Wildebeest ecological dynamics in the CKGR: The implications for potential isolation from the wider Kalahari ecosystem

By

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Disclaimer

I declare that work contained in this dissertation was completed by myself at the Okavango Research Institute, University of Botswana, between 01st August 2012 and 30th April 2017. The dissertation contains some journal articles, with co-authors. I also declare that data collection, analysis, key ideas and write up was conducted by myself. My supervisors (co-authors) provided guidance and corrections as required by the University regulations. The dissertation is an original work except where due reference is made and neither has been nor will be submitted for the award of any other University.

Signature ____________________

Date _____________________

Dedication

For my wife

I dedicated this work to “the bone of my bones”, for your support, for believing in me, and the strength I always got from you.

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Abstract

Survival of wildlife populations in arid savannahs depends on their mobility in regard to habitat heterogeneity as an adaptive response to large spatial and temporal resource variability over the annual cycle and with climatic change. The historic main wet season range of the blue wildebeest (*Connochaetes taurinus*) in the Kalahari ecosystem was a region with a high density of mineral-rich pans between the Central Kalahari Game Reserve (CKGR) and the Kgalagadi Transfrontier Park (KTP), commonly known as the Kalahari Schwelle. During drought years, wildebeest made long distance movements from the Schwelle through the CKGR to the permanent water of the Boteti River, Lake Ngami and Lake Xau in Northern Botswana and some to the south west towards the Nossob River. Access to water sources in the north has been prevented by fences, and movement routes from the CKGR to the Schwelle is increasingly encroached upon by human and livestock, and land use change. The drastic decline in wildlife populations in the Kalahari followed constructions of cordon fences. The populations have not recovered from the declines, and this may be exacerbated by the increasing trends in land use and habitat changes, with wildebeest being one of the most affected species. To address the loss of access to water, the government of Botswana introduced artificial waterholes in the CKGR. However, the wildebeest population has not recovered from the decline and it is not clear what may be preventing the recovery of the population. Understanding the relationship between the wildebeest population and the heterogeneity and variability of the CKGR environment is critical in determining the viability of the system as an independent entity and development of management interventions for sound species conservation. The main objective of the study was to investigate the ecological dynamics of the blue wildebeest population in the potentially isolated CKGR. I fitted GPS Plus satellite collars to ten female wildebeest in different herds (seven of them were found near waterholes) between August 2011 and July 2014 in the CKGR and Khutse Game Reserve (KGR), to examine seasonal wildebeest adaptive activity and movement patterns, habitat selection, sympatric diet composition and competition in relation to the environmental conditions variability and fragmented ecosystem. I also investigated water quality in artificial waterpoints and its potential impacts on the Kalahari ecosystem. Wildebeest coped with heat stress by maximising their activity in the cool hours of the day. They avoided predation pressure and loss of body condition (due to less food) by minimising activity at night and in dry seasons, respectively. Wildebeest favoured open, short-grass pan habitats in all seasons, probably in response to better forage quality and lower predation risk than the off-pan habitats. However, the ability to remain in pan habitats during the dry season was probably a result of artificial water provision. A wildebeest herd that had no artificial water in its home range migrated annually and survived the dry season, whereas most of those wildebeest that were accustomed to water provision died when their water points failed in the dry season. Wildebeest also face diet competition from gemsbok and springbok. Wildebeest are likely more negatively affected among the three species by inter-specific competition because they are unable to switch to a relatively, high-quality browse resource. Quality of water provided in the CKGR is poor and poses a health risk to both animals and humans in and around the CKGR/KGR. Most of the boreholes tested exceeded livestock maximum acceptable limits on TDS and some had potentially toxic levels of lead and arsenic. My study highlights that provision of water is a complicated and controversial tool to compensate and manage lost access to water in dryland ecosystems. Water provision alters acquired adaptive strategy and reduces resilience to arid environments. It is important to ensure consistent water provision to avoid mortalities. I therefore concluded that the viability of the CKGR wildebeest population can be improved with enough, strategic and consistent provision of good quality water, particularly if access to historic water sources cannot be restored.

These findings emphasise the sensitivity of arid regions to habitat change and highlight how habitat loss and fragmentation in arid regions create complex management challenges, especially where resources are distributed in distinct seasonal ranges. The findings call for detailed assessments of developments that include physical barriers along access routes of population. Migratory corridors or movement routes between key resources are established over a long term as adaptive strategies and they are critical to the sustainability of the populations, especially in dryland ecosystems where seasonal variability can be very high. Water provision as a last resort, may partially reduce the impacts of habitat loss and fragmentation but cannot replace the long-term established balance between populations and their environment. Water provision jeopardises the natural resilience of the populations and creates highly vulnerable populations that may struggle to survive the prevailing environmental variability, and unexpected disruption of water provisions. In conclusion, restoration of access to the natural water sources and grazing areas is a more natural and may be a more sustainable management intervention for the long-term viability and conservation of the Kalahari wildebeest population, than the current artificial water provision in the CKGR.

Key words: activity pattern, blue wildebeest, competition, diet composition, forage quality, water provision, water quality

Thesis Outline

Chapter one introduces general information on the Kalahari ecosystem and ecology of the blue wildebeest. The chapter discusses the history of the ecosystem and different factors that influence movement patterns, habitat selection and feeding ecology with some focus on ungulates, particularly wildebeest. Chapter two presents results on adaptive strategies of blue wildebeest to seasonal environmental variability in the Kalahari with focus on activity patterns in relation to ambient temperature and predation pressure. The chapter highlights the environmental factors that affect the timing of wildebeest activity, and how the population is coping with such factors. Chapter three presents results on habitat selection and movement patterns of the CKGR blue wildebeest population, in response to seasonal resource variability. The chapter highlights the importance of pans and valleys in providing high quality forage and safety against predators. The chapter emphasises the effects of inconsistent water provision on the movements and survival of the wildebeest. Chapter four presents seasonal diets and dietary overlap between sympatric herbivores (wildebeest, gemsbok and springbok) and potential implication of forage competition for the blue wildebeest. The chapter highlights how wildebeest population is facing competition over limited favoured forage resources. Chapter five presents results on water quality and potential implications for wildlife conservation in the CKGR. And finally, chapter six presents a synthesis of the results from chapter two to chapter five, and presentation of management implications of the results to wildebeest conservation, the fragmented Kalahari and arid lands ecosystems, the overall contribution to the field of arid and landscape ecology, and further present limitations of the study and recommendations for future research.

Chapter One: General Introduction

1.0 Introduction

In the face of climate change, habitat loss and fragmentation, and associated biodiversity loss, conservationists are concerned with maintaining at least viable populations to avoid extinction (Franklin & Frankham, 1998; Ganzhorn *et al.,* 2000; Reed *et al.,* 2003). Population viability defines the minimum number of individuals in a population that allows it to persist and avoid extinction over a specific time (Ruggiero *et al.,* 1994). The viability of a population depends on its reproductive rates relative to mortality rates, which are driven by the environment and population phenotype, structure and fitness (Gilpin & Soule, 1986). Population fitness is the proportionate contribution of individuals to the next generation (Begon *et al.,* 1990), enhanced by access to food, water and mating partners, and weakened by poor nutrition, disease and predation (McNamara & Houston, 1994; Parker *et al.,* 2009). Population phenotype includes all aspects of physical, chemical and biological manifestations of the population. The environment relates to both the biotic and abiotic aspects influencing the population; whilst population structure and fitness are a consequence of the environment and phenotype of the population (Gilpin & Soule, 1986). A change in the environment or phenotype of the population will result in a change in the structure and fitness of the population, eventually influencing the reproductive success and survival rates. Through evolution process, natural selection shapes ecosystems according to suitability or compatibility of population phenotypes to specific environmental opportunities and constraints, such that changes in the environment may require phenotypical plasticity to cope with the changes (Garland & Kelly, 2006; Williams *et al.,* 2008; Hetem *et al.,* 2010; Huey *et al.,* 2012). Unfortunately, where environmental changes are too drastic or too fast for the populations to adjust in time and cope, populations decline and in some cases local extinctions may manifest (Fuller *et al.,* 2008; Fuller *et al.,* 2010). In my study the population viability concept was explored to identify factors and measured some of the factors that could influence population fitness and contribute to the decline of the blue wildebeest (*Connochaetes taurinus*) population in the Central Kalahari Game Reserve (CKGR), without necessarily looking at the demographic patterns of the population. Key factors such as environmental characteristics and changes (including habitat loss and fragmentation), resource availability and quality that may potentially compromise the adaptability or resilience of the population were assessed. Food availability and quality (Johnson *et al.,* 2001; Bailey *et al.,* 1996), inter- and intra-specific competition, predation risk, thermoregulation and parasite avoidance are some of key factors that influence habitat selection and use by herbivore populations and alter their diets (Owen-smith, 2002; Valeix *et al.,* 2009), as they stride to meet their daily and seasonal energy and protein budgets (Johnson *et al.,* 2001).

1.1 Habitat fragmentation and loss

Climatic patterns in arid and semi-arid regions of sub Saharan Africa are highly variable (Bassett & Crummey, 2004) and wildlife populations in regions with highly-variable rainfall depend on their mobility to access spatiotemporal habitat heterogeneity and cope with environmental variability (Illius & O'Connor, 1999; Primack, 2002; Fryxell *et al.,* 2005) to meet seasonal nutritional requirements and avoid unfavourable environmental conditions. However, increasing human population, establishment of new settlements, expansion of agricultural activities, and anthropogenic developments have encroached into some of the habitats and have fragmented ecologically connected landscapes (Andren, 1994; Newmark, 2008; Fynn & Bonyongo, 2011), resulting in isolation of formally single or meta-populations (Primack 2002; Zhou & Wang, 2004). Habitat loss and fragmentation have restricted access to key seasonal resources and reproductive mates, as well as having restricted colonisation and dispersal to alternative resource-rich habitats, especially during unfavourable periods (Williamson *et al.,* 1988; Primack, 2002; Fahrig, 2007; Newmark, 2008). Restricted access to these resources reduces the populations' adaptive responses to environmental variability and may lead to depletion of local resources use and sustainability of the system (Noss *et al.,* 2006). These result in compromised survival rates (Hobbs *et al.,* 2008) and reduced reproduction success, with eventual decline, and possible extinction of the populations (Fahrig, 2007; Ozinga *et al.,* 2009).

As in many regions in Africa, the general decline in wildlife populations in the Kalahari is coupled with land use and habitat changes (Wallgren *et al.,* 2009; Ogutu *et al.,* 2016). In Kenya, the main cause of these effects was attached to policy, institutional and market failures (Homewood *et al.,* 2001; Ogutu *et al.,* 2016). This implies that these declines could have been avoided or could be addressed through formulation of relevant policies, and institutional improvements to reinforce the policies effectively. In Botswana, construction of veterinary cordon fences for foot and mouth disease (FMD) control has blocked wildebeest access to water during droughts, resulting is catastrophic mortalities in the late 70s and early 80s (DHV, 1980; Owens and Owens, 1984) with eventual loss of over 90% of the Kalahari wildebeest population. The cattle population has increased significantly over the last 30 years (Meyer *et al.,* 2010), and contributes 79% of the total animal biomass (DWNP, 2015). During the 30 year period, the wildebeest population has not recovered and continues to decline in some parts of the system. This trend, as well as human encroachment and associated activities, (like illegal hunting, increased fires) may have a negative impact on the access and utilisation of the areas by wildebeest (Williamson *et al.,* 1988; Bergstrom & Skarpe, 1999; Wallgren *et al.,* 2009). The wildebeest is the most affected species compared to other large ungulates like gemsbok (DWNP, 2015), understandably because they are the most mobile and water-dependent, and the least adapted ungulate to the dryland systems (Mills & Retief, 1994; Hayward & Hayward, 2012).

DHV (1980) concluded that the wildebeest population, estimated at over one quarter of a million, were essentially nomadic and opportunistic in their spatial and temporal movements, responding to the availability of green grass and melon crops (Bonifica, 1992). It seems that in average to good years, moisture from such foods enables them to reside in the Schwelle region throughout the year, while in drier years they move outwards to the north and north-east as well as to the south in search of surface water (Williamson *et al.,*1988; Bonifica, 1992).

Past reports and publications emphasised the importance of the Schwelle which forms part of Wildlife Management Areas (WMAs), especially Okwa and Matlhoaphuduhudu for the herbivore population of the southern and central Kalahari (Williamson *et al.,* 1988; Verlinden, 1994). Figure 1. A telemetry study on ungulates conducted between 1996 and 2003 in CKGR and KTP also showed that WMAs continue to play a significant role as wet season habitats, especially for wildebeest (Bonifica, 1992; Selebatso, 2007, unpublished). However, with the current land use changes it is likely that these movements or accessibility to these WMAs is limited or may not exist. Furthermore, there is a strong political movement by both the governments of Botswana and Namibia to develop a rail line from Botswana to Namibia across the Kalahari. The establishment of this development will present yet another physical barrier in the Kalahari, thus dictating that the CKGR and the KTP should function as independent ecosystems. Persistent demand for more land from the livestock farming community will exacerbate this habitat loss and further fragment the

Kalahari ecosystem. The poor or lack of community involvement and participation in wildlife tourism in these WMAs may further threaten the long-term use of these habitats (Ringrose & Vanderpost, 1997; Bergstrom & Skarpe, 1999). The communities in these areas are among the poorest in the country (Ditlhong, 1997; Statistics Botswana, 2014), and are expected to be highly dependent on natural resources. The ban on hunting stopped the main source of income for community. This potentially removed the motivation for conservation of this WMAs by the community (Mbaiwa, 2017)

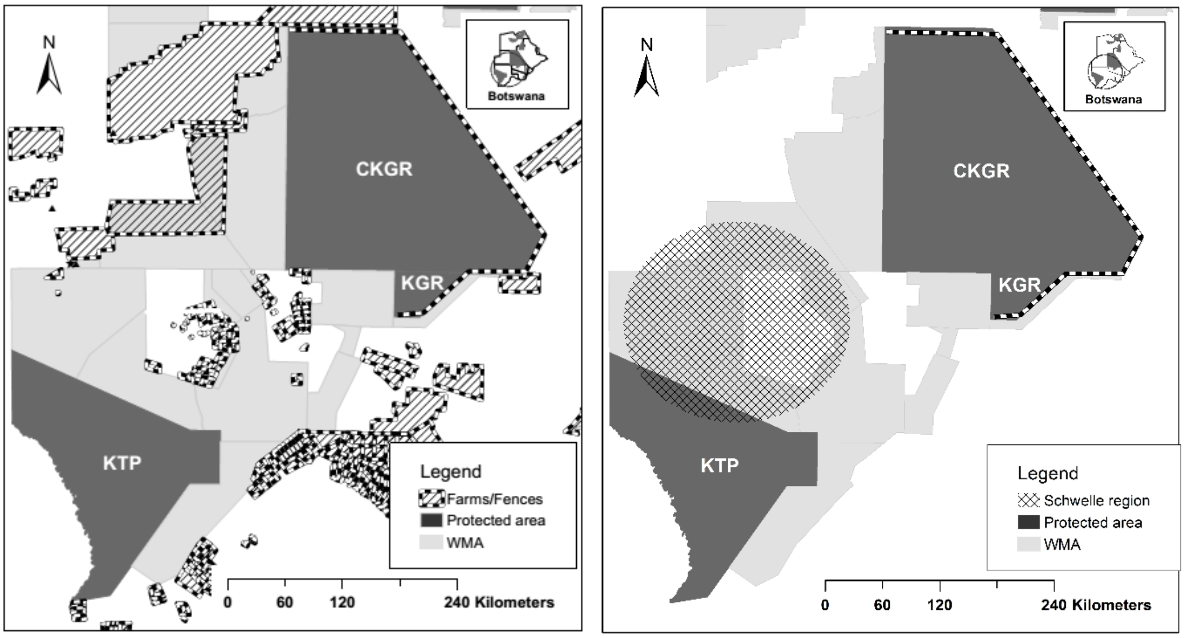

Figure 1. Landuse map of South Western Botswana showing the Central Kalahari Game Reserve and Kalahari Transfrontier Park surrounded by Wildlife Management Areas and farms/fences (Left), and Schwelle region (Right).

In the long term, the isolated population may also decline or go extinct due to inbreeding depression, genetic drift, Allee effects and environmental variations (Primack, 2002; Zhou & Wang, 2004). The possibility that some of these population isolation effects were realised in the Kalahari was reported by earlier biologists in the CKGR (Williamson & Williamson, 1985, unpublished; Verlinden, 1994). There were recommendations to provide water to minimise the impacts of habitat fragmentation and isolation of the population from natural surface water that were used in the dry seasons (Verlinden, 1994).

It is however, noted that there are recent positive ideas within the government of Botswana to create wildlife corridors between protected areas of Botswana. Consolidation of the ideas, and immediate development and implementation of the plan may potentially restore the Kalahari ecosystem. The feasibility study of the potential corridors, considering the existing human and livestock densities, farm fences, roads and community perceptions to conservation benefits, need to be undertaken sooner than later.

1.2 Landscape Heterogeneity and Herbivore foraging behaviour

In semi-arid and arid environments, resources availability and quality are highly variable, both spatially and temporally, in response to low, unpredictable rainfall and highly variable climatic conditions, with extreme temperatures (DHV, 1980, unpublished; Williamson & Williamson, 1985 unpublished; Illius & O'Connor 1999). Viability of populations in these arid landscapes depends on access to seasonal resources that meet nutritional requirements as well as low predation risk (Bjørneraas *et al.,* 2012). Populations are therefore expected to select habitats in accordance with nutritional requirements and resource availability. Habitat selection is an ecological process that influences both spatial and temporal distribution of populations (Johnson *et al.,* 2001), population dynamics and persistence, species interactions, and ecological communities (Schooley & Wiens, 2003). Biological and physical characteristics of the environment play a significant role in the timing and directions of selecting a suitable habitat (Smit *et al.,* 2007; Harrison *et al.,* 2008; Shannon *et al.,* 2009), and effectively affect the fitness of an individual and eventually survival of the population. The intensity of use of an area (or patch) can be assumed to define or reflect the environmental profitability of the patch across the landscapes (Barraquand & Benhamou, 2008).

Forage quantity and quality in selected habitats determine diet selection and food intake rate (Farnsworth & Illius, 1998), thus influencing population success in acquisition and fulfilment of nutritional requirements. Wildebeest in semi-arid savannas are believed to select habitats with a high abundance of nutritious and short grass species (McNaughton, 1990; Ben-Shahar & Coe, 1992, Arsenault & Owen-Smith, 2008). Wildebeest are also selective in the wet season, when most plants have new shoots and leaves (with high levels of crude protein). During dry season wildebeest tend to feed on the plants that they less preferred in wet season (Ben-Shahar & Coe, 1992; Knight, 1991; Ego *et al.,* 2003). Wildebeest can optimally graze on grass that is less than 5 cm tall and amount to 94 gm^{-2}, due their wide mouth gape, relative to their body size (Murray & Illius, 2000; Wilmshurst *et al.,* 2000; Arsenault & Owen-Smith, 2008). Knight (1991) recorded that wildebeest in the Southern Kalahari selected for *Eragrostis lehmmaniana* throughout the year and *Stipagrostis obtusa* was the most frequently eaten. Some grass species were avoided in different seasons, *Enneapogon desvauxii* and *Eragrostis porosa* in the hot-wet season; *E desvauxii* and *Schimidtia kalahariensis* in the cold-dry season; and *Brachiaria glomerata, Stipagrostis amabilis* and *S. kalahariensis* in the hot-dry season (Knight, 1991). Among these grass species, only *E. desvauxii* exists in the CKGR, and it will be interesting to determine the diet composition of *E. desvauxii* for the CKGR wildebeest population.

Seasonal variation in diet composition is dependent on seasonal forage availability and quality (Newman, *et al.,* 1995; Owen-Smith, 2002), which are driven by forage species physiology and anatomy, as well as grazing pressure (Owen-Smith, 2002). Grazing pressure is determined by the density and size of a herbivore population, coupled with diets of sympatric ungulates and competition for resources (Prins*,* 2000; Ogutu *et al.,* 2016). Herbivores cope with resource variability by exhibiting diet breadth expansion in relation to the diversity of available functionally-different plant species (Owen-Smith, 2002). Owen-Smith (2002) classified five functional generic resources that maintain herbivores over the annual cycle: (i) high quality resources that provides sufficient intake of energy and nutrients for growth and reproduction usually in the wet season, (ii) restricted intake resources that are high-quality but have restricted intake rates owing to being too short, too scarce or in the case of browse, protected by thorns, (iii) staple resources which provide the bulk of energy and nutrient intake over most of the year, (iv) reserve resources, lower in quality than staple resources, but maintaining herbivores through the dormant/dry season, and (v) buffer resources, usually unpalatable but eaten during drought periods thus preventing starvation. Acquisition of these functional resources maintain the herbivore population through periods of rich and poor resource availability and quality, thus ensuring survival and reproduction success of semi-arid herbivore populations (Owen-Smith 2002).

Acquisition and fulfilment of nutritional requirement is also limited by various factors such as optimal foraging time (Lima, 1998), morphological adaptation (Murray & Illius 2000; Arsenault & Owen-Smith 2008; Codron *et al.,* 2008) and digestive anatomy (Steuer *et al.,* 2011; Steuer *et al.,* 2013). Herbivores time their foraging activity to target better and accessible forage, within constraints of their morphology and mobility (Gordon & Illius, 1988), predation and heat stress (Green & Bear, 1990; Lima, 1998; Valeix *et al.,* 2009). In hot and dry ecosystems, herbivores forage during cool hours of the day, and sometimes at night, avoiding heat stress, especially when water is scarce (Hetem *et al.,* 2010; Lease *et al.,* 2014), though, nocturnal activity may expose herbivores to predation (Hayward & Slotow, 2009). Heat stress (or solar input) may be avoided or reduced by seeking shady habitat or positioning themselves parallel to the sun to reduce solar heat load (Cain *et al.,* 2006; Lease *et al.,* 2014). Some species have physiological ability to shed heat loads to minimise heat stress (Hetem *et al.,* 2009).

Mouth anatomy limits the amount of forage an animal can take in one bite. Herbivores with narrower mouths are better adapted to nibbling high quality parts from a plant, but limited in bite size on short swards (Jarman, 1974; Murray & Illius, 2000). Large bodied herbivores tolerate low quality forage and can ingest a larger amount of forage than small bodied herbivores (Jarman, 1974; Owen-Smith, 1988; Steuer *et al.,* 2011; Clauss *et al.,* 2013). Superimposed on the body weight and metabolic requirement, digestive anatomy (including absorptive gut surface), physiology and capacity limit retention time (Clauss & Hummel, 2005; Steuer *et al.,* 2011), and eventually limiting intake rates. Ruminants have a longer mean retention time compared to hind gut fermenters (Steuer *et al.,* 2011), and this gives ruminants a higher digestive efficiency of forage with a high fibre content (Steuer *et al.,* 2013). The high retention time allows them to maximise extraction of nutrients better than the non-ruminant. However, the longer retention time limits in nutrients intake rate (Owen-Smith, 2002), resulting in low nutrients assimilation particularly during dry seasons when forage quality is already low. This may compromise the fitness of the population especially where the population is restricted from accessing alternative foraging ranges with better forage quality.

1.3 Water provision in dryland ecosystem

Dryland regions are known for their lack of surface water, and dependence of wild animals of moisture from forage resource, and sometimes migrate to distant water bodies in drought years (Knight *et al.,* 1987; Williamson *et al.,* 1988). Provision of artificial water sources for wildlife has been implemented in other arid regions of the world to address lost access to natural water sources because of fragmentation and habitat loss (Rosenstock *et al.,* 1999). As noted by James *et al.* (1999), lack of water is more detrimental to animals and plants than any other essential resource. Artificial water provision can facilitate an increase of water dependent plants and animals (Owen-Smith, 1996; James *et al.,* 1999) and an increase of breeding habitats for invertebrates (James *et al.,* 1999). Nevertheless, water provision has not been without controversy. Indiscriminate distribution of watering points in a previously dry landscape may result in increased predation risk (Grant *et al.,* 2002), establishment of resident populations around waterholes (Verlinden, 1994, Thrash *et al.,* 1995) and redistribution of grazing and trampling effects (Andrew & Lange, 1986; Thrash, 1998), and eventual alterations of range resources (Thrash, 1998) or homogenization of landscapes (Sianga *et al.*, 2017).

In Botswana, the government developed artificial waterholes in the CKGR in 1984 and 1986, following mass die-offs of ungulates along veterinary cordon fences during droughts (Bonifica, 1992). Thouless (1997) hypothesized that the mass deaths of the Kalahari wildebeest during the 1980s droughts had selected against the migratory wildebeest population and that a more sedentary population was slowly establishing. The establishment of a sedentary population may lead to an eventual decline of the population, due to predation pressure (Fryxell *et al.,* 1988; Bonifica, 1992) and over utilization of the grazing resources around the waterholes (Rosenstock *et al.,* 1999; Shannon *et al.,* 2009). Nomadic movements centering around the Schwelle during the wet season and some dry seasons (Bonifica, 1992), could have been a strategy to escape predators during the calving period as the predation density is lower than in the protected areas (Knight, 1991). The movements also gave the wildebeest added advantage of access to the more nutritious grazing resources of the Schwelle than the CKGR, that would restore the wildebeest herds to full fitness before the ensuing dry season as well as provide optimal resources for pregnant and lactating females. A sedentary wildebeest population in the CKGR will most likely decline, because it does not have access to the resources that a migrant population had, and this may make it more vulnerable to climate change (Knight, 1991) and other unfavourable conditions, like disease and predation, especially of calves around waterholes as predators tend to use drinking places to ambush their prey. Dry season estimates of the wildebeest population show that the population in the CKGR is unstable and has not increased since 1999 (Figure 2).

