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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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).

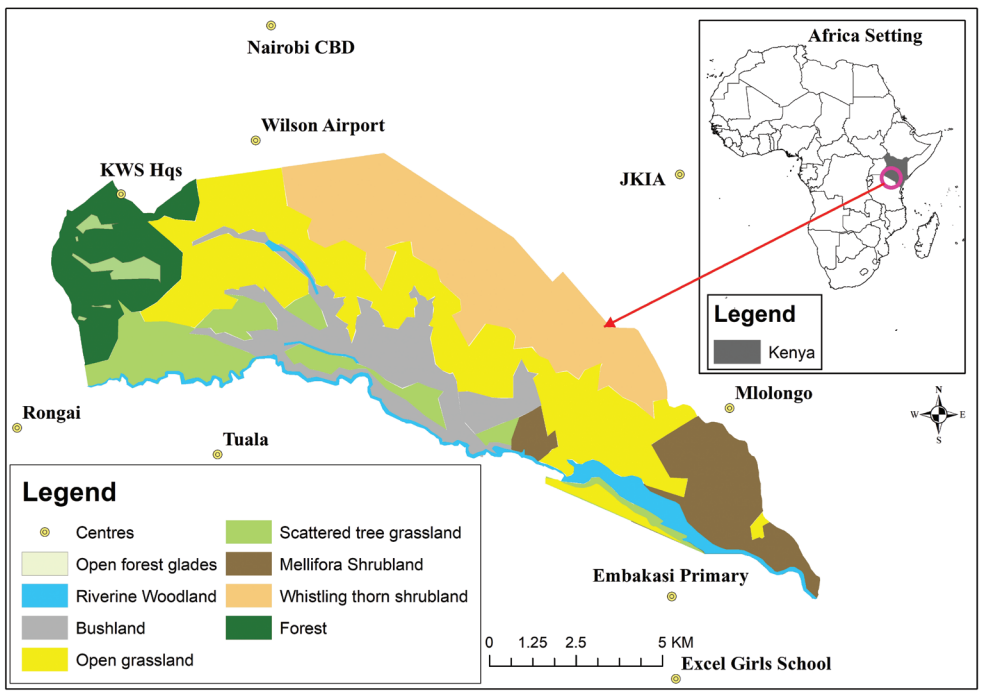

Figure 1.1
Map of Nairobi National Park showing the different habitat types. Vegetation data provided by the KWS GIS and Biodiversity Office (2011). (Designed in Arcmap 10.3.1 (ESRI Software, U.S.A.))

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).

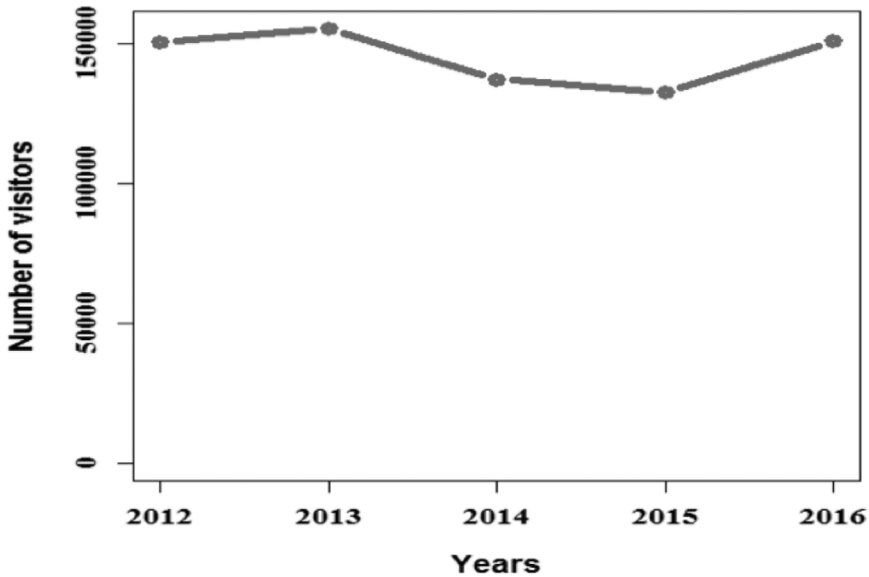

Figure 1.2
The number of visitors to NNP annually. The annual pass ticket holders were excluded during 2012-2016. (Source: this research)

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

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2

Population Size and Social Structure of Lions (*Panthera leo melanochaita)* in Nairobi National Park

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Abstract

We conducted a bi-annual lion survey during 2012 and 2014-2018 to monitor the lion population in Nairobi National Park (NNP). We also collared 12 lions from different prides to track them with radio telemetry and to identify other members of the pride. We developed a database of lion photographs using whisker spots, ear marks and body scars for individual and pride identification.

Our findings reveal that there are three lion prides in NNP. The lion population in NNP consists of 34-43 lions with a density of 26 lions/100 km^2 in 2018. The overall population size is estimated to be 29 lions (excluding cubs younger than one year). Our research shows that the NNP lion population is declining due to retaliatory killing of lions by the surrounding communities through spearing, poisoning and the use of snares. We conclude that human-related killing of lions impacts pride structure and could ultimately severely reduce the population of NNP lions.

Keywords
Nairobi City, retaliatory killing, African lions, GPS satellite tracking, pride

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2.1 Introduction

The African lion (*Panthera leo)* population has declined as a result of habitat fragmentation and retaliatory killing (Woodroffe & Frank 2005; Riggio et al. 2013). There are less than 45,000 lions in Africa (Bauer et al. 2004; Riggio et al. 2013). Kenya is estimated to host less than four per cent of the global lion population (KWS 2008); the population size declined from 7,000 individuals in 1990 to 2,000 in 2007 (KWS 2008). The Kenyan lions belong to the East African subspecies *Panthera leo melanochaita*, which was classified under the Endangered Species Act of 1973 and registered as threatened by the US, Fish and Wildlife Service in 2015 (USFWS 2015). In the 1970s, Rudnai (1979) estimated that the Nairobi National Park (NNP) lion population was 30 to 35 individuals from at least three different prides.

Geographically, lions are split into subspecies African lion (*Panthera leo leo*) and Asiatic lion (*Panthera leo persica*) (Bauer et al. 2016). African lions meet the criteria for vulnerable status (Bauer et al. 2016) and the West African subpopulation is critically endangered (Henschel et al. 2015) while the Asiatic lion subspecies is listed as endangered (Breitenmoser et al. 2008; Singh 2017).

The result of a phylogeographical study led to a revision of the taxonomic group and splits off African lions into a northern and southern subspecies (Barnett et al. 2014; Bertola et al. 2016; Kitchener et al. 2017). The South and East African subspecies of lion is called *Panthera leo melanochaita* (Bauer et al. 2016; Kitchener et al. 2017) while North, Central and West African lions are *Panthera leo leo.* Since Kenya is in East Africa, its subspecies is *Panthera leo melanochaita*, which was classified under the Endangered Species Act of 1973 and registered as threatened by the US, Fish and Wildlife Service in 2015 (USFWS 2015).

Knowing the population size and social status of species is paramount to the management of a conservation area. However, the fission–fusion (splitting and merging) nature of lions is complex and causes lion pride size, age composition, and social grouping to vary (Van Orsdol 1985) which makes it difficult to accurately estimate population size. The lion's cooperative hunting, territory defense and protection of cubs are essential for the survival of a pride (Schaller 1972; Rudnai 1979). As social cats, the pride is composed of between two and 35 individuals (Rudnai 1979; Van Orsdol 1985). A comparison of sex ratios reveals that females dominate prides (Van Orsdol 1985). The sub-adult males are displaced from the natal pride at the age of two and thereafter, lead a nomadic existence (Schaller 1972; Van Orsdol 1985; Elliot et al. 2017).

The last research undertaken on the NNP lion's ecology was in the 1970's when the human population of Nairobi City counted was less than one million people. Currently the population of the capital is growing at three per cent annually (KNBS 2009). This growth has increased the demand for resources and space. The rapid growth of human development towards the boundary of NNP is threatening the survival of large mammals, including carnivores, that historically have been ranging into the Athi-Kaputei Plains (Gichohi 2003). So, the NNP lion population is facing the threats of urban infringement, habitat fragmentation and isolation, reduction of prey populations, and retaliatory killing by local communities.

The aim of this research is to establish the present population size and structure and to identify factors contributing to the mortality and survival of NNP lions. We aim to answer the following questions: (i) What is the present population size of NNP lions? (ii) How many lion prides does NNP currently harbor? (iii) What is the social structure and sex ratio of NNP lions? (iv) What causes lion mortality in NNP?

2.2 Material and methods

2.2.1 Study area

Nairobi National Park (NNP) is adjacent to the southwestern part of Kenya's capital, Nairobi City (Owino et al. 2011) (Fig. 2.1). The park was established in 1946 with a surface area of 117 km^2 (gazette Notice no. 48 of 16th December 1948). It is situated between latitude 1° 20´-1° 26´ S and longitude 36° 50´-36° 58´ E (Ogutu et al. 2013) within an altitude ranging between 1533 m to 1760 m above sea level (Rudnai 1974; Owino et al. 2011). From West to East, the park is 6.5 km wide and North-west to South-west it is 24.8 km long.

Nairobi National Park has three distinct vegetation zones (Foster & Coe 1968) in eight distinct habitat type (Fig. 2.1): (i) The Western part of NNP is covered by semi-evergreen forest patches of *Croton macrostachys* and *Olea africana* with an open grass glade, occupying 10 km^2; (ii) The Athi Basin area is an open grass savannah with monocods like *Pennisetum meszzianum* and *Themeda triandra* and *Balanites spp* trees and egg-shaped *Acacia melifera* due to giraffe herbivory; (iii) The Mbagathi River is covered with riverine vegetation dominated by *Acacia xanthophloea Acacia mellifera* (Rudnai 1974). Dwarf woody plants are a result of controlled burning by park management (Foster & Coe 1968).

Due to its location next to Nairobi city, the National Park was partly fenced in 1955 (Steinhart 1994) with a chain-link fence and galvanized wire,

powered by electricity (6 kV) from the East, via the northern boundary, to the West to restrict wildlife from moving into the Nairobi metropolis (Foster & Coe 1968; Reid et al. 2008). The south-west boundary at the Mbagathi River (which the Maasai call Empakasi) and the southern border, which is beyond the Mbagathi River, provide open access to the Athi-Kaputiei Plains (AKP) with an area of rangeland of 2200 km^2 (Reid et al. 2008). This open access is necessary to maintain herbivore migrations in and out of the park especially during wet the season.

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

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).

Research conducted in Amboseli revealed that the cut-off point between the wet and the dry season was 28.3 mm a month (Tuqa 2015). Taking into consideration the high altitude of NNP and its relatively high rainfall, we set our cut-off point between the wet and the dry season at a mean 30 mm of rainfall per month.

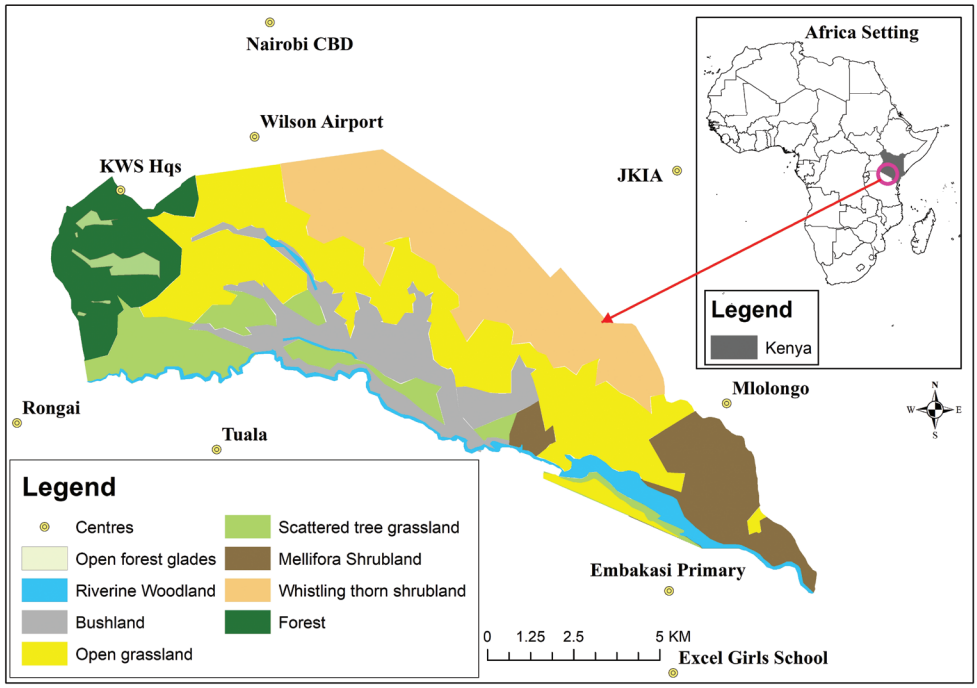

Figure 2.1
Map of Nairobi National Park showing habitat classification

2.2.2 Data collection

During 2014-2017, we collared 12 lions in the NNP (five males and seven females), following Tuqa et al. (2014) and Oriol-Cotterill et al. (2015) protocal of collaring lions, using Africa Wildlife Tracking (AWT, Pretoria, South Africa), Very High Frequency (VHF) Irridium satellite collars (Lesilau et al. 2018). Table 2.1 shows details of the lions that have been collared during the present study. A VHF model R-1000 Telemetry Handheld receiver with Telonics RA-14K rubber-duck "H" Antenna was used for the so called homing-in method during which the individual lions were tracked and visually identified by car, based on the radio signal. The signal is received from the VHF transmitter inside the lion's collar. The GPS location of the lion was then recorded and notes were taken on individual identification characteristics and group composition (number of individuals, sex ratio, age composition).

In order to identify individual lions, we took photos of whisker spots of both sides of the face using a Nikon D5100 with a 300 mm zoom lens, as described by Pennycuick & Rudnai (1970). As the whisker spot pattern can change from juvenile stage to adult stage, the method was only applied to adult lions (Penny-

cuick & Rudnai 1970) and cubs were not included as individuals for population analysis. Using these data, we created a database of photographs of NNP lions. We assessed age, sex and number of individuals per sighting, as described by Smuts et al. (1970) and Schaller (1972) and recorded GPS location (longitude and latitude). We also noted other distinguishable marks such as broken canines, ear notches, facial scars, behavior (feeding, hunting, resting, mating, walking) and body condition (health status).

Table 2.1

Details of collared NNP lions: resident pride (for females), the dates of collaring and the status of the collars and health status during the study period (2014-2017). Resident pride is not shown for males due to the frequent pride takeover.

S/n	Lion Name	Code	Animal Sex	Pride	Collar Id	Frequency	Start collaring	End of Collar	Status
1	Kiprono	L01	M		SAT1202	150.77	2014.01.25	2015.10.07	Dead (7 October 2015)
2	Nelly	L02	F	Southern	SAT1203	150.56	2014.01.26	2015.05.25	Neck injury and collar removed
3	Nelly	L02	F	Southern	SAT1203	150.56	2015.08.20	2015.11.14	Recollared
4	Dirk	L03	M		SAT1553	150.64	2015.02.02	2016.12.30	End of battery power
5	Nashipai	L04	F	Northern	SAT1552	150.62	2015.02.03	2015.10.10	Dead (10 October 2015)
6	Bertine	L05	F	Middle	SAT1552	150.62	2016.02.02	2017.03.16	End of battery power
7	Alex	L06	M		SAT1882	150.05	2016.02.02	2017.08.09	
8	Mumbi	L07	F	Northern	SAT1883	150.26	2016.02.26	2017.09.13	Dead (13 September 2017)
9	Nina	L08	F	Middle	SAT1975	150.78	2016.07.12		Active
10	Nala	L09	F	Middle	SAT2047	149.42	2017.01.23		Active
11	Tall Boy	L10	M	Northern	SAT2048	149.57	2017.01.23	2018.03.28	Dead(28 March 2018
12	Nelly	L02	F	Southern	SAT2050	149.89	2017.01.25	2018.5.17	Dead (17 May 2018)
13	Dirk	L03	M	Northern	SAT2049	149.68	2017.01.26		Active
14	Neema	L11	F	Northern	SAT2046	149.15	2017.01.30		Active
15	Karel	L12	M	Middle	SAT2045	149.03	2017.06.30	2018.04.11	Dead (11 April 2018)

* Two lions (L02 and L03) were collared twice and recollared: L02 after healing from injuries caused by a fight and L03 after the battery expired.

We conducted a bi-annual lion survey to visually identify individual lions in the months of February-April (the wet season) and July-September (the dry season) in 2012 and again during 2014-2018. In each bi-annual survey, all the data were collected by two observers for two days per week inside the park from 6.00 am to 6.00 pm. The searching effort was balanced in different areas of the park during the research. We carried out opportunistic searches, recording lion foot prints and lion roars, and we used reports from rangers and tourists to locate the lions in the park. The reports from rangers, tourists, foot print sighting and lion roars were not used for analysis, unless the research team observed the lions themselves and recorded details.

We acquired monthly rainfall data for the study period from Wilson Airport, through the Kenya Meteorological Department (KMD). We also obtained NNP vegetation data from the Kenya Wildlife Service GIS & Biodiversity Office (2011) to determine the habitat selections of lions (Fig. 2.1).

2.2.3 Data analysis and statistics

During 2012 and 2014-2018 we implemented a bi-annual lion population survey for which we used satellite tracking data and observations of new lions encountered. In order to determine the lion population size, each new sighting of a lion was cumulatively added to the number of previously identified lions per observation week (Fig. 2.3). This means that every lion is counted at least once per survey period. When the number of lions identified did not increase at the end of a lion survey period, we concluded that all adult lions in the population had been identified. The lion density as number of lions per 100 km^2 in the park was calculated based on a formula established by Tuqa (2015).

Individual lions were identified based on photos of their whisker spots pattern. A lion has whisker spots on the right and the left side of the face. The two rows were used to identify individual lions; Row A displays 17 cells and the row B has 9 cells. The number of spots in each cell is supposed to be unique for each lion (Pennycuick & Rudnai 1970). We used a grid template to place dots in the same pattern as was shown in the photo taken of the whisker spots, by zooming in on a computer. We aged the lions based on the classifications of Schaller (1972) and Whitman & Packer (2007), i.e. cubs (< 1 years), sub-adults (1-2 years) and adults (> 2 years).

We used the frequency of lion observations during surveys and sightings to determine individual pride members, age composition and group size. The number of occasions an individual lion was sighted and identified in a group of lions or alone was divided by the number of observations that group was sighted and multiplied by hundred. Any lion observed in > 50% of observa-

tions with the same group of lions during the study period, and did not show any sign of aggression to its group members during the observation, was considered to belong to that respective pride. Similarly, any lion that had not been associated with a particular group, and had been observed > 50% of the observations being alone was assumed to be a nomadic lion and makes occasional visit to natal pride. We named each pride according to its geographical location in the park. In addition, every adult and sub-adult lion identified was given a name (Table S1).

We monitored every known age cohort during 2012 and during 2014-2018 until reproductive maturity (until the first litter for females and until a male takes over a pride or forms a coalition with another pride male). We used the cohorts (set of cubs of same age) as the basis for calculating the surviving or age of first litter. Cohorts form closely related sub-prides and they also determine group size, pride demography and kinship (Van Orsdol 1985). To calculate survival rate, we divided the number cubs alive just before the next stage by the total number of cubs born in one year. The lion population growth rate was calculated by dividing the number of cubs that had reached productive adulthood by the total number of cubs of the same cohort born. We summarized the health status based on field observations. We conducted statistical analysis using the R program version 3.0.2 (R Core Team Foundation, 2016). We used a significance level of $p < 0.05$ for all tests.

2.3 Results

2.3.1 Population and prides

We found that NNP has on average 25.2 adult lions/100 km^2 (Fig. 2.2 and Table 2.2) and three prides (Northern, Middle and Southern prides, Fig. 2.4). In total, we encountered 1889 lions in 690 observations during 2012 and 2014-2018. The maximum population size was 29 lions, excluding cubs, in 2018 (Fig. 2.2 and 2.3). During 2012-2018, after excluding mortality and unsighted individual lions at the end of every study year, the NNP lion population including cubs fluctuated between 34 and 43 (Fig. 2.3 & Table 2.2). In the population of NNP, of the 11.7 cubs on average, 5 lions annually reach the reproductive stage (Table 2.3). We identified two nomadic females (Neema and Elsie) and four nomadic sub-adult males in NNP (Table S1). During our study period one female has never joined her natal pride even when she had cubs, although she was living within the territory of the pride. We did not observe mature nomadic males.

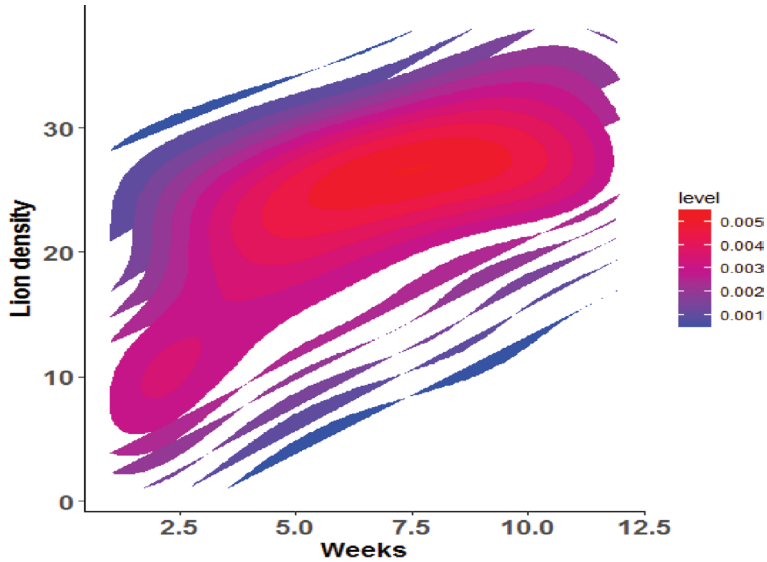

Figure 2.2
Lion density based on bi-annual lion survey during 2012, and 2014-2018

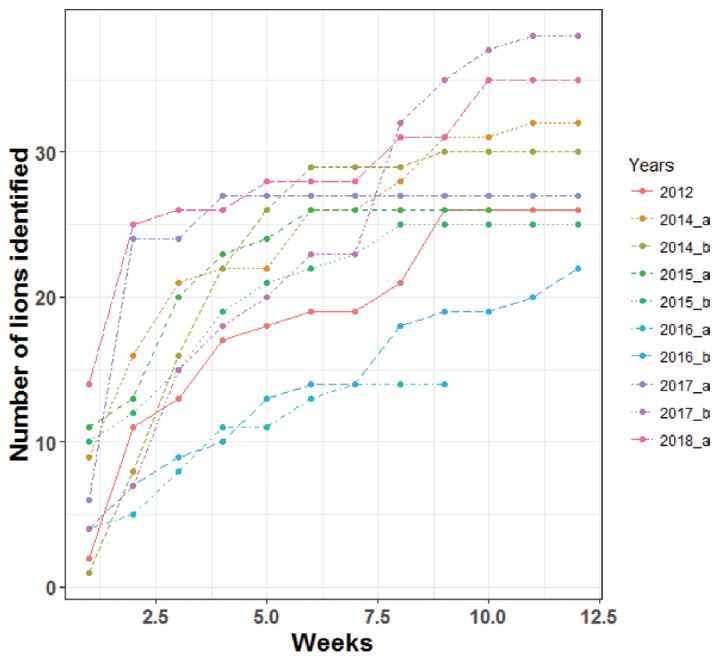

Figure 2.3
Total number of identified individuals (2 years and older) during lion survey from 2012-2018. In 2012, only one survey was carried out, during 2014-2018 two surveys per annum (a) = first survey and (b) = is second survey.

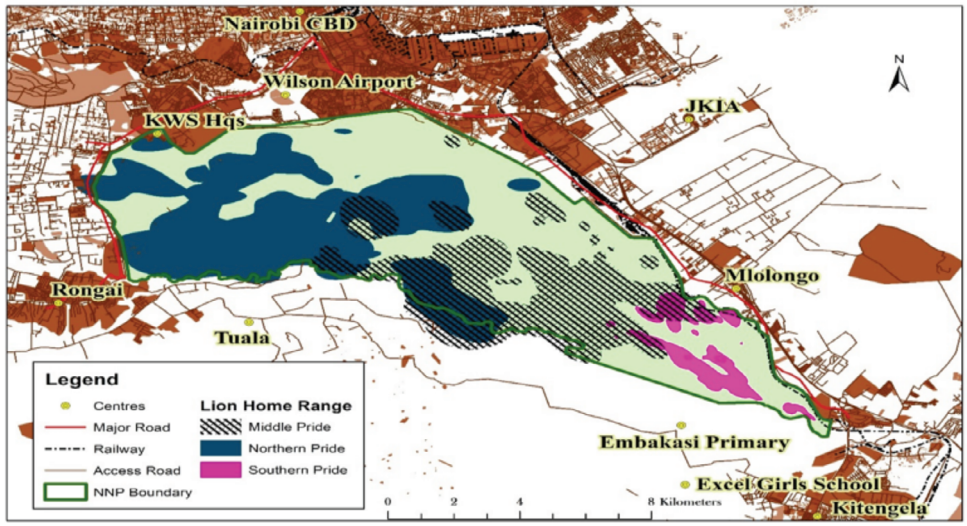

Figure 2.4
The home ranges of the three prides of Nairobi National Park prides (KDE 50%) based on collared females during 2014-2017.

