Human-Lion conflict around Nairobi National Park: Lion (Panthera leo melanochaita, Hamilton Smith, 1842) Population Structure, Landscape Use and Diet, in a Semi-Fenced Park

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1

Introduction

1.1 General background

Large carnivores are indicators of healthy ecosystems and contribute to the stability and resilience of an ecosystem (Pimm & Raven 2000). Extinction of large carnivores may result in cascading effects on ecosystems either directly or indirectly through various units in the food-web (Berger et al. 2001). Most larger carnivores are flagship species, contributing great value to the regional tourism industry (Sergio et al. 2008).

Large carnivore populations have shown a strong decline globally in recent decades (Woodroffe 2000; Chardonnet et al. 2010; Dickman 2010; Henschel et al. 2010). The observed decline concerns both population numbers and surface of suitable habitat (Riggio et al. 2013). Main factors contributing to the decline are habitat destruction, decline of prey populations, poaching for animal parts and retaliatory killing by poisoning or with guns/spears (Patterson et al. 2004; Packer et al. 2005; Carter & Linnell 2016).

In the past, human population growth and development have resulted in the destruction of wild habitats (Vitousek et al. 1997; Jetz et al. 2007). This is a result of changing land tenure systems from communal land where wildlife used to roam freely to a system of privatization, with a subdivision of the land into fenced private parcels (Gichohi 2003). As a consequence of these changes in land tenure systems, the land is fragmented and wildlife migration and accessibility of dispersal areas are generally restricted (Gichohi 1996). When species are restricted and confined in an area, they have limited access to resources acquisition, mates and are susceptible to hazards (Valeix et al. 2010; Vanak et al. 2013)

Lions are particularly vulnerable because they require large home ranges and undisturbed natural habitats to survive (Sillero-Subiri & Laurenson 2001; Patterson et al. 2004; Woodroffe & Frank 2005). Such undisturbed natural habitats, also sometimes called 'wildlands' allow diverse species interactions and facilitate ecosystem richness, thus improving lion access to diverse

prey species and catchability of prey (Ripple et al. 2014). However, most of the national parks in Africa have become "hard-edge parks" with no buffer from surrounding private lands (Bauer et al. 2010). The consequence of the absence of a 'soft edge' buffer zone, is that the hard edge restricts species migration into dispersal areas and this situation often makes the national park not ecologically viable, especially if its size is relatively small (Gichohi 2003).

In recent decades, a dramatic upsurge of human–wildlife conflicts has been reported (Woodroffe et al. 2005; Inskip & Zimmermann 2009). Henschel et al. (2010) suggested that human–felid conflicts and habitat destruction have resulted in a decline in lion populations and local extinctions in West and Central Africa. Inskip & Zimmermann, (2009) also found an exponential increase in the number of publications on human–carnivore conflicts, indicating an increasing interest from the scientific world in this phenomenon.

Carnivore conflicts resulting in human death, livestock depredation and disease transmission result in significant costs for livestock farmers (Woodroffe & Frank 2005). The situation is exacerbated in small, protected areas with high densities of carnivores, when carnivores leave the protected area in search of prey (Winterbach et al. 2013; Tuqa et al. 2014). Subsequently, carnivores are negatively impacted by retaliatory killing (Novaro et al. 2000; Sillero-Subiri & Laurenson 2001; Dickman 2010).

Carnivores are prolific breeders and under favorable conditions, are able to recover quickly (Packer et al. 2013). Rudnai (1979) suggested that, when there is suitable habitat adjacent to a national park for a surplus of lions to disperse into, the lion population could stabilize quickly.

The management of large carnivores continues to be a significant challenge for conservation managers given the animals' extensive home ranges, low densities and propensity for conflict with livestock (Bauer et al. 2010). Particularly sub-adult males moving away from their natal pride are more troublesome than mature adults with an established home range and territory (Woodroffe et al. 2007).

Their low densities increase the vulnerability of large carnivores to the impact of conflicts (Cardillo et al. 2004, 2005). In small, isolated populations, inbreeding depression often results in a loss of fecundity and reduces survival (Björklund 2003; Pimm et al. 2006). Being at the apex of the food chain, at lower densities large carnivores are more vulnerable to extinction compared to herbivore populations, which generally show higher densities (Sillero-Subiri & Laurenson 2001; Craigie et al. 2010).

Increasing human densities accelerate the rates of local extinctions of large carnivores (Woodroffe 2000). Consequently, large carnivores are the first victims when human populations expand into their habitats (Muntifering et al. 2006). Burkey (1995) suggests that the establishment of nation-

al parks alone are not sufficient to conserve wildlife, it is also necessary to extend conservation measures to the surrounding buffer zones of national parks. National parks are key to conservation of lions in Kenya. My study has a focus on Nairobi National Park (NNP). Lions in NNP have continued to face threats from humans, resulting in killing and translocation to other conservation areas. Due to these escalating threats, my thesis has focused on human-lion interaction in and around Nairobi National Park.

1.2 Status of lion population in Africa

With the exception of the spotted hyena (*Crocuta crocuta*), all species belonging to the African large carnivore guild, i.e. lion (*Panthera leo*), leopard (*Panthera pardus*), brown hyena (*Hyaena brunnea)*, striped hyena (*Hyaena hyaena)*, cheetah (*Acinonyx jubatus)* and African wild dog (*Lycaon pictus*), have declined in recent decades (Kumaraguru et al. 2010; Woodroffe & Sillero-Zubiri 2012; AbiSaid & Dloniak 2015; Bohm & Höner 2015; Henschel et al. 2015; Wiesel 2015). Between 1960 and 2010, the lions' historical range has decreased by 25% (Riggio et al. 2013). The estimated lion population in Africa is 32,260 (Riggio et al. 2013). The International Union for Conservation of Nature (IUCN) has listed the African lion on its global Red List of Threatened Species as vulnerable (Bauer et al. 2016).

However, different authors and diverse census techniques have produced different population estimates for lions in Africa, ranging from 16,000 to 47,000 (see Table 1.1) (Chardonnet 2002; Bauer & Van der Merwe 2004; Riggio et al. 2013). It is difficult to make a precise population size estimate for elusive, often nocturnal large carnivores such as lions (Riggio et al. 2013). Indeed, there is not a single census technique for lion population assessments (Ogutu & Dublin 1998). Generally, a combination of methods is recommended (Bauer & Van der Merwe 2004; Riggio et al. 2013).

The lion population trends differ across Africa. Southern Africa has generally reported growth in lion populations, whereas West, East and Central Africa have reported a decline (Bauer et al. 2015). Bauer et al. (2015) suggested that the lion in West Africa is regionally Critically Endangered, whereas the lion population in East Africa is considered regionally Endangered. Lion populations have declined by 67 per cent in West Africa and by 37 per cent in East Africa (Bauer et al. 2015).

