced sites based on feeding behaviour alone will improve success rates by ensuring there is adequate prey base to support the reintroduced population (Hayward & Somers 2009), but this fails to address other factors. Interspecific competition and the predator's social systems and life-histories, will have a profound effect on the carrying capacities of population and are vital to be considered (Hayward & Somers 2009. Carbone et al. 2005, Courchamp et al. 2000, Courchamp et al. 2002).

Interspecific competition, can affect the ranging behaviour of a pack (Mills & Gorman 1997) due to interference and competition through the direct killing and kleptoparasitism by lion and spotted hyena (*Crocuta crocuta*) (Creel & Creel 2002). The African wild dog is one of the smallest large vertebrate prey specialists within the African carnivore guild (Creel & Creel 2002), and are susceptible to competition by the larger members. African wild dog avoid areas rich in prey, where there are a high densities of lion and spotted hyena (Creel & Creel 1995, Mills & Gorman 1997, Van Dyk & Slotow 2003). The density of lions was around 101/1000 km^2 at the time of the study on the KGR, which is a similar figure to that in the Kruger National Park (Mills & Gorman 1997). This density of KGR lions is likely to have negatively affected the movements patterns of the pack, restricting them to areas with less available prey. Future research into such interspecific interaction between guild predators is needed. Kleptoparasitism by hyena was found (Carbone et al. 2005) to reduce the time African wild dog packs had access to their kills, particularly when the pack of dogs was small. In situations where the hyena densities are high and pack size smaller, kleptoparasitism may have a severe impact on the survival of wild dogs (Carbone et al. 2005). Another factor related to the co-existence of other African carnivore guild members present within an area, is the combined factor of depletion of prey, which neither model takes into account. The study of Hayward et al. (2007a) shows an overlap of prey preference for impala and bushbuck by leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and African wild dog, and for kudu by hyena and African wild dog, but this is not incorporated into the models' predictions for carry capacities. Depending on the densities of other guild members, the predicted number of African wild dog recommended for reintroduction into a particular sized area would be reduced significantly, and even found to be unsustainable if other predators were present within an area. For a more holistic and realistic approach to integrated predator management, more studies on interspecific guild feeding rather than to isolated feeding are needed to determine carrying capacities.

Often the social behaviour of carnivores is disregarded by wildlife managers during reintroductions (Hayward & Somers 2009). If the social behaviour of a carnivore is not considered in carrying capacity estimates, this could jeopardise the survival of the population and the success of a reintroduction. The African wild dog is an obligate co-operator, and suffers from inverse density dependency due to the need for helpers in the pack to ensure their collective survival and reproduction (Courchamp et al. 2000). Social compatibility of the reintroduced population prior to release has been shown to be important (Graf et al. 2006), as well as the Allee effect after release (Somers et al. 2008, Somers & Gusset 2009). Allee effect at a pack level, is where a critical pack size, typically around five adults (including alpha pair and helpers), is needed, as below which the capacity of the pack to maintain itself seriously compromised (Courchamp et al. 2002). These factors have to be seriously considered and relocation of a pack below or near this critical number, as predicted in Hayward et al. (2006) for this pack, should be discouraged based on sociality concerns. The opinion is that below five individuals the pack cannot successfully raise pups to independence due to the needs of this cooperative hunter in areas such as defence of kills, pup guarding and feeding (Courchamp et al. 2000). However, it should be noted that the founder population of the KGR pack consisted of only three adults, an alpha pair and one helper, which successfully bred 6 months after release, raising five of six pups born to 12 months old before relocation of three females to Shamwari Game Reserve (see Appendix C). Further, in June 2003 (when the pack consisted of three adults and two yearlings), they raised five of eight pups born to yearling age before relocation of four females to Kwandwe Game Reserve. Although management intervention relocated some off-spring (See Appendix D), this pack was one of the few packs of the metapopulation to successfully produce pups for relocation, despite the lower than critical number in the founder population. Although only a case study of a single pack, this challenges the current opinion, and needs to be investigated further.

