

The Ecology and Management of Kalahari lions in a Conflict Area in Central Botswana.

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The Australian National University
Fenner School of Environment & Society
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Declaration

I hereby declare that the work contained within these pages is wholly my own work and that where I have used the information from other work, I have made every effort to clearly cite the author of that information. Appropriate contributions to study design, analysis and editing are recognized in the acknowledgements section.

A handwritten signature in black ink, appearing to read 'K MacFarlane', with a small dot at the end.

Signed

Kevin MacFarlane

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Abstract

African Lions (*Panthera leo*) are an keys species in many natural ecosystems in Africa and provide income and ecosystem services to many human communities. They directly limit herbivore populations, which in turn maintain grasslands and associated systems. Those ecosystems have degraded in recent decades and the concurrent decline in lion population is believed to play a role. I investigated factors affecting lion behaviour and ecology including the effect of seasonal variation in wild prey herd size. Current levels of herbivore prey are significantly lower than before the creation of countrywide veterinary cordon fences and total lean season biomass was estimated at 375.5 kg.km⁻². I placed GPS position locating radio collars on 13 lions in 6 prides in a study area of approximately 9,911 square kilometres in the north of the Central Kalahari Game Reserve (CKGR), in central Botswana. The collars acquired total of 241,858 usable GPS fixes and I visited each lion monthly. Lion spatial behaviour appears to have changed in response to the decline in herbivores, although there is only a small amount of historical data. Lion home ranges were large (mean home range = 2116.5 km², range 798.3-4243.7 km²) compared to two prides from a study in the 1970s in the same area which had home ranges of approximately 337 km². Those prides increased their range to today's sizes only in severe drought years, but rainfall during the study period was high. I interpret this as evidence that seasonal lower herbivore densities have increased lion ranges, and reduced the number of lions in the CKGR. I estimate the current population in the study area at 307 adult lions, or 3.1 lions per 100km². During months of high herbivore group densities, lions travelled further on a daily basis (mean daily movement distance of 7,160 m at lowest density, to 8,616 m at the highest density), and males on average travelled significantly further each day than females (mean of 10,071.6m per day for male, SD = 7099.4, maximum 48,462m and a mean of 7,633.6m per day for females, SD= 5,069.3m, maximum 29,470m). Females moved similar distances daily even while supporting cubs under 3 months old. Lions significantly preferred hunting prey species above 90kg, but also hunted the smaller warthog (*Phacochoerus africanus*) and African porcupine (*Hystrix africaeaustralis*). This has implications for conflict mitigation and lion conservation. I investigate the economics and extent of the lion livestock conflict in Central Botswana and explore potential management options in light of this new data. Management options should be carefully selected with consideration for economics, politics and local conditions, and should target locations where conflict mitigation can have the greatest benefit for both lion conservation and economic improvement of stakeholders in order to have the best chance for success. After carefully examining the ecology of the Central Kalahari lions and the management of the reserve and farms in the area, I conclude that mitigating lion-livestock conflict is best achieved through improving grazing practices and not a change in reserve management.

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Glossary of Terms and Acronyms Used

B.P. - Before the Present

C.E. Common Era (equivalent to A.D. – *anno domini*)

Cattle-post- communal grazing homestead based around cattle grazing, see kraal

CKGR - Central Kalahari Game Reserve

Chobe - river on the northern border of Botswana

Depredation – predation upon livestock (in this dissertation). Compare predation.

D.W.N.P. - Department of Wildlife and National Parks

Eco-tone boundary – scale relevant transition area between two biomes

Ghanzi - town and political district to the west of the CKGR, farms directly adjoining the western boundary are usually known as the Ghanzi district farms, and are usually large-scale European style fenced cattle farms

Forbs – herbaceous flowering plants that are not grasses, usually of a very low profile i.e. hemicryptophytes.

Hainaveld - area to the north of the CKGR in the Ngamiland district. Farms directly to the north of the CKGR are a mix of fenced game and cattle farms, and areas with communally grazed grasslands with individual cattle-posts/kraals

Kernel Density Estimate – a home range estimator using a 2 dimensional implementation of kernel density methods: a non-parametric method for estimating the probability density function of the underlying data. Relies heavily on a smoothing parameter, *h*. Methods for finding *h* are controversial, models from the original calculations were based on simulated animal movements, which has been shown to differ in important ways to real animal movement data

Kgalagadi - political district in the south-west of Botswana and Trans-frontier park, containing lions and similar habitats and wildlife to the CKGR

Kraal – refers to the cattle enclosure at a family owned cattle-post comprising a few huts and a handmade stick/bush fence to corral the cattle at night. Often built around a water well, the family living there are generally impoverished and living at a subsistence level. In many cases the actual cattle are owned by businessmen that live in the towns, while family members are paid low wages to maintain the cattle-post. Afrikaans for corral(n)

KGR - Khutse Game Reserve

KTP - Kgalagadi Trans-frontier Park - Peace park in the South-west of Botswana, bordering South Africa and Namibia

Makgadikgadi - large salt pans to the north-east of the Central Kalahari for which the paleo-lake Makgadikgadi is named

Minimum convex polygon – A home range estimator, connecting the outermost points of an animals' spatial distribution without creating a concave perimeter. A robust, highly comparable and common method, although there is speculation about what can be implied from the results

Monophyletic – a grouping that includes all members of a common ancestor, and does not include non-members

Moremi - Game reserve covering about a third of the Okavango alluvial fan, lying to the north of the CKGR

M. Y. A. - Million Years Ago, before the present

Ngamiland - North western political district of Botswana. Includes lake Ngami and the Okavango Delta

Okavango - river and alluvial fan to the north of the CKGR, partially protected by the Moremi Game Reserve

Polygynous/Polygyny – males mate with more than one female

Polyandrous/Polyandry – females mate with more than one male

Polygamous/Polygamy – a pattern of mating in which animals have more than one mate

Predation – the act of one animal hunting and killing another animal. In context this is used when a predator kills natural prey. Compare: depredation

Rakops - town to the east of the CKGR in the Central District of Botswana. Farms are usually individual cattle-posts or kraals, with communal grazing and few fences

Spoor – tracks and signs of wildlife including broken grass, hair and faeces.

Thamalakane - river tributary that runs through Maun, Botswana after which the paleo-lake Thamalakane is named

Ungulate – a grouping of the hoofed mammals, although some members are not hoofed.

W.M.A. - Wildlife Management Area

Chapter 1 General Introduction

Humankind has appropriated a vast area of the earth, utilising an estimated 38% of the land for cultivation and grazing and an estimated 30-40% of the terrestrial net photosynthetic productivity to produce food (Haberl *et al.* 2007; Vitousek *et al.* 1986). Domestic vertebrates such as cattle, sheep and goats grown to produce food amount to more than 35 times the biomass of remaining terrestrial wild vertebrates (Smil 2003) and this new balance has a profound impact on ecosystems that support wild animals and humans (Diamond 2005; McShane & Adams 1997). Intact ecosystems provide services that are utilised by humans in many contexts, and being essentially free, are under-protected. With insufficient protection many ecosystems are deteriorating and those services are at risk. They include provision of clean water, clean air, protection from soil erosion and natural disaster and services to crops like fertilisation and pest control (Dirzo *et al.* 2014). In recent decades society has tried to come to terms with balancing our short-term expansion for access to food, minerals, waste management and water with the long-term health of the systems that provide basic resources, regulate our climate and provide a measure of protection from natural disasters (Wittmer 2010).

There are aspects to the natural world that directly compete with human interests, yet are integral to the ecosystem processes that eventually benefit humans. These include flood, drought, disease, fires and also carnivores which are a vital part of natural ecosystems (Estes *et al.* 2011). Carnivores play a role in regulating herbivore populations and buffer over-grazing, reducing disease outbreaks in prey species by removing diseased individuals and contributing to the recycling of nutrients through carnivory, scavenging, death and decay (Ripple *et al.* 2014). Indirectly, their removal from a system often results in lowered biodiversity and productivity and even ecosystem collapse or stagnation (Dirzo *et al.* 2014; Estes *et al.* 2011). Many large carnivores are charismatic and well managed tourism operations based on their conservation can help conserve larger biomes (Andelman 2000; Dalerum *et al.* 2008b). However, as carnivores directly and indirectly compete with humans for protein and are a danger to humans, they have been heavily persecuted across their ranges in both developing and developed nations (Ceballos & Ehrlich 2002). For as long as humans have needed food they have had to fight nature to grow more of it and have competed for protein with predators, more recently the predators have been losing the battle in terms of shrinking habitat, diversity and populations (Ripple *et al.* 2014). The African lion (*Panthera leo* Linnaeus) is no exception, and is now missing from greater than 90% of its range of 2000 years ago, and two of the eight recognised sub-species of lion have become extinct in the last 150 years (Barnett *et al.* 2009).

There are many reasons for the decline in African lion populations (IUCN 2006a), from active persecution by hunting, habitat loss, habitat fragmentation, decreases in wild prey populations and increasing susceptibility to disease epidemics in a fragmented population (Packer *et al.* 2013). Conservation organisations and governments are spending large amounts of money trying to address the decline, while juggling the needs of locals who are affected. However there is inadequate data on lion ecology and biology and even less on the effectiveness of livestock loss mitigation - a concern that is heavily emphasised

by both Non Governmental Organisations (NGOs) and government departments because of the economic impacts on farmers of developing nations and the prevailing public sentiment for the conservation of charismatic mammals. Large lion populations are prone to habitat and prey loss and smaller populations are often affected by direct killing due to livestock conflict (Dolrenry *et al.* 2014).

A robust and healthy ecosystem including natural vegetation, herbivores and carnivores exists in a complex multi-layered dynamic system for which consequences of disturbance can rarely be anticipated (Burgess *et al.* 2006; Mace *et al.* 2012; Walker & Salt 2006). For example it was common practice at the beginning of the 20th century for game park managers in Africa to remove carnivores from the system, anticipating growth in the desirable game antelope (Smuts, 1976, Curruthers, 1995). Commonly, the population of one or a few herbivore species would explode at the expense of others. Over-utilisation of the vegetation by increased and uncropped populations of herbivores leads to populations fluctuating and collapse in ecosystems (Fleishman *et al.* 2006; Sinclair *et al.* 2007). Although boom-bust cycles are also part of natural population fluctuations they have been exacerbated by human disturbance with unforeseen and undesirable outcomes.

The future conservation and sustainability of predators in Africa requires further research in order to better understand the ecosystem processes involved, the services they provide to neighbouring human populations and the effects that direct management and indirect pressures will have on those services (for examples, see Fuller and Sievert (2001) and Karanth *et al.* (2004)). Research demonstrates that protected areas alone are insufficient to continue to provide critical ecosystem services or to ensure the long-term viability of wild animals and plant communities (Young 1994). Creating more natural and healthy landscapes across multi-use zones is a key goal of future conservation and includes management techniques like building wildlife corridors and managing meta-populations (Estes *et al.* 2011; Tercek & Adams 2013). This is especially true when key species are migratory, live at low densities or have large ranges.

To stand a chance at long-term sustainability and food provision, current agricultural systems need to become more resilient, trading short-term benefits for long-term stability. Yet increasingly there is evidence that the short term economic goals of agriculture often contribute to the collapse of the resource those industries depends on (Conway & Barbier 2013; Walker & Salt 2006). Agricultural enterprises tend to displace natural landscapes to maximise short-term economic goals, with small successes spurring further manipulation of the environment to increase yields, sometimes until the system collapses. {Burmeister, 2008 #3756}. It is common to then blame externalities such as weather, governments and economic forces. Long-term successes of food production in a resilient framework usually rely on a mosaic of landscapes to provide the water, protection, seed dispersal, nutrient enrichment and protection from natural disasters such as floods, landslides, fires and storms. Pushes for efficiency often drive these systems to single crop stands over large areas, and while the output from any single crop system may be higher than mosaic systems, the mosaics can provide reliable outputs through disaster with sustained long-term output. For instance high efficiency, grain-fed cattle ranching may produce the highest mass of beef, but ignores external costs. This may include polluted water run-off reducing productivity in downstream industries. Cattle-ranching in Botswana is susceptible to unexpected disaster like drought,

disease and market fluctuations, whereas a diversified land-use system can be buffered by its diversity (Addison 1984). The same area of land with a complex mix of land use including some beef, timber, fish and hay production will produce more consistent and often higher total outputs (Walker & Salt 2006) and can have environmental benefits that in turn sustain the industry (Berglund *et al.* 2014; Fahrig *et al.* 2011). These industries are not viable in the Botswana landscape, and the primary alternative use involves wildlife for either production or tourism. African Lions are an important part of the natural African landscape and should be a part of a resilient future.

Lions, along with other carnivores, were historically considered pests which reduced valuable game populations, attacked livestock and occasionally attacked humans (Ray *et al.* 2005a). Within the ecological knowledge then available, it was inconceivable that lions could impact positively on grassland health or contribute to the landscapes humans rely on (Schaller 1972). For most of European occupation of Africa, lions and other predators were heavily persecuted with the view that this would boost wild game and keep domestic livestock and people safe (Schaller 1972). The results were varied but usually disastrous (for example, see Brashares *et al.* (2010)). Without a major predator, the population of a single herbivore would often expand rapidly, quickly deteriorating the grazing structure for both wild and domestic herbivores (Côté *et al.* 2004; Hübschle 1988; White *et al.* 2007), and if not controlled through expensive culling operations, resulted in disease outbreak or starvation in lean years at great cost to human industry (Bengis 2003; Daszak *et al.* 2000; Smithers 1986). Loss of large predators can also result in meso-predator release (Brashares *et al.* 2013), whereby medium sized predators expand their populations with flow-on effects down the food web. In farming landscapes in South Africa in which African lions were removed, problem populations of jackal and fox were created (Brashares *et al.* 2013). The time scale of this type of system re-adjustment initially made it difficult to connect the loss of apex predators to the expansion of meso-predators, yet the evidence is now compelling (Ripple *et al.* 2014).

Lion conservation should not be taken for granted. African lions are listed as vulnerable by the IUCN (IUCN 2006b), and locally endangered to extinct in every Central, West and North African country (Bauer *et al.* 2001; Henschel *et al.* 2014). Prominent researchers generally agree that globally, the African lion is not expected to go extinct, with several strongholds (each with more than 500 wild lions) acknowledged in at least nine countries in eastern and southern Africa (IUCN 2006a). Yet the lion is certainly facing severe challenges. The challenges are mostly in the form of genetic isolation of the remaining populations (Tende *et al.* 2014), habitat loss in unprotected areas that historically connected populations (Rodriguez *et al.* 2012), declines in herbivore populations (Gadd 2012) and direct persecution (Snyman *et al.* 2014). Conservation of the African lion, however, is not the only end goal worthy of pursuit; actions that help conserve the species have the potential to contribute to the larger environment, as well as many other naturally occurring species, local commerce, agricultural sustainability, cultural and social value (Dalerum *et al.* 2008a; Dolrenry *et al.* 2014)

Thesis Aim

The Central Kalahari Game Reserve (CKGR) has an issue with livestock conflict between resident carnivores and surrounding farms. Reserve management and neighbouring farmers say that stock-raiding lions are their

biggest concern. The conflict is defined by the desire for lion conservation within the reserve, balanced with the difficulty in protecting cattle in the farmlands. In this thesis I aim to explore the most prominent threats to that population, investigate factors that contribute to lion wildlife conflict, and discuss realistic potential solutions.

1.1 Botswana

The landlocked southern African nation of Botswana (Figure 1-1) has existed as an independent state since 1966. It has a small population (around 2 million people, Botswana national census, 2011 or around 4 people per square kilometre), a consequence of the arid nature of large parts of the country. Around 87% of the country is classified as semi-arid savannah receiving 250-500 mm of unpredictable rainfall on well-drained Kalahari sands (Tlou & Campbell 1997). The country is considered to have a comparatively intact natural ecosystem, with around 70% of the country under some form of wildlife management and an impressive 30.39% under complete protection with no consumptive use of wildlife (Mbaiwa 2005b), and a growing tourism industry based around photographic wildlife safaris. Botswana is the native home to 147 species of mammal and in 2013 banned all forms of sport hunting outside private property, allowing wildlife only to be killed in order to protect life and property, including livestock (Boyes 2012). The concept of protecting wildlife came late on the Botswana stage, beginning with the formation of the Game Department in 1956 (Tlou & Campbell 1997) while the first game reserve in neighbouring South Africa was designated as early as 1895 (Brooks, 1983). The department gazetted a large part of Botswana for protection with little disruption, as much of the landscape was considered unsuitable for farming.

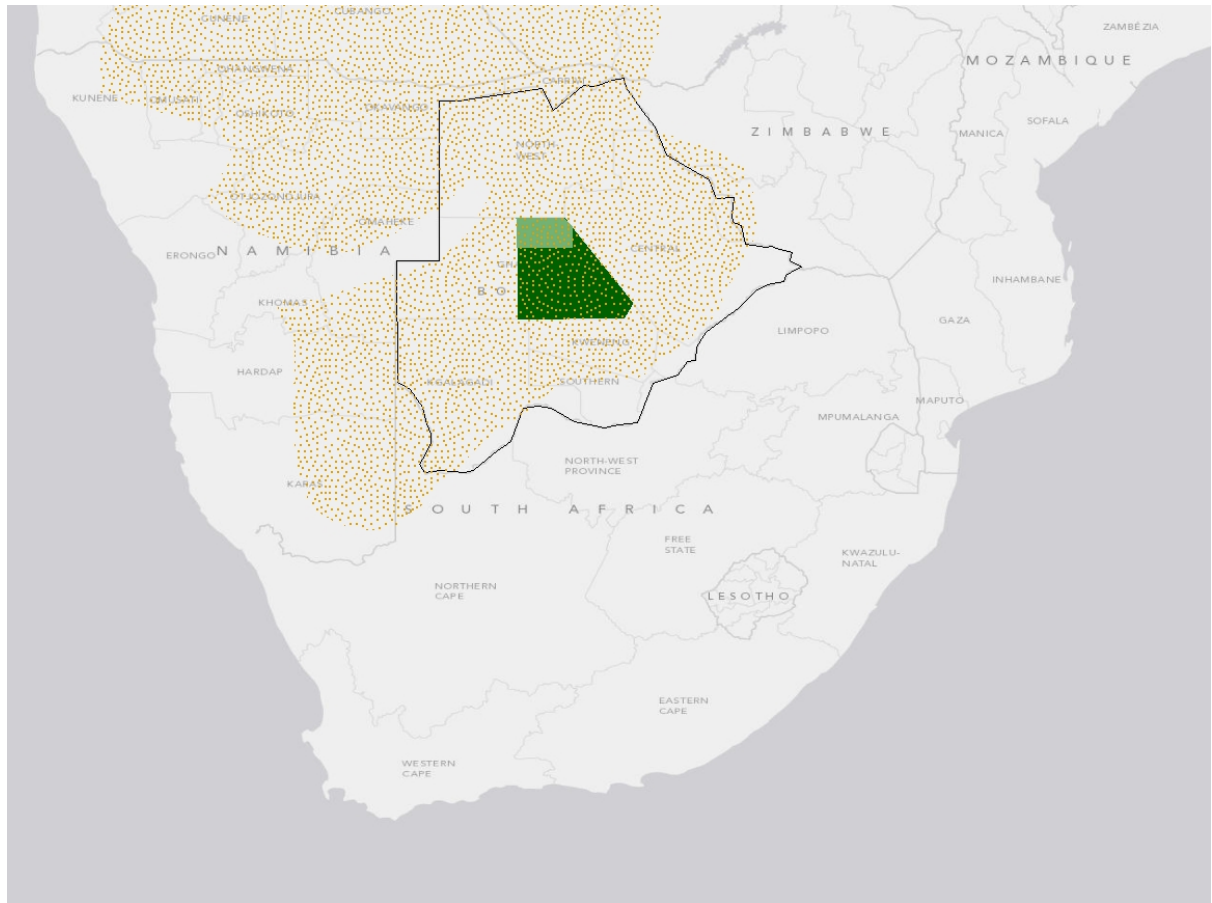


Figure 1-1 Map of southern Africa, Botswana as black outline, extent of Kalahari sands as beige stipple, the Central Kalahari Game Reserve (dark green) and the study area (light green).

Despite the low human population, Botswana's grassland shows signs of over utilisation by grazing (Moleele & Perkins 1998), and increasing levels of illegal poaching for meat (Hitchcock 2000). Even as photographic safaris have overtaken beef exports in value, national law continues to favour graziers by allowing the shooting of all predators that threaten livestock irrespective of their protected status. This disconnect is highlighted by two government organisations with opposing missions: the Ministry for Agriculture plans to double the national herd of cattle to 3.5 million in by 2020 (Ministry of Agriculture 2011) while the Department of Tourism, Ministry of Commerce and Industry aims to expand safari operations in the country and have considered doubling the number of beds available to safari tourists (Department of Tourism 2000). A number of management areas experience both tourism and livestock grazing side by side, but many valuable wildlife areas are not suitable safari destinations and expansion of the livestock industry would by necessity, be into areas currently inhabited by wildlife.

1.1.1 Wildlife

Botswana is home to an estimated 10% of the world's remaining African lions (IUCN 2006b). The country harbours important populations of other large

African predators, including up to 50% of the world's remaining African Wild Dogs (*Lycaon pictus*), healthy populations of leopard (*Panthera pardus*), and a few populations of cheetah (*Acinonyx jubatus*) (Botswana Environment Statistics Unit 2005). The nation's conservation record is mixed, yet it is generally accepted that amongst African nations, Botswana has several healthy and large wildlife communities. This is due in part to the arid conditions that support only a modest human population and lack of either colonial interest or civil conflict in recent history. Conflict in surrounding nations has added to Botswana's wildlife population through immigration (DeMotts & Hoon 2012). In the last few decades Botswana's economy has grown strongly with successful diamond mining operations bringing substantial wealth to the government. This wealth is shared through much of the population through high government employment rates and public works, such as roads, schools, healthcare and agricultural subsidies. The increased wealth throughout the country has kick-started a growth in human population, industry, grazing and wildlife tourism operations. Botswana faces new challenges as these processes threaten wildlife in a number of ways. Increased roads, vehicles, access to groundwater and veterinary cordon fences have allowed the expansion of livestock grazing. Grazing increases persecution of wildlife that competes with livestock for grass and many marginalised grazers view wildlife as a ready and cheap source of protein. Declines of around 90% in some ungulate species have been recorded in the Kalahari region between 1993 and 2004 (Crowe 1995; Department of Wildlife and National Parks 2014) , and eleven species of herbivores have declined by around 60% in the previous two decades in the district containing the Okavango Delta. Predators suffer from declines in herbivore numbers and from direct persecution, but there is insufficient data on predator population size, genetic diversity, life histories, movement, social structure (Botswana Environment Statistics Unit 2005) for the government to make important decisions concerning management and conflict response. Addressing this missing data for the Central Kalahari lion population is a chief aim of this study.

1.1.2 Land use

A variety of land use types, intensities, ownership styles and scales complicate the management of rangelands in Botswana. Agricultural intensity varies across the country, ranging from large-scale commercial ranching, freehold and leasehold fenced area farms that are typically 50 square kilometres or more (Kent 2011), to small-scale herding by family groups with few resources on shared communal grazing lands (Hemson *et al.* 2009). Small-scale grazing is the principal form of subsistence for the majority of rural residents of Botswana; the Botswana Central Statistics office listed 180 commercial cattle operations in the country, but 64,707 traditional (small-scale) cattle farms in 2005 (Botswana Central Statistics Office 2006). The motivations and attitudes towards grazing, wildlife and the role of government starkly differ between these two distinct farming scales (Kent 2011; Ogada *et al.* 2003; Stander *et al.* 1997). The commercial operations tend to be in the hands of a few individuals from established families that have operated in Botswana for many decades, and who control large areas of grazing land. In the Ghanzi district in particular, Kent (2011) noted that by far the greatest potential for enacting conservation outcomes

through agricultural paradigm shifts could be had by influencing a handful of individuals at this farming scale, as only a few families controlled a large proportion of land under grazing. The alternative is to change grazing practices amongst the numerous traditional farmers, and this is a much larger and likely less promising course of action, as each family controls such a small portion of the landscape. In other districts such as the Rakops district to the east of the study area, small area communal farmers dominate and while these small operators have much more to lose (every unit of livestock killed is a larger proportion of their own herd) they have fewer resources with which to pursue and kill predators, and so suffer greater livestock losses and impact less on the carnivore population (Schiess-Meier *et al.* 2007). The biggest environmental impact of small farmers is on the vegetation through changed grazing regimes, on the prey of carnivores by displacing wild herbivores with livestock and directly killing wild herbivores for cheap protein (Darkoh 1997; Hitchcock 1990; Moleele *et al.* 2002; Pratchett & Schirvel 1978; Saetnan & Skarpe 2006).

Sustainable conservation in Botswana requires recognition of the social and political importance of livestock even as its economic impact declines. In 2011, the Botswana Central Statistics Office counted just under 2.57 million cattle in the country, of which 294,000 head were in commercial enterprises, the rest (2.26 million) on small-scale communally-grazed lands. There were also about 1.8 million goats and 300,000 sheep, with the vast majority on traditional farms (Department of Wildlife and National Parks 2014). Urbanisation is a clear trend in Botswana, with 16% of people living in urban settlements in 1981, and greater than 50% in 2011 (World Bank Data on Urban Populations, 2012). As other industries grow, the contribution of agriculture to gross domestic product (GDP) has declined, accounting for 31% in 1974 to less than 2% in 2011 (Botswana Institute for Development Policy Analysis 2012). It should be noted that although agriculture may not contribute much to overall measured GDP, it contributes in a large way to subsistence and informal markets amongst villagers, providing food and livelihood to a great many of Botswana's citizens in a way that cannot be captured by domestic product measures. Cattle-grazing is a large part of the Botswana cultural identity, so much so that that economic argument against cattle grazing, or for mixed grazing holds less sway than they might otherwise. Cattle grazing also has a significant role in politics, with politicians owning cattle and paying respect to traditional lifestyles that many urbanised nationals identify with and valuing the activity. This is the framework within which conservation motives must be placed.

1.2 The Kalahari

The IUCN Cat Specialist Group recognises a large part of the greater Kalahari of Botswana as an important lion conservation unit (LCU) (IUCN 2006b). This area includes the Central Kalahari Game Reserve (CKGR) and the cross-border Kgalagadi Trans-frontier Park (KTP) spanning Botswana and South Africa and including an unprotected area of Botswana connecting the two parks (Figure 1.1). In this LCU, lions live at much lower densities than the Botswana's other protected areas of Moremi, Savute and Chobe, and their long-term viability is precarious despite the large area.

The Kalahari is a large sand-filled basin that spans deserts, dry woodlands and semi-arid savannahs over five countries, at about 1000m above mean sea level (Figure 1-1). The Central Kalahari Game Reserve protects a section of the semi-arid savannah and the present state of the landscape is a result of geological processes and current past climate. Kalahari sands extend from the jungles of the Congo in the north through Angola, Zambia, Namibia, Botswana, and South Africa in the south (Figure 1-1). A wide range of habitats can be found on Kalahari sands, and the Kalahari Desert biome is a prominent habitat that covers parts of Namibia, Botswana and South Africa. The majority of this desert biome is more correctly called a semi-arid savannah, receiving unpredictable rainfall of 250-500mm annually on a gradient from more rain in the south to less in the north (Stapelburg *et al.* 2007). In most years rain falls between November and April, and in this study is referred to as the wet season. May through October is referred to as the dry season, and incorporates both the coolest month, July and the hottest month, October.

The geological history of the Kalahari region began with the volcanic eruptions during the early Jurassic period (200-180 million years ago) that formed the igneous basalt covering much of southern Africa (Duncan *et al.* 1997) and are referred to as part of the Karoo super-group. The volcanic rocks include many obvious features of African countries such as the kopjes (boulder hills) of Zimbabwe, and the Drakensburg mountain ranges in South Africa. Rocky outcrops buried by Kalahari sands are noticeably scarce on the surface in but lie under 80m or more of the sand (Haddon 2005).

The existence of various ancient shorelines in parts of the Kalahari hinted at a great shallow lake that once covered much of central Botswana. Studies of fish evolutionary radiation in southern African rivers gave the most compelling evidence for the lake as modern river connections could not explain current distributions (Gutteridge & Reumermann 2013). The ancient lakes are now a generally accepted phenomenon, and are referred to as paleo-lake Makgadikgadi at 35,000 years B.P. and paleo-lake Thamalakane at 17,000-12,000 years B.P (Joyce *et al.* 2005) or sometimes referred to as the Kalahari super-lakes (Ives 2013). Three large rivers flowed south from present day Angola and Zambia to feed the lakes: the Kavango/Cubango, the Zambezi and the Chobe rivers. Over hundreds of thousands of years, the volcanic rock valleys were filled with the transported sands and this sandy lake bottom formed what is now the flat stretches of Kalahari sand typifying the Central Kalahari. The lakes dried up intermittently and then permanently when geological shifts re-directed two of the rivers east to drain into the Indian Ocean via the modern day Zambezi, about 80,000 years Before the Present (Y.B.P.). The Kavango /Cubango river still heads south into Botswana but flattens out in an alluvial fan known as the Okavango Delta. Up to 97% of the water that enters the fan evapo-transpires (Wolski *et al.* 2006), and the super-lakes further to the south were starved of water and slowly dried up. Since the most recent drying up of the super-lakes, shifting rainfall patterns from 80,000 Y.B.P. until the present have meant a dry, constantly shifting sand dune landscape dominating the Kalahari, but interspersed with wetter periods where dunes are stabilised by vegetation (Stokes *et al.* 1998; Wiggs *et al.* 1995). The present, relatively wet, vegetation covered landscape explains much of the vegetation patterns of woody shrub and savannah in the area (2,000 years Y.B.P. until now) seen in Figure 1-3, while the earlier dry history (100,000 to

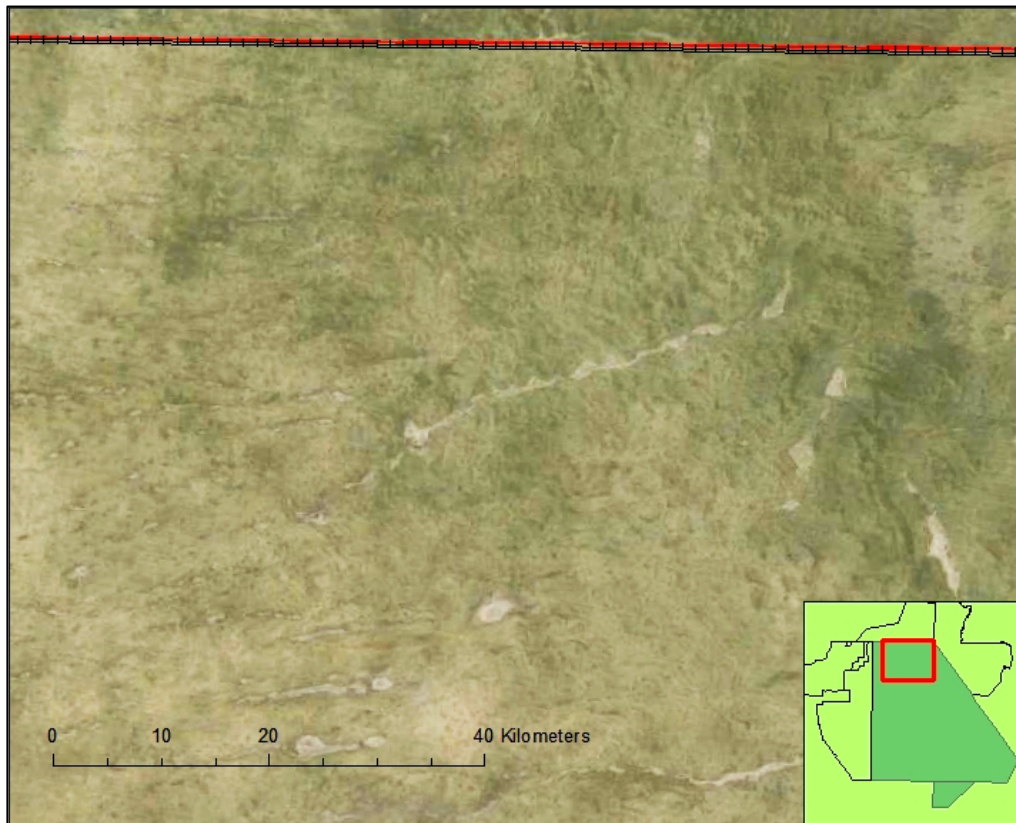


Figure 1-2 Map of the current and previous geological history of the region. The broad red arrow indicates the prevailing drainage patterns that eroded and brought Kalahari sand into the basin. The blue line indicates relevant tectonic uplifting the resulted in the formation of the super lakes. Paleo-lake extant shown is only one of the more recent and smaller paleo lakes identified (Paleo-lake Makgadikgadi). The older and larger Kalahari Super Lake has only a few sites identified as shore lines and it is more difficult to estimate the true extent, but is known to have extended across much of what is now the Central Kalahari Game Reserve.



Figure 1-3 Satellite imagery that highlights the stabilized dune formations of the study area. The Passarge Valley is central in each image and the effects of a 2011 fire that burned from the south east (Deception Valley) and burned some of Passarge valley are visible in the second image. Burned Tau Pan is bottom, left of centre. The visible dunes were formed in drier times, when wind blew free sand, while vegetation now holds the formations steady. (Google Earth 2013)

2,000 Y.B.P.) explains the dune-like patterns (Figure 1-2) evident in aerial photography of the region, and the very early history in the Pleistocene Epoch's intermittent glaciation (2.6 million to 11,800 Y.B.P.) explains the predominance of the sandy substrate (Figure 1-1). Current evaporation rates in the Kalahari are double the average rainfalls, and there are few natural year-round sources of water (Ives 2013). Two of the most important water sources, Lake Ngami and the Boteti River experience extended dry periods, such as from 1988 to 2006 C.E.

The Central Kalahari Game Reserve (CKGR) was established on 14 February, 1961 (High Commissioner's Notice No.33 of 1961) to protect resident populations of Kalahari San people as well as wildlife and unique ecological features (Hitchcock, 2002). The CKGR covers the entire eastern portion of the Ghanzi district of Botswana with the western-most border at E22.792° (decimal degrees, WGS1984, used throughout). The other borders correspond with the borders of the Ghanzi district at S21.000° in the north, S23.3000° in the south and an irregular boundary to E25.452° in the east (see Figure 1-5 for shape). The CKGR covers approximately 52,800 square kilometres, (Ministry of Environment, Wildlife and Tourism, but sometimes reported as 52,347 square kilometres), which is just under ten per cent of the country of Botswana, and making it the second largest game reserve in the world.

Alec Campbell, director of the DWNP during the 1960s stated that "many boundaries (of protected areas) were arbitrary lines drawn on the map, parallels of latitude, rivers, existing tracks or roads, and administrative boundaries. Generally, their shape was calculated to interfere with the existing settlements of as few people as possible." (Tlou & Campbell 1997). The original proposal of the CKGR included a statement about protecting the original inhabitants, the San Bushmen. While this was not mandated during the gazetting of the park, many San villages remained in the park for the next four decades. The population of people in the villages was unknown, but believed to have declined to about 1660 people in 1989 and to around 440 by 1999. Most left to seek employment in nearby ranches and towns. In the 1990s the small population subsisted on a few crops and by collecting traditionally from the landscape, but depended heavily on support from district councils and the central governments for water, education and healthcare (Hitchcock & Vinding 2001). From 2002 the government re-settled the remaining population to villages that were more accessible for delivery of government services but a small number have since returned to the reserve to live (Hitchcock & Vinding 2001). The settlements have always been and remain in the southern half of the reserve (Figure 1-4), while the north of the reserve where animals and clay pans are more common, was free of permanent settlements. The reserve hosts numerous basic campsites for visitors, operated by the DWNP and private companies, and two luxury safari lodges which opened in 2009 all in this northern area. The CKGR is remote, difficult to access and is under-utilised by tourists, receiving around 3,000 visitors per annum. For comparison, Botswana hosted a total of 390,681 leisure tourists in 2008, most tourists visiting several destinations (Department of Tourism 2011).

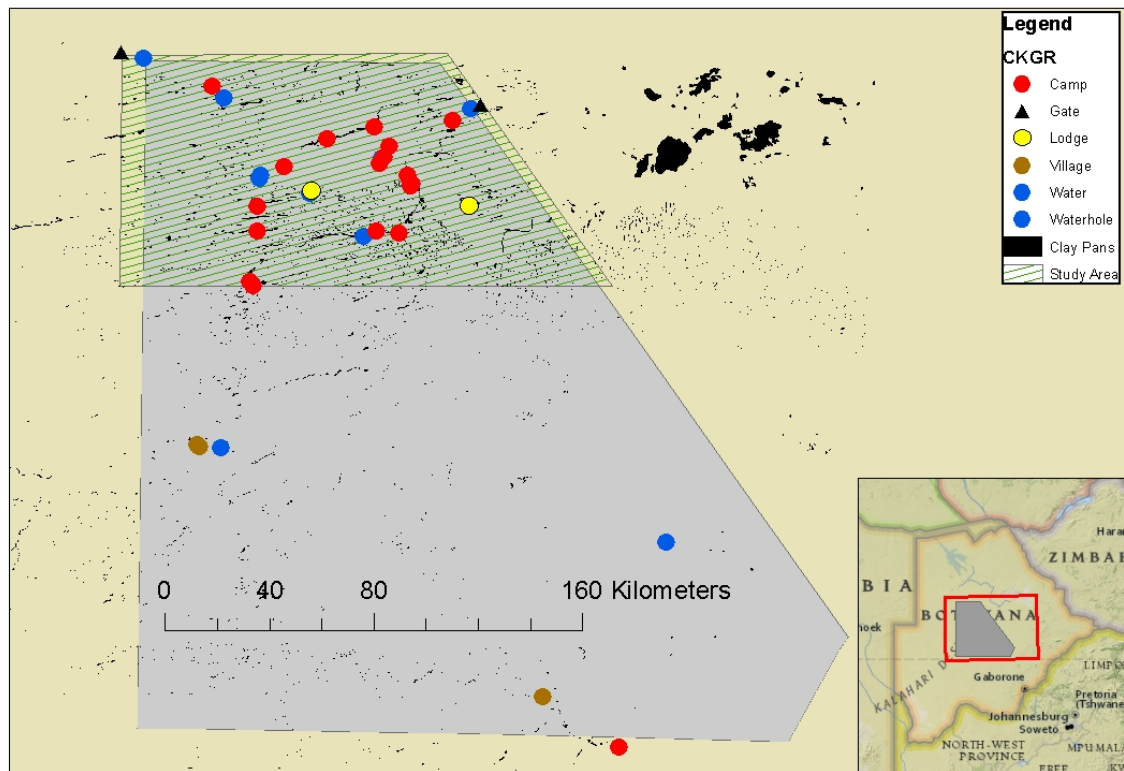


Figure 1-4 Map of the CKGR showing the predominance of clay pans and campsites in the north of the reserve where the study area was situated (green hashed box), and two San villages in the south.

Immediately adjacent to the game reserve are public and private land comprised of four land-use categories: large-scale cattle farming, large-scale game farming and hunting, small-scale rural communal cattle herding and wildlife management areas which may contain sparse traditional small cattle-posts. In the next section I will expand on the role of these categories in understanding the lion-livestock conflict.

1.3 Study Area

My study area comprised the accessible northern extremes of this system, which encompasses five land use categories, including the game reserve itself. It extends from South -20.877856° to South -21.667439° East 22.769744° to East 23.891975° , (Figure 1-4) an area I estimate at 9911 km^2 including a small buffer outside the reserve to include boundary transgressions by study lions.. It is an area known for lion activity and livestock predation by lions near the boundaries, This area incorporates the greatest network of established vehicle tracks accessing a complex system of clay depressions that provide the greatest opportunity for tourists to view wildlife and lions, and provided me with easier access to lions most often blamed for livestock loss near the reserve.

The Botswana Department of Tourism attributes the high numbers of large herbivores to the "sweet grasses" in this northern area (Department of Tourism 2000). Annual ungulate surveys of Botswana by the wildlife department indicate a

much higher density of ungulates in the northern area (Department of Wildlife and National Parks 2014), and this is the main reason that four fifths of the reserve are visited by fewer than 4% of CKGR visitors. The placement of campsites, lodges and tracks indicate that reserve management and tourism operators alike are aware the northern portion of the reserve is the most desirable from a wildlife perspective. Farms adjacent to this part of the reserve report the highest lion predation on livestock, and the selection of the study area flowed on from this.

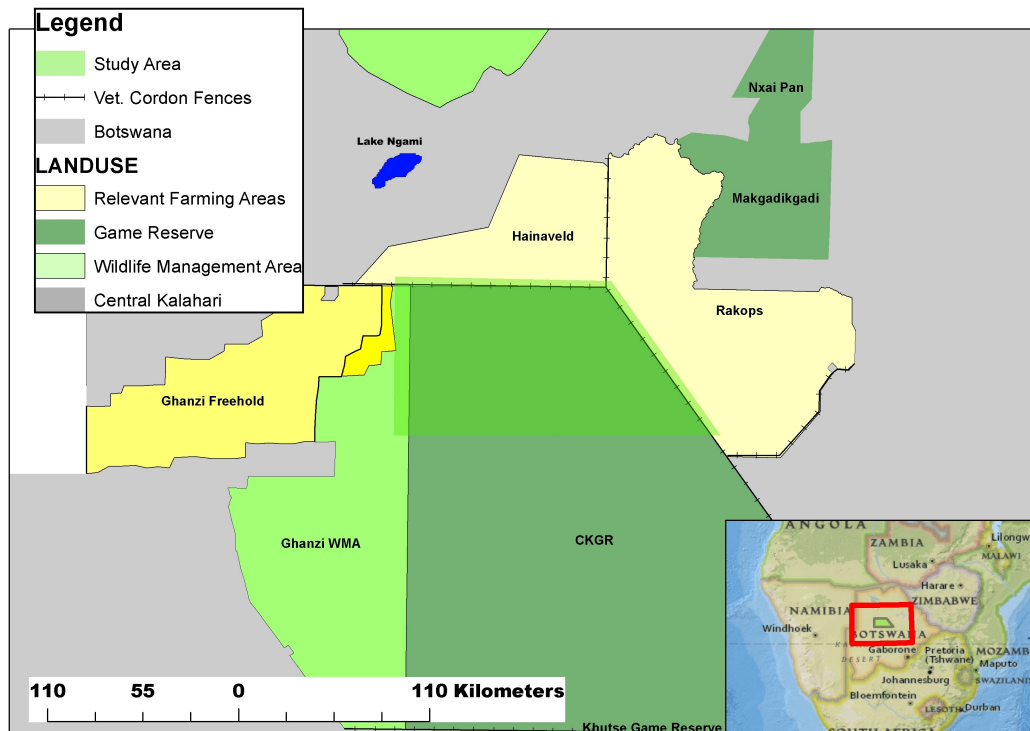


Figure 1-5 Map of relevant land usage to the CKGR lion-livestock conflict. The proximity of the Nxai Pan and Makgadikgadi Pans National Parks are evident. I have highlighted only the relevant commercial farming areas, Ghanzi, Hainaveld and Rakops. The CKGR is fenced on three sides by district fencing, as these coincide with the edge of the Ghanzi district, the western side is not fenced. These fences are permeable to lions and impermeable to most cattle and some large game; most noticeably wildebeest. The old migration of wildebeest would take them north of the Hainaveld to Lake Ngami.

In the 1970s, Mark and Delia Owens set up a research project that lasted 10 years, in the Deception Valley of the CKGR (Owens & Owens 1984a). At that time there were few tracks, tourists or rangers passing through the reserve. During their study, the Owens noted considerable numbers of gemsbok (*Oryx gazella*), wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*), steenbok (*Raphicerus campestris*) and red hartebeest (*Alcelaphus buselaphus*) in the Deception Valley. However the only figure reported was for 362.3 springbok per square kilometre, in clay pan habitats, in the rainy season (Owens & Owens 1978). They report that during the dry season, “almost no animals remained in the valley”, and springbok densities dropped to under 18 animals/km². They did not mention observing African ostrich (*Struthio camelus*), common duiker (*Sylvicapra grimmia*) or eland (*Taurotragus oryx*); the ostrich being a noticeable exception as it was common during my study. They did note trace evidence of all three in scats of brown hyaenas

(*Hyaena brunnea*). They observed the same major predators I observed; lion, leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), and jackal (*Canis mesomelas*), but noted the occasional spotted hyaena (*Crocuta crocuta*), which was not observed during my study. It is likely the spotted hyaena was an irregular visitor to the semi-arid CKGR and, increasingly, fences, roads and farms have prevented them reaching the reserve.

1.3.1 Areas surrounding and connected to the CKGR

There are three districts lying adjacent to the game reserve in the study area, Ghanzi, Ngamiland, and Rakops. Each district has different land use zoning and ownership types, farming styles and cultural histories that play a role in how lion conflict impacts on stakeholders and how those stakeholders address the issue. All farms within 40km of the CKGR use only borehole water, and in all areas the fences are permeable to lions. Beyond these areas there are several biomes that are considered connected to the study area, including the Makgadikgadi Pans National Park (East), the Okavango Delta (North), Khutse Game Reserve (South), Kalahari Gemsbok National Park (further South), and Xai Xai (north West). While all areas contain a mixture of the farming types typical in Botswana, the ratio is very different.

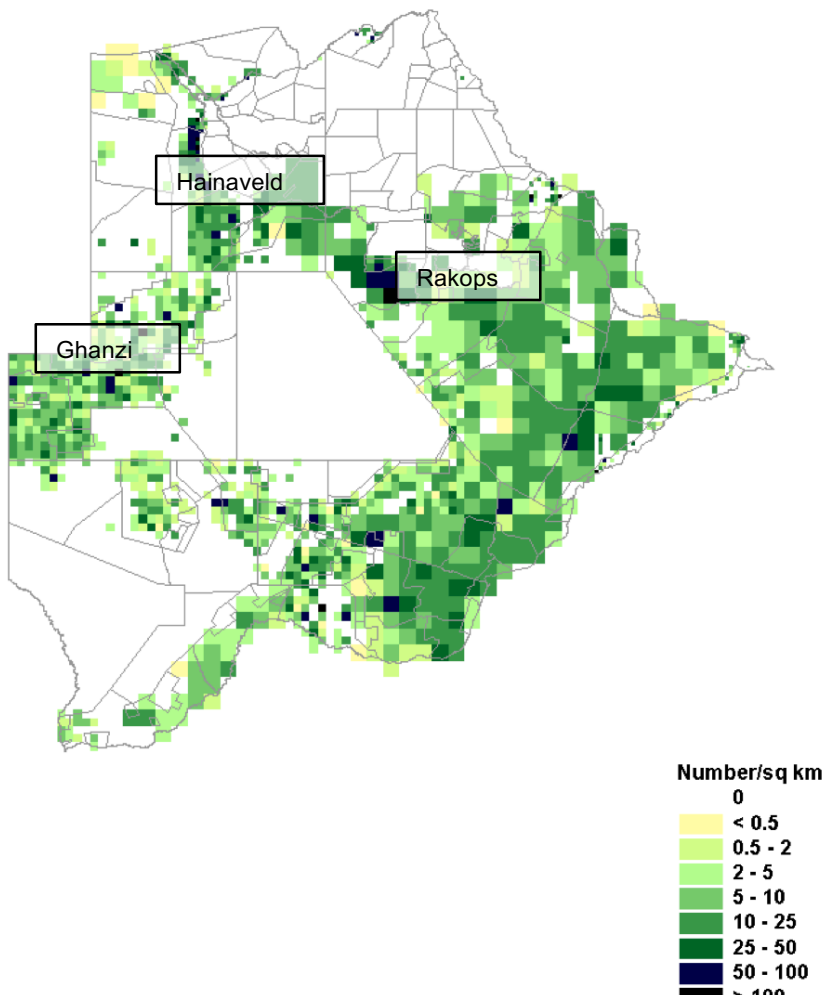
1.3.2 Ghanzi district

The Ghanzi district lies to the west of the CKGR, and the farms there are referred to as the Ghanzi farms (sometimes 'Gantsi'). In 2011, the area had 146,682 cattle out of Botswana's 2.26 million cattle on 2,118 properties, with every property served only by borehole and rain water (Agricultural Statistics Unit 2011). Early European explorers visiting the area prior to 1900 noted large numbers of wild ungulates and predators in the region, most of which are now much reduced in population (Kent 2011). It is the area of Botswana settled the longest by European farmers, and Dutch heritage is very strong, with most farm owners' families identifying themselves as Afrikaans (Dutch speaking Caucasians). A few wealthy families control the majority of farms in the area which are under long-term (99 year) leasehold or freehold. The majority are cattle farms, and each is delineated by a fence around the perimeter. It is one of the few regions in Botswana where most land is a delineated farm as opposed to communal unfenced grazing lands.

In the last decade, six of the eight farms immediately adjacent to the reserve have been combined into a single lion-friendly game-hunting ranch. Previously, those farms had been utilized for grazing cattle and were the 'front line' of livestock lost to lions from the park, reporting high levels of lion depredation. Now, farms further west are reporting higher-than-ever levels of livestock predation as the lions include the game ranch in their range. The cattle farmers of the Ghanzi district are intolerant of predators on their property and have the means to mobilise, track and shoot offending lions and other predators easily. Within these properties, cattle are able to roam freely, with several watering points and salt licks throughout the typical farm to spread grazing to all parts of the property. Cattle are not brought into a kraal for safekeeping at night, when the majority of lion predation occurs. On some farms, calves are protected for the first few months of their life in fenced areas called kraals, but standard

practice is to allow them out with their mother and herd. This is because kraaled calves lose condition but Flower and Weary (2001) showed that short-term condition losses were only temporary. Outer fences on cattle farms are designed to stop cattle leaving and are not an effective barrier to lions. Even the higher, stronger diamond mesh game fence around the game ranch does not stop lions which use holes dug by porcupines, honey badgers or jackals to quickly pass fences. In the conflict zone, cattle farming properties have several species of wild animals present, whose numbers are kept low through hunting to reduce grazing pressure. Most Ghanzi farmers complained of bush encroachment (woody shrubs replacing grass) as a serious problem, reporting that grassland health and herd carrying capacity of farms had declined in the last few decades.

Due to the large numbers of farms in the hands of a few key families, Kent (2011) stated that the greatest amount of change in farming techniques on a per area basis could be achieved by convincing only a handful of individuals to change. Records were not available of how many lions were shot, but one farmer complained about having to shoot more than 10 lions in a 2 month period in 2011 (J.Vorster, pers. comm.). This farmer is the closest cattle farmer in the Ghanzi district to the CKGR and as such is likely the most extreme case, but from informal reports and discussions with farmers, I estimate as many as 20-30 lions have been shot in the district every year since 2008. The Ghanzi region is classified as Foot and Mouth Disease (FMD) free, and as a result is classified as a green zone, from which meat can be exported to the largest importer of Botswana's beef products, the European Union.



1.3.3 Hainaveld, Ngamiland district

To the north of the CKGR is the Ngamiland district of which, the farms immediately adjacent are the Hainaveld farms. Far north Ngamiland is characterised by the Okavango delta, an important tourist attraction for tens of thousands of visitors to Botswana. Close to the CKGR the area is dry for many months, most farms relying on borehole water for cattle, game and humans. This stark difference is best served by referring to the area adjacent to the study area specifically by name; the Hainaveld. Two rivers and a shallow lake in the north of the Hainaveld mark the northern boundary of the farms, and prior to 2008, these rivers and the lake had been mostly dry during the middle of the year.

A significant wild herbivore in the region is the African buffalo (*Syncerus caffer*) which naturally harbours high levels of Foot and Mouth Disease. The Botswana Ministry of Agriculture considers FMD to be the most economically important disease threat to the beef industry (Benza 2013). FMD outbreaks are common in cattle close to the Okavango Delta and the district is classified as a red zone to reflect this. All cattle in a red zone are currently excluded from export and as such draw a lesser market value than cattle from other districts. Beef is sold for local consumption only. Hainaveld farms consider themselves to be quite separate from the Okavango Deltas' ecological processes and the farms near the delta, but because of historical zoning, they are included in the district for disease management and share low beef and cattle prices. The Hainaveld farms are a mixture of large-scale farms with fences delineating property boundaries, some game farms and communally grazed cattle areas (cattle roam freely between kraals, and as there is mixing between cattle-posts, ownership is distinguished on sight using brands). In 2011, the Minister for Agriculture announced a new veterinary fence separating Hainaveld into a new district, and in 2014 this will become a new green zone from which beef may be freely exported. During the extent of this study, Hainaveld was a red zone.

Immediately adjacent to the CKGR all farms are fenced, but further from the reserve some are not fenced. Game farms and tourism-based properties are accepting of lions, the cattle farms are not. Communal grazing begins one farm north from the first line of farms in some places. Wealthier farmers have been able to fence their properties and have used simple three strand fences to stop cattle leaving their property. A few game farms generally have tall diamond mesh, high tensile fences to enclose antelope species, but as in Ghanzi, neither of these fence types protect wild or domestic stock from predation at night as the fences are permeable to lions. Communal farmers' attitudes are usually antagonistic towards lions, but they are less able to persecute offending lions with the limited resources at their disposal, often sharing vehicles and guns between several cattle posts. Records were not available of how many lions were shot in this area. While the district Problem Animal Control (PAC) office keeps records of trophy lions shot when some part of the carcass was destined for sale, this set of records is incomplete and did not cover many of the lion deaths for livestock loss.

1.3.4 Rakops district

The Rakops district to the east of the CKGR is comprised almost entirely of un-fenced cattle posts that graze communally. Cattle posts are always situated at boreholes dug for water access, and families live at each cattle-post at a subsistence level. A cattle post consists of several simple mud and thatch huts and some crudely fenced areas for livestock called kraals. Kraals are usually constructed in layers from thorn-brush collected from nearby. Cattle are not usually herded, and are expected to return to the cattle-post for water and salt licks. Hemson (2003) showed that typically 80% of cattle in the nearby Makgadikgadi region returned to the cattle-post at night with some seasonal variation, while farmers believed the number was closer to 87%. The social and ecological aspects of the farming communities are similar enough to anticipate similar figures in the Rakops district. The less wealthy cattle managers had fewer resources to persecute problem lions, and generally believed that the predators they encountered belonged in the game reserve and that it was the government's obligation to deal with problem lions. They were more likely to report depredated cattle to the Department of Wildlife and National Parks, who may attempt to relocate problem lions back to the reserve. This area is of less concern than areas further from the game reserve, as the DWNP assumed that the reported lions had already returned to the reserve before translocation teams could arrive, and that moving lions only a short distance was not an efficient way to deal the conflict. We do know that a few lions were shot in the Rakops farms every year, as DWNP Problem Animal Control (PAC) records indicated 2-5 lions reported as shot each year from 2009 to 2012.

1.3.5 The Makgadikgadi Game Reserve and Makgadikgadi salt pans

The Makgadikgadi region further to the east beyond Rakops district is in many ways a similar ecosystem to the CKGR, and a related study in the Makgadikgadi by Hemson (2003) provides some insight to the CKGR conflict. It is semi-arid with seasonal rainfall supporting a large number of herbivores that usually migrate to track resources. A small population of lions hunt these wild herbivores during the rainy season. It is common that kraal based farmers make the economic decision to use water and salt licks to entice cattle to return rather than herding every night of the year. When a cow is killed by a lion, farmers track the lion and attempt to shoot it. Contrary to farmers' opinions, Hemson (2003) showed that lions preferred wild prey to cattle, choosing to kill wild prey even when each was equally abundant, and only switching to cattle when they greatly outnumbered wild prey. He noted that most losses occurred at night outside of the kraal, and could be prevented if all animals were herded back in to protection at night.

1.3.6 Khutse Game Reserve

Adjacent to the southern end of the Central Kalahari Game Reserve is the Khutse Game Reserve (KGR, see Figure 1-5). The area of the CKGR between the study area in the north of the CKGR and the KGR in the south is less populous in terms of large herbivores and large predators, as shown in aerial herbivore surveys conducted by the DWNP (Department of Wildlife and National

Parks 2014). Several villages made up of indigenous peoples called Basarwa or Kalahari bushman live in proximity to the KGR. The KGR is similar to the northern part of the CKGR, and has several clay depressions called salt pans, waterholes and high levels of wildlife sightings. Adjacent to the reserve, cattle graziers raise animals in communal grazing areas and come into conflict with predators. In 2009, a fence was completed around the KGR, but it was poorly constructed and many natural holes let in cattle and let out wild game and predators. Originally, research there focused on leopards and more recently has focused on lions (Bauer 2010). PAC records indicated that leopards are of uniform concern to livestock despite distance from the reserve, and that although they killed many more domestic animals than lions, they tended to kill smaller, less valuable stock like goats, sheep and chickens (Schiess-Meier *et al.* 2007). Predation from lions was inversely correlated with distance, indicating that lions were resident in the park, occasionally leaving to kill livestock. Farmer attitudes towards lions were such that lions were economically significant while predators such as jackal and leopards were not considered economically significant. The habitat is similar to the CKGR, and attitudes and conflict are likely to be similar in communal grazing areas.

1.4 Veterinary cordon fences

Veterinary cordon fences are a measure used extensively in Botswana to curb the spread of diseases. They are specifically designed to restrict the movements of wild ungulates and cattle, along with the endemic carrier of foot and mouth disease, the Cape buffalo, which is the main target for movement control. Transport of cattle from low value areas to high value (labelled as disease free) areas is a disease concern to Botswana's Department of Agriculture, and is illegal under national law. The impact of fences on wildlife can be substantial, reducing their ability to disperse to find food and water, cause direct deaths through entanglement and have been shown to worsen the conflict between people and wildlife, rather than aid it (Gadd, 2012).

In the 1980s, Mark and Delia Owens began a global media campaign against the network of fences that were being installed around Botswana. They brought to the attention of the world the deaths of tens of thousands of wildebeest as they attempted to escape the drought in the CKGR (Owens & Owens 1983; Owens & Owens 1984a). The fences are considered economically important to Botswana's cattle industry. The government's compromise was to install waterholes in the CKGR so that the wildebeest would not have to leave. During my observations, I found that the waterholes were highly saline (unpublished data) and poorly visited by animals (personal observation). The few remaining wildebeest were still migrating from the area during dry times heading south rather than north (M. Selabatso, pers. comm.). Protein and moisture content in the grass seems to be of greater importance to retaining wildebeest than the availability of drinking water (Ben-Shahar & Coe. 1992; Murray 1995) or the wildebeest are rejecting the saline water.

Douglas and Jane Williamson reported on the same cause of mass deaths of wildebeest in the Linyanti area (Northern Botswana) at around the same time, and firmly laid the blame on the fences (Williamson *et al.* 1988; Williamson & Williamson. 1984; Williamson & Williamson. 1981). They argued that the numbers of herbivores they counted during flying transects was far below the

well-established carrying capacity of large Kalahari herbivores. The installation of the fences around the country began in the 1950s and continues to the present day, such as the 2012 announcement of the Hainaveld veterinary cordon fence mentioned above.

1.5 The future of predator conservation in Botswana

Frank *et al.* (2006) concluded that all the tools necessary to ensure lion conservation exist in Africa, but that the possibility of conflict resolution lay "in the realm of policy, social science and politics", while science will continue to play a role informing these sectors. Hemson *et al.* (2009) noted that benefits from lion tourism were largely restricted to employees and owners of tourism organisations, and were rarely disbursed to the greater community, which is an important pre-cursor for conflict resolution. They noted that the livestock owners who bore the brunt of the cattle predation by lions were not prepared to improve care and herding of the cattle, despite demonstrations that all livestock lost occurred to stray animals outside kraals, and could potentially be easily remedied without lethal control. The authors advocated a system to re-distribute benefits from lion tourism to the greater community in ways that help reduce the cost of the conflict or incentivise better management of farming to reduce the incidence of conflict.

The Ghanzi farm block contained a diversity of carnivore species and a reduced, but healthy, naturally occurring prey base (Kent 2011). Densities of cheetah and leopard were low (0.68 and 0.48 animals / 100 sq.km respectively), but comparable to, or better than, those reported for other similar environments in the region. A substantial population of brown hyaena was found in the area, which could be of importance to the conservation of the species as a whole. The farming community were supportive of conservation in protected areas, but generally intolerant of predators that killed their livestock. A wide variety of land management and livestock husbandry practices were apparent, with some farmers prepared to do more than others to actively protect their livestock. Farmers with small stock suffered from greater levels of depredation than those who farmed only cattle, while some species of predator elicited feelings of antipathy. Many farmers professed a distrust of government interference in their affairs, which hampered efforts to obtain reliable data on livestock depredation and monitor the lethal control of predators (Kent 2011).

Amongst mammals, carnivores are particularly vulnerable to decline. Terrestrial carnivores are necessarily limited to much smaller populations than their prey species, and much of their diet conflicts with human interests. The African lion's vulnerability has a long well-documented history, having first been extirpated from mainland Europe and much of Africa by around 2,100 years ago (Harrington, 1969). The total population is estimated at 18,000 to 27,000 in the wild (Bauer & van der Merwe 2002). The lion tends to maintain higher populations than other large cat species, which results from several interacting factors including their large size, ability to bring down the largest of African herbivores and their sociality, unique amongst felids (Bygott *et al.* 1979; Packer *et al.* 1990; Schaller 1972). The fission-fusion society plays an important role in coping with tough conditions, and is often less pronounced, that is more stable, in

lion populations with access to stable territories, food and water supplies (Schaller 1972).

The continued survival of populations of carnivore species will depend on their ability to persist outside protected areas despite conflict with humans and their livestock. Knowledge of these wildlife populations and of the perceptions and attitudes of the stakeholders in the areas in which they live is of critical importance in the quest for coexistence. Little research has been conducted into either the wildlife or the difference in farming techniques between traditional African style farms and large-scale farmers who own the majority of the land west of the reserve. This study aimed to fill some of these gaps in knowledge.

There is little research on how retaliatory killing of problem lions affects prides of lions although there has been some work into the effects of trophy hunting (de longh 2012; Packer *et al.* 2011; Whitman *et al.* 2007; Whitman *et al.* 2004). However, it is difficult to separate the effects of trophy hunting from other effects due to the many associated anthropogenic causes of lion population decline, primarily habitat loss and fragmentation, and loss of herbivore food supply. Packer *et al.* (2011) found a significant correlation between levels of trophy hunting and population decline in lions in Tanzania and found that retaliatory killing by farmers had much less impact than trophy hunting in the region; areas with increased trophy hunting experienced greater declines than comparable areas with increased retaliatory killing. This is likely to vary in other locations.

In 2001, Botswana banned lion trophy hunting due to concerns about Feline Immunodeficiency virus, but re-instated hunting in 2005, and then in 2013, Botswana banned all forms of trophy hunting due to an aerial census indicating declines in most major herbivore species. Trophy hunting differs from retaliatory hunting in two major ways: firstly, trophy hunting is primarily directed at male lions in their prime, while retaliatory killing disregards gender and the status of the lion; secondly, the significant resources at the disposal of the trophy hunters means that they are more likely than retaliatory hunters to kill the lion, but collateral deaths are unlikely. Collateral deaths from retaliatory killing can be low as associated lions often react quickly and at speed to gunshots and vehicles, however it can be especially high when the deaths are caused by poisoning and can affect many other species such as vultures, jackals, hyaenas and corvids. (Packer *et al.* 2011) show that hunting has the potential to have minimal impact if well managed; which would include well conducted regular censuses of the lion population and observation of a strict age minimum.

Setting aside tracts of protected areas large enough to conserve large carnivores makes their continued protection problematic, but there are many benefits. Large carnivores are charismatic, represent totemic and mythical importance to local residents, and their conservation is more assured than smaller, less charismatic wildlife (Carvell *et al.* 1998),. When conserved they may act as umbrella species, where the large areas required to be conserved covers a range of habitats of several scales of heterogeneity, conserving species (Caro 2003; Noss 1990) and raising the awareness of environmental degradation or habitat loss (Gittleman *et al.* 2001) that would otherwise receive little to no attention.

The Botswana Environment Statistics Unit (2005) reports drastic declines in important ungulate species. Red hartebeest (*Alcelaphus buselaphus*) numbers fell from around 270,000 in 1979 to 40,244 and blue wildebeest in 2003

(*Connochaetes taurinus*) numbers from 260,000 to 14,154 in the same period (Crowe, 1995 and Botswana Environment Statistics Unit, 2005). Kent (2011) interviewed farmers from the Ghanzi district, many of whom were from families that were the first to settle in the farmlands around the Ghanzi district, now adjacent to the western boundary of the reserve. Even into the 1980s the number of wildlife in that area was “impressive” (Kent 2011), and included stories of countless springbok (*Antidorcas marsupialis*) (Bryden & Stanford 1893), and “hartebeest and wildebeest herds stretching across horizons”, (Livingstone and Oswell (1852). The lethal combination of the arrival of the four wheel drive and the high-powered rifle have contributed to the great losses in wild herbivores in the area (Kent 2011).

The area has historically supported a large biomass of ungulates that are adapted in several ways to survival through long spells without rainfall. Prior to modern times, the highly mobile ungulates could cope with long dry periods by migrating to rivers or following the rainfall. In recent years, large tracts of the Kalahari have been opened to cattle-ranching by tapping fossil water while building roads and fences (Tlou & Campbell 1997). The fences impede movement of wild herbivores and increasingly, large parts of the Kalahari are being lost to provide farmlands each year.

African lions benefit humans in two main ways: direct economic use as part of the safari hunting and tourism industry, and, indirectly, through the regulation of natural herbivores and landscapes that are the basis of natural capital that human populations rely on. In Botswana, there is a history of embracing the direct benefits with a thriving and well-supported tourism industry, while remaining unwilling to acknowledge, or act to protect, the indirect benefits. Ideally acknowledging both sources of benefits will do more for meta-population conservation. Where there is acknowledgement, farmers generally argue that the onus of ensuring healthy lion populations falls to other organisations (national parks, wildlife services, tourism), insist that lions belong only in protected areas, and deny their own capacity to act in favour of lion conservation (Kent 2011).

Scientific paradigms for understanding the conservation needs of large carnivores include island biogeography (Whittaker & Fernández-Palacios. 2007) and meta-population theory (Trinkel *et al.* 2010), and in these contexts data from studies on movement, migration, and genetic flow of lions and other carnivores indicate that protected areas are rarely enough to ensure the longevity of large animals or the ecosystems services they provide (Tende *et al.* 2014). A meta-population study of lions in Kenya showed that limiting the dispersal ability of females has strong implications for localised extinction and the chances of re-colonization, because even though females rarely disperse, they have a stronger ability to colonise a new patch (Dolrenry *et al.* 2014). To ensure long-term survival of lions, a degree of tolerance outside of protected areas is essential so that lions can continue to disperse between populations.

Current management of conflict lions consists of the Botswana Department of Wildlife and National Parks (DWNP) translocating 60 problem lions per year from all over Botswana to the CKGR (pers. comm. Dr. M Rueben, DWNP), and another 40 to other reserves. There is little data to determine whether these lions perish, return, integrate or disrupt local prides. Three translocated lions were followed in 2011 and 2012. In one instance a lioness walked 80 km to return to the spot where she was originally darted for translocation (pers comm. David Mills, Khutse Game Reserve Leopard Ecology)

while two males perished. From a conservation perspective, translocating lions achieves nothing for the source population, and can disturb the social dynamics of the population into which the lion is inserted and only temporarily benefits the farmers affected. It can also be an important tool for gene flow between disconnected populations, but if so should only occur after genetic research of the two populations is complete, and when genetic transfer is deemed necessary; 60 lions per annum is overkill for gene flow requirements. If the translocated lion remains in the CKGR, it may be detrimental to local genetics, spread disease (Craft *et al.* 2011) and disrupt social structures. Lion populations have a density dependent response, where elevated densities result in high levels of infanticide by males (Packer 2000). The most likely result of translocation of adult males to the reserve is an unnaturally high level of infanticide, thereby putting undue strain on reproduction, and is truthfully a political strategy with few over-all benefits even to livestock losses.

There are no real barriers to lions exiting the CKGR in any direction. Based on interviews from farmers and the incomplete records from the government, I estimate that 20-50 lions exiting the CKGR are shot every year. This is a significant portion of the estimated 420 adult lion population, notwithstanding input from translocations. I began this study to estimate the size and demographics of the population, and relate its movements and health to that of the prey species and other variables. I had initially intended to maintain equal numbers of collar on lions in the centre of the reserve and near the border of the reserve. However due to the higher than expected mortality of collared lions in the latter group, the study had to be adjusted, and collars were not replaced in cross-border areas. The data forms the basis for further investigation into the viability of the population and its propensity as a source for other smaller populations of lions in nearby protected areas. Six of the fifteen collared lions in this study were shot before the study was completed. Farmers may shoot a lion on private property legally in the protection of livestock; there is no requirement for the farmer to try and protect his livestock in any other way.

CKGR lions have undergone a catastrophic transformation in behaviour since the introduction of veterinary cordon fences in the 1970s. Current levels of livestock depredation are causing great anxiety amongst farmers alongside the reserve. Comparing causes of lion behaviour between the period before 1975 and now would be disingenuous as there are many contributing factors to lion behaviour. At that time, there were many more wildebeest, very many fewer farmers and cattle, few fences restricting movement, and there are no good records of the numbers of livestock, or wild herbivores, lions or the numbers of livestock damaged. Variation in lion behaviour and demography across small and large scales can be attributed to many factors such as prey density, suitable hunting habitat, interspecific competition and density dependence (Bauer *et al.* 2003; Borge 1998; Dagg 1999; Davidson *et al.* 2011; Joubert 2006; Lehmann *et al.* 2008; Mosser 2008; Stander 2007).