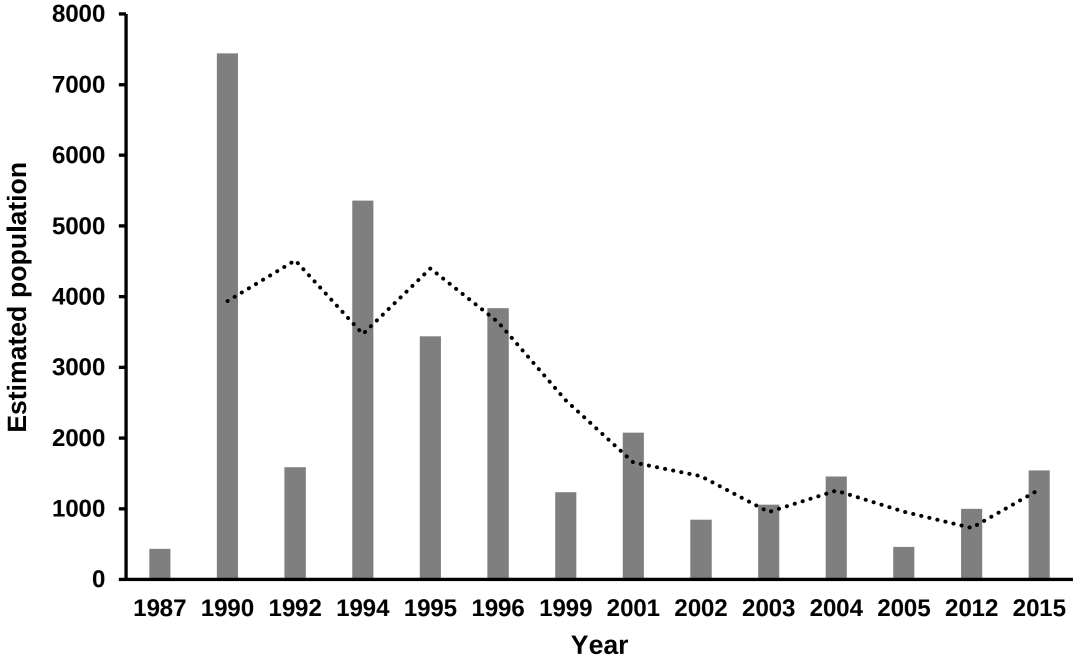

Figure 2. Dry season estimates of the Central Kalahari Game Reserve wildebeest population since 1987 (Source: DWNP, 2015).

Poor water quality can affect the health of wildlife populations (Rosenstock *et al.,* 1999) and so compromise the survival of populations (Stanley *et al.,* 1994; Knight, 1995). Despite this there are no water quality standards for wildlife, making it difficult to determine precise levels of impacts on wildlife populations. There have been reports of wildlife dying near the waterholes (Glyn Maude, per comm.), and this brought some concerns about the potential effects of the quality of the water in the waterholes. However, there has never been formal analysis and monitoring of the quality of the water provided in the CKGR, except the Total Dissolved Solids (TDS) as recorded by

Department of Water Affairs (Bonifica, 1992). Bonifica (1992) had recommended provision of water with a maximum total dissolved solids (TDS) of 5000 ppm. Four of the nine boreholes that existed in 1992 were above this recommended limit (Bonifica, 1992), but they have been used to provide water to wildlife since then. It is unknown how these solids and other impurities in the water may be affecting the wildlife population in the reserve. Understanding the effects of the artificial water points on animal physiology, movement patterns and habitat selection is important for decision making processes that balance the need for biodiversity conservation, population management and tourism development (Shannon *et al.,* 2009).

Habitat loss and fragmentation in the Kalahari has potentially isolated the CKGR from the wet season range and disrupted access to water sources that are allowed the wildebeest to survive drought. Isolation of the CKGR wildebeest population and other herbivores may have restricted sympatric ungulates to depend on the limited resources within the boundaries of the CKGR, resulting in competition, and depletion of forage resources, and eventually decline of the populations. Artificial provision of water which was intended to compensate for lost access to the natural drought ranges may have created a hunting ground for predators, as well as introduced a high risk of forage depletion around the waterholes due to grazing pressure. The quality and availability of the water to wildlife in the CKGR, and its impact on the populations has not been established. This study attempted to test these potential consequences of habitat loss and fragmentation in the Kalahari, and water provision with focus on the viability and adaptability of the CKGR wildebeest population.

1.4 Problem Statement

Wildlife populations in semi-arid savannah regions have to contend with large spatial and temporal resource variability of over the annual cycle (Illius & O'Connor, 1999). The survival of the populations in the system depends on their mobility in response to ecological gradients, to patchy fire and rainfall, to the spatial and seasonal food and temperature variability and to climatic change (Smith & Smith, 2001). The Blue wildebeest in Botswana were recorded to make long distance movements between the Kalahari Transfrontier Park (KTP) and the Boteti through the Central Kalahari Game Reserve (CKGR), Lake Ngami and Lake Xau (Williamson & Williamson, 1985; Bonifica, 1992; Verlinden, 1994; Verlinden & Masogo, 1997) during drought periods. Access to the Boteti River, Lake Xau and Lake Ngami was prevented from the southern part of the system by the veterinary cordon fence along the north and north-eastern boundary of the CKGR. There has also been a lot of habitat loss between the CKGR and the KTP through human and livestock encroachment, and landuse changes (Cooke, 1985; Williamson *et al.,* 1988; Bergstrom & Skarpe, 1999). The general decline in wildlife populations in the Kalahari is comparable with the increasing trends in landuse and habitat changes (Wallgren *et al.,* 2009). The decline is mainly attributed to the establishment of cordon fences (DHV, 1980; Owens & Owen, 1984; Perkins, 1996). Botswana developed cordon fences since 1950s (Williamson & Williamson, 1981), following the Beef Protocol Agreement known as Lomé Convention/Cotonou Agreement (Laaksonen *et al.,* 2007), which resulted in mass died off of large ungulates in the Kalahari (Williamson & Williamson, 1981). The wildebeest is one the most affected species, understandably because they are one of the most mobile and water-dependent ungulates in the region. The wildebeest population has not recovered from these catastrophic effects of the fences and continue to struggle, especially in the CKGR. The population is fluctuating around a thousand individuals (Figure 2).

In an attempt to address the effects of habitat loss and fragmentation, the CKGR management introduced artificial waterholes in the reserve in 1984 (Bonifica, 1992). However, Verlinden (1994) cautioned that provision of artificial waterholes would make the population resident around the waterholes exposing them to high predation pressure (Fryxell *et al.,* 1988; Bonifica, 1992) and overutilization of the grazing resources around the waterholes (Thouless, 1997; Rosenstock *et al.,* 1999; Shannon *et al.,* 2009). Wildlife surveys show that the wildebeest population in the region fails to recover and they are estimated to be about 1500 individuals in the CKGR (DWNP, 2015).

It has been suggested that the main cause of population decline and failure to recover could be loss of access to key habitats (water and forage) and fragmentation associated with fences, and livestock and human population increase (Perkins, 1996; Ngwamotsoko, 1997; Bergstrom & Skarpe, 1999; Dube & Pickup, 2001) and overexploitation (Perkins & Ringrose, 1996). The existing fences around the CKGR, fenced farms, encroachment and increase of livestock and human population, road infrastructure in and around the Schwelle area, isolate the CKGR from the larger Kalahari system and deny the population access to critical resources beyond the reserve boundaries. The 2015 aerial surveys showed that livestock dominated animal biomass by 79% in south western Botswana (DWNP, 2015). In the absence of corridors to these critical historic water and water resources, the survival, and persistence of the wildebeest population (and potentially other herbivores) in the CKGR will therefore depend on availability of functional resources within the boundaries of the reserve. Spatial heterogeneity of food resource plays a major role in the distribution of potential competing grazers (Cromsigt *et al.,* 2009), therefore a less heterogeneous landscape could result in interspecific competition, and so contribute to the decline of the wildebeest population. Poor water quality can also affect the health of wildlife populations (Rosenstock *et al.,* 1999) and may compromise the survival of populations. Understanding the relationship between the wildebeest population and the heterogeneity and variability of the CKGR environment is critical in determining the viability of the system as an independent entity and development of management interventions for sound species conservation.

1.5 Objectives

The main aim of the study was to assess the viability of the CKGR in maintaining a wildebeest population without access to historic water sources and grazing resources in the Kalahari ecosystem. The study was guided by the following specific objectives;

1.6.1 To investigate the adaptive strategies of the isolated blue wildebeest population of the CKGR, with a focus on daily activity schedule in response to seasonal environmental variability and predation risk in semi-arid Kalahari ecosystems.

1.6.2 To determine habitat selection and movement patterns of the CKGR blue wildebeest population in response to seasonal resource variability.

1.6.3 To determine seasonal diets and dietary overlap between sympatric herbivores in the CKGR.

1.6.4 To test water quality from the artificial waterholes within the CKGR and Khutse Game Reserve (KGR) to determine the potential of water quality to negatively affect wildlife in the ecosystem.

1.6 General material and methods

1.6.1 Study area

The Central Kalahari Game Reserve (52,145 km^2) is in Ghanzi District, Botswana and was gazetted in 1961. The CKGR northern, eastern and western boundaries and Khutse Game Reserve (KGR) defined the extent of the study area at 21°00' – 23°00' S and 22°47’ – 25°25' E. KGR (2,550 km^2) was gazetted in 1971 in Kweneng District, Botswana. The study area is surrounded by cordon fences in the north and north east. The south-eastern boundary of CKGR and the southern boundary of KGR have an electric fence developed as a human wildlife conflict resolution. The western boundary is surrounded by wildlife management areas, which act as a corridor to the Schwelle region.

The study area is in a semi-arid and hot region, with temperatures as cold as –6°C and hot as 43°C in winter and summer, respectively (DHV, 1980, unpublished; Williamson & Williamson, 1985 unpublished). Very high temperatures, especially between October and January, and the open landscapes are the main drivers of moisture loss through evaporation (Bonifica, 1992). Temperatures recorded in Gantsi Township (the nearest reliable station), between 2004 and 2014, show a slightly higher minimum and lower temperature in winter and summer, respectively (Figure 3), than the recorded CKGR temperature. Mean annual rainfall ranges from 350 to 400 mm (DHV, 1980 unpublished), with 35% variations from average annual rainfall patterns (Bonifica, 1992). The Kalahari climate is also known for its oscillations of droughts and wet years that drive the dynamics of the savannah ecosystem (Bonifica, 1992).

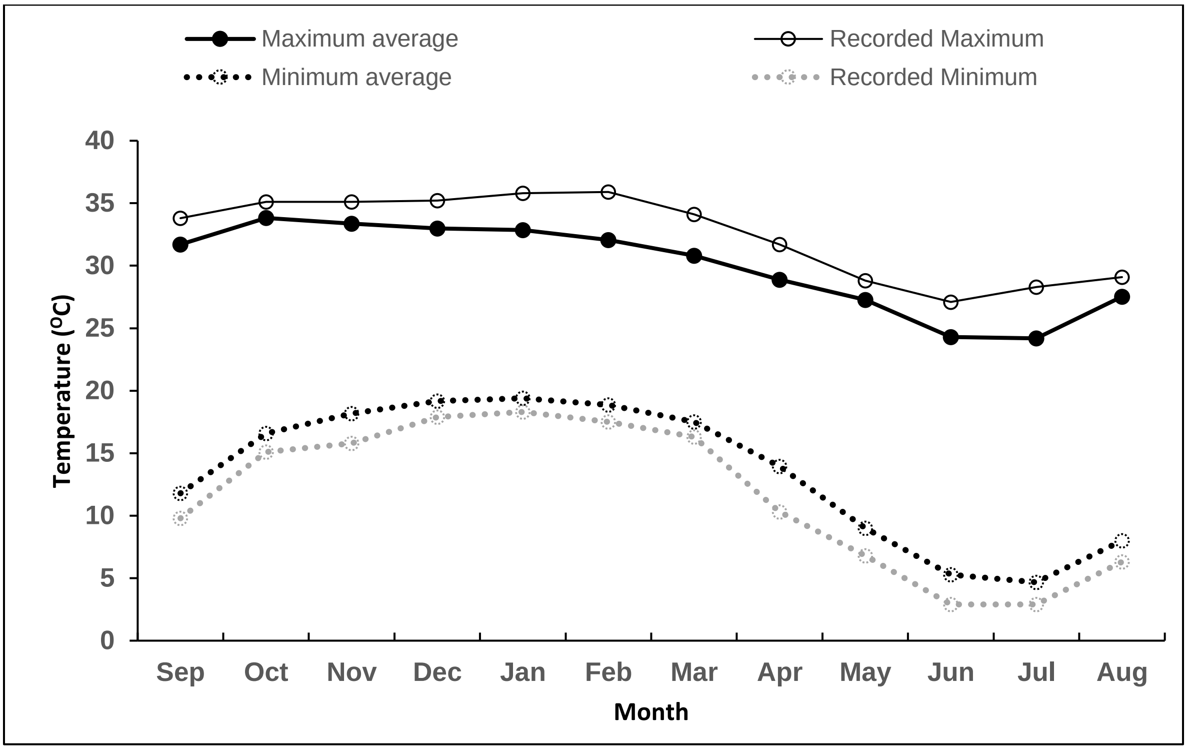

Figure 3. Average temperature recorded between 2004 and 2014 by the Department of Meteorological Services in Gantsi Township,

There is no natural permanent surface water in either of the reserves and the vegetation is a shrub and low tree density savannah with a ground cover of tufted perennials. However, there are currently 13 artificial waterholes developed in the reserves for wildlife use (Figure 4). The area is dominated by Kalahari sandy arenosols with a wide distribution of pans and fossil river valleys on the Karoo basalt rock (DHV, 1980 unpublished). The reserve is generally flat, with depression of pans and valleys and a few immobile sand dunes (Makhabu *et al.,* 2002). Pans and fossil river valleys consist of calcrete and clay soils that are rich in calcium carbonate (Makhabu *et al.,* 2002).

Herbivore populations in the study area include springbok (*Antidorcus marsupialis*), kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), red hartebeest (*Alcelaphus buselaphus*), steenbok (*Raphicerus campestris*) and common duiker (*Sylvicapra grimmia*). Carnivores in the study area include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), spotted hyaena (*Crocuta crocuta*), brown hyaena (*Hyaena brunnea*), and black-backed jackal (*Canis mesomelas*). There have been occasional sightings of elephants in the CKGR, and some elephants establishing temporary stays around artificial waterholes (*per obs*).

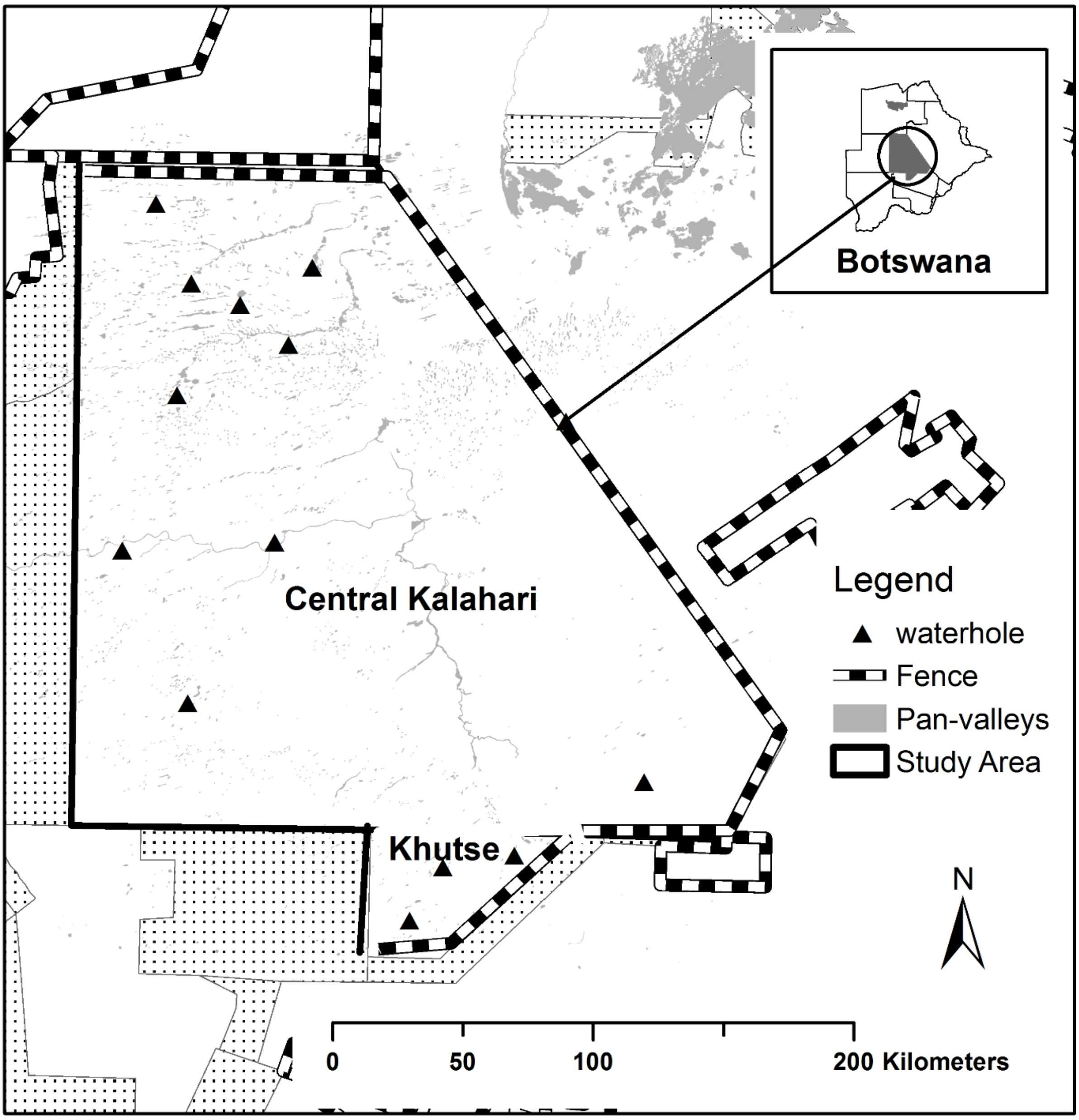

Figure 4. Map of the study area showing both Central Kalahari Game Reserve (Central Kalahari) and Khutse Game Reserve (Khutse), and distribution of the 13 artificial waterholes.

Pans and valleys habitat is dominated by *Leucosphaera bainesii, Eriocephalus sp., Sporobolus ioclados, Enneapogon desvauxii*, and *Cenchrus ciliaris*. This habitat has islands of *Acacia erioloba, A. tortillis, A. mellifera* and *Boscia albitrunca,* with R*higozium trichotomum* and *Catophractes alexandrii* dominant on the edges of the habitat. The off pans and valleys habitat consists of dune, interdunal and plains habitats, which are composed of savanna and woodland. The northern part of the reserve is dominated by *Terminalia prunioides*, *Croton gratissimus* and A. erioloba, whereas *Colophospermum mopane*, *Lonchocarpus nelsii* and *A. luederitzii* dominate the south-eastern part of the reserve (Mishra & Crews, 2014). *Terminalia sericea, A. luederitzii*, *A. mellifera* dominate the southern part of the study area. Herbaceous layers on habitats off the pans and valleys are dominated by *Anthephora pubescens, Schmidtia pappophoroides, Stipagrostis uniplumis* and *Urochloa trichopus*.

1.6.2 General study design

I fitted GPS Plus satellite collars manufactured by Vectronic Aerospace GmbH (Vectronic Aerospace, Berlin, Germany) to ten female adult wildebeest in different herds, between August 2011 and July 2014 in the CKGR. Four collars were deployed 2011, six in 2012 (Table 1). I am confident that the 10 wildebeest herds are representative of the CKGR population because efforts were made to locate new herds across the reserve using existing roads that go through pans and valleys. Wildebeest spend most of the times in the pans and valleys. Intense spoor surveys across the reserve in 2013 did not find additional herds. The darting and collaring of the wildebeest was conducted and supervised by experienced wildlife veterinarians registered with the government of Botswana. All darted animals were in good condition and were not obviously pregnant or with a young calf. Every effort was made to minimise the stress to darted wildebeest and their herds. All the animals were darted from a vehicle and were immobilised with 5mg of Etorphine and 100mg Azaperone, and the tranquilizer was reversed with 25mg of Diprenorphine.

Table 1. Details of blue wildebeest fitted with Vectronic satellite collars and monitored in the CKGR and KGR between August 2011 and July 2014.

Collar ID	Date of collaring	Months	Hourly fixes	Fate of animal/collar
5751	Dec 2012	6	4634	Collar failure
6397A	Apr 2012	6	3370	Lion kill
8137	Nov 2012	21	14261	Survived
8511B	Sep 2012	19	14143	Collar failure
10183A	Aug 2011	3	2681	Unknown kill
10183B	July 2012	19	12606	Survived
10187A	Aug 2011	11	9318	Lion kill
10187B	Dec 2012	14	10786	Collar failure
10188A	Aug 2011	11	8146	Dehydration
10189	Aug 2011	11	8521	Unknown kill

All the collars were programmed to record hourly Geographical Positioning System (GPS) fixes. The collars were also equipped with 3-axis acceleration sensors that measured relative forward/backward, sideways and up/down movements of the wildebeest four times every second and averaged every 5 minutes. I used the forward/backward movements to represent activity rhythms of animals to determine the activity patterns of the wildebeest.

Data from the study animals were analysed between three seasons. I divided each year into wet, cold early-dry and hot late-dry seasons, based on the average rainfall and temperature patterns for the area. I used data from January and February to represent the wet season, June and July for the cold, early dry and September and October for the hot, late dry seasons. I used the data from the collars to determine seasonal activity patterns, movement patterns and habitat selection of the wildebeest population.

I divided the study area into two main habitat types: pan-valley and off-pan. During each season, I randomly sampled five 0.5m x 0.5m quadrats from the two habitat types. I recorded grass height, aerial cover and species composition on site. I then clipped grass samples to determine biomass and analyse for crude protein, phosphorus, sodium and calcium in the laboratory. Wildebeest seasonal location data from the satellite collars were assigned to pan-valley and off-pan habitats to quantify and explain the wildebeest habitat selection patterns in relation to habitat and forage characteristics.

I collected dung samples from wildebeest, springbok and gemsbok to determined seasonal diet composition of three ungulates using microhistological analysis. I collected the dung samples in the dry (August and September 2013) and wet season (January 2014). The results were also used to determine seasonal diet overlap and niche breadth of the ungulates. I also assessed diet quality of the wildebeest by determining the crude protein content of the dung samples using a LECO nitrogen analyser. I further compared forage availability with use by the wildebeest (% in the diet) to determine food preference.

Water provision has been a major management operation in the CKGR/KGR. I However, formal assessment of the quality of the water and potential effects to wildlife population has not been conducted for decades. I collected water samples from 12 of the 13 waterholes in September 2013, January 2014 and June 2014 and tested for quality. I tested for pH, Electrical Conductivity and Total Dissolved Solids (TDS) using standard procedures and analysed for calcium, magnesium, lead and zinc using Atomic Absorption Spectrometry (AAS). I used Flame Photometer to analyse for sodium, and arsenic concentration using Inductively Coupled Plasma Optical Emission Spectrometry (ICS-OES). I then compared the water quality to the Botswana Standards for livestock and poultry specification (BOS 365:2010) and international guidelines summarised for wildlife water development by Rosenstock et al. (2004).

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Chapter Two: Adaptive activity patterns of a blue wildebeest population to environmental variability in fragmented, semi-arid Kalahari, Botswana. Short Communication. *Journal of Arid Environments*, published

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Abstract

*The blue wildebeest (*Connochaetes taurinus*) population in semi-arid savannah regions faces intense spatial and temporal environmental variability over the annual cycle. The population in the Kalahari has lost critical seasonal ranges outside the protected areas due to human induced landscape changes. The population is faced with sparse and patchy forage availability, seasonally very high day temperatures, high predation pressure and limited availability and variable quality of water. We investigated the adaptive strategies of wildebeest in the Central Kalahari Game Reserve with a focus on how daily activity patterns respond to environmental variability in semi-arid Kalahari. The population coped with heat stress by maximising their activity in the cool hours of the day. They avoided predation pressure and loss of body condition by minimising activity at night and in dry seasons, respectively. We conclude that seasonal variations in temperature and light play a critical role in the timing of foraging activity.*

Keywords: *Botswana; Central Kalahari Game Reserve, predator-sensitive foraging*

Introduction

African herbivore populations in semi-arid savannah regions have to contend with large spatial and temporal variability of forage quantity and quality over the annual cycle (Illius and O'Connor 1999). The regions are characterised by high diurnal temperatures and low rainfall (Williamson and Williamson 1985). These conditions lead to heat stress and dehydration in animals and plants (Shrestha et al. 2014), which is expected to worsen with increasing aridity associated with reduced rainfall combined with increased temperature (New et al. 2006). Adaptive behavioural characteristics such as timing their activity schedule (Green and Bear 1990), and feeding strategies (Lima 1998, Valeix et al. 2009) have helped animals cope with scarce water, forage variability, heat stress, and high predation risk.

In the Central Kalahari Game Reserve (CKGR), Botswana, the blue wildebeest (*Connochaetes taurinus*) has lost seasonal ranges beyond reserve boundaries due to human induced landscape changes (Williamson and Williamson 1985, Conservation International, 2010). Preferred habitats are limited, and forage is highly variable between seasons (Selebatso et al, in review). The blue wildebeest is water dependent (Knight 1991) and its dark colour makes it vulnerable to heat loads and as a consequence depends on shade seeking which limits the times of the day they can forage in (Lease et al. 2014). The CKGR, including Khutse Game Reserve (KGR) has no permanent natural surface water and ungulates depend upon moisture from grasses or thirteen artificial waterholes with saline water dispersed over a vast region (54,695km^2). Availability of water in the waterholes is inconsistent (*pers. obs.*). Consequently, the CKGR has a low density and declining population of large ungulates (Conservation International, 2010), which presents a high probability of wildebeest predation by carnivores (Smuts 1978). Large carnivore population spoor surveys estimates for the CKGR and KGR are brown hyaena (874), lion (552), wilddog (383), leopard (328), spotted hyaena (213), and cheetah (137) (Maude and Selebatso 2014, unpublished). Thus, wildebeest face sparse and patchy forage availability, seasonally very high day temperatures, high predation pressure and limited, unreliable and poor quality of water.

