Demography and ranging behaviour of lions (*Panthera leo*) within a human-occupied landscape in northern Kenya

A thesis submitted to the University of Oxford for the degree of Doctor of Philosophy in Zoology

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DECLARATION

The thesis presented here represents a project that I developed as a D.Phil. student of the Zoology Department, University of Oxford. I implemented all aspects of this project, analysed the results and wrote all of the material in the thesis. While others assisted with the project at various stages including fieldwork, data entry and analysis, it represents a work entirely of my own doing and I assume full responsibility for the work presented here.

The text, excluding figure legends, tables, references and appendices, does not exceed 50,000 words. All photographs included in the thesis are the copyright of the Ewaso Lions Project, except where stated.

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Date: 18th April 2017

ABSTRACT

Lion populations across Kenya are threatened, primarily as a result of habitat loss and human persecution in response to livestock depredation. This study provides the first population insights into lions within the Samburu-Isiolo ecosystem; considering both the protected area network and the surrounding human-occupied landscape. These results are particularly pertinent given Kenya's low lion population.

The demography of the lion population in the Samburu-Isiolo ecosystem was studied to provide data on the area's basic lion population structure. Due to the small size of the protected areas within the study area, it was expected that lions would frequently move outside the Reserves into the human-occupied landscapes that surround the protected areas and, therefore, their ranging behaviour was also assessed. Community Conservancies exist around the protected areas, where wildlife conservation is encouraged. However, the increasing human and livestock populations within these areas conflicts intensely with the spatial requirement of lions. This has numerous implications; from direct mortality to reducing the opportunities for immigration of new lions into the protected areas, or safe dispersal from them. Therefore, the presence of suitable habitat in one community area adjacent to the protected areas was examined using a Habitat Suitability Model (HSM) in order to explore these issues.

The demography of the lions within the study area was found to be comparable to other populations across Africa, although displayed higher sex ratios, and lower cub dispersal figures. Whilst the ranging behaviour of the prides displayed core ranges along the rivers, it was noted that they each had their distinct areas of intensive use. Male ranges were larger than females and shrunk during the drought in 2009 and expanded again in 2010. Despite displaying ranges within the limits of the protected areas, it is known that between 2008 and 2010, 10 lions disappeared and moved outside the protected areas. The HSM showed that highly suitable habitat did exist within the Community Conservancy, highlighting the presence of safe refuges for carnivores, with more suitable habitat found to be available at night compared to during the day. Despite the presence of highly suitable habitat, human-lion conflict was a common occurrence in these areas.

Anthropogenic factors will have an impact on the demography of lion populations, whether they exist inside or outside protected areas. If suitable habitat did not exist within the human-occupied landscape, it is expected that there would be reduced immigration of new males, longer pride tenures within protected areas and the potential risk of inbreeding. Conflict mitigation measures are important in reducing human-lion conflict, however, this study also recommends the presence of safe refuges in the form of Conservation Areas within the Community Conservancy network in northern Kenya. The model of Conservation Areas acting as safe refuges is essential for the conservation of lions outside protected areas throughout remaining parts of their range in northern Kenya.

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I dedicate this thesis to Jeremy Lucas, who loved Samburu, its people and wildlife. You are always missed.

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ACRONYMS AND ABBREVIATIONS

ANOVA	Analysis of Variance
BP	Borana Pride
BSNR	Buffalo Springs National Reserve
CA	Conservation Area
CITES	The Convention on International Trade in Endangered Species of Wild Fauna and Flora
DPhil	Doctor of Philosophy
ELP	Ewaso Lions Project
GIS	Geographic Information System
GPS	Global Positioning System
HSM	Habitat Suitability Model
IUCN	International Union for Conservation of Nature
KDE	Kernel Density Estimator
KM	Kilometre
KP	Koitogor Pride
KWS	Kenya Wildlife Service
M	Male lion
MCP	Minimum Convex Polygon
MSc	Master of Science
NMP	Ngare Mara Pride
ShNR	Shaba National Reserve
SNR	Samburu National Reserve
SP	Sasaab Pride
STE	Save the Elephants
WGCC	Westgate Community Conservancy

Chapter 1

Introduction

"In many cultures lion epitomize ferocity, strength, courage, dignity, and majesty."

Parker, 1989

1.1. Introduction to lion ecology

The lion, *Panthera leo*, the largest of the African felids, is an integral part of the continent's ecological community (Schaller, 1972). The lion is the only member of the Felidae family to live and hunt in stable, fission-fusion social units, known as prides (Schaller, 1972; Packer *et al.,* 1990). The core of a lion pride is a group of two to 18 closely related females; mothers, daughters, sisters and aunts, that occupy a territory (Schaller, 1972; Packer and Pusey, 1982; Pusey and Packer, 1987). Sixty percent of the animals within a pride may be cubs (Bertram, 1975).

Within lion populations, cub dispersal is important as population size is correlated with the number of prides and the size of each pride is determined by density within the group; the only way lion populations can increase in number is through the formation of new prides (Packer *et al.,* 2005). Cohesion amongst age-mates is greatest amongst individuals of the same sex (Hanby and Bygott, 1987). Females within a pride of similar age will most often remain with their mother's pride for the duration of their lives (Packer and Pusey, 1987). Adult females live in prides in the optimal size range (Packer *et al.,* 1990). Those in groups containing three or more females are more likely to emigrate, especially when the number of females in their natal pride exceeds 10 (Bertram, 1973; Hanby and Bygott, 1987). Pusey and Packer (1987) found that 30% are expelled and establish new prides near their natal home range. Single sub-adult females may be pushed out of their pride earlier than if they had age-mates. As a result of this dispersal pattern amongst females, most females live in prides of three to 10 individuals (Packer and Pusey, 1987). Their *per capita* reproductive success is highest in prides of this size (Packer *et al.,* 1990). VanderWaal *et al*., (2009) also found that the chances of dispersal declined with increasing numbers of females in unrelated neighbouring prides. Therefore, subadult females are likely to disperse when pride sizes are large but less likely to disperse if competition with neighbours is high. Also, high quality territory means that there are more unrelated neighbours (Mosser, 2008), and this could mean subadult females may not disperse because of a high number of neighbours.

A pride may also comprise a coalition of one to seven adult males (Packer and Pusey, 1982). These cooperative coalitions are composed of related and non-related individuals, especially within smaller coalitions (Pusey and Packer, 1987). Male cubs will generally leave the pride at about four years of age (Packer and Pusey, 1987) and will travel nomadically for one to three years, after which they will take over a resident pride and its area (Bertram, 1975). Bygott *et al.,* (1979) have shown that male lions in large coalitions gain reproductive advantages. A coalition of males may simultaneously gain tenure of several prides, giving them access to more oestrus females. The larger the male coalition, the more reliably they can gain tenure of female prides and they are expected to hold tenure over a pride for a longer period of time. Bygott *et al.,* (1979) found that coalitions numbering one or two males have pride tenure for under 25 months and coalitions of three or more males have tenure for more than 25 months. Coalitions of four to six males have tenure for over 46.5 months. This suggests that females whose prides are defended by the largest male coalition would possibly be able to rear their cubs more successfully (Packer and Pusey, 1983a). 'Male takeover' is the replacement of one male coalition (or single male) by another, for exclusive access to female groups (Packer and Pusey, 1983a). This is a male reproductive strategy where males stop females from investing in the offspring of other males, and consequently speed up the return of the females to sexual receptivity (Bertram, 1975; Packer and Pusey, 1987). New males are intolerant of all individuals, except females who are sexually receptive (Hanby and Bygott, 1987).

Lionesses give birth in isolation in dense thickets or bush (Schenkel, 1966; Schaller, 1972) and usually keep their cubs hidden for the first 4-8 weeks (Packer and Pusey, 1983a). If a female does conceive after a gestation period of 3.5 months, it is expected that she will produce between one and four cubs (Bertram, 1975) with a mean litter size of 2.3 (Packer and Pusey, 1983a). Lions produce litters of cubs (Schaller, 1972; Packer *et al*., 1988) approximately every two years (Pusey and Packer, 1987). Inter-birth intervals may also be as high as 40 months in some instances (Schaller, 1972; Funston *et al.,* 2003).

Cub mortality is very high (Packer and Pusey, 1983a) with more than 50% of cubs dying before attaining one year. Bertram (1975) states that if a cub reached two years of age, it would be more likely to survive until adulthood. Infanticide by immigrating males during a male takeover leads to a sharp increase in cub mortality (Bygott *et al*., 1979; Packer and Pusey, 1983a), with the eviction of the resident coalition causing 100% cub mortality (West and Packer, 2002). Twenty-seven percent of cub mortality is as a result of infanticide (Packer *et al.,* 1990). Small cubs are killed and older cubs and sub-adults are evicted (Packer and Pusey, 1983b). However, Bertram (1975) states that if cubs are born synchronously, they experience lower mortality as mothers can provide greater resistance to the new males after they pool all their cubs together to form a highly stable "crèche"; the function of which appears to be defense (Packer *et al*., 1990). Increased cub mortality also occurs as an indirect presence of the new males (Bertram, 1975), where the females produce less milk or hunt less efficiently and they could neglect their cubs altogether due to the stress induced by the new males (Packer and Pusey, 1983a). Rudnai (1973b) found that in Nairobi National Park, lionesses abandoned single cubs either at birth or when littermates died before the age of three months, whilst successfully raising litters later on. Additionally, cubs may die of starvation when lions leave territories in search of food (Schaller, 1972). Cub survival to 12 to 18 months is correlated with the amount of food available during prey scarcity (Van Orsdol *et al*., 1985). Bertram (1975) stated that more cubs would die during such times when there was no large prey available.

Rudnai (1973b) found that the sex ratio of lions is usually 1:1 at birth. Over time, the number of males will decline due to intra-sexual competition for pride tenure and mating rights, and Schaller (1972) reports that most lion populations have a bias towards females. Van Orsdol *et al.,* (1985) found that prides occupying small, isolated habitats may have higher female:male ratios. This occurs as a result of increased mortality amongst the emigrating males and decreased immigration of potential male rivals, as well as the multiple pride tenure of male coalitions (Loveridge *et al.,* 2010a). In contrast, Rodgers (1974) found that in the Eastern Selous Game Reserve in Tanzania, the sex ratio is unusually high in the proportion of adult male lions. Lions can bias their sex ratios to favour males because through cooperation, males enhance each other's expected reproductive success (Packer and Pusey, 1987). Other studies reported skewed sex ratios for cubs in favour of males as a result of removal of adult males from the system (Creel and Creel, 1997; Whitman and Packer, 1997; Loveridge *et al.,* 2007; Funston, 2011; Dolrenry, 2013). Bias in sex ratio as a result of the removal of males can cause adverse effects, however, reproductive collapse will only be caused if there are extreme skewed sex ratios (Milner-Gulland *et al.,* 2003).

Lions are wide-ranging animals (Packer and Pusey, 1983a) and as Loveridge *et al*., (2010a) and Funston (2011) found, a single lion pride's range can exceed 1000 km^2 (Loveridge *et al*., 2010a: range 101-1156 km^2). The distance lions travel depends on the number of potential prey animals available (Bertram, 1978), making prey abundance an important factor influencing the distribution and space use of lions (Van Orsdol *et al*., 1985; Hayward *et al*., 2009; Loveridge *et al*., 2009). The availability of abundant prey and high quality habitat results in smaller lion ranges while scarce prey results in larger ranges (Gittleman and Harvey, 1982; Macdonald, 1983). Lions are conservative in their movements (Schaller, 1972) and if they are able to catch prey without travelling long distances, they may stay in the same place for days (Bertram, 1978). Prey abundance and availability is in turn influenced by the presence of water because many ungulate species are water dependent (Hopcraft *et al*., 2005; Loveridge *et al.,* 2009; Valeix *et al.,* 2010). Other social factors such as group size and territoriality also influence lion's home range sizes (Schaller, 1972; Loveridge *et al.,* 2009). When group size increases, home range size will generally increase in response to higher demands for prey (Van Orsdol *et al.,* 1985).

Lions tend to avoid their neighbouring prides, and therefore their range size is limited by the proximity and threat of these prides (Loveridge *et al.,* 2009). They may move more into neighbouring territory when they find it difficult to find food within their own territories leading to spatial overlap in areas used by adjacent prides (Schaller, 1972; Funston *et al.,* 2003) but direct confrontations are rare in these interactions (Schaller, 1972). Extensive overlaps between prides may also be the result of small groups of lions and the low importance they place on associating with each other to defend their territories from rival prides. When home ranges are large, the chances of encountering a neighbour is expected to decrease (Hemson, 2003; Davidson *et al*., 2011).

Female home ranges are smaller than the male ranges (Schaller, 1972; Loveridge *et al.,* 2009; Tuqa *et al.,* 2014). This is to be expected as females defend smaller areas that provide sufficient resources and are suitable for their cubs, whereas males need to defend larger areas and are also affected by female distribution (Schaller, 1972; Funston *et al.*, 2003; Loveridge *et al.,* 2009).

When ranges are so large, there is a greater chance that they will overlap park boundaries and therefore there is an increased risk in mortality (Loveridge *et al*., 2010a). Males are more vulnerable to anthropogenic threats due to their large home ranges (Bannerjee and Jhala, 2012). Stochastic events, such as droughts, can also potentially lead lions to go beyond protected areas in search of prey, especially if protected areas are small (Tuqa *et al.,* 2014). Such events can create challenges for lion conservation and the potential of human-lion conflict increases if lions move outside the protected areas. Therefore, home ranges can actually predict lion's extinction probability (Woodroffe and Ginsberg, 1998).

Lions are found in varied habitat including forest and desert, however they are most commonly associated with savannah ecosystems (Nowell and Jackson, 1996; Riggio *et al.,* 2013). Habitat influences lion predation rates as it mediates the successful identification, pursuit and capture of prey (Kauffman *et al.,* 2007). Lions are stalk-and-ambush carnivores (Hopcraft *et al*., 2005) and mainly do this in dense cover (Peterhans and Gnoske, 2001; Hopcraft *et al.,* 2005). Lions make use of available dense cover in order to remain undetected by prey and increase their foraging success (Hopcraft *et al.,* 2005). Other attributes that are important for lion habitat include high quality landscape which provide shelter for cubs, water and minimum human disturbance (Packer *et al*., 2005; Mosser, 2008; Kissui *et al*., 2010; Schuette *et al.,* 2013; Oriol-Cotterill *et al.,* 2015b).

1.2. Lion conservation status

The conservation status of lions is Vulnerable, as reported by the International Union for Conservation of Nature (IUCN) red list (Bauer *et al.,* 2008; IUCN, 2012; IUCN, 2015). Lions are facing escalating threats with numbers declining in areas (Riggio *et al.,* 2013; Ripple *et al*., 2014; IUCN, 2015; Funston *et al.,* 2016) which historically were their strongholds, such as in East Africa (IUCN, 2015).

Lions are declining in number largely due to habitat loss (Funston *et al*., 2016) with most lion populations increasingly being confined to reserves and isolated protected areas (Bauer and Van der Merwe, 2004; Bauer *et al*., 2008; Loveridge *et al*., 2010a; Riggio *et al*., 2013; Dolrenry *et al*., 2014) due to increasing amounts of human settlements in dispersal areas (Ottichilo *et al.,* 2000; Funston *et al*., 2016). It is on the perimeter of these areas, that most human-lion conflict occurs (Woodroffe and Ginsberg, 1998; Loveridge *et al.*, 2010a) often leading to retaliatory killing of lions (Woodroffe and Ginsberg, 1998; Hazzah *et al.,* 2009; Hazzah *et al.,* 2017). Lions are often considered a serious problem animal, and the main reason stems from the killing of livestock by lions (Woodroffe, 2000), that are in turn killed by the local people to avenge their loss and to protect their livestock from further predation (Frank *et al*., 2005; Kissui, 2008; Hazzah *et al.,* 2009; Funston *et al.,* 2016). Lions are vulnerable to these types of killings as they often defend a livestock carcass, in contrast to other carnivores (Funston *et al.,* 2016).

Reduction in prey numbers is also an important factor leading to decline in lion numbers (Ogutu *et al*., 2011; IUCN, 2015; Lindsey *et al*., 2017) and often this may lead to more contact with humans and livestock (Sillero-Zubiri *et al*., 2006; Goldman *et al.,* 2013) due to lions searching for a prey base. Bushmeat poaching of wild prey is now identified as a serious threat to lions across Africa (Lindsey *et al.,* 2017) and is leading to a global crisis (Ripple *et al*., 2016). Lions are also often caught in snares that have been set for herbivores for bushmeat and in the Niassa Reserve in Mozambique, snaring accounts for 52% of lion mortalities (Funston *et al.,* 2016).

Encroachment in to protected areas is now thought to be one of the top three threats to lions (Funston *et al.,* 2016; Lindsey *et al*., 2017). Livestock grazing in protected areas leads to competition with herbivores and often leads to degraded habitat. Lions often encounter livestock here, increasing the potential of human-lion conflict. Lion killing is also embedded in some pastoralist cultures, such as the Maasai and Samburu (Pavitt, 2006), as a rite of passage for young men (warriors) and as a symbol of strength and prestige (Hazzah *et al*., 2009; Goldman *et al*., 2013; Hazzah *et al.,* 2017). Nowadays, this practice is no longer common especially in northern Kenya (*pers. obs*.) and traditional lion hunts are now illegal in Kenya (Schuette *et al.,* 2013). Additionally, the rise in the lion bone trade is of increasing concern (IUCN, 2015), as is poor management of trophy hunting which has led to further reduction in numbers (Loveridge *et al*., 2007; Packer *et al.,* 2009; Packer *et al.,* 2010; Groom *et al.,* 2014). Insecurity (see section 2.4.3.2.) has also led to increasing killing of lions (*pers. obs.*). Over the past three years in northern Kenya, warring ethnic groups and ranch invasions by herders, has led to a number of lions being killed. The exact numbers of lions killed has been difficult to document due to the insecurity. The decline in lion numbers in recent years means that their future is very much in doubt unless effective conservation measures are employed at the landscape level.

1.3. Lions in Africa

Riggio *et al*., (2013) calculated the potential range in Africa currently available for lions is 3,390,821 km^2. Over the past 100 years, lions have lost three-quarters or more of their original habitat (Funston *et al.,* 2016). Figure 1.1 illustrates the contraction of the lion's range across Africa, and lions now occupy only 8% of their historical range. In 2013, it was reported that there were between 32,000 and 35,000 free-ranging lions remaining throughout the African continent in 67 areas with over 40% of Africa's lions contained in Tanzania alone (Riggio *et al.,* 2013). However, recent reports state that approximately 20,000 lions remain in Africa (Funston *et al.,* 2016; Lindsey *et al.,* 2017). Only six countries in Africa, Kenya being one of them, contain at least 1000 lions (Riggio *et al*., 2013; Funston *et al.,* 2016). Lions across East Africa in particular have a metapopulation structure where there are key populations within a much larger landscape (Dolrenry *et al.,* 2014). Dolrenry *et al.,* (2014) explains that due to anthropogenic influences, populations across East Africa are fragmented where lions are living in isolated habitat patches within a matrix of unsuitable habitat.

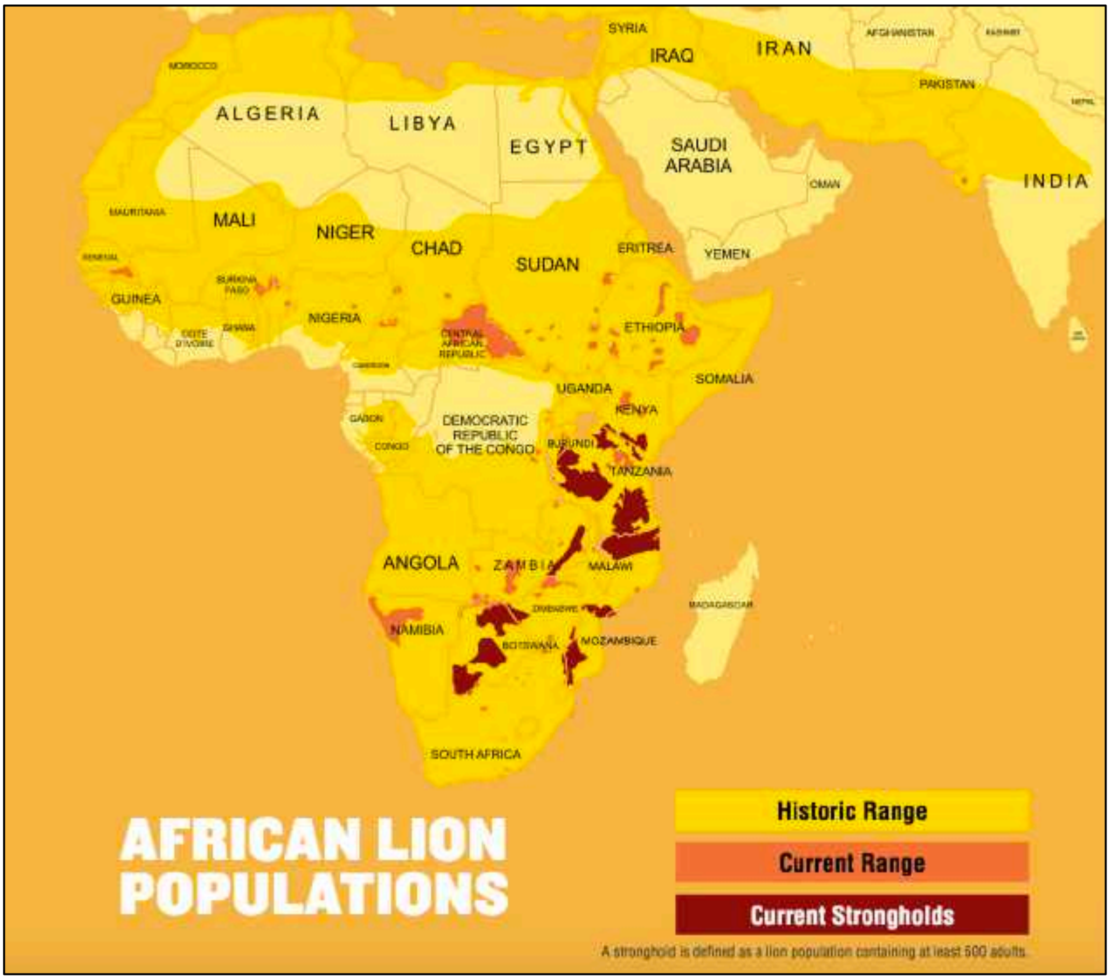


Figure 1.1. Map showing the historic and current range of lions in Africa (Funston *et al.,* 2016).

1.4. Lions in Kenya

It is widely accepted that lions in Kenya are threatened (Dolrenry *et al*., 2014) with an estimated population of 1,970 (Omondi *et al*., 2009). The National Large Carnivore Task Force (2010) states that there has been a 30% decline in lion numbers between 2000 and 2010 in Kenya. Earlier estimates of Kenya's lion population include 3,500 (Johnstone, 1999), while Chardonnet (2002) estimated 2,749 lions, and Bauer and Van Der Merwe (2004) calculated a population size of 2,280. The estimate for lion numbers provided by the Kenya Wildlife Service (KWS) is shown in Table 1.1, with Samburu and Isiolo regions supporting an estimated 100 lions.

Table 1.1. Estimated lion numbers in Kenya (Source: Conservation and Management Strategy for Lions and Spotted Hyenas in Kenya, Omondi *et al*., 2009).

Region	**Estimated No: of Lions**
Maasailand	825
Tsavo	675
Laikipia	230
Meru	40
Samburu/Isiolo	100
Northern Kenya	100
Total	**1970**

Kenya's first management strategy for lions was produced by the KWS in 2009 and included a map that documented lion distribution across different range categories (Figure 1.2). The strategy estimated that 18% of Kenya's total land surface has a permanent lion presence where it is known that lions are resident (Omondi *et al.,* 2009), with a further 16% of the country listed as having a possible lion presence.

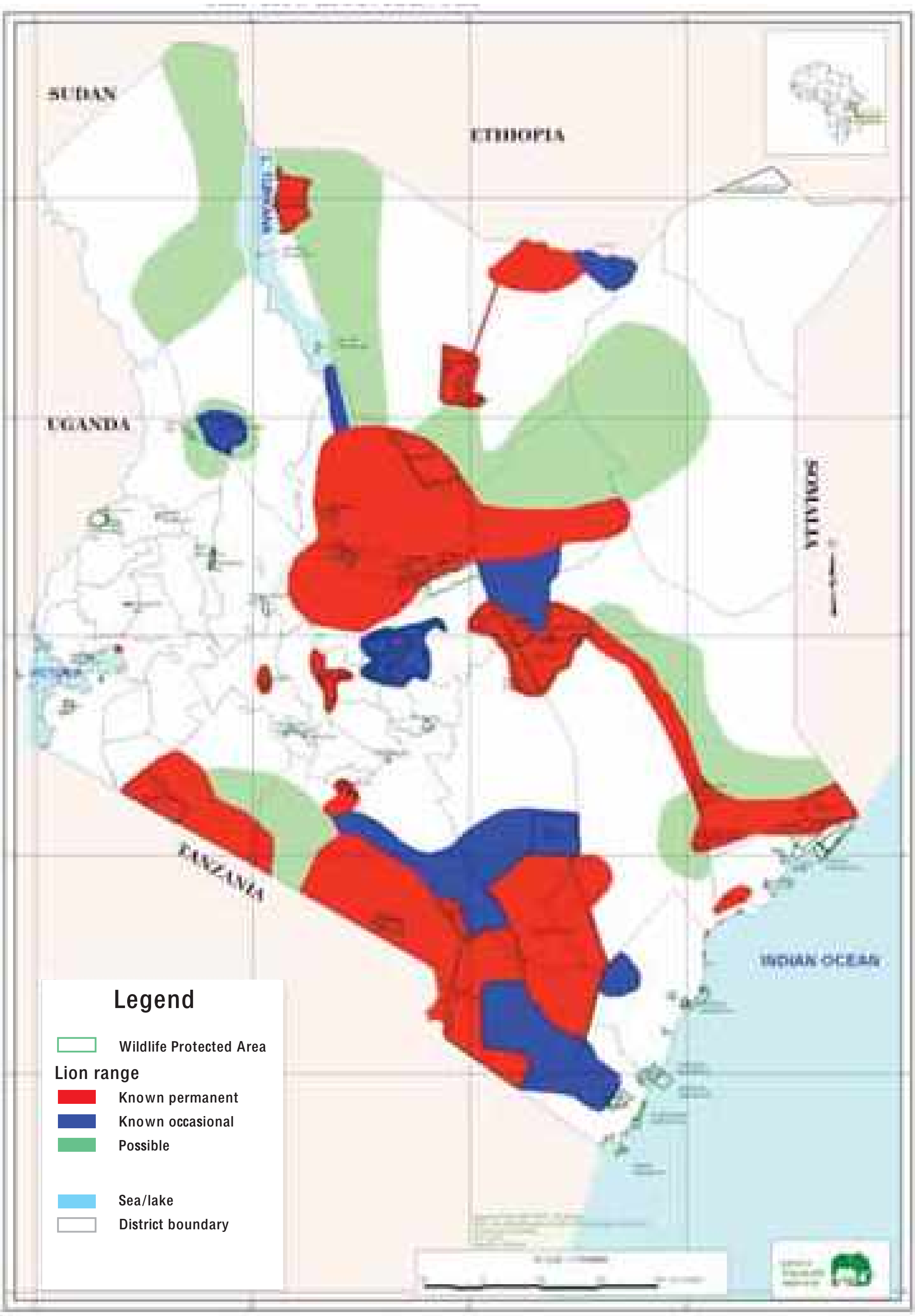


Figure 1.2. Map showing lion distribution across different range categories (Source: Conservation and Management Strategy for Lions and Spotted Hyenas in Kenya, Omondi *et al.,* 2009).

Kenya's lions are found in many of the country's network of National Parks and Reserves. Large areas that contain viable lion populations include the Maasai Mara and Tsavo ecosystems (Omondi *et al.,* 2009). Most of the remaining populations are confined to smaller protected areas. Although Chardonnet (2002) stated that 65% of Kenya's lions exist in unprotected areas, their status in these areas is mostly unknown with population sizes merely rough estimates (Omondi *et al*., 2009). Over the past 10 years, Community Conservancies (see section 2.3.4.) have been created in southern and northern Kenya, a few of which host small lion populations; one example being the Olare Orok Conservancy adjacent to the Maasai Mara National Reserve which contained at least 50 lions in 2011 (*pers. obs.*). In general, lions continue to roam outside parks and reserves but it is clear that obtaining accurate estimates of numbers and distribution of lions is a time-consuming exercise that requires extensive resources and vast areas of Kenya remain largely undocumented.

1.5. Lions in the Samburu-Isiolo ecosystem of northern Kenya: an unknown population

George and Joy Adamson brought fame to northern Kenya's lions through the story of '*Elsa*' the lioness and their trilogy of books (Amin and Eames, 1985). Samburu National Reserve attracted world attention due to 'Kamunyak', the 'Miracle Lioness', who in December 2001, adopted several young oryx calves, (*Oryx gazella beisa),* before her disappearance in 2003.

Prior to 2003 no detailed study had been conducted on lions in the Samburu-Isiolo region. The Wildlife Planning Unit (1981) conducted one-off ground counts in Samburu and Buffalo Springs National Reserves in 1973 (10 lions). Some estimates were presented in a paper published by Bauer and Van Der Merwe (2004) for parts of Samburu and Isiolo Counties (100 lions). The first detailed lion study within the National Reserves (Samburu and Buffalo Springs) was conducted as part of a Master of Science research degree in 2003 and 2004 (Bhalla, 2003) which gave a population estimate of 38.

The aim of the study was to identify the population structure, movements and predation of lions in Samburu and Buffalo Springs. Interviews were conducted to obtain information on earlier estimated numbers of lions. The lions' dry season ranges were mapped to show their ranging behaviour. The study further investigated prey preferences amongst lions, including the extent of livestock predation.

Although the study was limited in scope due to time restrictions, baseline information collected in the dry season for the lion population in Samburu and Buffalo Springs was presented. The study found that in those areas surrounding Samburu and Buffalo Springs, where the bush is relatively dense, prey is more sparse and where the human population is relatively high, the lions are more vulnerable and face constant threat. The reduction of human caused mortality was identified as the single most important factor safeguarding the survival of the lions in this region. The study highlighted the importance and necessity for a long-term demographic study of the lions in not only the protected areas of Samburu, Buffalo Springs and Shaba National Reserves, but also the lions in the human-occupied landscape. This study therefore seeks to address this.

1.6. The importance of lion conservation in Kenya

Kenya relies on tourism as a key economic activity, making it the country's third largest foreign exchange earner after tea and horticulture (Ikiara and Okech, 2002; Ministry of Tourism and Wildlife, 2006; Ministry of Tourism and Wildlife, 2008). Tourism contributes to approximately 13.7% of the gross domestic product and over 10% of the national formal sector employment (Ogutu *et al.,* 2016). The country's main tourist attractions are its wildlife and diverse landscapes which are ideal marketing tools for tourism. In 2011, wildlife-based safaris contributed approximately US$ 1.16 billion to Kenya's national revenue. Therefore, wildlife conservation must play a vital role in the safekeeping of the rich biodiversity of Kenya. Wildlife is a precious resource which needs to be harnessed, whilst also being understood and protected at the same time. With 65 National Parks and Reserves, Marine Parks and Reserves, and National Sanctuaries, comprising 8.2% of the nation's land area (Kenya Wildlife Service, 2000; Ondicho, 2000; Western *et al.,* 2009; Ogutu *et al.,* 2016), Kenya recognises the importance of conserving its wildlife.

As one of the “Big Five”, lions are one of the main attractions that bring tourists to Africa (Rudnai, 1973a) and Thresher (1982) calculated the value of a maned male lion to photographic tourism in a National Park in Kenya as being USD 515,000 over a period of 10 years. National Reserves, like Samburu and Buffalo Springs in northern Kenya, are very popular with tourists who bring much-needed revenue to the local county councils and overall, in the Samburu region, the conservation of large carnivores directly supports local development (Ating’a and Kimokoti, 2012; Lalampaa, 2012). One of the main attractions in these National Reserves is the lion (Wildlife Planning Unit, 1983; Bhalla, 2003).

Lions are also very important in some regions for cultural reasons (Loveridge *et al.,* 2010b). In the Samburu region, local people have lived with lions for generations and have strong beliefs about their importance and presence (*pers. comm. Jeneria Lekilelei*). The Samburu people believe that if a lion is heard calling at night, it means that drought will not affect them that year and if there is silence for months, drought will arrive. Therefore, having lions present means positive things for the Samburu communities.

The KWS has identified the Samburu-Isiolo ecosystem in northern Kenya as one of three remaining important areas in the country for the survival of Kenya's large carnivore species (Omondi *et al*., 2009). As lion numbers reduce and become more fragmented, an understanding of the factors affecting their populations, such as habitat loss and conflict with humans, is necessary to prevent further population decline. This study seeks to address this by understanding the status of the Samburu-Isiolo population and exploring suitable lion habitat within a human-occupied landscape.

1.7. Lion conservation in a human-occupied landscape

Lions are the most reviewed and studied carnivore in Africa (Becker *et al.,* 2012; Packer *et al*., 2013), with most of the research undertaken in protected areas, especially in the Serengeti National Park in Tanzania where lions have been studied since the 1960s (Schaller, 1972; Packer, 1986; Packer *et al.,* 1988; Packer, 2000).

However, parks and reserves do not guarantee the safety of the lion populations, as most protected areas are too small to conserve genetically viable populations (Linnell *et al*., 2005; Slotow and Hunter, 2009). There is also a risk of disease, such as canine distemper virus, which can wipe out an entire population (Packer *et al.,* 1999) and inbreeding (Snyman *et al.,* 2014), which can cause reduction in reproduction rates (Kissui and Packer, 2004). Additionally, if a protected area is small in relation to a lion's home range size, then it will be insufficient to protect a sustainable lion population (Harcourt *et al.,* 2001; Loveridge *et al.,* 2010a).

Within Kenya, extensive studies on lions have previously been conducted in protected areas such as the Maasai Mara National Reserve (Ogutu and Dublin, 2002) and Nairobi National Park (Rudnai, 1979). Few conservation / research projects in Kenya work outside the parks and reserves, with most concentrating within the safety of the protected regions (Dolrenry *et al.,* 2014). Within the human-occupied landscape in Kenya, there have been some studies conducted in the Laikipia region (Woodroffe and Frank, 2005; Frank, 2011; Oriol-Cotterill *et al.,* 2015a) and also in southern Kenya (Schuette *et al.,* 2013; Dolrenry *et al*., 2014). However, other than these few studies, very little is known about lions living in a human-occupied landscape and it is widely accepted that, although protected areas are essential for long-term persistence (Woodroffe and Ginsberg, 1998), it is the human-occupied landscape outside these protected areas that are required for carnivore survival (Nowell and Jackson, 1996).

Carnivores that live outside protected areas where human densities are high, face threats when: tolerance levels are low, there is a high propensity to kill lions, settlements are widely distributed, there is a low prey density, there is a lack of safe habitat and there are overlaps in the activity periods of both humans and carnivores (Oriol-Cotterill *et al.,* 2015b). These are all factors that increase the vulnerability of carnivores in a human-occupied landscape, and community areas are frequently associated with high anthropogenic mortality for lions ultimately affecting their population demographics (Loveridge *et al.,* 2010a; Dolrenry, 2013; Snyman *et al.,* 2014; Loveridge *et al.,* 2016). In areas where lions are persecuted, either through hunting or through retaliatory killing, lions are more secretive and nocturnal compared to areas where they are safer (Mogensen *et al.,* 2011; Schuette *et al.,* 2013; Oriol-Cotterill *et al*., 2015b). In Community Conservancies in northern Kenya, lions are more active at night when the presence of people is limited (*pers. obs.).* This was also found in ranches in the Maasai Mara (Ogutu and Dublin, 2004; Mogensen *et al*., 2011) and Laikipia (Frank and Woodroffe, 2001; Oriol-Cotterill *et al.,* 2015a; Oriol-Cotterill *et al.,* 2015b).

The availability of suitable habitats for carnivores in such areas is therefore essential in order to promote a "Landscape of Coexistence" with people living in these regions granting access to habitat where human caused mortality is low (Oriol-Cotterill *et al*., 2015b). These safe refuges, for example Conservation Areas in Conservancies, can help carnivores survive and avoid conflict even if the size of these safe areas is small (Schuette *et al*., 2013; Oriol-Cotterill *et al.,* 2015b). Wild prey numbers can increase in these small core regions, minimising livestock loss to carnivores as well. Carnivores often use refuges when hiding their young, resting or feeding on a carcass (Oriol-Cotterill *et al.,* 2015b). These refuges within a human-occupied landscape are often areas that are not used by people, such as rocky areas and thick bush which offers good cover for large carnivores, as people are less able to penetrate such habitat (Schuette *et al*., 2013). These habitats are deemed important to carnivores and if humans were to occupy them, it would pose a problem for the carnivores with reduction in wild prey and an increased probability of detection by humans (Oriol-Cotterill *et al.,* 2015b).

Promoting tolerance and coexistence will ultimately determine the fate of large carnivores (Woodroffe, 2000; Ripple *et al.,* 2014), including lions. Costs within community areas incurred as a result of carnivores need to be minimised in order to promote coexistence (Macdonald *et al.,* 2010). In addition to this, coexistence is more likely when the community is engaged in conservation and is able to build an appreciation and tolerance to having lions and other wildlife present in the area (Low *et al.,* 2009; Gurd, 2012; Hazzah *et al.,* 2014; Western *et al*., 2015). While people and lions have lived together for millennia; there is considerable need to rekindle local knowledge and to learn how to coexist with lions.

1.8. Big cats and conflict with humans

Human-carnivore conflict is a global issue, affecting carnivores in many countries (Woodroffe *et al.*, 2005; Inskip and Zimmerman, 2009; Seoraj-Pillai and Pillay, 2017). Wildlife species are often in competition with people for space and food (Woodroffe, 2000; Inskip and Zimmerman, 2009) and often livelihoods of local people who live adjacent to protected areas are in conflict with wildlife (Seoraj-Pillai and Pillay, 2017). Inskip and Zimmerman (2009) and Seoraj-Pillai and Pillay (2017) found in thorough literature surveys, that high-scale conflict species include lions, cheetahs *Acinonyx jubatus*, leopards *Panthera pardus*, jaguars *Panthera onca*, tigers *Panthera tigris*, amongst others. Typically, it is such high-scale conflict that often leads to retaliation and makes these carnivores extremely vulnerable. Carnivores are prone to conflict with humans due to their large home ranges and dietary requirements (Treves and Karanth, 2003; Inskip and Zimmerman, 2009). Often their home ranges overlap between protected areas and surrounding community or agricultural landscapes and carnivores go beyond these protected area boundaries making them more vulnerable (Woodroffe and Ginsberg, 1998; Woodroffe, 2000).

Seoraj-Pillai and Pillay (2017) found that leopards, were the leading carnivore causing conflict. African lions and tigers were the joint second carnivore involved in conflict. This short narrative below looks at tigers, leopards and jaguars and includes a few global case studies.

The world's population of tigers is in decline (Walston *et al.,* 2010), with three sub-species already extinct (Seidensticker and Christie, 1999). Tigers have declined across their range and exist now in only 13 countries (Saif *et al.,* 2016). Similarly to lions, tigers are often killed in retaliation due to both human and livestock loss. Habitat loss is a huge challenge for tigers (Walston *et al.,* 2010) due to their large range requirements (Kinnaird *et al.,* 2003). Tiger prey is also reducing (Karanth and Smith, 1999) and tigers go to villages to look for food, therefore causing conflict. Tigers often target livestock due to poor livestock husbandry practices (Wang and Macdonald, 2006). Additionally, man-eating is increasing especially as prey numbers decline (Walston *et al.,* 2010). In the Sundarbans in Bangladesh, human-tiger conflict is more common than anywhere else and tigers kill people frequently (Neuman-Denzau and Denzau, 2010). It was found that this was mainly because of the number of people entering forests (forest resource users), which appeared to provoke man-eating behaviour. Packer *et al*., (2005) and Kushnir *et al*., (2014) studied man-eating lions in Tanzania, where over 1000 people have been attacked in the last 20 years (Kushnir *et al*., 2014). Man-eating is not known to be a problem with lions in the Samburu region (*pers. obs*.). Saif *et al*., (2016) found in the Sundarbans that people are killing tigers for safety, professionally and opportunistically. Additionally, poachers are killing tigers for money and also tiger parts for local medicine. There are a number of efforts to protect tigers and their habitat. For example, in Nagerhole National Park in India, wild prey management was very successful through increased efforts in protecting habitat, law enforcement to prevent encroachment, limiting human access to parks and anti-poaching patrols (Karanth and Smith, 1999). This resulted in prey increasing by 80% and conflict with tigers reduced.

Leopards are the most widespread carnivore globally and able to live in a diversity of habitats (Gavashelishvili and Lukarevskiy, 2008; Constant *et al.,* 2015). However, in Southern Africa alone, the leopard's range has reduced by 37% over the past 100 years (Ray *et al.,* 2005; Swanepoel *et al.,* 2013; Constant *et al.,* 2015). Leopards across Africa and Asia are struggling due to habitat loss and natural prey depletion, similarly to tigers and lions. This is resulting in increased human-leopard conflict (Bhandari, 2015) and in India, leopards are involved in more conflicts than any other large carnivore (Odden *et al.,* 2014). Human loss is one of the factors leading to retaliatory killing of leopards as Bhandari (2015) found in the Kathmandu Valley, Nepal. Results from Bhandari's 2015 study indicated that the average leopard death rate is 4.66 per year in the Kathmandu Valley. Partasasmita *et al.,* (2016) found that in addition to loss of habitat due to forest conversion and lack of prey affecting leopards, Javan leopards were also being killed for their skins and body parts in Sukabumi, Indonesia. Despite the Javan leopard being listed in Appendix 1 of CITES, numbers of leopards continued to decline due to illegal hunting and between 2010 and 2016, 14 leopards were captured (Partasasmita *et al.,* 2016). Leopard meat is also consumed because people believe it has medicinal properties. Additionally, leopards are being poached to meet the illegal trade demand (Athreya *et al.,* 2004) and recent reports stated that between January and March 2017, 53 leopards were poached in India to fuel the illegal wildlife trade (Chatterjee, 2017). 154 leopards across India were killed by poachers in 2016 for the same reasons.

Alam and Kumar (2012) conducted a study in the Gir Protected Areas of Gujarat, India, and reported that leopards use agricultural plantations and orchards to find food, shelter and water. Leopards have adapted to living in these human settled areas and even breed in the cultivated fields. However, conflict has increased here and despite there being some acceptance of livestock predation, human loss is not accepted and leopards were soon seen as a "symbol of terror" (Alam and Kumar, 2012). Growth in human population is one reason for the conflict, with the concurrent increase in livestock numbers. The vast numbers of livestock have also attracted leopards to approach settlements, and loss of the leopard's natural prey base is a huge problem. Odden *et al*., (2014) also found that leopards in India are able to move around in areas where there is human activity and can be found in areas with high human densities. Through the use of collared data, results showed how closely leopards lived with people and how they moved closer to settlements especially at night (Odden *et al*., 2014). Lions, cheetahs and tigers are more vulnerable to human impact but leopards less so. They are a highly adaptable species that are able to tolerate humans. Their feeding habits are very diverse and in areas where there is limited wild prey, leopards can prey on livestock. They have a strategy of minimising as little contact with humans but still depend on livestock.

Jaguars, a keystone species, are also suffering from population declines (Zimmerman *et al.,* 2005; Altrichter *et al.,* 2006; Boron *et al.,* 2016). Jaguars have lost over 50% of their historical range and are also affected by habitat loss, loss of prey and conflict over livestock depredation (Hatten *et al.,* 2003; Zimmerman *et al.,* 2005; Silveira *et al.,* 2008). As with other large carnivores described previously, jaguars have large range requirements (Silveira *et al.,* 2008; Boron *et al.,* 2016). This makes unprotected areas important within their landscape as they are used for dispersal and connectivity. In Colombia, it was found that jaguars can live in unprotected and agricultural landscapes, as long as natural areas persist and hunting of jaguars and their prey is limited (Boron *et al.,* 2016). Protected areas are too few to contain jaguars (which is similar to other carnivores) and a landscape approach is needed for their conservation, encompassing both protected areas and unprotected areas.

Various studies have been conducted and methodologies used to identify suitable habitat for carnivores around the world. Imam *et al.,* (2009) used a Geographic Information System (GIS) model to evaluate habitat suitability for tigers in Chandoli National Park in India. Binomial multiple logistic regression was combined with GIS for the modelling. Swanepoel *et al.,* (2013) used maximum entropy-based habitat modelling techniques to assess suitable habitat for leopards in South Africa. Gavashelishvili and Lukarevskiy (2008) also used a GIS model combined with logistic regression to construct a predictive model of leopard habitat selection in west and central Asia. Hatten *et al.,* (2003) created a habitat suitability map for jaguars in the state of Arizona, which historically used to have resident jaguars. A GIS was used to create and analyse the data, and map the suitable habitat.

Overall, it is clear that large carnivores globally are exposed to similar threats, largely habitat loss and loss of a natural prey base, resulting in human-carnivore conflict. Management of human-carnivore conflict is a key issue that needs to be addressed and is a key conservation priority for a number of carnivore species, including lions. It is clear through understanding more about these global carnivore species, that protected areas are not enough for them due to their large ranges. Investigating what suitable habitat exists and knowledge of their habitat requirements for carnivores outside the safety of protected areas is essential since they persist in these landscapes, and in the case of leopards, thrive in such landscapes. In this study, we investigate suitable habitat for lions in a human-occupied landscape and understand what factors influence their presence.

1.9. Thesis aims

In light of the conservation status of lions and the concern over declining population numbers across Africa, this thesis seeks to examine the population demographic parameters (to establish the status of the population) and the ranging behaviour of the Samburu-Isiolo lion population (to establish their movements considering their requirements for large ranges). Since habitat loss is a serious concern for lions, the study further assesses the availability of suitable habitat for lions within a human-occupied landscape to determine the potential for safe dispersal and persistence of lions outside of protected areas and opportunities for their effective conservation with the goal of reducing human-lion conflict. This was a key objective of the thesis.

1.10. Thesis objectives

Key Objective: To develop a Habitat Suitability Model for lions within the human-occupied landscape.

The following research questions gave structure to this research and thesis planning. These questions helped address the key objective and led to the creation of the Habitat Suitability Model.

Objective 1: Establishing the lion population demographic parameters temporally.

» Data is presented in Chapter 3.

Objective 2: Establishing the ranging behaviour of the lions to understand their spatial requirements.

» Data is presented in Chapter 4.

Objective 3: Development of a Habitat Suitability Model for the lions for their effective conservation.

» Data is presented in Chapter 5.

This thesis will provide detailed knowledge of lion demographics and range, temporally and spatially, which is fundamental to lion conservation within the Samburu-Isiolo ecosystem. It will further address issues relevant to the anthropogenic interface. The overall demographics and home ranges are first explained, followed by a model that identifies suitable locations for lions in a Community Conservancy. The initial data chapters provide the underpinnings leading to the model.

1.11. Thesis structure

This thesis has been organised into six chapters including this introduction. The study area is described in detail in the second chapter, followed by three data chapters, ending with a discussion.

Chapter 1: Introduction

Chapter 2: Study area

Chapter 3: The demographic parameters of the lion population in the Samburu-Isiolo ecosystem

Chapter 4: Lion home ranges in the Samburu-Isiolo ecosystem

Chapter 5: Suitability modelling to identify potential lion habitat in Westgate Community Conservancy, Samburu

Chapter 6: Discussion

Chapter 2

Study area

"Northern Kenya is a country of sand rivers known as luggas, of isolated mountains rising sheer from the plains, of long droughts and sudden torrential rainstorms. Here, doum palms rustle in the hot dry winds and the thorn scrub stretches to the distant horizon. Kenya's north has a wild beauty all its own, irresistible to those who fall under its spell."

Wilson, 1989

2.1. Introduction

Carnivores, including lions, are important indicators of functioning ecosystems (Macdonald, 1995; Ripple *et al*., 2014). For effective wildlife conservation, the study of large carnivore populations is a necessity, especially due to their current vulnerability and importance in regulating ecosystems. In addition to studying carnivores, encouraging local communities to embrace conservation is essential to ensure the long-term persistence of carnivore populations. The importance of this is further emphasized due to the large ranges that carnivores need and their frequent movements outside of protected areas.

In northern Kenya, local people have always lived with wildlife and there has been a general appreciation and tolerance towards wildlife (Saidia, 1991). Within the study area (see 2.2.1), the interest to have Community Conservancies (further explained in section 2.3.4.) was initiated through the community members themselves (Kantai, 2012). The community came together to discuss conservancy formation and from the onset, involved the community members in all decision-making processes and employment opportunities. Ogutu et *al.,* (2016) states that this is critical for conservancy success. Wildlife protection was listed as one of the main reasons Westgate Conservancy was established (in addition to tourism) after Kantai (2012) interviewed community members. Members related wildlife to increased benefits they receive (for example through the provision of school bursaries, establishment of health clinics and provision of water – *pers. obs*.), and pledged to keep wildlife safe to accrue additional benefits. From personal observations between 2013 to date, there has been a change of view towards wildlife conservation amongst the community in Westgate Conservancy. Initially during the early years, wildlife was viewed with much optimism and appreciation for cultural, tourism and ecological reasons. With recent development in the area, it appears that the intent to have wildlife has changed and the community tolerate wildlife primarily for economic reasons. Kantai (2012) states, "For the Western sponsor or top manager of community conservation, development is the means and conservation is the end. For the community member, development is the end and conservation is the means." Overall, considering the decline in wildlife numbers across Kenya, Ogutu *et al*., (2016) suggest that empowering communities so they are able to use, manage and receive economic benefits from wildlife, will enhance the importance of wildlife as a component of livelihoods and development. The Samburu people have always lived with wildlife and generally do not kill any wild animals (Saidia, 1991). They have always ensured that the environment they live in is well protected for the benefit of their livestock. Elders were interviewed in 1991 by the Saidia Project regarding their attitudes towards the land and the environment, and they stated that wildlife tourism was not something they were keen on as it imposed boundaries on where they can take their livestock and how they need to keep away from wildlife – yet they have always lived with wildlife. Secondly, it was recorded that their nomadic lifestyle kept the environment and wildlife well protected but pressures to change this led to degradation of the environment.

2.2. Abiotic/biotic aspects

2.2.1. Location

This study focuses on the Samburu, Buffalo Springs and Shaba National Reserves, and Westgate Community Conservancy, located in northern Kenya. These areas form part of the Greater Ewaso Nyiro Ecosystem. The study area lies at latitude 0º30'N and longitude 37º30'E (Barkham and Rainy, 1976).

Samburu National Reserve (SNR) is situated in the southeastern corner of Samburu County in Rift Valley Province and covers an area of 165 km^2. Both Buffalo Springs National Reserve (BSNR) and Shaba National Reserve (ShNR), are located in Isiolo County, in the Eastern Province and cover 131 km^2 and 239 km^2, respectively (Kenya Wildlife Service, 2000). Refer to Table 2.1. to see how this compares to other protected areas in Kenya. SNR and BSNR are adjacent to ShNR (please refer to Figure 2.1). Westgate Community Conservancy (WGCC) is in the Waso West location in Waso West Division, Samburu County, and lies adjacent to the western boundary of SNR, covering an area of 406 km^2. The Ewaso Nyiro River flows between Samburu and Isiolo Counties transecting the National Reserves. The combined size of this unfenced region that comprises the study area is 941 km^2.

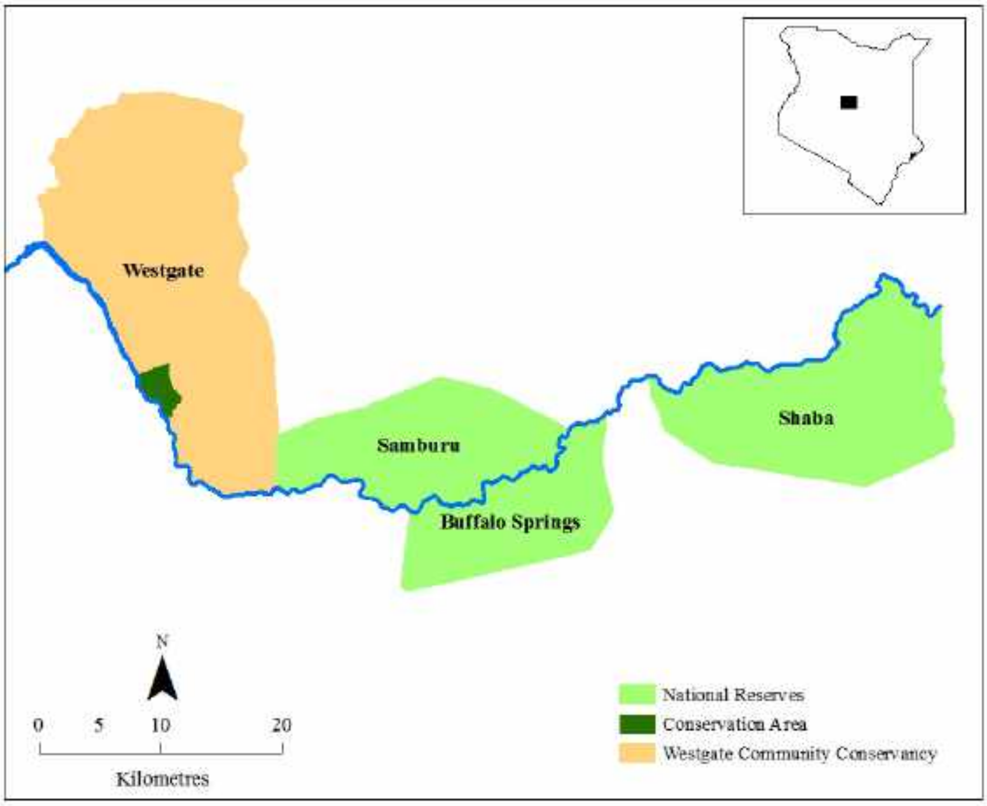


Figure 2.1. Map of Study Area within Kenya. For a close up view, refer to Appendix 1.

Table 2.1. Size of protected areas in Kenya (Source: http://www.protectedplanet.net/country/KE)

Name of protected area	Size (km^2)
Aberdares National Park	766
Amboseli National Park	392
Nakuru National Park	188
Meru National Park	870
Tsavo East National Park	13747
Tsavo West National Park	9065
Maasai Mara National Reserve	1510

The Samburu County Council manages SNR while the County Council of Isiolo has jurisdiction for managing the tourism and wildlife issues in BSNR and ShNR. The Kenya Wildlife Service (KWS) cooperates with both County Councils and provides additional monitoring and security for the area's wildlife and tourism. Within KWS's conservation area network, SNR and WGCC fall under the Mountain Conservation Area, while BSNR and ShNR fall under the Eastern Conservation Area.

WGCC, which was registered in 2004, is part of Ngutuk Ongiron Group Ranch, and is managed by the local community and divided into 4 sub-locations: Lpus Leluai, Ngutuk Ongiron, Remot and Lengusaka. While the National Reserves are gazetted and exclusively used for tourism and wildlife, WGCC is a Conservancy where local people, their livestock and wildlife live together with a Core Conservation Area designated for wildlife (Figure 2.1).

2.2.2. Climate

The area's climate is generally hot and dry, with cool nights. The average annual maximum and minimum temperatures are 30°C and 20°C respectively (Wilson, 1989). The annual rainfall for the area varies between 250 mm and 500 mm (Esilaba *et al.*, 2007), with peak rainfall in April, during the long rains and in November, during the short rains (Wilson, 1989). Rain tends to fall as widely scattered, short and heavy showers; which tend to be localised and far below the expected minimum. The rainy seasons vary from year to year and the rainfall is extremely unreliable (Figure 2.2). Dry conditions usually prevail from June to early October, and January to April. There was a prolonged drought in 2009, as indicated in Figure 2.2.