2.3.2 Social structure and sex ratio

During 2012 and 2014-2018, the annual mean number of adult lions in NNP was 16.17 ± 3.18 (range 11-19); the annual mean number of sub adult lions was 9.83 ± 3.34 (range 3-13); and the annual mean number of cubs was 16.00 ± 2.83 (range 12-20) (Table 2.2). We only once observed a group of 17 lions (including < 1 year cubs) together. The largest pride was in the northern part of the park and the least pride was in the southern part of the park. During the wet and dry season, the group size has remained at 1.23±0.7. The adult female group size was 1.2. The average number of adults and cubs in the population was 37.9% (range = 29.3-52.7%) and 38.7% (range = 27.5-50%) respectively (Table 2.2). Approximately 22.8% of the population comprises of adult females and 38.9% of cubs annually (Table 2.2). The annual average of newborn cubs is 11.7 ± 3.48 (range 7-18) from 2012 and 2014-2018 (Table 2.3). We observed that 7 lionesses synchronized their denning period 14 times (87%) out of 20 observations, with an average inter-birth period of 27 months (range = 24-33 months) (Table S2).

After excluding mortality and lions that were not observed for over a year, the annual average ratio of male to female adults was 1:1.56 and this is significantly from 1:1 ($c^2 = 6.18$, df = 1, p-value = 0.013). The ratio of adult females to cubs is 1:1.71. Similarly, the ratio of adult to sub-adult was 1:0.61 and adults

to cubs was 1:0.99. During 2015, NNP had the highest female to cub ratio (1:2.50) while and the male to female ratio was 1:2.67 (Table 2.2).

Most of the cubs (78.2 percent, 43 of 55 newborn cubs, in 16 out of 20 observations) were born between the months of September and February (Table S2; $c^2 = 7.2$, df = 1, p-value = 0.007). The lioness with the largest litter had four cubs in one litter and we recorded litters of four cubs four times during our study period. The mean number of cubs per lioness was 2.5 ± 1.11 (range = 1 to 4, n = 23).

Five lionesses have been observed denning in 2014. Of these five, three were observed denning in 2016 at different den sites, while the remaining two used the same den in 2017 (Table S2). Three of the females born in September 2014 had their first litter in March 2017 (Table S2). Only one female (Nashipai; Table S2) denned twice in the same year (February and August 2015) due to early cub mortality caused by African buffaloes. We also identified two nomadic females (Neema and Elsie) and some nomadic sub-adult males in NNP (Table S2). As mentioned, Neema has never joined her natal pride even when she had cubs. It looked like she had formed a sub-pride with her cubs.

We observed that NNP sub-adults start to move away from the natal pride after 18 months. We found sub-adult females to associate with sub-adult males, especially if they are from the same cohort of same pride. We have not observed a new lion from nearby areas, except for a returning NNP resident after roaming in the community land for 2-5 days.

Table 2.2

Changes in lion population density per 100 km² and ratios of sex and age, annual population number and structure (excluding missing and mortality lions during 2012 and 2014-2018.

	Population structure					Percentages (%)					Ratio			
Years	M	F	SA	C	T	M	F	SA	C	D	A:SA	A:C	M:F	F: C
2012	9	10	3	14	36	25.	27.8	8.3	38.9	21	1:0.16	1:0.74	1:1.11	1:1.40
2014	5	10	10	18	43	11.6	23.3	23.3	41.9	25	1:0.67	1:1.20	1:20	1:1.80
2015	3	8	9	20	40	7.5	20.0	22.5	50.0	20	1:0.82	1:1.82	1:2.67	1:2.50
2016	6	10	12	14	42	14.3	23.8	28.6	33.3	28	1:0.75	1:0.88	1:1.67	1:1.40
2017	6	9	13	18	46	13.0	19.6	28.3	39.1	28	1:0.87	1:1.20	1:1.67	1:1.80
2018*	7	9	12	12	40	17.5	22.5	30.0	30.0	29	1:0.71	1:0.71	1:2.40	1:10
Average	6.0	9.3	9.8	16.0	41.2	14.8	22.8	23.5	38.9	25.2	1:0.61	1:0.99	1:1.56	1:1.71

The ratio of adult to sub-adult was skewed due to the killing of six lions in 2011. Asterix (*) stand for data analysis done during March 2018. (D) stands for Density (>1yr) per 100 Km², (SA) stands for sub-adults, (A) stands for adults, (C) stand for cubs, (M) stands for male, (F) stands for female and (T) stand for total population.

Despite several mating events, we found that lionesses in NNP could delay conceiving. One lioness (L11) mated multiple times over 2 years and only got cubs in the third year of the study. We observed that a female lion with young cubs (L08) even mated with a male when her cubs were around. She mated with the male near the den, although she could have left the cubs in the den and taken the male away from the site. Male lions are usually maned (Schaller 1972), but also one maned female was observed in NNP and she was able to conceive and raise cubs.

2.3.3 Threats to the NNP lion population

During 2012-2018, of 47 lions, mortality and others missing (including cubs), the park lost 17 (36%) lions due to retaliatory killing by the community following livestock depredation incidents, while 23 (45%) lions have gone missing (i.e. no direct observations or reports) during the period of our study (Fig. 2.5). For this study, these missing lions were considered dead after one year of not being sighted. The majority of missing individuals were cubs younger than two years. Evidence from our lion observation data suggested that buffalo killed five (11%) cubs, while two male lions (4%) died due to injuries from fighting and two lions (4%) died due to disease (Fig. 2.5). One cub (< 1 year) died after having been trapped in a snare. One juvenile lion (and 1 hyena) was successfully de-snared by our research team.

Our analysis on the survival rate of the cohort of cubs up to reproductive maturity reveals that between 21.4 and 38.9 per cent (mean =31.2%) of the cubs make it to adulthood (Table 2.3). The survival rate of cubs to sub-adults is 59%. The survival rate of sub-adults to adults is the lowest (46%). During 2018, of the 10 pride members of the southern pride, 9(90%) were lost to retaliatory killing and missing cubs (Table S1).

Of 30 lions, we observed 15 (50%) lions that were sick or injured as a result of territorial fights (5 males), defending cubs (4 females), or during hunting (6). During our study, 4 (13%) (1 adult twice and 2 sub-adults) lions that were observed to show signs of sickness were successfully treated by KWS Veterinary personnel and 2 (7%) emaciated sub-adults died (Fig. S1).

We found that the NNP lions showed fidelity to their denning sites. Two females (Nelly and Nina) gave birth at their previous den site twice during the study period, while another lioness (Neema) denned at her mother's denning site. We also observed a cub with an injured scrotum in 2011 and this individual later became a maneless male. We did not observed females of the same pride denning at the same site in the same season. Each lioness denned at a preferred, but different sites. Lioness bring the cubs together for care.

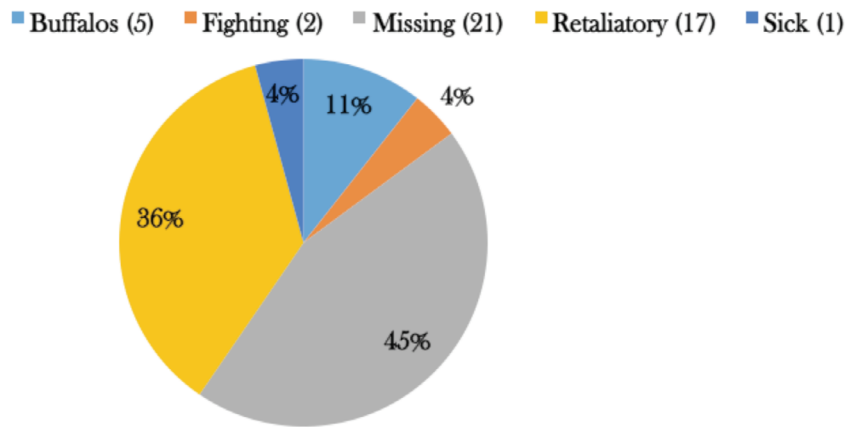

Figure 2.5
Causes of mortality and number of missing lions during 2012-2018.

Table 2.3
New born and survival of cubs into adulthood. A lion is considered a reproductive adult when a newborn cub of a particular year has reached maturity and is able to mate or be active in a takeover process. The figures in brackets are the percentages of survival from one stage to another.

Cohort	Cubs	Sub-adult	Adult	Reproductive adult	Percentage (%) Survival from cub to reproductive adult
2012	14	9 (64%)	4 (44%)	3 (75%)	21.4%
2014	18	14 (78%)	11 (79%)	7 (64%)	38.9%
2015	9	5 (56%)	4 (80%)	3 (75%)	33.3%
2016	10	6 (60%)	*	*	
2017	12	7 (58%)	*	*	
2018	7		*	*	
Total	70	41 (59%)	19 (46%)	13(68%)	
Average	11.7	8.20	6.33	5	31.2%
sd	3.59	3.19	3.30	1.63	

*In these cases, the cubs have not reached the age of reproductive adults.

2.3.4 Coalitions and pride takeovers

At the beginning of our study, there were four mature pride males in the park (Table 2.4). Two of the males formed a coalition as pride males for the central pride, while one belonged to southern pride and one was a member of the northern pride. All four males successfully stayed in their pride without any known conflict between 2012-2015. After the death of one male, suspected to be poisoned in 2015, the two males from the middle pride moved to the south and took over the southern pride (Fig. 2.6a). Only a single lioness and her sub-adult son survived in this pride, after all other pride members had died in 2011due to retaliatory killing. The two males could remain visiting their former females from the middle pride. During 2016, the sub-adult male from the southern pride, was chased away by a two-male coalition. The displaced male then moved to the northern pride, where he was observed fighting another adult male, that subsequently was killed in 2016 on community land by the park management due to it causing human-wildlife conflicts (Table 2.4).

In July 2016, the coalition of the two males moved back from the southern part of the park to the north (Table 2.4) and fought the middle pride male. They subsequently chased him into the community area before settling in the central area of the park after forming a coalition with a sub-adult male born in the northern pride. While two males were fighting over the northern pride, two sub-adults from the northern pride were chased away. These two took over the middle pride. At the same time, the two sub-adults from middle pride were then chased away from the pride. A sub-adult lion from middle pride took over the southern pride after the death of the pride male in the south. This coalition of two sub-adults from northern pride, subsequently took over the middle pride from two sub-adults in 2017 from the north.

In 2018, a sub-adult in the middle pride was chased away by a coalition of an adult and a sub-adult male to the southern part of the park, which was the territory of a sub-adult. At the same time, the maneless male remained in the central area of the park. Mohawk II is a sub-adult lion from the middle pride but he took-over the southern pride in 2017 after the coalition of two males moved to the northern pride in 2016. Later, a sub-adult from middle pride and one from southern pride fought and the sub-adult from the middle pride died (in March 2018) of his injuries, while the maneless male remained in the central area of the park and was killed by the coalition of one adult and one sub-adult. Average male tenure in the pride was 2.6±1.3 years (range =1-4.5 years) and could be longer (See Table 2.4).

Table 2.4

The chronology of pride male coalition, tenure and pride takeover.

Pride takeover and coalitions			
Years	North	Middle	South
2012	Mohawk	Alex & Cheru	Kiprono
2014	Mohawk	Alex & Cheru	Kiprono
2015	Mohawk	Alex & Cheru	Kiprono
2016	Mohawk/Dirk	Alex & Cheru	Alex & Cheru
2017	Alex & Cheru	Dirk/Tallboy & Pretty boy/ Kitili	Mohawk II
2018	Alex & Cheru	Dirk & Kitili	Mohawk II
b)Tenure (Years)			
Mohawk	4.5	0	0
Alex&Cheru	2	4.5	1
Kiprono	0	0	4
Dirk	1	1	0
Dirk & Kitili	0	3	0
Tallboy &Pretty boy	0	1	0
Mohawk II	0	0	2

Dark gray = pride male; black = coalition pride male; light gray = nomadic sub-adult.

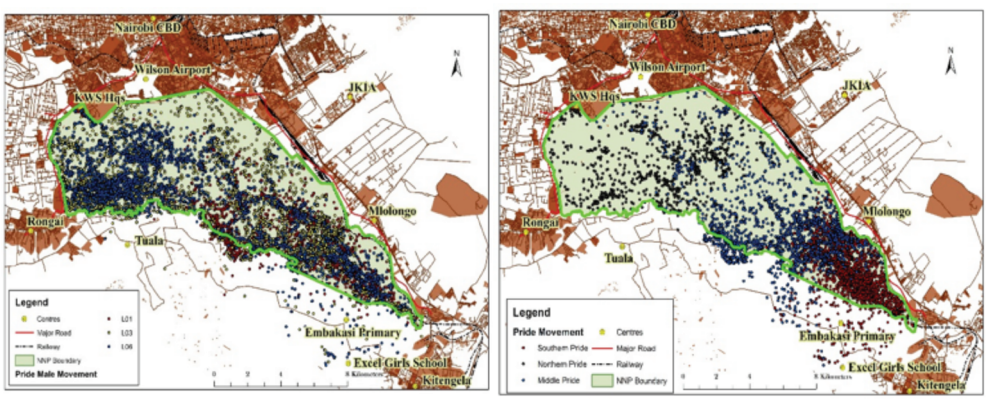

Figure 2.6

a) Pride male (L01, L02 & L06); b) female movements based on the collared males and females from 2014-2018, in Nairobi National Park.

2.4 Discussion

2.4.1 Population size and number of prides

The NNP lion population size varied between 34-43 lions annually (including cubs < 1 year) (Fig. 2.3 and Table 2.2) in three pride (Fig. 3.3). Most of the cubs were born between September and February, showing that the female lions were observed to synchronize mating and births, possibly to enhance cub survival (Table S2; Schaller 1972). The lion population of NNP is regulated by human related factors (retaliatory killing) as well as natural factors (attacks by buffaloes and/or fights) (Fig. 2.5; Table S1). Our findings support Rudnai (1979) who reported that the reproductive rate of NNP lions, and the dispersion of sub-adult and adult lions into the community land (Lesilau in prep), have allowed the park to sustain a stable, female-dominated population of around 29 lions excluding cubs.

In the context of lion densities in East African parks, NNP is among the top three, with the highest density of lions (26.2 lions/100 km^{2}, Fig. 2.2 and Table 2.2) after Ngorongoro Crater, Tanzania (38.8 lions/100 km^2 (Hanby et al. 1995) and Masai Mara National Park, Kenya (37 lions/100 km^2 (Ogutu et al. 2005). This high lion density is associated with a low density of competitors, such as spotted hyena *(Crocuta crocuta)* and leopard *(Panthera pardus)*, for medium-sized prey and a high prey density (Ogutu & Dublin 2002; Trinkel & Kastberger 2005; Hayward 2006; Bauer et al. 2008). During our study, we observed 12 hyenas, 6 leopards and 1 cheetah in the park. When hyena clan sizes are small, which is the case in NNP, they seem to be unable to recruit sufficient clan members to take over lion kills or deter lions from their own kills (Trinkel & Kastberger 2005). In absence of comptetition by other predators for prey and carcasses, lions are able to consume their kill undisturbed. This also suggests that it is unlikely that cubs or sub-adults are killed by the competators.

2.4.2 Social structure and sex ratio

The sex ratio of male to female (1:1.56) in NNP and this is similar to that described in literature, i.e. 1:1 in Maasai Mara Kenya, (Ogutu & Dublin 2002) and 1:1.6 Amboseli National Park, Kenya (Tuqa 2015) but different from the ratio of 1:3 in Waza National Park, Cameroon (Tumenta et al. 2010). Van Orsdol et al. (1985) suggested that the tendency towards higher number of females may be accentuated in small, isolated reserves, where sub-adult males are forced to leave their natal home ranges, and where immigration by new males is unlikely. In NNP, males survive by forming coalitions (Table

2.4). One explanation for the small group size regardless of the seasons follows Bauer et al. (2003), who believe that it is associated with livestock depredation and, in particular, nocturnal boma attacks (Lesilau et al. 2018).

The NNP pride structure differs to that found in other studies (Schaller 1972; Van Orsdol 1985). The pride size is small with few females and long male pride tenure (2.6 ±1.3 year), which could be prolonged due to coalition. Males without prides and nomadic sub-adults often become victim of fighting or retaliatory killing (Schaller 1972). Loveridge et al. (2009) found that anthropogenic activities around and within protected areas are known to affect the social structure.

Compared with a mean adult group size of 2.8 in Serengeti National Park, Tanzania (Schaller 1972), 4 in Kruger National Park, South Africa (Funston, 2003), 1.6 in Waza, Cameroon (De Iongh et al. 2009) and an average group size of 3.7 in Amboseli, Kenya (Tuqa et al. 2014), NNP has the smallest mean female adult group size at 1.2. A pride may have more females, but sometimes they split up into small sub-groups consisting of one adult female with several sub-adult lions hunting together. Small lion group size is related to disturbance and the density and weight of available prey (Van Orsdol 1985; Bauer et al. 2008). NNP serves as a dry season concentration area for most migrating wildlife and thus has a high prey density and wide prey weight spectrum (Rudani 1979; Gichohi 2003). The relatively small group size in NNP could therefore possibly be explained by retaliatory killing, other disturbance factors emanating from urban fringe (noise, lights, and pollution) and a shift towards selecting livestock as prey.

We found a remarkable fidelity of lionesses to their cub denning site. Two females (Nelly and Nina) gave birth at the same denning site twice. Another lioness (Neema) showed similar behavior, when she selected the same den as her mother had used previously. This is evidence of spatial memory in lionesses and even suggests a transfer of knowledge on suitable denning sites from mother to daughter.

We observed one maneless male in NNP. This male was originally a cub that had sustained severe injuries to its scrotum in 2011. Maneless lions are rarely documented (Schaller 1972; Kays & Patterson 2002; Patterson et al. 2006), but Schaller (1972) also described a situation in which a male lion's manes disappeared following a bad scrotum injury. Our observation of a lioness with manes is also extremely rare. The only known reports of maned lionesses are from Moremi Game Reserve and the Okavango Delta, Botswana (Gilfillan et al. 2017).

2.4.3 Threats to the NNP lion population

During 2012 to 2018, NNP lost a significant portion of its lion population to i) retaliatory killing due to livestock predation, ii) due to natural threats (mortality due to fights, due to injuries inflicted by prey during hunting) and iii) mortality of emaciated sub-adults which was suspected to be a result of hunger caused by the inability to hunt large and medium size prey alone after breaking away from the natal pride (Fig. 2.5 and S1). Whereas the mortality as a result of injuries sustained after aggressive encounters with other lions was relatively low, the small home range size, restricted by the park's fences and in combination with high vigilance may have contributed to these fights and subsequent fatalities. This may have an effect on the pride size and population structure of the lions in the future. A large pride with a coalition of males has better chances of successfully defending its territory and cubs against other prides (Van Orsdol 1981). In 2016, a sub-adult (Mohawk II) male took over the southern pride without a fight or coalition. This would have had an influence on the NNP lion population in terms of defending other coalition males from pride takeover and protect young cub's infanticide from incoming males.

The survival number of newborn cubs, rate and successful transition of cubs to adulthood, has fluctuated slightly over the years. The cub survival rate to sub-adult (> 2 years) in NNP of 59% is low in comparison to the 80% which was found for Kruger National Park in South Africa (Funston et al. 2003) and the 77% in Maasai Mara (Ogutu 2002). The possible reason for lower survival rate of cubs below two years is that when the female move with cubs into the community and they are chased by herders, females abandon cubs and they died of hunger or are killed by herders. Cub survival in NNP was however higher compared to the Serengeti Ecosystem where it was 20% (Schaller, 1972). The reason for lower survival in Serengeti is due to starvation during wildlife migration (Schaller, 1972). In general, cub mortality is high during periods of prey scarcity (Van Orsdol et al.1985). The low recruitment of cubs into reproductive adulthood could have had an impact on the overall population size of the lion population in NNP. Low recruitment into reproductive lions caused lion population to stagnant. Our analysis of cohort follow-up during 2012-2018 shows that out of 14 cubs born in 2012 and 18 cubs born in 2014, three (21.43%) and seven (38.9%), respectively, have made it to early reproducing adult (Table 2.3). Our comparison revealed that the annual population growth rate of NNP lions is 31.2% which is higher than the 25% found for Karongwe Game Reserve in South Africa (Lehmann et al. 2008). The killing and missing cubs of the southern pride has impact on the overall population and pride numbers in the park. The only surviving male

(Mohark II) has no pride of his own. Unless he forms a coalition with sub-adult's male to takeover one of the two remaining prides.

2.4.4 Coalitions, pride take-overs and pride tenure

Several fights that resulted in injuries and pride takeovers and retake-over were observed during the study period (Fig .2.6a; Table 2.4). Average male tenure in the pride was 2.6±1.3 years (range = 1-4.5 years) and could be longer (See Table 2.4). Our study shows a very dynamic interaction of pride males and pride take overs.

Not only adult males were involved in pride take overs. For instance, Mohawk II is a sub-adult lion from middle pride but he took-over the southern pride after the death of lion Kiprono). A comparison of NNP pride male tenure with other parks revealed that Queen Elizabeth National park in Uganda had a male average tenure of 7.5 years (Van Orsdol 1981), the Ngorongoro Crater had a pride male average tenure of 3 years (Hanby et al. 1987) and the Serengeti pride tenure was 2 years (Hanby et al. 1987). Van Ordsol et al. (1985) also found that two unrelated males can form a coalition and perform a takeover of a pride. Packer and Pusey (1982) stated that in lion male coalitions, kinship is not a primary factor of cooperation. We did not observe adult females switching prides (Fig. 2.6b). The sub-adult females may leave the natal pride with a nomadic male from her kinship in order to roam within the natal pride home range and occasionally join the pride. They may mate with the pride male and, soon after, leave and join the nomadic sub-adult male. After giving birth, such a lioness would rejoin the main pride for care.

My results suggest that lions in NPP are compensating for mortality by increasing the period of pride male tenure and possibly also through synchronized female birth, which have increased cub survival rates by joint nursing and care. The average of 27 months' inter-birth is associated with food availability, long male tenure and small size of the park which increase frequency of male female interaction.

Although overall lion density in NNP is relatively high, my research suggests that male lions are at a risk of (fatal) injuries due to fights, and of retaliatory killing than natural mortality resulting from illness and old age, because of the 'hard edge' which characterizes NNP. If the issue of retaliatory killing of lions is addressed, the NNP lions could repopulate other areas where there is are no lions or low density of lions, provided that the corridor to other habitat is secured.

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Table S 1

Summary of NNP lion pride, population, age classification, mortality and coalition. asterix (*) specifying male lion coalitions, plus (+/-) stands for cub' mortality in the same year of birth, minus (-) stands for death, double asterix (**) stands for nomadic, (M) stands for male and (F) stands for female during 2012 and 2014-2018.

	2012			2014		
Pride	**Adult**	**Sub-Adult**	**Cub**	**Adult**	**Sub-Adult**	**Cub**
Southern	Nelly (F) Kiprono (M)		Dirk (M)	Nelly (F) Kiprono (M)	Dirk (M)	Kijana (+) Killy (+) Mawenzi (+)
Middle	Alex (M) Cheru (M) Mumbi Selenge 50 Nina Bertine MF- 1 Mom Bertine LM 5 Granny	Elsie (F)** SA 4	Lemek (+) Cub 5 (+) Cub 6 (+) Cub 1 (+) Cub 2 (+) Cub 4 (+) Nani (+) Mohawk II (+) Nala (+)	Cheru (M) Alex (M) Bertine's mom Granny Bertine Nina MF-5 M7-Charlie	Sas 3 (-) Sas 4 (-) Lemek Nani Mohawk II Nala Cub 2 (-) Cub 4 (-) Ruff Cub 6 (-)	Karel (+) Sabuk (+) Serena (+) Sasab (+)
Northern	LM 3 Mohawk (M) LM 6 LM 7 LM 8 LM 9 Floppy ear Nashipai Lara Mumbi	LF 8_Cub1	Neema (+)** Ruff (+) Pretty Boy (+) Tall Boy (+) Pretty Girl (+) (+)	Mohawk (M) Nashipai Floppy Lara Mumbi	Pretty Boy (M) Pretty Girl Tall Boy (M) Neema** Elsie **	FeCub 1 (+) FeCub 2 (+) FeCub 3 (+) FeCub 4 (+) Alamaya (+) Amani (+) KFCub 3 (+) Kitili (+) Moran (+) Lebolia (+) KFCub 4 (+)
	2015			**2016**		
Southern	Nelly (F) Kiprono (-)		Kijana (M) Killy Mawenzi	Nelly (F)	Kijana (M) Killy (F) Mawenzi (F	
Middle	Cheru (M)* Alex (M)* Dot (F) Shipa Mom_Bertine Bertine (F) Selenge (50 gt)	Lemek (M) Mohawk II (M) Nani Nala Heena (M)	BeC1 (+) BeC2 (+) BeC3 (+) BeC4 (+) BmC1 (+) BmC2 (+/-) Karel (M) Sabuk (M) Sasaab (M) Serena	Bertine Bertine's mom Mumy Alex Cheru Nina	) Mohawk II (M) Lemek (M) Nala (F) Karel (M) Sabuk (M) Sasaab (M) Serena (F)	BeC1 BeC2 BeC3 BeC4 BmC1 SeC1(+) SeC2 (+)

Northern	Floppy (F) Lara (F) Mumbi Mohawk (M) Nashipai	Elsie (F) Dirk (M) Pretty Boy (M) Pretty Girl Ruff (M) Tall Boy (M) Neema (F)**	Nashi cub 1(+/-) Nashi cub 2 (+/-) Nashi cub 3 (+/-) Kitili Morana (F) Alamaya (F) Lobolia (F) Amani (F) Mambi (F) KFC_7 (-)	Mumbi (F) Floppy (F) Dirk Elsie (F) Dirk Mohawk (M) Lara (F) Mohawk	Neema (F) Pretty boy (M) Tall boy (M) Kitili (M) Morana (F) Alamaya (F) Lobolia (F) Amani (F)	MuC1(+) MuC2(+) MuC3(+) FloC1(+) FloC1(+) FloC2(+) LarC1(+) LarC2(+)
	2017			**2018**		
Southern	Nelly (F) Killy (F) Mawenzi (F) Kijana (M) (-) Mohawk II (M)		Nelly C1 Nelly C2 Mawenzi C1 Mawenzi C2 Mawenzi C3	Nelly (F) (-) Killy (F) (-) Mawenzi (F) (-) Mohawk II		NeCub 1 (-) NeCub 2 (-) MueCub 1(-) MueCub 2 (-) MueCub 3 (-)
Middle	Dirk (M) Tall Boy (M) Pretty Boy (M) Nala(F) Bertine (F) Nina (F) Bertine's Mom (F) Granny (F)	Karel(M) Sabuk (M) Sasaab (M) Serena (F) BeCub 1 BeCub 2 BeCub 3 BeCub 4 BeCub 5 BeCub 6	Ni Cub 1 NiCub 2 NiCub 3 NaCub 1 NaCub 2 NaCub 3 NaCub 4 (-)	Bertine's mom(F) Bertine (F) Nina (F) Nala (F) Pretty oy (-) Tall boy (-) Dirk Kitili Karel (-) Sasab (-) Sabuk Serena (F)	Be-3_Cub 1 Be-1_Cub 2 Be-1_Cub 3 Be-1_Cub 4 Be-1_Cub 5 Be-1_Cub 6	Ni3-cub 1 Ni3-cub 2 Ni3-cub 3 Na1-Cub 1 Na1-Cub 2 Na1-Cub 3
Northern	Alex (M)* Cheru (M)* Mumbi (F) (-) Floppy (F)(-) Lara (F) Neema (F)**	Kitili (M) Morana (F) Alamaya (F) Lebolia (F) Amani (F)	MuC1 MuC2 MuC3 FloC1 FloC1 FloC2 LarC1	Alex Cheru Alamaya (F) Amani (F) Lara (F) Morana Lebolia (F) Neema (F)	KfC1 KfC2 KfC3 KfC4 KfC5 KfC6	MoCub 1 LeCub 1 LeCub 2 Neecub 1 Neecub 2 Neecub 3

Table S 2

The months of birth synchronization and average inter-birth. Green colour stands for the months in which females of the same pride synchronize births, yellow colour stand for the months in which either mother or daughter of same cohort synchronized births, grey colour stand for months when there was no synchronization and unshaded area of the table are the months when there was no births recorded in the park.