Table 1.1
Summary of studies estimating the number of free-ranging African lions (adapted from Bertola, 2015)

Year of estimate	Authors	Number of African lions	Method
1980	Ferreras & Cousins (1996)	75,800	GIS-based model
1990s	Nowell & Jackson (1996)	30,000-100,000	"Guesstimate"
2002	Chardonnet (2002)	39,000 (range: 29,000-47,000)	Extrapolation from known populations
2004	Bauer & Van der Merwe (2004)	range: 16,500-30,000 (23,000*)	Mail survey
2013	Riggio et al. (2013)	32,000-35,000	GIS-based model

* protected areas only

DNA (deoxyribonucleic acid) evidence has resulted in the identification of two subspecies of lion: *Panthera leo melanochaita* (Hamilton Smith 1842) in East and Southern Africa, and *Panthera leo* (Linnaeus 1758) in West Africa and Asia (Kitchener et al. 2017). However, current scientific findings suggest four subgroups of lions, based on phylogenetic analyses of microsatellites and mitochondrial DNA (mtDNA): 1) West/Central Africa; 2) East Africa; 3) Southern Africa; and 4) India (Bertola et al. 2016). All four subgroups are involved in livestock depredation (Woodroffe et al. 2007; Tumenta et al. 2013; Tuqa 2015). Globally, apart from Africa, lions are still found in Asia, in the Gir Reserve in Gujarat, India (Schnitzler 2011; Riggio et al. 2013).

Lions symbolize power and they are a flagship species for the tourism industry (Dalerum et al. 2008; Sergio et al. 2008). In Kenya, lions feature in the coat of arms as a symbol of justice and they are used as a public seal and as a symbol of authority (G.o.K 2010). The lion is also imbedded in all of Kenya's local currency.

After the Second World War, there was a re-emergence in Kenya of the conservation movement and national parks were established following the model of the USA, where the first national park worldwide was established in 1872 (Yellowstone National Park) (Steinhart 1994). Following the model of Yellow Stone Park, the Colonial Administrators in Kenya, established several parks and reserves for the conservation of flora and fauna (Steinhart 1994). There are currently 22 national parks, 26 national reserves and five wildlife sanctuaries in Kenya (www.kws.go.ke). In total, 8% and 11% of Kenya's land area is covered by national parks and community conservancies respectively, which are primarily managed for the conservation of wildlife. Some of these areas are considered either lion strongholds or Lion Conservation Units (LCU) (Riggio et al. 2013; KWS 2015; KWCA 2016).

Kenya has six lion strongholds (see Table 1.2) (Riggio et al. 2013; KWS 2008). With the exception of the non-border zones like Laikipia-Samburu and Meru-Kora, other strongholds, such as Serengeti-Mara, Tsavo-Mkomazi and Arawale-Boni Bush (which extends into Somalia), are cross-border strongholds (Riggio et al. 2013). Maasai Mara, Tsavo West and Tsavo East are considered to be the most important lion strongholds, while the lion conservation status of other areas such as northern Kenya and the cross border population are unknown (KWS 2008).

Lion populations in Kenya have declined from an estimated 2,700 in 2000 to 2,000 in 2010 (KWS 2008). The declining lion population in Kenya is a major concern to the Kenya Wildlife Service (hereafter, KWS). The decline has occurred in spite of a prohibition of trophy hunting by the Government of Kenya in 1977. This decline in the lion population of Kenya is probably a result of intensifying human pressure on habitat and increasing human–carnivore conflicts in recent decades (Woodroffe 2000; Tuqa 2015).

Table 1.2
Lion population estimates in different areas in Kenya (based on Chardonnet 2002; Bauer & Van der Merwe 2004; KWS 2008 and Riggio et al. 2013)

	Area	Chardonnet et al. 2002	Bauer & Van der Merwe 2004	KWS 2008	Riggio et al. 2013
1	Aberdares NP	162	7		
2	Amboseli NP	130	20		
3	Arawale				750*
4	South and East of Rift Valley	20			
5	North of Tan, East of Rift Valley	271	650		
6	Galana Game Ranch		150		
7	Nairobi NP		22		30
8	Hells Gate & Kedong	9			
9	Lake Nakuru NP	37	28		
10	Laikipia plateau	362	120	230	271
11	Masai Mara NP	558	547	825	3673*
12	Surrounds of Masai Mara	394			
13	Meru Complex	65	80	40	40
14	Tsavo NPs	750	675	675	880*
15	Northern Kenya			100	
16	Samburu/Shaba/Barselinga		100	100	
17	Kora N. Reserve		40		
	Total	**2780**	**2439**	**1970**	**5644**

*These are the estimates of cross-border populations

1.3 Review of relevant scientific literature

Lion social and population structure

The African lion *(Panthera leo)* lives in a "fission–fusion" social unit (pride) of 4-12 related adult females together with their young. Pride males form coalitions of, on average, 2-3 adult males originating from different prides (Schaller 1972). The lion pride is the largest social unit and the core of lion social organization (Schaller 1972; Bauer et al. 2003). Defense of the territory is done by both males and females (Schaller 1972). Although temperature has an influence on lions' hunting and feeding, the peak in these activities is generally between 18:00-22:00hrs and 4:00-6:00hrs (Schaller 1972).

The morphological variation such as body size and mane are the two characteristics for distinguishing the difference between male and female. A mature male is larger and has a thick mane (Schaller 1972). However, in Tsavo, Kenya, males are maneless (Kays & Patterson 2002) and in the Okavango Delta, Botswana, a female with thick black mane was observed (Gilfillan et al. 2017). Upon maturity (2-3 years), juvenile pride-born males either leave the pride voluntarily, or are expelled by the adult male lion; coalition males are exiled when new pride males take over the pride (Schaller 1972). Inbreeding is avoided in all but small, isolated populations, e.g. in fenced reserves (Schaller 1972). Lions often disperse within the pride into small subgroups and form small social units within different home ranges (Stander 1991; Bauer et al. 2003; Elliot et al. 2017). The social factors of a pride are influenced by pride demography, kinship and sub-prides and pride size is not a good indicator of food abundance (Van Orsdol et al. (1985).

Female associations with a pride are more stable compared to young male associations, as young males become nomadic at 2-3 years (Schaller 1972). However, if a male successfully takes over a pride, its territory and the survival of its offspring can be maintained for some years (Hanby & Bygott 1987). In order to induce estrus in the female following a pride take over, the new pride male either kills or evicts all present young individuals from the pride, forcing young males to become nomadic (Schaller 1972). The expelled young males then usually stay inside the natal pride home range before establishing their own pride (Elliot et al. 2017).

Besides the infanticide events during such pride takeovers (Schaller 1972; Rosenblatt et al. 2016), other factors influencing cub survival include: lack of prey; extreme flooding or drought events; disease; and mortality due to attacks of e.g. spotted hyena or African buffalo (Schaller 1972). The ability of a pride to protect their cubs also indirectly influences cub survival, e.g. when female pride members have insufficiently synchronized their breeding, the communal cub care could be compromised (Packer et al. 2001).

Lion family units are highly susceptible to anthropogenic pressure where there is no transitional buffer between the park and surrounding communities (Tumenta 2012). Scheel and Packer (1991) state that, "lion cooperative hunting behavior is situational, depending on the size of the prey, difficulty to kill, and hunting distance." In open savannah grassland, cooperative hunting becomes beneficial and results in a higher kill rate, while hunting by solitary lions occurs mostly when prey size is small or when prey densities are low (Schaller 1972; Bauer et al. 2003; Hayward & Kerley 2005).

The loose nature of a lion pride and group size is influenced by prey dynamics, prey density, prey body mass and season (Schaller 1972; Macdonald 1983; Bauer et al. 2010). Smaller prey body mass may result in a smaller group of lions (Bauer et al. 2010). Several authors have indicated that lion populations in a disturbed environment generally have a lower pride size and lower group size, and often hunt in singles or in pairs (Bauer et al. 2003; Packer et al. 2013; Tuqa 2015). Also external factors resulting from human activities affects lion social structure (Creel & Creel 1997). Therefore, individual identification and documentation are critical to studying the social structure of lions (Sogbohossou et al. 2014). For this thesis I intended to establish the population structure and prides in Nairobi National Park for management and conflict mitigation with a view of developing a strategy to enhance the conservation of lions in close proximity to the City of Nairobi.