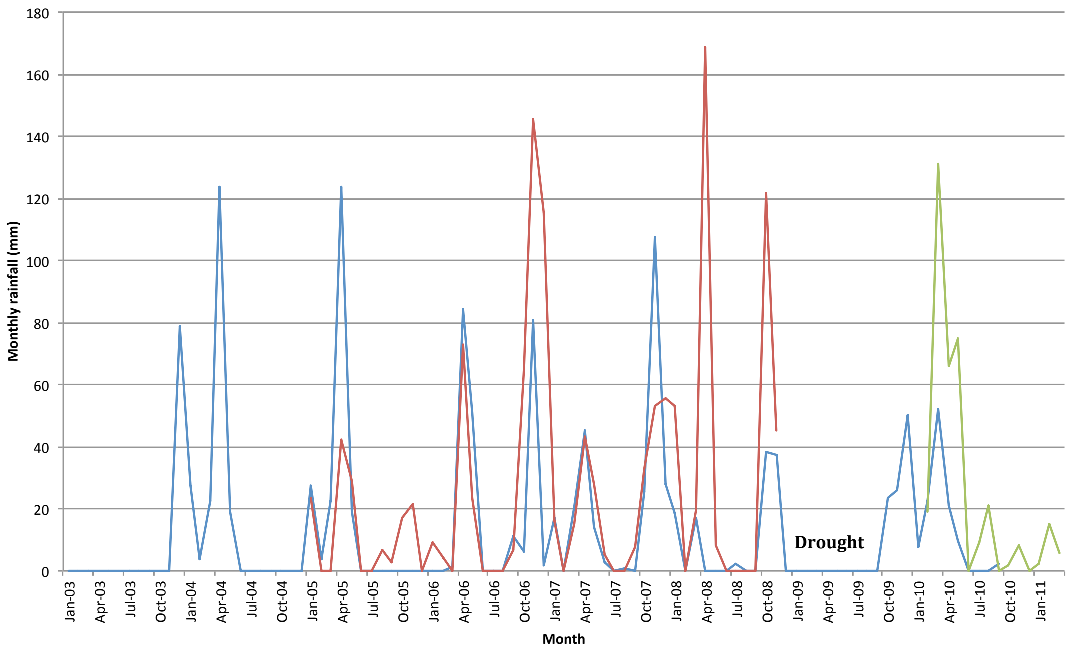


Figure 2.2. Monthly rainfall within the study area. The blue line represents rainfall data from Save the Elephants in SNR, the red line representing data from Archers Post Weather Station and the green line representing data collected by Ewaso Lions Project (ELP) in WGCC.

2.2.3. Hydrology

The scenic beauty and ecological importance of both SNR and BSNR centres around the Ewaso Nyiro River, which means 'River of Brown Water' in the Maa language (Figure 2.1) (Wilson, 1989). Spanning 32-kilometres through the study area, the Ewaso Nyiro River, is a central feature of the Reserves and forms the largest river system in northern Kenya. It originates from the Aberdare Range, from where it flows north and then eastwards between Mt Kenya and the Mathews Range. The three Reserves lie within the floodplains of the Ewaso Nyiro River drainage system which forms a natural boundary between SNR and BSNR. It borders WGCC and SNR to the south (Wilson, 1989; Colley and Crowther, 1997) and runs through ShNR in the east, forming the northern boundary of the Reserve (Figure 2.1).

Over the years, the amount of water in the Ewaso Nyiro River has been dwindling rapidly (Georgiadis, 2011). This is as a result of increased settlements and over-exploitation in its upper catchment area, especially in Laikipia, where there are uncontrolled irrigation practices (SICA, 2010; Georgiadis, 2011).

An important feature of the Reserves is the presence of permanent water (Wilson, 1989). Even when the Ewaso Nyiro dries up (a common occurrence in recent times), BSNR and ShNR have several sources of year-round water, although SNR relies solely on the Ewaso Nyiro. The Isiolo River in BSNR continues to flow and there are three deep waterholes near the Ngare Mara River (see Appendix 1). ShNR has 10 springs (NRT, 2015) scattered throughout the Reserve, the largest being the Chaffa Gafarssa Swamp. The springs and swamps are permanent and provide drinking water for the wildlife in the area.

During the wet season, the *luggas* or dry river-beds fill with water and provide a temporary water source for the wildlife in the area. This is especially the case in WGCC, where 10 main *luggas* provide temporary water sources for both livestock and wildlife. There are 10 man-made and 21 natural water dams in WGCC and five boreholes that supply water to the local people and their livestock. These sources lack water during the dry seasons.

2.2.4. Vegetation

Riverine vegetation, *Acacia–Commiphora* semi-arid scrub, and *Acacia* wooded grasslands dominate the Reserves (Wilson, 1989). Vegetation in SNR comprises mainly of thorny scrubland, while much of BSNR has large areas of the umbrella acacia, *Acacia tortillis*, particularly at Champagne Ridge in the eastern section of the Reserve (see Appendix 1). The finger grass, *Cynodon dactylon*, is the dominant grass cover in both Reserves (Shorter, 1981). ShNR has numerous alkaline grass species along the swamps (*pers. obs.*).

The most common tree along the Ewaso Nyiro River is the river acacia, *Acacia elatior* (Wilson, 1989). Narrow riverine woodland of Doum Palm, *Hyphaene compressa*, dominates part of the central river section (Colley and Crowther, 1997). Low-lying pans adjacent to the River become seasonally waterlogged and the dominant halophytic species present here is saltbush, *Salsola dendroides* (Wilson, 1989), to be found to the east of Samburu Lodge (see Appendix 1). In less saline areas, the '*mswaki*' or 'toothbrush bush', *Salvadora persica*, form dense thickets. *S.persica* dominates the western zone of SNR. *S.dendroides* and *S.persica* are seldom browsed, but they provide shelter and shade for many animals (Shorter, 1981) and provide perfect safe habitat for carnivores especially living in the human-occupied landscape (*pers. obs.*).

The vegetation in WGCC is characterised by a diversity of vegetation types and is dominated by shrub and grassland savannah enriched with scattered *Acacia* trees and riverine woodland (Hitimana, 2008). *S.persica* thickets dominate the riverine edges along the southern boundary of WGCC.

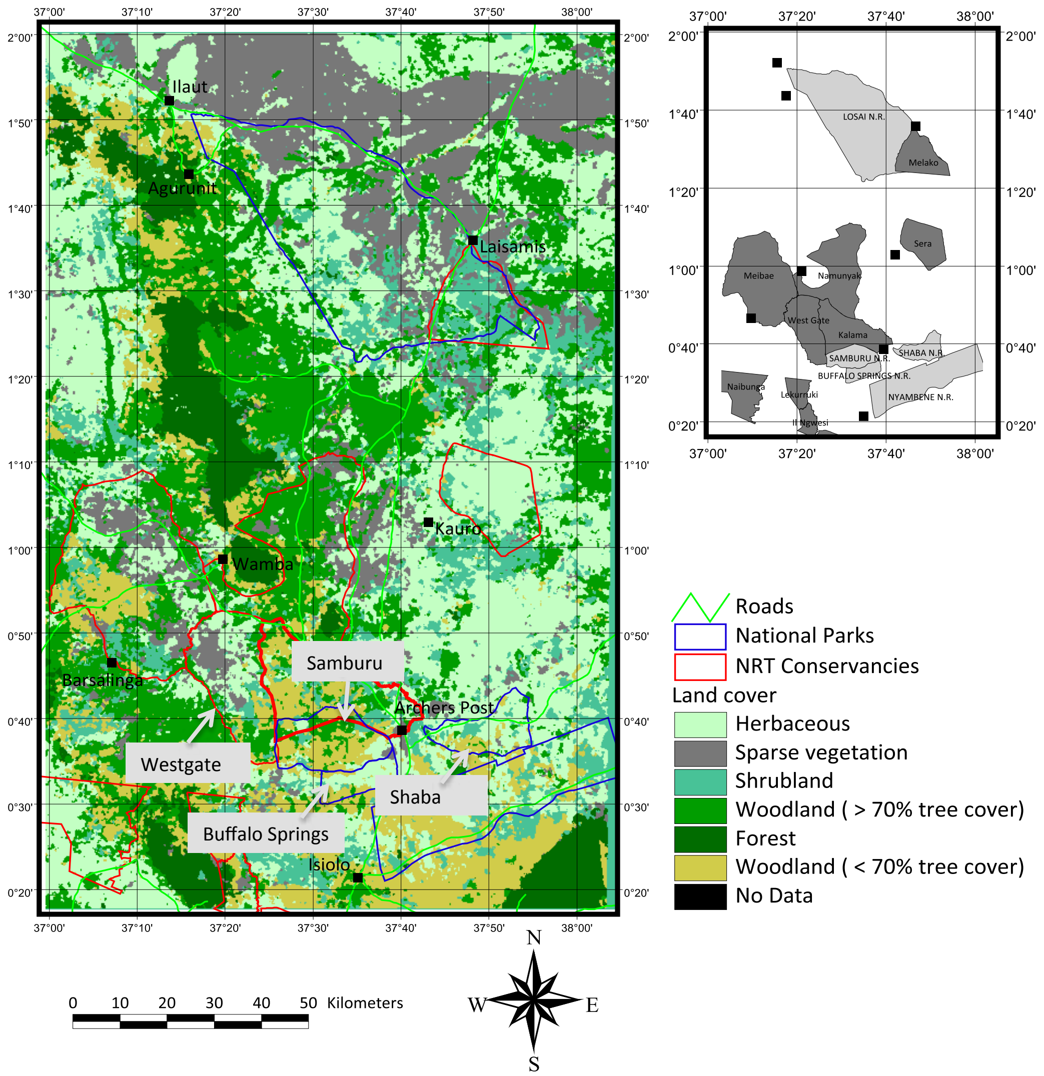


Figure 2.3. Vegetation map showing all land cover types within the study area (Source: Northern Rangelands Trust, 2010).

Figure 2.3 shows the land cover types within the Samburu-Isiolo landscape where WGCC has more sparse vegetation compared to the three Reserves, and the Reserves contain more woodland (< 70% tree cover) compared to WGCC. ShNR also contains more herbaceous vegetation compared to its neighbouring Reserves.

2.2.5. Topography

Mountains, hills and rocky outcrops form the backdrop to the Reserves (Wilson, 1989). The volcanic Nyambene Hills to the southeast of the Reserves are the source of most of the permanent springs within BSNR and ShNR.

SNR rises gently from the Ewaso Nyiro River, at an altitude ranging from 850 to 1250 metres above sea level (Wilson, 1989). However, most of the area lies below 1050 metres. SNR is a lava plain with steep-sided gullies and rounded basement hills. The sharp hill of Koitogor rises in the middle of SNR and is the main feature of the Reserve (see Appendix 1). On the horizon, 30 kilometres north, rises the Ol Donyo Sabache mountain (see Figure 2.4). BSNR has open plains with small hills. ShNR has a dramatic landscape with rocky outcrops and rugged hills, including the Bodech mountain. WGCC has mixed topography with plains and hills. The largest hills are Lmooti and the Lalasai range.

Figure 2.4. Photo showing mountains, hills and rocky outcrops that form the backdrop of the Reserves with Ol Donyo Sabache in the background.

2.2.6. Wildlife

The study area is home to some of Kenya's unique mammal and bird species, adapted to the arid north and only found in this region (Amin and Eames, 1985; Wilson, 1989; Leeuw *et al.,* 2001). This dry ecosystem is prone to large variations in animal populations as they move in search of water and pasture (Leeuw *et al.,* 2001). The Ewaso Nyiro River and the forest shade on its banks, draw abundant wildlife in the dry season and maintain many of the less nomadic species during the rest of the year.

The only non-riverine sectors that support large animal densities are near the Buffalo Springs "Swimming Pool" and the well-developed shade from *A.tortilis* at Champagne Ridge (see Appendix 1).

WGCC has both resident and transient wildlife species. Small numbers of eland (*Taurotragus oryx)*, giraffe (*Giraffa camelopardalis reticulata)* and numerous other prey species (see Appendix 2) are residents. WGCC is also strategically located as an important seasonal grazing area supporting the overflow of migratory species from the Reserves, including elephants (*Loxodanta africana)* and Grevy's zebra (*Equus grevyi*) (Hitimana, 2008; Low *et al.,* 2009). WGCC will continue benefiting from these migratory species as long as wildlife corridors and routes that transverse it, are preserved.

The Reserves and WGCC have a large diversity of carnivore species. Lions, cheetahs, *Acinonyx jubatus*; leopards, *Panthera pardus*; wild dogs, *Lycaon pictus*; striped hyaena, *Hyaena hyaena*; and spotted hyaena, *Crocuta crocuta*, are all found within this area. WGCC has a higher number of spotted hyaena, leopards and resident wild dog packs, compared to the Reserves which have more striped hyaena and transient wild dog packs (*pers. obs*.). In WGCC, it is also possible to catch glimpses of rarely seen carnivores such as caracals, *Caracal caracal* and aardwolves, *Proteles cristata*.

Wildlife populations in the region have greatly reduced as a result of the long drought and heavy poaching that took place between 1970 and 1977 (Wildlife Planning Unit, 1983). The period between 1973 and 1980 witnessed a decline of nearly 50% of the area's animals. Rainy and Worden (1997) report that the decrease in the numbers of wild herbivores still continues, and predicted that by 2010 numbers would fall to as low as half the 1990 population sizes.

A team of scouts collected data using transect sampling in WGCC, where the observer walks along a line and records wildlife sighted (all herbivores), and the distance and angle from the transect line (Buckland *et al.,* 2010; Thomas *et al*., 2010). These three-kilometre-long transects were one kilometre apart from each other and placed to cover the accessible part of the study area (see map in Appendix 3 – Figure

3a). Data analysis was conducted using the programme Distance version 6.2. Results from these transects indicated that between 2011 and 2014, the average density of all wild herbivores in the study area was 4.9 animals/km^2. Gerenuk (*Litocranius walleri*) and Grevy's zebra represented the two most common herbivores found in WGCC. Impala (*Aepyceros melampus*) and Grant's gazelle (*Nanger granti*) were uncommon and their estimated densities fell below 1 animal/10 km^2. When comparing the four years, herbivore densities averaged 30 individuals/10 km^2 in 2011, increased in 2012 and 2013, and then decreased in 2014 to 24 individuals/10 km^2 (refer to Figure 3b in Appendix 3).

Across Kenya, wildlife numbers have declined on average by 68% between 1977 and 2016 (Ogutu *et al.,* 2016). For Samburu County in particular, Grant's gazelle reduced by 82%, gerenuk reduced by 84%, warthogs (*Phacochoerus africanus*) reduced by 73%, impala reduced by 94%, waterbuck (*Kobus ellipsiprymnus*) reduced by 73% and Grevy's zebra reduced by 84%. All these species are typically lion prey in the region (Bhalla, 2003).

2.3. Anthropogenic influences

2.3.1. Tourism

SNR, BSNR and ShNR are part of the northern tourism circuit and are popular destinations for tourists due to the ready visibility of the rarer northern wildlife species. This ecosystem is second to the Maasai Mara in popularity with visitors to the country (SICA, 2010). 2005 saw a record breaking number of 14,000 tourists visiting the three National Reserves (Beh and Bruyere, 2007). Peak tourism season is generally in July and August each year with elephants present in vast numbers and the big cats are often seen in the Reserves (*pers. obs*.). As described in section 1.6, tourism plays a key role in creating a source of income for the local people.

At the start of the study in 2007 there were 13 tourist lodges within SNR and BSNR (see Appendix 1), however, this reduced to 11 facilities after the March 2010 floods when two lodges were permanently destroyed (Samburu Serena and Samburu Sentrim

Lodges). Five other establishments were also affected by the floods, but reopened after repairs. In WGCC, there is one permanent tourist facility, Sasaab Lodge, which provides WGCC with a bed-night fee revenue. Temporary and mobile camps are also present at times. The presence of the adjacent SNR, influences tourism related activities in WGCC through tourist visits to school and villages (*pers. obs*.).

2.3.2. Human demography

Samburu County, where part of the study area is located, is a semi-arid area comprised of communal lands inhabited by the nomadic Samburu pastoralists (Wildlife Planning Unit, 1985; Pavitt, 2006). The Borana and Turkana ethnic groups who are also nomadic pastoralists, mainly live in Isiolo County, south of the Ewaso Nyiro River.

SNR is bordered to the west and north by Ngutuk Ongiron and Girgir Group Ranches, respectively. Three main villages, Kiltamany village in the north and Lorubae village to the east of SNR and Loruko village in the west of BSNR, are on the peripheries of the Reserves (see Appendix 1). The Kalama Conservancy lies to the north of SNR. BSNR and ShNR are separated by Archers Post (east of SNR) and Ngare Mara (south of BSNR); both rapidly developing settlements (Figure 2.5). A newly established tarmac road connecting Isiolo town to Archers Post and beyond has resulted in a rapid growth of villages along this highway (*pers. obs*.). WGCC is also developing with an increased number of settlements (see Figure 2.6), clinics, schools and permanent houses.

Population census data from the Kenya Bureau of Statistics shows that there has been a population increase in the area between 1999 and 2009. Figure 2.5 shows the change in population size in six locations across an area of 985.9 km^2. These were the only locations where data was collected by the Kenya Bureau of Statistics that fell within the study area. The total number of people in 1999 was 10,198 in the six locations. This increased to 14,532 in 2009, representing a percentage increase of 42%.

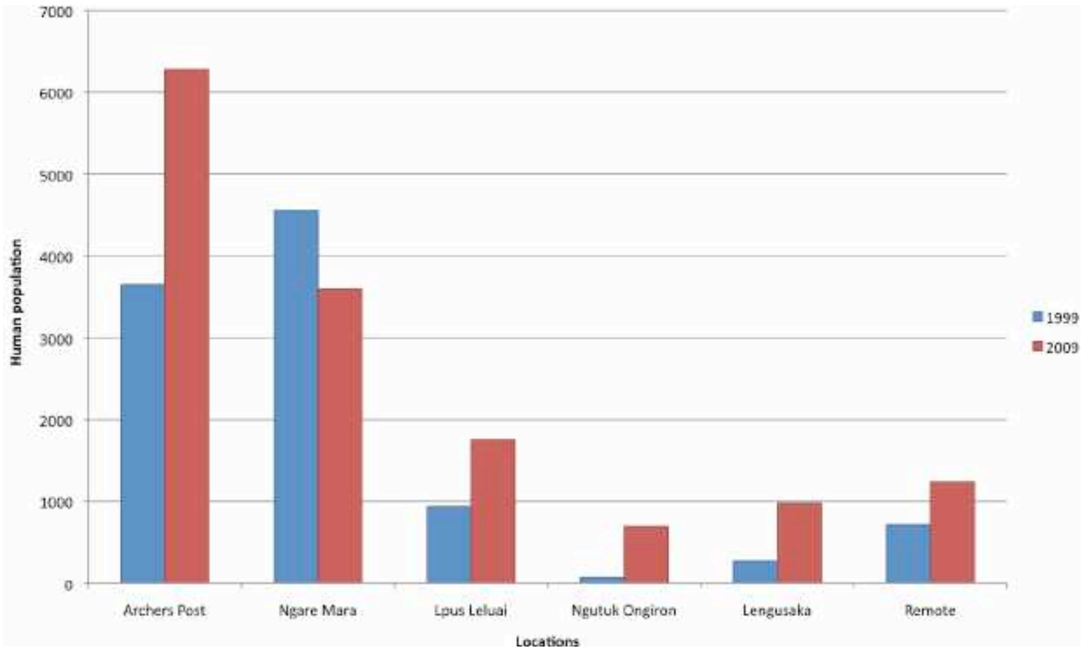


Figure 2.5. The change in population numbers between 1999 and 2009. The censuses were conducted by the Kenya Bureau of Statistics.

Ngutuk Ongiron Group Ranch forms part of the least densely populated areas of Samburu County, mainly due to the insecurity troubles in 1997 and 1998 leading to people migrating away (Hitimana, 2008). However, since then the area is now one of the more stable in the region after the formation of the Conservancy (WGCC), and this has led to an influx of people in recent years. There are six main settlement areas, mainly developed as a result of access to water and preferred vegetation for livestock; Lpus Leluai, Sasaab, Ngutuk Ongiron, Kiltamany, Naisunyai and Remot (see Appendix 1), with an average of 50 people per house (Hitimana, 2008). The population projection for the Group Ranch was three people per km^2 in 2008, compared to two people per km^2 in 1999. Data collected in 2011 by the Ewaso Lions Project showed that the number of people in WGCC between March and August, was 2,336. This included men, women, warriors and children.

Figure 2.6 shows the change in settlements in WGCC from 2008 to 2010. It can be seen that settlements became larger and in some locations, joined together to form a continuous line of settlements. There were 58 additional settlements in 2010 compared to 2008, representing a percentage increase of 54.2%.

(a) (b)

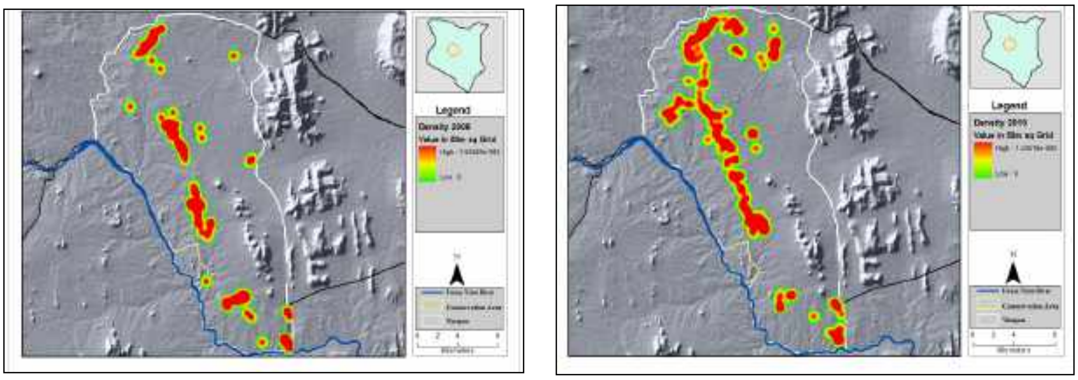


Figure 2.6. Maps showing settlement change in WGCC between (a) 2008 and (b) 2010.

2.3.3. Livestock keeping

The main economic income of the local population within Samburu and Isiolo Counties comes from livestock in the form of camels, cows, sheep, goats and donkeys (Spencer, 2004; Hitimana, 2008; Campbell *et al*., 2009; Low *et al*., 2009). Eighty percent of the population hold livestock and rely on their cattle as their livelihood and main source of income. Livestock is an indicator of wealth and prestige among the Samburu, Turkana and Borana people (Amin and Eames, 1985; Konaka, 1997) and they also have a strong cultural significance, encompassing social, political and cultural values (Spencer, 2004; Dickman *et al.,* 2011).

In WGCC, various livestock including cows (8%), donkeys (4%), camels (3%), sheep and goats (a combined 85% of total livestock – see Table 2.2.) roam through the Ngutuk Ongiron Group Ranch in search of pasture and water (Spencer, 2004). According to Hitimana (2008), the number of cattle per household has been decreasing but their absolute number in the ranch has increased. Factors such as drought, insecurity and disease have played a role in the change in livestock numbers in this area. The numbers of livestock changes frequently depending on security within the region and the consequent movement of people. There has been a slight shift from nomadism to sedentarism in WGCC over the last few years (Hitimana, 2008).

Table 2.2. Livestock census in Westgate Conservancy between 2012 and 2014. (Source: Ewaso Lions Project, 2014).

Year	Sheep and goats	Cattle	Donkeys	Camels	Total
2012	34380	2272	1279	974	38905
2013	27906	1664	1233	1618	32421
2014	33000	4875	1943	978	40796
Mean	31762	2937	1485	1190	37374
SD	3410	1706	340	371	4392
% of total	85%	8%	4%	3%	-

Using the same methodology explained in section 2.2.6 and the data collected by scouts, results indicated that the average density of all livestock within WGCC between 2011 and 2014 was 139.92 individuals/km^2. Sheep and goats had the highest densities of all livestock species in all four years, averaging 84.9 individuals/km^2. Camels were the second most abundant livestock species with an average of 21.36/ km^2, followed by donkeys (20.13/km^2), and cattle (10.36/km^2). The highest densities of all livestock occurred in 2012, with roughly 173 animals/km^2. The lowest densities of livestock were in 2013 (refer to Figure 3c in Appendix 3).

Figures 3b and 3c (Appendix 3) show that that herbivore densities have reduced within WGCC since 2012 and livestock densities have increased since 2013. Extreme wildlife declines with concurrent increases in livestock numbers has been reported by Ogutu *et al.,* (2016). In Kenya, between 1977 and 2016, cattle numbers decreased by 25.2% but sheep/goats (76.3%), donkeys (6.7%) and camels (13.1%) all increased. For Samburu county in particular, sheep and goats increased by a staggering 168% and camels by 99%. Between 2011 and 2013, livestock biomass was 8.1 times greater than that of wildlife, compared to 3.5 times between 1977 and 1980.

2.3.4. Community Conservancies

The Northern Rangelands Trust is the umbrella organisation for 27 Community Conservancies that have been established in northern Kenya and encompass over three million acres (Source: www.nrt-kenya.org accessed on 10th August, 2014). Conservancies are community-led initiatives which recognise the value of wildlife as an alternative livelihood strategy and contributor to development for local people.

Conservancies provide security for the local residents and wildlife outside of protected areas. There is a direct link between conservation and community development in Conservancies.

2.4. Importance and fragility of the study area

2.4.1. Importance of the Ewaso Nyiro ecosystem

SNR, BSNR and ShNR are critical components of the arid and semi-arid ecosystems of northern Kenya, providing safe refuges for the endangered and vulnerable northern wildlife species. The National Reserves form part of a larger ecosystem and, together with the neighbouring communal lands, act as critical dispersal areas for wildlife. The absence of fences within this landscape allows for an interconnected ecosystem throughout the region, providing free movement for the wildlife.

Twenty percent of the elephant population within the Laikipia-Samburu ecosystem uses the Reserves, highlighting the importance of connectivity between Laikipia and Samburu (Wittemyer, 2001). These northern counties also host the largest population of elephants outside of protected areas (Gadd, 2005). However, poaching still occurs in the region, where unsustainable rates of illegal killing took place between 2009 and 2012, escalating from a mean of 0.6% (SD=0.4%) between 1998 and 2008 to a high of 8% in 2011 (Wittemyer *et al.,* 2014). SNR and BSNR are known as 'safe havens' for the elephant population in the region (Wittemyer, 2001). WGCC also acts as a safe refuge for elephants, with high levels of poaching occurring in the surrounding areas (nearby Sera Conservancy reporting five deaths to poaching between January and June 2014) and only one unknown cause of death within WGCC itself (Northern Rangelands Trust, 2014). The Reserves are also focal areas for calving, indicating that the study area is of reproductive importance to the elephant population (Wittemyer, 2001).

The endangered Grevy's zebra have disappeared from their former range in southern Somalia and are now rare in southern Ethiopia (Wilson, 1989). Northern Kenya is their last stronghold (Low *et al*., 2009). A survey conducted in 2008 reported 2,407

Grevy's zebra in northern Kenya, with the highest concentrations in the Reserves and the adjacent Conservancies including WGCC, Meibae, Kalama and Namunyak Conservancies (Low *et al.,* 2009). The Reserves are dry season refuges and provide the Grevy's zebra with water, which is especially important for foals.

During periods of high rainfall, many ungulates disperse into the surrounding areas, but in the dry season the animals show a preference for the Reserves (Wilson, 1989). At times, the River may dry up altogether and elephants dig wells in the riverbed, whilst other animals converge around these elephant waterholes (Klumpp, 1992).

2.4.2. Importance of the Reserves for lions

In January 2006, at a workshop facilitated by the Wildlife Conservation Society, information on lions and the study area was presented using a broad platform of the Ewaso Nyiro landscape which takes into account Samburu, Laikipia and Isiolo Counties (Didier *et al*., 2009). The information included key areas, current distributions, areas of vulnerability and potential recovery, conservation costs associated with this, and mapping conservation priorities for lions. One of the key outcomes of the workshop was the creation of a map showing areas of current importance for lions, representing the contribution that the respective areas make towards supporting their current lion populations (Figure 2.7).

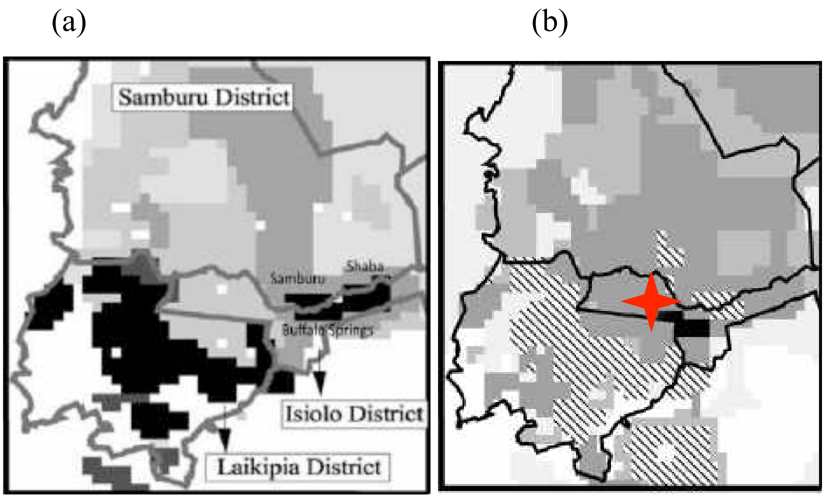


Figure 2.7. Maps showing (a) areas of priority for lions within the Samburu and Isiolo Counties, and (b) areas of conservation priorities (Source: Didier *et al.,* 2009). Dark regions indicate areas of high importance for lions and the red star indicates the Kipsing Corridor.

SNR, BSNR and ShNR were shown to be high priority areas for lion conservation and research within Samburu and parts of Isiolo County within the Ewaso Nyiro landscape. This is indicated by the dark coloured area in Figure 2.7a. The areas around the Reserves, for example in WGCC, also displayed high priority areas. However, more investment was required for lion conservation, thus allowing for dispersal of lions between the Reserves and surrounding community areas. Figure 2.7b highlights the crucial Kipsing corridor, indicated as a red star, which was referred as a key area for movement of lions between the Samburu and Laikipia landscape. This lion population that roams the Samburu-Laikipia ecosystem is critical for connectivity within East Africa's lion population (Riggio, 2011).

2.4.3. Ecosystem dynamics

2.4.3.1. Extreme environmental events; 2009 drought and 2010 floods

Over the course of the study, the region experienced a devastating drought, followed a few months later by destructive floods. The drought in 2009 which was as a result of failed rains earlier in the year (Figure 2.2) led to the death of numerous wildlife and livestock species. As a result, people within WGCC migrated to areas in Laikipia and near Mt Kenya where there was pasture (*pers. obs*.). During the drought, most community members together with their livestock moved closer to the Ewaso Nyiro River for easy access to waterholes. However, this is prime carnivore habitat and in order to reduce potential conflict with livestock, the bushes were burned eliminating existing carnivore habitat (*pers. obs*.).

In 2010 the area experienced heavy floods that led to most areas becoming completely inaccessible to vehicles as a result of the accumulation of mud. Access to BSNR from SNR was also affected as the main Uaso Bridge (see Appendix 1) connecting the two Reserves collapsed during the floods. This bridge was subsequently repaired in November 2010, however for eight months prior to this, BSNR could only be accessed through Archers Post town doubling the travel distance and time to enter BSNR from WGCC. As a result of the flood, several tourist lodges were closed and resident lodge drivers were not able to go out on game drives leading to a lower than usual tourist and guide presence within the Reserves. The floods also damaged 55 lion faecal samples that had been collected for a study analysing lion's preferred prey, and stored at the Save the Elephants Research Camp, which was washed away. There was a dramatic change in vegetation along the River during and after the floods; large trees were uprooted, huge thickets of *S.persica* and other bushes were flattened and washed away. In addition, vast sand deposits layered the riverbanks and covered most of the riverine vegetation (*pers. obs*.).

2.4.3.2. Ethnic tension, clashes and insecurity

Samburu is plagued by insecurity associated with natural resource scarcity and resulting conflict as well as ethnic antagonism (Campbell *et al*., 2009). During the course of this study, there was frequent tension between the various ethnic groups (Samburu, Borana, Turkana, Rendille and Somali) that live in the region. Cattle raiding was a frequent occurrence, at times taking place within the protected areas. In March 2009, the presence of government militia led to the Samburu people migrating and hiding to prevent their cattle from being forcefully removed from their homes. This resulted in temporary closure of the research base and reduced data collection until stability returned to the area. As a result of the insecurity and ethnic tensions in the area, research and monitoring activities were greatly restricted and ShNR was excluded from the study in 2010.

Chapter 3

The demographic parameters of the lion population in the Samburu-Isiolo ecosystem

"... it was easy to see why the lion has always fascinated man and become a symbol of something he admires. The king of animals, as they have called him, is a tolerant monarch; true he is a predator, but predators are essential to keep the balance of wildlife..."

Adamson, 1962

Abstract

Knowledge on the demographic status of lions is essential in understanding how populations change, especially within the anthropogenic landscape. Studies have shown that exposure to anthropogenic threats, especially human caused mortality on boundaries of protected areas can lead to changes in lion demography.

In this chapter, the overall population demographic parameters of the lions in the Samburu-Isiolo ecosystem are presented. The various methods used to obtain this baseline information are discussed, including the advantages and disadvantages of the direct observation method. The demographic parameters considered include: pride sizes, male tenure periods, age and sex ratios, cub dispersal, birthing interval, mortality, cub survival and population density.

The study found the male tenure periods, age ratios, cub survival and population densities in the study area were comparable to those of various lion populations across Africa. Cub dispersal and birthing interval were however slightly lower than what has been recorded in other populations across Africa, whilst sex ratios were higher.

Lion populations within small protected areas are at risk of, and more vulnerable to, human caused mortality and possible localised extinction. It is important for conservationists to understand how lion population demography may respond to human caused mortality especially in small protected areas such as in this study. This study, therefore, examines lion population demographics both within, and outside, protected areas in order to gain a better understanding of the status of the Samburu-Isiolo lion population and to examine any changes in its demography over the years.

3.1. Introduction

Studying large carnivore populations and obtaining reliable estimates is important for conservation management (Stander, 1998; Rosenblatt *et al*., 2014). Understanding lion demographics provides essential insight into how populations change over time and what factors affect them. Knowledge of the baseline information is crucial in order to determine the extent of any change and this is especially important in light of the current threats that lions face. There is an urgent need to describe and identify population trends, and what underlies these changes (Rosenblatt *et al.,* 2014).

There are many small and isolated lion populations across Africa and conserving and protecting them is very important (Snyman *et al*., 2014). These populations are often exposed to many threats that this directly compromises their viability, making them more vulnerable and slow to recover (Hayward *et al*., 2007; Snyman *et al.,* 2014) from environmental and demographic stochasticity and therefore, more prone to localised extinction (Frankham, 1995; Bannerjee and Jhala, 2012). It is therefore imperative for conservationists to understand how lion population demography may respond to human caused mortality (Loveridge *et al*., 2010; Dolrenry *et al.,* 2014).

Wide-ranging lions occupying small protected areas are more at threat and within such areas, lion demographics can vary between the boundaries and core regions of the protected area (Loveridge *et al.,* 2010a). For instance, lion cub survival in boundary regions has been found to be lower than within the core regions of parks (Loveridge *et al.,* 2010a). Pride sizes are also smaller closer to boundaries compared to within core regions. It is these prides, occupying the peripheries of protected areas that are most likely to go extinct. In addition, disruption of population numbers and demographics in the protected areas could lead to problems with not just lion numbers, but also impacts on prey species and competing carnivore species (Loveridge *et al*., 2007).

The most common objective in a carnivore conservation project is to determine population size and look at trends (Rosenblatt *et al.,* 2014). Direct methods of assessing population sizes are often time-consuming and expensive (Stander, 1998), especially as carnivores are wide-ranging and often occur at low densities (Rosenblatt *et al.,* 2014; Midlane *et al.,* 2015). A wide variety of carnivore survey tools are recommended for field biologists (Rosenblatt *et al*., 2014). These include direct observation techniques, telemetry, observation of effects such as scat and tracks, opportunistic data (Bertram, 1976; Loveridge, 2001), camera trap surveys (Karanth and Nicholls, 1998), call-up surveys (Ogutu and Dublin, 1998; Mills *et al*., 2001) and capture-mark-recapture (Loveridge, 2001). Midlane *et al.,* (2015) reported that two of the most widely used methods are call-up surveys and track counts (Stander, 1998; Funston *et al.,* 2010).

The method of direct observation was used in this study. The advantages of this method include the definite observations, locations and a high percentage of accuracy in lion identification. There have been other studies that have employed this method of direct observation (Nairobi National Park – Rudnai, 1973; Serengeti National Park – Schaller, 1972; Maasai Mara Reserve - Ogutu and Dublin, 2002).

Individual recognition is the most accurate method to identify lions and estimate a population's size (Schaller, 1972). Although a challenging and lengthy process, particularly within human-occupied landscapes, individual recognition was one of the main methods used.

This chapter looks at the demographic parameters of the lion population in the Samburu-Isiolo ecosystem. Data collected between 2003 and 2007 was analysed in addition to a more substantial dataset obtained between 2008 and 2011. The pride size and composition were established together with the age and sex ratios, cub dispersal and survival, and birthing intervals. The density and mortality of the lion population was also obtained. The overall aim of this chapter is to therefore present lion demographic parameters between 2003 and 2011. It is recognised that this population did exist before the study started and this baseline study was a snapshot in time, where the population could be recovering from a previous perturbation and may not have started at a stable state. This is the first time that the demographic parameters have been described for this population in northern Kenya.

3.2. Methods

3.2.1. The study area

The study area covered for the lion census included Samburu (SNR) and Buffalo Springs (BSNR) National Reserves, and Westgate Community Conservancy (WGCC). These areas form part of the Samburu-Isiolo ecosystem (see Chapter 2 for details and Appendix 1 for maps). Shaba (ShNR) National Reserve was initially included in the study but later removed.

3.2.2. Methods for sighting lions

A number of lion sighting methods were used to obtain the population demographic data within the study area. A summary of these methods is presented in Table 3.1.

Table 3.1. Methods used to obtain population demographic data.

Methods	Location	Notes	References
Direct Observations	Samburu, Buffalo Springs and Shaba National Reserves, and Westgate Conservancy (Conservation Area)	Lions tracked and individually identified using whisker spot pattern. Data was filled out in Lion Monitoring Sheet (see Appendix 4).	Pennycuick & Rudnai, 1970 Schaller, 1972 Estes, 1997
Tracking	Samburu and Buffalo Springs National Reserves	Extensive road network within the Reserves was covered. Tracks were followed and eventually lions located.	Schaller, 1972
Visiting known preferred locations	Samburu and Buffalo Springs National Reserves	Areas which were known to be preferred habitat for lions, were targeted more intensely.	Bhalla, 2003
Tourist presence and reports from guides	Samburu, Buffalo Springs and Shaba National Reserves	Followed clusters of tourist mini buses as they often indicated carnivore presence. Guides also gave reports of lion sightings.	Bhalla, 2003
Call-in surveys	Westgate Community Conservancy	Call-in surveys used to observe lions. This method failed and has not been described further.	Ogutu and Dublin, 1998 Mills *et al.,* 2001 Midlane *et al*., 2015

Camera traps	Westgate Conservancy (Conservation Area)	5 camera traps were deployed at 3 fixed locations. This method failed and has not been described further.	Gerber *et al.,* 2010 Karanth and Nichols, 1998
Lion identification photos	Samburu and Buffalo Springs National Reserves	Randomly collected photographs (including tourists) were entered in a database and lions identified through whisker spot patterns.	Pennycuick and Rudnai, 1970 Rosenblatt *et al.,* 2014

3.2.3. Estimating population size and the identification of lions

One of the most accurate ways of determining the population size is by recognising all the animals in the population individually (Stander, 1991). All the individuals in a pride are rarely together at one time, highlighting the importance of individual recognition. All the animals are identified from natural markings following the method outlined by Pennycuick and Rudnai (1970). This is based on individual variations in the spots pattern, marking the position of the vibrissae between the upper lip and nose.

When recording new lions in the field, pencilled outlines of the lion's profile were drawn, as seen from both sides (Figure 3.1). Other identifying marks were looked at, including nicks in the ears, faulty dentition and nose patterns. However, tears in the ears could change over long periods (Bertram, 1976). Temporary noticeable marks, including scars and injuries would be noted for ease of daily and quick identification of lions. Mane size and colour amongst males was recorded. The animal was given an identification number and name; and its sex, approximate age, and pride affiliation (if known) was determined.

Photographs were taken of both facial profiles, with the whisker spots clearly defined, as well as face-on to include close-ups of the nose colouration pattern. Each lion had its own identity card with photographs and sketches (Figure 3.1).

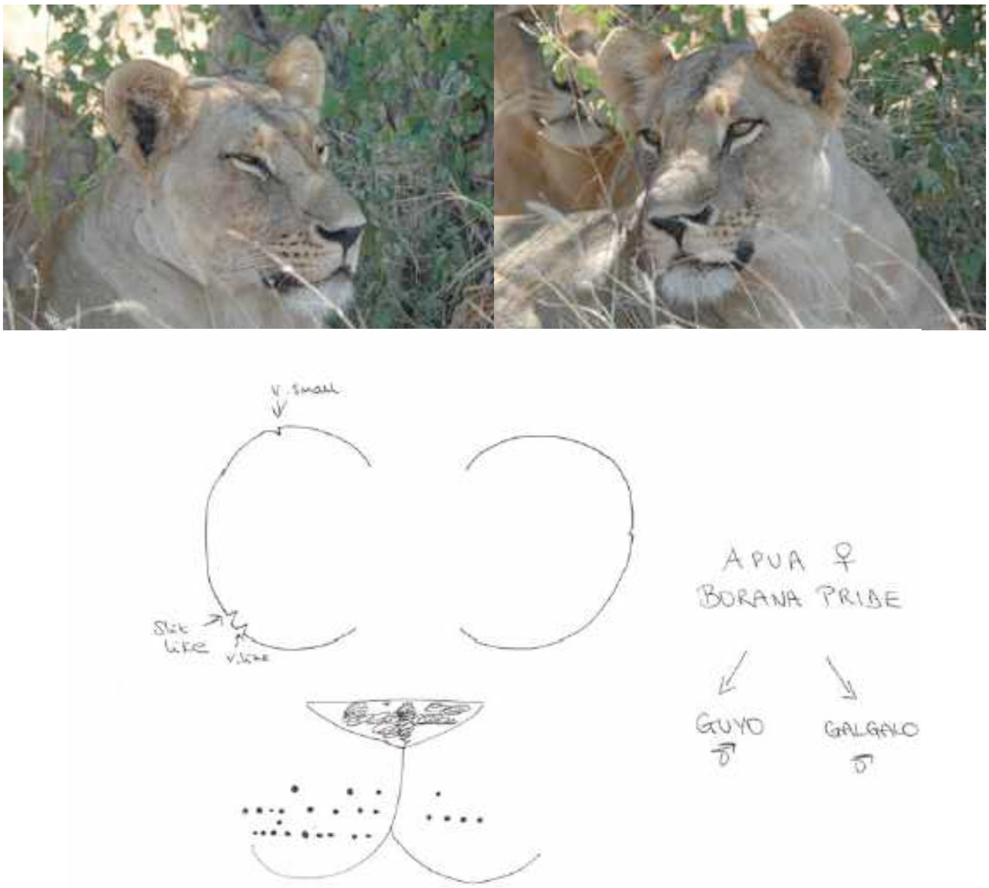


Figure 3.1. Identity card showing the female Apua, BP1, from the Borana Pride. The card shows photos of her left and right sides. Underneath the photo images is a sketch of the female's ears indicating nicks and her whisker spot pattern. Her nose pigmentation is coloured in.

Cubs under six months of age were too young to be distinguished individually and were monitored as frequently as possible whilst they were growing to ensure full identification at the earliest possible time. This was generally when they reached 12 months old. It gradually became easier to identify all the lions and with time, a quick glance at the face was sufficient to recognise each individual.

Schaller (1972) categorized lions into 'residents' and 'nomads'. These definitions were used in the study. The identified lions were assigned to pride or nomadic status using peaceful or agonistic behaviour and by looking at their space use. Residents were generally within the protected areas and WGCC, and nomads who were nervous were not present permanently in the Reserves.

3.2.4. Establishing the population structure

The lion population density was estimated by counting the number of known individuals, including both adults and cubs. Sex classification was achieved by looking at manes in adult males or tufts around necks of young males. The sex ratio was estimated by using all sightings of lions that could be sexed, not relying on the assumption that males and females are equally likely to be seen (Creel and Creel, 1997).

The age ratios were assigned using the information obtained on all age classifications. Using Schaller's (1972) classification method (see Appendix 5), each lion identified was allocated to one of the following age classes:

- Small cubs (0-1 year)
- Large cubs (1-2 years)
- Sub adults (2-4 years)
- Adults (4+ years)

Age was estimated from size, degree of speckling on nose and dentition (Whitman, *et al.,* 2004). Until two years, age was estimated on the basis of body size. Afterwards, age was estimated using nose colour. Young lions have pink noses, which become increasingly darker until it is entirely black between 8-10 years of age and beyond. The blackening occurs due to the development of several black pigment spots at different points on the nose (Bertram, 1978). These spots gradually grow and merge with one another (Figure 3.2). Tooth wear is looked at for adults older than 10 years.

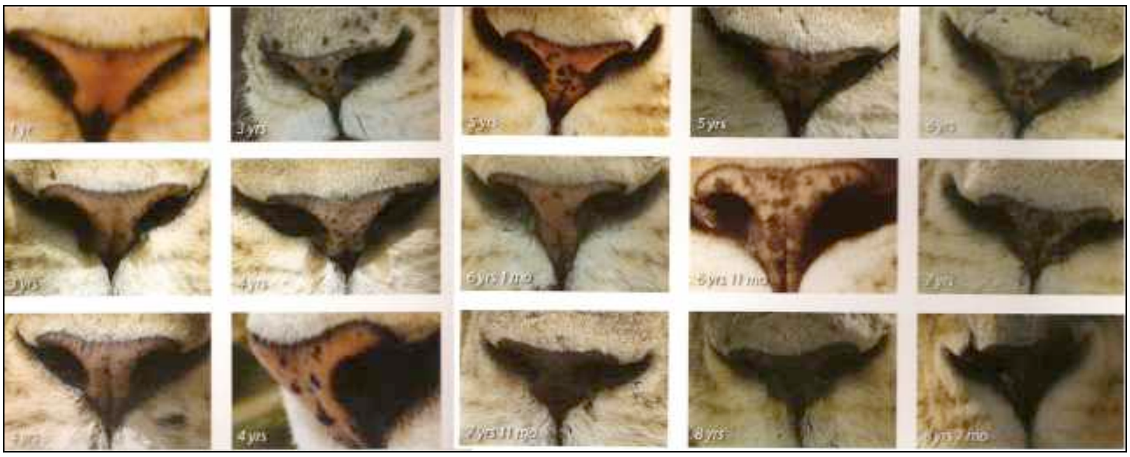


Figure 3.2. Nose pigmentation of lions showing different ages (Whitman and Packer, 2007).

In addition to using the chart from Figure 3.2, the same method that Creel and Creel (1997) used for their classification method was adopted, where the following classes for nose pigmentation were used:

2-4 years	black speckling	**5-8 years**	50% black – splotched
4-5 years	25% black – mottled	**8-10 years**	75% black – livered

The age when cubs leave their mothers (cub dispersal) is calculated by examining the difference between the estimated age when the individual was first seen and the first sighting when it was seen alone without its mother. Subsequent sightings where females were clearly antagonistic towards their cubs further helped identify this split. The birthing interval for the population's females was calculated by looking at the difference in time from the age of their first litter and subsequent litters.

3.2.5. Population mortality

All lions in the study area that were killed in conflict or died of natural causes were recorded. The lions were identified and, when possible, the cause of death established. Signs of injury were looked for on the body of the dead lion and all signs of violence in the vicinity were examined. Lions that disappeared and were presumed dead were also recorded in addition to lions that were removed from the region. This was entered in a mortality database and submitted to the Kenya Wildlife Service (KWS).

3.2.6. Cub survival

In order to assess cub survival taking into account different birth dates and years, the staggered Kaplan-Meier method was used (Kaplan and Meier, 1958), together with log rank tests to compare the survival curves of males and females (Pollock *et al.,* 1989; Dolrenry, 2013). The Kaplan-Meier method and the estimates of the survival data that it produces has become a familiar way of dealing with different survival times (times to an event), especially when not all the subjects continue in the study.

The survival rate is expressed as the survivor function:

$$S(t) = \frac{\text{number of individuals surviving longer than } t}{\text{total number of individuals studied}}$$

where t is a time period known as the survival time or the time to failure or the time to an event (such as the death of the cub in this instance).

In analysing survival data, the survival function S(t) is defined as the probability of surviving at least to time (t) (Pollock *et al.,* 1989). The graph of S(t) against t is known as the survival curve. The Kaplan–Meier method is based on the basic idea that the probability of surviving k or more periods from entering the study is a product of the k observed survival rates for each period (i.e. the cumulative proportion surviving), given by the following formula:

$$S(k) = p_1 \times p_2 \times p_3 \times ... \times p_k$$

Where; p_1 is the proportion surviving the first period, p_2 is the proportion surviving beyond the second period and conditional on having survived up to the second period, and so on. The proportion surviving period i having survived up to period i is given by:

$$p_i = \frac{r_i - d_i}{r_i}$$

Where; r_i is the number alive at the beginning of the period and d_i the number of deaths within the same period.

Assumptions of the Kaplan-Meier method in this study include:

i. That at any time cubs who are censored (alive) have the same survival prospects as those who continue to come in to the system.

ii. That the survival probabilities are the same for subjects recruited early and late in the study. If there were enough subjects in both the groups, contingency table tests of this assumption could be made. In practice, however, the animals will often be added in very small groups thereby not allowing a quantitative assessment of this assumption. The usual application of the Kaplan-Meier method assumes that all animals are released at one time and they are followed during the study until they die or are censored.

However, new animals are released at each occasion (in this case every few months); this entry is therefore 'staggered' (Pollock *et al*., 1989).

iii. That the event happens at the time specified. This means that the time of the event (in this case death of the cub) and the exit point of the subject is known.

Advantages of the Kaplan-Meier method include:

i. The Kaplan-Meier curve represents the distribution of survival times.

ii. Drops only occur at event times, that is, when the cub dies. Censoring is easily accommodated in this method (cubs that did not die are considered censored; it is known that they survived a specific amount of time, but do not know the exact time of the event, that is, death).

iii. If the last time is not an event, the curve does not reduce to 0.

A comparison of two survival curves was done using the log rank test, a statistical hypothesis test. It is used to test the null hypothesis that there is no difference between the population (male and female) survival curves (i.e. the probability of an event occurring at any time point is the same for each population). The test is calculated as follows:

$$\chi^2(\text{log rank}) = \frac{(O_1 - E_1)^2}{E_1} + \frac{(O_2 - E_2)^2}{E_2}$$

O_1 and O_2 are the total numbers of observed events in groups 1 and 2, respectively, and E_1 and E_2 are the total numbers of expected events.

3.2.7. Statistical analyses

All the aspects of population dynamics discussed were used to describe the demographic parameters of the Samburu-Isiolo lion population. In most instances, these analyses were restricted to the population of SNR and BSNR only, since this is the region where the lion population was completely identified. The population studied here is small with only three separate prides, and as such the majority of the analyses did not qualify for assessment with parametric statistics, thus equivalent non-parametric tests were used. All analysis was conducted using the statistical software

R version 3.22 (R Core Development Team) and SPSS 16. Standard errors have been calculated unless otherwise stated.

3.3. Results

3.3.1. Effort

The intensive study period began in January 2008 and ended in March 2011 however, lions were not seen everyday. Since lions of the same pride are at times dispersed over a wide area, and with the difficulty in locating individuals, there were gaps in observations of several days. Additionally, due to various climatic variables, such as flooding which destroyed the majority of the Reserves' roads, certain areas were avoided for many months at a time. Due to security concerns, there were some areas that were avoided during certain times of the year.

An average of 15.5 ± 1.42 days per month were spent in the field between 2008 and 2011. In total, 605 days were spent in the field during this period (Figure 3.3).

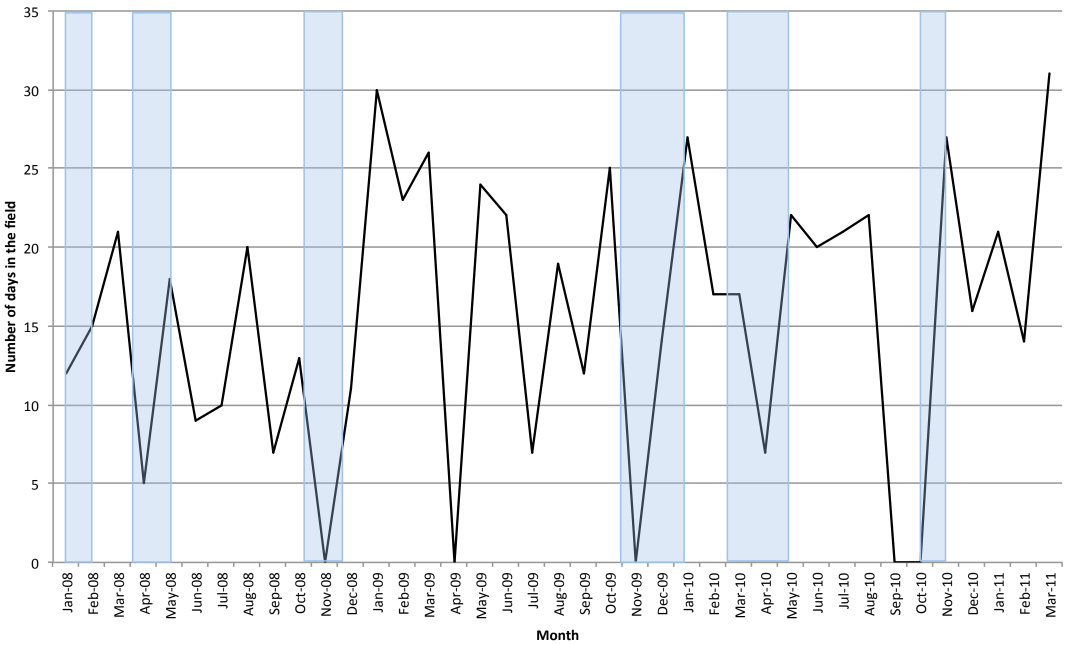


Figure 3.3. The number of days spent in the field per month between January 2008 and March 2011. The blue shading indicates the wet seasons.

Each morning, different routes were taken to cover as much ground as possible. The routes would vary between SNR, BSNR, ShNR, WGCC and the Core Conservation Area (CA) in WGCC. 225 days were spent in SNR, 148 days in BSNR and on 51 of these days, fieldwork was conducted in both SNR and BSNR while 333 days were spent in the CA and 83 days in remaining areas in WGCC (outside the CA). The total number of months when fieldwork was conducted during the study period is 39 and the mean number of days spent in each location per month is presented in Table 3.2.

Table 3.2. Mean number of days in each location per month

Location	Mean no: of days / month
Samburu National Reserve	5.77 ± 0.72
Shaba National Reserve	0.38 ± 0.13
Westgate Community Conservancy	2.13 ± 0.4
Conservation Area (Westgate)	8.54 ± 1.22
Samburu and Buffalo Springs Reserves - combined	1.31 ± 0.25
Buffalo Springs National Reserve (before 2010 floods)	4.62 ± 0.73
Buffalo Springs National Reserve (after 2010 floods)	2.15 ± 0.31
Buffalo Springs National Reserves (overall)	3.79 ± 0.64

The maximum distance travelled was in SNR (31%), followed by BSNR (25%) and in the CA (28%). Only 11% of the entire mileage was covered in WGCC and 5% in ShNR (Figure 3.4a), however the greatest distance driven was in ShNR (53%; Figure 3.4b).

(a) (b)

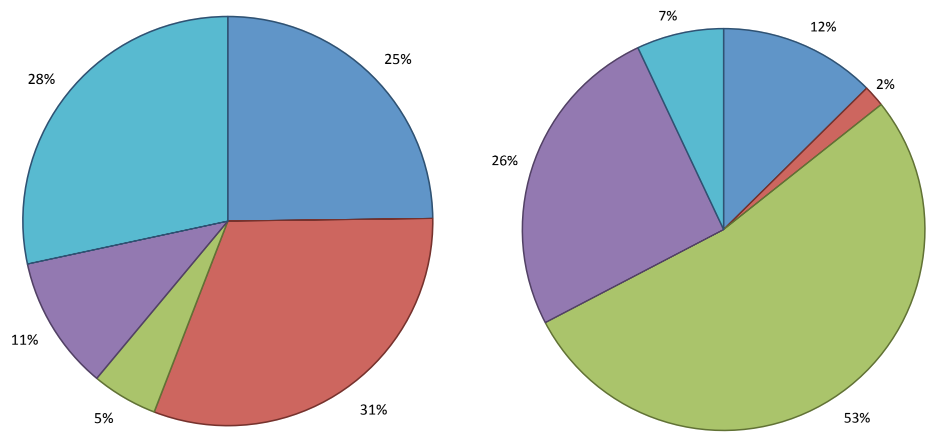


Figure 3.4. The sampling effort within Samburu (red), Buffalo Springs (blue) and Shaba (green) National Reserves, and WGCC (purple) and the Core Conservation Area within WGCC (turquoise) is represented as (a) the proportion of the total mileage expended within each area and (b) the proportion of sampling effort (approximated by distance driven) in each location corrected by the area of the location.