Names	Pride	2014	2015			2016			2017			2018		Average inter-birth (Months)
		Sept-Dec	Jan-Apr	May-Aug	Sept-Dec	Jan-Apr	May-Aug	Sept-Dec	Jan-Apr	May-Aug	Sept-Dec	Jan-Apr	May-Aug	
Nelly	Southern													30
Mawenzi	Southern													
Floppy	Northern													24
Mumbi	Northern													24
Lara	Northern													24
Neema	Nomadic													
Morana	Northern													
Nina	Middle													33
Nala	Middle													
Lobolia	Northern													
Nashipai	Northern													
Bertine	Middle													
Bertine Mom	Middle													
Granny	Middle													

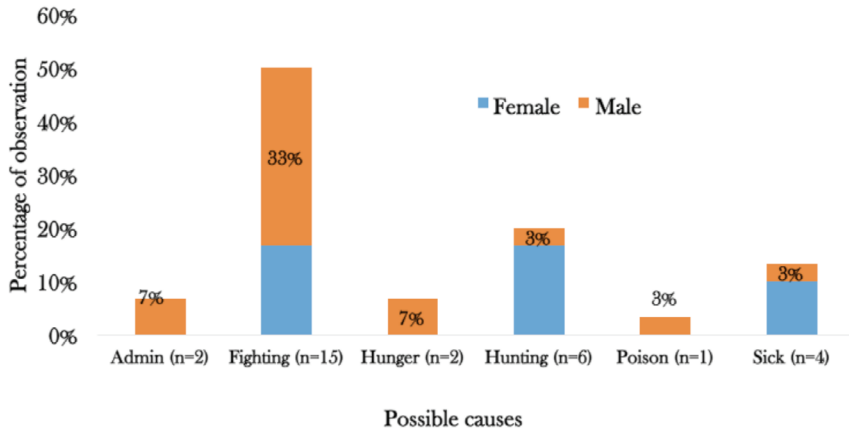

Figure S 1

Summary of the health condition of NNP lions based on observations of 2012, 2014-2018 and causes

3

Home Range Size, Dynamics and Movements of Nairobi National Park Lions (*Panthera leo melanochaita*)

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Abstract

During 2014-2017, we collared 12 lions (five males and seven females) in Nairobi National Park (NNP) with iridium satellite collars in order to study their seasonal and annual movements and home ranges. We programmed the collars to download the GPS locations at intervals of one fix per three hours via satellite. The data is then accessed at a website.

The average annual home range for NNP lion is 34 km^2 and there are significant differences between males and females, but no significant differences between seasons, age and years. Some home range core areas (Kernel 50%) overlap with community land (outside the park) where human density was relatively low, whereas no core area has been established near the urban fringe of the park. However, we found spatial shifts in home ranges, which related to pride takeovers u dominant males.

We conclude that male home ranges and movements are dependent on their status (pride male or not) and that females may therefore provide a more realistic indication of home range size than males. The lack of core areas at the urban fringe of Nairobi City is an indicator that lions avoid high disturbance areas (noise, light, smell). The urban fringe zone is primarily used for transit and hunting when human activity is low.

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In order to reduce disturbance, we recommend NNP management to establish a buffer of natural habitat. Such a buffer zone could possibly also include planted trees to filter noise and reduce artificial illumination from human settlements.

Keywords
African lions, disturbance, home range, GPS satellite tracking, urban fringe, Nairobi National Park

3.1 Introduction

Apex carnivores, such as the African lion (*Panthera leo)*, cheetah (*Acinonyx jubatus)*, leopard (*Panthera pardus*), and the African wild dog (*Lycaon pictus*) show global declines (Woodroffe 2000; Bauer & Van der Merwe 2004; Riggio et al. 2013). The main threats have been identified as habitat destruction, decline of prey populations, and human–carnivore interaction (Riggio et al. 2013; Winterbach et al. 2015). Large carnivores are particularly vulnerable to these causes because they have large home ranges and require extensive, intact habitats to survive (Sillero-Subiri & Laurenson 2001).

A home range is defined as the area used by an individual animal for its regular activities of food gathering, mating and caring for its young (Burt 1943). Lion home ranges vary substantially, depending on habitat and season, prey abundance, interaction with lions from neighboring home ranges, human presence and geographical boundaries (Bauer & De Iongh 2005; Davidson et al. 2012; Loveridge et al. 2009; Oriol-Cotterill et al. 2015). The sex of an individual is also suggested to be an important factor for home range size and movement patterns. Females prefer territories where they can deliver and care for newborn cubs and that harbor sufficient prey to sustain their offspring (Loveridge et al. 2009; Packer et al. 2001). Male home ranges are generally larger than female home ranges (Van Orsdol 1985; Funston et al. 2003; Loveridge et al. 2009).

Lions generally occur in prides. A pride is defined as a "fission–fusion" social unit. The home range of individual lions may be defined by the pride's territory. A pride territory is the area that is avoided by other lions or from which other lions are actively excluded (Schaller 1972). Sub-adults that have been forced to become nomadic, usually remain close to the natal territory and may establish a new home range near the natal pride's territory (Elliot et al. 2014; Funston et al. 2003). Valeix et al. (2011) have suggested that lion movements within the pride territory is based on the patch-disturbance theory, where lions leave an area, even if they could hunt successfully, due to

behavioral changes, i.e. prey becoming more vigilant. Of all the ecological variables, prey density is the core determinant influencing home range (Gittleman & Harvey 1982).

Several studies in East, southern and West/Central Africa have shown pride home ranges sizes in Kernel Density Estimator (95% KDE) varying between 56.4 – 641 km^2 (Tumenta et al. 2013; Tuqa 2015). In the Pendjari Biosphere Reserve, Benin, the average annual home range (95% KDE) was 256 km^2 (Sogbohossou 2011). In Waza National Park, Cameroon, it was reported to be 641 km^2 (95% KDE) (Tumenta et al. 2013) and in Amboseli National Park, Kenya, the average home range (95% KDE) was 56.4 km^2 (Tuqa 2015).

Despite having similar activity patterns, the home range size of nomadic lions is generally much larger compared to pride members and less vigorously defended (Tumenta 2013; Tuqa 2015). Nomads also tolerate other lions in their home range without strong opposition (Schaller 1972). Temporary changes to home ranges occur due to fluctuations in prey densities, water (availability), habitat suitability or social structure, resulting in contraction and expansion of the home range and, consequently sometimes an associated increase in human–lion interaction (Bauer & De Iongh 2005; Loveridge et al. 2009; Ogutu & Dublin 2002; Patterson et al. 2004; Tuqa 2015). This effect is even more pronounced when vital resources (i.e. prey, water, space) become scarce.

In a fragmented habitat, movement is an important mechanism to ensure genetic fitness (Clobert et al. 2012). Lions are known to move up to 20 km in 24 hours and can cover hundreds of kilometers over several months (Tuqa 2015). When this happens, there is a high likelihood that the lion's home range extends beyond the boundary of the national park. The expansion of home ranges into the surrounding community land increases the likelihood of contact with people and their livestock, which may ultimately result in livestock depredation conflicts. Lions sometimes also become more or less dependent on livestock for their survival (Bauer & De Iongh, 2005; Tumenta, Visser, et al., 2013).

An understanding of how lions occupy and utilize the landscape is a requirement for the management of protected areas. Fundamentally, the fixed boundary system of protected areas has been a challenge in the management of large carnivores outside national parks (Dolrenry 2013; Tuqa 2015). Precise information on lion home ranges outside national parks would help wildlife conservation authorities to prevent and mitigate human–lion conflicts. Additionally, demographic information would help further clarify what the factors are that lead to intra-specific variations in lion home ranges (Loveridge et al. 2009).

Our study focused on the lions' seasonal home range size and movements outside and inside NNP. As Nairobi City is expanding, the borders of NNP have become more densely inhabited, and conflicts between wildlife and humans occur more frequently. Lions have limited options to range into the community land without being disturbed. Six lions from NNP have been reported to be killed in the community land in 2011 and there were also reported cases of lions wandering in the Capital City (Smith 2011; Kushner 2016; Ombati 2017). Although NNP is a small, partially fenced, protected area, surrounded by dense urban human settlements, little is known about the movement and the dynamics of lion home ranges in NNP. A recent dramatic increase in the number of lions roaming into the community area and the suburban city (Smith 2011; Dolrenry 2013; Kushner 2016) has resulted in increased conflicts between lions and the growing human population in Nairobi (Lesilau et al. 2018).

We aimed to establish spatial movement patterns, including lions' exit locations from the park and the duration of their stay in the surrounding community land. We also aimed to get insight into the factors influencing home range size. Prior knowledge of lion (potential) movement patterns and ecological needs would help to establish an early warning system for local livestock owners. We therefore intend to address the following research questions: i) What is the seasonal and annual mean MCP (100%) and KDE (50%, 95%) home range size of males and females? (ii) What are the activity patterns of lions and where are the possible exit and entry points along the park's boundary? (iii) What is the maximum travel distance for lions? (iv) Which factors influence lions to roam into community land?

3.2 Material and methods

3.2.1 Study area[1]

Nairobi National Park (NNP) is located to the south-west of Nairobi City in Kenya (Owino et al. 2011) (Fig. 3.1). The park was established in 1946 with a surface area of 117 km^2 (gazette notice No. 48 of 16th December 1946). It is situated between latitude 1° 20´-1° 26´ S and longitude 36° 50´-36° 58´ E (Ogutu et al. 2013) within an altitude ranging between 1533 m to 1760 m above sea level (Owino et al. 2011; Rudnai, 1974). From West to East, the park is 6.5 km wide and North to South it is 24.8 km long.

1 This section is partly based on section 2.2.1.

Nairobi National Park has three distinct vegetation zones (Foster & Coe 1968): (i) The western part of NNP is covered by semi-evergreen forest patches of *Croton macrostachys* and *Olea africana* with an open grass glade, occupying 10 km^2; (ii) The Athi Basin area is an open grass savannah with monocods like *Pennisetum meszzianum* and *Themeda triandra* and *Balanites spp* trees and egg-shaped *Acacia melifera* due to giraffe herbivory. (iii) The Mbagathi River is covered with riverine vegetation dominated by *Acacia xanthophloea Acacia mellifera* (Rudnai 1974). Dwarf woody plants are a result of controlled burning by park management (Foster & Coe, 1968).

Being adjacent to Nairobi City, the National Park was partly fenced in 1955 (Steinhart 1994), with a chain-link fence and galvanized wire, powered by electricity (6 kV). The fence was erected from the East, via the northern boundary, to the West in order to separate wildlife from the Nairobi metropolis (Foster & Coe 1968; Reid et al. 2008). The south-west boundary at the Mbagathi River (Maasai call it Empakasi) and the southern border, which is beyond the Mbagathi River, provide open access to the Athi-Kaputiei Plains (AKP) with an area of rangeland of 2200 km^2 (Reid et al. 2008). This open access is necessary to maintain herbivore migrations in and out of the park during wet season.

The NNP and AKP forms the Athi-Kaputiei Ecosystems (AKE) (Reid et al. 2014). Considering the small size of NNP this park cannot meet the ecological requirements of migrating wildlife. As a consequence, AKP was declared as a wildlife conservation area in 1946 this was never officially gazetted (Gichohi 2003). During the rainy season, NNP becomes swampy, muddy and the grass becomes unpalatable for large herbivores due to the absence of control burning and as a result wildlife migrates into AKP for feeding and calving (Owino et al. 2011). However, the herbivores still depend on the park, since the artificial dams and rivers in the park provide water to wildlife throughout year (Rudnai 1979; Gichohi 2003). In contrast AKP has no permanent surface of water during the dry season.

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

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 www.naturekenya.org/content/important-bird-areas). In Amboseli, the cut-off point between the wet and the dry season was 28.3 mm a month (Tuqa 2015). We considered the high altitude of NNP and relatively higher rainfall and determined our cut-off point to be a mean of 30 mm of rainfall per month.

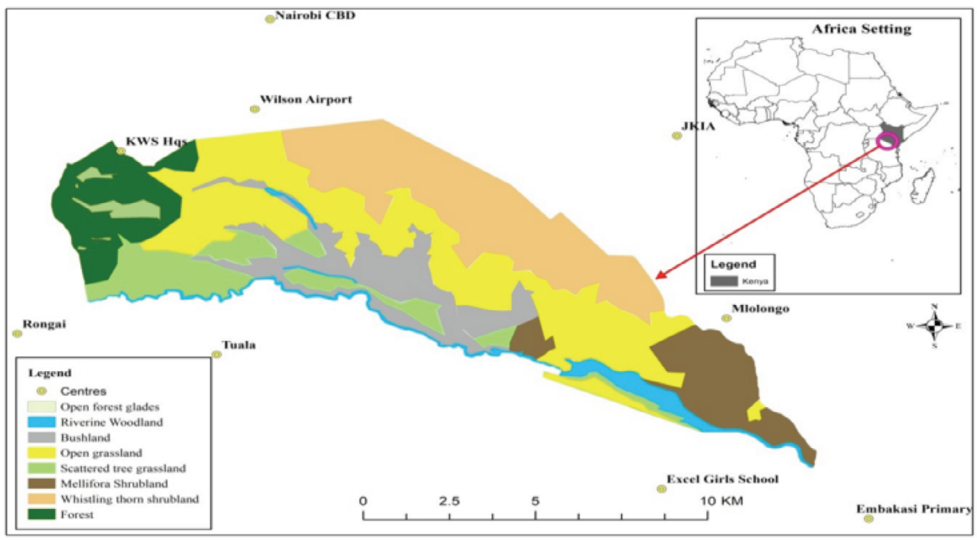


Figure 3.1
Map of Nairobi National Park showing habitat classification

3.2.2 Data collection[2]

Between 2014 and 2017, we collared 12 lions (five males and seven females) in NNP, following Tuqa et al. (2014) and Oriol-Cotterill et al. (2015), with Africa Wildlife Tracking (AWT, Pretoria, South Africa), Very High Frequency (VHF) iridium satellite collars (Lesilau et al. 2018). We monitored the movement of the 12 collared lions via the AWT website. Table 3.1 shows details of collared lions, date of collaring, and status of the collars. The collar weight

2 This section is partly from section 2.2.2.

was 1.5 kg and this was <1% of the animal's weight (Oriol-Cotterill et al. 2015). Some collars were removed, i.e., at the end of battery life or when the animal had a neck or other injury. During our study, only one lioness (L02) had a neck injury due to a fight to defend her cubs and she was decollared on 25 May 2015. After healing, she was recollared on 20 August 2015 (Table 5.1). We collared four sub-adult lions from three different prides in January 2017. We monitored sub-adult lions and adjusted collars in November 2017.

Table 3.1

Summary data for collared lions during the study period (2014 - 2017).

S/n	Lion Name	Code	Animal Sex	Pride	Collar Id	Freq	Start collaring	End of Collar	Status
1	Kiprono	L01	M		SAT1202	150.77	2014.01.25	2015.10.07	Dead (7 October 2015)
2	Nelly	L02	F	Southern	SAT1203	150.56	2014.01.26	2015.05.25	Neck injury and removed
3	Nelly	L02	F	Southern	SAT1203	150.56	2015.08.20	2015.11.14	Recollared
4	Dirk	L03	M		SAT1553	150.64	2015.02.02	2016.12.30	End of battery power
5	Nashipai	L04	F	Northern	SAT1552	150.62	2015.02.03	2015.10.10	Dead (10 October 2015)
6	Bertine	L05	F	Middle	SAT1552	150.62	2016.02.02	2017.03.16	End of battery power
7	Alex	L06	M		SAT1882	150.05	2016.02.02	2017.08.09	End of battery power
8	Mumbi	L07	F	Northern	SAT1883	150.26	2016.02.26	2017.09.13	Dead (13 September 2017)
9	Nina	L08	F	Middle	SAT1975	150.78	2016.07.12		Active
10	Nala	L09	F	Middle	SAT2047	149.42	2017.01.23		Active
11	Tall Boy	L10	M	Northern	SAT2048	149.57	2017.01.23	2018.03.28	Dead (28 March 2018
12	Nelly	L02	F	Southern	SAT2050	149.89	2017.01.25	2018.5.17	Dead (17 May 2018)
13	Dirk	L03	M	Northern	SAT2049	149.68	2017.01.26		Active
14	Neema	L11	F	Northern	SAT2046	149.15	2017.01.30		Active
15	Karel	L12	M	Middle	SAT2045	149.03	2017.06.30	2018.04.11	Dead (11 April 2018)

* Two lions (L02 and L03) were collared twice and recollared: L02 after healing from injuries caused by a fight and L03 was recollared after the battery expired.

We programmed all the collars to download the GPS location of each lion (one fix per three hours) for research through a satellite, accessible via the AWT website (http://www.awt.co.za). The collars recorded date, time, longitude, latitude, altitude, temperature, and present distance from previous location of the collared lion. When livestock depredation incidences increased in the wet season, we modified the GPS collars, using the AWT website, to collect data every 30 minutes for the analysis of entry and exit points and also for the movements of lions outside the park.

The length of stay of a lion outside the park was calculated as the time span between the last point inside the park, before crossing the Mbagathi River, and the first point inside the park at the lion's return. A straight-line movement path between these two connecting points was created with ArcGIS 10.2.2 (ESRI Software, Redlands, CA, USA). We took GPS coordinates of livestock bomas around NNP and geo-fenced livestock bomas – using AWT's geo-fencing mode – in order to warn the park management and researchers when a lion had left the park and was in the vicinity of a livestock boma. The collars were programmed such that a short message service (SMS) was received from the network providers when a collared lion was 500 m from a livestock boma.

We acquired monthly rainfall data for the study period from Wilson Airport, through the Kenya Meteorological Department (KMD). We obtained NNP vegetation data from KWS GIS and Biodiversity Office (2011) to determine the lions' habitat selections (Fig. 3.1). We assigned a vegetation class to each GPS location using the Spatial joint tool in ArcGIS 10.2.2 (ESRI Software, Redlands, CA, USA) to determine the proportion of time spent in each habitat type. For the habitat analyses all GPS locations outside the park were excluded since there was no habitat classification available.

3.2.3 Data analysis and statistics

GPS data was downloaded into Microsoft Office Excel 2010 so that it could be cleaned up before use. A consistent dataset containing only three-hour fixes was created. The maximum of potential minimum distance moved in 3 hours and in 24 hours is indeed the distance covered between two GPS points. Since it is not known whether the lion moved in a straight line between the two GPS points or not, this distance of the straight line between the two GPS points is called 'minimum potential distance moved' because theoretically the lion may have moved a longer distance between the two GPS points. The maximum of potential distance (km) travelled in three and in 24 hours was calculated between two fixes, i.e. a straight line between two points and the sum of distances respectively (Hunter 1998). The distances covered in 3 hours and 24 hours (Table 3.2) refers to the maximum distances recorded for minimum potential distance covered by collared lions during the entire collar operational life time. The average travel distance can be shorter because it is the sum of all (potential minimum) distances covered by an individual lion per 24 hrs divided by the sum of days the lion had a collar.

We analyzed the data using ArcGIS 10.2.2 and projected the results in the Universal Transverse Mercator (UTM) WGS-84, zone 37 ° S. The Spatial An-

alyst tool and the Geospatial Modelling Environment software (www.spatialecology.com/gme/) were used to analyze the GPS data. We determined the resolution bandwidth with least-squares cross (LSC) validation for fixed-kernel home ranges (Seaman & Powell 1996). We considered two seasons (dry and wet) based on the monthly rainfall (mm) with a cut-off point of 30 mm of rainfall per month.

Home range sizes of each collared lion were estimated using KDE and MCP (Powell 2000) based on GPS locations downloaded from the collars into a computer. KDE takes into account the density estimation of GPS locations when estimating home ranges, while MCP only considers the outer GPS locations. The boundary of the home range areas was defined as 95% of KDE, the core home range as 50% of KDE and the heart of the core area as the 10% of KDE (Hemson 2003; Powell 2000). Bi-annual lion survey sightings were used to allocate lions to specific prides based on the frequency of sightings in a specific group (Lesilau in prep). Home ranges of individual lions belonging to a particular pride were then extrapolated to pride home range, through overlap (Fig. S3). We excluded males from overall home range estimations due to their frequent involvement in pride takeovers.

To investigate the potential impact of urban disturbance at the park border, we created a 500m buffer zone from the park boundary inside the park and used spatial ArcGIS 10.2 to calculate all GPS locations of lions within this buffer zone. We divided the zone into East (near the city) and West (few human settlements).

We used t.test for seasonal movement (wet vs. the dry) exit and roaming in the community land and Chisq.test for the differences between males and female's seasonal distances traveled. We used Kruskal wallis test for the difference between males and females in maximum potential distance travelled between two points (three-hour interval). We tested the relationship between maximum of potential minimum distance travelled in 24 hours and temperature of males and females using a spearman correlation coefficient. We compared the lions' core home ranges with lion scat distributions in the park (Fig. S1). We also counted the number of occasions when sms was received and number of times the lion was located outside the park and no sms was received.

To test home range sizes, seasonal effects and pride, we used a mixed model (lme4) with year and lion identity as a random factor for statistical analysis. We performed a Likelihood Ratio Test (LRT) with Chi-square test in program R version 3.0.2 (R Core Team Foundation 2016). We used a significance level of $p < 0.05$ for all tests.

We used a Manly's selection index (Manly et al. 2006) to assess lion habitat preference. The selection index was measured using the formula: $w_i = o_i p_i$

where w_i = ratio for vegetation type i (Table 3.5); o_i = proportion or percentage of time spent (corresponding to number of fixes) in vegetation i and p_i = proportion or percentage of vegetation i available in the park. Values above 1.0 indicate preference, while values less than 1.0 indicate avoidance. The standardized index B_i allows comparisons: $B_i = w_i / \Sigma^n{}_i = w\hat{}_i$, where B_i is the standardized selection index for vegetation i and $w\hat{}_i$ is the ratio for vegetation i. Values below 0.125 (corresponding to 1/number of vegetation types) indicated relative avoidance, while values above indicate relative preference.

Table 3.2

Average home range (km²) size per annum and distance travelled by 12 collared lions in NNP, 2014-2017 and summary of maximum of potential minimum distance (km) travelled per 24hrs by collared lions. (Average and maximum calculated over number of collared days).

		KDE			MCP	Travel Distance			
Code	Sex	5%	50%	95%	100%	Total	Maximum of potential minimum distance (km) in 3 hrs	Maximum of potential minimum distance (km) in 24hrs	Average of potential minimum distance per 24hrs
L01	M	10.8	40.3	52.4	121.3	3443.7	14.2	29.9	7.1±4.7
L02	F	2.1	10.8	14.4	34.4	2584.0	5.8	13.9	2.9±2.3
L03	M	9.4	38.8	51.3	136.6	4146.0	8.1	16.3	4.1±3.0
L04	F	9.9	43.5	54.1	75.3	1092.3	6.8	19.9	4.4±3.4
L05	F	10.0	39.0	50.6	88.4	1561.0	5.0	13.3	3.8±2.7
L06	M	15.7	66.6	84.5	140.8	3865.7	16.3	24.8	7.5±4.8
L07	F	13.0	42.4	52.2	95.1	2167.3	6.6	20.9	3.9±3.3
L08	F	11.2	38.9	48.5	82.5	2025.3	5.3	12.3	3.8±2.7
L09	F	6.3	23.5	29.4	65.4	1351.5	6.8	13.6	4.0±3.0
L10	M	11.3	45.3	59.4	92.2	1293.3	7.5	14.7	3.8±2.8
L11	F	11.5	36.3	45.2	66.3	1420.6	5.0	12.8	4.3±2.6
L12	M	14.5	56.9	71.7	92.9	734.0	7.3	13.1	4.1±2.3
Average		10.5	40.2	51.1	90.9	2140.0	7.9	17.1	4.5
Sd		3.4	13.5	17.0	29.3	1087	3.5	5.4	1.3

3.3 Results

3.3.1 Home range size

The annual MCP (100%) home ranges of males were significantly larger than those of females as in the Chi-square test was the result of a LRT: (LRT: χ^2 = 8.78, df = 1, p-value = 0.003) and home range sizes between prides also differ significantly (LRT: χ^2 = 7.41, df = 2, p-value = 0.025). However, there is

no significant difference in home range size between different seasons (LRT: χ^2 = 0.17, df = 1, p-value = 0.680) or different age classes (Tables 3.2 & 3.3; LRT: χ^2 = 0.79, df = 1, p-value = 0.375). The 100% MCP annual mean home range size of males is 124.4±31.7 (range = 92.2–179.7 km^2) and of females is 70.2±35.0 (range = 18.7–153.9 km^2) for the whole study period (Table 3.4). L06 has the largest home range with 96.4 km^2 at KDE (95%) and 179.7 km^2 at MCP (100%). The annual mean of all the lions' home ranges, across sexes, pooled in MCP 100% is 93.4±43 (range = 18.7–179.7 km^2). Avoidance of the urban fringe section of the park is significant (Fig. 3.2 and S3; χ^2 = 5836, df = 1, p-value = 0.001).