Lion home range and movement

Large carnivores require extensive home ranges to meet their energetic demand (Gittleman & Harvey 1982; Macdonald 1983). The dispersion and abundance of prey in relation to vegetation cover affect home range size (Macdonald 1983; Ogutu & Dublin 2002). Seasonal changes in habitat quality and prey density result in spatial and temporal differences of lion home range size (Coe et al. 1976; Hemson 2003).

Several studies in East, southern and West/Central Africa have shown lion home range sizes (95% KDE) varying between 56.4 – 641 km^2 (Tumenta et al. 2013; Tuqa 2015). E.g. in the Pendjari Biosphere Reserve, Benin, the average annual home range (95% KDE) was 256 km^2 (Sogbohossou 2011) while in Amboseli National Park, Kenya, the average home range (95% KDE) was 56.4 km^2 (Tuqa 2015).

In Waza National Park, Cameroon and Amboseli National Park, Kenya, home range sizes increased during the wet season and decreased during the dry season (Bauer & Iongh 2005; Tuqa et al. 2014). This is contrary to findings by Hemson (2003), who suggested that in Botswana's Makgadikgadi Pans National Park, the lion's home ranges increase when lions are searching for livestock during the dry season in the community land. Male lions generally have

larger home ranges than females due to territorial behavior and depredation on larger prey by male lions (Schaller 1972; Funston et al. 2001; Lehmann et al. 2008).

A species' energetic requirement, territorial surveillance and search for mates are achieved through movement, explaining the relatively large home range sizes seen in lions (Nathan et al. 2008). Movement and protecting territory by lions will expend theirenergy through daily travel distances covered for hunting and surveillance (Pontzer & Kamilar 2009). In order to optimize energy, gain and cost, lions spend less hours walking and hunting than eating and resting (Schaller 1972). The changes in daily or seasonal activity of lions, affect their home ranges size, shape and time to be active. In Nairobi National Park (hereafter, NNP), we assumed that given the density of lions and the size of the park, lions do not cover long distances.

Although females can become nomadic, their acceptance into a new pride is possible (Schaller 1972). This is unlikely for young males, except during pride takeovers. So, male lions are more nomadic compared to female lions, since their stay in the pride depends mainly on pride takeover. This social system of pride takeover, eviction of young males and nomadism forms the nature of the pride and facilitates gene flow and fitness into the population, since the strongest male lions take over the pride for reproduction (Schaller 1972). The nomadism phase of lions increases their home ranges and movement (Eliot 2017). The nomadic phase ends when the nomad, or a coalition of nomadic males, successfully expels a pride male or seasonal dominant males in an existing pride and takes over the pride (Schaller 1972).

Reports on the incidence of NNP lions roaming into community land have increased (Smith 2012; Dloniak 2012; Kushner 2016). This pattern of increased roaming into community land has a direct impact on retaliatory action by the local community, which often results in the killing of lions (Dloniak 2012; Lesilau et al. 2018). Therefore, understanding how NNP lions utilize the landscape is important for the management of NNP.

Lion diet and prey choice

Lions are diet generalists. They feed on a wide variety of small to large animals depending on region, species vulnerability, species availability, season and protective vegetation (Bauer & Iongh 2005; Hayward & Kerley 2005; Tumenta et al. 2013). The medium-sized and water-dependent prey such as African buffaloes (*Syncerus caffer*), kudu (*Tragelaphus strepsiceros*), and wildebeest (*Connochaetes taurinus*) are vulnerable to depredation by lions, especially during the dry season when water points become scarce (Druce et al. 2004; Hayward & Kerley 2005; De Boer et al. 2010). A recent study by Love-

ridge et al. (2006) revealed that lions even prey on elephant calves in the dry season. A similar observation was reported by Tuqa (2015).

Vegetation providing cover for lions and abundance of prey increases the chance of lion success in hunting herbivores (Davidson et al. 2012). Lion hunting success is limited by prey anti-predatory strategies (such as grouping by African buffalo) and prey morphology (horns) (Hayward & Kerley 2005).

The feeding strategy of a predator is determined by natural selection and is aimed at maximizing intake of energy and nutrients (Hayward & Kerley 2005). In hunting, abundance and accessibility play a primary role in prey choice (Hayward et al. 2011). Where the biomass of potential prey is considerably lower, sound and smell contribute to the initial location of prey and sight is the primary sense during hunting (Schaller 1972). Some species, such as wildebeest, are more responsive to food quality and quantity than to depredation pressure (Hopcraft et al. 2014). In contrast, zebra avoid dense cover and prefer open grassland at night when lions are active, thus reducing catchability (Fischhoff et al. 2007). African buffalo defend themselves against lion attacks by forming large herds (Prins & Iason 1989). Sinclair et al. (2003) stated that top-down depredation and resource limitation (bottom-up) could lead to the extinction of large carnivore populations, including lions.

Understanding the feeding ecology and prey choice of lions is important for improved conservation and management of lions. Globally, there is a decline in prey populations and this decline has a direct impact on large carnivore populations (Craigie et al. 2010). Responding to this alarming situation, the KWS formulated large carnivore's conservation and management strategy. As a contribution to this strategy in this thesis a question on the dynamics of lion diets in and around NNP is addressed.

Human–lion interactions in Kenya

Livestock depredation by lions has been reported throughout the lions' range, in West, South and Eastern Africa (Patterson et al. 2004; Tumenta et al. 2013; Tuqa 2015). Human–lion conflicts occur around all national parks in Kenya (Patterson et al. 2004; Woodroffe & Frank 2005; Tuqa 2015). Conover (2002) defined human–wildlife interactions as "situations occurring when an action by either humans or wildlife has an adverse effect on the other." Young et al. (2010) suggested that a clear distinction should be made between interactions and the related impacts of wildlife on humans on the one hand, and underlying human–human conflicts related to wildlife conservation strategies on the other hand. Human–wildlife conflicts arise when non-domesticated animals threaten the livelihood and safety of people and their property (Inskip & Zimmermann 2009).

The Sessional Paper No. 3 of 1975 entitled, "A Statement on Future Wildlife Management Policy in Kenya," emphasized the importance of including communities in conservation activities in order to minimize human–wildlife conflicts (KWS 2011). The ongoing wildlife policy review in Kenya points out a lack of implementation of The Sessional Paper No. 3 of 1975 as the major cause for largely failing to address the human–wildlife conflict problem in Kenya, including the lack of compensation (KWS 2011). This has negatively affected the conservation of threatened species, especially large carnivores.

In small national parks, human–lion conflicts can cause more damage compared to such conflicts in larger parks (Lesilau et al. 2018). NNP is a small, protected national park (117 Km^2) near the capital city, Nairobi. The park is surrounded by urban settlements and livestock areas. The proximity and densities of livestock around a protected area may increase the magnitude of human–lion conflicts (Patterson et al. 2004; Van Bommel et al. 2007; Tumenta et al. 2013). As most of the local pastoralists are dependent on livestock, depredation by lions results in economic losses (Hemson 2003; Dickman et al. 2014).