Although the mean number of days in ShNR was less than one per month and the percentage of field days spent in ShNR was only 2%, the kilometres covered per day here was the greatest (>87km; Figure 3.5) because the entire Reserve was covered on each occasion that the area was visited.

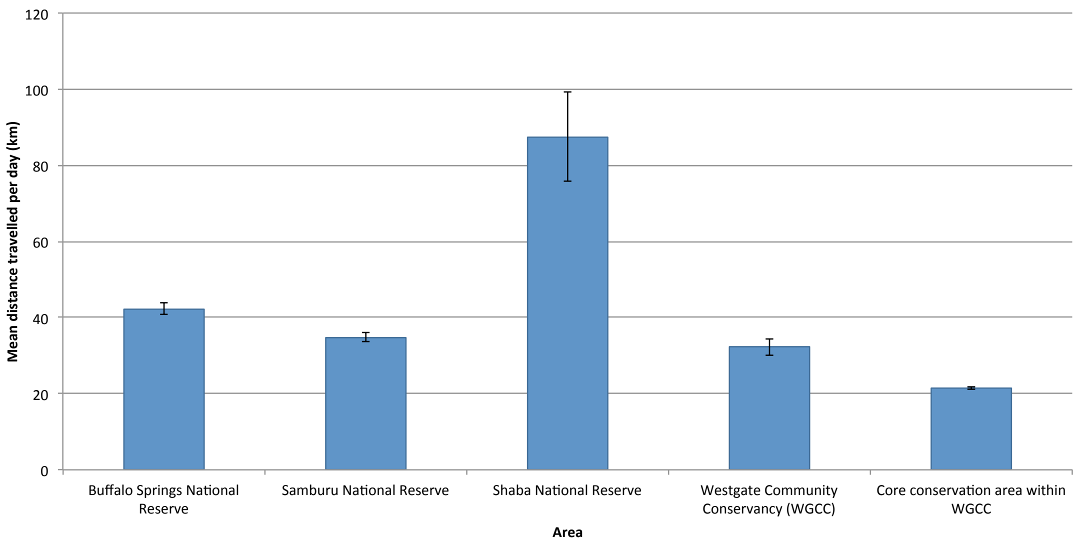


Figure 3.5. The mean distance travelled per day in each of the locations within the study area.

3.3.2. Lion sightings

The total number of all lion sightings between 2003 and 2011 was 507. The majority of these sightings were in SNR (n=332) and the least number of sightings were in ShNR (n=4; Table 3.3).

Table 3.3. Lion sightings in the four areas between February 2003 and March 2011.

Area	2003	2004-2007	2008-2011	Total
Samburu National Reserve	89	71	172	332
Buffalo Springs National Reserve	18	20	97	135
Shaba National Reserve	0	0	4	4
Westgate Community Conservancy	0	0	36	36
Total	**107**	**91**	**309**	**507**

Between January 2008 and March 2011, lions were seen on 208 days out of 605 days in the field. Out of the 208 days, 309 lion sightings were recorded. The majority of lions were found opportunistically (n=139), followed by receiving information from tour drivers (n=66) and tracking (n=50).

During a previous study in 2003, the baseline lion population that was identified included 107 sightings which comprised 29 individually identified lions (Bhalla, 2003). Following this, between 2004 and 2007, 91 opportunistic sightings were recorded and 40 lions identified from photographs. During this period, 12 sighting records from a photographer in SNR were also acquired. Through these photographs and descriptions, it was possible to identify the lions and the areas where the photographs were taken. Between 2008 and 2011, photographs from tour guides provided information on seven separate sightings.

The timeline in Appendix 6 shows all lions seen between 2003 and 2011 in the entire study area. The timeline is a graphical representation of the lion population over time and their age and sex categories. In the timeline, the years go back to the year 2000 after estimating the age of the individual lions at the first sighting.

3.3.3. Pride size and composition

Between 2003 and 2011, 98 lions were identified and monitored in all regions of the study area. This included cubs (ones that also disappeared or died), and also lions only sighted on one occasion, as was mainly the case in ShNR. Some individuals were identified during a previous study (Bhalla, 2003), thus allowing the complete identification of the population within SNR and BSNR. Appendix 7 provides a breakdown of all lions identified with their names and identification numbers between 2003 and 2011. All analyses where stated have been conducted annually and for this reason, the data for three months (January to March) in 2011 has been removed.

There are three prides within SNR and BSNR: Koitogor Pride (KP), Ngare Mara Pride (NMP) and Borana Pride (BP). The resident pride within WGCC is the Sasaab Pride (SP). Figure 3.6 shows how the pride sizes, excluding small cubs, have changed annually between 2003 and 2010.

The KP had the largest mean pride size (10.08 ± 0.34). The BP size, despite being higher initially in 2005 and 2006, reduced considerably in 2007 (overall mean pride size between 2008 and 2010 is 2.08 ± 0.15). The NMP gradually increased in size from 2006 onwards (overall mean pride size between 2008 and 2010 is 9.22 ± 0.32) and the SP was only seen from 2008 onwards yet remained very small (mean pride size of 1.56 ± 0.15) which was to be expected of a pride living within the human-occupied landscape.

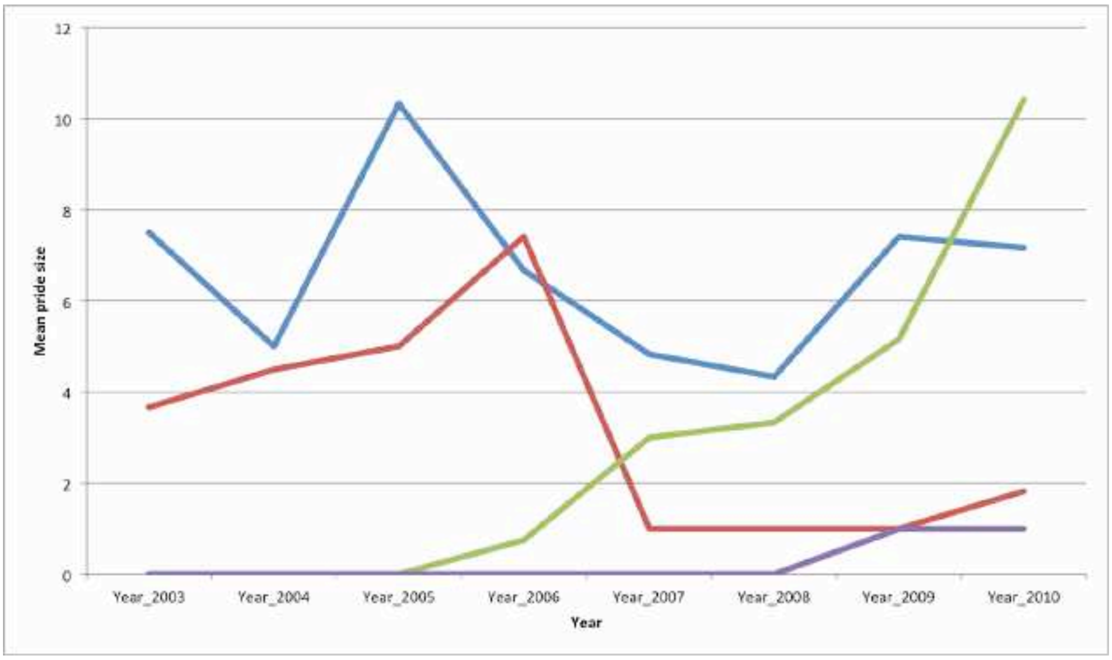


Figure 3.6. The change in pride size (excluding small cubs) for the prides in the study area between 2003 and 2010: Koitogor Pride (blue), Ngare Mara Pride (green), Borana Pride (red) and Sasaab Pride (purple).

The following detailed pride descriptions provide an accurate representation of the entire population.

3.3.3.1. The Prides

When the study started, the KP in SNR was the first to be identified and monitored. This was the largest pride at the time, with seven adult females, although the numbers reduced considerably before 2008 leaving three adult females and their surviving cubs. Cubs left their mothers and were forced out of SNR, becoming resident in neighbouring Kalama Conservancy and WGCC (see Appendix 1). It appeared that the KP had split in to three groups, and had become resident in three different areas; SNR, Kalama and WGCC.

It is unclear from observations prior to 2007 whether the NMP existed as a pride unit or as individuals that were not clearly identified. Their pride structure was well established from 2007 onwards. Between 2008 and 2010, the pride comprised of 13 individuals, and included four lions that immigrated into the area. This pride also split in to two groups, with two females in each group giving birth to their cubs and raising them independently.

Prior to 2008, the BP consisted of nine females. The pride reduced in size from nine adult females to one adult female (BP1) and her two subadult male cubs, M13 and M14 (see Appendix 7). The fate of the remaining females is unknown, although it was suspected that they had moved south of BSNR in the wet season and BP1 was the only individual who returned.

During the study period, the SP in the CA of WGCC comprised of three individuals; one female (SP1) and her two cubs, M15 and M16. Due to the nervous disposition of the lions in this human-occupied landscape, it took 16 months before an accurate whisker spot pattern was drawn and SP1 was identified.

The composition within all prides was assessed annually between 2008 and 2010 and is presented in Table 3.4.

Table 3.4. The summary composition of each pride

Pride	**Koitogor Pride**		**Ngare Mara Pride**		**Borana Pride**		**Sasaab Pride**	
Composition	**Mean**	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**
Adult Females	2.47	0.08	2.33	0.13	1.00	0	0.50	0.08
Adult Males	2.25	0.08	2.25	0.08	0.08	0.05	0	0
Subadults	0.61	0.20	1.33	0.16	0	0	0.50	0.08
Large Cubs	1.50	0.32	1.81	0.34	0.33	0.13	0	0
Small Cubs	3.25	0.43	1.50	0.37	0.67	0.16	0.56	0.15
Whole Pride	**10.08**	**0.34**	**9.22**	**0.32**	**2.08**	**0.16**	**1.56**	**0.15**

Within the KP, adult male numbers were similar to that of adult females, and small cubs were greater than large cubs. Subadult numbers were the lowest within the KP. Within the NMP, the number of adult females and adult males is similar to that of the KP, with adult males and females being close in number. Subadults, large cubs and small cubs comprised low numbers. Within the BP, it is clear that the pride is small (in all age categories) although it used to be larger prior to 2008.

The mean sizes across all prides for the entire population between 2008 and 2010 is presented in Table 3.5. The overall mean pride size was 5.83 ± 0.71.

Table 3.5. The summary composition for all prides

Composition	Mean	Standard Error
Adult Females	1.61	0.14
Adult Males	1.13	0.20
Subadults	0.70	0.15
Large Cubs	0.99	0.27
Small Cubs	1.40	0.35
Mean pride size	**5.83**	**0.71**

3.3.3.2. Lone female and single sightings

There was one female, NAI (see Appendix 7) seen alone during the study period on three occasions. She was seen in SNR and clearly not part of the KP. There were also a number of lions seen only once. This was all across the study area and included sightings in SNR, BSNR and ShNR. Within ShNR, the Dakadima Pride (DP) was seen only once and consisted of two females and their two cubs.

3.3.3.3. Males and coalitions

Between 2003 and 2004, and thereafter until 2008, it appeared that none of the prides identified had more than one adult male at the same time. The males were not an integral part of any one pride. Insufficient observations complicated the classification of seven males as nomads or residents. Between 2008 and 2010, nine adult males were seen and these males formed three coalitions; two of which were in SNR and BSNR and one in WGCC. Resident males M24 and M25 (see Appendix 7) disappeared from the Reserves when M26, M27 and M28 arrived from WGCC, in 2008. M24 had remained in the area for 31 months and M25 had remained for 24 months before leaving. M28 disappeared soon after his arrival, and it was suspected he was killed by another male. M26 and M27 remained within the Reserves, often moving between the KP in SNR and the NMP in BSNR. The average pride tenure in months between the males is 34.6 ± 5.67.

Two males, M29 and M30, were sighted in WGCC, but were difficult to identify clearly as a result of their nervous disposition. The two males were nomads and were not seen again after February 2009.

3.3.4. Age and sex ratios

The age and sex ratios have been calculated annually. The mean numbers for each age class for the lion population between 2003 and 2010 is shown in Figure 3.7.

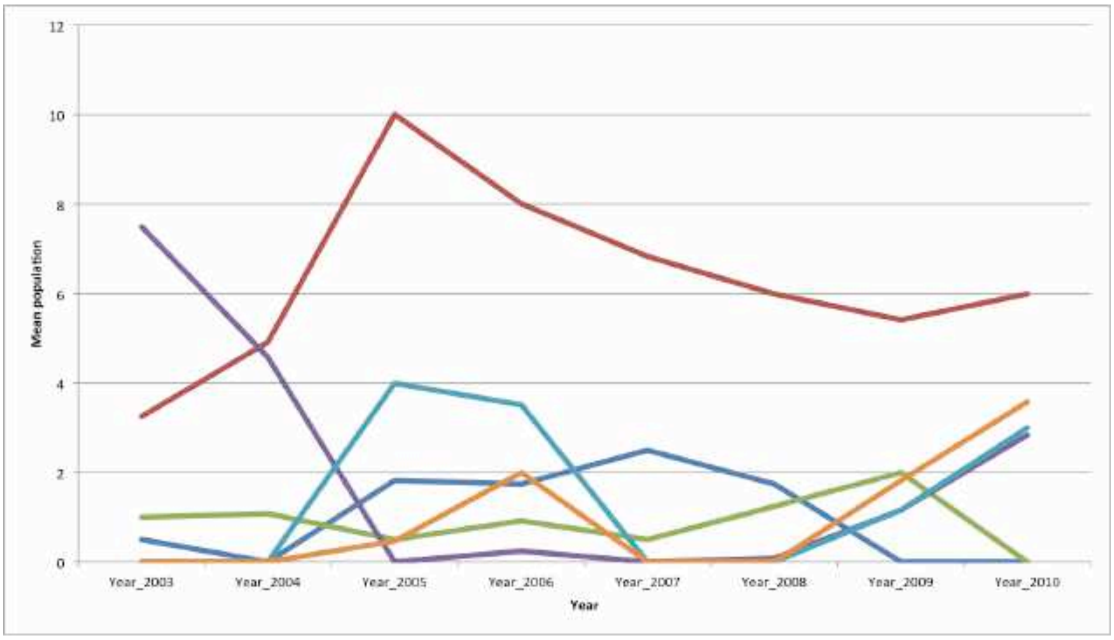


Figure 3.7. The mean numbers within each age class (excluding small cubs) for the lions in Samburu and Buffalo Springs National Reserves between 2003 and 2010. Adult males (dark blue), adult females (dark red), subadult male (green), subadult female (purple), large male cub (light blue), large female cub (orange) are all displayed on the graph.

Figure 3.7 shows that the mean of the adult female population was larger (6.33 ±0.22) compared to any of the other age categories. Subadult females (2.11 ±0.27) although initially high, reduced, but remained higher than both adult males (1.33 ± 0.11) and subadult males (1.17 ± 0.12).

In 2003, all lions were identified during this initial part of the study, showing an increase in number of adults. Following this, the adult population was fairly stable in the subsequent years from 2004 onwards. The subadult population was larger between 2003 and 2004 and reduced in 2005 with the disappearance of a number of individuals – mainly females. The mean number of individuals in SNR and BSNR that fall into each age category including small cubs is presented in Table 3.6.

Table 3.6. Mean lions in each age group between 2003 and 2010 (including small cubs)

Age class	Mean	Standard Error
Adults	7.65	0.29
Subadults	3.29	0.29
Large Cubs	2.82	0.35
Small Cubs	4.71	0.43

The mean age ratio over the whole study period as adult: subadult: large cub: small cub was 1:0.42:0.36:0.62. There were twice as many small cubs compared to large cubs, and adults were more than subadults.

Between 2003 and 2004, the number of male lions was low, with a sharp increase recorded in late 2004 (Figure 3.8). This number dropped again in mid 2006 and was low in 2007. An increase in male numbers followed from 2008 onwards with the arrival of new males. There was an increase in numbers of female lions during the initial part of the study as new females were identified, and they were therefore not new to the population and could have been present prior to 2003. There was another drop in female numbers in 2006 when females from the BP disappeared, followed by a stable period where numbers were low. There was a gradual increase in female numbers from 2008 onwards and cubs that were born stayed in the population. Overall, the average number of females is greater than that of males. The adult female: male ratio was 4.80:1, and the adults and subadults together was 3.36:1 (Table 3.7). Males outnumbered females only in the large cubs category (0.80:1).

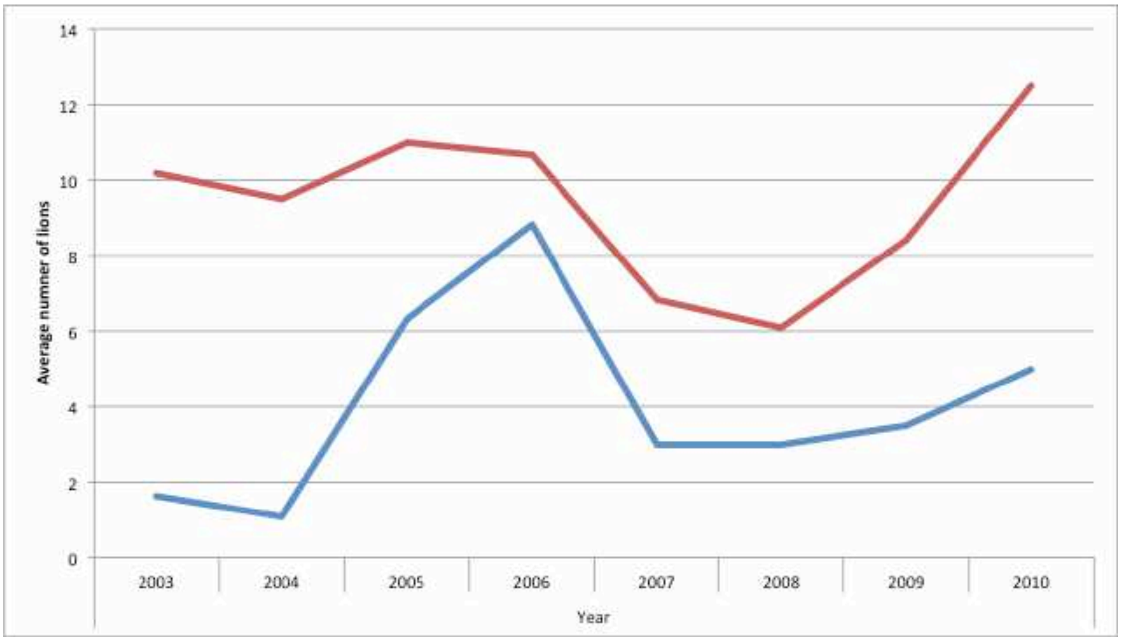


Figure 3.8. The number of female (red) and male (blue) lions within the known population in the study area (excluding small cubs).

The mean number of females and males is reported, alongside the ratio of females to males within each age category. This is shown in Table 3.7.

Table 3.7. The sex ratio within the breeding population, and the adult, subadult and large cub demographics separately from 2003 to 2010. The sex ratio is represented as the number of females per male.

	Female		Male		Ratio
Age demographic	**Mean**	**S.E.**	**Mean**	**S.E.**	
Adults, Subadults & Large Cubs	9.68	0.31	4.07	0.30	2.40:1
Adults & Subadults	8.44	0.21	2.50	0.12	3.36:1
Adults	6.33	0.22	1.33	0.11	4.80:1
Subadults	2.11	0.27	1.17	0.12	1.75:1
Large Cubs	1.24	0.18	1.57	0.23	0.80:1

3.3.5. Cub dispersal

Table 3.8 shows ages when cubs dispersed from their mothers. The mean age in months of cub dispersal is 19.85 ± 0.84.

Table 3.8. Approximate ages when cubs dispersed from their mothers.

Name of Cub	Pride ID Number	Approximate age when cub dispersed (months)
Kengeza	M1 (KP)	27
Loboito	M2 (KP)	27
Lotuunyi	M3 (KP)	24
Loyeyo	M4 (KP)	24
Layeni-lai	M5 (KP)	17
Lekume	M6 (KP)	17
Loterenkwe	M7 (KP)	17
Napono	KP23	27
Naramat	KP24	18
Nanyiro	KP25	20
Namelok	KP26	20
Nanai	KP27	17
Nabulo	KP28	18
Sipen	KP29	18
Lmalmali	M8 (KP)	20
Lmelitaa	M9 (KP)	18
Guyo	M13 (BP)	18
Galgalo	M14 (BP)	18
Ltangenoi	M15 (SP)	16
Sikiria	M16 (SP)	16
Mean age of cub dispersal (n=20) over the entire period		**19.85 ± 0.84**

3.3.6. Birthing interval

As shown in Table 3.9 which presents birthing intervals for eight lionesses, KP10 had a very small birthing interval because she abandoned her first litter of cubs who were then cared for by another female, KP1. KP13 is the only female to have had five birthing intervals. Her first and second birthing intervals were higher than her third, fourth and fifth intervals. Her second interval was the longest being 30 months. Although mating between the females and males was regularly observed during this period, the females did not conceive. KP13's last and most recent birthing interval was only 12 months. It is unknown whether KP17 had cubs prior to 2008, and her first birthing interval is between May 2008 and December 2009. KP18 had a birthing interval of 17 months after her first litter died. For the NMP, only one birthing interval has been recorded as these were newly identified females. The mean birthing interval in months is 21.25 ± 2.27.

Table 3.9. Birthing intervals for all lionesses within the population that had multiple litters of cubs.

Female	Pride ID	1st Interval	2nd Interval	3rd Interval	4th Interval	5th Interval
Sempei	KP10	10				
Nashipai	KP13	21	30	18	17	12
Nabo	KP17	19	18			
Ntito	KP18	17				
Kofafeth	NMP1	33				
Jalalo	NMP2	27				
Jabdu	NMP5	23				
Korti	NMP6	20				
Mean birthing interval (n=8)		**21.25±2.27**				

3.3.7. Population mortality

3.3.7.1. Confirmed deaths

Between 2003 and 2011, eight lions were confirmed to have died (Table 2 in Appendix 8). Three of the deaths were of unknown lions whose identities were not confirmed because the carcasses were considerably decomposed.

3.3.7.2. Lions that disappeared

Between 2003 and 2011, 55 lions disappeared, dispersed or were taken away (Table 3 in Appendix 8). Out of these, 24 are presumed to be dead. Between 2008 and 2010, 10 lions disappeared. M1-M7, KP23, M29 and M30 were presumed dead because of their sudden disappearance and the lack of any information coming from within the human-occupied landscape indicating their whereabouts and status. The vast network of scouts, researchers, guides and rangers would continuously provide reports on lions but none came through indicating their presence. M8 and M9 were presumed alive because of the continuous stream of information coming from the community scouts and warriors on tracks and sightings of two male lions in an area where they were known to have frequented often and where they were last seen.

Seventeen adults disappeared with nine of them having an unknown status and eight presumed dead. Within the subadult category, eight subadults disappeared with three of unknown status and five presumed dead. Within the large cub category, 15 disappeared, 11 presumed dead and two presumed to be alive. Within the small cubs, 15 disappeared with 11 of unknown status and four cubs removed by the KWS.

3.3.8. Cub survival

Table 3.10 shows the percentage of cubs that died in the first year, within the first two years and the percentage that survived to subadulthood. The total number of cubs that were assessed was 51. 31.4% died in their first year with a total of 62.8% dying within two years of birth, and 37.3% of all 51 cubs sampled survived to subadulthood.

Table 3.10. Total cub survival within the population

Cub survival	N	Percent
Cubs that died in 1 year	16	31.4%
Cubs that died in 2 years	16	31.4 %
Cubs that survived to subadulthood	19	37.3%
Total	51	100%

Using the log rank test, it was possible to ascertain that the survival time of the three (male, female and unknown) groups is significantly different ($\chi 2$=13.80, df=2, $p<0.05$, log rank test). The survival distributions of the different types of groups are not equal in the population.

Proportionality was checked by including the time-dependent covariates in the model. The time-dependent covariate for this case was not significant (p=0.153) indicating that there was no violation of the proportionality assumption. Cubs were censored if they died, were taken away or disappeared.

The sex of the cub was found to be a significant predictor for survival (p = 0.0004). The cub survival rates for the 25-month period by gender is shown in Figure 3.9.

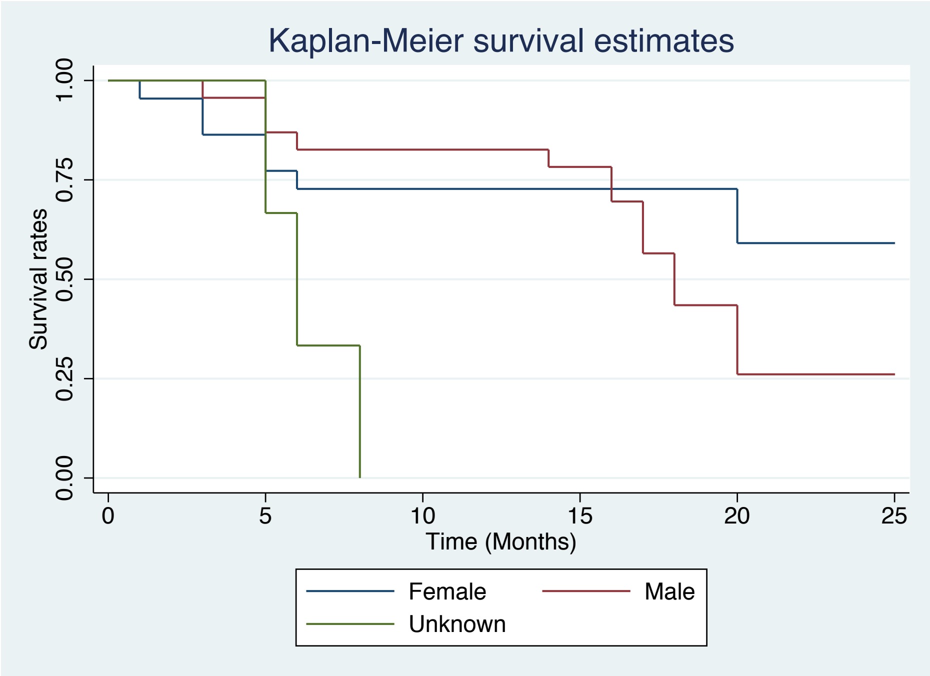


Figure 3.9. Survival curves for cubs

It was found that 40.91%, 73.91% and 100% of the cubs were censored for the females, males and unknown gender respectively. The male cubs males had a two-fold hazard rate in comparison to females (HR = 2.07, 95% CI [0.92-4.67], p = 0.08), while cubs having unknown sex had a seven-fold hazard rate in comparison to females (HR = 7.86, 95% CI [2.44 – 25.33], p = 0.001).

Table 3.11. Hazard ratio calculations

Characteristic	Percentage censored n (%)	HR (95% CI)	p value
Females	9 (40.91)	*ref.*	
Males	17 (73.91)	2.07 (0.92-4.67)	0.08
Unknown	6 (100.00)	7.86 (2.44-25.33)	0.001

3.3.9. Population density

The population density was calculated in two ways;

i. for the total research period from 2003 to 2011 excluding small cubs, because it was likely that some were missed during this period.

ii. with the whole population from 2008 to 2011.

The combined size of the study area for SNR and BSNR is 296 km^2. The population density was lower between 2003 and 2011 (0.046 km^2), compared to between 2008 and 2011 (0.067 km^2) (Table 3.12).

Table 3.12. The lion density in Samburu and Buffalo Springs

Population	Mean (km^2)	Standard Error
2003-2011	0.046	0.0017
2008-2011	0.067	0.0030

3.3.10. Summary of key population parameters

The following are the results of the key population parameters:

i. The mean lion pride size in the study area was 5.83.
ii. The mean age ratio over the whole study period as adult: subadult: large cub: small cub was 1:0.42:0.36:0.62.
iii. The overall adult male: female sex ratio was 4.80:1 and the overall adults and subadults sex ratio was 3.36:1. There was a bias towards females except for large cubs.
iv. The mean birthing interval is 21.25 months.
v. 55 lions disappeared during the study and eight lions were confirmed dead. 10 lions disappeared between 2008 and 2010.
vi. Cubs dispersed at 19.85 months.
vii. The average pride tenure was 34.6 months.
viii. 37.3% of the cubs survived in to sub-adulthood with 31.4% dying in their first year, and 62.8% dying within two years.
ix. The population density between 2008 and 2011 including small cubs was 0.067 km^2.

3.4. Discussion

3.4.1. Direct observations of lions

Lions are very difficult to census (Stander, 1991) and in this study the method of direct observation was used to identify and produce results on the lion population. There are a number of advantages and disadvantages of using such a technique for studying wildlife. Using the technique in this study highlighted a number of advantages that have also been found in other studies, not just on carnivores in Africa, but worldwide.

Using direct observation on wildlife has been extremely useful, for example it has been possible to learn about diet in various primates (Aguiar and Moro-Rios, 2009), hunting behaviour in wolves (MacNulty *et al.,* 2007), hunting habits and prey preferences in cheetahs (Durant, 2000) and interactions between spotted hyaenas and lions (Funston *et al*., 1998). All observations can be made and recorded in real time. Aguiar and Moro-Rios (2009) state that it is possible to understand reproductive success and knowledge of infanticidal behaviour in some species. It is a low-cost technique and has been used successfully with primates due to the ease in habituating the primates that are being followed and monitored. It has been suggested that this success can be replicated to shy and cryptic animals such as forest felids, where forest blinds can be used for observation. Becoming familiar with the individuals and their behaviour also allows the observer to design and identify the best way in monitoring the subject that is being studied. With the challenging and difficult terrain in this study area, this helped with monitoring the lion population.

Despite the numerous benefits of using direct observation as a study technique, there are a few disadvantages that have been observed:

i. It is argued that it is a time-consuming technique and requires a skilled observer. However, it is stated here that taking time with the method of direct observation can make an unskilled observer a more proficient one.

ii. In habitats with high forest cover where the animal being observed is crepuscular, using direct observation may be problematic (Aguiar and Moro-Rios, 2009).
iii. Additionally, looking at space use in a wide-ranging animal may be challenging and can only be looked at through other indirect techniques such as radio-telemetry.

Aguiar and Moro-Rios (2009) state that observers must be careful to reduce bias and plan a way that does not interfere with the subject's movements or behaviour. They agree that although habituation takes a long time (for example it can take over a decade to habituate apes) and considerable investment, it can enlighten you about social structure, territorial behaviour and more. However, it is argued here that habituation of lions within a human-occupied landscape could affect their survival. The threat of human caused mortality represents a cause of fear for lions (Oriol-Cotterill *et al*., 2015b) and they often adjust their behaviour in order for them to survive in human-occupied landscapes (Oriol-Cotterill *et al*., 2015a). Habituation may lead to reduced fear of humans. Lastly, many wildlife species have nocturnal habits that make the technique of direct observation difficult to use. This can be overcome, for example, by the use of night vision binoculars, previously used successfully to study the *Aotus*, night monkeys (Estrada and Coates-Estrada, 1985).

3.4.2. Lion monitoring

The number of days spent in the field per month varied during the study period (Figure 3.3). During the wet seasons, it was not possible to be present in the field due to the Reserves being inaccessible and the difficulty in finding lions at this time. Rudnai (1979) also found that during the wet seasons in Nairobi National Park, less regular lion sightings did not necessarily mean that the lions were not present.

Only 15 days were spent in ShNR and this was a result of security concerns in the area. This vast wilderness area is rarely monitored by security personnel; thus, it became a raiding area between various ethnic groups and a poaching hotspot.

After the flooding in March 2010, when the main connecting bridge from SNR to BSNR collapsed (see Appendix 1), the mean number of days in BSNR was almost reduced by half. With the collapse of the bridge, the travel time to BSNR increased tremendously, vehicles received increased wear, and there was a lack of secure places to camp overnight in BSNR. In comparison, the mean number of days spent in the Conservation Area (CA) in WGCC was very high, largely because of its easy access and close proximity to the research base (see Appendix 1).

The greatest distance was covered in SNR (Figure 3.4a). Located between WGCC and BSNR, SNR was well situated for lion monitoring. However, the greatest number of kilometres covered per day was in ShNR prior to removing it from the study area. This is because of the limited number of days spent in ShNR and when the opportunity arose to visit the Reserve, the entire area was covered as much as possible. The mileage covered per size of the area was greatest in the CA in WGCC, again due to the proximity of the region to the research base.

During the study period, lions were seen on 208 days out of 605 field days. This indicates the challenge in finding lions in this area, where the thick bush and terrain make it difficult to spot lions. The lack of roads in the area, especially north of SNR and south of BSNR, also posed a challenge as lions are often present in areas where they are undisturbed by vehicles (Loveridge *et al*., 2010a). Generally, with a larger number of roads in a particular area, there is a positive effect on the precision of the data (Stander, 1998). More than half of the lion sightings were in SNR where the greatest kilometres were covered, followed by BSNR and the Conservation Area in WGCC (Table 3.3).

3.4.3. Pride sizes

There may be as many as 40 lions in a pride (Estes, 1997). ShNR was famed for large prides of 20 or more individuals (Wilson, 1989) while prides of between 8 to 48 individuals have been observed in the Maasai Mara National Reserve (Ogutu and Dublin, 2002). The largest pride in this study area consisted of 14 individuals (KP), and the smallest consisted of three individuals (SP). The likelihood of overlooking a large number of lions or prides within the study area is slight due to the intensive coverage of the protected areas and the regular and consistent communication with the resident tourist guides and rangers.

Schaller (1972) reports that in the 1960s, 347 groups were tallied in East Africa with an average of six individuals per group. The mean pride size for all ages within the SNR and BSNR lion population is compared to other mean pride sizes across Africa.

Table 3.13. Mean pride sizes in Samburu and Buffalo Springs National Reserves relative to other lion populations across protected areas in Africa.

Area	Mean pride size	Source
Serengeti National Park	15.3	Van Orsdol *et al*., 1985
Ngorongoro Crater	20	Hanby *et al*., 1995
Maasai Mara National Reserve	22	Ogutu and Dublin, 2002
Maasai Mara National Reserve	17.1	Mogensen *et al*., 2011
Kruger National Park	11.8	Smuts, 1976; P.Funston (*pers. comm.*)
Etosha National Park	12.5	Stander, 1991
Waza National Park	7.3	Bauer *et al*., 2003
Nairobi National Park	6.7	Rudnai, 1973a
Hwange National Park	2.7	Loveridge *et al.,* 2007
Zakouma National Park	13.7	Vanherle, 2005
South Luangwa National Park	3.27	Rosenblatt *et al*., 2014
Kgalagadi Transfrontier Park	11.3	Funston, 2011
Amboseli Group Ranches	1.62	Dolrenry, 2013
Samburu and Buffalo Springs	*5.83*	*Bhalla, this study*

The mean pride size of 5.83 is smaller than the range of prides sizes recorded in the literature across Africa, except for the protected areas of Hwange and South Luangwa National Parks (compared to the ones listed in Table 3.13) which had smaller mean pride sizes. Dolrenry (2013) also reported a small mean pride size for the lions living outside the protected area of Amboseli National Park.

In the study area, the BP reduced in number, whilst the numbers of individuals in the other prides increased over time (Figure 3.6). The BP became very small after a number of females left the safety of BSNR and moved into community areas where wildlife was not tolerated by the local people. These females did not return and it is suspected that they were killed in the community areas south of BSNR (*pers. comm.* Abdi Sukuna). Removing females from a population has also been shown to expose that population to decline (Loveridge *et al*., 2007). In this case, the BP has not recovered since losing their females in 2006, and only one adult female remains.

Most of the lion sightings belonged to the KP. Their location within SNR made this pride more accessible for viewing compared to the other regional prides. Their pride composition was similar to that of the NMP (Table 3.4). Likewise, the pride composition of both SP and BP was similar although the prides fall in entirely different regions (Tables 3.4). The SP was resident within a human-occupied landscape (WGCC) and BP was resident within a protected area (BSNR). This highlights the importance of areas surrounding protected areas (see Chapter 5). Small protected areas may not protect prides, as has been seen within the BP.

The number of breeding males and females within the KP and the NMP were similar in number, indicating the small numbers of adult female numbers that were present within both prides. One theory is that the prevalence of smaller prides is related to the ratios of lions to prey biomass or vegetation density (Bauer *et al.,* 2008; Trinkel *et al.,* 2008; Funston, 2011), and also may be due to infrequent kills of large prey (Elloff, 1984). However, Snyman *et al.,* (2014) argues that it is the human caused mortality that leads to the small groups, once adult numbers are reduced below a certain threshold. Bauer (2003) agrees that in many smaller protected areas, where lions are exposed to human caused mortality, lions do not occur at their predicted densities and often comprise smaller prides. Dolrenry (2013) also found small groups (mean group size was 1.62) and the presence of solitary lions in the community group ranches of Amboseli, which was as a result of human presence. Oriol-Cotterill *et al.,* (2015b) confirms that large carnivores may in fact become more solitary when the risk of human caused mortality is high. This is why there is a greater chance of either solitary lions or small groups existing outside protected areas, as Dolrenry (2013) found in addition to results from the SP in this study. However the BP which was within the protected areas, also comprised a small group towards the end of the study, highlighting that human caused mortality affected this park population as well.

3.4.4. Males and coalitions

It was observed that males were not integral to any pride in the study area prior to 2006, except for M18 who remained in the area and associated with various prides for 22 months. Dolrenry (2013) found that similarly, within the Amboseli Group Ranches, males did not associate with females except during mating. Other instances when they would associate included when large prey was killed. Males were generally seen alone, which is not typical for lions in Africa (Dolrenry, 2013). In this study, new males M24 and M25 arrived in August 2006, and this was the first male coalition to have been seen within the Reserves during the entire study period. The second male coalition M26 and M27, who arrived in August 2008, remained until the end of the study period.

The average male tenure within the study area for the five males was 34.6 months. This average pride tenure is longer than what has been reported in the Serengeti National Park (18 months) but lower than that reported in Queen Elizabeth National Park (90 months) (Van Orsdol *et al*., 1985). Bygott *et al*., (1979) and Packer *et al*., (1988) report the average male tenure length as two years in the Serengeti. Schaller (1972) reported that the longest tenures of males with a pride were two instances of six years in Nairobi National Park. Male tenure in Kruger National Park was rarely more than two years (Orford *et al*., 1988). In Etosha National Park, Orford *et al*., (1988) and Stander (1991) state that some male lions had tenure for a minimum of four years, which is comparable to this study. They further state that the low lion density in Etosha may have led to the longer pride tenure. In one case in the Ngorongoro Crater, small nomadic coalitions have entered the Crater but have not been able to establish themselves as they face competition from the larger resident coalitions (Packer *et al.,* 1991), however, this was not seen within the SNR and BSNR lion population.

Funston *et al.,* (2003) found that for multiple prides within Kruger National Park, coalitions retained tenure over multiple prides at the same time and stayed resident within each pride for 17 months. This was similar to what was found within the SNR and BSNR lion population. After M24 and M25 arrived, the males associated with two prides, moving frequently between the regions where KP and NMP ranged. Similarly, M26 and M27 associated with both the KP and NMP after they became resident in the Reserves. This has been found in other areas too, such as in Hwange National Park (Loveridge *et al*., 2007), and Rudnai (1973a) also found that one of the males studied in Nairobi National Park was not a permanent resident of one of the prides, but he associated with females from four different prides. In small ecological units, such as Nairobi National Park, successful male coalitions are more likely to hold multiple pride tenure.

3.4.5. Age and sex ratios

Packer *et al*., (1988) states that females generally live up to 18 years of age and males up to 14 years of age. Lion survival also increases with growing age (Schaller, 1972). In SNR and BSNR, no known individuals have reached between 14 and 18 years of maturity.

The mean age ratio over the whole study period was 1:0.42:0.36:0.62 (adult:subadult:large-cub:small-cub). This indicates that there were almost twice as many small cubs as large cubs. This is an average over the entire study period, and many large cubs did not reach their first full year prior to dispersing. Within the Serengeti, 20% to 25% of the population were subadults, and large cubs outnumbered small cubs by 15% to 12% (Schaller, 1972). This is in contrast to the lion population within SNR and BSNR. The adult proportion of the population is more than the subadult proportion, similar to what Ogutu and Dublin (2002) found in the Maasai Mara and to what Snyman *et al.,* (2014) found in the Northern Tuli Game Reserve (adults comprised 69%). Both studies found that adults formed more than half of the lion population, with adult females outnumbering adult males. Dolrenry (2013) found that in the community Group Ranches of Amboseli, adults comprised 66%, subadults only 2% and cubs 32%.

The overall adult sex ratio in this study was 4.80:1 (female:male). This is compared to other lion populations across Africa (Table 3.14).

Table 3.14. Sex ratios in Samburu and Buffalo Springs National Reserves relative to other lion populations across Africa.

Area	**Sex ratio**	**Source**
Serengeti National Park	3:1	Packer *et al*., 1988
Ngorongoro Crater	1.9:1	From Celesia *et al*., 2009
Maasai Mara National Reserve	2:1	Ogutu and Dublin, 2002
Kruger National Park	2.5:1	Funston *et al*., 2003
Etosha National Park	1.4-1.6:1	Stander, 1991
Waza National Park	3:1	Tumenta *et al.,* 2009
Nairobi National Park	2.3:1	Rudnai, 1973a
Hwange National Park	6:1	Loveridge *et al*., 2007
Zakouma National Park	1.6:1	Vanherle, 2005
Northern Tuli Game Reserve	1.6:1	Snyman *et al*., 2014
Kgalagadi Transfrontier Park	1.2:1	Funston, 2011
Amboseli Group Ranches	0.91:1	Dolrenry, 2013
Amboseli National Park	1.5-1.7:1	Dolrenry, 2013
Chobe National Park	5.7:1	Cooper, 1991
Samburu and Buffalo Springs National Reserves	*4.80:1 (Adults)* *3.36:1 (Adults and Subadults)*	*Bhalla, this study*

Overall, females outnumbered males across populations in Africa, yet the female to male sex ratios reported in SNR and BSNR are higher compared to other populations across Africa (for both adults, and adults and subadult age categories). It appears that only Hwange National Park has a higher ratio (6:1; Loveridge *et al.,* 2007) from the selected examples shown in Table 3.14. The low number of males has led to a higher female ratio compared to male numbers as a result of long tenure periods and limited immigration.

The sex ratio for subadults alone in the SNR and BSNR lion population is 1.75:1 and the ratio for large cubs is 0.8:1, which is the only instance where the female ratio is lower than the males (Table 3.7). Rudnai (1973a) also found in Nairobi National Park that large cubs have a more even sex ratio compared to the breeding population and are more similar to the sex ratios at birth. If there are fewer males in the population for a specific reason, there could be a resultant shift in the sex ratio. Creel and Creel (1997) found that in the Selous Game Reserve, the population compensated for the removal of adult males (by hunting) by producing a higher percentage of male cubs.

Loveridge *et al.,* (2007), also states that skewed sex ratios are reported often in areas where males are hunted. By removing old males, the subadult male mortality rate could increase due to the increased turnover of pride-holding males. Schaller (1972) and Whitman and Packer (1997) also found that if there was a high turnover of adult males, this could lead to male bias within the cub sex ratios. Funston (2011) and Dolrenry (2013) revealed similar results in their study areas of Kgalagadi Transfrontier Park and the Amboseli Group Ranches, where the sex ratio of cubs was biased in favour of males.

3.4.6. Cub dispersal

In this study, there were only two adult females on two occasions when females dispersed from their mothers. It appeared that there was increasing intolerance by the older lions towards the younger ones and the large cubs were treated as trespassers, similar to what Schaller (1972) witnessed in the Serengeti when cubs were between 1.5 and two years of age. Bertram (1973) also states that eviction can at times be done by one particularly hostile adult female.

In 2006, the three youngest cubs from the eight in the KP, who dispersed at 17 months, had the support of other 10-month old lions to help them after they dispersed. These cubs were between 17 and 19 months old when they were abandoned by their mother and left to survive on their own. They were too young to mate with the new males and pre-pubertal females generally avoid encounters with new males and at times, leave permanently, becoming peripheral (Hanby and Bygott, 1987). In addition to this, if pride ranges are large enough, females can avoid new males until they are ready to mate, and generally all subadults are better able to avoid hostile new males (Hanby and Bygott, 1987). However, pride ranges in the study area are small (see Chapter 4) and therefore, it appears that the females preferred to leave the area entirely and not return. Additionally, vacant areas containing suitable habitat and resources can be colonised by emigrating females (Loveridge *et al*., 2007; Davidson *et al.,* 2011), which appears to be the case for these females in the KP who eventually moved permanently to the Kalama Conservancy, north of SNR (see Appendix 1).

In SNR and BSNR, the mean age of cub dispersal over the entire period, was 19.85 months. Some studies found that this age was generally at two years (Rudnai, 1979; Stander, 1991; Dolrenry, 2013). In the Serengeti, cub dispersal occurred at approximately three years of age (Schaller, 1972; Bertram, 1973; Pusey and Packer, 1987). Hanby and Bygott (1987) found that 87% of the males in their study population in the Serengeti had left by 48 months and none stayed longer than 65 months. They also found that no females emigrated later than 48 months. Funston *et al*., (2003) found that in contrast to lions in the Serengeti, subadult males associated with their natal pride for longer periods in the Kruger National Park and in most cases remained close to their natal territory. When they did disperse, it was on average at 38 months.

The age of cub dispersal in SNR and BSNR is lower compared to the cub dispersals reported in the literature across other populations reported here. Dolrenry (2013) suggested that the earlier age of dispersal that was witnessed in the Amboseli Group Ranches could be due to the low lion population densities and small groupings, leading to subadults moving to new areas where territorial adults were absent.

Interestingly, other more solitary cats become independent at younger ages compared to lions (Schaller, 1972). Cheetah young are independent at about 16 months. Leopard and tiger young become independent between 20 and 24 months. It is possible that lion cubs need extra time to learn how to hunt cooperatively; therefore, the age at which independence is achieved is later than in other solitary cats.

3.4.7. Birthing interval

In SNR and BSNR, the mean birthing interval was 21.25 months (Table 3.9). Rudnai (1973a) found in Nairobi National Park that the intervals between litters was on average two years, although when a female lost her cubs, the intervals were six and eight months or, after loosing the litter, 3.5 and six months. Assuming some cub mortality, Schaller (1972) found in the Serengeti, the birthing interval was more than 18 months if at least one cub in the litter survived and Bertram (1975) stated that the interval was nine months after the last of the previous litter had died. Six lionesses in the Serengeti had cubs after 18.5, 22, 22, 25, 26 and 26 months respectively (Schaller, 1972). Most of the females conceived after their young were between 19 to 23 months old. However, assuming no cub mortality, the birthing interval was 24 months (Packer *et al*., 1988). Despite being slightly lower in this area, the SNR and BSNR mean birthing interval fell within the range of what was found in the Serengeti. Funston *et al.,* (2003) found that the birthing interval in Kruger National Park was 40 months, which is longer compared to the Serengeti because of subadult males dispersing at a later age. Dolrenry (2013) also found a large birthing interval in Amboseli and suggests that there could be a lot of unobserved mortality due to the secretive nature of the females, especially in the group ranches where the lions were being studied.

KP13's second interval was very long and unusual as the frequency of copulation was high between the resident males and the females. It is uncertain as to why there were no births during this second interval, though there are several potential explanations. Schaller (1972) found that in the Serengeti, 80% of all sexual contacts did not result in young. A number of reasons were suggested for this; one being the lioness was already pregnant. Furthermore, 30% of the sexual contacts were typical of the kind leading to conception, yet there were no births. Lastly, females could be in false oestrous and had failed to come into heat fully. Bertram (1975) confirms that most oestrous periods do not result in cubs and concludes that a high abortion rate is also a possibility, although Packer and Pusey (1983a) argue that it is difficult to determine whether newly pregnant females abort. Additonally, West and Packer (2002) suggest that dark-maned males suffer from abnormal sperm. The males, M24 and M25, were dark-maned lions originating from the Lewa Wildlife Conservancy, south of BSNR. KP13's last interval was very short because of human interruption as her cubs were separated from her as a result of aggressive behaviour from tour drivers (*pers. obs.*). The cubs died from starvation soon after separation.

3.4.8. Mortality

Schaller (1972) found that most lions die from disease, starvation, old age, abandonment or violent interactions with other lions or other species. Human caused mortality also leads to lion deaths as explained in section 1.2. Lion mortality is difficult to measure and often, when known animals disappear it is uncertain whether they are dead or alive, and at times if found dead, it is difficult to determine the cause of death. Stander (1991) concurs that in particular, cub deaths are rarely witnessed and it is usually difficult to determine their exact cause of death.

Table 3 in Appendix 8 showed the number of lions that died, disappeared, dispersed or were taken away. Clearly a large number of lions died or went missing from the region. Lions often left the safety of SNR and BSNR and entered community areas where wildlife were not tolerated by the local people and where lions killed livestock (*pers. comm.* Abdi Sukuna). Rudnai (1979) found that the main reason for the lack of a sizeable lion population in Nairobi National Park was the presence of pastoralists and resulting conflicts. Tuqa *et al.,* (2014) found that in Amboseli National Park, lions increased their movements outside the park as they widened their home ranges in search of prey after the drought in 2009. This put them into closer contact with the local communities living around Amboseli. Mogensen *et al*., (2011) found that during drought conditions in the Maasai Mara, there were heightened movements of livestock searching for food and water. Lions were forced to prey on livestock and this increased the chances of retaliatory killing of lions by pastoralists. The authors conclude that drought occurrences accentuate threats to lions and human-lion conflict increases.

In Zimbabwe, Loveridge *et al.,* (2007) found that prides and females on edges of parks had a lower survival in comparison to lions within the core areas of the park. Large carnivores such as lions are often attracted to boundaries of protected areas due to the presence of livestock (Loveridge *et al.,* 2010) which are easier to prey on. This then leads to increased human-lion conflict. Snyman *et al*., (2014) also found that most of the lion mortalities that took place in the Northern Tuli Game Reserve were close to the boundary of the park. Edge effects have profound effects on lions (Woodroffe and Ginsberg, 1998). In contrast, during this study, the lions shot by herders were in the middle of the protected areas as the herders were grazing their livestock illegally within park boundaries during the drought. It is such mortality that could lead to entire prides being eliminated (Funston, 2001). In BSNR, four cubs were removed and taken to the Nairobi National Orphanage after their mother was shot as a direct effect of livestock encroachment. If a mother dies whilst she still has dependent cubs, other lionesses could potentially raise her cubs (Rudnai, 1973a). However, in this situation, the other females in the area did not make any attempts to associate with the cubs. The cubs were too young to hunt for themselves or compete successfully at kills at this age (seven months) and were therefore removed. Male takeover (see section 3.4.4) resulted in one confirmed death of a male lion, killed by another. Bertram (1978) confirms that fights between rival males are serious and could lead to death, as was found in the Serengeti.

3.4.9. Cub survival

In this study, 37.3% of the cubs survived to sub-adulthood. 31.4% of the total cubs died in their first year, and a total of 62.8% died within two years of birth. Rudnai (1973b) found that the lions in Nairobi National Park had a 51% survival rate, with 32.7% of those born, reaching two years of age. Ogutu and Dublin (2002) found that cub survival in the Maasai Mara was high at 77% and Funston *et al*., (2003) also found that cub survival in the Kruger National Park was high with 84% surviving their first year, compared to a low survival of 33% in the Serengeti. In the Kgalagadi Transfrontier Park where lions faced persecution, Funston (2011) found that 59% of cubs survived to one year. Woodroffe and Frank (2005) monitored the survival of 30 cubs in the neighbouring Laikipia County and reported a high cub survival where 77% survived to one year with 83% surviving to two years of age. In the Amboseli Group Ranches, 132 cubs were monitored and it was found that 34% died in their first year, 17% of the remainder died in their second year and 48.8% survived to sub-adulthood (Dolrenry, 2013). Results from cub mortality studies in the Amboseli Group Ranches (human-occupied landscape) and Nairobi National Park (protected area) are more similar to what was found in this study. There were no cubs lost as a result of infanticide or predation by other carnivores in SNR and BSNR, which is similar to what Funston *et al.,* (2003) found in the Kruger National Park.

Van Orsdol *et al.,* (1985) found in their study that cub survival to 12 to 18 months was correlated with the amount of food available during prey scarcity. Packer *et al*., (2005) stated that in a “good year” the primary demographic response was increased cub survival. Rudnai (1979) also found that an unusually large number of cubs were born when wild prey numbers were high and especially when in a weakened condition, thus forming an easy prey base for lions. During the drought in 2009, five large cubs from the KP were abandoned by their mothers and struggled to hunt for themselves. An elephant died at this time in BSNR and four of the cubs crossed the river from SNR to BSNR to feed on the carcass. One cub was left behind and was unable to hunt by herself. Her condition weakened at this time and she was struggling to move after the separation period lengthened. The warden of SNR intervened and fed her an impala. After feeding on the impala for two days, she obtained the strength to look for her siblings. Schaller (1972) found that cubs revive very quickly after a few meals and thin lions can transform into energetic ones with their recent deprivation not apparent. After the cub was reunited with her siblings, the large cubs eventually survived through the drought mainly through feeding on carcasses. The cub's hunting abilities were not yet refined and their survival appeared to be dependent on the availability of weakened prey or from prey that had succumbed to the severity of the drought. Schaller (1972) found that lions readily scavenge food and will eat animals that have died from disease and other causes. Creel (2001) also states that carcasses are more valuable compared to live prey, as hunting is dangerous and costly in terms of energy expenditure.

When new males arrived in 2008, small cubs were present within the KP. Upon their arrival, the mothers aggressively attacked the males to defend their cubs and were able to drive them away (*pers. obs.*). This is similar to what Packer and Pusey (1983a) witnessed in the Serengeti, where mothers of cubs vigorously attacked infanticidal males, allowing the cubs to escape. Soon after hiding the cubs, the females from the KP continuously mated with the males to deceive them, whilst keeping their cubs hidden, until possibly the cubs odour was not foreign after the males had been in the pride for a while and they were not considered as strangers any more (Bertram, 1975). Rudnai (1973b) found that females in the Nairobi National Park did occasionally mate at the same time as raising their young and yet they did not conceive. Schaller (1972) found that lactating females with small cubs courted on two occasions. Lionesses can also sometimes appease an aggressive male by presenting herself sexually to him. This appeared to be the case for both females in the KP, allowing their cubs to survive.

3.4.10. Population density

The overall mean population density between 2003 and 2011 excluding small cubs was lower (0.046 km^2) compared to the mean between 2008 and 2011 where small cubs are included (0.067 km^2; Table 3.12). Lion densities across Africa vary regionally with lower densities in desert ecosystems, such as the Kalahari and Etosha, and higher densities in grassland ecosystems such as the Serengeti and Ngorongoro (Celesia *et al.,* 2009; see Table 3.15). The population density in SNR and BSNR appears to fall in between densities reported in the literature across various lion populations in Africa. Populations in the Serengeti, Ngorongoro, Maasai Mara and Nairobi all had higher densities, although populations in Kruger, Etosha, Waza, Hwange and Zakouma all had lower densities compared to SNR and BSNR.

Table 3.15. Lion population density estimates in Samburu and Buffalo Springs National Reserves, relative to other lion populations across Africa.

Area	**Size (km^2)**	**Lion density (km^2)**	**Source**
Serengeti National Park	2,700	0.110-0.180	Mosser *et al.,* 2009; Packer *et al.*, 2011
Ngorongoro Crater	250	0.21-0.40	Hanby and Bygott, 1995; Packer *et al.*, 2011
Maasai Mara National Reserve	1,530	0.2-0.4	Ogutu and Dublin, 2002
Kruger National Park	4,280	0.016-0.02	Funston *et al.,* 2003
Etosha National Park	14,645	0.01-0.02	Stander, 1991
Waza National Park	1,700	0.008-0.012	Tumenta *et al.*, 2009
Nairobi National Park	117	0.24	Rudnai, 1973a
Hwange National Park	5,884	0.027	Loveridge *et al.,* 2007
Zakouma National Park	3,050	0.039	Vanherle, 2005
Kafue National Park	4,720	0.018	Becker *et al.,* 2012
Northern Tuli Game Reserve	720	0.101	Snyman *et al.,* 2014
Amboseli Group Ranches	3,684	0.012	Dolrenry, 2013
Amboseli National Park	390	0.095	Dolrenry, 2013
Samburu and Buffalo Springs National Reserves	*296*	0.067	*Bhalla, this study*

Data from the Wildlife Planning Unit (1983) stated that in 1973, the lion density in SNR and BSNR was 0.03 km^2 and in 1980, it was 0.01 km^2. These figures were based on one-off ground counts and showed that both resident and migratory lions in the population were stable. This shows that the lion density may have increased since 1980. In the 1970s, although wildlife populations had greatly reduced, lions were believed to be increasing in numbers (Wildlife Planning Unit, 1983). However, this does not conform to opinions and views of Reserves authorities. The general consensus is that there has been a decline in the number of lions and this is mainly due to conflict between livestock owners and lions (*pers. comm*. Abdi Sukuna). Reports of visitors seeing 27 or 30 lions in BSNR were common (*pers. comm.* David Letiktik). Jamlick Lepuyapui, a ranger in SNR, adds, "*Now, a person can drive for a full week within the Reserves and not see a lion*." There are some studies that have shown that lion populations with small group sizes have low density populations (Dolrenry, 2013). For example in the Makgadikgadi Pans in Botswana, the lion population density was 0.0074/km^2 when group sizes were 1.2 (Hemson, 2003).