Management implications

Tools to predict carrying capacities and prey of predators, based on abundance and preferences, are invaluable to conservation managers today (Hayward et al. 2007b), but they have limitations that need to be considered. Encouragingly, our findings seem to support the suggestion that the potential for African wild dog reintroduction may be larger than previously thought, and reintroduction could occur on reserves smaller than the average size of the home range of African wild dog (Lindsey et al. 2004). However, caution should be exercised in the interpretation of results of carrying capacity models that do not take into account the specific circumstances of a reserve (Morgan et al. 2009), or prey and predator community. Also models which are based solely on feeding behaviour of carnivores, not considering other important limitations and stresses on a reintroduced population such as interspecific competition and social behaviour requirements, should be used with caution. Interspecific competition and the simultaneous take off of prey by other members of the African carnivore guild will have a profound effect on the prediction, lowering the carrying capacity. If the essential social requirements of the pack pre and post release of a reintroduction (Somers & Gusset 2009, Courchamp et al. 2000) were considered in the models, then the carrying capacities would be increased to ensure the success of the reintroduction and survival of the population. Both these models use feeding preference alone to predicted carrying capacities of African wild dog. They predicted low carrying capacities for KGR, which the pack size on KGR was near to or, in the case of Hayward et al. (2007b), exceeded the recommended population. Although more information is needed, we predict that, if interspecific competition was taken into account, the predictions are likely to decrease the recommended carry capacity further, which would compromise the critical number, vis. an Allee effect, needed to survive, and thus predicting that the KGR pack is unsustainable. As a consequence we recommend that neither should be used by conservation managers at this time as a tool to predict carrying capacities for wild dog in relatively small reserves.

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CHAPTER 4

General Discussion

The broad aim of this study was to investigate the feeding ecology of a pack on a small fenced reserve, to contribute to the assembly of descriptive accounts of the feeding behaviour of African wild dog reintroduced into relatively small reserves. Also, we aimed to determine if this population showed similar patterns in feeding ecology to those previously recorded in Pilanesberg National Park (Van Dyk & Slotow 2003) and Shambala Game Reserve (Rhodes & Rhodes 2004). Using the feeding data presented in Chapter 2, the predictive prey preference models (Hayward et al. 2007a) were tested to determine their suitability as predictive tools for packs reintroduced into small reserves. With these findings, we hope to enhance current knowledge about the reintroduction of African wild dogs and assist in predicting management strategies to achieve not only the management objectives, but also, importantly, the conservation objectives concerning this species and other large carnivores.

The recent studies in relatively small reserves showed a possible shift from small or medium sized prey toward larger species, through the use of fences as hunting aids (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004, Davies- Mostert et al. 2009). However, the findings of this study do not follow this pattern with regard to larger prey in the diet, but this study did find that the pack use the fence as a hunting aid. This study found that this pack of African wild dog feed opportunistically rather than adopting a rate maximising foraging strategy, feeding on a similar prey base to studies in larger open systems (Mills & Biggs 1993, Mills & Gorman 1997).It should however be noted that this is only a single case study, and the contrasting results found here may not be good representation of populations in relatively small reserves and more detailed evaluations of reintroductions in these areas are needed to determine if there is in fact a common feeding behaviour of these reintroduced populations. Using this information, managers can undertake more appropriate evaluations and management plans can then be implemented for small, fenced reserves to ensure success in future reintroduction efforts and the conservation of the African wild dog in South Africa.

After a two-year continuous study, the diet of the pack was found mainly to include small to medium sized prey, although larger species, such as kudu and waterbuck, were included in the diet. Unlike results in previous studies, the majority of species were killed in relation to abundance, with no strong prey preferences, or tendency toward rate maximizing foraging techniques (Krűger et al. 1999). This population does not follow same pattern as other packs studied in relatively small, fenced reserves with regard to high proportions of larger prey species killed. However, there was evidence of the use of the barriers as effective hunting tools, but not as a tool to assist in killing larger prey species as found in Pilanesberg National Park and Shambala Game Reserve (Van Dyk & Slotow 2003, Rhodes & Rhodes 2004, Davies- Mostert et al. 2009). There are a number of suggested reasons that could explain why our results are contrary to our expectations regarding preference for larger prey. These include possible biases in data collection in the two previous studies, where the majority of data was collected along the fence line, possibly exaggerating this pattern. Also the pack sizes in KGR were smaller than those in previous studies and large pack sizes are known to increase hunting success and mass of prey killed (Creel & Creel 1995) which may account for the smaller prey items selected for. We must also take into account the fact that these results only represent a small sample size and the founding population was only three. As a result the impact of individual differences in behaviour and selectivity, particularly for a highly social species like African wild dog could have an effect on the results. One individual can substantially bias the decisions of the pack, which could result in substantial bias in interpretations.