Livestock husbandry is the mainstay of employment for the majority of the residents of Botswana, but contributes less to the economy than diamond mining and wildlife tourism. Both these industries employ many fewer people, but bring back great financial benefits to their families, many of whom are cattle farmers. There is a disconnect between the money the families receive from tourism and its source, and if these perceptions are addressed has some implications for lion conservation. Cattle are traditionally seen as the ultimate investment, but the

return of a typical communal cattle farm is extremely low, probably less than 3% per annum (Bauer 1995; Reed *et al.* 1974), and income is at the mercy of market forces, climate, disease and depredation. Tourism has proved a more dependable source of income in Botswana, maintaining high visitation through the 2008 global financial crisis (Department of Tourism 2011), having greater sustainability potential, and utilising only a small part of the country's natural resources. An important employer in the country, the tourism industry in Botswana is controlled by a handful of multi-national companies that keep a large part of the profits from tourism overseas, thus paying less tax in country (Mbaiwa 2005a). It also does not have the potential to provide employment for many more citizens living in rural Botswana; much of which is unsuitable for photographic tourism. While much is made of the great income that mining and tourism bring to Botswana, it will require both these industries to actively employ many more local citizens than they currently do to drive the reliance that the majority of the population has on livestock for day to day income.

The Botswana government has a compensation scheme for livestock lost to protected predators. The value of cattle was 700 Botswana Pula (BWP) from 2000 until 2013 without adjustment; in 2012 a single beef cow could be valued at around BWP3-4000. Values for compensation of other livestock and USD equivalence can be seen in Table 1.1. Compensation relies only on proof of the identity of the offending species; while some predators are not covered.

Table 1.1 Botswana Pula (BWP) and 2013 United States Dollar (X-rates.com 2014) value of livestock compensation when killed by protected predators (MEWT 2013)

Livestock	BWP	US\$ (2013)
Cow	700	82.39
Horse	1400	164.78
Heifer	700	82.39
Calf	350	41.195
Goat	120	14.124
Donkey	120	14.124
Foal	350	41.195
Mule	700	82.39
Ox	900	105.93
Bull	900	105.93
Tolly	900	105.93
Sheep	300	35.31

Various stakeholders in the region affected by CKGR predators have suggested many changes to current management in order to alleviate lion predation of livestock and lethal retaliation as a response. Farmers suggested that park management should do more to keep lions within the reserve, such as: building more waterholes, releasing more herbivores into the park, building better, taller and even electrified fences, implement chemical breeding control of lions and other predators and allowing farmers affected to acquire trophy licenses and sell hunts for the worst offending predators in order to provide some incentive for leaving other lions alone. These suggestions are short-term in scope

and display a clear lack of acceptance that wildlife may be beneficial to rangeland health. They reflect the long-held view by farmers in Africa that wildlife has no place on farms. There is some evidence to the contrary, as farms that have persecuted herbivores and carnivores on their properties have suffered from reduced grassland health and bush encroachment (Archer 2010; Blaum *et al.* 2007; Gadd 2012). The push for higher efficiencies with low market prices and rising costs has made the farmers work the land even harder, putting strain on their range and cattle and having little in reserve for natural catastrophes like fires and floods (Walker & Salt 2006, 2012).

1.6 The African Lion

The lion has long been a symbol of strength, courage, even wisdom throughout western, Mediterranean and eastern culture (Schaller 1972). The ubiquity of the lion as a symbol recalls its once-great historical range throughout Africa, Europe, the middle East and Asia. Prehistoric ancestors of modern lions roamed from Russia across the ice-covered Bering Strait and into the American continents (Nowell & Jackson 1996). By 1950, the modern lion was extirpated from all locations except Africa, and a small relict population in India's Gir Forest. In Africa, lions are estimated to have once numbered around one million in pre-colonial times, falling to 200,000 in 1975, and to less than 100,000 in the early 1990s (Frank *et al.* 2006). The current population is estimated at 18,000 to 27,000 (Bauer & van der Merwe 2002) with nearly 30% of that in Tanzania alone. Botswana is estimated to have a stable population of around 2700 lions (IUCN 2006b), or at least 10% of the world's population. Despite the precipitous decline in so short a span of time, the International Union for the Conservation of Nature (IUCN) lists the African lion as vulnerable rather than endangered (IUCN 2006b). This reflects the well-documented strength of the remaining populations, primarily in large but discontinuous protected areas in southern and eastern Africa. Many remaining small and isolated populations of lions are at great threat of localised extinctions, particularly in central and western Africa. The primary cause of historical decline has been a mix of both habitat and prey loss (Ray *et al.* 2005a), with direct persecution, originally for game management and more recently for livestock depredation, an emerging threat to smaller populations that remain (Bauer *et al.* 2008; Frank *et al.* 2006).

1.6.1 Ecology

Many researchers have contributed to our current understanding of lion's ecology. Here I discuss some relevant examples before discussing the current status of lions and the threats they face. Between populations, lion density is positively correlated with lean season prey biomass (van Orsdol *et al.* 1985) and there is a linear positive correlation with prey abundance (Carbone & Gittleman 2002). Hayward *et al.* (2007b) found a stronger relationship between lion density and prey in preferred weight categories. Long-term stable home range sizes are inversely correlated with prey abundance (Packer, 1986; Viljoen, 1993) but may vary on a fine temporal scale to track spatiotemporal variation in prey abundance (Hemson 2003). The distance between waterholes has a strong effect on home

range size in Hwange, Zimbabwe (Valeix *et al.* 2012b) with larger home ranges in areas where waterholes are more dispersed.

The lion is Africa's largest terrestrial carnivore, and is largely but not exclusively nocturnal (Hayward *et al.*, 2009). The body size and group hunting skills of lions allow access to several large herbivores unavailable to other African predators such as giraffe, buffalo and elephant (Power & Shem Compion 2009). Lions can be very active on cool days, walking great distances, hunting and fighting in daylight hours. The lion is polygamous and sexually dimorphic (Clutton-Brock 1989) although there are records of both maned females and maneless males (Gnoske *et al.* 2006; West *et al.* 2006). There is a large difference in mass between the genders, with a female mean mass of 150-170kg, and 200-270kg for males (Gutteridge & Reumermann 2013). Lions are considered to be highly adaptable, and there are records of lions living in most habitat types throughout the Africa including mountainous regions, deserts, beaches, dense woodlands and snow-dominated landscapes (Smithers 1983). Recent research into genetics, morphology, ecology and behaviour highlight the need for understanding complex lion response on a multitude of scales (Patterson 2007) to explain its adaptability. On average, males live much shorter lives than females - in some areas the average life expectancy is 7 years for males and 15 years for females (Gutteridge & Reumermann 2013). While males have the capacity to live as long, as seen in captive lions, natural situations result in high mortality from fighting to defend and acquire territories and mates, or the difficulties of living alone for males who have lost control of a pride group. Most mammals bias in utero sex allocation to contain more males, and there is evidence that a lioness will bias even further in areas where there is trophy hunting (Stander 2004).

1.6.2 Sociality

Lions are set apart from other big cats in their tendency to sociality, living in fission-fusion groups called prides (Bygott *et al.* 1979; Schaller 1972) based on related females and their offspring (Packer & Rutten 1988). In some more arid areas like the CKGR, it is rare to find the whole pride together, usually small groups form spontaneously of females in similar reproductive status (Packer *et al.* 1990). The transient nature of the males position in the pride means that researchers generally define pride size by adult females: 7.1 per pride in Tanzania's Serengeti (Schaller, 1972), 9.2 females per pride in the Masai Mara (Ogutu & Dublin, 2002), 4.2 females per pride in Namibia's Etosha woodland (Stander, 1990), 4.2 females per pride in Kruger National Park, South Africa (Smuts, 1976), 3.5 females per pride in Luangwa Valley, Zambia (Yamazaki, 1996) and 4.2 females per pride in Kalahari Transfrontier Park (KTP) (Mills *et al.*, 1978). In the Serengeti, prides sizes are density dependent (Bertram 1975; Bertram 1978).

Lions are the only large cat that regularly forms social groups, although the reason for this is a point of contention. Theories range from a social paradigm of cooperative hunting (Stander 1992a), exclusive access to a niche of large item prey animals (Scheel & Packer 1991), mutual defense of kills (Cooper 1991), and cooperative defense of territory and young (Packer *et al.* 1990). Ecological paradigms include the patch size hypothesis (Chapman *et al.* 1994), the resource abundance hypothesis (Wrangham *et al.* 1993), the prey renewal hypothesis

(Waser 1981) and the temporal food availability hypothesis (Malenky & Wrangham 1994). Many of these hypotheses are not mutually exclusive, and although their predictions may conflict; empirical data from field studies has so far been unable to categorically rule out most of these hypotheses and it is likely that many play some role in group formation by lions. For instance, the resource dispersion hypothesis may be unable to explain the formation of groups in entirety, (Revilla 2003) but facilitates the evolution of a group when paired with effects described by other hypotheses such as territorial defence and cooperative hunting (Valeix *et al.* 2012b).

Male lions leave their natal pride between 1.5 and 3 years of age, forming cohorts of brothers or cohorts with strange males, or sometimes becoming solitary, and lions in this phase are commonly called nomadic (Schaller, 1972). After a few years attempting to mate pride females and testing their strength in fights, they will attempt take-over of a pride by fighting the dominant male. Fights can be fatal (Schaller, 1972; Grinnell *et al.* 1995). Though there some data on dispersing lions there are records of lions walking 120km distant from the natal range. Elliot *et al.* (2014) used data from 50 dispersing lions through the Kalahari area to demonstrate the dispersing lions use radically different criteria for habitat while moving through fragmented and human dominated landscapes. This behaviour should inform the creation of animal corridor schemes to facilitate meta-population viability. In the Kruger, males often settled very close to the natal range (Funston *et al.*, 2003; Hanby & Bygott, 1987; Pusey & Packer, 1987). If they win the fight for a pride, males will have the opportunity to sire cubs and defend the territory. Infanticide at this time has been documented (Packer 2000; Packer & Pusey 1983; Packer *et al.* 1984; Parmigiani 1994) and it is generally thought to bring the female into oestrus; in an informal publication, Kat (2000) claimed research evidence that females continued their normal cycles throughout lactation, but refused to mate with pride males while rearing cubs. Killing the cubs therefore brought about not a physiological ability to mate, but a behavioural change. Lioness produce large litters of between 1 and 6 cubs and intervals between litters can be as high as 40 months (Funston *et al.*, 2003; Packer *et al.*, 1988; Schaller, 1972). Packer (2000) collected long-term data-sets where the ages of cubs during take-overs played a major role in infanticide, with a sharp increase in cub survival rates at 12 to 14 months of age. Infanticide will play different roles in population regulation at different densities of lions, with the greatest effect in regulating high-density populations that experience regular take-overs of prides. Loss of males through non-combative processes such as trophy hunting has the potential for nontrivial increases in infanticide (Whitman *et al.* 2004). Trophy hunting is currently banned throughout Botswana, pending a review of the lion census methods and the hunting industry in general. Some authors argue that trophy hunting has the potential to boost conservation in areas with low potential for photographic conservation, if the regulations and hunters work closely with science and effective lion populations censuses (Packer *et al.* 2011; Whitman *et al.* 2004). Offtake rates are usually only 2–5% and concentrated on male populations meaning that trophy hunting is often sustainable and low risk if well managed (Bond *et al.* 2004). The alternative in many currently hunted areas is not for photographic wildlife tourism, but usually for low value agro-pastoralism as many hunting areas are not considered aesthetically suitable for tourism (Lindsey *et al.* 2006a).

Mortality of cubs and sub-adults is skewed towards males, and sex-ratios of litters often contain higher numbers of male. For example in the Kalahari Trans-frontier Park (KTP) the ratio is two male cubs to one female (Funston 2011). Sex ratios of adults are usually female biased. For example, one male to 1.2 females in KTP (Funston 2011). Funston attributes both to the high male mortality during dispersal.

Roaring and scent marking are routinely observed and play a role in defending territorial boundaries and avoiding fights. Lions have a vomeronasal organ located in the top of their mouths, which they use to identify particular smells for information on breeding status on females, individual recognition and possibly social cues (Gutteridge & Reumermann 2013). This enables lions to maintain large territories and avoid conflict in low-density areas such as the CKGR, where mate guarding may replace territory defence.

Lionesses are induced ovulators, and experience regular menses without releasing ova; instead they are released by stimulation during copulation. Thus it is common for extended bouts of mating every 25 minutes lasting up to 4 days; a behavioural adaption to ensure the male defends the female from the advances of other males (Clutton-Brock 1989). Nevertheless there are high levels of mixed paternity in litters; which is likely to be a strategy by the females to protect cubs from the males (Packer & Pusey 1983). Lions are able to identify individuals through their calls and assess the number of lions calling (Heinsohn 1997) in order send large enough groups to defend the pride.

Individual lionesses show a preference for particular positions in hunting formations, with some lions reluctant to join the hunt and others usually do not punish individuals who continually refrain from hunting (Stander 1992a) or meeting intruders (Heinsohn 1997; Heinsohn & Packer 1995; Heinsohn *et al.* 1996).

1.6.3 Habitat and density of lions

Before the first century CE, lions were the second-most widespread of large mammals on the planet, apart from *Homo sapiens* (Harrington, 1969), which is indicative of their adaptability and dispersive abilities. Today, they are still found in a diverse array of habitats including monsoon forest, desert, swamp, plains, scrub, deciduous woodland and savannah (Nowell & Jackson 1996), albeit on a much reduced scale. Habitat influences the sex bias of pride hunting, with females doing most of the hunting in the open savannahs and pride males scavenging from these kills (Schaller 1972 ; Stander 1992b). In woodland habitats like the Okavango Delta and Kruger National Park, males frequently hunted (Funston *et al.* 2001; Funston *et al.* 1998). High-density lion populations are more likely to hunt in complete prides, reducing the need for males to hunt, and low density populations are more likely to have females dispersed in small groups, and males will hunt more often (Hermann *et al.* 2002).

The CKGR lion population follows the low-density pattern.

1.6.4 Diet

The diet of lions is as diverse as their habitat range, but tends to consist predominantly of the 2-5 most common large herbivores in their range (Hayward & Kerley 2005; Mills & Shenk 1992; van Orsdol 1982), with a marked preference

for species between 190kg and 550kg in mean mass, and some preference for species that are commonly found in larger herds (Hayward & Kerley 2005) but hunted when they are in smaller groups (Scheel 1993a). For example, buffalo are commonly in large herds, and easily located by lions, but lions will choose to hunt small groups that have broken from the larger group. Three smaller species commonly depart from this preferred weight range pattern, being accessed in accordance with their abundance: the common warthog (*Phacochoerus africanus*), the bushpig (*Potamochoerus larvatus* – not found in the study area) and the African porcupine (*Hystrix africaeaustralis*).

1.7 Research Questions

My aim in this thesis is to ultimately explore the realistic and best management options for the CKGR lion-livestock conflict. Since data on the ecology of the CKGR lion population is missing, I set out to determine some much needed specifics, including an estimate of the population size, mean pride sizes and typical home ranges. I also investigated the typical movement patterns, diet preferences and aspects of lion hunting that are relevant to the conflict I sought to determine factors that caused variation in lion ecology to understand the temporal and spatial nature of the conflict, and the ramifications for suggested management options. A reduction in conflict benefits both farmers and wildlife.

The flexibility of lions in ecological and behavioural adaptations requires a local understanding of their current ecology in order to understand and manage a local conflict. Initially, I set out to understand lion responses to environmental changes in a livestock predation setting by comparing lions that ranged across the reserve boundary with lions that resided wholly within the reserve. Over the course of the study, lions from these cross boundary prides were often chased by farmers and some were shot. Although I had anticipated this to some degree, I had not anticipated the scale of the threat to those lions. By the end of the study, six of the seven lions from the boundary prides had been shot and killed by farmers. While two collars were returned, another two collars were irreparably damaged and two more lost, at great financial cost to the project. Apart from the inconvenience to the research in economic and time costs, a moral question was raised about interference from the study. To deploy collars on lions, naturally I had to be quite close to the lions, and collecting social and health data over the course of the study involved a measure of habituating the lions. In this setting I quickly realised that the actions of the study could increase the threat to individual lions. At that point, actions that would increase habituation were minimised and I decided not to deploy replacement collars on more boundary lions. It is possible that my actions did not increase the risk to individual lions at the short time scale (some lions became visibly less habituated; others were clearly already comfortable with vehicles).

Despite this regrettable setback, I maintained focus on the key research questions by analysing the movement and range of lions as a response to ecological drivers. An important driver is the density and composition of prey herbivores and I set out to quantify the state of the wild prey as a baseline for comparison to other lion habitats and the variation of the same over a suitable timescale to observe lion responses.

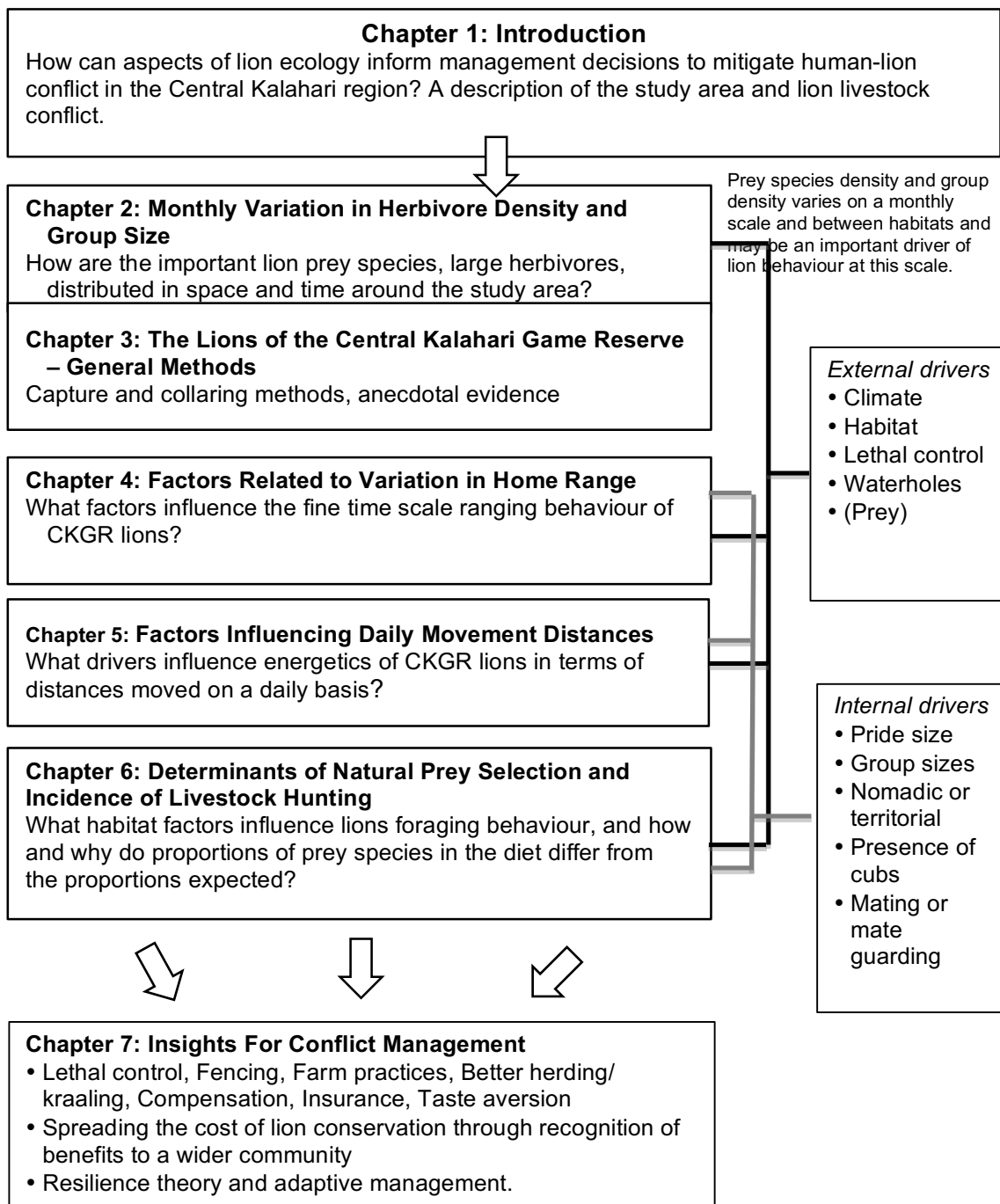


Figure 1-7 A diagrammatic representation of the thesis logic

1.9 Thesis Structure

In this introductory chapter, I describe the study area, historical context, habitats, seasons, lion ecology and other aspects that are relevant to the whole study, such as ethical approval and permits acquired. In Chapter 2, I describe data collection and analysis for herbivore density and cluster density estimation, which is important for understanding lion behavioural responses but does not directly deal with lions. Chapter 3 introduces the lion data section of the thesis, and I begin by describing the darting and collaring procedures, and give some detail about each study lion, including a map of the GPS data collected for that individual. Some relevant, primary observations are given here. I also describe the set of GPS data, including how gross spatial behaviour compares to studies of lions elsewhere and discuss the estimates for the lion population in the study area.

Chapters 4 and 5 describe the collection, analysis and results of two major aspects of lion spatial ecology, daily movement distance variation and home range variation. The estimated herbivore densities and cluster densities from Chapter 2 form a major component of this analysis, as does various data from climatic sources. In Chapter 6, I use data collected from kill sites of lions and scats to explore the role diet plays in the ecology of CKGR lions, from the habitats in which hunting generally occurs, to the preferred prey species as a subset of available prey species.

Finally, in Chapter 7 I discuss the results from Chapters 2-6 in light of the historical and political context of the conflict, and discuss management options that have been suggested by stakeholders, and other frameworks that prove useful to moving towards conflict reduction. In this section I will briefly summarise the chief findings and implications of this study.

The life histories, movements, and density and distribution of prey species of African Lions of the Central Kalahari region in Botswana were studied over a two-and-a-half-year period commencing in July, 2009. Fifteen lions of both genders in six prides were collared for between three months and two and a half years, and the method and summaries of each lion are discussed in Chapter 3. The collars were GPS enabled radio collars that allowed fine-scale positional data to be collected remotely, and allowed continuous contact with the lions for direct observation. Collars were changed several times on some lions as batteries became depleted. Several lions died during the course of the study, and the remaining collars were then removed from the surviving lions. Two collars failed completely, and two collars failed such that the data was unusable in some contexts. In light of this, I will refer to a sample size of eleven lions where appropriate. Data from a pilot study lion may also be referred to where appropriate. Using a calling station methodology, I estimated the lion population to be around 307 adults in the 10,800 sq. km. study area. The eleven collared lions associated regularly with sixty-six other lions, allowing me regular contact with 25% of lions in the study area. Occasional data was kept on another 51 lions as they were encountered.

At the same time as following and collecting data on lions I conducted regular transects of the study area, counting large herbivores, and in Chapter 2 describe clear trends in prey density only in a rare but important habitat, the clay pan. Herbivore density of the major prey species did not vary predictably over the majority of the population. Instead, a clear trend was noted in the group formation

of the most important species: gemsbok and springbok. Wildebeest numbers were considerably lower than those reported in years prior to the 1970s and this may have dramatic effects on the predators of the reserve and other ecosystem services attributed to the reserve.

In Chapter 3, I focus on the daily movement distances of lions as a response to climatic and prey variation. Daily movement distances are an important indicator of processes limiting lions, and are useful in uncovering the most important drivers that could lead lions into conflict zones, such as a need to increase foraging or explore empty territory for mating opportunities.

I used a mixed effects spatial Analysis of Variance (ANOVA) to explain important contributors to lion movement behaviour. Most of the variation was accounted for by temporal autocorrelation and by individual variation, supporting the use of the robust ANOVA method. Further variation yielded several insights into lion spatial responses. I predicted and found that lions responded more in daily movement changes to changes in preferred prey, gemsbok (*Oryx gazella*) group sizes than group sizes of other herbivores, or to the density of any herbivores (including gemsbok). Foraging studies tend to use prey density as a predictor in predator behaviour, but in the highly clumped distribution typical of herbivores, and the response to predators in varying habitat conditions, the density and size of herbivore groups should be considered. Group density reflects the encounter rate of groups by lions and the number of opportunities that lions have to hunt. I also found that males moved further than females, and this was accounted for by females moving shorter distances more often, and males moving longer distances more often. Lions of both genders in the west walked longer distances than in the east, although this was a non-linear relationship, and a small effect size.

In Chapter 4, the home range of lions is investigated in light of prey density, prey group size, social status of the lions, lion group sizes and other variables. I discovered that CKGR lions live at relatively low densities. A short study in the 1970s on two prides indicated that the prides maintained ranges of around 40 square kilometres. In my study, I found that all lions maintained ranges an order of magnitude larger than the previous study, indicating a strong effect on lion demographics of the herbivore decline. Home range sizes of lions are influenced by food resources, mate guarding of females by males, territorial boundaries and other factors like fences, waterholes and habitat. The size of pride ranges interacting with pride sizes determine carrying capacities and also the impact of edge effects across reserve boundaries, most importantly causes of mortality including human wildlife conflict. Total home range estimates are compared with other lion populations. Cumulative monthly home ranges indicated that CKGR lions continued to shift or expand their range over long periods. Total range is therefore dependant on the time period chosen. Monthly home ranges in three measures were calculated for each lion and analysed with a mixed effects ANOVA in order to explore forces driving lion ranging behaviour and further discuss the impact of these factors on long term survival of the population and the conflict across the game reserve boundary. Individual variation was much higher than monthly variation for each lion, and no significant gender differences were found. An important negative correlation with a remotely sensed greenness index (NDVI) was found with all measures of home range. Lions expanded core ranges and total ranges during greener, wetter periods. Total minimum convex polygons were positively correlated with group sizes of the preferred prey,

gemsbok. Larger groups mean fewer groups and fewer hunting opportunities and I suggest that factors that causes lions ranges to expand, may increase risk of lion livestock predation.

I collected vegetation and line of sight measurements at 421 locations around the study area, visiting locations where lions had spent more than four hours during the night. I found evidence of kills at 102 of these points, and compared chosen kill sites with random comparative vegetation points. CKGR lions showed a preference for making kills in areas with more, taller trees, but not necessarily with thicker or taller shrubs and grasses. Despite this, kill sites had significantly more cover at distances 15m from the kill site. I also collected scats while following lions and analysed hair to study diet. A few extra small species were found in the scats, but together with identified kill site species, they confirmed that gemsbok, wildebeest, giraffe and eland were all highly preferred above their relative abundance. Springbok and steenbok were avoided. Kudu, ostrich and hartebeest selection was similar to abundance.

The importance of diet to Kalahari lions is further investigated in Chapter 6. The immediate availability of much of the GPS data via satellite link or remote download allowed investigation of night-time clusters of lion positions to find kill sites. Identified kill sites were compared to random locations within the study area, and I compared vegetation characteristics. This revealed that lions of the CKGR preferred to make their kills in areas with considerably more cover, taller trees and more tree canopy cover, but not more shrub cover. Lions preferred the larger herbivores, and accessed them in proportion to their density. There is evidence of avoidance of herbivores common in open habitats; most noticeably, the springbok and the ostrich. Wildebeest were too rare to contribute much to lion diet, but were still eaten in proportion to their abundance. In contrast, researchers in the 1970s noted that lions hunted often in open habitat, accessing the once considerable wildebeest resource. This change in available prey and behaviour of the lion is discussed with respect to its effects on livestock predation. From these, I hypothesize that lions have selective preference for larger mass prey that prefer woody habitats, and form smaller groups (and are therefore more numerous in group density and less vigilant).

Chapter 6 investigates the evidence of livestock predation for clues into the conflict problem. The Department of Wildlife and National Parks in Botswana maintains records of the predators that kill and injure livestock. As the government provides compensation for lost livestock upon inspection of the loss, it is anticipated that these records are an important and accurate indicator of levels of livestock depredation around the country. Records are available from three districts that are relevant to the lions of the study area. In one area, the Rakops district directly to the east of the CKGR, farming is mostly communal grazing with relaxed herding, and few fences except for the corrals into which most animals return at night. Active herding is rare, with farmers expecting livestock to return to farms for water and salt licks – the return rates are naturally lower in the wet season when water is abundant and livestock predation was high in the wet season in this region. In the other two regions to the north and west, farming is on large fenced farms and no herding is practiced. Water is usually available at many points across each property. The fences offer no barrier to lions, and here predation is highest during the dry season. These findings offer important directions for future wildlife and farm management to reduce conflict

with the vulnerable African lion, and increase the benefit from ecosystem services to people living near the reserve.

In Chapter 7, I bring all the data from the preceding chapters together in the context of human livestock conflict and discuss how management could address the conflict issues. The two major farm types exhibit seasonal differences in lion predation on livestock, and I propose that certain attitudes to herding, fencing, waterholes access and management can increase risk of predation by lions. I bring together the risk factors from Chapters 2 to 6 that may help the Botswana Department of Wildlife and National Parks (DWNP) and farmers plan better for lion depredation, and discuss mitigating techniques from the literature and their potential for the CKGR conflict.

1.10 Ethics, Permits and Approvals.

Capturing and collaring of lions conformed to requirements of the Botswana Department of Wildlife and National Parks (DWNP) and American Society of Mammalogists' guidelines (Gannon *et al.* 2007). All field work for this project carried out within the protected area of the CKGR was pre-approved and all permits were sought including research, vehicle and personnel permits as required by the Botswana Ministry for Environment Wildlife and Tourism, Department of Wildlife and National Parks (Permit Number EWT 8/36/41 (80)), with full permission and knowledge of Reserve Management. All access to private property was done under prior permission, with full disclosure. The appropriate animal handling protocol was presented to and approved by the Australian National University Animal Experimentation Ethics Committee (Protocol ID A2011/44) and adhered to at all times, as well as adherence to the Australian Code for the Care and Use of Animals for Scientific Purposes.

Chapter 2 Monthly Variation in Herbivore Density and Group Size.

Chapter Summary

Farms bordering the Central Kalahari Game Reserve (CKGR) in Botswana experience seasonally different livestock predation rates from threatened wild predators. Of these predators, lions cause the greatest economic loss, with only elephants causing greater financial damage (Botswana Problem Animal Control Records, Ghanzi, Rakops and Ngamiland Offices, 2009-2012). The prevailing view of the reserve management is that predation upon livestock near the reserve is related to low stocks of wild herbivores in the reserve, yet data are lacking on behavioural responses of lions to varying levels of herbivore density. Reserve fences also prevent seasonal migration of herbivores to areas outside the reserve; contributing to low prey densities and degraded rangelands on farms. I studied seasonal variation in the density of the important natural prey of the lions involved: wild herbivores larger than six kilograms. I used the line transect method from a vehicle to survey density on a monthly basis to understand how herbivore density changes on various spatial and temporal scales and how different herbivores are using the reserve. The density of the ten most common large herbivore species varied seasonally across habitats. Five were at higher densities in the dry season than the wet: gemsbok (*Oryx gazella*), wildebeest (*Connochaetes taurinus*), ostrich (*Struthio camelus*), warthog (*Phacochoerus africanus*) and strongly so for the hartebeest (*Alcelaphus buselaphus caama*). Five showed strong signs of declining density going into the dry season: duiker (*Sylvicapra grimmia*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*) and less so for springbok (*Antidorcas marsupialis*). Gemsbok, springbok, ostrich, giraffe, hartebeest and wildebeest densities were high in pan habitats (<3% of the study area) while the remaining dune savannah habitat (~97% of study area) accounted for a larger population of these herbivores, but at lower densities. Total lean season biomass was estimated at 375.5 kg/km², of which gemsbok accounted for 36.7%, kudu 21.2% and giraffe a further 20.0%. This estimate is less than 50% of the conservative prediction for herbivore carrying capacity of the study area and indicates that the ecosystem has not recovered after major herbivore losses roughly 30 years ago. Where herbivore herds are spatially clumped, herd densities provide a measure of herbivore spatial structure that may influence predator responses. The number of herds per square kilometre of giraffe, hartebeest, kudu and ostrich varied significantly between months. The number of gemsbok herds per square kilometre varied between habitats. This variation may be as important as herbivore density in explaining why predators switch to livestock. My study suggests that natural herbivore densities and density of groups vary across time scales for questions explaining loss of livestock to large predators around the reserve.

2.1 Introduction

Predator density and behavioural response are related to density of prey species (Hayward *et al.*, 2007a). Predicting herbivore density in a biome can allow for fine scale understanding of predator responses. However, prey selection by predators, is influenced by multiple effects, including prey availability (potential prey may occupy niches in space and time which preclude capture), energetic constraints (some prey items may not be worth the effort) and grouping (large vigilant herds provide fewer hunting opportunities than homogeneously dispersed individuals). Measuring herbivore density, group size and the incidence of groups in the landscape allows for a better understanding of herbivore species and the causes of predator responses (Bagchi *et al.* 2003 ; Elliott & Cowan 1978; Funston 2011; Schmidt 2008).

Several studies investigating herbivore carnivore dynamics have highlighted the importance of considering prey group size in predator-prey relationships (Cresswell & Quinn 2011; Ioannou *et al.* 2011; Krause & Godin 1995). Herbivores in larger groups of prey are more conspicuous to predators but this is countered by the three following properties of grouping. The dilution effect states that for any individual, the chance of mortality decreases as the size of its group increases (Wrona & Dixon 1991), and often groups are better able to deter predators (Bertram 1980). Secondly, in the absence of migration, as group size increases, the total number of groups become fewer and the rate at which foraging predators can expect to encounter prey decreases (Ioannou *et al.* 2011). And finally the vigilance of larger groups is higher with a lower time cost of vigilance to individuals in the group (Krause & Godin 1995; Scheel 1993a; Treisman 1975). However larger groups are also more conspicuous; Krause and Godin (1995) showed that larger groups of guppies suffered more attacks from cichlids, demonstrating that large groups are more conspicuous. Fitzgibbon demonstrated the same effect with cheetah and Thomson's Gazelles, (FitzGibbon, 1990). The hunting tactics of some predators favour prey conspicuousness. Hebblewhite and Pletscher (2002) showed that medium sized groups of elk experienced the highest threat to individuals and found that elk preferred either very small or very large groups. Evolutionary theory states that the herbivores should choose the best trade-off between the benefits of avoiding predation risks and the costs of grouping such as reduction in food intake rates (Preisser *et al.* 2005). As vegetation condition changes and available surface water disappears, herbivores change the size of their groups (Fryxell 1991) and move between habitats. This may result in disaggregation. Aggregation may be an emergent property of foraging behaviour in open spaces by non-territorial ungulates (Gerard & Loisel 1995). This behaviour is both influenced by predation, and influences predation (Heard 1992). Larger groups are also more likely to be constrained in their position in the landscape. For example, Hebblewhite and Pletscher (2002) showed that wolves in Banff National Park killed more elk from large groups than expected based on the number of encounters, because large groups of elk are predictably restricted to the valley floor and lack the mobility of small groups.

As pressure from grazing livestock increases throughout sub Saharan Africa, reserves are becoming increasingly isolated. This affects species richness and population sizes in the reserve (McNaughton & Georgiadis 1986; Williamson *et al.* 1988). The spaces between reserves also become less porous to all

species, especially predators, which are not tolerated by farmers and experience reduced recruitment between protected areas (Gusset *et al.* 2009; Schiess-Meier *et al.* 2007). Spinage (1992) found declining populations of many typical prey species throughout the Kalahari region. This was attributed to recurring natural drought cycles with animal movements and recovery being restricted by veterinary cordon fences, and an increased incidence of meat poaching (Hitchcock 2000; Owens & Owens 1984a). The spatial response of herbivores to the extreme climate of the Kalahari habitat between seasons and between years is poorly understood.

In the 1970s, Owens and Owens indicated that CKGR herbivore density was relatively high in their small study area (Owens & Owens 1984a), and later, a larger survey in the early 1980s documented a decline that was expected to continue following the construction of veterinary cordon fences through the area (Williamson *et al.* 1988). An understanding of the current density and dynamics of the prey species of the reserve is crucial for reserve management, for managing the impact on surrounding farms and, in particular, for understanding the causes of predation on livestock.

The effects of group size are an important ecological factor. Reduction in the number of groups benefits predators that follow large herds (e.g. Cheetah following springbok), while a decrease in the size of groups may benefit predators that hunt by ambush or must forage for new groups after unsuccessful hunts (e.g. lions (Hopcraft *et al.* 2005)). Typically, studies concentrate on density, one aspect of how predators interact with their food, or on the mean prey group size, which puts the focus on the prey species, incorporating aspects of vigilance and survival prospects. (Amundson & Arnold 2011; Fay & Greeff 2006; Fay *et al.* 2006; Jeschke & Tollrian 2007; Mills & Shenk 1992; Seip 2010). In this chapter I argue that a measure of group density (counts of whole groups of any size of herbivore per square kilometre), shifts the focus back to the predator's viewpoint of prey encounter rates as the predators forage, and is directly related to hunting opportunities and therefore foraging success.

In the case of the CKGR, resident predators often depart the reserve to farmland where they are not tolerated and are confronted with lethal control, reducing the populations and destroying crucial meta-population connectivity. Lethal control has knock-on effects to predator social structure within the reserve (Woodroffe & Frank 2005). To gain an understanding how the structure of herbivore populations in the CKGR impacts this lethal conflict, I first undertook research to explicitly document seasonal variation in spatial structure (namely density and herd density patterns) of large herbivores (>6 kg) on a useful temporal scale and then related this to the drivers of herbivore group formation and movement such as vegetation production, rainfall and habitat. I focused on herbivores of a size that competed with livestock, both for food and as prey for predators.

Methods for estimating the density of species can be inadequate in any given habitat, with quickly diminishing returns on any scaling up of survey methods, and several untested assumptions in the more sophisticated options. The oldest method is a simple strip sampling method (Thomas *et al.* 2002). The centre-lines of the strips are randomly placed within study habitats and the total count of animals divided by the total area searched is the basis of estimate for all areas of that habitat type. The width of the block is limited to the distance from the line to which the researcher is confident of being capable of seeing 100% of

target animals, and a major assumption is that no animal is missed; yet this assumption is rarely tested (Burnham *et al.* 1985; Marsh & Sinclair 1989). A modern method to account for this detectability issue is called the line transect method or distance sampling (Buckland *et al.* 1993; Buckland *et al.* 2001; Thomas *et al.* 2002; Trenkel *et al.* 1997). The only assumption is that all animals on the line are detected, and proceeds to estimate a function of detectability at distances from the line is calculated from the sample data, and this function is used to improve the abundance estimate. In order to compare the seasonal density of prey species, detectability should not vary between seasons, which is not often true, but is likely in the dune savannah of the CKGR for prey sizes that lions prefer and this can be tested for. Detection functions should be calculated separately for each species where possible. Critics argue that the assumption that all animals on the line are detected and that detectability is correctly modelled by the function is flawed because the same data used in the sampling is used to explore possible detection functions (Barry & Welsh 2001; Welsh 2002). However, it is generally considered a robust method for estimating abundance. Older methods such as strip transect sampling suffer from a variation in detection abundance that is also difficult to estimate and makes comparison of seasonal estimates or estimates from difficult locations difficult.

2.2 Methods

Distance sampling transects were conducted throughout the reserve on a monthly basis between April 2009 and December 2010. As well as assuming that all animals on the line of the transect were counted, two further assumptions were that animals were stationary during the survey and not counted twice and that the blocks were representative either through random or stratified design. It became apparent during pilot surveys that randomly placed transects seriously limited distances surveyed, because off road sampling in the deep Kalahari sand was too slow and tough on vehicles. Typically, only 10km was covered in around 3 hours and this placed unacceptable strain on the research vehicles and animals were warned of our approach at this slow pace with a highly strained engine. Moving the transects to the nearest motor-able track was the only solution (see Figure 2-3). As I was concerned with relative changes in herbivore density rather than estimating actual density in this study, I did not consider this modification of the survey design to be likely to influence the results.

A single observer sat on top of a vehicle, while a driver drove the vehicle at a walking pace along the 60km track. The observer noted where animals were on approach and stopped the vehicle when perpendicular to the original location. The distance to this location was measured with a laser rangefinder (Bushnell Scout 1000 Rangefinder). Animals separated by less than 50m were considered a single group, and the centre of the group was estimated as the location of the cluster. Time, GPS location, species, number of young, habitat and if possible, numbers of each gender were recorded. Two of the surveys were also conducted as double observer studies to estimate observer bias.

2.2.1 Habitat classes

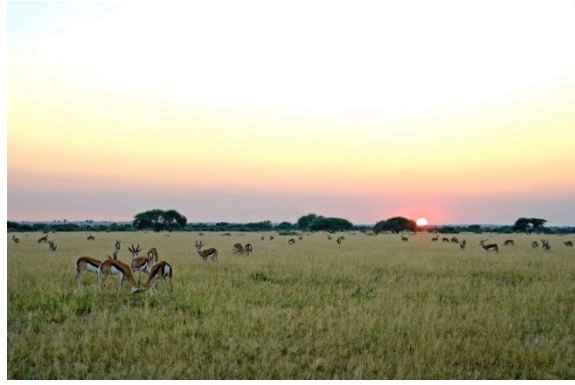
A comprehensive vegetation survey was completed between November 2008 and July 2009, and mapped to remotely sensed images of high quality (Mishra *et al.* 2015). Where possible, plant species are listed in order of relative abundance as noted by habitat surveys described in this thesis. Please note that at the time of writing the taxonomic status of many species that formally belonged to the *Acacia* genus are in a state of flux due to numerous studies showing the genus is not monophyletic (Kyalangalilwa *et al.* 2013; Miller & Seigler 2012). The African subgenera are also still being typed into two new genera: *Senegalia* and *Vachellia* (Brummitt 2010). Although they are still polyphyletic and these groups may be further revised (Kyalangalilwa *et al.* 2013).

2.2.1.1 Pans

Clay pans are open habitats found in low lying depressions between sand dunes and are characterized by calcium-rich clay soils. They are sometimes bare ground, exposing a white, hard clay substrate, but in the CKGR mostly comprise well-grazed *Schmidtia kalahariensis* grasses and a variety of forbs (families Acanthaceae, Asteraceae, Amaranthaceae, Aizoaceae and Scrophularaceae), with the occasional tall tree (see habitat categories below for examples of species). Pan habitats are preferred by grazing herbivores for much of the year for high nutrient grasses and provision of salt licks (Williamson *et al.* 1988). They frequently contain shallow depressions that collect water in the rainy season and last for variable periods into the dry season. Pans usually have calcium tolerant plants at the ecotone boundary of sandy habitats. These plants include *Cataphractes alexandri* and *Vachellia nebrownii*, shrubs which only occasionally cover entire, small pans. I used Landsat 5 satellite imagery (USGS, 2010) and compared to direct ground measurement to estimate the coverage of pan-type habitats at approximately 2.8% of the study area or 277.5 square kilometres.



A)



B)



C)



D)



E)



F)

Figure 2-1 **Pan habitats**. A) Aerial view of a north-east section of the Passarge Valley. A road runs through the valley's pan habitat, skirting the ecotone boundary to dune savannah habitats in the top left and top right of the image. In the bottom right of the image is a woodland habitat. (Google Earth 2013). B) Springbok on a pan in Deception valley. C) Bare earth is often visible on pans (foreground) and the sloping dune savannah habitat in the background can be clearly delineated in this case by dense vegetation. D) Small pockets of tall (2-4m) thornbushes are found through the pan habitats. E) Aerial view of a pan habitat with a research vehicle traversing a pan road that comprised part of the herbivore transects, showing short grass to the right and short shrubs to the left of the vehicle F) Pans provide some refuge from bush fires. If pans burn, it is quick, and relatively cooler than fires in dune savannah habitat. I observed most herbivores avoid fires by using this habitat.

2.2.1.2 Dune Savannah

Dune savannah or mixed shrub savannah (Dawson & Butynski 1975) are open grassy habitats on a sandy substrate with varying levels of shrubs, dominated by the grasses *Cenchrus ciliaris*, *Digitaria eriantha*, *Stipagrostis uniplumis* and *Panicum spp.* Shrubs include *Lonchocarpus nelsii*, *Terminalia sericea*, *Cataphractes alexandri*, *Bauhinia petersiana*, *Senegalia mellifera detinens*, *Senegalia fleckii*, *Grewia flava*, *G. bicolor*, *G. flavescens*, *Dichrostachys cinerea*, *Vachellia nebrownii*, *Senegalia ataxacantha*, *Boscia albitrunca*, *V. hebeclada*, *V. erioloba*, and *V sieberiana*. This habitat is characterised by finer grained substrates, deeper bedrocks, and lower rainfall than woodland habitats (Moore & Attwell 1999). I had originally intended to classify this varied habitat into sub-categories to capture the density and heights of shrubs within, however the algorithms employed to categorise the remotely sensed images were unable to distinguish sufficient differences along the subtle spectrum, and field categorization was similarly difficult.

2.2.1.3 Woodland

Woodland habitat is found mostly in the north-east of the study area and to the east of Leopard Pan and Sunday Pan and is a result of coarser grained soils with a shallow depth to bedrock and of higher rainfall. The predominant tree types are *Terminalia prunioides*, *T. sericea*, *Albizia anthelmintica*, *Vachellia erioloba* and *Combretum imberbe*. These trees are also found in much sparser numbers occasionally throughout all of the other habitat types. I defined the woodlands to be greater than 30% tree canopy cover as used by other authors, for example Moore and Attwell (1999). In the CKGR this is a rare habitat and insufficient herbivore counts made estimating density separately for woodlands questionable. I have not provided photographs for this habitat, as a relatively closed habitat it is difficult to photograph. However the scale of the trees is similar to those in Figure 2-1D, and an aerial view of woodland habitat is seen in the lower right corner of Figure 2-1A



A)



B)



C)



D)



E)



F)



G)



H)

Figure 2-2 **Dune savannah habitat**. Soft sandy substrates characterised this varied habitat from open grasses, or with short shrubs, to tall dense shrubs. A) aerial view with open grassland in foreground, to denser shrubland at greater distances. B) Open grassland. Grass is typically shoulder height on a lion/lioness (shown) C)-G) Increasing densities of shrubs in the tall grasses and occasional trees can provide excellent cover for lions. H) Lions often rest in the shade of unexpectedly short vegetation.

2.2.2 Remotely sensed data

I collected very high quality satellite imagery accessed through a generous grant from the GeoEye Foundation (1mx1m) (GeoEye 2010) and accessed high quality imagery from the freely available USGS datasets (30m x 30m)(U.S. Geological Survey 2008-2012). This was combined with vegetation data collected on the ground and used to validate the imagery classification at various spatial scales, to form hybrid supervised/unsupervised habitat classification on a 30mx30m grid. For the purposes of this study habitat was divided into the two major types described as dune savannah and pan. Imagery based on the Normalised Difference Vegetation Index (U.S. Geological Survey 2008-2012) was used for both seasonal classification (see Figure 2-4) and as a factor in herbivore density and group density modelling, after clipping the monthly imagery into polygons and defining each portion of the transect. The NDVI uses the ratio between Visible and Near Infra-Red light to estimate vegetation cover and has proven useful for estimating seasonal changes in vegetation (Bartlam-Brooks *et al.* 2013). Vegetation height and cover was assessed throughout the study, and compared with NDVI values. Very good rainfall was experienced prior to and throughout the study, and the grass was long throughout the study area, although its greenness was variable. A large variation in NDVI in the CKGR biome translates mostly as increased grass biomass, which will primarily effect the detectability of small species such as duiker and steenbok in grasslands but not on pans. Clipping into each transect portion on a monthly basis was achieved in the ArcGIS 10.1 software package (Environmental Systems Research Institute 2012), and 6% had to be estimated from nearby polygons of similar habitat due to their small size. I reasonably assume that the differences will not affect the interpretation using the interpolated values, due to the large differences in estimated values between months, and small variation within month across the imagery.

2.2.3 Large herbivores of the CKGR

The CKGR is home to eleven species of large herbivores that form the basis of the diet of resident African lions. In this study I ignore rare vagrant herbivores such as African elephants (*Loxodonta africana*), Cape buffalo (*Syncerus caffer*) and itinerant lost livestock that may wander into the park. Instead, I concentrate on those herbivores that are likely to contribute to variation in predator behaviour. The typical prey species available to the large predators of the CKGR comprise nine varieties of ungulate and two non-ungulates. Four of these 11 species aggregate in herds of larger than a family unit; the rest are typically found in smaller family groups.

The four herding species are usually heterogeneously distributed, forming small to large aggregations that dynamically redistribute themselves across the landscape. They often aggregate on the large pans found in the reserve in the wet season. They are the large blue wildebeest (*Connochaetes taurinus* ~ 150kg Mean Female Mass or MFM), gemsbok (*Oryx gazella*); African ostrich (*Struthio camelus*, ~90kg MFM) and the small springbok (*Antidorcas marsupialis*, ~ 39kg MFM). During the wet season these four species congregate in herds of up to several hundred along the pans and valleys. The largest groups counted were

395 springbok, 222 gemsbok, 45 ostrich and 35 wildebeest. Individuals of any of these were also regularly seen. Wildebeest are the most water dependent of the four species, and migrate large distances in dry periods in most years (pers comm. M Selabatsi). Verlinden (1998) observed that ostrich, springbok and gemsbok do not undergo annual changes in distribution at the reserve scale, but they do show localised changes in aggregative behaviour and habitat use. There are records of irregular, "once in twenty year", large-scale springbok migrations in severe drought years (Roche (2005) reported this in the order of hundreds of thousands of individuals). This phenomenon was not observed during the study period or in recent years and may no longer occur at such scale.

The other seven herbivore species only form small groups. These are the giraffe (*Giraffa camelopardalis*), red hartebeest (*Alcelaphus buselaphus*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*) and the common warthog (*Phacochoerus africanus*). The non-herding herbivores are usually solitary or in small family groups and are more homogeneously distributed throughout the reserve both spatially and temporally.

I note the presence of other prey items including the African porcupine (*Hystrix africaeaustralis*) and armadillo (*Oryzomys afer*), the honey badger (*Mellivora capensis*), black-backed jackal (*Canis mesomelas*), springhare (*Pedetes capensis*), helmeted guinea fowl (*Numida meleagris*) and the bat-eared fox (*Otocyon megalotis*). These species were not considered for the prey abundance estimates as they do not contribute substantially to the diet of lions and therefore, are unlikely to influence lion behaviour.

2.2.4 Line transects and abundance estimation

Sets of seven 60km long were conducted over seven consecutive days at the beginning of each month (Figure 2-3). The line transects methods, (also called distance transects) included data out to 1500m from the track (the limit of the rangefinder used) (Thomas *et al.* 2002). Large transect lengths were needed for estimates on rare species and for feasibility, transects were started at 8 am every day and continued until finished, which was sometimes after midday. Line transects were alternately performed in different directions to account for time of day bias and separate time of day bias studies were conducted, and are also presented in the results. Transects were conducted once each, each month for the duration. Each transect was naturally divided into unequal lengths at the interfaces between the two main habitat types, resulting in portions of variable lengths. This was accounted for by an effort variable included in the analysis, species were estimated separately in each habitat type as detection is likely to be different. Variation was high for monthly transects and no replication was possible at this division, therefore months with similar NDVI values were pooled to provide seasonal estimates (wet season above 3500 NDVI and dry season below 3500 see Figure 2-4).

Lean season biomass for the CKGR is estimated from the mean density for the 6 months in each year during the dry season (May - October). The total number of animals is estimated from density in each habitat and multiplied by the mean female mass from Smithers (1983).

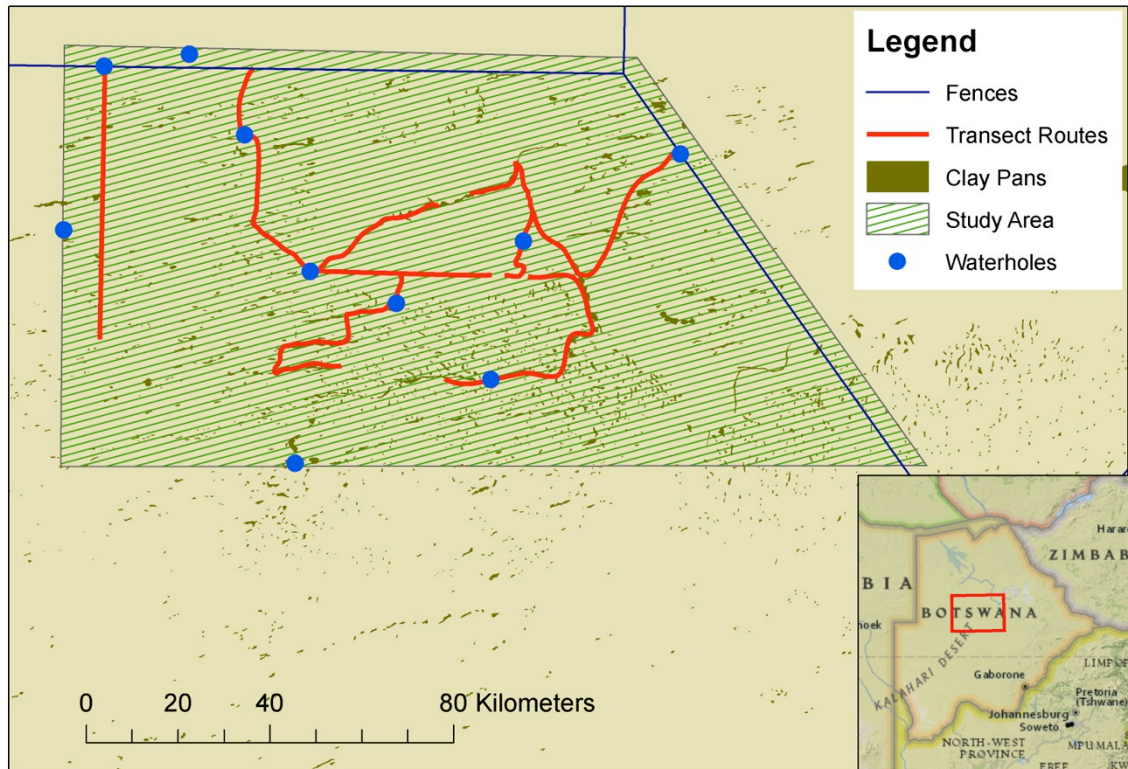


Figure 2-3 Map of the study area showing transects in red. Dune savannah transects are fixed width (400m), clay pans are variable width green areas. Extant fences are visible as a blue line. No fence exists on the western boundary of the reserve. Inset is Botswana highlighting larger map with a red rectangle.

Observation data was analysed using the Distance Software package (Thomas *et al.* 2010). A full set of detection function models were explored for each species and models that satisfied Goodness of Fit tests were distinguished by lowest Akaiques Information Criteria.

Herbivore clusters were analysed using Generalised Linear Mixed Effects Models (GLMMs) as described for animal density using numbers of groups per square kilometre in place of numbers of animals. I intended to use the number of groups of a species per square kilometre acted as a proxy for the encounter rate of herbivores by lions. For solitary animals there is no distinction between density and group density, as with the common duiker which was discarded from group density analysis ($R^2 = 96.6\%$) and was high with steenbok ($R^2 = 88.6\%$) and kudu ($R^2=70.1\%$). My aim was to distinguish which herbivore group sizes were not correlated with density and were rather a function of changing foraging behaviour and habitat use resulting in fission of larger herds.

The resulting group density model was used to estimate the density of each species across the space and time of the lion study. A prediction grid of 100m x 100m was generated in the bounds of the study area, and populated with the information about the habitat type. Predictions were applied using the selected GLMM's for each month of the study period, and grid files from each

prediction were saved. This was repeated for the group density for each species. This generated 418 group density maps, of which an example is Figure 2-12, and were used in herbivore co-variables with respect to lion behaviour.

Mean crowding graphs use representations of animal counts to explore variation in group size from the perspective of the counted animal (Iwao 1977; Iwao & Kuno 1968). By example, while standard histograms represent two counts of 50 animals with a height of 2 at the 50 value, a mean crowding histogram places a 100 at this point (Lloyd 1967). 40 counts of single animals is still represented by a height of 40 at the 1 value. These figures are presented to explore information about crowding that is missed when expressing the groups as mean sizes.

2.3 Results

Seasonal patterns of rainfall and vegetation greenness as measured by NDVI are graphically represented in Figure 2-4, and a slight lag in the greenness after rains is visible, as well as a stark contrast between the greenness of wet months (values above 3500) and dry months (below 3500) as well as year-to-year variation in which months constitute wet and dry.

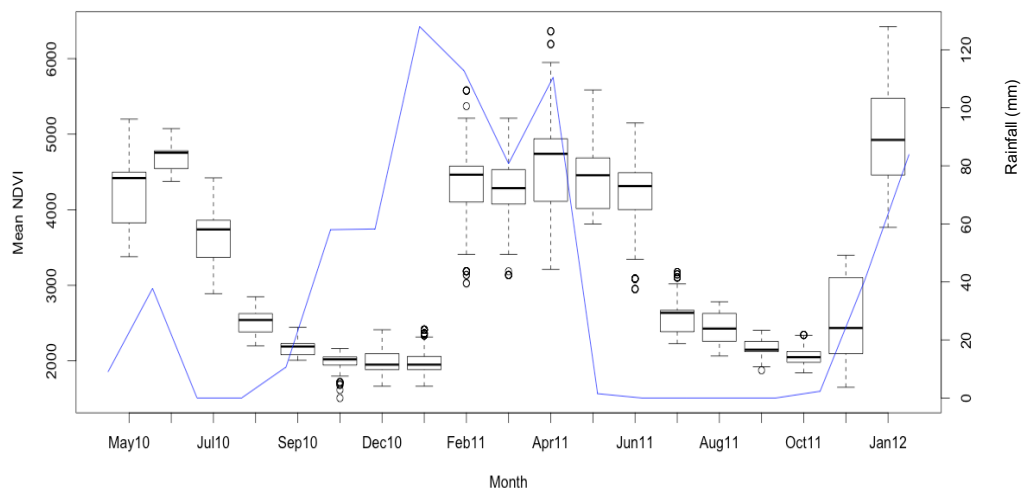


Figure 2-4 Normalised Difference Vegetation Index provided a clear distinction between wet seasons at values above 3500 and dry season values which were below 3500 and also more tightly clustered. The blue line indicates mean rainfall for the study month as measured at three stations on the edges of the study area.

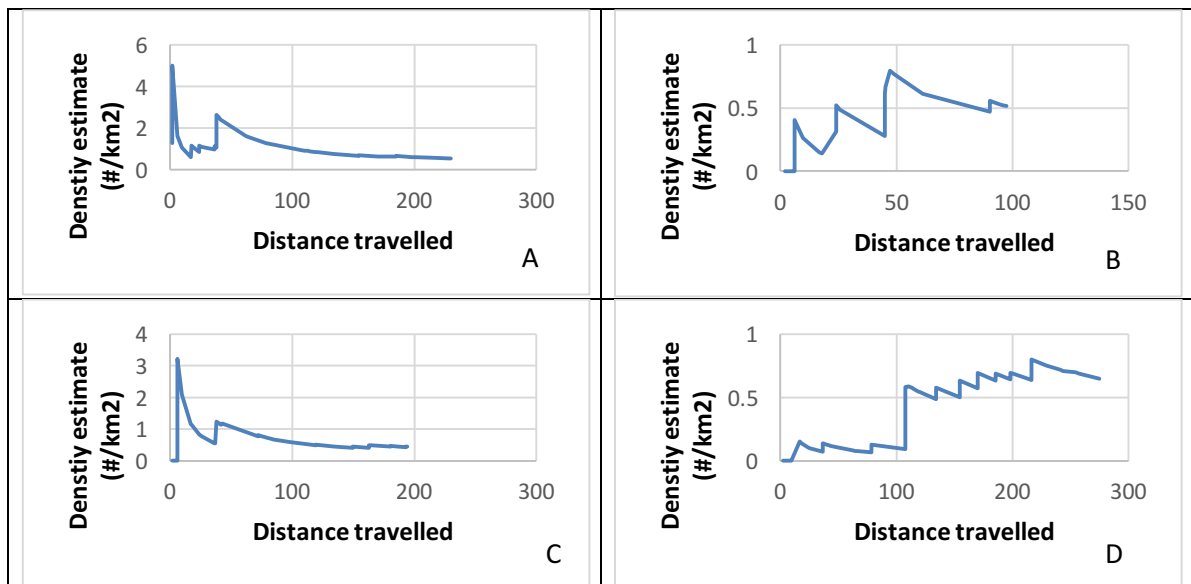


Figure 2-5 Selected graphs of density calculated by length of transect travelled. Density estimates usually converged with longer distances travelled. Gemsbok density estimate for A) April, 2009, B) May, 2009 C) June 2009 D) July, 2009. Confidence intervals are not appropriate in raw data graphs displaying the change in mean estimate with increasing distance.

Transect accuracy is estimated by observing convergence of estimates over distance travelled and four of the 209 graphs are presented in Figure 2-5. Estimates tended to be stable after 200km of transects but were more variable for rare species. Detection functions for rare species were calculated from more common species of a similar mass, separately for each habitat.

2.3.1 Estimates of large herbivore density

A total of 7278.6 km of herbivore transects were conducted. Eland were seen occasionally during other times, but never counted during herbivore transects. Only 28 Duiker were counted on 26 occasions in 19 months of transects. This species is considered rare in the study area. A total of 15, 434 springbok with a mean group size of 13.75 ± 0.86 S.E. were counted, 91.4% in pan habitats and 15,038 gemsbok were counted, with an average group size of 7.42 ± 0.28 S.E., 80.2% of which were in pans. Results for other herbivores are found in Table 2.1 and Table 2.4.

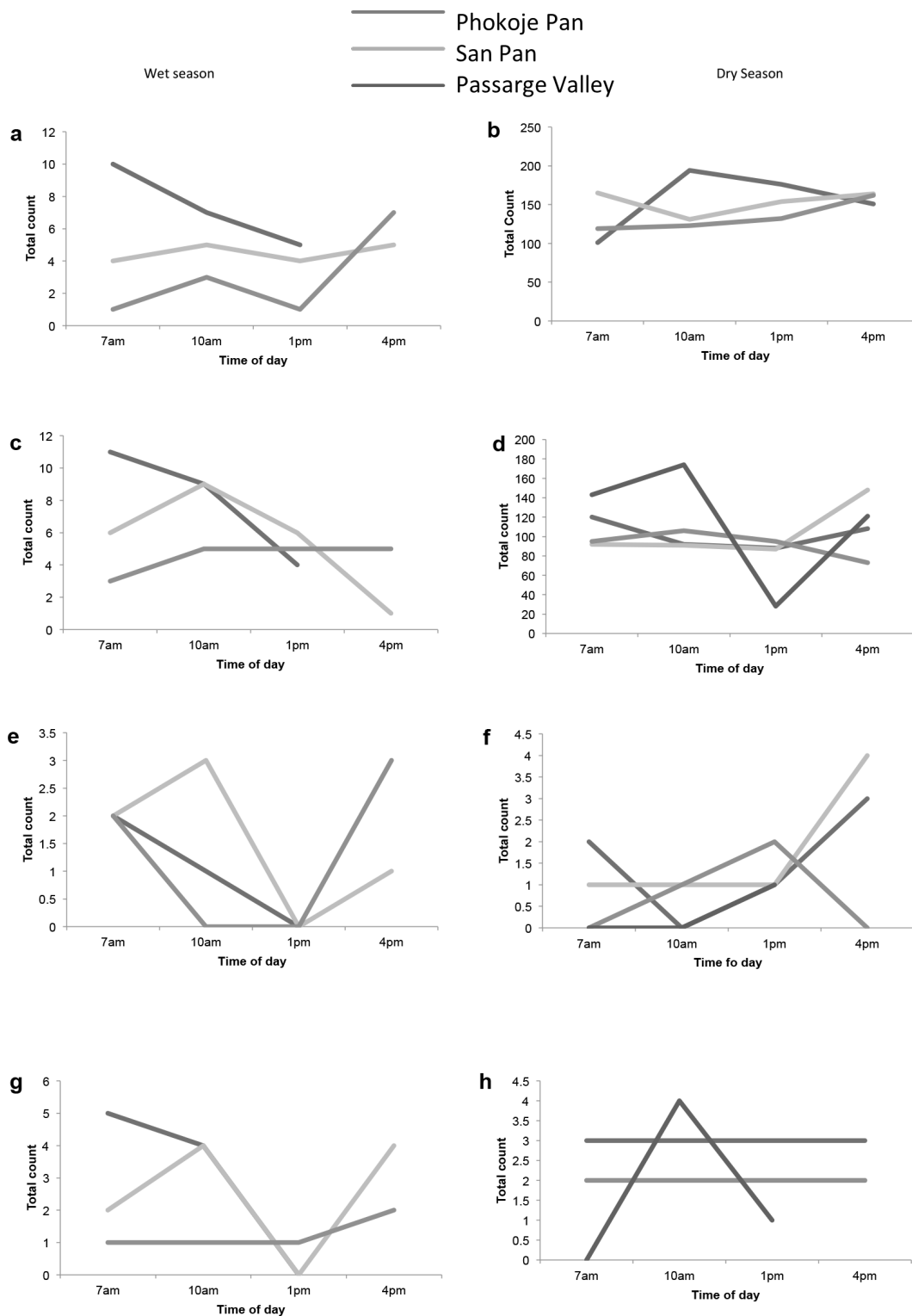


Figure 2-6 Time of day bias surveys were conducted at three locations in the wet season (left column) and again in the dry season (right column). Rarer species showed some signs of time of day count bias, but the animals that make up the bulk of the biomass (oryx, springbok, wildebeest) in a CKGR lions diet were not clearly changing their locations between 7 am and 4pm. a) gemsbok wet season b) gemsbok dry season, c) springbok wet season d) springbok dry season e) steenbok wet season (1pm seems to be problematic) and f) steenbok dry season g) ostrich wet season (again 1pm shows evidence of bias) and h)wildebeest dry season.

Table 2.1 Summary of total counts, density, group sizes and the ratio of density between habitats of large herbivores in the Central Kalahari. This represents the actual data before estimation analysis

	Total Count	Mean density (Number per km ²)	Mean Group Size + (Range)	Pan/Dune Ratio of total counts
Gemsbok	15038	5.63	7.42 (1-222)	0.803
Springbok	15434	5.78	13.75 (1-395)	0.914
Kudu	593	0.22	3.71 (1-15)	0.121
Wildebeest	907	0.34	4.76 (1-66)	0.890
Duiker	27	0.01	1.038 (1)	0.037
Ostrich	1398	0.52	4.76 (1-45)	0.648
Hartebeest	443	0.17	4.83 (1-23)	0.535
Giraffe	444	0.17	5.48 (1-32)	0.536
Steenbok	776	0.29	1.769 (1-2)	0.205
Warthog	81	0.03	1.857 (1-5)	0.543

2.3.2 Regional and seasonal variation in prey density

A sample set of six of the 23 modelling results for gemsbok is shown in Table 2.2. Final models for all 10 species are presented in Table 2.3 and final density estimates in Table 2.4. There was insufficient data for eland, (3 observations, all greater than 200m from the transect line). The duiker data was sparse (n=26) and estimates were treated with caution (refer to Table 2.1 for all sample sizes).

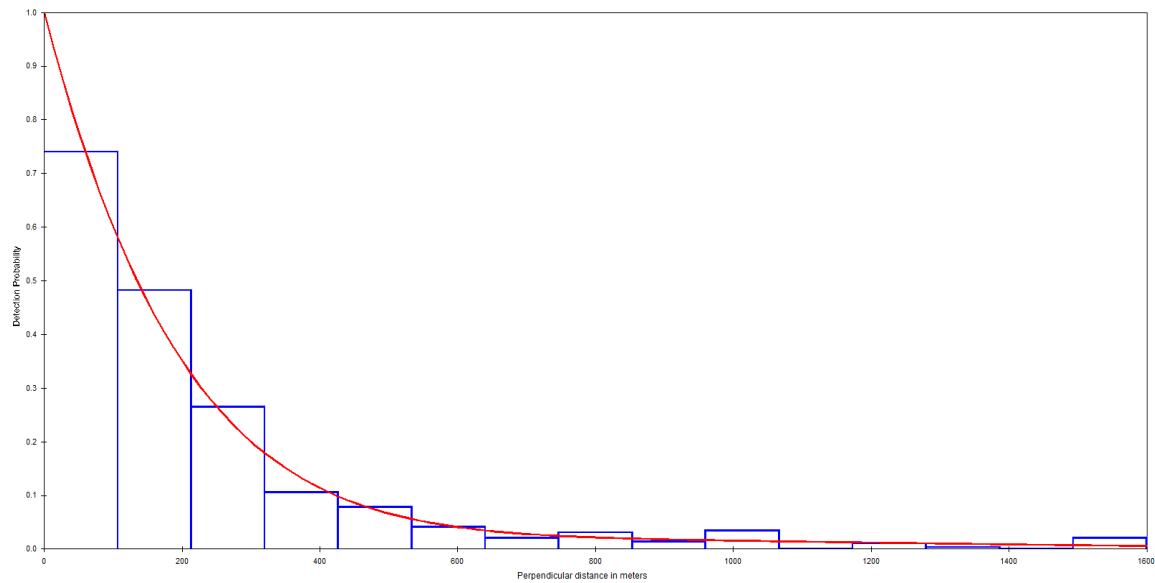


Figure 2.7a An example of the detection function created by the Distance software. This is the resulting detection function for the Gemsbok data in dune habitats, which established the Negative Exponential key function with an Hermite Polynomial series expansion as the best fit for detection.