3.4.11. Summary

This chapter has presented the overall demographic parameters for the Samburu-Isiolo lion population. The parameters considered include: pride sizes, male tenure periods, age and sex ratios, cub dispersal, birthing interval, mortality, cub survival and population densities. These parameters were compared with those of various lion populations across Africa. The pride sizes, male tenure periods, cub survival, birthing interval and population density were comparable to other studies across Africa. The cub dispersal in this study was lower compared to other places in Africa – a key outcome in this study. The sex ratios were higher compared to most other regions across Africa. This study highlighted the fact that human caused mortality did in fact affect the lion population demography not only through edge effects, but also within the protected areas. The lack of male immigration and safe dispersal of lions is a concern highlighted throughout this thesis.

Chapter 4

Lion home ranges in the Samburu-Isiolo ecosystem

"A Samburu story states that there are three long distance trekkers; a Samburu warrior, an elephant and a lion."

Gabriel Lepariyo, 2003

(Warden Samburu National Reserve)

Abstract

The spatial dynamics of lions is of great relevance to conservation especially within an anthropogenic landscape. This chapter assesses the home ranges of the lion prides within the Samburu-Isiolo ecosystem. Pride ranges were assessed annually between 2008 and 2010. The prides that were considered were the Koitogor Pride, Ngare Mara Pride and Borana Pride inside the protected areas. Due to the lack of sufficient sightings for the Ngare Mara and Borana Prides, certain years were excluded from the range calculations and mapping. Additionally, the ranging behavior of males who were part of a coalition were examined between 2008 and 2010. Methods used for the range analysis included Minimum Convex Polygon (MCP) and Kernel Density Estimator (KDE). The MCP method included 100% range calculations and the KDE method included 95% and 50% home range calculations. The methods used to establish the home ranges are discussed, in addition to the drawbacks experienced.

Overall, the ranging behaviour of all three prides was confined within the limits of the protected areas. All pride home ranges were centred near the water sources that were present in the protected areas (the Ewaso Nyiro River for the Koitogor Pride, the Ngare Mara River for the Ngare Mara Pride, and the Isiolo River for the Borana Pride). Core home ranges between all prides showed no overlap and each pride had its own distinct regions of intensive use. Male ranges were larger than those of the females from the Koitogor Pride, except during the drought of 2009. Overall, male ranges were smallest during the drought of 2009 and increased in 2010. The Koitogor Pride also displayed an increase in core range size following the drought. The largest pride range at 62 km^2 belonged to the Koitogor Pride, which is also the largest pride in the study area. The extent of their home range was lower than that reported for other prides in various protected areas across Africa. Lions have large ranges and within small protected areas, it is expected that lions move close to park boundaries and areas beyond. This could potentially mean that there is an increased risk of human caused mortality.

4.1. Introduction

The spatial dynamics of species are of fundamental interest to ecology and, subsequently, of great relevance to conservation practice (Lehmann *et al.,* 2008; Struve *et al*., 2010; Tuqa *et al*., 2014). For the conservation of ecosystems, it is important to understand the home range behaviour of lions and to consider variations (Loveridge *et al*., 2009), especially within human-occupied landscapes.

Home ranges are able to provide insights into how animals use their surroundings (Powell, 2012). A home range is described as a common pattern of space use and can provide an understanding of any variations in sizes (Loveridge *et al.,* 2009). The home range of a carnivore is as large as is necessary and its ranging behaviour is affected by ecological, demographic and behavioural factors. An animal's home range is dependent on the abundance and dispersion of resources, such as prey (Macdonald and Carr, 1989).

Fluctuations in the extent of an individual lion's home range size may occur in response to different factors across different timescales (Hayward *et al.,* 2009; Loveridge *et al.,* 2009). Therefore, it is essential to examine a lion's space use over time to determine whether factors such as seasonality, climate variability, including the prevalence of droughts, influence and affect home range size (Tuqa *et al*., 2014).

With extensive home ranges, lions often come into contact with a growing human population which frequently leads to conflict (Loveridge *et al.,* 2009). Funston (2011) concurs that when home ranges are the approximate size of the protected areas, it creates more of a challenge for the carnivores. It is for these reasons that the ranging behaviour was assessed; to ascertain whether the lions were in fact moving outside the limits of the protected areas.

Maps delineating the spatial extent or outside boundary of an animal's movement in the course of its daily activities can be constructed using a set of location points (Funston *et al.,* 2003). Such data for lions are typically collected automatically using Global Positioning System (GPS) radio-collars fixed on individuals that transmit at regular intervals, and allow for constant monitoring of the collared lions (Tuqa *et al.,* 2014). The boundaries of a home range from a set of location data allows for the construction of the smallest possible convex polygon around the data. This approach is referred to as the Minimum Convex Polygon (MCP) method (Burt, 1943; Mohr, 1947). Kernel Density Estimator (KDE) can also be used to demonstrate home range and is thought to be more efficient. This study employed both methods, using GPS points of pride sightings over a period of three years, following failed attempts to radio-collar several lions. All sightings were plotted and ranges mapped during the three-year period (2008-2010). Variations between the years are then discussed, especially with respect to the Koitogor Pride as this was the only pride to have three years of sufficient data. In addition to the three-year dataset, an overall dataset of nine years (2003 to 2011) was plotted. However, this nine-year dataset was not as comprehensive as the detailed study period between 2008 and 2010.

4.2. Methods

4.2.1. Radio-tracking

Radio-tracking greatly increases efficiency in finding more lions per day (Bertram, 1976; Loveridge *et al*., 2001). It further allows for the understanding of lion range and movement, indicating when the lions go outside their normal ranges. Variations between ranges in the dry season and wet season can be mapped through the use of radio-tracking data. Unfortunately, there were no successful attempts at collaring the lions, despite considerable time, effort and resources put towards attaching collars on some key lions within the study area.

4.2.2. GPS locations of lions and mapping

The methodology for sighting lions is described in detail in Chapter 3 (section 3.2.2). The position of the known individuals was collected each time a lion was sighted. The prides' locations were recorded using a GPS unit. These were then mapped using a Geographic Information System (GIS) and the spatial use of the various prides examined within the study area. Maps were created according to the prides, and males were further grouped together in their coalitions. It was this study's aim to map the ranges of the Sasaab Pride (see Chapter 3). However, due to limited sightings in a small section of the Conservation Area (CA), mapping presented more of a linear profile compared to a polygon feature along the River and therefore the maps of the Sasaab Pride were excluded from this Chapter.

4.2.3. Range analysis

Home ranges were estimated using both the MCP and the KDE method. The 100% MCP method is the most common and oldest used method for home range estimation (Burt, 1943; Mohr, 1947). It is a standard method most often used where the only kind of spatial data available is presence-only data (Burgman and Fox, 2003) and is often used for discontinuous data (Funston *et al.,* 2003) where the smallest convex polygon is created (Powell, 2000) using, in this case, lion locations. These were plotted with the outermost points of locations the lions were sighted connected to give the range (Mohr, 1947). The computer programme ArcGIS 10.0 was used to generate the maps.

Home ranges can also be estimated using KDE. The KDE method is more efficient and unbiased (Worton, 1989; Börger *et al.,* 2006) and has been used in this study in addition to the MCP 100%. The KDE method uses the harmonic mean of all the locations to assess core density areas. The areas are defined as the boundaries of the lion's home range (KDE 95%) and the core home ranges (KDE 50%), both of which are used in this study (White and Garrott, 1990). The 95% home range corresponds to the area in which the probability of finding or relocating the animal is equal to 0.95 and the 50% home range is the core utilisation area, where there is a 0.50 relocation probability of finding the animal. Powell (2000) defines this as the area most intensively used, that is, the animal's main activity area.

Using ArcGIS 10.0, the kernel density tool was run with each pride's data being used as the input point feature. A grid cell size of 20 metres was used. The KDE values were then extracted using the "Extract values to point" tool located in the Spatial Analyst Toolbox. This created a new shapefile with the KDE value added to the specific pride data. In order to get either 50% or 95% of the range, the total number of points were either halved to get the 50% or 95% of the points taken to get the KDE 95%. The KDE raster created was reclassified into two classes using the reclassify tool, with the KDE 50% value as the break value separating the two classes. The reclassified raster was then converted to a polygon which represents the 50% core range or the 95% home range.

4.3. Results

4.3.1. Range estimators

Home ranges for the prides and male coalitions within Samburu National Reserve (SNR) and Buffalo Springs National Reserve (BSNR) were obtained using the MCP and KDE methods.

4.3.1.1. Koitogor Pride

The pride ranges for the Koitogor Pride (KP) are displayed in Figures 4.1, 4.2, 4.3 and 4.4. Annual maps have been created for 2008, 2009 and 2010. An overall map combining all sightings between 2003 and 2011 is also presented. MCP (100%) indicated by the outermost black line, KDE (95%) by red lines and KDE (50%) as the light green lines, are included in each map.

Figure 4.1. shows that in 2008, the KP were centred along the Ewaso Nyiro River with one core range at Wire Bridge (see Appendix 1). The lions were mainly in SNR (34 sightings), with limited sightings in BSNR (20 sightings). The size of the core range was very small. Despite a large number of sightings (n=54), compared to subsequent years, the pride's movement was fairly restricted, remaining in close proximity to the River. The KDE 95% are smaller compared to the following years.

Figure 4.2. shows in 2009, there was more movement by the pride in BSNR (36 sightings compared to 24 in SNR). There were three core ranges; a small one in BSNR, and another two along the River encompassing both SNR and BSNR. The core ranges were in the Green Bush region, near Larsens Camp and along White River (see Appendix 1). 2009 was a drought year in the region and the Ewaso Nyiro River was the only source of water (in SNR) for the KP, which is mainly resident in SNR. Examining the MCP 100% in this year, there was a sighting towards the western section of SNR, near the Elephant Watch Camp. This appeared to be an outlier compared to all other sightings and it was not common for this pride to be as far west as the Elephant Watch Camp.

Figure 4.3. displays two core ranges in 2010; a larger one overlapping SNR and BSNR at Wire Bridge, and a smaller one in SNR near Leopard Rock. From the map, the pride's KDE 95% ranges are very clear and cover the Wire Bridge, Green Bush, Leopard Rock and Sierra 4 areas. Movements were largely confined to SNR (19 sightings) compared to BSNR (seven sightings).

Figure 4.4. shows that between 2003 and 2011, although the pride's range (MCP 100%) extended as far as Elephant Watch Camp and south of Girgir Plains, the KDE 95% and KDE 50% ranges showed a concentration along the Ewaso Nyiro River mainly around Wire Bridge, Green Bush, south of Koitogor Hill and Larsens Camp. Interestingly, the pride - mainly known to be resident in SNR (161 sightings) - also shows its range extending considerably into BSNR where the pride was seen on 132 occasions (KDE 95%). The two core ranges are centred at Wire Bridge, Green Bush and Larsens Camp.

Figure 4.1. Range sizes for the Koitogor Pride in 2008 displaying MCP (100%), KDE (95%) and KDE (50%)

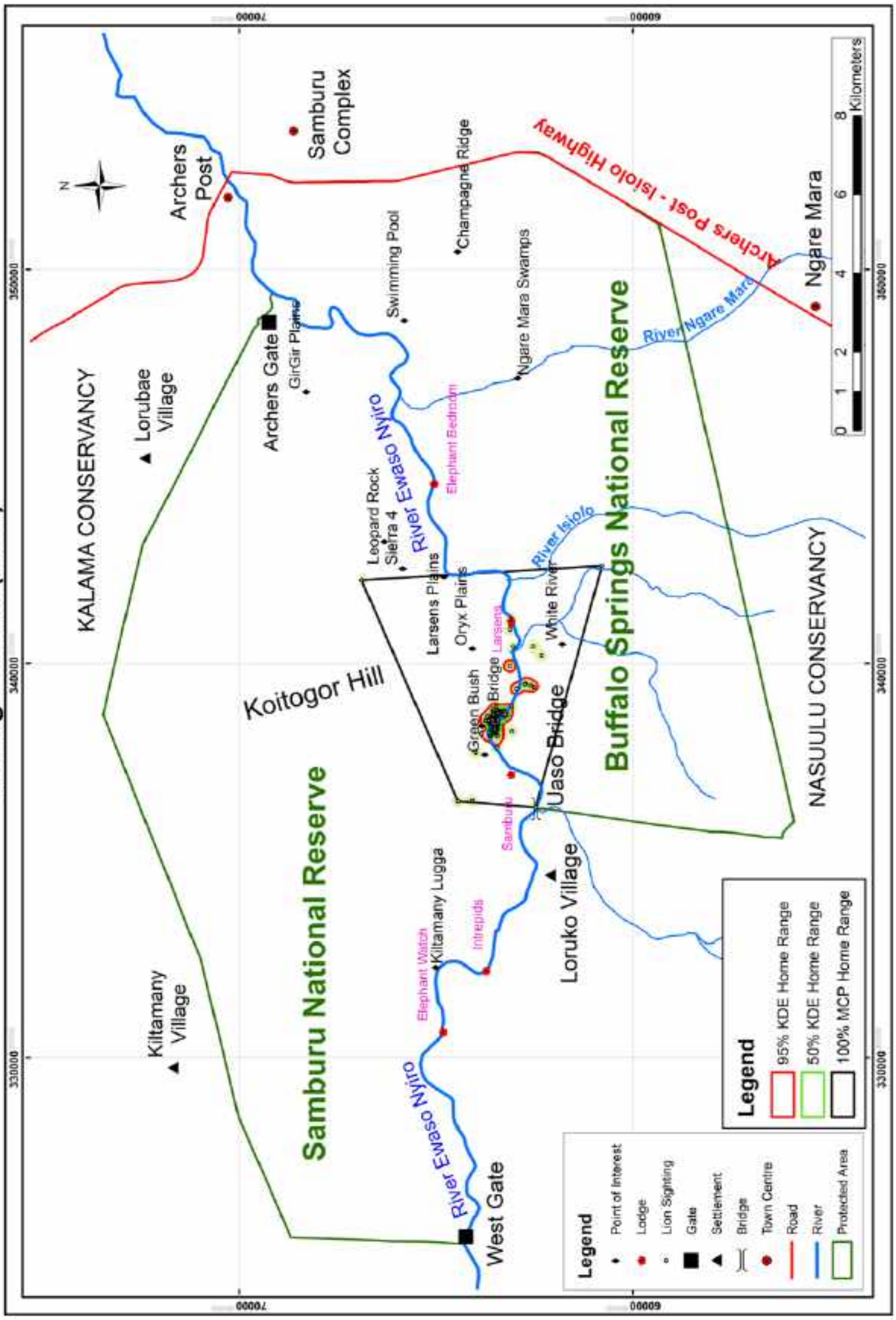


Figure 4.2. Range sizes for the Koitogor Pride in 2009 displaying MCP (100%), KDE (95%) and KDE (50%)

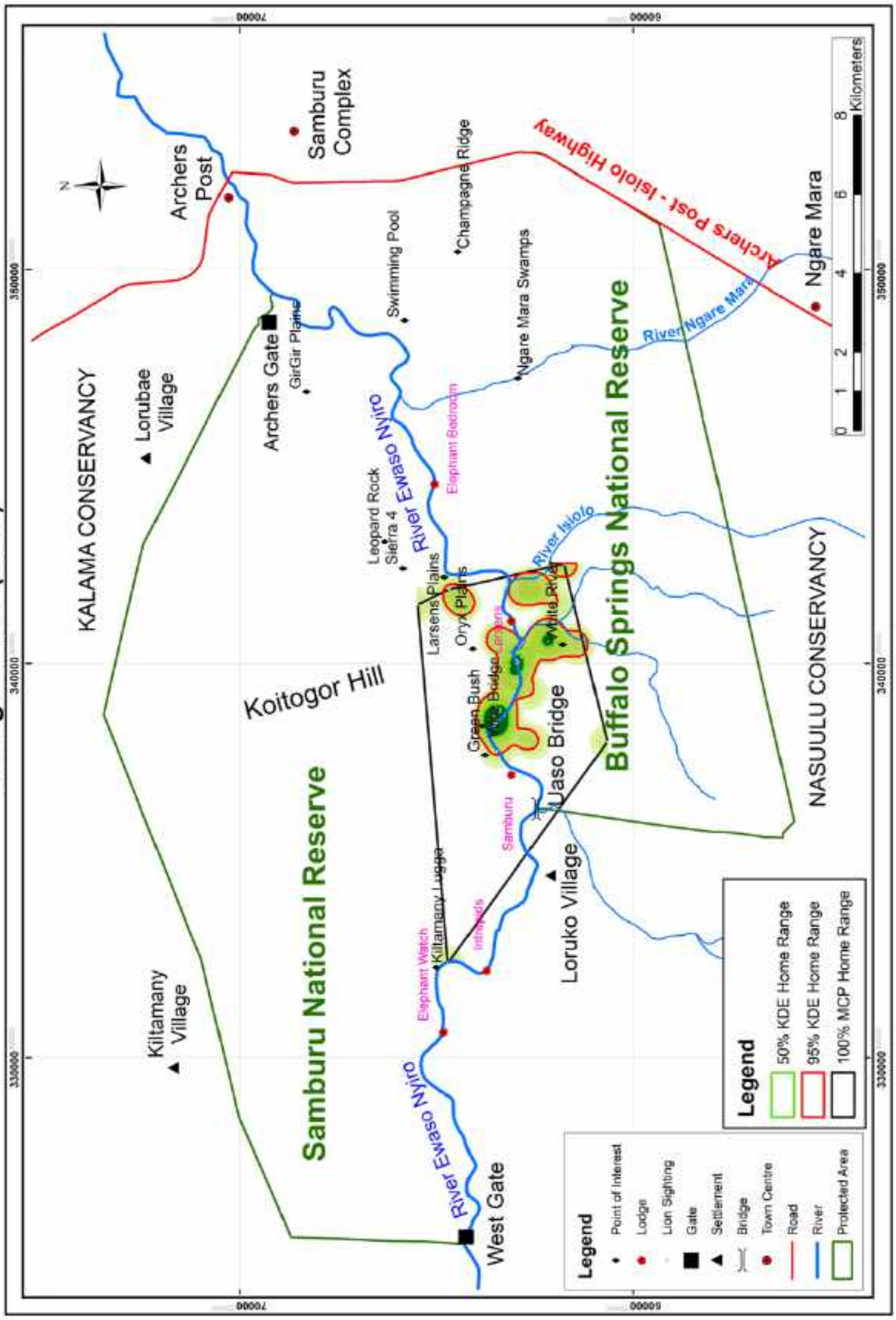


Figure 4.3. Range sizes for the Koitogor Pride in 2010 displaying MCP (100%), KDE (95%) and KDE (50%)

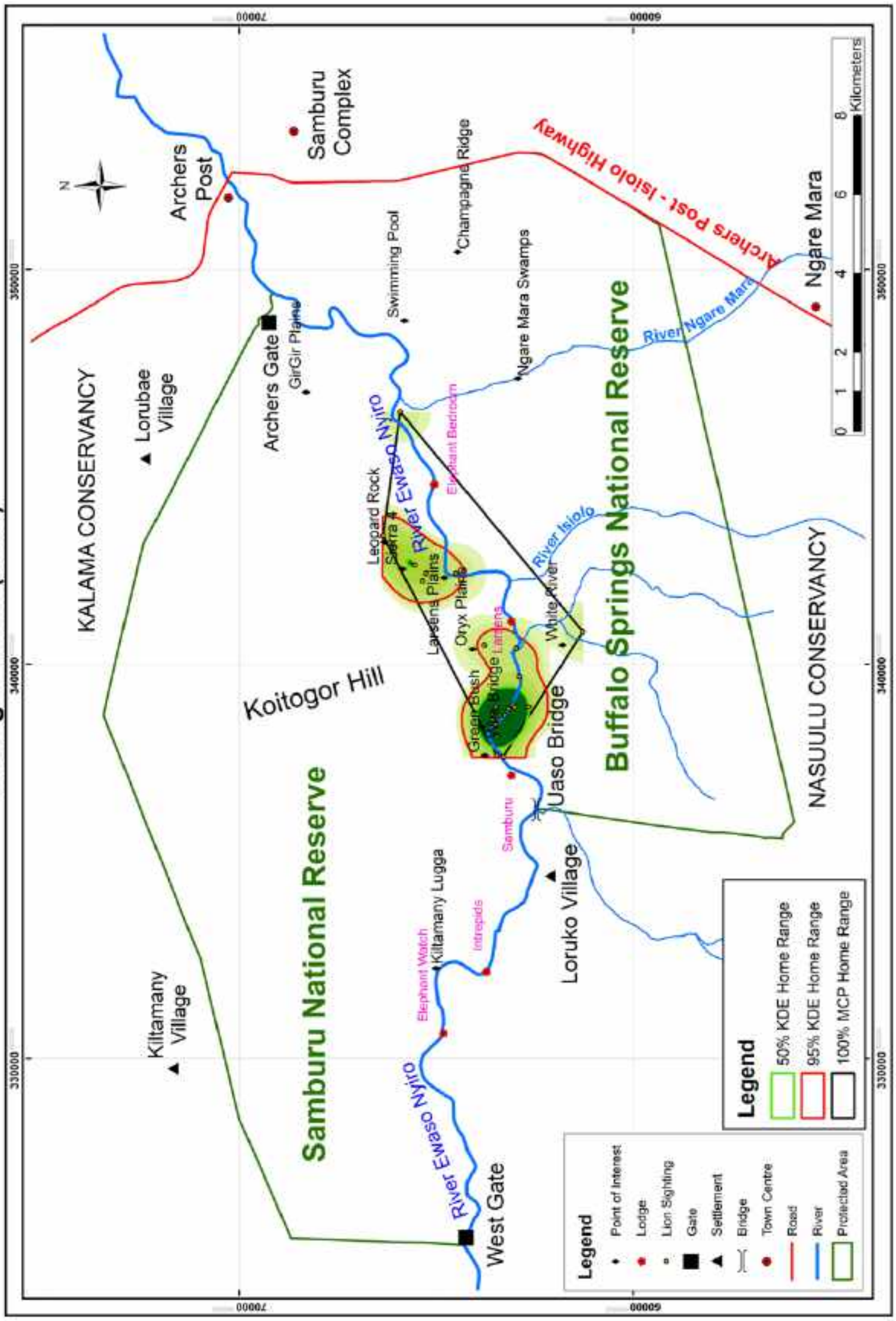
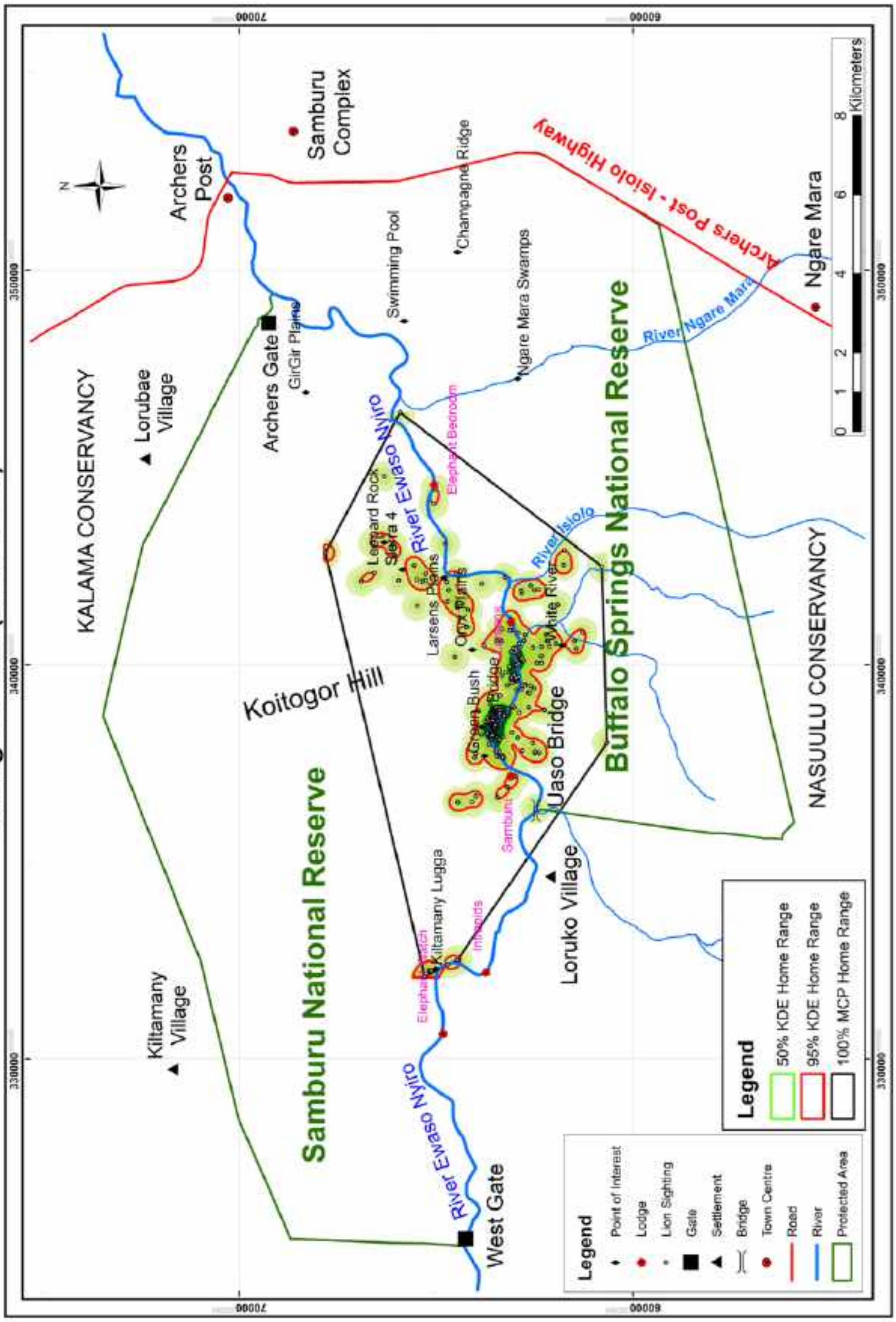


Figure 4.4. Range sizes for the Koitogor Pride in 2003-2011 displaying MCP (100%), KDE (95%) and KDE (50%)



4.3.1.2. Ngare Mara Pride

The home ranges for the Ngare Mara Pride (NMP) are displayed in Figures 4.5, 4.6 and 4.7. There were only two sightings of the NMP in 2008 and 13 sightings in 2009. A 2008 map was not developed and the 2009 map only included the MCP 100% as the KDE maps could not be created due to the limited number of sightings. Seaman *et al*., (1999) recommends that home range studies which include kernel estimates require at least 30 observations of the subject. An overall map combining all sightings between 2006 and 2011 has also been included, as the NMP were not sighted prior to 2006. MCP (100%) shown as the outermost black line, KDE (95%) shown as the red line and KDE (50%) shown as the light green line, are included in each map.

Figure 4.5 shows only the MCP 100%, indicating ranging behaviour around the Ngare Mara River and Swamps. It is acknowledged that although the MCP is an over-representation of NMPs range, it does indicate that in 2009, the NMP were solely in BSNR, and mainly around the Ngare Mara River and Swamps as confirmed by the ground sightings where the pride was seen on 13 occasions.

In 2010, NMP's ranging behaviour was extensive (MCP 100%) as shown in Figure 4.6, extending as far as Champagne Ridge and Swimming Pool. Sightings were mainly in BSNR (n=17) with some sightings in SNR (n=6) near Elephant Bedroom and south of Girgir Plains. There were two core ranges; a large core range along the Ngare Mara River encompassing the Swamps and a smaller core range further south heading towards the boundary of BSNR and Nasuulu Conservancy.

Figure 4.7 shows the overall pride ranging behaviour between 2006 and 2011. One large core range exists along the Ngare Mara Swamps with most sightings in BSNR (n=38) and fewer sightings in SNR (n=12). Between 2010 and 2011, the NMP moved in to SNR, whilst previously, they were predominantly in BSNR along the Ngare Mara River area.

Figure 4.5. Range sizes for the Ngare Mara Pride in 2009 displaying MCP 100% only

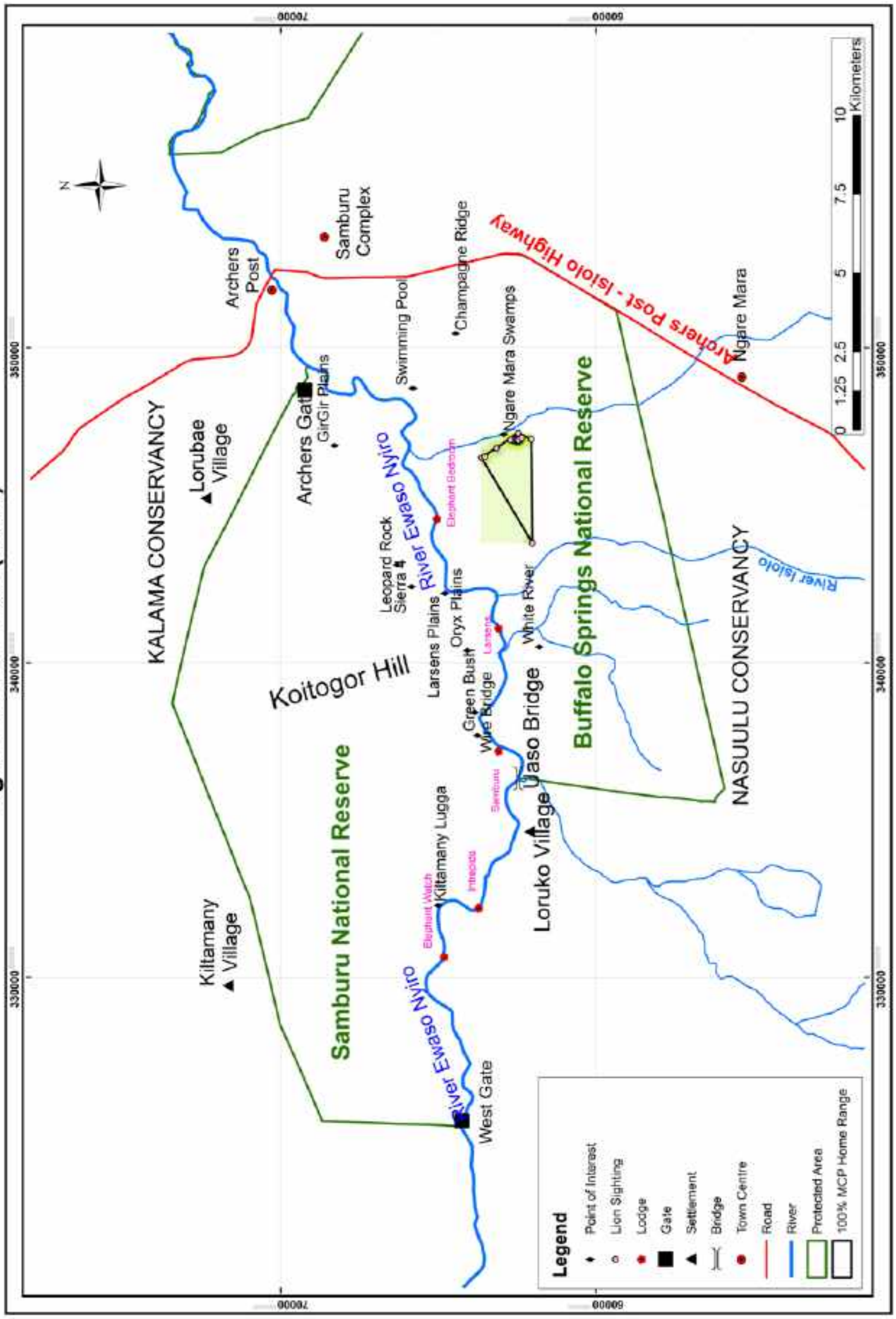


Figure 4.6. Range sizes for the Ngare Mara Pride in 2010 displaying MCP (100%), KDE (95%) and KDE (50%)

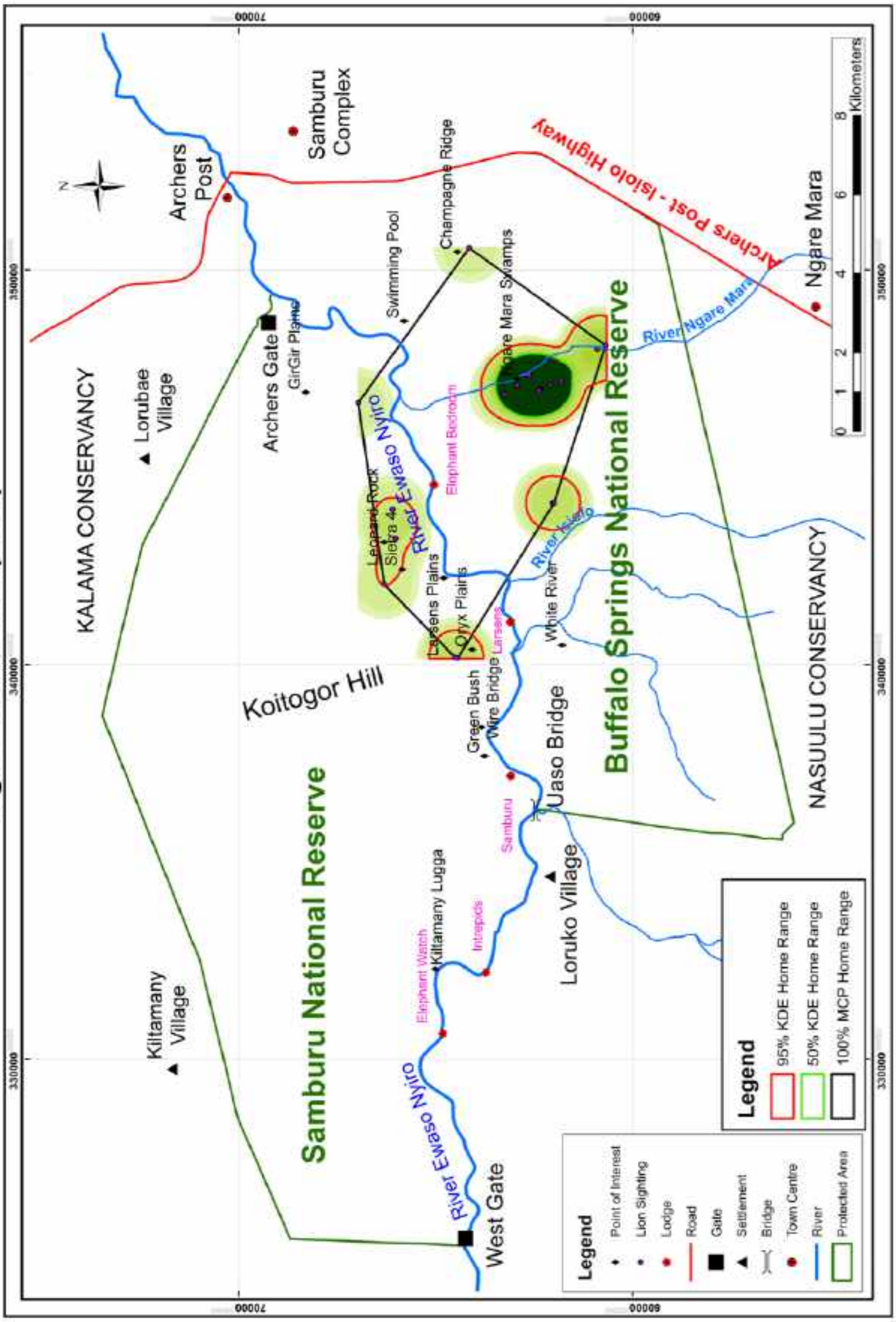
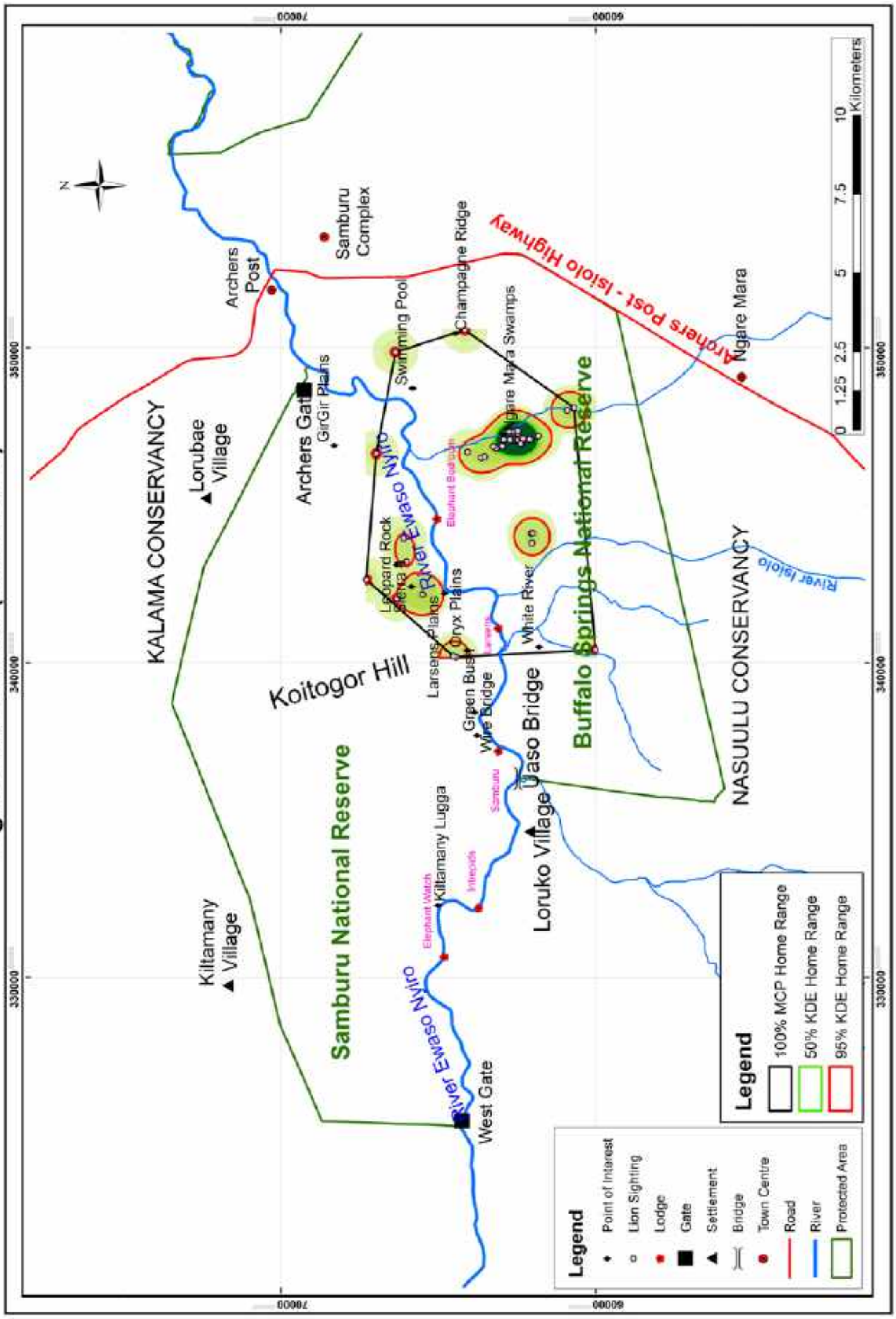


Figure 4.7. Range sizes for the Ngare Mara Pride in 2006-2011 displaying MCP (100%), KDE (95%) and KDE (50%)

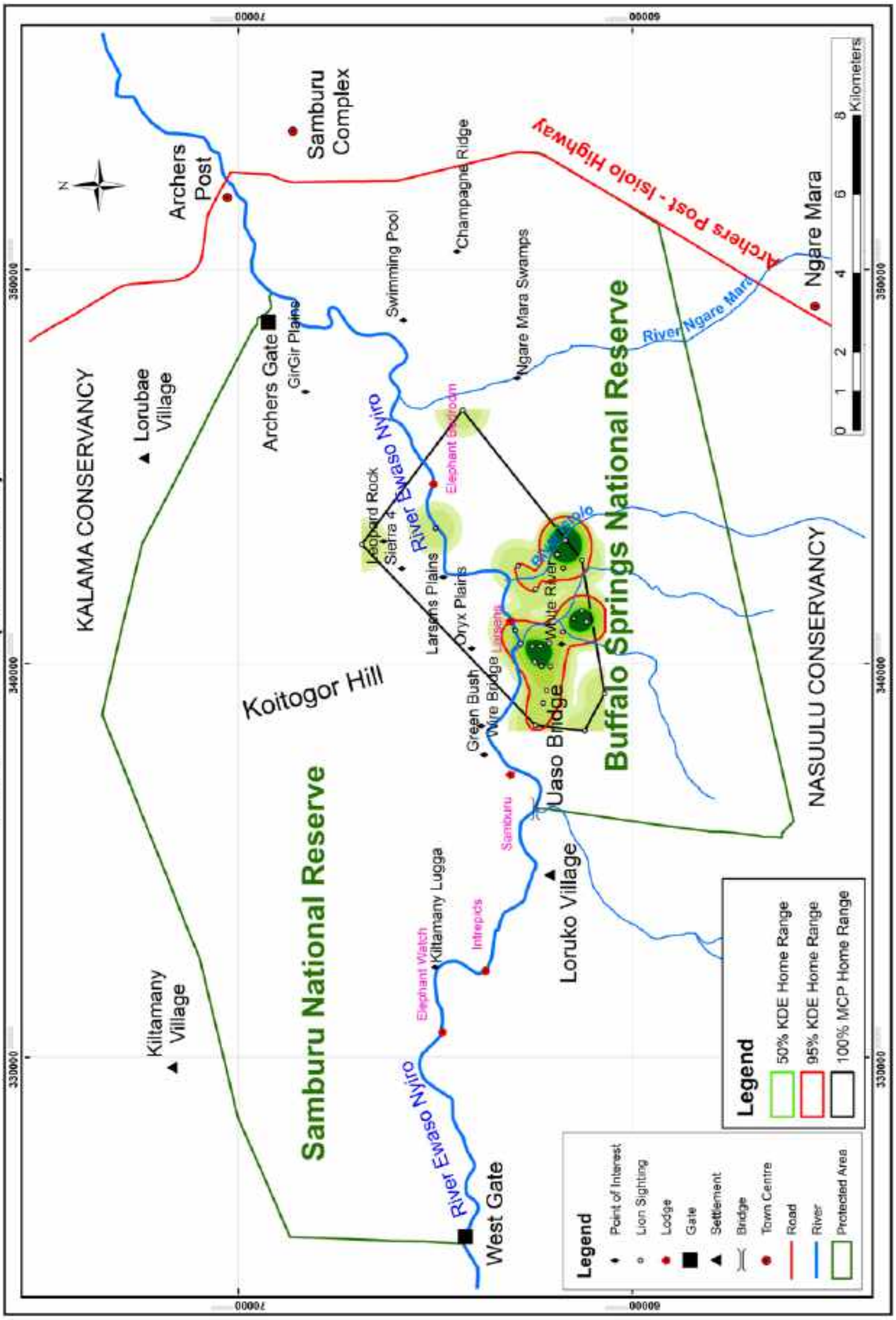


4.3.1.3. Borana Pride

The pride range for the Borana Pride (BP) is displayed in Figure 4.8. It was not possible to produce annual maps between 2008 and 2010 as the number of sightings were less than four, with at least 30 sightings required to create KDEs (Seaman *et al.,* 1999). In order to establish their home range, an overall map combining all sightings of the BP was created and is shown in Figure 4.8.

Figure 4.8 shows most of the sightings of the BP are in BSNR (31 sightings) and along the Isiolo River, where the largest core range exists. Two smaller core ranges exist along White River. The BP was seen only twice in SNR. The pride's home ranges were noted as being greater earlier in the study period, shrinking gradually over the years after the number of lions in the pride reduced to one female and her two cubs (see Chapter 3).

Figure 4.8. Range sizes for the Borana Pride in 2003-2010 displaying MCP (100%), KDE (95%) and KDE (50%)



4.3.2. All prides

All sightings of the different prides within SNR and BSNR were mapped to examine if there were any overlaps in their core ranges (Figure 4.9).

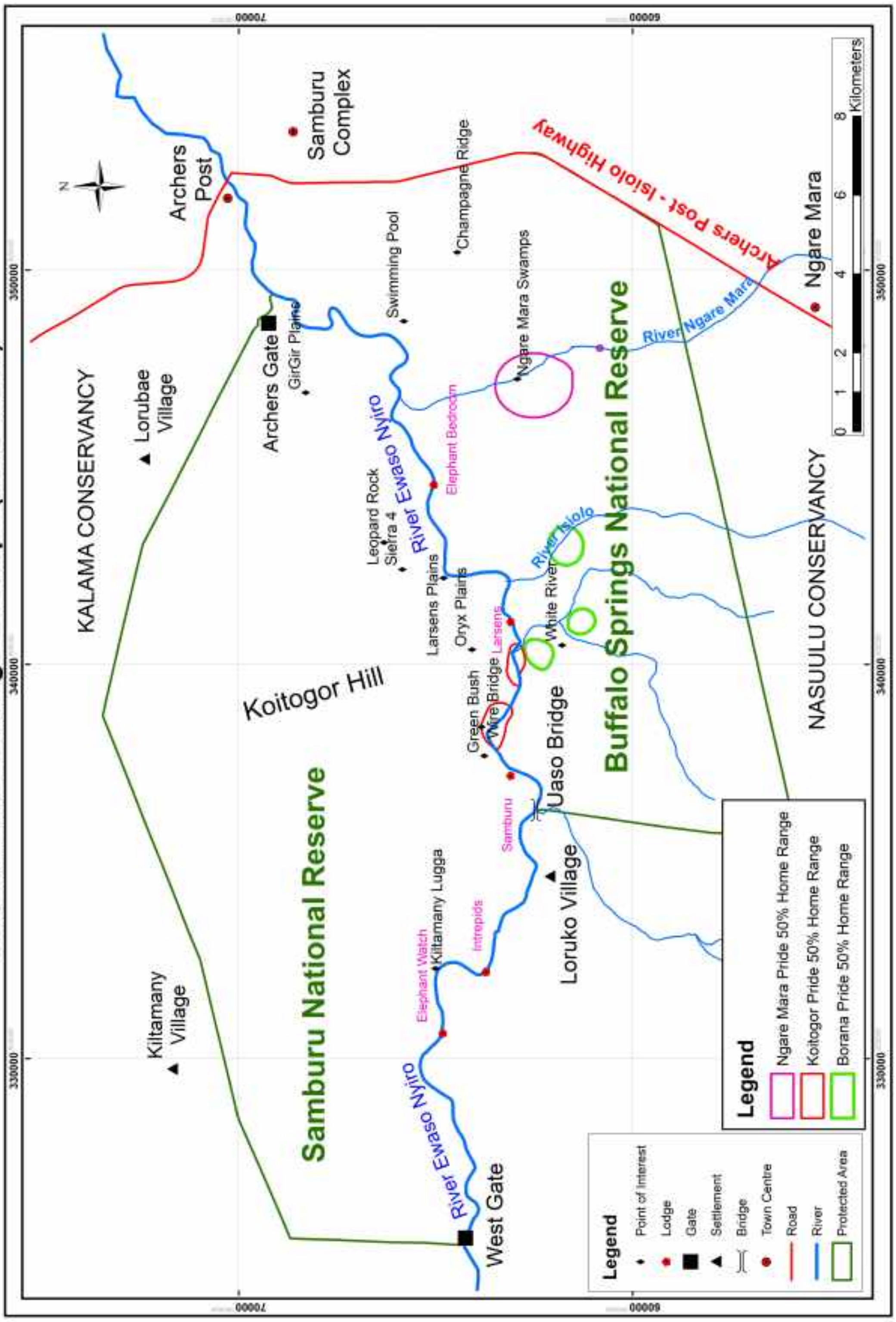
Figure 4.9 on the following page displays KDE 50% of the three prides and shows no overlap, as they each intensively utilise distinct regions of the study area. The KP core ranges are mainly along the River in SNR, at Wire Bridge and Larsens, with the BP mainly ranging in BSNR and along the Isiolo River and White River. The NMP has its core range mainly along the Ngare Mara River and Swamps in BSNR.

Table 4.1 shows the range sizes in km^2 for all the prides using the two methods (MCP and KDE). These were calculated by generating range polygons and areas were computed automatically using ArcGIS 10.0. The number of sightings during the various years has been included. See section 4.3.4. which highlights the variation in sizes. The areas shaded in grey do not have figures because their ranges could not be calculated due to the limited numbers of sightings.

Table 4.1. The range sizes (km^2) for all prides using MCP (100%), KDE (95%) and KDE (50%)

Prides	No: of sightings	MCP (100%)	KDE 95%	KDE 50%
KP 2008	54	23.75	0.86	0.28
KP 2009	60	29.87	5.82	0.76
KP 2010	26	19.37	8.29	1.6
KP 2003-2011	293	62	8.38	0.96
BP 2008	2			
BP 2009	2			
BP 2010	4			
BP 2003-2011	33	25.81	6.35	1.45
NMP 2008	2			
NMP 2009	13	2.89		
NMP 2010	23	38.43	9.84	2.57
NMP 2006-2011	50	59	8.6	1.32

Figure 4.9. The KDE (50%) core ranges of the Koitogor Pride (red), Ngare Mara Pride (pink) and Borana Pride (light green) between 2003 and 2010 in Samburu and Buffalo Springs National Reserves.



4.3.3. Male coalitions

Chapter 3 provides a description of the males and the coalitions that were formed. The ranges of the coalition of males that were present in the Reserves between 2008 and 2010 are mapped using the two methods – MCP and KDE.

Figure 4.10 shows the male ranges in 2008 with one core area encompassing Wire Bridge and along the Ewaso Nyiro River. The males were sighted in both SNR and BSNR as they had tenure over two prides (KP in SNR and NMP in BSNR) with their ranges extending as far as Ngare Mara River in BSNR, and up to Leopard Rock and Sierra 4 in SNR.

Figure 4.11 shows the ranging behaviour for the males in 2009, a drought year in the region. The males were mainly in BSNR, staying very close to the Ewaso Nyiro River. However, their range extended as far as Ngare Mara Swamps to the east with their core range at Wire Bridge along the River. This core range was similar to that of 2008 (although smaller). Their MCP 100% was overall smaller in 2009 compared to 2008.

Figure 4.12 shows the ranging behaviour for the males in 2010, following the drought year. They have two core areas; one at Wire Bridge in SNR and the other along the Ngare Mara River and Swamps in BSNR. The males had control over two prides at this time; the KP and NMP and their core ranges reflected the core areas for the two prides.

Figure 4.10. Range sizes for the males in 2008 displaying MCP (100%), KDE (95%) and KDE (50%)

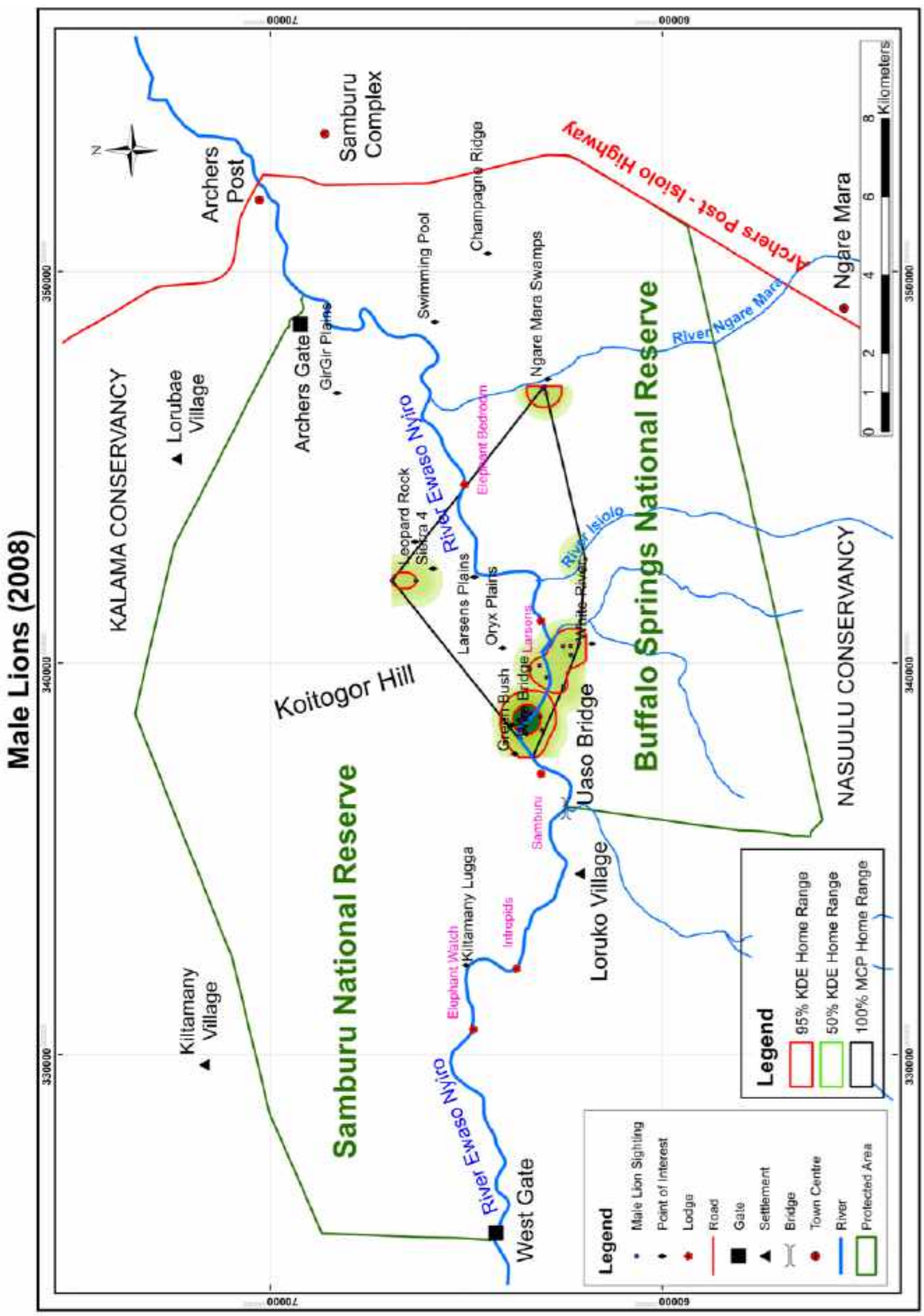


Figure 4.11. Range sizes for the males in 2009 displaying MCP (100%), KDE (95%) and KDE (50%)

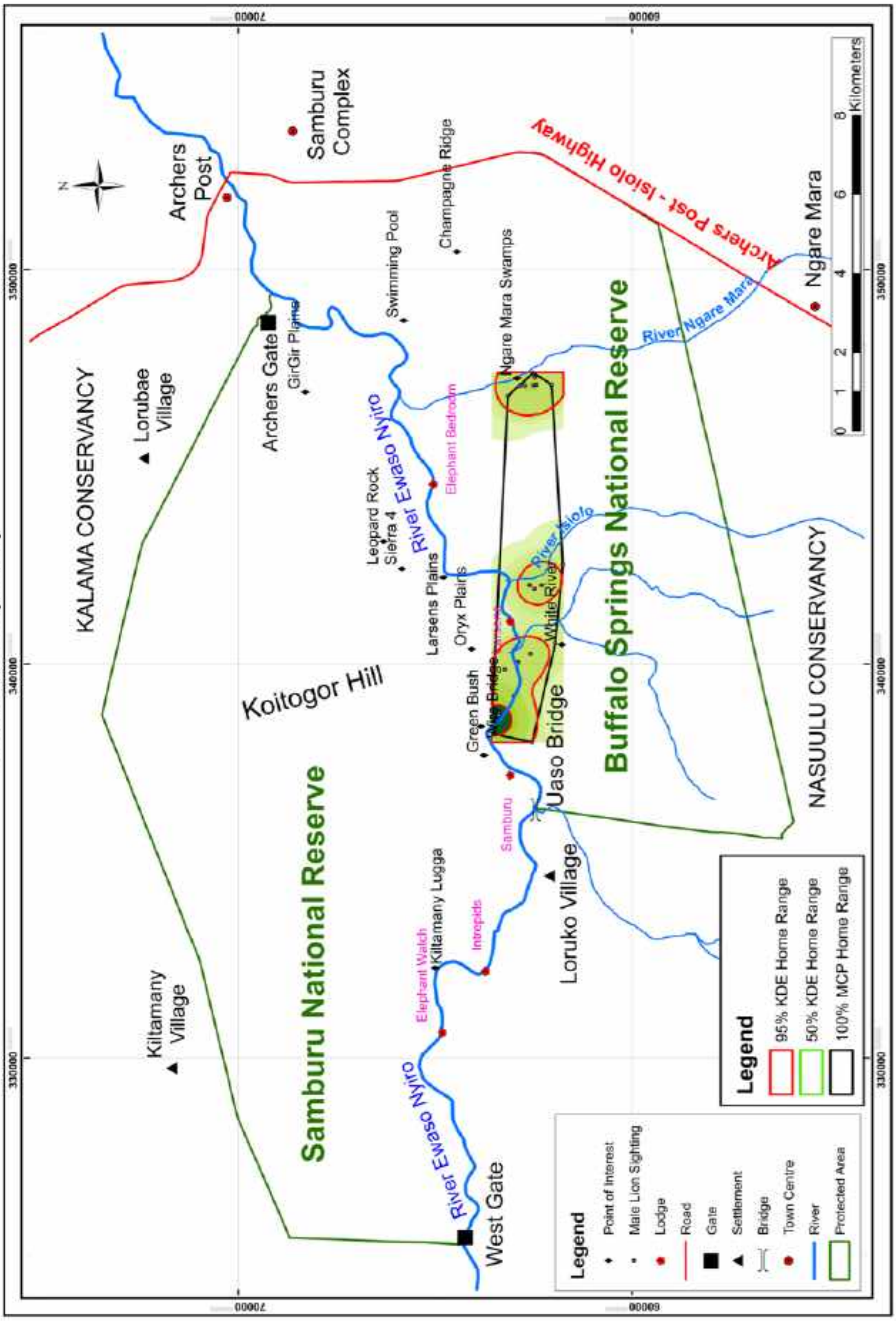
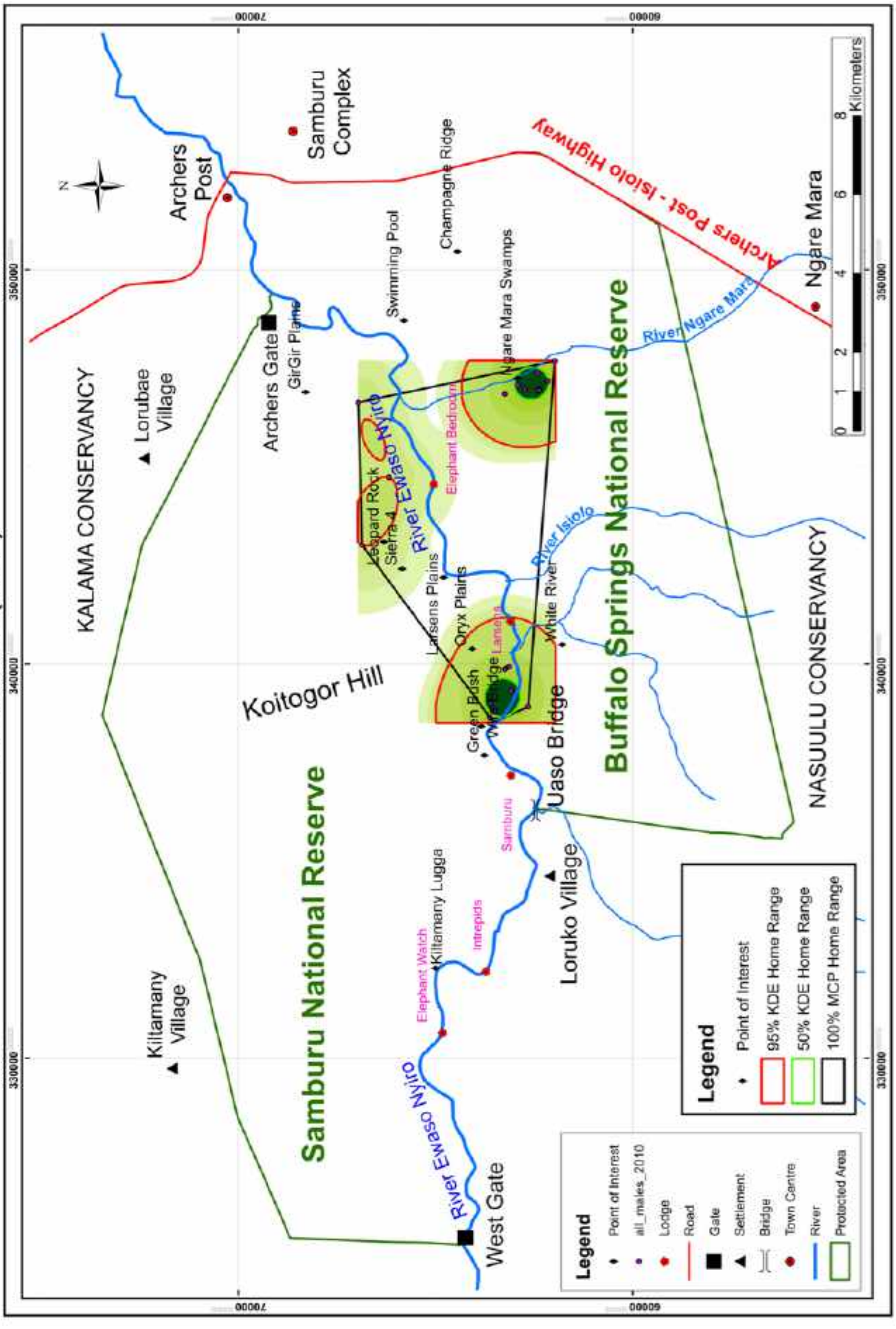


Figure 4.12. Range sizes for the males in 2010 displaying MCP (100%), KDE (95%) and KDE (50%)



The range sizes for the males between 2008 and 2010 are shown in Table 4.2. The range sizes of the male coalition decreased between 2008 and 2009 (despite having more observations of the lions), but increased again in 2010 (despite having a lower number of observations of the males).