It is interesting to note that results from studies carried out on reintroduced populations of a closely related canid and other large carnivore species may lead us to possible explanations for the variations found in this study. The reintroduced population of wolf (*Canis lupis)* in the Yellowstone National Park, USA, showed a strong preference for elk (*Cervus elaphus),* preying on calves in early winter and cows throughout the year (Smith & Bangs 2009). However the pattern of prey selection of the wolves changed over time (Smith & Bangs 2009) which was attributed to drought conditions, behaviour learning by elk and intraspecific competition (Smith & Bangs 2009). It was found that there were variations in prey preferences even within regions of the park where climate and prey densities varied. Here the wolves were found to adapt their prey preferences to these different conditions. Flexibility in feeding ecology was also observed in other large carnivores, including the jaguar (*Panthera onca*) which tends to feed relative to abundance of prey. The jaguar has also been found to have a high degree of behavioural and ecological flexibility (Kelly & Silver 2009), subsisting on large prey (>20kg) in some and medium sized prey (10-20kg) in other areas, and even feeding on small prey in marginal areas. Likewise the Australian dingo (*Canis dingo*) have a wide prey range from grasshoppers to swamp buffalo (*Bubalus bubalis*), but a preference for prey closer to its own size (Dickman 2009). They have flexible hunting strategies, hunting alone for small prey or working cooperatively to hunt and kill larger prey (Dickman 2009). All these findings highlight the need for long-term monitoring to determine if differences seen in this study regarding prey preference and foraging behaviour of the KGR pack when compared to other studies on African wild dog, are in fact simply due to temporal differences, small pack size, and/or behavioural and ecological flexibility. With more detailed long term information we may find that the KGR pack does indeed show distinct differences to all previous studies or either showed more tendencies towards the feeding preferences in other small reserves or toward open systems.

Interestingly it seems that the use of barriers as a hunting tool is not exclusive to the African wild dog in small fenced reserves. Wolves have also been found to use landscape features as barriers, such as streams, valleys bottoms and roads to facilitate kills. Here kills were more strongly associated with landscape features rather than elk density (Smith & Bangs 2009). More monitoring on African wild dog in both enclosed and open systems may reveal that the use of barriers is not restricted to relatively small fenced reserves and should be given priority for further studies.

The predictive model of prey preferences (Hayward et al. 2007a) for large carnivores was tested and compared with the actual diet composition found in the KGR and the Shambala Game Reserve study (Rhodes & Rhodes 2004). Although the model of Hayward et al. (2007a) was found to be accurate for lion (*Panthera leo*), it was found to be unreliable for the case study presented here and in Shambala Game Reserve. Factors that may limit the applicability of the model include the combined effect of KGR pack showing no strong species preference in the diet unlike those used to develop the model, variations in prey availability over time, the fact that no consideration for interspecific competition and interference was made, and the fact that the simultaneous depletion of prey by other guild predators was not considered. If, in general, a pattern in relatively small reserves is found with regard to prey preferences and feeding behaviour of populations of African wild dog as compared to more open systems, then this predictive tool needs to be modified to account for variations, before it can accurately be used to predict the diet of large predators on relatively small, fenced reintroduction sites. I also propose that other large carnivore species reintroduced into small enclosed reserves may be found also to show feeding behaviours which differ from previous studies in more open systems, as suggested by Bissett (2004) in cheetah (*Acinonyx jubatus*). Further monitoring and evaluation of other reintroduced large carnivores on relatively small reserves, should also be considered, with specific reference to diet and expected impact on the prey population, before guidelines for their reintroduction are finally determined. It is imperative that as far as possible more accurate prior understanding of feeding ecology is available to conservation managers, primarily to decide more accurately whether a reintroduction is a viable option, and secondarily to enable pre-planning of management to avoid *ad hoc* and reactive decisions. Therefore, recommendations for the reintroduction of all large predators within relatively small reserves, particularly endangered species, should be re-evaluated to ensure the most appropriate guidelines and decisions are being made.