Maximising energy gains under these various constraints, demands that wildebeest make substantial calculated risks with regards to heat stress during the day and predation at night. The trade-offs associated with maximising energy intake, water demands and antipredator strategies may compromise the survival of the population (Sinclair and Arcese 1995, Lima 1998). Wildebeest are expected to take greater risks of predation while foraging when their body condition is low (Sinclair and Arcese 1995, Lima 1998). This is likely to occur during the hot, late dry season when individuals have been subjected to 4-5 months of low quality, dry grass since the end to the wet season. In addition, conservation of moisture becomes a key survival priority during the hot, late dry season, when heat stress and moisture loss are greatest and moisture content of forage is lowest. Under the predation-sensitive foraging hypothesis (Sinclair and Arcese 1995) we predicted that during the moisture-limited, hot, late dry season when body stores are declining and moisture constraints greatest, wildebeest would take greater risks by foraging more at night in cooler conditions but when visibility is worst and predators most active (Sinclair and Arcese 1995). The alternate hypothesis is that wildebeest would simply reduce activity in the late dry season to conserve body stores while avoiding taking excessive risks by extending foraging bouts into the night. Our objective was to investigate the adaptive strategies of the isolated blue wildebeest population of the CKGR, with a focus on daily activity schedule in response to seasonal environmental variability and predation risk in semi-arid Kalahari ecosystems.

Materials and methods

Study Area

The Central Kalahari Game Reserve (52,145 km^2) and the Khutse Game Reserve (2,550 km^2) formed the study area. The area falls within 21º00' – 23°00' S and 22°47.5’ – 25°25' E. The area is hot and dry, with extreme temperatures ranging from –6°C to 43°C in winter and summer, respectively (DHV 1980, Williamson and Williamson 1985). Mean annual rainfall ranges from 350 to 400 mm (DHV 1980). There is no permanent surface water in the reserves, however, there are 13 artificial waterholes developed for wildlife. The CKGR contains four main habitats; (1) pans/valleys with open, high-quality short grassland on the higher clay soils of lacustrine origin, (2) dunes and (3) interdunes both with open to dense savanna/scrub and taller coarse grasses and (4) plains with open and mixed savanna (Williamson and Williamson 1985). Larger ungulates are giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), blue wildebeest, gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*) and springbok (*Antidorcus marsupialis*) while larger carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog *(Lycaon pictus*) and brown hyaena (*Hyaena brunnea*) (Williamson and Williamson 1985).

Method

Ten female wildebeest from different herds were immobilised and fitted with a Vectronic Aerospace’s GPS Plus satellite collars between August 2011 and July 2014. High mortality and the low population of study herds led to less than 5 study animals surviving in any one season; we therefore used cumulative data from 2011 to 2014. We divided each year into wet (January-February), cold, early dry (June-July) and hot, late dry (September-October) seasons. Due to high inter-annual variability at the onset of the rains and associated effects on forage quality the other months were not included in the analysis. Sometimes rains start any time from November to December- March and April can be wet or dry season depending on the timing of rainfall during the wet season. We therefore focused comparison between months of the seasons that have minimal annual variations. We had eight animals in each season.

The collars were equipped with 3-axis acceleration sensors that measured relative forward/backward, sideways and up/down movements of the wildebeest four times every second and averaged every 5 minutes (Krop-Benesch et al. 2012). We used the forward/backward movements as they are known to represent activity rhythms of animals (Krop-Benesch et al. 2012, Krop-Benesch et al. 2013). We developed an activity chart (Actogram) using Vectronic Activity Pattern (software1.2.3) program (Krop-Benesch et al. 2012, pg 41-43) to display mean hourly activity intensity. We also divided each day into four distinct two-hourly periods (dawn, midday, dusk and night) that we believed represent functionally different periods with regards to adaptive and predator-sensitive foraging strategies. Dawn and dusk have low temperature and enough light for foraging and visibility, while midday temperatures are too high and night has high predation risk. We used www.sunrise-and-sunset.com to estimate dawn and dusk. We extracted mean hourly activity data for these periods and used these data for relative activity analysis. Due to variations between individual collars associated with the circumference of the animal neck and the circumference of the collar (Krop-Benesch et al. 2013) we standardised the activity data for each sensor as a percentage of the maximum activity recorded by respective sensor (Hetem et al. 2012). Repeated measures ANOVA and Tukey's post-hoc tests in R (R Core Team, 2014) were used to test for differences in the seasonal and time of the day activity patterns. A two-way ANOVA with repeated measure in R (R Core Team, 2014) was used to test for difference in night activity between seasons. To test for increase in the night activity, only data set for 8pm to 11pm was used.

Results

Wildebeest activities peaked during the cooler periods of daylight hours (sunrise and sunset) but contrary to our first hypothesis, wildebeest did not display greater activity at night during the hot, late dry season compared to the wet season (Figures 1 and 2) ($F_{6,\ 16}=0.654$, $p > 0.05$). There was a little increase in their activity from 8pm until midnight in all the seasons.

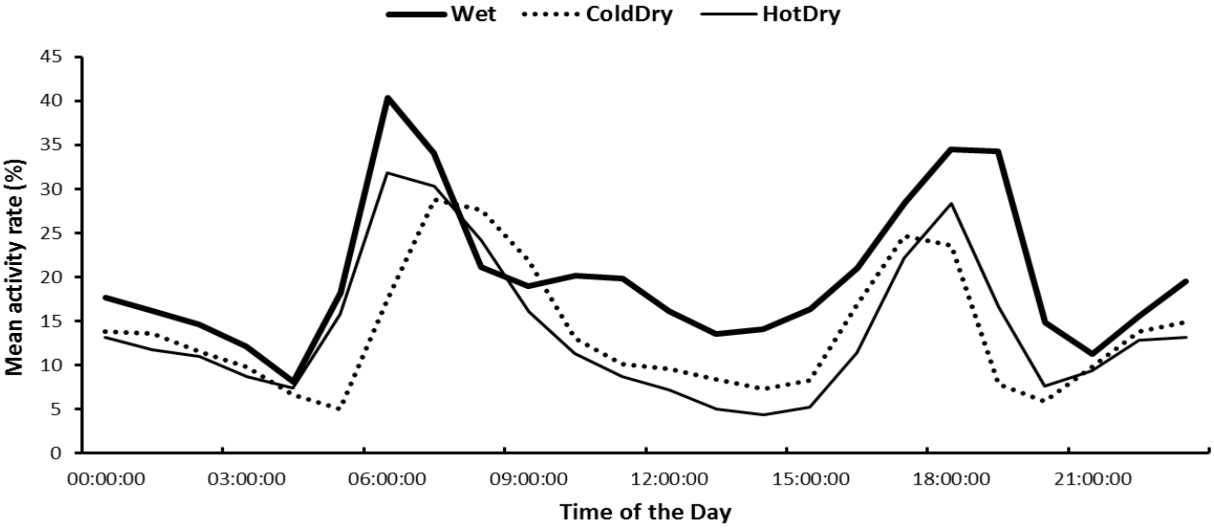

Figure 1. Seasonal patterns in mean activity levels of 10 blue wildebeest in a 24 hour cycle, in the Central Kalahari Game Reserve, Botswana between 2011 and 2014.

The peak activity levels differed significantly between seasons ($F_{2,\ 13}=11.93$, $p < 0.01$) and between different times of the day ($F_{3,\ 24}=210$, $p < 0.001$). All seasons were different from each other, with greatest activity during the wet season then the cold, early dry and hot, late dry seasons (Figure 1). There was no difference in activity between mid-day ($p = 0.727$) and mid-night ($p = 0.866$) during dry seasons; between mid-day and mid-night ($p = 0.854$) during the wet season; and between mid-day and dawn ($p = 0.638$) during the cold early dry season. The hour with the relatively lowest activity at night was 4am - 5 am in both wet and hot late dry seasons and from 4.30 am - 5.30 am in the cold, early dry season.

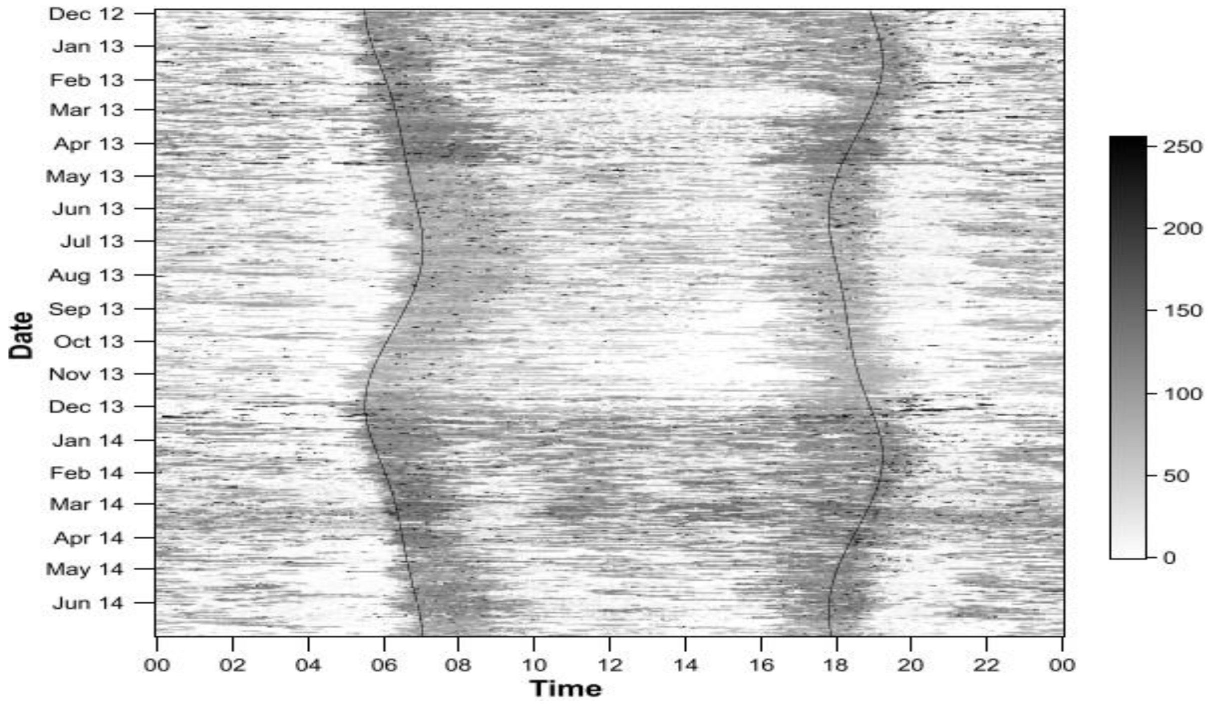

Figure 2. Actogram showing an example of one blue wildebeest activity pattern against the sunrise and sunset (vertical curves on the graph), between 2012 and 2014. The activity rates are represented by the intensity of darkness on the graph, ranging from white to dark black, as represented on the bar on the right.

Discussion and Conclusion

During the hot, late dry season forage abundance and moisture content are lowest although moisture content increases in Kalahari grasses to some extent at night (Williamson and Williamson 1985). Owing to the extreme heat during the day, wildebeest foraging activity is strictly limited to cooler periods in the early morning and late afternoon. During the hot, late dry season, when body stores of wildebeest are declining, they would likely not get enough intake of energy and protein as forage quality is at its lowest (Selebatso et al, in review) and diurnal foraging greatly restricted. We therefore predicted that wildebeest would risk predation by foraging at night to increase daily intake (the predator sensitive foraging hypothesis), as well as take advantage of increased grass moisture content. However, our results did not support the predator-sensitive foraging hypothesis. Our collared wildebeest did not display greater activity at night during the hot, late dry season compared to the wet season; instead wet season activity was highest at this time suggesting that their strategy was to conserve body stores over the dry season (Fig. 1). Unlike the Arabian Oryx (Hetem et al. 2012), which has low predation risk, the wildebeest avoided predation risks and chose to conserve energy by reducing activity in forage limited dry seasons. While food is abundant during the wet season, temperatures are generally high and thus we had expected wildebeest to rest longer in the wet season when they could eat plentiful high-quality food in early morning and late afternoon. However, wildebeest chose to maximise foraging in the wet season, probably to accumulate enough body reserves to take them through the dry season (e.g. Parker et al. 2009). Forage quality is very high in the wet season (Selebatso et al. in review) and so it makes sense to maximise intake before the quality declines. The wet season is expected to have some cloudy and so cooler days, enabling wildebeest to continue grazing into the midday. The cold, early dry season activity was even lower, with minimal activity in the morning because temperatures are low at this time (Williamson and Williamson 1985) and the sun rises a little later than in the hot, late dry season. Wildebeest, minimised activity in the dry season when conditions are bad, and only become active in the not too cold and not too hot times of the day, with evident avoidance of night activity. Our results suggest that the wildebeest obtain enough forage in the dry season or acquire enough fat reserves in the wet season, and so could afford to avoid predation by not foraging during risky periods. This adaptive strategy is expected to sustain the population as long as forage quality and quantity is sufficient to maintain the population. Periods of drought or persistence of below-average rainfall and occasional heat waves associated with climate change would probably push wildebeest to either predation or heat risk.

Contrary to findings by Knight (1991), wildebeest in the CKGR did not increase their activity during midday in any season. The CKGR wildebeest population showed reasonably high activity between the morning peak and noon in the wet season compared to other seasons. In the Kalahari Transfrontier Park (KTP), Knight (1991) reasoned that the wildebeest population had an optimal water supply and so could afford to graze longer on hot days and later dissipate the heat. The scenario at KTP suggests that the population did not get enough daily food intake during cool hours, such that they even when it was hot to maximise foraging. The CKGR wildebeest population chose to be active during the cool hours of the day to avoid heat stress but only when sufficient light enables them to detect predators.

To conclude, the foraging activity of the CKGR blue wildebeest population was constrained by high day temperatures and predation risk at night suggesting that avoidance of immediate threats (heat stress and predation) dominates the hierarchy of foraging decisions. Our findings support our alternate hypothesis that the strategy of wildebeest in the CKGR is to build body stores during the wet season and then to conserve those body stores during the dry season, while avoiding heat stress in both seasons. The persistence of this adaptive strategy may be compromised by inconsistence climatic conditions resulting from climate change and increased variability.

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Chapter Three: Water provision alters wildebeest adaptive habitat selection and resilience in the Central Kalahari, *African Journal of Ecology*, published https://doi.org/10.1111/aje.12439

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Abstract. Wildlife populations in semi-arid regions require unrestricted mobility along ecological gradients and across large landscapes to enable adaptive responses to seasonal variability and patchy resources. In the Kalahari region of Botswana, herbivore populations historically depended on seasonal access to the nutrient-rich Schwelle area in the wet season and to water from the Boteti River during drought periods. Blue wildebeest *Connochaetes taurinus* in the Central Kalahari Game Reserve (CKGR) have lost access to these key habitats due to fences and encroachment of livestock and humans. We deployed satellite collars onto ten female wildebeest in the CKGR to examine seasonal movements and habitat selection in relation to the environmental conditions and fragmented ecosystem. Wildebeest favoured open, short-grass pan habitats in all seasons, probably in response to better forage quality and lower predation risk. The ability to remain in pan habitats during the dry season was a result of artificial water provision. A wildebeest herd that had no artificial water in its home range survived the dry season, whereas those wildebeest that were accustomed to water provision died when their water points failed in the dry season. Thus, water provision altered adaptive behaviour and reduced resilience of the population to the arid environment.

Key words: *Artificial water provision, blue wildebeest*, *Kalahari, daily distance, forage quality, migration*

INTRODUCTION

Habitat loss and fragmentation compromise the resilience of wildlife populations to variable climatic conditions in semi-arid regions by restricting their mobility in response to stochastic patchy resources and habitat heterogeneity (Illius & O'Connor, 2000; Owen-Smith, 2004; Fryxell *et al.,* 2005). In the 1970's, the Kalahari region of Botswana was home to some of Africa's most abundant herds of ungulates, with an estimated 250 000 blue wildebeest *Connochaetes taurinus* a similar number of red hartebeest *Alcelaphus buselaphus* and an estimated 100 000 springbok *Antidorcas marsupialis* (DHV, 1980). Owing to the low, patchy, and unpredictable rainfall distribution of the region, these herds were extremely mobile, following a nomadic strategy in response to the rainfall-driven spatiotemporal mosaic of grazing resources in the landscape (Williamson, Williamson & Ngwamotsoko, 1988; Verlinden & Masogo, 1997). The main wet season range of the blue wildebeest, hartebeest and springbok populations in the Kalahari ecosystem was a region with a high density of saline pans (Lancaster, 1978) between the Central Kalahari Game Reserve (CKGR) and the Kgalagadi Transfrontier Park (KTP), commonly known as the Kalahari Schwelle. The saline pans of the Schwelle probably enabled pregnant and lactating females to meet their elevated mineral requirements through access to mineral-rich forage and geophagy (Williamson *et al.,* 1988; Ayotte, Parker & Gillingham, 2008).

During dry seasons and mainly drought years, wildebeest made long distance movements from the Schwelle through the CKGR to the permanent water of the Boteti River, Lake Ngami and Lake Xau (450 km), and some to the southwest towards the Nossob River (150km) (Williamson *et al.,* 1988; Verlinden, 1998). Fences in the north, east and south of the CKGR, as well as human and livestock encroachment in the Schwelle (Cooke, 1985; Williamson *et al*., 1988; Bergstrom & Skarpe, 1999) have increasingly restricted access to these various ancestral ranges. Furthermore, a recent review of national land use designated some of the Schwelle area (a part of a semi protected wildlife management area) to the west of the CKGR as livestock ranches (Department of Lands 2009). This change will potentially exacerbate the isolation of the CKGR wildebeest population from the rest of the Kalahari population in the KTP and the Schwelle. These effects of habitat loss and fragmentation, and landscape change are believed to be responsible for the decline of the Kalahari ungulate populations, especially wildebeest, over the last 30 years (Wallgren *et al.,* 2009), potentially through denied access to water, high quality forage (Sinclair & Fryxell, 1985; Fryxell, Greever & Sinclair, 1988, Oliver, Brereton & Roy, 2013) and compromised persistence of plant-herbivore interactions (Fryxell & Sinclair, 1988). Wildebeest are the most water-dependent ungulates in the Kalahari and so loss of access to water in drought years results in mass die-offs (Williamson *et al.,* 1988). Up to 80,000 wildebeest mortalities were cited in each drought year of 1961,1964 and 1970 (Owens & Owens, 1984) and more than 50,000 were recorded in 1987, primarily as a result of veterinary cordon fences blocking access to water (Owens & Owens, 1984; Williamson *et al.,* 1988).

The government of Botswana addressed the loss of access to drought ranges by establishing artificial waterholes in the CKGR in 1984 (Bonifica, 1992). Artificial water provision could remove the need to seek water, thereby selecting for a sedentary population, which may then decline due to local depletion of forage resources and ambush by carnivores around waterholes (Rosenstock, Warren & James, 1999; Shannon *et al.,* 2009). It is unknown how the population that is potentially restricted within the CKGR is utilising the landscape/habitat heterogeneity and its spatiotemporal variability within the reserve.

We studied habitat selection and movement patterns of the CKGR blue wildebeest population in response to seasonal resource variability. Pans and valleys usually have short, highly nutritious grasses compared to off-pan habitat (Milton, Dean & Marincowitz, 1992); therefore, we expected that pan-valley habitat would have higher forage quality than off-pan habitat. However, in low rainfall areas, the herbaceous layer in the pans and valleys becomes moisture-limited earlier in the dry season than that in the sandy off-pan habitats, mainly because larger pore spaces in sands result in loss of hydraulic conductivity and conservation of soil moisture much later into the dry season than in clay soils (Alizai & Hulbert, 1970; Noy-Meir, 1973). This suggests that the off-pan habitat could provide greener forage during the dry season. We also expected a decline in forage abundance in the pan-valleys due to limited moisture and grazing. We predicted that wildebeest would select pan-valley habitat in the wet season. The forage maturation hypothesis propose that herbivores aggregate to keep forage biomass at immature growth stages that are more nutritious than the mature forage (Fryxell, 1991; Wilmshurst, Fryxell & Bergman, 2000). We expected wildebeest to remain in the pan-valleys during the wet season and maintain grazing lawns that provide high quality forage and optimal levels of herbaceous biomass (Arsenault & Owen-Smith, 2008; Bonnet *et al.,* 2010). We also predicted that wildebeest would select the off-pan habitats during the dry seasons where forage is expected to be greener than in the pan-valley habitat.

Predation risk avoidance may dominate the hierarchy of decision making in habitat selection choices (Rettie & Messier, 2000). Thus wildebeest would be expected to select pan-valley habitats with their open short grassland, not only for the better forage quality of the pans but also for the lower predation risk that pans provide (Martin *et al.,* 2015). Artificial waterholes are also located in the pan-valley habitat, so in the dry season, wildebeest may be forced to use the pan-valley habitat to drink and sleep, even if they forage in the off-pan habitat, thereby extending their foraging area in the dry season. We therefore further predicted that wildebeest would cover shorter daily distances during the wet than dry seasons.

MATERIAL AND METHODS

Study Area

The CKGR northern, eastern and western boundaries and Khutse Game Reserve (KGR) defined the extent of the study area at 21º00' – 23°00' S and 22°47’ – 25°25' E (Fig. 1A). The northern and eastern boundaries of the CKGR, as well as the eastern and southern boundaries of the KGR are fenced. The CKGR and the KGR cover 52,145 km^2 and 2,550 km^2, respectively. The area is hot and dry, with extreme temperatures ranging from –6°C to 43°C in winter and summer, respectively (DHV, 1980, unpublished; Williamson & Williamson, 1985 unpublished). Mean annual rainfall ranges from 350 to 400 mm (DHV, 1980 unpublished). Although there is no permanent natural surface water in the reserves, water is provided for wildlife at thirteen solar panel powered artificial waterholes. The area is dominated by Kalahari sandy arenosols with a wide distribution of pans and valleys on the Karoo basalt rock (DHV, 1980 unpublished).

The CKGR and KGR contain five main habitats: pan and valley short grassland habitats, which are open and largely treeless with similar grass composition, and dune, interdunal and plains habitats, which are composed of savanna and woodland. For the purpose of this study, pans and valleys were classified as pan-valley habitat, and dunes, interdunal and plains as off-pan habitat because they generally have similar grass species. The herbaceous layer in the pan-valley habitat is dominated by *Leucosphaera bainesii, Eriocephalus* sp*., Sporobolus ioclados, Enneapogon desvauxii,* and *Cenchrus ciliaris*, whereas the off-pan habitat is dominated by

Anthephora pubescens, Schmidtia pappophoroides, Stipagrostis uniplumis and *Urochloa trichopus.*

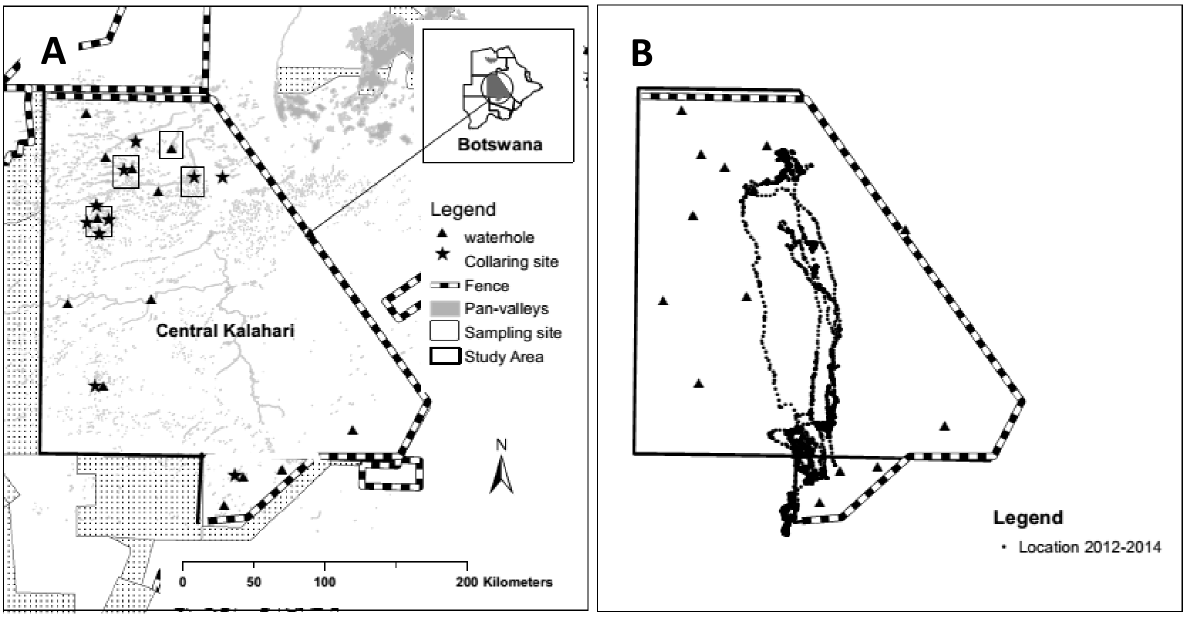

Fig. 1. Map (**A**) of the study area showing both CKGR (Central Kalahari) and Khutse Game Reserve (Khutse), vegetation sampling, waterholes and collaring sites. Map (**B**) movement locations of a migratory herd between 2012 and 2014. The wet season range was in the northern CKGR (November to March), whereas the dry season range was at southern CKGR, KGR and south-west of KGR (April to October).

The pan-valley habitat contains islands of *Acacia sp.* and *Boscia albitrunca*, and the off-pan habitat is dominated by *Rhigozum trichotomum, Catophractes alexandrii*, *Grewia sp., Acacia sp., Albizia anthelmintica, Lonchocarpus nelsii*, *Terminalia sericea* and *B. albitrunca* (Bekker & de Wit, 1991). Nomenclature for all plant names is according to Germishuizen et al. (2006). The faunal composition includes ungulates such as giraffe *Giraffa camelopardalis*, eland *Taurotragus oryx*, blue wildebeest, gemsbok *Oryx gazella*, kudu *Tragelaphus strepsiceros* and springbok. Carnivores are also present, such as lion *Panthera leo*, leopard *Panthera pardus*, cheetah *Acinonyx jubatus*, wild dog *Lycaon pictus*, spotted hyaena *Crocuta crocuta*, brown hyaena *Hyaena brunnea*, and black-backed jackal *Canis mesomelas*. Nomenclature for the animals is according to Skinner & Chimimba (2005).