In recent years, lions in NNP have experienced a serious threat due to retaliatory killing of lions by local communities outside the park as a result of livestock depredation (Lesilau et al. 2018). The southern part of NNP is not fenced and is accessible for wildlife as a migratory corridor (Gichohi 1996; Reid et al. 2008). Prior to this research, lions have been leaving the park and causing conflicts. In 2011, the community (close to NNP) killed six lions in retaliation for attacks on livestock (Smith 2012). A lioness was observed with cubs in a suburban area of Mukoma Road in Nairobi (Dloniak 2012). As per KWS Veterinary report (2012), the lioness was captured and translocated to Meru National Park, while her four cubs were being raised in the animal orphanage, Nairobi. It is suggested that either the lioness followed warthogs, by sneaking through the fence, or that she had escaped with her cubs in order to hide from a male pride takeover (Dioniak 2012).

Successful conflict resolution between humans and lions is an important outcome for both human development and species conservation (Woodroffe et al. 2007). Several authors have suggested different techniques and methods for addressing human–lion conflicts, including fencing, lethal removal, improved herding and adopting a *boma* structure, among others (Ogada et al. 2003; Woodroffe et al. 2007; Lesilau et al. 2018). *Boma* is a Kiswahili term for a livestock enclosure built to protect against predators (Manoa & Mwaura 2016).

During 2012, several livestock *bomas* around NNP were equipped with flashlights, invented by a school pupil, Richard Turere, (http://edition.cnn.com/2013/02/26/tech/richard-turere-lion-lights/) to deter lions from attack-

ing livestock *bomas* at night. The system uses solar energy to charge a car battery and, at night, the battery feeds light emitting diode (LED) bulbs connected to the battery by wire. The flashlights were installed around the *bomas*, facing outwards. To date, scientific proof of the effectiveness of flashlights in deterring nocturnal lion depredation remained speculative. My research intends to assess the impact of this flashlight application.

Lion management in Nairobi National Park

The Nairobi National Park was established in 1946 and in 1955 the western part of NNP bordering the Langata-Karen area was fenced to deter lions from roaming into the streets and gardens of Nairobi City (Steinhart 1994). Kenya Wildlife Service (KWS) was established as a state corporation in 1989 by an Act of Parliament, CAP 376, with a mandate for wildlife conservation and management in Kenya (G.o.K 1989). KWS developed and implemented a "Carnivore Conservation and Management Strategy" (KWS 2008). In addition, KWS established a large carnivore Task Force to advice and implement this strategy, which emphasizes law enforcement, research and monitoring. KWS seeks public support through public-private partnerships to ensure effective conservation of large carnivores (KWS 2008).

1.4 Research objectives and research questions

The main objective of my PhD research is to analyze factors influencing livestock depredation by lions around Nairobi National Park, to assess the impact of climate variability and to investigate mitigation measures used by livestock farmers to prevent livestock depredation.

The specific objectives for this research have been defined as follows:

- **i** To analyze population size, structure and factors affecting the Nairobi National Park lion population
- **ii** To determine home range and movement dynamics of the Nairobi National Park lions in time and space
- **iii** To analyze the impact of climate variability on the feeding ecology of lions
- **iv** To determine the contribution of livestock to the lion's diet and the impact of independent factors (the presence/absence of fences and rainfall) on livestock raiding and the related economic costs incurred by livestock farmers.
- **v** To investigate the response by lions to the installation of LED flashlight technology on livestock *bomas* to prevent nocturnal livestock depredation

In relation to these objectives, I have defined the following research questions, that were addressed in detail in the following 5 chapters:

1 What is the population size and social structure of NNP lions in time and space?
2 What are the home range sizes and movements of lions in time and space?
3 What is the diet composition of lions in time and space and which independent factors (climate variability, carcasses and scats) influence the diet?
4 What is the livestock contribution to lions diet and which independent factors influence livestock raiding and economic costs incurred by farmers?
5 What is the response of lions to LED flashlights installed on livestock *bomas*?

1.5 Study area

Location of Nairobi National Park

Nairobi National Park (NNP) is located 7 km southwest of Nairobi City in Kenya (Owino et al. 2011). According to the 2009 population census of Kenya by the Kenya National Bureau of Statistics (KNBS), Nairobi City has a population of 3,138,369 people with an average growth rate of three per cent per annum (KNBS 2009). The park was established in 1946 with an area of 117 km^2 (gazette Notice no. 48 of 16th December 1948). It is situated between latitudes 1° 20´-1° 26´ S and longitudes 36° 50´-36° 58´ E (Ogutu et al. 2013) within the altitude ranging between 1533 to 1760 m above sea level (Rudnai 1974; Owino et al. 2011). The broadest part of the park is 6.5 km and the longest is 24.8 km.

Because the park is adjacent to Nairobi City, the park was fenced in 1955 (Steinhart 1994). A chain-link fence and galvanized wire are installed, powered by electricity (6 kV), which covers the perimeter of the park from the East, via the northern border, to the West in order to separate wildlife from the Nairobi metropolis (Foster & Coe 1968; Reid et al. 2008). Approximately 56% (36.3 km) of the park perimeter was fenced. The southwestern boundary of the park is the Mbagathi River (the Maasai call it Empakasi) and the southern border is beyond the Mbagathi River. There is a wildlife migratory corridor that grants access to the Athi-Kaputiei Plains (AKP), which has an area of 2,200 km^2 (Reid et al. 2008).

Vegetation (plains, woodlands, grassland)

Nairobi National Park has three vegetation zones, with distinct vegetation types, covered with grassland and acacia (*Themeda triandra, Bothriochloa*

insculpta, Acacia depanalobium (Rudnai 1974). (i) The western part is covered by semi-evergreen forest patches of *Croton macrostachys* and *Olea africana* with some open grass glades, occupying 10 km^2 (Foster & Coe 1968). (ii) The Athi Basin is open grass savannah with monocods like *Pennisetum meszzianum* and *Themeda triandra Balanites* tree and an egg-shaped *acacia melifera* due to giraffe herbivory. (iii) The Mbagathi River is covered with riverine vegetation dominated with *Acacia xanthophloea* Benth *Acacia mellifera* (Vahl) Benth (Rudnai 1974). Small woody and dwarf plants are the result of controlled burning (Foster & Coe 1968). The three vegetation zones can be classified in eight distinctive habitat types (Fig. 1.1)

Geology and soil

The NNP is covered with friable clay soils (Deshmukh 1985). Almost half of the park's total area is covered with grey or black, generally neutral, alkaline soil that is popularly known as "black cotton". This soil becomes waterlogged during the rainy season and it cracks during the dry season (Deshmukh 1985).

The central part of the park has steep valleys and gorges. These steep valleys and gorges descend from north to south to join the Athi River on the park's southern boundary. They are characterized by poor drainage and a number of fairly restricted plant communities' distribution.

Wildlife populations

The Athi-Kapiti Plains, the Ngong Hills, across the Mombasa Road to Thika have historically provided the majority of Nairobi Park's wildlife dispersal zone (Foster & Coe 1968). Today, all these areas are dominated by human settlements. In the early 1970s, dams were constructed to enhance carrying capacity for and water provision to wildlife in the park, and to create a tourist attraction (Gichohi 1996).