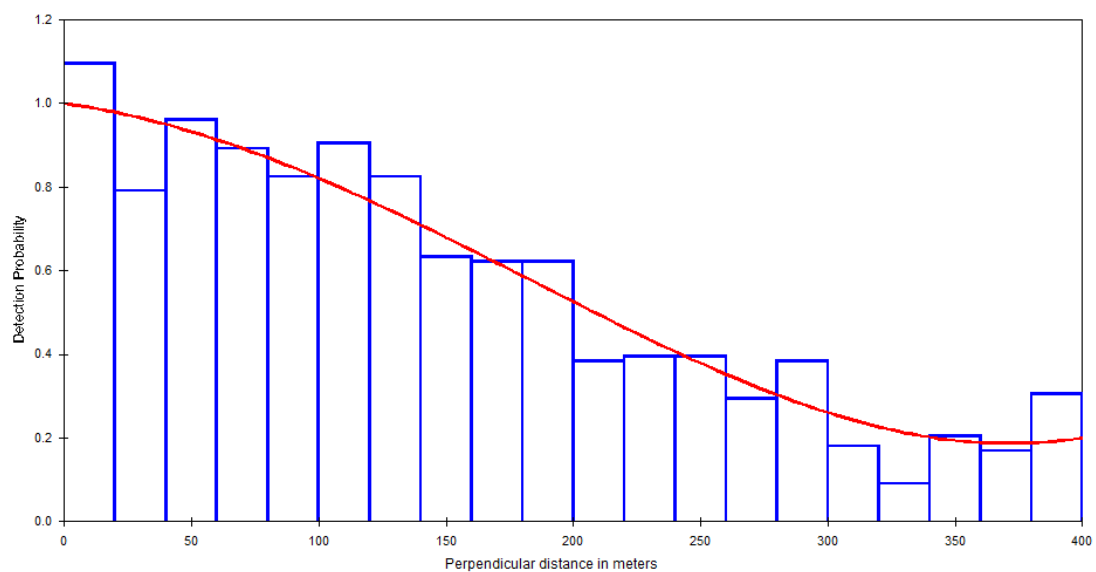


Figure 2-7b An example of the estimated detection function for Springbok counts in the pan habitat. Data from pans is truncated to 400m

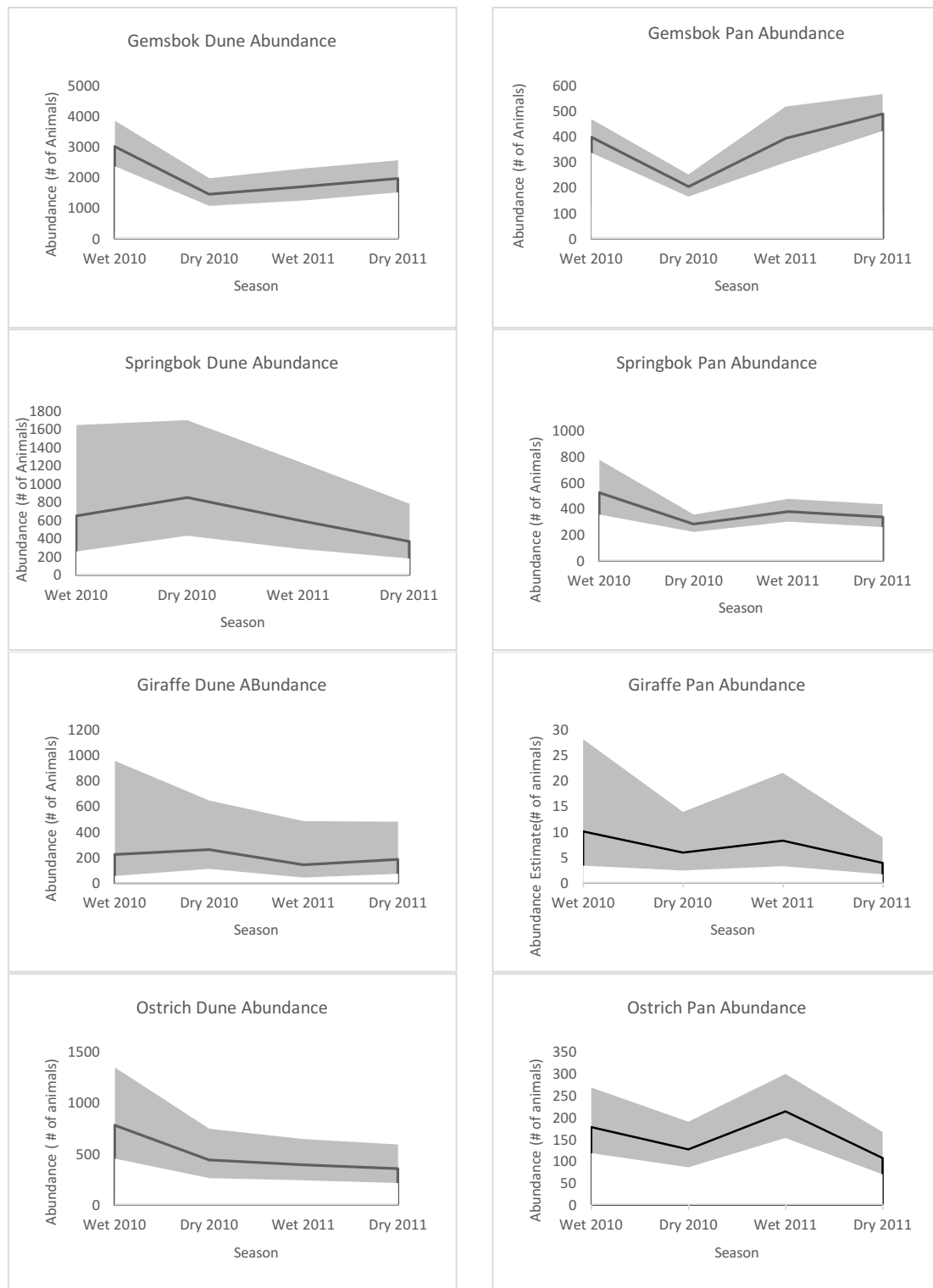


Fig 2.8a

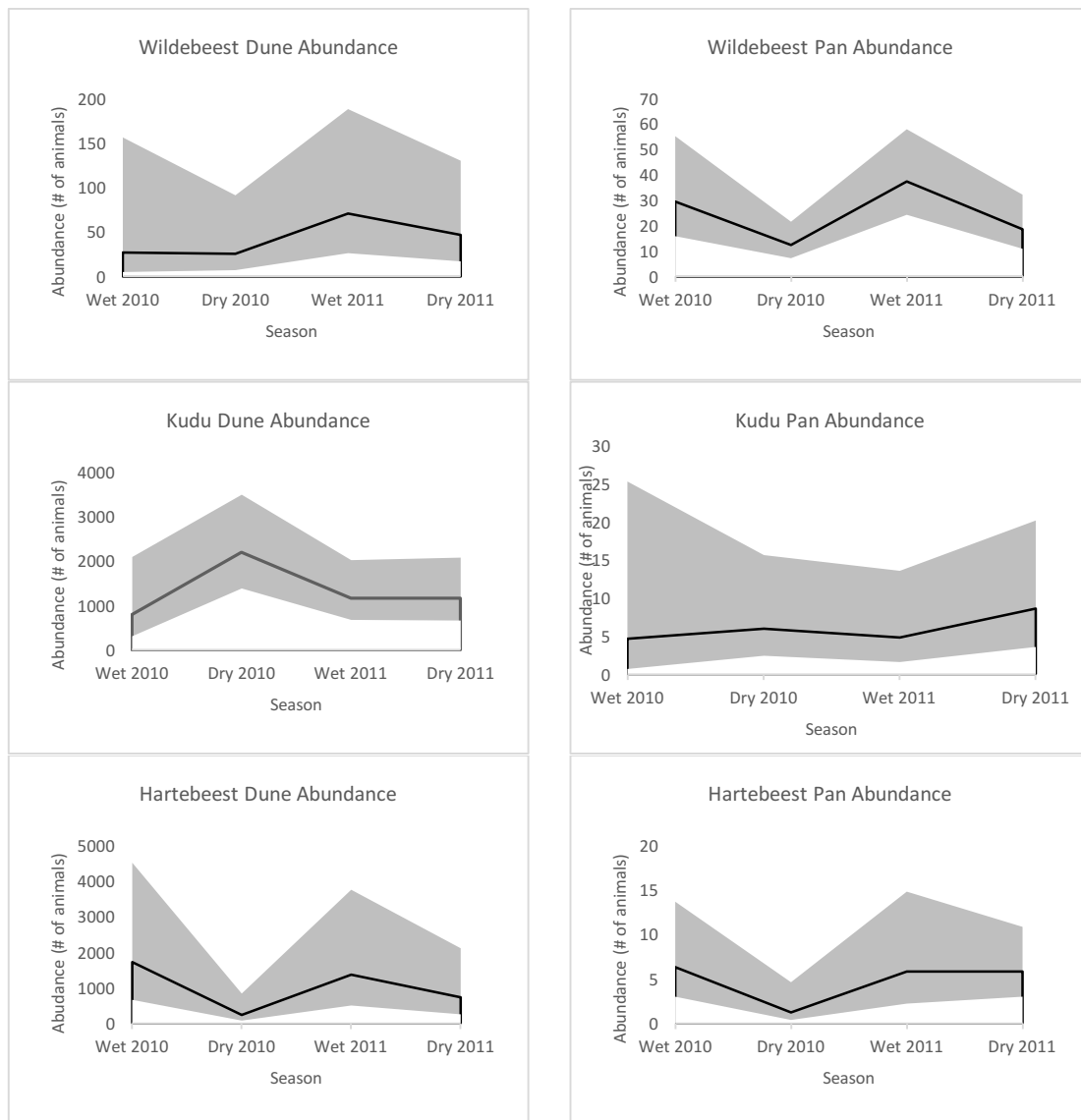


Figure 2-8 Estimated number of each species in the study area, by habitat over the four seasonal breaks identified by remotely sensed greenness (NDVI). Grey area is the 95% confidence interval of the mean value estimated from distance sampling.

Table 2.2 Akaike's Information Criteria results for GLM modelling of group densities of all large herbivores, (>100kg) lumped. Each equation represents the configuration of the dependent terms where "+" indicates no interaction, and "X" indicates both separate and interaction terms. Various distributions were explored as the data displayed Poisson characteristics (count data) some evidence of over-dispersion and zero inflation. These tables represent some of the models explored for all species.

Group Density =	Distribution	AIC	ΔAIC
NDVI + X + Y + Month + Habitat	Poisson	4,125	307
NDVI + X + Y +Month X Habitat	Poisson	4,072.21	255
NDVI + X + Y + Month X Habitat	Negative binomial	3,826.67	9
NDVI + X + Y +X²+Y²+Month X Habitat	Negative binomial	3,817.63	0
NDVI + X + Y + Month + Habitat	Negative binomial	3,832.73	15
NDVI + X + Y +Month X Habitat	Zero inflated Poisson	4,533.71	716
NDVI + X + Y +Month + Habitat	Zero inflated Negative binomial	3,838.54	21

Table 2.3 Summary of selected models for prey species group density models including the over-dispersion parameter, theta. Full model can be devised by taking column header and adding terms from rows. 'X' indicates crossed terms. i.e. Month + Habitat + Month:Habitat. Location terms were kept in all models. X and Y are latitude and longitude (in metres) from a UTM projection, X² or y² indicates squared terms showing that location influenced density in a non-linear fashion. Although habitat and month terms were always retained due to the purpose of modelling (to construct density maps for each month), the terms were not always significant and in the last three columns a * is used to denote whether habitat, the crossed terms (X) or month was significant according to the outcome of the ANOVA t-test and 0.05 p-value.

		AIC	Model - Density of groups = Habitat*Month+ NDVI+	theta	Habitat	x	Month
Duiker			(No difference to animal density model as single animals only observed)				
Giraffe	Negative Binomial	340.5538	$Y+Y^2$	0.2785			*
Hartebeest	Negative Binomial	338.01	$X+Y+X^2+Y^2$	1744.6	.		*
Kudu	Negative Binomial	660.3435	$X+Y+Y^2$	1.066			*
Gemsbok	Negative Binomial	2876.1	$X+Y+X^2+Y^2$	1.57	*		
Ostrich	Negative Binomial	1071.6	X	2.16	.		*
Springbok	Negative Binomial	1942.618	X+Y	1.16	.		
Steenbok	Negative Binomial	1836.735	$X+Y+Y^2$	2.6			*
Warthog	Negative Binomial	319.9	$X+X^2$	340.1			
Wildebeest	Negative Binomial	929.0515	$X+X^2$	1.27			

Time of day did not significantly account for variation in herbivore density; this had originally been supported by a pilot study investigating the effect of time of day (Figure 2-6). A clear delineation between wet and dry periods is shown in data from NDVI imagery of the study area (Figure 2-4), where vegetation greenness lagged behind rainfall by about one month into the wet season and by two months as the region became drier.

GLMM models for density of most CKGR herbivores was modelled by Habitat, Month, NDVI and combinations of linear and non-linear location terms measured in metres on the Universal Transverse Mercator(UTM) - Zone 34S projection. This means that density of many herbivores can be predicted by combinations of these data. More specifically, maps of density should retain location information such that changes in density from one area to another of the study area are reflected in the prediction maps. This prediction maps or grids, form the basis of prey estimation in chapter 4 and 5.

Rainfall did not significantly contribute to variation in herbivore density. Instead, greenness as estimated by the NDVI was a better predictor (see Table 2.3 for t and P values for each species). Density estimates and clustering responses of most herbivores varied on a markedly finer temporal scale than a simple seasonal difference as month was a significant term in all density models except for duiker, while season was dropped from all models (Table 2.3). The mean estimates using various models are summarised in Table 2.4, using season for brevity, and presented in Figure 2-9. The clearest pattern emerged for the gemsbok, where the dry winter periods correlated with larger group sizes and higher densities on pan habitats. Month was an important term for all herbivores except the duiker (potentially due to small sample size) and this term interacted with habitat for all of these except for steenbok and gemsbok. Total lean season biomass for the CKGR is estimated at 375.48 kg/km².

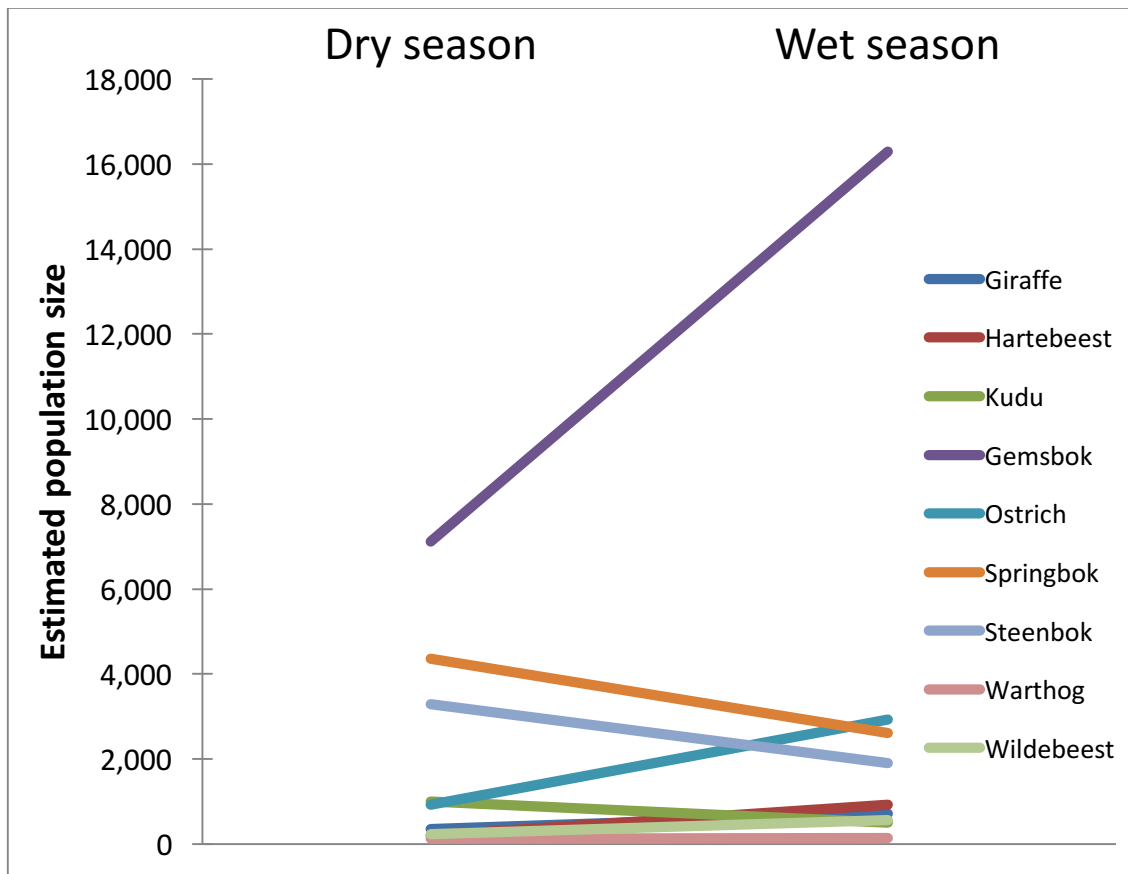


Figure 2-9 Seasonal changes in estimates of herbivore numbers for the 9911 km² study area,

Table 2.4 Density and total number of animal estimates for large wild herbivores in the study area, summarized by season (mean of monthly estimates) and habitat for the chosen transect method. Mean female mass (kg) and lean season biomass calculations (kg/km²) are shown. Total numbers are the results of the density for each habitat, multiplied by the total area of that habitat (277.5 km² for pans, and 9633 km² for dune savannah) within the study area.

	Pan - Dry	Dune - Dry	Pan - Wet	Dune - Wet	Total estimated animals		Mean Female Mass	Lean Season Biomass estimate
	animals / km ²				Dry season	Wet season	(kg)	(kg/km ²)
Duiker	0.000	0.026	0.004	0.011	250	104	6	0.15
Giraffe	0.116	0.137	0.201	0.064	1,353	675	550	75.09
Hartebeest	0.084	0.079	0.156	0.197	787	1,941	95	7.54
Kudu	0.137	0.603	0.081	0.319	5,843	3,098	135	79.60
Gemsbok	4.676	0.762	6.894	0.727	8,641	8,915	158	137.77
Ostrich	0.838	0.453	1.222	0.446	4,597	4,631	70	32.47
Springbok	6.603	0.236	6.264	0.197	4,109	3,633	26	10.78
Steenbok	0.825	2.722	0.845	1.331	26,452	13,052	8	21.35
Warthog	0.054	0.060	0.196	0.069	598	715	45	2.72
Wildebeest	0.498	0.047	0.746	0.054	588	723	135	8.01
							Total	375.48

2.3.3 Group size

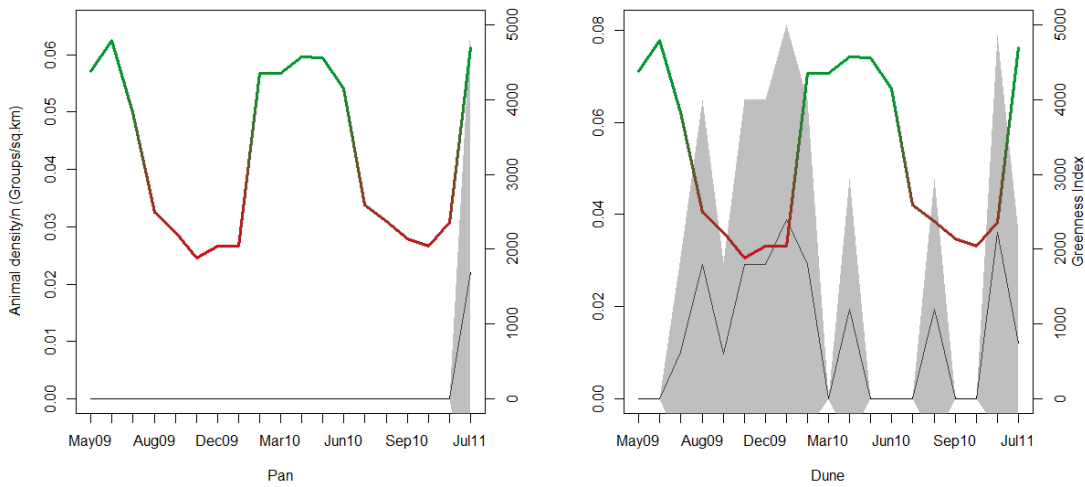
Group sizes of hartebeest and gemsbok were significantly different between habitats, groups were larger on pan habitats. There was no such relationship for other herbivores (Table 2.5).

Graphs of the mean estimates of both herbivore density and mean group size are presented in Figure 2-10 and best demonstrate the stochastic seasonal nature of the density and cluster responses shown by herbivore populations in the study area.

Table 2.5 Mean group sizes and significant differences between habitat and season. Unequal sample size Students t-test was used, and t and P values are shown using a significance level of 0.05.

	Pan	Dune	t	P	Wet	Dry	T	p
Duiker	1.040	1.000	0.000	1.000	1.000	1.06	0.62	0.54
Giraffe	5.40	5.14	-0.23	0.82	5.60	5.04	-0.31	0.76
Hartebeest	4.25	5.31	2.54	0.0186*	5.70	2.78	0.00	1.00
Kudu	4.06	4.33	1.32	0.19	3.55	4.34	NA	NA
Gemsbok	4.52	7.02	3.04	0.00244*	7.61	5.12	0.34	0.74
Ostrich	3.66	3.92	0.20	0.84	5.32	2.58	0.51	0.61
Springbok	10.57	11.05	0.29	0.77	13.61	9.36	-0.67	0.50
Steenbok	1.19	1.23	1.24	0.22	1.22	1.19	-1.25	0.21
Warthog	2.31	1.94	-0.88	0.39	2.10	2.15	0.06	0.96
Wildebeest	4.25	5.34	0.20	0.84	6.18	4.34	-0.63	0.53

Duiker



Giraffe

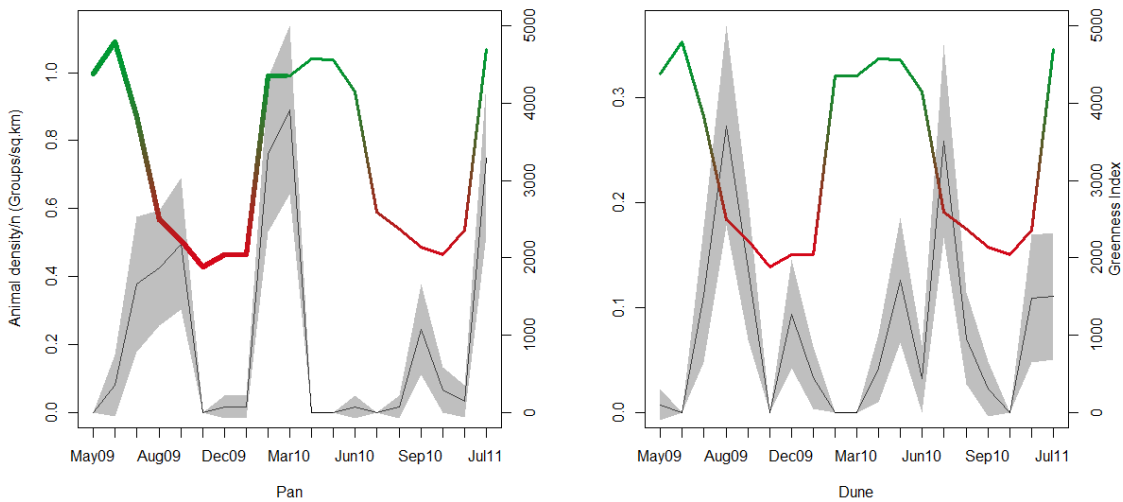
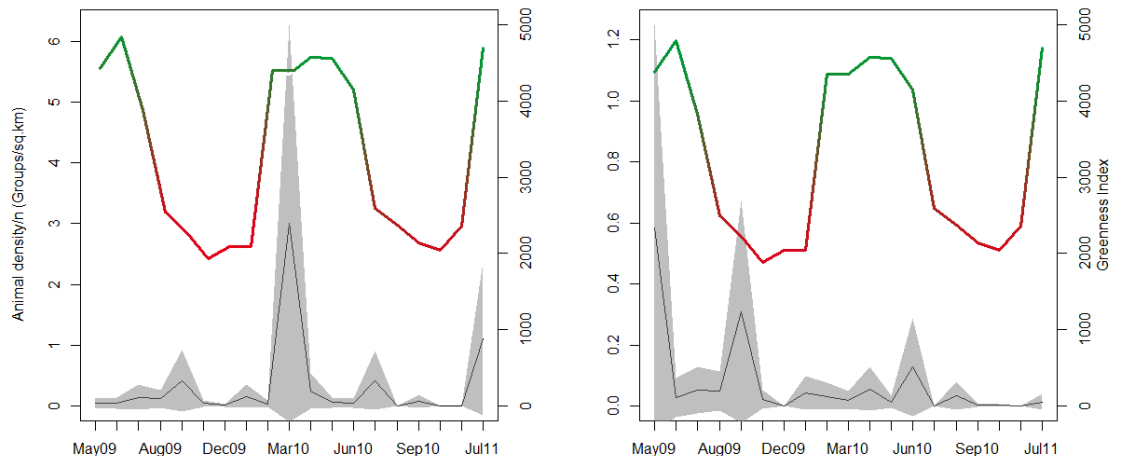
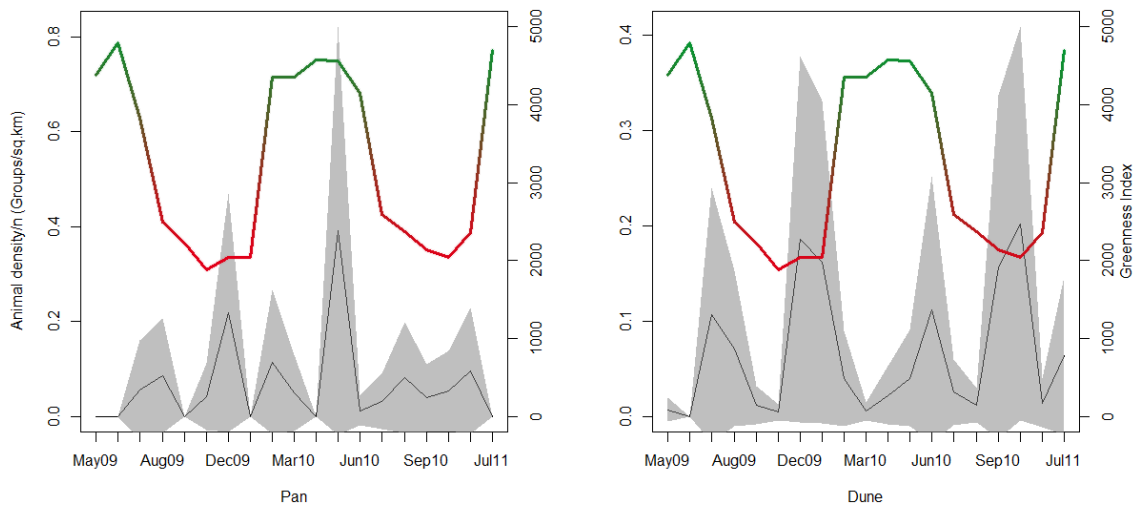


Figure 2-10 Herbivore density estimates from the mean model (black line) with 95% confidence intervals (grey shading) for species density (Y-axis) by month (X-axis) and habitat (separate panels labelled "Pan" and "Dune"). The coloured line is the NDVI, a significant variate in all models except duiker; for ease of comprehension, higher values are shaded in green and indicate greater vegetative production, lower production values are shaded red. More species on subsequent pages.

Hartebeest



Kudu



Gemsbok

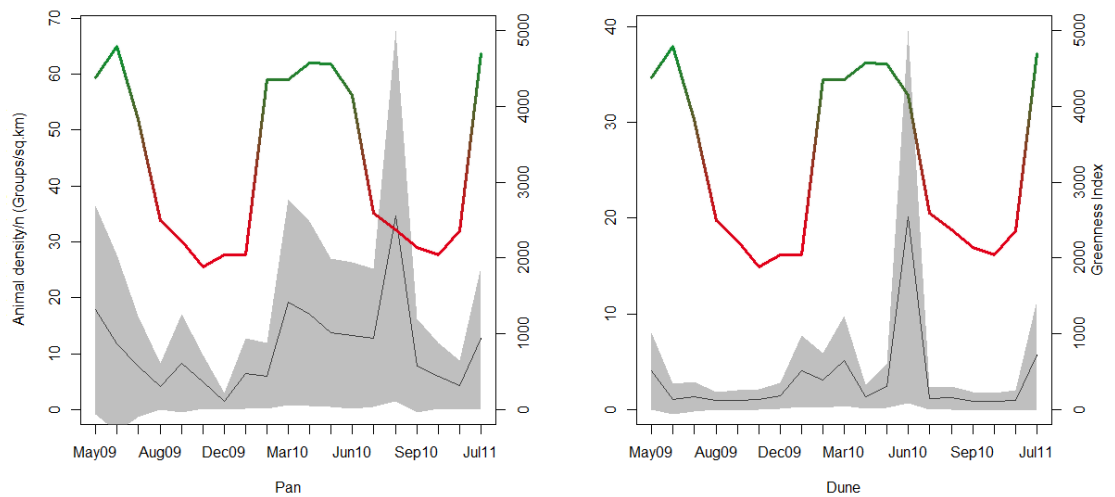
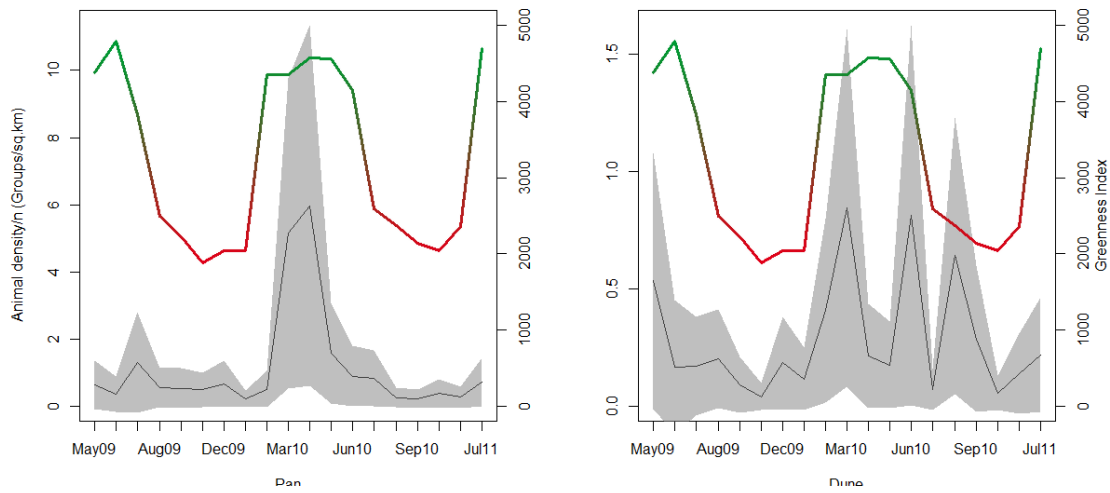
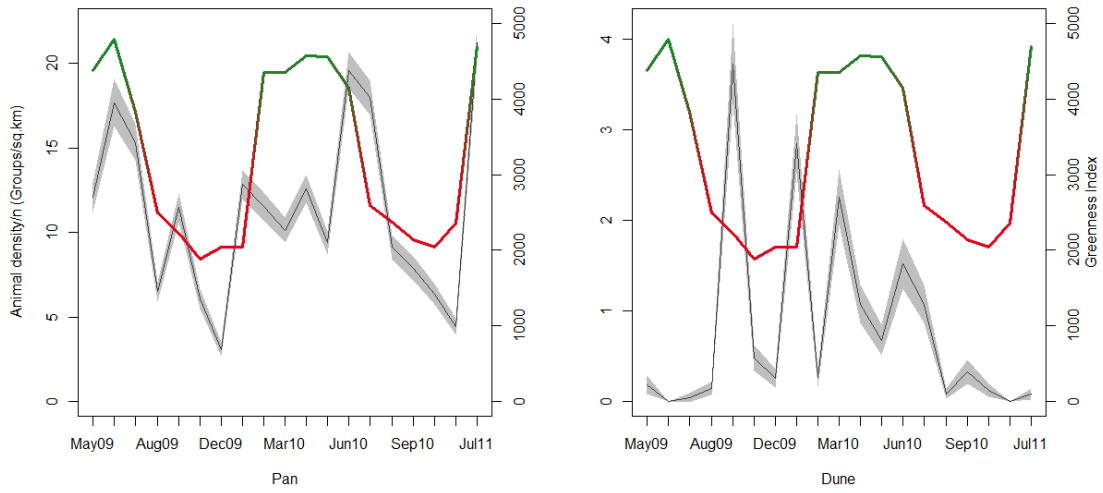


Figure 2.10 Continued. Herbivore density estimates from the mean model

Ostrich



Springbok



Ostrich Steenbok

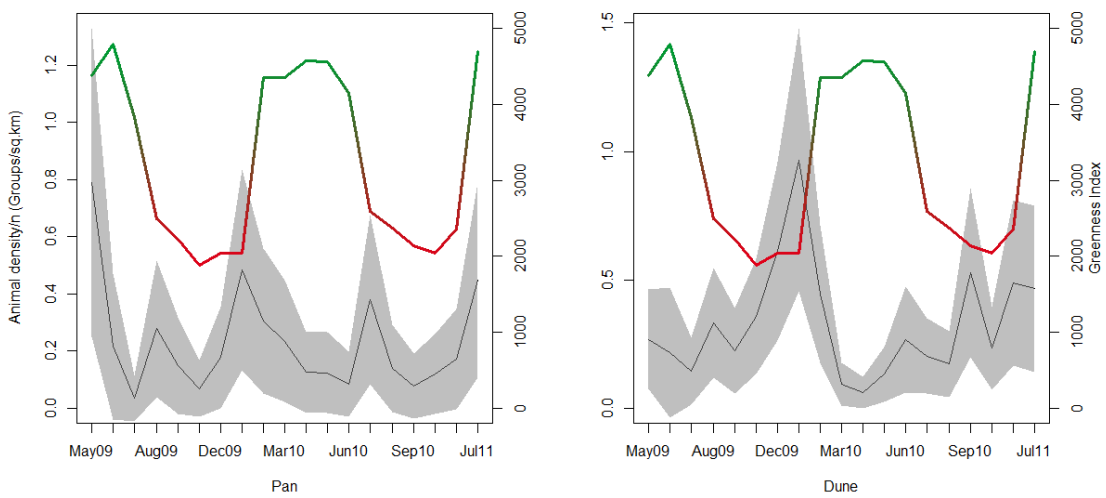
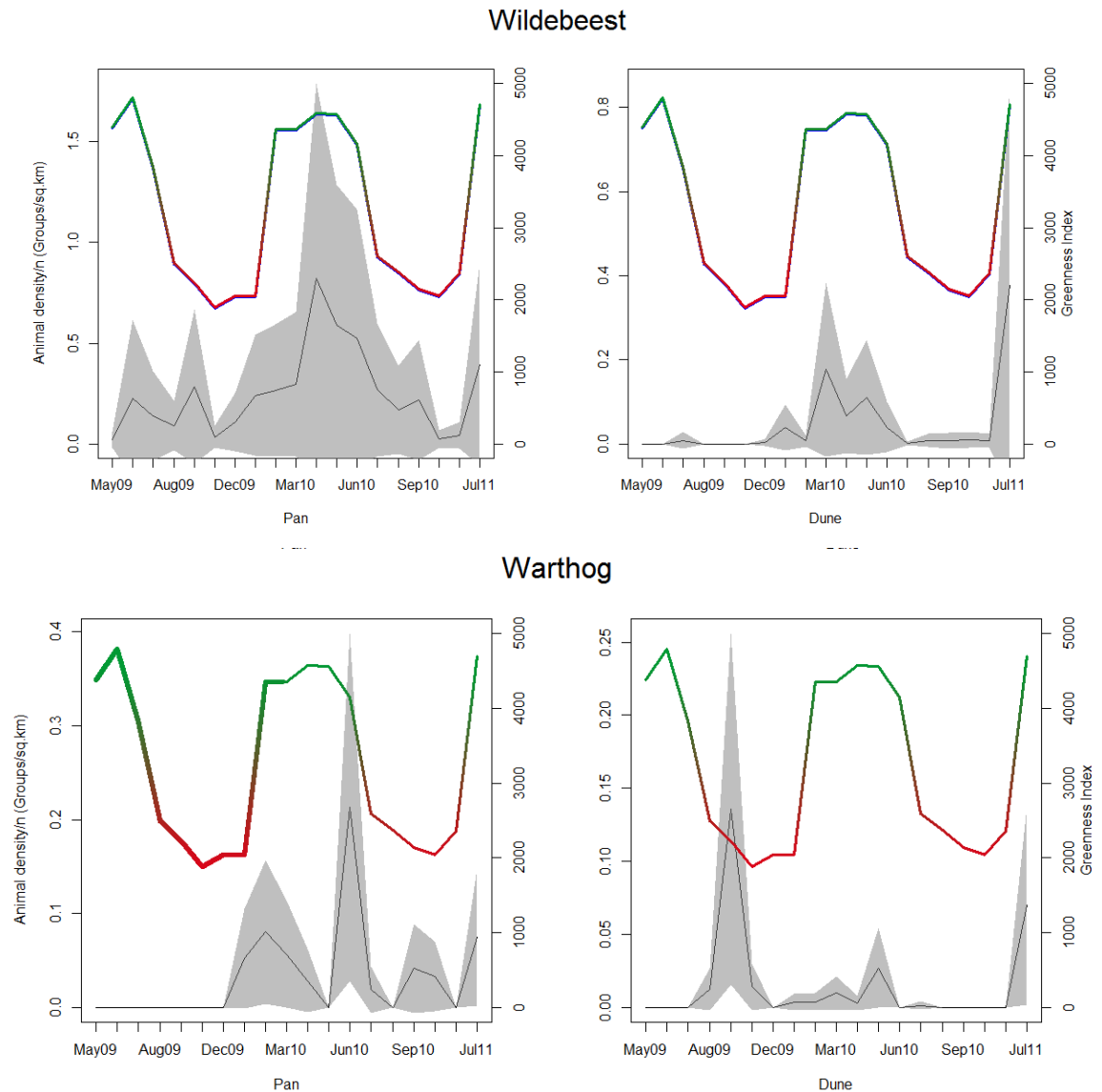


Figure 2.10 Continued. Herbivore density estimates from the mean model



2.3.4 Regional and monthly variation in group density.

Photosynthetic productivity, as measured by NDVI, was an important co-variate in group density for all species. Habitat and month were retained in all models as per study aims. The mean estimates are presented graphically in Figure 2-9. Habitat was an important variate only for gemsbok (Table 2.3), with higher densities of groups in the pan habitats. Month was an important co-variate for giraffe, hartebeest, kudu, ostrich and steenbok, but not for gemsbok, warthog and wildebeest. Mean group sizes were significantly different for gemsbok with an interaction between season and habitat ($t_{3,663} = 3.38$, $p < 0.01$, $n = 663$), with no difference between seasons in dune habitats (9.1 in the dry season and 12.8 in the wet season), and a large increase in pan habitats into the wet season (19 in the dry season to 41.7 in the wet season). In the main effects, there was no significant difference in group size between seasons ($t_1 = 0.86$, $p = 0.39$), while the habitat was significantly larger in pan habitats ($t_1 = 2.5$, $p < 0.05$). The model for steenbok did not exhibit a significant interaction ($t_{3,316} = 1.633$, $p = 0.097$), there was no difference in mean group size in pan habitats

(1.6 in both) and a significantly larger mean group size in the dune habitats during the dry season (3.1 as compared to 2.1 in the dry season). There were no significant habitat or seasonal differences in mean group sizes for ostrich, kudu, giraffe, springbok, warthog or wildebeest.

Figure 2-13 is a summary of the crowding of each species. This graph demonstrates the bias of the mean measure towards small groups for some species, in particular wildebeest, hartebeest, ostrich and giraffe, for which many more individuals were found in a few large groups, but a number of single individuals reduced the mean group size. Mean group sizes of hartebeest is 7.14 animals, reduced by the many single individuals in the pans, while the bulk of the population usually finds itself in much larger groups of 15 or more individuals. This effect is particularly evident in wildebeest, hartebeest and giraffe.

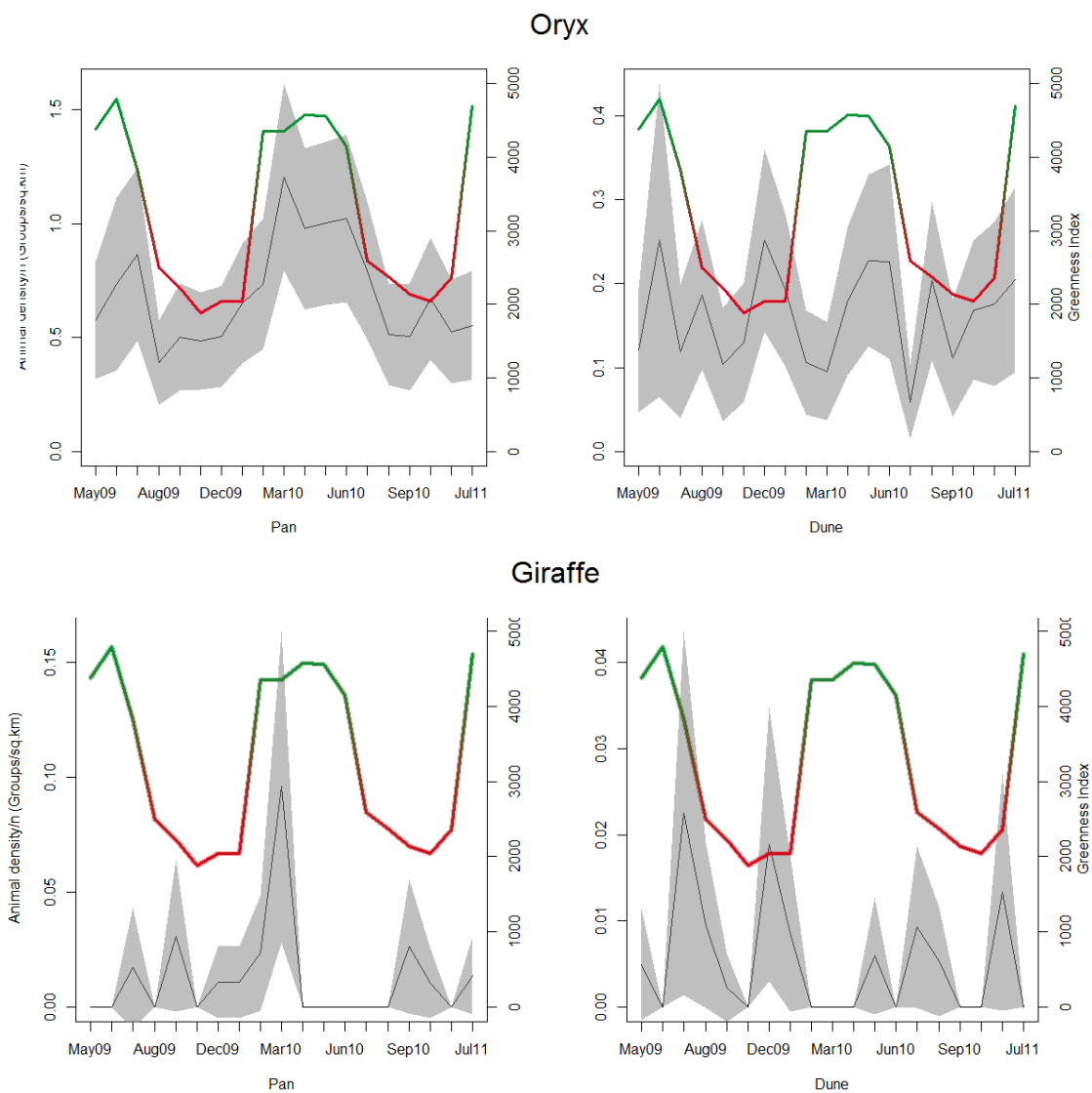
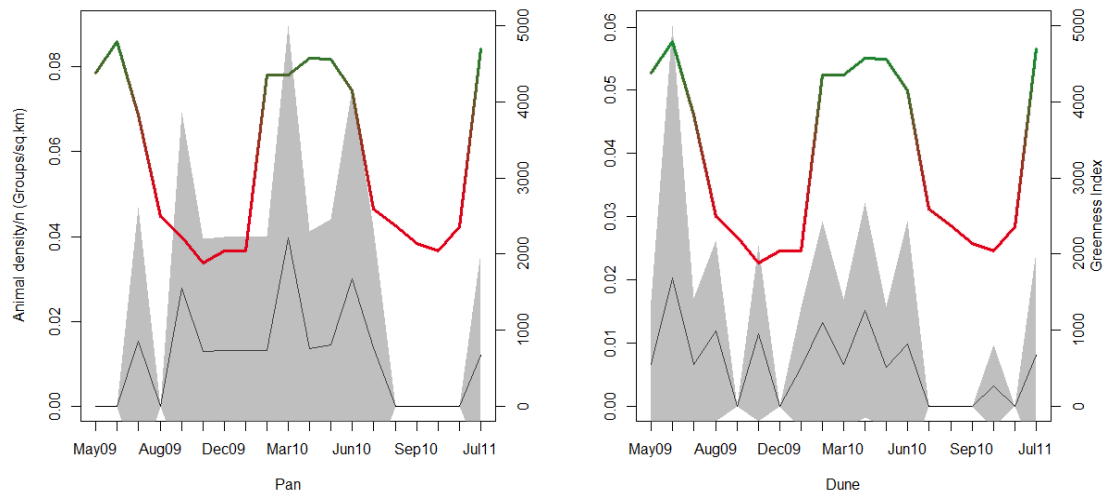


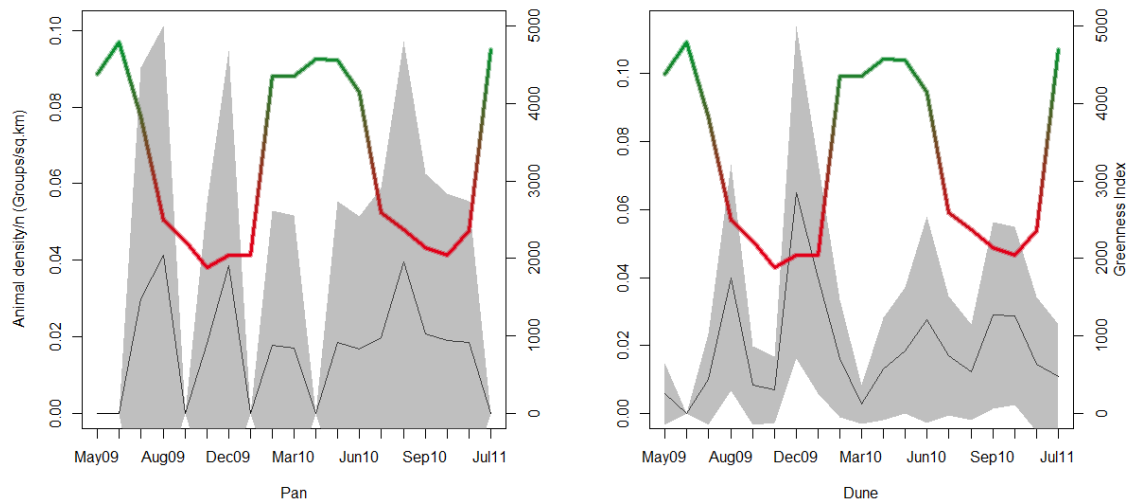
Figure 2-11 The above graphs show estimated density and 95% confidence intervals of herbivore groups from the mean model (GLMM). The coloured line is the NDVI which correlates with greenness in vegetation. Peaks in the greenness correspond with peaks in group density for gemsbok and wildebeest in pan habitats, but there is little

relationship with group density of other species. More group densities for other species are in subsequent graphs.

Hartebeest



Kudu



Ostrich

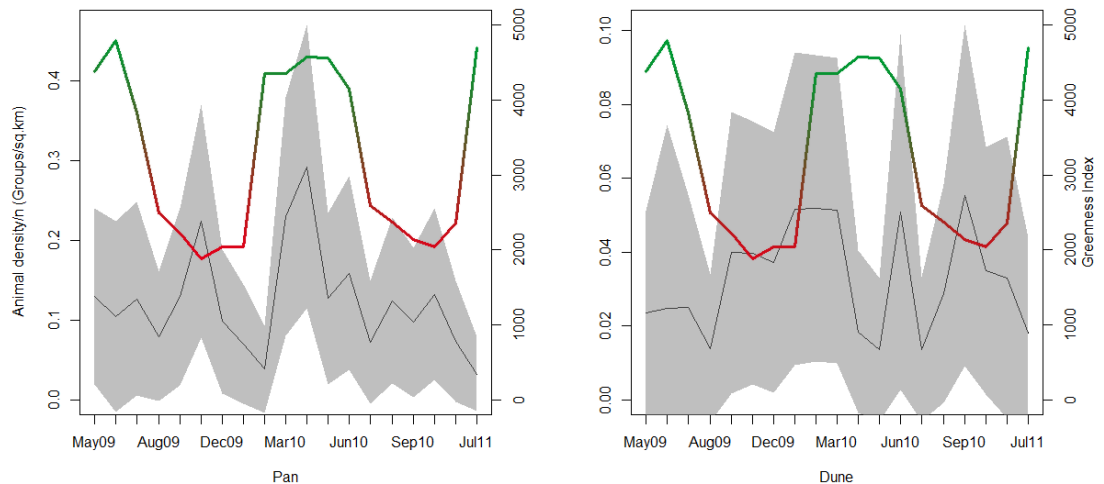
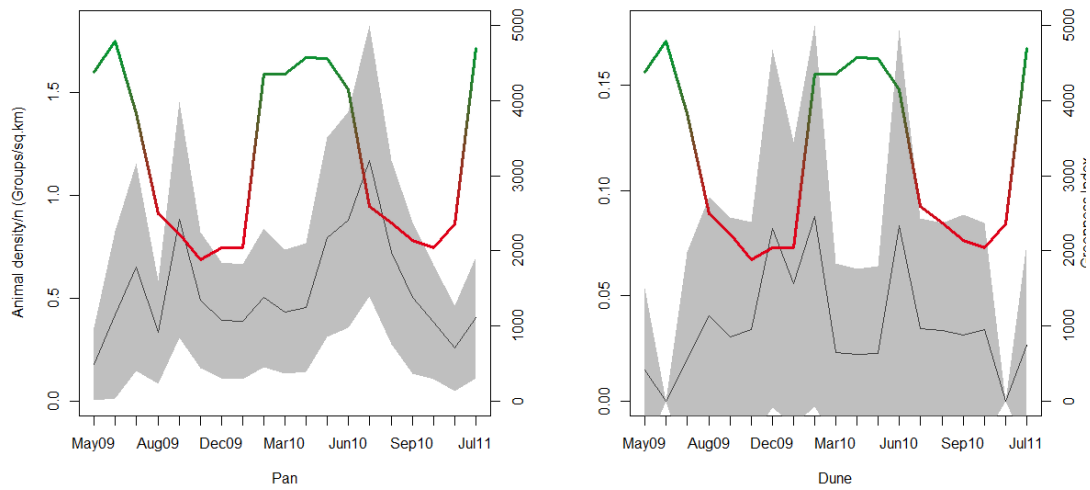


Figure 2.11 continued. Group densities of CKGR herbivores.

Springbok



Steenbok

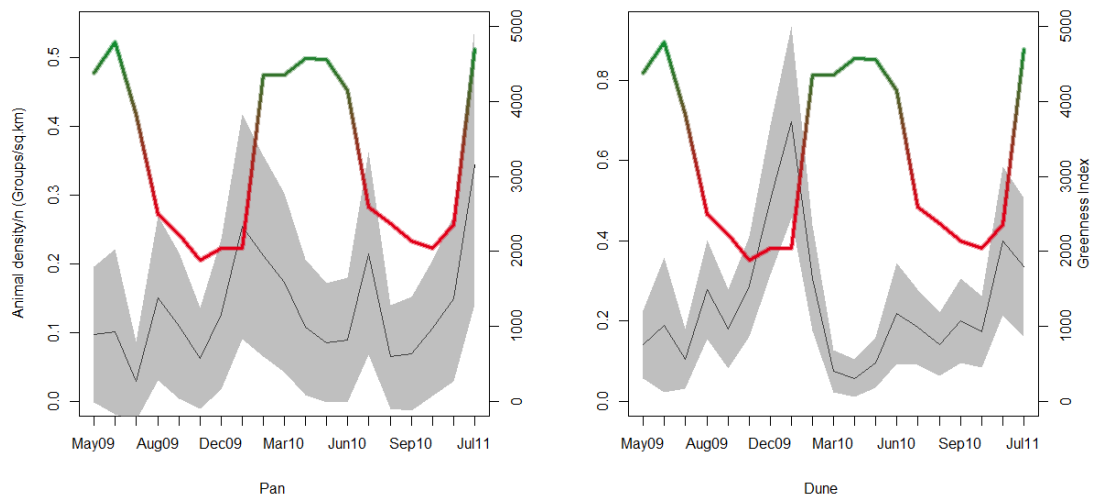


Figure 2.11 continued. Group densities of CKGR herbivores.

Figure 2.11 continued. Group densities of CKGR herbivores.

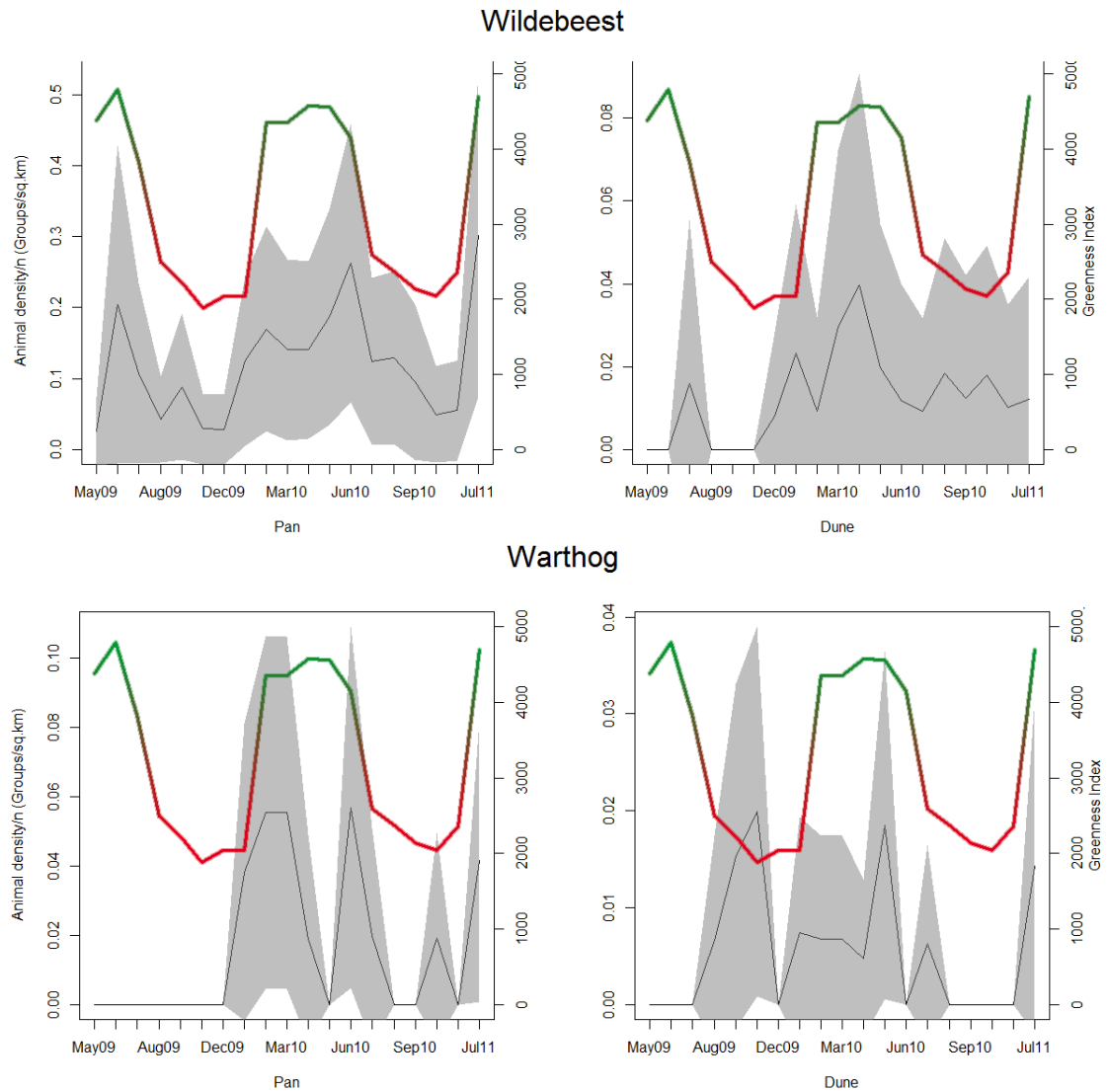
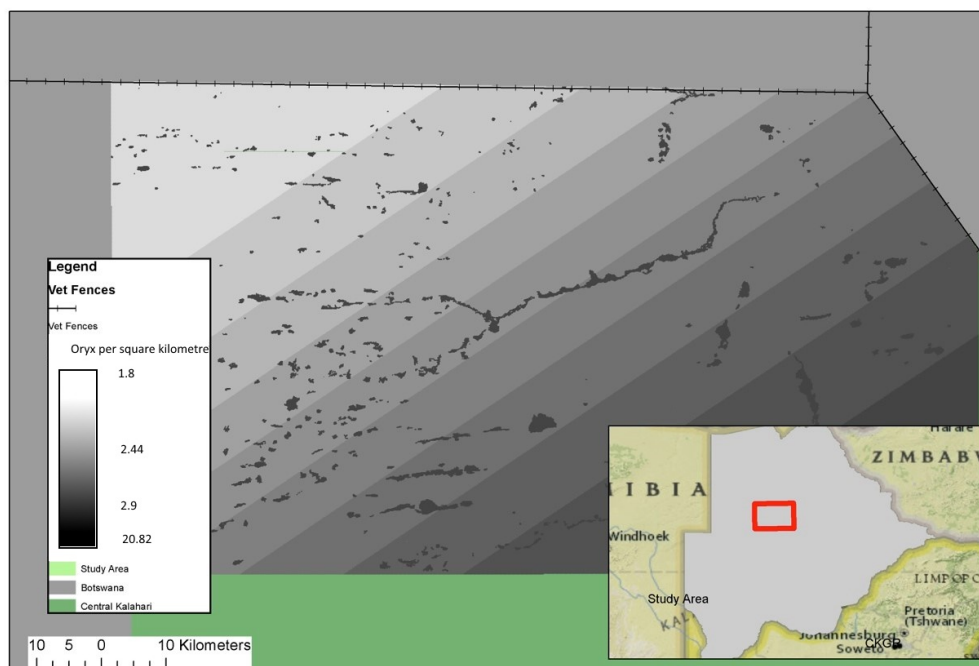


Figure 2-12 Estimated gemsbok density (animals per square kilometre) across the study area for one month (July 2009). This is one example of the 190 such graphs created from the modelling exercise.



Numbers of animals in each group

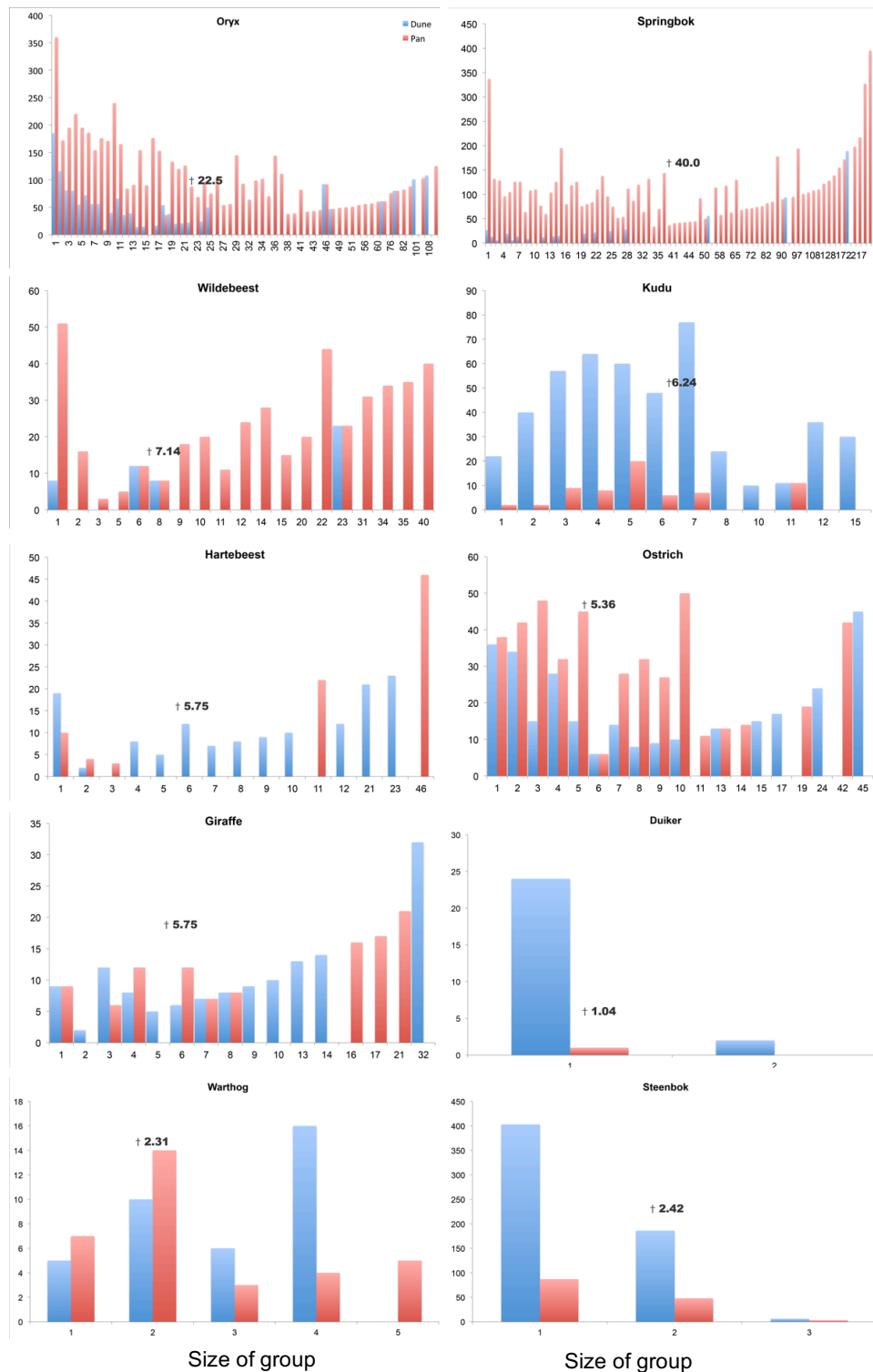


Figure 2-13 Crowding effects histogram by habitat. Blue bars represent dune habitats, and red is pan habitats. The mean measure for group size sometimes masks where the bulk of the individuals are. This is most striking in the wildebeest, where presence of a number of single individuals brings the mean value down to 7.14, but the bulk of the biomass is in a few larger groups. † Arithmetic mean group size for comparison.

2.4 Discussion

In this study I explored the current densities and abundance of large herbivore species in the CKGR. Variation in density in pan habitats was high, but lower and less variable in the more common dune habitat. Gemsbok group size and the group density of giraffe, hartebeest, kudu, ostrich and steenbok varied on a monthly scale in response to vegetation greenness and the response varied across the study area. The factors predicting herbivore density and group sizes have implications for variation in predator behaviour, and these factors are useful predictors of characteristics of herbivores in the landscape. Total lean season biomass was low compared to a conservative estimate of carrying capacity, and wildebeest numbers were exceptionally low. This may indicate a lack of recovery from disease cordon fences that have interrupted migration routes since the 1960s.

2.4.1 Habitat

Density of herbivore species in a region can be used to estimate predator carrying capacities, and patterns of herbivore density over seasons can enhance our understanding of predator responses. I found that herbivore densities of the most common species varied considerably in clay pan habitats. Densities were much higher in the wet season months in pan habitats. To visitors to the CKGR, the clay pans seem significant but at 2.7% of the study area, pans accounted for a small part of the area and therefore a small percentage the overall biomass. Herbivores on pans provide limited hunting opportunities for stalking predators like lions and leopards who prefer thicker habitat (Hopcraft *et al.* 2005; Scheel 1993b). Therefore, high variation in pans is unlikely to account for variation in predator behaviour. Overall herbivore biomass in the CKGR remains low, and is predominantly represented by gemsbok, with only a small proportion of the number of wildebeest reported in the 1970s, prior to the large die-offs reported around 1980 (Owens & Owens 1978).

2.4.2 Group Size

Gemsbok group size and the group density of giraffe, hartebeest, kudu, ostrich and steenbok varied on a monthly scale and this may have implications for variation in predator behaviour. Mean group sizes are important for an actor looking into the system, such as a predator, but skew the viewpoint of the animals within the herds. Mean crowding estimates are one way to explore whether an animal is more likely to be in a larger herd, and buffered from predation by the dilution effect. When I plotted contributions of each group size to the total population (

Figure 2-13) it was apparent that several species were more likely to be in larger groups than indicated by the mean group size; these included wildebeest, hartebeest, ostrich and giraffe, all of which are large animals and likely to be a part of the diet of lions. The presence of many individuals in single or small groups provides many hunting opportunities for the predators, but means that most individuals of the population of these herbivores find themselves in large groups with relatively low risk of predation. Gemsbok and Springbok are two most abundant prey species in the CKGR. However they use habitats very differently, and group dynamics between season is so different

that predators will respond to each very differently. Springbok do not substantially change their density between seasons, showing a slight decline in the dry season, mostly owing to mortality of young, but also as a result of short time-scale migration out of the park. Springbok are rarely found in the dune savannah habitat, and cluster sizes of this species are larger in the wetter peak season.

2.4.3 Trends in herbivore numbers

Several studies of the fauna of the Central Kalahari Game Reserve have attempted to define patterns of herbivore movement and occupancy (Owens & Owens 1978; Verlinden 1997, 1998) though rarely have they reported actual densities of the important herbivores. Few researchers anywhere report group densities and mean group sizes. Owens and Owens (Owens & Owens 1978) reported peak season densities in one clay pan habitat, Deception Valley, of 362.3 springbok per square kilometre. In our study over 30 years later, densities of this magnitude were only possible at a very small scale; for instance, if the entire transect had been in a short section of the Deception Valley pan habitat. I saw large herds of up to 400 springbok in small areas, but did not see mean densities above 18 animals per square kilometre across the park at any time of year in any habitat. This is not, however, clear evidence of a decline in springbok, as the Owens study was very small in scale and concentrated in the area where springbok numbers are still high today. It is difficult to comment on the trend in density over the last four decades but there is evidence of substantial decline in the last decade (Department of Wildlife and National Parks 2014).

Owens and Owens (1984b) also reported "considerable numbers" of gemsbok, red hartebeest, giraffe, greater kudu and steenbok in the dune savannah without giving estimates. Following Fritz and Duncan (1994) the estimated potential carrying capacity of the study area is 883.8 kg/km² (I used conservative values of 350mm mean rainfall and 'low' soil nutrient availability) while estimated actual ungulate biomass from strip transect sampling and mean female mass was only 375 kg/km² (refer to Table 2.4). This clear sign of an understocked game reserve may indicate long-term effects of the veterinary cordon fencing program on herbivore numbers and therefore on the resilience of herbivore populations in drought periods in the CKGR. Estimates of peak season wildebeest numbers prior to the construction of the veterinary cordon fences are rough but centre around 100,000 (Verlinden 1998). If, for instance, an additional 70,000 wildebeest were to enter the system then the herbivore biomass would reach that predicted using Fritz and Duncan's method. This method is for resident species and does not account for the migratory behaviour of wildebeest; if the population were eating elsewhere for a substantial part of the year, typically the lean or dry season, the CKGR could potentially support an even larger population. Williamson and Williamson (1984) described the decline in wildebeest numbers beginning in the 1950s as a result of fences and estimated a 90% drop to around 10,000 animals. They estimated in 1983 that population of all ungulates in the CKGR was as low as 11% of the carrying capacity for the given vegetation. Our study's peak estimate of 601 wildebeest in a study area in one fifth of the reserve may only represent a lack of recovery rather than a further decline, as there is some evidence that wildebeest now

prefer the middle of the park, south of the study area (M. Selabatso, unpublished data).

The declines in wildebeest numbers due to the construction of the veterinary cordon fences can both contribute to declines in other herbivore species and a shift in vegetation structure in and out of the reserve. (Milchunas & Lauenroth 1993; van de Koppel & Rietkerk 2000). Herbivore decline will result from predators shifting to the remaining herbivores. Changes in herbivory by the remaining herbivores is likely to lead to a shift in vegetation structure and net primary productivity (Milchunas & Lauenroth 1993). The grazing system around the CKGR is increasingly being impacted upon and is further changed by increased single-species grazing from cattle and this will impact vegetation in and out of the reserve. The effects are far reaching, as evidenced by declines in national herbivore surveys (Department of Wildlife and National Parks 2014). Since wildebeest migrate from the study area during a typical lean season, and predator biomass relates to lean season prey biomass (Carbone & Gittleman 2002; van Orsdol *et al.* 1985), predator populations are indirectly affected by the loss of wildebeest (Preisser *et al.* 2005) through changes in pressures on remaining herbivores, and changing vegetation structure affecting hunting chances and success.

2.4.4 Addressing sources of bias

The scale of the prey estimates is relevant to predator carrying capacity, and various modelling techniques produced different scales of predictions. Model choice has an element of subjectivity, and with no other information available, more conservative estimates are potentially more useful for conservation, but there is evidence of a separate process (most likely observers missing small groups) generating extra zeroes in the dataset. The more conservative negative binomial models were similar in magnitude to the line transect estimates, and selected as more suitable. Larger prey estimates would have resulted in larger predator carrying capacity estimates, but since the chosen estimates were already high for the four predators given current information, the currently modelled prey estimate is considered the most suitable.

Herbivore density and herbivore group density are related in the CKGR's open pan habitats, but less so in dune habitats. Gerard and Loisel (1995) describe a mechanism by which herbivore grouping is an emergent property of non-territorial herbivores in open habitats as their density increases. This mechanism arises spontaneously and better explains grouping as an evolutionary response to some ancestral pressure such as the dilution effect for protection from predators (Wrona & Dixon 1991). Herding allows animals significantly more time foraging and less time looking out for predators (Jarman 1987) but the groups are unstable and costly to maintain. Groups that are based on families are stable and do not fluctuate seasonally, while groups that are not based on family ties are unstable, fluctuate seasonally and are more likely to grow in open habitats and to break up in denser vegetation (Rodgers 1977). In the CKGR, Gemsbok and springbok form the largest herds, although wildebeest did historically (Williamson 2002). Gemsbok group sizes increased as density increased but springbok herds did not. Most springbok were in pan habitats, where larger groups are more stable. Both may suffer quite high

predation, gemsbok from the lions, and springbok from African wild dogs and cheetah. Aggregating behaviour might best be explained by the sit and wait predators that gemsbok most often encounter, lions, while springbok are more likely to be chased at high speeds in the open pan by cheetah.