Collaring and movement dataset

We fitted GPS Plus satellite collars manufactured and programmed by Vectronic Aerospace GmbH (Vectronic Aerospace, Berlin, Germany) to ten female wildebeest in different herds each ranging in size from 6 to 33 individuals, between August 2011 and July 2014. Four collars were deployed in August 2011, one each in May 2012, July 2012 and September 2012, and three in November and December 2012. All ten herds were located in the pan-valley habitat when they were darted. One of three experienced wildlife veterinarians registered with the government of Botswana carried out each darting and collaring operation, as approved by the Ministry of Wildlife Environment and Tourism through a research permit, capture and darting permits. All darted animals were adult females in good condition that were not obviously pregnant or with a young calf. Every effort was made to minimise the stress to darted wildebeest and their herds. All the animals were darted from a vehicle and we avoided darting during the hottest time of day. We drove approached herds until animals were comfortable around with our vehicle before darting, which took between ten minutes and two hours depending on the responses of the herds. The wildebeest were immobilised with 5 mg of Etorphine and 100 mg Azaperone, and the tranquilizer was reversed with 25 mg of Diprenorphine. The Etorphine and Diprenorphine were manufactured by Novartic, Switzerland, and Azaperone by Kyron laboratories, South Africa. Reusable Palmer Cap-Chur aluminium dart syringes with barbed needles were used with a Pneu-dart Model 389 remote delivery system. The animals were monitored after drug reversal, and we left as soon as they re-joined and were accepted by the herd. All the satellite collars were removed from the animals after the study, including three that had stopped transmitting prematurely.

Collars were programmed to record hourly Geographical Positioning System (GPS) fixes. We screened all the recorded GPS locations and removed locations with a high Dilution of Precision (DOP > 9) and a low number of satellites (<3D) (D'Eon &

Delparte, 2005; Lewis *et al*., 2007; Frair *et al.,* 2010). We converted all data from decimal degrees to a UTM coordinate system to allow distance and area estimations. We determined location error of the satellite collars by calculating the distance between the true location of the collar and the collar GPS locations from a stationary collar (Lewis *et al*., 2007). The location error (mean ± SD) was 6.8±4.9m. High mortality of study animals (associated with water availability as discussed later in the results), combined with the overall small size of the study population, led to fewer than five datasets during any one season; we therefore used cumulative seasonal data from 2011 to 2014.

Seasonal analysis

We divided each year into wet, early dry and late dry seasons, based on average rainfall and temperature patterns for the area, which influence surface water availability and forage conditions. Wet and late dry seasons are usually very hot (up to 43^0C) while early dry season is very cold (-6^0C). Due to high variability of the onset date of the three seasons, we focused our analysis on two peak seasonal months to create a clear distinction between seasons. We used January and February for the wet, June and July for the early dry, and September and October for the late dry seasons, respectively.

Forage quality and quantity between habitats

During each season, we randomly sampled vegetation in five 0.5 m x 0.5 m quadrats from eleven sites in each of the two habitat types: pan-valley and off-pan. The pan-valley sites were in northern pan-valley system, and the off-pan sites were around these pan-valley sites (Fig. 1A). At each site, the first quadrat was thrown randomly to provide a starting point and the other four quadrats were systematically located 5m from the first quadrat in the four cardinal directions. We recorded the height (to the tip of inflorescence or culm) of five grasses in each quadrat, selected at random. Grass samples were clipped to 1 cm above ground from all quadrats. Due to extremely low amounts of grass in some seasons and habitats, grass samples from the quadrats were combined for each site. We air-dried the samples in the field and further dried them in an oven at 60^0C for 48 hrs. Dry biomass was used as a measure of forage quantity. We ground each sample and mixed it well to get a homogeneous representative subsample and analysed it for crude protein (nitrogen %), with a LECO nitrogen analyser at the Biological Sciences Department, University of Botswana. We then analysed subsamples for mineral content (phosphorus, sodium and calcium), using ICP-AES spectrometry at the Okavango Research Institute, University of Botswana.

We used generalised linear mixed models (lme4 package; Bates *et al*., 2015), in R version 3.2.4 to compare grass quality (protein, calcium, sodium, and phosphorus) and quantity (biomass and height) between habitats and seasons. Response values were all positive but did not follow a normal distribution, so we used a gamma distribution. Habitat, season and the interaction between the two were used as fixed effects and replica within site was used as a nested random effect.

Habitat selection

Shapefiles of pans and valleys were obtained from the Department of Survey and Mapping, and used to develop a habitat map at a scale of 1: 3,600,000. We used the “Minimum Bounding Geometry” tool in ArcGIS 10.3 to calculate 100 % Minimum Convex Polygons (MCP) from seasonal movement data to determine the potential area available to each animal. We used the movement-based kernel density estimation (MKDE) method from the adehabitatHR package in R (R Development Core Team, 2015) to calculate the seasonal utilisation distribution (UD) and home range (HR) for each individual (Benhamou, 2011). We set the minimum distance threshold (MDT) to 10 m, the distance below which the animal was considered to have been inactive or resting and set the minimum smoothing parameter to 30 m. We used UD-weighted grids within the HRs to estimate pan-valley and off-pan use and availability to determine third order habitat selection patterns (Johnson, 1980). We used Jacobs' index to calculate habitat selection ratios (Jacobs, 1974; Kauhala & Auttila, 2010)

$$(D) = (r - p)/(r + p - 2rp)$$

where r is the proportion of habitat used and p the proportion of habitat available. D varies from -1 (avoidance) to +1 (preference), and values close to zero indicate that the habitat is used in proportion to its availability. We used Multivariate Analysis of Variance (MANOVA) in R version 3.2.4 to determine whether selection ratios differed between seasons.

Daily distance analysis

We used hourly location data from collared wildebeest to calculate the minimum daily distance covered. We adopted the method of distance calculation from Ensing *et al.,* (2014), as modified in http://www.movable-type.co.uk/scripts/latlong.html, to calculate hourly distance, and summed the hourly distances for each day and for each animal. We used generalised linear mixed models (Bates *et al.,* 2015) to compare the daily distance covered between seasons, with the fixed effect of year to account for annual differences and the random effect of individual. During the study, four artificial waterholes used by study animals dried up due to borehole breakdown and there was some observed change in the foraging behaviour of the animals. We compared our results with and without the affected collared animals. We also demonstrated the effects of changing water availability, by comparing wildebeest movement a month before and after the waterhole dried up. The generalised linear mixed models (lme4 package; Bates et al., 2015), in R version 3.2.4, were used to compare pre- and post-period waterhole drying periods. Response values were all positive but did not follow a normal distribution, so we used a gamma distribution. All statistical analyses were done in R 3.2.4 (R core team, 2015).

Model selection

We ran all possible combinations of models for the above variables (except for habitat selection analysis) and identified the most parsimonious based on Akaike's Information Criterion (AIC; Akaike, 1974). We considered models to be competitive if their AIC values were within two units of the best model, and slightly competitive if there were between 3 and 7 (Burnham & Anderson, 2002).

RESULTS

Forage quality

Our results confirmed that forage quality in terms of protein, phosphorus and calcium, in the pan-valley habitat was higher than in the off-pan habitat, except during the late dry season. The full models, with or without an interaction term, provided the best fit for protein, calcium and phosphorus (Table 1). Protein content decreased from the wet season to the early dry and late dry seasons in the pan-valley habitat, but the decrease in the off-pan habitat was small between the dry seasons (Fig. 2A).

In the pan-valley habitat, calcium decreased from the wet season to the early dry and late dry seasons, but did not change between the early dry and the late dry seasons in the off-pan habitat (Fig. 2B). Phosphorus was higher in the wet than the early dry and the late dry seasons. Phosphorus was higher in the in the pan-valley than off-pan habitat (Fig. 2C). For sodium, the most parsimonious model included both fixed effects of season and habitat. Sodium was higher in the wet than the early dry season and the late dry season (Fig. 2D).

Table 1. Ranking of possible models for forage quality and quantity. **Delta (Δ) AIC** = difference between model AIC and lowest AIC in the model set. **ω** = Akaike model weight, "weight of evidence" in favour of model, adding to 1. **k** = number of estimable parameters in the model. **Deviance** = measure of model fit. The model covariates include habitat and season. Only models with Δ_{AIC} values less than 4 units and the null model are presented.

	Model variables	**Δ_{AIC}**	**ω**	***k***	**Deviance**
Protein	Habitat*Season	0	0.737	3	2.009
	Habitat+Season	2.203	0.245	3	2.258
	Null	45.239	0.000	2	4.521
Calcium	Habitat*Season	0	0.706	3	9.460
	Habitat+Season	3.377	0.130	3	10.601
	Season	2.919	0.164	2	10.547
	Null	28.066	0.000	2	16.294
Phosphorus	Habitat+Season	0	0.4724	3	18.759
	Habitat*Season	1.638	0.2083	3	20.425
	Season	0.7838	0.3193	2	20.756
Sodium	Habitat+Season	0	0.452	3	28.843
	Habitat*Season	1.118	0.258	3	30.095
	Season	0.884	0.290	2	31.167
	Null	46.171	0.000	2	63.344
Height	Habitat*Season	0	1	3	509.977
	Null	102.967	0.000	2	563.469
Biomass	Habitat*Season	0	0.984	3	103.718
	Null	23.159	<0.001	2	154.405

For grass biomass, the model with the best fit was the global model, which included the fixed effects of season and habitat, and the interaction between the two terms. Biomass was lower in the pan-valley habitat than in the off-pan habitat, but within the off-pan habitat there was no seasonal difference. In the pan-valley habitat there was a difference between the wet and early dry seasons but not between the early dry and late dry seasons (Fig 3A).

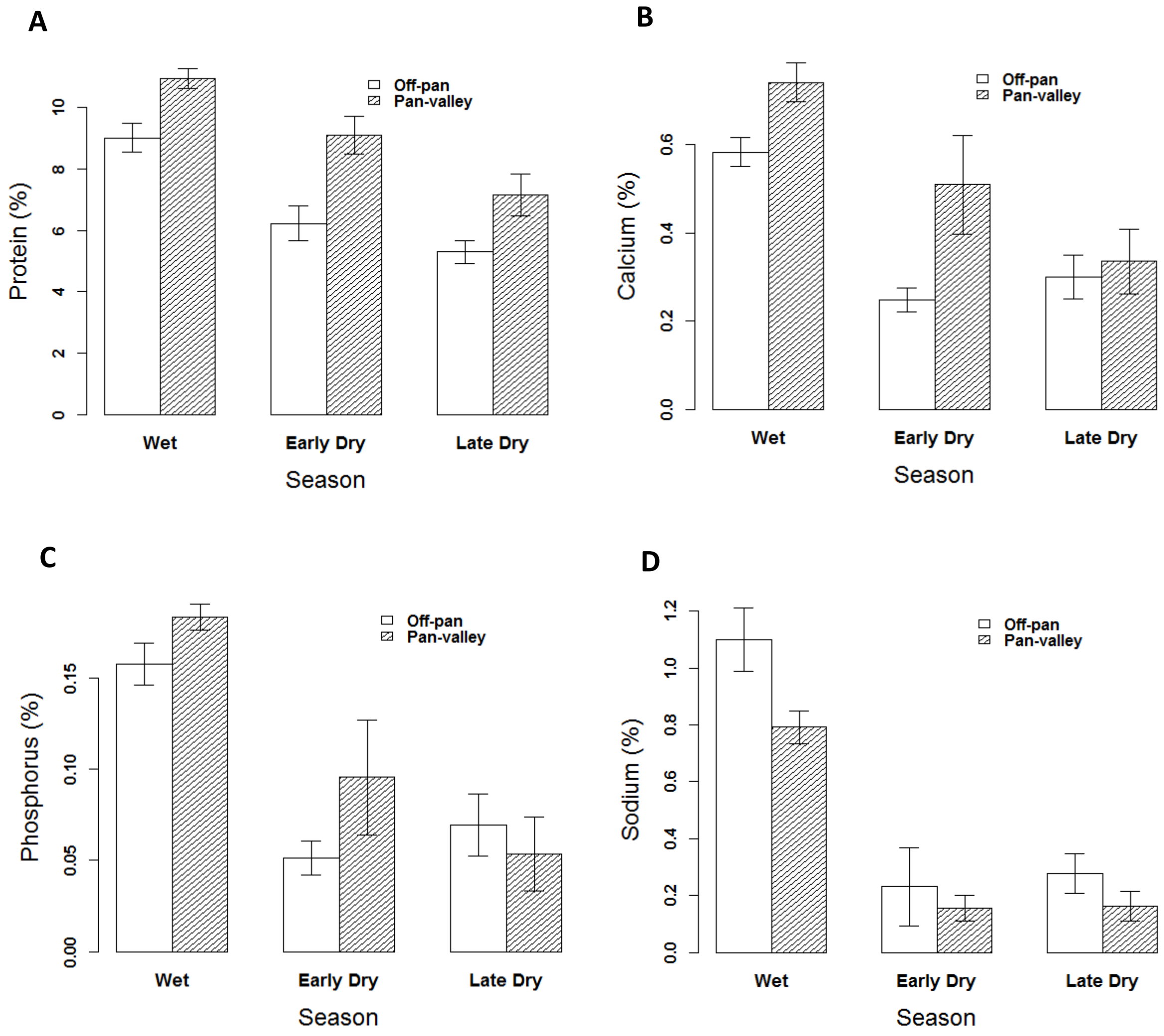

Fig. 2. Seasonal mean dry mass percentage (±SE) for grass crude protein (**A**), calcium (**B**), phosphorus (**C**) and sodium (**D**) between pan-valley and off-pan habitats in the CKGR and KGR.

For grass height, the model with the best fit was the global model, which included the fixed effects of season and habitat, and the interaction between the two terms. Grass height was lower in the pan-valley than in the off-pan; it decreased from the wet season to the early dry season in the pan-valley habitat, but increased from wet to early dry in the off-pan habitat (Fig. 3B). Therefore, sandy off-pan habitats had higher grass biomass and height than pan-valley habitats throughout the year.

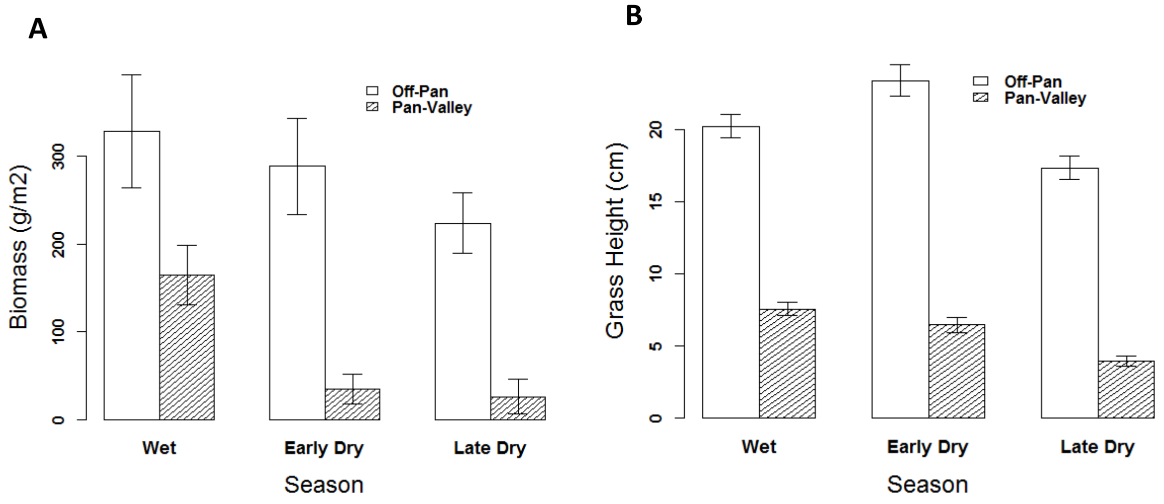

Fig. 3. Seasonal mean (±SE) values for grass dry biomass (**A**) and height (**B**) in between pan-valley and off-pan habitats in the CKGR and KGR.

Wildebeest habitat selection

Wildebeest strongly selected for the pan-valley habitat in the CKGR, with a mean (± SE) Jacob's index of 0.64 ± 0.065, 0.68 ± 0.10, and 0.60 ± 0.10 in the wet, early dry and late dry seasons, respectively. However, habitat selection did not change significantly between seasons (Table 2). Although most herds selected the pan-valley habitat throughout the year, one was migratory, occupying distinct seasonal home ranges: wet, early dry and late season ranges in the northern CKGR, the southern CKGR and KGR, and outside the western KGR, respectively (Fig. 1B). There was a distance of over 200 km between the wet and dry season home ranges.

Daily distance

One wildebeest covered extreme daily distances at an average of 40.56 ± 15.64 km/day during the late dry season of 2011, with a longest minimum daily distance of 84.48 km. Data from this animal were not included in the analysis for the population because it was a substantial outlier.

Table 2. MANOVA results for seasonal comparison of habitat selection ratios. No significant results found.

Season	Habitat	MANOVA output
Wet vs Early Dry	Overall	$\text{Pillai}_{2,14}$ = 0.0983, p = 0.510
	Pan-Valley	$F_{1,14}$ = 0.848, p = 0.775
	Off-pan	$F_{1,14}$ = 0.102, p = 0.754
Wet vs Late Dry	Overall	$\text{Pillai}_{2,15}$ = 0.237, p = 0.131
	Pan-Valley	$F_{1,15}$ = 0.124, p = 0.730
	Off-pan	$F_{1,15}$ = 1.401, p = 0.254
Early vs Late Dry	Overall	$\text{Pillai}_{2,11}$ = 0.0580, p = 0.720
	Pan-Valley	$F_{1,11}$ = 0.252, p = 0.625
	Off-pan	$F_{1,11}$ = 0.558, p = 0.469

Wildebeest covered mean ± S.E. daily distances of 6.89 ± 0.15 km, 7.59 ± 0.28 km, and 6.71 ± 0.17 km during the wet, early dry, and late dry seasons, respectively. The most parsimonious model included the effect of year and season; the null model was not competitive (Δ_{AIC} = 0, ω =1, k = 8, Deviance = 346.2347). Wet and early dry season distances were not different, whereas the late dry season distance was shorter than in the early dry season. Daily distances in late dry season of year 2011, early dry season of 2012 and wet season of 2013 were longer than the other years, respectively. When data from wildebeest that were affected by waterholes drying up were included, mean daily distances increased, and the wet season distance was not different from the late dry season, whereas the early dry distance was longer than the other seasons. Daily distances early dry season of 2012 and wet season of 2013 were longer than the other years, respectively.

For daily distances travelled before and after the waterholes dried up, the most parsimonious model included the effect of water availability; the null model was not competitive ((Δ_{AIC} = 0, ω =1, k = 2, Deviance = 126.538). Distance travelled was shorter before (5.93 ± 0.97) than after (13.35 ± 0.25) the waterhole dried up. Seven (70%) of the ten collared animals made long distance movements (up to 275 km) when the waterholes they depended upon dried up. Five (71%) of the seven collared wildebeest that left their range after a waterhole dried up died before finding an alternative waterhole. Lions killed three collared wildebeest inside the reserve, while two left and died outside the reserve, one from apparent dehydration and the other from unknown causes.

DISCUSSION

Our results show that wildebeest strongly select for the pan–valley habitat in the CKGR throughout the year. Pans were favoured year-round because of their shorter grasses, and higher crude protein, calcium and phosphorus content. Unlike in other areas where forage quantity during the dry season influenced habitat selection of large herbivores (Anderson *et al.,* 2005; Saïd *et al.,* 2009), the decline in abundance and quality of forage from the wet to dry seasons did not influence wildebeest foraging patterns. Thus, they are not limited by forage quantity in this ecosystem. Wildebeest are adapted for foraging on relatively short swards grasslands (Murray & Illius, 2000; Wilmshurst *et al.,* 2000; Arsenault & Owen-Smith, 2008), which may explain why they did not select taller grass in the off-pan habitat, even during the dry season.

The key wet season range of wildebeest in the Serengeti is a vast treeless saline grassland, similar in grass composition and function to the smaller-scale pans in the CKGR. Most pans in the CKGR are dominated by halophytic grasses such as *Sporobolus ioclados,* as are the short grass saline plains of the Serengeti (McNaughton, 1983), suggesting functional similarities between these key wet season ranges. Habitats selected by wildebeest in the Kruger National Park (Grant & Scholes, 2006; Yoganand & Owen-Smith, 2014) and by some zebra in northern Botswana (Fynn, Chase & Röder, 2014) show similar functional similarities, with relatively high protein and phosphorus content. A higher concentration of protein and minerals help to meet the elevated resource demands of pregnant and lactating females during the wet season (Kreulen, 1975; Murray 1995; Voeten *et al.,* 2010) and build body stores from abundant forage to survive the dry seasons (Parker, Barboza & Gillingham, 2009).

Habitat quality is likely to be a key determinant of habitat selection for Kalahari ungulates (e.g. Milton *et al.,* 1992), but it is difficult to disentangle the relative influence of habitat quality and anti-predator behaviour on selection for pan habitats (Fryxell, 1991; Yoganand & Owen-Smith, 2014). The open high-visibility nature of the pans, greatly reduces predation risk (Hernandez & Laundré, 2005; Valeix *et al.,* 2009), but strongly co-varies with the higher forage quality of the pans. Therefore, predation risk could also contribute to selection for the pan-valley habitat, especially at night (Martin *et a*l., 2015), when predators are most active (Hayward & Slotow, 2009). All the predation events on collared animals were in the off-pan habitat, emphasizing that pan-valleys provide a much safer habitat. Therefore, the extent and hierarchy of the influence of forage quality and predation-risk factors cannot be easily defined and ranked. Thus, in the Kalahari and other savanna ecosystems, wildebeest take advantage of the low predation risk nature and higher forage quality of the pan habitats, thereby maintaining growth and reproductive processes and reducing predation events.

Our results also suggest that water is a critical component of wildebeest home ranges, especially when they become accustomed to artificial water provision (Western, 1975; Williamson *et al.,* 1988; Owen-Smith, 1996), and therefore influences movement patterns across the landscape (Smit, Grant & Devereux, 2007). During the wet season, the pan-valley habitat had above-optimal grass height and biomass for a grazer the size of a wildebeest (Wilmshurst *et al.,* 2000), but wildebeest remained on the pans during the dry season when grass height and biomass had dropped to 25 gm^{-2}, well below optimal levels (94 gm^{-2}) for wildebeest (Wilmshurst *et al.,* 2000). Provision of artificial water points in the pans seemed to have influenced the dry season movement patterns. One wildebeest herd at a pan without a water point migrated away during the dry season, and other wildebeest left pans when artificial water points failed during the dry season. This suggests that water availability during the dry season was a key limiting factor that influenced habitat selection.

The migratory herd moved over 200km from its wet season range to the southern CKGR, apparently attracted to a high abundance of tsamma melons *Citrullus lanatus* and gemsbok cucumber *Acanthosicyos naudinianus* (pers. obs.), and to a burned area during the late dry season. The southern migration of this herd might be driven by a need for water provided by the tsamma melons and the likelihood of green regrowth following fires. Moisture provided by these melons could explain why this herd survived the entire dry season without access to a waterhole. Knight, Knight-Eloff & Bornman (1987) suggested that wildebeest in the KTP depended on these water-bearing plants when they did not have access to water. In support of this, all the other herds that had access to artificial water were sedentary and did not leave the high quality pan-valley habitat as long as water was available. This suggests that water provision has resulted in a loss of adaptive foraging knowledge in water-dependent individuals because all those that were unable to find alternative water points after the water point in their favoured pans dried up died, whereas the migratory herd survived both dry seasons without evidence of accessing a waterhole.

Contrary to our predictions, but consistent with findings by Hopcraft *et al.* (2014) in East Africa, wildebeest daily movement distances were smaller in the late dry season than in the other seasons, though not significantly different from the wet season. The late dry season was when forage availability was lowest and temperatures were generally very high. Wildebeest probably attempted to conserve energy and avoid heat stress during the late dry season by minimising their movements (Selebatso, Fynn & Maude, 2017). The inconsistent availability of water seems to not only affect habitat selection, but also energy expenditure and risk, as the wildebeest had to extend their daily distances following the loss of water. The non-migratory wildebeest made long distance movements after the artificial waterholes in their home ranges dried up. The drying up of artificial waterholes seemed to push wildebeest to take greater risks through increased exposure to predation and the potential to lose condition in an attempt to seek alternative sources of water. Collared wildebeest made exploratory searches for alternative water sources, and the majority died during the search. Our results emphasise the need for water provision, especially that removal of anthropogenic factors such as fences and land use changes are highly unlikely. The provision of artificial water for wildlife in arid environments disrupt natural processes (Andrew & Lange, 1986; Thrash, 1998; Grant et al., 2002), but when access to key resources are restricted, much of the natural ecosystems resilience is lost (Primack, 2002; Fahrig, 2007). Maintenance of water dependent species in drylands may therefore depend on such artificial water provision, especially given the continued human induced habitat fragmentation and connectivity loss. Furthermore, Owens and Owens (1984) reported high mortalities of wildebeest due to illegal hunting and range degradation by livestock in and around Lake Xau, where most of the wildebeest went in the last recorded drought migration. We therefore emphasise the need for timely maintenance of existing waterholes in the CKGR to reduce future mortalities that could result from the drying of the waterholes.

In conclusion, high quality forage in pans and valleys, combined with access to water and reduced predation risk, are important determinants of the habitat selection and movement patterns of Kalahari wildebeest. Seasonal forage availability, temperature and water availability limited the movement patterns and home ranges. Artificial water provision in arid ecosystems is important to compensate for lost access to natural water sources; however, it promotes a sedentary strategy and loss of adaptive resilience to shocks, such as water points failing. Our results reveal how loss of connectivity and access to seasonal resources could lead to complex consequences for species reliant on access to distinct seasonal ranges and key resources. If artificial water development is a necessary option for wildlife management in arid environments, a clear maintenance program is required to ensure consistency in the provision of water.