The park is home to four species of the so-called Big Five: lion (*Panthera leo)*, leopard *(Panthera pardus)*, African buffalo *(Syncerus caffer caffer)*, and eastern black rhinoceros (*Diceros bicornis*). The blue wildebeest (*Connochaetus taurinus)*, Burchell's zebra (*Equus quagga burchelli)* and associated smaller ungulates such as Grant gazelle (*Gazella granti)*, Thompson's gazelle (*Eudorcas thomsoni)* and warthog (*Phacochoerus africanus*) tend to range into community land during the wet season (Gichohi 1996). Other resident ungulate species include: White rhinoceros (*Ceratotherium simum),* Common eland *(Tragelaphus oryx)*; hartebeest *(Alcephalus buselaphus*); giraffe *(Giraffa Camelopardalis)*; impala (*Aepyceros melampus),* waterbuck (*Kobus ellipsiprymnus),* Bohor reedbuck *(Redunca redunca)* and Common reedbuck *(Redunca arundinum)* (Owino et al. 2011). The park is an important bird

area with a high diversity of bird species (see http://www.naturekenya.org/content/important-bird-areas).

Climatic conditions of Nairobi National Park

Kenya has two periods of rainfall, one longer wet season from March to May and a short wet season from November to December (Deshmukh 1985). The monthly mean of the long rainfall period is 150 mm during March to May and for the short rainfall period it is 90 mm for November to December (Deshmukh 1985). The temperature range is between 13.6 °C and 25.3 °C (Deshmukh 1985; Muya & Oguge 2000).

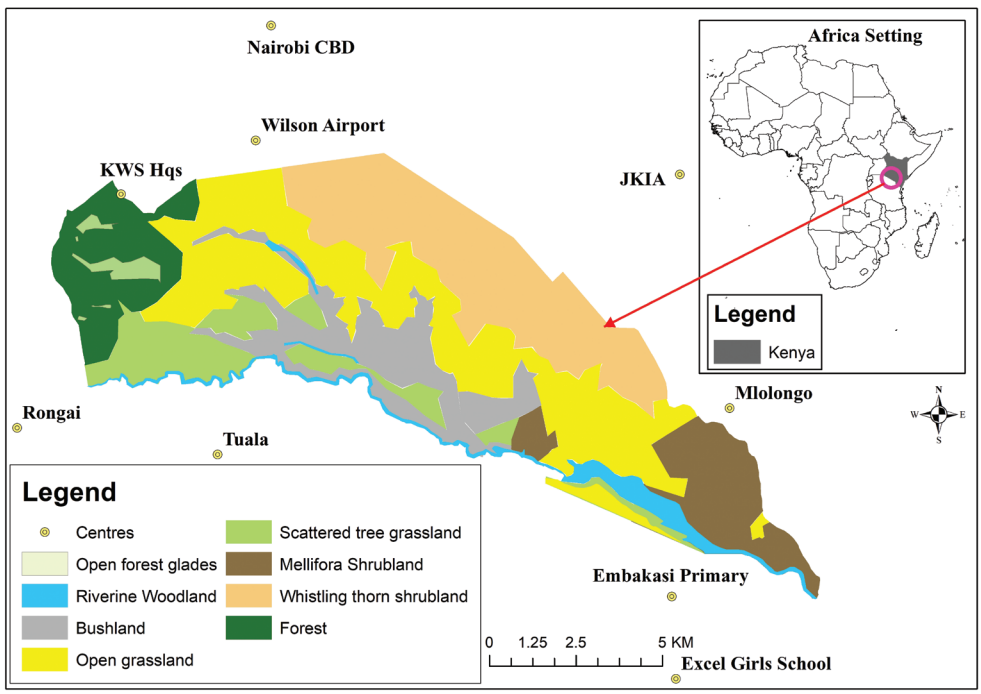

Figure 1.1
Map of Nairobi National Park showing the different habitat types. Vegetation data provided by the KWS GIS and Biodiversity Office (2011). (Designed in Arcmap 10.3.1 (ESRI Software, U.S.A.))

Tourism

Humans derive pleasure from flora and fauna and the lion tops the list of species attracting tourists into national parks (Macdonald & Sillero-zubiri 2002). Adjacent to Nairobi City, NNP is the most accessible and frequently visited park by Kenyan citizens (Fig. 1.2). Foreign visitors arriving at Jomo Kenyatta International Airport and those departing from Wilson Airport get a good

glimpse of this green island of forested savanna landscape, surrounded by human settlements. The park received between 132,304–150,464 visitors per annum during 2012 to 2016.

Due to a lack of revenue sharing with the surrounding communities and without any intervention to address the land challenges in the Athi-Kaputei ecosystem, the viability of the wildlife migratory corridor in the community land is currently in jeopardy (Matiko 2014).

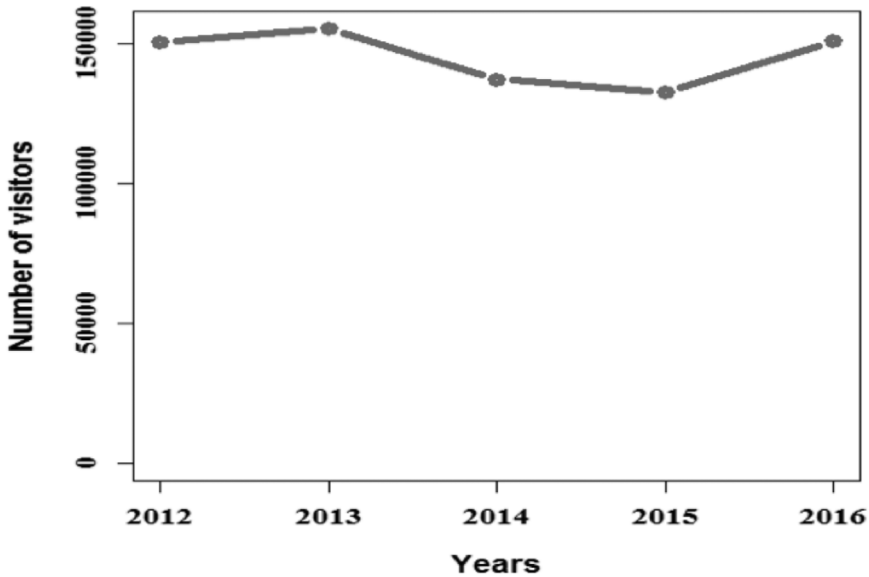

Figure 1.2
The number of visitors to NNP annually. The annual pass ticket holders were excluded during 2012-2016. (Source: this research)

1.6 Rationale and thesis structure

Nairobi National Park is in Nairobi's backyard and it includes the headquarters of the Kenya Wildlife Service, an institution mandated by an Act of Parliament to protect, conserve and sustainably manage wildlife in Kenya (Wildlife Conservation and Management Act) (GoK 1989). NNP is the oldest park (gazetted 1946) in Kenya and the management of lions within its perimeter is an important part of Kenya's wildlife conservation efforts. The proximity of the park to the capital city does make lion conservation and management here more complex. Prior to this study, lions in NNP have faced retaliatory killing by pastoral communities around the park (Rudnai 1979; Smith 2012;

KWS 2014). The park's management has witnessed lions entering urban and suburban areas. To date little is known about the NNP's lion population in terms of pride structure, home ranges, movements and diet. The communities around NNP have become more sedentary and wildlife habitat in the community land is shrinking due to human population growth, fencing and industrial development. This has led to more incidences of human–lion conflicts in recent years.

A better understanding of the factors influencing human–lion conflicts would improve conservation of the NNP lions and assist the development of science-based solutions to resolve human–lion conflict. These science-based solutions to resolve human–lion conflict are required to prevent retaliatory killing of lions. Therefore, the aim of this study is to ensure conservation of lions in NNP and in the surrounding areas, specifically in relation to human–lion conflicts. It focuses on population size and pride structure, home ranges and movements by employing iridium satellite collars from Africa Wildlife Tracking Ltd. This study covers the factors influencing human–lion conflict, the lion's prey choice and diets and examines the socio-economic aspects of lion–livestock conflicts.