Table 4.2. The range sizes (km^2) for the males using MCP (100%), KDE (95%) and KDE (50%)

All Males	No: of sightings	MCP (100%)	KDE 95%	KDE 50%
Males 2008	35	24.37	4.02	0.42
Males 2009	39	12.45	5.67	0.32
Males 2010	22	31.58	13.27	1.27

4.3.4. Description of ranging behaviour

Overall, the lion's core home ranges were concentrated along the Ewaso Nyiro River, especially the KP, while BP was predominantly in BSNR and the NMP mainly along both the Ngare Mara River and Swamps in BSNR.

In comparison to MCP 100% and KDE 95%, KDE 50% provided a more accurate description of this population's ranging behaviour, as it highlights areas most intensively used (Powell, 2000). Between 2008 and 2009, the core range of the KP increased by 0.48 km^2. Between 2009 and 2010, the core range of the KP increased yet again by 0.84 km^2. The largest core home range was in 2010 (1.6 km^2), however this was based on the fewest number of sightings (n=26).

It is possible to compare the sizes of the three prides ranges over nine years, however because the NMP were not seen prior to 2006, it is restricted to a comparison between 2006 and 2011. Despite the number of sightings of each pride being vastly different (see Table 4.1), the largest range belonged to the KP with 62 km^2 (MCP 100%), followed by the NMP with 59 km^2 and the BP's range stood at 25.81 km^2. With respect to the KDE 95% ranges, both the KP and NMP's ranges stood at 8.38 km^2 and 8.6 km^2 respectively, with the BP range lower at 6.35 km^2. With respect to the core ranges, the KP core range was the smallest at 0.96 km^2, with BP's core range at 1.45km^2 and NMP's core range at 1.32 km^2.

The male coalition is compared to the KP between 2008 and 2010, in order to examine whether male home range sizes were larger than females. In 2008, the male ranges were larger compared to the KP (for MCP 100%, KDE 95% and KDE 50%). However, in 2009, their ranges were all smaller compared to the KP. In 2010, the male ranges were larger, except their core range (1.27 km^2) which was smaller than the KP core range in 2010 (1.6 km^2).

4.3.5. Some observations on lion movement

M23 (see Chapter 3 and Appendix 7) was first seen on the 25th of December 2004 in BSNR together with females from BP. He was later seen on one other occasion alone on the 19th of February 2006 again in BSNR. Following this, he was not seen again until the 29th of March 2011, when he was sighted in Shaba National Reserve (ShNR – see Figure 2.1). This was the first confirmed instance where lions moved from BSNR to ShNR. According to reports from rangers in BSNR, it is suspected that this lion moved across the Isiolo-Archers Highway near Champagne Ridge of BSNR (see Appendix 1) to access ShNR.

During the course of this study, it was observed that between February and August 2006, two male lions (M24 and M25 – see Appendix 7) moved from Lewa Wildlife Conservancy to SNR and BSNR. Lewa is mainly fenced and has a small gap designed for elephant access (Douglas-Hamilton *et al.*, 2005). Through information received from the local community, it is suspected that the male lions avoided the populated Isiolo region and moved through the gap to Ngare Ndare, before reaching the Ewaso Nyiro River. They followed the River in an easterly direction towards the Reserves. M22 (see Appendix 7) also moved frequently between Lewa and, SNR and BSNR, and it is believed that he followed the same path.

Three male lions (M26, M27 and M28 - see Appendix 7) moved from Westgate Community Conservancy (WGCC) to SNR. The warriors from the region were able to piece their movement together as they left WGCC and entered SNR from the north. They were initially sighted on the 24th of July and 11th of August 2008 in WGCC and their first sighting in SNR was on the 24th of August 2008. Between the 11th and 24th of August, the three lions travelled north of WGCC, through the Kiltamany village and into the Kalama Conservancy (see Appendix 1). Here, they spent a few days and were seen by local tour guides, after which they moved south into the Oryx Plains of SNR.

Each of these scenarios illustrate lions travelling long distances through densely populated areas. Additionally, this was the first time in this area that there were confirmed movements of known lions from the human-occupied landscape to the protected areas, a concept which is central to this thesis (see Chapter 5). Lastly, the movement of lions described here highlights the importance of connectivity within the entire landscape (see Chapter 6) as there is clearly lion movement within the human-occupied landscape.

4.3.6. Key results

The key results and outcomes of mapping the prides and males home ranges are summarised below:

Prides

i. The core range for the KP increased between 2008, 2009 and 2010. The largest core range was in 2010, following the drought year. Between 2003 and 2011, the largest MCP 100% range belonged to the KP (62 km^2), the largest KDE 95% range belonged to the NMP (8.6 km^2) and the largest core range belonged to the BP (1.45 km^2).
ii. There were no overlaps in the core ranges between the prides; each pride had their own distinct core range in different regions of SNR and BSNR.
iii. Over time, the home range of the BP reduced after a number of lions disappeared from the area, leaving only one female and her cubs.
iv. There is strong evidence that the Ewaso Nyiro River forms a boundary between the prides.

Males

i. During the drought year of 2009, males were mainly along the Ewaso Nyiro River, encompassing areas in SNR and BSNR. Following the drought, males had two core ranges; one in SNR at Wire Bridge and another in BSNR at Ngare Mara River, which is further away from the Ewaso Nyiro River.

ii. The size of the core ranges for the males decreased during the drought year of 2009 and increased again in the following year after the rains.

iii. Male ranges were larger than that of the KP in 2008 and 2010 (except the core range in 2010), however in 2009 displayed smaller ranges compared to the KP ranges.

4.4. Discussion

4.4.1. Minimum convex polygons and Kernel density estimators

One of the main strengths of using MCPs is the simplicity of the method to make area statements and its ease in computing coordinate data. However, this method is biased (Burgman and Fox, 2003) and often provides an overestimate of the range and the range boundary encompasses locations that are beyond the main area of activity (Funston *et al.,* 2003). Douglas-Hamilton *et al*., (2005) also state that this method is outdated and often misleading, however it has been found to be a better estimate of the total area available for lions in this case. This technique is highly sensitive to sample size and outlying points (Börger *et al*., 2006) and is also affected by the spatial and temporal distribution of the sampling effort, which is often not always under the control of the scientist. Sampling is most often concentrated in accessible areas where there are more roads (Burgman and Fox, 2003). In this study, efforts were concentrated along the roads that are located centrally in the protected areas and less so towards the north and south of the Reserves, where roads are lacking. Where and whether the lions are found depends on where the observer looks (Bertram, 1976). If the lion had not been found after looking in its normal range, there was uncertainty as to whether it was there, but unseen, or whether it was outside its normal range. ArcGIS 10.0 automatically computes MCPs of 100% of all the points including the outliers. Other studies suggest using a Concave Clusters approach (Hemson, 2003) or removing 5% of the outlying points to create MCPs of 95% (Tuqa *et al.,* 2014). Despite the limitations in these two methods, the home ranges for the three prides in the protected areas were calculated using MCP and KDE and were found to be very useful indicators and methods of home range analysis for the type of data that was available.

4.4.2. Home ranges

Overall, it was found that the core ranges for all the prides were along the Ewaso Nyiro River in SNR (for the KP) and Ngare Mara River and Swamps (for NMP) and along the Isiolo River (for the BP) in BSNR. The core ranges were very small, ranging between 0.28 km^2 to 2.57 km^2 and displayed regions of the prides' main activity. These were the areas where the females gave birth to their cubs in the respective prides. Rudnai (1973b) found in Nairobi National Park that lionesses gave birth to their litters in the same zones where they themselves were born, showing a strong attachment to a site, and may indicate that the area offers favourable conditions for raising cubs. These could be considered as core areas for reproduction. In this study it is also recommended that such regions be considered as an important variable when selecting suitable habitat that can be set aside for lion conservation (see Chapter 5).

Despite the ranges encompassing areas both in SNR and BSNR, the majority of the KP sightings and their range were in SNR between 2003 and 2011. Despite some movement into SNR by the NMP and BP, they were mainly resident in BSNR, with the Ewaso Nyiro River appearing as a boundary between the prides. The BP stayed on the west of the Isiolo River, whereas the NMP stayed on the east of the Isiolo River. Funston (1999) found that rivers are often natural borders between lion home ranges.

As the number of sightings for the KP was the greatest between 2003 and 2011, this home range has been compared in size to the ranges of lions in parks and reserves across Africa as shown in Table 4.3, which also indicates the home range estimator used. These comparisons are however made cautiously noting that the choice of estimator used to determine the range sizes differs in each case and will therefore influence the results (List and Macdonald, 2003).

Table 4.3. Range size in km^2 for the Koitogor Pride in Samburu and Buffalo Springs National Reserves, compared to other lion ranges in various parks and reserves across Africa.

Location	**Range size (km^2)**	**Estimator**	**Source**
Serengeti National Park	200	MCP	Schaller, 1972
Etosha National Park	1100	MCP	Stander, 1991
Waza National Park	824	MCP	Bauer *et al.*, 2003
Hwange National Park	388	KDE	Loveridge *et al.,* 2009
Kgalagadi Transfrontier Park	1462	MCP	Funston, 2011

Amboseli National Park	24	KDE 95	Tuqa *et al.,* 2014
Amboseli Group Ranches	954	MCP	Dolrenry, 2013
Amboseli Group Ranches	375	KDE 90	Dolrenry, 2013
Samburu and Buffalo	*8.38*	*KDE 95*	*This study*
Springs National Reserves	*62*	*MCP 100*	*This study*

The largest range size amongst the three prides in the study area was 62 km^2, belonging to the KP. Table 4.3 displays lion home ranges larger than in this study. The comparative protected areas listed are however larger in size than SNR and BSNR and the studies utilised radio-tracking data to acquire more accurate assessments of ranging behaviour. The KDE 95% figure for the KP is smaller (8.38 km^2) in comparison to those of lion prides in Amboseli National Park (24 km^2 - Tuqa *et al.,* 2014). Comparing the core range for females between Amboseli National Park and this study, shows that the core range in SNR and BSNR for the KP is 0.76 km^2 during the drought year while in Amboseli, it was 4.85 km^2 in this same year (Tuqa *et al.,* 2014).

No actual territories were established during the study and non-pride interactions were never observed. Figure 4.9 shows that there was no overlap in core ranges between the three prides; each pride had their own distinct core range. Looking at their MCP 100% and KDE 95% ranges, there is some overlap in regions especially when the KP occasionally moved into BSNR and the NMP and BP occasionally moved into SNR. The zone between adjacent prides tended to be used less intensively and effectively as a buffer zone (Bertram, 1978). As Loveridge *et al*., (2009) found in Hwange National Park in Zimbabwe, prides did avoid their neighbours and their range sizes were affected by the proximity to the next pride.

The male ranges displayed a reduced range size during the drought year (2009) compared to 2008 and 2010. The males only had one core range during the drought, compared to two after the drought. Additionally, the KP's core range in 2009 was only 0.76 km^2 and showed an increase in size after the drought to 1.6 km^2. In group living species, the spatial distribution of key resources may influence home range size (Macdonald, 1983; Hayward *et al*., 2009; Kissui *et al*., 2010) and it is believed that this is what led to the variation in the males and the KP ranges. Prey was concentrated along the Rivers in 2009, but dispersed in 2010. During the dry season in the Savuti, lions expand their home ranges to search for prey that have moved away (Hayward *et al*., 2009). This conforms to what Owens and Owens (1984) found in the Kalahari. However, in other areas, where prey is sedentary during dry seasons, lion ranges decrease, especially when prey are concentrated along water points (Stander, 1991; Hayward *et al.,* 2009). Dolrenry (2013) concurs that inside Amboseli National Park, lion ranges were small (20-97 km^2) and were centred on permanent water sources and consequently areas of high prey density. This is similar to observations made in 2009, where home ranges were smaller and the locations of the lions were centred along the Ewaso Nyiro River, Ngare Mara River and Isiolo River. When the water availability reduced, the prey concentrated where water was available and in SNR and BSNR, this was confined to the Isiolo River and a few waterholes that tourist lodges had dug outside their establishments. These are known as patches according to Macdonald (1983) who confirms that resource patches may be aggregations of ungulates at waterholes, especially during the late dry season (Valeix *et al*., 2010). This reinforces the crucial role that water sources play in lion spatial ecology (Mosser *et al.,* 2009; Valeix *et al.,* 2010; Valeix *et al.,* 2011). During this time, lions found it relatively easy to find prey. Animals, including Grevy's zebras and warthogs, increased in number along the River; both moving to the River in search of water. Rudnai (1973b) also found that during the severe drought in Nairobi National Park between 1960 and 1961, the prey biomass significantly increased as animals from the surrounding areas moved into the park to access the permanent water that was available. There were also several carcasses of animals that had succumbed to the drought. During this drought period, livestock had encroached into the protected areas and their mortality was also high.

Tuqa *et al.,* (2014) found that after the drought in Amboseli National Park in 2009, the lions expanded their home ranges and sought new territories. The drought in Amboseli caused the death of key lion prey which is why after the drought they had to search further for food. During the drought, their ranges shrank initially but then expanded as their prey disappeared. Dolrenry (2013) concurred that lions moved out of Amboseli National Park in search of prey during the wet season as did Rudnai (1973b) who found that during the wet season in Nairobi National Park, prey dispersed and lions moved further in search of prey which was harder to come by.

Such areas that are adjacent to protected areas have been found to play a role as an additional hunting area for resident lions, especially during the wet seasons when herbivores disperse. This was reflected in 2010, when the KP's core range increased as they followed prey that had dispersed away from the river.

Male ranges were greater than female ranges in 2008 and 2010, and this was also found in Amboseli National Park (Tuqa *et al*., 2009). Increases in range size could also be due to increasing social group sizes (Loveridge *et al*., 2009). This was found in this study where the largest pride, KP (see Chapter 3) did indeed have the largest home range size. Larger prides will require more prey to fulfill their metabolic requirements and therefore they need to search over larger areas, especially when prey is scarce (Macdonald, 1983). The size of the BP pride reduced over time (see Chapter 3) and their home range size also reduced when the group size decreased.

Due to the large home ranges of lions, looking beyond the boundaries of protected areas is, therefore, essential in understanding their chances of survival in human-occupied landscapes.

Chapter 5

Suitability modelling to identify potential lion habitat in Westgate Community Conservancy, Samburu

"Promoting tolerance and coexistence with large carnivores is a crucial societal challenge that will ultimately determine the fate of Earth's largest carnivores and all that depends on them, including humans."

Ripple et al., 2014

Abstract

Lion populations within Kenya are exposed to a rapidly changing human-occupied landscape. Lions are subjected to habitat loss, prey depletion and human-lion conflict. At the heart of this conflict, is the need for lions to have a sufficient prey base and safe refuges within human-occupied lands. This chapter seeks to explore the availability of suitable habitat for lions in the Westgate Community Conservancy (WGCC) in northern Kenya. In order to achieve this, constructive site suitability models using Geographic Information System (GIS) modelling techniques and multi-criteria decision analysis was applied to identify suitable lion habitat. Two models were employed – day and night, as lion preferences vary temporally, especially within human-occupied landscapes.

The results indicate that this community landscape has only 20.6% of highly suitable habitat for lions during the day, but this increases to 28.9% during the night. The Core Conservation Area (CA) emerged as highly suitable during the day and, especially at night, a contiguous region of highly suitable habitat is available between the CA and Samburu National Reserve. Despite there being highly suitable habitat available for lions, conflict still occurred within these areas, predominantly during the day. Conflict was also observed within the CA (15% of all lion conflict in WGCC), highlighting the need to manage livestock encroachment in such vital habitat.

The results from the maps were validated using known lion sightings and tracks, with most lion sightings occurring within highly suitable habitat. However, when lions move through areas of lower suitability habitat there is the potential for increased human-lion conflict, as shown in the region between Lempaute and Loijuk. This area is highlighted as one where conflict mitigation measures should be put in place in order to reduce livestock depredation, thereby reducing human-lion conflict and increasing lion survival.

This study provides the first maps of suitable lion habitat outside protected areas in the Samburu-Isiolo ecosystem, using WGCC as a case study. It demonstrates how modelling can be applied to an area to understand lion habitat requirements. In

addition to WGCC, this modelling approach can be applied to other Community Conservancies neighbouring the protected areas, to advise on potential habitats that may be set aside as safe refuges for lions, therefore, allowing for the provision of contiguous high suitability habitat and enabling lions' safe dispersal from the protected areas.

5.1. Introduction

In Kenya, lion populations have been exposed to a rapidly changing human landscape. Lions are subjected to habitat loss, prey depletion and human-lion conflict, often associated with increasing human populations (Woodroffe and Frank, 2005). Rapid population growth has discouraged pastoralism in some areas and encouraged permanent human settlement (Homewood *et al*., 2009). These land use changes have fragmented important lion habitat and removed dense cover which is important for these stalk-and-ambush carnivores (Hopcraft *et al*., 2005). In addition, livestock densities and the subsequent high intensity of grazing have displaced numerous herbivore species (Groom and Harris, 2010). With depleting sources of lions' natural prey (Ripple *et al.,* 2015), human-lion conflict increases (Mogensen *et al.,* 2011; Ogutu *et al*., 2011; IUCN, 2015) and with high levels of conflict between humans and lions, there tends to be increased retaliatory killing (Woodroffe and Ginsberg, 1998; Ogada *et al*., 2003; Hazzah *et al*., 2009). Clearly, as described in Chapter 1, the anthropogenic landscape is a significant cause of lion population loss.

Human-occupied lands outside protected areas are important for lion populations, with unprotected arid regions in Kenya supporting an estimated 65% of the country's lion population (Chardonnet, 2002). Lions that live outside, or on the edge of, protected areas are threatened by anthropogenic factors (Woodroffe and Ginsberg, 1998; Loveridge *et al.,* 2010a) as they have a greater chance of encountering people, livestock and roads (Loveridge *et al*., 2010a). Such areas are hotspots for conflict.

Wittemyer *et al.,* (2008) found that protected areas did attract settlements resulting in accelerated human population growth at the edges. Small protected areas that occur in regions with high human densities surrounding them can be subjected to human-caused mortality as they are often sited in more unfavourable locations (Harcourt *et al*., 2001). Harcourt *et al.,* (2001) reported a risk of extinction for the Samburu lion population after accounting for the size of the protected areas and the density of humans. Looking beyond Samburu's protected areas is, therefore, important in exploring the possibility for lion presence, safe dispersal and persistence outside the protected areas.

It is important to explore the presence of suitable habitat for lions within human-occupied lands, which have implications for their conservation, and to understand how people and lions can live together. In addition, it is imperative to understand whether lions in community lands adjust their movements to avoid people in response to human caused mortality risks and how they adapt to the constant changes within these landscapes (Valeix *et al.,* 2012; Schuette *et al.,* 2013; Oriol-Cotterill *et al.,* 2015a; Oriol-Cotterill *et al.,* 2015b). Within protected areas, prey abundance may play the largest role in lion ecology, but in human-occupied lands, the potential of conflict with people is a major driver of lion ecology (Oriol-Cotterill *et al*., 2015a).

Carnivores within human-occupied landscapes adjust the timings of when they are active, showing a greater preference for darkness (Frank and Woodroffe, 2001; Schuette *et al.,* 2013; Oriol-Cotterill *et al.,* 2015b). Oriol-Cotterill *et al.,* (2015a) found that collared lions in Laikipia used areas closer to livestock *bomas* when people were least active (between 11:00pm and 4:00am), moving faster and in straighter directions when using these areas. It was also noted that lions tended to be closer to livestock settlements when it rained heavily and when there was less moonlight, despite people still being active in the settlements. Oriol-Cotterill *et al.,* (2015b) further observed that lions hunt when people are not active, as hunting in the daytime in human-occupied areas increases chances of detection. Valeix *et al.,* (2012) noted that lions in their Botswana study area, avoided use of areas near cattle settlements between 6:00am and 8:00pm.

This study examined Westgate Community Conservancy (WGCC) to establish whether the community area provided sufficient suitable lion habitat during the day and night. In order to achieve this, a Habitat Suitability Model (HSM) was created using a Geographic Information System (GIS). Remote sensing and GIS have the potential to provide useful information for wildlife through the use of predictive models (Obade, 2008). This study's main objective was to use GIS analysis methods, including multi-criteria decision analysis (MCDA), to integrate variables influencing lion patterns into models to determine whether suitable habitat exists in WGCC. This HSM intends to identify suitable habitat for lions, making it a powerful tool for conflict mitigation and land use planning. It further intends to explore the possibility of applying this type of model elsewhere.

5.2. Methods

5.2.1. Introduction

Habitat Suitability Models (HSM) are useful tools for learning more about the appropriateness of a given area; they allow investigation of undocumented areas to determine regions where species could be present and evaluate the variables which may influence habitat selection (Austin, 2007). HSM provides a prediction of potential habitat by evaluating areas of known species' presence against a series of selected variables (Hirzel and Le Lay, 2008). Suitability models are created using a GIS that computes selected criteria. Site selection analyses make use of GIS-based MCDA (Greene *et al*., 2011). MCDA is a decision support technique that uses geographical data and the decision maker's preferences to obtain useful information for decision-making (Estoque, 2011; Greene *et al*., 2011; Amoke, 2012). It provides a collection of procedures and algorithms for designing and evaluating alternative decisions (Arafat *et al.,* 2010; Estoque, 2011), and is also viewed as a data conversion process that adds extra value to the original data (Drobne and Anka, 2009).

5.2.2. Variables

The combined use of GIS and MCDA provides a powerful tool for suitability assessments and the development of suitability models, with GIS computing the selected criteria and the MCDA grouping them in to a suitability index capability (Florent *et al.,* 2001; Amoke, 2012). To run this model, baseline data gathered from various datasets were evaluated and analysed to identify the relevant variables (Table 5.1) which were then extracted using spatial analyst tools in ArcGis 10.0. The Spatial Analyst Toolbox contains tools and functions that are able to extract desired information from multiple vector layers to provide a comprehensive modelling environment for spatial analysis. The variables employed in this study's HSM have been selected taking into account those factors that influence lion habitat selection and movement (Elliott *et al*., 2014). Anthropogenic factors evident in the area including settlements and roads were also included in the model. Oriol-Cotterill *et al.,* (2015b) noted that such factors promote a "Landscape of Coexistence". Overall, the variables take in to account what lions need in order to survive within a human-occupied landscape (river, protected area, herbivores, cover) and what they need to avoid which poses a significant threat to them (settlements, roads, livestock). The variables employed in this study's HSM are listed in Table 5.1.

Table 5.1. Variables used in the Habitat Suitability Models - both daytime and nighttime

Variable	Description	Source
Distance to river	Distance to the Ewaso Nyiro River.	Northern Rangelands Trust (2010)
Distance to roads	Distance to the major road network in WGCC.	Ewaso Lions Project (Field data, 2010)
Distance to settlements	Distance to human settlements and villages.	Ewaso Lions Project (Field data, 2010)
Distance to protected areas	Distance to Samburu National Reserve and the Conservation Area in WGCC.	Ewaso Lions Project and Northern Rangelands Trust (2010)
Vegetation cover	Includes habitat in the ecosystem. Categories: Forest, herbaceous, shrubland, sparse vegetation, woodland (< 70% tree cover) and woodland (> 70% tree cover).	Northern Rangelands Trust (2010)
Herbivores	This data includes presence data.	Ewaso Lions Project (Field data, 2010)
Livestock	This data includes presence data.	Ewaso Lions Project (Field data, 2010)

For this HSM, human density was excluded due to the linear distribution of the settlements and therefore the settlements zone of influence was looked at instead, irrespective of the number of people per settlement. Livestock was also excluded due to the poor quality of the data and this is explained in section 5.2.4. Dry river-beds known as *luggas* were also excluded because of the temporary water availability within these *luggas* which only flow briefly during the wet season. *Luggas* were not looked in terms of habitat in this HSM.

Buffer distances were applied to the shapefiles that were either provided or created, using the ArcGIS model builder as shown in the flow charts (Figures 5.1 and 5.2). These buffers (based on Euclidean distances) were then converted to rasters in order to be processed in ArcGIS 10.0. A raster is a matrix of cells organised into grids where each cell contains a value representing information for the area covered by that cell (ESRI, 2009). The resulting rasters were extracted to fit WGCC boundaries using the Extract Tool in the Spatial Analyst Extension of ArcGIS. The final steps included re-classifying the raster according to suitability levels.

5.2.3. Conceptual models

The conceptual models for the HSM on the following pages (Figures 5.1 and 5.2 for day and night models) illustrate the variables included in the models, highlighting the spatial processes undertaken to assess their degree of suitability and assigning weights to each variable. Captions for the figures are below.

Figure 5.1. Flow chart detailing suitability mapping steps for the daytime model (after the model has run). Blue indicates the original data, yellow shows the processing tool with the shadow indicating that the tool has been successfully executed, green shows the resultant data after processing with the shadow indicating that the results were successfully derived.

Figure 5.2. Flow chart detailing suitability mapping steps for the nighttime model (after the model has run). Blue indicates the original data, yellow shows the processing tool with the shadow indicating that the tool has been successfully executed, green shows the resultant data after processing with the shadow indicating that the results were successfully derived.

Figure 5.1. Flow chart for the daytime model

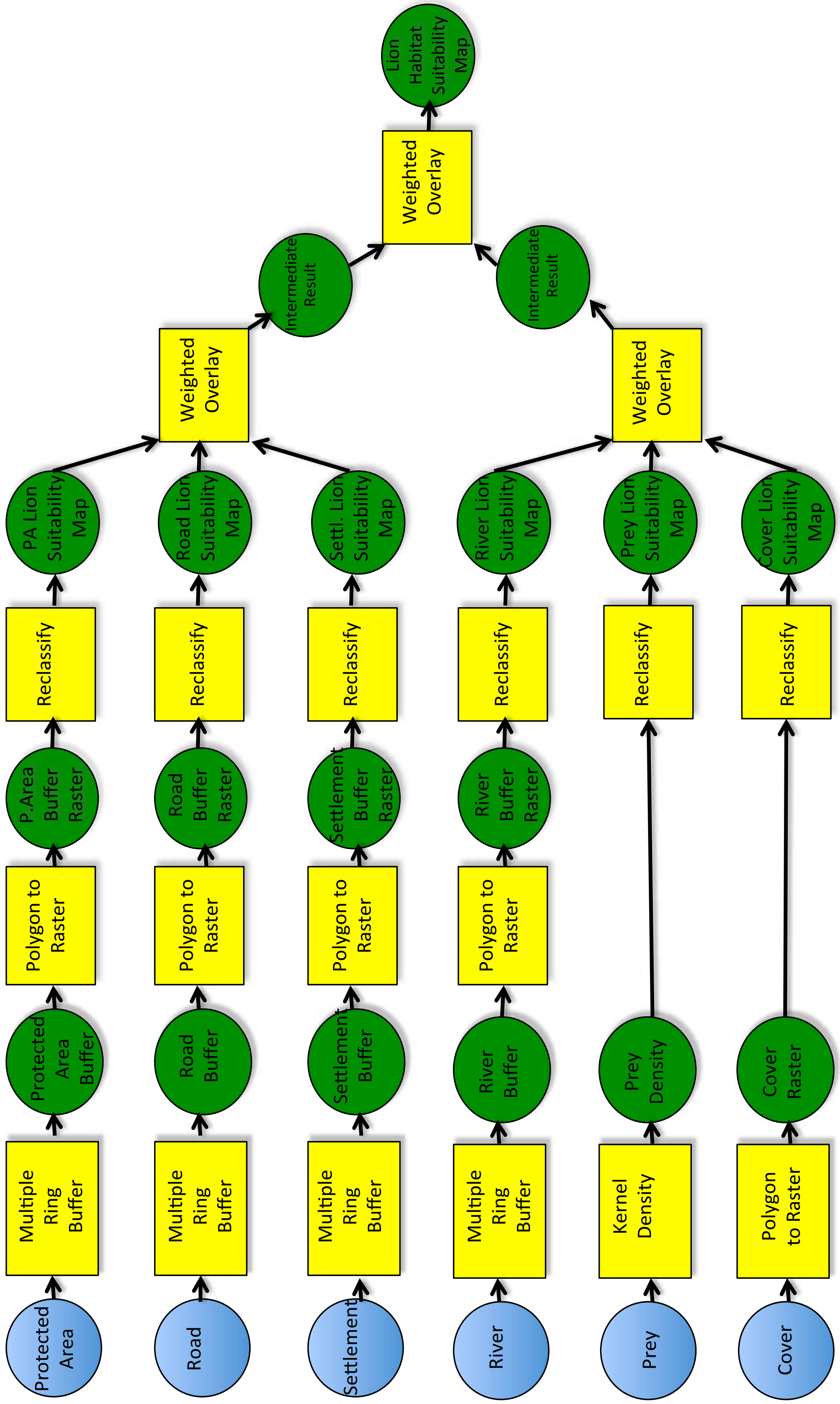
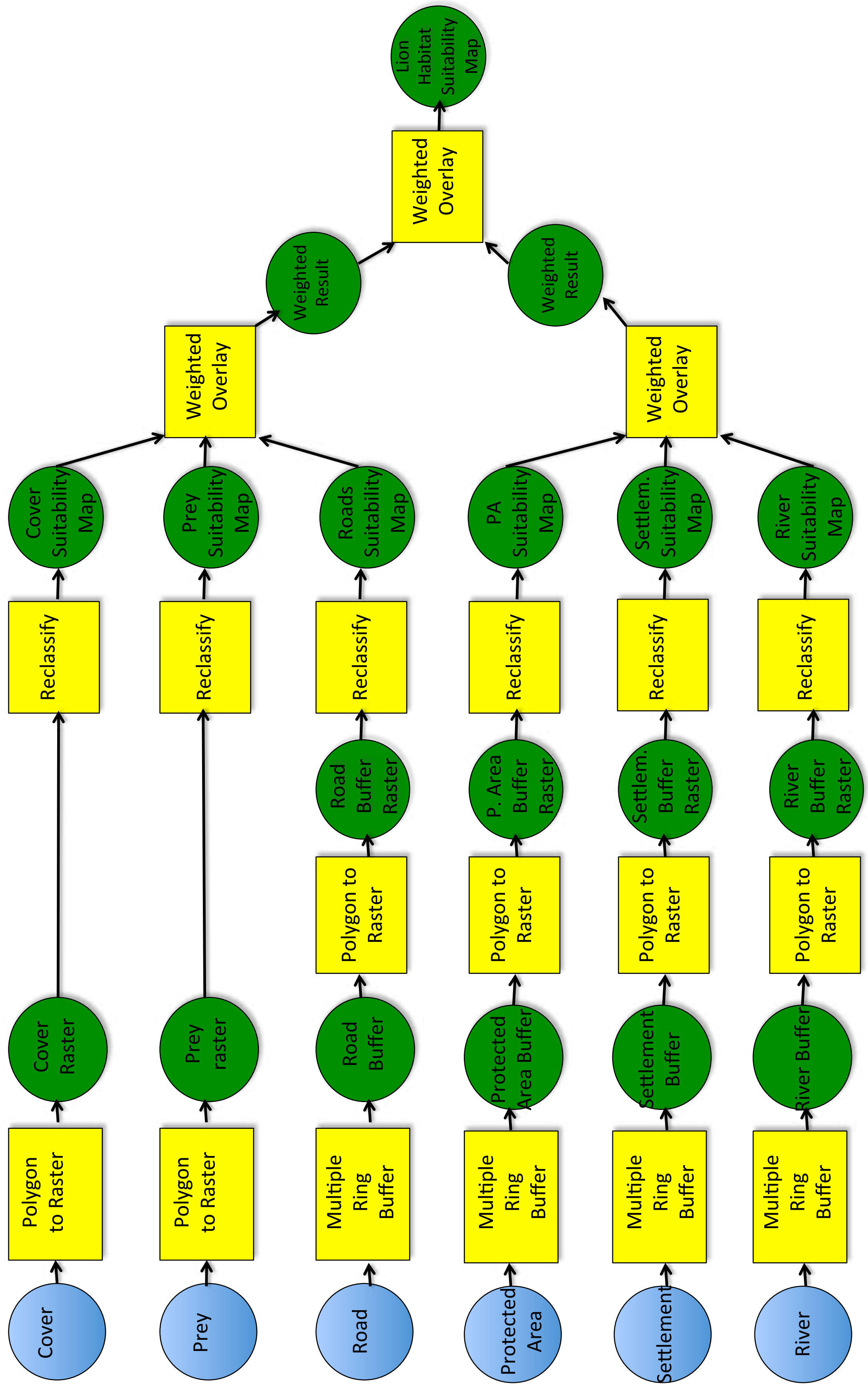


Figure 5.2. Flow chart for the nighttime model



5.2.4. Selection parameters for the day and night HSM models

Accessibility of the Ewaso Nyiro River

Lion hunting and reproductive success increases with close proximity to water sources and dense vegetation (Mosser, 2008; Kissui *et al.*, 2010) as a result of increased water availability and more shelter for cubs. Areas near rivers are considered population sources due to the long-term reproductive success in these areas (Mosser *et al.*, 2009). Additionally, water sources are essential as they influence prey distribution with lions having higher chances of capturing prey in areas around waterholes (Hopcraft *et al.*, 2005; Valeix *et al.,* 2010). Herbivore distribution is highly dependent on the distribution of surface water especially for water-dependent grazers, making the location of water sources in WGCC key to lion distribution. In human-occupied landscapes such as the arid north of Kenya, it has been observed that livestock compete with wildlife for water, with livestock remaining close to water sources and wildlife further away (Leeuw *et al.,* 2001). The distance from water sources by wildlife may be attributed to livestock herders who have been found to scare wildlife away from those water sources or to burn critical wildlife habitat to open up spaces for livestock along the river (*pers. obs.).* The Ewaso Nyiro River is the only water source during the dry season and has been considered as a variable affecting lion presence in the HSM. The shapefile of the Ewaso Nyiro River was made available by the Northern Rangelands Trust. The suitability scores and weighting influence for Distance from the Ewaso Nyiro River during the day and nighttime are presented in Tables 5.2 and 5.3.

Table 5.2. Suitability scores for Distance from the Ewaso Nyiro River - Daytime

Distance from the river	**Suitability**	**Rationale and expected outcome**	**HSM influence**	**Source**
0 to 5 kms 5 to 10 kms Over 10 kms	High suitability Medium suitability Low suitability	The expected outcome is that lions will stay close to the river, however, areas close to the river may be avoided during the day because of people and livestock. But if thick cover is present lions may hide close to the river. There is no unsuitable category as lions can survive away from the river – it is just more	20%	Leeuw *et al*., 2001 Schuette *et al*., 2013 Personal communication with Alayne Oriol-Cotterill

		difficult for them and they will choose prey over water.		
Discussion on how weightings were established: During the day, the river is less of an influence for lions because they would not risk going to drink from the river due to the presence of humans. Herders often take their livestock to drink from the river during the day. However, habitat along the river is preferable due to thick cover so although lions may be there, they would not emerge from the thick habitat to drink.				

Table 5.3. Suitability scores for Distance from the Ewaso Nyiro River - Nighttime

Distance from the river	**Suitability**	**Rationale and expected outcome**	**HSM influence**	**Source**
0 to 5 kms 5 to 10 kms Over 10 kms	High suitability Medium suitability Low suitability	During the dry season, the Ewaso Nyiro is the only source of water. Lions will stay close to the river because of higher prey density and their HSM influence is therefore high.	20%	Schuette *et al*., 2013
Discussion on how weightings were established: At night the weighting influence remains at 20% because lions will tend to drink at night as there is generally no human activity along the river and lions are less threatened at this time. At night, lions are present along the river because of access to water and not cover as they will remain active for hunting purposes. Herbivores may also come to drink from the river at night as often they are displaced during the day by livestock. Lions can stay close to the river to hunt these herbivores.				

Distance to roads

Road density and their level of use can have an impact on wildlife (Loveridge *et al.,* 2010a). Roads provide access to people who live in settlements close to protected areas, however they also provide access to poachers. The increased access to poachers and others involved in illegal killing of wildlife could have an impact on prey populations (Loveridge *et al*., 2010a). Mogensen *et al*., (2011) found that lions in the Maasai Mara avoided heavily used roads due to their fear of humans in community areas. Prior to mapping the roads within WGCC, the Ewaso Lions Project (ELP) team members constructed basic maps using local knowledge to indicate locations of the Conservancy's roads, especially those not frequently accessed. Using knowledge of the roads travelled on over the past few years and the maps drawn by the ELP team, a comprehensive map of all roads and tracks of WGCC was created. The mapping was achieved by driving along the roads with the "tracking" setting on the GPS activated. The tracks were downloaded onto ArcGIS 10.0 directly from the GPS, and then converted to shapefiles. The suitability scores and weighting influence for Distance to roads during the day and night are presented in Tables 5.4 and 5.5.

Table 5.4. Suitability scores for Distance to roads - Daytime

Distance to roads	Suitability	Rationale and expected outcome	HSM Influence	Source
0 – 0.5 km > 0.5 km	Low suitability Highly Suitable	Roads can be suitable during the day as long as there is thick cover near the roads where lions can hide. However, being close to roads does increase the chance of encountering people and it is expected lions would want to avoid roads. Roads and settlements are combined with cover for this HSM.	5%	Loveridge *et al.*, 2010 Mogensen *et al.*, 2011 Elliott *et al.,* 2014 Personal communication with Alayne Oriol-Cotterill
Discussion on how weightings were established: There are not many roads within WGCC and therefore traffic is minimal, especially during the day. It is acknowledged that this could change in the future but currently usage of roads is too limited to have a huge weighting influence.				

Table 5.5. Suitability scores for Distance to roads – Nighttime

Distance to roads	Suitability	Rationale and expected outcome	HSM Influence	Source
0 – 0.5 km > 0.5 km	All suitable	At night, all roads are suitable for lions. These roads have little activity in darkness as the local people are in their villages.	5%	Personal observation and communication with Alayne Oriol-Cotterill
Discussion on how weightings were established : At night, there is even less human traffic than during the day and lions may use some roads however will avoid the main road due to the close proximity to villages.				

Distance to settlements

Lions may alter their movements according to shifts in settlements, and in response to human and/or livestock presence (Oriol-Cotterill *et al.*, 2015a; Oriol-Cotterill *et al.*, 2015b). The locations of settlements have therefore been found to play a large role in lion presence and movements within human-occupied landscapes. The ELP team mapped all the settlements within WGCC in 2010. Eight locations were visited (see Appendix 1) and each house within each group of houses (known as a *manyatta*) was geo-referenced. The suitability scores and weighting influence for Distance to settlements during the day and night are presented in Tables 5.6 and 5.7.

Table 5.6. Suitability scores for Distance to settlements – Daytime

Distance to settlements	Suitability	Rationale and expected outcome	HSM Influence	Source
Over 3 kms	High suitability	Thick cover close to settlements may be suitable for lions during daytime but generally lions will avoid settlements because of the presence and activity of people.	15%	Valeix *et al.,* 2012
2 to 3 kms	Medium suitability			Schuette *et al*., 2013
1 to 2 kms	Low suitability			Elliott *et al.,* 2014
0 to 1 km	Unsuitable			Oriol-Cotterill *et al*., 2015a &b
Discussion on how weightings were established: Settlements were given a weighting of 15% during the day because lions will generally not go close to settlements due to intense human activity. Being close to the protected areas, or near the river are higher influencing factors compared to settlements.				

Table 5.7. Suitability scores for Distance to settlements – Nighttime

Distance to settlements	Suitability	Rationale and expected outcome	HSM Influence	Source
>1km	All suitable	When people are asleep, lions are able to go close to settlements, if there is prey in the vicinity. Darkness provides cover and lions are not likely to be detected near settlements. These settlements are small scale where there is little activity after dark. Although lions utilise areas close to human habitation at night, they make behavioural changes that could be costly (in terms of how much energy is used) within 1.5 km of settlements.	15%	Schuette *et al.,* 2013
<1km	Low suitability			Oriol-Cotterill *et al*., 2015a
Discussion on how weightings were established: This was given a weighting influence of 15% again due to the same reasons that generally lions will avoid settlements. Access to herbivores, distance to the river and cover for ambushing their prey, have a higher weighting influence.				

Distance to protected areas

The two protected areas considered in these models were Samburu National Reserve (SNR) and the Core Conservation Area (CA) in WGCC. Within the context of this chapter, the western boundary of SNR is the most relevant as this is adjacent to WGCC's eastern boundary. The CA is located within WGCC and is not a gazetted protected area but has been set aside by the community as an area free from human activity (settlements or livestock grazing). The shapefiles for these areas were made available by the Northern Rangelands Trust and additional details on SNR and WGCC can be found in Chapter 2. The suitability scores and weighting influence for

Distance to protected areas during the day and night are presented in Tables 5.8 and 5.9.

Table 5.8. Suitability scores for Distance to protected areas – Daytime

Distance from the protected areas	**Suitability**	**Rationale and expected outcome**	**HSM Influence**	**Source**
0 to 3 kms 3 to 6 kms Over 6 kms	High suitability Medium suitability Low suitability	Lions prefer to be closer to protected areas due to better cover (less livestock overgrazing) and less people/livestock. In addition, protected areas represent higher prey densities that lions need access to. Walking far away from these represents an energetic cost to lions. There is no distance to protected areas that would be unsuitable because lions can survive permanently outside protected areas.	30%	Schuette *et al*., 2013 Personal communication with Alayne Oriol-Cotterill
Discussion on how weightings were established: The weighting for distance to protected areas was the highest at 30% because it is the closest area for safety within a human-occupied landscape. Humans are the greatest threats to lions and protected areas often are the safest places for them.				

Table 5.9. Suitability scores for Distance to protected areas – Nighttime

Distance from the protected areas	**Suitability**	**Rationale and expected outcome**	**HSM Influence**	**Source**
0 to 5kms 5 to 10kms Over 10 kms	High suitability Medium suitability Low suitability	During the night being close to SNR or the CA means that lions have a shorter distance to walk and less energy expenditure to return during the daylight hours.	15%	Personal communication with Alayne Oriol-Cotterill
Discussion on how weightings were established: The weighting reduces to 15% at night because lions do not need to hide from humans as much at this time. There are less people at night that can pose a threat to lions, and therefore, distance to protected areas is a lesser influence on lions at this time.				

Vegetation cover

Thick bush habitats offers very good cover for large carnivores as people are often less able to penetrate through them (Oriol-Cotterill *et al*., 2015b). Large carnivores will especially use this thick bush where human caused mortality could be high and Schuette *et al*., (2013) found that lions in the Shompole region of southern Kenya would use thick bush even more when they were in close proximity to people. This pattern of staying in thick cover is even more apparent when carnivores are resting, feeding or hiding their young (Oriol-Cotterill *et al*., 2015b). The data source for the cover was provided by the Northern Rangelands Trust from a previously created vegetation classification map. From the vegetation map provided, the vegetation classes were digitised as polygons. These were then converted to rasters and reclassified according to the suitability levels (how well they provide cover for lions for hiding from people or hunting). The suitability scores and weighting influence for cover during the day and night are presented in Tables 5.10 and 5.11.

Table 5.10. Suitability scores for Vegetation cover – Daytime

Type of cover	Suitability	Rationale and expected outcome	HSM Influence	Source
Very high/dense cover (>70% tree cover) High cover (<70% tree cover) Medium cover (scrubland) Little/no cover (Herbaceous and sparse vegetation)	High suitability Medium suitability Low suitability Unsuitable	This has the second highest influence on lions during the day as they need to hide from people. If lions are close to settlements or the river (which attracts people), only dense cover is considered suitable. Medium cover is also suitable if it is further away from settlements.	25%	Schuette *et al*., 2013 Oriol-Cotterill *et al*., 2015b
Discussion on how weightings were established: This is the second highest weighting influence at 25%. Good cover is essential for lions but not as important as being close to protected areas or safe habitat. Lions in protected areas can feel safe even in open areas. Lions can also be vulnerable in dense cover in human occupied areas if humans are in the vicinity and they know lions are present. Therefore, distance to protected areas had a greater weighting influence compared to cover.				

Table 5.11. Suitability scores for Vegetation cover – Nighttime

Type of cover	Suitability	Rationale and expected outcome	HSM Influence	Source
Very high/dense cover (>70% tree cover) High cover (<70% tree cover) Medium cover (scrubland) Little/no cover (Herbaceous and sparse vegetation)	High suitability Medium suitability Low suitability Unsuitable	Cover matters less at night except for hunting purposes. As an influencing factor, cover is less significant at night compared to the day.	20%	Schuette *et al*., 2013

Discussion on how weightings were established: At night, lions use cover for hunting but not for hiding from people as there is less human activity at night. For this reason, the weighting influence was reduced from 25% to 20%. Compared to distance to protected areas, this weighting is much higher (20% compared to 15%), because hunting is a priority at night, regardless of how far the lions are from the protected areas.

Herbivores (Prey base)

Lion density is regulated by prey (Van Orsdol *et al.,* 1985) and therefore it is essential that prey abundance is monitored and estimated reliably. Within a human-occupied landscape such as WGCC, herbivores are threatened by competition with livestock and landuse changes such as habitat loss (Ripple *et al.,* 2015). In the study area, livestock production continues to increase and this encroaches on land needed for wild herbivores. The upsurge in livestock numbers results in competition for grazing leading to less forage and water available for the wild herbivores.

It was not possible to collect systematic presence-absence data on herbivores for this study. The methodology employed to collect this data is explained in section 5.2.5. After plotting point data of herbivore locations, the data was explored to assess its fitness for use through ArcGIS 10.0 software. Using the spatial statistics tools, the data was found to consist of clusters and appeared unfit for use in mapping the herbivore distribution (see Appendix 9). As a result of this, local knowledge was combined with expert opinion to produce an alternative distribution map for herbivores based on areas in WGCC where herbivore densities are generally observed to be high, medium or low. After creating the regions, the data was converted into polygons which were then converted to rasters (for the nighttime model only, as prey is most relevant for lions during this time). After conversion to rasters, they were reclassified according to the suitability levels. The suitability scores and weighting influence for herbivores during the day and night are presented in Tables 5.12 and 5.13.

Table 5.12. Suitability scores for Herbivores – Daytime

Herbivores	Suitability	Rationale and expected outcome	HSM Influence	Source
	All highly suitable	This model assumes that lions only hunt at night and not much during the day. They will show more preference for cover than prey density	5%	Personal communication with Alayne Oriol-Cotterill

		during the day. Its influence on the HSM is small.		
Discussion on how weightings were established: The weighting influence was very small at 5% because lions will generally not hunt during the day and therefore the other variables play a larger role in what influences suitable lion habitat. However, if there was no human activity, lions may opportunistically hunt which is why a 5% influence was decided on.				

Table 5.13. Suitability scores for Herbivores – Nighttime

Herbivores	Suitability	Rationale and expected outcome	HSM Influence	Source
		Lions will mainly hunt at night resulting in higher influence at night compared to during the day.	25%	Schuette *et al.*, 2013
Discussion on how weightings were established: This was the greatest influence for lions at night because this generally will be the only time when they will hunt. The search for food is the priority and therefore herbivore locations and availability is key.				

Livestock

Within the human-occupied landscape, livestock may at times constitute a prey base for lions, especially when wild prey is scarce (Loveridge *et al.,* 2010a; Valeix *et al.,* 2012). Livestock may also affect lion presence due to human disturbance as a result of herders who accompany their livestock and who often chase lions away (Oriol-Cotterill *et al.,* 2015b). Furthermore, outside protected areas, livestock are easier to catch and their numbers far greater than those of wild prey (Valeix *et al*., 2012; Oriol-Cotterill *et al*., 2015b). Their movements can also be predicted both spatially and temporally (Valeix *et al.,* 2012). It is expected that carnivores will focus on livestock within the human-occupied landscape (Oriol-Cotterill *et al.,* 2015b). However, this has not been confirmed (Woodroffe *et al.,* 2007; Hemson *et al.,* 2009) and it appears that carnivores do not regularly prey on livestock due to the risk of human caused mortality (Oriol-Cotterill *et al*., 2015b). Monitoring livestock is, therefore, essential and was considered important for this model. However, it was not possible to collect systematic presence-absence data on livestock due to field constraints. The methodology of how the data was collected is explained in detail in section 5.2.5. After plotting the point data of livestock locations to assess its fitness for use using ArcGIS 10.0 (see Appendix 9), it was decided that livestock would be removed from the model due to the bias in areas of data collection and the clustered presence it showed within WGCC. There was no confidence in the knowledge of unpredictable grazing patterns to be able to produce an alternative distribution map for livestock.

5.2.5. Engaging local people in data collection for herbivores, lion records and livestock

With the lack of roads in the area, drawing on the expertise of warriors (young Samburu men) and scouts patrolling the region proved to be the most effective way in gathering information on herbivores, livestock and carnivores. Local community scouts have been effective in other conservation projects in the Samburu region (Low *et al*., 2009). They have been able to provide valuable conservation insight and also improve the local people's attitudes towards conservation. Lion scouts and warriors collected data on sightings and tracks of all large carnivores, herbivores and livestock, using a species list (see Appendix 2). A Conflict Officer also recorded all livestock depredation incidents. All the conflict reports recorded between 2007 and 2013 that were accumulated over the years were analysed and mapped to determine the distribution of conflict incidents across WGCC and to obtain an index of human-carnivore conflict in the area.

5.2.6. Validation

For the purposes of this model, all of the scouts and warriors observational data of lion presence were included (both direct sightings and tracks). Lions in this area are nervous of people and are rarely observed directly, however the scouts and warriors were well trained in identifying lion tracks and this was the most common indication of lion presence in an area. All tracks and sightings were mapped and overlaid on the model outputs to validate whether the areas of highest suitability were in fact areas where lions were present.

In order to assess whether the areas of highest suitability experience human-lion conflict, livestock depredation incidents were overlaid on the final HSM daytime and nighttime models in a GIS. It would be expected that in areas where habitat is the most suited for lions, human presence (and therefore livestock) would be low in numbers.

5.2.7. Creating the Habitat Suitability Model

Six suitability maps were created (for both daytime and nighttime) and assigned weights that were based on research and expert opinion. The suitability maps were then combined using MCDA to produce two final lion HSM (one for day and another for night). The weighted overlay tool was used to combine the individual suitability maps to produce the final maps.