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Chapter Four: Sympatric ungulates dietary overlap: Food resource competition for a blue wildebeest population in the Central Kalahari, Botswana *African Journal of Wildlife Research*, Under Revision

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Abstract. *Competition among herbivores for limiting forage resources can affect the viability of populations and lead to range displacements. Blue wildebeest in the Central Kalahari Game Reserve (CKGR) depend on high-quality grasslands in pans and valleys, a limited and key habitat for them, gemsbok and springbok. We used microhistological techniques on dung samples of these ungulates to determine their seasonal diet composition. Our results showed that wildebeest face competition from gemsbok and springbok, which deplete favoured grasses, leading to competition. Protein-rich short grasses, such as* Sporobolus ioclados *and* Enneapogon desvauxii*, dominated the diets of all three species during the wet season. During the dry season, wildebeest expanded diet breadth to less nutritious grasses, whereas gemsbok and springbok switched to dicots. Thus, wildebeest are more negatively affected among the three species by inter-specific competition because they cannot switch to relatively, high-quality browse. In addition, springbok, can likely tolerate a lower height of grass than wildebeest. The fragmentation from the core wet season range of the Schwelle therefore limits the ability of the CKGR wildebeest population to adapt spatially to local competition. This may contribute to the decline of their population. This demonstrates the need to restore and maintain corridors to the Schwelle for the survival of the wildebeest population in the Kalahari.*

Keywords. Adaptive foraging, Central Kalahari, Diet selection, Microhistology, Seasonal resources

INTRODUCTION

Herbivores face the challenge of consuming sufficient energy and protein in the face of severe spatial and temporal variability of resources in African savannas (Owen-Smith, 2002; Fryxell et al., 2005; Hopcraft, Olff, & Sinclair, 2010). Superimposed on this variability and limitation, inter-specific competition or facilitation may further influence the dynamics of energy and protein intake (Vesey-FitzGerald, 1960; Verweij, Verrelst, Loth, Heitkonig & Brunsting, 2006; Fynn et al., 2016). In resource-limited ecosystems, dietary overlap among sympatric species may indicate interspecific competition for food (de Boer & Prins, 1990). However, for herbivores, dietary overlap may result in either competition or facilitation depending upon how one species modifies grass height in relation to the other species' optimal height requirement, which is determined by body size and mouth anatomy (Murray & Illius, 2000; Wilmshurst, Fryxell & Bergman, 2000; Arsenault & Owen-Smith, 2008). Competition for forage results in reduced intake, growth rates (Derner, Detling & Antolin, 2006; Odadi Karachi, Abdulrazak & Young, 2011), and home range restriction or displacement (Grobler, 1981; Bhola et al., 2012). However, facilitation may also play a critical role in maintaining habitat quality and the viability of populations, especially for smaller-bodied herbivores such as gazelles (Western & Gichohi, 1993; Fryxell et al., 2005)

Body size determines absolute resource requirements (Illius & Gordon, 1987; Wilmshurst et al., 2000). A smaller-bodied herbivore is more tolerant of competition for grazing (arising from reduced forage height and biomass under grazing) than larger-bodied species because of their lower absolute resource requirements (Illius & Gordon, 1987; Wilmshurst et al., 2000). For example, both springbok and wildebeest favour short-grass habitats but the smaller-bodied springbok likely maintains weight better on very short grass owing to its much smaller body size (Illius & Gordon, 1987; Wilmshurst et al., 2000). Conditions affecting grass regrowth following defoliation also influence the potential for competition. For example, grass cannot regrow during the dry season and rates of regrowth will be much lower on shallow dry soils or saline soils compared with deeper moister soils. As a result, competition is generally greater during the dry season owing to forage depletion in the absence of regrowth (Derner et al., 2006; Augustine & Springer, 2013; Fynn et al., 2016).

The strength of density-dependent feedbacks on herbivore population growth tends to decline with increasing access to spatial heterogeneity, which facilitates adaptive foraging in relation to environmental variability and competition for grazing (Wang et al., 2006; Hobbs et al., 2008). Different resources, distributed on environmental gradients at landscape and regional scales (Hobbs et al., 2008; Hopcraft et al., 2010; Fynn et al., 2016), play variable roles in enabling herbivores to adapt to environmental variability (Owen-Smith, 2002). Thus, restricting herbivore movements reduces access to critical resources seasonally and increases spatial coupling of herbivores to their resources (Hobbs et al., 2008; Fynn, 2012). Consequently, ecosystem fragmentation should increase competition for forage, negatively impacting body stores and associated survival, reproduction, and ultimately population size (Ottichilo, De Leeuw & Prins, 2001; Parker, Barboza & Gillingham, 2009; Voeten, van de Vijver, Olff, & van Langevelde, 2010).

Wildebeest are short grass grazers (Arsenault & Owen-Smith, 2008) and in the sand-dominated Kalahari ecosystem they prefer pans and valley habitats, which have saline lacustrine soils dominated by high-quality short grasses (Selebatso et al., 2017). These habitats represent less than 3% of the Central Kalahari Game Reserve (CKGR), but represent critical habitats not only for wildebeest but also for other ungulates, such as springbok (Antidorcus marsupialis) and gemsbok (Oryx gazella) (Milton, Dean, & Marincowitz, 1992).

Prior to erection of fences, ungulates in the Kalahari ecosystem could move over vast areas between the CKGR, the Schwelle region (the favoured wet season range with the highest pan density and open grassed woodland), and the adjacent Kalahari Transfrontier Park (KTP). However, migration corridors between these regions are becoming increasingly restricted and ungulates in the CKGR no longer appear to migrate between these regions (Selebatso et al., 2017). Exclusion of the CKGR wildebeest and springbok populations from the historic wet season range in the Schwelle limits those populations to the CKGR, thereby likely increasing competition for resources. Knight (1991) reported overlap in the wildebeest and gemsbok diet in the KTP. We therefore predicted a high level of interspecific diet overlap, a potential source of competition for the limited high-quality forage in the pans and valleys.

We investigated seasonal diets and dietary overlap between sympatric herbivores (wildebeest, gemsbok and springbok) to understand how interspecific competition may affect wildebeest populations in the CKGR. Our specific objectives were to determine: (1) Seasonal diet composition for the three herbivores; (2) Seasonal diet preference for wildebeest; (3) Protein content in wildebeest diets; (4) Seasonal niche breadth; and (5) Seasonal diet overlap. We predicted (i) that diet herbivores and preference for wildebeest would vary between seasons as forage resource quality and quantity varied; (ii) that protein content in wildebeest diets would decrease as forage quality decreased in the dry season; (iii) an increase in diet breadth for all species between wet and dry season; (iv) greater overlap in the wet season, when the 3 ungulates prefer pan habitats (Knight, 1991; Milton et al., 1992); and iv) greater diet overlap between wildebeest and gemsbok given their similar body masses (Illius & O’Connor, 2000).

MATERIAL AND METHODS

Study area

The Central Kalahari Game Reserve’s boundaries defined the extent of the study area [Figure 1), covering 52,145 km^2. The area falls within 21°00' – 23°00' S and 22°47.5’ – 25°25' E. The CKGR is in the semi-arid and hot region, with temperatures ranging between –6°C to 43°C in winter and summer, respectively (DHV, 1980; Williamson & Williamson, 1985). Mean annual rainfall ranges from 350 to 400 mm (DHV, 1980). The area has a wide distribution of pans and valleys. Vegetation is defined by two main habitats, pan-valley and off-pan habitat. The off-pan habitat includes all vegetation types outside the pans and valleys, with soils having lower clay and fertility compared to pans and valleys. The herbaceous layer in the pan-valley habitat is dominated by *Cenchrus ciliaris*, *Enneapogon desvauxii*, *Eriocephalus* spp., *Leucosphaera bainesii*, *Sporobolus ioclados*, and *Tragus berteronianus*, whereas the off-pan habitat is dominated by *Anthephora pubescens*, *Schmidtia pappophoroides*, *Stipagrostis uniplumis,* and *Urochloa spp*. The pan-valley habitat has islands of *Acacia* spp. and *Boscia albitrunca*, whereas *Rhigozum trichotomum*, *Catophractes alexandrii*, *Grewia* spp., *Acacia* spp., *Albizia anthelmintica*, *Lonchocarpus nelsii*, *Terminalia sericea and B. albitrunca* dominate the off-pan habitat.

The wildlife population includes herbivores such as giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), blue wildebeest, gemsbok, kudu (*Tragelaphus strepsiceros*) and springbok and the most common carnivores include lion (*Panther leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), spotted (*Crocuta crocuta*) and brown hyaena (*Hyaena brunnea*) and black-backed jackal (*Canis mesomelas*).

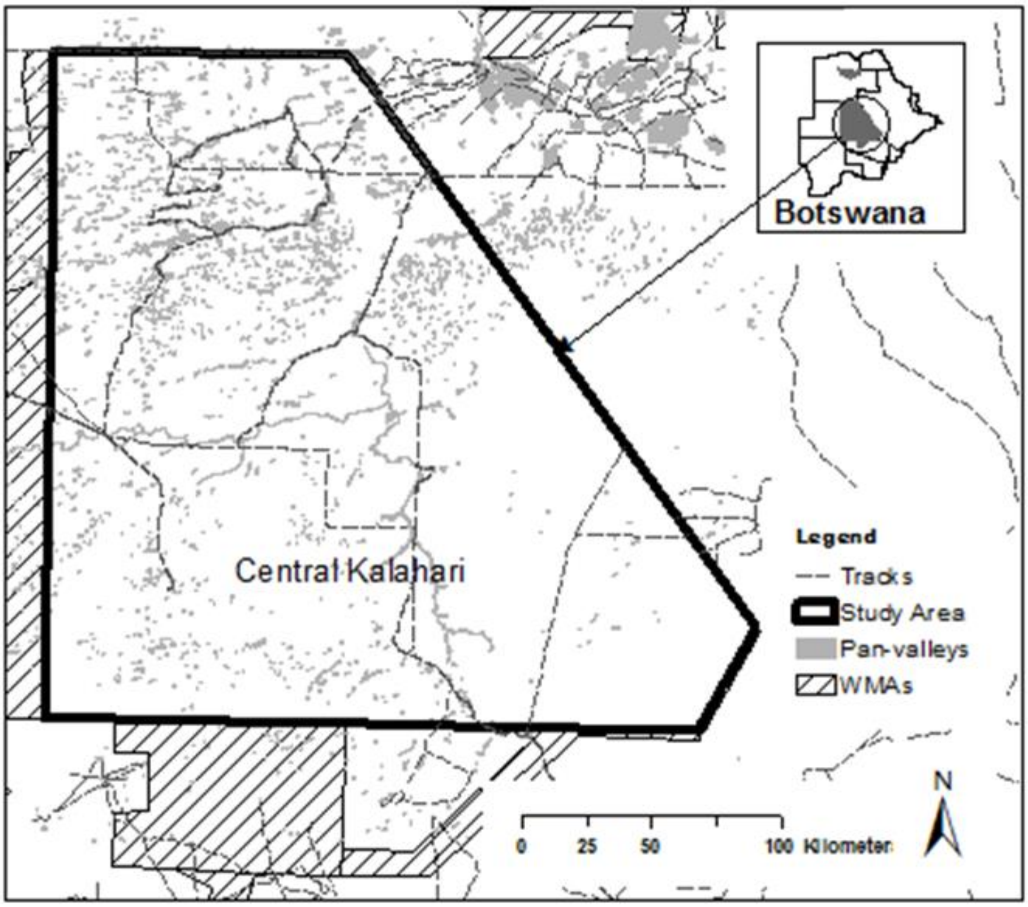

Figure 1. Map of the study area showing the Central Kalahari Game Reserve

Methods

Data collection

To determine vegetation composition and availability of different grasses to herbivores, we randomly sampled vegetation in five 0.5 m × 0.5 m quadrats from 11 sites in each of two habitat types (pan-valley and off-pan) during the wet and dry season. The wet season ranges between December and March, whereas the dry season ranges between April and November, basing on long-term average rainfall patterns (DHV, 1980, Bonifica, 1992). At each site, we threw the first quadrat randomly to provide a starting point, with the other four quadrats systematically located 5 m from the first quadrat in the four cardinal directions. We estimated aerial cover (as a proportion of the quadrat area) of each grass species rooted within the quadrat. Average cover from all the quadrats was used to represent forage availability for each site. We compared forage availability with use by the wildebeest (% in the diet) to determine food preference.

We determined diet composition of three ungulates (wildebeest, springbok and gemsbok) using microhistological analysis of faecal samples. We initially attempted to use direct observation of diet selection, but found it impossible to get close enough to individuals to clearly observe species selected. Thus, while some researchers criticise microhistological techniques (Holechek, Vavra & Pieper, 1982), it is often the only viable method and has been widely used for decades to determine herbivore diet composition (Bartolome, Franch, Gutman & Seligman, 1995; Jung, Stotyn & Czetwertynsk, 2015; Mphinyane, Tachela & Makore, 2015).

We collected samples of leaves from common grass species in the study area to prepare species reference slides. We scraped grass leaves with a sharp scalpel blade to obtain the lower epidermal layer and mounted the epidermal layers on microscope slides. We located wildebeest and collected at least five fresh (less than 2 hours old) dung samples from five different herds. We also collected five samples from the nearest (within 2 km) gemsbok and springbok herds near the same vegetation sampling site. We collected dung samples in the dry (August and September 2013) and wet season (January 2014), resulting in five samples per species per season. We sun dried the faecal samples in the field and then oven dried them at 60 ^{o}C for 48 hrs in the laboratory before grinding them with a 1 mm screen in a Wiley mill. A 1 g of subsample from the composite sample was placed in a test tube with 5 ml concentrated nitric acid (HNO_3). We boiled the solution for 90 seconds and then diluted the suspension with 100 ml of water, before boiling it for another 2 minutes. To minimise bias associated with fragment sizes, we washed the samples with water and passed them through a sieve with 1 mm and 0.25 mm openings. We placed subsamples of fragments that were between 1 mm and 0.25 on a microscope slide with glycerine. We then covered the sample and examined it under a microscope (Bartolome et al., 1995). We classified 100 epidermis fragments from each subsample to species level, where possible. We determined diet composition by estimating the area of each fragment using a stage micrometer. We then calculated the proportion of each plant species in the diet as the sum of the fragment area of each plant species relative to the summed area of all 100 fragments (Jung et al., 2015). All dicotyledonous species were lumped as single group (dicotyledon) as we focused primarily on wildebeest, a grazer.

We assessed diet quality of the wildebeest by determining the crude protein content of the dung samples using a LECO nitrogen analyser at the Biological Sciences Department, University of Botswana. We also determined the protein content of grass species whose leaves were used as reference samples.

Data Analysis

We considered plant species (or class) that contributed ≥ 10 % to the diet an important forage resource for the animal in that season (Jung et al., 2015). We used a paired t-test to compare these important forage resources between seasons for each ungulate.

We used Jacobs' Preference Index (Jacobs, 1974) to determine the diet preference for the wildebeest. We did not estimate preference for springbok and gemsbok because that was not our objective. The Jacobs Preference Index = $(u - a)/(u + a) - (2 \times u \times a)$, where "u" is the proportion of grass species in the diet, and "a" is the proportion of the grass species available. Jacobs' index varies from -1 (avoidance) to +1 (preference), and values close to zero indicate that the grass was used in proportion to its availability.

We calculated seasonal Food Niche Breadth (FNB) for all the three ungulates using the Levin's measure of niche breadth [adopted from 34]. The FNB = $((\sum p_i^2)^{-1}-1)/(n-1)$, where “n” is the number of species in the diet and “p_i” is the relative proportion of fragments of the i^{th} species). FNB varies from 0 when “a” species dominates to 1 when there is equal representation of species.

We used modified Morisita index of similarity, C_λ, (Morisita, 1959) to determine diet overlap between ungulates for the wet and dry season. $C_\lambda = (2 \sum n_{ij} n_{ik}) / [(\lambda_1 + \lambda_2) N_j N_k]$, where n_{ij}, n_{ik} = Number of individuals of species *i* in sample *j* and *k; J* and *k* can represent any two ungulates (wildebeest, gemsbok or springbok*); $N_j = \sum n_{ij}$*= Total number of individuals in sample *j; $N_k = \sum n_{ik}$* = Total number of individuals in sample *k;* $\lambda_1 = \sum [n_{ij} (n_{ij}-1)]/N_j(N_j-1)$ and $\lambda_2 = \sum [n_{ik} (n_{ik}-1)]/N_k(N_k-1)$ (Krebs, 1999). This widely used method compares similarities in composition (Jung et al., 2015; Mphinyane et al., 2015) with low bias (Wolda, 1981). We classified diet overlap values of $C_\lambda < 0.26$ as low, $C_\lambda = 0.26–0.74$ as moderate, and $C_\lambda > 0.74$ as high, as described in Jung *et al.,* (2015). We used paired *t*-tests to compare diet selection for grass species by each herbivore in the wet and dry season; to test for seasonal difference in diet quality for wildebeest; and to test dietary overlap between ungulates.

RESULTS

E. desvauxii, S. ioclados and *T. berteronianus* dominated the pan-valley habitat, whereas *Urochloa spp, S. pappophoroides* and *S. uniplumis* dominated the off-pan habitat (Table 1). We recorded the highest protein content (> 12 %) in the two most common species in the pan-valley habitat, *E. desvauxii* and *S. ioclados,* as well as in *P. coloratum* and *S. acinifolius* during the wet season. *S. pappophoroides* and *Urochloa* spp. were most common in the off-pan habitats, but they contained lower protein content than individuals in the pan-valleys habitat.

Table 1. Wet season protein content (% of dry mass), Seasonal cover and relative availability (%) of common grass species in the Central Kalahari Game Reserve.

Grass species	**Mean Protein content**	**Percentage cover**		**Relative Availability**	
		Wet	**Dry**	**Wet**	**Dry**
Aristida congesta		2.00	0.00	1.60	0.00
A. pubescens	8.73	0.00	0.80	0.00	1.45
Brachiaria advena	10.31	0.63	2.05	0.50	3.71
Cenchrus ciliaris	8.89	5.6	0.19	4.48	0.34
Chloris virgata	10.87	3.81	2.88	3.05	5.20
D. giganteum	9.02	1.6	0.00	1.28	0.00
D. eriantha	10.41	2.2	1.63	1.76	2.94
E. cenchroides	7.73	1.00	6.89	0.80	12.46
E. desvauxii	13.39	42.31	0.00	33.83	0.00
Eragrostis spp	9.34	1.73	0.26	1.38	0.47
Melinis repens	11.07	3.83	1.04	3.06	1.88
Panicum coloratum	13.51	9.31	0.50	7.45	0.90
S. acinifolius	17.18	0.69	5.25	0.55	9.49
S. ioclados	15.26	7.69	6.29	6.15	11.38
S. pappophoroides	7.95	16.63	16.88	13.29	30.52
S. uniplumis	9.16	10.48	7.45	8.38	13.47
T. berteronianus	11.93	8.30	0.00	6.64	0.00
Urochloa spp	11.80	7.30	3.20	5.82	5.80

Collectively, *S. ioclados* and *E. desvauxii* contributed more than 57%, 64%, and 46% to the wet season diet of the wildebeest, gemsbok and springbok, respectively (Table 2). *S*pringbok consumed *Eragrostis* spp. and dicotyledons as additional important food items during the wet season. *S. ioclados* remained important for the wildebeest during the dry season (t = -0.95, df = 4, p = 0.398). The proportion of *E. desvauxii* decreased significantly from the wet to dry season diet of wildebeest (t = 5.28, df = 4, p < 0.01), and springbok (t = -2.94, df = 4, p = 0.042). We found a significant increase of *Urochloa* species in wildebeest (t = 2.66, df = 4, p = 0.057) and gemsbok diets during the dry season (t = 3.82, df = 4, p < 0.05). There was an increase, though not significant, in the proportions of *Eragrostis* spp*.* in wildebeest (t = -1.56, df = 4, p = 0.193) and gemsbok diets (t = 2.11, df = 4, p = 0.102) during the dry season. We found a large dietary overlap between the three ungulates during the wet season, with more overlap between wildebeest and gemsbok (Table 3). Dietary overlap between gemsbok and springbok remained high during the dry season. Wildebeest and gemsbok diets overlapped moderately in the dry season, but was not significantly lower than in the wet season overlap (t = -2.28, df = 4, p = 0.08). The diet overlap between wildebeest and springbok was significantly lower in the dry season than in wet season (t = -4.52, df = 4, p < 0.05). Seasonal diet overlap between springbok and gemsbok did not differ significantly (t = -0.086, df = 4, p = 0.94). Dicotyledonous species proportions increased significantly for springbok (t = 6.59, df = 4, p < 0.01) and gemsbok (t = 7.00, df = 4, p < 0.01) during the dry season with the proportion of dicotyledonous plants contributing over 55% to the diet of springbok during the dry season. Analysis of wildebeest diet preference showed that they strongly selected *B. advena, E. cenchroides*, *S. ioclados* and *Eragrostis* species during the wet season and *C. ciliaris, E desvauxii*, *Eragrostis* spp. and *T. berteronianus* during the dry season (Figure 2). Wildebeest preferred pan and valley grasses, while avoiding most of the off pan/valley species. Wildebeest had wider and springbok narrower niche breadths in both the wet and dry seasons (Table 2). There was no significant change in the seasonal niche breadth of the three ungulates. Though not significant, both wildebeest and gemsbok increased their niche breadths during the dry season; however, springbok decreased their niche breath in the dry season.

Table 2. Seasonal proportion (%) of food items in the ungulates diet. Bolded show food items that contributed an average of ≥ 10% to the diet, regarded as important food resource.

	Wildebeest		**Gemsbok**		**Springbok**	
Species (or plant group)	***Wet***	***Dry***	***Wet***	***Dry***	***Wet***	***Dry***
A. congesta	3.0 ± 3.86	-	-	-	0.6 ± 0.73	-
A. pubescens	-	-	1.1 ± 1.99	1.2 ± 2.14	-	-
B. advena	5.2 ± 4.65	1.6 ± 2.31	-	-	1.8 ± 2.51	-
C. ciliaris	2.2 ± 4.11	2.6 ± 1.79	1.1 ± 1.95	-	1.6 ± 1.90	0.7 ± 0.80
C. virgata	9.9 ± 12.5	2.2 ± 4.02	9.4 ± 5.84	4.9 ± 2.94	6.8 ± 3.69	1.3 ± 2.43
D. giganteum	-	-	0.04 ± 0.08	0.6 ± 1.10	0.3 ± 0.43	0.7 ± 0.85
Dicotyledons	1.1 ± 1.73	5.9± 3.04	3.0 ± 2.3	**29.3 ± 12.56**	**16.1 ± 7.6**	**55.7 ± 12.78**
D. eriantha	-	-	-	-	0.3 ± 0.41	-
E. cenchroides	0.2 ± 0.38	0.3 ± 0.55	-	-	-	-
E. desvauxii	**26.6 ± 7.30**	8.7.0 ± 4.33	**36.1 ± 5.52**	1.7 ± 1.87	**19.4 ± 8.55**	3.9 ± 4.59
Eragrostis sp	7.6 ± 3.82	**20.7 ± 14.59**	7.1 ± 2.13	**15.3 ± 7.08**	**14.1 ± 13.3**	7.2 ± 2.32
M. repens	-	-	1.9 ± 2.21	-	-	-
P. coloratum	6.5 ± 8.62	0.8 ± 1.38	4.0 ± 2.82	0.5 ± 0.61	5.7 ± 3.77	-
S. acinifolius	0.3 ± 0.43	3.2 ± 4.49	1.7 ± 2.0	0.9 ± 1.19	0.8 ± 0.90	6.1 ± 7.70
S. ioclados	**30.5 ± 14.29**	**18.0 ± 15.62**	**28.0 ± 9.21**	3.7 ± 2.99	**26.8 ± 15.35**	7.0 ± 5.18
S.pappophoroides	-	4.6 ± 4.05	0.8 ± 1.47	7.7 ± 7.41	0.4 ± 0.71	2.0 ± 1.31
S. uniplumis	0.4 ± 0.86	1.5 ± 1.32	1.5 ± 2.45	1.5 ± 2.80	0.4 ± 0.71	0.3 ± 0.64
T. berteronianus	2.9 ± 3.32	1.0 ± 1.36	1.1 ± 2.03	4.3 ± 4.69	2.2 ± 1.55	0.8 ± 1.32
Urochloa sp	0.8 ± 1.44	**18.0 ± 12.23**	0.3 ± 0.54	**24.0 ± 12.83**	0.5 ± 0.87	9.0 ± 7.6
Unidentified	2.9 ± 0.85	**10.4 ± 5.79**	2.8 ± 2.3	4.3 ± 2.72	2.28 ± 1.75	5.1 ± 2.11
Levin's FNB	0.38 ± 0.05	0.45 ± 0.12	0.37 ± 0.06	0.41 ± 0.07	0.38 ± 0.11	0.27 ± 0.11
FNB seasonal t-test	t = 0.780, df = 4, p = 0.479		t = 1.131, df = 4, p = 0.321		t = -1.093, df = 4, p = 0.336	

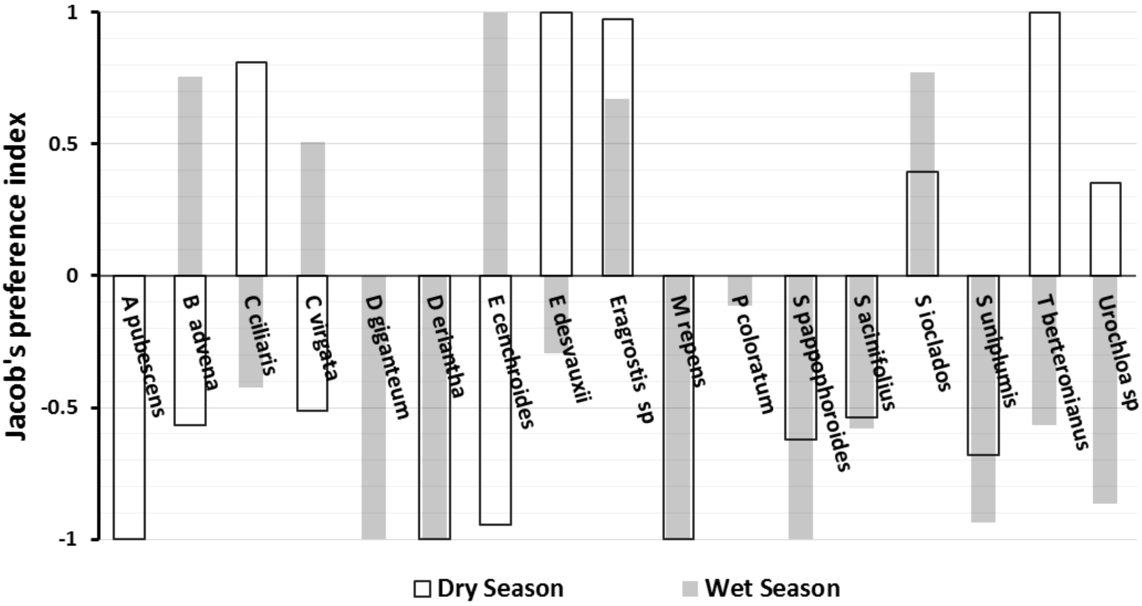

Figure 2. Grass species preference of wildebeest in the Central Kalahari Game Reserve between wet and dry season.