Dune savannah habitat comprised 35 times the area of pan habitats and this difference prevents a complete understanding of movement of prey animals between the habitats, as even large numbers of animals moving away from pans to dunes will not be smaller than the error in dune estimates. Lower lean season pan density may be attributed primarily to both shifting grazing from the pans to the dune savannah and loss of young and weak animals to predators. Fine-scale temporal changes in pan density are therefore much clearer than changes in dune estimates, and this study does have the data to determine where the high numbers of herbivores found in pans go to in the dry season. While gemsbok most likely disperse into the dune habitat, wildebeest have been shown by other research to disperse out of the park in various directions, but primarily southwards (M. Selabatsi, Central Kalahari Predator Research, pers. comm.).

In the study area, there was a strong correlation between vegetation productivity and the density of herbivores in the CKGR. The densities varied spatially, between habitat types and on a fine monthly scale for most species. The resulting estimates make an important contribution to considering the behavioural drivers of predators. Our study points to added attributes of prey spatial structure that may be useful for predicting predator responses. Predator-prey encounter rates are an important consideration for foraging success and as a predator moves through the landscape each cluster or herd is counted as a single encounter – an unsuccessful attempt would alert the herd regardless of herd size (Ioannou *et al.* 2011). To a predator, densities of herds in the landscape will be of similar if not greater importance to foraging success. Where total density of the prey does not vary between seasons, I propose that densities of groups in a landscape may provide the cue for predators to change behaviour between seasons, and should be reported in similar studies when regarding predator responses to herbivore spatial structure. Both measures will be the basis for co-variables in investigating lion behaviour in this study. There were no significant differences between mean group sizes of any species between season, and for any species between habitats except gemsbok and hartebeest. Mean group sizes for both species were larger in dune habitats. This could be an expression of grouping behaviour in the habitat where prey are vulnerable, to protect individuals from lions in their preferred hunting habitat, due to an observer effect where small groups of individuals are harder to spot than larger groups, or as a result of an ecological response of these little studied species (e.g. males guarding open territories to attract females). Whatever the reason for the variation in herbivore density, I now have a clearer picture of herbivore population structure in time and space, to better understand lion behaviour in the CKGR.

Chapter 3 The Lions of the Central Kalahari Game Reserve – General Methods

3.1 Introduction

In this chapter I describe the process of locating, darting and collaring the study lions, and describe the most relevant aspects of each lion and the prides to which they belong. These descriptions are important as some will lead to insights about the conflict and potential solutions, which cannot be drawn from the data.

In a study in the 1970s, Owens and Owens did research into the CKGR Brown Hyaena (*Hyaena brunnea*), and managed to put radio-collars on lions from two prides resident in the valley which they talk about in a popular science article (Owens & Owens 1984c). Most strikingly they noted an interesting behaviour after rains failed for two years and the savannah dried up. Members of the two opposing prides were antagonistic during the preceding few years of the study, and their research indicated that lion ranges were 100 to 130 square miles (259-337km²) during this time. The mean range increased to 1500 square miles (3885 km²) during the dry spell and lions became solitary and were found up to 50miles (80km) apart from pride members. After a long period alone, two previously antagonistic females from the opposing prides met and became a solid and amicable hunting pair. Owens and Owens claimed this was the first evidence that strange lionesses could interact peacefully and even form a new pride. Where previous research indicated that all friendly female lions were related through maternal lines, they suggested that during very hard conditions, single lioness were able to pair with strange females. However, since their study had been going just a few years it seems entirely possible that the females had originally been part of a single pride many years before, which split up in the usual fission-fusion way, which despite relations, included young lionesses in each that did not know lionesses in the other pride and were naturally antagonistic. Over time, the two related lionesses acted as they must, antagonistically towards an entire pride of mostly strange lions with which they were in competition and only when they were alone were they able to reform bonds. While this scenario is speculative, it is as plausible as the reasoning of Owens and Owens and only a long-term study or an in-depth genetic analysis of the lion prides may uncover the truth of the Kalahari lions that "broke all the rules". The CKGR is a unique system for lions, in between the diverse habitats of the dry woodlands in the Kruger National Park, South Africa, to the extreme aridity of the Namib deserts.

3.2 History

Prior to beginning the research in 2008, there was little information on CKGR lion pride sizes, numbers, ranges and movements. I placed a single satellite transmitting GPS collar on a male lion in Passarge valley, in November 2008. I refer to this lion as PM001, the first letter corresponding to the

“Passarge pride”, named after the area in which the male was first encountered, the second letter to the gender, and then every lion was assigned a unique number as encountered, regardless of gender or pride. PM001 had a male companion, referred to as PM002, both with very distinctive features. Over the course of 5 months, PM001 walked 1321.9 kms, at a rate of 9.1 ± 6.8 km per day. A minimum convex polygon (MCP) of the locations (connecting the outermost locations without creating a concave intrusion) encompassed an area of 1,734.2 square kilometres. The collar was recovered after the lion perished naturally 5 months later (see section 3.5.2.1). This early data gave a great amount of insight into logistics of the proposed study, particularly that home ranges could be expected to be very large, and lions were not expected to be found in pan habitats as much as indicated by tourism guides and limited lion research in the 1970s by (Owens & Owens 1984c)

Seven more lions were collared with store-on-board GPS collars between July and December of 2009, one using the refurbished satellite collar. The oldest male lion died of natural causes a few months later, and when his store-on-board collar was opened, all the data were accidentally lost at the manufacturer. The second store-on-board collar was removed, the data were collected successfully, but it was found that the desired GPS fix schedule had not been uploaded. The manufacturer determined that all deployed store-on-board collars suffered the same problem. Instead the default 24 hour, hourly fix rate had been implemented. When funds and logistics allowed I began to replace these collars with remote download and satellite collars, on which the schedule could immediately be checked and new schedules could be uploaded. These collar types are expensive and more energy intensive. More lions were added over the next few years as budget and logistics allowed, some using VHF only collars to allow greater observation on social aspects including dispersal. A total of 18 lions were collared using 28 collars. All store on board collars and three remote download collars were manufactured by African Wildlife Tracking (Pretoria, South Africa) and all other remote download and all satellite collars were manufactured by Vectronics GMBH (Berlin, Germany). Some collars were re-used. One collar produced data intermittently and the data as such was unusable (MM102), and a collar on a younger female was removed after 3 months to allow her to grow. Six collared lions disappeared, assumed shot by farmers, which meant that for some lions a few days to months of data were lost. A summary of the data collected on each lion is presented below in Table 3.1 and a schematic for the timeline for the main study and collars worn by individual lions is shown in Table 3.2.

Table 3.1 Summary of study lion collar data and demographic information, Collar type summary: VHF: Radio only, SToB: GPS store on board + Radio, RD: GPS remote download+ Radio, Sat: GPS transmitted daily by satellite + Radio. Reason for death code: A: Alive at end of study, NC: died of natural causes, SK: Confirmed shot for livestock killing, ASK: Assumed shot for killing livestock; DMD = Daily Movement Distance

Code	Nickname	Gender	Estimated age (Years)	Collar Types	Conflict/ Reason for death	Pride	Start Month	Length of study (days)	GPS fixes	Pride Size (adults)	Mean Foraging Group Size (adults)	Permanent Waterhole Within Range	100% MCP estimate (km ²)	50% KDE estimate (km ²)	KDE95 (km ²)	GPS Fixes	Total distance walked (km)	Mean DMD (km)
BM052	Marco	Male	11	Sat	Yes, SK	Bokamoso	December, 2009	408	18,753	5	1.2	Yes	3,213.4	143.6	1038.5	18,753	4,360.2	10.7 ± 3.4
PM014	Tristan	Male	12	SToB, RD, Sat	No, A	Passarge	August, 2009	964	30,401	12	2.5	No	3,316.3	318.1	1728	30,458	8,935.1	9.3 ± 1.3
PM001	Passarge	Male	16	Sat	No, NC	Passarge	December, 2008	149	2,008	12	2.5	No	1,734.2	132.4	905	2,008	1,321.9	9.1 ± 3.9
TM059	Bart	Male	6	RD, Sat	No, A	Tau Pan	March, 2010	743	26,206	3	2	Yes	4,243.7	476.1	2513.5	26,206	5,113.1	7.9 ± 1.0
JM058	Wasp	Male	9	Sat	No, A	none	August, 2010	244	12,587	5	2.5	No	919.6	165.5	793.3	12,587	2,375.1	9.7 ± 2.2
MM102	Mogoto	Male	7	Sat	Yes, ASK	Motopi	December, 2010	132	868	12	2.5	Yes	798.3	245.4	977.4	868	199.6	6.7 ± 9.0
PF015	Isolde	Female	10	SToB, RD, Sat	No, A	Passarge	August, 2009	627	19,732	12	3.5	No	1,459.6	196.8	876.5	19,732	4,457.2	7.7 ± 1.0
SF010	Steph	Female	9	SToB, Sat	No, A	San pan	July, 2009	805	27,560	11	3	No	2,076.6	204.3	1176.1	28,082	6,177.3	8.4 ± 0.9
BF053	Cally	Female	9	SToB, RD	Yes, SK	Bokamoso	November, 2009	632	23,760	2	1	Yes	1,563.4	44.8	343.4	23,762	2,869.5	4.8 ± 0.8
MF013	Rata	Female	3	SToB	Yes, A	none	July, 2009	116	2,546	5	5	Yes	3,085.1	740.5	3064.5	2,546	881.0	8.0 ± 2.2
HF012	Tata	Female	8	SToB, RD	No, A	Hills	July, 2009	852	27,821	7	2.5	No	1,915.3	281.4	1126.3	27,822	6,543.4	7.8 ± 1.1
SM009	Scar	Male	13	SToB, Sat, Sat	No, NC	San pan	July, 2009	604	25,491	9	1.5	No	1,632.6	169.33	904	25,491	6,614.6	11.0 ± 2.3
JM068	Sega	Male	9	Sat	No, A	Junction	October, 2010	543	24,125	11	2.5	Yes	1,674.8	189.3	844.8	24,125	6,188.6	11.5 ± 3.2
JM011	Madala	Male	12	SToB	No, NC	Junction	July, 2009	136	0	6	2.2	Yes	-	-	-	-	-	-
BM060	Chico	Male	4	VHF	Yes, SK	Bokamoso	October, 2010	108	0	3	3	Yes	-	-	-	-	-	-
JM067	Bee	Male	7	VHF	No, A	Junction	March, 2011	493	0	2	2	No	-	-	-	-	-	-
TM040	Nkosi	Male	5	VHF	Yes, ASK	Tau Pan	May, 2011	57	0	4	4	Yes	-	-	-	-	-	-
MM105	Corkwood	Male	5	VHF	Yes, ASK	Motopi	May, 2011	41	0	5	2.5	Yes	-	-	-	-	-	-

Table 3.2 Schematic of the time frame of the study, from June 2009 to July 2012 when the last collar was removed. This time frame excludes lion PM001 from 2007-2008. Collar types are distinguished by colour (see key), and each month is coloured by the dominating seasonal attribute (red for dry and blue for wet season). Sum of GPS fixes excluding extra fixes (e.g. daily of 5 minute fix schedule fixes) are shown in final column. (X = lion death. ER – Collar failure lead to insufficient GPS fixes). Lion JM014 and MM107 were excluded from the final analyses.

2009					2010					2011					2012					Points				
Num		JJ	A	S	O	N	D	JF	M	A	M	J	J	A	S	O	N	D	JF	M	A	M	JJ	
JM014	♂	ER	ER	ER	X																			0
SM009	♂																				X			22,967
PM014	♂																							20,238
TM059	♂																							23,775
BM051	♂																				X			12,928
JM057	♂																							22,650
MM107	♂																				ER	ER	ER	1,308
JM068	♂																							10,022
SM010	♀																							45,444
PF015	♀																						?	26,899
HF016	♀																							26,344
MF017	♀																							2,548
BF052	♀																						X	17,763
		Store on board					Remote download					Satellite												

3.3 Methods

3.3.1 Lion population survey

Lion numbers were estimated in the study area only, using a call up survey spanning thirteen consecutive days in October 2011. I used 46 call up stations evenly dispersed 8km apart through the study area. Following Loveridge *et al*, (2001) I played a recorded sound of an injured buffalo through four 150 watt megaphone type speakers, amplified to a measured 90dB at 5 metres from the speakers. Each speaker pointed in directions at 90 degrees from each-other, horizontal to the earth, 2 metres above the ground. The sound was played for 1 minute, with a 5 minute rest and then another 1 minute of sound. I remained at the location for 1.5 hours from the start of initial sound, before moving to the next location. Beginning at 9pm, calling stations were separated by two hours, and up to four were conducted each night. On the first night, seven lions 3 km distant from the calling station team were under observation by a second vehicle and responded immediately to the sound. Five females walked briskly to the location, while two males clearly heard the sound, but waited 3.5 minutes before following slowly behind the females. On the second night, two male lions were under observation at 4 km away, and responded immediately to the sound, walking briskly to the location, arriving 50 minutes later. On the third night two lionesses at 5km away did not respond to the recorded sound. On the seventh night a lioness was encountered 3.8 km from the site of the previous call-up station. She showed signs of having recently fed and I assume she would not respond, but may also have moved to that location (within the radius of hearing) after the call up survey from nearly 2 hours earlier. No other chances to directly observe lions at distance with a second vehicle were available, and I conservatively estimated the radius of the survey method at 4km. Study area population estimates were calculated from the total number of adult lions counted divided by the total area surveyed ($46 \times 4^2 \times \pi = 1808.64 \text{ sq. km}$ or 18.25% of the 9911 square kilometre study area). Upper and lower limits of the population estimate of 20% are used as per Bauer and van der Merwe (2004). A lion generally walks at about 4km an hour or less, and could only reach the calling station in 1 hour. Thus we expect the total estimate to be a conservative estimate of the lower limit of the lion population. The response rate of the few observed individuals was high. I checked my assumption by using the mark-recapture technique to also estimate the study area population.

3.3.2 Animal handling and collaring

Experienced Botswana registered veterinarians darted lions using a combination of Medetomidine hydrochloride (Domitor, ZooPharm), Ketamine hydrochloride (Ketamine, ZooPharm), and Tiletamine (Telazol, Pfizer). Doses varied according to gender, age, size and condition of the lion, as judged by the veterinarian, doses and response times were recorded. Measurements of the lions body parts including teeth and health indicators were made following de Waal *et al*. (2004) and the anaesthesia reversed with atipamezole hydrochloride (Antisedan, Pfizer). The lions were followed for between 29 and 965 days (mean 500 days), after which all collars were removed. The collars were replaced up to twice each, when batteries were low. All collars were less than

1kg in mass (less than 0.5% of male lion or 0.75% of lioness body mass). All males and four of the five females were adult sized (estimated age older than 3 years) when darted. Several collar failures and lion deaths from farmer retaliation before data collection occurred resulted in data from five other lions collared as missing or unacceptable. Mean estimated age of study animals was 10.4 years for males and 8.4 years for females as at each first collaring, using tooth wear and methods in (Whitman & Packer 2007). I originally intended to dart one male and one female in each area, but no prior information on pride ranges was available. In one instance a male (JM067) from a cohort of 2 individuals was collared and then moved into the area occupied by another male cohort of 2 individuals, one of which was already wearing a collar (PM014). The data from these two males were considered independent for the purposes of this study, as the lions only interacted on rare occasions (they were within 400m of each other in 0.3% of GPS locations, and observed interactions were antagonistic). Thus two males were studied in largely overlapping ranges. One male and one female were found to be nomadic (that is they displayed a large overlap with established pride ranges and not regularly socialising with the resident females).

3.3.3 Assessment of the accuracy of the GPS locations

GPS error is indistinguishable from small movements by the study animal (D'Eon & Delaporte 2005; Frair *et al.* 2004), and lions are more likely to move substantially or only short distances. Therefore error rates were determined for each collar in a stationary position before deployment for at least 24 hours and subsequently all movements registered as within 2 standard deviations of this value were reset to 0m. The cut-off value for different collars varied from 11m to 34m. Statistical analyses were repeated using this procedure based on cut-off values between one and three standard deviations to check the effects of this assumption on significant terms. This stationary test also allowed me to compare the three different collar types from the two manufacturers. Collar error varied between individual collar types, satellite collars (Vectronics GMBH, Berlin Germany) provided the most precise measurements at 13.95m $\pm$ 3.31 (SD), remote downloads were nearly as precise at 14.11 $\pm$ 7.057m with store-on-board collars all from African Wildlife Tracking (Pretoria, South Africa), with a relatively low precision of 35.80 $\pm$ 10.19m.

3.4 Site fidelity of CKGR lions

The lions of the Central Kalahari Game Reserve used most of their total range in each season, but less of it in the dry season. During the wet season, the eleven study lions on average used $83.2 \pm 21.6\%$ (SD) of their total minimum convex polygon range (MCP) and $59.0 \pm 27.6\%$ during the dry season. Lions used quite different areas between years of study, (see Figure 3-1 for one example).

Legend

Year

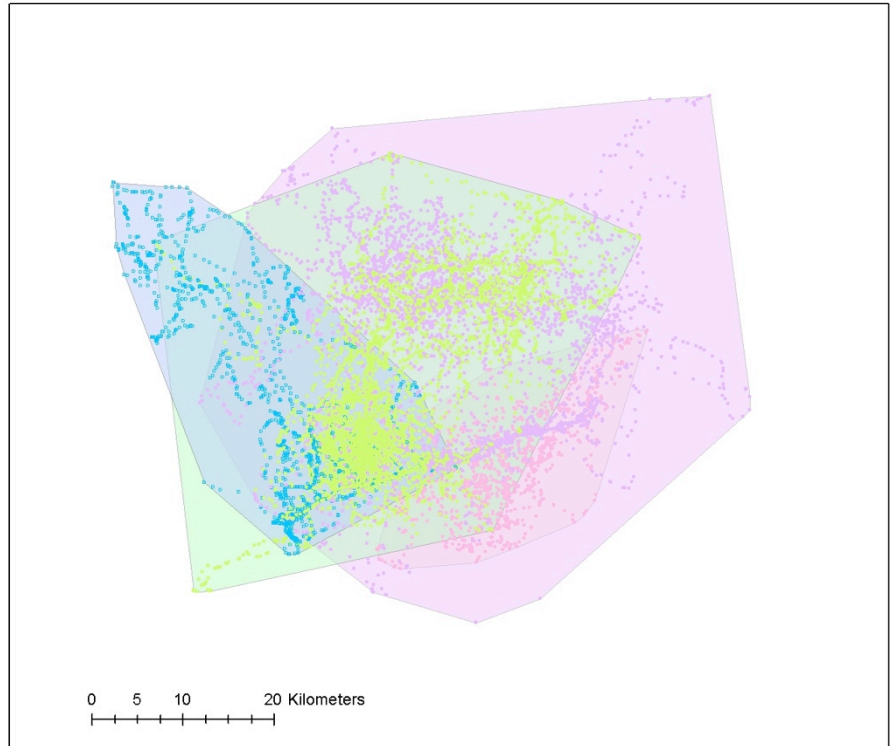


Figure 3-1 Lion home ranges for different years of lion SM059.

Table 3.3 Estimated CKGR lion pride sizes and numbers of males and females wearing collars in each pride.

Pride	Lions with GPS collars	Max Pride Size (females only)	Male Cohort size
Passarge	2M, 1F	10	2
Bokamoso	1M, 1F	2	1
Deception	-	8	3
Pipers	-	6	3
Hills	1F	4	2
Junction	2M	9	2
Letiahau	-	7	2
Motopi	1F	9	2
BokamosoN	-	5	2
San Pan	1M, 1F	9	1
Tau Pan	1M	3	2
Sunday Pan	-	7	2
Nomadic	1M, 1F	-	-
Mean		6.6	2

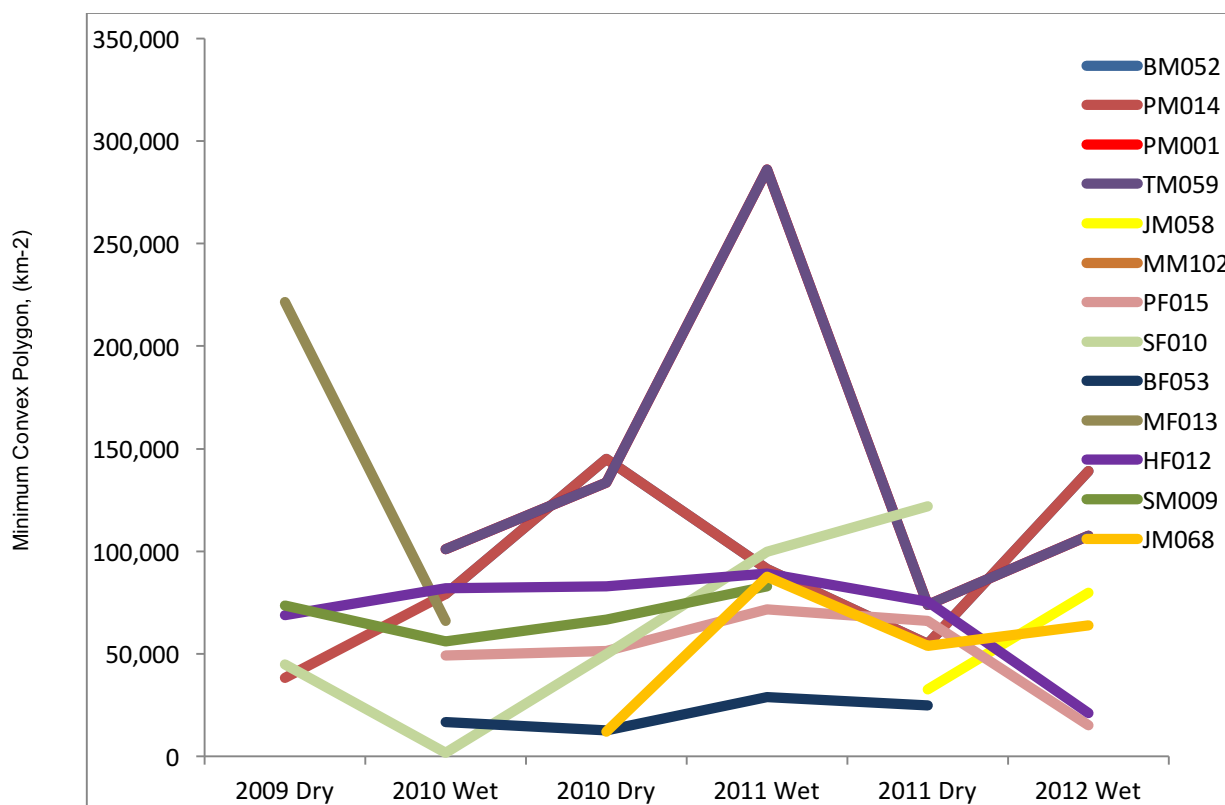


Figure 3-2 Change in seasonal minimum convex polygon size for each study lion.

3.5 Results

3.5.1 Lion Population estimates

The estimated density was 3.09 lions per 100 km². For the total study area (9911 km²) the estimate is therefore 307 individual adult lions. This density is not expected to reflect the entire reserve, as habitat characteristics and herbivore densities are known to differ dramatically. A full reserve spoor survey

was conducted in 2011 not part of this research and the results are addressed in Chapter 6.

3.5.2 Description of study individuals

Some anecdotal evidence appears here, as I feel that some of this information concerning events that occurred once or seldom can augment the more substantial data presented in following chapters. Lions were numbered as encountered with a three digit identifier beginning at 001. For ease of reference they were also designated with a gender identifier, and pride range identifier from where they were first encountered, although some were later found not to belong to that original pride. For instance PM001 refers to the first lion encountered, a male from the Passarge pride area. Although I endeavoured to collar lions from 8 prides, there were substantial logistical and financial hurdles, unfortunate loss of data and also loss of lions to causes outside of the research. At least some data was recovered from six pride ranges, and three of those had both genders represented: Passarge valley, Bokamoso and San Pan.

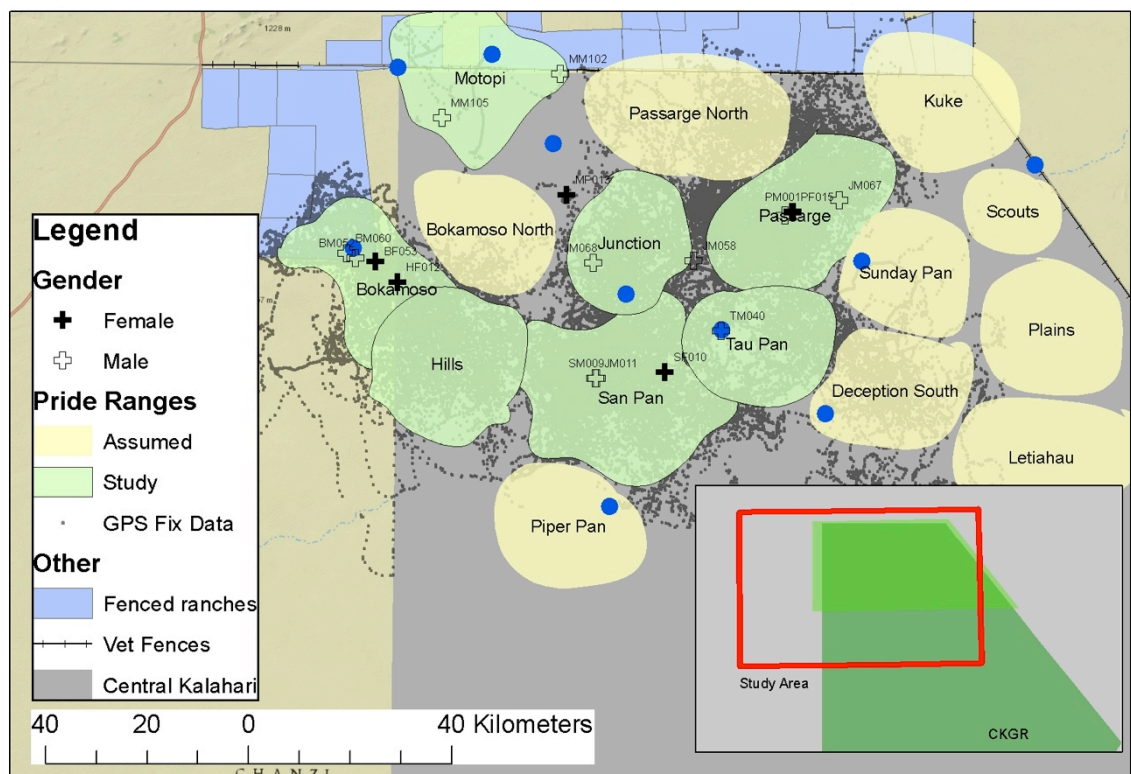


Figure 3-3 Estimated pride range from GPS data (green) and assumed from visual observation (yellow) pride ranges of lions in the study area (inset is the northern CKGR showing the study area). Blue circles represent waterholes. Crosses represent the geographic location at which lions were darted and collared. I have included the first two farms bordering the reserve in blue, which are clearly absent in the east of the reserve (Rakops district).

3.5.2.1 Lion PM001

The first lion tracked for this study was collared on the 5th of December, 2008 in Passarge Valley and was designated PM001 (**P**assarge – **M**ale – **001**). This lion had a male companion (PM002, not collared) and I estimated both lions to be at least 10 years of age as they had rugged and recognizable facial features and scars. For three months the lions were observed around the Passarge Valley area, and GPS data indicates movement of several kilometres either side of the valley with a central tendency towards this landscape feature. The hard clay pan surfaces are substantially easier to walk on than the surrounding dunes and appear to be used by lions for socializing, locating pride mates and taking shortcuts through the range. This movement pattern was common for lions with ‘valley’ landscapes in their range. High visibility in the pan habitats leads to a bias amongst tourist and safari guides who believe lions favour the pans and kill often there. My data on lion locations and their kills in the CKGR demonstrated otherwise. Pans habitats comprised 3% of the available habitat, but was used 6% of the time and was almost used never for making kills; ~1% of kills were in pan habitats. Lions including PM001 and pride-lions would often rest in dune habitats just a few hundred metres from pans or valleys, under short bushes as often as large shady trees.

PM001 utilised a home range area of 905 square kilometres (95% KDE, see Chapter 4 for description of home range estimators used). After 3 months, PM001 changed behaviour dramatically and departed from usual walking patterns that would normally return him to the valley. It is unknown if lion PM002 was with him. He walked quickly outside his normal range, ending up alone, at a waterhole in the Deception Valley area with little movement for several days and in a visible state of decline. He was observed *in-situ* for a few days until the Department of Wildlife’s veterinarian anaesthetized the lion but the lion passed away of undetermined causes. The collected data were very informative concerning what the rest of the study could expect in terms of range size and walking speeds and distances, and played an integral part in planning further collars.

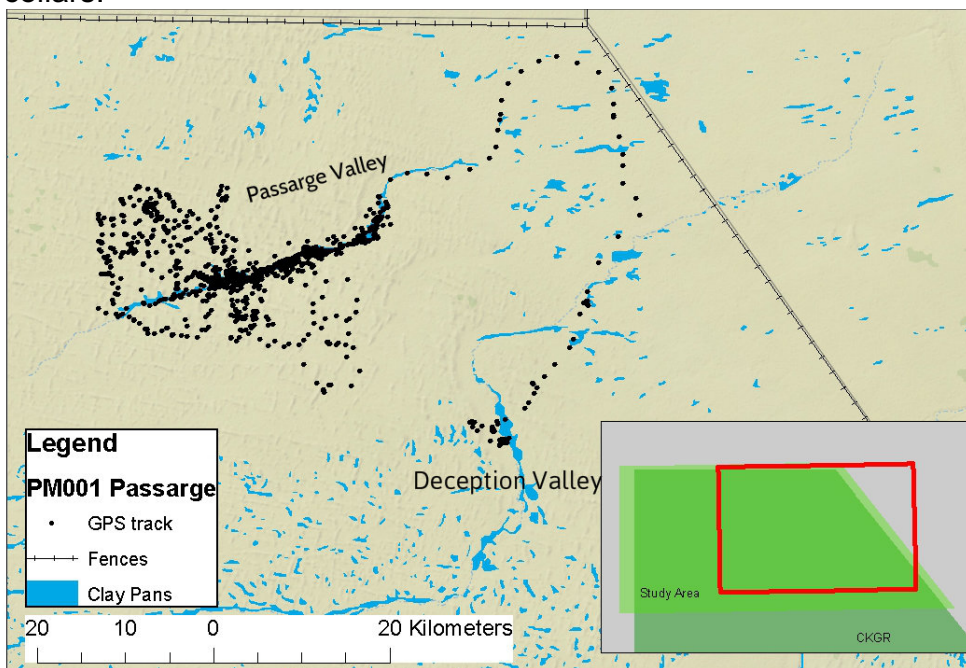


Figure 3-4 GPS data of lion PM001. Heavy use of the Passarge Valley Pan habitat is evident, with several excursions outside the valley. In the last month of life, April 2009 PM001 can be seen wandering north east, and then south into Deception valley. PM001 was observed in an injured state at a waterhole there, and an inspection by the Department of Wildlife Vet was too late to aid him or ascertain the cause of injury, and he soon died.



Figure 3-5 An anaesthetised lion, PM001, during collaring. The short grass and sparseness of the pan habitat during the dry season is evident.

3.5.2.2 Lion SM009

This lion was first observed in December 2008, with a female and two large cubs (approx. 8 months old) at Tau Pan. By the time he was collared in August 2009, this large male, who did not appear to be part of a cohort and had distinctive scarring controlled a large area incorporating at least seven adult females around the San Pan area. He was collared during the day on the far western end of San Pan, and his range from there on centred on San pan, incorporating the two pans to the north and south. He appeared to father several quite successful litters with the females he defended, but never again was seen to visit Tau Pan or the female and cubs observed in 2008.

His behaviour, range and daily movements were typical of other lions in the study, but remarkable in the control by a single lion over a very large area for such a long time with a reasonable number of females at distant locations. By comparison; his neighbours, the two lions that at the time controlled Tau Pan (not part of the collared study) seemed unable or uninterested to defend more than a small area and only two females. Mobile safari operators were able to recognize lion SM009 from several years ago from a cub due to the distinctive scarring acquired at a young age, and were able to state that his natal pride lay to the southern end of Deception Valley, about one average pride range width distant (about 25km). After two years of observations, SM009 perished in the middle of his range, coinciding with an intrusion by a male pair from a pride directly to the north. A lethal fight is the most likely cause of death. At that time all known cubs (5) were older than 1.5 years, survived for another six months, and were likely to do well.

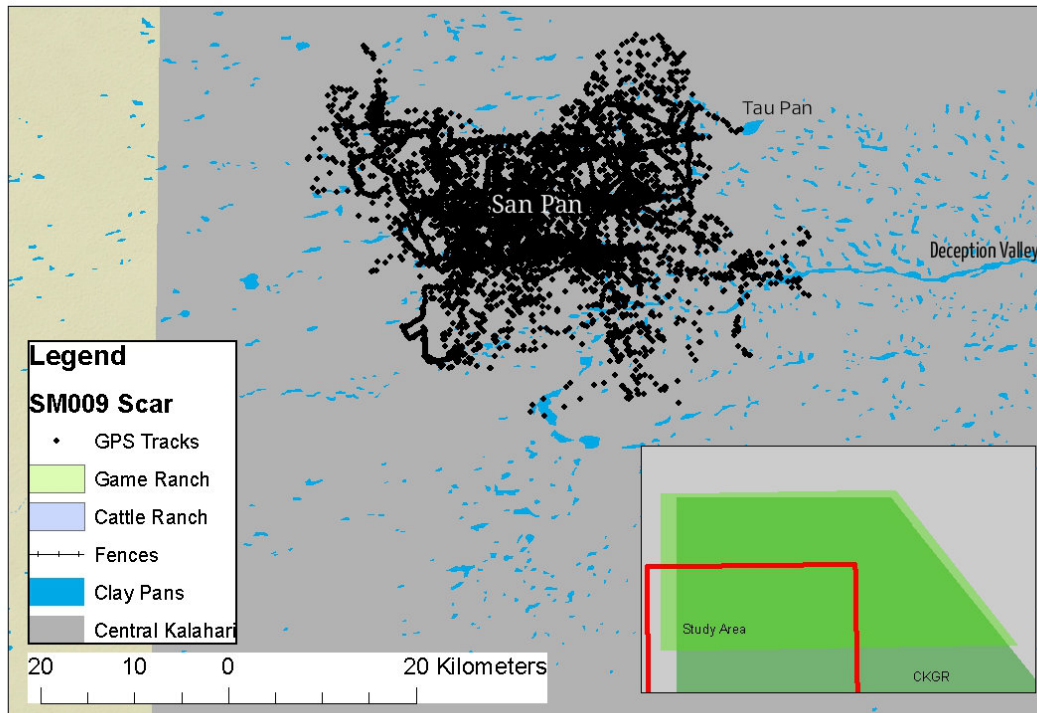


Figure 3-6 GPS data from lion SM009



Figure 3-7 Lion SM009 was easily recognized by his scar on the spine, shown here. Safari guides recognized the pattern from a cub in Deception valley in approximately 2006.

3.5.2.3 Lioness SF010

On the evening of same day that male SM009 was collared, a female was collared from the eastern end of San Pan, as part of a group of four

lionesses. After darting the vet immediately recognized that she was pregnant. She gave birth a few weeks later hiding the new cubs, and soon mixed her cubs with another female's of a very similar age. Milk feeding was shared, and as such it was never determined how many, or of what gender were her cubs. Between the two lionesses, three male and two female cubs were raised until the collars were removed two and a half years later. SM010 was always shy of the vehicle, but I was able to approach the cubs and the other lionesses quite easily. Adult females were constantly joining and leaving the group and group size varied between two and five adult females of a total of seven distinct individual adults during observations. SF010's ranging behaviour, daily distance moved were otherwise very similar to that of other resident lioness studied.

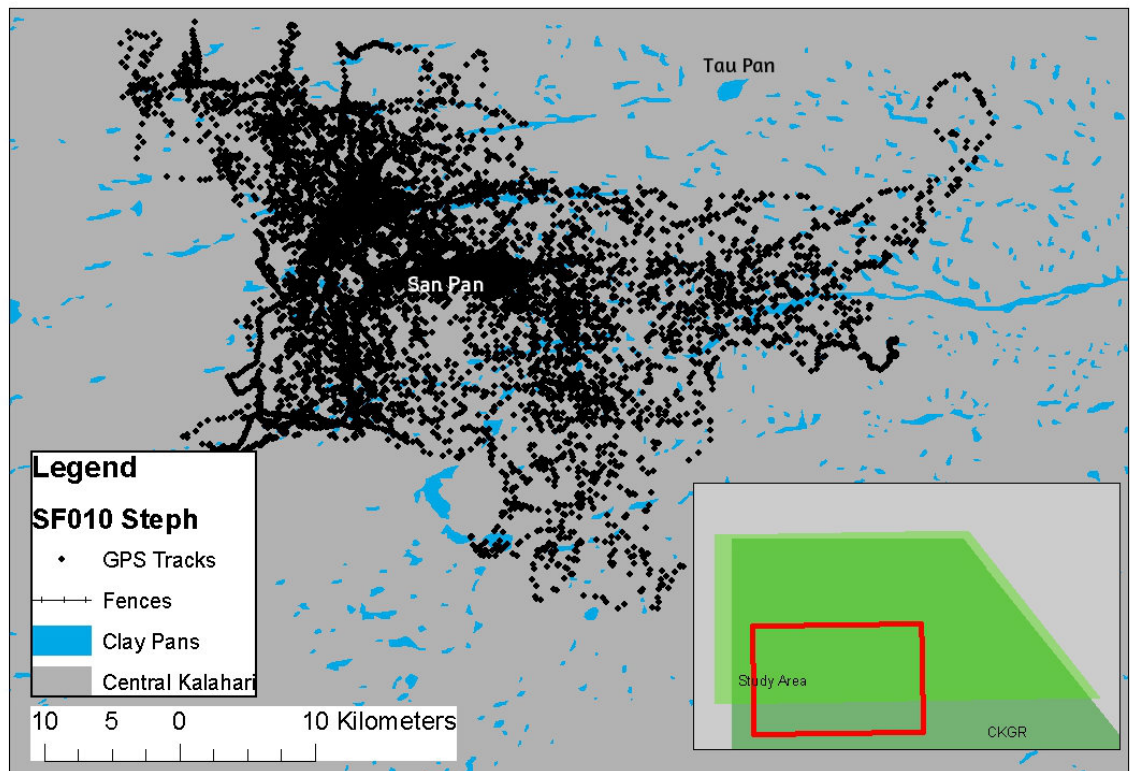


Figure 3-8 GPS Data from lioness SF010



Figure 3-9 Lioness SF010 and cubs rest on a pan, during the wet season.

3.5.2.4 Lion JM011

In August 2009 an older lion was darted and collared north of the San Pan Area, in a pride are called the Junction pride (see Figure 3-3). This lion was observed six times before perishing of unknown causes approximately 135 days after collaring. The collar was recovered and was the first Store-on-Board type collar returned to the manufacturer. Unfortunately the microchip holding the GPS data was broken at the factory during data recovery and no further information is known about this lion. Seven other lions were wearing Store-on-board collars, but this incident prompted a move to the much more expensive remote download and satellite type collars for which the data could be checked continuously and the schedule updated as needed. The next store-on-board collar to be retrieved indicated that my original schedule had not been implemented on all Store-on-Board collars and this switch became even more critical.



Figure 3-10 Lion JM011 was an older lion whose collar failed and no GPS data was collected.

3.5.2.5 Lioness HF012

Lioness HF012 responded to playbacks of prey animals in distress on the western boundary of the CKGR. This lioness travelled with a single female partner, and very occasionally with a pair of males about which little was known, as no vet was available when the males were encountered. This lioness acted as a resident with a reasonable static boundary range and had very similar range sizes and movement distances to the other resident females SF009 and PF015, but included two noticeable journeys outside the usual range.

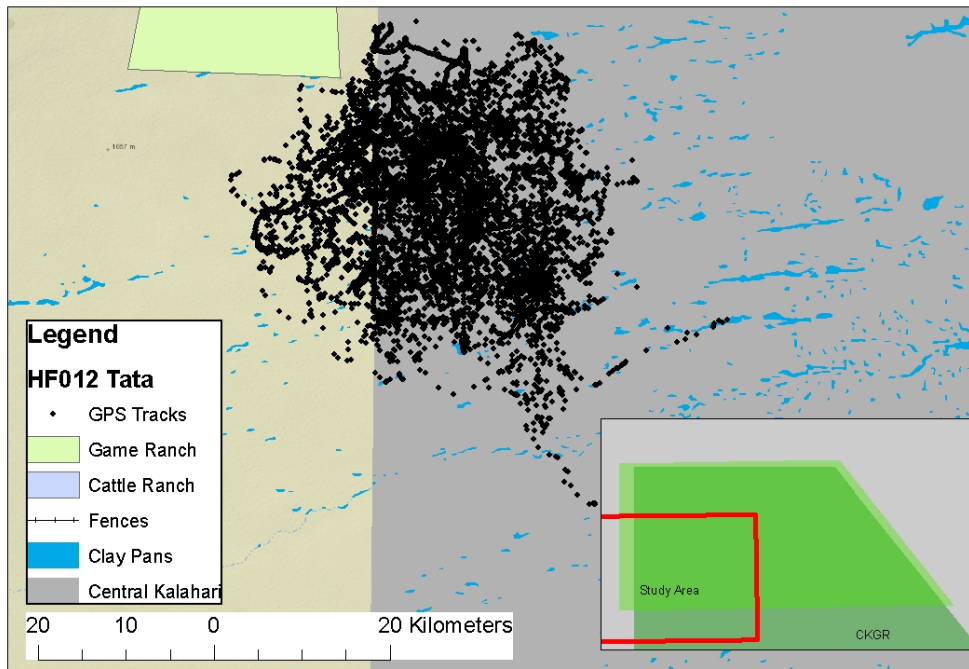


Figure 3-11 GPS tracks for the lioness HF012 who displayed a full range usage of a typical size for a resident female.



Figure 3-12 Lioness HF012 lived on the border of the CKGR and remained very shy of the vehicle.

3.5.2.6 Lioness MF013

Lioness MF013 was collared near the centre of the Junction pride's territory, but had soon departed from this area, and was not part of the Junction pride. She travelled in a group of five lions, apparently her mother, sister and two brothers, judging from age and behaviour. In contrast to the resident females of other prides, lioness MF013 and her cohort appeared to be a part of a roaming family unit with typical nomadic behaviour with no clear boundary (Figure 3-13), when they encountered resident lions, I observed antagonistic behaviour towards the family unit. The distinction of home range on a long-term scale had less meaning from this lioness and was by far the largest calculated total minimum convex polygon for a female at 3,085.1 square kilometres. This very large range was utilized by moving on average 8.0 ± 2.2 s.e. km per day similar to the mean daily movements for all CKGR lionesses. After three months the collar was removed for use in residential females, and total MCP calculated included occasional sightings over the rest of the study.

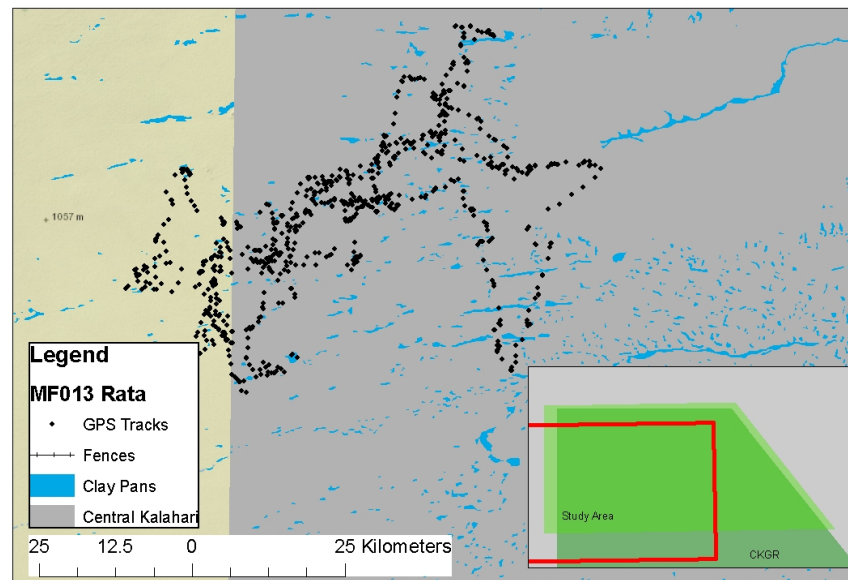


Figure 3-13 Young lioness MF013 and her family of five ranged over a very large area, crossing the boundary of the reserve and then returning, with no evidence of central tendencies.



Figure 3-14 Lioness MF013 during darting.

3.5.2.7 Lion PM014

In the north west of the study area is a long patch of pan habitat (about 50km in length) known as Passarge valley. The male successors to the Passarge pride, PM014 and PM016 were encountered in August 2009 and one of them, PM014 was darted and collared. These two maintained a large territory that included a group of nine adult lionesses. During their tenure there were no signs that either lion fathered any cubs with lionesses in the pride, despite several mating sessions observed with various females, including PF015. Nine months after beginning observations, the two lions began to spend most of their time in the northernmost extreme of their range with three lionesses that were not part of the Passarge pride, and averaged less than one known interaction per month with the Passarge females for fifteen months (from May 2010 until August 2011). A nomadic pair of male lions (JM067 and JM068 see section 3.5.2.15) of notably divergent ages moved into the Passarge area and proceeded to mate with the females, producing 4 litters of cubs. However when PM014 and PM016 returned, the two usurpers were unable to defend the territory against the original two lions. All known cubs perished (15 cubs from 4 females) presumed killed by the returning males or abandoned by females. The behaviour of PM014 and PM016 towards the new males was always antagonistic and yet the two new males remained in the area at least until observations ceased eight months later. While the original males displayed in-oestrus mate guarding behaviour and occasionally copulated with pride females, the new pair would socialize with other female members of the pride just a few kilometres or more away. An impasse seemed to have been quickly reached where it was not economical for the original males to continue pursuit of the intruders and perhaps more economical to concentrate on excluding the new males from accessing females in oestrus. It is interesting to note this behaviour, likely a common behaviour in a semi-arid environment where mate-guarding is a more economical strategy to territory defence. Territorial defence is common in high lion density areas such as the Okavango Delta (Kat 2003), and Ngorongoro crater, Tanzania (Elliott & Cowan 1978). There was no evidence of new cubs or pregnancies at the termination of the study.

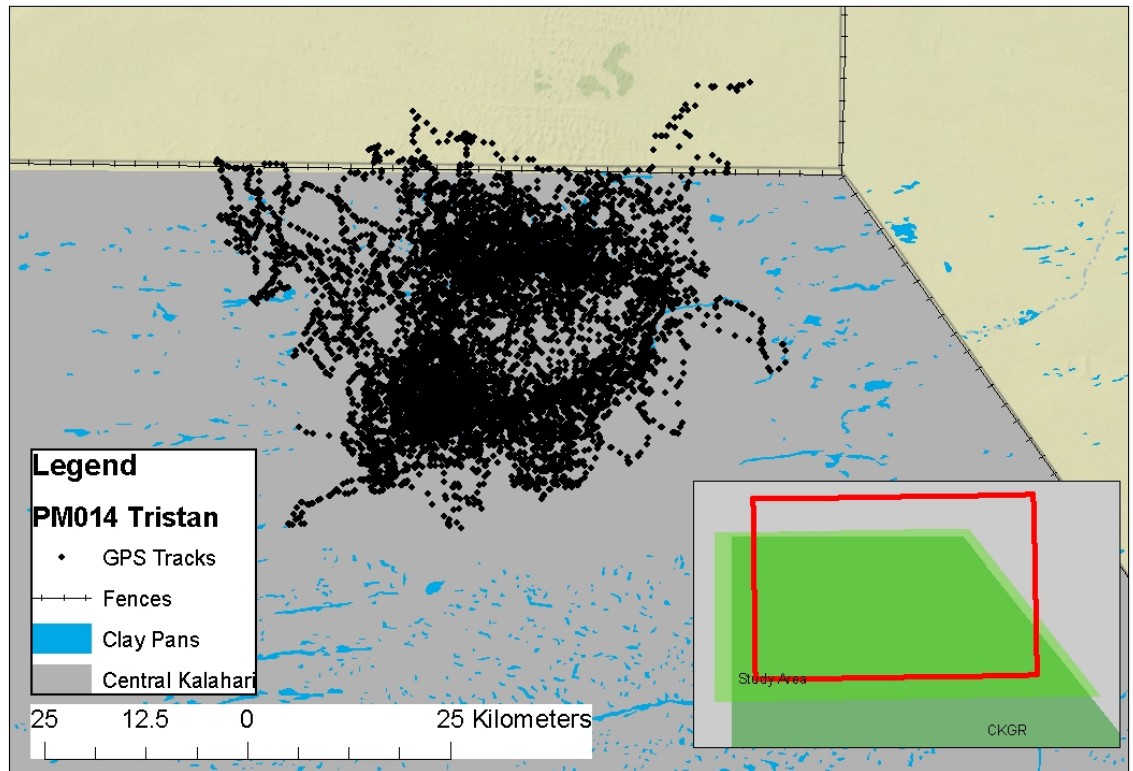


Figure 3-15 GPS locations of lion PM014. The southern part of this range was utilized during this lions tenure with the Passarge Valley pride, including PF015, while the north-western extent of this range represents time spent with females of an unstudied pride. Several excursions outside the reserve to the north can be observed, during times of heat and water stress.



Figure 3-16 Male PM014 in Passarge Valley showing the distended belly associated with a recent meal.

3.5.2.8 Lioness PF015

This lioness was part of a group of nine females that I was able to observe very regularly. The nine were rarely all together, but formed smaller foraging groups on a regular basis. PF015 and PM014 were collared at the same time, during bouts of mating and the two males PM014 and PM016 were often accompanying one of the groups of lionesses, until May 2010. Despite the mating, PF015 was never visibly pregnant during this time, until the interlopers JM067 and JM068 arrived, and most of the Passarge females became pregnant. PF015 gave birth to cubs shortly before the 26 April, 2011 when three cubs were first observed. While PF015 kept her cubs apart from the other pride lionesses, she would join them to hunt through the night, until returning after dawn. PF015 therefore had to return to the position of the cubs every morning and find the other lionesses every evening. This behaviour is common to protect the cubs at this vulnerable stage (Schaller 1972), and it meant she therefore walked greater distances than other lionesses, during the period before the cubs were introduced to them, the distance they walked and the distance to and from the cubs. This behaviour adds substantial energy requirements to a lactating lioness, and emphasises the importance of the group to the lioness. The cubs of PF015 and other lionesses were observed several times until the return of PM014 and PM16.

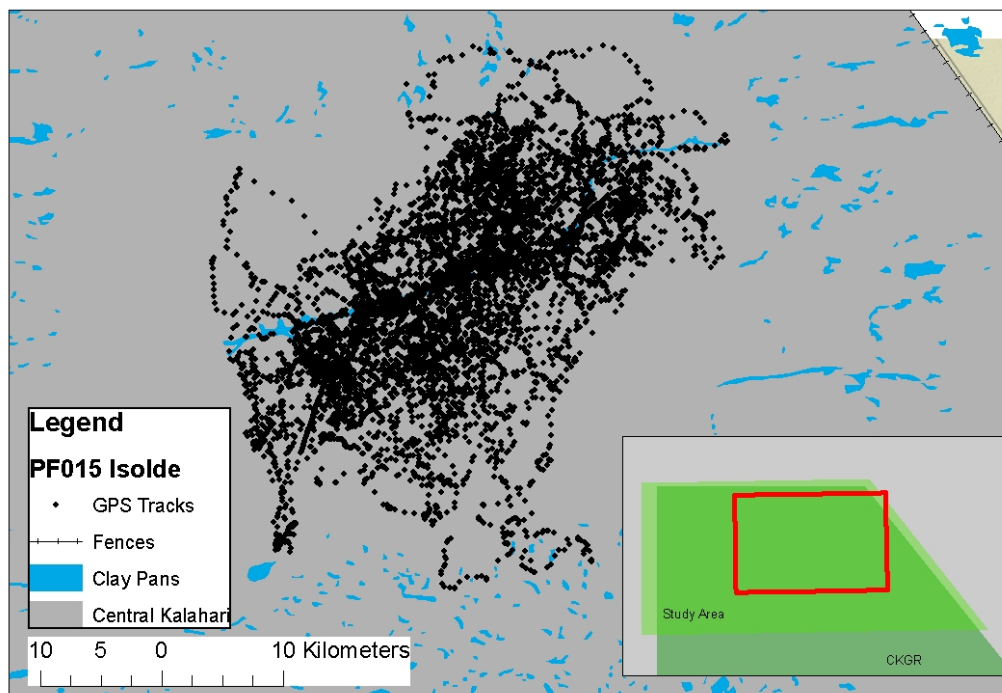


Figure 3-17 A map of the range that lioness PF015 used during the study.



Figure 3-18 Lioness PF015 receives a dart to replace the collar she wears while resting with pride lions in Passarge Valley.

3.5.2.9

Lion TM040

A new lodge was opened at Tau Pan in 2007 and began pumping water to a small waterhole in front of the lodge. This waterhole attracted some game during the dry season, but was hardly used when rainwater was available, being very salty. Two male and two female lions began to use this waterhole regularly in 2010, and lion TM040 was collared in May, 2011 with a VHF collar. After locating the lion four times at less than 4 km from the waterhole, the collar bindings broke and it dropped off. We were able to observe the hunting behaviour of the group, where the males trailed behind the females who killed gemsbok, young giraffe and kudu. There were six cubs in total who joined in feeding at about 4 months of age. Antagonistic behaviour was only observed once in this pride, when the females and interlopers from Passarge Valley came to the waterhole during an extreme heat wave in October 2011. They injured one of the Passarge lionesses, who remained near the lodge for a week, losing a lot of condition before returning to Passarge Valley.



Figure 3-19 TM040 wore a GPS collar for five months. He was part of the very small Tau Pan pride of two lionesses and his companion, TM041

3.5.2.10 Lion BM052

Lion BM052 was darted and collared in the wildlife management area (WMA) corridor between the CKGRs western boundary and the farms further to the west. He never associated with another male, chasing several younger males for considerable distances. When travelling west out of the reserve, lion BM052 encountered a game farm that tolerated lions and he spent a considerable amount of time there. He consumed several species of antelope that could survive only inside the well watered fenced farm such as black wildebeest (*Connochaetes gnou*) and waterbuck (*Kobus ellipsiprymnus*) and enjoyed access to constant fresh water through the year. Despite this, BM052 regularly made extremely long journeys inside the boundaries of the reserve, making the rounds to various groups of females. On the game farm he defended a lioness (lioness BF053, see section 3.5.2.11) with three small cubs and one sub-adult male cub. BM052 barely tolerated the sub-adult as it grew to a similar size, which then left the group in February, 2011, and was later reported as shot. In October 2011, BM052 started to make extreme journeys to the south and west of his usual range travelling nearly 40km further south than ever before, then returning to the game farm. Finally BM052 walked a considerable distance in two days including walking 7km after 9am to the extreme east of his range then 28 km to the extreme west. While in the west BM052 killed a cow on the neighbouring farm and was shot. Up to that time the particular farm had experienced only three incidences of livestock loss to lions all connected to BM052 by the GPS data. The same farm had experienced high but undisclosed levels of losses to lions on a different property to the north. After shooting BM052, the farm began to experience the worst cases of livestock loss on the southern farm. They wrote an open letter in which they

claim to have lost 49 cattle to lions and blamed the game farm for tolerating lions. They remained uncooperative but the evidence seems to suggest that lion BM052 was in fact acting to hold back nomadic and exploring lions who were naïve to farmer persecution. After his death the numbers of lions exploring the territory rose dramatically and cattle losses increased instead of being mitigated by the culling. It is difficult to study this phenomenon due to the fatal and legal response by farmers, and at this time I began to withdraw my studies of lions on the boundary of the CKGR for political and ethical reasons.

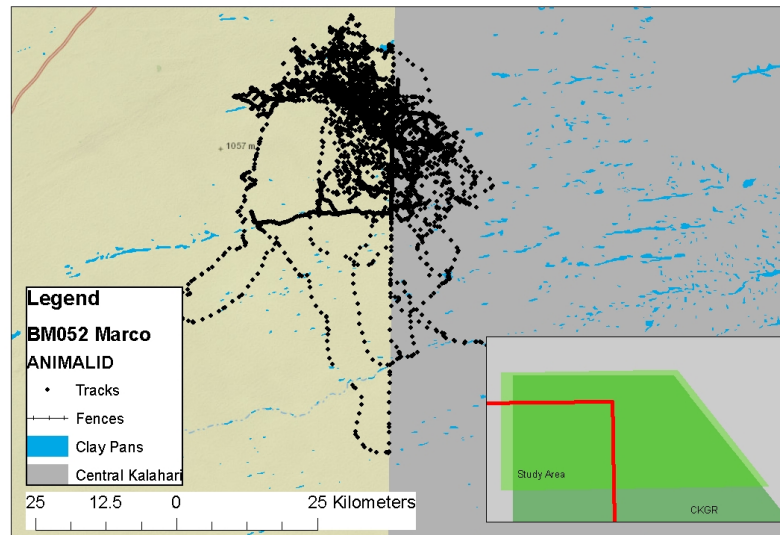


Figure 3-20 A map of the range of lion BM052, showing utilization of park, WMA and private property.



Figure 3-21 Lion BM052 and two of the cubs he tolerated as his own on the Game Farm Bokamoso.

3.5.2.11 Lioness BF053

A very shy lioness was darted at the western boundary of the CKGR, and darted at the same time as male BM052 while they had been mating for about 20 hours beforehand. At the time BF053 had one single large cub, approximately 1.5 years of age, whom BM052 had chased away from the scene. After darting she returned to mate with BM052, and gave birth to cubs about three months later, three survived to be observed. BM052 was tolerant of the young cubs and to a lesser extent the sub-adult. BF053 confined herself to a very small range on the game farm and a little to the east and south (Figure 3-22). The area to the east and south was wildlife management area, and was largely unoccupied by people or livestock. She remained extremely wary of vehicles throughout observation, despite the managers on the game farm being very tolerant of lions. The cattle farm directly to the west was not tolerant to lions and actively pursued problem carnivores, though she did not venture on to the cattle farm. The wary behaviour of BF053 seemed to indicate a history of persecution and reflect her lack of membership with any pride – pride females are usually less wary than unaffiliated females. Her range was severely restricted while she raised the small cubs. The sub-adult left the small family after another 20 months. I was unable to track him, but was told by a farm manager that he was shot on another farm. 26 months after the original darting took place, female BF053 increased her range slightly to include the cattle farm to the west (blue polygon in Figure 3-22) and was subsequently shot in February 2012. The fate of the three small cubs is unknown, but had been healthy when last seen about one month prior although completely dependent on the mother.

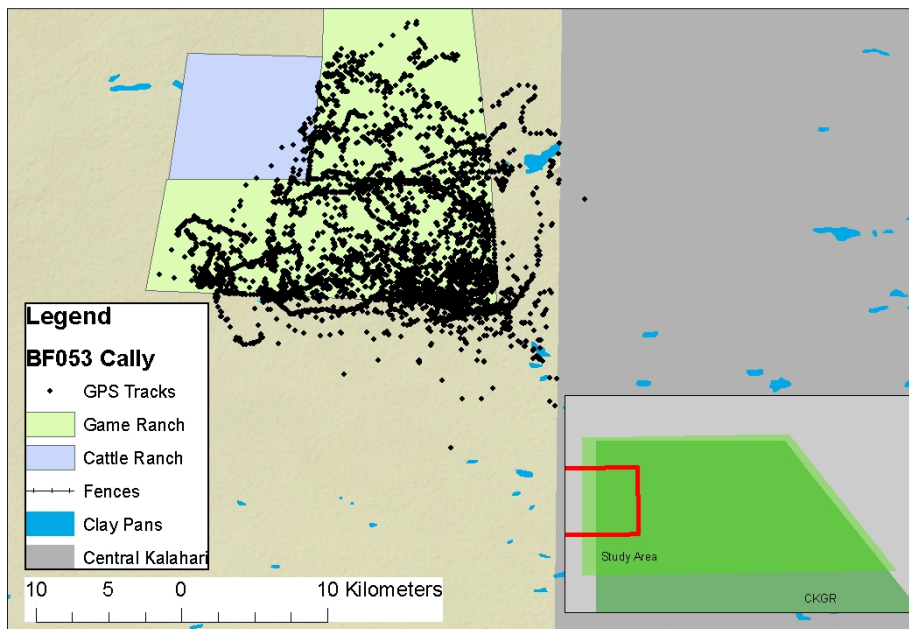


Figure 3-22 GPS tracks for lioness BF053, indicating an extremely restricted ranging behaviour limited to the safe areas of the game farm (light green) and the wildlife management area between the farms and the game reserve. For over 26 months she raised three small and one large cub before being shot on the cattle ranch indicated in blue.

3.5.2.12 Lion JM058

Lion JM058 was part of a pair of 6 year old lions first observed in November, 2009 in the Junction Pride range (see Figure 3-3) but were not part of the pride there and were apparently nomadic. Two years later they were observed inside the mostly undefended Passarge area in August, 2011, mating with a Passarge Pride female. I placed a collar on JM058, and a VHF collar on JM059 a few weeks later. The two were more often apart than other pairs of male lions and proceeded to mate with eight of the nine females in the pride at that time. At least five became pregnant and gave birth to cubs. The original pride males, PM014 and PM016 returned, and several antagonistic encounters followed. As the females were usually split into two or more groups, one male pair usually accompanied a group of females, while the other pair accompanied another group. Within a few weeks, there was no sign of any cubs (at least 15 had been observed prior to the return of the original pair) and I presume that the original pair recognized that they could not be the fathers and swiftly disposed of them. A tense stand-off ensued where the two pairs occupied a mostly overlapping range, while usually avoiding direct interaction, and this lasted for the 8 months until the cessation of observations. A particularly hot week in October, 2011, while the original pair left the CKGR to find a waterhole on a game farm to the north, the females and the intruding pair went south, into the middle of the Tau Pan prides range to drink from the water hole there. It was a relatively new waterhole, built in 2008 by the new safari lodge there and it seems unlikely that the female lions knew of its existence. The males may have experienced it during their previous nomadic phase. The group encountered the local pride, and despite outnumbering them considerably, the resident Tau Pan pride managed to severely injure one Passarge female and chase the others away, but not before they had a good drink. The injured female was left behind, resting under the lodge's cabins for six days and losing noticeable condition in not eating, before returning to her pride. The main advantage that the resident pride had over the Passarge pride was that they were well watered during the heat wave, when daytime temperature maxima were above 42 degrees Celsius for the 6 day period.

This incident highlights two important factors relevant to the lion livestock conflict; the response of some prides without access to permanent water to extreme heat during the dry season, and their vulnerability. The injured Passarge female showed no fear of humans during her injury time. It is clear that lions ignore pride boundaries, fences and humans when they are desperate for a resource, which may include more things than water – for instance if food was difficult to find. This story serves to question the general argument used to defend lethal control of lions; that some, but not all lions are problem lions. The argument continues that, as only a few lions are problem lions, lethal control can minimise livestock losses while having little impact on the lion population. The evidence from the CKGR indicates that any lions are potential livestock killers, given the right circumstances.

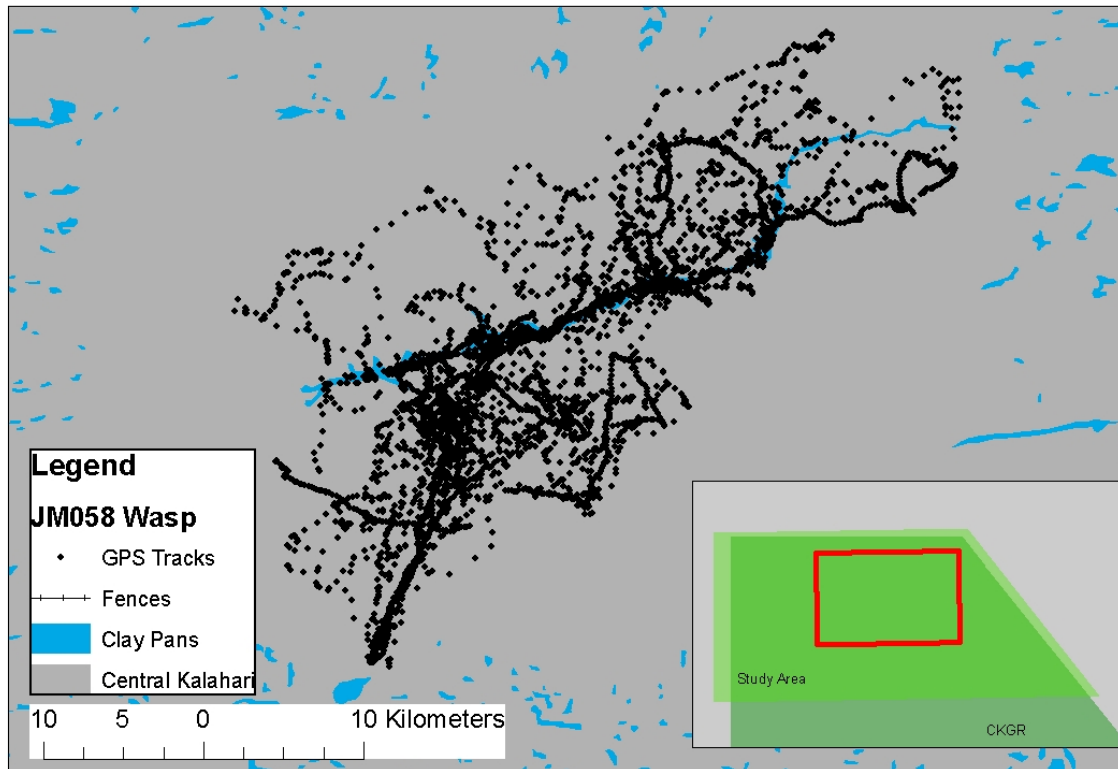


Figure 3-23 Map of GPS collar tracks of male JM058. Utilisation of the pan/valley habitat is evident. The south-westerly movement tracks the transgression into Tau Pan Pride territory to access a waterhole.



Figure 3-24 JM058 receives a cleaning by tongue from companion, JM057

3.5.2.13 Lion TM059

This young male with very striking facial features was part of a cohort of three young males. He was observed singly on several occasions and was estimated to be about 4 years old when collared in March, 2010. He spent a little time around Tau Pan, but did not associate with the four territorial lions of the Tau Pan pride. Instead the three young males wandered over one of the largest areas of any males that I observed, coming into contact with females of many other prides. Often these interactions were amicable, but on one occasion I was following TM059 and his two companions as they roared and approached two females. When they were within a few hundred metres they began to give chase and the females fled. After running for around 1.5km they caught up with one of the females and proceeded to attack her until she was subdued. They sniffed her, and then left with apparent interest in locating the other female. This location was the furthest north east they had ever been, and it was unlikely they had ever encountered these females before. Over the final few months of observation, TM059 was only ever observed without his two companions, in the far south east of his range.

While TM059's range was the largest of any of the study males, while his mean daily movement distance was the smallest. This highlights the lack of relationship between range and daily movement distances, instead pointing to the effort that pride required for males to defend appropriately sized areas. These large arid ranges require constant patrolling and effort to ensure that intruders do not have access to undefended females at the critical times when they are prone for the mating phase of oestrus.

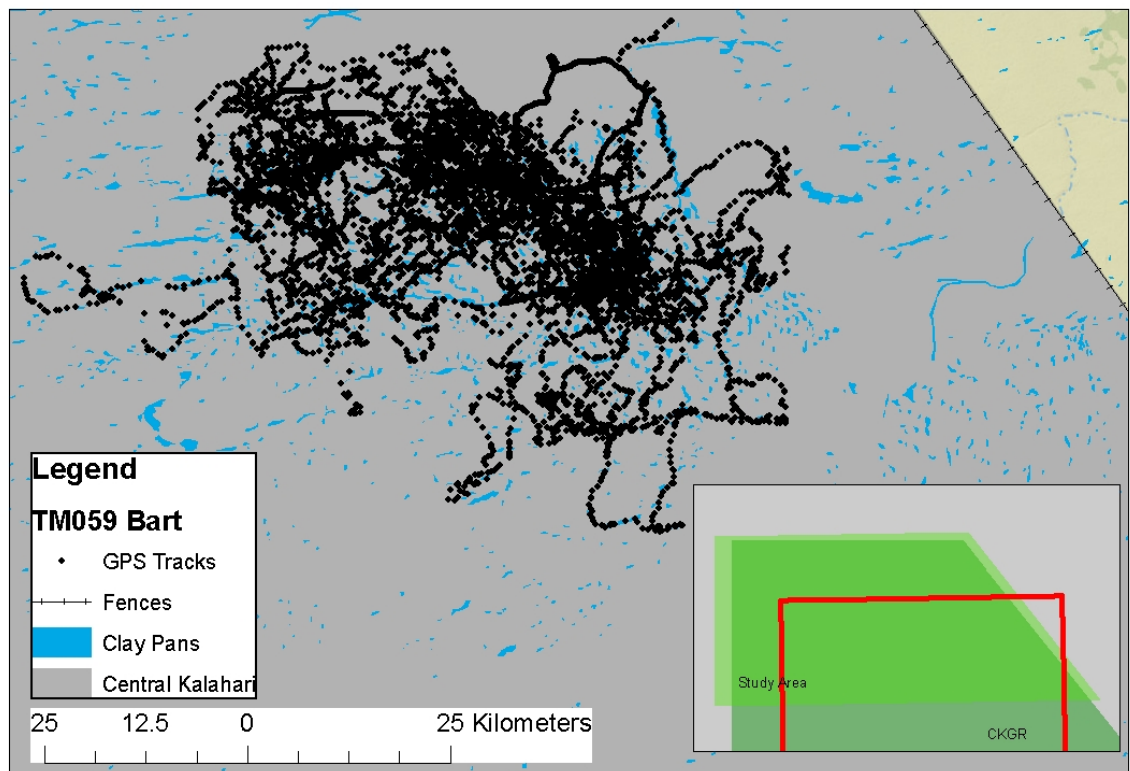


Figure 3-25 Maps of the GPS tracks of lion TM059, a nomadic young ion with two companions.