The findings of this research can be used to identify exit point in NNP of the lions' dispersal movements into the community land for identification of potential depredation hotspots and conservation zones. It can also be used for rapid response for conflict mitigation and planning for land use around NNP.

This study comprises of seven chapters and each chapter covers a specific research objective. Chapter 1 of this thesis provides a general introduction to the ecology of the African lion (*Panthera leo*) by giving a global overview of its population status, recent scientific publications on home range and movements, diet, livestock raiding behavior and threats. Chapter 2 focuses on the NNP lion population size, the number of prides, social structure and factors affecting lion population size and grouping. Chapter 3 is on the movement and seasonal variation of home range size. Chapter 4 covers the feeding ecology of lions using carcass counts and microscopic prey hair morphology prints from lion scats. This method is combined with deoxyribonucleic acid (DNA) analysis of lion scat, and a prey estimate from carcass counts. The emphasis of Chapter 5 is on the contribution of livestock to the lions' diet, partial fencing of the park, and the occurrence of human–lion conflicts and economic losses incurred by livestock farmers. The level of human–lion interaction is evidenced by reported livestock depredation events and reports of NNP lions roaming in the community land. We used lion scats with microscopic analysis of livestock hair morphology and correlated these data with livestock depredation records from the Kenya Wildlife Service (KWS), Friends of Nairobi

National Park (FoNNaP) and The Wildlife Foundation (TWF). I also used the average livestock market price to assess the economic costs incurred by livestock farmers. Chapter 6 covers the impact of lighting emitting diodes (LED) flashlights and livestock husbandry techniques on lion-livestock depredation. I evaluated the application of LED flashlights to livestock bomas to deter nocturnal livestock depredation. Chapter 7 provides a synthesis of my research. This chapter integrates the findings of all the chapters and includes conclusions and recommendations for management actions, NGO's and communities in order to conserve the lions of Nairobi National Park.

NAIROBI NATIONAL PARK

It lies close to the boundary of the busy city's rights
A tiny little sanctuary in which the game delights.
The remnants of the vast herds which used to roam the plains,
Still at dawn the vultures circle round the lions' grim remains.
By dark the gorges echo to wild voices of the night
By day to droning engines of the aeroplanes in flight.
But the birds and beasts and flowers by water-hole and stream
Pay no heed and rest contented. It's a nature lover's dream.

K. P. BEATON
Warden
24th May, 1951

References

AbiSaid M, Dloniak SMD. 2015. Hyaena hyaena. The IUCN Red List of Threatened Species 2015: e.T10274A45195080.

Bauer H, Chapron G, Nowell K, Henschel P, Funston P, Hunter LTB, Macdonald DW, Packer C. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. Proceedings of the National Academy of Sciences **48**: 14894-14899.

Bauer H, De Iongh H, Sogbohossou E. 2010. Assessment and mitigation of human-lion conflict in West and Central Africa. Mammalia **74**:363–367.

Bauer H, De Iongh H. 2005. Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. African Journal of Ecology 43:208–214.

Bauer H, De Iongh H, Di Silvestre I. 2003. Lion (Panthera leo) social behaviour in the West and Central African savannah belt. Mammalian Biology 68:239–243.

Bauer H, Packer C, Funston PF, Henschel P, Nowell K. 2016. Panthera leo. The IUCN Red List of Threatened Species 2016: e.T15951A115130419.

Bauer H, Van der Merwe S. 2004. Inventory of free-ranging lions (*Panthera leo*) in Africa. Oryx **38**:26–31.

Berger J, Stacey B, Bellis L, Johnson P. 2001. A Mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. Ecological Society of America **11**: 947-960.

Bertola LD, Jongbloed H, van der Gaag KJ, de Knijff P, Yamaguchi N, Hooghiemstra H, Bauer H, Henschel P, White PA, Driscoll CA, Tende T, Ottosson U, Saidu Y, Vrieling K, & de Iongh HH. 2016. Phylogeographic Patterns in Africa and High Resolution Delineation of Genetic Clades in the Lion (*Panthera leo*). Scientific Reports, Nature Publishing Group **6**:1–11.

Björklund M. 2003. The risk of inbreeding due to habitat loss in the lion (Panthera leo). Conservation Genetics **4:**515–523.

Bohm T, Höner OR. 2015. Crocuta crocuta. The IUCN Red List of Threatened Species 2015: e.T5674A45194782.

Burkey TV. 1995. Faunnal collapse in East African Game reserves revisted. Biological Con. **71**:107-110.

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005. Multiple Causes of High Extinction Risk in Large Mammal Species. Science **309**:1239–1241.

Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology **2**:909–914.

Carter NH, Linnell JDC. 2016. Co-Adaptation Is Key to Coexisting with Large Carnivores. Trend in Ecology and Evaluation **31:** 575-578

Chardonnet P. 2002. Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA: Pp102–171.

Chardonnet P, Soto B, Fritz H, Crosmary W, Drouet-Hoguet N, Pellerin PM, Mallon D, Bakker L, Boulet H, Lamarque F. 2010. Managing the conflicts between people and lion. Review and insights from the literature and field experience. Wildlife Management Working Paper **13**:1–69.

Coe MJ, Cummings J, Phillipson J. 1976. Biomass and production of large herbivores in relation to rainfall and primary production. Oecologia **22**:341–354.

Conover MR. 2002. Resolving Human-Wildlife Conflicts: The Science of Wildlife Damage Management. Publishers, CRC Press LLC, Boca Raton, FL. Pp 1-440

Craigie ID, Baillie JEM, Balmford A, Carbone C, Collen B, Green RE, Hutton JM. 2010. Large mammal population declines in Africa's protected areas. Biological Conservation **143**: 2221–2228.

Creel S, Creel NM. 1997. Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. African Journal Ecology **35**: 83–93.

Dalerum F, Somers MJ, Kunkel KE, Cameron EZ. 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. Biodiversity and Conservation **17**: 2939–2949.

Davidson Z, Valeix M, Loveridge AJ, Hunt JE, Johnson PJ, Madzikanda H, Macdonald DW. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. Journal of Mammalogy **93**: 677–685.

De Boer WF et al. 2010. Spatial distribution of lion kills determined by the water dependency of prey species. Journal of Mammalogy **91**: 1280–1286.

Deshmukh I. 1985. Decomposition of grasses in Nairobi National Park, Kenya. Oecologia **67**: 147–149.

Dickman AJ. 2010. Complexities of conflict: The importance of considering social factors for effectively resolving human-wildlife conflict. Animal Conservation **13**: 458–466.

Dickman AJ, Hazzah L, Carbone C, Durant SM. 2014. Carnivores, culture and "contagious conflict": Multiple factors influence perceived problems with carnivores in Tanzania's Ruaha landscape. Biological Conservation **178**: 19-27.

Dloniak MS .2012. Suburban Lions Present a Conundrum. Available from https://www.nytimes.com/2012/09/11/science/suburban-lions-present-a-conservation-conundrum-in-africa.html. (accessed on 19 September, 2014).

Druce D, Genis H, Braak J, Greatwood S, Delsink A, Kettles R, Hunter L, Stow R. 2004. Prey selection by a reintroduced lion population in the Greater Makalali Conservancy, South Africa. African Zoology **39**: 273-284

Elliot NB, Cushman SA, Loveridge AJ, Mtare G, Macdonald DW, Elliot NB, Cushman SA, Loveridge AJ, Mtare G, Macdonald DW. 2017. Movements vary according to dispersal stage, group size, and rainfall: the case of the African lion. Ecological Society of America Stable **95**: 2860–2869.