5.2.8. Enhancements of the Habitat Suitability Model

There were no technical limitations in this HSM and the GIS software (ArcGIS 10.0) used was powerful enough and contained sufficient tools to process the model. However, there are a number of problems encountered with respect to the data used in this HSM.

i. The effort between the scouts was different over the study period. Whilst collecting presence data, their efforts varied each month, as they often collected data on different days. The effort of the warriors was also variable over time, with a greater effort made later in the study period, after the warriors learned how to read and write.
ii. All data collection was also heavily dependent on the security in the area.
iii. The livestock data that was collected showed heavy bias with clusters in some areas due to the fact that it was only the scouts that were collecting this data, and not the warriors. The scouts were located in only three locations compared to the warriors whose data collection efforts were more widespread.
iv. The herbivore data also displayed some unreliability due to sampling bias. Local knowledge and expert opinion was used to verify the data to allow it to be utilised in the model. Limited sample size and biased sampling is a common problem in carnivore studies (Abade *et al*., 2014).

v. A challenge of recording lion data based on the presence of tracks is that the probability of detection varies with substrate; there is a higher probability of observing tracks in sandy areas such as on roads or in *luggas*, and very little or no chance of seeing them in areas with a lot of ground cover, vegetation or rocks. It is therefore possible that additional tracks may have been present but not recorded.

vi. The habitat data received from the Northern Rangelands Trust was coarse, highlighting only five broad habitat categories found within WGCC, and with the vegetation feature classes not directly related to lion habitat. It is recommended that for future modelling, a habitat map be created as part of the study.

vii. Going forward for a future study which could include human density as a variable, 500 m^2 blocks will be divided per location and human density will be accounted for in each block. It is assumed that more people within a village will have a greater influence on lions, compared to less people within a village of the same size.

viii. For future studies, weightings can be established using results from lion collar data to see the extent to which lions prefer, for example, cover (safe habitat) over distance to the river and other water bodies.

ix. For future studies, the study area will be divided into patrol (sampling) blocks covering the whole area. Each patrol block will be allocated a number of warriors or scouts depending on the size. The scouts and warriors will patrol each of their blocks a number of times each month recording the following details whenever they observe wildlife or livestock: wildlife/livestock species, total number, GPS point. This sampling design is akin to the method described by MacKenzie *et al.,* (2003) when estimating occupancy. The patrol blocks will be larger than the home range of any of the target species (MacKenzie and Royle 2005; MacKenzie *et al.,* 2006) because the interest is to measure the occupancy and not the intensity of habitat use by the wildlife/livestock. In order to create the density maps, the total number of individual species sighted per patrol block will be used in ArcMap by dividing the total number of observations per block by the size of the block, using the Kernel Density method. In order to create this, all the blocks within the study area will be surveyed (Karanth *et al.,* 2011).

5.3. Results

5.3.1. Lion sightings

Lion sightings have been included and overlaid in the final HSM outputs. These sightings and tracks of lions were collected by the scouts, warriors and the ELP field team and are shown as white circles. The warriors mainly saw lions (tracks and sightings) along the River and scattered throughout WGCC. The scouts and field team saw lions in the CA, the Loijuk area and the Sasaab area, including the Buffer Zone (see Appendix 1).

5.3.2. Variables

The following figures show the results of the day and night variables. Red indicates areas that are unsuitable, yellow indicates areas of low suitability, light green show areas of medium suitability and dark green show areas of high suitability.

Distance to the River

Figures 5.3 and 5.4 show the areas of suitability with respect to distance from the Ewaso Nyiro River during the day. Areas of highest suitability are all along the Ewaso Nyiro River, encompassing the entire CA and the boundary of WGCC to SNR. The top section of WGCC, where Naisunyai and near Sukuroi are located, have lower suitability due to the extensive distance from the River.

Distance to Roads

Figure 5.5 shows the road network within WGCC, with the majority of the roads in the CA and between Sasaab and Lpus Leluai locations, and one main road running through the entirety of WGCC. Areas along the roads are all classified as low suitability, including areas within the CA and the boundary of SNR. Areas between Naisunyai and Loijuk, and southeast of Ngutuk Ongiron all show high suitability areas due to their extensive distance from the roads of WGCC.

Figure 5.6 shows that at night, all areas on and around roads are highly suitable. There are no areas of medium or low suitability with respect to roads. This is because there is very little human activity along the roads at night.

Distance to Settlements

Figure 5.7 shows that all areas within close proximity to settlements during the day are unsuitable for lions. These include areas around all locations of WGCC and the boundary of WGCC to SNR. Areas that contain low and medium suitability habitat include part of the CA and some sections on the boundary of SNR. The northernmost tip of the CA is classified as low suitability due to its close proximity to Ngutuk Ongiron settlement. Regions that are of highest suitability include along the Ewaso Nyiro River, Loijuk and south of Naisunyai. There is only one open corridor connecting the River to the Buffer Zone and the Lalasai range (see Appendix 1), which is located on the southern tip of the CA.

Figure 5.8 shows that only areas immediately at or surrounding the settlements contain low suitability habitat at night. The remainder of WGCC is highly suitable with respect to settlement distribution as people are in their villages at night where there is little human activity and therefore there is no disturbance to lions.

Distance to Protected Areas

Figure 5.9 shows the protected areas suitability buffers. The areas of highest suitability are all areas in and surrounding the CA and the boundary of WGCC to SNR. The northern sections of WGCC are too far from the protected areas and therefore have low suitability. These include most of the locations in the settled areas namely Sukuroi, Naisunyai, Lempaute, Remot and Loijuk.

Figure 5.10 shows that highly suitable locations are closest to the CA and the entire area bordering SNR. The northern sections of WGCC are of low suitability due to their extensive distance from either the CA or SNR. The area at Sasaab has emerged as highly suitable at night including more of the region surrounding Ngutuk Ongiron. Loijuk area also emerges as an area of medium suitability.

Vegetation cover

Figures 5.11 and 5.12 show the suitability of vegetation cover within WGCC during the day and night. There is no forest cover present in WGCC. Most of the areas in the northern parts of WGCC contain sparse vegetation and therefore are unsuitable for lions, with woodland cover increasing towards the southern parts of WGCC and towards SNR. There is one section on the northern boundary to SNR which is unsuitable and has sparse vegetation. This area is located close to a large settlement area, Kiltamany (see Appendix 1), with overgrazing as a result of high livestock numbers having led to the sparseness of vegetation.

Herbivores

Figure 5.13 shows that WGCC contains herbivores throughout WGCC and it is suitable for lions due to the availability of the herbivores as a source of food. As this is during the day, the presence of herbivores in this area does not play a huge role in lion habitat suitability since lions will mainly hunt at night in this human-occupied landscape.

Figure 5.14 shows that highly suitable areas for lions include the CA and all along the boundary to SNR. Medium suitability locations include the middle sections of WGCC and a section along the Ewaso Nyiro River towards Remot. Low suitability areas include the northern sections of WGCC, including the areas around the settlements of Lempaute, Remot, Sukuroi and Naisunyai.

Figure 5.3. Suitable locations during the day with proximity to the River as priority selection criteria.

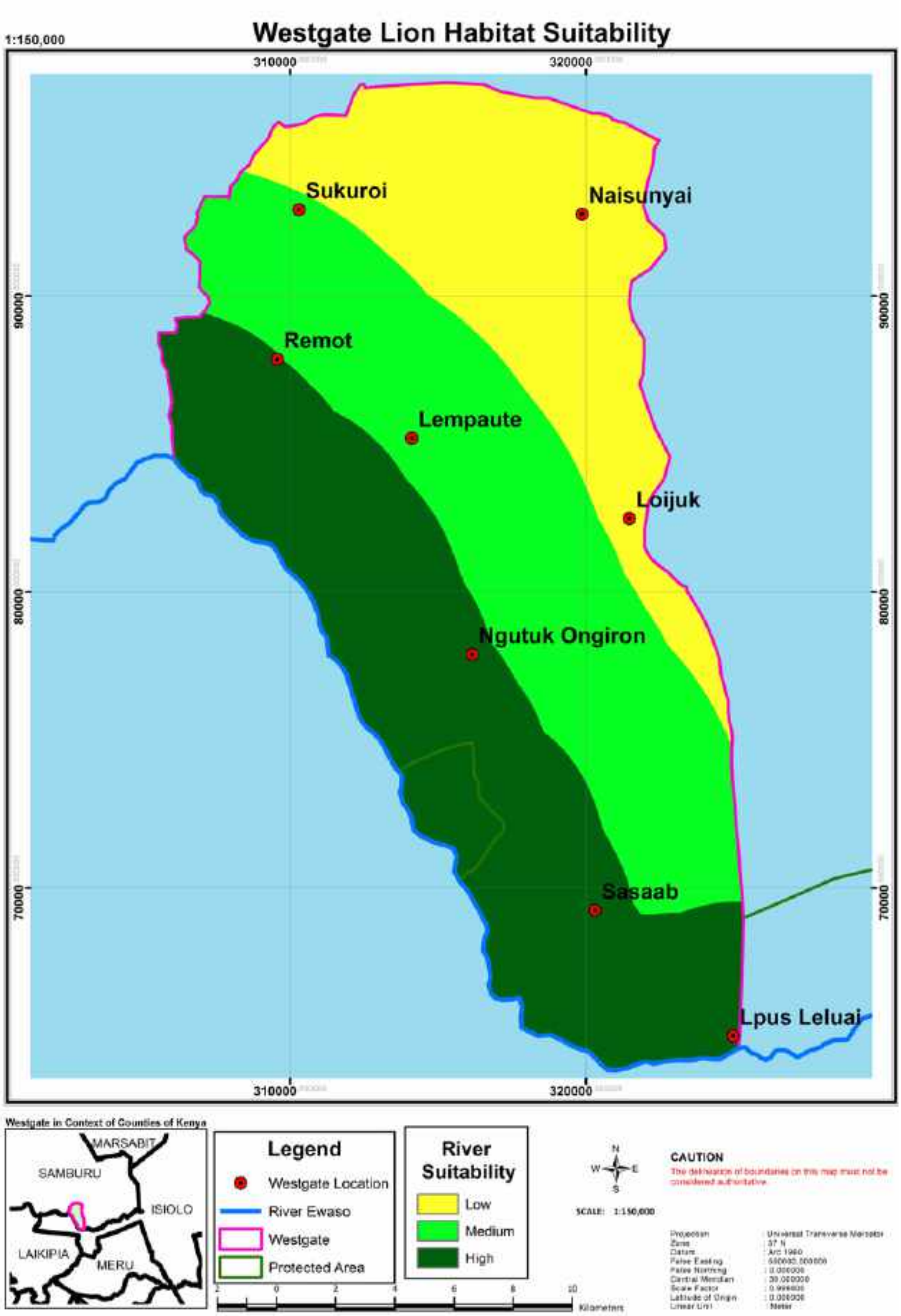


Figure 5.4. Suitable locations during the night with proximity to the River as priority selection criteria

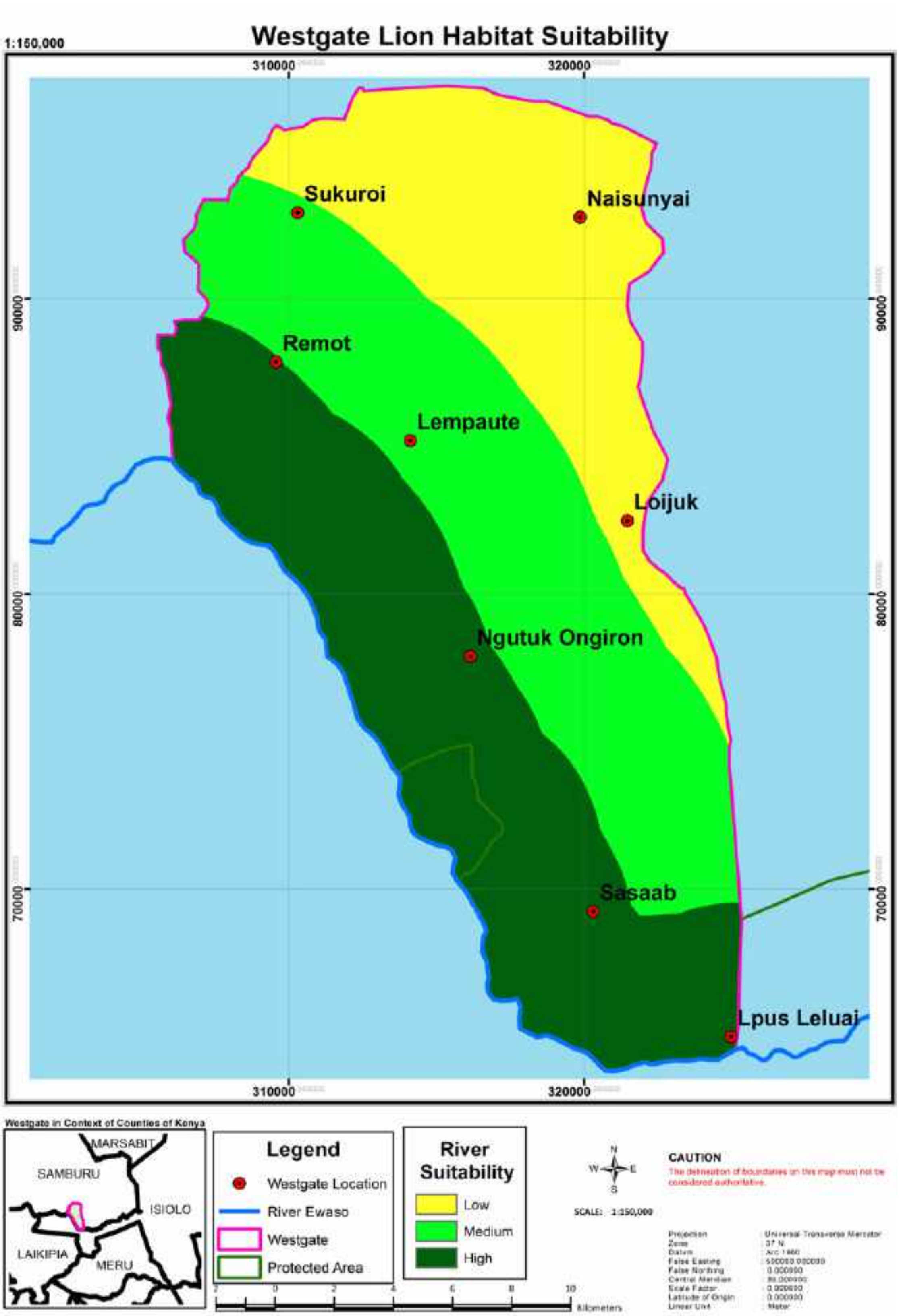


Figure 5.5. Suitable locations during the day with proximity to roads as priority selection criteria

Figure 5.6. Suitable locations during the night with proximity to roads as priority selection criteria

Figure 5.7. Suitable locations during the day with proximity to settlements as priority selection criteria

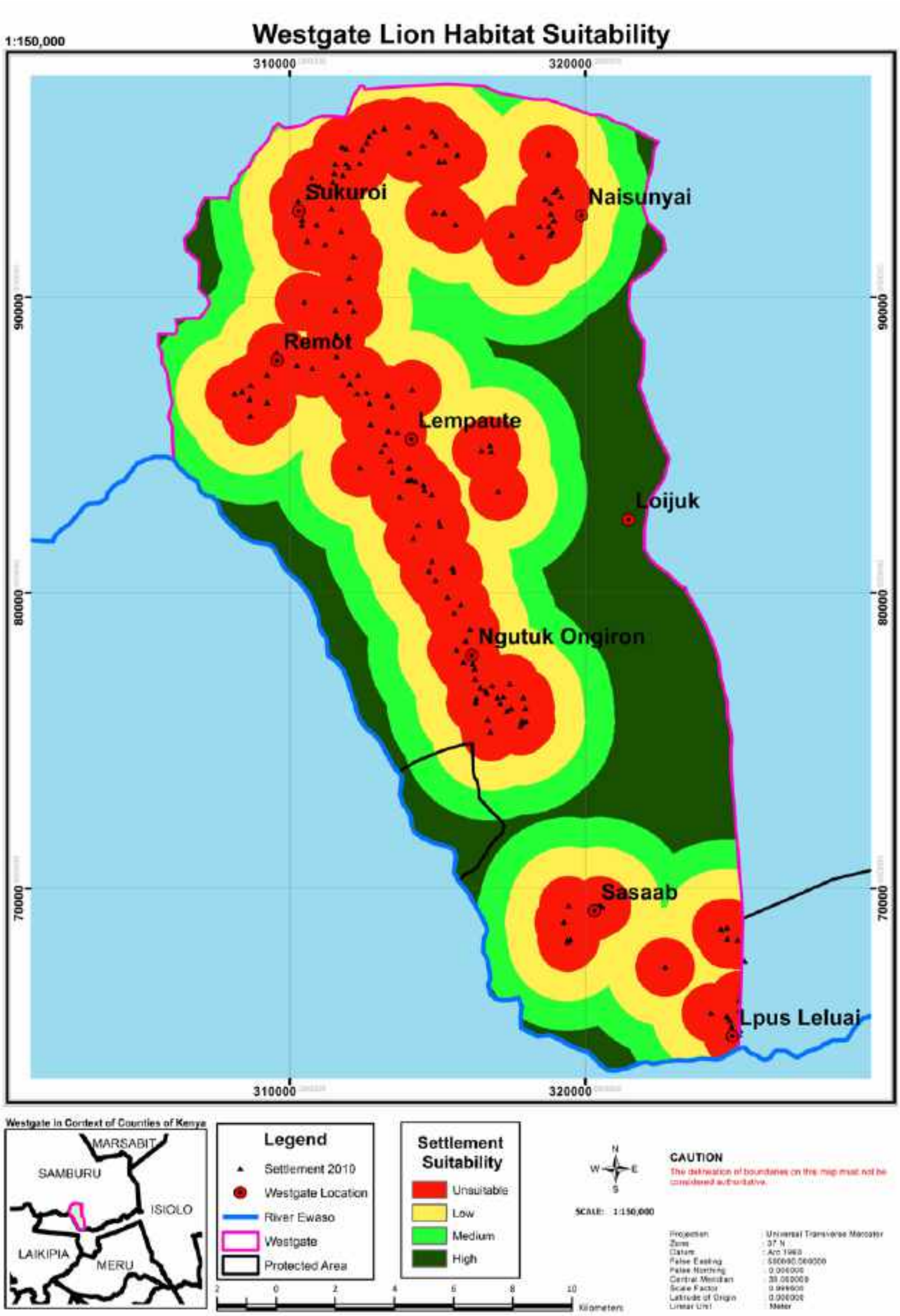


Figure 5.8. Suitable locations during the night with proximity to settlements as priority selection criteria

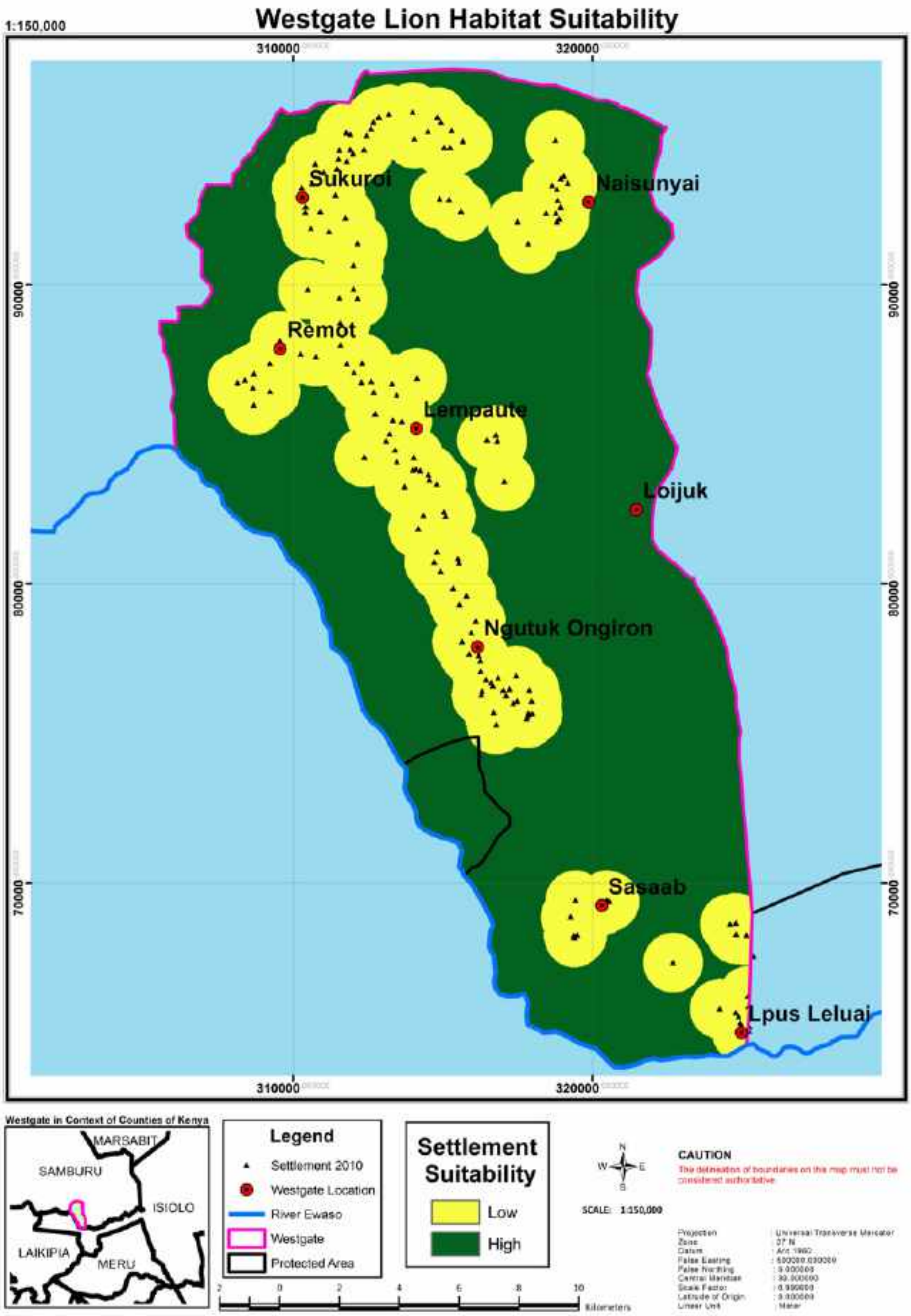


Figure 5.9. Suitable locations in the day with proximity to protected areas as priority selection criteria

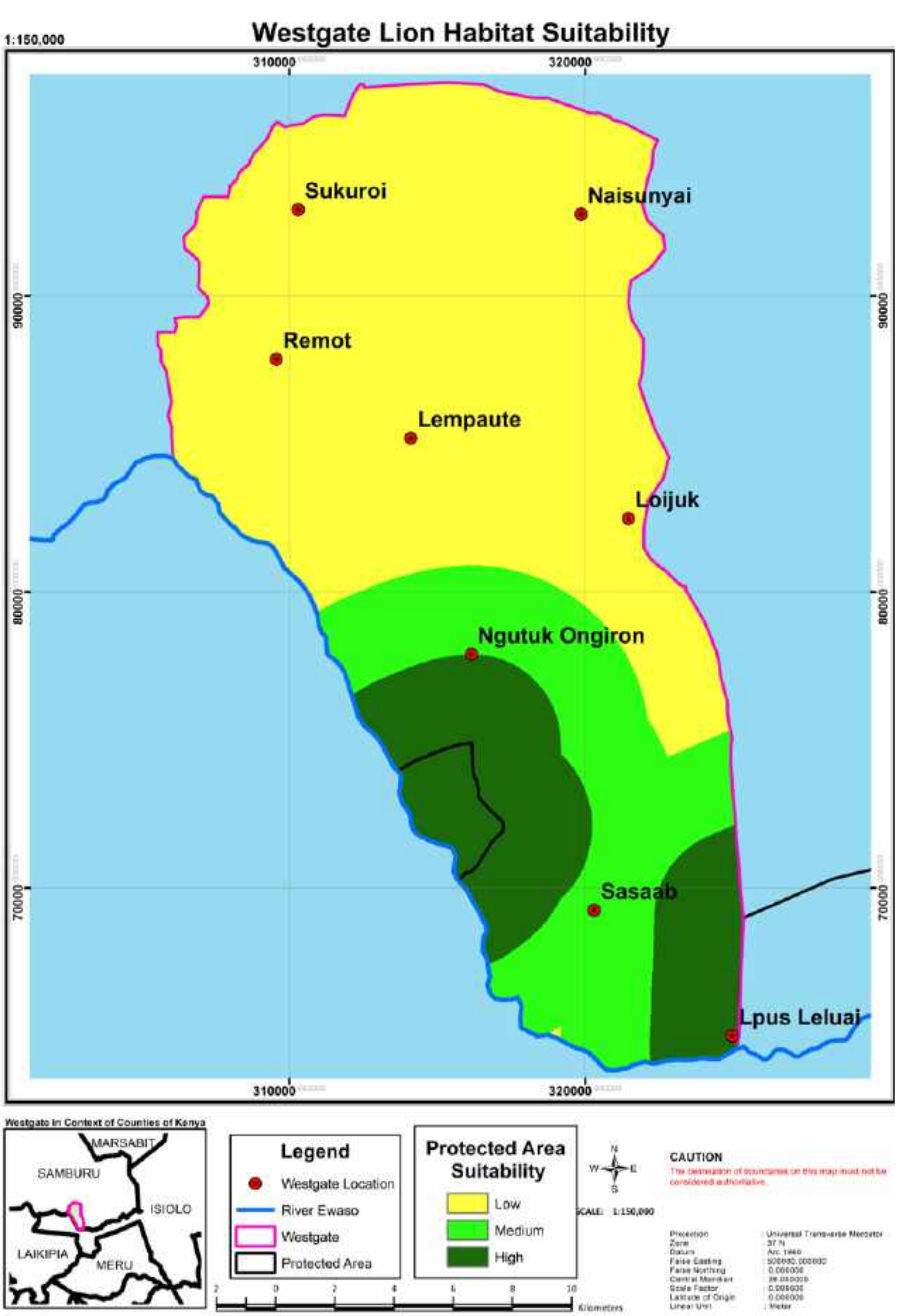


Figure 5.10. Suitable locations during the night with proximity to protected areas as priority selection criteria

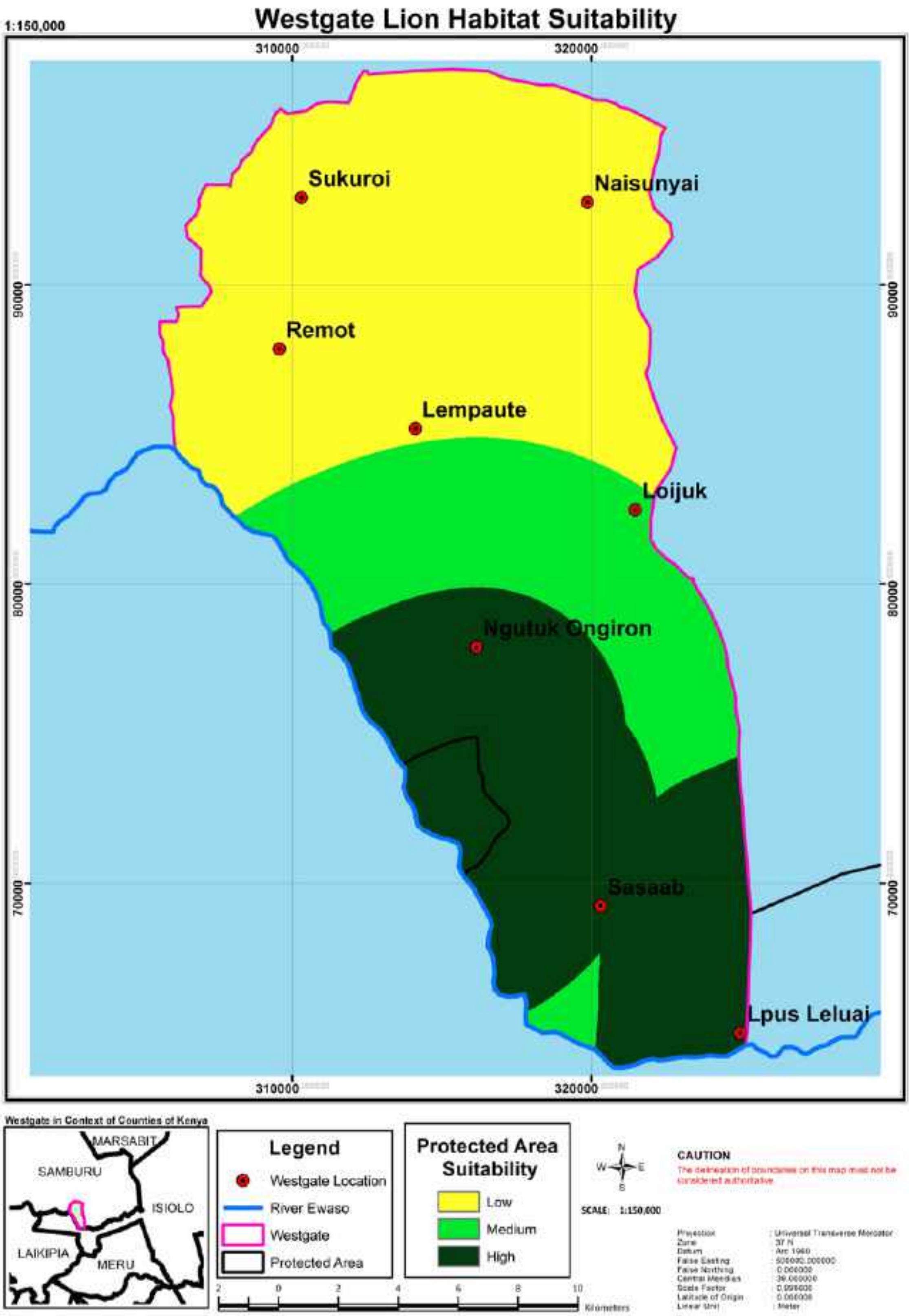


Figure 5.11. Suitable locations during the day for vegetation cover as priority selection criteria

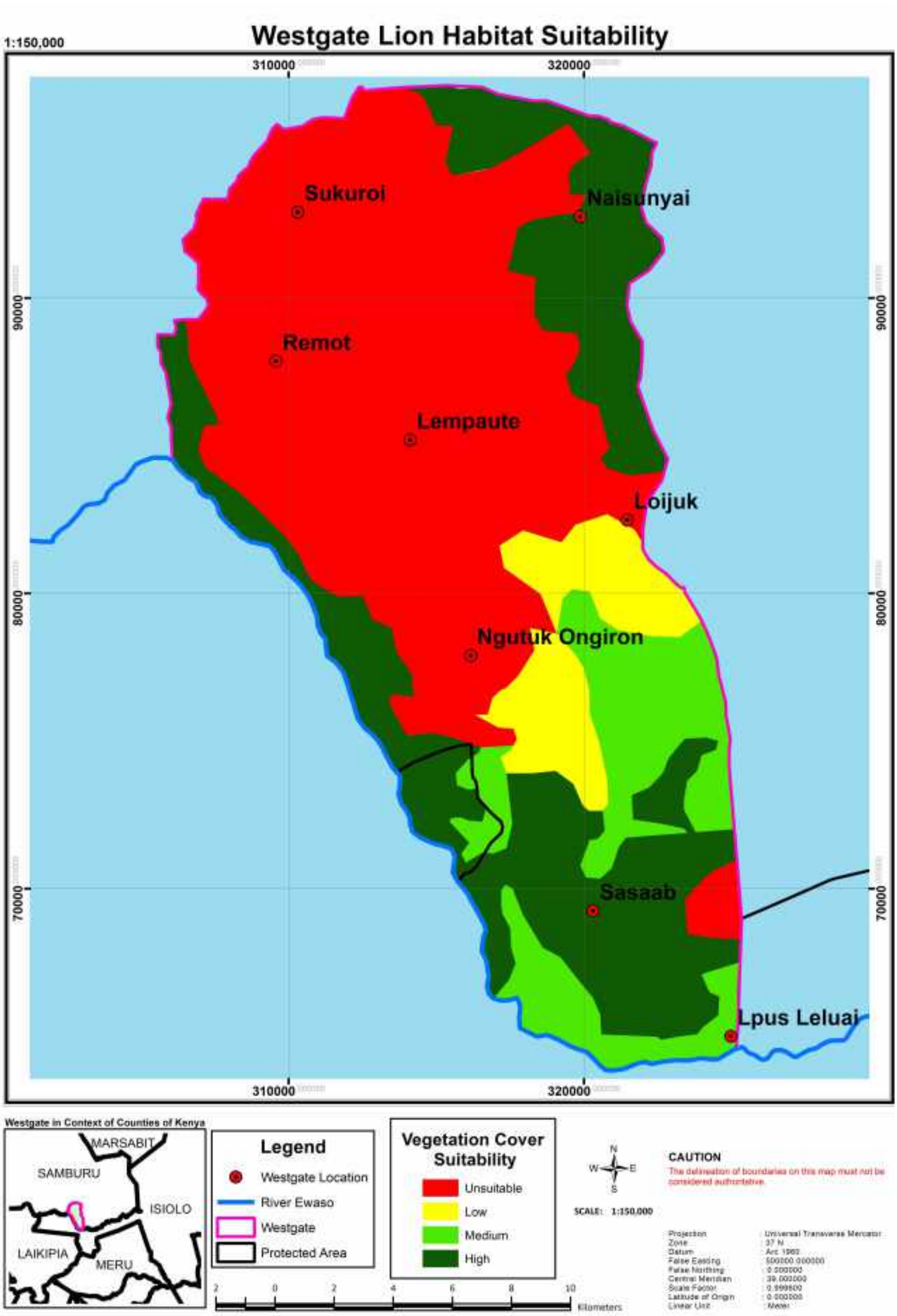


Figure 5.12. Suitable locations during the night for vegetation cover as priority selection criteria

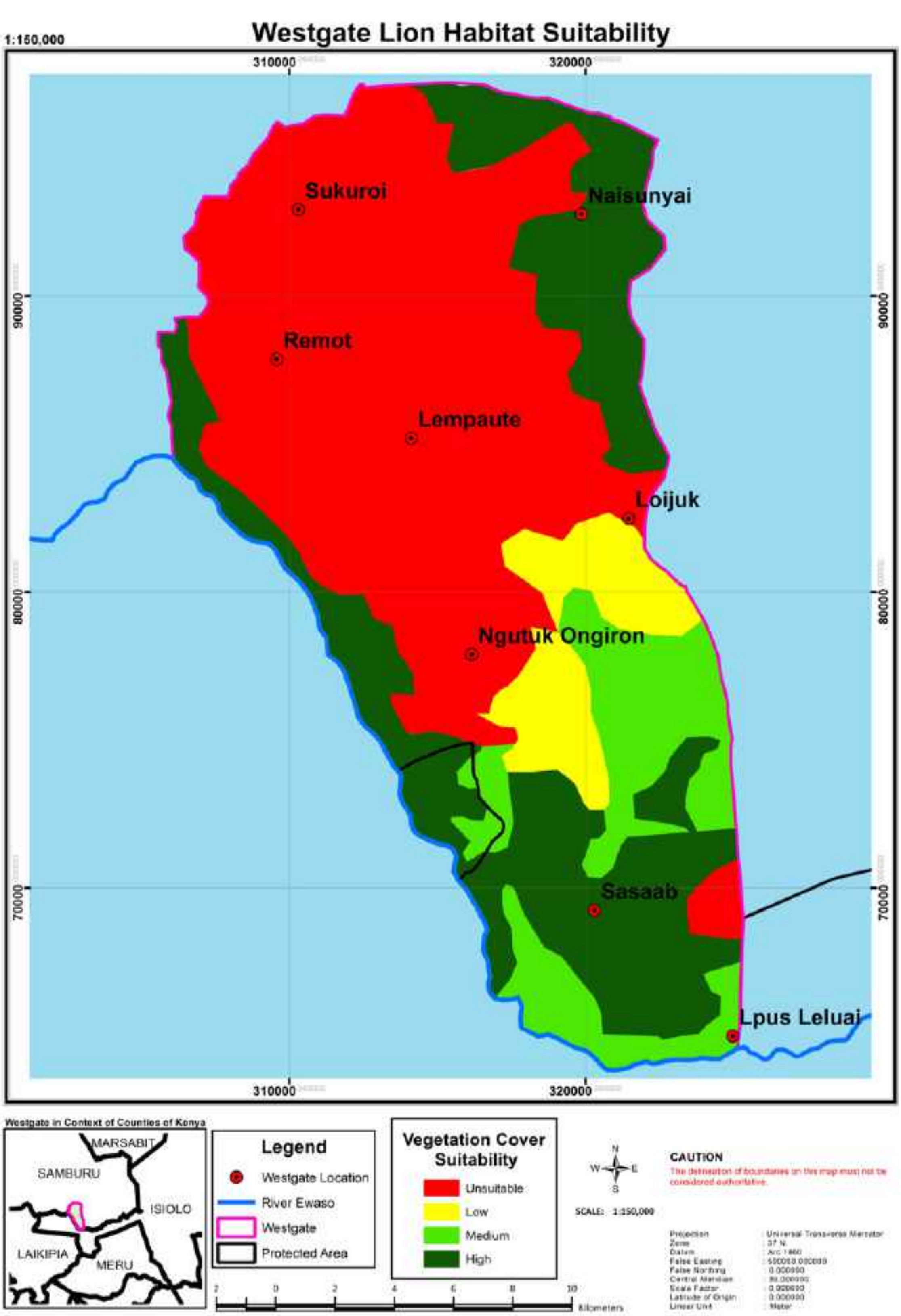


Figure 5.13. Suitable locations during the day for herbivores as priority selection criteria

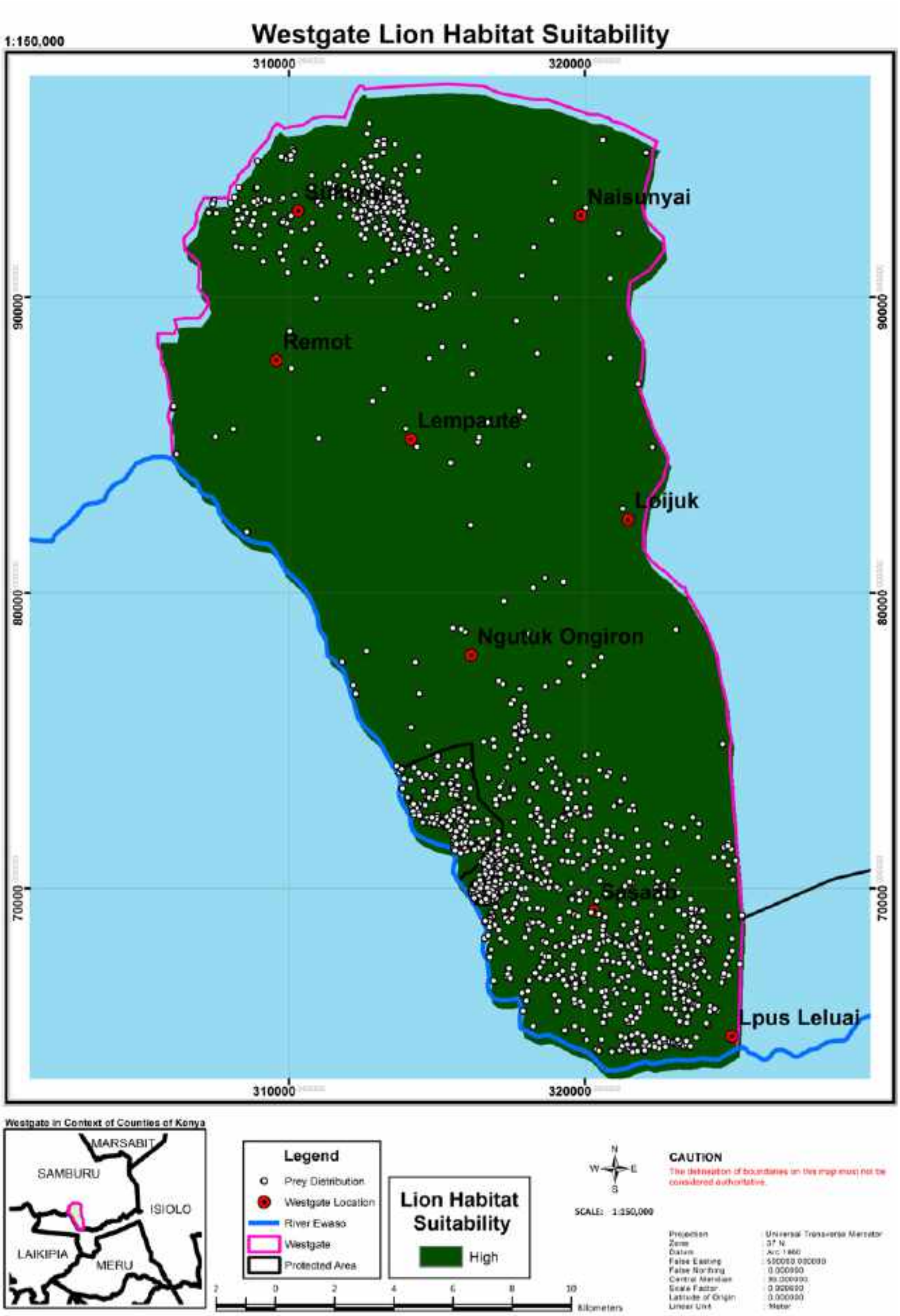
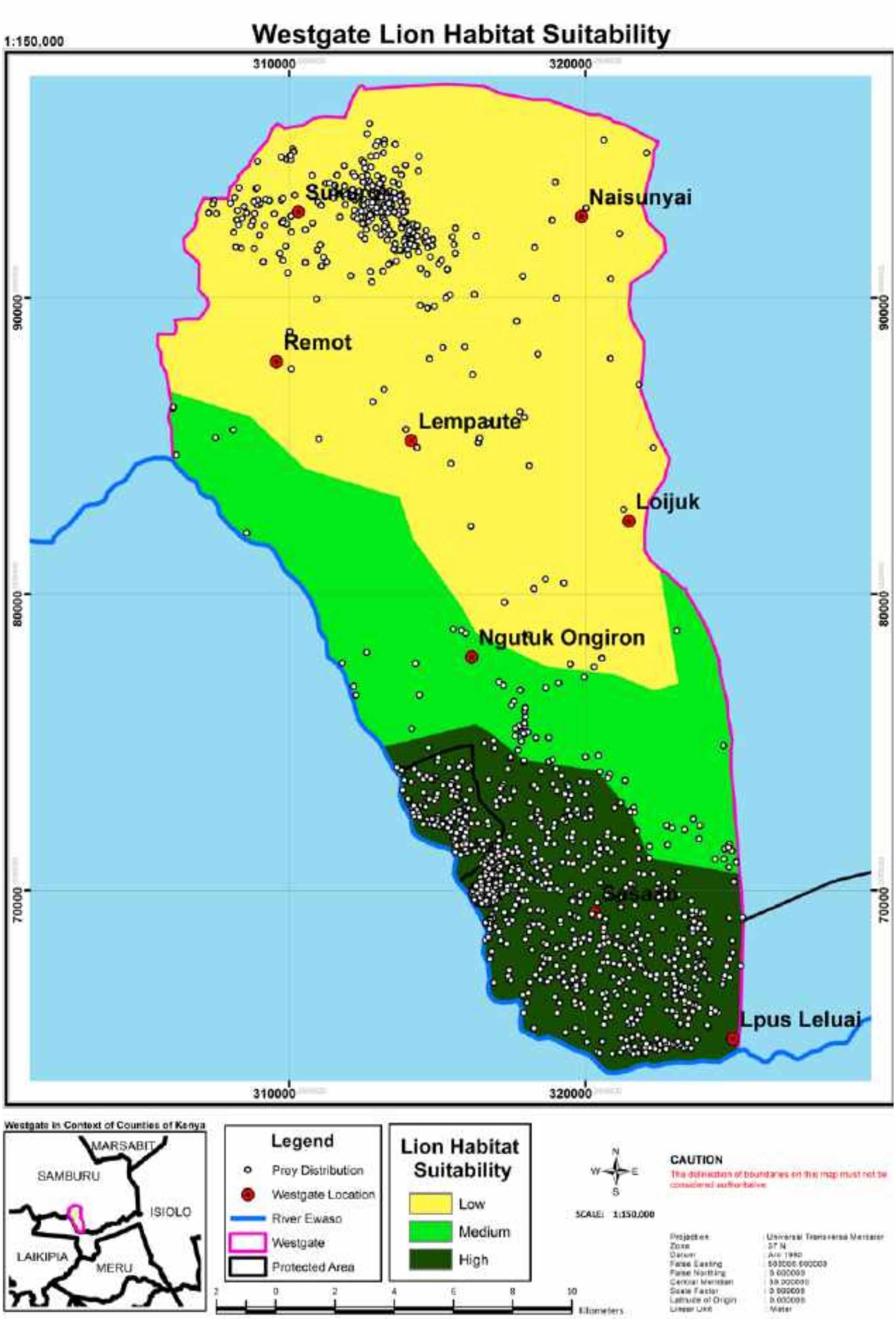


Figure 5.14. Suitable locations during the night for herbivores as priority selection criteria



5.3.3. Suitable habitat during day and night

One of the key outputs of this study is the suitability map documenting suitable habitat for lions both during the day and at night. Figure 5.15 has been created to show the suitable habitat that is available for lions during the daytime. Figure 5.16 has been created to show the suitable habitat available for lions at night. Lion data (tracks and sightings) have been overlaid (in white circles) on these maps in addition to settlement locations within WGCC (in red circles).

Figure 5.15 shows that highly suitable habitat for lions during the day includes the CA, all areas bordering SNR, and all along the Ewaso Nyiro River as well. However, further upstream, the area of high suitability reduces as shown by the thinner band of dark green as you approach Remot. Between Lpus Leluai and Sasaab, there are pockets of medium suitability including the northern most point of the boundary of SNR and WGCC. Areas around Naisunyai and Loijuk all contain medium suitability areas. The northern most sections of WGCC are all low suitability areas, which include the locations of Sukuroi, Remot and Lempaute, and the edge of Ngutuk Ongiron. There were no areas that were classified as unsuitable for lions during the day within the whole of WGCC.

By comparing these areas of suitability with areas where lions were sighted (both tracks and sightings), all the sightings in the CA are in areas of high suitability. Additional records of lions include along the Ewaso Nyiro River in areas of high suitability. However, lions were also seen in areas of medium suitability such as in areas around Ngutuk Ongiron (showing a limited number of lion records), and in low suitability areas in the region between Lempaute and Loijuk (showing more lion records).

Figure 5.16 shows the suitable habitat available for lions at night. Overall, there is more high and medium suitability habitat compared to during the day and less habitat containing low suitability locations. Areas all along the River contain highly suitable habitat. Areas around the Sasaab location that contained medium suitability habitat during the day are all highly suited to lions at night and there is now a contiguous section between the CA and the boundary to SNR that contains highly suitable habitat, including the Lpus Leluai location. There is only a small tip at the northern boundary of WGCC to SNR that contains medium suitability habitat. Some areas that contained low suitability habitat during the day are now more suited at night, for example the region around Loijuk. Areas of low suitability persist in the northern section of WGCC, namely in and around the locations of Sukuroi and Remot. The majority of the lion records fall in regions of high and medium suitability at night. Very few lion records fall in the low suitability areas.

Figure 5.15. Habitat Suitability Model for lions during the daytime

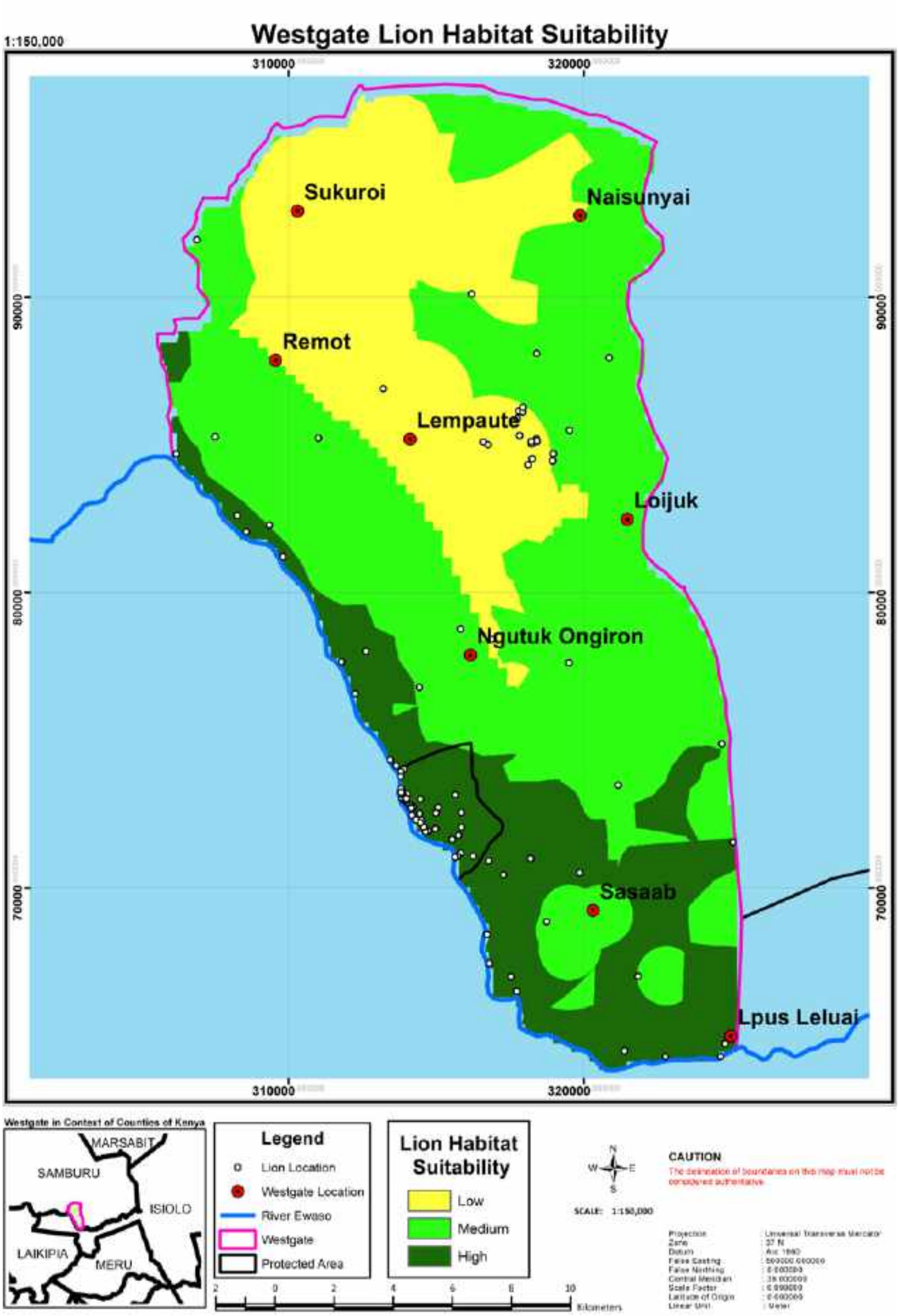


Figure 5.16. Habitat Suitability Model for lions during the nighttime

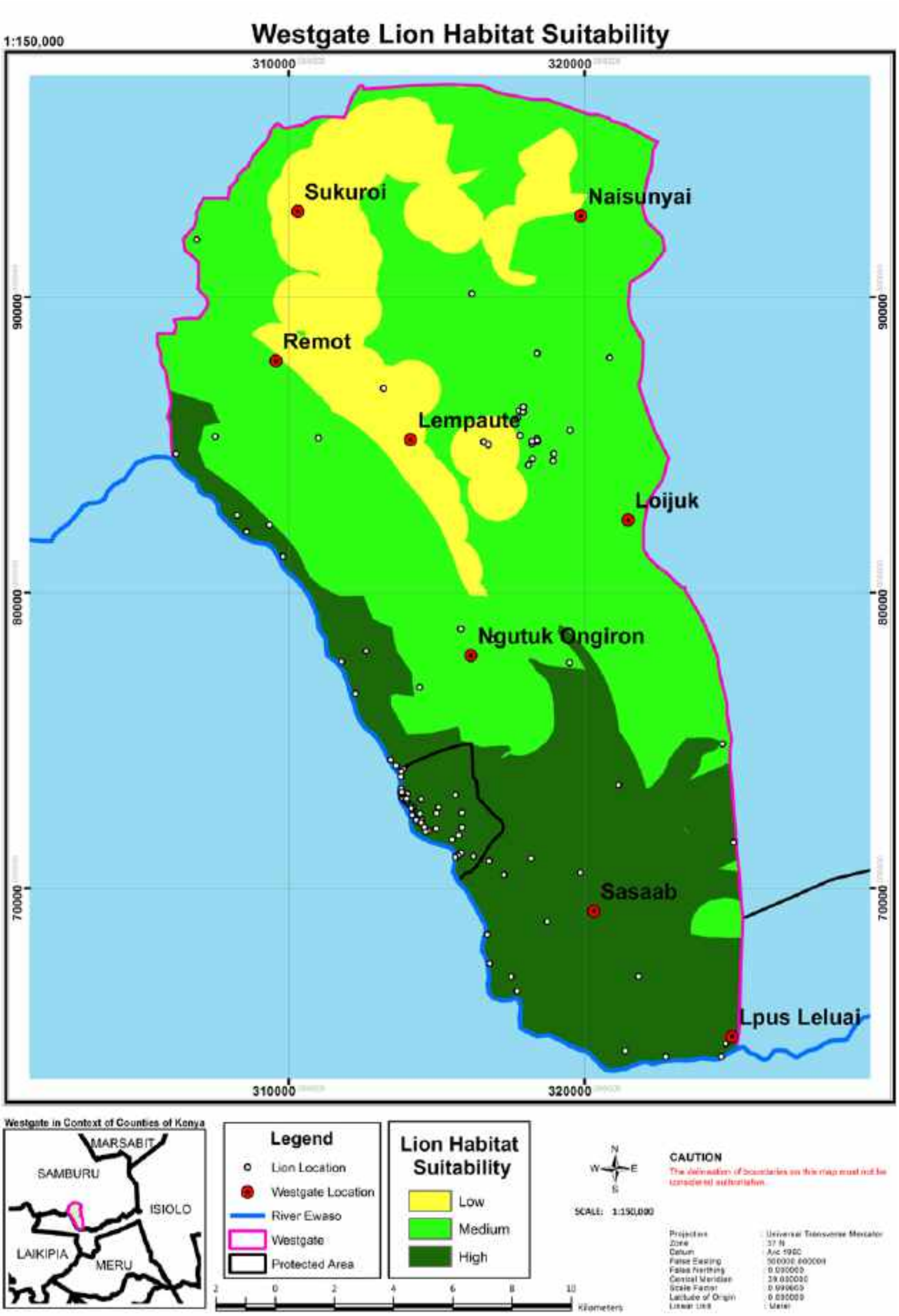


Table 5.14 shows the percentage of suitable habitat during the day and night as calculated from the final outputs.

Table 5.14. Suitable habitat available during the daytime and nighttime

Model	Highly Suitable area (km^2) (% of study area)	Medium Suitable area (km^2) (% of study area)	Low Suitable area (km^2) (% of study area)
Daytime	82 (20.6%)	207 (51.9%)	110 (27.6%)
Nighttime	118 (28.9%)	223 (54.5%)	68 (16.6%)

Overall, the distribution of the highly suitable habitat for lions covers less than 30% of WGCC. However, there was an increase in the extent of highly suitable habitat between day and night. In total 82 km^2 (20.6% of WGCC) emerged as highly suitable during the day and 118 km^2 (28.9% of WGCC) emerged as highly suitable during the night. Of this, 9 km^2 was within the CA during both day and night. Medium suitability habitat also increased between day and night, from 51.9% to 54.5% of the total study area. Comparing the day and night model, the extent of low suitability habitat reduced from 27.6% to 16.6% of the total study area.

Table 5.15 shows the number of lion records (n=253) that fall within the different suitability types during the day and night as calculated from the final outputs.

Table 5.15. The number of lion records (tracks and sightings) per suitability type

Model	Highly Suitable area (% of total)	Medium Suitable area (% of total)	Low Suitable area (% of total)
Daytime	170 (67.2%)	56 (22.1%)	27 (10.7%)
Nighttime	173 (68.4%)	75 (29.6%)	5 (1.98%)

Table 5.15 clearly indicates that the majority of all lion records in WGCC during the day (67.2%) and night (68.4%) were in highly suitable areas. 22.1% of all lion records were in medium suitability areas for the daytime model and 29.6% for the nighttime model. Only 10.7% of all lion records were in low suitability areas for the daytime model and 1.98% for the nighttime model. Out of the lion records located within highly suitable areas, 25% of these were located within the CA.

5.3.4. Results showing livestock depredation incidents overlaid on the daytime and nighttime models

Looking at the final day and night outputs of suitable habitat available for lions, Figure 5.17 and Figure 5.18 show the suitability overlaid with livestock depredation incidents (shown in small red circles) within WGCC. The purpose of this is to investigate whether human-lion conflict takes place in areas of high suitability for lions or areas of low suitability. It is expected that in areas of high suitability for lions, human presence and activity is low and therefore conflict would be low as well. Overall livestock depredation results are first explained.

Between 2007 and 2013, 326 livestock depredation reports were collected in WGCC. 8.7 attacks/10 km^2 were reported during the study period, averaging 1.75±0.56 attacks/year/10 km^2. Out of the 326 reports gathered, 16% (n=63) were attributed to lions. 87% (n=55) of lion attacks on livestock took place away from livestock enclosures, when livestock were lost (n=15) or grazing (n=40). All the GPS referenced locations were mapped using the UTM 37N coordinate projection system.