Figure 3-26 Male TM059 was a young lion with striking blonde highlights on his face, shared to a lesser extent with his two brothers. The three lions kept close to the Tau Pan area for the first five months before roaming the entire study area. After seven months of this, TM059 was only observed alone.

3.5.2.14 Lion JM068

A single male dominated the Junction pride after the death of JM011 and JM011's partner (see section 3.5.2.4). Lion JM068 was collared in July 2009 and was observed to defend two cohorts of three females each. These females had not been observed with the original males, and the females that spent most time in the north had cubs that were young enough to be sired by JM068. He behaved as though he believed the cubs were his own. A likely interpretation is that JM068 held a small territory to the north of the original Junction pride range, before expanding the territory to include the vacated Junction territory and three females after the death of JM011. After the death of SM009 in July 2011 further to the south, male JM068 again frequented the empty territory for several weeks at a time. See Figure 3-27 for a visualization of his range before and after the death of SM009). He had shown no interest in this territory prior to the death, evidence that territories are defended and delineated by scent and roaring and are respected to some degree. Upon cessation of those cues, it appears that both nomadic lions and those with their own territories readily

explore undefended territories.

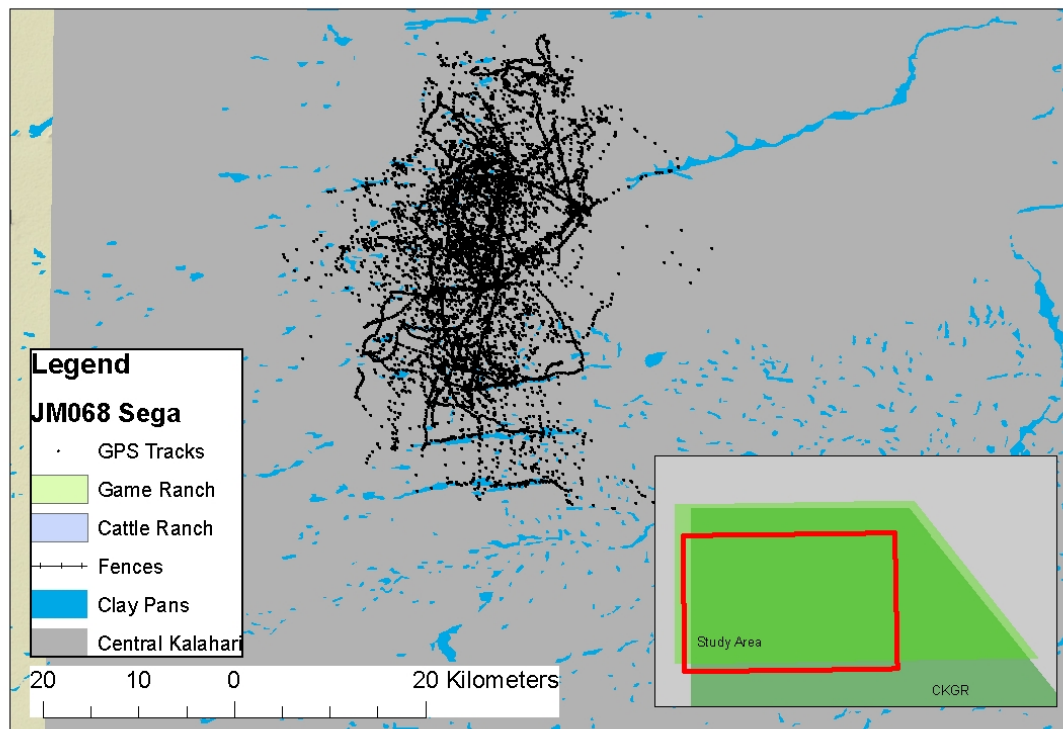


Figure 3-27 The GPS data from JM068 shows how the lion spent most of his time in his territory, the northern half of the GPS points shown here, until the lion to the south perished, and he incorporated several forays into this open territory.



Figure 3-28 Lions JM068 sits on green grass in an area that burned several weeks previously. Normally the grass would be above his head (at least shoulder height on a standing lion).

3.5.2.15 Lion MM102

A male was collared in the north west of the reserve to fill an important gap in the developing pride map. Almost immediately the satellite collar failed and only occasionally returned sporadic data. After 132 days the collar was removed with 24 days worth of data, no GPS enabled collar was available at the time, and I decided not to attempt a collaring of the lionesses in the area. The lion was part of a pair of males that spent extensive time on lion friendly properties to the north of the game reserve, with free access to drinking water for wildlife. The lion was observed nine more times over the next few months usually on this property. At about the same time the study concluded, an unsubstantiated report was relayed to me that the lion had been shot by neighbouring cattle graziers.



Figure 3-29 The collar on Lion MM102 failed and returned no usable data. He was shot by farmers north of the CKGR in an area known as the Hainaveld.

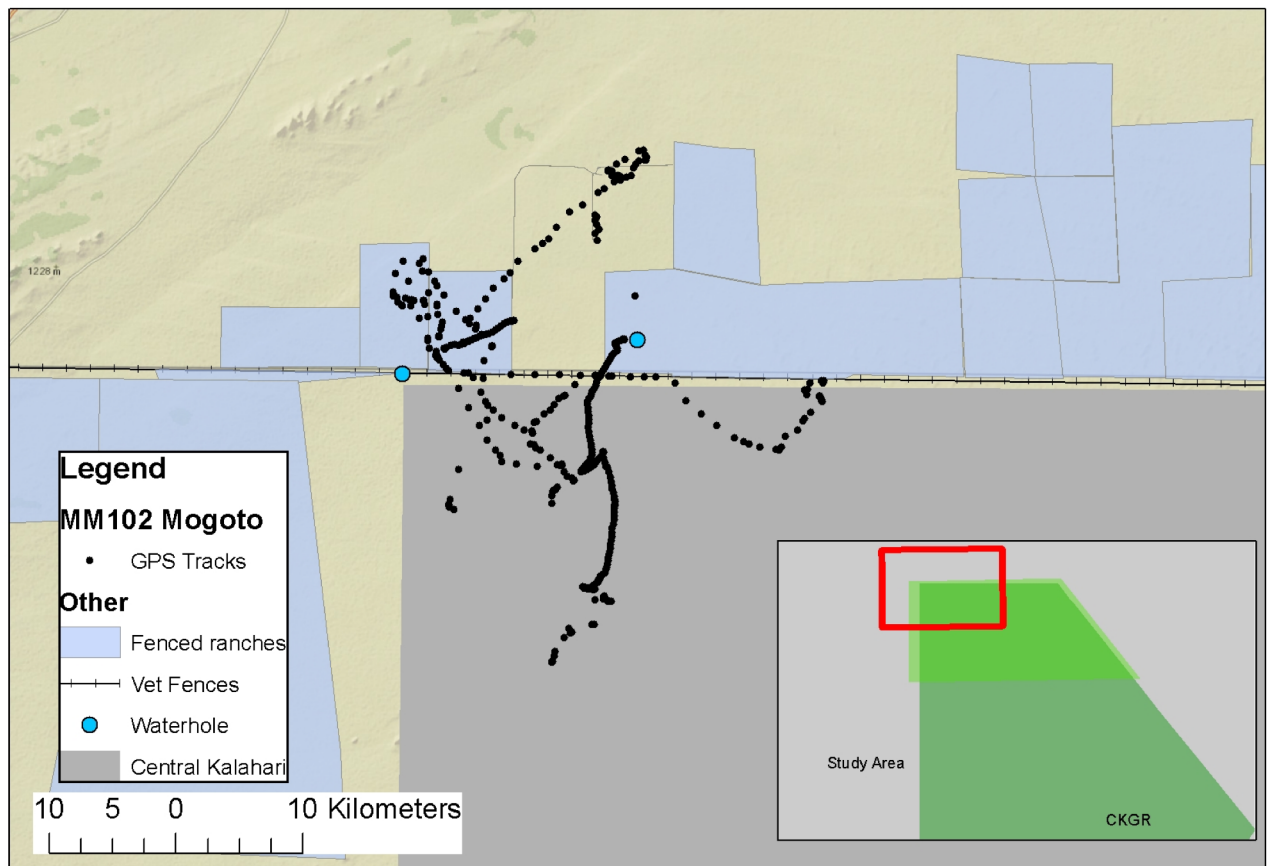


Figure 3-30 Map of the GPS tracks of lion MM102, sporadically transmitted before early removal of collar. The lion pair was observed many times with a pair of lionesses with three cubs on the property with the eastern most waterhole shown on the map. I received an informal report that the collared lion was shot in the unfenced grazing area to the north of this property.

3.6 Summary of lion body measurements.

Every effort was made to follow the protocol suggested in de Waal *et al.* (2004) to standardise the measurements of individual lions. For safety reasons the vet had complete control of personnel during the darting phase, and occasionally we were unable to complete some measurements. Mean values for collected measurements and sample size are shown in Table 3.4. Skinner and Chimimba (2005) reports the mean adult mass of lions Kruger National Park lions to be 190 kg for males and 126 kg for females. The CKGR lion population may represent some large lions, respective averages 19 and 21kg greater than lions from Kruger. More information is available in Appendix 4.

Table 3.4 Mean values of available measurements for male and female lions. Column headings include sample sizes unless otherwise shown in data table. Methodology follows (de Waal *et al.* 2004). More details on measurements can be found in appendix 4.

	Male (n = 4)	Female (n = 4)
Upper Right Canine Length (mm)	50.05 (n = 4)	38.921 (n = 3)
Upper Right Canine Length (mm)	35.73 (n = 3)	32.48 (n = 3)
Mass (kg)	209 (n = 7)	147.625 (n = 5)
Body Length (cm)	199.57 (n = 7)	170.83 (n = 5)
Tail Length (cm)	84.64	80.17
Body+ Tail Length (cm)	257.79	253.00
Tail Circumference (cm)	27.48	24.80
Neck Girth (cm)	73.11	60.50
Chest Girth (cm)	121.79	107.71
Abdomen Girth (cm)	123.93	109.93
Front Right Leg Length (cm)	60.20	56.00
Rear Right Leg Length (cm)	66.13	62.33
Front Left Leg Length (cm)	52.93	58.25
Rear Left Leg Length (cm)	66.25	61.75
Front Right Leg Circumference (cm)	47.00	66.17
Front Left Leg Circumference (cm)	51.67	43.75
Rear Right Leg Circumference (cm)	47.00	62.00
Rear Left Leg Circumference (cm)	59.25	60.75
Front Right Paw Length (cm)	12.40	10.80
Front Left Paw Length (cm)	12.20	10.75
Rear Right Paw Length (cm)	12.62	10.30
Rear Left Paw Length (cm)	12.75	9.93
Rear left Paw Length (cm)	12.75	9.93
Front Right Paw Width (cm)	10.82	9.13
Front Left Paw Width (cm)	11.02	9.87
Rear Right Paw Width (cm)	9.45	7.88
Rear Left Paw Width (cm)	9.75	8.25
Shoulder Height (cm)	111.83	92.33
Head Length (cm)	40.75	34.75

Chapter 4 Factors Related to Variation in Home Range in Central Kalahari Lions (*Panthera leo Linnaeus*).

Chapter Summary

Human-Lion conflict in Botswana leads to large losses of livestock to depredation on farms close to game reserves, and retaliatory killings of lions. Depredation is often the result of extra-home range excursions that lead lions in to farms, rather than lions seeking livestock per se. Home range sizes of lions are influenced by food resources, mate-guarding of females by males, territorial boundaries and other factors like fences, waterholes and habitat. I tracked the movements of eleven lions in the Central Kalahari Game Reserve (CKGR) in Botswana between 2008 and 2012, collecting intensive GPS locations every thirty minutes or more during the night. I calculated total and monthly utilisation distributions (UD) as various measures of home range and used generalised linear mixed models to explore factors that influence variation in UD's. Male lions used large total areas (minimum convex polygon (MCP) of 2500.1 km², SD = 1276.5), and smaller core areas (estimated 95% kernel density estimates (KDEs) of 1303.7 km², SD = 684.8, and 50% KDEs of 243.7 km² S.E. = 129.7). Female lions had smaller total ranges than males (MCP = 2020 km², SD = 646.4) and utilised slightly larger core areas (95% KDE = 1317 km², SD = 1031, 50% KDE = 293 km², SD = 264.2). Cumulative monthly home ranges indicated that CKGR lions continued to shift or expand their range over extended periods, while the short term sizes of home ranges are maintained by lions with prides. The different measures of utilisation were affected differently by measured variates. Gender and age played no role in monthly variation in UD size, mean rainfall was negatively correlated with all measures of UD, and temperature was positively correlated with the two KDE measures. Foraging group size of lions was positively correlated with 95% KDE size, and females with large cubs had significantly smaller monthly 95% KDE. This variation may help explain the incidence of lion-livestock conflict, and provide insights into managing the conflict. In general, home ranges were larger than that of many lions around Africa (Smuts, 1976; Smuts, 1979) but smaller than other arid area lions (Stander 2000a; Stander 2000b).

4.1 Introduction

Carnivores play an important role in the health of many ecosystems (Callan *et al.* 2013), the far reaching effects of which can have many negative impacts on many human interests (Heal 2003). Removal of carnivores can alter ecosystem function and composition (RAY *et al.* 2005b; Winterbach *et al.* 2013). Comparing similar sites with and without predators has shown that loss of carnivores can result in cascading effects on other trophic levels (Callan *et al.* 2013) reducing herbivore, plant and avian diversity and health (Berger *et al.* 2001) and even insect and rodent diversity (Carter & Rypstra 1995). The interdependent nature of systems means that effects may extend to outside carnivore ranges, reducing rangeland health, impacting fodder and domestic

animal stocking rates (Berkes *et al.* 2000b; Pickett *et al.* 2008). Predators continue to be heavily persecuted due to their real and perceived cost to livelihoods (Baker *et al.* 2008) and reducing the conflict or perception of conflict will have direct economic benefits. Conflict is costly to both humans and wildlife, and reducing conflict can increase predator numbers, benefitting the ecosystem and, indirectly, humans living alongside the game reserve. Despite decades of effort in a few conflict areas such as South Africa - (Lagendijk & Gusset 2008; Snyman *et al.* 2014), Zimbabwe - (Butler 2000; Gandiwa 2011; Rasmussen 1999; Sibanda & Omwega 1996), Kenya - (Holmern *et al.* 2007; Kaltenborn *et al.* 2005)) and Tanzania (Hazzah *et al.* 2009; Hazzah 2006; Mwangi 2007; Ogutu *et al.* 2005; Patterson *et al.* 2004) progress has been slow and any lessons learned are often not relevant in different regions (Treves & Karanth 2003). It is important that predators are studied *in situ* to further the understanding of ecological drivers and correlates of lion behaviour and space use in order to manage and mitigate conflict.

Home ranges constitute a more or less restricted area within which an animal conducts its normal business e.g. foraging and reproduction (Harris *et al.* 1990) and variation of range size between genders, ages, and social group types of animals can inform stakeholders about the current and potential effects of possible management actions. African lions (*Panthera leo*) maintain home ranges for which lower limits are constrained by food availability (Funston *et al.* 1998) and the upper limits for maximising territory and other resources are constrained by energy expenditure (Packer *et al.* 1991) and the interaction with the territorial boundaries of neighbours (Potts *et al.* 2012). A lion's territory is largely contiguous with home range and defended passively through roaring and scent-marking during patrolling, and actively with physical aggression (Lehmann *et al.* 2008).

Variation in home range size in short time scales within populations can reflect drivers of lion behaviour and identify constraints. Knowledge of the correlates of home range area with dependable climatic variates such as rainfall or prey density can allow management to predict and respond to lion behaviour to better manage conflict between wild populations and humans living near reserves (Baker *et al.* 2008). Between population comparisons of home ranges have found important large-scale patterns, but "within-population studies are needed to investigate the extent of, and the factors underlying, intra-specific variation in home range size" (Loveridge *et al.* 2009). Various home range estimators can be used to discriminate between variation in size, shape and structure between individuals under different pressures (Kenward *et al.* 2001), and can be useful measures of drivers of behaviour see (Carroll *et al.* 2003).

Home range estimators have been used for decades to account for relationships between the area an animal needs and uses and measures of behaviour, body size and resource requirements (Burt 1943). More recently they have been used to study individual variation and the effects of age, gender and social status (Borger *et al.* 2006). There is some argument as to the utility of some measures of home range. For instance there is agreement that occasional forays should be excluded but identifying such forays is problematic. Utilisation distributions are mathematical solutions that discriminate areas of high use. They are useful in answering questions regarding foraging, central tendency behaviour (returning to burrows, dens, favourite patches of defended

areas), socialising and access to other resources (water, scratching posts, and cleaning stations). A variety of available home range estimators are relevant to different scientific questions, and usually focus on utilisation that is pertinent to the scientific question being asked. As such, they are referred to as Utilisation Distributions (UD).

Kernel density estimates (KDE) focus on utilisation by highlighting areas of high use through statistical methods, but are reliant on the choice of smoothing parameter, h (Hemson *et al.* 2005). Animals rely on small core areas for socialising and dependable food and water resources and a 50% KDE is an estimator of this area. The normal range of a lion should exclude once-off forays into neighbouring or unoccupied territories but include regularly patrolled parts of the territory and the 95% KDE is a useful measure of this. By contrast, estimators that include outlier locations can answer questions for which occasional use is extremely important, such as exploration in response to death of competitive neighbours or searching for extra-group mating opportunities. These outliers are correctly discarded by studies interested in the most common behaviours of foraging, but outliers become important when occasional behaviour may bring the animal into conflict with humans resulting in death (Loveridge *et al.* 2007). For this reason a robust measure of ranging behaviour, the 100% minimum convex polygon is valuable to encapsulate this behaviour. Both are used in this study to address different hypotheses on range utilisation.

An important determinant of predator carrying capacity and range size is prey biomass (Carbone and Gittleman, 2002 and papers therein) with a better prediction of carnivore population size obtained by using biomass of preferred prey by weight range (Hayward *et al.* 2007b). Celesia *et al.* (2009) found that at a continent wide scale (34 habitats) herbivore biomass showed no independent contribution to lion demographic parameters, such as lion density, and home range size. This is most likely to be because herbivore abundance is dependent on the same climatic correlates as lion survival, such as water in Kgalagadi Trans-frontier Park (van Vuuren *et al.* 2005). Wolff (1993) however points out that animals can maintain territories in defence of different resources such as females or den sites, and that home ranges are also limited by such considerations. Sociality and group territoriality also have the potential to influence inferences about space use and resource selection with stronger social groups monopolising territory disproportionately. For instance, a small strong population could control a large territory, while a weak large population (perhaps of young adults) could remain in a small undesirable area. Research into these two populations might conclude that the higher density population indicates a desirable resource when the reverse is true. Variation in home range between groups of animal species can highlight responses to variation in resources, climatic constraints and social needs at a variety of scales.

Large-scale variation can highlight different approaches to gross environmental variation in which populations of the species is found. Within population variation can highlight the seasonal response, or differences in behaviour between gender, age cohorts and social structure. Due to their diet, carnivores often have to roam large distances to fulfil their daily nutritional need. Depending on the distribution and abundance of available resources, carnivore societies exhibit a large degree of structural flexibility (Gittleman 1996) with home range size typically being negatively correlated to prey availability (Ramsauer 2006). For instance, in lion social systems, pride and foraging unit

sizes vary in responses to seasonal resources as observed in Kalahari lions which were observed foraging singly in extreme drought periods (Owens and Owens, 1984).

I used three measures of home range to investigate various drivers of lion ecology: extra-territorial exploration with 100% minimum convex polygons, territorial maintenance with 95% kernel density estimation, and core range minimum limit with a 50% kernel density estimate. Each range estimate was calculated monthly, using one GPS location per day for MCPs and all data for KDEs. I compare present ranges of CKGR lions with those from other populations. I also compare my measures to measures from CKGR lion research in the 1970s. I hypothesise that gross changes in the herbivore assemblage of the study area have resulted in changed territory and ranging patterns of lions, and therefore, the likely carrying capacity of lions in the CKGR.

4.2 Methods

4.2.1 Data Collection

Lions were located by radio signal and, when possible, visited monthly to download GPS and activity data and collect social data (pride size, group size, and cubs). As lions are largely nocturnal (Hayward and Slotow, 2009) and known to move little during daylight hours each collar was set to attempt a GPS location every 30 minutes between 5 pm and 8 am, and one location at midday. Extra locations were taken over a few days to estimate bias (e.g. 5 minute locations at night or hourly locations during the day for up to a week, 81,832 locations of this type were made, including some that were also 30 minute fixes) but were excluded from the main analyses. Failed or inaccurate fixes were removed, and a total of 173,826 locations from 6295 lion-days were gauged as suitably accurate for further analysis.

I used GPS location to estimate proximity and time spent together for the four male-female within-pride lion pairs. I plotted proximity and time spent together, and noted an inflexion at 400m at which percentage of time spent at any distance becomes unrelated to proximity. This figure agrees well with observations, where two interacting lions can be separated by two to three hundred metres for long periods, resting under separate vegetative cover and 400m was chosen as the distance at which lions were associating. Conflicting data was randomly removed from either lion on a day by day basis. I assumed that males and females from the same pride moved independently of each other when not associating. Visual inspection of movement patterns satisfied me that this was so.

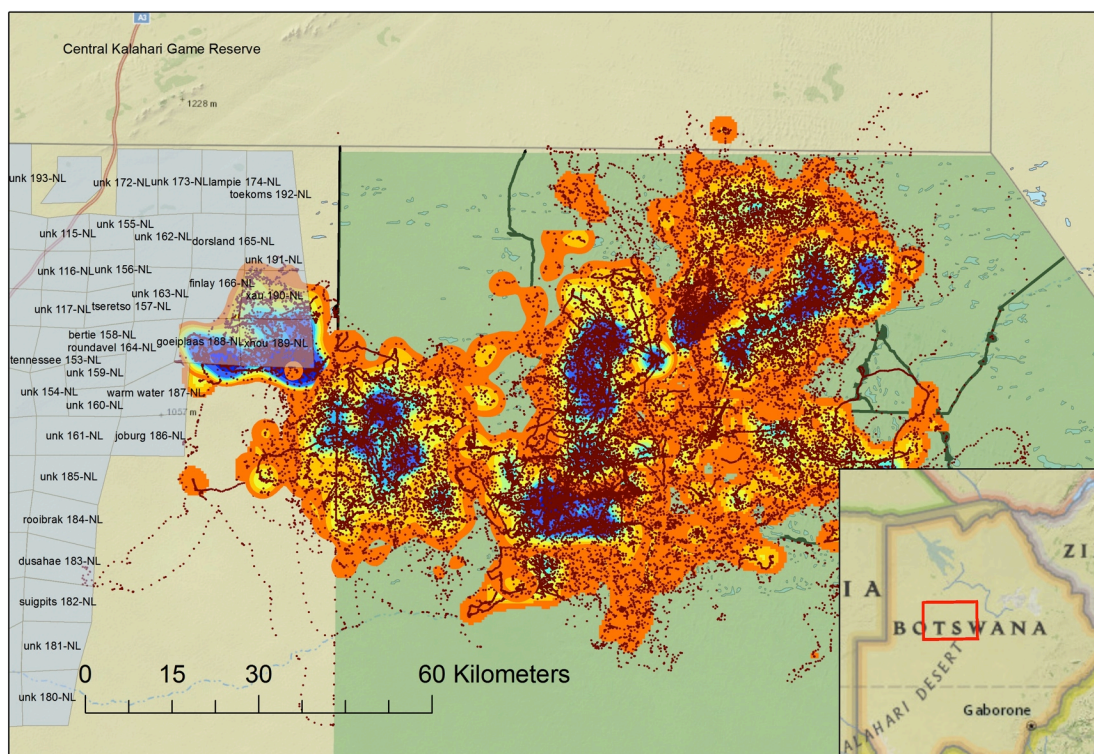


Figure 4-1 Map overlay of all individual lion kernel density estimates starting at a 95% utilization estimate (Orange through yellow to green and blue for highest estimated utilization). This map served to show the coverage of collected lion data. Some tracks are seen outside the kernel density estimates, indicating movements that the methodology considers outliers. Green shaded area is the CKGR, blue shaded polygons are freehold farms. Inset is Botswana, with view highlighted by red rectangle

4.2.2 Prey abundance estimates.

Monthly road transects of nine large herbivores to estimate changes in herbivore abundance and herd structure are taken from chapter 2. The monthly densities were estimated with a spatial model, such that densities could be estimated for each herbivore species each month in the area used by each study lion. To achieve this, density maps were constructed for each species, for each month, using the GIS software package, ArcGIS 10.0 (Environmental Systems Research Institute 2012). Data points for density are the mean value of the density within polygons representing the lion's home range (MCP) for that month. Estimates from months where herbivores were not explicitly counted were made from modelled data in similar months in other years (e.g. March 2009 was estimated from March 2010 data, April 2011 was estimated from the average of April 2009, and April 2010). The majority (84%) of lion home range estimates coincided with prey survey months. Analyses were repeated with those months removed to validate inference.

4.2.3 Climatic Data.

The Botswana Bureau of Meteorology provided monthly rainfall data from the three stations located at gates of the park at Xade, Matswere and Tsau

gates for the period of the study. The mean of these three values was used to estimate daily temperatures. Daily temperature maxima were estimated from sensors on several collars and the mean value used for all lions. This is reasonable as the total relief of the study area is less than 110m. Normalised Difference Vegetation Index (NDVI) data from the MODIS MYD13A collection were acquired from the USGS collection. (U.S. Geological Survey 2008-2012). The NDVI is retrieved from near daily imagery on-board NASA's Terra and Aqua satellites by the Moderate Resolution Imaging Spectroradiometer. By leveraging the strong absorption of red light but reflectance of near-infra-red by productive vegetation, the index has proven a useful measure of gross primary productivity (Bartlam-Brooks *et al.* 2013; Wiegand *et al.* 2008; Wittemyer 2011). During this study, the value of this unitless index varied from 2040 coinciding with dry periods with no surface water and brown vegetation, to a value of 4330 which correlated green vegetation and a productive time of year, see Figure 2-4. Herbivores are expected to respond strongly to vegetative productivity, and in time lions in turn will respond to variation herbivore distribution and abundance.

4.2.4 Data analysis

Home range values of two types were calculated each calendar month: minimum convex polygon (MCP) and kernel density estimate (KDE) using a Generalised Linear Mixed Effects Model with individual lion ID as the random effect (therefore home range for the month is the repeated measure). I used the utilisation distribution functions for MCP and KDE calculation in the Geospatial Modelling Environment v0.7.2.1 (www.spatialecology.com, 2012) software. This software in turn used R software v 2.12 (R Core Team 2013) for the mathematical operations and ArcGIS 10.1 (Environmental Systems Research Institute 2012) for spatial operations. I excluded some months where the lion collar was placed or removed in the middle of the month, or where fewer than 20 days of GPS fixes were recorded, as ranges would be unrepresentative. KDEs were made with all available 30 minute locations, while MCP were calculated with every available data point. The KDE is prone to an arbitrary selection of the smoothing parameter (bandwidth), denoted h (Hemson *et al.* 2005). Large values result in over-smoothing and incorporation of larger utilisation distributions, and there is some debate as to the best method for selecting h , based on given data. For this study I calculated h using the reference value, which can be found by minimizing the mean-integrated-square-error of the utilisation distribution fitted to the data.

After investigating histograms on an individual lion basis, home range estimates were normalised with square root transformations. Variables tested initially in the full model for home range models were the monthly means of rainfall and NDVI, monthly means of preferred prey density in two habitats, month of the year, mean NDVI for the region (U.S. Geological Survey 2008-2012), age of lion, average foraging group size, presence of cubs under 3 months, and under 12 months, full pride size, gender, and presence of a waterhole in usual range of lion. Incremental Area Analysis (Kenward, 1992, Hawyard, 2009) demonstrated that total home range size did not stabilise for the lions of the CKGR over the period monitored. Data were analysed using generalised linear mixed effects models (GLMMS) in the lme4 package in the R

program v 2.12 (R Core Team 2013), with individual lion included as a random term following a repeated measures strategy (Pinheiro & Bates 2000). Model selection was made by dropping terms from the model as indicated by Akaike's Information Criteria (AIC) values of nested models. That is terms were dropped if models were improved by $\Delta AIC > 2$.

4.3 Results

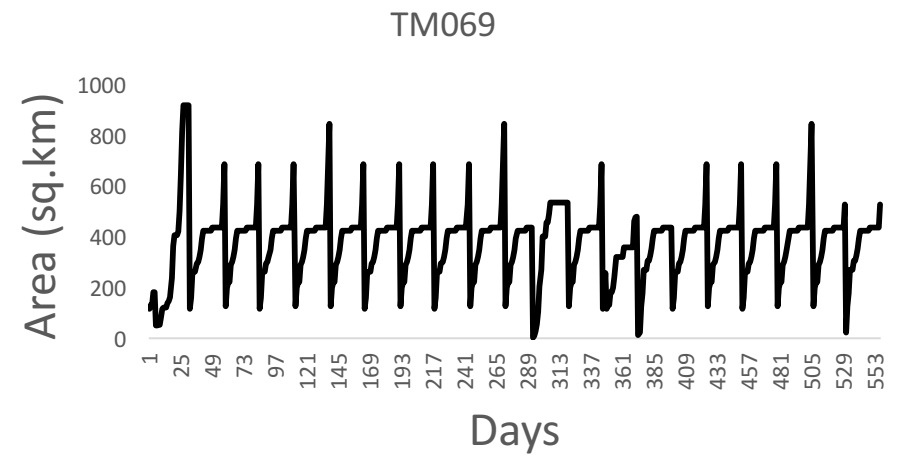
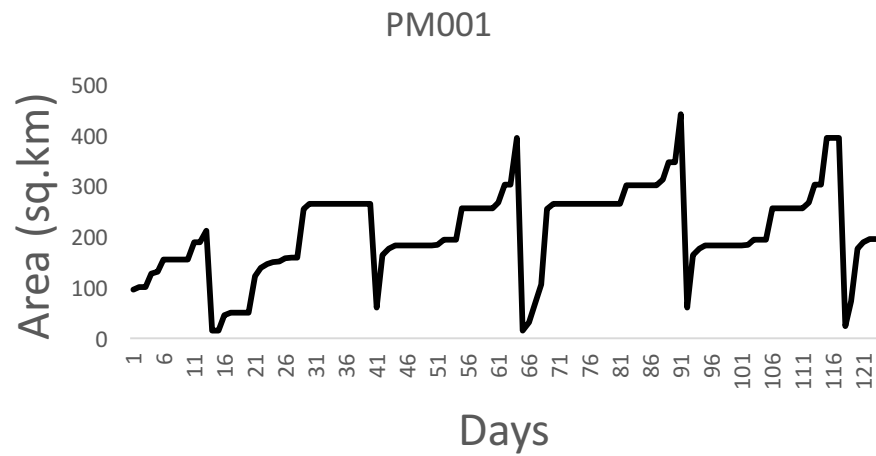
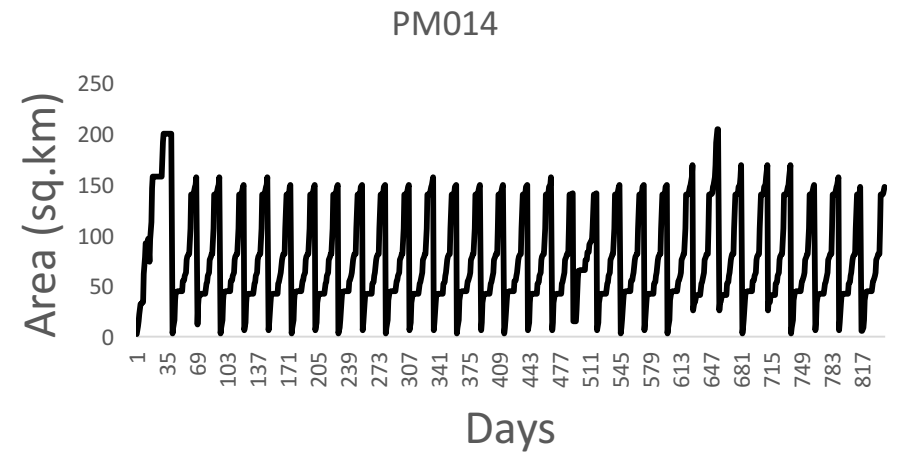
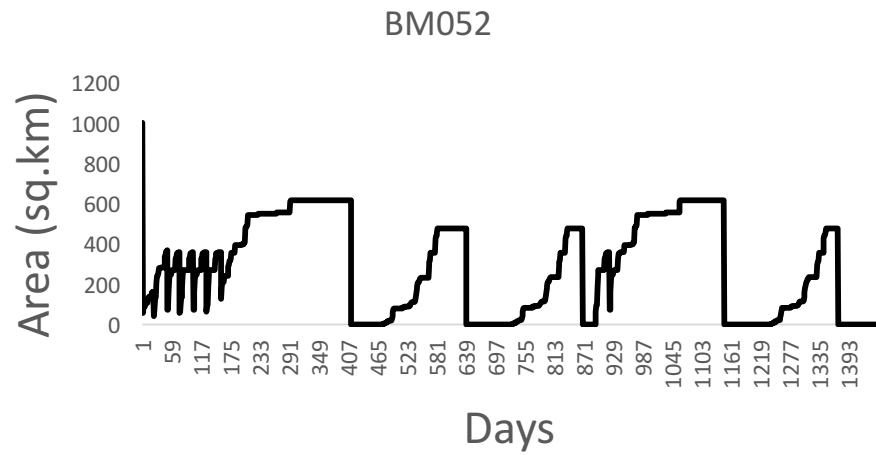
4.3.1 Home Ranges

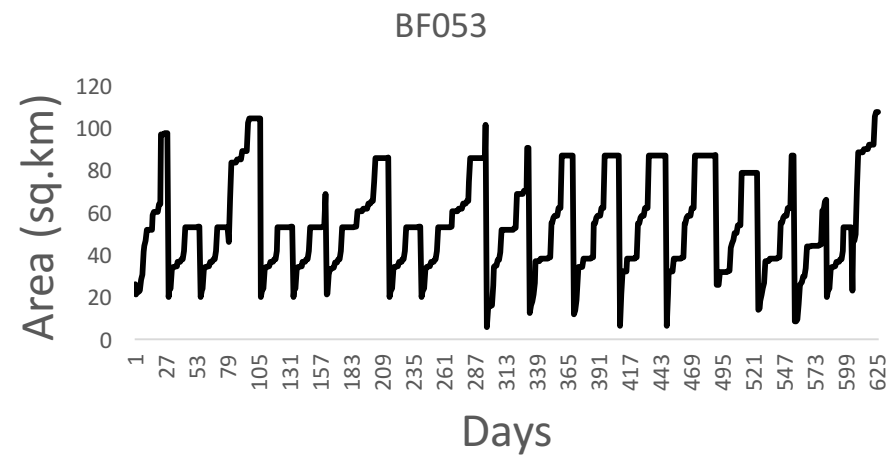
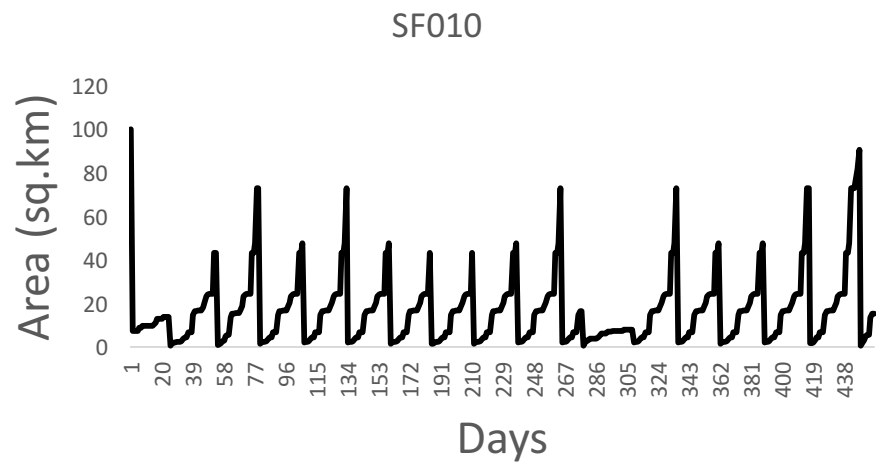
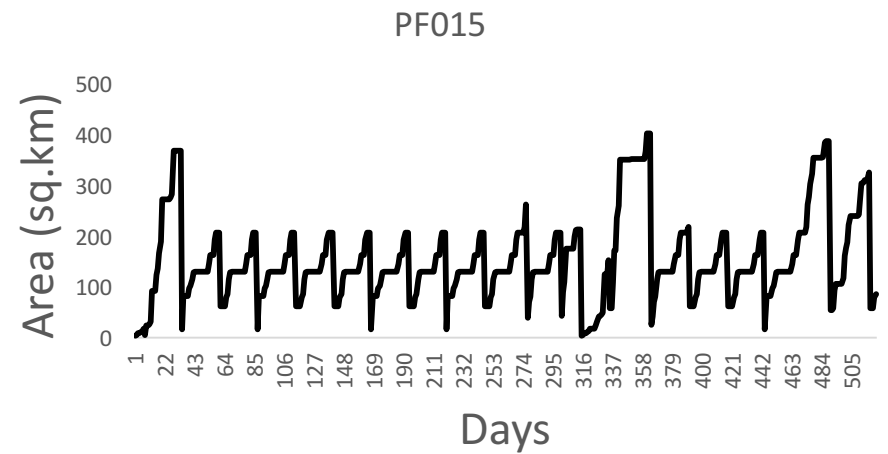
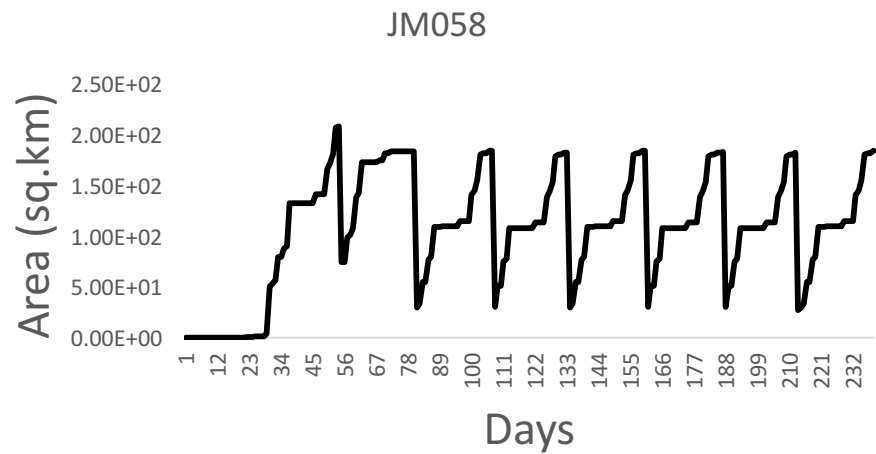
Monthly home ranges were calculated for 11 lions, 5 females and 6 males (see Table 4.1). The total home range (MCP and 2 KDE estimates) for most lions continued to increase even after considerable time (Figure 4.3 a-c) casting doubt on the long term fidelity to a small range over this period of time for any of the lions. This precluded an analysis on the total home range.

Mean monthly home range areas varied between lions. Male lions used large total areas (minimum convex polygon (MCP) areas of 2500.1 km^2 , S.E. = 212.7), and small core areas (95% kernel density estimates (KDEs) of 1303.7 km^2 , S.E. = 114.1, and 50% KDEs of 243.7 km^2 S.E. = 21.6). Female lions had smaller total ranges (MCP = 2020 km^2 , S.E. = 129.3) and utilised slightly larger core areas (95% KDE = 1317 km^2 , S.E. 206.2, 50% KDE = 293 km^2 , S.E. = 264.15), but these values were more variable.

Table 4.1 Summary of study lions and data collected. The number of days that each study lion was wearing any of the three collar types if shown, and various measures about the pride the lion belongs to such as pride size, average foraging group size, and the presence of a waterhole in the pride range. Home range values are total study values, and were not used in the modelling. The total number of usable GPS fixes is shown.

Lion	Sex	Age	Store on Board	Remote Download	Satellite	Pride Size	Avg Forage Group Size	Waterhole Within Range	MCP 100%	KDE 50%	KDE 95%	GPS Fixes	Mean DMD
			(Days wearing collar type)						(km ²)	(km ²)	(km ²)		(m)
SM009	M	13	244	0	349	9	1.5	N	1632.6	169.33	904	25491	11099
PM014	M	12	218	487	251	12	2.5	N	3316.3	318.1	1728	30458	9527
BM052	M	11	0	0	403	5	1.2	Y	3213.4	143.6	1038.5	18753	10830
JM058	M	9	0	0	243	12	2.5	N	919.6	165.5	793.3	12587	9799
JM059*	M	6	0	404	239	3	2	Y	4243.7	476.1	2513.5	26206	8221
TM068	M	9	0	0	532	11	2.5	Y	1674.8	189.3	844.8	24125	12081
SF010	F	9	214	201	319	5	3	N	2076.6	204.3	1176.1	28082	8563
JF012	F	10	428	401	0	12	3.5	N	1915.3	281.4	1126.3	27822	8350
HF013*	F	8	106	0	0	7	2.5	N	3085.1	740.5	3064.5	2546	8330
PF015	F	9	0	362	212	2	1	Y	1459.6	196.8	876.5	19732	7808
BF053	F	6	309	301	0	5	5	Y	1563.4	44.8	343.4	23762	5201





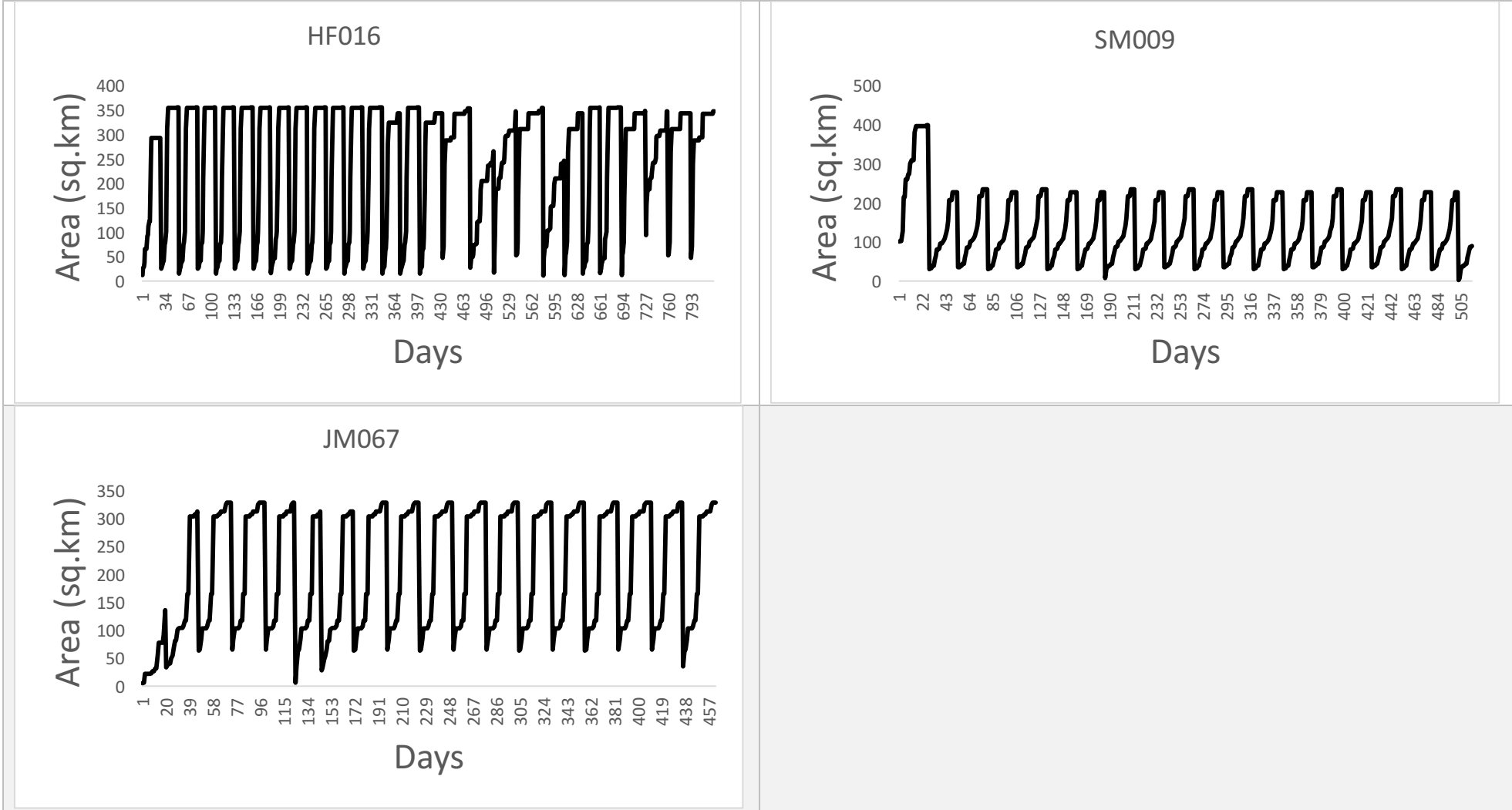


Figure 4-2 Home range sizes re calculated every month, showed some signs of consistency with many lions

4.3.2 Predictors of CKGR home ranges

There was no significant correlation with gender and any measure of utilisation distribution. Males had slightly smaller monthly mean estimates of 95% utilisation (mean 95% KDE = 484.7, SD = ± 349.2 km² and females of 385.1 (SD = ± 339.8) km² but did not differ significantly (ANOVA 95% KDE : $t_{(6)} = 1.853$, $P = 0.1133$). Of the five females, the three that belonged to prides had extremely similar mean ranges (386.2, 415.2 and 333.7 km²) and two that did not have prides had divergent ranges (106 and 1039 km²). These last two lionesses belonged to small family units with strategies that minimised exposure to danger. The lioness with the small range had young cubs and lived on a game farm with plenty of food near waterholes, but danger on nearby farms, whereas the lioness with the large range had adult cubs and lived in the game reserve but was regularly chased out of pride ranges by resident females.

Lions that hunted in larger groups had larger monthly home ranges (ANOVA 95% KDE : $t_{(6)} = 2.91$, $P = 0.027$) ranging from individuals with 228 km² to groups of 5 at 701.7 km². Range size was inversely correlated with rainfall (ANOVA 95% KDE : $t_{(197)} = -1.999$, $P = 0.047$), with ranges averaging 370 km² when there was no rain, to 233.7 km² in months with around 100mm of rainfall. All measures of utilisation distribution were positively correlated with monthly rainfall (ANOVA 95% KDE : $t_{(197)} = 1.98$, $P = 0.049$), ranging from 242.3 km² when the mean temperature was 18 °C to 417 km² when the mean temperature was 28 °C. Cubs played a role in home range size (ANOVA 95% KDE : $t_{(197)} = -3.6$, $P < 0.001$), but not when they were very young (ANOVA 95% KDE : $t_{(197)} = 0.96$, $P = 0.339$). Mean range size was 382.8 km² when there were no cubs and 191.7 km² with cubs.

Age of the lions had no significant correlation with range size, nor did some factors usually considered important in reducing lion conflict around the reserve, such as density and herd density of favoured prey species and the presence of waterholes.

Table 4.2 Best model results for the Minimum Convex Polygon GLMM. Significance column legend: * <0.05, ** <0.01, ***<0.001. Brackets show the base value for factor type variates.

Term	Value	Std.Error	DF	t-value	p-value	Sig.
(Intercept)	4.482	1.605	181	2.792	0.006	**
Gender (Male)	0.826	0.252	2	3.274	0.082	.
Mean Forage Group Size	0.519	0.199	2	2.605	0.121	
Mean Rain (mm)	-0.006	0.002	181	-2.597	0.010	*
Temperature (°C)	0.048	0.027	181	1.792	0.075	.
Young cubs (0 = no cubs under 3 months)	-0.779	0.427	181	-1.823	0.070	.

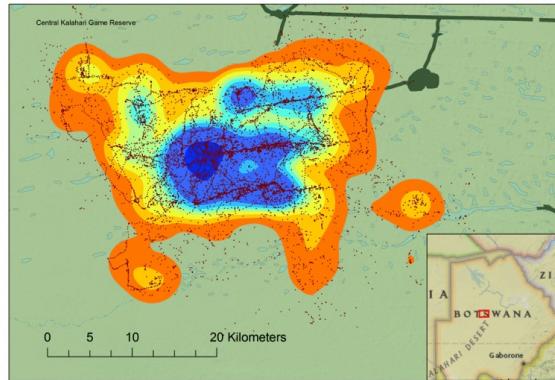
Table 4.3 Best model results for the 95% Kernel Density Estimate GLMM. Significance column legend: * <0.05, ** <0.01, ***<0.001.

Term	Value	Std.Error	DF	t-value	p-value	Sig.
(Intercept)	4.345	0.792	197	5.485	0.000	***
Gender (0 = Male)	0.331	0.178	6	1.853	0.113	
Mean Forage Group Size	0.280	0.096	6	2.908	0.027	*
Mean Rain (mm)	-0.005	0.002	197	-1.999	0.047	*
Temperature (°C.)	0.054	0.027	197	1.981	0.049	*
Large cubs (0 = no cubs <1year)	-0.694	0.193	197	-3.598	0.000	***

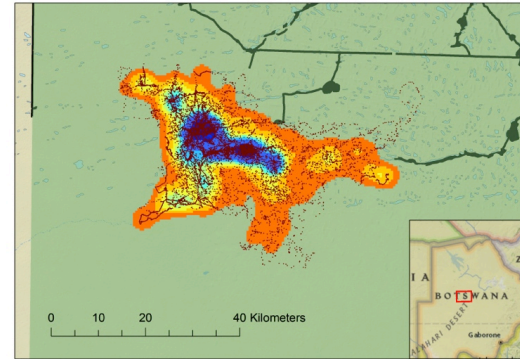
Table 4.4 Best model results for the 50% Kernel Density Estimate GLMM. Significance column legend: * <0.05, ** <0.01, ***<0.001.

Term	Value	Std.Error	DF	t-value	p-value	Sig.
(Intercept)	3.858	3.029	196	1.274	0.204	
Mean Rain (mm)	-0.005	0.002	196	-2.192	0.030	*
Temperature (°C)	0.080	0.031	196	2.564	0.011	*
Large cubs (0 = no cubs <1year)	-0.595	0.451	196	-1.318	0.189	
Young cubs (0 = no cubs <3 months)	-0.452	0.361	196	-1.254	0.211	

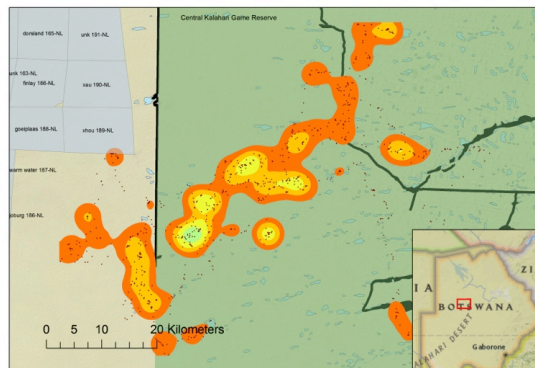
Figure 4-3 Individual kernel density estimates for CKGR lions. The orange outline is the 95% estimate, light blue coincides with the beginning of the 50% estimate. Inset is Botswana, with view highlighted by red rectangle



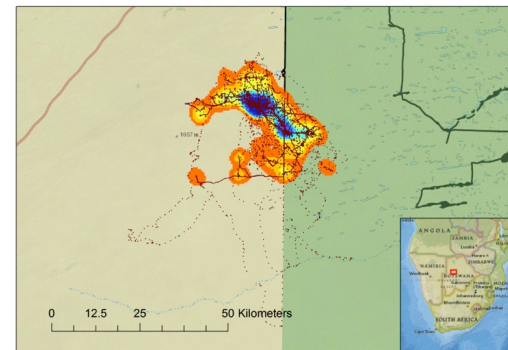
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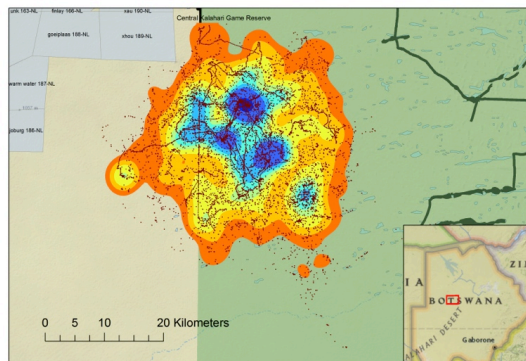
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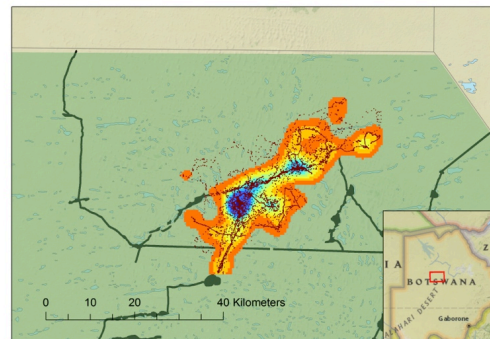
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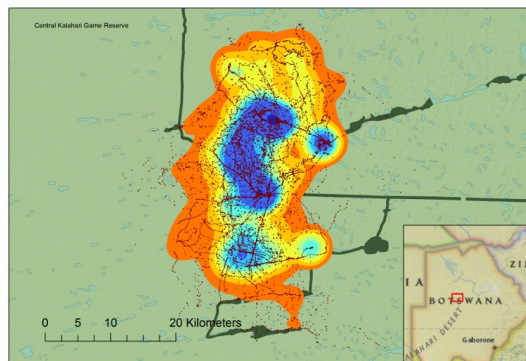
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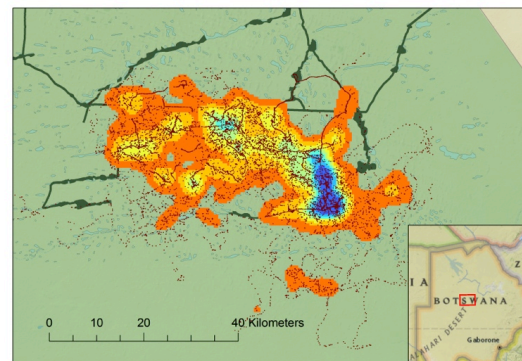
Lioness HF012



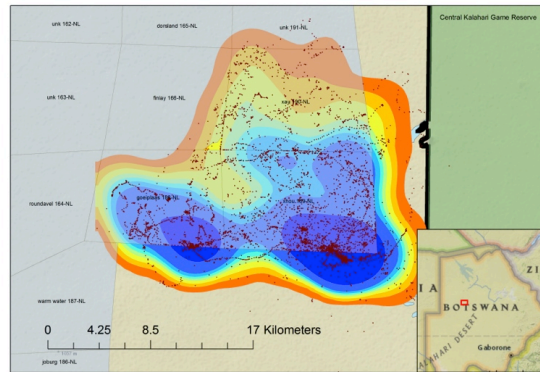
Lion JM058



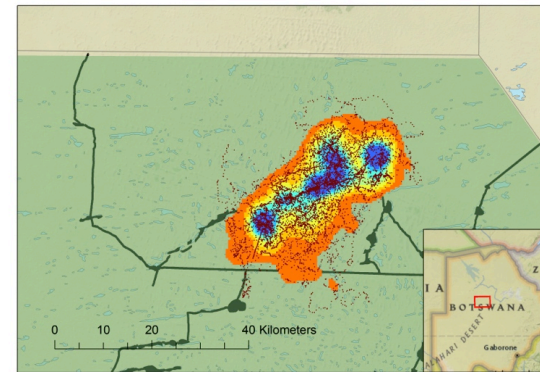
Lion JM068



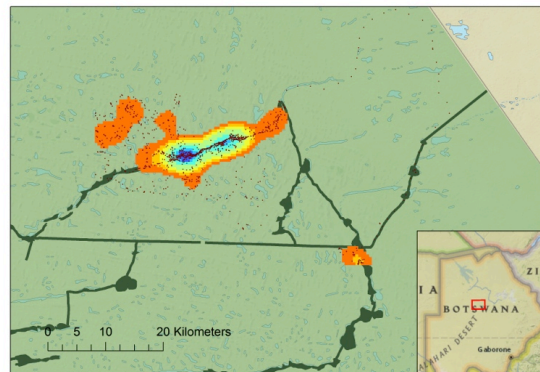
Lion TM069



Lioness BF053



Lioness PF015



Lion PM001

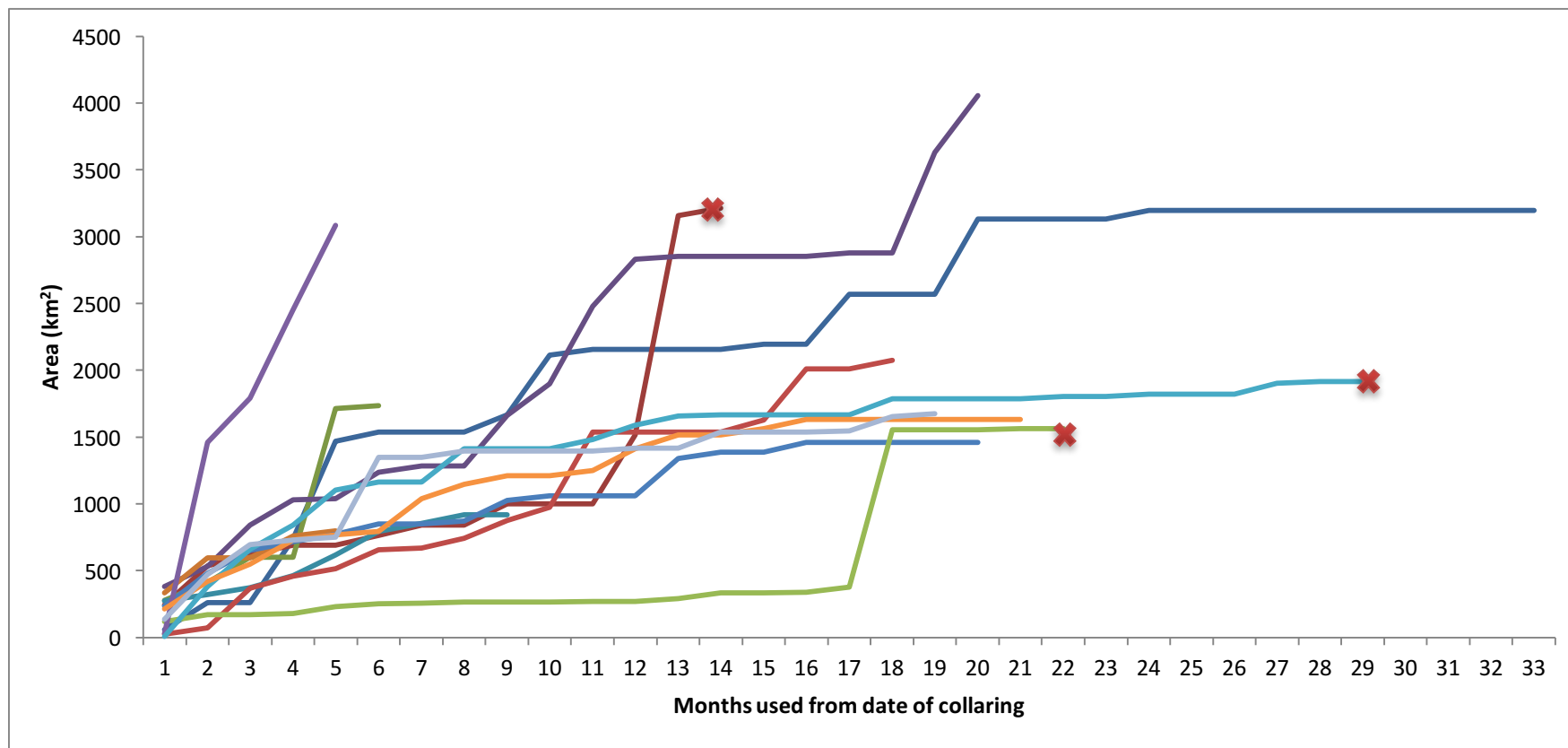


Figure 4-4 Cumulative MCP area over the time that lions were wearing their collars. There are large jumps for many lions after a long period of stability bringing into question if an asymptotic range had been reached for any lions. The nature of the MCP calculation is such that it can only increase in size, and only if GPS fixes are recorded outside previous polygons. Crosses indicate death by farmer retaliation. Two of three lions that were shot, were shot soon after significantly expanding their range.

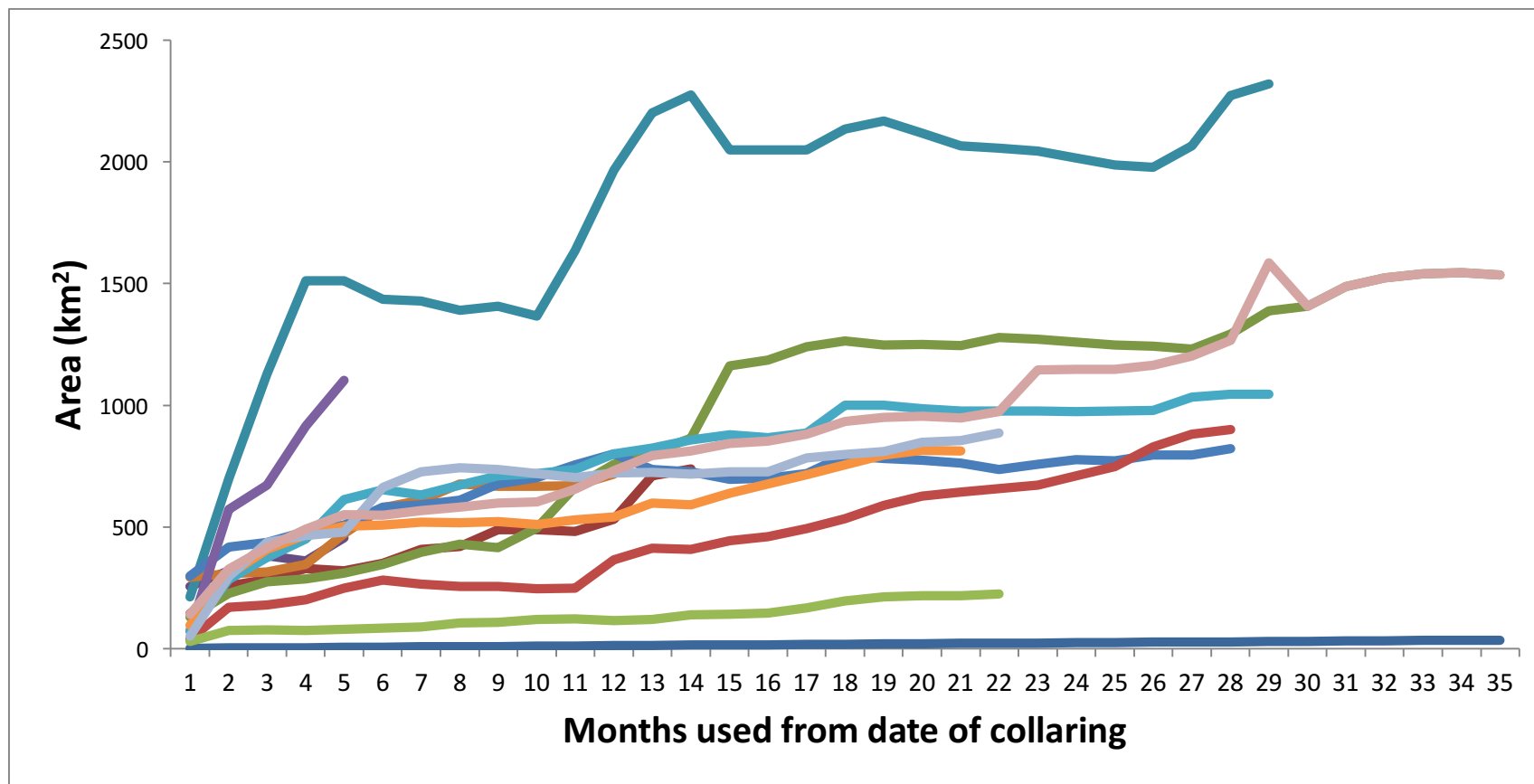


Figure 4-5 Cumulative 95% KDE for individual lions. The nature of the KDE means that the estimate will sometimes shrink as more points are added, but the trend to continued increased size in the estimate is clear.

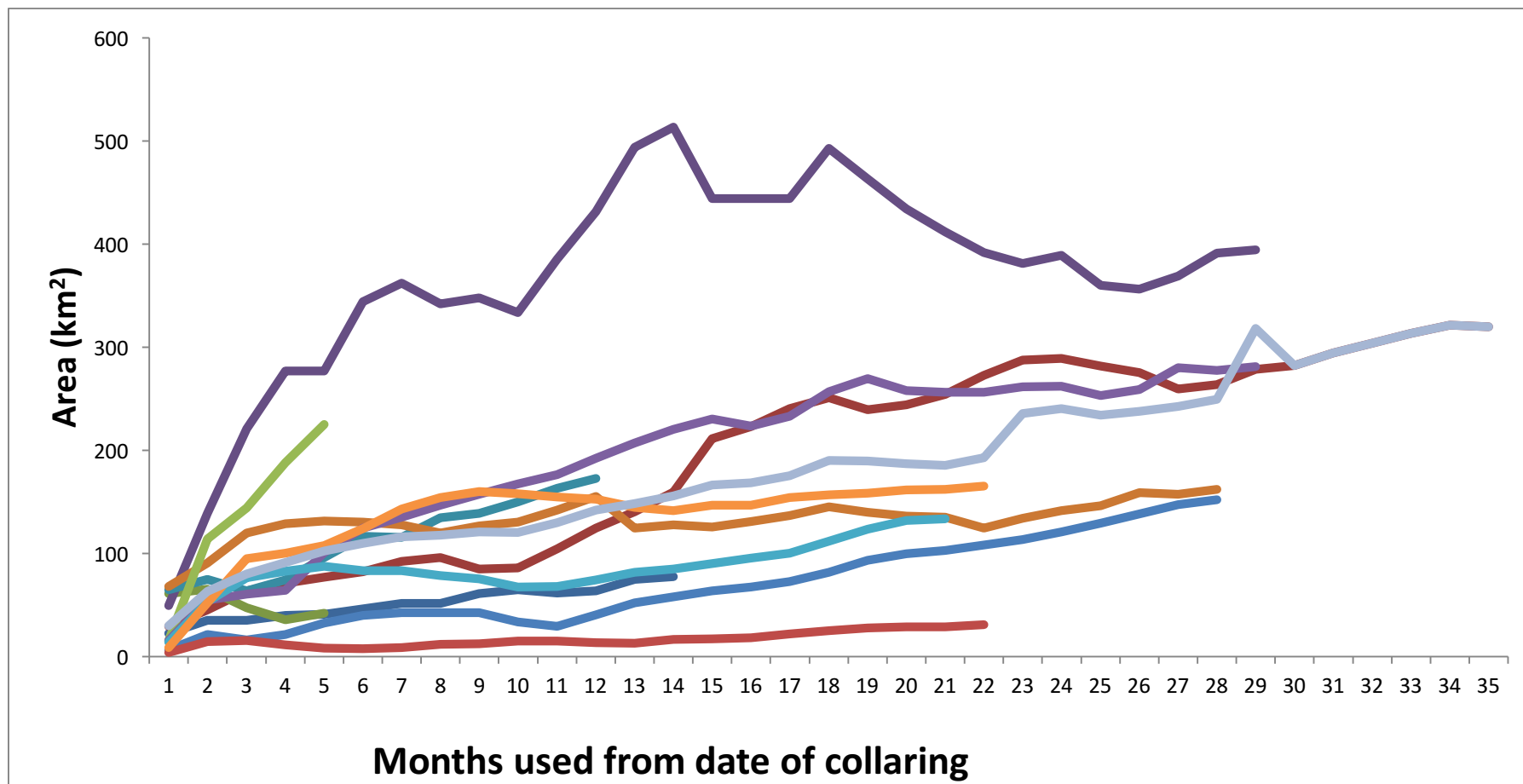


Figure 4-6 Cumulative 50% KDE values for individual lions indicated that ranges in CKGR lions were unstable and continued to grow.

Table 4.5 Comparisons of area estimates of utilisation distributions with previous research, and research on populations from elsewhere. Namib Desert, South Kalahari and Kunene regions are more arid.