However, another problem facing conservation managers is how to determine the carrying capacity for reintroducing a population of large carnivores. There are two common and key questions for managers (1, 3) put forward by Armstrong and Seddon (2007) for priority reintroduction biology studies. The first of these is the size the release group should be, the second concerns what resources are needed for persistence of the reintroduced population to ensure it remains sustainable based on available resources. The common management approach is to estimate carrying capacity for a specific area based on resource availability and quality (Hayward et al. 2007b). New predictive tools, appropriate for large carnivores, developed by Hayward et al. (2007b) and Lindsey et al. (2004), apply predator-prey relationships to predict predator carrying capacities and area requirements. Using the data presented in Chapter 2, we were able to determine the carrying capacities the models predicted for the KGR. The predictions for KGR varied considerably between the two different methods and also within methods depending on whether a correction factor was used (Owen-Smith & Mills 2008). This emphasises the importance of corrected game count figures being used in calculations to give more accurate predictions. Also, both the methods warrant further attention before they should be used as decision making tools regarding reintroductions. The ability to predict diet and carrying capacity of predators at reintroduced sites based on feeding behaviour alone, will improve success rates of reintroduction. As it will ensure there is adequate prey base to support the reintroduced population (Hayward & Somers 2009). However, these models fail to address other factors, which will have a profound effect on the carrying capacities of population, and which are vital to success. These include interspecific competition and the predator's social system and life-history. Suggestions for further investigation would be to look at the specific impact of the pack on the prey populations of KGR to see, if the recommendations of carrying capacities are indeed appropriate. Simultaneous data on kills made by the other guild predators on KGR, during the same time period as the African wild dogs would need to be analysed in order to determine the direct impact of the African wild dog on the reserves prey population. An analysis on this scale is beyond the scope of this study but remains a possibility for future publications. Also if management did maintain the pack number below the recommended critical number of five then intense observations on how this affects the breeding success and survival of the pack on small reserves would be needed. The importance of demographic and genetic considerations in the success and survival of the reintroduced population was also highlighted in studies on other reintroduced populations of other large carnivores, including bears (*Urus Americanus*, Clark 2009) and the Eurasian lynx (*Lynx lynx*, Linnell et al. 2009). Many reintroductions of the Eurasian lynx involved very small numbers in the founder population which raised issues of long term genetic viability of the population.

The main limitation of this study was the small sample size of one reintroduced pack. However, as recommended (Gusset et al. 2008, Armstrong & Seddon 2007) we hope that this study will be combined with others to establish what determines a successful reintroduction, and to assist in the development of appropriate management decisions regarding metapopulations. An improvement in the methods would have been the use of the additional indirect method of scat analysis in assessing diet (Krűger et al. 1999, Bissett 2004). Scat analysis allows for continuous determination of feeding habits (Krűger et al. 1999), reducing the bias towards larger prey species associated with short-term observations (Mills 1992). Another limitation of the study was the lack of analysis of spatial movement, when determining the precise prey available to the pack. African wild dog are known to be limited by competition from lions and spotted hyenas (*Crocuta crocuta)* (Creel & Creel 2002). Lions in particular may limit African wild dog numbers in areas of high prey density (Mills & Biggs 1993) and as a consequence sub ordinate predators (African wild dog and cheetah) use refuge habitat to avoid competitive interactions (Hayward et al. 2007c). Within the enclosed area of the KGR where lions are present, their presence influences the African wild dog movements (Niemann, pers. obs., unpublished data), and this may exclude them from specific areas, including areas of high prey density. This competitive dominance has been observed in another large carnivore, the Australian dingo, in the relation to the presence of foxes and cats. The dingos were found to have a negative effect the subordinate carnivores densities and movements through interference competition and dietary overlap (Linnell et al. 2009). Prey availability data presented in this study were calculated from annual game counts of the reserve, not the availability specifically of prey related to the pack's spatial movements. Spatial separation of African wild dog and lion has been observed in KGR with the pack seeming to avoid areas of lion activity (Niemann pers. obs.). A more accurate indication of the prey preference and foraging strategies may have been determined by incorporating data on the actual prey available to the pack. This could have been done by matching distribution maps of prey by using the method of quarterly road transects (Hirst 1975), overlaid by the actual home ranges of the pack. The absence or presence of competing dominant carnivores (lion and spotted hyena) could have had a profound effect on the actual available prey in relation to their spatial movements of subordinate predators (Hayward 2009). This could have affected our results, and thus needs further attention.