Figure 5.17 shows the conflict incidents that took place within WGCC overlaid on the daytime HSM. Conflict occurred in areas where there were lion records present, with incidents taking place in high, medium and low suitability areas for lions. Conflict occurred in the CA, between Lempaute and Loijuk, with other incidents scattered throughout WGCC. Table 5.16 shows that the number of incidents (daytime model) that took place in areas of high suitability (n=18) were more compared to other areas of medium suitability (n=13) and low suitability (n=8).

Figure 5.17. Habitat Suitability Model (day) overlaid with lion records and all conflict incidents

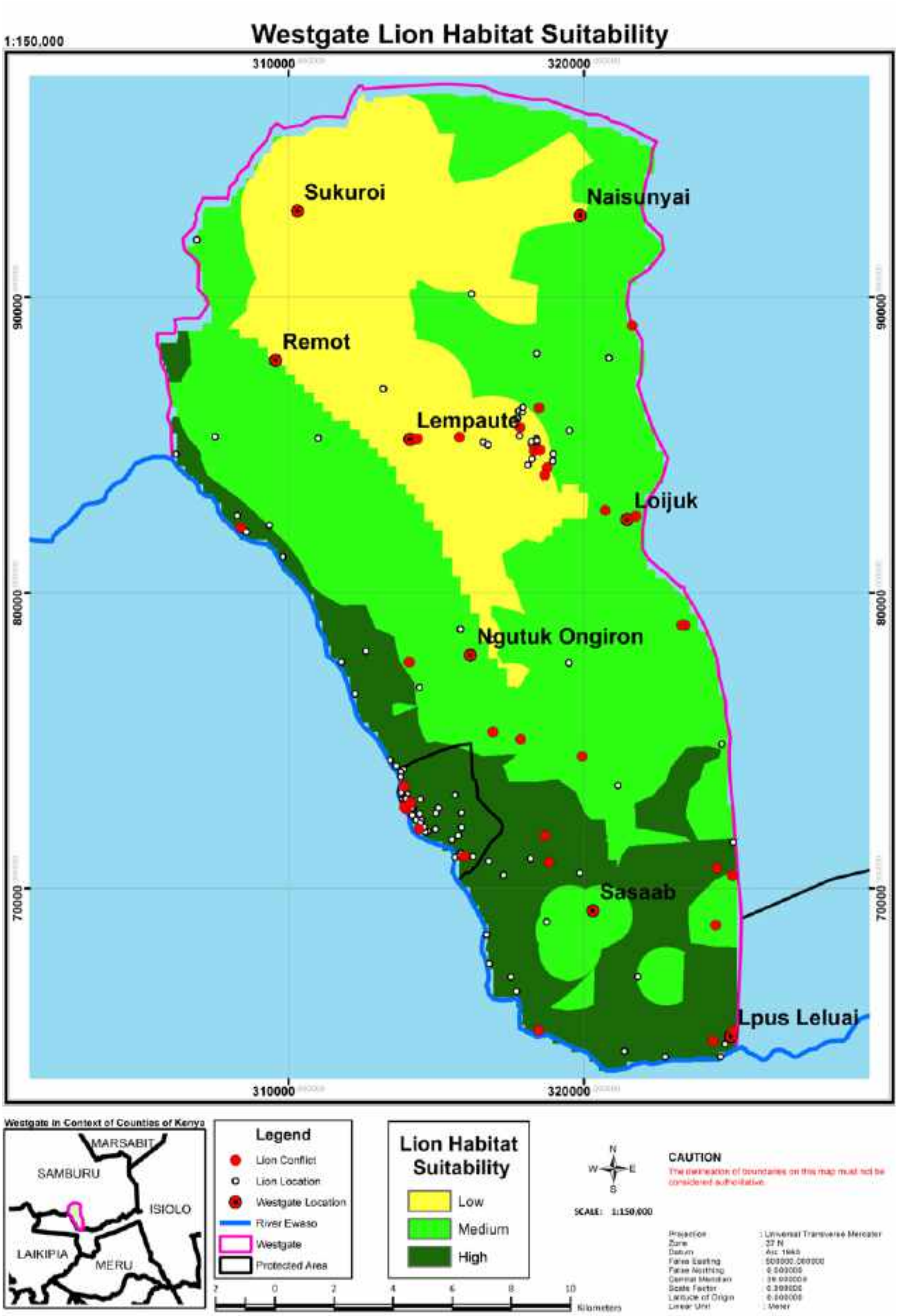


Figure 5.18. Habitat Suitability Model (night) overlaid with lion records and all conflict incidents

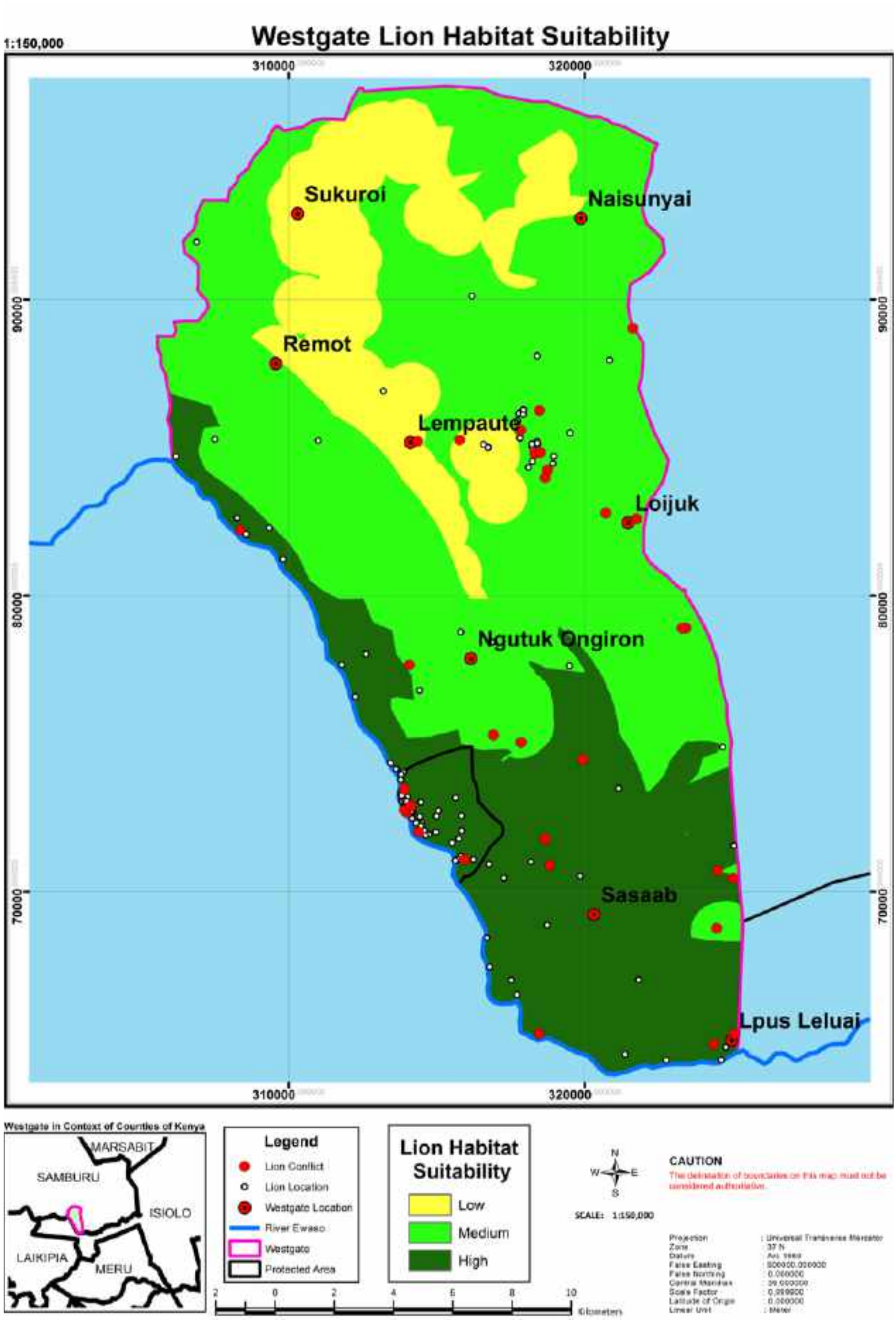


Figure 5.18 and Table 5.16 shows that overall, most of the conflict incidents (nighttime model) are located within high (n=19) and medium (n=18) suitability areas, with only two incidents in low suitable areas.

Table 5.16 shows the number of conflict incidents (n=39) located within each suitability type.

Table 5.16. The number of conflict incidents per suitability area during day and night

Model	Highly suitable area (% of total)	Medium suitable area (% of total)	Low suitable area (% of total)
Day	18 (46.15%)	13 (33.3%)	8 (20.5%
Night	19 (48.7%)	18 (46.15%)	2 (5.1%)

Overall, there was conflict recorded in most parts of WGCC except the northern most sections of WGCC including Sukuroi, Remot and Naisunyai, where the number of lion records was also very low. Interestingly, there were six incidents of conflict (15% of total lion conflict in WGCC) that took place within the CA indicating that livestock encroachment was a problem. Five of these conflict incidents took place during the day and one at night. Eleven conflict incidents took place within the low and medium suitability areas between Lempaute and Loijuk. This correlates to the number of sightings and tracks of lions that were seen in this area, that were high as well (n=37).

The day and night models reveal that the conflict incidents that took place between Lempaute and Loijuk were in medium suitability areas at night, in contrast to during the day when they were in low suitability areas. For these reasons, it is important to look at the timing of the conflict incidents and whether livestock were attacked during the day or night. The timing of conflict incidents have been overlaid on the daytime HSM and the nighttime HSM (Figures 5.19 and 5.20).

Figure 5.19. Conflict incidents that took place during the day (n=30) overlaid on the day HSM

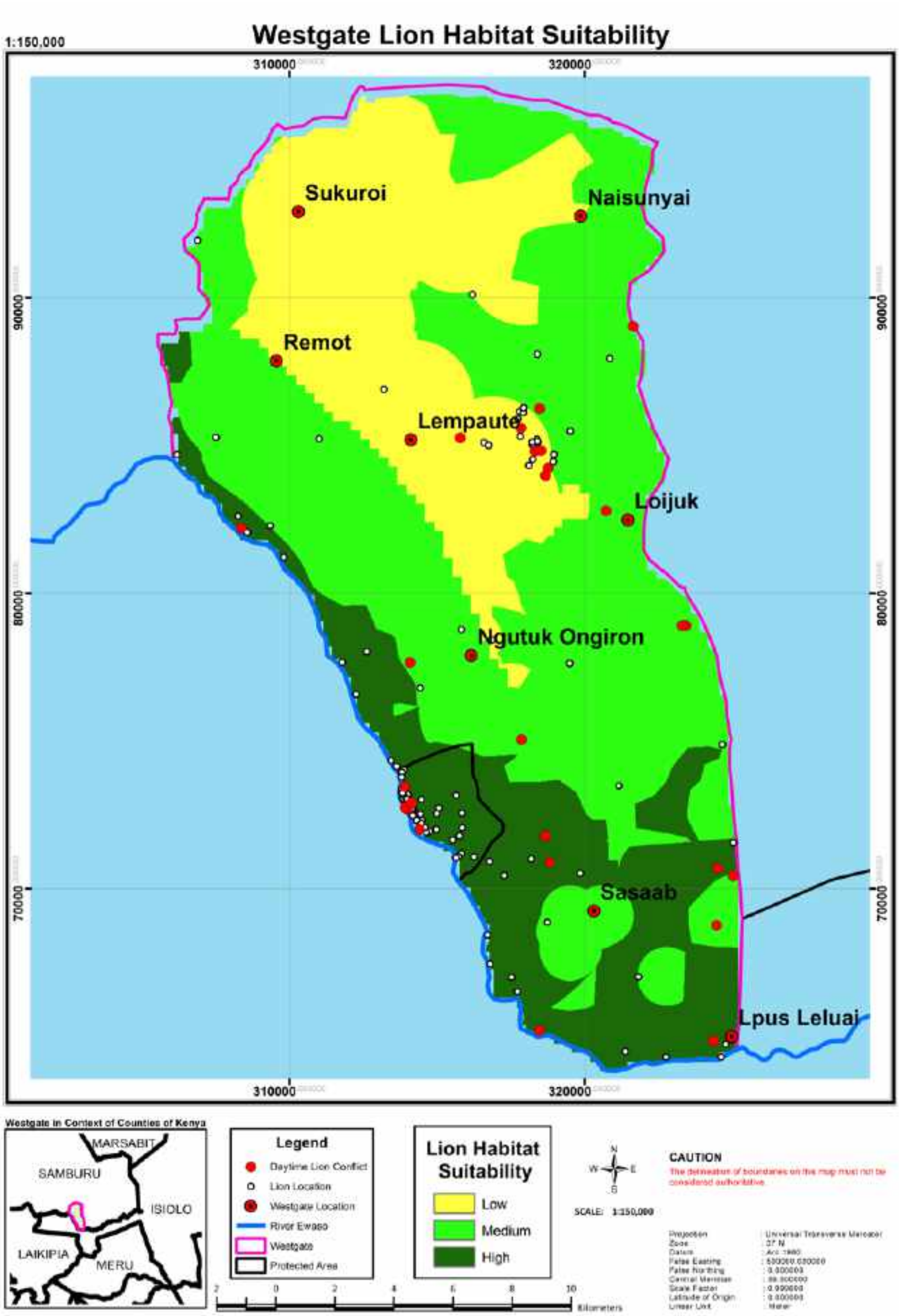


Figure 5.20. Conflict incidents that took place during the night (n=8) overlaid on the night HSM

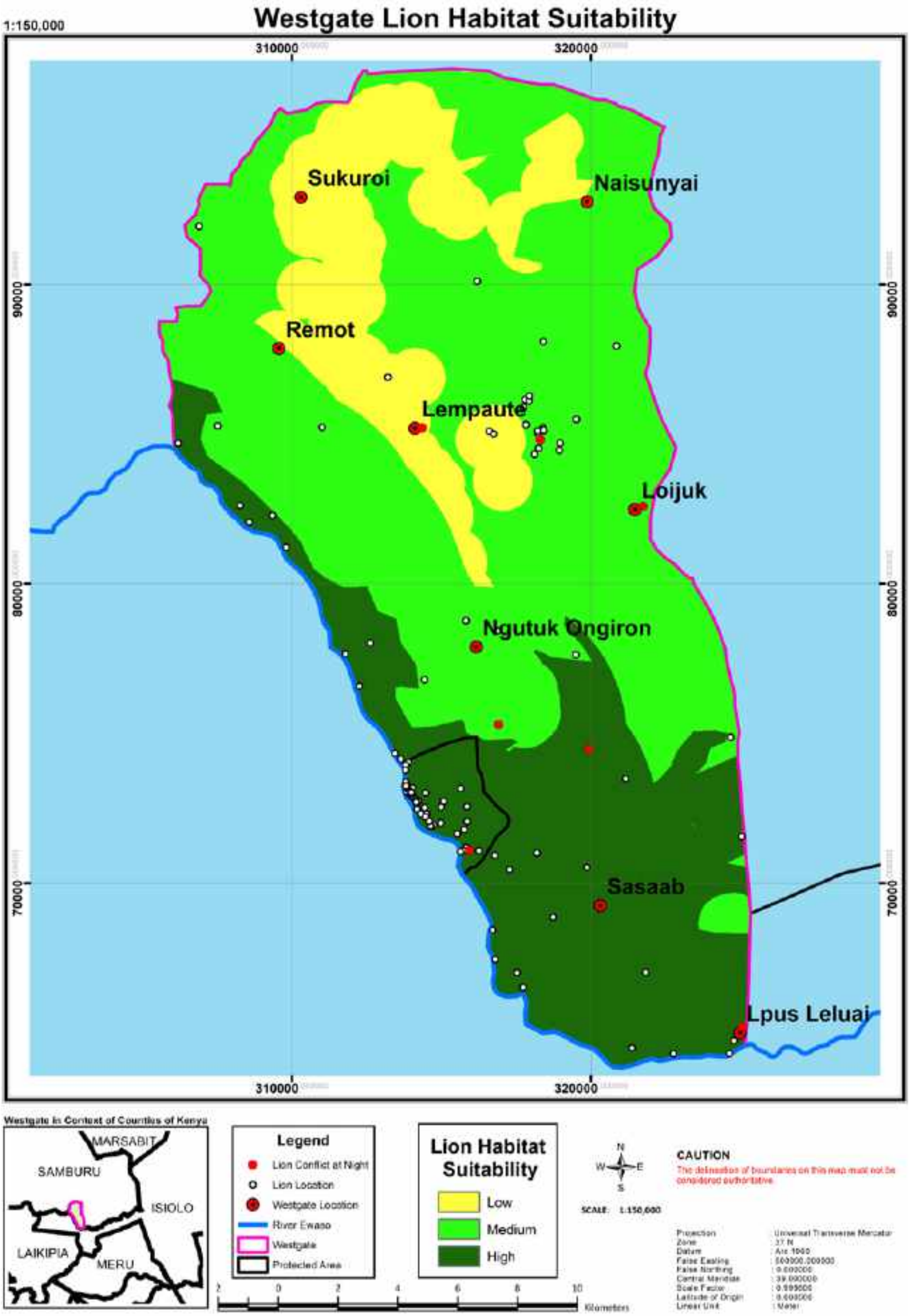


Figure 5.19 shows that conflict incidents that took place during the day occurred in all areas of suitability. Conflict mainly occurred in the CA, and between the CA and Sasaab, in areas of high suitability. In areas of medium suitability, conflict occurred near the boundary to SNR (the northern tip), and conflict in areas of low suitability took place in the region between Lempaute and Loijuk.

Figure 5.20 shows that conflict incidents that took place at night occurred in mainly high (CA and Lpus Leluai) and medium suitability areas (Loijuk and between Lempaute and Loijuk) with one incident in an area of low suitability (Lempaute).

Out of 39 conflict incidents, 30 incidents took place during the day and eight at night, with one incident's timing unrecorded. Table 5.17 shows the number of day (n=30) and night (n=8) conflict incidents that took place per habitat type. Most of the day and night conflict incidents took place in highly suitable habitat for lions (day=14 and night=4), with the least number of day and night conflict incidents taking place in low suitability habitat.

Table 5.17. The number of day and night occurring conflict incidents per habitat type

Conflicts	**Highly suitable area**	**Medium suitable area**	**Low suitable area**
Day incidents	14	10	6
Night incidents	4	3	1

The region between Lempaute and Loijuk appears to be important for lion conservation as it displays areas of low suitability, and when lions are present here, conflict is shown to be taking place. Of the 11 conflict incidents in this area, seven took place during the day while three took place during the night (one incident's timing was not recorded). The boundary to SNR displayed seven conflict incidents, with six taking place during the day and one at night. Another region of importance is the CA and despite it displaying an area of high suitability both during the day and night, conflict has been recorded as occurring here mainly in the daytime due to livestock encroachment.

5.3.5. Summary of key results

i. There was an increase in the amount of highly suitable habitat available for lions at night compared to during the day, with more medium suitability habitat available for lions at night compared to during the day and less low suitability habitat for lions available at night compared to during the day.
ii. The region between Lempaute and Loijuk which contained low suitability habitat during the day emerged as medium suited at night.
iii. The CA emerged as highly suitable for lions both during the day and night.
iv. Most of the lion records collected were in areas of highly suitable habitat (both day and night).
v. Most of the livestock depredation incidents took place during the day.
vi. The highest number of livestock depredation incidents took place in areas of highest suitability for lions – for both the day and night models.
vii. Out of the total number of livestock depredation incidents that took place during the day and night, most of them occurred in high suitability areas.
viii. 15% of all lion conflict in WGCC took place inside the CA. 83% of these took place during the day.
ix. There were seven livestock depredation incidents that took place on the boundary of SNR (18% of total lion conflict in WGCC). 86% of these took place during the day.
x. The region between Lempaute and Loijuk is highlighted as an area for concern where 28% of WGCC's total lion conflict took place in low and medium suitability areas for lions, with 64% taking place during the day.

5.4. Discussion

5.4.1. Introduction

Expanding human populations often results in fragmentation of suitable wildlife habitat and increased occurrences of human-carnivore conflict (Nowell and Jackson, 1996; Macdonald *et al.,* 2010). In the Samburu-Isiolo ecosystem, despite the fact that the small protected areas are more susceptible to the lethal effects of conflict (Woodroffe and Ginsberg, 1998), providing safe habitats at a small scale around the protected areas can still be effective and this will ultimately improve the viability of the protected areas in the long-term.

In this study, an HSM was used as a tool to establish the availability of suitable habitat for lions during the day and night within WGCC by looking at their preferences temporally. Models are considered very helpful in identifying areas of importance for lions in community areas and can assist with future conservation planning strategies (Abade *et al*., 2014).

GIS based MCDA was used to create the HSM. However, using MCDA does pose some disadvantages (Greene *et al.,* 2011).

i. The variety and complexity of MCDA methods means that this extensive set of tools is often not easily accessible to users.
ii. The decision makers may have vastly varying assumptions and this could lead to biases in the technique.
iii. Although the use of MCDA continues to expand, it has not yet received widespread acceptance and is often considered to be only an element of spatial support.

Despite the highlighted disadvantages, MCDA's greatest strength is its ability to simultaneously consider both qualitative and quantitative criteria, and its techniques can be designed for individuals and applied in group decisions (Greene *et al*., 2011). MCDA can also be used to understand spatial problems and its growth and applicability has increased in environmental fields. If well applied, MCDA can be successfully used by conservationists to determine the suitability of proposed wildlife areas, as well as determining suitable locations in underutilised areas (Amoke, 2012).

5.4.2. Suitable habitat for lions

It is essential that refuge habitats are available for lions to persist within human-occupied landscapes (Schuette *et al.,* 2013; Oriol-Cotterill *et al*., 2015b). Other global studies looking at suitable habitat for carnivores in human-occupied landscapes had similar findings after using various modelling techniques to understand carnivore habitat. Gavashelishvili and Lukarevskiy (2008) used a GIS model to look at leopard habitat selection in west and central Asia. Results from their model showed that leopards avoided deserts, areas with snow cover that persisted, and areas near urban settlements. The model used can predict corridors and connectivity patterns. The study also used presence/absence data but failed to incorporate prey densities as the data was not available in adequate form (similar to this study). Imam *et al*., (2009) used a GIS model and results indicated that 50% of the forested areas within Chandoli National Park in India were suitable for tigers and were deemed appropriate for consideration for a Tiger Reserve. The Chandoli National Park was later classified as a Tiger Reserve, reflecting that the model developed was not only statistically sound but can be considered during wildlife management decision making. Hatten *et al.,* (2003) created an HSM for jaguars in Arizona. Through an extensive literature review, they looked at what variables influenced jaguars. Similarly to lions, they learned that jaguars had a close association with water, preferred dense cover, required sufficient prey and avoided highly disturbed areas. Results indicated that there was between 21% to 30% of suitable habitat for jaguars in the state of Arizona.

This study showed that there was between 20% and 29% of highly suitable habitat (for both day and night) within WGCC. Cotterill (2013) found that 34% of the Laikipia region where the study was conducted was highly suited for lions. Laikipia ranches differ from community areas such as WGCC, as most of the ranches are fenced and have limited pastoralist settlements. The majority of the suitable habitat for lions, during both the day and night, was within the CA, the region between the

CA and the boundary to SNR, and along the Ewaso Nyiro River. The majority of the lion records were located within this highly suitable habitat. Schuette *et al.,* (2013) also found that lions in the Shompole region of southern Kenya increased their use of the Conservation Area and thick bush when people were in the vicinity and also to avoid settlements. This adjustment in response to human presence reduced the lion's access to permanent water but not to prey. However, in Ruaha National Park, a protected area in Tanzania, suitable habitat for lions was found to be influenced by proximity to water (Abade *et al.,* 2014). In this study, the highly suitable habitat is shown to follow the Ewaso Nyiro River, providing lions access to water. The section along the boundary to SNR is all highly suited both during the day and night and is considered to be an important area for lions that move between SNR and WGCC frequently.

The areas of high suitability habitat for lions were all in regions where there was dense cover. Lions in ranches in the Maasai Mara ecosystem were also noted to prefer thick bushes compared to open plains (Mogensen *et al*., 2011) and would only venture onto open plains when there was reduced pressure from livestock and herders. Elliott *et al.,* (2014) also found that lions selected for bushland and avoided settlements in Hwange, Zimbabwe. This highlights the fact that dense cover is not only necessary for hunting success, but is also an important feature in providing a refuge from potential encounters with people and livestock.

Overall, there was increased high and medium suitability habitat available for lions at night compared to during the day and less low suitability habitat for lions available at night compared to during the day. Despite vegetation cover having a higher weighting influence during the day, the comparison between day and night did not reveal much change in suitable locations with respect to vegetation cover. However, there was a change with respect to proximity to settlements; locations such as the CA had some areas of low suitability habitat during the day due to its close proximity to Ngutuk Ongiron and areas along the SNR boundary were unsuitable due to their close proximity to Lpus Leluai and Kiltamany settlements. However, at night, the CA and SNR boundary emerged as highly suited with respect to proximity to settlements, and the region near Sasaab, which was of medium suitability during the day, also emerged as highly suitable at night. This indicated that settlements may have played a role in determining the suitability of habitat in areas such as the CA and along the SNR boundary. Settlement locations may also have played a role in the region between Lempaute and Loijuk which contained low suitability habitat during the day but emerged as a region of medium suitability at night. This region was unsuitable with respect to vegetation cover during the day and night, showing that the sparse vegetation cover had a lower influence on lion habitat compared to settlement locations.

Additionally, the region around Sasaab varied between day and night where it contained a ring of medium suitability habitat during the day but was highly suited at night. The variation was reflected in Figure 5.9 and Figure 5.10 (distance to protected areas). During the day, being closer to protected areas is better for lions due to the potential disturbance from the presence and activity of people, whereas at night, lions are able to move further away from protected areas due to reduced human activity. Oriol-Cotterill *et al.,* (2015a) found that in the Laikipia region, lions would only come close to settlements in the safety of darkness when people were confined to settlements and human activity was at its lowest. Lions were able to adjust their behaviour in response to the risk of human caused mortality. A recent study by Loveridge *et al.,* (2016) reported that lions will avoid risky areas and make behavioural decisions based on perceptions of risk.

5.4.3. Conflict mapped within the suitability models

The requirements of large carnivores often conflict with those of local people (Woodroffe, 2000). Most of the livestock depredation incidents within WGCC took place during the day in areas of highest suitability for lions (as shown in both the daytime and nighttime models). This suggests that lions utilise these areas, but that livestock are also present as conflict is taking place. An area of concern is the CA where conflict took place. Despite the fact that the CA has been set aside for wildlife, and livestock are excluded, livestock encroachment is a concern especially when the number of conflict cases are examined in this highly suitable area for lions. Daytime livestock encroachment needs to be controlled to avoid conflict from taking place. In contrast, in the Shompole region in southern Kenya, Schuette *et al.,* (2013) found that conflict was very low because when people were in the vicinity, lions would make use of dense cover and the Conservation Area. This highlights the fact that areas that have been set aside for wildlife such as Conservation Areas, need to remain livestock free, as that is exactly what will promote coexistence as Schuette *et al.,* (2013) further states. Another area of high suitability was the boundary of SNR where conflict occurred as well. The extent of livestock depredation may be closer to protected areas boundaries where resident large carnivores may be more in number compared to further away within the human-occupied landscape (Ogutu *et al.,* 2005; Western *et al.,* 2009).

Conflict incidents also took place during the day in areas of low and medium suitability, such as in the region between Lempaute and Loijuk which has also been highlighted as an area for concern. Lions are known to attack livestock at any time during the day, either whilst livestock are grazing or in *bomas* (Patterson *et al.,* 2004; Woodroffe *et al.,* 2007). This emphasizes the need to improve or implement conflict mitigation measures in such areas to reduce the occurrence of conflict when lions move through these less suitable areas. Abade *et al*., (2014) found that if there were areas of low suitability near park boundaries, this can help identify areas of potential conflict where mitigation measures can be put in place.

Schuette *et al.,* (2013) found that the creation and setting aside of Conservation Areas was very effective in providing important habitat for wildlife and reducing conflict, and noted that due to shifts in the grazing patterns of livestock and subsequent adjustment of lion movement, there was no increase in conflict. Schuette *et al.,* (2013) further noted that carnivores can persist with people and livestock, even at high densities, and an unfenced, open landscape allowing such adjustments of grazing and movement of lions, can promote this.

Despite conflict taking place across all levels of habitat suitability, only one lion was killed in retaliation to livestock loss (April 2010). Outside of this study area, livestock loss has led to considerable numbers of lions being killed. Between 2009 and 2012, 17 lions that were part of a research study were killed by local people in the neighbouring Laikipia County (Oriol-Cotterill *et al.,* 2015a) and Woodroffe and

Frank (2005) found that the retaliatory killing of lions in the same region reduced the lion population by approximately 4% per year.

Possible reasons for the lack of retaliatory killing could be that lions are not the main animal that causes depredation and so are tolerated or the local people have less of a propensity to kill lions in these high conflict areas. Two studies were conducted by students affiliated with the (Ewaso Lions Project) ELP and investigated these topics:

i. Spira (2014) found that out of 443 depredation incidents, only 16% were attributed to lions, whereas leopard and spotted hyaenas caused more conflict. Leopards and spotted hyaenas appear to be the most problematic carnivore as Kolowski and Holekamp (2006) and Woodroffe *et al.,* (2007) found, and are more abundant than any other large carnivore.
ii. Additionally, Maggi (2014) found after conducting surveys with 200 people across WGCC, the majority of respondents would either never kill a lion after it killed livestock or would only kill it after a threshold was reached of the number of livestock lost.

Out of the lion attacks on livestock, 29% were on camels, 19% on cows, 17% on donkeys and 32% on shoats (goats and sheep) (Spira, 2014). Cows and camels are direct indicators of wealth and have a higher financial value than shoats or donkeys. Cattle and camels are also used as gifts during weddings and thus have a larger cultural significance (Spencer, 2004). The fact that the livestock (shoats) killed most frequently were not as financially valuable may be another reason why the presence of lions was tolerated.

Furthermore, the results of a detailed questionnaire survey conducted within WGCC (Gurd, 2012), found lions were ranked 5th – behind spotted hyaena, wild dogs, leopards and elephants – as a species local people would prefer not to be present in the Conservancy. Despite this, attitudes towards the conservation of carnivores remained very positive, supported by a relatively high tolerance stated for all carnivores, except spotted hyaena, which contrasts with other pastoralist communities (Gurd, 2012). However, the lion population in WGCC is low and if this were to change, a concomitant change in tolerance might also occur.

Overall tolerance thresholds were high throughout WGCC, including the Lpus Leluai and Sasaab locations (Maggi, 2014). These locations are the closest to SNR and lions traverse through these areas when they disperse from the protected area. The local people here are tolerant towards the presence of lions and livestock loss. On the other hand, results from Maggi (2014) showed that the local people within the Naisunyai location had no tolerance at all for livestock loss to lions. Figures 5.17 and 5.18 show Naisunyai as having no conflict taking place here. Therefore, despite this area hosting low and medium suitability areas for lions, conflict is low.

The results from Maggi's 2014 study were encouraging as they indicated that people in WGCC could be more tolerant than expected of dispersing lions even if their livestock were killed, except in Naisunyai. The fact that people in WGCC were more tolerant to losing livestock compared to other areas included in this specific study, could perhaps be related to the presence of the ELP and the community programmes that have been established to promote coexistence. This is supported by Gurd's study in 2012 where community members agreed that their tolerance levels towards lions had improved as a result of the ELP.

It appears that human-lion conflict is not a main factor preventing lions from persisting within this pastoralist-dominated area. This infers that other factors such as settlement locations and human activity may have a greater influence on the presence and persistence of lions in WGCC. It is known that in areas where there are settlements and livestock grazing, mammal diversity and densities are kept low (Caro, 1999; Ogutu *et al.,* 2016). Georgiadis *et al.,* (2007) also reported that in Laikipia, increasing numbers of sheep and goats contributed to wildlife declines, as does Ogutu *et al.,* (2016) – see section 2.3.3. A report published in 1983 (Stiles, 1983), stated that environmental degradation in Samburu was caused by the increasing human population, and Saidia (1991) concurred with this and added that pressure from the government to develop pastoralist areas and become more sedentary contributed to environmental degradation.

5.4.4. Recommendations for Westgate Community Conservancy

Various components of this HSM have already been implemented as a guide to policy for lion conservation action within this ecosystem. This has been presented in italics below. The following recommendations are directed towards WGCC with a view of improving the effectiveness of safe refuges for carnivores:

i. Regular patrols by scouts and warriors should be conducted to prevent livestock encroachment and disturbance from communities within the CA, including to ensure that thick habitat is not burned by the local people as this thick cover is essential in keeping lions safe, away from human disturbance. *This has happened on a regular basis since results of this HSM were presented back to the scouts and management team of WGCC.*

ii. Overall, all disturbance within the CA, which is a highly suitable area for lions, should be minimised. This includes the prohibition of visitors/tourists from camping or walking within the boundaries of the CA, and other areas of high suitability for lions. Additionally, firewood should not be collected from any areas of high suitability for lions as this leads to further removal of habitat and disturbance from the people collecting firewood. *A policy document has been drawn up regarding disturbance within the CA outlining places where tourism activities can take place (outside of the CA).*

iii. Vehicles should keep to the main roads and tracks to reduce disturbance to lions in all areas of high suitability.

iv. Pastoralists who are migrating from Mpus Kutuk Conservancy (see Appendix 1) to WGCC, should be encouraged to travel adjacent to the CA and settle in an identified area outside the boundaries of the CA. For this to be implemented successfully, close communication and dialogue between the management boards of WGCC and Mpus Kutuk is essential. *A meeting with Mpus Kutuk board has been arranged to discuss this in early 2017.*

v. In all areas of high suitability for lions in WGCC, scouts and warriors should provide adequate space for the lions rather than following them closely during their routine patrols and data collection activities. *This has been discussed at a scouts meeting in 2016 and implemented.*

vi. The conservation importance of all areas of high suitability (CA, areas between CA and SNR, and all along the River) need to be explained and management of these areas discussed with the local people at meetings. *Since the HSM was developed, there have been numerous meetings with the local community regarding the areas of high suitability. Encroachment has been better controlled and conflict in areas between the CA and SNR has also reduced.*

vii. Settlement planning is vital in WGCC to ensure that settlements are not sited too close in the first instance and, where already established, do not expand to identified areas of high suitability. Settlements in Ngutuk Ongiron in particular have been observed to be increasing in number along the main road towards the CA. *Since the development of the HSM and the presentation of results back to the management of WGCC, there have been no additional settlements along the main road and settlement planning is a core topic now frequently discussed at WGCC management meetings. This has also been incorporated in WGCC's management plan (2017-2021).*

viii. The corridor between the CA and the Buffer Zone needs to remain open (see Figure 5.7). *Since the development of the HSM and the presentation of results back to the management of WGCC, this corridor has remained open and is always discussed at WGCC management meetings.*

ix. Conflict mitigation measures should be implemented in areas of low suitability for lions where conflict is taking place for example the region between Lempaute and Loijuk. Such measures include better daytime livestock husbandry (as most of the conflict is taking place during the day). *The ELP team has recently set up a permanent outpost in this region to implement measures to address conflict.*

5.4.5. Recommendations for adjacent and neighbouring Conservancies

The following recommendations are directed towards the adjacent and neighbouring Community Conservancies:

i. Baseline data should be collected in each of these Conservancies by scouts and warriors following transects to collect information on herbivores, carnivores and livestock in a systematic and appropriate manner to ensure high quality data that can be used for modelling. Settlements should be mapped in each Conservancy, together with counts of the number of people and their livestock to monitor change.

ii. Modelling, such as this study's HSM, should be run to identify areas of high, medium and low suitability for lions in the different Conservancies.

iii. Based on the outputs of these models, the management of areas of high suitability for lions should be discussed with the residents of the Conservancy to see whether there is potential for the creation of Conservation Areas. These safe refuges or Conservation Areas need to contain sufficient cover, a healthy prey base, access to water, and be located away from settlements. The size of these resulting safe refuges will be dependent on the number and distribution of settlements, number of people and livestock and the overall size of the Conservancy.

iv. Baseline data should be collected in the designated Conservation Areas before they are well established. This will allow for a measure of effectiveness of the Conservation Areas.

v. A Conservation Area in Mpus Kutuk Conservancy (see Appendix 1) should be set up directly across from WGCC's Conservation Area to ensure that there is contiguous high suitability habitat available for lions on either side and along the Ewaso Nyiro River. This will help alleviate livestock encroachment problems that WGCC's Conservation Area currently faces and increase the size of the safe habitat for lions.

vi. Settlement planning should be implemented in each Conservancy which is deemed suitable for lions and other large carnivores. People should be discouraged from locating near the Conservation Areas or areas of high suitability for lions since this inevitably will lead to the problem of livestock encroachment and potential of conflict.

vii. Community meetings should be held in each Conservancy to discuss the importance and relevance of safe habitat and Conservation Areas. The impact that livestock encroachment has on these areas of high suitability for lions should be explained as this leads to more conflict as shown in this study.

viii. Despite the fact that current Conservation Areas in Conservancies were initially established for tourism purposes (*pers. comm.* Jeff Worden), it is argued here that these areas are more beneficial for providing safe habitat for lions and other carnivores, and providing areas of connectivity between Conservancies. Numerous Conservancies in northern Kenya do not currently have tourism potential and this should not be perceived as a hindrance by the communities to setting aside highly suitable habitat for lions in the form of safe refuges or Conservation Areas. However, in areas where there is potential for tourism, Conservation Areas or areas of highly suitable habitat for lions could provide tourists with access to game viewing in a natural wildlife setting although proper game viewing etiquettes need to be adhered to prevent disturbance to the already nervous carnivores.

ix. Currently only six out of 27 Conservancies have Conservation Areas. To maintain connectivity of lions and other carnivore populations, and to provide regions for their safe dispersal, it is recommended that additional high suitability areas in the form of Conservation Areas be established in each Conservancy. Several Community Conservancies link Laikipia and Samburu Counties (see Appendix 10 for a map showing lion dispersal between Laikipia to Samburu and the Conservancies they traverse through).

5.4.6. Conclusion

The influences of the landscape's features and anthropogenic factors in WGCC created a mosaic that varied between day and night with respect to suitable habitat for the area's lion population. Having suitable habitat for lions in WGCC will, to some extent, ease the pressure on lions in the area and their long-term persistence is contingent upon adequate settlement planning, effective core areas and lion refuges. Although protected areas often serve as ecological sources whilst neighbouring community lands often act as ecological sinks, Community Conservancies in northern Kenya could potentially function as sources, especially if suitable habitat can be created for lions. Considering the extensive network of Community Conservancies in northern Kenya, models such as the one created in this study should be replicated to ascertain whether contiguous high suitability lion habitat can exist not only in individual Conservancies, but between connected ones. Highly suitable habitat will help guide the establishment of safe refuges or Conservation Areas within these Conservancies. These areas will provide wildlife with a safe region away from the threats posed by humans and their livestock. If located in suitable habitat for carnivores, not only is conflict reduced but lions and other carnivores are able to move from one safe area to another in an otherwise human-occupied landscape. This is what will encourage human-carnivore coexistence in this region. Lions are able to recover quickly from the impacts of anthropogenic factors as long as conditions improve for them, such as reduced human pressure and sufficient prey availability in the form of safe refuges. Conservation practitioners should consider various anthropogenic and biophysical factors when addressing lion conservation across the landscape. Otherwise, edge effects and even reserve pride mortality could lead to population declines. Factors such as drought and livestock encroachment are threats that need to be addressed, and collaborating with local people who coexist with lion populations is the best method for designing conservation measures that will have lasting success.

Chapter 6

Final Discussion

"The realistic conservationist should recognise that the present range for the lion in Africa could be reduced to a string of isolated patches before the end of the century. Whether that is sufficient to guarantee the lion a future in the wild is doubtful."

Norman Myers, The Silent Savannahs, 1975

6.1. Final discussion

6.1.1. Introduction

Lion numbers are decreasing within Africa, mainly due to habitat loss and conflict with humans (Woodroffe and Ginsberg, 1998; Bauer and Van der Merwe, 2004; Hazzah *et al*., 2009; Riggio *et al*., 2013). Knowledge of current lion numbers, their movements and distribution is vital for the effective conservation and management of the species, and is required for defining strategies and setting conservation priorities. Protected areas are important for lions as these are areas where human caused mortality is at a minimum and are often known as the source for lion populations (Didier *et al.,* 2009). The protected areas in this study were highlighted as regions of high importance for lions (see section 2.4.2.), however, the human-occupied landscape surrounding these protected areas is also essential for lion survival (Nowell and Jackson, 1996).

The overall goal is to reduce human-lion conflict and to secure a future for lions in northern Kenya. Considering the lions' wide ranges and their presence within the human-occupied landscape, the lack of habitat and sufficient prey, this study is crucial to understand the survival of lions in northern Kenya. This thesis has in the first instance described the lion population parameters within the protected areas of Samburu (SNR) and Buffalo Springs National Reserves (BSNR), and the human-occupied landscape of Westgate Community Conservancy (WGCC), and examined changes in their population annually. The population demography is discussed, followed by a description of the lions ranging behaviour. The thesis concludes with an exploration of available suitable habitat within the surrounding human-occupied landscape of WGCC.

6.1.2. Conservation management of lions

It has been stated often throughout the thesis that the lion's future hangs in the balance. Lion populations are facing extreme pressures and it has been widely accepted that the large-scale decline of lions need urgent action, requiring conservation management to maintain existing populations and recover populations where there is potential for recovery. Across Africa there are many conservation management actions that are either in place or proposed to ensure a future for lions.

One proposed solution is compensating pastoralists when their livestock is killed by lions (Maclennan *et al.,* 2009). Pastoralists are rarely, if at all, compensated for the loss of livestock which serves as their valuable asset and means of livelihood. There are attempts in Kenya to address this through the Wildlife Conservation Management Act (2013) where livestock loss is compensated for. However, it has been observed that despite being announced countrywide, County Compensation Committees are yet to start working efficiently and compensation has not commenced in northern Kenya. This has caused additional friction between local people and wildlife authorities (*pers. obs*.). Furthermore, although this Wildlife Act may be seen as an improvement to carnivore conservation, such schemes do not address the root causes of conflict (Sillero-Zubiri *et al*., 2006) and may not be effective in reducing livestock loss to carnivores (Breitenmoser *et al*., 2005). Compensation by the Kenyan government had failed previously due to high administrative costs and false claims by herders (Western and Waithaka, 2005) and herders tended to neglect livestock husbandry as compensation removes the incentives for applying conflict mitigation measures (Treves *et al.,* 2006; Dickman *et al.,* 2011). A study in southern Kenya found that although compensation reduced lion killing to some extent, lions were still killed and in some instances lions were killed to demand higher compensation payments (Hazzah *et al.,* 2014). Lastly, sustaining compensation payments is a challenge to both governments and private bodies and some believe that lions will be killed if compensation payments were to eventually stop (Nyhus *et al*., 2003; Dickman *et al.,* 2011; Hazzah *et al.,* 2014). Others have suggested that "performance payments" have significant potential and are more effective than compensation, as this gives lions a direct value (Dickman *et al*., 2011; Funston *et al.,* 2016). This means that communities are paid for the lions and other wildlife that share the landscape with them, and if there is evidence of breeding, premium payments are made. Performance payments are often made in the form of educational opportunities or improving healthcare for example (Funston *et al.,* 2016).

It has been suggested that fences will help alleviate a few of the challenges that lions face, especially where encroachment of people and livestock in to protected areas is a problem (Packer *et al*., 2013; Funston *et al.,* 2016). In South Africa, fencing has helped some smaller reserves (<1000 km^2) successfully conserve their lion populations (Bauer *et al.,* 2015; Funston *et al.,* 2016) and Packer *et al*., (2013) states that the management of lions inside fenced areas require less financial resources compared to in unfenced areas. Packer *et al.,* (2013) concludes that nearly half the unfenced lion populations in Africa could possibly decline to near extinction over the next 20-40 years. However, fencing also has numerous disadvantages, including genetic isolation of populations, fencing wire being used for snaring, cutting off of migratory and dispersal routes, and fragmentation of the ecosystem (Becker *et al.,* 2013; Creel *et al.,* 2013).

Strengthening protected areas has been suggested as one of the key solutions to recover lion populations across Africa (Funston *et al.,* 2016; Lindsey *et al.,* 2017). Most protected areas in Africa are underfunded and lack the resources to effectively maintain wildlife, including lions. Vast amounts of funds are required for law enforcement, maintenance of park infrastructure, providing aerial support, engaging with communities and implementing measures to address human-wildlife conflict, and ensuring there are adequate human resources for patrols and management (Funston *et al.,* 2016). Support in this form must come from the African governments, and also the international community as recovering lion populations requires a global response. Recently, Lindsey *et al*., (2017) stated that with effective management of Africa's protected area network, the protected areas could support up to four times of the existing lion population in Africa.

Mitigation tools are urgently needed to reduce conflict between people and carnivores at a local level (Woodroffe, 2000). Resolving conflict will allow viable lion populations to exist in these areas. Reducing livestock loss to carnivores will lower the mortality of lions as there will be less motivation for retaliation (Ogada *et al*., 2003; Woodroffe *et al*., 2007; Hazzah *et al*., 2014). Ogada *et al*., (2003) states that there are effective ways to reduce livestock loss to carnivores such as having livestock closely herded during the day and kept in effective *bomas* at night with intensive human and domestic dog presence. Valeix *et al.,* (2012) and Tumenta *et al.,* (2013) confirm that improved herding and husbandry practices should be employed when livestock loss to lions is high. This has been successful in many places including northern Namibia, where new corrals led to reduced livestock depredation and a significant decline in the number of lions that were killed (Funston *et al.,* 2016). Woodroffe *et al.,* (2007) also found in the Laikipia region of Kenya, the risk of lion attacks on lions was lowest when livestock were kept in dense, walled *bomas.*

An effective solution to address conflict is to employ community members to engage with herders informing them of lion locations, and also empathise when livestock are killed (Dickman *et al*., 2011; Gurd, 2012; Dolrenry, 2013; Hazzah *et al*., 2014). Giving the community a sense of ownership over lions and conservation is another effective tool of conservation management. Tied in with education programmes and cultural connections, local people can protect lions based on their strong traditional values and role that they have been given in conservation management.

Translocation has been suggested as a management tool for lions, although is recognised to have very little conservation value (Slotow and Hunter, 2009). Translocation often displaces problematic lions to another area where there could still be depredation, and often there are high rates of post translocation mortality (Linnell *et al.,* 1997; Treves and Karanth, 2003). In South Africa, other management tools used in overpopulated reserves are female contraception, male vasectomy, culling, male replacement and prey supplementation (Slotow and Hunter, 2009), however, these have a number of challenges well described in Miller *et al.,* (2013).

Tourism can also help with encouraging communities to live with lions, as a result of attaching a value to a lion (Funston *et al*., 2016). However, tourism often does not benefit the communities who are living with lions and is also not a viable option in remote and unsafe areas.

It has been suggested that zoning could be a useful management option, through reducing "the spatial overlap between large carnivores and unmitigated sources of conflict" (Linnell *et al.,* 2005). Across the landscape, there could be different management zones, where either carnivores or people are given priority to various levels. However, zoning does not always prevent livestock depredation where wildlife and people are sharing the same region (Treves and Karanth, 2003) and often causes resentment amongst communities (Saidia, 1991).

Trophy hunting is a controversial topic whereby proponents of it argue that trophy hunting generates significant revenue for wildlife authorities in many parts across Africa, in addition to creating economic incentives to retain large areas of land for wildlife (Loveridge *et al.,* 2006; Loveridge *et al.,* 2007; Funston *et al.,* 2016). Local people also receive incentives to live with wildlife as long as they receive hunting benefits. In some places, hunting organisations also contribute to anti-poaching efforts, and at times, hunting concessions are in places where tourism may not be viable (Loveridge *et al.,* 2006). Opponents to trophy hunting argue that lions are vulnerable to overhunting, and hunting can lead to population declines as prime males are often targeted and this leads to increased infanticide (Whitman *et al.,* 2004; Loveridge *et al*., 2007; Packer *et al.,* 2009; Funston *et al.,* 2016). Often hunting may occur on the edges of protected areas, and protected area populations may be affected as they venture outside. Revenues are at times not fairly distributed amongst communities (Funston *et al*., 2016). There have also been numerous reports of widespread abuse of regulations, highlighting that trophy hunting is hard to control. If trophy hunting is to continue in various countries in Africa, there is an urgent need to reform it (Whitman *et al.,* 2004; Rosenblatt *et al.,* 2014; Funston *et al*., 2016).

A number of conservation management solutions have been proposed here. It is believed that especially in northern Kenya, fencing and compensation will not help with the conservation management of lions. Fences will prevent the movement of wildlife across the Community Conservancies and cause ecosystem fragmentation. Laikipia and Samburu will contain isolated populations of wildlife, if the protected areas are fenced. Strong cultural connections and values that the Samburu people have with wildlife will also be eroded if fences were put in place. Compensation has already exacerbated the current situation, with promises of compensation being made, however not implemented. This has led to more anger and resentment towards lions and other large carnivores. Compensation for loss of livestock is also not supported within the Samburu culture. Trophy hunting is banned in Kenya and therefore not considered. Improving husbandry methods of livestock especially during daytime herding is an important option, as are keeping dogs and having effective *bomas* (Ogada *et al.,* 2003; Woodroffe *et al.,* 2007; Spira, 2014).

It is proposed that this population exhibits a metapopulation structure (Dolrenry *et al.,* 2014) – distinct populations within a wider landscape with limited migration in between due to human influence. With population numbers in Samburu County increasing significantly from approximately 10,000 in 1912 (Bronner, 1990), to the current 320,000 in 2017 (Samburu County Plan, 2013), wildlife are facing increasing challenges as a result of human pressure. As previously stated, lions are wide-ranging and lion conservation needs to be approached on a landscape-scale to prevent surviving populations from becoming isolated and vulnerable to local extinction. Laikipia and Samburu Counties are home to the third largest population of lions in Kenya (Omondi *et al.,* 2009). Most of these lions survive outside protected areas, sharing the landscape with people and livestock. Movement corridors for lions are becoming increasingly difficult to navigate successfully, threatening to break the Laikipia-Samburu lions into fragmented isolated populations. Overall, addressing issues related to landscape connectivity within this unfenced human-occupied landscape will enhance coexistence between people and lions in this part of Kenya, in addition to building tolerance levels and improving attitudes towards lions, and finally, working on conflict mitigation. In order to further the understanding of the conservation management of lions within this landscape, the following research themes are suggested.

6.1.3. Future research themes

6.1.3.1. Dispersal and energetics of lions through the use of GPS collars

A research project looking at the movements of dispersing lions will help identify areas on the landscape that are key to their movements and areas they feel safe in. Securing these corridors and safe refuges for lions will ensure safe habitat for lions and continued movement between Laikipia, Samburu, and beyond, thus maintaining connectivity and the resilience of this important lion population. Using research collars fitted with GPS, it will be possible to map lion movements across the human-occupied landscape, providing valuable information on dispersal areas, high conflict zones and safe refuges.

Energetics: This study will measure the impact that humans have on lion persistence in the landscape through analysis of their energy budget. There is limited knowledge about the field energetics of African lions. In this project, data will be collected to measure how many calories adult male and female lions expend in the course of their average day and how these energetic costs are impacted by human activity. To measure this, specially designed GPS collars that collect fine-scale data will be used. *This study is already underway in collaboration with conservation partners.*

Dispersal: The project will aim to collar dispersing adults – males that are looking for new prides and territories, and females that have already dispersed and are living outside protected areas in the human-occupied landscape. Through this, it will be possible to accurately measure the impacts humans have on these dispersing lions. By mapping the movements of these young adults, it will be possible to identify areas that are important for lion connectivity and areas lions feel safe in. *This study is already underway with conservation partners.*

Additionally, northern Kenya is currently undergoing rapid development which is expected to accelerate with the country's Vision 2030[1] plans for a Resort City around Isiolo town (Njiru, 2011). The impact that the region's development, its growing human population, settlements and livestock will have on the lions and wildlife of the region needs to be assessed. A study is needed to assess the impact of developments on lions and their habitats, with threats identified and measures put in place to ensure connectivity. The use of GPS collars will produce results which will examine the impact of such development on lions and data can be presented to development authorities to assist with mitigation measures.

[1] http://www.vision2030.go.ke/index.php/pillars/project/Economic/27

6.1.3.2. Long-term monitoring of lion population

Results in Chapter 3 indicate that lions are often alone or in very small groups, cubs are dispersing at earlier ages compared to in other landscapes and female:male sex ratios are higher. This needs to be investigated further to see whether this is a tactic of survival – to see how lions are surviving within human-occupied landscapes, or a result of prey density within the landscape. This can be achieved by intense monitoring of the lion population and prey density data (see section 6.1.3.5.) collection in both the protected areas and human-occupied landscape.

6.1.3.3. Assessing suitable lion habitat in other Community Conservancies and exploring the potential of creating Core Conservation Areas across the landscape

As lions were found to move north to Kalama Conservancy and south to Nasuulu Conservancy (see Appendix 1), it is recommended that the anthropogenic factors and biophysical factors in these areas be assessed as a priority, to explore the presence of suitable lion habitat and existing threats. Ultimately, all areas surrounding the National Reserves need safe refuges and the identification of suitable habitat will help with the potential establishment of Core Conservation Areas in other Community Conservancies. As much as possible, these Conservation Areas need to be connected via Conservancy boundaries to provide a contiguous network of highly suitable habitat for lions and other large carnivores. Conservation Areas are designated for wildlife and constant monitoring is essential to ensure that that livestock do not encroach. Additionally, developmental planning is important to ensure that human settlements and associated infrastructure are located away from designated Conservation Areas. An HSM can be applied within each Conservancy as per the methodology presented in Chapter 5.

6.1.3.4. Understanding the metapopulation structure of the lion population across the landscape using metapopulation analysis techniques

Conservation planning across this landscape requires an understanding of the metapopulation structure of the lions. Lions exist in distinct populations in Laikipia and Samburu, across a landscape with little remaining connectivity that is reducing rapidly as a result of human pressure. This population can therefore be called a metapopulation – a collection of local populations (Levins, 1970; Hanski and Gilpin, 1991). The populations are at risk of becoming isolated and isolation of wildlife species could lead to regional extinction (Dolrenry *et al.,* 2014). It is clear that lion home ranges are small within this northern Kenyan landscape and this is partially because of the landscape matrix where suitable habitats are fragmented. Key questions needs to be looked at, including how the landscape can be better managed, taking into account the fragmented habitat for lions, and female dispersion and how it impacts at the metapopulation level. If the population is threatened with extinction, recolonisation will not occur if distances between suitable patches exceed female dispersal ability or if females are unable to survive as they move across the landscape matrix. These distances and barriers need to be understood.

Using the methodology and analyses described by Dolrenry *et al.,* (2014), and an incidence function model (Hanski, 1994), the effect of sex-specific dispersal characteristics on metapopulation connectivity, impact of humans, and the threat of isolation, can be considered in this research. This model is applicable within real systems and provides projections of the viability of the metapopulation, the importance of patches and corridors that connect them.

6.1.3.5. Influence of prey density on lions

Carnivore distribution and densities are affected by prey abundance (Carbone and Gittleman, 2002), and therefore the influence of prey on lions within this landscape needs to be investigated. The conservation of prey populations is important for lions (Frank *et al*., 2005; Ripple *et al.,* 2015), however northern Kenya is now severely degraded, with soil erosion being extremely high (Vagen and Winowiecki, 2015). About 37% of the Community Conservancy landscape in northern Kenya experienced an increase of soil erosion higher than 10% between 2002 and 2012. This land degradation with large increases in numbers of livestock has led to decreased lion prey numbers (see section 2.2.6. and 2.3.3.). A study looking at the densities of prey within the human-occupied landscape versus the protected areas, is important within this landscape. Additionally, investigating whether lions in human-occupied landscapes are targeting smaller prey to feed quickly and move away, remaining undetected by humans, may be a survival tactic and needs further investigation.

6.1.3.6. Assessing landscape-level variations in human propensity to kill lions within various ethnic groups

Lions have disappeared from areas south of BSNR, and it is suspected to be as a result of human-lion conflict and retaliatory killing. A study involving the Turkana and Borana, the ethnic groups in this area, is important to establish and understand their tolerance levels to carnivores and the extent to which human-lion conflict occurs in the region. Maggi (2014) conducted a similar study with the Samburu communities and to a smaller extent with the Turkana ethnic group. Both qualitative and quantitative methodologies were used in this study and included semi-structured interviews using questionnaires and participatory mapping exercises. The same methods can be applied here.