Table 3.3
Summary of lions' home range test results and variables

Variables	Kernel Density Estimator Test Results		Minimum Convex Polygon
	KDE (50%)	KDE (95%)	MCP (100%)
Sex	χ^2 = 2.22, df = 1, p-value = 0.136	χ^2 = 5.31, df =1, p-value =0.021	χ^2 = 8.78, df = 1, p-value = 0.003
Seasons	χ^2 = 0.36, df = 1, p-value = 0.546	χ^2 = 0.18, df =1, p-value =0.678	χ^2 = 0.17, df = 1, p-value = 0.680
Years	χ^2 = 3.74, df = 3, p-value = 0.292	χ^2 =5.16, df = 3, p-value=0.160	χ^2 = 3.55, df = 3, p-value = 0.314
Pride	χ^2 = 8.72, df = 2, p-value = 0.128	χ^2 = 9.31, df = 2, p-value = 0.01	χ^2 = 7.41, df = 2, p-value = 0.025
Age	χ^2 = 0.001, df =1, p-value = 0.985	χ^2 = 0.67, df =1, p-value =0.802	χ^2 = 0.79, df = 1, p-value = 0.375

Model 1; 100% MCP modelsex<-lmer(MCP~Sex+(1|Years)+(1|Names))
drop1 (modelsex, test="Chisq")
model 2; 95% KDE: modelseason<-lmer(X0.95~Season+(1|Years)+(1|Names))
drop1 (modelseason, test="Chisq")

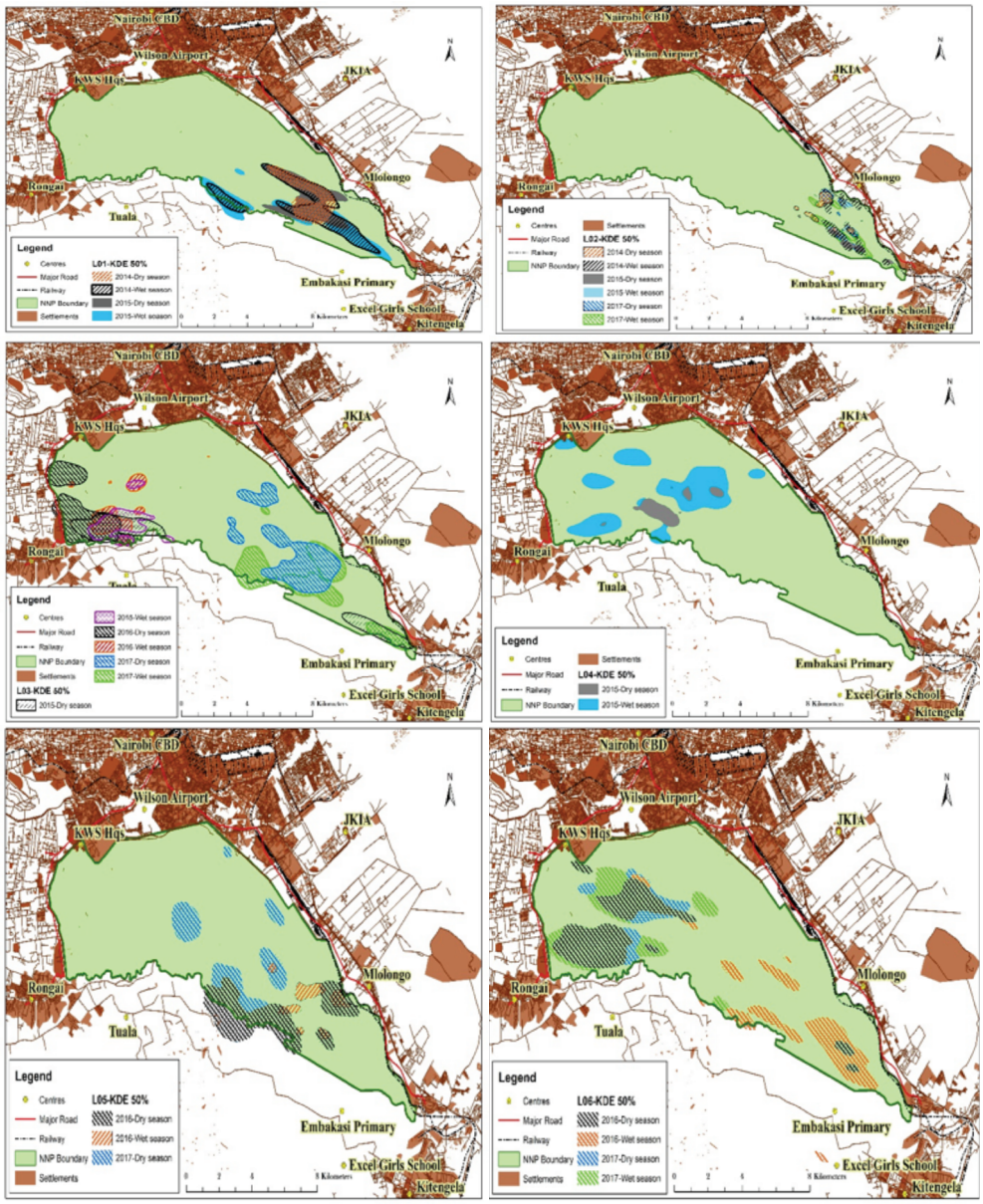
The mean seasonal core area estimate (50% of KDE), averaged across sexes, ranges between 0.4–18.1 km^2 (mean = 8.6±4.9) and the KDE 95% was 5.27–91.7 km^2 (mean = 43.72 ± 22.4). The NNP lion's avoidance of the eastern border of the park near urban fringe (Fig. 3.2). The mean home range size of males was significantly larger than that of females at 95% KDE (χ^2 = 5.31, df = 1, p-value = 0.021) but not at 50% KDE (χ^2 = 2.22, df = 1, p-value = 0.136). There is no difference between the dry and the wet season home range size at 50% KDE (χ^2 = 0.364, df = 1, p-value = 0.546), at 95% KDE (χ^2 = 0.180, df = 1, p-value = 0.680) and in 100% MCP (Fig. 3.3; χ^2 = 0.170, df = 1, p-value = 0.680).

The annual core area estimate when all years of lions are averaged at KDE (50%) shows no significant difference between males and females (χ^2 = 2.22, df = 1, p-value = 0.136). However, at 95% KDE, there is a significant difference between males and females, with males showing both a larger home range (χ^2 = 5.31, df = 1, p-value = 0.021) and 100% MCP (Table 3.4; χ^2 = 8.78, df = 1, p-value = 0.003).

A comparison of NNP prides shows that the southern pride has the smallest annual mean home range of 14.4± 5.9 (range = 6.2–19.7), the middle pride home range size is 45.5±11.1 (range = 29.4–59.5) and the northern pride has the largest home range, with 50.9±23.6 (range = 19.1–85.2) at 95% KDE) (Table 3.4c). In the South, home ranges extended outside NNP into the community land (Figs. 3.2, S 2 & S 3). The annual average is 34 km^2 (95% KDE).

Table 3.4
Summary of home ranges by season, sex, pride and year at 50% and 95% KDE and 100% MCP

4 a)	Seasonal home ranges					
	Females			Males		
	All seasons	Dry seasons	Wet seasons	All seasons	Dry seasons	Wet seasons
50%	0.4–16.1 7.3±5.4	0.8-16.1 7.9±5.6	0.4–15.5 6.5±5.1	4.0-18.1 10.3±3.2	6.5-13.2 10.4±2.2	3.98-18.1 10.2±3.9
95%	5.3–76.4 34.7±22.1	5.5-76.4 38.9±22.9	5.3–75.1 30.0±20.2	27.6–91.7 55.3±15.9	27.6-70.1 52.6±12.2	29.4-91.7 58.0±18.2
MCP	10.4–144.4 55.5±32.3	10.4–105.8 57.6±28.7	15.1-144.4 53.1±35.6	35.5-177.2 98.6±32.4	35.5-149.6 92.5±30.2	52.4-177.2 106.7±33.4
4 b)	Annual			4 c) Pride Home Range(Female)		
	Annual home range for all lions	Females	Males	Northern	Middle	Southern
50%	0.4-17.7 10.0±5.4	0.4-22.8 8.5±6.1	6.4-17.7 11.9±3.3	3.2-22.8 11.9±7.1	6.2-14.9 9.8±3.6	0.4-2.7 2.1±1.2
95%	6.2-96.4 49.2±22.2	6.2-85.2 39.5±21.5	44.7-96.4 62.1±15.6	19.1-85.2 50.9±23.6	29.4-59.5 45.5±11.1	6.2-19.7 14.4±5.9
MCP	18.74-179.7 93.4±43.0	18.7-153.9 70.2±35.0	92.2-179.7 124.4±31.7	36.3-153.9 82.9±43.5	62.9-113.8 81.4±18.2	18.7-44.9 34.4±11.3
4 d)	Annual home range					
	2014	2015	2016	2017	Dry	Wet
50%	3.2-10.1 6.7±3.6	0.4-11.5 7.0±4.3	6.7-11.8 14.0±6.0	2.7-14.5 9.8±4.3	0.74-16.1 9±4.6	0.4-18.1 8.19±5
95%	19-54.4 37.1±17.4	6.2-54.1 38.8±19.1	44.8-96.4 66.4±20.9	17.4-72.5 47.2±19.6	5.4-76.4 44.8±20.3	5.3-91.7 42.6±23.9
MCP	44.9-130.1 87.5±42.6	18.7-155.7 90.6±50.3	84.4-179.7 125.0±36.3	36.3-160.8 79.9±34.0	10.4-149.1 72.5±34.1	15.1-177.2 76.4±43.1


Nairobi CBD
Wilson Airport
KWS Hqs
JKIA
Mlolongo
Rongai
Tuala
Embakasi Primary
Excel Girls School
Kitengela
Legend
Centres
Major Road
Railway
NNP Boundary
Settlements
L01-KDE 50%
2014-Dry season
2014-Wet season
2015-Dry season
2015-Wet season
L02-KDE 50%
2014-Dry season
2014-Wet season
2015-Dry season
2015-Wet season
2017-Dry season
2017-Wet season
L03-KDE 50%
2015-Wet season
2016-Dry season
2016-Wet season
2017-Dry season
2017-Wet season
L04-KDE 50%
2015-Dry season
2015-Wet season
L06-KDE 50%
2016-Dry season
2016-Wet season
2017-Dry season
2017-Wet season

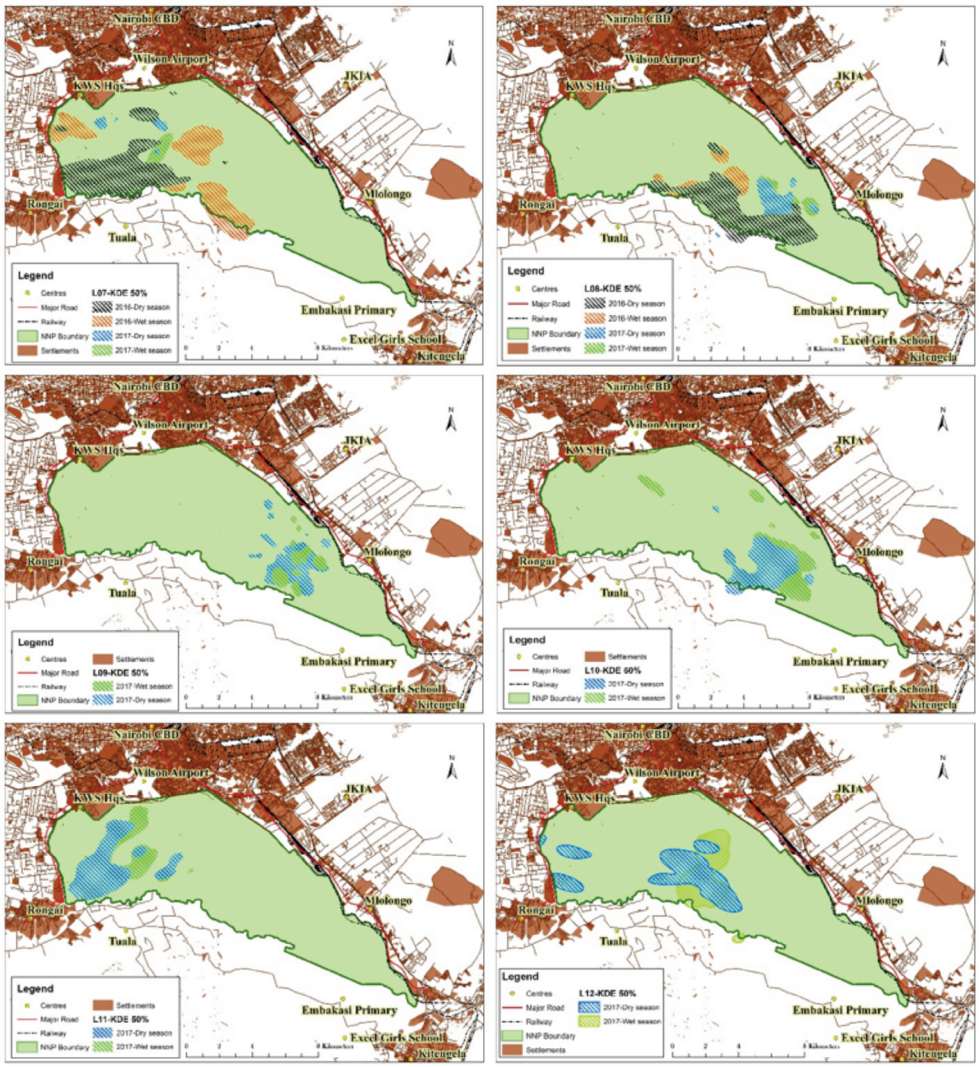


Figure 3.2

Seasonal 50% KDE core areas of all collared lions from 2014-2017. L01-L12 are the code of collared lions.

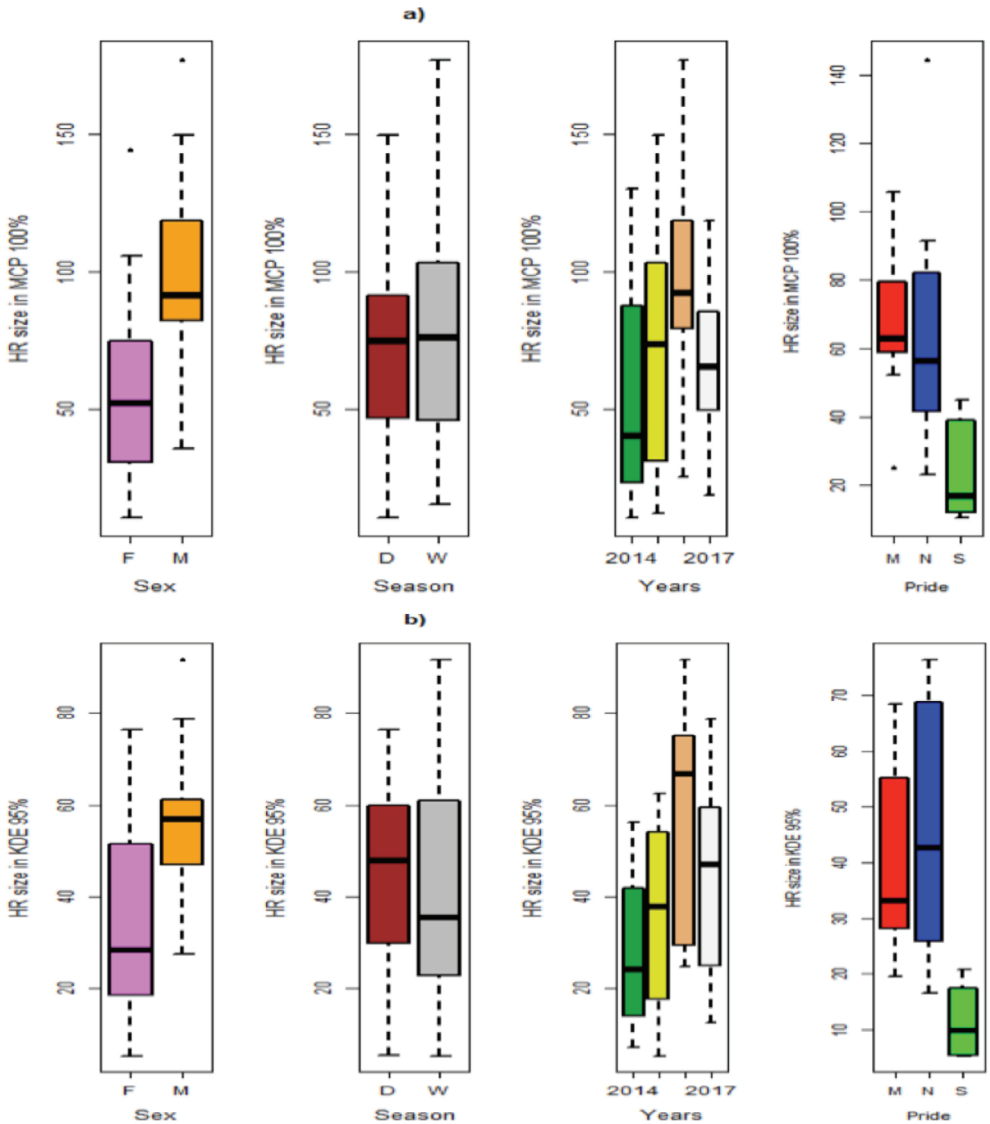


Figure 3.3

Comparison of home range size of NNP lions: a) MCP 100% home range sizes b) KDE 95% home range sizes. Dry season (D), Wet season (W), Female (F), Male (M), Middle Pride (M), Northern Pride (N), Southern Pride (S), Home Range (HR).

3.3.2 Seasonal movement, exit and re-entry

Activity patterns show consistent peaks during nighttime (20:00-04:30hrs) (Fig. 3.4) and a dip during the heat of the day (Fig. 3.5). There is a significant difference in the duration of lions roaming into the community land between wet and dry season. Lions roam in community land significantly more during the wet season compared to the dry season (Fig. 3.4; t = -2.4, df= 175, p–value = 0.017,); however, a comparison of seasons shows no significant difference in the frequency of lions leaving the park (t = -1.187, df = 120.5, p-value = 0.06). The duration of roaming is not significantly different between males and females (t = -1.012, df = 150.47, p-value = 0.3) and there is also no significant difference in the frequency of leaving the park and roaming into community land between males and females (t = -1.86, df = 123.7, p-value = 0.06).

Most of the lions made short trips in and out of the park and some lions remained entirely inside the park (e.g. L04). The southern section of the park is the main exit and re-entry point into the community land (Fig. S2). The annual mean temperature from the lion reading is 27.8±4.4 (range = 9.5 - 45). Our results show that lions require an optimum temperature range of between 18 - 32 degrees to be fully active (Fig. 3.5; R^2 = 0.05454, p-value: < 0.001).

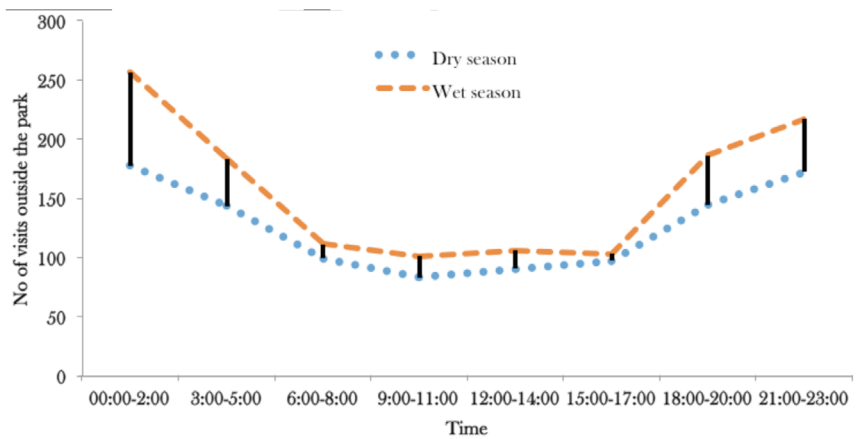


Figure 3.4

Number of collared lion visits outside the park during the dry and the wet season. (The black lines show the difference between the wet and dry season based on GPS data of all 12 collared lions during 2014-2017).

The results on geo-fencing of livestock bomas using an AWT option in order to alert the park management and research team when a collared lion had left the park showed that lions are mostly close to livestock bomas during the

day while the collared is actually in the park. On 127 occasions delays have been reported in receiving the SMS when lions approached livestock bomas. In addition, in 53 cases a false alert was received during the day when the collared lion was still in the park.

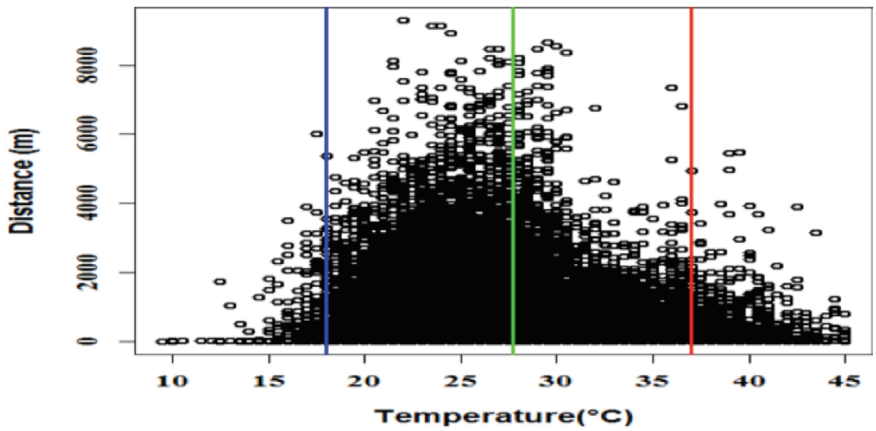


Figure 3.5
Relationship between the ambient temperature reading from the collars and the distance travelled by the lions between two points. (The blue vertical line = minimum, green = the mean and red = maximum. Between blue and red is the ambient temperature).

3.3.3 Travel distance

Table 3.2 provides an overview of distances travelled by the different lions. The movement analysis shows that the three pride males (L01, L03 and L06) have the longest potential maximum travel distances between two GPS points (16.31-29.9 km^2) within 24 hours (Table 3.2). Males travel significantly longer distances than females (Fig. 3.6a; χ^2 = 4.28, df = 1, p-value =0.038). There was no difference between distances travelled in the wet vs. the dry season (Fig. 3.6b; χ^2 = 1.44, df = 1, p-value = 0.230) except between years (Fig. 3.6c; χ^2 = 0.05, df = 1, p-value = 0.019). During fieldwork, we observed that all three pride males were able to travel from the northern part of the park to the undisturbed southern section. The three males show the longest travel distance (average and maximum in 24 hours). The mean travel distance in 24 hours is 17.1 ± 5.4 (ranges = 12.3-29.9 km). The average distance for the whole period is 4.5 (range = 2.9-7.5, Table 3.2). There was a significant difference between males and females in maximum potential distance travelled between two points (three-hour interval) (W = 8.13, p-value = 0.001).

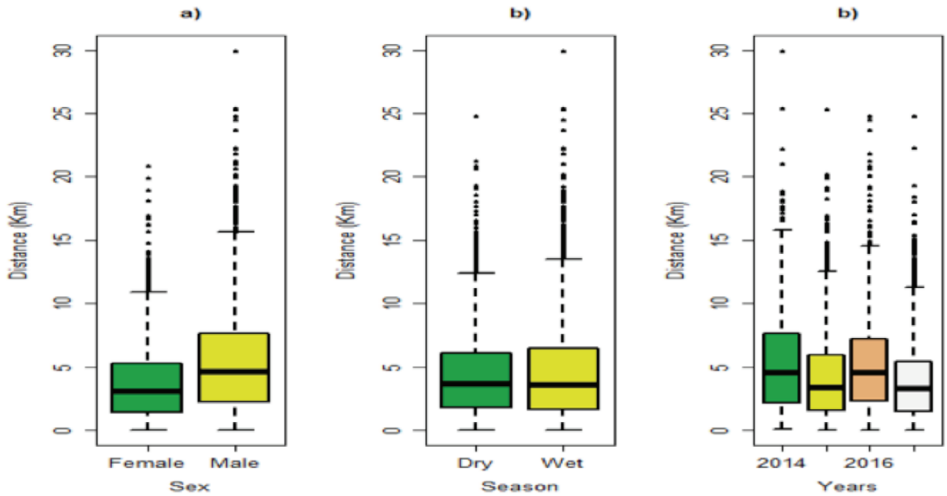


Figure 3.6
Differences in distances travelled by collared lions during 2014-2017 based on a) sex, b) season, c) year.

3.3.4 Habitat factors

Our analysis of habitat preference shows that the lions preferred the riverine woodland (w_i = 1.733, B_i = 0.205), followed by bushland (w_i = 1.396, B_i = 0.774) and scattered trees grassland (w_i = 1.16, B_i = 0.150). Most of the lions selected the riverine woodland as their core zone (Table 3.5 and Fig. S2). The largest habitat in the park is open grassland (28.4%) and this habitat is the fourth most selected when comparing all habitat preferences (w_i = 1.050, B_i = 0.137). The most avoided habitats are the forest (w_i = 0.495, Bi = 0.053) and open forest glades (w_i = 0.495, B_i = 0.174). Despite the whistling thorn shrubland being the second largest habitat (23.3%) in the park after the open grassland (28.41%), our analysis indicates that lions avoided this area (w_i = 0.851, B_i = 0.107). Although there was an incidental presence of lion scats (Fig. S1 in the zone close to Wilson Airport and Mulolongo (the urban fringe), our comparison of habitat choice demonstrated that none of the lions had its core (KDE 50%) on this eastern side of the park (Fig. S2). Our results show that lions tend to avoid the urban fringe section of the park (c^2 = 5836, df = 1, p-value = 0.001). Figs 2 & S 3 shows the average annual home ranges of all collared lions at 50% KDE and this figure it also shows the spatial avoidance by lions of the eastern border of the park which represents the urban fringe.