Although there are still gaps in our knowledge regarding the reintroduction of African wild dog, the metapopulation programme was one of the most extensive and successful endangered species reintroduction efforts to date (Davies-Mostert et al. 2009, Gusset 2009 Gusset et al. 2008). Many other reintroduction programmes could learn much from these studies. The metapopulation framework for African wild dog was coordinated by a national level body called the Wild Dog Action Group (WAG), which ensured that the objectives at the reserve level were achieved as well as contributing to the conservation of this endangered species at a national and even global level (Slotow & Hunter 2009). The documentation and evaluation of this metapopulation programme, has facilitated the accumulation of extensive knowledge and technical expertise with regard to reintroduction and metapopulation management. This could be of benefit to the management of African wild dog populations in other African countries, as well as other large carnivore species globally. South Africa has faced challenges with the conservation of large carnivore due to fragmentation of conservation areas and now other countries face similar issues. Countries with comparable land changes (Slotow & Hunter 2009) could benefit from the successful framework of the African wild dog metapopulation programmes.

Despite the successes of the past, our knowledge of African wild dog natural history and reintroduction biology should not be seen as exhaustive. Even though the extensive research has been carried out, we have shown in this thesis that we still have much to learn to further develop the framework of reintroductions and enhance integrated management tools specifically for African wild dog. Other large carnivore conservation efforts, such as the population recovery programme of the Eurasian lynx (*Lynx lynx*, Linnell et al. 2009) and lion (Slotow & Hunter 2009), lacked such detailed documentation. Past efforts to assist in the population recovery if these species have largely been successful despite a rather *ad hoc* approach to reintroduction and management. Unlike the African wild dog, in both cases these was little coordination and science based approaches were not used as well as the fact that only a few reintroductions were well studied. This limits our ability to evaluate the reintroduction processes and our understanding of what contributes to the success or failure of a reintroduction (Linnell et al. 2009, Slotow & Hunter 2009). For example in Europe over 170 lynx were introduced in 15 different sites in eight countries over a 37 year period, the majority of which were poorly planned or followed up. A similar situation occurred in South Africa where the reintroduction of lions has been common practise since the 1960’s, but unlike the African wild dog, no national level coordinating body controlled these practises. As a consequence decisions regarding reintroduction and management have been based mainly on a local reserve level, where local agendas have been reached but not larger conservation goals.

Although there is a worldwide decline in large carnivore populations, unequal efforts in reintroduction have taken place across the globe (Johnsingh & Madhusudan 2009). In some regions the reintroduction of large carnivore species has not been an important conservation theme in the past, but it is now being given more serious consideration as the number of animals at risk of extinction grows. This is the case in India with the Asiatic lion (*Panthera leo perisca*) and tiger (*Panthera tigris*, Johnsingh & Madhusudan 2009) and the jaguar (*Panthera onca*) in tropical America (Kelly & Silver 2009). Successful conservation management of these and other large carnivores will only be reached through greater collaboration amongst scientific disciplines. This will ensure important information concerning the pitfalls and lessons learnt from other reintroduction of large carnivores will be shared. Global sharing of information will enable consolidation of research via *post hoc* meta-analysis to establish and improve the emerging science of reintroduction biology.