Fischhoff IR, Sundaresan SR, Cordingley J, Rubenstein DI. 2007. Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. Behavioral Ecology **18**: 725–729.

Foster JB, Coe MJ. 1968. The biomass of game animals in Nairobi National Park, 1960 - 66. Journal of Zoology **155**: 413–425.

Funston PJ, Mills MGL, Biggs HC. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. Journal of Zoology **253**: 419–431.

G.o.K. 1989. The Wildlife (Conservation and Management) Act,1989. Government Printers, Nairobi Kenya. Pp 29901-19978

G.o.K. 2010. The Constitution of Kenya. Kenya Law Reports, Nairobi Kenya. Pp 1-191

Gichohi HW. 1996. The Ecology of a Truncated Ecosystem - The Athi-Kapiti Plains. University of Leicester UK. PhD Thesis. Available from http://hdl.handle.net/2381/34356 (Accessed on 20th April, 2016)

Gilfillan GD, McNutt JW, Vitale JDT, De Iongh HH, Golabek K. 2017. Rare observation of the existence and masculine behaviour of maned lionesses in the Okavango Delta, Botswana. African Journal of Ecology **55**: 383–385.

Gittleman JL, Harvey PH. 1982. Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology **10**: 57–63.

Hanby JP, Bygott JD. 1987. Emigration of subadult lions. Animal Behaviour **35**:161–169.

Hayward MW, Hayward GJ, Tambling CJ, Kerley GIH. 2011. Do lions (*Panthera leo*) actively select prey or do prey preferences simply reflect chance responses via evolutionary adaptations to optimal foraging? PLoS ONE **6**: e23607

Hayward MW, Kerley GIH. 2005. Prey preferences of the lion (*Panthera leo*). Journal of Zoology **267**: 309–322.

Hemson G. 2003. The Ecology and Conservation of Lions: Human-Wildlife Conflict in semi-arid Botswana. University of Oxford Uk. PhD Thesis. Available from http://www.africanindaba.co.za/Conservation/hemson (accessed on 12 June, 2017).

Henschel P, Azani D, Burton C, Malanda GUY, Saidu Y, Sam M, Hunter L. 2010. Lion status updates from five range countries in West and Central Africa. Cat News **52**: 34–39.

Henschel P, Bauer H, Sogbohoussou E, Nowell K. 2015. The IUCN Red List of Threatened Species: *Panthera leo* (West Africa subpopulation). IUCN Red List of Threatened Species 2015: e.T68933833A54067639.

Hopcraft JGC, Morales JM, Beyer HL, Borner M, Mwangomo E, Sinclair ARE, Olff H, Haydon DT. 2014. Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. Ecological Monographs **84**: 355–372.

Inskip C, Zimmermann A. 2009. Human-felid conflict: A review of patterns and priorities worldwide. Oryx **43**: 18–34.

Jetz W, Wilcove DS, Dobson AP. 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology **5**: 1211–1219.

Kays RW, Patterson BD. 2002. Mane variation in African lions and its social correlates. Canada Journal of Zoology **80:** 471-478.

Kissui BM. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Animal Conservation **11**: 422–432.

Kitchener AC, Breitenmoser-Würsten Ch, Eizirik E, et al. 2017. A revised taxonomy of the Felidae Executive. The final report of the Cat Classification Task Force of the IUCN/ SSC Cat Specialist Group. Cat News Special Issue **11**: 80 pp.

KNBS. 2009. Kenya Population and Housing Census: Analytical Report on Mortality Volume VIII. Kenya National Bureau of Statistics, Nairobi Kenya. Pp 1-250

Kumaraguru A, Saravanamuthu R, Brinda K, Asokan S. 2010. Prey preference of large carnivores in Anamalai Tiger Reserve, India. European Journal of Wildlife Research **57**: 627-637

Kushner J. 2016. Lions Are Wandering Out of Parks and Into Cities. National Geographic. Available from https://news.nationalgeographic.com/2016/04/160401-Kenya-lions-leaving-Nairobi-National-park-conflict/ (Accessed on 12th March, 2017).

KWCA. 2016. State of Wildlife Conservancies in Kenya Report 2016. Kenya Wildlife Conservancies Association, Nairobi Kenya. Pp 1-84 KWS. 2008. Conservation and Management Strategy of Lions and Spotted Hyena in Kenya. Kenya Widlife Service, Nairobi, Kenya. Pp 1-52.

KWS. 2011. Draft Wildlife Policy. Kenya Widlife Service, Nairobi, Kenya. Pp 1-38

KWS. 2015. Annual Report 2015. Kenya Widlife Service, Nairobi, Kenya. Pp 1-94

KWS. 2014. Veterinary Field report 201-2014. Kenya Widlife Service, Nairobi Kenya. Pp 1-10

Lehmann MB, Funston PJ, Owen CR, Slotow R. 2008. Home Range Utilisation and Territorial Behaviour of Lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. PLoS ONE **3**: e3998.

Lesilau F, Fonck M, Gatta M, Musyoki C, Van 't Zelfde M, Persoon GA, Musters KCJM, de Snoo GR, de Iongh HH. 2018. Effectiveness of a LED flashlight technique in reducing livestock depredation by lions (*Panthera leo*) around Nairobi National Park, Kenya. PLOS ONE **13**: e0190898.

Loveridge AJ, Hunt JE, Murindagomo F, Macdonald DW. 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. Journal of Zoology **270**: 523–530.

Macdonald DW. 1983. The ecology of carnivore social behaviour. Nature **301**: 379–384.

Macdonald, DW and Sillero-Zubiri, C. (2002). Large carnivores and conflict: Lion conservation in context. Pp. 1-8 in A.J. Loveridge, T. Lynam and D.W. Macdonald (Eds.) Lion conserva- tion research. Workshop 2: modelling conflict. Wildlife Conservation Research Unit, Oxford University.

Manoa DO, Mwaura F. 2016. Predator-Proof Bomas as a Tool in Mitigating Human-Predator Conflict in Loitokitok Sub-County Amboseli Region of Kenya. Natural Resources **7**: 28–39.

Matiko D. 2014. Wildlife Conservation Leases are Considerable Conservation Options outside Protected Areas: The Kitengela - Nairobi National Park Wildlife Conservation Lease Program. Journal of Ecosystem & Ecography **4**: 2–9.

Muntifering JR, Dickman AJ, Perlow LM, Hruska T, Ryan PG, Marker LL, Jeo RM. 2006. Managing the matrix for large carnivores: A novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling. Animal Conservation **9**: 103–112.

Muya SM, Oguge NO. 2000. Effects of browse availability and quality on black rhino. African Journal of Ecology **38**: 62–71.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. PNAS **105**: 19052–19059.

Novaro AJ, Funes MC, Susan Walker R. 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. Biological Conservation **92**: 25–33.

Ogada MO, Woodroffe R, Oguge NO, Frank LG. 2003. Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. Conservation Biology **17**: 1521–1530.

Ogutu JO, Dublin HT. 1998. The response of lions and spotted hyenas to sounds playbacks as a technique for estimating population size. African Journal of Ecology **36**: 83-93

Ogutu JO, Dublin HT. 2002. Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. African Journal of Ecology **40**: 120–129.