Table 3.5
Habitat selection indices.

Type area		bush-land	open forest glades	forest	mellifera shrubland	open grass-land	riverine wood-land	scattered tree grassland	whistling thorn shrubland
(km²) area(%)		**13.030 (11.18%)**	**1.380 (1.18%)**	**10.920 9.37%)**	**13.440 (11.53%)**	**33.120 (28.41%)**	**5.050 (4.33%)**	**12.480 (10.70%)**	**27.170 (23.30%)**
L01	wi	**1.081**	0.000	0.086	**2.014**	**1.402**	**3.226**	0.729	0.099
	Bi	**0.125**	0.000	0.010	**0.233**	**0.162**	**0.374**	0.084	0.011
L02	wi	0.000	0.000	0.000	**5.186**	0.016	**4.612**	0.093	0.030
	Bi	0.000	0.000	0.000	**0.522**	0.002	**0.464**	0.009	0.003
L03	wi	1.086	**1.746**	1.017	0.453	0.818	1.524	**3.070**	**3.609**
	Bi	0.082	**0.131**	0.076	0.034	0.061	0.114	**0.230**	**0.271**
L04	wi	**1.260**	0.398	0.300	0.000	0.289	0.185	0.564	**2.900**
	Bi	**0.214**	0.068	0.051	0.000	0.049	0.031	0.096	**0.492**
L05	wi	**1.106**	0.000	0.014	**1.058**	**1.780**	**1.975**	0.662	0.391
	Bi	**0.158**	0.000	0.002	**0.151**	**0.255**	**0.283**	0.095	0.056
L06	wi	**1.682**	0.517	0.782	0.000	**1.141**	**2.323**	**2.568**	0.141
	Bi	**0.184**	0.056	0.085	0.000	**0.125**	**0.254**	**0.280**	0.015
L07	wi	**2.493**	**1.856**	**1.286**	0.036	0.693	0.866	**2.680**	0.231
	Bi	**0.246**	**0.183**	**0.127**	0.004	0.068	0.085	**0.264**	0.023
L08	wi	**2.153**	0.000	0.000	0.914	**1.243**	**2.171**	0.632	0.597
	Bi	**0.279**	0.000	0.000	0.119	**0.161**	**0.282**	0.082	0.077
L09	wi	0.555	0.000	0.000	**1.358**	**1.737**	**1.166**	0.302	0.880
	Bi	0.093	0.000	0.000	**0.226**	**0.290**	**0.194**	0.050	0.147
L10	wi	**1.897**	0.000	0.000	**1.004**	**1.468**	**1.818**	0.165	0.681
	Bi	**0.270**	0.000	0.000	**0.143**	**0.209**	**0.258**	0.024	0.097
L11	wi	0.083	**1.314**	0.830	0.000	**1.004**	0.367	**3.392**	0.334
	Bi	0.011	**0.179**	0.113	0.000	**0.137**	0.050	**0.463**	0.046
L12	wi	**3.356**	0.110	**1.479**	0.000	**1.005**	0.564	0.941	0.319
	Bi	**0.432**	0.014	**0.190**	0.000	**0.129**	0.072	0.121	0.041
Average of all lions	wi	**1.396**	0.495	0.483	1.002	1.050	**1.733**	**1.316**	0.851
	Bi	**0.174**	0.053	0.055	0.119	0.137	**0.205**	**0.150**	0.107

w_i selection index: Values above 1.0 indicate preference; values less than 1.0 indicate avoidance. B_i standardized selection index allowing comparisons: Values below 0.125 (corresponding to 1/number of vegetation types) indicate relative avoidance; values above 0.125 indicate relative preference. Indices in bold show most preferred habitat; grey boxes show the highest index per lion.

3.4 Discussion

3.4.1 Home range

In our study, we did not find a significant difference between the wet season and the dry season in the home ranges of NNP lions (100% MCP, 50% and 95% KDE, Fig. 3.2 and Table 3.3). As was suggested in other studies on lion home range use, the insignificant seasonal variation in home range size we found in our study area could be a reflection of prey abundance and accessibility (Van Orsdol et al. 1985, Bauer & De Iongh 2005). A possible reason is therefore, the relatively high accessibility lions have year round to wild prey inside NNP and to livestock at short distances from the park (Lesilau et al. 2018). However, several lions showed a shift in the home ranges southwards during the wet season, although the size remained similar compared with the dry season home range size (Fig. 3.2 and Table 3.2). This shift can be explained by the migration of prey through the southern corridor into community land. Other studies also found that lion follow prey when there is abundance of water outside the park during wet season (Loveridge et al. 2009; Tuqa et al. 2014; Valeix et al. 2012).

Pride home range size of NNP lions (excluding males) ranges between 14–51 km^2 (34 km^2 in KDE 95%, Table 3.4b). This is the smallest home ranges size in Africa, smaller than those in the Amboseli National Park, Kenya, which has a dry season home range of 56 km^2 (KDE 95%) (Tuqa 2015) and in the Serengeti ecosystem, Tanzania, with 52 km^2 (KDE 95%) for lions (Schaller 1972). The small size of the NNP home ranges are primarily attributed to the small size of the park as a whole, the presence of a fence and high prey densities during the dry season (Lesilau et al. in prep).

Some NNP lion home ranges include the community land in AKP (Figs. 3.2 & S 2) and important feeding grounds of several large migratory herbivores (Gichohi 2003). The community land is privately owned and is progressively being partitioned into small fenced plots (Gichohi 1996). Thus, lions have no space to roam during the day due to human settlement (Lesilau et al. 2018) and prefer stay in the park over the community land. More of the lion home ranges and movement is on the western side of the park where riverine forest habitat is dominant. Lions use the riverine forest to hide during the daytime and they roam the surrounding area at night (Figs. 3.4, S 2 & S 3).

Male lions that joined other prides following takeovers demonstrated adaptation to the new pride territory (Fig. 3.2). This pride takeover increased the home ranges of incoming pride male when moving from their pride to a new pride and to females that have large home ranges because avoidance of infanticide during a pride takeover (Table 3.2). This is similar to observation

by Bygott & Hanby, (1987) where sub-adults stay at periphery of natal home range. Life stage, such as reproductive status of males and females, is an important factor in shaping lions' home range size (Bauer & De Iongh 2005; De Iongh et al. 2009; Loveridge et al. 2009). Other studies have also confirmed that season, prey and reproductive status of a lion influence their home range size (Lehmann et al. 2008; Loveridge et al. 2009). We conclude that landscape features and the small size of the semi-fenced park determine the movement patterns of lions in and outside the park.

3.4.2 Activity patterns

The peak time for NNP lions leaving the park and moving into community land is between 20.00–05.00 hours (Fig. 3.4). Lions partition their activity in human dominated landscape by roaming when human activity is low, in combination with the cover of darkness (Oriol-Cotterill et al. 2015). Tumenta et al. (2013) suggested that in Waza National Park in Cameroon, as livestock leaves for the bomas from the grazing fields and water points near the park, lions move closer to the park border and roam in the community land in the evening. The timing of lions roaming into community land is related to a reduction in livestock activity in the grazing fields around the park border. However, lions roaming into community land is not a reflection of habitual livestock depredation behavior.

The geo-fencing of livestock bomas as an early warning system has been only partially successful. We observed that due to close proximity to the park border and occasional cloud cover, there is a delay in receiving SMS and sometimes an alert is only received when the lion is already back in the park.

Lions are inactive at extremely low and high ambient temperatures (Fig. 3.5). When in an area with optimum temperature (between 18°C and 28°C) lions would hunt for prey and patrol their territory during the day. In high altitude areas like NNP, lion activities are determined by the ambient temperature. This finding on ambient temperature is confirmed by others studies (Schaller 1972; Tumenta 2012; Tuqa 2015). Climate variability affects the small window that lions have to hunt (Tuqa et al. 2014). To adapt to changes in temperature, lions adjust their strategy and invest more energy to take advantage of periods of optimum temperature.

3.4.3 Distance travelled

The maximum of potential minimum travel distance of each collared lion as shown in Table 3.2 is much larger than the average potential minimum travel distance (Table 3.2). The 24 hrs distance is just a one-day travel distance

which might have been either a result of avoidance behavior in response to a particular situation (e.g. males fighting or female avoidance of infanticide during a pride takeover). We observed three cases (Mumbi & Bertine) in which lions left the park into community, thereby increasing their maximum (potential minimum) distance.

When we compared our results with those of Serengeti National Park, Tanzania (Schaller 1972), where the lions had an average distance of 14.5 km, and with those of Waza National Park Cameroon, where the annual average was 7.5 km (Tumenta et al. 2013), NNP lions have shorter travel distances (4.5 km, Fig. 3.6, Table 3.2). This is possibly the result of a territorial avoidance mechanism with other neighbouring lions and a reflection of the small home range size.

Male lions in NNP are very active in terms of marking their territory and are involved in nighttime surveillance of their small home range. Van Orsdol (1985) demonstrated that lions in a large park, with large prides, may split into sub-prides to protect the pride. Travelling of short distances within the park, reflects the small home range size of NNP lions and their need to defend themselves against other lions. Similarly, they range short distance into community land, possibly due to proximity of livestock bomas to the park border and access to livestock (Lesilau et al. 2018).

The reproductive status of the lionesses also influences their movements and home range size. Lionesses with small cubs (e.g. Nelly) generally had significantly smaller home ranges and travelled shorter distances per 24hrs compared to lionesses with larger cubs and lionesses without cubs (Mumbi; Table 3.2). Several other studies confirmed that females with cubs have smaller home ranges compared to females without cubs (e.g. Funston et al. 2003; Tumenta et al. 2013; Tuqa 2014). Small cubs are not able to travel large distances and need safe places to shelter (Funston et al. 2003). Males travel significantly longer distances (between two points) within three hours compared to females (Table 3.2).

3.4.4 Habitat factors

Although the location of lion scat with prey hair items (Fig. S1) and some carcasses show incidental lion presence in NNP (Lesilau et al. in prep), there is no single collared lion with its core home range (50% KDE) inside the park along the eastern border neighbouring Wilson Airport, the southern bypass and Mulolongo (Figs. 2, S 2 & S 3). Our results show that lions tend to avoid the urban fringe section of the park. Figs 2 & S 3 show the average annual home ranges of all collared lions at 50% KDE and this figure also shows the spatial avoidance by lions of the eastern border of the park which repre-

sents the urban fringe. It is our assumption that the increased artificial lights from the city, in combination with the smell and noise pollution from the road and airport in this region of the park is scaring the lions. Avoidance of high human densities and human disturbance was also demonstrated by Oriol-Cotterill et al. (2015). Furthermore, Rich and Longcore (2005) showed that artificial lights that have a similar intensity to moonlight and may disrupt nocturnal activity patterns, such as foraging behavior. NNP lions only utilized the urban fringe zone in order to transit to other parts of the park to stay, rest and hunt. Hölker et al. (2010) showed that, a change in nocturnal habits due to light pollution threatens biodiversity. In an open habitat with few barriers to block artificial lights from urban settlements, this light pollution may influence the distribution and behavior of predators (Longcore et al. 2016). In addition, Longcore et al. (2005) found that species tend to disperse away from the urban glow towards the darkest horizon. Moreover, species adjust their nocturnal hunting activities to coincide with darkness hours in order to increase hunting success (Van Orsdol 1985; Funston et al. 2001).

Lions in the southern and middle part of the park concentrate their home range along the riverine habitat and valleys (Fig. S2). Lions use habitat with better cover and available water to ambush both livestock and wildlife (Loveridge et al. 2009). Habitat preference is strongly influenced by the distribution of habitat and location of an individual in the national park. A pride male lion's choice of habitat is dependent on the pride they have taken over and female social status (with or without cubs). Consequently, the effective habitat within NNP used by lions is 25.64% less than the actual surface area of the park (117 km^2).

We conclude that the Nairobi National Park lions have small home ranges (Fig. S3 & Table 3.4) and that they avoid the high human disturbance zone (by tourism, retaliatory killings, light, noise) of the park (Fig. 3.2 & Fig. S3) and thus their movement patterns seem disturbed by the urban fringe (Fig. S2). However, the lions are able to partition their activity within their home range to both in the community land outside the park and in suitable riverine habitat inside the park (Fig. S2). To optimize the habitat use, we recommend that the NNP management re-instates a 'green line' of trees to act as a buffer zone and embankment to filter the noise and lights from the human settlements along the Mombasa road and southern bypass.

Acknowledgements

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Supporting information

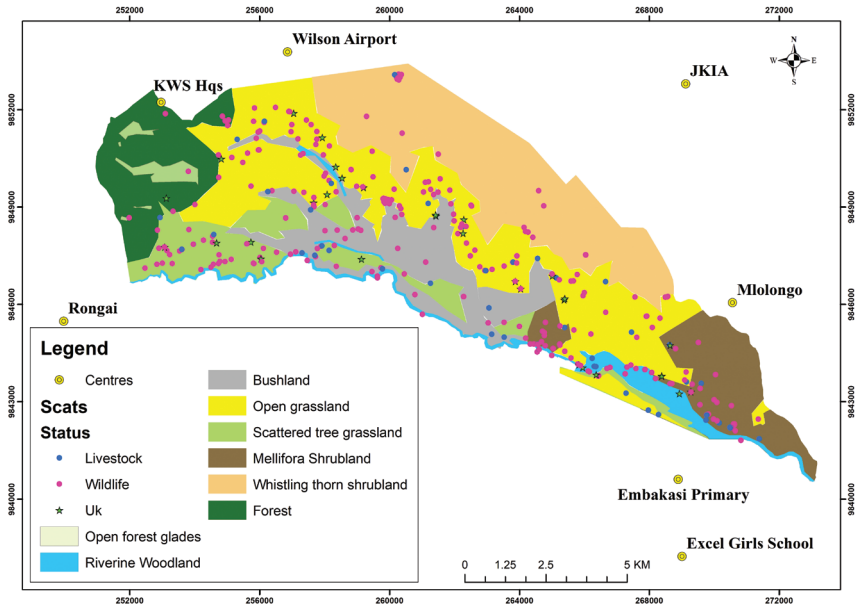

Figure S1

Map of NNP showing location of lion scats with different prey items.

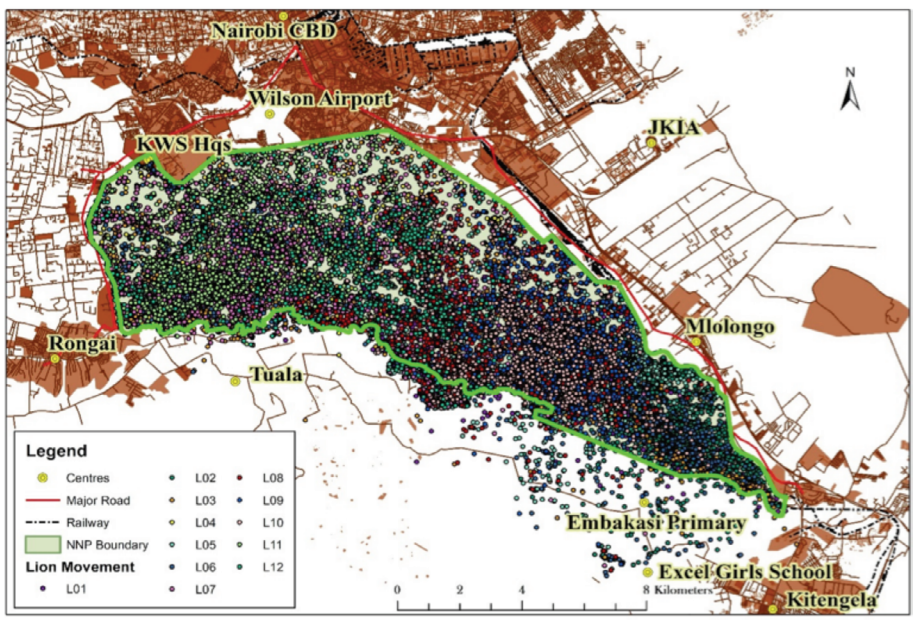

Figure S2

The GPS locations of collared lions inside the park and dispersal areas outside the park into the community land during 2014 – 2017.

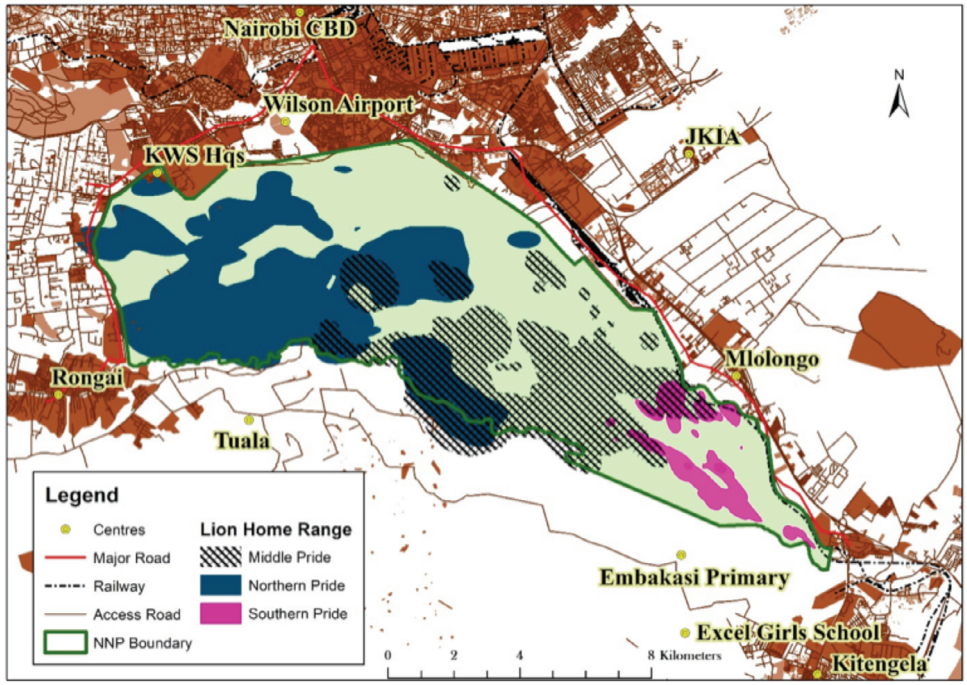

Figure S3
Pride home ranges at KDE 50%.

4

Impact of Climate Variability on Feeding Ecology of a Lion (*Panthera leo melanochaita*) Population under Urban Pressure in Nairobi National Park, Kenya

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Abstract

The aim of our study was to analyze the effects of climate variability and associated rainfall on the feeding ecology of lions in Nairobi National Park (NNP). We conducted carcass counts and collected scats to determine lion diets based on microscopic analysis of hair morphology, by DNA-metabarcoding.

Our results show that the lions of Nairobi National Park (NNP) have a mixed diet. They feed on large (< 200 kg), medium-sized (50-200 kg) and small-sized prey (5-50 kg), supplemented with very small prey (<5 kg). During and after three months of heavy rainfall more very small prey items were found in the lions' diet. Prey composition varied significantly between the dry and the wet season (also influenced by climate variability), showing different foraging strategies in different seasons.

Our findings validate the application of hair morphology and DNA-metabarcoding in a lion feeding study. We recommend further study of the role of very small prey in lions' diets by analyzing DNA from lion scats.

Keywords
Panthera leo, carcasses, Scats, DNA, Diet, Prey size

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4.1 Introduction

The free ranging lion *(Panthera leo leo)* populations in Africa are locally and regionally threatened as a result of habitat encroachment, a decline in prey populations and by conflicts with human communities (Bauer & Van der Merwe 2004; Craigie et al. 2010; Henschel et al. 2010; Riggio et al. 2013). The most important driving forces in this process are human population growth and economic development (McKee et al. 2004; Craigie et al. 2010; Stuart et al. 2010).

Male and female lions require a mean daily uptake of 10.4 and 7.5 kg of fresh meat respectively (Schaller 1972). They are considered to be opportunistic hunters and they can travel long distances (some 20 km per day) in search of prey and are therefore expected to encounter the full range of potential prey species occurring in their habitat (Hayward & Kerley 2005; Tuqa et al. 2014). However, prey abundance and density is subject to temporal changes (e.g. seasonal changes in rainfall, migration of prey species) and therefore will, differ within a lion's range (Hayward et al. 2007; Hayward & Kerley 2005). Other factors are: prey species characteristics (e.g. prey body mass, age, sex); temporal and spatial distribution; defense or anti-predatory tactics; morphological (e.g. sable horns); ecological (e.g. occurring at low density) and behavioral (e.g. the large herd size and increased vigilance of eland) characteristics; and preferred weight range and preference (Sunquist & Sunquist 1989; Hayward & Kerley 2005).

Different authors suggest different lion preferences and weight ranges, depending on region and species presence in that geographical area. Hayward & Kerley (2005), for example, conducted an analysis of 32 studies over 48 different spatial locations on the distribution of lions and showed that prey species within a weight range of 190–550 kg are preferred. The most preferred weight of prey is 350 kg and the mean mass of all preferred species was 201 kg (Hayward & Kerley 2005). Overall, gemsbok (*Oryx gazella*), African buffalo (*Syncerus caffer)*, wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and zebra (*Equus quagga*) were reported as the five most significantly preferred prey species in the analysis by Hayward & Kerley 2005. Being opportunistic feeders, lions regularly feed on medium-sized (50-200 kg) and large prey (>200 kg) (Bauer *et al.* 2008).

The dispersion of prey in a protected area is regulated by rainfall (Sogbohossou et al. 2011; Tumenta et al. 2013). Tuqa (2015) reported wildebeest and zebra as the most preferred species in Amboseli National Park. The Amboseli study analyzed prey preference before and after a period of drought, which resulted in mass mortality among wildebeest and zebra, forcing the lions to shift prey selection towards smaller prey species (such as impala and

warthog) and larger prey species (giraffe and African buffalo), in addition to livestock (Tuqa et al. 2014). After the drought, lions shifted back to medium-sized prey such as zebra and wildebeest, confirming the preference for these species (Tuqa et al. 2014). This largely coincides with the findings of Schaller 1972.

Nairobi National Park (NNP) is experiencing the impact of climate change and other human related changes (Owino et al. 2011). As a result, the human communities around the park are rapidly changing their strategies to cope with changes in their environment, shifting from pastoralism to urban livelihoods (Nkedianye et al. 2009). These changes have a direct impact on the lion's habitat and the feeding ecology of lions.

The role of large and medium-sized mammals in the lion's diet is well studied (Hayward & Kerley 2005; Bauer et al. 2008). However, it has been observed that occasionally very small prey species (body mass <5 kg), such as rodents or small birds, are also part of a lion's diet (Sogbohossou et al. 2011; Davidson et al. 2013). There are very few studies on the contribution of very small mammals and birds to the diet of lions. The detection of very small prey is more difficult with traditional methods of diet assessment, such as carcass counts and analysis of prey hair morphology in scats.

The use of DNA extracted from lion scats for diet studies of carnivores is an emerging field of research. In our study, we used a combination of carcass counts, microscopic analysis of prey hair morphology in scats and DNA techniques to detect the full range of prey in the lions' diet. This methodology was selected in order to fill a gap in research and determine the contribution of very small prey species to lions' diet.

Our aim is to assess the effects of climate variability and rainfall on the feeding ecology of lions. We hypothesize that NNP does not have sufficient wild prey all year round to meet the energetic demands of lions. Consequently, we suggest that lions in NNP need to supplement their diet with very small prey. The following research questions will be addressed: (i) What is the diet composition of lions in time and space? (ii) What is the prey choice of lions in time and space? (iii) What is the effect of climate variability and associated rainfall on lion diet? (iv) What are the trends in prey carcasses biomass in in time and space? (v) What is the added value of the meta DNA barcoding method compared to the diet methods based on the scat analysis and carcass counting?"

4.2 Materials and methods

4.2.1 Study area

Nairobi National Park (NNP) is located to the south-west of Nairobi City, Kenya (Owino et al. 2011) (Fig. 4.1). The park was established in 1946 with an area of 117 km^2 (Owino et al. 2011; Lesilau et al. 2018). It is situated between latitudes 1° 20′-1° 26 S and longitudes 36° 50′-36° 58′E (Ogutu et al. 2013) within an altitude ranging between 1533 m to 1760 m above sea level (Rudnai 1974; Owino et al. 2011). It has a long wet season from March to May with a mean of 150 mm of rainfall and a short wet season from November to December with a mean of 90 mm of rainfall; the annual temperature range is between 13.6°C and 25.3°C (Deshmukh 1985).

Nairobi National Park has three distinct vegetation zones: (i) semi-evergreen forest patches (*Croton macrostachys* and *Olea Africana*) with open grass glades (Foster & Coe 1968); (ii) an open grass savannah with monocods like *Pennisetum meszzianum* and *Themeda triandra* and trees like *Balanites spp.* and *Acacia melifera*; and (iii) riverine vegetation dominated by *Acacia xanthophloea Acacia mellifera* (Rudnai 1974). Dwarf woody plants are a result of controlled burning by park management (Foster & Coe 1968).

As a result of its locality, the park was semi-fenced in 1955 (Steinhart 1994). A chain-link fence with galvanized wire was erected along 36.3 km (56.1%) of the park's 64.7 km perimeter. The fenced is powered by electricity (6 Kv) and runs from the East via the northern boundary to the West in order to separate wildlife from the Nairobi metropolis (Foster & Coe 1968; Reid et al. 2008). The park's southern boundary is beyond the Mbagathi River and provides open access to the Athi-Kaputiei Plains (AKP) with an area of rangeland of 2200 km^2 (Reid et al. 2008).