		50% KDE $\pm$ S.D. (km ²)	95 % KDE $\pm$ S.D. (km ²)	100% MCP $\pm$ S.D. (km ²)
CKGR lions	Owens and Owens, 1984			~400
CKGR Males	This study	243.7 $\pm$ 129.7	1303.7 $\pm$ 684.8	2500.1 $\pm$ 1276.5
CKGR Females		293.6 $\pm$ 264.2	1317.4 $\pm$ 1031	2020 $\pm$ 646.4
Namibia Males	Stander, 2003,2009		2814 $\pm$ 2264	5498 $\pm$ 3701
Namibia females	"		818 $\pm$ 409	2398 $\pm$ 1135
Serengeti	"			60-220
Makgadikgadi	Woodroffe and Ginsberg, 1998			725
Chobe	Hemson, 2008			2152
South Kalahari	Funston, 2001			2823
Kunene Region	Stander, 2006			7337

4.4 Discussion

Until recently, studies on the home ranges of lions and other predators have relied on occasional locations via VHF radio collars. Researchers assumed that MCP home ranges based on these locations were not likely to miss outliers where an animal spends a short amount of time outside the normal range (both by virtue of the time interval between detections and that being outside of the expected range can greatly reduce the detectability of animals by radio tracking). However, a recent study with high frequency GPS locations has indicated that a sharp drop off in MCP estimation occurs as the time between locations increases (Mills *et al.* 2006), indicating that reducing the sampling intensity greatly effects home range estimation of fast moving animals. Our very high frequency GPS collection of positional data provides a clear look at how lions behave over short time scales, promising to detect farm transgressions and is the first attempt to understand drivers of lion behaviour on Central Kalahari Game Reserve that may result in livestock predation and losses of lions. Missing even just a few days of locations would greatly affect the estimated MCP home range, indicating the large contribution of unusual behaviour to large space use and ultimately exposure to human activity. In a VHF study, the extreme values are the most likely to be missed by researchers. Even so, direct observations I made on study lions at extreme distances from their usual range were often missed as I searched for them on the ground and occurred when the lions were at extreme distances from their usual range; possibly the most interesting time to observe them. Satellite collars provided daily positions and greatly increased the rate of direct observation of widely dispersed lions. The CKGR lions regularly explored into new territory, a behaviour that brought many onto farmlands. This is very interesting behaviour, as resident lions in other locations display greater site fidelity and more consistent ranges (Roxburgh 2008) and are known to usually explore when they are not part of a pride.

While home range was not correlated with traditional measures of season, there was some climatic influence of rainfall and temperature. The CKGR experiences high rainfall from October to April, and the data suggests that lions are more reliant on a small core range for regular access to water and meeting pride mates and that the dry period is associated with expanding ranges. There are two likely contributors to range expansion - the availability of surface water throughout the study area for fresh drinking water would allow animals to expand and move easily and the structure, and variation in density and availability of prey resources. I attempted to explain this relationship beyond greenness using measures concerning prey but only found that group sizes of the lions' preferred prey influenced range size. Of large kills that lions spent 4 or more hours to consume, 82% were gemsbok (see Chapter 6). Gemsbok group sizes were complex and more predictable in pan habitats, but lions did not respond directly to variation in group size, or density of herds, unlike in other studies (Funston 2011; Ikanda 2005. ; Loveridge *et al.* 2009). Between populations, prey density and availability plays a significant role in lion home ranges (Carbone & Gittleman 2002; Gittleman & Harvey 1982), but it is interesting to note that changes in prey densities as estimated in this study plays little role in explaining variation in home range of CKGR lions.

Lions reduce their ranges in the wet season. Rainfall is almost completely absent from May to September when lions increased their core range and the exploration of the extremes of their ranges, and were moving further per day. The wet green season has many complex effects that I was unable to capture with other measures, such as the presence of surface water for drinking, taller thicker grasses and shrubs which may help or hinder foraging and the movement or aggregation of herbivores. Larger ranges should coincide with more livestock discovery, predation and greater losses of lions to livestock conflict. My results indicate that CKGR lions have the greatest exposure during the wet months. Although territory size is related to energy expenditure, the energy usually comes from defending it and not patrolling it since range size did not vary with daily distances moved. In low lion density areas like the Central Kalahari, fights are uncommon and large and small territories can be maintained expending similar amounts of energy (Alberts *et al.* 1996). Observed males in the CKGR employed a mate guarding strategy that resulted in greatly different movement patterns depending on pride structure. Male BM052 and male SM009 guarded three groups of females that were regularly tens of kilometres apart. These males would cover the distances to search and check the status of each group of females regularly, sometimes covering 40km or more in a day, and all groups of females in 5-8 days. Another lion pair in the Tau Pan area, guarded only two females and rarely walked further than 10km from the females or the waterhole at Tau Pan. Thus the mate guarding strategy resulted in greatly differing movements and energetic outputs. Daily movement distances were not associated with home range size, indicating that lions were able to maintain large ranges without restrictions by energetics.

Behaviour usually considered as outlying becomes of utmost importance when the consequences are lethal and the animal in question is a vulnerable, slow breeding animal, like the African Lion. In October 2011, maximum daytime temperature exceeded 46 degrees Celsius for 6 consecutive days. The Passarge Valley lions left their usual range to find water. This happened to be during a period when two male cohorts of two lions each were competing for the

attention of the females. While the resident cohort monopolised any females in heat, the intruder cohort spent time when possible with other females of the pride. Fights were rare but very physical, the intruders seeming to try to avoid confrontation. Prior to this the Passarge Valley pride and the two competing male cohorts had survived comfortably without drinking water for around four months and in the previous two years had survived the entire 6-7 month dry period without drinking water. During the heat wave, all seven females and the two intruders walked south to a new waterhole maintained by a private lodge at Tau Pan. This waterhole is at the centre of a neighbouring small prides' range who aggressively defended the waterhole and left one Passarge Valley lioness seriously injured, unable to follow the hunt or to eat for eight days. The original male pair walked north and left the reserve for the first time during our observations of them and found waterholes in a game farm to the north of the reserve. Although the game farms tolerated the lions, their cattle farming neighbours did not, as most are known to kill lions to protect cattle. I estimate that less than half the lion prides in the study area have access to year round drinking water. This becomes an issue only in poor rainfall years or during extreme heat and may result in an increase in conflict with both humans and with prides defending water holes. These rare and extreme events could not be captured by a mean modelling analysis, but the anecdotal evidence is noteworthy.

Male lions staunchly defend access to females (Bertram 1975; Borge 1998; Smuts *et al.* 1978), marking their range with scent and loud vocalisations (Funston & Mills 1997). When lions die, their range is usually quickly invaded by neighbours seeking access to females (Schaller, 1972). The male SM009 died of natural causes around July 20th 2011. Two of his neighbours, both collared, explored most of his range for the first time in several expeditions in the two months after his death. New unknown males were also seen in the area and it is likely that some were missed. While I expected nomadic unattached lions to be interested in undefended territories, it was unexpected to see large scale exploration by neighbouring residents for such long periods of time. If this had been a lion whose range extended to farmland, the effect of removing the lion to protect cattle would increase exposure to lions and predation of cattle. This exact result was observed in January 2010 when lion BM052 was shot for killing cows in a farm to the west of the CKGR. After this, the numbers of male lions in the area dramatically increased; the farmer claims to have lost 49 cattle in next 3 months, in contrast to the 3 cattle in the 17 months prior during BM052s residency, all killed by this lion. The farmer claims that the situation is "getting worse" and shot an undisclosed number of the intruding lions. I propose an alternative explanation. A resident male lion that eats an occasional cow may be a better protection against cattle loss than lethal control because he keeps other lions away. BM052 may even have learned to avoid eating cattle as he was regularly scared off the carcass by farmers.

I compared home ranges of lions studied in the same location in the 1970s by Owens and Owens, who described two prides with small consistent territorial ranges over a four year period. They did not disclose values of ranges and the study was based on VHF detections. The researchers claimed that home ranges were small, and only in the worst drought year did the herbivore prey density drop to a level where the lion groups broke up, fissioning into smaller groups and roaming over areas "10 times larger than normal",

comparable to the current CKGR lion ranges (1500 square miles $\approx$ 3884 square kilometres). Owens and Owens (1984a) argue that wildlife fences surrounding the reserve have cut off important migrations causing a massive decline in the wildebeest population. Estimates of prior numbers are poor, but are usually around 100,000-200,000 wildebeest; the wildebeest population is less than 1000 today (Chapter 2). It seems that the CKGR lions have settled into a stable pride range much larger than prior to fencing and similar to bad drought years. This is further evidence of the destabilising effects on the wildlife assemblage of the CKGR. The effects on rangeland and other herbivores is unknown, but complaints by farmers of increased bush encroachment, rangeland degradation, lower stocking rates (on some farms to a quarter of historical stocking rates (Moleele & Perkins. 1998) and personal communication with farmers and DWNP officers) and increased predation are common since the 1980s. Hemson *et al.* (2009) demonstrated that lions prefer wildlife to livestock until the ratio of livestock to wild game is quite large. Large wildebeest herds would provide a buffer to predation on livestock and allow other wild herbivores to recover from predation possibly increasing their numbers too.

Chapter 5 Factors Influencing Daily Movement Distances of Central Kalahari Lions (*Panthera leo Linnaeus*)

Chapter Summary

Variation in daily movement distances by large carnivores can provide insights into their resource requirements, responses and management options for resolution of conflict with humans. I used high frequency GPS tracking data from 11 lions in the Central Kalahari Game Reserve to estimate the distances moved by lions and investigated factors that influence the mean daily movement and the extreme daily movement distances. During months of high herbivore group densities, lions travelled further on a daily basis (mean daily movement distance of 7,160 m at lowest density, to 8,616 m at the highest density), males on average travelled significantly further each day than females (mean of 10,071.6m per day for males, sd. = 7099.4, maximum 48,462m and a mean of 7,633.6m per day for females, sd= 5,069.3m, maximum 29,470m). Females moved similar distances daily even while supporting cubs under 3 months old. Temperature was negatively correlated with distances walked, while low temperatures correlated with higher incidence of extreme distances. Aspects of prey also influenced daily movement distances, with lions walking further on average when the density of herds of prey species increased and when the preferred prey species was more abundant, and slightly less per day as rainfall increased. Some of these results were unexpected and provide reserve managers with information on when to expect higher incidences of livestock predation.

5.1 Introduction

As human activity reduces the living space for wildlife around the planet, national parks and other protected areas become islands of conservation (Wilcox & Murphy 1985). Increasingly the viability of threatened populations relies on detrimental processes working at the boundaries of these protected areas. These include habitat edge effects (Shivik 2006); the need for further space to escape from fire, floods or droughts; interruption of gene flow between fragmented sub-populations (Olivier *et al.* 2009; Trinkel *et al.* 2008); transmission of diseases to and from livestock and other domestic animals (Woodroffe *et al.* 2004) and; direct impacts from humans including poaching of wildlife and retaliation for crop and livestock loss (Gusset *et al.* 2009; Kahler *et al.* 2013) . The 'boundary model' suggests that exposure of a reserve is a major determinant of its vulnerability (Schonewald-Cox & Bayless 1986).. This model acknowledges that the space requirements of animals will expose them to external processes more often in smaller reserves, or reserves with greater edge to area ratios, like long thin reserves, and that effectiveness of reserve protection is more dependent upon what happens at the boundary than any internal processes alone

The size of a reserve or the length of its boundary are not the only indicators of the exposure of wildlife populations to detrimental processes,

mainly because wildlife often move daily or seasonally in response to resource fluctuations. In particular the wildlife of arid biomes have larger ranges, move further on a daily basis, may be migratory and thus may have an increased exposure despite the small perimeter to area ratios of large conservation areas. In Africa key species with a significant contribution to the biological processes are often very large, (McNaughton *et al.* 1988). Large animals are at an increased risk of extinction due to longer time required for reproductive success, large home range requirements and small litter sizes (Cardillo 2003). As technology and human population pressure allow greater use of areas adjacent to protected areas, the study of conflict across these boundaries is gaining importance. Essential for understanding the viability of populations in these circumstances is knowledge of the way animals move through their landscape and how their movements change in response to changes in climate, density and important resources. These characteristics influence the portion of the population that experiences boundary effects, and how often they may transgress them and encounter harmful interactions with humans. In my aim to better inform management in techniques to reduce lion-livestock conflict, an investigation of the factors affecting how animals use the landscape is vital.

Measures of daily movement distance (DMD) provide an important perspective on the factors that limit animals. For example, after a reduction in their density due to tuberculosis, the DMD of red foxes (*Vulpes vulpes*) was shown to be a more consistent measure than range when studying their foraging and social requirements (Soulsbury *et al.* 2007). Foxes responded to low density from a disease outbreak by increasing their range considerably although there were no changes in resources, while moving similar distances per day. When densities returned to normal, ranges returned to normal. The interpretation of these data was that foxes filled territory gaps in the short term while waiting for them to be occupied by familiar (related) foxes rather than strangers, at almost no extra energetic cost. Increasing range did not reflect increasing energetic demand, but rather a social strategy. DMD often remains constant through a wide variety of home range sizes. Animals seem to be able to defend varying range sizes without varying energy expenditure significantly. Conversely, variation in DMD is a more dependable indicator of the ecological limitations facing animals. For example, badgers (*Meles meles*) move further each day when earthworm abundance is lower (Kowalczyk *et al.* 2006 ; Soulsbury *et al.* 2007)

I studied the daily movements of individual lions in a population in the northern 20% of the Central Kalahari Game Reserve (CKGR) with the aim of improving understanding of the drivers of conflict with cattle farmers near the reserve's edge. While average density across Africa is low, humans in conflict with lions along boundaries of protected areas of greatest conservation value naturally experience them at high densities (Frank *et al.* 2006; Schiess-Meier *et al.* 2007). Data on population dynamics and space use are required in order to identify which section of the northern Kalahari population is most at risk from lethal conflict with farmers (Celesia *et al.* 2009) and to identify processes that will maximise conservation outcomes. In this chapter I use the daily movement distances of Kalahari lions to identify the likely factors affecting their movements, in order to better understand when and why some lions leave the reserve and come into conflict with farmers.

5.2 Methods

5.2.1 Study Area

The study was conducted in the 9911 square kilometre area of the northern part of the Central Kalahari Game Reserve and surrounding farms (See Figure 5.1).

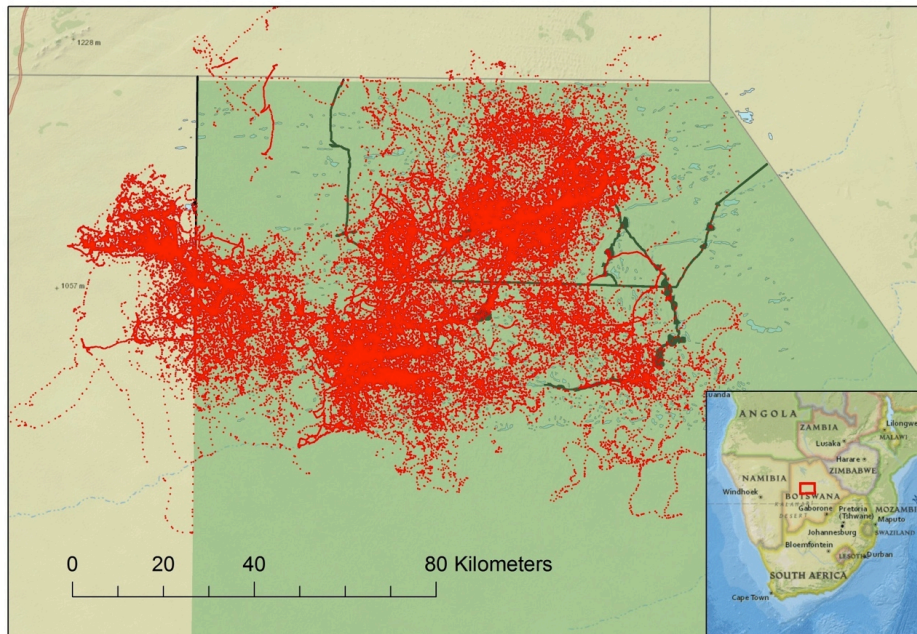


Figure 5-1 Map of the study area, showing collected GPS data points from lions used to calculate daily movement distances, across the northern part of the Central Kalahari Game Reserve. Inset is southern Africa. The game reserve (green) and various types of cattle and game farms, including farm buffer zones (beige) are shown.

5.2.2 Climatic Data.

The Botswana Bureau of Meteorology provided monthly rainfall data for the period of the study from the three closest stations, Xade, Matswere and Tsau gates on the borders of the game reserve, and a mean of these three values was used as the rainfall estimate. Daily temperature maxima were estimated from sensors on several collars, and the mean value used for all lions. This is reasonable as the total relief of the study area is less than 110m. Brightness from moonlight was calculated for each half hour of each night over the study period following Krisciunas and Schaefer (1991). The highest value for that night was included as a fixed term in the analyses.

5.2.3 Prey abundance estimates as co-variates for daily movement distance.

5.2.3.1 Herbivore density and Herd Density

In an environment with patchy resources, patch density can be of greater influence on movement dynamics and dispersal than the strict density of

resources (Hein *et al.* 2004; Knegta *et al.* 2007) and the impact of herbivore patch density is little understood with respect to carnivores. Territorial behaviour is likely to increase the importance of patch density. I modelled lion movement distances with respect to both prey density (animals per square kilometre) and prey herd density (groups of animals per square kilometre - patch density). Herbivore density in the landscape was modelled on a per species basis, and herd density was modelled as all possible herds of species in a lion's preferred weight range in the landscape. Monthly herbivore transects of large diurnal herbivores typically hunted by lions were counted along seven daily 60km road transects, described Chapter 2. Values for density and herd density were taken from the prediction maps from the spatial Generalised Linear Model (GLM) described there. I estimated the density of each herbivore species, and herd density species, specifically for each lion based on range for a specific month by estimating mean herbivore density from monthly transects within the lions home range polygon. Estimates from months where herbivores were not explicitly counted were made from data modelled in similar months in other years (e.g. March 2009 was estimated from March 2010 data, April 2011 was estimated from the average of April 2009, and April 2010). Analysis was repeated excluding these data to determine the impact on our conclusions. The majority of GPS data (>65%) collected fell in the months when herbivore density was directly surveyed, and running the analyses again showed that the interpretation of the main effects were unaffected by estimating densities from non-surveyed months.

5.2.3.2 Remotely sensed vegetation productivity

Vegetation productivity was estimated from freely available normalised difference vegetation index imagery (NDVI) courtesy of the USGS (U.S. Geological Survey 2008-2012). The NDVI image is calculated every 16 days using satellite spectral reflectance measurements and therefore varied on this time scale. The NDVI is the ratio of the values of near-infra red without visible light to the near infra-red plus visible light and is strongly correlated with vegetative biomass (Sellers 1985). Mean NDVI was calculated for the whole study area for a whole month from the image as close to the prey transect survey of the month as possible, using the Zonal Statistics tool in ArcGIS 10.1 (ESRI 2011, Redlands, California). There was much greater variation between months than spatially within a month, and months in a similar season were likewise very similar. This dataset acknowledges that rainfall has a dynamic and lagged effect on vegetation greenness and surface water availability that may be difficult to measure otherwise.

5.2.4 Lion movement data collection

I regularly located the eleven study lions (see Chapter 3) by radio signal and, when possible, visited monthly to download GPS and activity data. I collected social and body condition data including pride size, group size, number and status of cubs and a visual condition estimate such as belly size (Potgieter & Davies-Mostert 2012). As lions are largely nocturnal and known to often not move much outside daylight hours (Schaller 1972), and battery life of collars is a limiting concern, each collar was set to attempt a GPS location every

30 minutes between 5 pm and 8 am, and one location at midday. Extra locations were regularly taken over a few days to estimate bias (e.g. 5 minute locations at night or hourly locations during the day for up to a week, 81,832 locations of this type were made, including some that were also 30 minute fixes) but the extra locations were excluded from the main analyses. Failed or inaccurate fixes were removed, and a total of 173,826 locations from 6295 lion-days were used for the DMD analysis. Final distances per day were the sum of the straight line distances between GPS points.

I used GPS location to estimate proximity and time spent together for the four male-female within-pride lion pairings. I plotted proximity and time spent together, and noted an inflexion at 400m at which the percentage of time spent at any distance becomes unrelated to proximity. This figure agrees well with observations, where two associating lions can be separated by up to three hundred metres for long periods, usually daytime resting under the sparse vegetative cover. To avoid duplication, data was randomly removed from either lion for days on which they associated. I assume that males and females from the same pride moved independently of each other when not associating. These data formed the basis of comparative analyses.

5.2.5 Data analysis

Instantaneous GPS position data of lions were converted to UTM notation using ArcGIS 10.1 (ESRI 2011, Redlands, California). Distances moved by the lion were calculated in metres using simple Pythagorean geometry in two dimensions, ignoring altitude as differences in altitude between readings were less than mean GPS error. Daily movement distances (DMD's) were calculated as the sum of distances from midday to midday the following day, referenced by the earlier date. Altitude was ignored as the total variation in relief of the study area is less than 35 metres, and only 6 metres across most lion ranges.

Multiple regression was conducted on non-correlating, transformed variables to determine which factors influenced the dependent variable - daily movement distances of the lion, estimating parameters by restricted maximum likelihood in the lme4 package in the R program (R 3.0.2, R Core Development Team, 2013) with individual lion included as a random term following a repeated measures methodology (Pinheiro & Bates 2000). Multi-model inference was used to explore multiple candidate models and estimate parameter importance from inclusion in high-ranked models, ranked by Akaike's Information Criteria (AIC) (Burnham & Anderson 2002). Models with the lowest AIC were deemed more informative, however models with differences in AIC less than 2 are not considered significantly better.

The intention of the modelling exercise was to uncover factors correlated with variation in lion daily movement distances. Independent terms modelled were at the daily level for each lion: females with small cubs (under 3 months old), females with dependent sub-adults (under 2 years old), spatial X and Y terms; at the lion level: age and gender; at the group level: pride size, foraging group size and the presence of a waterhole in the pride territory; at the monthly level: rainfall, mean temperature and vegetation production; and at the month by lion level: mean density estimates for each of 10 herbivores and density of

large herbivore groups. Lion characteristics were used to estimate age by an experienced vet when in hand, or during monthly field observations.

An investigation of the autocorrelation functions revealed substantial temporal autocorrelation, DMD at day_t was correlated by 39% with day_{t+1} and this dropped to 4% on the second and lower on subsequent days. I tested the assumptions of models using all the data and then with every second row of data removed to test the effects of the temporal auto-correlation on interpretation of coefficients.

Two models were used to investigate factors influencing lion daily movement distance. A linear regression model looking at mean daily movement distances was normalised using a square root transformation because of positive skew in the distribution. Co-linear terms were not modelled, and a significance level of $p < 0.05$ was used to determine significance. Model averaging allows for greater confidence in terms significance, and I used a model averaging approach of all highest ranked models within 2 AIC of the highest ranked model (lowest AIC). This measure rates the relative importance of models by the ratio of the number of times that term appears from all the highly ranked models. The impact of spatial dependency was assessed by removing every second data point and running the analysis again, which had no significant change on interpretation of coefficients, significance values nor effect sizes.

Secondly to analyse factors associated with extreme daily movement distances, the data was then modelled in a quantile regression framework. However there were clear individual lion responses (i.e. repeated measures) which thus needed to be taken into account. This is best achieved with a random effect approach as above, but this approach is not yet available in quantile regression. Instead, I constructed box-plots of the daily movement distances which visually discriminates extreme distances between categories of variables of lion daily movements and is a more robust approach. For instance I can easily compare females with and without small cubs, days when the temperature was above and days when it was below 37 degrees Celsius and days when the temperature was above and days when it was below 6 degrees Celsius. I repeated the analyses for each lion to see how individuals responded to the variables under investigation.

5.3 Results

5.3.1 Proximity

Two separate pride pairs of lions and lionesses spent 19.6% and 30.3% of their time in close proximity, as indicated by GPS locations separated by less than 400m. In the area where two males overlapped substantially, one lion, M058, the intruder, spent 3% of time with the lioness F015 in the same pride area, while the dominant male M014 spent 23.6% of his time with this lioness, despite long bouts at the extremes of his range.

5.3.2 Daily movement distances

Mean daily distance moved by CKGR lions during the study period was 8,999.5m (SD = 6402.9m). There was a large difference between movements of

each sex in the raw data, (mean DMD = 10,071.6m for males (SD. = 7099.4, maximum 48,462m) and 7,633.6m for females (SD= 5,069.3m, maximum 29,470m)). Individual mean daily movement distances for each lion are listed previously in figure 3.1 (Chapter 3) and model outputs for the standard mean model are listed below in Table 5.1.

Analysis focussed on two aspects of lion daily movement distance: mean response and extreme responses. The mean modelling indicated that gender played a significant role in daily movement distances. After accounting for variation due to other variables, male DMD's from the mean model are estimated at 8174.7m and females distances at 6376.5m (ANOVA, $t_9 = 2.47$, $p=0.036$). Rainfall accounted for significant variation, decreasing DMD by 1100m over the range of 0mm-100mm of rain per month (ANOVA, $t_{209} = -2.18$ DF = 209, $p=0.03$). Larger prides moved greater distances, with range of predicted mean movements of small prides of two lions moving 5900m per day, to large prides of twelve lions moving on average 8600m per day but was not significant ($t_{10}=1.78$, $p = 0.11$). Increased rainfall was significantly correlated with decreased DMD ($t_{209}=-2.186$, $p = 0.03$), and increased densities of herds of herbivores was slightly correlated with increasing DMD. ($t_{209}=1.57$, $p = 0.12$, not significant). There was a significant interaction effect involving gemsbok density and giraffe density in dune habitats (ANOVA, $t_{209} = -2.33$, $p = 0.021$), though neither was significant on its own. At low densities of gemsbok density, giraffe densities had little correlation with lion DMD, but at high densities of gemsbok density, increasing giraffe density was correlated with lower DMD of lions ($t_{209} = -2.20$, $p = 0.029$) (Figure 5-5, Figure 5-4b).

Figure 5-2 Frequency histogram of untransformed daily movement distance, (female grey bars, male transparent bars.). Females moved shorter distances more often than males and longer distances less often.

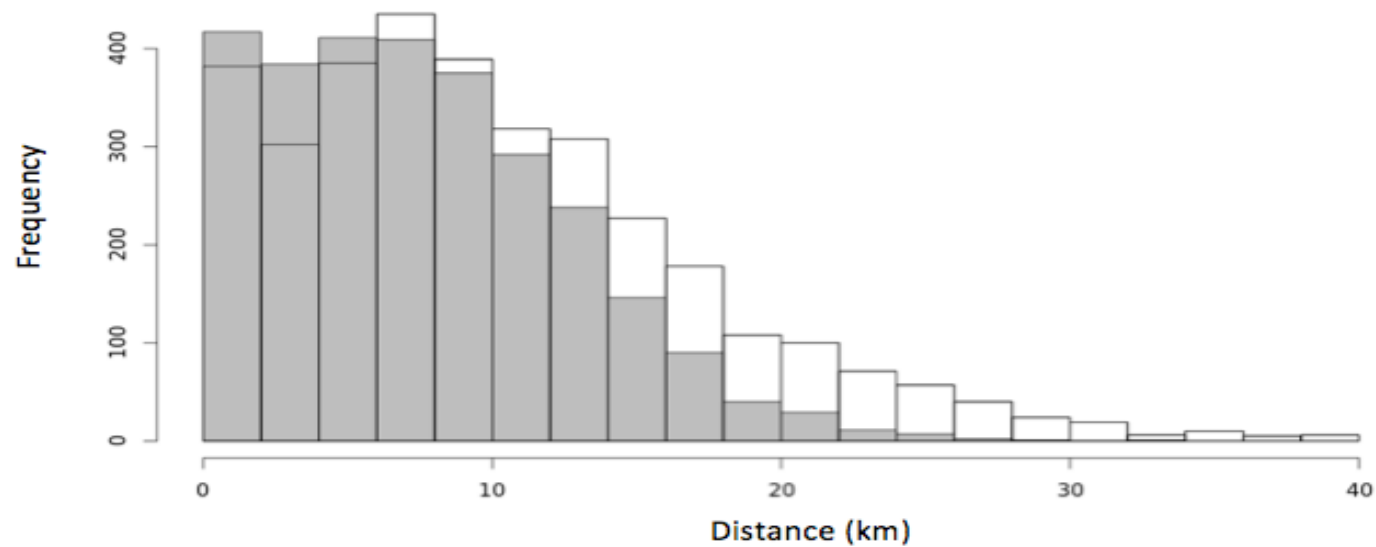


Table 5.1 Output of terms from the mixed effects regression model of the mean lion daily movement distances. Coefficients expressed in terms of the response term on the transformed scale (i.e. the square root of the daily distance moved.) * indicates terms significant at the 0.05 level.

Term	Coefficient	Std.Error	DF	t value	Significance(P)	
Intercept	71.55	6.162	5929	11.61	<0.001	*
Gender Male	10.56	4.358	9	2.42	0.0384	*
Mean Rainfall	-0.06	0.0220	210	-2.92	0.0039	*
Pride Size	1.06	0.602	9	1.75	0.1134	
Giraffe Density (Bush only)	20.75	12.537	210	1.66	0.0994	
Gemsbok Density (Bush only)	3.74	4.104	210	0.91	0.3629	
Herd Density	3.36	1.917	210	1.75	0.081	
Giraffe and Oryx Density Interaction	-57.47	24.713	210	-2.33	0.021	*

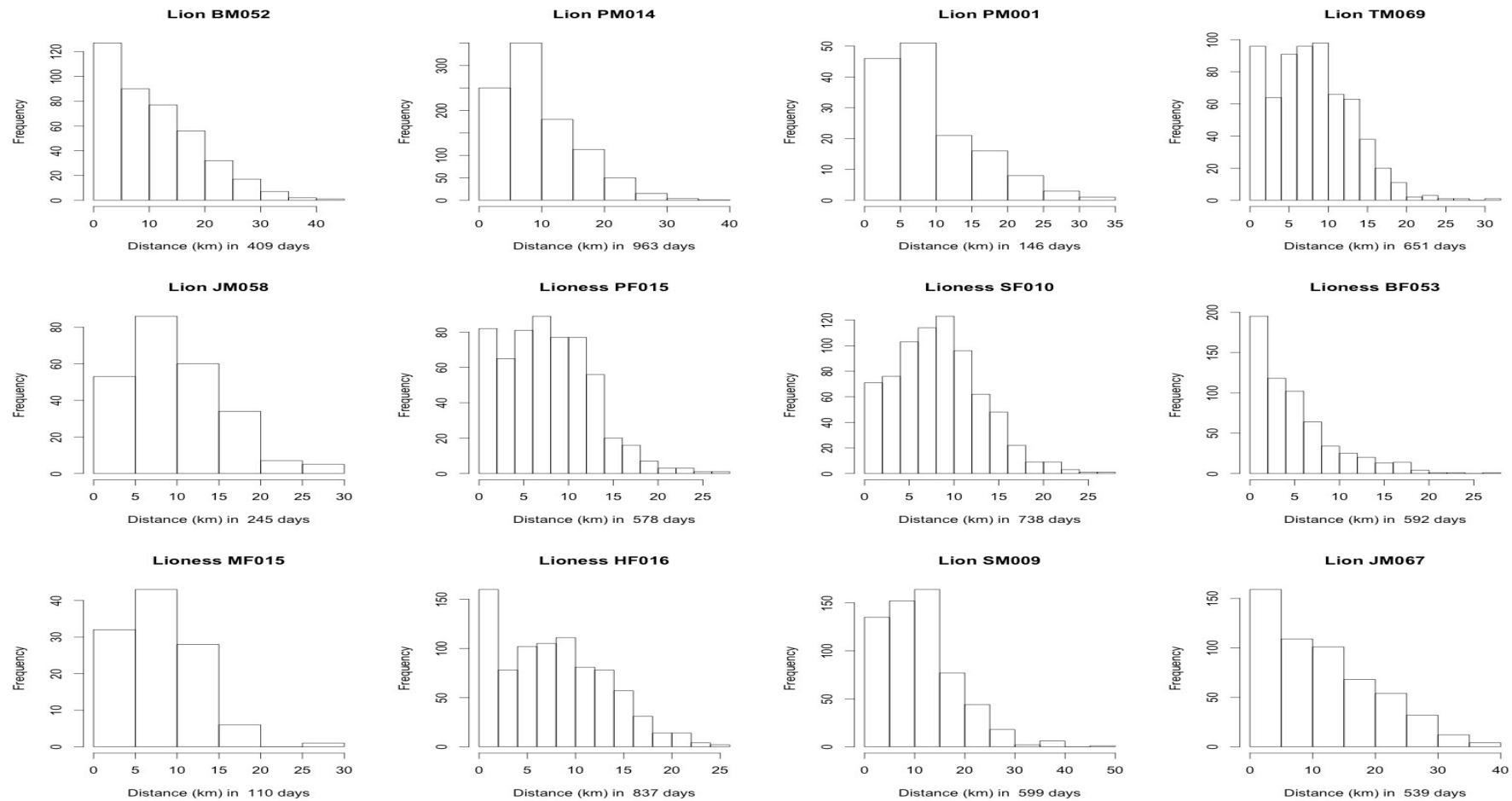


Figure 5-3 Frequency histogram for daily movement distance of individual lions by 5 km buckets. This highlights the long tail of extreme large distances as rare occurrences, yet common to all study lions.,

a)

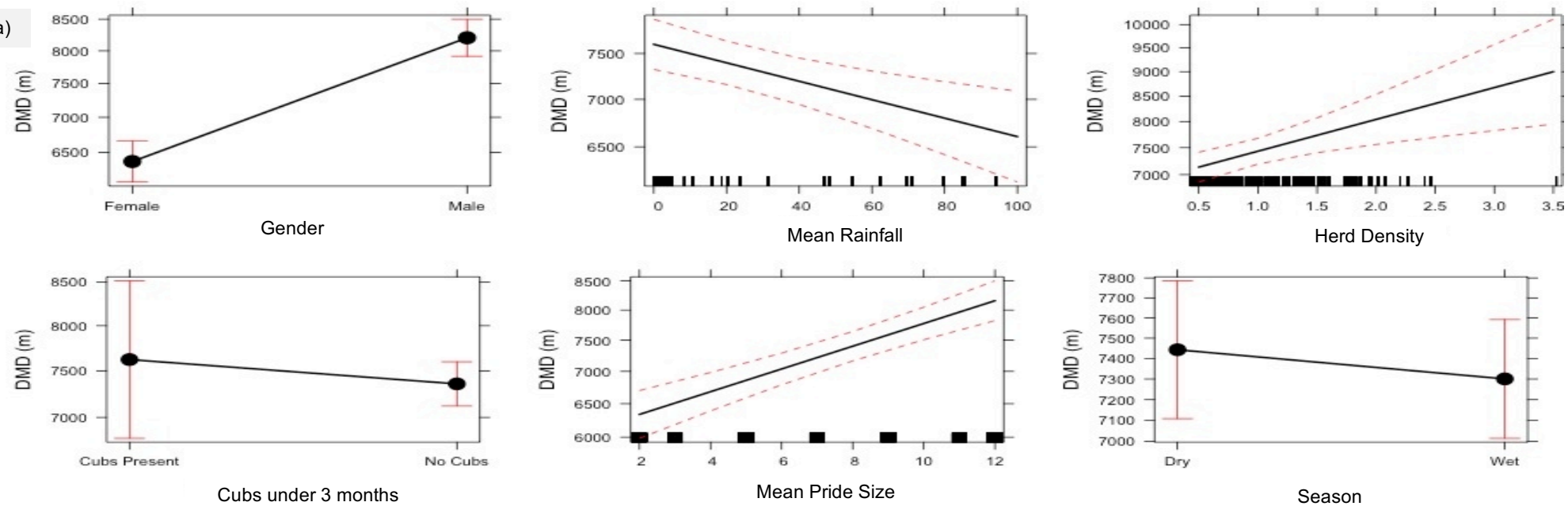


Figure 5-4 a) Main effects graphs of the estimated effect sizes of the mixed effects mean model for daily movement distance. Black dots and red error bars indicate mean values for factorial terms and 95% confidence intervals (C.I.), while black lines and red dashed lines indicated linear estimates and C.I.s of the effects for continuous terms. Note “cubs under 3 months” and season were removed from final model and are shown here to explain why this was done.

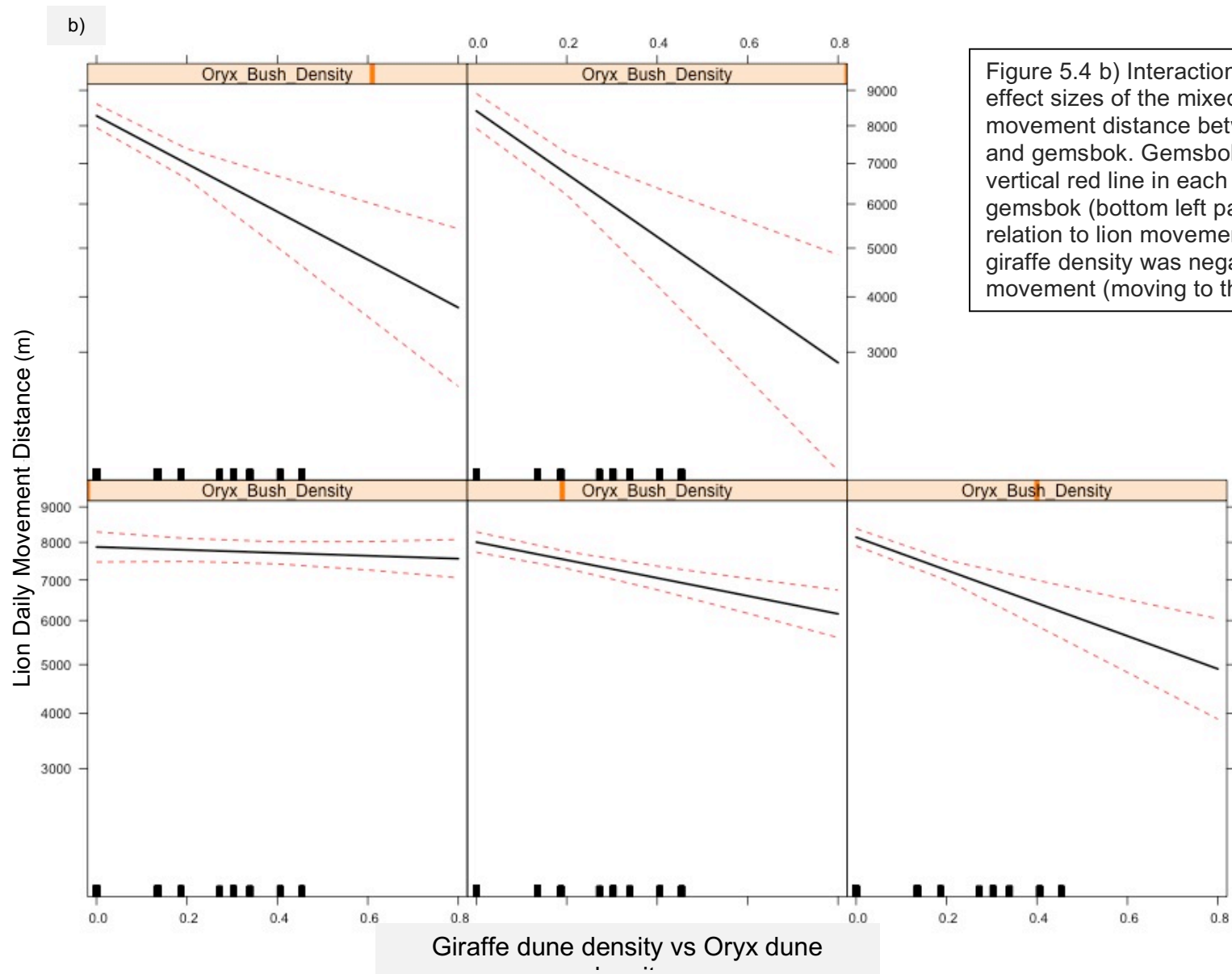


Figure 5.4 b) Interaction effect graphs of the estimated effect sizes of the mixed effects mean model for daily movement distance between dune densities of giraffe and gemsbok. Gemsbok density is indicated by a vertical red line in each title bar. For low densities of gemsbok (bottom left panel), giraffe density had little relation to lion movement at high gemsbok densities, giraffe density was negatively correlated with lion movement (moving to the right, then to upper panels).

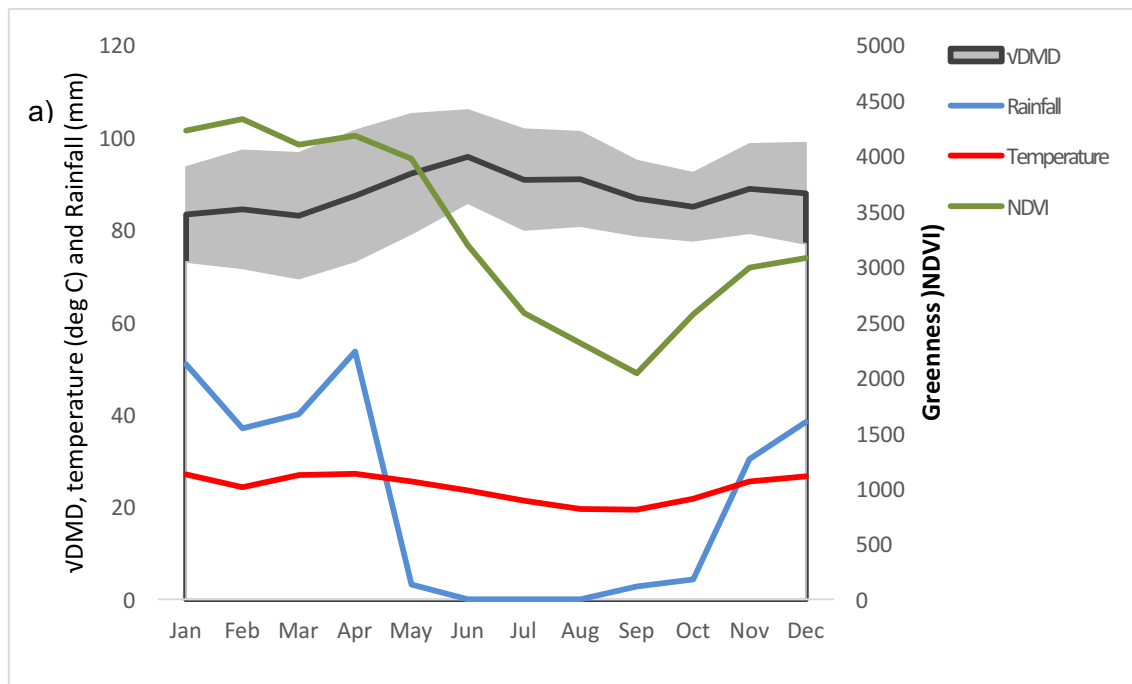


Figure 5-5 a) Model estimated mean response variable by month for $\sqrt{\text{DMD}}$ (Black line + 95% confidence interval in grey area) and co-variables. These two graphs represent the same estimates for the response on different scales, note the left hand axis. The mean response variable exhibited relatively little variation in response to larger environmental variation. There was an inverse linear relationship to rainfall, lions travelling further when there was less rain

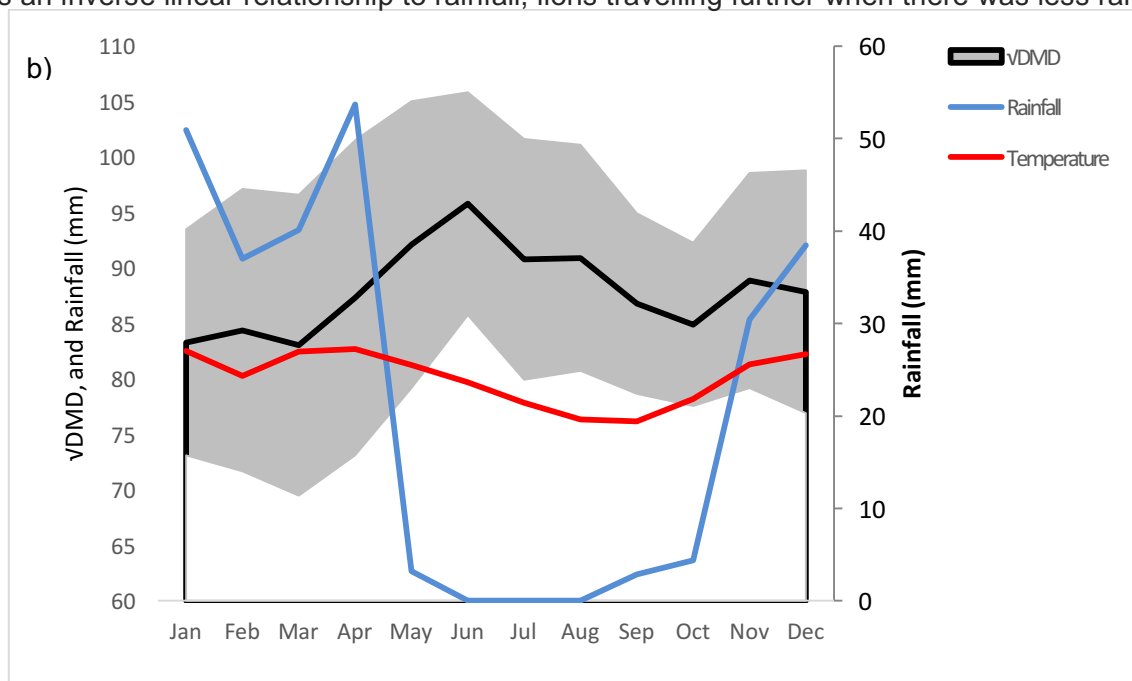


Figure 5-5 b) Emphasizing the variation in response on scale, $\sqrt{\text{DMD}}$ is plotted against the left axis (black line), and two climatic variates, temperature (red line) and rainfall (blue line) plotted against the right axis, for each month throughout the study period. There is a slight increase in daily movement distances coincident with the early dry period. The mean temperature of October was 26 degrees, however maximum temperatures exceed 37 °C regularly (and did not regularly exceed it in other months). This explains the severe dip in lion daily movements in this month.

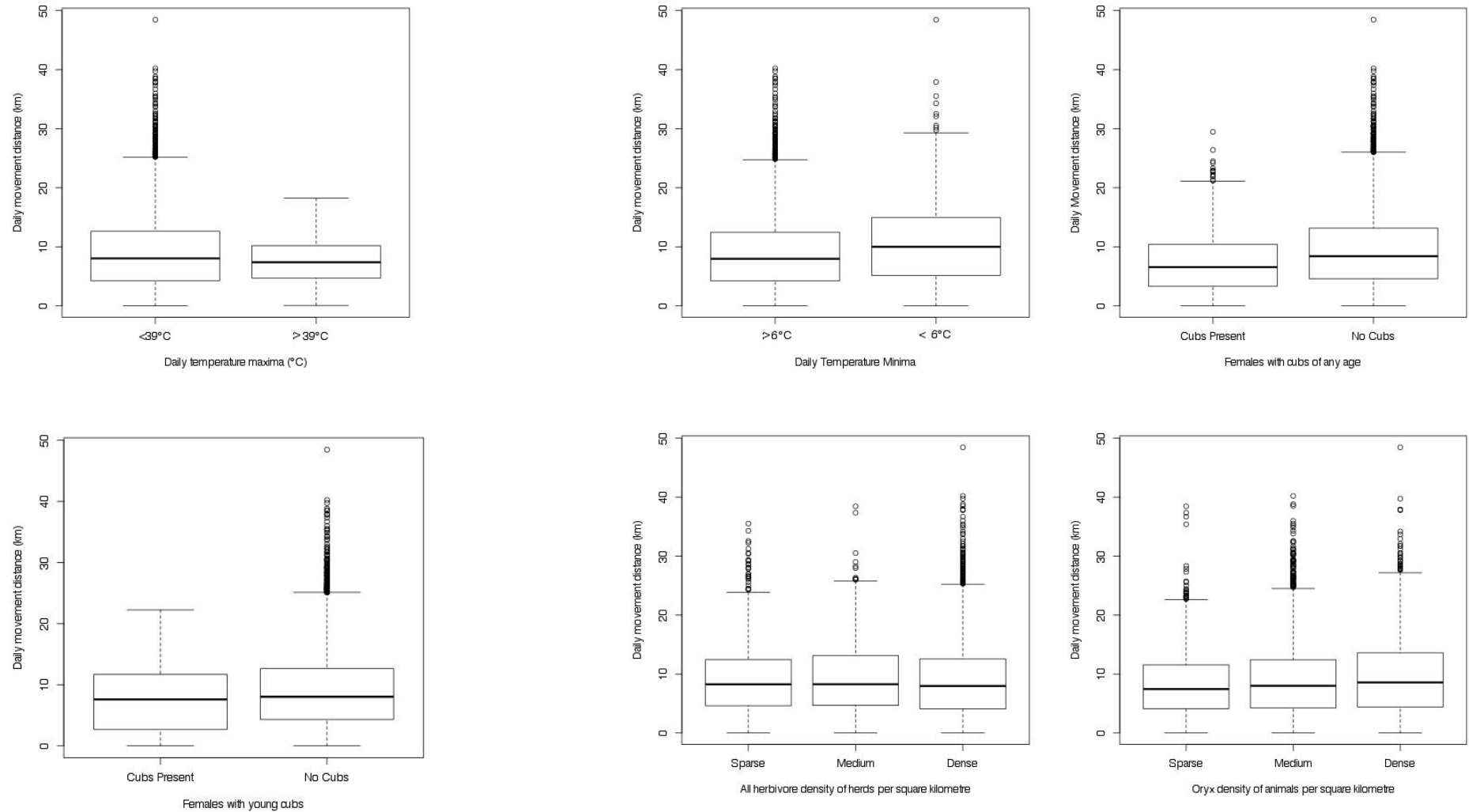


Figure 5-6 Boxplots of extreme daily movement distances are characterised by the existence of outlying points outside the 95% confidence interval (boxes the first and third quartiles, whiskers contain $1.58 \times \text{Inter Quartile Range}/\sqrt{n}$). Circles are data points outside this interval. Points further away indicate increasingly large or extreme movements on one day. Notable variates with increased incidence of extremely large daily movement distances include temperatures below 39°C , females that did not have cubs and especially cubs younger than 3 months and male lions generally were likely to make more extremely large movements.

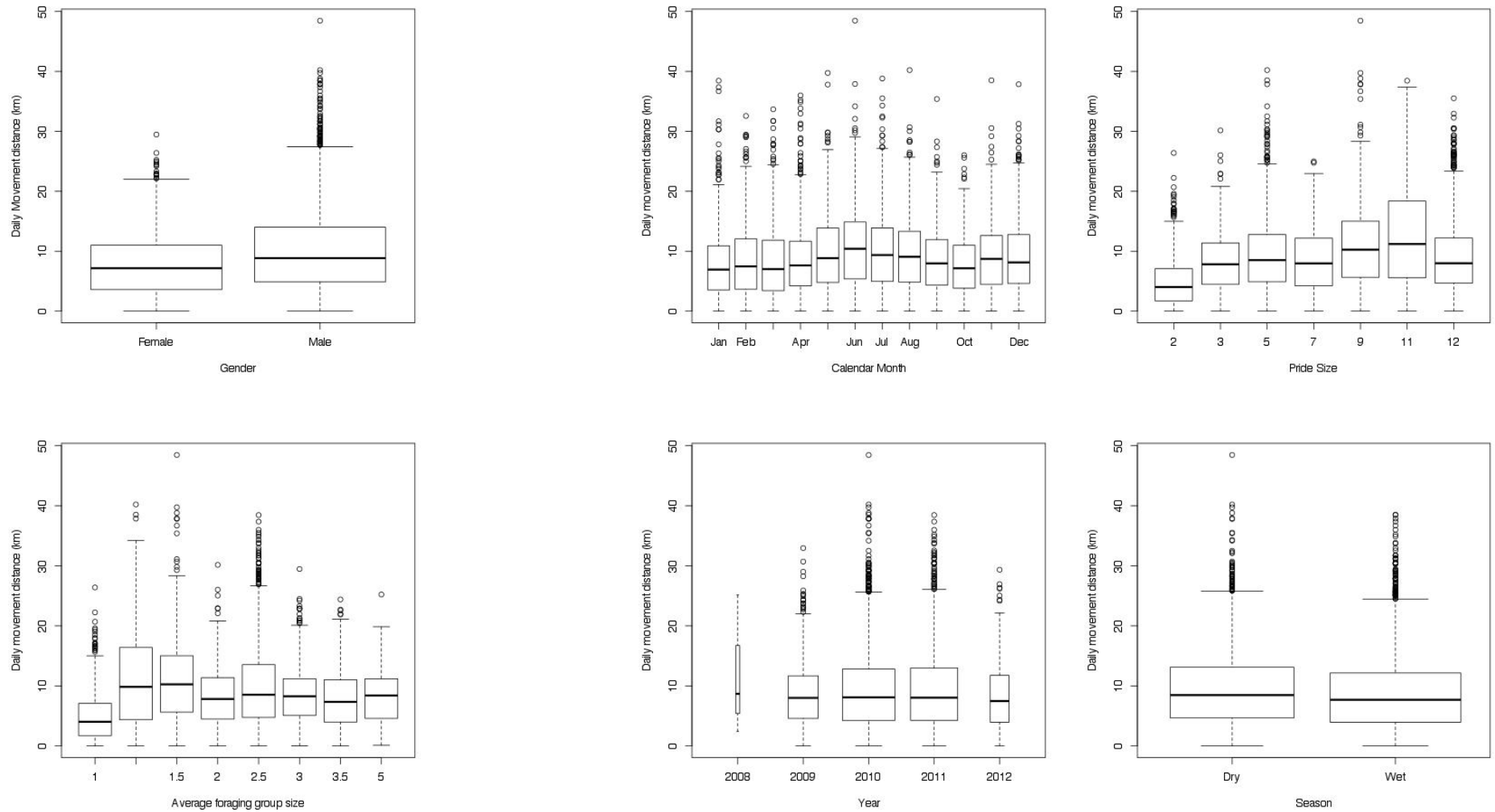


Figure 5-6 Continued. Boxplots of extreme daily movement

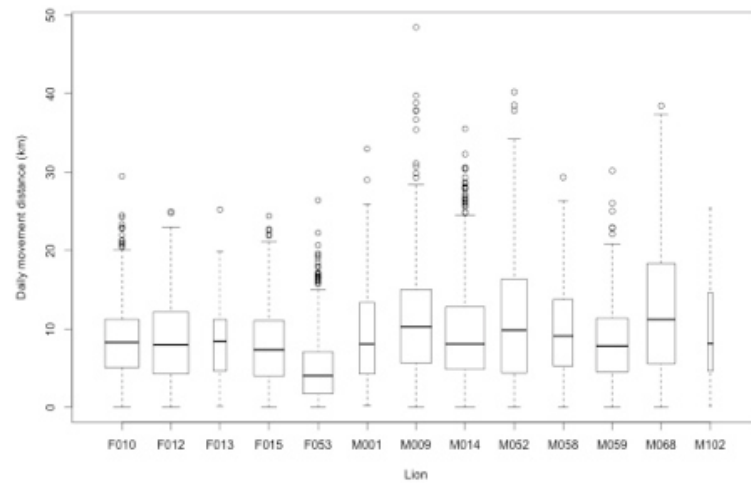
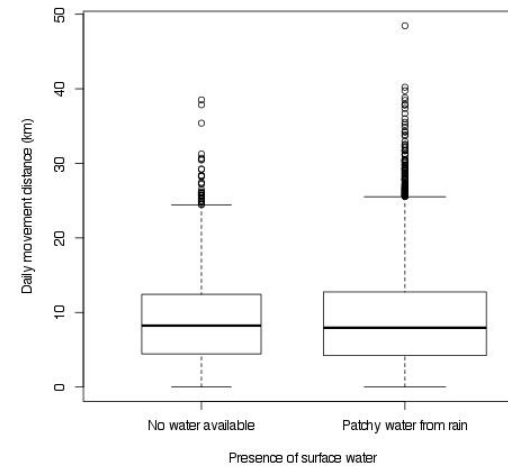
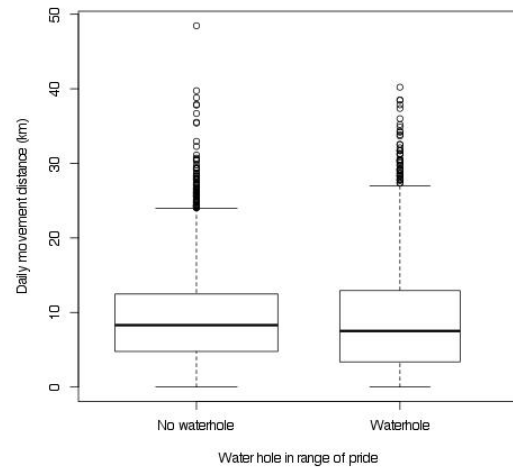


Figure 5-6 Continued. Boxplots of extreme daily movement distances

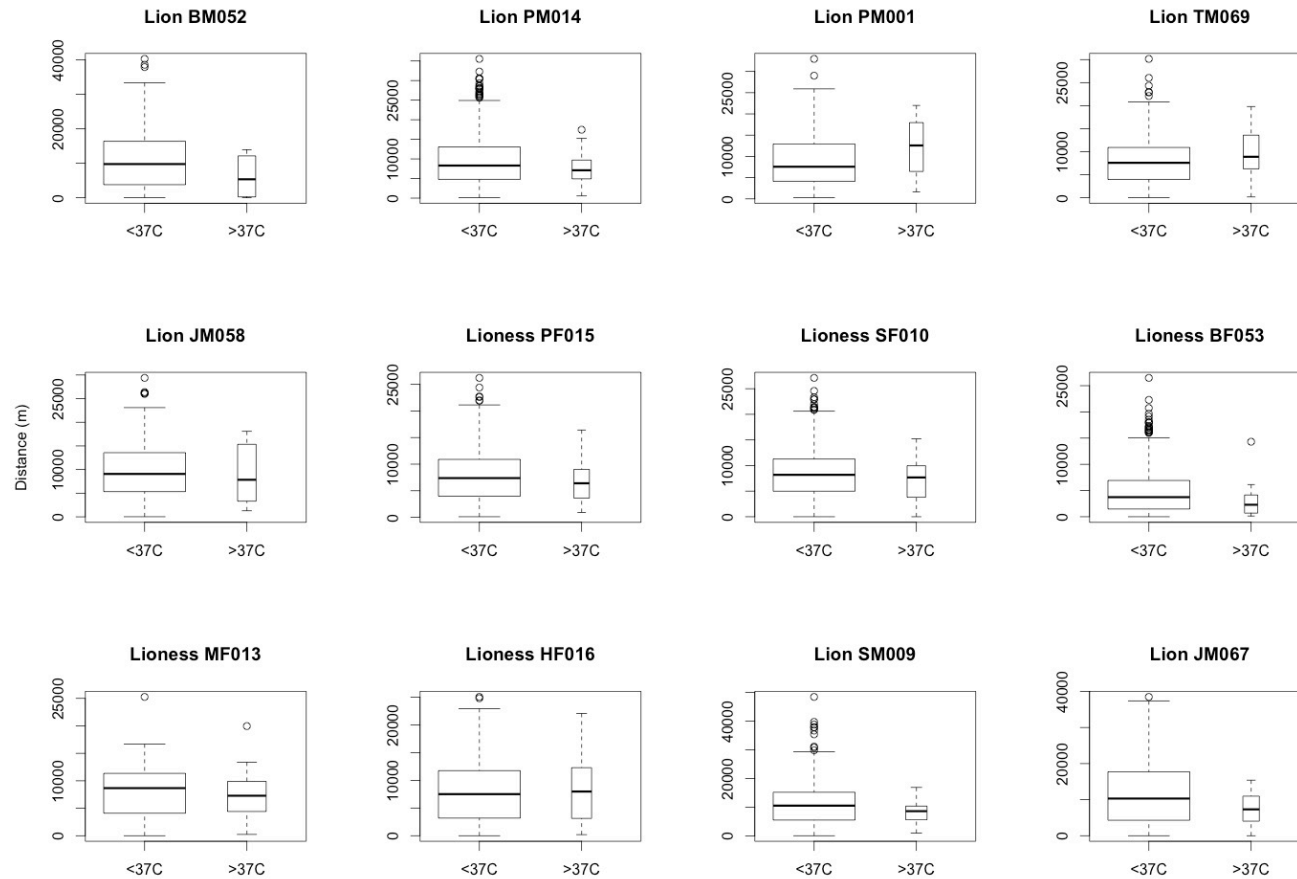


Figure 5-7 Boxplots of daily movement distances comparing days when the daily maximum temperature was above and when it was below 37degrees Celsius. The width of the boxes is relative to the number of data points in that category, open circles indicate points above 1.58x Inter Quartile Range/ $\sqrt{n}$. There is little evidence to support the hypothesis that extremely high temperatures during the day, may cause lions to move extreme distances looking for water that night.

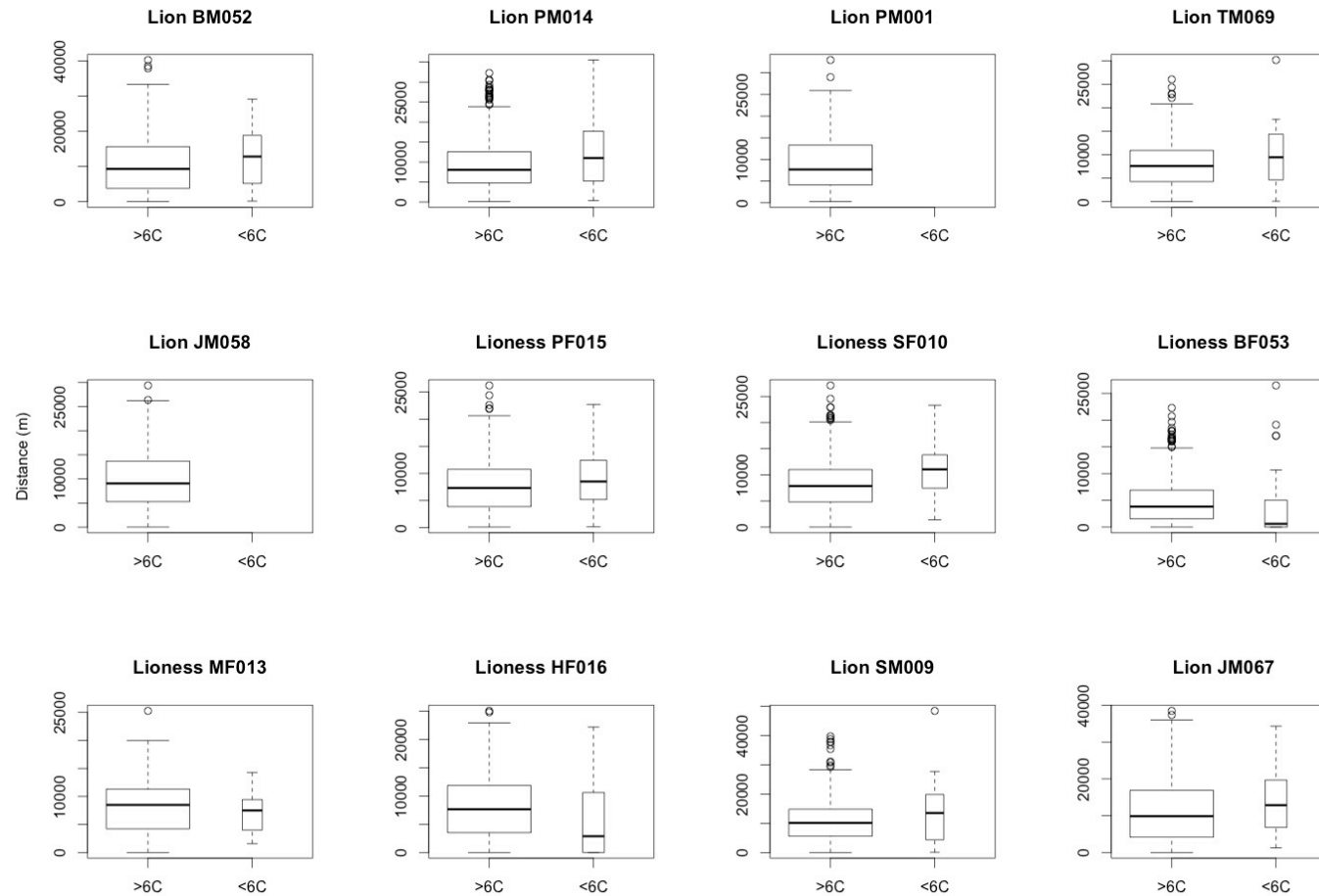


Figure 5-8 Boxplots of individual daily movement distances comparing days when the daily minimum temperature was above and when it was below 6 degrees Celsius. The width of the boxes is relative to the number of data points in that category, open circles indicate points outside the interquartile range.

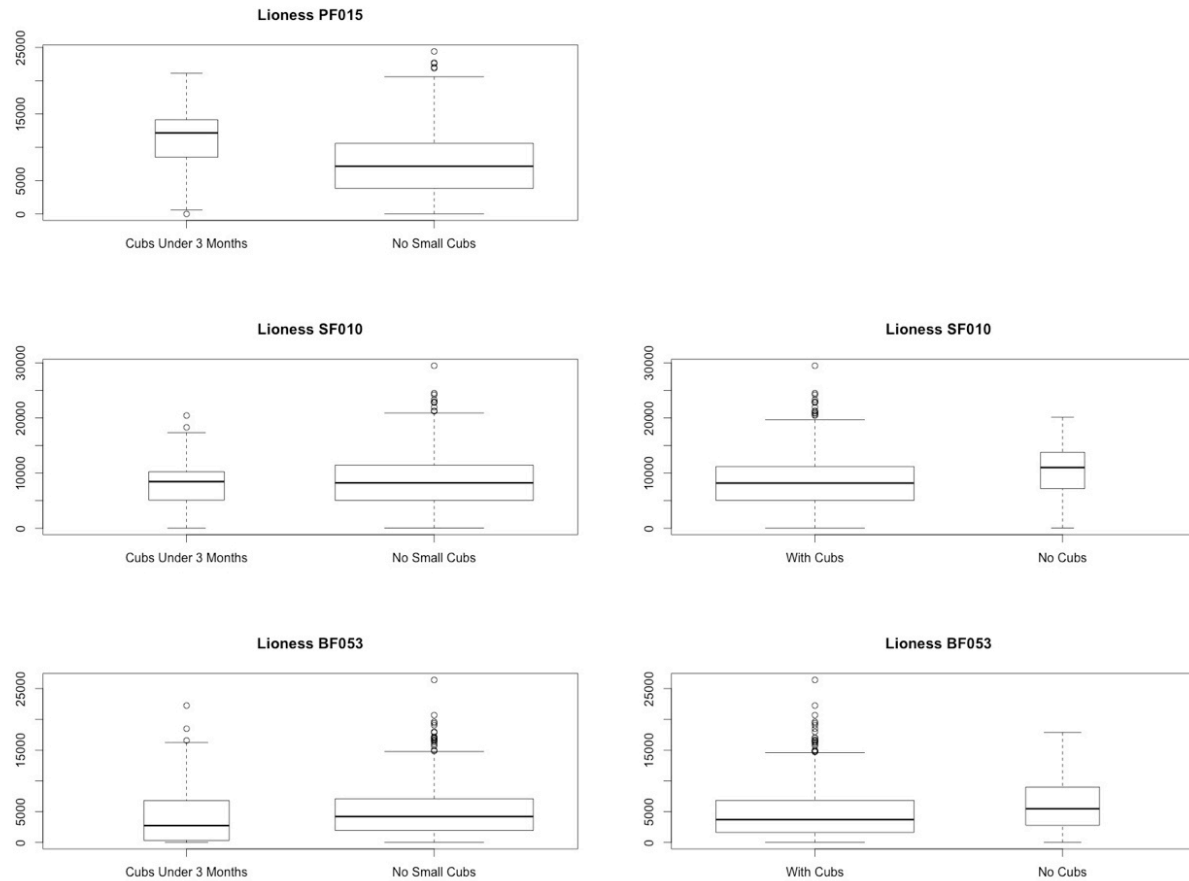


Figure 5-9 Boxplots for individual female lions comparing the daily movement distances of females with cubs with those of females without cubs. Box widths indicate relative number of data points. There is evidence that when females have small cubs (under 3 months, 3 graphs on the left side), they are less likely to move larger distances than when they did not have cubs, but those with cubs of any age (under two years, right hand graphs), they are less likely to move larger distances than when they have no cubs. It should be noted that the samples for having small cubs in the first instance (52, 91 and 86 days) and the sample sizes for no cubs of any size in the second instance (34 and 67 days) are small.

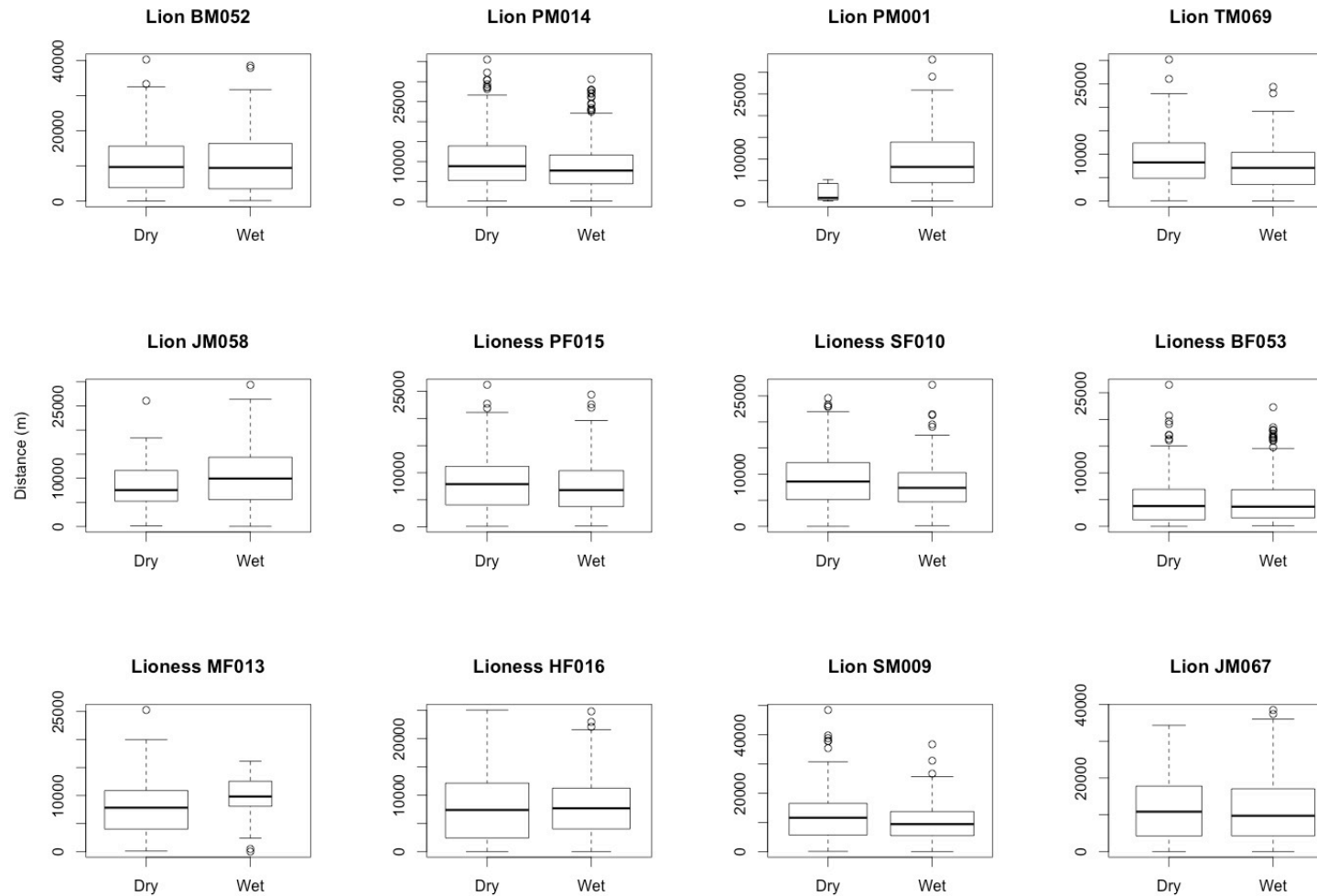


Figure 5-10 Boxplots for individual female lions comparing the daily movement distances of lions between the wet and dry seasons. Box widths indicate relative number of data points. For most lions there is little evidence that extreme daily movements are more likely in the wet or dry season, as defined by this study, and only PM001, with a very small sampling regime in the dry period stands out.