We note that we grouped dicotyledons together for analyses, which may have impacted springbok diet breadth in the dry season. Wildebeest dung analysis showed a significant decrease in mean protein content from 8.74 ± 0.34% in the wet season to 7.76 ± 0.88% in the dry season (*t* = -10.47, df = 4, *p* < 0.01).

Table 3. Seasonal diets overlap between the wildebeest and the other ungulates in the Central Kalahari Game Reserve. Index values range from 0-1, with 0 representing no overlap and 1 indicating complete overlap.

	MORISITA INDEX OF SIMILARITY	
SPECIES	Gemsbok	Springbok
WET SEASON		
WILDEBEEST	0.82 ± 0.13	0.79 ± 0.15
GEMSBOK		0.76 ± 0.25
DRY SEASON		
WILDEBEEST	0.48 ± 0.21	0.40 ± 0.16
GEMSBOK		0.75 ± 0.09

DISCUSSION

Animals adapt to strong seasonal variability in resources by moving between ranges and habitats at landscape to regional scales (Hopcraft et al., 2010) and by expanding their dietary breadth (Owen-Smith, 2002). The functional generic resource framework Owen-Smith (2002) identifies six functionally different forage classes that provide options to exploiting variable resources over the annual cycle: (i) High-quality resources that play a key role in providing sufficient energy and nutrients for growth and reproduction, but are generally depleted by the dry season. (ii) Restricted intake resources that are high-quality, but restricted in quantity though they may help supplement energy and protein requirements during key periods. (iii) Staple resources that provide the bulk of a herbivore's energy and nutrient needs annually. (iv) Reserve resources that are of lower quality than resources i- iii and are thus ignored during the wet season, but which offer a critical reserve of forage for the dry season (also known as a key resource – (Illius & O'Connor 2000)). (v) And Buffer resources that animals ignore in most years, but eat during drought and thus prevent population collapse (also a key resource). Our data on the protein content and the seasonal diet of wildebeest, springbok and gemsbok enabled us to classify the various plant species according to the functional generic resource framework, which provides insights into mechanisms of the adaptive foraging strategies of these herbivore species. This allows us to translate the local specifics of diet selection (in the CKGR) to other studies of diet selection elsewhere in Africa, thereby generalizing our results.

S. ioclados and E. desvauxii contained among the highest protein contents of the grasses (Table 1) and were the most abundant grasses in the diets of all three herbivores during the wet season (Table 2). These two grasses occurred much less in the diets of springbok and gemsbok during the dry season, whereas wildebeest maintained high levels of S. ioclados in their diets during both seasons (Table 2). We therefore classify these grasses as high-quality resources for all three herbivore species, except S. ioclados for wildebeest, which represents both a high-quality and a staple resource owing to its very high quality and a large, annual contribution to its diet. Similarly, S. ioclados is a dominant grass within the core wet-season range of ungulates in the Serengeti, occurring in more saline areas (McNaughton, 1983), thereby forming a critical forage, which facilitates meeting the elevated demands for minerals in pregnant and lactating ungulates (Murray, 1995). S. ioclados is taller and more leafy than E. desvauxii, making the former more profitable in terms of bite size. C. virgata contained a relatively high protein content (Table 2) and formed a significant proportion of the diet of all three herbivores during the wet season, but much less so during the dry season and could, therefore, also be classified as a high-quality resource for all three herbivores. C. virgata also forms a key forage species in the core wet season range of zebra at Mababe, northern Botswana (Sianga, 2014). A very similar species, Chloris pycnothrix, is an important grass in the Serengeti plains (McNaughton, 1983).

We expected wildebeest to favour P. coloratum and B. advena because of their high protein content, but these grasses contributed only around 5-6% of the wet season diet (Table 2). As such, we classify these species as restricted intake resources for all three herbivores, probably due to their lower availability (Table 1). Similarly, T. berteronianus, with its high protein content but very small size, probably functioned as a restricted intake resource, especially for gemsbok during the dry season. While not a large proportion of their diets, these latter three grasses likely play an important role in supplementing energy and protein during the resource demanding period of growth and reproduction over the wet season. Grazing lawns of Cynodon dactylon played a key role in supplementing protein intake for buffalo at Lake Manyara during the dry season, despite their restricted intake (Prins & Beekman, 1989).

We classify the taller lower-quality C. ciliaris, Eragrostis spp. and Urochloa spp. as reserve resources for the three ungulates, as they were mainly selected for during the dry season. Seasonal change in grass species selection is an example of diet breadth expansion, which may play a key role in optimizing energy intake annually (Owen-Smith, 2002). In addition, gemsbok and, especially springbok, consumed dicotyledons as a critical reserve resource during the dry season. Thus, non-grasses provided an important reserve resource for gemsbok and springbok in the dry season, but not for wildebeest, which switched to Urochloa spp. and Eragrostis spp. at this time. By selecting non-grasses over the dry season, springbok and gemsbok gain a competitive advantage over wildebeest when preferred grasses in pan-valley habitats become depleted during the dry season. Non-grass forage remains green longer into the dry season and so likely provides more protein and energy than the senescent grass species.

The trends in dietary composition that we observed in the CKGR support those found in East Africa (Ego, Mbuvi & Kibet, 2003). Those authors found that forage quality drives diet selection in the wet season when the resources are abundant, while quantity drives dry season selection as resources drop below optimal levels. Thus, competition becomes more pronounced during the dry season (Odadi et al., 2011; Fynn et al., 2016).

High levels of dietary overlap coupled with evidence of diet change that follows a reduction in preferred resources suggests competition (Smith, Grant, Grant, Abbott & Abbott, 1978). Wildebeest, springbok and gemsbok usually graze in the same habitat patch, and the three herbivores favoured high-quality grasses in the pan-valley habitats during the wet season. As resource abundance in the pan-valley habitat declined in the dry season (Selebatso et al., 2017), all the three herbivores expanded their diet to include lower-quality grasses and dicotyledons. These results suggest that as preferred grasses declined through the wet season ungulates changed their diets to maintain sufficient energy and protein intake. A reduction of standing biomass should impact wildebeest more than the other ungulates, because they are more dependent on grass than the three ungulates, and heavy, with the great food requirements (Illius & Gordon, 1987; Wilmshurst et al., 2000). Similarly, on grazing lawns in the Serengeti, larger ungulates left first (Bell, 1970). Based on body size, a wildebeest requires standing biomass of around 94.2 gm^{-2} of grass (Wilmshurst et al., 2000) that range in height between 6 and 10 cm (Arsenault & Owen-Smith, 2008). Biomass and height estimations in the preferred habitats in the CKGR exceeded these optimal limits in the wet season (160 gm-2 and 8 cm), but declined to less than 50 gm^{-2} and 5 cm in the dry season (Selebatso et al., 2017). Forage availability and height in the pan-valleys decreased to levels only sufficient to maintain a springbok, which requires 22.4 gm^{-2} of grass (Wilmshurst et al., 2000). However, wildebeest have specialized broad muzzles that enable them to forage effectively on much shorter grass than predicted for their body size (Murray & Illius, 2000; Arsenault & Owen-Smith, 2008), which may mitigate some of the impact of lower grass height. Nonetheless, wildebeest may have had some energy and protein deficit when grass height during the late dry season was below favoured grass heights observed in field studies (Arsenault & Owen-Smith, 2008). In support of this, faecal analyses demonstrated that protein intake by wildebeest at our study site during the dry season declined to less than 8 %, below the recommended minimum threshold of 8.5% for a grazer (Wrench, Meissner & Grant, 1997). Springbok and gemsbok dealt with the low biomass and shorter heights of preferred grasses by increasing browse in their diet. Browse maintains its nutrition better than grasses during dormant periods (Mphinyane et al., 2015), suggesting that springbok and gemsbok fared better during the dry season.

In conclusion, the reliance of all three herbivores on the high-quality grasses S. ioclados and E. desvauxii during the wet season likely led to competition for forage with wildebeest once favoured grasses had been depleted during periods when grass growth had ceased, such as dry periods within the wet season and by the late wet season/early dry season. The depletion of favoured grasses forced diet breadth expansion to lower quality grasses, mostly on sandy soils off the pans. Consequently, protein intake of wildebeest declined below desirable limits by the late dry season, which likely reduced reproductive potential and survival rates (Parker et al., 2009). Restricted access to historic wet and dry season ranges for the wildebeest population therefore exposes them to intensive exploitation competition that may reduce fitness and, eventually, population decline. Restoration and maintenance of corridors to the Schwelle will facilitate access to high quality resources, reduce competition and ensure survival and sustainability of the Kalahari wildebeest.

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Chapter Five: Quality of water available for wildlife in the Central Kalahari and its potential effects to wildlife populations, *Physics and Chemistry of the Earth*, Under review

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Abstract. *Arid and semi-arid environments have low and unpredictable rainfall patterns resulting in limited availability of surface water for wildlife. In the Central Kalahari Game Reserve (CKGR) wildlife populations have lost access routes to natural surface water mainly through veterinary cordon fences, as well as livestock and human encroachment. Artificial waterholes have been developed in the reserve to compensate for the loss. However, there has not been assessment of the quality of water provided for wildlife and how that may be contributing to populations declines in the CKGR. We assessed water quality from 12 of 13 artificial waterholes against Botswana and international livestock standards. Overall the quality of water provided is poor and poses a health risk to both animals and humans. Eight out of twelve boreholes we tested exceeded the maximum acceptable TDS limits while three and four have toxic levels of lead and arsenic, respectively. In some cases the provided water could effectively have more negative impacts on wildlife than positive thus defeating the intended management purpose. Failure to provide water of acceptable quality is a major concern for wildlife management in the CKGR and this may underlie some wildlife declines. This emphasises the need for water quality analysis and regular monitoring of artificial water for wildlife in semi-arid and arid environments where ground water may be saline and have toxic levels of heavy metals. Management interventions that includes closure and or desalination of some waterholes is recommended to reduce the potential effects of toxic substances on wildlife. This study findings further highlights the negative effects that arise from restricting populations from their natural water sources that had maintained the population for centuries.*

Keywords: *arsenic, artificial waterholes, heavy metals, lead, water quality*

Introduction

Arid and semi-arid environments have low rainfall and prolonged hot and dry periods. Wildlife populations in these environments are limited by access to water within commutable distance from food resources (Rosenstock *et al*. 1999). Similarly, natural surface water in the Central Kalahari Game Reserve (CKGR) is very limited and only available in pans for a short time with no natural surface water available in the reserve for most of the dry season, as is typical of the Kalahari ecosystem. Habitat loss and fragmentation have deprived wildlife populations' access to key water resources outside the reserve, which has resulted in drastic declines of herbivore populations, especially during drought periods (Williamson *et al.* 1988). Wildebeest in the Kalahari depended on the Boteti river system during drought, but this resource was cut from the population by veterinary cordon fences since the late 70s (Owens & Owens 1984). Artificial waterholes were developed since 1984 (Bonifica 1992) in the reserve to increase the viability of wildlife populations by compensating for lost access to permanent water sources outside the reserve.

Worldwide, development of artificial water for wildlife has become a major management intervention to address effects of habitat loss, especially in arid and semi-arid environments (Dolan 2006). However, this has not been without controversy and criticism, particularly on its effects on distribution and movement of wildlife (Smit *et al.* 2007), decline of some rare species (Harrington *et al.* 1999), as well as carnivore hunting strategies (Harrington *et al.* 1999; Rosenstock *et al*. 2004). Nonetheless, it possible that some ecosystems could collapse without artificial provision of water, especially where natural water has been lost or access prevented by human induced development (Williamson *et al.* 1988).

Both availability and quality of water have effects on population dynamics. Poor water quality reduces reproductive rates and survival rates of animal populations, resulting in potential population declines (Pokras & Kneeland 2009). Surprisingly, specific research on water quality and its possible effects on wildlife populations has been limited (Rosenstock *et al*. 1999; Wolanski & Gereta 2001), therefore neglecting the potential negative effects of artificial water provision for wildlife on animal health and production (Simpson *et al.* 2011). Other than a limited study on total dissolved solids (TDS) of the water from the developed waterholes (Bonifica 1992), after decades of provision of water to wildlife in the CKGR there has never been a comprehensive study conducted to investigate the quality of water at artificial water points and its impact on the ecosystem. Other water quality characteristics, such as presence of toxic heavy metals were not tested. Toxic levels of heavy metal can compromise the ability of prey to respond to potential predation (McPherson *et al*. 2004), thereby increasing vulnerability of prey.

Water from the boreholes is usually pumped into ponds for animals to drink. This exposes the water to seasonal atmospheric environmental variability such as wind and temperature (Vega *et al.* 1998), leading to evaporation into the air as well as and filtration of salts and solids as water sinks into the soil, potentially resulting in increase in the concentration of salts and other impurities that cannot evaporate or filtered into the soil. The increase in the concentration of salts may worsen the quality of the water available to animals.

There are records of elevated blood lead levels in vultures in and around the CKGR (Kenny *et al.* 2015). Sources of the lead have not been established. There is a strong suspicion that lead ammunitions are the source but underground water is also a possible source. Arsenic effects on humans have been well documented and it is regarded as a carcinogen (Vainio 1992; Ng *et al.* 2003). Effects of long term ingestion of arsenic include damages of internal organs such as kidney, liver, bladder and lungs (IARC 2004). These effects have been reported in animals as well (Biswas *et al.* 2000; Ng *et al.* 2003). Consumption of arsenic is generally caused through drinking water (Ng et al. 2003). We tested water quality from the artificial waterholes within the CKGR and Khutse Game Reserve (KGR) to determine the potential effects of water quality to wildlife in the ecosystem. The objectives of this study were to (1) to determine seasonal variations in water quality in the study area, (2) to compare water quality of the waterholes between the waterhole outlet and the pond, and (3) to compare water quality of the waterholes against Botswana (and international) water standards for livestock. We expected the quality of the water from the ponds to be poorer than that from the boreholes due to water evaporation and filtration of salts and other impurities. We also expected the water quality to worsen in the dry season due to lack of recharge from rainfall to neutralise the mineralisation of underground rocks and soil.

Study Area

The Central Kalahari Game Reserve (52,145 km^2) and the Khutse Game Reserve (2,550 km^2) formed the study area. The area falls within 21^{0}00' – 23°00' S and 22°47.5' – 25°25' E. The study area temperatures range from –6 °C in winter to 43 °C summer, with mean annual rainfall ranging from 350 to 400 mm (DHV 1980, unpublished). There is no permanent surface water in the reserves, but 13 artificial waterholes have been developed for wildlife (Figure 1). The wildlife population in the area includes large ungulates such as giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), blue wildebeest (*Connochaetes taurinus*), gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*) and springbok (*Antidorcus marsupialis*), and large carnivores such as lion, leopard (*Panthera pardus*), cheetah, wild dog and brown hyaena.

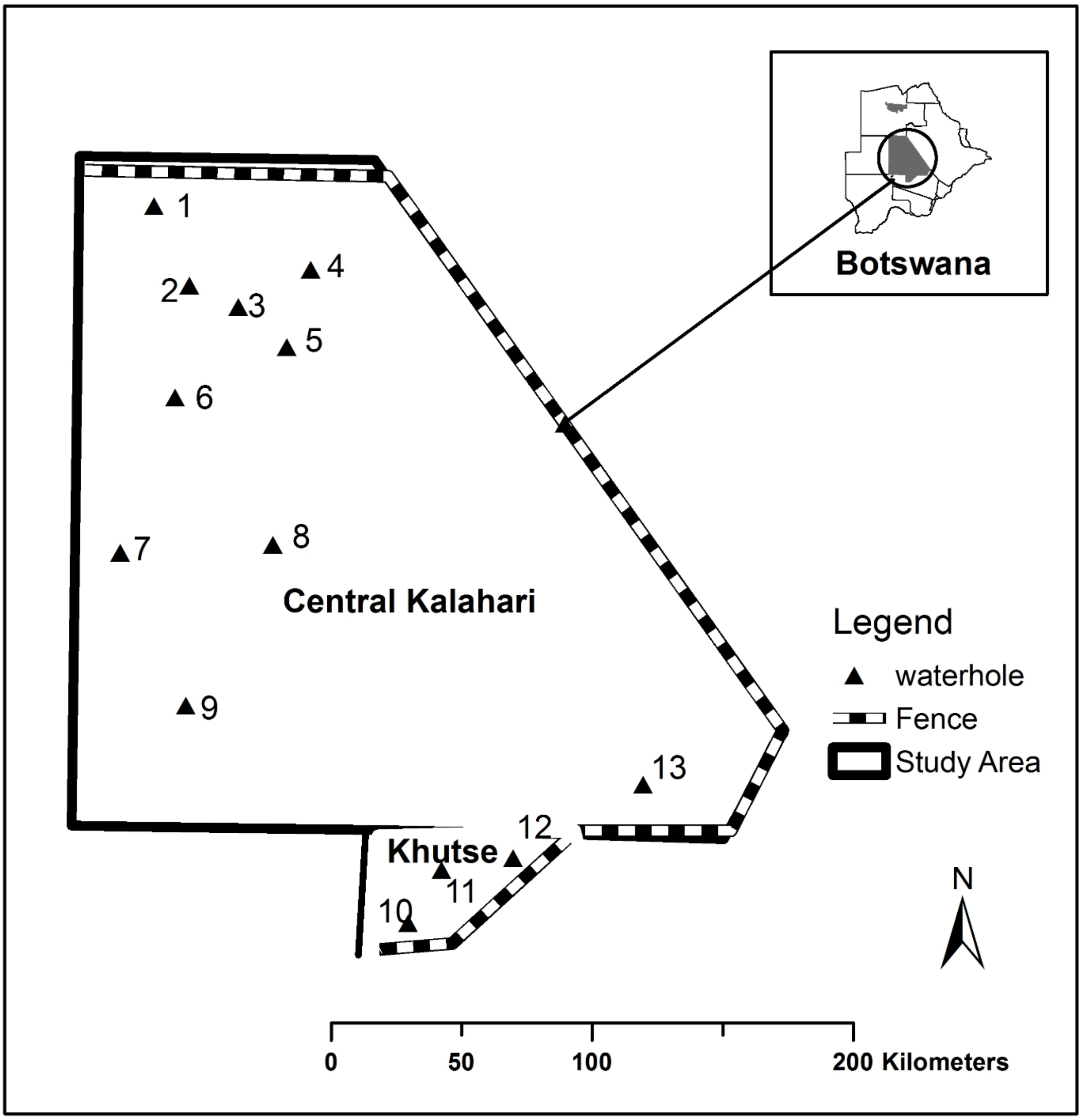

Fig. 1. Showing study area and locations of waterholes in the Central Kalahari and Khutse Game Reserves. 1 = Motlopi, 2 = Passarge, 3 = Tau, 4 = Sunday, 5 = Letiahau, 6 = Piper, 7 = Xade, 8 = Xaka, 9 = Quee, 10 = Moreswe, 11 = Molose, 12 = Khutse, 13 = New waterhole

Methods

Water samples were collected from 12 of the 13 waterholes in September 2013, January 2014 and June 2014 and tested for quality. The 13th waterhole could not be reached due to logistical reasons. Three of the waterholes were within KGR and the rest in the CKGR. We tested the quality of the source of the waterhole therefore we collected the samples from the outlet that releases water into the ponds. Samples were tested for pH, Electrical Conductivity and Total Dissolved Solids (TDS) using standard procedures at the Okavango Research Institute environmental laboratory in Maun. We analysed for calcium, magnesium, lead and zinc using Atomic Absorption Spectrometry (AAS). We used a Flame Photometer to analyse for sodium, and arsenic concentration using Inductively Coupled Plasma Optical Emission Spectrometry (ICS-OES). Due to lack of standards for wildlife, we compared the water quality to the Botswana Standards for livestock and poultry specification (BOBS 2010) and international guidelines summarised by Rosenstock *et al*. (2004). We compared concentrations of TDS between seasons and between water outlets and ponds of each waterhole using paired t-test. Lead and arsenic concentrations were not normally distributed; therefore, Wilcoxon paired test was used to compare concentration of lead and arsenic between seasons, and between outlets and ponds.

Results

All the artificial waterholes recorded levels of calcium, magnesium, potassium and zinc that were lower than the maximum acceptable levels (Table 1). Six of the waterholes recorded levels of sodium that are higher than the maximum limit, in at least one season. All artificial waterholes, except Letiahau, Khutse and Motlopi had pH values above the Botswana recommended range of 5.5 – 8.3 for livestock.

Table 1. Showing seasonal pH, calcium, magnesium, sodium and zinc levels for water in the Central Kalahari Game Reserve. Values in bold were above maximum acceptable limits. Values in parentheses represent maximum acceptable limits.

	EC (7800 µS/cm)		**pH** (5.5 – 8.3)		**Ca** (700 – 2000 mg/L)		**Mg** (400 mg/L)		**Na** (2000 mg/L)		**Zn** (20 – 50 mg/L)	
	Wet	**Dry**	**Wet**	**Dry**	***Wet***	***Dry***	**Wet**	**Dry**	***Wet***	***Dry***	***Wet***	***Dry***
Sunday	x	**17750**	x	**8.39**	x	3.72	x	11.39	x	**3059.01**	x	0.01
Passarge	**13130**	**13280***	**8.87**	**8.62***	7.31	7.43*	3.267	2.89*	**3163.36**	**2927.29***	0.01	0.01
Tau	**5840**	**6240**	**9.11**	**9.28**	3.52	1.42	1.051	0.38	1227.57	1220	0.01	0.06
Letiahau	**22700**	**23800**	8.00	7.45	386.65	314.64	91.9	86.54	**4721.44**	**3848.43**	0.02	0.08
Piper	3640	3810	8.26	**8.82**	3.67	2.78	3.678	5.10	736.54	819.03	0.00	0.05
Xade	2500	2600	**9.00**	**9.29**	1.30	1.03	0.241	0.27	585.46	562.46	0.00	0.05
Xaka	1067	1120	8.30	**8.96**	1.24	0.60	0.374	0.39	264.40	215.03	0.00	0.00
Khutse	**21900**	**23000**	8.15	7.67	386.90	279.25	178.15	179.89	**4627.01**	**4835.21**	0.03	0.12
Molose	**7010**	**7260**	**8.39**	**8.04**	14.84	11.64	3.466	4.01	1558.07	1539.37	0.00	0.08
Moreswe	**18470**	**25300**	**9.08**	**9.26**	2.07	1.62	1.183	0.83	**4202.08**	**4835.21**	0.02	0.08
Motlopi	**11880**	12440	8.09	7.91	105.72	81.21	104.76	113.34	**2407.93**	1776.20	0.02	0.07
Quee	1050	1093	8.06	**8.35**	9.48	8.25	6.775	6.67	221.91	226.96	0.00	0.06

Eight out of 12 waterholes recorded levels of TDS higher than the conservative recommended limit of 3000 mg/L, while six are above the highest recommended range. Only Quee, Xaka, Xade and Piper were below the TDS conservative limit (3,000 mg/L). Xaka and Quee had less than 1,000 mg/L TDS, whereas Khutse, Letiahau and Moreswe had over 10,000 mg/L (Figure 2). Seasonal comparison of TDS did not show significant difference between wet and dry season (t = -1.64, df = 10, p-value = 0.1322). However, the TDS concentration was higher in the ponds than in the waterhole outlet (t = -2.3472, df = 9, p-value < 0.05).

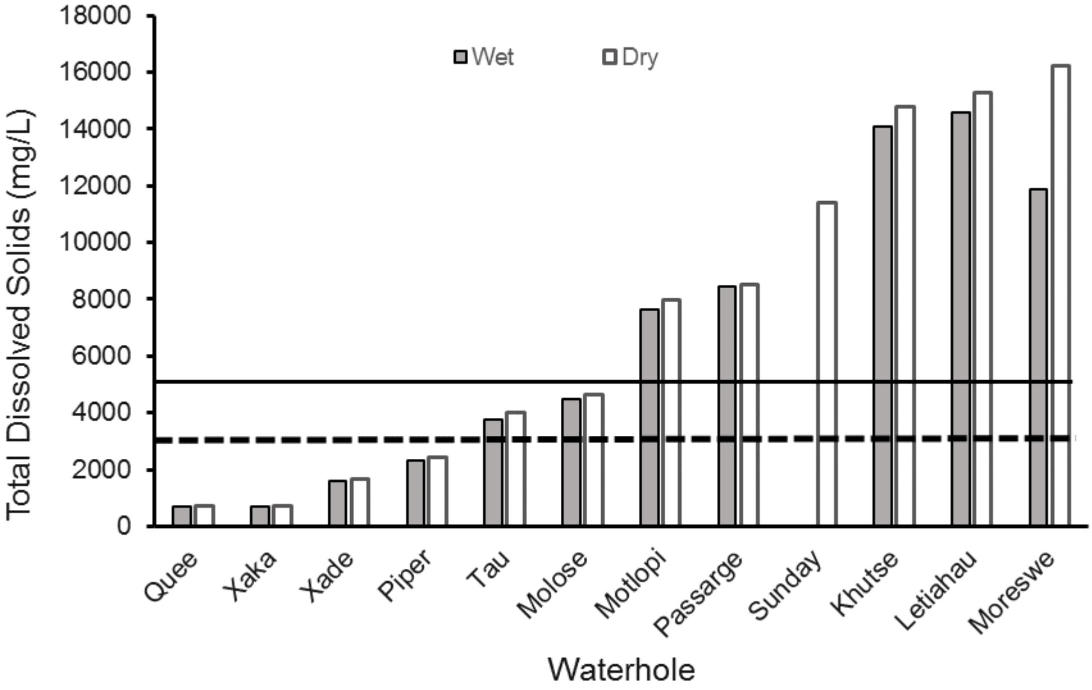

Fig. 2. Seasonal values for Total Dissolved Solids for the Central Kalahari/Khutse Game Reserve. Dotted and solid horizontal lines show recorded ranges of maximum acceptable limits, respectively (3,000 and 5,000 mg/L).