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).

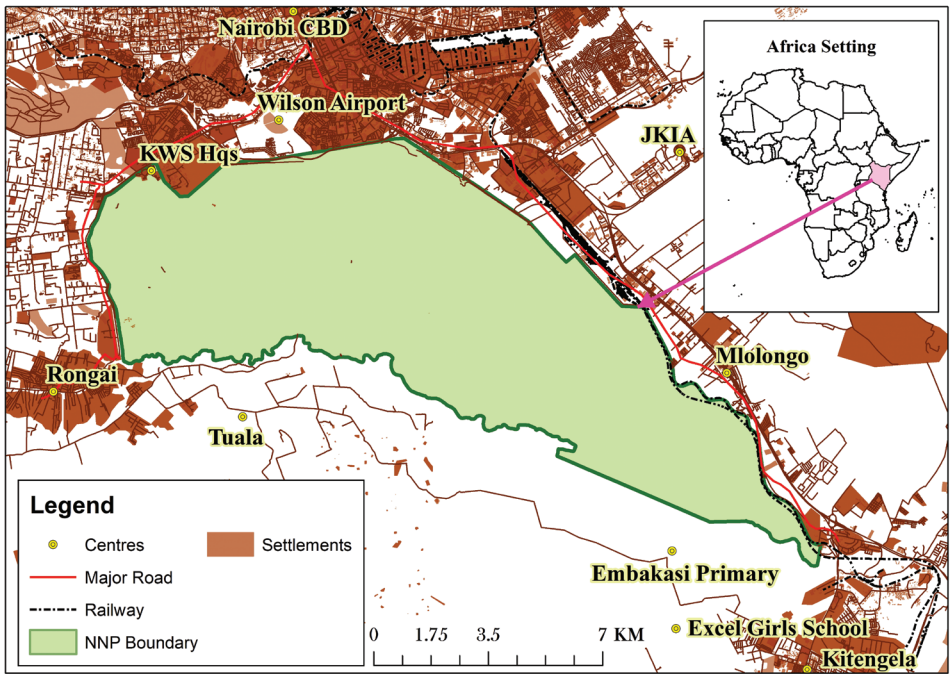


Figure 4.1
Map situating different habitat types within Nairobi National Park. Vegetation data provided by the KWS GIS and Biodiversity Office (2011). (Designed in Arcmap 10.3.1 (ESRI Software, USA))

4.2.2 Data collection

4.2.2.1 Prey hair in lion scats

Prey hairs in carnivore scat are usually unspoiled (Ramakrishnan et al. 1999). Lions live in family units and prides at the apex of their social organization (Stander 199; Bauer et al. 2003; Elliot 2017). Each adult member of a pride marks their territory using scats, urine and scents (Schaller 1972). As a result, scats from lions are commonly found throughout NNP. The scats were searched for at previously sighted lion resting sites, around prey carcasses killed by lions, along the roads while driving, and at opportunistic encounters with lions (Bisceglia et al. 2008; Tuqa 2015). Lion scats have a number of distinguishable features; they can be blackish, pungent smelling, segmented appearance, turning white when dry due to bones (Stuart & Stuart 2000). The

scats identified in the field were collected before sun drying and stored in a labelled zip-lock bags in a secure enclosure in order to prevent the samples from curious baboons, following Tuqa (2015). We recorded the GPS locations (including date and time) of the scats and later air-dried them. Lions do not necessarily feed on one prey at a time. For example, we observed (12 October 2015) a lion feeding on a hartebeest and a Thomson gazelle simultaneously, in which case hairs from both species would be present in the scat. Microscopic hair identification was prepared according to the procedure used by Reynold & Aebischer (1991) and Ramakrishnan, Coss & Pelkey (1999). We made a Prey Reference Hair Collection (PRHC) from fresh prey carcasses in NNP by collecting hair specimens from stuffed animals in the Natural History Museum, Naturalis in Leiden, The Netherlands, and from livestock encountered around the NNP. Prey hair items were identified using hair structure (cuticle scales) and color and by comparing them with previously prepared PRHC morphology (Corbett 1989). Prey weight categorization was adapted according to Bauer et al. (2008) into large (>200 kg), medium (50-200 kg) and small (5-50 kg).

We constructed a Prey Reference Hair Collection (PRHC) from fresh prey carcasses in NNP and from collected specimens in the collection of the Naturalis Biodiversity Centre (Leiden, The Netherlands) and from livestock encountered around the NNP.

4.2.2.2 Rainfall

We acquired Wilson Airport Meteorological station rainfall data from the Kenya Meteorological Department (KMD, 2012, 2014-2016). We considered the high altitude of NNP and high rainfall and chose 30.0 mm of rainfall per month to be the cut-off point for the transition between the dry and the wet season.

4.2.2.3 Prey DNA in lion scat

We only applied DNA (deoxyribonucleic acid) analysis of scat during the heavy rainfall year of 2015 to confirm the findings of hair morphology in the scats and carcasses. A sub-sample of the ten fresh scat samples collected in July – September 2015 from NNP was taken and preserved in a sterile DNA-free Eppendorf with 99.7% ethanol. The remaining scats was collected as described by Tuqa (2015) for prey hair analysis. The composition of lion diets was further determined using a recently developed method based on next-generation sequencing (Shezad et al. 2012).

We took samples from the center of the fresh lion scat using plastic gloves and a sterilized surgical blade and preserved them in a DNA-free Eppendorf tube containing 1.8 ml of 99.7% ethanol to minimize the collection of scats

with DNA degraded by ultraviolet light, or the collection of overabundant epithelial cells from the predator's intestinal tract. The tubes were labelled and stored in the dark at room temperature. The rest of the scats were collected and secured in labelled zip-lock bags for hair morphological and other remnants analysis.

We successfully extracted prey DNA from lion scats at the Leiden University molecular laboratory following previously optimized protocols (Bertola et al. 2011, 2016) using the Qiagen QIAamp DNA stool mini kit (Qiagen Inc., Valencia, California, USA). Controls were included to check for contamination during the extraction process.

4.2.2.4 Prey carcasses

We conducted prey carcass counts by searching for lions and prey carcasses. In addition, we collected ranger reports and reports from tour guides of sightings of fresh prey carcasses during 2012, 2014-2016. Finally, we counted carcasses during opportunistic encounters. The carcasses were inspected by the principal author who examined them for lion feeding signs and traces (e.g. claw marks and scats) in order to identify them as a lion feed, as described in Bauer et al. (2008). We excluded those carcasses showing no signs of lion feeding from the analysis. We recorded the Global Positioning System (GPS) coordinates of the carcasses (Garmin GPS), prey species, season (wet/dry) and condition of the carcass (fresh/old) in a pre-structured form.

4.2.3 Data analysis and statistics

4.2.3.1 Prey hair in the scats

We expressed occurrence of each prey hair item in each of the scat samples as presence or absence within the scats. We obtained the percentage frequency of occurrence by dividing the total prey hair items of a particular species by the overall number of prey hair items for all species and multiplied by 100%. The presence of bones, skull fragments, feathers, beaks, claws, jaws and teeth fragments of very small prey <5 kg (e.g. mice and birds) were determined only to genus or family level.

4.2.3.2 Rainfall

When analyzing the results of the prey hair analysis, we took into account rainfall data during the three months prior to scat collection. We carried out all statistical tests using the software R version 3.3.2 (R Foundation, Vienna, Austria). We used a significance level of $p < 0.05$ for all the tests.

4.2.3.3 DNA- Meta-barcoding

To amplify vertebrate prey DNA without any a priori knowledge of dietary composition, we conducted a polymerase chain reaction (PCR) with the highly conserved universal primer binding sites 12SV5F/12SV5R for all vertebrates with blocking primer for lion (Riaz et al. 2011; Shezad et al. 2012). This method has successfully been implemented with other felid species (Shezad et al. 2012, 2015). A PCR of the control, as well as a control PCR reaction were included to rule out contamination. We checked all PCR reactions on the Bioanalyzer (Agilent Genomics) and they were subsequently equimolarly (concentration 19.0 ng/μl) pooled for sequencing. We generated data using paired-end sequencing (Run length 125bp) on an Illumina HiSeq 2500 and subsequent quality control, as implemented by Baseclear (Leiden, The Netherlands). This includes Illumina Chastity filtering, removing reads containing the PhiX control signal and removing read containing partial adapters, while maintaining a minimum read length of 50 bp. We de-multiplexed all samples based on a unique combination of eight base pair tags attached to both the F and the R primers (tags were designed so that all the tags differ from each other by >2bp).

After quality control, sequence data were analyzed using a pipeline hosted at Naturalis Biodiversity Center. Sequence read were filtered, clustered and BLASTed using scripts implemented in the galaxy platform (Giardine et al. 2005). We used the Uchime de novo tool from the Usearch package to remove chimeric sequences from an amplicon set (Edgar 2010). We clustered rea above 100nt with CD-HIT-EST at 100% similarity and removed any clusters smaller than 10 reads (Fu et al. 2012). We used representative sequences from the clusters for BLAST search identification against a local copy of GenBank. Only 100% matches were selected (Camacho et al. 2009).

We performed a chimera check (as implemented in Galaxy – chimera removal). We chose these stringent options to reduce the noise and chances of false positives. The resulting list of identified prey species was further analyzed by excluding all hits that were represented by <3% of clustered reads. We compared the composition of the prey hair item identified from scats and prey carcasses counted with DNA scats results of the same season.

4.2.3.4 Prey carcasses

We first determined the total number of kills per prey species (Druce et al. 2004). We then split the prey species carcass data into seasons based on the monthly amount of rainfall (wet/dry). We used 30 mm of rainfall per month as a cut-off point between the wet and dry season. The percentage frequencies of prey species carcasses were calculated seasonally, based on the cumulative number of carcasses of each season, and biomass was multiplied

by ¾ of individual female weight, as in Hayward & Kerley (2005), to obtain the total carcass biomass for the dry and wet seasons. We excluded livestock carcasses from biomass analysis.

4.2.3.5 Comparison on data collection techniques

We compared the composition of the diets based on prey hair items identified from scats and from prey carcass counts, with diets based on DNA analysis of scats during the same (wet) season to determine the prey species presence and absent between the three methods.

4.3 Results

4.3.1 Prey diversity in lion scats

We collected 425 scats during 2012, 2014-2016 and 35 (8.4%) doubtful scats were excluded from analysis, either because they did not contain hair to match the PRHC, or because they were suspected to be from other carnivores. In 21 scats, bones, skull fragments, feathers, pieces of horn, beaks, claws, grass, jaws and teeth were found (Fig. 4.2a and b). After discarding doubtful scats, we were left with 390 scats. Of the remaining 390 scats, 298 were collected in the dry season and 92 scats in the wet seasons during 2012, 2014-2016. The dry season scats contained 265 prey hair items and the wet season scats contained 111 prey hair items based prey hair morphology and scale pattern from lion scats (Fig. 4.2c). There is a significant difference in the expected equal prey hair items between the dry season scats and the wet season scats ($\chi^2 = 64.7$, df = 1, p-value = 0.001). There are 20 different prey species hair items from the lion scats. Three wild large prey species, five medium-sized species, seven small species and five very small prey species were found, with a significant difference between prey biomass category found in the prey hair items (Table 4.1; $\chi^2 = 104.5$, df = 3, p-value < 0.001). In 102 scats we identified more than one prey species, with the highest being four different prey species in one scat.

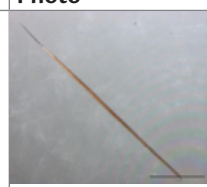
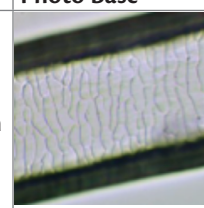
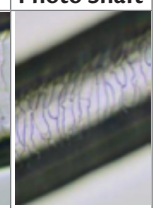
Species	Morphology	Photo	Scale Pattern	Photo Base	Photo Shaft
Impala	Reddish Brown (Raw Sienna) over entire length with black tip (0.8 mm)		**Base & Shaft**: regular waved mosaic, 2-3 scales across width, scale margin smooth. **Tip**: slightly irregular, scale margin smooth to ripple.		

Figure 4.2
(a) small prey carcass remains from lion scats; (b) Lioness feeding on a marabou stork (*Leptoptilos crumenifer*); (c) prey hair morphology and scale pattern from scats

The main species found in the scats during the dry season was zebra (23%), followed by African buffalo (14%), hartebeest (10%), rodents (9%) and wildebeest (7%). Results for the wet season were similar, with zebra (27%), African buffalo (11%), warthog (9%), hartebeest (9%) and impala (8%) (Table 4.1). During 2012 and 2014-2016, the result shows large prey contribute 31% of the prey hair items, medium size prey is 52%, small size prey is 17% and very small prey is 0% (Fig. 4.4c)

Table 4.1
Frequency and percentage of occurrence of different wildlife prey hair items in the scats of NNP lions (data are cumulative during 2012, 2014-2016, by season).

Class weight	Species	No. of prey hair items in the scats	Total in dry (Jul-Sept)	Total wet (Feb-Apr)	Dry season (%)	Wet season (%)
Large	Buffalo	48	36	12	14	11
	Eland	13	10	3	4	3
	Giraffe	9	5	4	2	4
Medium	Hartebeest	37	27	10	10	9
	Ostrich	12	7	5	3	5
	Waterbuck	10	5	5	2	5
	Wildebeest	23	18	5	7	5
	Zebra	91	61	30	23	27
Small	Bushbuck	4	2	2	1	2
	Bushpig	1	0	1	0	1
	Grant's gazelle	21	16	5	6	5
	Impala	28	19	9	7	8
	Reed Buck	1	0	1	0	1
	Thompson's gazelle	15	12	3	5	3
	Warthog	25	15	10	6	9
Very small	Bird	7	6	1	2	1
	Hare	1	0	1	0	1
	Rodent	28	25	3	9	3
	Snakelike	1	1	0	0	0
	Lizard	1	1	0	0	0
		376	265	111	100	100

4.3.2 Climate variability effects

The amount of rainfall of three months prior to data collection had a direct positive impact on the presence of very small prey in the lions' diet. As rainfall increased, the contribution of prey hair items of large ($r^2 = 0.5$) and medium (r^2 0.03) prey decreased, while the proportion of the small ($r^2 = 0.24$) and very small ($r^2 = 0.04$) prey hairs increased (Fig. 4.3)

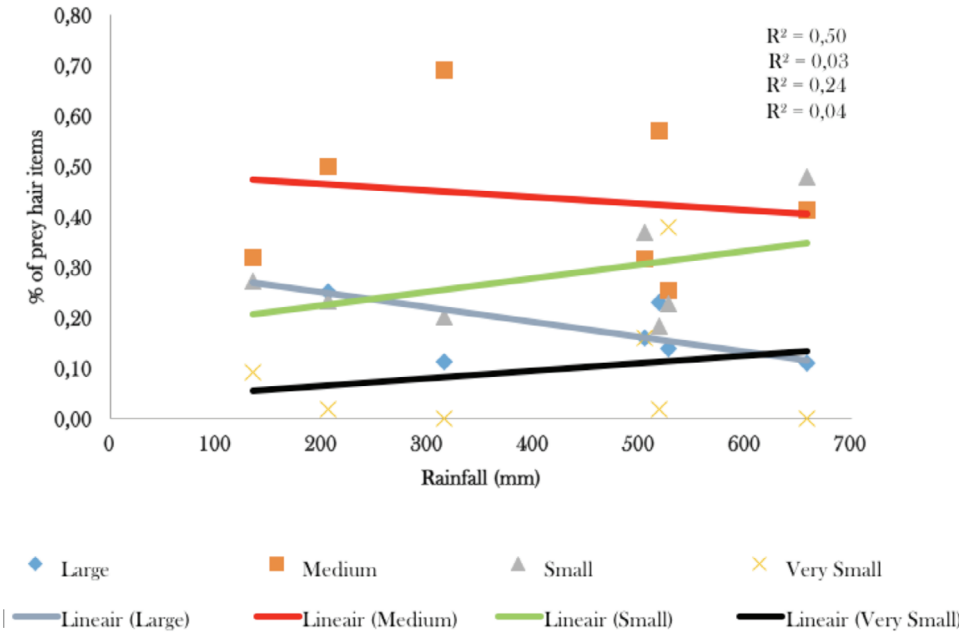


Figure 4.3

The El-Nino rainfall impact on lion diet, based on prey hair items in the lion scats. Rainfall is based on cumulative rainfall for three months prior to data collection months. Large (L), Medium (M), Small (S) and Very Small (V) prey size.

4.3.3 Meta-barcoding results

We used DNA to confirm the effects of rainfall on the diet already established from hair morphology in the scats. From the ten samples, we obtained a total of 546,768 reads, which were accepted after FastQC (version 0.10.0) quality control. We retained 97% of all reads after a chimera check. After removing clusters that represented <3% of all clustered reads, BLAST identification resulted in a list of two to six species per sample. Multiple clusters had identical BLAST identification.

We encountered lion DNA in all ten samples and this data was used as an internal control to check the identity of the scat samples. In one case, 63% of the reads were attributed to leopard. Leopard was also found in three other samples, albeit in a lower percentage. We identified serval DNA in three samples. The reads of leopard were interpreted as errors and not taken into account, although it cannot be excluded that lions eat leopards. We excluded the reads without other species from further analysis. The reads of other prey animals in the scats with leopard reads were still used for the analysis. So we analyzed 10 lion scat samples in total. We also found human DNA

in three samples. In two samples, BLAST returned tiger as a hit, which we attribute to damage in the DNA, resulting in a sequence change (1 bp) that resembles a tiger sequence. All other identified species are likely to be true prey species for the lion: blue wildebeest, zebra, suni (*Neotragus moschatus*), African buffalo, common eland, shoat and mole rat (*Tachyoryctes sp* as the only representative of a very small prey species.) (Fig. 4.4a, b and Table 4.2). With the exception of the DNA of tiger, leopard, human and serval cat, we had identified all other species either through carcasses or hair morphology. The aforementioned reads were not included in the statistical analysis, while a possible cross contamination was indicated by negative controls. We mention these findings here to highlight the diversity of prey composition that can be detected based on DNA analyses.

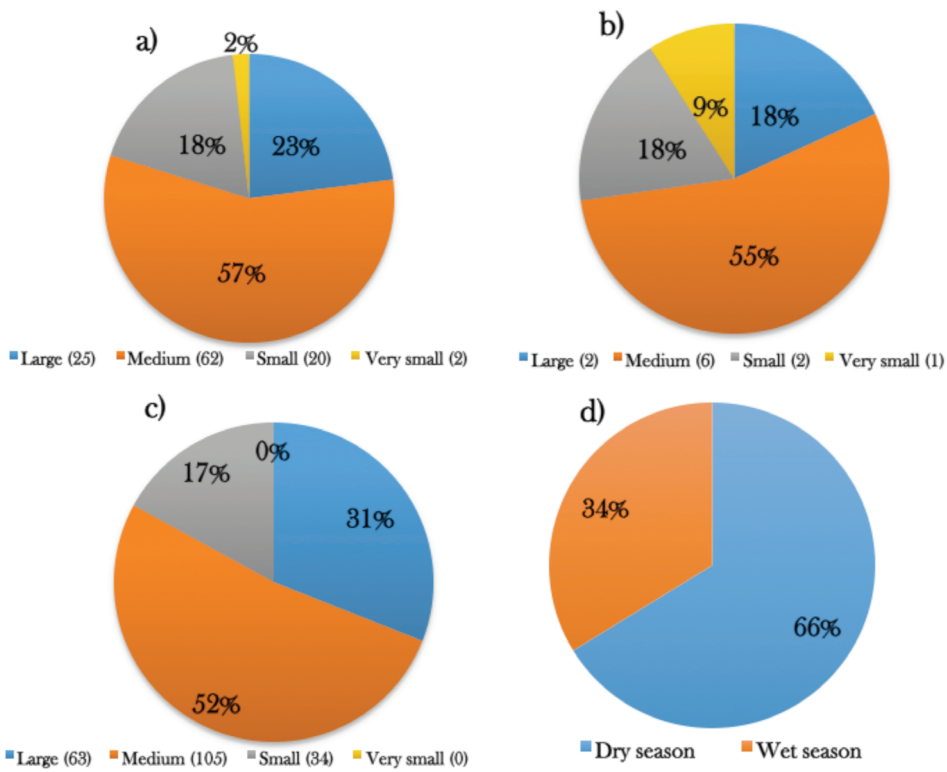


Figure 4.4

(a) Prey size proportions based on hairs from lions' scats of July – September 2015; (b) DNA-metabarcoding results of ten scats samples collected in NNP in July – September 2015 (excluding livestock and carnivores); c) Frequency of prey sizes occurrence in the park based on carcass surveys during 2012 and 2014-2016 (Large 200 kg, medium 50–200 kg, small <5–50 kg and very small < 5 kg, based on Bauer et al. 2008); d) Seasonal average of wild species biomass (kg) carcasses from 2012, 2014-2016 in NNP, based on average male and female weight, following Hayward & Kerley (2005).

Table 4.2
DNA, prey weight classification, counts and percentage in DNA analysis from ten scat samples

Weight class	Scientific names	Species	Count	Percentage
Large (>200 kg)	*Syncerus caffer*	African buffalo	1	9.1
	Tragelaphus oryx	Common eland	1	9.1
Medium (50-200 kg)	*Connochaetes taurinus*	Blue Wildebeest	4	36.4
	Equus burchellii	Zebra	2	18.2
Small (<5-50 kg)	*Neotragus moschatus*	Suni	2	18.2
Very Small (< 5 kg)	*Tachyoryctes sp*	Mole rat	1	9.1

4.3.4 Prey carcass diversity and biomass

A total of 234 carcasses of 14 wild prey species, three livestock prey species and four unknown prey species were recorded during 2012, 2014-2016. We excluded 28 livestock carcasses and four unidentified carcasses from the analysis, since livestock are not legally found in the park and carcasses could be as a result of unherded or stray livestock killed by lions, except when comparing DNA-metabarcording with hair and carcasses in the sample of July-September 2015. Of the 202 remaining carcasses, 148 carcasses were found during the dry season and 54 carcasses during the wet season (Fig. 4.4a; $\chi^2 = 43.7$, df = 1, p-value <0.001). Our average detection rate is 40 carcasses (62%) in the dry season and 25 in the wet season (38%). The average wild prey carcass biomass amounted to 8,356 kg/km^2 (66%) in the dry season and 4,259 kg/km^2 (34%) in the wet season (Fig. 4.4d). There is a significant 68% decline in carcass biomass (kg) from dry season to wet season (Fig. 4.4d, Table 4.3; t = 2.42, df = 15, p-value < 0.031). The six main prey species killed by lion amount to 55% of all carcasses in the dry season. In the wet season, the six main prey species amount to 25% of the total carcass biomass (Table 4.3). The overall average frequency of carcasses per body size class for the dry season are: large 21%; medium 35%; and small 11%. For the wet season, the contribution of large is 10%, medium 17% and small 6%, as shown in Fig. 4.4. A Chi-square test reveals a significant difference prey size class distribution between the wet and the dry season ($\chi^2 = 64.5$, df = 3, p-value < 0.001). We also found a significant negative correlation between log-monthly precipitation and log-number of prey species carcasses found in the park using Pearson correlation test: ($r^2 = -0.66$, p-value<0.004; Fig. 4.5).

Table 4.3

Seasonal wild species carcasses, contribution of each species from 2012, 2014-2016 in NNP on ¾ weight of female adult, based on Hayward & Kerley (2007).

Classes	Species	No of carcasses during study period			Seasonal averages of carcasses and biomass				Seasonal percentages (%)	
		Dry season carcasses	Wet season carcasses	Body Mass (kg) per species	Dry season average	Wet season average	Dry season Biomass	Wet season Biomass	Dry season	Wet season
Large	Bu	25(16.9%)	6(10.7%)	432	6	2	2592	864	31.0%	20.3%
	El	11(7.4%)	5(9.3%)	345	3	2	1035	690	12.4%	16.2%
	Gi	11(7.4%)	5(9.3%)	550	3	2	1650	1100	19.7%	25.8%
Medium	Os	2(1.4%)	2(3.7%)	70	1	1	70	70	0.8%	1.6%
	Wb	0(0%)	1(1.9%)	188	0	0	0	188	0.0%	4.4%
	Ha	13(8.8%)	6(11.1%)	95	3	2	285	190	3.4%	4.5%
	Wbz	13(8.8%)	3(5.6%)	135	3	1	405	135	4.8%	3.2%
	Ze	49(33.1%)	16(29.6%)	175	12	5	2100	875	25.1%	20.5%
Small	Im	8(5.4%)	3(5.6%)	30	2	1	60	30	0.7%	0.7%
	Gg	3(2%)	0(0%)	38	1	0	38	0	0.5%	0.0%
	Po	0(0%)	1(1.9%)	12	0	0	0	12	0.0%	0.3%
	Rb	2(1.4%)	0(0%)	16	1	0	16	0	0.2%	0.0%
	Tg	5(3.4%)	1(1.9%)	15	1	0	15	15	0.2%	0.4%
	Wa	6(4.1%)	5(9.3)	45	2	2	90	90	1.1%	2.1%
	Total	148	54	2146	38	18	8356	4259	100	100

Buffalo (Bu), Eland (El), Giraffe (Gi), Grants Gazelle (Gg), Hartebeest (Ha), Impala (Im), Ostrich (Os), Thompson's Gazelle (Tg), Warthog (Wa), Waterbuck (Wb), Wildebeest (Wbz), Zebra (Ze), and Porcupine (Po) and Bushbuck (Bb)

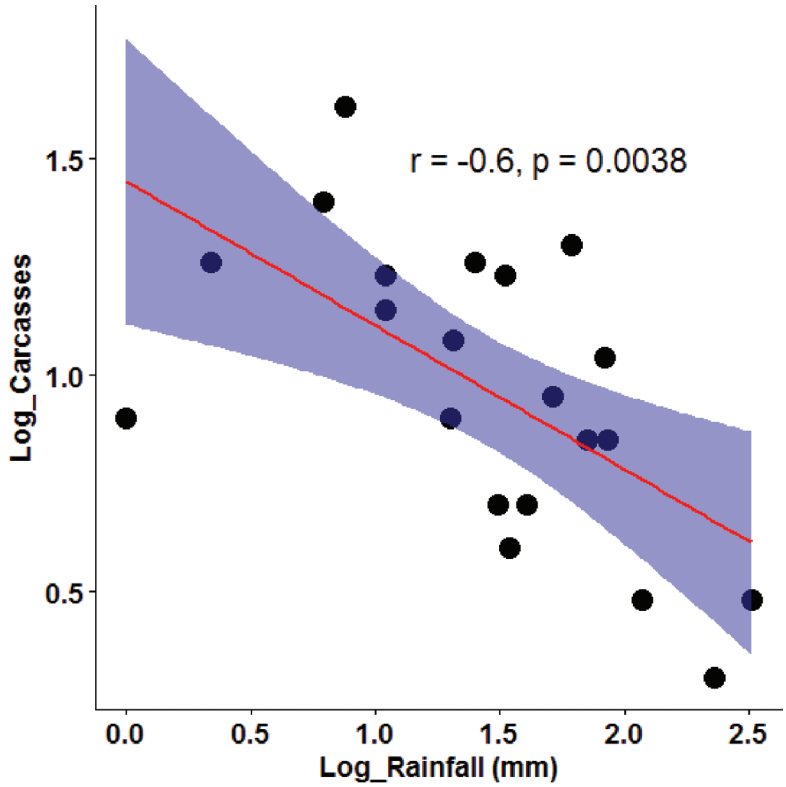


Figure 4.5
Correlation between the log-number of prey carcasses and log-maount of rainfall in NNP during 2012 and 2014-2017.