Conclusion

This thesis shows that the KGR pack does not follow the expected pattern of feeding behaviour as seen in other small reserves and as consequence the predictive model by Hayward failed to predict the prey preference for this population. Thus we highlight the need for more long term monitoring of other reintroduced populations on relatively small reserves to increase the sample size and determine if the KGR pack did indeed show contrasting behavioural adaptations, possible temporal variations in feeding behaviour or whether the pattern of preference for larger prey species in the diet as seen in Pilanesberg National Park and Shambala Game Reserve was due to biases in experimental methods. This study also highlighted the need for reintroduction guidelines to attempt to consider all aspects of a large carnivore's behavioural ecology, including their social behaviour is often disregarded by wildlife managers when reintroducing populations (Somers & Gusset 2009). Models that focus solely on one aspect of behavioural ecology, such as feeding behaviour to make a prediction of suitable carry capacities should be used with caution. Incorporating considerations on social behaviour and interspecific competition in conservation management would increase efficiency and effectiveness of large carnivore reintroduction programmes. These tools and the lessons learnt from the reintroduction programmes of African wild dog and other African large carnivores could have important and far reaching implications on the future successes of reintroduction of species in other countries. These may refer to the framework of African reintroductions as a basis for development of their own population recovery strategies. Meta-analysis of past and future attempts of reintroduction should therefore be a priority (Armstrong & Seddon 2007, Hayward & Somers 2009) in order to continue to improve and develop more appropriate and integrated decision making tools which are essential for the success of African wild dog reintroductions (Gusset et al. 2008, Morgan et al. 2009) and ultimately globally for other large carnivores.

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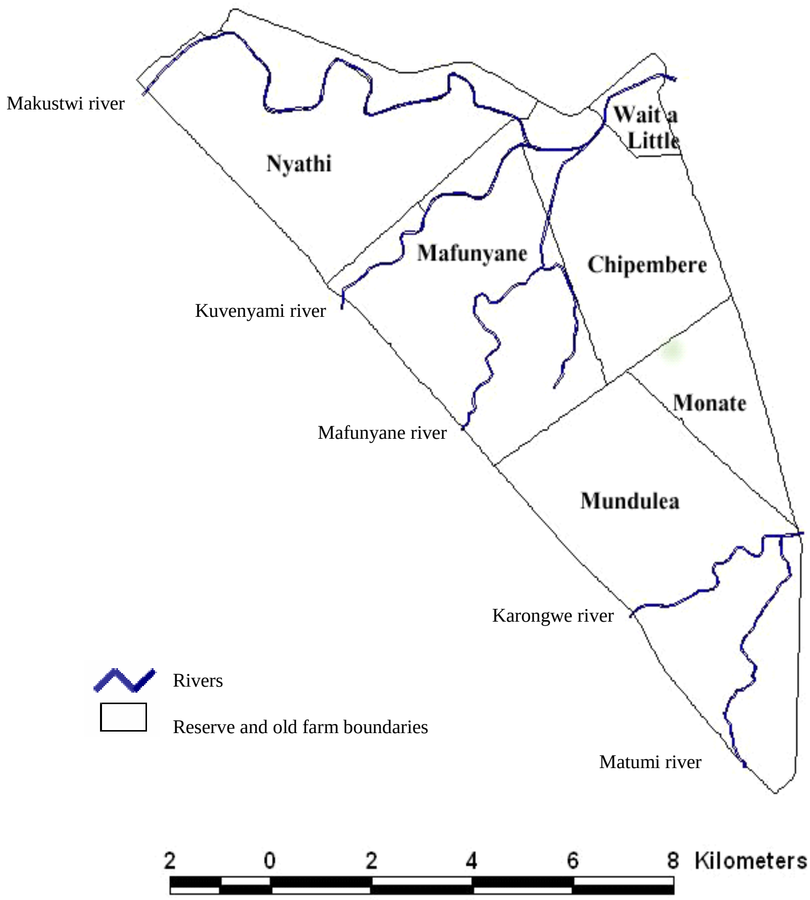
Appendix A: The Karongwe Game Reserve. The map indicates the various properties comprising the reserve, and the major rivers flowing from west to east across the reserve.