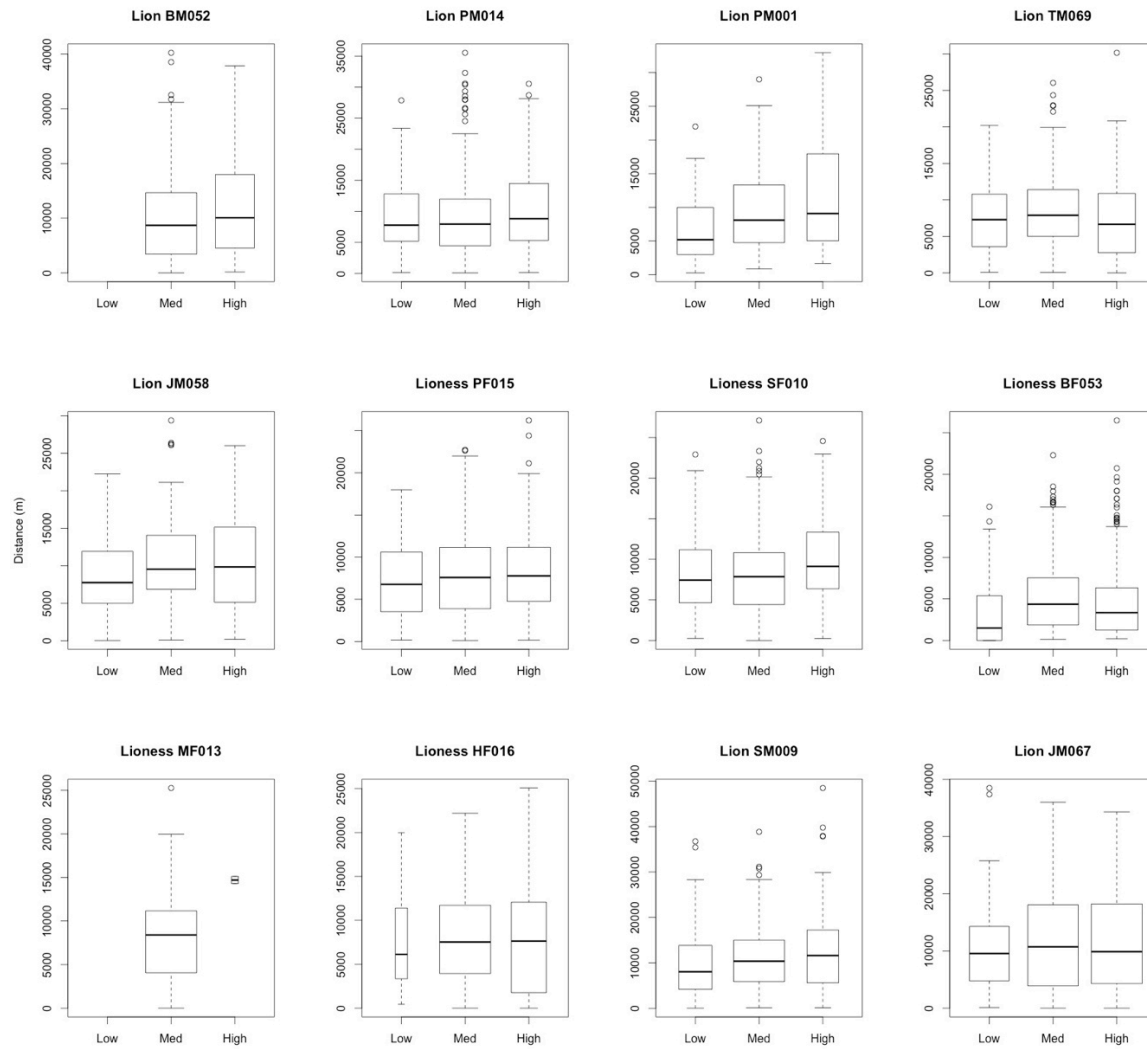


Figure 5-11 Boxplots for individual lions comparing the daily movement distances of lions exposed to low, medium and high densities of gemsbok. Box widths indicate relative number of

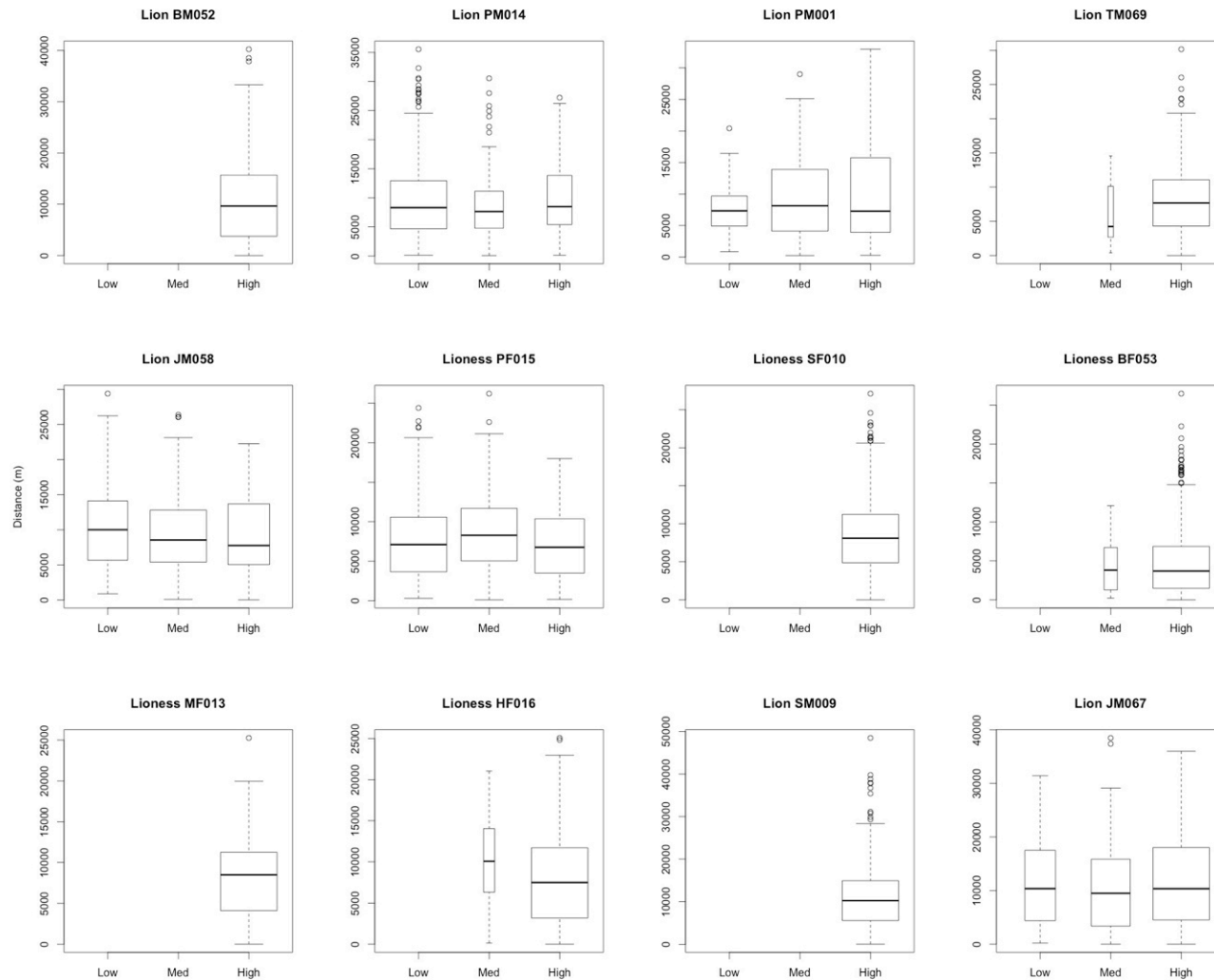


Figure 5-12 Boxplots for individual lions comparing the daily movement distances of lions experiencing varying levels of densities of herds of the herbivores measured in Chapter 2. Box widths indicate relative number of data points.

Extreme daily movement distances proved difficult to model in both quantile modelling and extreme distribution framework. This was due to the random effects being significant contributors to variation and the unbalanced nature of the data. However, clear patterns were visible in graphing boxplots of the DMD with respect to some variates. Important variables that were associated with increased incidence of extreme daily movement distances include days with temperatures below 39°C, females that did not have cubs (especially small cubs) and male lions generally were likely to make more extremely large movements (Figure 5-6). There was little evidence that density of herbivores, time of year, pride size or season impacted the likelihood of extremely large movements. Lions that usually foraged in larger groups seemed less likely to make large movements, but observations were only monthly and accurate foraging group size was not assessed. For the most part, individuals responded the same way to temperature extremes (Figure 5-7 and Figure 5-8), presence of cubs (Figure 5-9) and season (Figure 5-10). There was some correlation between extremely large movements and gemsbok density for several individuals. Four out of six males (BM052, PM014, TM069, JM068) and female SF010 made most or all incidences of large movements during periods of medium gemsbok density, while the highest incidence was for lioness BF053 during medium and high densities (Figure 5-11). The incidence of extreme movements with respect to herd density was varied and no clear patterns are evident (Figure 5-12).

Activity sensors indicated that most activity ceased 2 hours after sunrise and began a little before sunset (Figure 5-13). Activity on any given night was sporadic, long periods of inactivity were common, yet the probability of activity was evenly distributed throughout the night for most lions. During follows, hunting lions would often rest immediately following an unsuccessful hunt, even if that hunt did not involve a chase. Winter (between April and November) activity would occasionally continue for three hours after sunrise, but lions most often would remain inactive until sunset. One lioness, PF015 exhibited pronounced crepuscular (around sunset and sunrise) activity during the first three post natal months, until her cubs were lost. The fathers were recent intruders and her behaviour fits with infanticide avoidance by resident males. The two other study lionesses that gave birth to cubs wore store-on-board collars that did not collect activity data, but the GPS movement data of all three lionesses indicate a return to the denning site at morning for as long as the cubs were unable to join the pride. Without cubs, the lionesses would seek out rest close to wherever they were at sunrise.

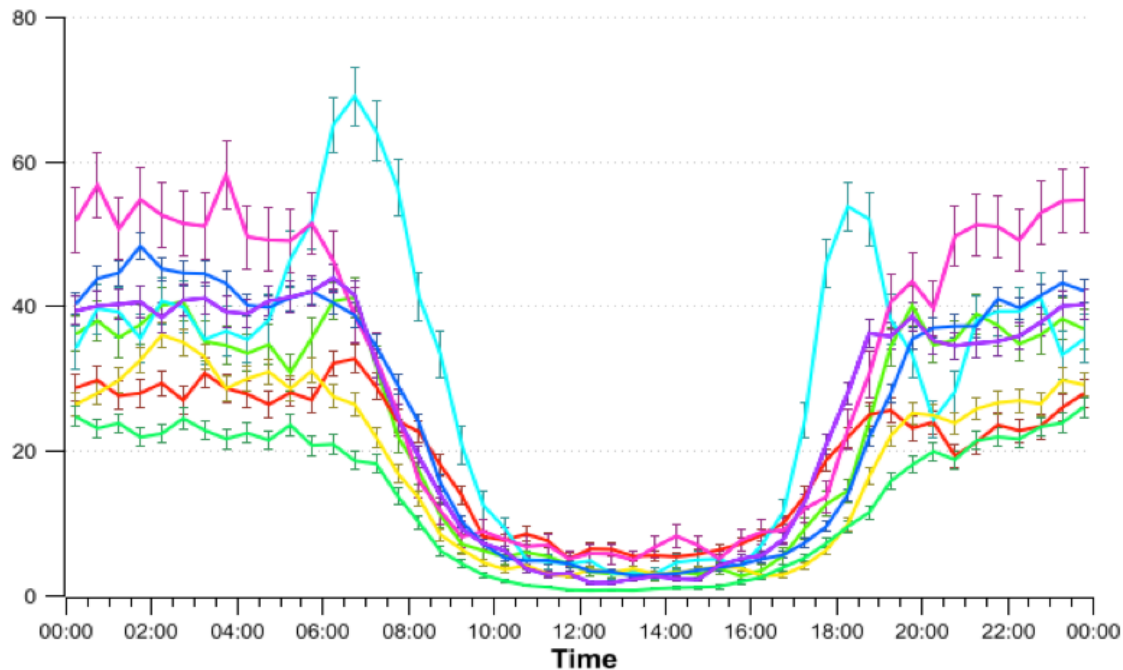


Figure 5-13 Mean activity readings for 24 hour periods for seven lions. Absolute values may vary between collars and should not be compared. Lions are shown by a single coloured line, except female F009 which is shown by two separate lines, light blue for post natal months (three months only), and dark blue otherwise. A clear crepuscular (dawn and dusk activity) trend is noticeable in the post natal months. No other females wore collars with activity sensors in the critical three month post natal period.

5.4 Discussion

Understanding the factors that contribute to variation in lions' daily walking distances is likely to reveal the risk factors leading to conflict between lions and humans, and may provide important insights for formulating management strategies. The findings from my research are important as they represent some of the highest frequency acquisition of GPS movement data on lions, and add a great deal of knowledge about a vulnerable predator at risk due to conflict with farmers. During the study, several study lions were shot after killing cattle, on farms that were only a small corner of the lions range. The continuous location data indicates that cattle could only be a very small part of their diet, as these lions rarely went on to farms. Extreme movements characterise the lions' spatial behaviour in the days before each depredation event and this may be prove useful in preventing future events. In Kenya, Maasai trackers are able to alert farmers when monitored lions are walking towards villages, so that they can protect their cattle. This resulted in a 99% drop in retaliatory killing in southern Kenya (Hazzah *et al.* 2014), and a similar program is having success in the low lion density desert areas of Namibia. It is unlikely that all at-risk lions can be collared and tracked in the CKGR, and knowing when lions are most likely to visit farms will enable farmers to better protect their cattle.

Male lions are at a greater risk of conflict, walking further distances on average and are more likely than females to walk extremely long distances in a

given night. This characteristic also means that females are less likely to cross large conflict zones, reducing the chance of recolonisation of patches such as the Boteti River in the Makgadikgadi Pans National Park to the east of the CKGR. There is currently no effective corridor program ensuring the passage of lions between reserves in Botswana, and lions in this small, protected area are at great risk of local extinction, although there has been a lot of interest in creating corridors. Elliot *et al.* (2014) found substantial movement of dispersing lions between the CKGR and the Makgadikgadi Pans National Park, and sets out the criteria well for the protection or establishment of corridors between parks and reserves. The CKGR itself may not be at high risk of local lion extinction, but is an important source population for smaller reserves. In an increasingly fragmented and hostile landscape this may be the case in the future.

The impacts of herbivore grouping effects are substantial, but only for two prey species, gemsbok and giraffe. This finding supported my hypothesis that lions with more food walked shorter distances. When both gemsbok and giraffe densities were high, lions walked on average 3km per day. This increases to around 8km when both prey species were at low densities. Lions are known for energy conservation and in arid environments are unlikely to expend extra energy (Hayward and Hayward 2009).

Being large terrestrial carnivores they are near the upper limit for energy expenditure (Carbone *et al.* 1999). I anticipated interactive effects concerning lions having to walk further to find water, yet waterholes and the presence of rainy season ephemeral pools had no effect on lion daily movements. It appears that during the wet periods lions would drink often without having to seek out pools, and in the dry season no such pools were to be found and lions therefore did not try to seek them out. Some lions with permanent waterholes in their range did not wander far from those waterholes, while others would return only after several days (typically three to four days). In both cases, this was done without increasing daily movement distance above lions without waterholes.

In arid environments where resources are sparse, such as the Kalahari, the greater daily movement distances imply that some resource limits the population, generally compelling arid lions to move further to acquire sufficient access (Carbone & Gittleman 2002 1640; Carbone *et al.* 2007). Food (Davis & Afton 2010), water and social contact (Getz *et al.* 2005) are resources commonly suggested as drivers of movements. Density of herbivore prey is likely to contribute to differences in distance moved between populations of lions, with females walking further to increase prey encounters, and attending males walking further to increase encounters with and defend disparate female groups. Lions in the Rwenzori National Park in Uganda moved 2.2-2.7 km per day (van Orsdol 1982), and 2.4 - 3.5 km in the Greater Makalali Conservancy, South Africa (Druce *et al.* 2004), much less than the 8.2 km that CKGR males and 6.4 km that CKGR females walked. These other areas are wetter, and have higher densities of herbivore prey. In similarly herbivore poor areas DMDs were similar, such as females in the neighbouring Khutse game reserve who walked 9.5 ± 4.7 km per day (Ramsauer, 2006) and the arid area lions of Etosha, Namibia, which walked similar distances to CKGR lions despite having much larger home ranges.

Another source of variation after gender differences was the density of herds in the dune savannah. I hypothesised that fewer groups, regardless of size of the groups, would mean fewer opportunities for lions to encounter prey, which would also result in greater vigilance and protection in large groups, and may cause an

increase in foraging distances in order for successful hunting. The effect was in the direction that I had expected, although weakly so. This seems to imply that CKGR lions capitalise on periods when herds are dispersed. Larger groups may be easier to find (Hebblewhite & Pletscher 2002), contain more vulnerable sub adults, or be easier to scatter into fragmented groups by lions using cooperative techniques (Stander & Albon 1993) but this seems to be offset by the advantage of encountering many more herds, more often. Daily movement distances were inversely correlated with rainfall but not temperature, although high temperatures decreased the frequency of extremely large movement distances. Periods of high rainfall hinders animals' progress in deep Kalahari sand and the availability of surface water for drinking also reduces the lions' need to travel long distances to find water.

Collar type and collar manufacturer seemed to play a role in daily movements distances calculated. Store-on-board collars and collars manufactured by African Wildlife Tracking (AWT, Pretoria, South Africa) regularly measured shorter distances than other collar types. Greater GPS error by some collars cannot account for this discrepancy, as location error would be expected to produce the same mean position with a greater variance, resulting in mean distances in a large dataset being equal. Since the lighter collars (850g vs. 1kg) produced the shorter measurement, it seems unlikely that collar weight caused the effect as suggested by (Brooks *et al.* 2008) in the case of plains zebra (*Equus quagga*, formerly *Equus burchelli* Linnaeus). I acknowledge this source of variation, but am unable to explain it. However, I have minimized its impact by incorporating this variate as a random effect in the model.

5.4.1 Application to human-wildlife conflict issues

Our data offers an insight into the drivers of conflict between lions and cattle farmers on the boundaries of the CKGR. Problem animal control (PAC) records listing livestock damaged by lions in the years 2001-2012 (DWNP Botswana, 2012) showed a seasonal interaction between fenced cattle farms, and communal cattle posts; lion depredation is higher in the wet season for communal grazing areas, and higher in the dry season for cattle ranching areas. In communal farming areas (to the east of the study area) cattle are kraaled (corralled) at night but move over a much greater area while grazing. Fenced cattle farms (common to the north and west of the study area) are typically 40 square kilometres and larger, and cattle are not otherwise restrained. PAC records indicated that fenced cattle farms experience the heaviest losses of livestock in the dry season. Our data indicate that a contributing factor may be increased movement by lions in response to variation in wild herbivore group size. On fenced farms, cattle are not more accessible in the dry season, but wild prey is less accessible. Communal farms to the east of the study area experienced the most predation in the wet season. The increase here is more likely due to livestock group density. Wild herbivores are highly clumped in the wet season which means they are less accessible to lions (fewer groups equals fewer encounters and more vigilant groups, (Grange & Duncan 2006)), and lions may compensate by ranging further, increasing range overlap without necessarily increasing daily movement. Conversely, livestock is less clumped, taking advantage of available surface water. Communal cattle are left to return to the kraal for water

at night, which they do reliably in the dry season but tend to spread out further from the overgrazed watering points in the wet season and many do not return to the kraal at night; they are at greatest risk in this period. In contrast cattle density does not change in the fenced farms in the same period as these cattle typically have access to many watering points year round and are free to roam within the fences at night. Schiess-Meier *et al.* (2007) found that of 2272 livestock predation cases at night, only three were inside a kraal.

Management that aims to address the lion-livestock conflict should include encouraging communal farmers to herd livestock back to the kraal in the wet season and encouraging fenced farms to consider a method by which their livestock were similarly protected at night. For example, intensive rotational grazing encourages the concentrated grazing of all cattle in very small spaces for periods of three days as a way of prompting grass vigour and recovery of grasslands. This would also have the side-effect of clumping cattle in a way that reduces lion's access to them. Hemson *et al.* (2009) showed that lions in a similar environment to the CKGR preferred wild prey to livestock when both were in similar densities, only switching to livestock when wild prey was very rare. This is attributed to the experience of being chased from livestock kills and other anthropogenic causes. Aggregating cattle in larger groups should amplify this effect. Collared lions have shown a great disregard for typical livestock fences, but rarely enter kraal walls, and twin strand cattle fences should not be expected to prevent livestock predation. Fenced cattle farms only kraal vulnerable calves, but kraaling all cattle each night or employing intensive rotational grazing management strategies while increasing wild herbivore numbers on their property has great potential for reducing lion predation.

As the result of a conflict is usually lethal for a lion, the causes of extreme or unusual movements by lions are difficult to study. However, some important and revealing unusual lion behaviour occurred during October, 2011, when temperatures exceeded 46 degrees Celsius for several days. All lions that did not have a waterhole in their range travelled beyond the bounds of their territory, either into the territory of other lions or into farming areas to access those waterholes. No study lions were shot during this heat wave, but highlights that extreme movement behaviour of lions may be important when considering the impacts of conflict. During the study three collared lions were killed by farmers and the collars destroyed resulting in loss of data for the few most important weeks prior to lethal conflict. Data recovered by satellite from one lion who was killed on a farm indicated a three week period where daily distances moved were substantial and often from one side of the lions range to the other. The cause of the movement is unclear and destroyed collars ensure that data to enlighten the cause is lacking, and would make a conflict study expensive.

Chapter 6 Determinants of Natural Prey Selection and Incidence of Livestock Hunting by Central Kalahari Lions (*Panthera Leo* Linnaeus).

Chapter Summary:

Lions of the Central Kalahari Game Reserve in Botswana live at low densities and have very large ranges, which makes studying their diet difficult. To gain an insight in to the selection of hunting habitat and preferred prey of lions, eleven lions were collared with VHF and GPS enabled collars. I investigated 421 locations, including 159 clusters of GPS points indicating a lion had remained in one location for more than 4 hours within 30 days of the even. I identified 102 kill sites, including 92 carcasses, of which 63 prey animals could be identified to species. The characteristics of these sites were compared to random sites in the range of each lion. Lions preferred to make kills in areas where cover was significantly greater and there were more trees. Height and ground cover of grass and shrubs made no further contribution when measures of predator cover and visibility had been taken into account. Prey was compared to herbivore density estimates and CKGR lions demonstrated a preference for some species over and above their abundance. This method may be biased towards large prey items, so I also opportunistically collected and analysed 44 scats for diet preference. Analyses of hair in the scats detected confirmed the data from the kill sites, but also indicated additional preference for warthog. Eland, giraffe, gemsbok and porcupine were highly preferred, while kudu and wildebeest were killed in accordance with their abundance. Ostrich, hartebeest, springbok and steenbok were avoided. The dominant species in the diet were gemsbok (70%), giraffe (8%), wildebeest (7%), kudu (6%) and springbok (3%). Smaller species and those that habitually lived in the open habitat were killed at a rate lower than expected from their abundance suggesting lions avoid open habitat hunting and smaller species that are difficult to catch with a low energetic return. This technique proves useful for understanding relationships between lions and large prey items. Some direct observations revealed that smaller prey items were likely to be missed by this technique, but they are likely to make only a small contribution to lion diet.

6.1 Introduction

Foraging strategies employed by a population of animals affects their viability through demographic parameters such as dispersal, survival and reproduction (Goss-Custard & Sutherland 1997). Understanding the diet of carnivores is an essential part of conservation (Mills 1992; Tambling *et al.* 2012) in order to better understand population level drivers of carnivore behaviour and threats both to and from carnivore populations. The African lion is widely distributed across the African continent and highly adaptable to a great variety of habitats. Recent studies have indicated a suite of behaviours to cope in the range of biomes in which lions are found. Yet they are well studied in only three areas: the Serengeti (Bertram 1973; Hanby *et al.* 1995; Makacha 1969). Southern Africa (Funston *et al.* 1998) and, to a smaller extent, Zimbabwe (Loveridge *et al.* 2009). Some studies describe unique hunting behaviour in Namibian lions (Stander & Albon 1993; Stander 1992a), tree

climbing behaviour in East Africa (Makacha 1969) and social behaviour in the Central Kalahari (Owens & Owens 1984c). Variation in lion behaviour to cope with the wide variety of biomes in which they are found is to be expected. The effect of diet on lion behaviour and social structure is complex, interacting with variable weather, density dependence, intra-specific competition, prey dynamics, habitat and anthropogenic effects. This requires in situ studying of each lion population to facilitate long term conservation management strategies (Jorgensen & Redford 1993; Macdonald 1983). Between populations, density of prey species correlates with lion density, but some prey species may be unavailable to lions (Hayward *et al.* 2007b). In Zimbabwe, the behaviour indicated that lions expected higher density of prey species around waterholes. In these locations, lions used shorter step lengths and higher turn angles as they moved indicating hunting behaviour and, the authors argued, an awareness of prey dynamics (Valeix *et al.* 2009). Studies using GPS clusters to identify leopard kills were very successful at estimating size and species of kill by combining handling time from GPS information, and vegetation and habitat characteristics (Tambling *et al.* 2010; Pitman *et al.* 2012).

There are a number of techniques available to investigate diet, each with benefits and limitations (Mills, 1992; Rapson & Bernard 2007; Tambling *et al.* 2012). Direct observation during follows is costly and may cause more interference than other techniques (Mills & Shenk 1992) and stomach content analysis is highly invasive and costly (Berry 1981; Ferreira & Bester 1999; Smuts 1979). More practical is faecal analysis and carcass observation via transects or GPS cluster analysis. Each method has some bias, over- and underestimating biomass respectively (Tambling *et al.* 2012). Combining these two techniques is the most feasible method for studying the diet of a carnivore population.

Previous analysis of lion diet has relied on opportunistic sightings (Schaller 1972), which may bias research to large kills and lions that hunt near roads; direct follows (Stander 1992b), which are costly per unit of data; stomach analysis (Rowe-Rowe 1986), which is lethal or when opportunistic yields little data in predators; scat analysis (Tambling *et al.* 2012), which is gaining favour but most effective in high density populations and more recently; GPS cluster facilitated kill site searches. Prior studies that used GPS clusters of collared lions to analyse their diet (Tambling *et al.* 2010; Valeix *et al.* 2011) found great utility of the method for producing high quality, reproducible information on diet. Lions are known to eat a variety of smaller prey items that are not amenable to GPS cluster search, but combining this with scat analysis provides for robust insights into diet.

6.2 Methods

6.2.1 Lion Kill Site Data Collection

Six male and five female lions in five prides were opportunistically darted and collared across the study area in 2009 and 2010, and fitted with GPS tracking collars (see Chapter 3). Between March 2010 and November 2011, GPS data was downloaded from the lion collars each month, either during observation from a short distance via remote download collars, or automatically to a website via satellite collars. Store-on-board collars placed on lions at the beginning of August 2009 were replaced from March 2010 for which GPS data was available after removal. Any available data was represented visually in GIS software ArcGIS 10.1 (Environmental Systems Research Institute 2012). Clusters of points for the same

lion indicating the lion spent 4 hours or more in the same place were identified. Data from daylight hours was ignored. Over the 17 month period, 941 clusters were mapped. An equal number of sites were chosen by a random computer algorithm in ARCGis 10.1, restricted to a minimum convex polygon generated from the range of all of the lions up to that time. Both sets were recorded in a database then mixed into a spatial file that did not identify to which category the site belonged, such that the list grew every month. These were transferred as GPS locations into a handheld GPS unit (Garmin GPS60cx, Garmin limited, Switzerland). I visited the sites that terrain and logistics would allow and searched a 100m radius area for evidence of a lion kill, within 30 days of the activity. This included bones, skin remains, cleared areas indicating feeding, vulture feathers and scats of lions and carrion eaters. Where possible the species, gender and age class of the prey species was identified.

Vegetation characteristics were collected using the carcass as a central point when present, or the centre of the GPS location when no carcass was identified. Due to the method of transferring data, my assistants and I were unaware whether locations were from GPS clusters or random sites, and all were investigated in the same way. Vegetation measurements were taken in a 15 metre radius area. The measurements taken were: percentage of shrub cover, average shrub height, percentage of tree cover, estimate of average tree height to nearest 50cm, estimated average grass height to nearest 10cm, habitat type (described in Chapter 2), dominant vegetation species in tree, shrub and grass classes and a measure of visibility. This last measure required one observer to remain at the centre of the location while a second observer moved to each cardinal direction (N,E,S,W.) at a distance of 15m, measured by laser range finder, and place a 40cm marked ruler on its end to the ground. The first observer would record the length of the ruler covered by vegetation at all four points from his vantage point, ranging from 0 cm as no cover, to 40cm as total cover. This method is a proxy for typical cover from the viewpoint of large herbivores that a lion might employ, being approximately 40cm at the shoulder, while hunting, and is adapted from Hopcraft *et al.* (2005). For analysis the measures from the four directions were summed to produce a single figure, or score out of 160cm. Although the places where carcasses were found are likely to have been a few hundred metres from where the lion may have stalked the prey, habitats were generally homogenous at this spatial scale and habitat around the carcass is likely to have been similar to habitat near where the prey was initially stalked. To test this I recorded if there was a clear ecotone boundary nearby, such that the analysis could assess whether changing habitats might affect the interpretation of the results.

6.2.2 Lion scat collection

Lion scats were opportunistically collected if it was deemed safe. I collected 28 scats during observations on study lions and a further 11 while following lion spoor. The size, characteristic smell and appearance of adult lion scats are such that they could not be confused with scats of other animals in the Central Kalahari Game Reserve. Scats were immersed in water in a 1 square metre open tray until they broke down and spread evenly in the tray. I then collected 20 hairs from all quadrants. Hairs were observed under a light microscope, and compared with known samples, when available, and photographic references (Keogh 1983, 1985). When hairs were difficult to identify, cuticle impressions were made in wet varnish

on a glass slide and the hairs were identified by examining the cuticular pattern under a light microscope.

6.2.3 Prey abundance estimates.

Monthly herbivore transects were conducted by road during a 20 month period as described in Chapter 2. The counts and group occurrence were modelled using ANOVA in R 15.2 (R Core team, 2012) and then predicted for each month on a 100m x 100m resolution map of the study area, primed with binary information of the habitat (pan or dune savannah). In this way I was able to estimate density of each herbivore, (e.g. Gemsbok per square kilometre) for the entire study area. Eland and porcupine densities were below the threshold for this method but since they were present at scats and kill sites I assigned a value of 0.001 animals per square kilometre, (half of the lowest animal density I did measure, warthog density : 0.002 warthog per square kilometre), as the maximum value for expected density.

6.2.4 Estimates of carrying capacity and abundance of predators

The prey densities were averaged between seasons for the 12 month period between November 2010 and October 2011, based on the findings presented in Chapter 2. Total biomass was estimated using mean female masses from Hayward *et al.* (2007b) and used to calculate the mean total study area biomasses in as per Carbone and Gittleman (2002). Prey species for which not enough information was available to model their density did not significantly contribute to the total biomass.

6.2.5 Habitat and prey preference analysis

Hypothesising that lions would more often make kills in habitats with more cover, I set out to test if types of cover (i.e. trees, shrubs or grasses) were important. I compared sites where kills were discovered with the randomly selected sites for each variable using unpaired one-tailed Student's T-tests. An uncorrected significance level of 0.05 was used.

Preference for prey species was calculated using the robust Jacobs' Index (Jacobs 1974; Manly *et al.* 2002) below:

$$\text{Preference} = \frac{r-p}{(r+p-2rp)}$$

Where r = observed proportion of selections (e.g. Number of gemsbok kills/number of kills of all species)

p = expected proportion of selection (i.e. proportion of abundance).

The Jacobs index scales selectivity from most preferred as +1 to most avoided as -1. A score of 0 indicates the species is selected in accordance with availability (no preference or avoidance). Herbivore mean female masses of prey species were taken from Hayward and Kerley (2005) for comparison and comprise three quarters of the mean species mass as listed in Stuart and Stuart (2000) and Estes (1999).

6.2.6 Lion population survey

Lion numbers were estimated in the study area only, using a call up survey spanning thirteen consecutive days in October 2011, which included 46 call up stations evenly dispersed at 8km intervals throughout the study area. Following Loveridge *et al*, (2001) I played a recorded sound of an injured buffalo through four 150 watt megaphone type speakers, amplified to a measured 90dB at 5 metres from the speakers. Each speaker pointed in directions at 90 degrees from the next speaker, horizontal to the earth, 2 metres above the ground. The sound was played for 1 minute, with a 5 minute rest and then another 1 minute of sound. I remained at the location for 1.5 hours from the start of initial sound, before moving to the next location. Beginning at 9pm, calling stations were separated by two hours, and up to four were conducted each night. On the first night, seven lions 3 km distant from the calling station team were under observation by a second vehicle and responded immediately to the sound. Five females walked briskly to the location, while two males clearly heard the sound, but waited 3.5 minutes before following slowly behind the females. On the second night, two male lions were under observation 4 km away from the calling station and responded immediately to the sound, walking briskly to the location, arriving 50 minutes later. On the third night two lionesses 5km away from a station did not respond to the recorded sound. On the seventh night a lioness was encountered 3.8 km from the site of the previous calling station. She showed signs of having recently fed and I assume she would not respond, but may also have moved to that location (within the radius of hearing) after the call-up survey from nearly 2 hours earlier. No other chances to directly observe lions at distance with a second vehicle were available, and I conservatively estimated the radius of the survey method at 4km. Study area population estimates were calculated from the total number of adult lions counted divided by the total area surveyed ($46 \times 4^2 \times \pi = 1808.64 \text{sq .km}$ or 18.25% of the 9910 square kilometre study area). Upper and lower limits of the population estimate of 20% are used as per Bauer and van der Merwe (2004). A lion generally walks at about 4km an hour or less, and could only reach the calling station in 1 hour. Thus we expect the total estimate to be a conservative estimate of the lower limit of the lion population. The response rate of the few observed individuals was high, and following Bauer and van der Merwe (2004) I used an upper limit of +20%.

I made a second population estimate using the Petersen mark-recapture formula (Peterson and Cederholm. 1984). This used the 121 identified lions at the time and the incidence that these 'marked' lions were encountered during the call up survey (Castley *et al*. 2002; Ogutu *et al*. 2006).

6.2.7 Value of livestock killed by lions

The problem animal control registers maintained by the Botswana Department of Wildlife offices at locations around the CKGR collate data on all livestock and property damaged by wildlife. Livestock killed by lions and some other predators is covered by compensation from the government. I judge reporting of losses should be high, particularly when the losses are substantial. In the case of lions attacking livestock, carcasses are inspected by DWNP officers for evidence of the lion attacks and an assessment is made about whether compensation is offered based on evidence of the lion kill. I requested records from these reports as far back as possible. Records were made available to me from the Hainaveld area

(Ngamiland district) from January, 2006, to August 2011; from the Ghanzi district from January 2001 to December 2012 and from the Rakops district January, 2000 to December 2010. I used the total Botswana Pula amount compensated rather than claims, as many were unsuccessful. Values compensated per type of livestock have not changed since the inception of the Wildlife Act in 2001. Since the compensation values do not reflect market values, this exercise tracks temporal changes in livestock losses caused by lions using the compensation value as an index (comparing regions and months of the year), rather than estimating market values or real economic cost.

This dataset covered farms from throughout the three districts and many farms were far from the study and closer to other game reserves and wildlife areas. I attempted to geolocate farms based on farm and farmer names from the PAC records. The Ghanzi district council maintains a GIS dataset of large farms and some cattle posts, and 314 of 480 listed farm names were geolocated (some were duplicate farms with differential spelling.) In the Ghanzi and Ngamiland areas the help of farmers and DWNP officials was used to geolocate as many farms as possible by cross-referencing with some property data and official data on boreholes in the areas. I geolocated 196 of 258 farms in the Rakops region and 205 farms of 930 in the Ngamiland district. Most of the unknown farms from the Ngamiland district were situated further than 50km from the study area, and I estimate that more than 90% of farms within 30km of the boundary of the CKGR were geolocated; farms not geolocated or further than 30 km from CKGR were dropped from the analysis.

6.3 Results

6.3.1 Diet of CKGR lions

I investigated 421 potential kill sites and identified 63 carcasses to species from a total of 92 discovered carcasses. Only 3 carcasses were considered small species, 2 springboks and 1 porcupine. A total of 44 scats were collected, and species representation was correlated with kill site representation ($R^2 = 0.97$ with unknown kills removed, see Table 6.1 for numbers of each species found by each method). This was overly influenced by the gemsbok data ($R^2 = 0.37$ excluding gemsbok). One scat contained warthog hairs, which were not represented in kill site data, and eland, porcupine and ostrich were represented at kill sites but not in any scats. There was also a much greater proportion of unknown species for the kill site methodology: 2.2% of scats but 23% of kill sites could not be identified.

Models explaining the proportions of each species at kill sites followed a similar pattern to models explaining proportions in scats and both included interacting terms of species mass, season and density of each species. The model explaining species representation in scats explained 91.5 % of variation (multiple R^2 , $F_{7,16} = 27.02$, $p < 0.01$) and that for kill sites explained 92.2% (multiple R^2 , $F_{7,16} = 24.44$, $p < 0.01$, see Table 6.1 for coefficients).

Lion kill sites did not differ in the height or percentage cover of grasses or shrubs. However, at kill sites there were significantly more trees than at randomly selected sites ($T_{99} = 2.37$, $p < 0.05$). Trees at kill sites were also significantly taller than trees at random sites (arithmetic mean height of 2.18 m at kill sites compared to 1.57m, $T_{99} = 1.664$, $p < 0.0$).

Table 6.1 Numbers of each prey species in scats and at kill sites for CKGR lions. Percentages do not include unknown species. Prey density is measured as animals per square kilometre, and animals for which density was too low for estimation were rounded up to 0.1 animals per square kilometre. A Jacob's index of +1 indicates highly selected for, -1 indicates highly avoided.

Prey species	Number In Scats	Proportion of representation in scats	At Kill Site	Proportion of representation at kill-sites	Estimated female Prey Density	Mean mass (kg)	Jacobs Index	Jacobs Index from meta- analysis (+/-1SE) (Hayward <i>et al</i> , 2011)
Gemsbok	24	57%	50	70%	0.472	158	0.75	0.70 (0.06)
Springbok	5	12%	2	3%	0.343	26	-0.36	-0.59(0.08)
Kudu	7	17%	4	6%	0.017	135	0.89	0.13(0.12)
Wildebeest	2	5%	5	7%	0.010	135	0.89	0.27(0.08)
Duiker	0	0%	0	0%	0.003	16	-1.00	-0.83(0.07)
Warthog	1	2%	0	0%	0.002	45	0.85	0.11(0.09)
Porcupine	0	0%	1	1%	0.001	10	0.92	0.58(0)
Eland	0	0%	1	1%	0.001	345	0.92	0.18(0.14)
Steenbok	0	0%	0	0%	0.060	8	-1.00	-0.86(0.08)
Ostrich	0	0%	1	1%	0.045	70	-0.30	-0.55(0.17)
Giraffe	3	7%	6	8%	0.035	550	0.74	0.24(0.10)
Red Hartebeest	1	2%	1	1%	0.010	95	0.66	0.02(0.13)
Unknown	1	2%	21	23%				
Total	44		92					

Table 6.2 Results of 2 tailed T - tests of variates between kill sites and randomly selected comparison sites

Variable	Kill sites expected to have:	DF	T value	Probability
Tree cover	More trees	99	2.37	0.0253*
Tree height	Taller trees	99	2.3117	0.0497*
Shrub cover	More shrubs	99	0.387	0.323
Shrub height	Taller shrubs	99	0.5536	0.275
Grass cover	More grass	99	0.895	0.195
Grass height	Taller Grass	99	-0.9344	0.85
Lion cover at 15m	More cover	91.5	2.398	0.0176*

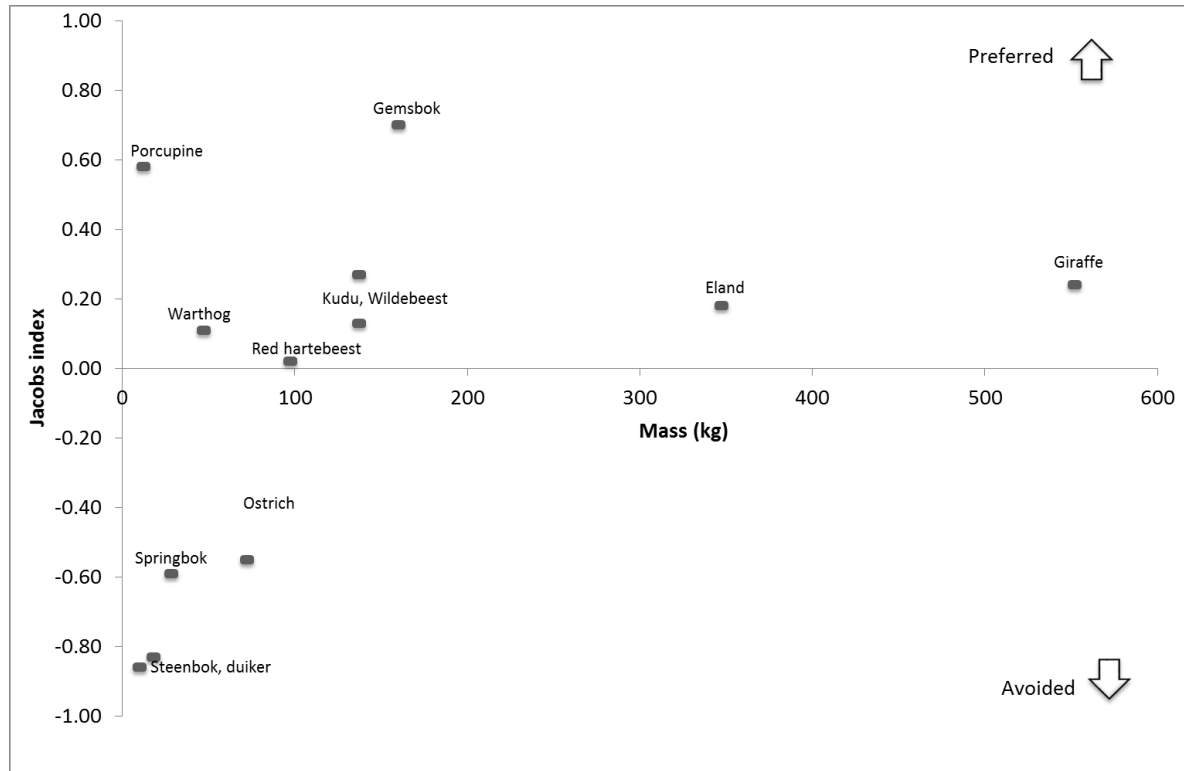


Figure 6-1 Scatter-plot of Jacobs index versus body mass. Large mass (>100kg) species were preferred, smaller mass species are generally avoided, the exceptions being porcupine and warthog.

Table 6.3 Linear Model results for species representation in kill site and scat.

	Coefficient	SE	T -value	Prob(> t)	Significance
Species at Scat site modelled by:					
Intercept	2.27E-03	3.57E-02	0.064	0.950125	
Mass	-2.53E-05	1.53E-04	-0.165	0.870631	
Season (Wet)	-3.81E-02	5.17E-02	-0.737	0.471806	
Density	-2.50E-04	1.57E-04	-1.588	0.131799	
Mass*Season	-1.22E-04	2.19E-04	-0.56	0.583182	
Mass*Density	1.16E-05	1.43E-06	8.139	4.43E-07	***
Season*Density	-2.54E-05	5.58E-04	-0.046	0.964219	
Mass*Season*Density	2.28E-05	4.85E-06	4.694	0.000244	***
Species at Scat site modelled by:					
Intercept	-1.31E-02	3.10E-02	-0.423	0.678	
Mass	2.36E-04	1.32E-04	1.787	0.0928	.
Season (Wet)	-6.98E-03	4.48E-02	-0.156	0.878	
Density	-6.95E-05	1.36E-04	-0.51	0.6171	
Mass*Season (Wet)	-4.02E-04	1.89E-04	-2.123	0.0497	*
Mass*Density	7.49E-06	1.24E-06	6.065	1.64E-05	***
Season*Density	-2.27E-04	4.83E-04	-0.469	0.6452	
Mass*Season*Density	2.46E-05	4.20E-06	5.845	2.49E-05	***

6.3.2 Carrying capacity

Total lean season estimated numbers of all prey species are taken from Chapter 2, Table 2.4, for the purpose of calculating the total biomass in Table 6.4, which also shows the estimated biomass for preferred weight range species for each predator, used to estimate predator carrying capacity (Table 6.5). Estimates from the latter method appear more reasonable for most species, although extremely low for leopard. Predator estimates from two recent surveys for lions and spoor counts for other predators are also shown. If estimated carrying capacity and predator density are correct, they indicate below optimal levels of predators in the CKGR, except perhaps for leopard.

Table 6.4 Lean season prey numbers estimated from road transects and mean female masses and resulting biomass estimate

Species	Lean season low estimate	Mass (kg)	Biomass (3/4*Mass*Pop.Estimate)
Oryx	5288	169	670254
Springbok	1156	39	33813
Kudu	2150	214	345075
Wildebeest	14	215	2258
Hartebeest	1208	134	121404
Giraffe	22	1240	20460
Ostrich	1104	93	77004
Steenbok	3660	11	30195
Duiker	200	13	1950
Warthog	363	45	12251

Table 6.5 Estimated carrying capacity of the CKGR predators, and estimated numbers from two techniques. The spoor survey conducted in 2012 (Maude & Selebatso 2012) estimated predators from the entire reserve, and the call-up survey in 2011 estimated only lions in the northern study area.

Carnivore species	Predator Mean Mass	Number per 10,000kg of prey biomass	Biomass of prey in preferred weight range	Estimated carrying capacity of predators	Estimate from Spoor Survey - Whole CKGR (#per 100km ²)	Estimate from Call Up Survey - Study Area (#per 100km ²)
Wild dog (<i>Lycaon pictus</i>)	25	1.61	823,803	132.632283	1.16	-
Leopard (<i>Panthera pardus</i>)	46.5	19	78209.25	148.597575	0.72	-
Cheetah (<i>Acinonyx jubatus</i>)	50	7	46064.25	32.244975	0.06	-
Lion (<i>Panthera leo</i>)	142	3.4	814375.5	276.88767	1.16	2.49

6.3.3 Value of livestock killed by lions

A total of 12,535 cases of wildlife damage were reported in the periods for which records were made available. This included 80 threats to human life and 5200 cases involving lions.

Lions accounted for 53% of the value of livestock lost, with a total of BWP3,776,913.90 (Botswana Pula) received in compensation for livestock lost to lions out of BWP7,148,000 wildlife damages in total. One United States Dollar (1USD) bought around 11.996 BWP on January 1st 2012 (X-rates.com 2014) and BWP is considered a relatively stable currency. Ghanzi farmers were compensated a total of BWP716,167 in 12 years. The Rakops district compensated a total of BWP2,010,429 over 11 years or BWP15,185 per month. The total amount compensated in the Hainaveld was BWP1,065,848 in 4 years 7 months or BWP19,033 per month. For other species 70% of the 2009 claims were compensated in the case of elephant damage, or BWP605 per claim and 79% of 2094 claims involving leopard at an average of BWP328.03 per claim, and 77.8% of 2457 claims for wild dog damage at an average of BWP526 per claim. For lions, 89.3% of 5073 claims were compensated at an average value of BWP747.58 per claim, the highest rate of successful compensation and highest value of compensation per claim.

To the east of the study area where most grazing is communal, compensation was sought equally in most months except for October when there was a drop in compensation sought (Figure 6-2). October is the hottest and driest month. The farms to the north and south showed that compensation was highest in the mid-year months (Figure 6-3 and Figure 6-4), after the rains had finished and the days and nights were getting cooler. These areas do not use kraals, relying on boundary fences to keep cattle on their property.

A greater monetary value of compensation for livestock damaged by lions was sought in proximity to the game reserves than at further distances (Figure 6-5), despite this region containing fewer farms and cattle posts due to the smaller area and remoteness of the locations. This indicates resident lion populations seek refuge in game reserves and cause the greatest value of livestock damage, and is consistent with the results of previous research to the south of study area in Khutse Game Reserve (Schiess-Meier *et al.* 2007). Table 6.6 Annual value of damage in Botswana Pula (BWP) by wildlife in each of the three regions surrounding the CKGR. Elephants caused the greatest value in damages to property per attack.

	Ghanzi	Ngamiland	Rakops
Brown Hyaena	700		
Jackal	1,400		
Cheetah	55,230	9,533	4,610
Croc		3,973	
Duiker	900		
Elephant	6,450	1,199,499	
Hippopotamus		82,729	
Jackal	4,950		
Spotted Hyaena	1,050		590
Kudu	2,100		
Leopard	422,610	185,154	79,130
Lion	716,167	1,065,848	2,010,429
Wild dogs	776,760	354,051	164,100

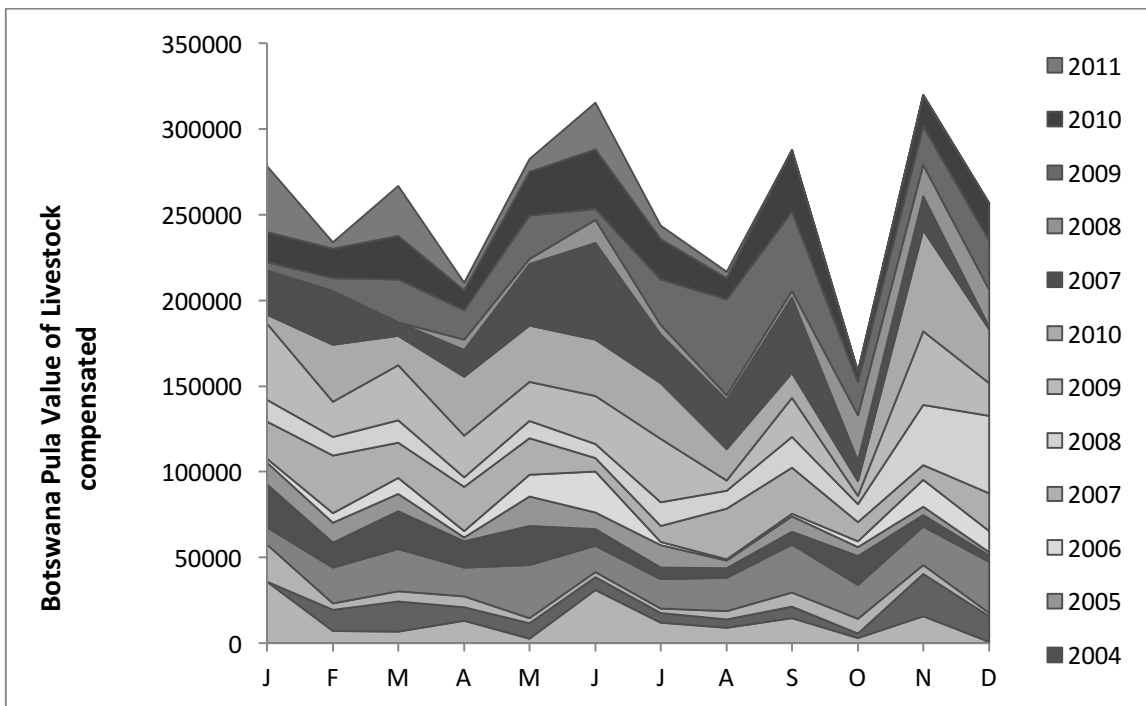


Figure 6-2 Monthly variation of reported livestock losses in the Rakops district varied little month by month for 10 years of data, with a clear drop in reporting in the hottest, driest month, October.

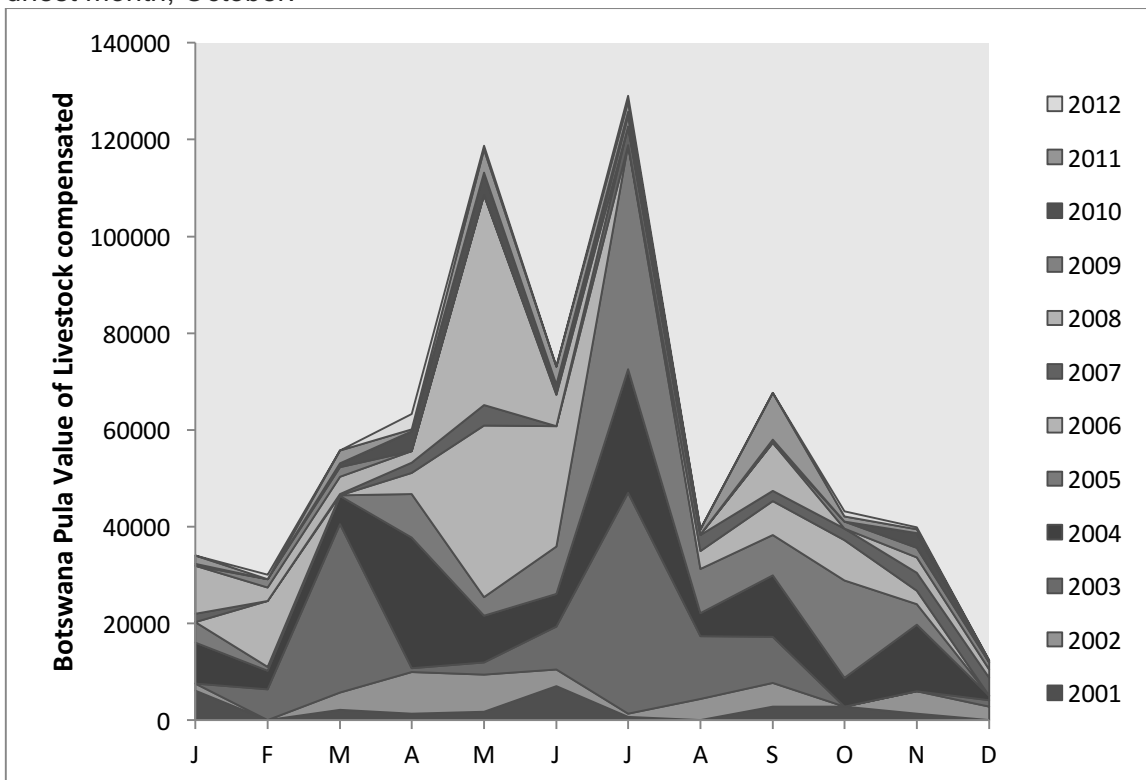


Figure 6-3 Monthly variation of reported livestock losses in the Ghanzi district showed low levels of reporting in the wetter months, with a few years contributing most to May and July reports.

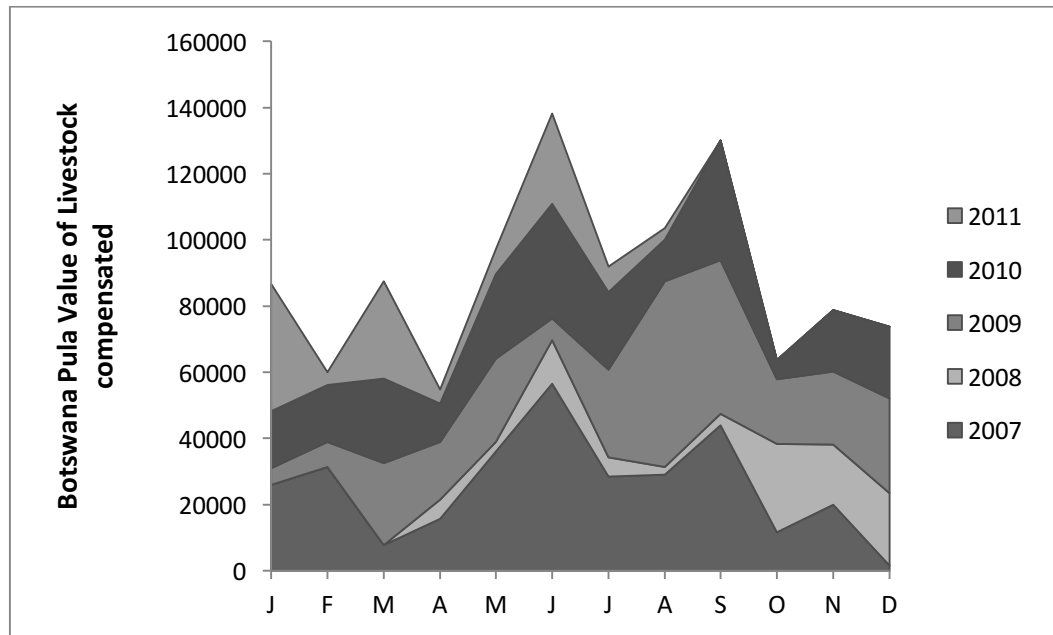


Figure 6-4 Monthly variation of reported livestock losses in the Hainaveld region (Ngamiland district) showed a similar pattern to Ghanzi with greater reported losses in dry cool mid-year months (4 months of data missing from the end of 2011.)

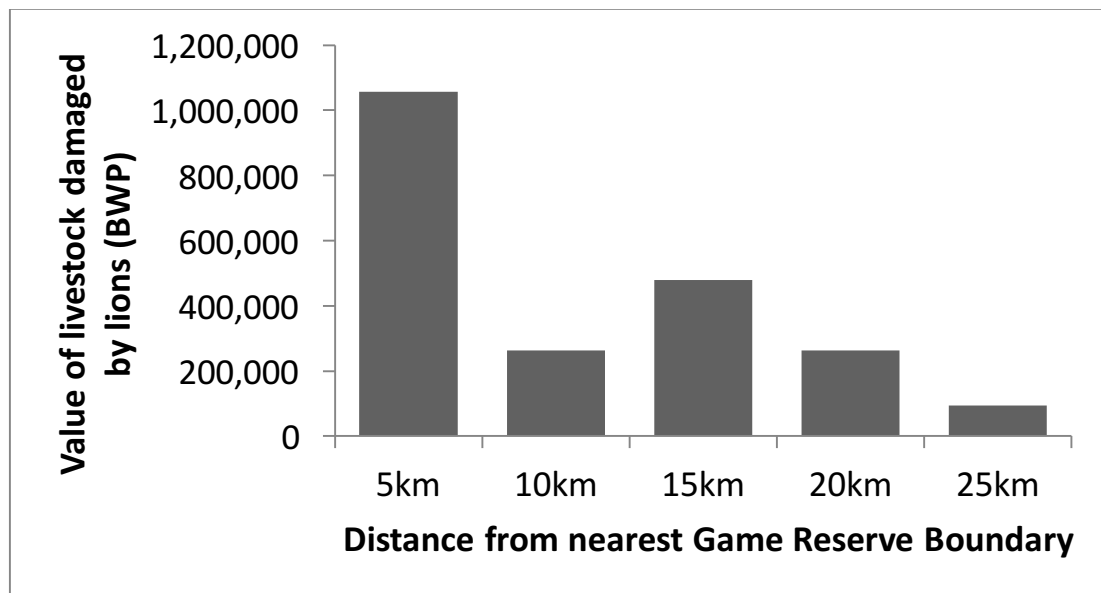


Figure 6-5 The value of livestock damaged by lions dropped off at increasing distance from a CKGR boundary, indicating reserve resident lions were responsible for the greatest amount of damage.

6.4 Discussion

The main prey of Central Kalahari Game Reserve lions are those species above 100 kilograms in mass; with smaller species generally avoided. The two exceptions are the warthog and the porcupine for which a precedence for lion preference is well established (Hayward *et al.* 2011) due to sympatry with the lion, low levels of vigilance and the slow speed of these prey species. The

abundant springbok was eaten by CKGR lions, but distinctly less than would be expected given their abundance. Preferences of the lion are likely to be driven by habitat availability (springbok in the CKGR are generally found in the open pans and avoid dune savannah) and effort/reward considerations of the lion hunting group. The preferences were largely consistent with other findings (Schaller, 1972; Hayward, 2005), although in some areas springbok are preferred by lions (e.g. Nxai pan in Botswana).

The dry 'lean' season is a good time for lions to hunt, as animals are dispersed in small groups so that encounter rates by lions and group vigilance is high; while the dilution effect is impaired (Wrona & Dixon 1991), however young of each prey species are fewer at this time. The GPS cluster methodology biases the study towards larger animals (Bacon *et al.* 2011) where intact skeletons and skulls are easily identifiable up to 18 months after a predation event. This is in contrast to GPS clusters from studies of smaller predators like leopards (Martins, 2010) which have successfully identified small prey items many months after kills; where cached remains are still somewhat intact. I have observed that the remains of small animals tend to be almost entirely consumed by a group of lions. It may be that many of the confirmed kill sites attributed as unknown prey (only bone fragments or flattened grass remained to indicate a kill) should be attributed to sub adults of large herbivore species or to small species. This underestimate of the proportion of a lion's diet that are smaller prey is noted but not expected to effect the interpretation of these data for two reasons. Small prey items are animals that are more homogeneously distributed in the landscape and throughout the year, with localised distributions curtailed by their territorial nature, particularly duiker and steenbok (Smithers 1983) and see Chapter 2 for relevant distributions. Small prey items are of substantially lower mass and are therefore unlikely to contribute to lion diets enough to influence their behaviour on the scale of interest in this study. This is more relevant for groups of lions, including single mothers with cubs, than for solitary individuals.

Predator kill rates are calculated by taking into account all kills over an extended monitoring period (Merrill *et al.* 2010), but finding the majority of kills over long periods requires continuous observation (Funston *et al.* 1998), which is often logistically not possible (Martins *et al.* 2011). Accurate knowledge of the biomass contribution to diet is important for considerations of carrying capacity (Hayward *et al.* 2007a). GPS clusters tend to underestimate the proportion of smaller species in lion diets in two main ways; the predator does not eat for long enough, and then moves on from carcass site before the chosen threshold to make a "cluster" is achieved and secondly by consuming almost all of the remains such that little is left to determine what happened and what was eaten (Franke *et al.* 2006; Tambling *et al.* 2012). During follows of lions, several small kills were observed independently of this kill site analysis. The prey items eaten were one bat-eared fox, three warthog, one steenbok, three juvenile gemsbok, a juvenile kudu and a newborn wildebeest. In many cases lions remained less than 20 minutes and moved considerable distance from the kill site. I inspected eight of these sites and very little remains were evident, sometimes the stomach or intestines of prey, a little hair, only the horns of the steenbok and the hooves of ungulates. Lions also killed porcupine on nine occasions, but the unique quills were always easy to locate. Combined with the short time the lions remained at the kill site, it seems likely that many of these types of small kills

were missed by the GPS cluster methodology which only discovered a single site with porcupine remains. However Tambling *et al.* (2012) showed that the under representation of small species did not significantly alter the estimated composition of lion diet because the large carcasses contributed much higher biomasses to the total diet, 94.8-98.2% in the case of that research. My study was interested in how habitat influences a lions kill site choice and success and how habitat might impact on the lion-livestock conflict. Although lions occasionally kill sheep and goats, their greatest economic impact is upon cattle and our inferences about CKGR lions kill site choice still hold.

Scat collection, on the other hand, over-estimates the contribution of smaller species to the diet of lions mainly because lions ingest more hair from small carcasses, partly while fighting with pride mates for the small meal. For this reason, I did not use hair in scats to estimate biomass. Hayward *et al.* (2011) showed that observed prey preferences of lions are reinforced throughout the hunting sequence, where the typical foraging patterns of lions led them to encounter preferred prey animals more frequently than expected from abundance. Non-preferred prey items were encountered less frequently and then hunted less than expected based on the encounters that they did have, although the initial response was varied. In the context of lion-livestock conflict, this provides a mechanism by which lions learn to avoid cattle when they are often disturbed from feeding by farmers and accounts for the lower than expected rates of livestock killed by study lions.

The most important result from the modelling exercise is that CKGR lions prefer areas with significantly more cover from which to hunt. A preference for greater lion cover at kill sites is more easily explained and confirms evidence from elsewhere (Hopcraft *et al.* 2005). The implication of this pattern also applying to the CKGR region is that farms with increased cover are at greater risk of livestock loss to lions. Overgrazing has led to difficult to manage bush encroachment on many farms, with decreasing carrying capacity that many farmers are very concerned about. While they naturally seek to remedy the bush encroachment, it is likely that a secondary benefit will be to reduce lion depredation. Cattle are also in the middle of the preferred weight range for lion prey. Despite this, lions take far fewer cattle than would be expected (Hemson 2003). This is more true of resident lions than of lions for whom cattle are novel, such as BM052, who had mostly learned to avoid the cattle in his range. There was also evidence that lions preferred areas with tall tree cover. This is surprising considering many of the hunts were conducted at night, and a direct selection for trees is difficult to connect with lion behaviour. Everywhere trees were sparse, and few gave cover close to the ground; cover for lions was not effected by tree presence in the study area. An indirect possibility may be that the tall trees grow in areas that are selected by herbivores for feeding or where lion hunting is more successful. Tall trees will correlate with other vegetation and unmeasured soil type variables that may influence the behaviour of either lions or prey species.

The seasonal and geographical variation found in lion compensation rates may reflect a change in behaviour of either the lions in hunting, the livestock in ranging behaviour (seasonal), or the farmers in kraaling their cattle and their ability to report (geographical). As the fenced farming area experienced greater variation in compensation rates throughout the year, it seems likely that lion behaviour plays a part here. In the drier months the lions

ranged farther afield, in part to seek water, and encountering un-kraaled cattle more often at this time; as traditional three strand cattle fences do not stop lion intrusions. In the communal grazing areas kraals used at night are an effective barrier to lions (Schiess-Meier *et al.* 2007), and almost all cattle taken are those that have not returned to the kraal at night. While both regions would benefit from more effective kraaling, it is a time consuming job requiring constant and considerable effort that many farmers are reluctant to pursue further. A major stumbling block is that many cattle farms are managed by people who do not own the majority of the cattle, are paid low wages and have less invested in the herd. The Ghanzi and Ngamiland regions would benefit greatly from using kraals over the winter months. These farmers currently complain that kraaling reduces productivity, as cattle would normally feed at night. They would prefer to leave all cattle to feed every night of the year, and retaliate by shooting lions on the few occasions they have a problem. On the nearest cattle farm to the CKGR in the Ghanzi district, 49 cattle were killed in a 3 months period, and it is hard to imagine that the productivity of the remaining herd improved enough from night-time grazing to cover this shortfall. The stagnancy of current farming practices is based, to some degree, on tradition, stubbornness and pride (Kent 2011).

The Botswana Wildlife Conservation and National Parks Act of 1992, protects all large carnivores in game reserves and national parks. It has provisions for hunting them on private land and wildlife management areas (WMAs) and controlled hunting areas (CHAs) with a hunting license and under a provisional quota. It also allows for the killing of any animal that threatens life or property, regardless of protected status. The hunting of lions was banned between 2005 and 2009. Then in 2013 a complete hunting ban in WMAs and CHAs was announced for the whole of Botswana in the wake of several government endorsed censuses that indicated many herbivores are in serious decline (BBC 2012). Retaliatory or protective killing of threatening carnivores is still allowed (Part IX, section 46 of the Act) and there is some ambiguity as to whether a farmer may chase a carnivore which has already killed livestock in order to kill it. The ambiguity arises over whether the carnivore remains a threat to livestock, but excludes the right of a landholder to chase the carnivore into reserves and national parks.

Under advice of myself and several others, the government has revised the implementation of the policy of compensation for livestock taken by carnivores. As of January 2014, the compensation value for livestock taken by lions has increased nearly 4.5 times to reflect the average market value (for cattle, from BWP700 to BWP3000). Secondly, while farmers may choose to protect livestock lethally, they will not be compensated if they kill a lion. These two factors were the greatest barriers to compensation as an effective protection for wildlife, and time will tell if there is a reduction of lions killed in the area.