4.3.5 DNA-metabarcoding analysis versus scat and carcass sampling

A comparison between the three sampling techniques shows that African buffalo, eland, zebra and wildebeest were found in the analysis of the carcasses, prey hair items morphology and in the DNA analysis of the same (wet) season (Table S1). Suni and Rodents were only present in DNA analysis and not in carcasses and prey hair analysis of the same (wet) season. For all techniques combined and throughout the study period, few very small prey such as birds, hare, rodents and some scales most likely to originate from snakes or lizards were only found in the scats. We observed a lion killing and feeding on a marabou stork (*Leptoptilos crumeniferus)* (Figs. 4.2a and b, Table S1).

4.4 Discussion

4.4.1 Diet composition

NNP lions have a mixed diet, consisting of a wide range of prey size classes. With the exception of very large prey, such as rhinoceros and hippopotamus, lions in NNP feed on very small prey to large prey (Figs. 4.2, 4.4 and Table 4.2). The long stay of wild prey in the community land would result into one lion roaming longer in the community by following migrating pay and intensity of human-lion conflict. Thus lion would have developed preference to livestock. Secondly, lion would put more pressure on non-migrating wild prey and cause "predator dip". Predator dip is a situation why a population of certain declined due to over depredation. The dominant presence of large-medium prey, supplemented by small-medium prey and fewer very small prey, confirm the findings of other studies (Hayward & Kerley 2005; Bauer et al. 2010).

The increased presence of bird feathers in lion scat during the dry season could possibly be attributed to the increased number of herbivore carcasses in the park, and consequently the higher availability, and possibly catchability, of scavenging birds such as vultures at such carcass sites (Fig. 4.2; Table 4.1).

Although Hayward & Kerley's (2005) diet analysis shows zebra to be the predated species in the majority of African lions, our analysis confirms the findings of Davidson et al. (2013) that zebras are consumed regardless of season due to abundance (Ogutu et al. 2013) based on carcasses and prey hair items from NNP (Table S2). In the 1970s, Rudnai (1979) found that wildebeest was the most abundant prey in the park. The difference in these findings on few carcasses of wildebeest can probably be explained by a strong decline of the wildebeest population in NNP recent decades, as previously suggested by Owino et al. (2011) and Ogutu et al. (2013).

NNP lions also predate on giraffes as evidence in carcasses count and hair morphology (Table S2). Predation on giraffe in NNP, could be partly due to the grouping behaviour of juvenile giraffes. We observed that, during the dry season, baby and juvenile giraffes mostly remain in the NNP's forest ecotone, while the adults browse in the forest and valleys. This provides lions with an opportunity to predate on the giraffe juveniles. In Lake Nakuru National Park, Kenya, a skewed age structure of Rotchild giraffe has resulted due to juvenile removal by lions (Muller 2018).

Despite African buffalo being least predated by lions in the wet season, this study confirms findings by Rudnai (1974), who found that they are the most predated species in the dry season, based on the carcasses and prey

hair items from scats (Table S2). This contradicts the findings of Hayward & Kerley (2005) and Davidson (2013), which suggested that African buffalo was most predated species regardless of the season. Hayward & Kerley (2005) stated that buffalo are weaker in the dry season and more vulnerable to depredation during drought.

Spatial-temporal fluctuation of herbivores in the park has a significant impact on the lions' diet (Tumenta et al. 2013; Tuqa et al. 2014). In the dry season, wild prey biomass is considerably higher in NNP when wild prey concentrates around the available water sources and man-made dams in the park, compared to the wet season when they migrate out of the park into AKP (Gichohi 1996; Owino et al. 2011; Ogutu et al. 2013). During the dry season, the constraints of low forage quality, drinking requirements and presence of ambushing predators increases the vigilance of prey (Valeix et al. 2009).

Although we rarely observed some of the species, such as, bushbuck, porcupine, hare and bushpig carcasses, in the park, prey hair analysis revealed that they are available species in the park and form part of lion diet, based on hair morphology from the lion scat data during the wet season (Table S2). It is possible that the carcass count method is not suitable for these rare and cryptic species. With the seasonal decline of large and medium prey density in the park (Owino et al. 2011), small and very small prey become more common food for lions in NNP as evidence in prey hair item (Table S2).

4.4.2 Climate variability effects

We found a direct relationship between rainfall and lion diet in terms of prey size composition (Fig. 4.3). With increasing rainfall, the consumption of large and medium prey declined, while small and very small prey increased (Figs. 4.3 and 4.5). Decline in herbivore density during the wet season carcasses (Fig. 4.4c and d) allows for the growth of vegetation and it favors rodent density and other very small prey (Tian et al. 2015). We found a significant relationship between the amount of very small prey hair items and bones with a cumulative amount of rainfall in the three months prior to data collection (Fig. 4.3). The contribution of small prey (18%) and very small prey (<5 kg, 9%) in the lions' scats collected in NNP during 2015-2016 (Fig. 4.4b), confirms the diverse feeding ecology and opportunistic nature of lions (Table 4.1). Although the majority of prey hair items were found between cumulative rainfall of 400-500 mm, the data suggest the frequency of very small prey hair items in the scats is positively related to rainfall (Fig. 4.3).

A research project in China, conducted during 2005-2012 in Xi'an, found that a period covering three months' rainfall prior to sampling has an in-

fluence on rodent populations (Tian et al. 2015). Leirs et al. (1994) suggested that new vegetation growth stimulates rodent breeding. Rainfall and increased cloud cover enhance the activity of rodents and decreases the activity level and detectability of rodent predators which enhances their chances of survival (Lahaye et al. 2004; Wróbel & Bogdziewicz 2015). It is possible that the NNP lions hunt small and very small prey species when they encounter them by chance, as a possible 'snack', and they may also opportunistically take dead rodents, reptiles and birds killed, e.g. on the park roads as a result of dense traffic in the park. The main author observed a lion stalking, killing and consuming a marabou stork (*Leptoptilos crumeniferus)* in NNP on 21 January 2017 (Fig. 4.2a). We suggest that the high contribution of very small prey (< 5 kg) to the diet of NNP lions is partly due to the effects of extreme climate variability, which caused prolonged rainfall during 2015-2016.

Herbivores have a spatial-temporal impact on the ecosystem (Schippers et al. 2014) and modify vegetation composition and structure (DeWalt et al. 2003). The congregation of herbivores during the dry season in NNP (Gichohi 2003) changes the land cover and may affect the activity of rodents. As rodents move from cover to cover, they are exposed to risks of being killed by e.g. snakes, birds or traffic in the park. This may explain why there is an increase in hair, bones and feathers in NNP lion scats in the dry season (Fig. 4.3).

4.4.3 DNA-metabarcoding

We also found a broad spectrum of prey species with DNA-metabarcoding (Fig. 4.2c and Table 4.4). The fact that DNA-metabarcoding only identified mammals (Table 4.2) may be the result of a bias of the primers and sample size (ten samples from 2015), which are known to perform poorly for reptiles and potentially also for birds. Even when lowering the threshold and including even those clusters with very low numbers of reads, we encounter bird species in the DNA. However, we have chosen not to include these results as they may potentially represent false positives.

In the second analysis of the same set of samples, including a blocking primer to reduce the representation of lion DNA, four more species were identified after processing the samples: black-backed jackal (*Canis mesomelas*) (this may not be part of the lion's diet and can possibly be attributed to marking over the lion sample or scavenging of the lion kill, although this cannot be excluded), African pygmy mouse (*Mus minutoides*), chicken (*Gallus gallus*) and pig (*Sus scrofa*). Presence of leopard and serval cat in the DNA may be the result of territorial marking of a previously deposited lion sample.

Despite three cases of lions attacking humans in NNP reported to KWS during 2012-2017 (Ombati 2017), there was no human hair in any of the lion scats collected from the park. Human DNA found by DNA-metabarcoding is likely a result of sample processing in the lab. We assumed that the absence of human hair in the lion scats is due to the relatively low number of human attack cases in the park and few scat samples for DNA analysis. Therefore, our study cannot confirm that humans are part of the lions' diet or the existence of a man-eating lion in NNP.

4.4.4 DNA-metabarcoding versus prey hair analysis and carcass counts

Our results show that DNA-metabarcoding is a complementary method for the analysis of lion diets, when compared with prey hair analysis from scats and carcass counts, despite overestimating the larger prey size during carcass counts (Fig. 4.4), and underestimating smaller species in lion scats because of the small body mass and low amounts (or absence, in case of reptiles) of hairs from small species present.

A major advantage of microscopic analysis of prey hair and DNA-metabarcoding is therefore that it also allows for the identification of smaller prey species, which are not detected through carcass counts or microscopic analysis of hair morphology in lion scats (Biswas & Sankar 2002; Bagchi et al. 2003; Ogara et al. 2010).

Ackerman et al. (1984) stated that large prey has more flesh with fat and thus, lions feeding on more meat alone, rather than skin, bone and hooves, produce more liquid scats which dry quickly, and these would probably not be collected during field studies or may have few hairs. Our analysis of scats from the same season shows more very small prey in the DNA analysis (9%) compared to the diets based on prey hair items (2%). We recommend the application of DNA to assess the role of very small prey in lions' diet.

Despite well-known limitations, such as DNA-amplification bias, this technique shows great promise for obtaining additional insights into dietary composition of species (Yoccoz 2012; Pompanon et al. 2012; Bohmann et al. 2014; Mumma et al. 2015).

Application of DNA technique on lion scats has added value of detecting more species in the lion diet compared to carcass count and microscopic hair morphology analysis. We recommend the application of DNA to assess the role of very small prey in lions' diet.

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Supporting Information

Table S1

Proportion of prey hair items found in lion scats, carcasses and DNA-metabarcoding based on results of ten scat samples collected in NNP in July – September 2015. The shaded boxes with grey colour represents the species with highest proportion in scats, carcasses and DNA.

Size	Species	Hair	Proportion	Carcasses	Proportion	DNA	Proportion DNA
Large	Buffalo	21	0.17	11	0.16	1	0.09
	Giraffe	0	0.00	5	0.07	0	0.00
	Eland	4	0.03	3	0.04	1	0.09
Medium	Cow	1	0.01	1	0.01	0	0.00
	Hartebeest	17	0.14	4	0.06	0	0.00
	Ostrich	5	0.04	0	0.00	0	0.00
	Waterbuck	5	0.04	0	0.00	0	0.00
	Wildebeest	11	0.09	6	0.09	4	0.36
	Zebra	24	0.20	25	0.37	2	0.18
Small	Impala	4	0.03	1	0.01	0	0.00
	Pig	1	0.01	0	0.00	0	0.00
	Shoats	12	0.10	3	0.04	0	0.00
	Thompson's gazelle	3	0.02	3	0.04	0	0.00
	Warthog	6	0.05	2	0.03	0	0.00
	Bushbuck	1	0.01	0	0.00	0	0.00
	Reedbuck	0	0.00	2	0.03	0	0.00
	Grant's gazelle	6	0.05	2	0.03	0	0.00
	Suni	0	0.00	0	0.00	2	0.18
Very Small	Bird	1	0.01	0	0.00	0	0.00
	Rodent	0	0.00	0	0.00	1	0.09
	Snakelike	1	0.01	0	0.00	0	0.00

Table S2

Comparison on seasonal prey carcasses, prey hair items and their proportion based on the data collected during 2012 and 2014-2017 at NNP. The shaded boxes with grey represent, the species with the highest representation per seasons.

Category	Species	Total number prey carcasses for the study period, per season and their proportion						Total number of prey hair items for the study period, per season and their proportion					
		Carcasses	Proportion of whole period	Dry	Proportion of prey carcasses in dry season	Wet	Proportion of prey carcasses in wet season	No. of prey hair	Proportion of whole period	No. dry season scats	Proportion of prey hair in dry season	No. of prey hair wet	Proportion of prey hair in wet season
Large	Bu	31	0.15	25	0.17	6	0.11	48	0.13	36	0.14	12	0.11
	El	16	0.08	11	0.07	5	0.09	13	0.03	10	0.04	3	0.03
	Gi	16	0.08	11	0.07	5	0.09	9	0.02	5	0.02	4	0.04
Medium	Wb	1	0.00	0	0.00	1	0.02	10	0.03	5	0.02	5	0.05
	Wbz	16	0.08	13	0.09	3	0.06	23	0.06	18	0.07	5	0.05
	Ze	65	0.32	49	0.33	16	0.30	91	0.24	61	0.23	30	0.27
	Ha	19	0.09	13	0.09	6	0.11	37	0.10	27	0.10	10	0.09
	Os	4	0.02	2	0.01	2	0.04	12	0.03	7	0.03	5	0.05
Small	Gg	3	0.01	3	0.02		0.00	21	0.06	16	0.06	5	0.05
	Im	11	0.05	8	0.05	3	0.06	28	0.07	19	0.07	9	0.08
	Bb	0	0.00	0	0.00	0	0.00	4	0.01	2	0.01	2	0.02
	Bp	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	1	0.01
	Po	1	0.00	0	0.00	1	0.02	0	0.00	0	0.00		0.00
	Rb	2	0.01	2	0.01	0	0.00	1	0.00	0	0.00	1	0.01
	Tg	6	0.03	5	0.03	1	0.02	15	0.04	12	0.05	3	0.03
	Wa	11	0.05	6	0.04	5	0.09	25	0.07	15	0.06	10	0.09
Very Small	Ro	0	0.00	0	0.00	0	0.00	28	0.07	25	0.09	3	0.03
	Sn	0	0.00	0	0.00	0	0.00	1	0.00	1	0.00		0.00
	Hr	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	1	0.01
	Li	0	0.00	0	0.00	0	0.00	1	0.00	0	0.00	1	0.01
	Bi	0	0.00	0	0.00	0	0.00	7	0.02	6	0.02	1	0.01
		202	1.00	148	1.00	54	1.00	376	1.00	265	1.00	111	1.00

Buffalo (Bu), Eland (El), Giraffe (Gi), Waterbuck (Wb), Wildebeest (Wbz), Zebra (Ze), Hartebeest (Ha), Impala (Imp), Ostrich (Os), Grant gazelle (Gg) Bushbuck (Bb), Bushpig (Bp), Porcupine (Po), Thomsons gazelle (Tg), Warthog (Wa), Snake (Sn), Hare (Hr), Lizard (Li), Bird (Bi), Rodents (Ro) and Reedbuck (Rb)

5

Impact of Partial Park Fencing and Costs of Livestock Depredation by Lions (*Panthera leo melanochaita*) around Nairobi National Park, Kenya

Francis Lesilau[1,2], C. J. M. Musters[1], Gerard A. Persoon[3], Hans. H. de Iongh[1] and Geert. R. de Snoo[1]

Abstract

We examine the contribution of livestock to lion diet and to investigate the impact of the partial fencing of the park on livestock depredation, to assess the relationship between rainfall and livestock depredation and to determine the number of heads of livestock killed by lion and economic losses incurred by livestock farmers. A comparison was made between a scat sampling method and depredation records.

Our findings show that the presence of livestock remains differs per season and section of the park and that depredation on livestock is probably facilitated by the absence of fences in the south-west part of the park, resulting to a significant livestock depredation and high economic losses to livestock farmers.

We concluded that the partial fencing of parks is not a solution to human-lion conflicts and that the unfenced portion of the park is a corridor for high livestock depredation during the wet season and during the period when livestock is in close proximity to the park. Consequently, this section is

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linked to a higher annual percentage of livestock depredation and economic losses incurred by livestock farmers than the fenced section of the park.

We recommend that the park authority improves park fences, establishes a problem lion control station in the unfenced section of the park for rapid response to problem lions and implements compensation schemes.

Keywords
Panthera leo, Scats, Livestock, Conflict, Nairobi National Park, Community compensation scheme

5.1 Introduction

Across the world, where large carnivores are in contact with humans and livestock, both humans and carnivores have suffered negative consequences (Inskip & Zimmermann 2009; Riggio et al. 2013). Local farmers in the proximity of large carnivores often suffer substantial losses through livestock depredation and such incidents are frequently followed by persecution and retaliatory killings, either by authorities (animal control) to avoid future attacks or by locals (Bauer & De Iongh 2005; Van Bommel et al. 2007). Different authors have defined human-wildlife interaction based on underlying causes, the adverse effects on people and the threat levels to and safety of people (Conover 2002; Inskip & Zimmermann 2009; Young et al. 2010). Redpath et al. (2013) have suggested using the term "impact", when there is interaction between wildlife and people, i.e. instigated by the wildlife, and the term "conflict" when there is interaction with wildlife initiated by people and/or wildlife authorities. It should be noted, however, human–carnivore interactions are not limited to livestock depredation, but also include attacks on humans that result in injury or even death and man-eating report in Tanzania among others (Packer et al. 2005).

This is also true for the lion in Africa (*Panthera leo*): increased human populations and the associated expansion of human settlements have largely confined lions to protected areas (Woodroffe 2000; McKee et al. 2004; Stuart et al. 2010). Human development has resulted in a decrease in lion populations in Africa in recent decades (Bauer & Van der Merwe 2004; Kolowski & Holekamp 2006; Riggio et al. 2013). The interaction between humans and lions may have a negative effect on the livelihood of local communities and it may also result in increased mortality of lions due to retaliatory killing (Sogbohossou et al. 2011).

The level of livestock depredation differs per season and depends on the accessibility of domestic stock to lions (Woodroffe et al. 2005; Sogbohossou

et al. 2011; Valeix et al. 2012; Lesilau et al. 2018). Livestock depredation has a significant impact on the livestock owner's economy (Bauer et al. 2010). Livestock owners bear the costs of livestock depredation, but they may receive few benefits from wildlife tourism (Hemson 2003; Winterbach et al. 2013; Hazzah et al. 2014).

Livestock encroachment is now a problem in most protected areas in Africa (Vijayan et al. 2012). In these locations, lions incorporate both wild and domestic prey species in their diet (Table 5.1) (Hayward & Kerley 2005; Tuqa et al. 2015). Where livestock farmers are financially compensated for livestock losses and participate in effort to conserve wildlife, they tend to be more tolerant, which in many cases, it has prevented retaliatory killing of lions (Hazzah et al. 2014; Blackburn et al. 2016).

Table 5.1
Livestock depredation analysis from various parks in Africa

Country	Protected Area	Livestock Contribution to lion diet (%)	Source
Kenya	Tsavo N. Park	5.8	Patterson et al. 2004
Botswana	Makgadikgadi Pans	10-26	Hemson 2003.
Kenya	Samburu N. Reserve	6.2	Ogara et al. 2010
Benin	Pendjari Biosphere Reserve	18	Sogbohossou et al. 2011
Cameroon	Waza N. Park	21.6	Tumenta et al. 2013
Kenya	Amboseli N. Park	6-9	Tuqa 2015
Kenya	Mbirikani group Ranch	7	Maclennan et al. 2009

During 2012-2013, in a scheme to increase local pastoralists' tolerance to livestock depredation around Nairobi National Park (NNP) was implemented to compensate for their losses (http://www.thewildlifefoundationkenya.org). The process for claiming compensation for livestock killed is described in Lesilau et al. (2018). Only confirmed livestock depredation by Kenya Wildlife Service (KWS, 2017), The Wildlife Foundation (TWF) and Friends of Nairobi National Park (FoNNaP) were compensated. In our study, the term 'shoats' covers sheep and goats while livestock is a combination of cattle, shoats and donkeys (Ottichilo et al. 2000). In the area around NNP, the local conservation organization (The Wildlife Foundation) has been compensating one head of cattle at US $150, one head of donkey at US $50 and one head of shoat at US $25. The loss of dogs and pigs was not compensated (www.thewildlifefoundationkenya.org).

Although the compensation offered was only a third (average 64% lower) of the market value of a head of livestock, the purpose was to console owners who had lost livestock to depredation and to reduce the retaliatory killing of carnivores. In another area, the Amboseli ecosystem (Kenya) at the Mbirikani Group ranch, one lion was lost annually due to retaliatory killing, despite the community being compensated for depredated livestock (Maclennan et al. 2009) largely provoked by depredation on livestock, and there is debate as to the usefulness of financial instruments to mitigate this conflict. Intending to reduce local lion-killing, the Mbirikani Predator Compensation Fund compensates members of Mbirikani Group Ranch for livestock depredation at a flat rate (close to average market value. This suggests that, the solution to, addressing human-wildlife conflict may not be purely monetary. A combination of tackling the underlying social problems, compensating economic losses, and evaluating alternative conflict management approaches is required (Redpath et al. 2013)

NNP is partially fenced with a chain-link fence (Steinhart, 1994) and galvanized wire powered by electricity (6 kV). The park has an open access corridor to the Athi-Kaputei Plains (AKP) at the south-west border (Reid et al. 2008). During the 1970s, the park harbored approximately 30 lions in three prides (Rudnai 1974). There are no resident lions in AKP but it is a dispersal area for surplus lions from NNP and serves as a hunting reservoir (Rudani 1979).

To our knowledge, to date, no study has explored the use of livestock hairs from lion scats to demonstrate the spatial distribution of livestock–lion interactions. The results from our study could help farmers and wildlife authorities to better understand; the spatial distribution of human–lion interactions; the number of heads of livestock killed annually; the economic losses incurred by farmers; and depredation hotspot zones around the park. They can also assist in identifying factors influencing livestock depredation by lions. With these new insights, the management of NNP would take proactive measures to address the negative effects of human–lion interactions in the community land by monitoring and conduct education and awareness program.

Although other large carnivores in NNP, such as leopard *(Panthera pardus)*, cheetah (*Acinonyx jubatus)* and spotted hyena (*Crocuta crocuta*), interact with livestock in the community land as well, our study focuses on lions. During our study, from 2012 until 2018, the park lost 14 lions due to retaliatory killing in response to killing of livestock (Smith 2012; Kushner Jacob 2016; Ombati 2017). The management of NNP believes that problem lion management, in combination with improved knowledge about the lions in NNP, is urgently needed.

Based on our aims we designed the following research questions: (i) Which kind of livestock is killed by lions, based on the scats and official records? (ii) What is the influence of fences and rainfall on livestock raiding? (iii) What is the annual economic losses of livestock for farmers around the NNP? (iv) What is the difference between depredation records and scat sampling? (v) How can knowledge of management on NNP lions be improved?

5.2 Material and methods

5.2.1 Study area

Nairobi National Park (NNP) is located in the south-western part of Nairobi City in Kenya (Owino et al. 2011) (Fig. 5.1). 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 an altitude ranging between 1533 m to 1760 m above sea level (Rudnai 1974; Owino et al. 2011).

Nairobi National Park has three distinct vegetation zones, as described by Foster & Coe (1968) and Rudnai (1974). Dwarf woody plants are a result of controlled burning by park management (Foster & Coe 1968). Kenya has two periods of rainfall, longer wet one from March to May with a mean of 150 mm of rainfall, and a shorter one from October to December with a mean of 90 mm of rainfall. During 1980-1981, the annual mean temperature was 19.6 °C with daily minimum 12- 14°C and maximum range 23-28°C (Deshmukh 1985).

As a result of its location, adjacent to Nairobi city, the National Park was semi-fenced in 1955 (Steinhart 1994) with a chain-link fence and galvanized wire. The fence, which is powered by electricity (6 kV), was erected from the east via the northern boundary to the west in order to separate wildlife from the Nairobi metropolis (Foster & Coe 1968; Reid et al. 2008). The southern boundary is beyond the Mbagathi River and provides open access to the Athi-Kaputiei Plains (AKP) with an area of rangeland of 2200 km^2 (Reid et al. 2008).

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 www.naturekenya.org/content/important-bird-areas).