Appendix B : **Game count figures, large herbivore and predator numbers generated from aerial game counts undertaken annually on KGR from 1999 – 2004 .**

Species	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**
Small herbivores						
Bushbuck (*Tragelaphus scriptus)*	178	58	96	127	56	14
Duiker (*Sylvicapra grimmia*)	32	11	16	18	0	29
Eland (*Taurotragus oryx*)	4	4	0	0	0	0
Gemsbok (*Oryx gazelle)*	10	3	0	0	0	0
Giraffe (*Giraffa camelopardis*)	65	85	79	80	90	66
Hartebeest (*Alcepaphus buselaphus*)	42	21	17	7	4	2
Impala (*Aepyceros melampus*)	1816	1953	2140	1782	1252	930
Kudu (*Tragelaphus strepsiceros)*	161	183	166	144	140	154
Nyala (*Tragelaphus angasii)*	27	19	20	27	30	11
Steenbok (*Raphicerus campestris)*	8	1	3	0	0	1
Warthog (*Phacochoerus aethiopicus)*	146	244	261	266	119	113
Waterbuck (*Kobus ellipsiprymnus)*	278	254	231	205	185	149
Wildebeest (*Connochaetes taurinus)*	289	282	239	321	298	219
Zebra (*Equus burchelli*)	172	195	171	206	190	159
Large Herbivores						
Elephant (*Loxodonta africana)*	0	10	12	13	15	15
Hippopotamus (*Hippopotamus amphibious)*	3	11	12	15	16	16
White Rhinoceros (*Ceratotherium simum)*	0	5	5	4	4	5
Large predators						
Cheetah (*Acinonyx jubatus)*	5	13	9	15	12	9
Hyaena (*Crocuta crocuta)*	0	0	0	5	7	11
Leopard (*Panthera pardus*)	10	16	19	27	23	12
Lion (*Panthera leo)*	0	6	8	10	8	10

A diverse range of fauna are found on the reserve with all herbivore being present prior to 1999 and only zebra (*Equus burchelli*) being introduced between the formation of the conservancy and the end of the study. Introductions of large mammal species during this time included elephant (*Loxodonta africana*), lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), serval (*Felis serval*), white rhino (*Ceratotherium simum*), and hippopotamus (*Hippopotamus amphibius*).

Appendix C – Vegetation map procedures

Vegetation map developed by Victor Bangamwabo, School of Biological and Conservation Sciences, Westville Campus, University of KwaZulu-Natal, Private Bag X54001, Durban 4000, South Africa, 204503168@ukzn.ac.za

Data description

The primary satellite imagery used in this study was an orthorectified Landsat Enhanced Thematic Mapper (ETM+) image mosaics obtained from NASA's Landsat circa 1999/2000 coverage database at https://zulu.ssc.nasa.gov/mrsid/ .

The image has a spatial resolution of 14.25 meters sharpened with using the panchromatic band and three spectral bands, namely Band 7, Band 4 and Band 2 covering the mid-infrared, near-infrared and the green wavelengths, respectively. The image product comes ready projected with a Universal Transverse Mercator (UTM) projection. Additionally, contrast enhancement, geometric and radiometric corrections had already been applied to maximize image processing procedures.

A colour aerial photograph was used as reference dataset in creating signatures and identifying training sites alongside GPS points describing various vegetation types.

Image processing

Prior to image classification, it was important to identify different vegetation and land cover types at the study site.

Using this information in conjunction with GPC points collected, it was then necessary to identify and create training samples / signature creation that are essentially required for a supervised classification.

Identification of training samples / signature creation and image classification

Major vegetation types were identified using the GPS points then spectral signatures / training sites required for a supervised classification processes were created using ERDAS IMAGINE 9.0 regional growing (seed) tool (Leica Geosystems, 2005). A supervised image classification using a Maximum Likelihood algorithm was used.

Reference

https://zulu.ssc.nasa.gov/mrsid/docs/GeoCover_circa_2000_Product_Description.pdf

Appendix D:

Details of the study animals and their fate from reintroduction of captive female and then during the study period (January 2002 to January 2004).

(re-introduced; African wild dogs born on the KGR)