Sunday, Khutse, Letiahau and Moreswe waterholes had higher levels of lead than the maximum limits (Figure 3). Lead concentrations were not different between the wet and dry season (t = -0.44042, df = 10, p-value = 0.669). The dry season levels for

Khutse, Letiahau and Moreswe were more than twice recommended limit. Concentrations of lead between ponds and waterhole outlets were not different (V = 21, p-value = 0.5382) (Table 2).

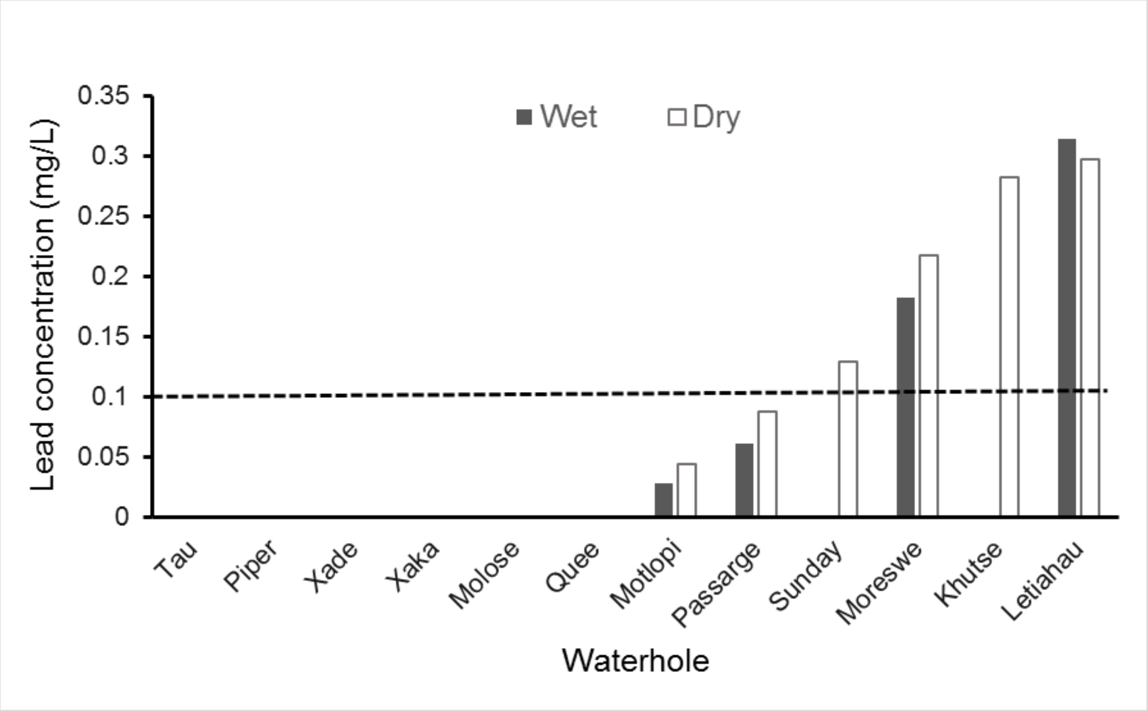

Fig. 3. Dry season values for lead for the Central Kalahari/Khutse Game Reserve. Dotted horizontal lines show maximum acceptable limits (0.1 mg/L).

Arsenic levels for all the waterholes were above the most conservative guidelines (0.02 mg/L). Piper, Tau and Moreswe waterholes were above Botswana's recommended limits (0.2 mg/L). None of the waterholes were above highest recorded maximum acceptable limit of 0.5 mg/L (Figure 4). There was no difference between the wet and dry season concentration of arsenic in the water (t = 0.55902, df = 10, p-value = 0.5884). Arsenic concentrations were not different between ponds and waterholes outlets (V = 19, p-value = 0.4316).

Table 2. Showing Total Dissolved Solids, lead and arsenic concentrations (mg/L) compared between ponds and waterholes outlets.

Waterhole	**Total Dissolved Solids**		**Lead**		**Arsenic**	
	Pond	**Outlet**	**Pond**	**Outlet**	**Pond**	**Outlet**
Tau	4571.04	3614.46	<0.001	<0.001	0.161	0.1514
Sunday	10541.64	10323.36	0.176	0.161	0.02594	0.02802
Letiahau	19067.4	14637.6	0.41	0.282	0.04987	0.04003
Piper	3903.36	2388.24	<0.001	<0.001	0.4491	0.312
Xade	1649.94	1726.98	<0.001	<0.001	0.07754	0.06806
Moreswe	13032.6	13032.7	0.198	0.204	0.02686	0.02795
Molose	5611.08	4320.66	<0.001	<0.001	0.02797	0.03779
Khutse	14830.2	7832.4	0.352	0.284	0.06283	0.2018

Discussion

Most the boreholes exceeded the conservative TDS and pH limits. TDS and pH are commonly used as easily measurable indicators and monitoring parameters of water quality (www.safewater.org). TDS is regarded as a measure of ions in water and these can be contributed by calcium, magnesium, sodium, and potassium cations and carbonate, hydrogen carbonate, chloride, sulphate, and nitrate anions. Elevated TDS may not necessarily mean a health hazard. Water taste deteriorates with increasing TDS and water with high TDS is less preferred by both humans and wildlife. Furthermore, very high concentration of salts in water will not be helpful for quenching thirst (Sengupta 2013). High pH, just like TDS affects the taste of the water (www.watersystemscouncil.org). High levels of TDS result in diarrhoea (BOBS 2010). pH values above 9 cause digestive upset and decrease intake of water and food (BOBS 2010). Our results show that the salinity of the water was high in the ponds compared to the outlets. This is probably due to accumulation of salts because of evaporation of water, and in some cases, poor filtration due cemented bases of some waterholes.

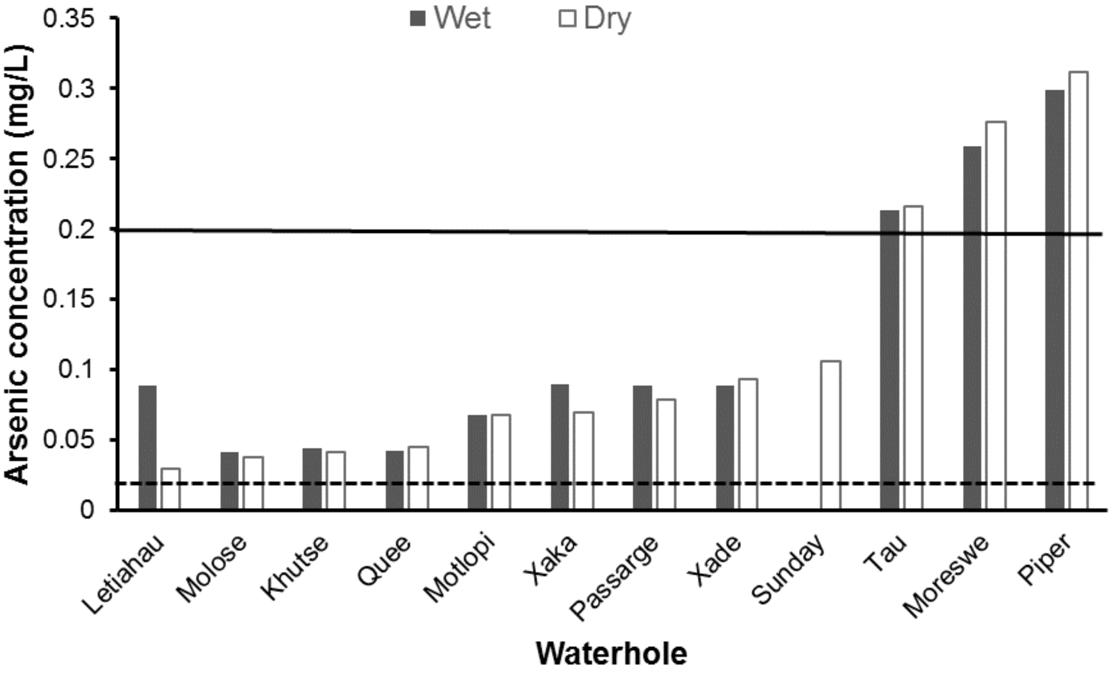

Fig. 4. Seasonal values for arsenic for the Central Kalahari/Khutse Game Reserve. Dotted and solid horizontal lines show recorded ranges of maximum acceptable limits, respectively (0.02 mg/L and 0.2 mg/L).

Some of the waterholes have high levels of heavy metals (lead and arsenic) thus exposing animals to toxins. Lead is known for health risks such as neurological impairment and malfunctioning of the central nervous, digestive and circulatory system (Ekong *et al.* 2006, Pokras & Kneeland 2009). Unfortunately, most of these studies were on human health. Pokras & Kneeland (2009) rightfully highlighted that our understanding of effects of lead on humans can help us to protect non-human species. In their review, Pokras & Kneeland (2009) revealed that exposure to lead can interfere with mental processes and behaviour that are critical to reproductive success of animals. Furthermore, birds that ingest lead are known to suffer negative effects such as an impaired digestive system (de Francisco *et al.* 2003). Vultures in Botswana have elevated blood lead concentration in 30% of vultures tested (Kenny *et al.* 2015), and it is currently unclear what has caused these elevated levels. Coincidentally, most of the waterholes that had high levels of lead (Letiahau, Khutse and Moreswe), had very high levels of salinity (TDS). The high salinity of the water my discourage animals from drinking the water, therefore reducing their chances of exposure to lead. Unfortunately, limited options of water sources may force the animal to drink the saline water. Arsenic is classified as a carcinogen and has effects such as increased prevalence of cancer; vascular, cardio- and cerebro-vascular diseases; injury to the nervous systems (Biswas *et al.* 2000, Thomas *et al.* 2000, Ng *et al.* 2003).

Overall the water provided in the CKGR for wildlife has very poor quality and poses a health risk to both animals and humans. It is key to note that water in artificial water points is pumped from deep ground water, which would not be accessible to wildlife under natural conditions; hence the argument that wild animals would be better adapted to saline water than livestock or humans does not hold. Among the Kalahari ungulates, the blue wildebeest is the least adapted to drylands (van Hoven 1983), and provision of artificial waterholes in the reserve was primarily meant to compensate for the lost access to water outside the reserve. Studies show that wildebeest have become dependent on waterholes (Mills & Retief 1994, Selebatso *et al.* 2017), especially Piper and Tau pans waterholes (Moses Selebatso, per obs), and spent most of the time around these sources. This implies that these wildebeest herds and many other wild populations such as gemsbok, giraffes, vultures, etc, are exposed to this heavy metal and may have compromised survival and reproductive rates (Biswas *et al.* 2000, Thomas *et al.* 2000, Ng *et al.* 2003). Hayward & Hayward (2012) also highlighted the importance of water provision in the conservation of African herbivore populations in dry savanna landscapes. The quality of water provided for wildlife in the CKGR could lead to mortalities of some resident wildlife or compromise the overall fitness of the populations. A study in the Kalahari Gemsbok National Park (KGNP), the current South African side of the KTP, showed that animals preferred to use waterholes with better water quality than those with lower quality (Child *et al.* 1971), and that mortalities of wildebeest was correlated with poor water quality (Knight 1995). In the KGNP wildlife had access to 250 times higher density of waterholes in the CKGR. There were 86 waterholes in the 9.591 km^2 KGNP compared to 13 in 54696 km^2 CKGR (including KGR).

Khutse, Moreswe and Letiahau were the worst quality waterholes failing standards for most parameters measured (especially Moreswe), though Piper and Tau had excessive levels of arsenic, a health hazard, and these waterholes need to be dealt with. Treatment of the water to improve its quality can be a very expensive. Therefore, exploration and equipping of alternative boreholes, particularly to replace Khutse, Moreswe, Letiahau and Piper would be cheaper in the long-term. Otherwise, Motlopi and Passarge water may be improved by desalination only because all other quality determinants are not as bad.

Conclusions

The quality of some water provided for wildlife in the CKGR is below acceptable standards and poses a health risk. The current failure to provide water of acceptable quality is a major concern for wildlife management in the CKGR and may underlie some wildlife declines in the CKGR. These findings have important implications for water provision in conservation areas, especially in semi-arid and arid regions, and calls for further research to quantify effects of water quality on wildlife and development of specific standards for wildlife. We also emphasize the need for water quality analysis and regular monitoring of artificial water for wildlife in semi-arid and arid environments where ground water may be saline and have toxic levels of heavy metals. We strongly recommend management intervention that involves desalination of water, seek alternative water sources and closure of those sources (particularly Letiahau, Moreswe, Sunday and Khutse) that have extreme excess of impurities. Where possible samples from animals should be tested for both lead and arsenic levels. These findings confirm that restriction of populations from natural water sources create complex management challenges, especially where save and sustainable alternative sources are scarce.

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Chapter Six: Synthesis

6.0 Foreword

Habitat loss and fragmentation are major factors driving global wildlife population declines and biodiversity losses (Owen-Smith, 2004; Fryxell *et al.,* 2005; Harris *et al.,* 2009). Increasing human and livestock populations, as well as associated land use demands, continue to put pressure on wildlife and its habitats (Bergstrom & Skarpe, 1999; Wallgren *et al.,* 2009; Schieltz & Rubenstein, 2016). These pressures and fragmentation of habitat resulting from farms and veterinary fences, lead to an increased rate of declines and biodiversity losses. Global commitment, through the Convention on Biological Diversity (CBD) to reduce the rate of decline, did not show positive results (Butchart *et al.,* 2010). As in many dryland ecosystems, herbivore populations in the Kalahari depended on mobility to access stochastic patchy rainfall, fire events and key functional seasonal resource areas (Williamson *et al.,* 1988; Verlinden & Masogo, 1997). The area available for movement is a major determinant of a herbivore's ability to forage adaptively to patchy rainfall or fire events, which can influence viability of a population (Fryxell et al., 2005). The blue wildebeest population historically depended on seasonal access to the nutrient-rich Schwelle area between the CKGR and the KTP in the wet season, and to water from the Boteti River, Lake Xau and Lake Ngami during drought periods (Owens & Owens, 1984; Williamson *et al.,* 1988). However, the access to these key resources by wildebeest were blocked by fences and encroached by livestock and humans (Williamson *et al.,* 1988; Wallgren *et al.,* 2009), which has contributed significantly to the decline of wildebeest in the Kalahari. These habitat losses will eventually isolate the CKGR from the rest of the Kalahari ecosystem. However, specific effects associated with habitat loss and fragmentation have not been clearly defined or described. The CKGR is one of the largest game reserves in the world, but its viability to sustain a highly-mobile wildebeest population in a variable and harsh waterless ecosystem is not known. Functional heterogeneity of a landscape determines the viability, and stability thereof, of the supported populations (Owen-Smith, 2004). The primary aim of the study was to assess the viability of the CKGR in maintaining a wildebeest population without access to historic water sources and grazing resources in the Kalahari ecosystem. The study investigated possible factors that could be limiting the wildebeest population in the CKGR. These include reduced adaptive foraging options, low quality and availability of forage, low quality and availability of water, high competition for resources with other herbivores, as well as high predation pressure and heat, and their effects on the activity patterns of the wildebeest. In this chapter I present an integration of major findings and discuss theoretical and practical implications of the findings to the CKGR population, Kalahari ecosystem and arid ecosystems management. I also present limitations of my study.

6.1 Major Findings and Discussions

The semi-arid Kalahari regions are characterised by very high diurnal temperatures and low and patchy rainfall (Williamson & Williamson, 1985), which lead to spatial and temporal variability of forage availability and quality (Illius & O'Connor, 1999; Fryxell *et al.,* 2005). Large spatiotemporal variability of water and forage quantity/quality demands that animals must (i) move nomadically over extremely large areas to be able to find distant patches of green grass associated with stochastic patchy rainfall (Verlinden & Masogo, 1997; Fryxell *et al.,* 2005) and (ii) vary their seasonal selection and use of habitats in order to cope with seasonal variability (Owen-Smith, 2004; Hobbs *et al.,* 2008). The selection and use of habitats, therefore, likely reflects the profitability of the landscapes in supporting survival and reproduction of the population (Cain *et al.,* 2008). Habitat selection patterns are often underlain by a hierarchy of factors limiting individual fitness at large to small scales, in order of importance (Rettie & Messier, 2000; Dussault *et al.,* 2005). These limiting factors include climate, predation risk (including hunting), food availability, disease and water availability (Dussault *et al.,* 2005), and define the spatial and temporal limits of animals' foraging patterns. Optimal foraging, therefore, describes the decisions by animals on where to look for food, the timing and duration for food search and acquisition and/or consumption (Schoener, 1971; Pyke *et al.,* 1977; Stephens & Krebs, 1986). At a large spatial scale, wildebeest in the Kalahari ecosystem preferred the Schwelle region with its high density of mineral-rich pans during normal or above normal rainfall years for the better forage, low predation risk and salt licks (Williamson *et al.,* 1988; Ayotte *et al.,* 2008). During dry seasons, wildebeest depended on water bearing plants such as tsamma melons (*Citrullus lanatus*) for moisture requirements (Knight, 1995). However, during drought years it appears the wildebeest were forced to move to permanent water sources, such as the Boteti River, Lake Ngami and Lake Xau, and some to the south west towards the Nossob River, and return to the Schwelle as soon as it rained (Williamson *et al.,* 1988; Verlinden, 1998). This adaptive strategy by the wildebeest and other ungulates, such as springbok and hartebeest, is disrupted by cordon fences, farms fences, and encroachment by humans and livestock (Owens & Owens, 1984; Williamson *et al.,* 1988). Movement patterns of the wildebeest study herds in the CKGR confirmed that the population was mainly sedentary around waterholes and there was no movement to the Schwelle area (Chapter Three). The lack of movement to the Schwelle could mean the population is sedentarised or confined in the CKGR, implying that the wildebeest no longer have access to the range of functionally-different habitats and resources and to extensive spatial options needed to adapt to stochastic patchy rainfall and fire effects that maintained them in the past. The population does not access wet season, high quality resources in the Schwelle, and is unable to reach water in the Boteti River system during droughts. These factors suggest that the CKGR population may not acquire its annual nutritional requirements and potentially die of thirst during droughts, therefore, compromising fitness to reproduce and persevere in the highly variable dry and hot Kalahari environment. Williamson and Williamson (1985) reported that CKGR population was relatively low, and an occasional increase in the CKGR wildebeest population coincided with a decrease of the population in the Schwelle area. Owens and Owens (1984) also reported that they seldom saw wildebeest in Deception valley (Northern CKGR) between 1974 until 1978. Bonifica (1992) estimated less than 200 wildebeest in between 1989 and 1990. The low number of wildebeest in the CKGR and its seasonal fluctuations imply that the CKGR did not provide the full suite of functional resources (as described by Owen-Smith, 2002) combined with reliable water availability, that could maintain a larger population in the face of large seasonal and inter-annual variation in water and forage availability.

It becomes particularly interesting to determine how then do the wildebeest survive in the CKGR landscape, independent of access to the historic landscape heterogeneity that sustained the Kalahari ecosystem. I investigated how the wildebeest population select and utilise the CKGR landscapes to survive. Habitats with low predation risk, high-quality forage (Fryxell, 1991; Milton *et al.,* 1992; Hernández & Laundré, 2005; Valeix *et al.,* 2009) and water (Smit *et al.,* 2007) are usually favoured in a landscape. All collared wildebeest in the CKGR strongly selected pans and valleys (Chapter Three): they concentrated their activity in pans and valleys in wet seasons, and those that had access to water in these habitats remained there during the dry season, while those that had no access to water migrated 200 km and were found to settle in areas with abundance of water bearing plants in the south. Pans and valleys were favoured because of their shorter grasses, and higher crude protein, calcium and phosphorus content. Favourable sward heights and nutritional content of pans and valleys forage were preferred throughout the year, despite a decline in quantity during the dry season. This analysis of seasonal habitat selection was further confirmed by a significant contribution of pan-valley grasses such as *Sporobolus ioclados* and *Enneapogon desvauxii*, to the wildebeest diet throughout the annual cycle (Chapter Four). A significant increase of the off-pan grasses such as *Eragrostis* and *Urochloa* sp in the wildebeest dry season diet (Chapter Four), confirmed that wildebeest do spend some time grazing off the pans and valleys during the dry season, as predicted.

In both wet and dry season, predation risk seemed to be a possible explanation or determinant for wildebeest habitat use at night. I compared habitat use between day and night to determine whether the use could qualify the use of pans for safety. I removed dawn (5am-6am) and dusk (6pm-7pm) periods to create a clear distinction between day and night time. I then compared proportions (%) of GPS locations inside and outside pan-valley habitat between day and night. I then used paired t-test to determine if pan-valley habitat use was indeed used more at night than during the day. Proportion of pan-valleys use by wildebeest was significantly higher at night than during the day ($t = -2.9391$, $df = 17$, $p < 0.01$). The wildebeest spent 78.75 ± 4.80 % of the time in the pan during the day and 87.63 ± 3.31 % at night (Figure 1). In chapter Two I showed that wildebeest are inactive at night. This suggests that wildebeest use pans and valleys at night when they are resting or sleeping as it is safer than off pan-valleys. The open high-visibility nature of the pans, greatly reduces predation risk and therefore contributed to selection for the pan-valley habitat in both seasons (Hernández & Laundré, 2005; Valeix *et al.,* 2009), despite lower forage quantity in the pan-valleys than in the off-pan habitat. These findings suggest that predation risk was the main determinant of habitat selection at night, while forage quality and water availability were important during the wet and dry season, respectively.

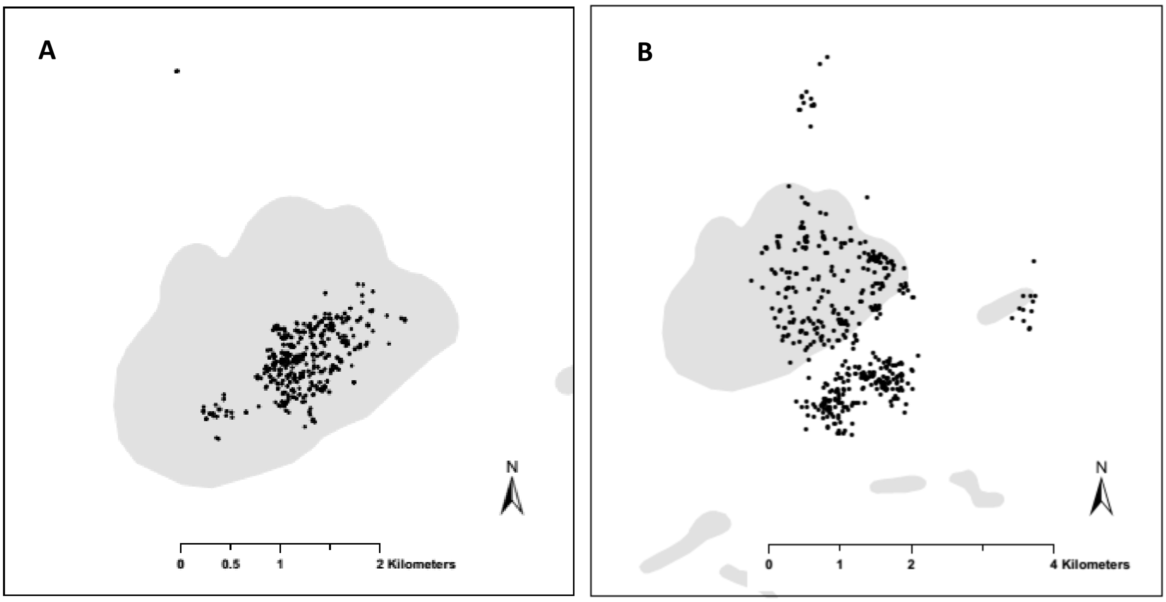

Figure 1 Example of dial habitat selection showing that wildebeest were exclusively using pans at night (**A**) and use both the pan and off-pan during the day (**B**). Grey background is a pan, and black dots are individual hourly location data from a collared wildebeest in the early dry season.

Investigation into the diet composition of gemsbok and springbok showed a significant overlap with wildebeest, especially during the wet season (Chapter Four). This suggests that pan-valley habitats are very important to the Kalahari ungulates for high quality food in the wet season, and for security. However, these habitats are very limited in the CKGR, as they form less than three percent of the whole reserve and there is, therefore, much potential for competition. In resource limited landscapes, interspecific competition results in reduced intake and growth rates (Derner *et al.,* 2006; Odadi *et al.,* 2011). Preferred grasses are depleted in the dry season, mainly due to competition with gemsbok and springbok (Chapter Three and Four). Unlike the wildebeest, springbok and gemsbok switched to browsing in the dry season to meet their nutritional needs. The wildebeest only increased its diet breadth by grazing on less nutritious grasses off the pan-valleys. Diet breadth expansion and partitioning in the dry season coincided with reduced quantity of the preferred forage, suggesting that competition may have led to this niche partitioning of the sympatric ungulates (Putman, 1986). The resultant change in the diet by wildebeest to less nutritious forage during the dry season suggest that the population is vulnerable to drought. The population cannot access other potential grazing areas during droughts, as they are limited by water availability and fences.