Ogutu JO, Owen-Smith N, Piepho H-P, Said MY, Kifugo SC, Reid RS, Gichohi H, Kahumbu P, Andanje S. 2013. Changing Wildlife Populations in Nairobi National Park and Adjoining Athi-Kaputiei Plains: Collapse of the Migratory Wildebeest. Open Conservation Biology Journal **7**: 11–26.

Ripple WJ, Estes JA, et al. 2014. Status and ecological effecs of the world's largest carnivores. Science. **343**: 1241484- 1241484

Owino AO, Kenana ML, Webala P, Andanje S, Omondi PO. 2011. Patterns of Variation of Herbivore Assemblages at Nairobi National Park, Kenya, 1990-2008. Journal of Environmental Protection **2**: 855–866.

Packer C, Pusey AE & Eberly LE. 2001. Egalitarianism in Female African Lions. *Science* **293**: 690-693.

Packer C et al. 2013. Conserving large carnivores: Dollars and fence. Ecology Letters **16**: 635–641.

Packer C, Hilborn R, Mosser A, Kissui B, Borner M, Hopcraft G, Wilmshurst J, Mduma S, Sinclair ARE. 2005. Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. Science **307**: 390–393.

Patterson BD, Kasiki SM, Selempo E, Kays RW. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biological Conservation **119**: 507–516.

Pimm SL, Dollar L, Bass OL. 2006. The genetic rescue of the Florida panther. Animal Conservation **9**:115–122.

Pimm SL, Raven P. 2000.Extinction by numbers. Nature **403**: 843-845

Pontzer H, Kamilar JM. 2009. Great ranging associated with greater reproductive investment in mammals. Proceedings of the National Academy of Sciences of the United States of America **106**: 192–196.

Prins HHT, Iason GR. 1989. Dangerous Lions and Nonchalant Buffaloes. Behaviour **108**: 262–297.

Reid RS, Gichohi H, Said MY, Nkedianye D, Ogutu JO, Kshatriya M, Kristjanson P, Kifugo SC, Agatsiva JL, Adanje SA, Bagine R. 2008. Fragmentation of a Peri-Urban Savanna, Athi-Kaputiei Plains, Kenya. Pages 195–224Fragmentation in Semi-Arid and Arid Landscapes. Springer.

Riggio J, Jacobson A, Dollar L, Pimm S, Bauer H, De Iongh HH, De Dickman A, Becker M, Funston P, Groom R, & Henschel P . 2013. The size of savannah Africa: A lion's (Panthera leo) view. Biodiversity and Conservation **22**: 17–35.

Rosenblatt E, Creel S, Becker MS, Merkle J, Mwape H, Schuette P, Simpamba T. 2016. Effects of a protection gradient on carnivore density and survival: An example with leopards in the Luangwa valley, Zambia. Ecology and Evolution **6**: 3772-3785.

Rudnai J. 1974. The Pattern of Lion predation in Nairobi. African Journal of Ecology **12**:213–225.

Schaller GB. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press. Chicago, IL, USA.

Scheel D, Packer C. 1991. Group hunting behaviour of lions: a search for cooperation. Animal Behaviour **41**: 697–709.

Schnitzler AE. 2011. Past and present distribution of the North African-Asian lion subgroup: A review. Mammal Review **41**: 220–243.

Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, McHugh K, Hiraldo F. 2008. Top Predators as Conservation Tools: Ecological Rationale, Assumptions, and Efficacy. Annual Review of Ecology **39**: 1–19.

Sillero-Zubiri, C., and K. Laurenson. 2001. Interactions between carnivores and local communities: Conflict or co-existence? Pp. 282-312 in J. Gittleman, S. Funk, D.W. Macdonald and R.K. Wayne (Eds.). Proceedings of a Carnivore Conservation Symposia. Zoological Society of London, UK.

Sinclair ASE, Mduma S, Brashares JS. 2003. Patterns of predation in a deverse predator-prey system. Nature **425**: 288–290.

Smith D. 2012. Six wild lions speared to death after livestock killed in Nairobi area. The Guardian. Available from https://www.theguardian.com/world/2012/jun/21/six-lions-speared-death-nairobi-livestock. (accessd on 14 July, 2014)

Sogbohossou EA, Bauer H, Loveridge A, Funston PJ, De Snoo GR, Sinsin B, De Iongh HH. 2014. Social Structure of Lions (*Panthera leo*) Is Affected by Management in Pendjari Biosphere Reserve, Benin. PLoS ONE **9**: e84674.

Stander PE. 1991. Demography of lions in the Etosha National Park, Namibia.pdf. Madoqua **18**: 1–9.

Steinhart E. 1994. National Parks and Anti-poaching in Kenya, 1947-1957. The International Journal of African Historical Studies **27:** 59-76.

Tumenta P, Kok J, Van Rijssel J, Buij R, Croes B, Funston P, De Iongh HH, Udo De Haes H. 2010. Threat of rapid extermination of the lion (*Panthera leo leo*) in Waza National Park, Northern Cameroon. African Journal of Ecology **48**: 888–894.

Tumenta PN, Visser HD, Van Rijssel J, Müller L, De Iongh HH, Funston PJ, De Haes HAU. 2013. Lion predation on livestock and native wildlife in Waza National Park, northern Cameroon. Mammalia **77**: 247–251.

Tuqa. 2015. The Impact of Climate Variability on the Ecology of a Lion (*Panthera leo Linnaeus 1758*) Population and Lion-Livestock Conflicts in the Amboseli Ecosystem-Kenya. Leiden University. PhD Thesis. Pp 1-166

Valeix M, Loveridge JA, Davidson Z, Madzikanda H, Fritz H, Macdonald DW. 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecol **25**: 337–351

Van Orsdol, KG, Hanby JP, & Bygot JD. 1985. Ecological correlates of lion social organization. Journal of Zoology Zoology, London **206**: 97–112.

Van Bommel L, Bij De Vaate MD, De Boer WF, De Iongh HH. 2007. Factors affecting livestock predation by lions in Cameroon. African Journal of Ecology **45**: 490–498.

Vanak AT, Fortin D, Thaker M, Ogden M, Owen C, Greatwood S, Slotow R. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology **94**: 2619-2631

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human Domination of Earth' s Ecosystems. Science **277**: 494–499.

Wiesel I. 2015. Parahyaena brunnea. The IUCN Red List of Threatened Species 2015: e.T10276A82344448

Winterbach HEK, Winterbach CW, Somers MJ, Hayward MW. 2013. Key factors and related principles in the conservation of large African carnivores. Mammal Review **43**: 89-110

Woodroffe R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation **3**: 165–173.

Woodroffe R, Frank LG. 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. Animal Conservation **8**: 91–98.

Woodroffe R, Frank LG, Lindsey PA, Ole Ranah SMK, Romañach S. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: A case-control study. Biodiversity and Conservation **16**: 1245–1260.

Woodroffe R, Lindsey P, Romañach S, Stein A, Ole Ranah SMK. 2005. Livestock predation by endangered African wild dogs (*Lycaon pictus*) in northern Kenya. Biological Conservation **124**: 225–234.

Woodroffe R, Sillero-Zubiri C. 2012. African Wild Dog (*Lycaon pictus*). The IUCN Red List of Threatened Species. IUCN Red List of Threatened Species **8235**:e.

Young JC, Marzano M, White RM, McCracken DI, Redpath SM, Carss DN, Quine CP, Watt AD. 2010. The emergence of biodiversity conflicts from biodiversity impacts: Characteristics and management strategies. Biodiversity and Conservation **19**: 3973–3990.