Chapter 7 Central Kalahari Lions: Insights For Conflict Management

7.1 Introduction

Humans benefit directly and indirectly from natural ecosystems (Walker and Salt 2012), receiving many of the benefits without paying for them. The scale of current progress and industry is damaging many ecosystems and the cost will be high. Great potential for nature conservation lies with acknowledging social, health and economic benefits to humans of keeping ecosystems intact and this may be the most powerful conservation tool at hand in the coming decades (Mace *et al.* 2012). This can be achieved by governments legislating for long-term sustainability over short term gains. A successful example of this is the establishment of no-take marine parks in New Zealand. The fishing industry originally opposed marine parks in light of expected losses to their already declining catch, but the marine parks provided refuge for many young fish, and ultimately improved the stocks and catches of some important species outside the marine parks (Gell & Roberts. 2003) with unforeseen benefits to sea grass beds, and long-shore drift erosion processes further afield. Many of the fishermen in this study originally opposed to no-take parks are now supporters of their existence and have benefited in greater income. In this case the benefits were directly observable and occurred within a few years. Benefits of a terrestrial ecosystem that includes large carnivores will need to address the disconnect between those who benefit directly from these ecosystems such as the tourism industry and those in conflict who may benefit indirectly or at longer time-scales, such as farmers. While there are benefits of wildlife conservation to farmers (Knowler & Bradshaw 2006), it is important to address negative attitudes caused by the large time lag before farmers benefit (Gillingham & Lee 1999). Short-term benefits such as free protein from bush meat and reduced livestock loss are powerful drivers of biodiversity loss in Botswana but ultimately cause long-term economic, social, environmental and cultural losses.

There are many reasons why reducing the level of lethal control of lions would be of benefit beyond the conservation of lions. Hunting to control numbers lowers the mean age of lions, resulting in populations of younger predators that are naïve to humans (Sogbohossou *et al.* 2014). They are less likely to be shy of humans compared to the older more experienced predators and often cause more damage amongst livestock, even attacking people. Tracking, stalking and shooting shy problem lions is time intensive, expensive and politically sensitive. In Botswana, farmers often expect the government to control the predators and the two small translocation teams are usually overworked and unable to attend two thirds of proposed translocations in time (pers. comm. Maadi Ruben, Botswana Department of Agriculture). This leaves the organisation in charge of protecting wildlife, the Department of Wildlife and National Parks, the job of shooting problem lions. Lions can retreat across farm boundaries, causing tension between neighbouring farmers. There is a potential for shooting non-problem lions, injury to humans and damage to vehicles and to property. Farmers most often select this method in order to mitigate future

livestock losses to lions, despite the costs. However, anecdotal evidence from this study indicates that shooting resident lions that occasionally take livestock can dramatically increase future depredation in the short term. Young, naïve felids are known to kill livestock more often than older felids (Patterson *et al.* 2004) and North American mountain lions are known to behave in exactly this fashion to newly opened up territories (Maletzke *et al.* 2014, Peebles *et al.* 2013). Each location where lions are in conflict with human activity has numerous differing factors such that management to reduce livestock loss and lion deaths will need to carefully consider local conditions. Initial reductions in lion livestock conflict may lead to localised increases in lion populations, and an increase in the lion population may change the dynamics of livestock loss reducing the effectiveness of particular solutions. Management should therefore be adaptable and resilient. This includes a built in buffer to absorb unexpected fluctuations. The CKGR conflict zone is characterised by low quality farms, dry conditions, lions with large home ranges and a range of farming types from European style fenced farms to unfenced communal grazing. In this chapter I will explore how the information found in Chapters 2 to 6, combined with the local conditions of this conflict, influence and limit the choice of management options that are available. I will first recap the history of the conflict in the CKGR, before addressing current and suggested solutions to the conflict.

7.2 History of the conflict

In the CKGR lion density is low (3 per 100km² (Botswana Environment Statistics Unit 2005) ; 2.8 lions per 100 km², this study) compared to the Moremi Game Reserve in Botswana (8.0 to 11.5 lions per 100 km², (Bauer & van der Merwe 2004)), Kruger National Park, South Africa (9.3- 12.6 lions per 100 km², (Bauer & van der Merwe 2004; Smuts 1978)) and Serengeti National Park Tanzania (4.4-8.1 lions per 100 km², (Packer 1990)) but slightly higher than other Kalahari areas like the Kalahari Transfrontier Park (1.1-1.3 lions per 100 km², (Funston 2011)) and Etosha National Park, Namibia (0.8-1.2 lions per 100 km², (Bauer & van der Merwe 2004)). Initial estimates of other predators like cheetah, wild dog and leopard from spoor transects are tentative but also seem to be very low (pers. comm. G. Maude, Central Kalahari Predator Research Group). As terrestrial carnivore densities are always much lower than densities of their prey (Farlow & Pianka 2003), populations of predators require very large areas to remain viable and those in arid and semi-arid environments more so. Meta-population theory states that connecting small population areas with corridors or even translocations can be effective at bolstering long-term population and genetic viability (Dolrenry *et al.* 2014; Olivier *et al.* 2009). It is no longer sufficient to discount small protected areas that contain “unviable” populations and large reserves should be seen as reservoirs required for long-term viability of these small reserves. In this regard CKGR should not be considered on its own but as an important resource for the greater Botswana lion population. Increased connectivity between reserves is tantamount to lion conservation on a national and international scale (Elliot *et al.* 2014).

The continued health of herbivore communities is often dependent on a healthy predator guild for maintaining biodiversity and productivity through cropping (Wallach *et al.* 2009) and mitigating trophic cascade changes in the ecosystem (Berger *et al.* 2008; Callan *et al.* 2013). The low densities of both

herbivore and carnivores in the CKGR is offset by the large size of this reserve. Its populations of globally vulnerable African predators is important in terms of conservation. The presence of the vulnerable cheetah and the endangered African wild dogs is important. As for lions, the IUCN (2006b) lists the species as vulnerable and the Central Kalahari Game Reserve as an essential part of the Kgalagadi lion conservation unit (LCA). The Kgalagadi LCA contains the CKGR in the centre of Botswana, the Kgalagadi Trans frontier Park in the south of Botswana, the area adjoining the two, and an area to the west incorporating Xai Xai and Ghanzi district. A comprehensive lion conflict management strategy for the CKGR should consider the presence, conflict situation and conservation of other predators, herbivores, water resources, grassland health, who will bear the economic burden of conflict reduction and who will benefit from it. Current schemes such as compensation and lethal control spreads benefits thinly across the whole country, but a directed management plan should consider that targeting particular areas may achieve conservation goals much more economically. The aim of conflict management in this situation needs to be explicitly addressed.

Reduction of the human lion conflict has two major objectives reflecting the major stakeholder positions. The first is to reduce the loss of livestock to owners and the second is ensuring the future of lion populations. Two main stakeholders make up the bulk of the stakeholder position interested in livestock loss reduction; the government, who has reduced cost in investigating and compensating losses and a benefit in redressing a political concern. The second is the farmers for increased productivity in cattle and reduced man hours devoted to mitigating or preventing loss (fence repair, lethal control, loss reports etc.). There are many stakeholders that benefit from the reduction of lion lethal control, including the owners and operators of tourist enterprises, the guests that visit the CKGR, the herbivores and any who benefit from a more intact ecosystem and the services it provides (clean water, air, a carbon sink etc.). Reducing the livestock conflict need not be a zero sum game as both stakeholder sides can benefit from conflict reduction. Reducing the instances of conflict can be achieved by novel methods, but as yet stakeholders from either position are unable or unwilling to bear the costs. Using the information from this study I hope to discuss the likely outcomes of management options in the CKGR setting as many options may not survive a simple cost benefit analysis.

Early attempts to reduce predator populations by culling were very successful in Africa with greatest reductions in populations occurring with the introduction of high powered rifles and four wheel drive vehicles since the 1950s (Schaller 1972). In a climate where lions are desirable by at least some stakeholders (and I argue, all stakeholders), the efficacy of current conflict mitigation techniques in the CKGR area does little to address both objectives or benefit all stakeholders. Two neighbouring forces are at odds and are set to remain that way; a conservation area where lions are desirable adjacent to a farming zone where lions are undesirable and lethal control is practiced. The decline of lions has continued despite compensation schemes, and reports of livestock losses have also increased in some areas. In the Rakops district the values compensation claims has increased by on average P17,000 per year, while the general trend in Ghanzi is a decrease in claims. These seemingly contrary results are possible because of the steady increase in the number of farms in the Rakops area, while some Ghanzi farms have recently converted to

game, losses of which are not compensated. Ghanzi farmers indicated that it was usually “not worth their while” to claim for cattle losses, as it involved several trips to town (personal communications). Current management strategies in Botswana focus on the lion, include translocation, lion proof fences and population control (Hermann *et al.* 2002; Macdonald & Sillero-Zubiri 2002; Stander 1997). These methods tend to be expensive and costs grow as the two objectives are met: as livestock populations expand or as lion populations recover. The effectiveness of current techniques is doubtful (Hemson 2003). Alternatively, conflict mitigation strategies aimed at the farmer such as improving herding and kraaling or mixing game in the landscape offer benefits to the farmers such as better livestock husbandry, improved productivity and improved rangelands. While costs of current lion-focussed strategies grow as they are effective, farmer-focussed strategies have the potential to off-set the cost and so ensure their continued adherence (Frank *et al.* 2006; Hemson *et al.* 2009). If adhered to they have the potential to eliminate much conflict, while lethal control and compensation have no way to do this while lions continue to survive in the protected areas.

While lethal strategies will continue to dominate conflict in the foreseeable future (Baker *et al.* 2008) it is apparent that in many cases little is understood about factors contributing to livestock predation and the effectiveness of both lethal and non-lethal methods. Human and economic considerations continue to dominate the political response to carnivore conflict. In Botswana where protected animals such as lions and African wild dogs are considered protected species, conflicting legislation protecting property outweighs the predators protected status and allows for lethal control. Policy that target improved farmer practices such as herder accreditation or tax incentives for improving rangeland and herding culture can be effective and offer a lucrative way to improve general productivity and reduce conflict (Gillingham & Lee 1999).

Estimates of actual rates of predation from reports by farmers underestimate predation for various reasons. Capital and resource poor farmers in remote areas are less able to report losses and some carcasses are removed or never found. It is possible that there is over-reporting by farmers who assume that all missing livestock can be attributed to protected predators (Vos 2000) and the accuracy of DWNP investigations is not well known. In Botswana when spotted hyaenas were removed from the list of predators for which compensation was available, the numbers of spotted hyaena reports decreased while those of listed predators increased (pers. comm. DWNP office Rakops). In Chapter 6 I only used successful compensation claims, which require proof of carnivory and identification of the predator from spoor or carcass sign. Even so, the perception of predation may be more important than actual levels of predation, as it is upon the perception that livestock owners respond and kill predators. This is especially true when considering smaller predators and scavengers, such as brown hyaena (*Hyaena brunnea*) which are unlikely to ever kill livestock, but being often found on dead livestock are heavily persecuted. Lions are elsewhere known to be opportunistic scavengers and may be mistakenly blamed for kills (Schaller 1972).

Stakeholders continue to emphasise the importance of livestock when sometimes predation can be a minor component of livestock loss. Losses to disease, poor rangeland management and natural disaster can be much

greater, but many farmers feel they cannot combat these problems and underestimate these losses when forming attitudes (Schiess-Meier *et al.* 2007). Predators generally consume more wild prey than livestock, despite livestock outnumbering wild prey (Gazzola *et al.* 2005; Marker *et al.* 2003; Meriggi & Lovari 1996; Valeix *et al.* 2012a) but farmers generally do not accept this, arguing without evidence that cattle are easier targets. It may be difficult to change farmer perceptions, but this knowledge may lead to other ways to increase wild game in farm areas which will act as natural buffers to livestock predation.

7.2.1 Defining the problem in reducing lion - human conflict: Appropriate goals.

Although the conflict is a relatively simple one, there are two different farming strategies in the conflict that need to be considered. European style fenced ranching of cattle and game, and traditional cattle-posts with shared communal grazing. Both experience conflict with lions killing their cattle, yet each has different approaches to cattle ranching, a different capacity for dealing with lions and differing attitudes to farming and willingness to change farming practices (Kent 2011). There is a geographic correlation between farm styles in the immediate surrounds of the CKGR arising from historical land acquisition: European ranching in the west, traditional ranching in the east, and mixed in the north (see section 1.3.1). Some fenced game ranching occurs in the north and west which generally does not consider lions a threat. For lions dispersing to the west there is great difficulty in crossing the farms, as a lion will find little refuge or wild game, many roads and antagonistic farmers in this direction. It is a 184 km walk to the Namibian border through an inhospitable region before a dispersing lion might find a pride to take over or an area to settle without persecution. In this direction lions encounter the greatest resistance and from reports experience the greatest loss to retaliatory killings. If a solution to conflict was sought in the west, the greatest reduction in lion shootings may result (Kent 2011), however without anywhere to expand to it is unlikely that this result will contribute to the meta-population. While lethal control here may reduce the CKGR population, considering the large population and growth rates of study prides as long as the levels of lethal control remain stable there should be no impact on the total population. However, reducing the need for lethal control will please both farmers, DWNP officials and create political goodwill. The economic benefit to farmers in this area is low as a percentage of total income, as farms are productive, typically experiencing calving rates of greater than 80% (H. *et al.* 1974) which is indicative of farm profit.

For lions that exit the park to the east it is 39 km to the Makgadikgadi Pans National Park (MPNP), a day's walk through communal grazing for a determined lion. The local farmers here have few fences and generally share old vehicles and weapons that are barely adequate to find and kill lions. A dual carriageway highway crosses from north to south and substantial numbers of wildlife cross this road regularly. There is a small resident lion population in the MPNP which experiences high levels of conflict with farmers between the two reserves, especially as the migratory population of Burchells Zebra (*Equus quagga*) ebbs and flows across the park, following the rainfall. An estimated

population of 50 lions in the proximate region of the MPNP (the Boteti River) was reduced by half in 2008, and this population would potentially benefit most from preserving the current levels of movement of lions from the CKGR (Elliot *et al.* 2014), both genetically and to bolster population losses to conflict. There is evidence that the MPNP population is itself connected with other populations of lions in Africa, namely the Chobe National Park population in the north, and the Zimbabwean populations like Hwange, to the north-east (Hemson 2003). Therefore a reduction in lethal control to the east of the CKGR will contribute both to farms as well as the greater lion meta-population.

Since calving rates are considerably lower in the area at around 30-50% and cattle mortality and productivity is generally low (Reed *et al.* 1974). Here, any reduction in livestock lost to predators has great economic benefit to individual farmers; much more so than in the Ghanzi region. The same could be argued to a lesser extent to the north of the study area where mixed farming is practiced and the Okavango Delta lion population is close at hand. It is desirous to reduce the conflict in all zones but in a sector with restricted resources I would argue that the Rakops and Hainaveld region is of a higher priority for both farmers and lion conservation goals.

Although the distance between the CKGR and the MPNP is short, it is increasingly difficult for lions to cross the farmland separating the two, with numerous cattle-posts. Wild game is reduced in this zone and it is unlikely that lions are able to regularly cross the region. As farm numbers increase, this area will only become less permeable to lions. Ranchers here are less able to carry the burden of livestock loss, but are also less able to kill lions. Compensation records indicate larger livestock losses to lions in this region, but the trophy records suggest that fewer lions are killed here. The political climate differs between the regions; European style farmers have greater political influence per individual as they are successful businesses with many employees and contribute significantly to the agriculture sector and the political life of Botswana. European descended farmers prefer to handle issues such as problem lions themselves (Kent 2011), while the majority of traditional cattle-post owners have stated that they believe the government is responsible for problems caused by wildlife and insist on government assistance (Schiess-Meier *et al.* 2007).

Both farmers and reserve management have called for solutions to the conflict with lions, but they both emphasise techniques that do not redress lion population conservation. The main problem they want to solve is the loss of cattle, the effort in tracking down, translocating or killing problem lions and the bad publicity associated with lethal control. The Botswana government has the unenviable position of balancing angry farmers and a critical international community that values the existence of lions and natural ecosystems.

It is common to label any lion that kills livestock as a 'problem lion', yet the study lions encountered during my research did not neatly fit the definition. Linnell *et al.* (1999) proposed that predators will be divided into two sets of individuals, those that kill livestock as they are encountered amongst their natural prey, and those that favour livestock. The latter can be considered "problem individuals". It is generally accepted that livestock have lost almost all of their natural anti-predator mechanisms and are at greater risk of depredation. Farmers disproportionately value their own livestock over any nearby wildlife that may feed lions, and so conclude that any lions nearby are almost exclusively killing cattle, while my experience following lions near the border of

the reserve showed the opposite to be true (see Chapter 3, section 3.5.2.10 and 3.5.3.11). This neglects important evidence that livestock are afforded some of the greatest anti-predator mechanisms by virtue of vested human interest – herders, fences, dogs, vehicles and rifles. In this setting only some lions will gain the skills necessary to access livestock. Young predators and cautious females are less likely to overcome this obstacle. Only the few lions who regularly access livestock for which standard protection mechanisms are insufficient should be considered problem lions. Lions that kill livestock generally do so at rates much lower than expected, most likely learned due to experience with human responses to depredation (Hemson *et al.* 2009; Valeix *et al.* 2012a).

The evidence from my research into CKGR lions as problem animals points to the majority of lions killing cattle at a much lower rate than expected from the cattle/wild game ratio, but the overwhelming response is to label this group as problem lions. The reason this is important is that farmers believe that removing only the problem individuals will reduce the conflict over-all by leaving only non-problem lions. However, I have observed the opposite to be true. Resident lions near farms, which kill livestock at a much lower than expected rate, when shot are replaced by naïve lions that kill livestock at higher rates. This is evidenced by the high mortality amongst collared lions near the boundary despite a preference for wild game, the reporting of problem females and young lions, and the seasonal variation in livestock hunting in the Rakops region. Here, predation is higher during the dry period when cattle are more likely to spend the night in the boma (Chapter 6). It also reflects similar conclusions in other studies (Hemson *et al.* 2009). This has important implications for conflict management. Problem lion are typically considered to be only a small part of the population, and the current removal paradigm insists on the need to cull or translocate problem individuals to allow co-existence with non-livestock hunting lions. I interpret the observations of my study lions as evidence that problem lions do not exist, and the current labelling categorises all lions that are simply in the wrong place. The evidence presented in Chapter 3 and 6 indicates that lethal control is counterproductive. When livestock is unprotected and lions highly mobile, potentially all the lions that reside in the protected area could become problem lions and this is unsustainable. Lethal control both increases livestock loss and decreases lion conservation, which is in direct opposition to the goals of reducing lion human conflict. Real conflict mitigation can only begin when herding practices change. The main obstacle to improving farming methods remains the political dilemma of “telling farmers how to do their jobs better”, but smart incentives from government and private initiatives have great potential to overcome this. I will now explore proposed mitigation strategies including lion focussed and farmer focussed strategies in light of both mine and general research and the particulars of the CKGR conflict.

7.3 Potential solutions for the conflict

Farmers, conservation groups and the Botswana government have proposed a variety of solutions to the conflict. Historically lions have been shot

as problem animals, extirpated across grazing areas, and kept away from cattle by bomas. Grazing practices have changed and boma use at night has declined in recent decades (Hemson *et al.* 2009). In traditional cattle-post areas there are no fences, and cattle are expected to return to the boma in the evening for watering; some proportion do not (Hemson 2003). Large-scale cattle farms leave the cattle to roam the whole property hemmed in by the fence line. Doing little by way of preventing access to cattle, and then shooting problem lions has been the preferred loss mitigation method. There is little evidence to back up its efficacy, and evidence from this study that it is less effective than a preventative strategy and causes greater livestock loss and knock on effects in the social structure into the reserve.

Sections 3.5.2.2, 3.5.2.9 and 3.5.2.10 describe the death of lions who mostly preyed on wild game, but were killed after eating between one cow (two lions) and three cows (one lion). This highlights the complexity of problem animal control for reducing livestock loss to predators next to protected areas. The government and people of Botswana has shown that many value lions, and seek to protect them through legislation and by implementation of national parks and wildlife management areas. Yet it still places greater value on livestock, and allows the lions to be killed to protect the livestock.

Two examples from my research highlight the impact that lethal control has on the lion-livestock conflict. In the first example, lion SM009 died of natural causes, and his territory was explored by neighbouring resident lions within a few days. In the second example the lion BM052 was killed by cattle farmers after eating three cattle in 408 days of study, and several wild animals per week otherwise. The subsequent damage by neighbouring lions exploring the empty territory resulted in the deaths of a reported 49 cattle in less than 90 days. Saying that another way, the livestock lost to lions before lethal control was on average 0.22 cows per month, and after lethal control greater than 17.3 cows per month in the short term. I was told that more lions were shot but they were not part of this study, and the number was not disclosed. While the farmer blamed a general trend to a “worsening of the situation”; there was a clear misunderstanding about what makes a problem lion. Inexperienced lions that emerged from the protected area were a real problem when they encountered slow unprotected cattle. The original “problem” lion, averse to human cars and their cattle, had acted as an unwitting protector, preventing other lions from accessing the farms and livestock. While BM052’s ‘costs’ of three cattle had been too high for the farmers to bear, the costs of losing his protection seems to me to be much higher. A nearby female, BF053, spent most of her time preying on only wild game in 632 days of study, and was shot after killing one cow on the same farm.

There are several examples where lion populations well below carrying capacity have increased substantially when left undisturbed, that is, no hunting of lions, and a hitherto underutilised prey base (Anderson 1981; Hunter *et al.* 2007; Smuts 1978). In some ways this points to the inadequacy of removing problem lions when protected areas exist nearby. Removing problem lions may have little impact on the population as a source of more potential problem lions, but does hinder meta-population dynamics, genetic flow and immigration. Lion populations have decreased across Africa due to habitat and prey animal loss, urbanisation and historical predator persecutions and not so much because of problem animal control. Instead removing problem animals is costly and causes

greater problems and may have little or detrimental effects on livestock productivity due to ecosystem degradation, meso-predator release and allowing access to inexperienced lions.

There is also little evidence to support many proposed solutions and inadequate resources to attempt all of them. In this section I will explore the suggestions I have encountered interviewing farmers and other stakeholders, with respect to the data acquired during the course of this study and considering local conditions.

7.3.1 Lion focused strategies

7.3.1.1 Provision of waterholes or greater prey numbers in the protected area

It has been suggested that lions exit the park to seek water during the dry season and that providing more waterholes in the reserve may curb this behaviour. This was mostly suggested by farmers in the west, and the problem animal control records there seem to bear out that livestock loss was greatest in the dry season (see Figure 6-3 and Figure 6-4). However the pattern was not observed in the Rakops region over a ten year period (see Figure 6-2) indicating that the problem is more complex and more likely related to farming techniques than water provision. Historically there was no freshwater available in the region for around six months of the year, and around half of the prides I studied did not have access to any of the new waterholes. Most managed the long dry period without water. Additionally the quality of the deep ground water provided at the existing waterholes is extremely saline and of poor quality. Waterholes have been successful at boosting wildlife numbers elsewhere in Africa (Valeix *et al.* 2009) but there may be unintended consequences in a system for which year round water provision is novel (Smit *et al.* 2007).

In similar reasoning it has been suggested that boosting numbers of wild game in the reserve would reduce the incidence of livestock loss, as farmers assume the perpetrating lions are hungry. This could be achieved as has been done in the past, where game farms were legally obliged to release some proportion of their stocks. Again my research seems to argue against this line of reasoning on two fronts. There may be room for more herbivores in the form of a migratory species like the wildebeest, but with the migration route cut-off, non-migratory species are unlikely to be able to fill the void. Resident populations of gemsbok, hartebeest, eland and springbok are restricted by dry season productivity and the CKGR is likely to calibrate to carrying capacity for resident herbivores. From the lion's point of view, the main reasons for forays outside the reserve are social, either increasing or seeking new territory, or searching for mating opportunities (Chapter 4 and 5). Livestock loss in the CKGR setting is usually incidental to this. While I would like to see an increase in the wildebeest migration in the CKGR, this strategy and the provision of waterholes will only lead to a new equilibrium for the lions and herbivores of the park, and just as likely increase the conflict. The data from this study does not support providing more waterholes or wild game as a means to reduce lion livestock conflict.

7.3.1.2 Fences

Multi-variate analysis into the viability of protected reserves of Africa and the factors that lead to the greatest success in long-term lion population survival showed that predator proof fencing of reserves has the greatest potential to conserve lion populations (Packer *et al.* 2013). In the study, most reserves were much smaller than the CKGR, and a small effect was noted concerning the size of the protected area involved. Other important factors included the management budget available, the size of the adjacent human population and governance of the park. When the insights are applied to the CKGR, it indicates that the reserve is not likely to suffer from complete loss of lions anytime soon, and is more than likely a viable source population of lions without the need for fencing to conserve. Predator proof fencing could reduce the number of cattle being killed every year, but the potential for economic savings does not approach the cost of building and maintaining a fence. Packer *et al.* (2013) estimate current costs of predator proof fencing at USD3000 per km, and the CKGR needs a further 860 km for a total of USD 2.6 million. I estimate that real world losses to cattle farmers bordering the CKGR are USD244,000 per annum based on reported numbers of livestock lost (Chapter 6), and 2013 market values and mean weights (Botswana Central Statistics Office 2011) rather than compensation values paid out. Notwithstanding maintenance costs (likely prohibitive because of the occasional presence of African elephant, *Loxodonta africana*), a predator proof fence will only recover costs after 10.67 years of service. A fence would further reduce the ability of wild herbivores like blue wildebeest to migrate properly. Fences similar to that proposed for the CKGR have been less than successful. For instance the national park fence at the Boteti River boundary of the Makgadikgadi Pans National Park has no regular maintenance to fill small holes dug by small animals, or make regular repairs to the electrification systems, and that around the Khutse game reserve was so poorly built at great expense that it does not stop movement of lions or even herbivores. Generally game fences around private farms are maintained only enough to hold game, and are ineffective at stopping lions. However fencing is a popular political move that engenders general goodwill and support from farmers, conservation bodies and the international media alike and continues to be proposed by the DWNP for serious consideration.

Respected ecologists familiar with the African stage disagree about the future of fences as conservation tools. Woodroffe *et al.* (2014) showed concern that fences impede migration and stifle meta-populations and should be last resort tools in conservation. Pfeifer *et al.* (2014) responded pointing out that in the current developing world where conservation conflicts are high-stakes, fences have proven the only tool that allows co-existence of wildlife alongside impoverished and hungry human populations. Fences are more economical when both livestock and wild game is at higher density, and the low density of both in the CKGR suggests to me that this is unlikely to be a useful strategy for reducing conflict.

7.3.1.3 Conditioned Taste Aversion Therapy

Conditioned taste aversion (CTA) therapy involves the training of wild predators to avoid livestock despite proximity and a lack of protection, by

exploiting this well-studied phenomenon. This strong physiological response occurs when an animal feels nauseas shortly after consuming a particular food item and associating that feeling with the food item, whether or not the food caused the illness (Silva & Soto-Blanco 2010). It is so well established that researchers use the expectation of CTA to test for memory, memory loss and learning behaviour in neuroscience (Bures *et al.* 1998; Dragoin *et al.* 1971). In one study 75% of foxes (*Vulpes vulpes*) were shown to avoid a particular meat on seven consecutive occasions after initially consuming it with a harmless drug (Levamisole) that induced nausea (Massei *et al.* 2003). Coyotes (*Canis latrans*) were similarly shown to stop killing live sheep after being administered doses of lithium chloride (Gustavson 1979).

There is considerable promise for this approach in the CKGR, where current herding practices could continue and theoretically part of the predator population could learn to avoid livestock. Untreated or unaffected individuals would be removed in line with current problem animal removal strategies, effectively creating for the first time a population that will not be considered problem lions by management. This could make an effective buffer population surrounding the reserve. However the high cost associated with constant interference makes this option less sustainable than a change in herding culture. Training of herders in animal husbandry, disease recognition, range management and supplemental feeding can be positively associated with tighter herding has additional economic benefits for the farmers that would endear this paradigm and ensure its long-term sustainability without constant contribution from an outside organisation. In 2012 CTA was demonstrated with a number of captive Kalahari lions (Glyn Maude & Bill Given, unpublished data) with some success and in situ trials have begun, but logistical constraints have not allowed for demonstration of the method in the field.

7.3.2 Non-lethal population control

Hormonal contraception has been promoted to control lion populations (Orford 1996; Orford *et al.* 1988; Orford 1988), and seriously suggested by stakeholders of the CKGR lion conflict. The main argument in favour of the method is as a counter to lethal control which cannot take into account variation in future populations from unforeseen disasters such as the 1980 drought in Etosha, Namibia. The methodology is touted as more humane but consideration should be given to the high cost to the lions of finding, chasing, darting, the immobilisation drugs, the minor operation and the effects of hormone treatment. The economic costs of darting sufficient lionesses to control the population and the treatment itself are prohibitive and an in depth cost benefit analysis is beyond the scope of this study. My experience in darting lions required many of the same resources and suggests that this is unlikely to be an economical solution in the CKGR. It may however be a useful stepping stone when applied in smaller areas where other solutions are problematic.

7.3.3 Farming technique focussed strategies

The conservation of lions is part of the conservation of Botswana's natural ecosystem which has benefits for many people around the country. However the costs of lion conservation under current management is borne by

a relatively few, namely the farmers who live adjacent to protected areas. By acknowledging the benefits of intact wild systems through taxation, education programs and opening reserves to the public, the cost of conserving lions and their environment may be shared amongst more of the real stakeholders who are set to lose the benefits. Here I explore some of the ways in which lions offer value to a greater number than currently recognise it. They mainly rest on the theory that top predators like lion regulate the herbivores which in turn regulate habitats and ecosystem as a whole (Blaum *et al.* 2007; Blaum *et al.* 2009).

7.3.3.1 Adaptive management and resilience theory

The term resilience is used in many contexts as a desirable state for most systems. However resilience theory, as advocated by Brian Walker and colleagues argues that a resilient system is resistant to change, but adaptable in the face of change (Peterson *et al.* 1998; Walker & Salt 2012). Further they argue that productivity may have to be sacrificed for true resilience, but this is more desirable than most fragile yet productive systems. Resilient systems are usually costly as they ensure the system can withstand great disturbances that cannot be anticipated. An example given is the Deforestation (Walker & Salt 2012). Forests can handle a certain level of forest removal and recover naturally, but may have a threshold where erosion and key species loss causes a domino effect leading to unrecoverable change and loss of forest. Agricultural systems are increasingly brittle systems, pushed there by the increasing economic demand for cheaper, more efficient food supplies that can meet demand year around. Agricultural systems have met these demands by becoming increasingly single product based, using many highly technical mechanisms to increase productivity from fertilisers to hormones to pumping deep fossil water sources and pushing stocking rates on marginal land (Anderies *et al.* 2006). High-pressure brittle systems have little give when the unexpected occurs, or often bailed out by governments' intent on stabilising food production and often have little room for consideration of externalities, such as run-off of chemicals or trophic cascades of nearby wildlife zones.

In contrast a resilient system seeks to redress the importance of natural systems for buffering the effects of climate change or catastrophic weather (Tompkins & Adger 2004). Externalities are important as a resilient manager with a long-term view acknowledges the impact of the run-off from their property or resource use like groundwater extraction can have unknown impacts at some future time. Short term productivity is reduced in favour of more stable long-term productivity at some lower level. In the context of the Kalahari lion-livestock conflict, farm managers would seek to increase their long-term viability by reducing cattle stocking rates on their marginal properties in anticipation of lower productivity cycles, and mix game farming or non-consumptive use of wildlife on their properties so that they have a diverse land usage. Overall productivity may be expected to increase as mixed use lowers bush encroachment of woody shrubs and a mix of browsers and grazers tend to produce a greater yield of meat for unit area. This resilient system would acknowledge the role that lions play in reducing meso-predators, protecting cattle from naive predators and stabilising game populations which in turn promote the greatest grass yields. While the theory alone cannot address the

unique Kalahari system, the principles of an adaptive management strategy (Berkes *et al.* 2000a), where novel methods can be tried, monitored, tested and evolved has a great chance of success within the resilience framework.

7.3.3.2 Small area cattle grazing (“Holistic Management”)

The Kalahari grazing belt is a marginal yet profitable area for beef cattle, and farmers complained that stocking rates had declined in previous decades and blamed increased woody shrub encroachment (Kent 2011). On the typically large properties in the area, woody shrub removal is prohibitively expensive. There has been considerable recent interest in improving grazing potential for marginal and degraded lands by changing grazing patterns of cattle (Estrada *et al.* 1997). Janzen (2011) showed that a particular planned grazing farming strategy allows rangelands to recover from traditional grazing while allowing cattle to feed, and did so better than resting the rangelands. The method is called Holistic Management by the Savory Institute and I will refer to it as Savory Intensive Grazing Management (SIGM). According to Savory, it is distinct from rotational grazing; the method claims that concentrating cattle numbers in very dense herds to remove the hardest of vegetation through both hoof impaction and browsing. Where selective grazing under other systems by cattle allows cattle to avoid woody shrubs, here they will be removed by the high cattle density, allowing grasses the greatest window to establish in the longer recovery periods, gradually reducing bush encroachment. The important aspect here is the high densities maintained in a small area (a Zimbabwean system example is 400 head of cattle in less than one hectare for three days) by a few herders and a cheap, mobile fencing system. The SIGM method claims to reduce bush encroachment, and if this were true would inhibit lion hunting in farmlands. Despite fantastic claims by proponents of SIGM in Australia, North America, South America and Africa (Sherren *et al.* 2012), there is little published research that can be said to support the methods claims for increased animal productivity or rangeland improvement and several peer-reviewed articles that show no such effects, reviewed in (Briske *et al.* 2014). However if SIGM has similar levels of productivity to continuous grazing, there are two main reasons why adoption of some of its methods would be of benefit to the lion-livestock conflict for both farmers and lions, decreased exposure to lions, and tolerance of wild game for lions to hunt.

As no other fences are needed to be maintained on the property (30 - 90 km of fencing is needed on typical Ghanzi or Hainaveld farms), and a diversity of wild game on the property is encouraged, predators moving through the landscape will have access only to food of little value to the farmer and no access to livestock. In the Kalahari grazing system this method would be much cheaper than the current techniques used on European farms, whereby large work forces are employed to maintain expensive long fences, the many water holes around the large properties and there is little contact with cattle for long periods. The main premise of SIGM involves keeping an entire farms worth of cattle in a less than half an acre using a simple portable fence, usually some trained dogs and minimal staff. Three or four workers can manage herds of several hundred. The cattle remain in the enclosure for several days, grazing and browsing the woody shrubs, before moving a few metres to the next

position where they will remain for a few more days, and SIGM only requires the nearest waterhole to be maintained. SIGM would also allow for faster determination of disease in cattle and allow for greater control and husbandry of the animals. If the method also improves stocking rates and overall productivity of the farm, it may be encouraged without direct mention of lion conservation goals, and could be adopted on the economic and effort merits. The Ghanzi community has been slow to trial the new methods but the method has had great uptake in neighbouring Namibia and farmers there claim to see an improvement. Perception of improvement and the wellbeing and reduced workloads of farmers can also be worthwhile drivers of new farming techniques.

The SIGM method is intriguing but its major claims about carbon sequestration, reversing desertification and increasing cattle productivity should be approached with scepticism. Some aspects may provide benefit to the lion-livestock conflict situation and should be trialled within an adaptive management framework on farms around the CKGR.

7.3.4 Valuing lions

The benefits of conservation of native species are widespread and thus the costs of conservation should not be borne by a few. In the case of the lion-livestock conflict in farms around the CKGR, lion conservation is desirable by those involved in the tourism industry, reserve management, visitors from foreign countries, and as I've argued, indirectly by farmers who desire improved rangelands. In this conflict situation the immediate costs of conservation are borne by farmers alone, while reducing the incidence of conflict will benefit all stakeholders. The problem is complex yet not intractable. In this section I explore some strategies to spread the costs of lion conservation between more stakeholders by acknowledging benefits that an intact CKGR ecosystem including lions has farther afield and employing a system of environmental economics to demonstrate that value.

7.3.4.1 Invasive species and climate change

A major effect of climate change is the shift in distribution of species (Altmann *et al.* 2002) and communities of native species should be preserved where possible in order to buffer the worst effects of climate change. Novel communities are established as species move at different rates and even in different directions according to various drivers like rainfall or temperature. Some are restricted in moving due to human barriers such as roads and the network of fences that criss-cross southern Africa (Gadd 2012). While some species will flourish it may often be at the expense of others. Lions for instance are very adaptable with respect to temperature and rainfall, but rely on their prey species which may be less adaptable. Many species are expected to decline due to climate change and those that might adapt will be slowed by recent human disturbances to the landscape (Andrews & O'Brien 2000; Thuiller *et al.* 2006). Ripple *et al.* (2014) demonstrated that apex predators such as lions are important buffers for ecosystems during disturbance like climate change. Re-introduced Gray wolves (*Canis lupus*) in Yellowstone National Park buffer the boom and bust cycles of carrion availability to scavengers as diverse as

corvids and grizzly bears by stabilising the timing and abundance of carrion. Predators play an important role in reducing over-abundance of any one particular species in their target weight range by *de facto* selection of the most abundant species (Sergio *et al.* 2008). Both native and introduced species are less likely to become invasive when ecosystem inter-dependencies remain undamaged (Ripple *et al.* 2014). The Kalahari is large ecosystem with productive grasslands. It currently acts as a substantial carbon sink, although it would perform better if it were less degraded (Kulichenko 2011). As global climate is on a course to add 2 to 4 degrees Celsius by 2100 (Allen *et al.* 2014), the adaptable and resilient Kalahari lion has a role to play in mitigating trophic cascades in wildlife and vegetation of the area, and buffering the effects of climate change and greenhouse gas emission.

7.3.4.2 Environmental economics: Valuing lions and natural ecosystems

Environmental economics is an accounting technique that recognises the relationship between productivity, human and environmental health and long-term sustainability (Dyar & Wagner 2003). Traditionally, externalities such as water, air, pollution, health of workers, and climate change are not included on the balance sheet of any business. Environmental accounting instead draws data from best available data sources to estimate the value in fiscal terms of these externalities. For instance environmental accounting of a typical farm would consider the cost of erosion both on the farm and downstream, any loss of provision of clean water to nearby settlements, as a buffer against natural disaster and as part of a larger system that provides tourist viewing of wildlife. Some of these values are real values that can be estimated using financial risk management techniques, while others are less tangible in a financial sense (e.g. peace of mind), but the benefit can be acknowledged at some level (Walker & Salt 2006). Some uncertainty is built into the model and variation in this uncertainty can be explored (Walker & Salt 2012). In this way business proposals that classically would be approved on financial grounds can be seen to be indefensible due to downstream costs and long-term feedback. An example from Walker and Salt (2006) the ability of coral reefs to recover from storms. Prior to the escalation of human disturbance, coral reefs in the Caribbean would recover from storm damage. The current level of human impacts from tourism, fishing, pollution and climate change have not allowed the reefs to recover. In the same way disturbance of the Kalahari system by fences and farms does not allowed for natural ecosystems to recover from natural fluctuations like drought.

In the Kalahari system farmers should attribute many extra costs that they currently omit. Problem animals are removed as a direct response to loss aversion, without consideration of full costs even to livestock productivity. In the course of this thesis I uncovered evidence that lethal control of lions causes greater livestock losses. It is unlikely that farmers in the area will acknowledge these data and so it can only be used by other organisations to mitigate perceived costs to the farmers and discourage lethal control. This might be achieved by increased compensation and no compensation in the event of lethal control, but this should be monitored for desired outcomes, as they are not assured.

Translocation of problem lions is used and farmers desire that it occurs more often. The costs are high and the data on translocations indicates a very low level of success (Weilenmann *et al.* 2010). In this thesis I have also demonstrated that tolerating wild game on farms is an effective method for reducing livestock lost to lions. Many farmers are averse to mixing game with livestock due to the perceived threat of disease but if the government were to encourage game ranching through a relaxation of transportation and export laws perhaps by finding new markets with less strict import laws, the economic incentives would encourage many to consider tolerating game. A few select farms supply a small domestic market, but the recent success of the South African game market should be encouraging.

The Botswana government uses several long and expensive fences to stop movement of wildlife and livestock between districts and prevent the spread of Foot and Mouth Disease (FMD). Removal of these fences would mitigate some lion livestock conflict by re-establishing the wildebeest migration routes and providing an alternative food source to CKGR lions. Historically the main purchaser of Botswana beef was the European Union which insisted on the quarantining, subsidizes the fences and only buys from districts where FMD has not been recently recorded. There are several expanding markets in Africa, the Middle East and Asia interested in buying beef at a premium without necessitating quarantining, and Botswana is beginning to explore these markets.

7.3.4.3 Reducing meso-predator release

Meso-predator release theory (Brashares *et al.* 2013; Elmhagen & Rushton 2007) is used to describe the observed changes in some ecosystems after the removal of top predators and subsequent increase in mid-trophic level predators. Lions are shown to be very aggressive towards species like hyaena, jackal, wildcats and foxes, killing their young and generally excluding them. When top-predators such as lions are removed from a system, meso-predators numbers grow and small to medium sized prey animals experience very high predation (Berger *et al.* 2008). The effect has been observed in only a few systems (Berger *et al.* 2008; Lloyd 2007), but is assumed to explain structure of a number of other systems for which prior data is unavailable (Ripple *et al.* 2014). While the full cascade of effects remains poorly understood, due to their small size and capacity for rapid population growth in the absence of larger predators, meso-predators can be very difficult to control and have significant economic impacts on livestock farms. This indicates that a key goal of removal of apex predators from agricultural areas may have less of an improvement on livestock success than indicated by apex predators kill rates suggest. Further research in this area would be desirable, which would compare the productivity of farms that exclude top predators and those that do not. Within the study area, meso-predators are likely only to be a direct problem for smaller livestock such as sheep, goats and chickens, which are of lesser economic importance. However a fair study would analyse the problem over large time scales where meso-predator release effects include cascades to small herbivores, soil erosion and total primary productivity.

7.3.4.4 Existence value

Alexander (2000) formulated a generalised model exploring the economics of species extinction, acknowledging that previous models used by the United Nations CITES research were unable to model the prevention of species extinction without consideration of the global public value of endangered species. Prior models typically could only consider consumptive factors (such as hunting), and locally significant non-consumptive factors (such as photographic tourism) due to the national sovereignty barrier that prevents foreign governments appropriating existence value funds where they can assist. As most of the world's biological diversity is concentrated in a small number of generally poor states (McNeely *et al.* 1990), the appropriable funds exist in other wealthy nations with no mechanisms to tax the citizens who benefit from knowing that the species exist and are wealthy enough to contribute directly to improving its existence. Alexander (2000) acknowledge that there are a few international funds which attempt to remedy this such as the United Nations' World Heritage Fund and many small charities, but the current funds are negligible.

7.4 Conclusion

This research is important because it exposed some serious flaws in understanding CKGR lion ecology and behaviour, with ramifications for proposed conflict strategies. All stakeholders and lion conservation will benefit from a move away from lethal control, to a farmer focussed strategies that improve productivity and reduce lion's access to livestock. Lethal control is a reactive strategy with little evidence, and the Botswana government can greatly improve the situation by taking a pro-active stance by encouraging resilient methods in animal husbandry that allow predators to better co-exist with livestock.

In January 2014, the Botswana government increased the compensation values to reflect the mean weight and price of livestock listed by the Botswana Meat Commission (Botswana DWNP gazette, 2013), see Table 7.1. These values reflect a large burden on the Botswana government to compensate recent levels of livestock losses, but are directed only at damages caused by lion and elephant. The increased cost of compensation will be balanced by stipulations about the conditions under which farmers are eligible for compensation. This includes for the first time, the stipulation that the lion was not killed or injured in retaliation and that the cattle are herded during the day and kraaled in a substantial kraal at night. This is a substantial improvement over the system prior to 2014, where lions could be shot and compensation still awarded, and most compensation was awarded for cattle that were away from the boma at night. Whether this works as incentive for inducing better livestock husbandry remains to be seen. Many farmers will not change their practices, particularly on the large-scale European style farms. In my thesis I have discovered some important factors influencing lion behaviour in the CKGR which is relevant to reducing livestock loss and benefiting both farming and conservation minded stakeholders.

Table 7.1 New values of compensation for damages caused by lion and elephant (as of 1st November, 2013). The prices are based on mean market values provided by the Botswana Meat Commission. The 1992-2013 were the same for all protected carnivores.

Livestock	BWP (1992- 2013)	BWP (2014)	U\$ (2014)
Cow	700	3000	\$353.10
Horse	1400	2500	\$294.25
Heifer	700	3000	\$353.10
Calf	350	1000	\$117.70
Goat	120	450	\$52.97
Donkey	120	200	\$23.54
Foal	350	1000	\$117.70
Mule	700	2500	\$294.25
Ox	900	3000	\$353.10
Bull	900	5500	\$647.35
Tolly	900	3000	\$353.10
Sheep	300	450	\$52.97

Despite heavy pressure on lion populations across the boundary of the Central Kalahari Game Reserve, I have shown that the CKGR lion population is strong and should be a source population for nearby lions. Recent efforts to highlight the serious plight of lions across Africa, where more than half the unfenced populations are expected to go extinct in the near future (Packer *et al.* 2013) have often concentrated on reducing the killing of lions in sport hunting and retaliation killings. While this is a contributor to lion population decline, it is more important in fragmented and smaller populations. It also distracts from the much more serious threat of habitat loss and incidence of fragmentation; the cause of most past and anticipated future decline. Efforts to conserve lions should focus on the most important actions that would most economically and realistically achieve desired conservation outcomes. To this end I have given reasons why efforts by the Botswana government and any concerned conservation organisation might better direct their attention to the eastern boundary and northern boundary of the CKGR reserve, foremost of which is connectivity with the meta-population of Kalahari lions.

In the CKGR, heavy emphasis on lion conflict should not eclipse the fact that livestock losses are of a real concern and can have significant fiscal impact on farmers (for example see (Holmern *et al.* 2007), and a highly politicised problem demanding resolution. Of greater immediate conservation concern should be the state of the herbivore populations within the CKGR, the recovery of which would directly benefit lions without necessarily adding to the conflict, and connectivity of CKGR lions to small reserves where the more secure population can support more threatened ones. It seems clear from my research that future park management should be directed at best practice for herbivore management and at reducing the economic impact of lions in the immediate surrounds. However strategies that focus on lions tend to increase the conflict when successful. Future management techniques that address farming techniques, rangeland management and reducing the availability of cattle to lions are more likely to succeed in the long-term. To this end I advocate an

adaptive management strategy where farming strategies are monitored in areas adjacent to the CKGR. Incentives that encourage farmers to improve livestock husbandry should be revised often, in line with the best results. Livestock availability to lions can be reduced by keeping the herd together, increasing the numbers of wild games on rangelands, decreasing woody shrubs that act as cover for lions and most importantly kraaling the cattle at night in bomas. Techniques like holistic farm management show some promise if they can be applied to the Kalahari rangelands.

All aspects of livestock husbandry, grassland health, disease, herding, water and business management should be emphasised such that herd productivity is the primary goal and reducing predator access to herds a useful by-product. Only in this way can expenses be lessened and the future of the mitigation strategy ensured. While it is not clear yet which methods would most suit this region, it would be best not to rule out any likely land uses. For instance, mixing game on ranch-lands may help hold back bush encroachment, promote grass production and provide alternatives for predators. Sport hunting of game and perhaps predators should be considered if monitoring, licensing and adherence are possible and if these endeavours prove fiscally sound and beneficial to the ecosystem. Re-establishment of the large-scale wildebeest migrations through the Kalahari would do much to recover wild herbivores, grasslands and also provide alternative prey for lions. In the event that migration of wild herds cannot be re-established, a real substitute for the effects that migration has on the ecosystem should be sought. Farmers should be encouraged to allow wild game like kudu and hartebeest to feed on their rangelands. Improving livestock husbandry is probably the single most cost-effective way to reduce predation.

Encouragement of methods to improve livestock husbandry must come from oversight organisations with influence amongst stakeholders, for example, farmers peers, farmers cooperatives or the Botswana Ministry of Agriculture, rather than those that appear to have alternative motives such as predator conservation organisations and the Department of Wildlife and National Parks. Incentives that promote the trial and uptake of successful methods should be well thought out and strategically deployed and likely schemes should include tax break incentives or insurance schemes for livestock loss that hinge on the implementation of the methods. For example, if holistic farming (high density/long pause grazing) is found to be a realistic method for improving pastures, a scheme that insures livestock against predation and disease could rest upon the display of regular employment of the method.

The CKGR lion population is strong but does not exist in a vacuum. It is part of many other systems, including the African lion meta-population, the Kalahari biome, the trophic pyramid in the immediate surrounds, and a human system that includes a very lucrative tourism industry. Lions require large intact ecosystems to survive, but those large intact ecosystems can also provide many benefits to humans living both near and far from the CKGR. It will require close management of many parts, an interested government and a willingness for stakeholders to come to the table, and be prepared to bear some costs between them.

It is possible to reduce the lion-livestock conflict and at great benefit to many stakeholders. I believe that an adaptive and pro-active strategy can benefit the lion meta-population and bolster genetic diversity, enhance farmer

productivity and sentiment, improve rangelands and tourism and ultimately benefit all stakeholders involved in the CKGR lion conflict. The data I have collected on lions' prey, lion movements, their home ranges, habitat use, feeding habits and the costs of the lion conflict can contribute to better management decisions going forward, but constant monitoring of livestock losses, and lion responses to any methods used will be an integral part of any new strategy.

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Appendices

Appendices are indexed for online access at
<http://www.kalaharilionresearch.org/thesis>

Appendix 1. GeoEye and Landsat 5 imagery used in

This chapter describes the collection of *in-situ* vegetation data used to construct the vegetation map in ground trothing remotely sensed imagery. The imagery used to create the maps was kindly made available from the GeoEye foundation and was acquired by GeoEye-1 satellite, in May 2010, coinciding with vegetation surveys. Each image covers 200 square kilometres at a resolution of 1m², and 2 images from my allocation were combined with 2 images from a colleague's allocation within the study area. Individual image codes were from the 20100527084643216030316008772010052708464321603031 line of section and these codes are:

20100527084643216030316008772010052708464321603031600877_002
20100516084603416030316065012010051608460341603031606501_001

These were combined with a lower with lower resolution (30m²) Landsat 5 imagery that is freely available from the United States Geological Survey at <http://earthexplorer.usgs.gov> . A single image that coincided with vegetation surveys and displayed minimal cloud cover was selected from Surface Reflectance data products from Landsat 5 Thematic Mapper (TM). That image code is LT51740752010097JSA00, acquired on the 7th April 2010.

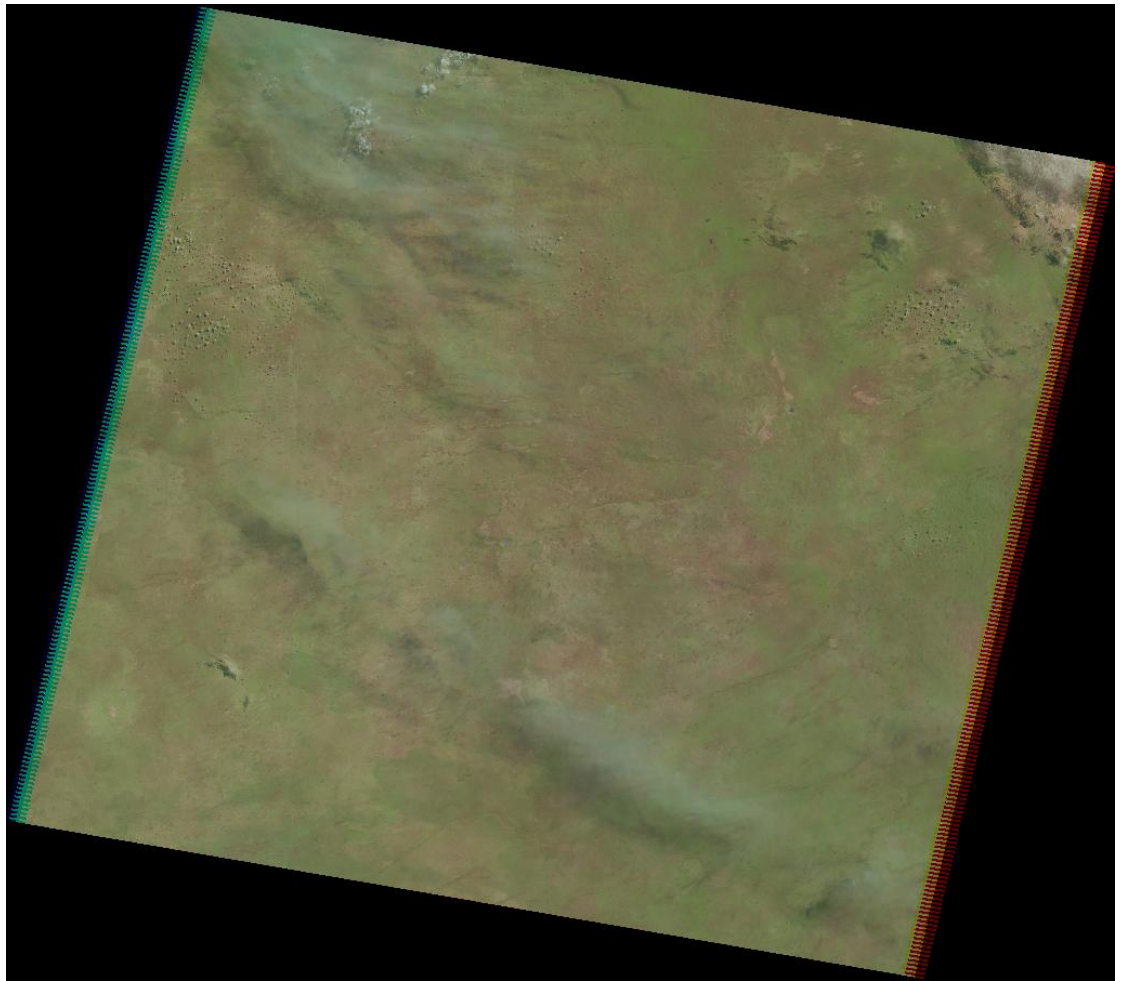
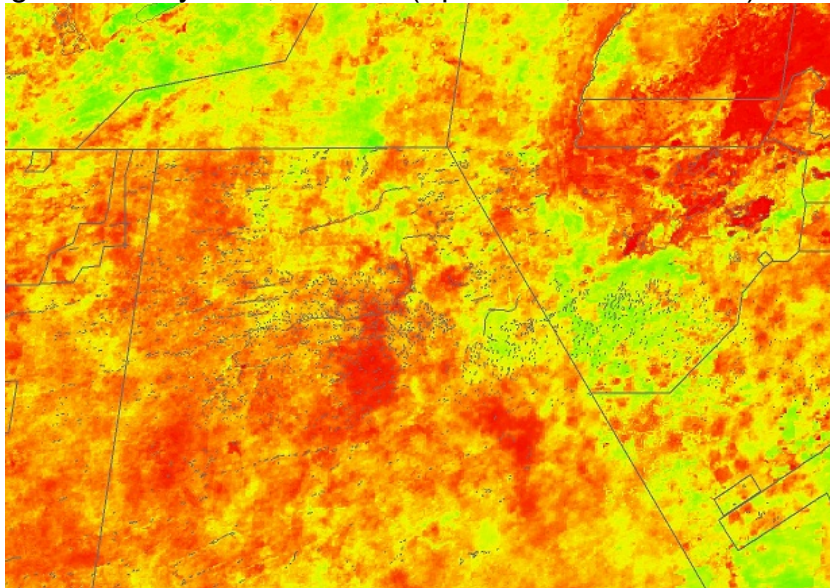


Figure 7-1 True colour Landsat 5 surface reflectance thematic mapper imagery used to classify the habitat map in Chapter 2.

The resulting paper is published by Niti Mishra in the International Journal of Remote Sensing: Relating Spatial Patterns of Fractional Land Cover to Savanna Vegetation Morphology Using Multi-scale Remote Sensing in the Central Kalahari (vol 35, pg 2082, 2014). DOI: 10.1080/01431161.2014.885666

Appendix 2. NDVI

An informative animated GIF visualising the variation in NDVI through the timeframe of the project can be viewed at: <http://www.kalaharilionresearch.org/thesis/KalahariNDVI.gif> and is approximately 4.5 megabytes in size. Example imagery, cropped to highlight the study area, is below (April 2010, false colour).



All imagery can also be viewed at the full extent in thumbnail form in Table 1.1, which details the exact image names and dates used. All imagery listed was used in lion behaviour modelling, while only those with dates listed in the column entitled “Herbivore Transect Month” were used to model herbivore densities. Each file is publicly available and can be sought and downloaded from <http://Earthexplorer.usgs.gov> and are approximately 60 megabytes in size per file.

Appendix 3. Herbivore density maps

The spatial grid derived from the habitat classification and used in chapter 4 and 5, is available for download in Microsoft Excel format at <http://www.kalaharilionresearch.org/thesis/PredictDataFile100m.xlsx> and is approximately 60 megabytes in size. It details the best prediction from ground trothing the high resolution imagery described in section Appendix 1 of the habitat at each point in a 100x 100m grid of the study area, as described in section 2.2. A thumbnail version of this prediction grid is visualised in Figure 7-2.

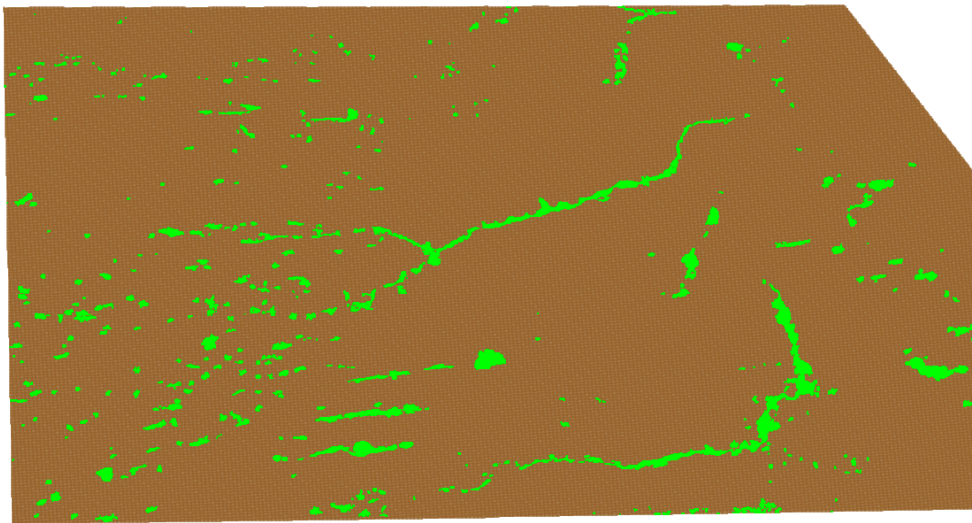


Figure 7-2 Visual summary of the habitat prediction grid classified in Chapter 1, and for which the data formed the basis of several calculations for data in Chapter 4 and 5.

171 herbivore density maps and 19 herbivore group density maps were created from the analyses in Chapter 2. These maps were constructed on a grid space of 10m across the 9911km² study area, and are too numerous to include all them even in an appendix. The data has been preserved and is available on the project website at

www.kalaharilionresearch.org/thesis/PreyTransectData.csv

A visual spatial representation of the NDVI data used for this study can be viewed at www.kalaharilionresearch.org/thesis/KalahariNDVI.gif. False colour has been used to represent productive values as green through orange to red as the least productive values.

Appendix 4. Lion body measurements

In the interest of comparability, we followed de Waal *et al.* (2004) for measuring anaesthetized lions in hand. We specifically used a cocktail of drugs with a proven track record for least-harm to the lions, including fastest recovery time. This cocktail means that lions are exceptionally “lightly” anaesthetized, and care must be taken not to provoke a response from the unconscious lion. At

all times the vet was in control of the situation and dictated what measurements could be taken if any. Taking the mass of the lion was the noisiest and potentially dangerous. Here we provide a list of actual measurements from lions. Three lions that were otherwise not part of this study are included here. They were fitted with VHF collars for social research.

LionID	Date Collaring	Name	Age estimate (years)	Scars	Pride	GPS(E) DD	GPS(S) DD	Sex
PM001	5/11/2008	Passarge	8	Abscess-like wound on lower lip, large dorsal scar on mid-back, folded and full of ticks	Passarge	23.5478	21.2504	M
SM009	28/07/2009	Scar	6-8		San	23.1805	21.5518	M
SF010	28/07/2009	Steph	4-5		San	23.3104	21.5386	F
JM011	29/07/2009	Madala	8-10	Much facial scarring, older lion, abscess on lower lip	Junction	23.1782	21.5518	M
HF012	30/07/2009	Tata	7-8		Hills	22.2976	21.3843	F
MF013	29/07/2009	Rata	3.5		Motopi	23.1189	21.2252	F
PM014	14/08/2009	Tristan	4-5	Nice scimitar shaped scar on right shoulder	Passarge	23.5478	21.2504	M
PF015	14/08/2009	Isolde			Passarge	23.5478	21.2504	F
BM052	24/11/2009	Marco	6-7		Bokamoso	22.7198	-21.343	M
BF053	25/11/2009	Cally	4-5	Small facial scars	Bokamoso	22.7575	-21.349	F
TM059	22/03/2010	Bart	3-4		Tau Pan			M
BM060		Chico	2-3		Bokamoso	22.7015	-21.335	M
JM068	9/10/2010	Segafetso	5-6	Mid spine, large flap, full of ticks	Junction	23.1712	-21.346	M
MM106	19/12/2010	Mogoto	4-5		Motopi	23.1035	-21.011	M
SM009	28/01/2010	Scar	8-9		San	23.2486	-21.535	M
SF009		Steph	5-6		San	23.2171	-21.594	F
MF013		Rata	2-3		Junction			F
PF015	21/03/2010	Isolde	6-7		Passarge	23.5911	-21.233	F
PM014		Tristan			Passarge			M
BF053	8/09/2010	Cally	5-6		Bokamoso	23.6742	-21.329	F
HF012		Tata	4-5		Hills	22.8767	-21.415	F

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LionID	Canine Length				Canine short width				Canine long width			
	UR	UL	LR	LL	UR	UL	LR	LL	UR	UL	LR	LL
	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)
PM001												
SM009												
SF010		45		37		16.4		17.2		22.2		21.2
JM011												
HF012	40.3	43.35	32.45	36.3	17.1	17.5	13.8	16.6	21.35	21.2	20	22
MF013	38.05		30.5		16.5		17.3		16.2		14.5	
PM014												
PF015												
BM052	51.7	50.8	28	40.75	17.5	18.5	16.9	16.3	27.2	27.75	25.7	25.6
BF053	38.4	42.1	34.5	40.4	15.	16.2	14.8	13.5	21.1	18.2	18.4	20.3
TM059												
BM060	49		38		19.2		18		25.5		24	
JM068		49		42.2		18.6		18		26.2		24.2
MM106	44					41			21		28	
SM009	55.5		41.2		20.1		20.5		29.2		25.7	
SF009												
MF013												
PF015												
PM014												
BF053												
HF012												

Key: UR =Upper Right, UL = Upper Left, LR = Lower Right, LL = Lower Left

Lion ID	Weight	Body Length	Tail Length	Total Body Length	Tail Circumference	Neck Girth	Chest Girth	Abdomen Girth
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	(kg)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)
PM001								
SM009	222	205	85	290	27	72	129	135
SF010	172	158	79	249		60	111	114
JM011	200	194	86	280	28		123	118
HF012	152	172	89	261	27	65	117	112
MF013	107	169	74	243	24	59	99	100
PM014	206	203	83	286	29.4	76	124	131.5
PF015	148	175	78	253	25	65	115	117
BM052	229	193	89	282	25	76.5	127	116
BF053	149	184	82	266	24	61	109	120
TM059						76.5		
BM060	188	206	85	206	27.5	72.5	119.5	131
JM068		197	83	280		77	119	122
MM106	172	199	81.5	180.5	28	69	111	114
SM009	246					71.5		
SF009	183					60		
MF013	114					54	99	104
PF015	156	167	79	246	24	60	104	102.5
PM014						67		
BF053								
HF012								

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LionID	Leg Length				Leg Circumference				Paw Length				Paw Width				Head Length
	FR	FL	RR	RL	FR	FL	RR	RL	FR	FL	RR	RL	FR	FL	RR	RL	
	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)
PM001																	
SM009	62	61	65	64			32	31			15	14			10	10	
SF010		58		61		43.5		61	11	11		10.5	10	10		9	35
JM011		62		72		53		71	15	14	12	12			9	9	39
HF012	57		63		114.5		66		11.2	11	11.2	11.2	8.5	9.6	7	7.5	35
MF013	53		61		42		55			10.5	8.5	8.5			8.5	8.5	33.5
PM014	57	58		65		51		69.5	12	12	12	12	11	10	9.5	10	40
PF015																	
BM052		63		64		51		65.5	12	12			12	12			
BF053	58		63		42		65		10		12		8.5		8		
TM059																	
BM060	58	11.6	63.5								13.2		12.1	12.1	10.2		
JM068	62	62	69						12	11	12.5	13	11	11	10	10	46
MM106	62		67		47		62		11	12	11		8	10	8		38
SM009																	
SF009																	
MF013																	
PF015		58.5		62.5		44		60.5	11	10.5	9.5	9.5	9.5	10	8	8	35.5
PM014																	
BF053																	
HF012																	

Key: FR = Front right, FL = Front Left, RR = Rear Right, RL = Rear Left

Appendix 5. Lion GPS raw data

The raw GPS data for Chapter 4 and Chapter 5 has been uploaded to the MoveBank repository and will be made publicly available after submission of this dissertation. Early access is available with the following credentials:

Website: www.movebank.org

User Name: KalLionCollab

Password: WgstVDf83e]t"[+"

For the sake of brevity, we present here data for the monthly home ranges of lions (total home ranges are presented in Table 3.1 in Chapter 3), and the raw dataset that was used for the analysis described in Chapter 4 can be downloaded www.kalaharilionresearch.org/thesis/HR_Data.csv

Appendix 6. Scripts for clipping and analyzing herbivore density data into lion home ranges

The script used in the Geospatial Modelling Environment software package is available at

<http://www.kalaharilionresearch.org/thesis/Appendix6.html>.

The purpose of this script is to estimate on a month-by-month basis, the mean density of each herbivore species estimated from Chapter 2 density maps (Appendix 3) within the home range for each lion for each month (Appendix 7). This method takes into account density of herbivore in both major habitat types, at different points across the study area, using all the information that was deemed important in the Generalised Linear Modelling exercise from Chapter 2, such as NDVI, month and latitude and longitude.

Appendix 7. Raw data and analysis script for lion home range analysis

This raw data used in Chapter 4 can be downloaded in comma delimited .csv format from www.kalaharilionresearch.org/thesis/CKGR-Lion-HR-Raw.csv and the R script which follows can be downloaded from www.kalaharilionresearch.org/thesis/CKGR-Lion-HR-Stats.R. Several R packages were used, are listed at the beginning of the script and may need downloading. All were available on the CRAN R servers at the time of writing. These packages may have been updated since use. The version of R used at the time of analyses was R 2.12

```
# The following code constructs spatial files of the lion MCP measures
used in Chapter 4. These spatial files are specifically for use in the ARCMAP
10.1 software package.
```

```
library("adehabitatHR")
```

```
library(rgdal)
```

```
myproj4utm <- CRS("+proj=UTM, +zone=34, +datum=WGS84,
+units=m")
```

```
thresholddays <- 10
setwd("~/LionUD")
lionDMD_all <- read.csv("CKGR-Lion-HR-Raw.csv")
SeasonYear <- read.csv("SeasonYear.csv")
#Temporarily remove 1003 as only 1 mdiday point, also need to fix 1005
#lionDMD2 <- lionDMD_all[lionDMD_all$ANIMALID != 1003,]
lionDMD_all <- merge(lionDMD_all, SeasonYear)

lion1001 <- lionDMD_all[lionDMD_all$ANIMALID == 1001,]
lion1002 <- lionDMD_all[lionDMD_all$ANIMALID == 1002,]
lion1003 <- lionDMD_all[lionDMD_all$ANIMALID == 1003,]
lion1004 <- lionDMD_all[lionDMD_all$ANIMALID == 1004,]
lion1005 <- lionDMD_all[lionDMD_all$ANIMALID == 1005,]
lion1006 <- lionDMD_all[lionDMD_all$ANIMALID == 1006,]
lion1007 <- lionDMD_all[lionDMD_all$ANIMALID == 1007,]
lion1008 <- lionDMD_all[lionDMD_all$ANIMALID == 1008,]
lion1009 <- lionDMD_all[lionDMD_all$ANIMALID == 1009,]
lion1010 <- lionDMD_all[lionDMD_all$ANIMALID == 1010,]
lion1011 <- lionDMD_all[lionDMD_all$ANIMALID == 1011,]
lion1012 <- lionDMD_all[lionDMD_all$ANIMALID == 1012,]
lion1013 <- lionDMD_all[lionDMD_all$ANIMALID == 1013,]

i = 1013
lionNOW <- lion1013
xy <- cbind(lionNOW$POINT_X, lionNOW$POINT_Y)
LionsLev <- data.frame(factor(lionNOW$YearK))
coordinates(LionsLev) <- xy
lionNowMCP <- mcp(LionsLev, percent = 100)
writeOGR(lionNowMCP, dsn = "MCP/lionMCPYear", driver = "ESRI
Shapefile", layer = paste("lionMCPYear",i, sep = ""));
plot(lionNowMCP)
lionNowMCP

lionNOW <- lionDMD_all
xy <- cbind(lionNOW$POINT_X, lionNOW$POINT_Y)
LionsLev <- data.frame(factor(lionNOW$ANIMALID))
coordinates(LionsLev) <- xy
lionNowMCP <- mcp(LionsLev, percent = 100)
writeOGR(lionNowMCP, dsn = "MCP2", driver = "ESRI Shapefile", layer
= paste("lionMCPTotal",i, sep = ""));
-----
```

Appendix 8. Raw data and analysis script for lion daily movement distance analysis

The raw data used in Chapter 5 can be downloaded in comma delimited .csv formatted from www.kalaharilonresearch.org/thesis/CKGR-Lion-DMD-Raw.csv and the R script which follows can be downloaded from

www.kalaharilionresearch.org/thesis/CKGR-Lion-DMD-Stats.R Several R packages were used, are listed at the beginning of the script and may need downloading. All were available on the CRAN R servers at the time of writing. These packages may have been updated since use. The version of R used at the time of analyses was R 3.02.

Appendix 9. Raw data for the analysis of lion problem animal control data

These data is made available for download from
www.kalaharilionresearch.org/thesis/PAC_LionData.csv