To persist under limiting resources, wildlife populations would be expected to maximise foraging time to meet energy and nutrient intake requirements (MacArthur & Pianka, 1966; Sinclair & Arcese, 1995). Maximising foraging time is most important where they have to overcome competition for food and avoid predation. In hot and arid environments where water is limiting, herbivores avoid moisture loss and heat stress by limiting their activities to cool hours of the day, including increasing nocturnal activity on very hot days (Dussault *et al.,* 2004; Maloney *et al.,* 2005; Hetem *et al.,* 2010). Similarly the wildebeest (and other animals) in the CKGR faces limited and inconsistent availability of water (Chapter Three) as well as predation pressure from a substantial population of large carnivores (Maude & Selebatso, 2014, unpublished). Maximising energy and nutrient gains under these constraints (spatio-temporal forage variability, heat stress, limited water availability and predation pressure), demands that wildebeest make some trade-offs through diel and seasonal cycles (Sinclair & Arcese, 1995; Lima, 1998; Dussault *et al.,* 2005; Hetem *et al.,* 2010). Like the Arabian Oryx in similar climatic conditions (Hetem *et al.,* 2012), wildebeest would be expected to increase their nocturnal activity in the late dry season when forage availability was lowest, and day temperatures highest. Contrary to expectations, the wildebeest did not increase their nocturnal activity during seasons of low forage availability and hot temperature (Chapter Three). The CKGR wildebeest, unlike the Arabian Oryx, is faced with high predation pressure, and most predators are active at night (Hayward & Slotow, 2009), thus it appears the disadvantages of increased risk of predation at night overrides the advantages of foraging during the cool of the night. Instead, the wildebeest reduced their overall activity during the late dry season likely as a strategy to conserve body stores and moisture. The wildebeest appeared to adopt a foraging strategy that maximised energy gains and built body stores during the wet season, and conserved body stores during the dry season, with activity peaks limited to cool hours of the day while avoiding predation at night. It appears, therefore, that heat and predation risk are key factors limiting wildebeest activity in this hot and dry environment.

The good forage quality and quantity, in terms of biomass, optimal grass height, calcium, phosphorus and protein (Chapter Three), as well as the activity of the wildebeest in the CKGR (Chapter Two), suggest that the population copes well in the wet season. However, the population seems vulnerable in the late dry season, when they are faced with very high temperatures, low amount and quality of forage, as well as limited surface water availability. Most females drop their calves from November to January. Pregnant mothers are expected to have elevated nutrient demands as they approach parturition (McDowell, 1985), which coincides with the time when the population struggles to get enough food to maintain body requirements – unlike other populations that can make use of green grass up on floodplains during the late dry season (e.g. Taylor 1985). Any delay in the onset of the wet season means that the pregnant females go into critical stages of pregnancy under resource-limited conditions, which may result in severe negative effects on reproductive output, including foetal abortion, delayed calving and small and weak calves (White, 1983; Cook *et al.,* 2004). Weak calves are also vulnerable to predation and diseases, therefore contributing to the poor recruitment of the population. As a result, poor nutrition pre and post parturition can cause a suite of “multiplier effects” greatly reducing population viability (White, 1983; Cook *et al.,* 2004).

I also found that artificial water provision in drylands ecosystems is a good intention but can be a detrimental management intervention. In arid and semi-arid environments, water availability is limited and it is usually the primary determinant of habitat selection (Coughenour*,* 2008). Like in other arid regions, low rainfall patterns and high summer temperatures make it difficult to have surface water in arid Kalahari. The unpredictability of rainfall patterns in the region makes water dependent ungulates vulnerable to drought periods, therefore water provision in the Kalahari ensures survival of the population, especially during droughts (Williamson et al., 1988).

This study confirmed the importance of water in the home range of the wildebeest population in the CKGR, especially during the dry season (Chapter Three). As in the in Kruger National Park (Pienaar, 1985), artificial water provision in the CKGR was a management decision to compensate for the lost water access due to fencing and growing human population pressure, which collectively have reduced access to critical water sources during drought years (Bonifica, 1992). Thousands of wildebeest died along the Kuke fence in the droughts of the 1980s as they attempted to access water sources beyond the CKGR boundaries (Williamson *et al.,* 1988; Spinage, 1992). Although artificial water provision has good intentions, it can result in loss of biodiversity due to depleted forage resources around water points, increased vulnerability to predation (Walker *et al.,* 1987; James *et al.,* 1999; Grant *et al.,* 2002) and change in the ranging patterns of animals (Smit *et al.,* 2007; Shannon *et al.,* 2009). The predicament or controversy of provision of artificial water to wildlife is evident in the CKGR system, and potentially in other arid ecosystems. As mentioned earlier, the Kalahari wildebeest remained in the Schwelle during both the wet and dry season, except during drought periods when they were forced to move long distances to reliable water sources (Williamson *et al.,* 1988; Bonifica, 1992). The population could meet their water and nutritional requirements within the Schwelle mainly through forage moisture and other water bearing plants. One of the wildebeest study herds had no access to a waterhole, and migrated between wet and dry season ranges. This herd selected the Deception Valley (northern CKGR) during wet seasons, possibly for its high quality forage (Chapter Three), and migrated more than 200 km south to Khutse Game Reserve and neighbouring WMAs at the beginning of the dry season to where they could survive on water bearing plants like tsamma melons (Chapter Three). These water bearing plants are highly dependent on sufficient rainfall during the wet season to produce a crop of moisture-rich melons, such that they may not be available in very dry years. This herd seemed to cope well (as they returned to the Deception Valley consistently), despite having to travel long distances risking predation and exhaustion, as well as risk miscarriage by pregnant mothers. However, this migration strategy will not persist during droughts as wildebeest cannot survive without access to water when it is too dry and water bearing plants are absent (Knight *et al.,* 1987; Williamson *et al.,* 1988). It is not clear, however, why they would leave pans and valleys in and around Khutse Game Reserve and migrate to Deception Valley, when they could use the pans in the Khutse Game Reserve. It is presumed that forage quality is better in the northern pans, which drives this northerly migration in the wet season, and availability of water bearing plants in the south drive the dry season movement. Further investigation on these presumptions will be of importance for management of the population.

Wildebeest that had access to waterholes spent time in the vicinity of the waterholes, and only moved away as soon as the waterhole dried up (Figure 2). This suggests that a sedentary population established around waterholes, and became accustomed to drinking water. This population loses resilience to arid environment and its adaptive behaviour of seeking water bearing plants, thus becoming highly dependent on water, and vulnerable when the water supply ceases. Most of the wildebeest that left the dry waterholes and could not find an alternative waterhole did not survive longer than two months (Chapter Three). It needs to be noted that drying up of these waterholes was usually due to mechanical failures and it usually took weeks to be repaired. The resultant mortalities following the drying up of waterholes confirmed the vulnerability of a wildebeest population dependent upon artificial waterholes, especially seeing that these waterholes are not reliably maintained. According to Mr Dimakatso Ntshebe (pers comm), former park manager, water availability is currently more reliable or consistent with solar panels than during the engine operated period (1984-2008). Many more animals were likely to have died before the solar panel operated boreholes were put into place as in the past there were more problems with older borehole engines maintenance, and some waterholes were very far from camps for regular operations.

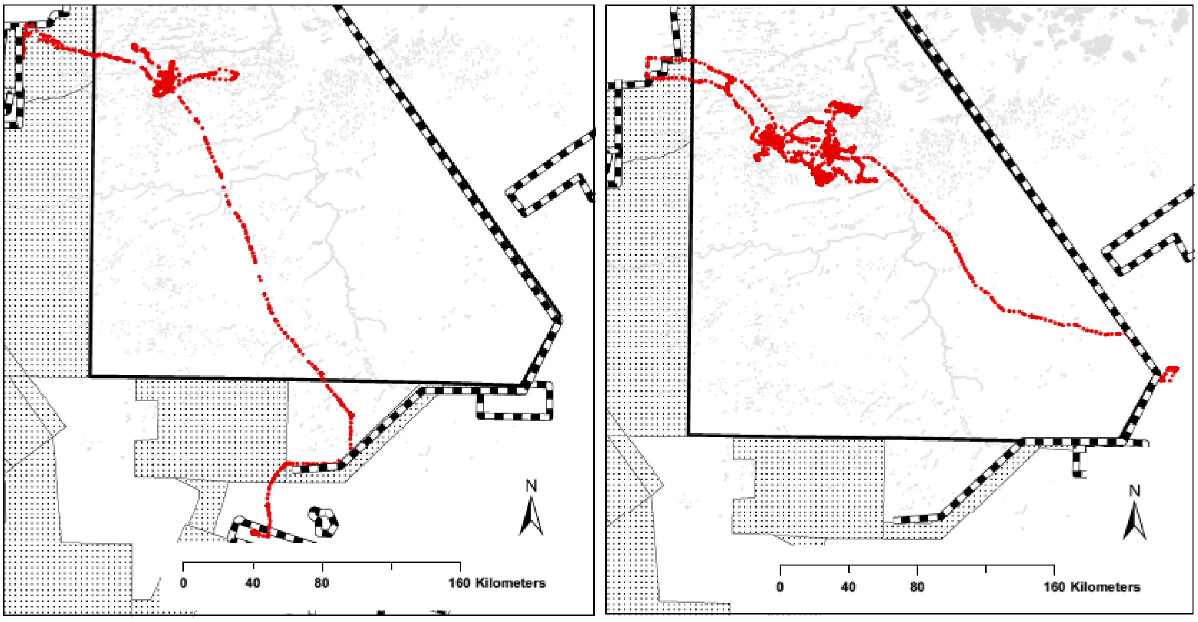

Figure 2. Movement of wildebeest herds after the drying up of Piper waterhole in 2012. Most of the mortalities of the study animals happened when waterholes dried up. The red dots show the long-distance movements of the two collared wildebeest after the waterhole dried up. The wildebeests died outside the reserve in the southern farm (left) and outside the south-eastern boundary of the reserve (right).

The mortality of the study wildebeest and evident reductions in herds size were observed during the periods when waterholes dried up, suggesting that regular maintenance of the waterholes would reduce the rate of population decline. The migratory herd showed an increase, at least double the herd size, in the wet season and decrease during dry season (Figure 3). This suggests that the herd split during the dry season. The migratory herd size continued to decrease in the dry season until they reached the wet season range. These findings are consistent with reported fluidity in group dynamics of the migrants of the CKGR in the 90s (Bonifica, 1992). In my study, the migratory herd traversed through wooded areas to reach seasonal ranges. As reported in Chapter 3, most of the recorded mortalities were outside pan/valley areas, and the decrease in the migratory herd could be due to predation between the seasonal ranges, especially in the dry season where the range is in woodland landscapes. The distance that the migratory herd persistently travelled in woodland landscapes, despite predation risks, confirms that wildebeest as opposed to zebras are more driven by forage quality than predation risk (Hopcraft *et al.,* 2014).

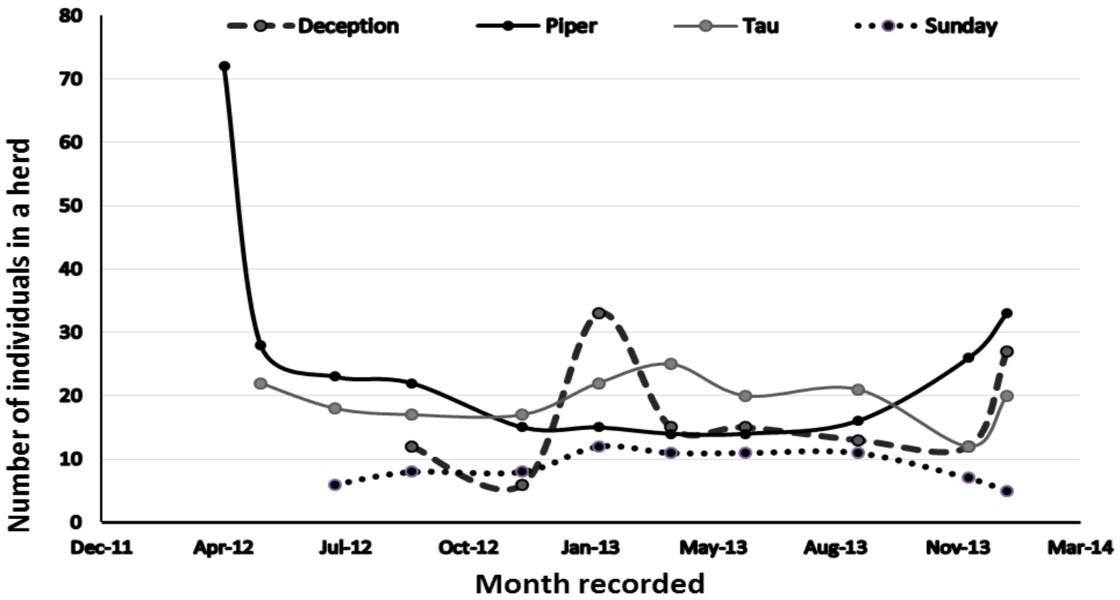

Figure 2. Number of individuals in study herds between May 2012 and Jan 2014 in the Central Kalahari Game Reserve. The migratory herd is labelled as Deception, which was its wet season range.

These findings reveal that provision of water creates sedentary populations and reduces the adaptation and resilience of the wildebeest to the arid Kalahari environment. However, as discussed earlier lack of water makes wildebeest vulnerable to droughts events. This raises a question of whether water provision really alleviates or worsens the population decline. To try and address this question, I listed some of possible effects of provision or no provision of water (Table 1). Provision of water creates an artificial environment that is greatly independent of natural environmental variables like rainfall and temperature. This development presents a comparatively more reliable water source than natural rainfall such that animals lose their resilience to natural variability. The established population become highly vulnerable to the unanticipated loss of water as discussed in Chapter 3. The development also creates permanent central foraging landscapes and eliminates the need for seasonal migrations, especially if the water source is developed in or around key foraging resources like pans. Furthermore, the artificial landscape creates a reliable hunting ground for predators, and this increases predation pressure on the population (Owen-Smith, 1996). In their review, James *et al.* (1999) revealed that provision of water enhances population increase of water dependent predators such as scavengers. This eventually exacerbates predation pressure on prey populations. Provision of water promotes radial destruction of vegetation and/or depletion of forage resources from the centre of the watering point, as phenomenon termed the piosphere by Lange (1969). However, as suggested by Makhabu et al. (2002), this piosphere effect may not be manifested in the CKGR or dryland scenario where wildlife populations are sparse, and presence of large herbivores as such as elephants is limited. These listed effects show that provision of water has the potential to cause population declines. However, lack of water in an isolated dryland population may cause worse consequences, especially in drier or drought years, when the animals are forced to find a water source. Previous studies demonstrated that wildebeest migrated in response to water demands, triggered by previous year's low rainfall. Under average rainfall patterns, wildebeest in the CKGR and Southern Kalahari would survive well without water (Williamson *et al.,* 1988), except those accustomed to drinking water. Lack of water in the regions becomes a threat during droughts, as animals would have no access to any other source of water, as a result of fences and other barriers on their access routes to water. This suggests that water provision in the “isolated” CKGR is a requirement to ensure survival of the wildebeest population during periods of low or no rainfall events. Under this water provision predicament, water could be provided during drought years only. However, this approach could also prove futile. Animals rely mainly on memory to access resources (Börger *et al.,* 2008; Van Moorter *et al.,* 2009). It cannot be guaranteed that the wildebeest and other animals that would need water during droughts would locate the developed waterholes. One of the herds that ended up dying after a dry Piper Pans waterhole, had missed Xaka waterhole by less than 5 km. This suggests the poor detection ability of the wildebeest. The best option in this predicament would be provision of water in dry seasons only. One of the herds did not appear to access a water source, and this was also shown by the historic Schwelle population (Williamson *et al.,* 1988), suggesting that wildebeest may not need to drink water in the wet season. The option of water provision in the dry season allows the population to still retain some dryland adaptation (like depend on forage moisture in the wet season), and also allows the population to spread away from the waterhole locations in wet seasons, thus spreading grazing pressure. While water provision may not be critical in the dry season when grass moisture may be sufficient, consistency in pumping water ensures that the population get used to where water may be found. The option reduces borehole maintenance costs as the borehole operation is reduced, as well as preserve underground water for periods when wildlife need it.

Most wildlife populations in the reserve depend on these artificial waterholes, as was shown by aggregation or regular sightings of animals around the waterholes.

Table 1. Possible effects of provision and no provision of water for the Central Kalahari Game Reserve population

Water provision	**No water provision**
Loss of resilience to drylands	Elevated vulnerability to droughts
Loss of migratory populations	Loss of animals that are already water dependent
Increased predation risks around waterholes	
Animals become water dependent	
Vulnerable to loss of water	
Poor water quality effects	

These include wildebeest, springbok, gemsbok, giraffe, lions and many bird species. Provision of water is therefore critical for survival of herbivores in dry land ecosystems that have lost access to natural sources. However, quantity and quality of underground water in these drylands is still a huge challenge. The quality of pumped water provided for wildlife in the CKGR has high Total Dissolved Solids, high arsenic and lead levels (Chapter 5). All the boreholes that existed in 1992 have fairly similar salinity after 20 years, except Sunday pan borehole that doubled the TDS value from 5072 ppm (Bonifica, 1992) to 11396 ppm (Chapter 5). It should be noted, that the location of the current Sunday borehole is about 30 m from the old borehole (a factor that may explain the variations in the salinity). There are no tolerance standards or guidelines that may be used to confidently qualify the effects of “poor” water quality on wildlife. For the purpose of highlighting the potential of water quality, I used standards that were compiled for wildlife water development assessment by Rosenstock *et al.* (1999) as well as livestock standards from Botswana Bureau of Standards (BOBS, 2010). High total dissolved solids do not help reduce thirst in water dependent species such as wildebeest. High levels of arsenic and lead in the water are likely to compromise the health of the wildebeest population, thereby reducing its fitness and eventually contributing to the decline of the population. These effects would not only affect the wildebeest, but also other animals and birds that use the waterholes. In their review, Michaelidou *et al.* (2002) emphasised the importance of water quantity and quality in maintaining natural ecosystems and ecological integrity. It is, therefore, highly possible that both the availability, unavailability and quality of water in the CKGR contributes to the decline of the population. However, more specific studies on how water quality affects wildlife and hopefully establishment of tolerance standards will be needed to guide future water developments for conservation.

This finding suggests that the current management intervention may not be sustainable and calls for a need to immediately explore the option of creating corridors as a more natural and potential more sustainable intervention. This option, though ecologically sound, may not be feasible. Owens and Owens (1984) described the Lake Xau as “nemesis” considering further mortalities that were associated with hunting by communities, range degradation by livestock, and that wildebeests had to make daily round trips of 50 miles to access water and forage. An overview of the possible corridors between the CKGR and Makgadikgadi National Park suggested that it may be unlikely that livestock owners and communities would buy into the idea of a corridor (Department of Environmental Affairs and Centre for Applied Research, 2010:49)

6.2 Management implications for the CKGR and other arid ecosystems

My study shows that fragmentation of habitats in the arid ecosystem of the CKGR is detrimental to its wildebeest population as it deprives access to the abundant resource rich habitats, thereby limiting the size of the population. Nevertheless, the pans that do occur within the CKGR provide relatively high forage quality and are probably sufficient to support a small wildebeest population within the CKGR because they only make up around 3 % of the total surface area. Losing access to the high density of resource-rich pans in the Schwelle limits the reproductive potential of the population whereas losing access to the Boteti river results in the population being highly-vulnerable to droughts. Loss of access to these resources subjects the population to interspecific competition, predation pressure, and extended risks to extreme environmental effects, that would otherwise be avoided, and so compromising the resilience of the population to accustomed environmental variability. The study demonstrated that water provision in isolated landscapes is necessary to compensate for lost access to natural sources. However continuous provision of water increases water dependency of the various herbivore populations, and usually establishes resident populations (Shannon *et al.,* 2009), that lose their former adaptation to arid environments. This study shows that water provision is a complex management intervention and needs thorough planning. It should be implemented with a clear water provision policy and practical management and maintenance plans to avoid catastrophic effects that may result from failure of the water provision development. This complexity emphasises the detrimental effects of habitat loss and fragmentation in a dryland ecosystem whose survival in the face of severe environmental variability was dependent on access to various spatially distributed resources.

In isolated dryland ecosystems where water development is required to compensate for lost access to water, enough waterholes, with acceptable quality, need to be provided, and the water should only be provided in dry seasons when animals need to drink, not only in drought years as suggested by Bonifica (1992). Consistency of this approach will ensure that populations know when and where they can access water in times of need, as well as allow them to migrate elsewhere in the wet season to access alternative foraging sites when water is not pumped into the waterholes. The approach will also prevent piosphere effects that may be manifested when water resources are limited in the landscape.

The quality of water provided in the reserve may pose a health threat to the population. It is therefore important that water of good quality is provided to wildlife, to avoid potential physiological effects that may result from exposure to poor quality water. Otherwise provision of poor water quality will not reduce the effects of loss to natural water source, and the population will ultimately perish. For the CKGR, I recommend a follow up study on how the quality could be affecting wildlife in the reserve. This may require opportunist collection of blood samples as well as post-mortem on dead animals to assess potential effects of water quality. There is need for regular monitoring of water quality parameter, possibly at seasonal intervals.

6.3 Limitations of the research

During the study period, the population of the wildebeest in the CKGR was estimated to be below 1000 individuals (DWNP, 2012). However, there was a total of eleven identified main herds in the reserve. Among these, three of the herds did not allow us to get close enough to deploy a satellite collar. Although the problems were experienced in simultaneously placing sufficient collars on this small population, the results of the study represent close to true representation of the population as the data is from more than 80% of the identified wildebeest herds in the CKGR/KGR. It should also be noted that most of the identified herds proved to be sedentary, and I cannot rule out the possibility that there could be other herds that would still access the CKGR from the Schwelle, despite the encroachments. However, during the study period there were intense efforts to locate wildebeest in the CKGR using existing road networks that are mainly following pans and valleys that are preferred by wildebeest. Above that, there were predator spoor surveys conducted in the reserve in 2012 that covered all the road networks in the reserve, including boundaries using over 13 vehicles in a week. All teams were requested to report any sightings of wildebeest. Only some of the 10 herds described above were located, and no new herd was recorded, except a number of lone and territorial males. The low density of the wildebeest population was also recorded in the 1989-1992 study where only eight herds of a total of 150 were located in the whole reserve using a helicopter (Bonifica, 1992).

There was very high mortality of the study wildebeest, which made it impossible to have continuous data on enough individuals. While this was a problem in getting ideal continuous data, the events were important as they reflected the mortality rates of the population, that may help unpack the factors leading to the overall recovery failure of the CKGR population.

Diet overlap between populations can represent exploitation competition, but may also reflect facilitation between the species. My study showed some noticeable depletion of the shared forage resources, which suggests some competition. However, this observation could have been validated by observation of the ungulates during grazing to document the grazing patterns on these sympatric herbivores.

The lack of wildlife water quality standard limits the inferences that can be made on the quality of the water provide for wildlife in the CKGR. I acknowledge that the water quality standards for livestock are based on public health, and that some of the effects on humans may not necessarily be presented at the same magnitude on wildlife. However, as a precautionary measure, the high levels of heavy metals and high salinity in some of the waterholes should not be ignore as they pose a potential threat to both wildlife and humans. Where possible alternative waterholes need to be developed to alleviate the possible effects on the existing waterholes. This may be done through exploration of new boreholes or reticulation from existing boreholes that have better water quality.

6.4 Overall Conclusions

Loss of connectivity can lead to complex consequences for species reliant on access to functional resources in distinct seasonal ranges. It is evident that the CKGR population does not access the historic wet season and drought years range, probably due to fences, livestock and human encroachment and provision of artificial waterholes in the CKGR. The wildebeest population faces competition during dry seasons for the limited high-quality forage in the reserve. Forage quality and quantity in the reserve drop significantly during the dry season forcing the wildebeest to graze on low quality resources to take them through the dry season. The onset of wet season is therefore critical for the fitness of the population, as any delay may comprise reproductive success and survival rates of the populations. The wildebeest population survive the heat and limited water supply of the CKGR through maximisation of energy and nutrient intake in the wet season and reduce activity in the late hot dry season. Wildebeest are active during cool hours of the day in both seasons. Wildebeest also avoid activity at night to avoid predation. Provision of water is important to compensate for lost access to water, and noted as a powerful but controversial tool to manage dryland ecosystems (James *et al.,* 1999), as it alters acquired adaptive strategy and reduces resilience to arid environments. Where access to natural water sources cannot be restored, it is important to ensure consistent artificial water provision to avoid mortalities of the transformed populations. Increasing the number of boreholes with better quality can spread grazing pressure, and may improve the survival and reproductive success of the population. Provision of water during the dry season would allow wildebeest to migrate to alternative grazing areas, while ensuring that they are not severely affected by the dry and hot climate of dry seasons.

In conclusion, habitat loss and fragmentation restrict dryland populations from access to key grassing and watering ranges. These result in mass die-offs on population, especially in drought years when forage quality and quantity are lowest, coupled with low moisture content. Water provisions in these isolated landscapes transform populations to sedentary and water dependent populations that become extremely vulnerable to water loss. Ideally access to these resources should be restored or maintained to avoid transformation of populations through unsustainable management interventions. These findings call for a need to immediately explore the option of creating corridors as a more natural and potentially more sustainable intervention for the long-term viability of the CKGR and the Kalahari wildebeest and other ungulates. However, in cases where access to the natural resources is unlikely, consistent water provision in these drylands may offset some negative effects that followed disrupted access, especially to natural water systems. It is therefore concluded that the CKGR cannot support a viable wildebeest population with the current management where water provision is unreliable, especially when historic access to water sources is still disrupted and provision of water is unreliable, and therefore unsustainable.

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6.6 Appendix One: Authors contributions

It is hereby declared that the primary study design, data collection, analysis, key ideas and write up were conducted by Mr Moses Selebatso, the student. Dr Richard Fynn provided academic guidance and corrections, as well as ensured that the student's work fall within the University regulations and ensured that the work meet the University standard. Dr Glyn Maude provided guidance in some of the study design and development of manuscripts and the Dissertation. Dr Emily Bennitt provided much of the guidance in the approach to data analysis as well as development of Chapter Three of the Manuscript.

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