6.1.3.7. Investigating livestock depredation across the landscape

Finding effective conflict mitigation strategies requires research on livestock depredation and their patterns (Ogada *et al.,* 2003; Woodroffe *et al.,* 2007). Livestock depredation can only be reduced if the spatial and temporal characteristics of conflict incidents are better understood. Spira (2014) conducted a study in Samburu and constructed a framework for understanding the processes which contributed to livestock depredation. Conflict events and husbandry practices were also analysed in this study using data collected between 2007 and 2013. A follow-up study based on data collected since 2013, including the use of control data, will help gain a better understanding of conflict incident patterns within the study area and how that has changed spatially and temporally.

6.1.4. Recent developments within the lion population

Following the data collection, analysis and write-up stage of this thesis, additional developments, between 2012 and 2016, have occurred within the lion population. As expected, dispersal was observed outside the protected areas, where known lions were identified and monitored in WGCC. Their movements appear to be more extensive than those between 2008 and 2010. There was continuous movement of lions between the protected areas, WGCC and Kalama, and lions became resident in the Community Conservancies of WGCC and Kalama. Lion sightings outside the protected areas mainly comprise solitary females and males. The lions were sighted in areas predicted by the model in Chapter 5 to contain highly suitable habitat.

Although there has been previous movement of male lions from WGCC to SNR (see Chapter 4) this has reduced since 2008. Should male lions not be able to move from WGCC and other community areas into SNR and BSNR, this could have severe consequences on the lion population inside the protected areas. The current males would persist if nomadic males were not able to disperse and replace the current resident male. Van Orsdol (1984) suggests that in small confined areas, immigration of mature males is low, and males that are born within small regions are evicted into unsuitable habitats, where prey is limited. There could be increasing mortality amongst these males, as Funston (2011) found in the Kgalagadi Transfrontier Park. Extended pride male tenures can, in turn, result in incestuous matings (Orford *et al.,* 1988). Inbreeding is a risk in small isolated populations and could result in lower reproductive rates or lead to individuals becoming more susceptible to disease, as has been seen in the Ngorongoro Crater (Kissui and Packer, 2004). Snyman *et al.,* (2014) found that inbreeding was occurring in Northern Tuli Game Reserve and is likely to occur in populations affected by human caused mortality. In this study, since the movement of males ceased in 2008, inbreeding within the park prides has been observed and is a primary concern within this study population with females recorded as reaching reproductive age while their fathers continue to hold tenure within the area. The movement of male lions out of Lewa Wildlife Conservancy has also reduced due to development between Lewa and BSNR and the resulting lack of suitable lion habitat between the two regions (*pers. obs.*). This has led to inbreeding in Lewa as well (*pers. comm.* Zeke Davidson). Maintaining connectivity between the lions in Samburu and Laikipia Counties is essential to prevent populations becoming isolated and the presence of suitable habitat between the two Counties will allow for safe dispersal of lions.

Human-lion conflict has continued and since 2012, five known lions have been killed in retaliation. M26 was killed in Kalama, close to the boundary of SNR, after attacking 10 camels in three months. Two lion cubs from the Ngare Mara Pride (NMP) were also poisoned inside the protected area of BSNR following livestock encroachment and the NMP attacking camels. This highlights that not only are edge effects having an impact on the park lions, but anthropogenic factors in the form of livestock encroachment also have an impact on these populations. A young male lion was killed and a one-year old cub also shot dead in 2016 in WGCC after livestock were killed, showing that human-lion conflict and the pressures surrounding lions in human-occupied landscapes are increasing, thereby leading to retaliatory killing.

6.1.5. Conclusion

Samburu and Buffalo Springs National Reserves are small protected areas in comparison to other parks and reserves in Kenya, such as Tsavo or Maasai Mara (see Table 2.1). Their effectiveness in terms of maintaining a viable lion population is therefore dependent upon the constant movement of lions, including their immigration into the protected areas and their dispersal and survival outside the protected areas. This is especially important with respect to young males who disperse from their natal prides in search of new territories. Lack of information on population characteristics creates concern for the viability of a population, highlighting the need to collect data on basic lion population structure in order to inform conservation action (Funston, 2011). This study was the first of its kind in northern Kenya where lion demography was examined inside the protected areas and outside, within the WGCC. The demographic parameters of the study area's lion population were generally comparable to other populations across Africa. During the course of this study, it was discovered that over a period of nine years, 51 lions had disappeared. Whilst it is assumed that the lions must have left the protected areas, little was known about their movement or presence in the surrounding human-occupied landscape.

Home ranges were investigated to determine whether lions were in fact moving outside the protected areas due to the small size of the protected areas and lions' wide-ranging behaviour (Packer and Pusey 1983a; Funston, 2011). Results indicate that lions stayed within the boundaries of the Reserves and very close to the Ewaso Nyiro River. The study period included a drought year (2009), where the Ewaso Nyiro River was the only source of water available for carnivores and their prey, especially in SNR. Although the study showed that the lion's ranges were restricted to the protected areas, a more accurate assessment of lion ranging behaviour would have been possible if radio-tracking collars could have been deployed on the lions and their movements monitored over a number of years.

Human-occupied landscapes surround the protected areas of SNR and BSNR and lions are dispersing to and originating from these areas. If suitable habitat for lions does not exist outside protected areas, when lions disperse and at times become livestock raiders, there is a higher chance of them being killed especially in areas where the local communities are not tolerant of lions (Woodroffe, 2000; Hazzah *et al.,* 2009). Lions are often the first carnivore to be eliminated outside protected areas (Woodroffe and Frank, 2005) and young males who are dispersing are especially vulnerable and more prone to human-lion conflict (Elliott *et al*., 2014; Oriol-Cotterill *et al*., 2015b). Lack of sufficient habitat may also mean there is less prey, as well as less cover for lions to hide from people or hide their new born cubs (Packer *et al*., 2005; Oriol-Cotterill e*t al.*, 2015b). These factors all play a role in affecting lion survival within the anthropogenic landscape (Oriol-Cotterill *et al.,* 2015b). Additionally, if suitable habitat outside protected areas does not exist, it reduces the likelihood of new males coming in to replace pride males within protected areas.

A habitat suitability model was created and run to investigate the presence of suitable habitat in WGCC. Results showed that despite there being suitable habitat present for lions, the growing human population and resulting settlements need adequate monitoring and planning to ensure that lions are still able to move from one safe refuge to another and, whilst doing so, have a sufficient prey base. Without adequate numbers of wild prey, lions turn to livestock; thus causing increased conflict with the local people. Conflict between people and carnivores needs to be resolved in order to effectively conserve carnivores both inside and outside of protected areas (Woodroffe and Frank, 2005). Conflict issues can be resolved if the impact that carnivores have on people is reduced to a level that is tolerable (Gurd, 2012; Maggi, 2014). There is hope for the future, particularly if all the demographic groups within the local community can be effectively engaged in conservation. Samburu elders in the study area expressed the need for conservation education for the younger generation as they found that the youth did not understand the importance of wildlife as much as they did (Kuriyan, 2002). Conservation efforts such as the Ewaso Lions Project have been, and continue to be, instrumental in changing people's attitudes and engaging them in the conservation process (Gurd, 2012; Maggi, 2014; Spira, 2014).

6.1.6. A final word

The future of lions, the symbol of Africa, is uncertain. Lions are becoming more rare outside protected areas, and if action is not taken they will probably only persist in large protected areas which have adequate conservation management. Lion populations across Africa are becoming more fragile and the threat to lions is real. With lion numbers having fallen so dramatically in the past two decades, the continent is faced with their possible fatal fragility especially with there being so many small and isolated populations across Africa. The Kenya Wildlife Service has stated that Kenya could lose its lions in 20 years if current rates of decline persist. Habitat loss and human-wildlife conflict are issues that need to be addressed as a priority. Finding solutions that are realistic and achievable is of paramount importance. Kenya's wildlife is a unique natural resource, whose destiny ultimately is in the hands of the local people who live alongside these animals. Conservation, not just of a single species, but of whole ecosystems must be pursued in close collaboration with local people.

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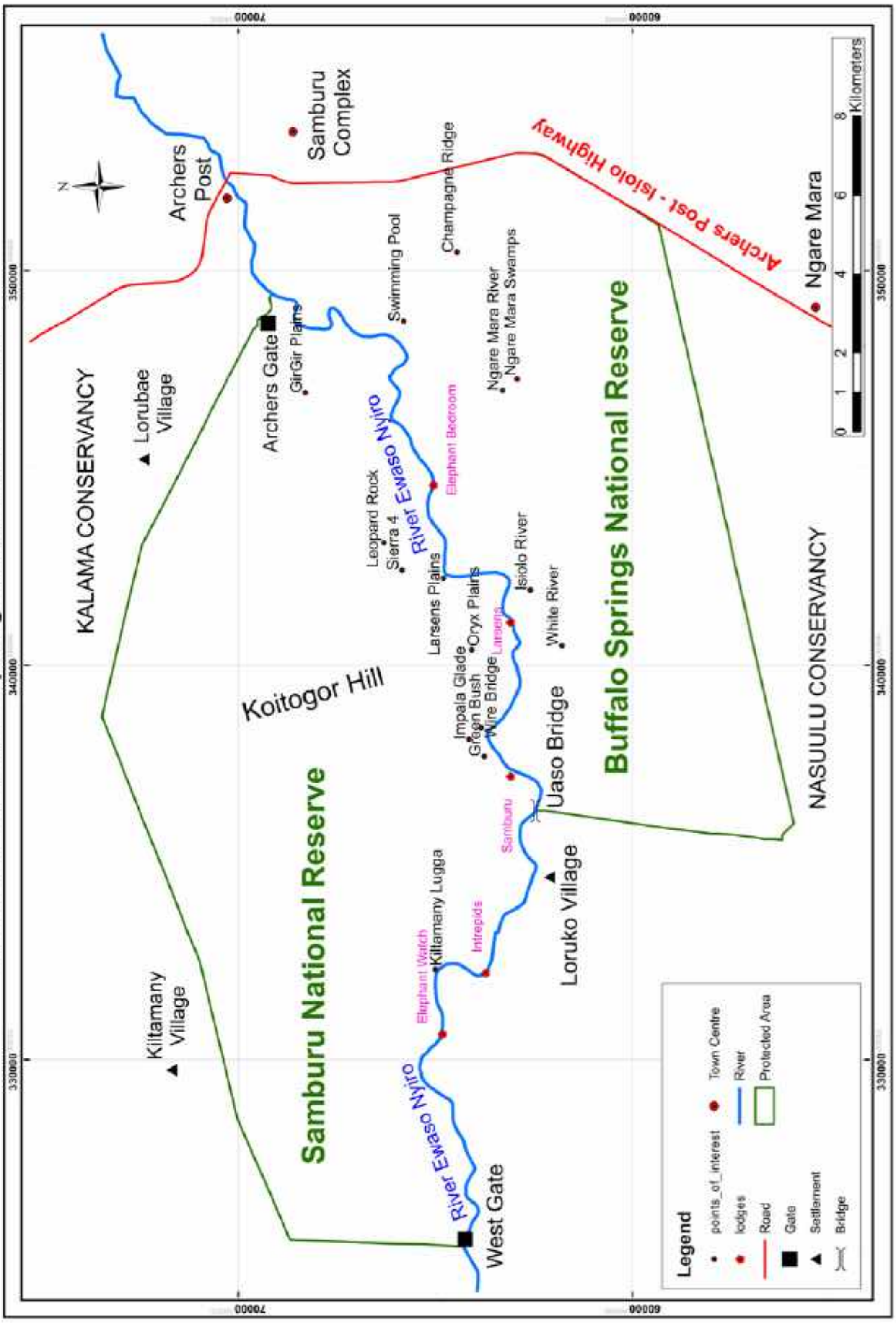
APPENDICES

Appendix 1: The Study Area

Figure 1 Samburu and Buffalo Springs National Reserves. Area names and features are in black and lodge names in pink.



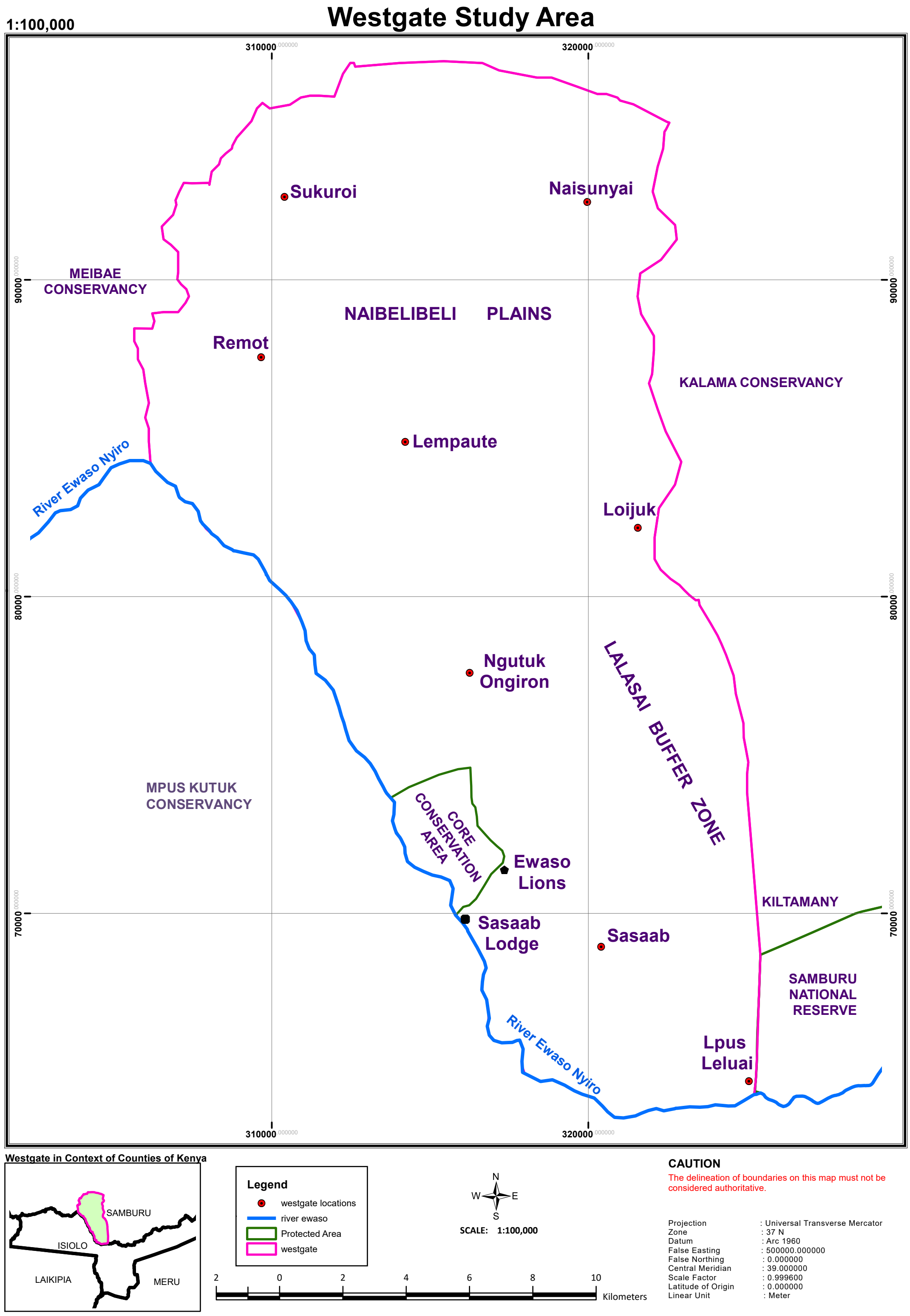


Figure 2. Westgate Community Conservancy which is part of the study area representing the human-occupied landscape. The Conservation Area is marked in green and locations in red circles.

Appendix 2: Wildlife and livestock species

Name of animal	**Scientific name**
Aardwolf	*Proteles cristata*
Bat-eared fox	*Otocyon megalotis*
Buffalo	*Syncerus caffer*
Burchell's zebra	*Equus burchelli*
Caracal	*Caracal caracal*
Cheetah	*Acinonyx jubatus*
Eland	*Taurotragus oryx*
Elephant	*Loxodonta africana*
Gerenuk	*Litocranius walleri*
Giraffe	*Giraffa camelopardalis reticulata*
Grant's gazelle	*Gazella granti*
Greater kudu	*Tragelaphus strepsiceros*
Grevy's zebra	*Equus grevyi*
Impala	*Aepyceros melampus*
Jackal	*Canis mesomelas*
Leopard	*Panthera pardus*
Lesser kudu	*Tragelaphus imberbis*
Lion	*Panthera leo*
Oryx	*Oryx gazella beisa*
Ostrich	*Struthio camelus molybdophanes*
Spotted hyaena	*Crocuta Crocuta*
Striped hyaena	*Hyaena hyaena*
Warthog	*Phacochoerus africanus* (common) and *Phacochoerus aethiopicus* (desert)
Waterbuck	*Kobus ellipsiprymnus*
Wild dog	*Lycaon pictus*

Type of livestock

Camel, Cow, Dog, Donkey, Goat, Sheep (including young ones).

Appendix 3: Wildlife and Livestock Densities in Westgate Community Conservancy

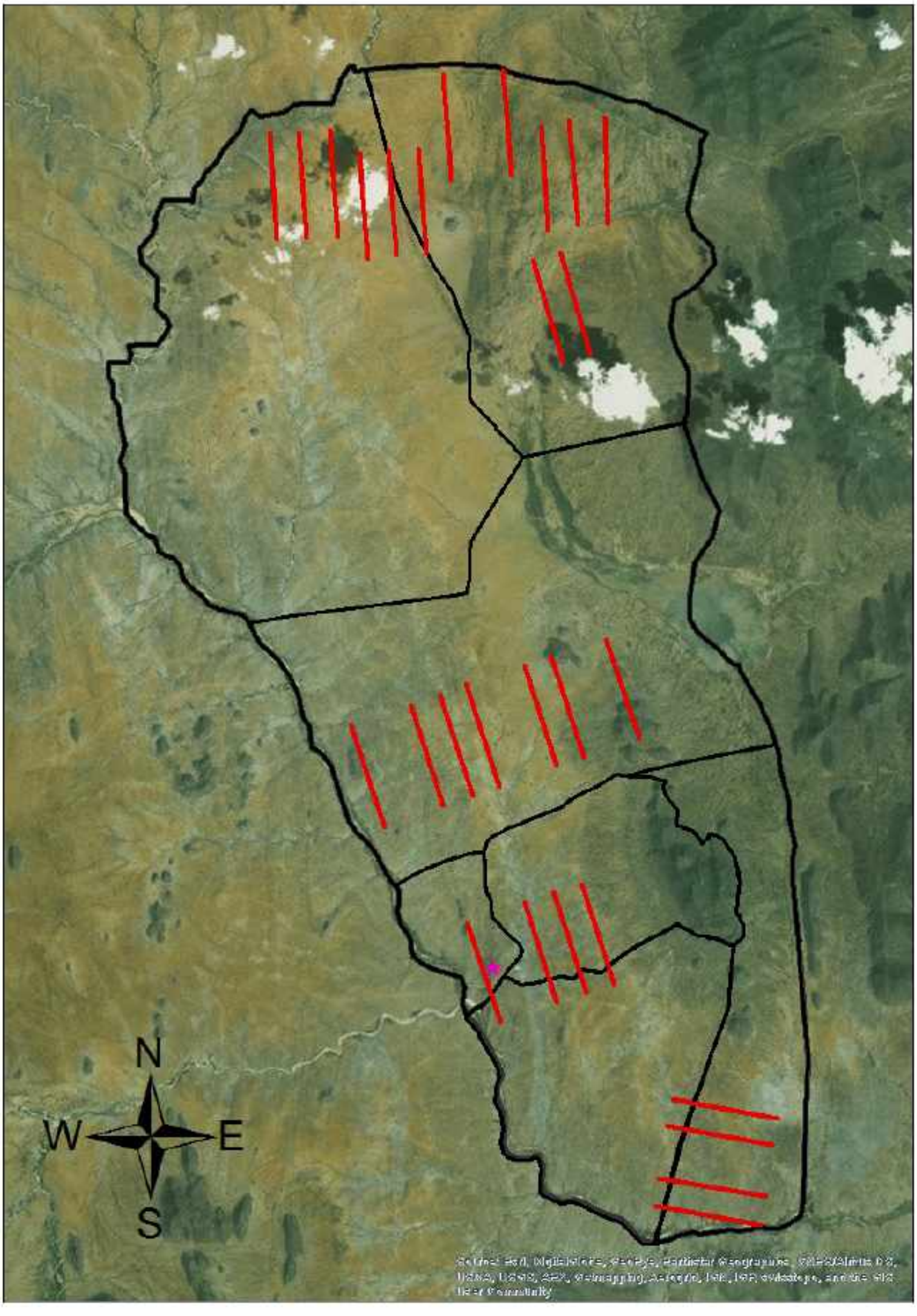


Figure 3a. Transects conducted within Westgate Conservancy

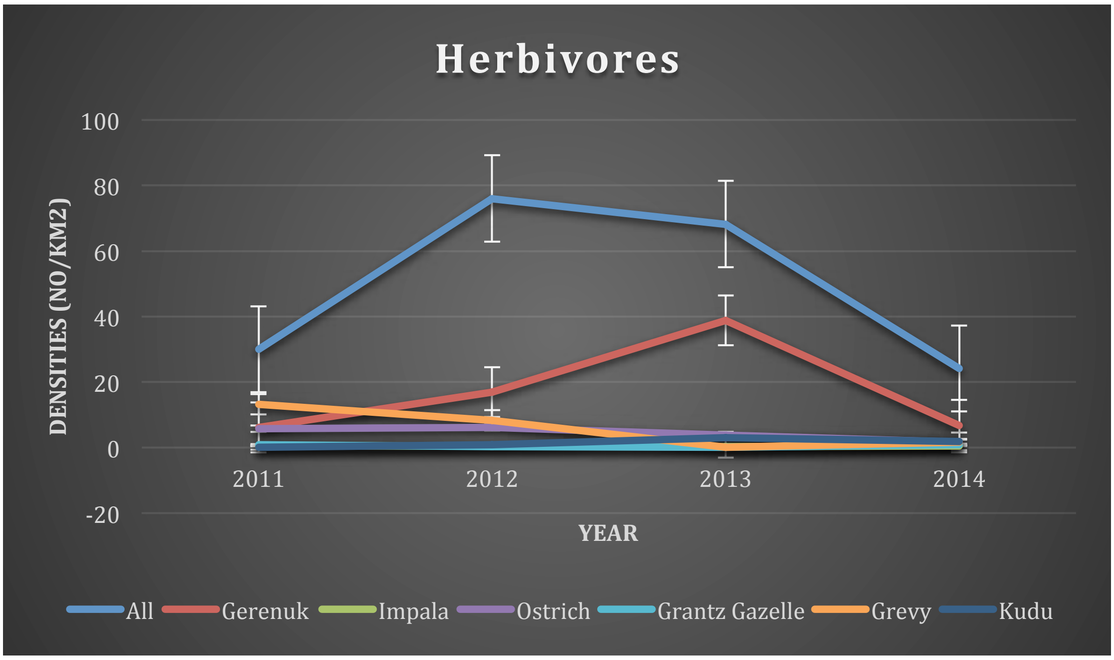


Figure 3b. Herbivore densities recorded between 2011 and 2014 in Westgate Conservancy

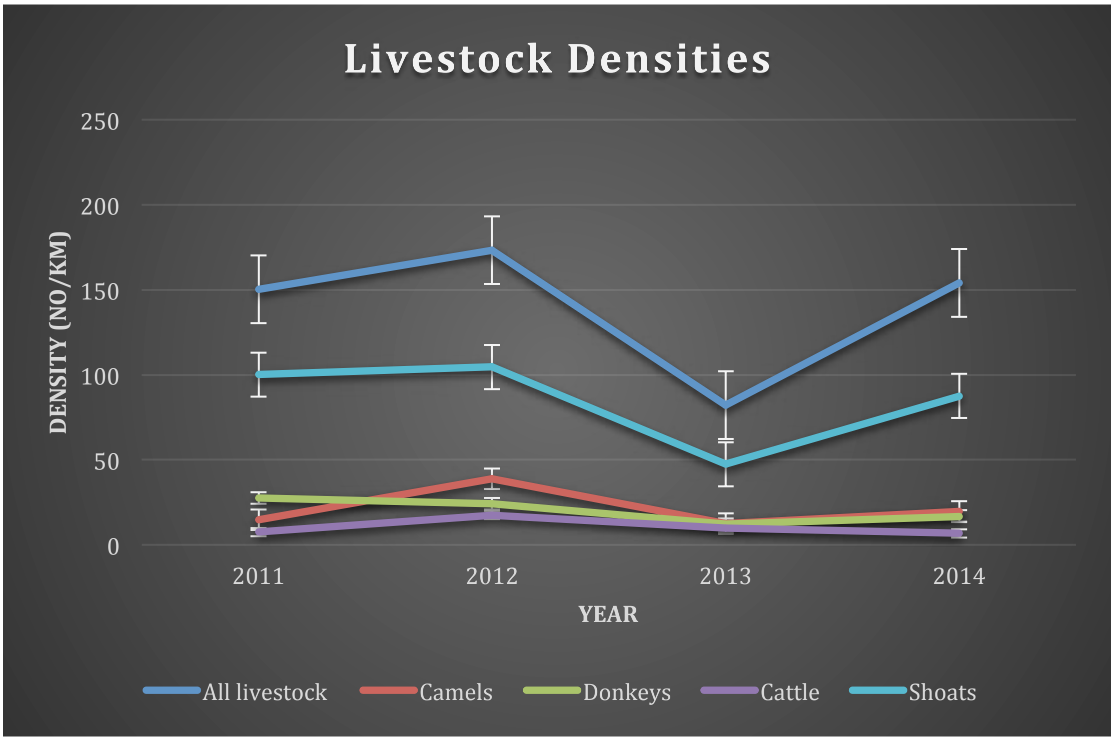


Figure 3c. Livestock densities recorded between 2011 and 2014 in Westgate Conservancy

Appendix 4: Lion monitoring data sheet

EWASO LIONS PROJECT
LION MONITORING DATA SHEET

DATE

TIME OF DEPARTURE **TIME OF ARRIVAL**

TIME OF LOCATING LIONS **TIME OF LEAVING LIONS**

HOW LIONS WERE FOUND (Key 9)

ROUTE

NAME OF AREA

TYPE OF COVER (Key 8)

LAST RAIN

GPS OF LIONS

COMPOSITION OF PRIDE (Key 1)

PRIDE IDENTIFICATION (Key 2)

IF LIONS UNKNOWN, PAGE NUMBER OF DRAWING

PHOTO NUMBERS

LION ACTIVITY UPON ARRIVAL (Key 3)

LION ACTIVITY UPON DEPARTURE (Key 3)

ACTIVITES DURING OBSERVATION

IF HUNTING, ON WHAT SPECIES (Key 4)

DID LION HUNT AND MISS? Yes or No

IF FEEDING, ON WHAT SPECIES? (Key 4)

SCAT COLLECTED -Yes or No. IF YES, ID NUMBER?

CONDITION OF LION (Key 5)

TYPE OF PREY IN AREA AND DISTANCE FROM LION (Key 4)

OTHER PREDATORS IN AREA AND DISTANCE FROM LION (Key 6)

PRESENCE OF VEHICLES / TOURISTS and BEHAVIOUR (Key 7)

INFORMATION FROM DRIVERS/TOUR VEHICLES/LODGES

ANY INTERESTING SIGHTING / OBSERVATION /DESCRIPTION

(if adding notes, put page number of section in field note book)

OBSERVER ....

KEY 1 Composition of Pride (Number and sex)
Adult male (AM), Adult female (AF), Sub-adult male – 12-24 months (SAM), Sub-adult female (SAF), Male large cub – 1-2 yrs (MLC), Female large cub (FLC), Male small cub – 0-1 year (MSC), Female small cub (FSC), Unsexed small cub (USC)

KEY 2 Pride / Lion Identification
Koitogor Pride (KP), Borana Pride (BP), Ngare Mara Pride (NM), Other (O) specify

KEY 3 Lion activity upon arrival / departure
Resting (R), Walking (W), Hunting (H), Feeding (F), Stopped feeding (SF), Other (O) specify

KEY 4 If hunting or feeding, on what species?
Grant's gazelle (GG), Impala (I), Ostrich (Ost), Zebra (Z), Oryx (Or), Gerenuk (G), Buffalo (B), Giraffe (Gir), Other (O) specify

KEY 5 Condition of lions
Relaxed (R), Unrelaxed (UR), Pregnant (Pr)   General: Good (G), Poor (P), Injury (I), Skin problem (SP)

KEY 6 Other predators in area and distance from lion
Cheetah (C), Hyaena (H), Leopard (L), Jackal (J), Other (O) specify

KEY 7 Tourism activity
Number of vehicles, Behaviour of tourists/drivers, Time spent with animal, Distance between vehicle and animal

KEY 8 Type of cover
Salvadora (Sal), Saltbush (SB), Acacia (A), Commiphora (C), Doum (D), Rocks (R), Indigofera (I), Cynodon (Cy), Bush (B), Other (O) specify

KEY 9 How Lions were found

Prey alarm call (specify which prey)	Researchers information
Tracking	Drivers information
Opportunistic sighting	Other

Appendix 5: Age classes

Using Schaller's (1972) classification method, each lion identified was allocated to one of the following age classes:

Small cubs (0-1 year)

- Amber eyes at 2-3 months old
- Woolly, grayish-yellow coat with dark spots on forehead
- Sleek, short haired tawny coat at 5 months
- Tail tuft becomes evident at 5 ½ months and prominent at 7 months
- Scrotum of males is visible and therefore easy to distinguish sex of cub
- Males are stockier and have a broader head then females
- Males have slight throat ruff by 6 months
- All young up to ⅓ the weight of an adult female (Bertram, 1976)
- Rudnai (1973a) adds: cubs aged between six to eight weeks would have dark, solid spots all over the body. These markings gradually fade away.

Large cubs (1-2 years)

- Deciduous canines are replaced by permanent ones between 13 and 15 months
- Males have massive shoulders and crested mane on the top of the head at 2 yrs
- Males have tufts on cheeks and scraggly patches on neck and chest
- All young between ⅓ and ⅔ of the weight of an adult of the same sex (Bertram, 1976)

Subadults (2-4 years)

- Females have inconspicuous nipples and a taut abdomen
- Males grow rapidly when they are 3 ¼ to 3 ½ yrs old
- All animals more than ⅔ of adult weight, but are still noticeably young (Bertram, 1976)

Adults (4+ years)

- Both males and females grow rapidly until 6 yrs
- Mane of the male becomes heavier and grows backward and downward
- All animals of full weight (Bertram 1976)

Appendix 6: Time-line for lion population (2003-2011)

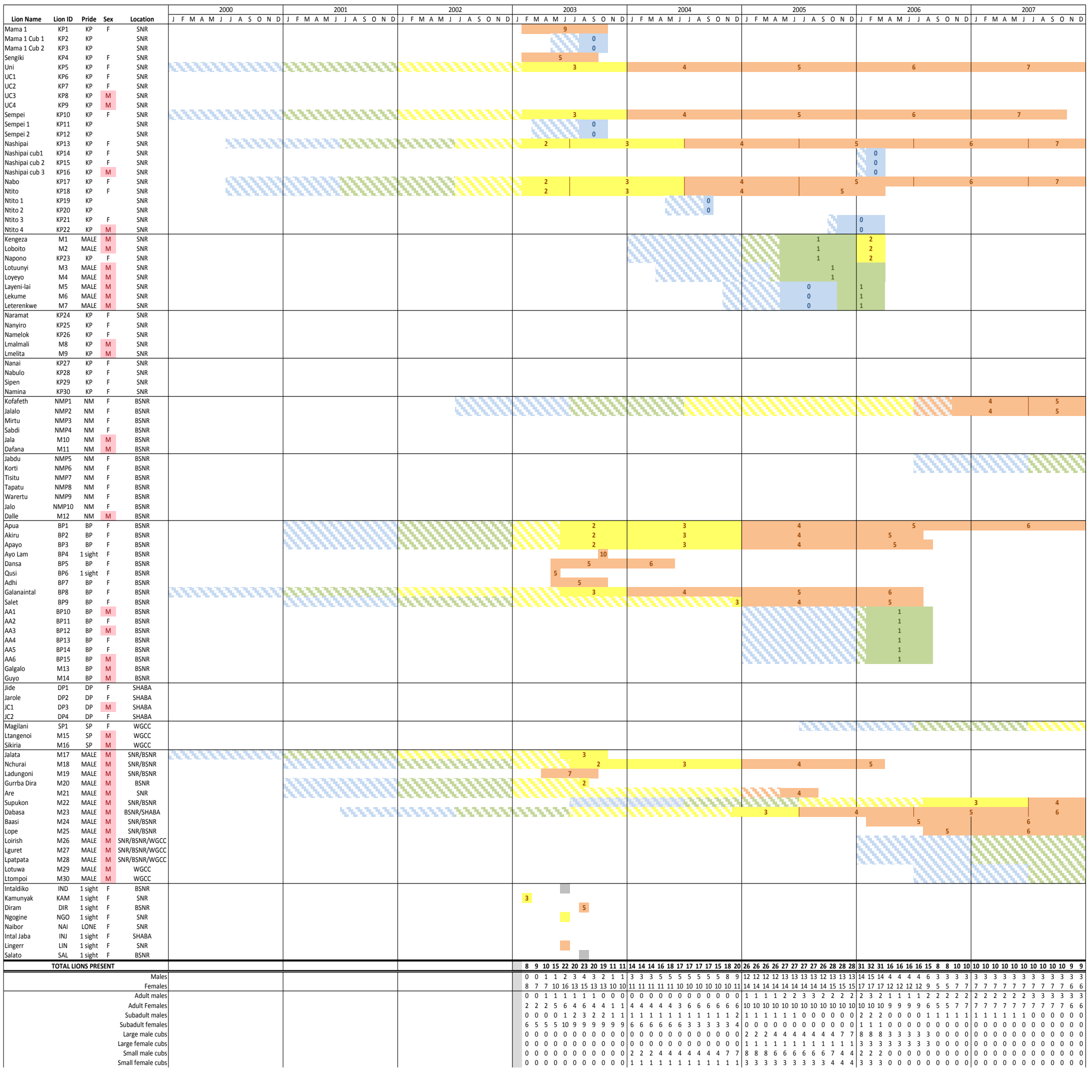


Figure 4a. A close-up view of the time-line representing the lion population between 2000 to 2007. Small cubs are represented in blue, large cubs are represented in green, subadults are represented in yellow and adults are represented in orange. The hatched lines indicated the estimated age of lions and grey indicates lions that were not aged.

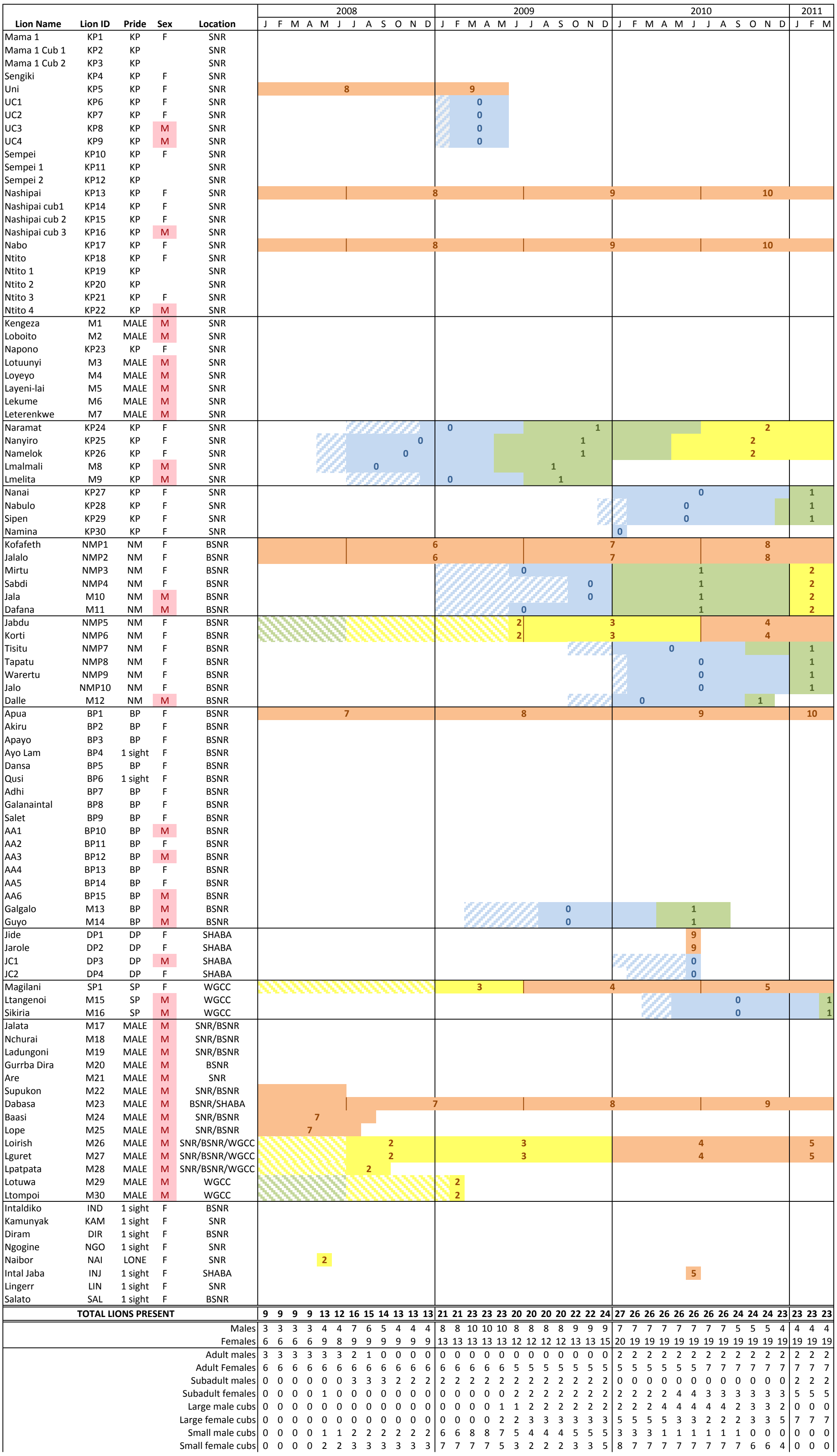


Figure 4b. A close-up view of the time-line representing the lion population between 2008 and 2011.

Appendix 7: Lion names and identification numbers

Table 1. The prides, names of lions and identity numbers for the lion population in Samburu, Buffalo Springs and Shaba National Reserves, and Westgate Community Conservancy.

Name	ID No	Name	ID No
Koitogor KP		**Borana Pride BP**	
Mama 1	KP1	Apua	BP1
MC1	KP2	Akiru	BP2
MC2	KP3	Apayo	BP3
		Ayo Lam	BP4
Sengiki	KP4	Dansa	BP5
		Qusi	BP6
Uni	KP5	Adhi	BP7
UC1	KP6	Galanaintal	BP8
UC2	KP7	Salet	BP9
UC3	KP8	AA1	BP10
UC4	KP9	AA2	BP11
		AA3	BP12
Sempei	KP10	AA4	BP13
SC1	KP11	AA5	BP14
SC2	KP12	AA6	BP15
		Guyo	M13
Nashipai	KP13	Galgalo	M14
NC1	KP14		
NC2	KP15	**Sasaab SP**	
NC3	KP16		
		Magilani	SP1
Nabo	KP17	Ltangenoi	M15
		Sikiria	M16
Ntito	KP18		
NtC1	KP19	**Males (Lone)**	
NtC2	KP20		
NtC3	KP21	Jalata	M17
NtC4	KP22	Nchurai	M18
		Ladungoni	M19
Kengeza	M1	Gurrba Dira	M20
Loboito	M2	Are	M21
Lotuunyi	M3	Supukon	M22
Loyeyo	M4	Dabasa	M23
Layeni-lai	M5		
Lekume	M6	**Males (Coalitions)**	
Loterenkwe	M7		
Napono	KP23	Baasi	M24
		Lope	M25

Naramat	KP24
Nanyiro	KP25
Namelok	KP26
Lmalmali	M8
Lmelitaa	M9
Nanai	KP27
Nabulo	KP28
Sipen	KP29
Namina	KP30

<u>Ngare Mara Pride NMP</u>

Kofafeth	NMP1
Jalalo	NMP2
Mirtu	NMP3
Sabdi	NMP4
Jala	M10
Dafana	M11
Jabdu	NMP5
Korti	NMP6
Tisitu	NMP7
Tapatu	NMP8
Warertu	NMP9
Jalo	NMP10
Dalle	M12

Loirish	M26
Lguret	M27
Lpatpata	M28
Lotuwa	M29
Ltompoi	M30

<u>Single Lion Sighting</u>	**<u>(Includes DP)</u>**
Diram	DIR
Salato	SAL
Lingerr	LIN
Ngogine	NGO
Intal Jaba	INJ
Intal Diko	IND
Kamunyak	KAM

<u>Dakadima DP</u>

Jide	DP1
Jarole	DP2
JC1	DP3
JC2	DP4

<u>Individuals</u>

Naibor	NAI

Cubs under one year of age are given identity (ID) numbers but not names. Male cubs under one year have been allocated a pride ID number and not a male ID number. Their sex is indicated in the time-line (Appendix 6).

Appendix 8: Population mortality

Table 2. The confirmed deaths of lions within the Samburu-Isiolo ecosystem between 2003 and 2011.

Lion ID	Sex	Age	Cause of death	Date
KP10	Female	Adult	Unknown	27th October 2007
M28	Male	Sub-Adult	Fight with male lion	28th October 2008
Unknown	Male	Adult	Herdsmen shooting	1st April 2009
KP5	Female	Adult	Herdsmen shooting	27th May 2009
Unknown	Female	Adult	Unknown	4th January 2010
KP30	Female	Small Cub	Unknown	Suspected March 2010
Unknown	Male	Adult	Herdsmen shooting	3rd April 2010
M12	Male	Large Cub	Choked on impala bone	7th November 2010

Table 3. The lions that either disappeared, dispersed or were removed from the study area. This excludes 11 lions that were only seen once.

Lion ID	Sex	Age	Cause of disappearance	Date of last sighting
BP6	Female	Adult	Presumed dead	14th May 2003
M20	Male	Subadult	Unknown	23rd August 2003
M19	Male	Adult	Unknown	12th September 2003
KP4	Female	Adult	Unknown	24th September 2003
KP1	Female	Adult	Unknown	19th October 2003
KP2	Unknown	Small Cub	Unknown	19th October 2003
KP3	Unknown	Small Cub	Unknown	19th October 2003
BP4	Female	Adult	Presumed dead	20th October 2003
BP7	Female	Adult	Presumed dead	20th October 2003
M17	Male	Subadult	Unknown	22nd October 2003
BP5	Female	Adult	Presumed dead	28th May 2004
KP21	Female	Small Cub	Unknown	3rd September 2004
KP22	Male	Small Cub	Unknown	3rd September 2004
KP11	Unknown	Small Cub	Unknown	14th March 2005
KP12	Unknown	Small Cub	Unknown	14th March 2005
M21	Male	Adult	Unknown	23rd June 2005
M18	Male	Adult	Unknown	2nd March 2006
KP14	Female	Small Cub	Unknown	7th March 2006
KP15	Female	Small Cub	Unknown	7th March 2006
KP16	Male	Small Cub	Unknown	7th March 2006
M1	Male	Subadult	Presumed dead	13th March 2006
M2	Male	Subadult	Presumed dead	13th March 2006

M3	Male	Large Cub	Presumed dead	13th March 2006
M4	Male	Large Cub	Presumed dead	13th March 2006
M5	Male	Large Cub	Presumed dead	13th March 2006
M6	Male	Large Cub	Presumed dead	13th March 2006
M7	Male	Large Cub	Presumed dead	13th March 2006
KP23	Female	Subadult	Presumed dead	13th March 2006
KP18	Female	Adult	Unknown	16th March 2006
KP19	Unknown	Small Cub	Unknown	16th March 2006
KP20	Unknown	Small Cub	Unknown	16th March 2006
BP2	Female	Adult	Presumed dead	25th July 2006
BP8	Female	Adult	Presumed dead	25th July 2006
BP9	Female	Adult	Presumed dead	25th July 2006
BP3	Female	Adult	Presumed dead	11th August 2006
BP10	Male	Large Cub	Presumed dead	11th August 2006
BP11	Female	Large Cub	Presumed dead	11th August 2006
BP12	Male	Large Cub	Presumed dead	11th August 2006
BP13	Female	Large Cub	Presumed dead	11th August 2006
BP14	Female	Large Cub	Presumed dead	11th August 2006
BP15	Male	Large Cub	Presumed dead	11th August 2006
NAI	Female	Subadult	Unknown	13th May 2008
M22	Male	Adult	Unknown	17th June 2008
M25	Male	Adult	Unknown	5th July 2008
M24	Male	Adult	Unknown	24th August 2008
M29	Male	Subadult	Presumed dead	16th February 2009
M30	Male	Subadult	Presumed dead	16th February 2009
KP6	Female	Small Cub	Mother shot: cub removed	30th May 2009
KP7	Female	Small Cub	Mother shot: cub removed	30th May 2009
KP8	Male	Small Cub	Mother shot: cub removed	30th May 2009
KP9	Male	Small Cub	Mother shot: cub removed	30th May 2009
M8	Male	Large Cub	Dispersed–Presumed alive	15th December 2009
M9	Male	Large Cub	Dispersed-Presumed alive	15th December 2009
M13	Male	Large Cub	Unknown	1st August 2010
M14	Male	Large Cub	Unknown	1st August 2010

Appendix 9: Livestock and Herbivores Graphs (Screenshots) for HSM

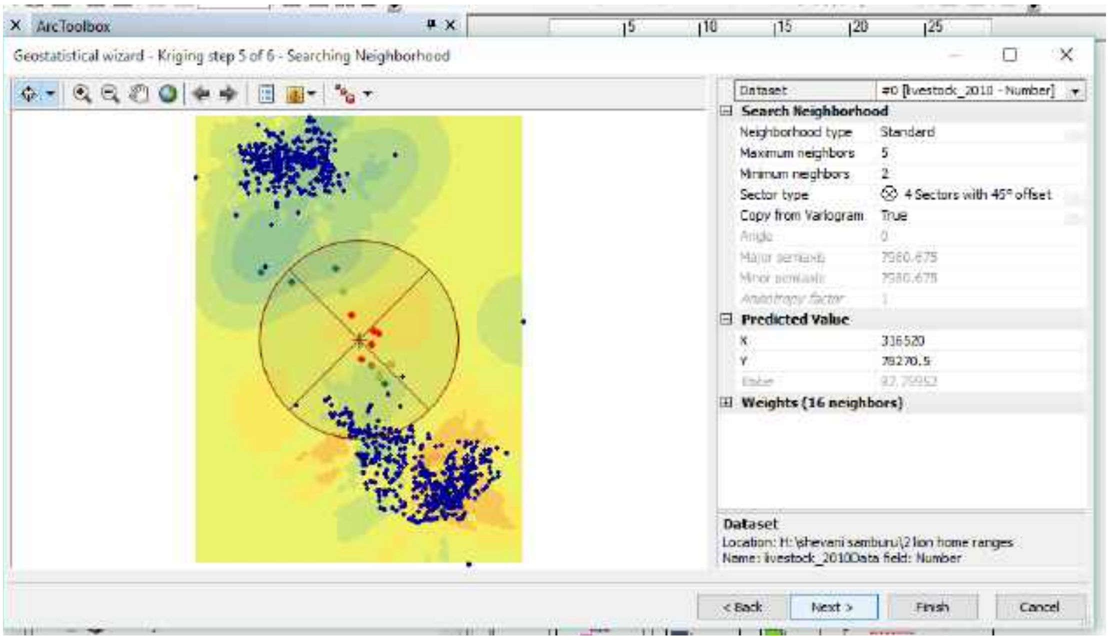


Figure 5. Screen shot showing results after searching the neighbourhood with livestock data. Graph shows the data was mainly in the form of two clusters and the central region of WGCC had no data samples.

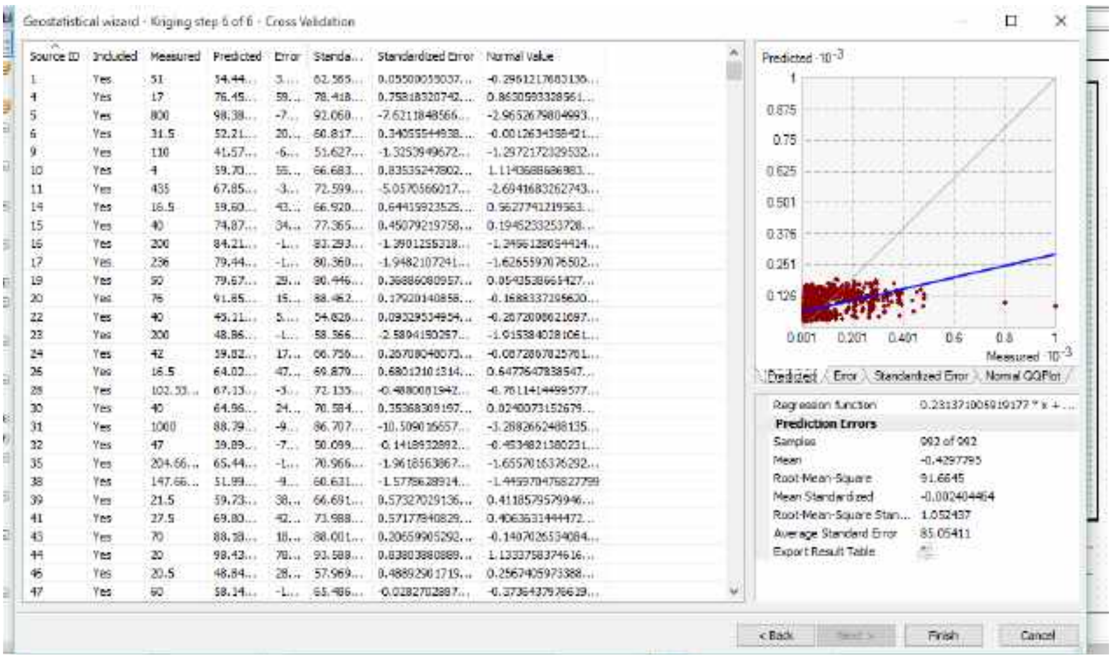


Figure 6. Screenshot showing the livestock data displaying a 85% prediction error, i.e. a very high degree of unreliability and was therefore not fit for use in distribution mapping.

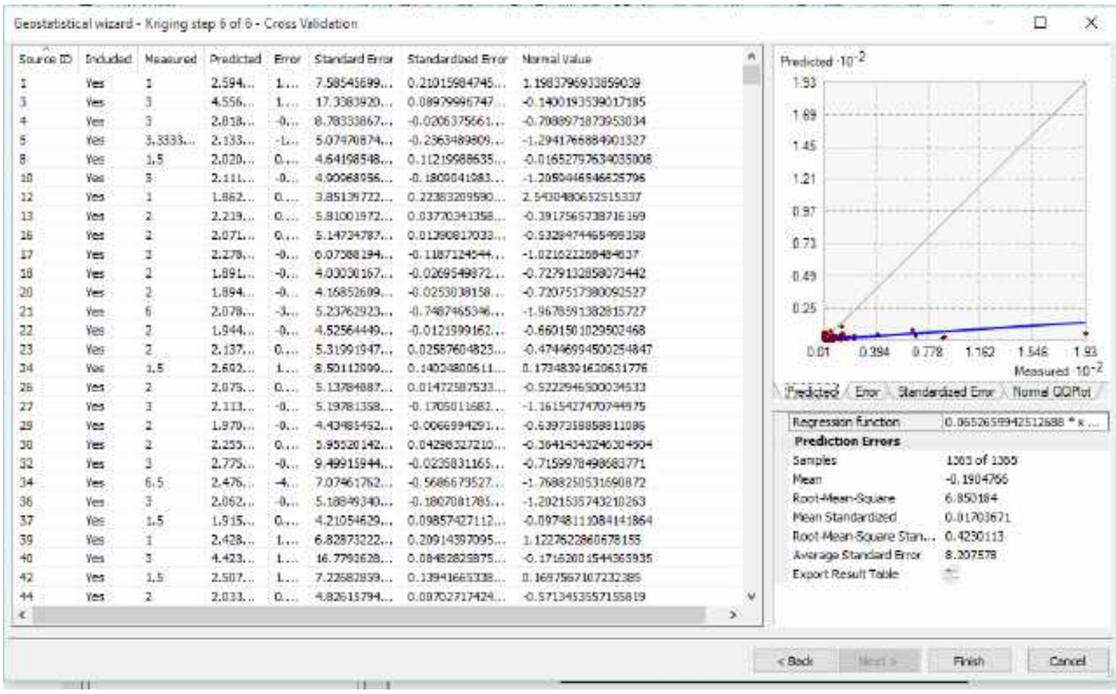


Figure 7. Screenshot showing herbivores with a prediction error of 8% indicating the degree of reliability as being low.

Appendix 10: Map of lion dispersal between Samburu and Laikipia counties

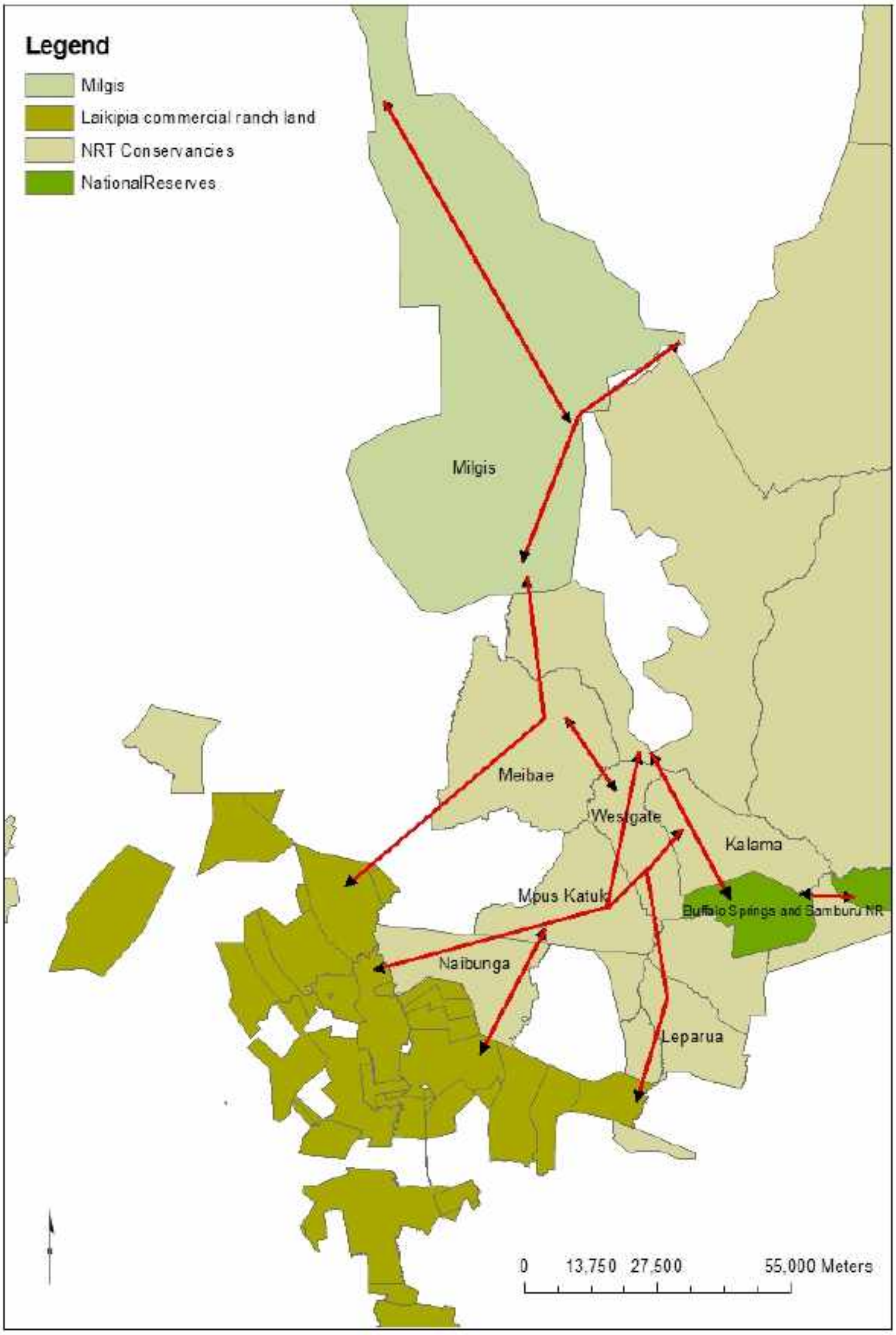


Figure 8. Map showing lion dispersal between Samburu and Laikipia Counties (Source: Alayne-Cotterill, Lion Landscapes, Laikipia).