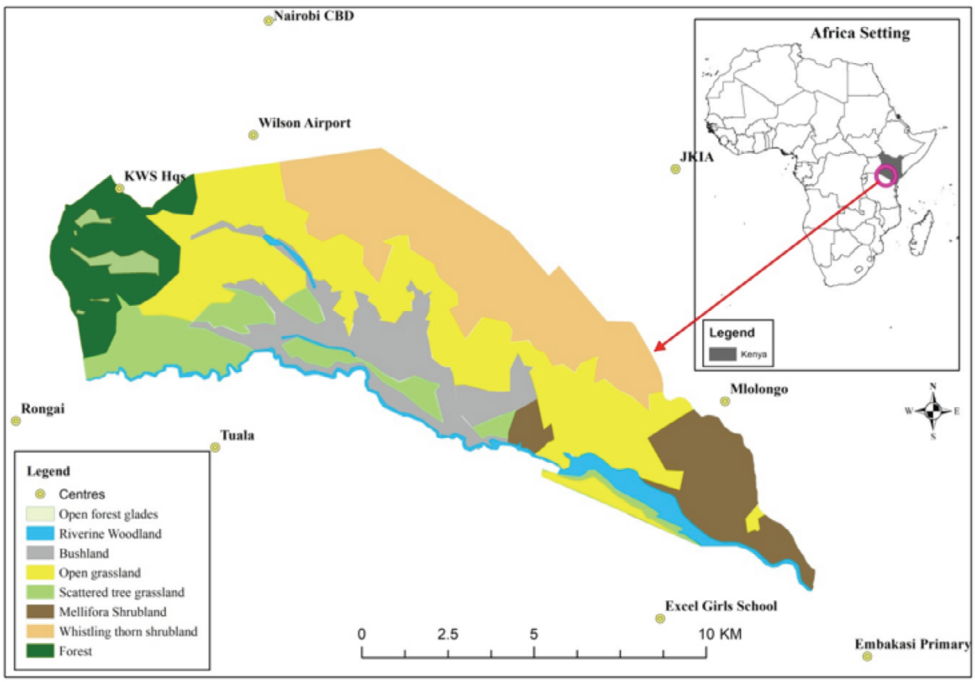

Figure 5.1
Map situating the different habitat types within Nairobi National Park. Vegetation data provided by the KWS GIS and Biodiversity Office (2011). (Designed in Arcmap 10.3.1 (ESRI Software, USA))

5.2.2 Data collection[3]

Lions live in family units and prides at the apex of their social organization (Stander 199; Bauer et al. 2003; Elliot 2017). Each adult member of a pride marks their territory using scats, urine and scents (Schaller 1972). As a result, scats from lions are commonly found throughout NNP. The scats were searched for at previously sighted lion resting sites, around prey carcasses

3 This section is partly from section 4.2.2.

killed by lions, along the roads while driving, and at opportunistic encounters with lions (Bisceglia et al. 2008; Tuqa 2015). Lion scats have a number of distinguishable features; they can be blackish, pungent smelling, segmented appearance, turning white when dry due to bones (Stuart & Stuart's 2000). The scats identified in the field were collected before sun drying and stored in a labelled zip-lock bags in a secure enclosure in order to prevent the samples from curious baboons, following Tuqa (2015). Microscopic hair identification was prepared according to the procedure used by Reynold & Aebischer (1991) and Ramakrishnan, Coss & Pelkey (1999). We made a Prey Reference Hair Collection (PRHC) from fresh prey carcasses in NNP by collecting hair specimens from stuffed animals in the Natural History Museum, Naturalis in Leiden, The Netherlands, and from livestock encountered around the NNP. Prey hair items were identified using hair structure (cuticle scales) and color and by comparing them with previously prepared PRHC morphology (Corbett 1989; Tuqa 2015).

The livestock depredation data of 2012-2016 were obtained from the Kenya Wildlife Service (KWS 2017), The Wildlife Foundation (TWF) and Friends of Nairobi National Park (FoNNaP) depredation database. When livestock owners reported a depredation incident it was recorded in the Service incident book, after which a team of Problem Animal Control experts was dispatched to the scene of depredation to verify the report (i.e. determination of predator by claw marks on the kill, paw prints on the ground, scats, predator hairs) and to take GPS coordinates, scene photographs and details of the property owner, time and location of the incident. Further details on data collection for this database are described in Lesilau et al. (2018).

ArcGIS 10.3.1 (ESRI Software, Redlands, CA, USA) was used to determine the length of fenced and unfenced sections of the park (Fig. 5.2). We used GPS locations of 12 collared lions for lion distribution, and movement, and location of pride (Lesilau inprep). We also conducted a bi-annual lion survey to visually identify individual lions in the months of February-April and July-September in 2012 and again during 2014-2018 inside the park (Lesilau inprep). We obtained rainfall data from Wilson Airport Meteorological station through Kenya Meteorological Department (KMD, 2012, 2014-2016). Taking into account the high altitude of NNP and high rainfall, we chose a mean of 30 mm of rainfall per month as our cut-off point between the wet and the dry seasons.

Several authors have applied different techniques to determine the costs of livestock depredation. Patterson et al. (2004), for example, used weights and retail economic value, while Butler (2000) used economic value survey techniques and Woodroffe & Frank (2005) used average market prices. The livestock market price data for our study area (Kitengela livestock market,

Kenya) was not available. Therefore, we used existing livestock prices from Loibor Siret market in Tanzania based on the average livestock market prices recorded by Lichtenfeld et al. (2015), since Kitengela livestock market in Kenya and Loibor Siret market in Tanzania are similar (Table 5.2). The inhabitants of our study area (around NNP) and those in Loibor Siret belong to the same ethnic community (Maasai) and due to the nomadic nature of this community, they have unrestricted access to both markets.

Table 5.2
Economic loss caused by lions for different livestock types. Cumulative livestock depredation data from 2012-2016

Livestock	No. of Livestock predated	Percentages (%) of livestock predated	Average prices per head of livestock (US$)	Total value of livestock loss	Percentages (%)
Cattle	296	19.4	450	133,200.00	66.9
Donkeys	36	2.4	200	7,200.00	3.6
Goats	241	15.8	50	12,050.00	6.1
Sheep	933	61.1	50	46,650.00	23.4
Dogs	20	1.3	0	0	0
Total	1526	100		199,100.00	100

The average livestock market value is from Lichtenfeld et al. (2015)

5.2.3 Data analysis and statistics

The scats were grouped into seasons of data collection (wet and dry season). The occurrence of hair items from each prey species in all scat samples was expressed as presence or absence of the prey species within the scats (Reynold & Aebischer 1991; Bisceglia et al. 2008; Tuqa 2015). Presence of prey remains (hair, bones, nails, teeth, feathers, and scales) were identified to genus or family level only (Pearson 1995; Bisceglia et al. 2008). Each identified prey hair was grouped as either of livestock or wildlife origin and classified based on the species weight according to Bauer et al.'s (2008) classification. We used the frequency of occurrence of the prey hair item in the lion scats as an indicator for the contribution to lion diet, rather than the number of prey hair items or body mass. We used a Chi-square test to determine differences in occurrence of prey species (livestock vs. wildlife) between sections and seasons.

We used two methods to identify recorded events of livestock attacks and to determine the risk of an attack. The first one were the actual recorded attacks, irrespective of the number of livestock killed, so that each attack

was counted as a single event (Kissui 2008). For the second one, we analyzed and plotted GPS coordinates, whenever there were available, at every report from villagers, confirmed by KWS rangers and research, of the presence of a lion, irrespective of an actual attack or no attack. We emphasized events, rather than attacks, since not all inhabitants around the park own livestock. We have witnessed two incidences of "mass – killings" and each is treated as a single event. "Mass-killing" refers to a situation where lion kill many livestock either in a boma or in the grazing field. Thus, an event is a single incident where a lion killed livestock or has been observed in the community land. The Fishers Exact Probability test was used to establish the difference between the number of prey hair items per species and the number of depredation records per species.

For spatial analysis, we divided the park arbitrarily into two parts: the North-West (NW) section and the South-West (SW) section (Fig. 5.2). We plotted the GPS locations of the twelve collared lions and the scats using ArcGIS 10.2.2 and projected these into the Universal Transverse Mercator (UTM) WGS-84, zone 37 ° S. The Spatial Analyst tool and Geospatial Modelling Environment software were used to determine lion movements and location of scats (www.spatialecology.com/gme/). We used the frequency of lion observations during surveys and sightings to determine individual pride members, age composition and group size in the park (Lesilau inprep). We did not determine livestock density since these animals are not allowed to graze in the park and sometimes they illegally grazed at night. The NW section borders an urban environment with high human settlement. This area does not provide a wildlife dispersal corridor, while the SW section borders a rural environment with a wildlife dispersal corridor. Both sections were semi-fenced but the surface of the unfenced portion of the NW section is much smaller than the SW section. We compared livestock prey hair items in the scats from the northern section with those from the southern section that is partially fenced and has some open access to the surrounding rangelands. We classified prey hair items in the scats as being from the "NW section" or the "SW section", based on the GPS location where the scats with livestock prey hair items were collected.

We determined a possible relationship between monthly precipitation, livestock attacks and the number of incidences of lions being outside the park (KWS 2017). We log-transformed the monthly rainfall data to normalize distribution (McKee et al. 2004; Kolowski & Holekamp 2006; Kuiper et al. 2015) and applied a linear regression model to determine the relationship between rainfall and log-number of livestock depredation events. We calculated the value of every head of livestock predated by lions and multiplied this by the number of livestock killed and then by the livestock market price to deter-

mine the economic losses incurred as stated in Lichtenfeld et al. (2015). We then divided the cumulative value of livestock predated by five years to get annual expenses incurred by the farmers around NNP. We excluded dogs, since they have no market price.

All statistical tests were carried out using the software R version 3.3.2 (R Foundation, Vienna, Austria). A significance level of ($p < 0.05$) was used for all tests. In all cases, normality was tested using the Shapiro-Wilk test.

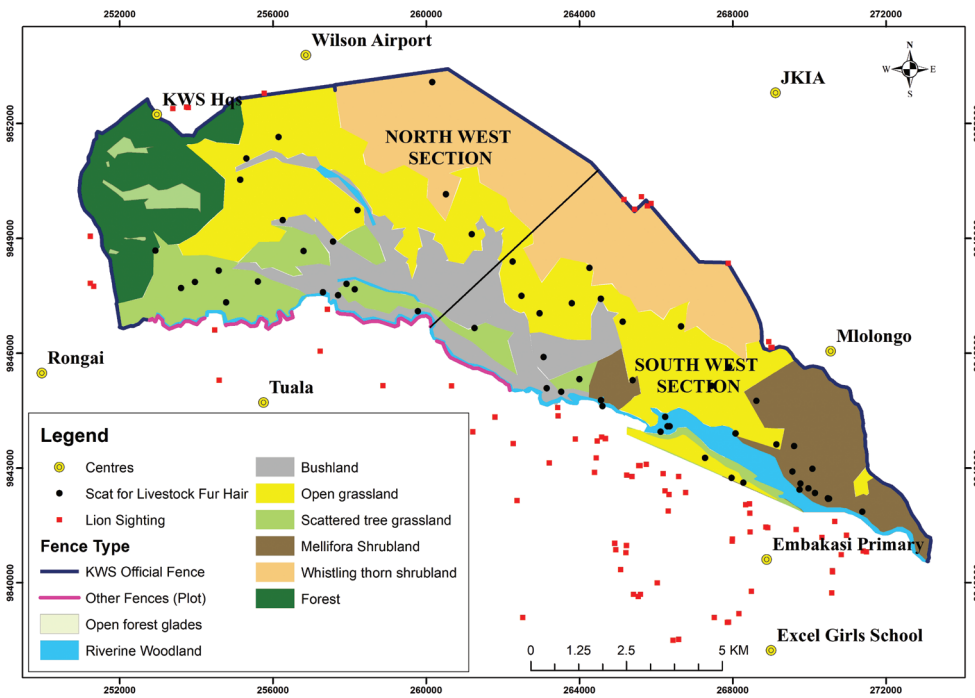

Figure 5.2

Locations of scats containing livestock prey hair items and the locations of livestock attacks or events of a lion being outside the NW and SW sections of NNP (based on data from 2012, 2014-2016). The black dots = GPS locations of scats with livestock prey hair items; red squares = GPS location of lion attack or report of a lion being outside the park.

5.3 Results

5.3.1 Livestock presence in lion scats

Of the 390 scats collected, 61 contained livestock items. The total number of prey hair items found in the scats was 442, of which 69 were livestock items. A total of 3 scats with inaccurate GPS locations were excluded from analysis.

Our analysis focused on prey hair items of different prey in each lion scats with verified GPS location, resulting in a total of 66 (15%) of all the scats items with livestock prey hairs from 58 scats used for analysis.

We identified six different livestock prey species based on hair identification in the lion scats (Fig. 5.3a). We found 40 (61%) livestock prey hair items in the dry season and 26 (39%) in the wet season, which represents a significant difference (Fig. 5.3e & f; $\chi^2 = 47.91$, df = 1, p-value =<0.001). The most predated livestock by lions around NNP are shoats (72%) followed by cattle (12%), donkey (9%), dogs (5%) and pig (2%) (Fig. 5.3a). Furthermore, 73% of livestock prey hair was found in the SW section of the park and 27% was found in the NW section of the park, which is also a significant difference (Fig. 5.2, 5.3c and d; $\chi^2 = 18.45$, df = 1, p-value < 0.001).

The relative contribution of 26 (39%) livestock hair prey items in the dry season and 40 (61%) livestock hair prey items in wet season in relation to the total number of 150 prey hair items in the dry season and 292 prey hair items in the wet season is 8.9% and 26.7% respectively (Fig. 5.3e and f). Relative to all prey hair items identified, 18 (4%) livestock prey hairs were found in the NW section and 48 (11%) livestock prey hair were found in the SW. This means that, there is relatively more livestock consumption by NNP lions in the wet season than in the dry season and more in the SW than in the NW section. Simultaneous to the larger percentage of livestock prey hair items in lion scat during wet season compared to the dry season, the wild prey carcasses biomass in the park during the dry season is larger (8,20 kg/km^2) and this drops to 3,837 kg/km^2 in the wet season (Lesilau in prep).

5.3.2 Livestock depredation

Official records reported a total of 1,088 lion depredation events during which 1,526 heads of livestock were killed, around NNP during 2012-2016 (Fig. 5.3b). The annual average of depredation is 305±128.1 (range = 227-560). We found five categories of livestock prey species in the records. The majority of the attacks were on sheep (61%), followed by cattle (20%), goats (16%), donkeys (2%) and dogs (1%) (Fig. 5.3b). In one case, the depredation records and the local news media (Kiplagat 2018) reported the depredation of 110 shoats by a pride of lions in a single night. The Fishers Exact Test shows a significant difference between livestock depredation in official records and livestock prey hair items in the scats in relative to number per species ($p < 0.001$). There are more species variety in the scats than in the depredation records.

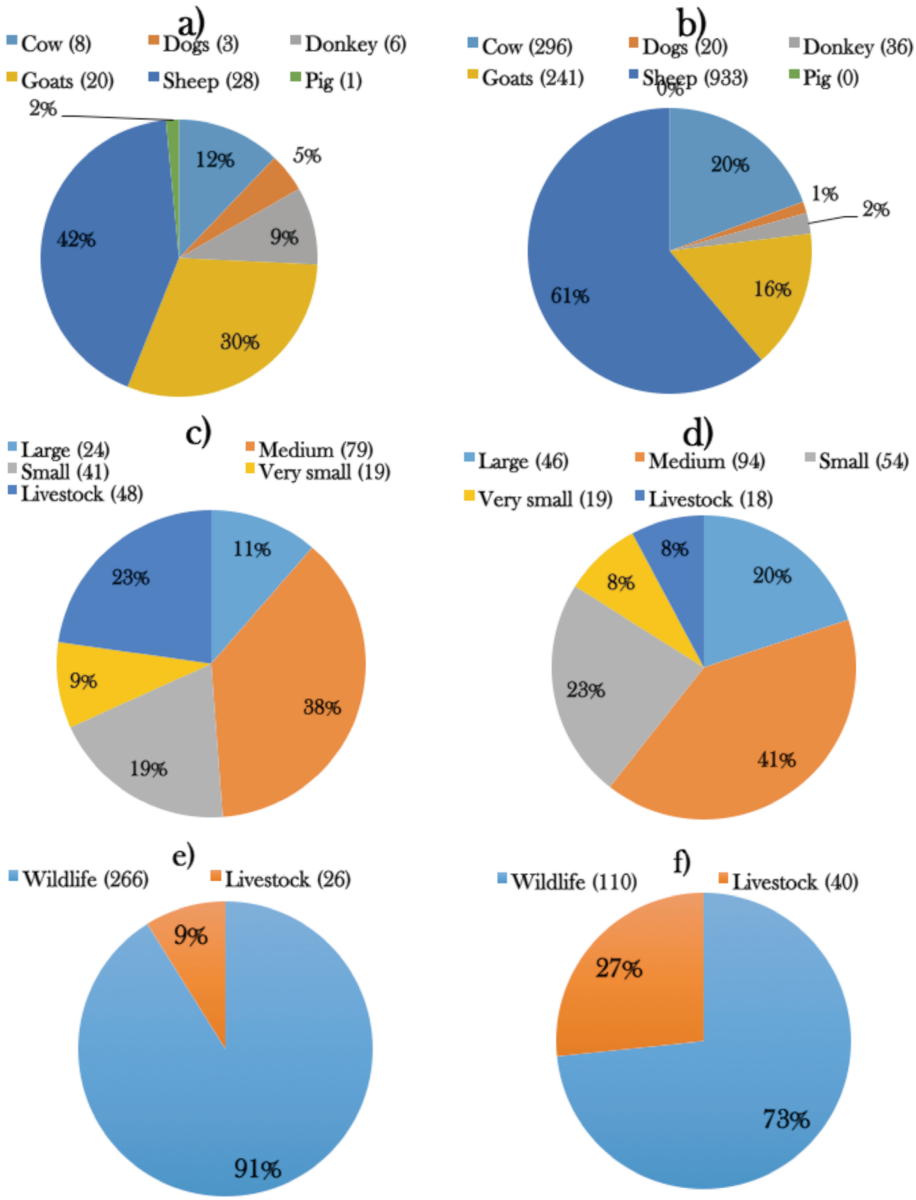

Figure 5.3

Comparison based on the percentage analysis of livestock prey hair items and different categories of prey species of different body mass between sections: (a) livestock prey hair items found in scats; (b) predated livestock records; (c) NW section; (d) SW section; e) relative contribution of wildlife and livestock prey hair items in dry season, and f) relative contribution of wildlife and livestock prey hair items in wet season. The figures in brackets = livestock depredated and prey hair items found in lion scats. Species category is based on Bauer et al. (2008) (Large is 200 kg, medium 50 – 200 kg, small <5 - 50kg and this study on very small < 5 kg).

5.3.3 Impact of fencing and rainfall

The park's perimeter (64.7 km in total) is fenced over a stretch of 36.3 km (56.1%). This fence encompasses 21.5 km (59.2%) of the NW section perimeter and 14.8 km (40.8%) of the SW perimeter (Table S1). However, the lions could still detour some of the fences through the valleys and thus have access to livestock. The log-transformed number of depredation events and the log-transformed rainfall per month in the park were significantly correlated (Fig. 5.4; r = 0.87, p-value = 0.001) to depredation. Livestock depredation is generally higher in the wet season, compared to the dry season (except in 2013; Table S2). During 2012-2016, there were 905 reported cases of lions being outside the park in the wet (83%) of all cases, which is significantly more than the 183 (17%) in the dry season depredation cases (Fig. 5.5) in which lions ventured beyond the park's perimeter with a mean of 217.6 (range = 149-299), which was significant (χ^2 = 1262.7, df = 1, p= 0.001). Based on Satellite Collars' GPS locations of lions, shows a spatial shift into the community area at the south-west of the park on 1005 (44%) occasions in the dry season and on 1263 (56%) occasions in the dry season (Fig. S4; χ^2 =29.35, df = 1, p = 0.001), with a mean of 567 (range 300-972).

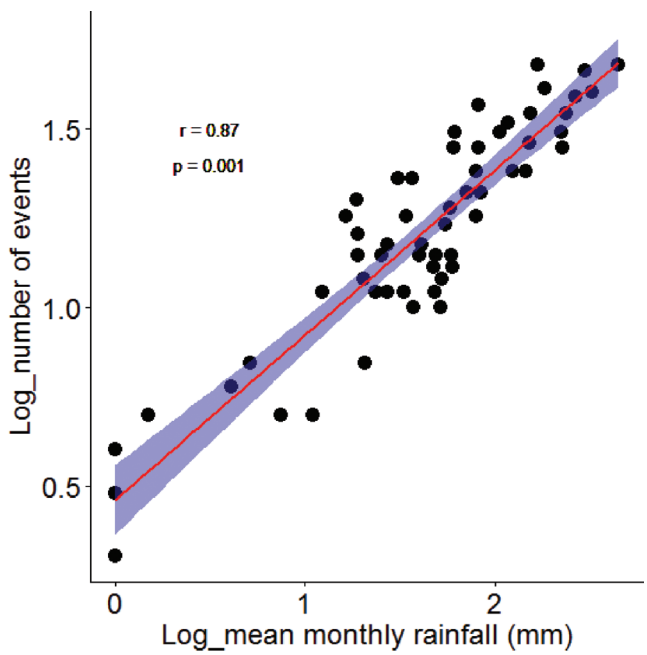

Figure 5.4

Relationship between the logged monthly mean rainfall and monthly logged number of events of lions outside NNP during 2012-2016. The shaded grey band = 95% confidence band; black solid line at the center of the grey = the regression line; black dots = events.

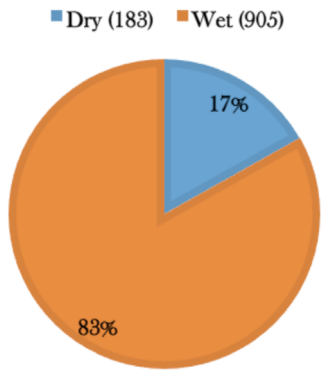

Figure 5.5
The number of confirmed reported cases of lions sighted in the community land, either by community members or the wildlife authority. In some cases, the lions attacked *bomas*; in others, they were chased into the park or sedated by veterinary personnel and released in the park.

5.3.4 Costs of lion attacks

We found that in terms of 'economic loss', among the categories of livestock, cattle (66.9%) were the most valuable (Table 5.2). The farmers around NNP incur livestock depredation losses, amounting to 39,820 USD annually due to lions alone. Shoats contributed only 29.5% to the total losses of depredation.

5.3.5 Comparison with depredation data from scats

The scat results showed that domestic pigs are eaten frequently but not often reported as being killed by lions. Dogs and donkeys are the least reported depredations. In terms of both scats and depredation records, shoats are common prey for all livestock species. We compared the prey hair items per month a particular species of predated livestock per month and found a significant ($p < 0.001$) relationship between predated shoats and the prey hair items of livestock in the Fishers Exact Test (Fig. S1). The data of other livestock species like pigs, donkeys and dogs, were too few to be analyzed.

5.4 Discussion

5.4.1 Depredation on livestock based on hair analysis

Our findings from the scat analysis show a significant contribution of livestock to the NNP lions' diet. We found a broad spectrum of livestock prey hair in the scats, including cattle, shoats, donkeys, pigs and dogs (Fig. 5.3a). Larger wild prey contributed more to the lions' diet in the NW section compared to the SW section of the park (Fig. 5.3c and d) due to fence restriction in the north and not body mass. This suggests that, the pride in the SW section of the park supplement their wild prey diet in this area with livestock (Fig. 5.3c, d and S4). The higher frequency of livestock items found in scat in areas adjacent to the unfenced portion of the park is most probably the result of this easy access for lions to the surrounding rangeland. Our results confirm that measuring the contribution of livestock hairs in lion scats is a good indicator of depredation (Fig. S1).

A number of studies have identified lions as major livestock predators, often killing more and larger livestock compared to other large carnivores, such as leopard and spotted hyena, which generally prefer goats and sheep (Hemson 2003; Bauer & De Iongh 2005). Although it was not recorded in the depredation data, the presence of pig hairs in the lion scats shows that lions going through the fence into sub-urban area also depredate pigs. Moreover, hairs from domestic dogs were found in the lion scat. In addition to observing domestic dogs in the park, on one occasion we encountered dogs scavenging a lion kill either in the park or in the community land on 14 July 2015 (Fig. S3), thus dogs make themselves vulnerable to lion depredation.

5.4.2 Livestock depredation

We found that the most predated livestock around NNP are shoats (Table 5.2). Lions mostly predate at night, sometimes even killing shoats inside bomas. A lion can kill as many as one hundred shoats in a single night, partly as a result of the panic caused by the attack, resulting in multiple fatalities among the stampeding herd (Lesilau et al. 2018).

Although Bauer et al. (2008) and Kissui (2008) stated that lions prefer medium-sized prey such as cattle and donkeys, the small-sized shoats were the most targeted in our study area. The fact that lions can jump over the livestock boma fence while carrying this relatively small prey, may have attributed to this. Furthermore, killing shoats requires a lower energy investment by the lions. The fact that some livestock, like sheep, lack a distress call to alert human guardians could be a further contributing factor to the lions' prefer-

ence for shoats in our study area, as it gives lions more time in the boma to continue killing (Lesilau et al. 2018).

Little energy is needed to find shoats when they are housed inside permanent bomas, therefore the profitability is high. In such a situation, the benefits of livestock raiding are high and as long as they outweigh the energy costs, livestock attacks are likely to continue. The costs of livestock raiding for lions rise from risks involved in encounters with humans, the energy spent on travel, and the energy spent on entering well-protected bomas and crossing the park's fence. The risk of being killed or wounded by humans is the highest cost and this is reflected in the lions' hunting behavior i.e., usually depredate at night when human activity and visibility is low (Valeix et al. 2012; Oriol-Cotterill et al. 2015). The localized high abundance of livestock and their highly predictable distribution in combination with their inability to escape bomas, make livestock a favorable type of prey for lions in our study area.

Although depredation data reveal significantly more attacks during the wet season compared to the dry season, our NNP scats analysis indicates that livestock is included in the diet of the lions irrespective of the availability of wild prey. We speculate that initial livestock depredation events will occur during periods of low prey availability. Once livestock raiding has proved to be an efficient and beneficial hunting strategy, it seems to be practiced by lions even when wild prey is more commonly available. The higher than expected livestock depredation revealed by the scat analysis in comparison to reports of depredation events during the dry season could also be a result of illegal livestock grazing inside the park during the dry season at night. In this case, it is likely that lion events are underreported, since pastoralists are aware of the illegal nature of their activity. By making the costs of livestock depredation higher than the benefits for the lions, it may be possible to force them to adapt their prey choice to focus on wild prey. This is possible with improved herding, predator-proof fencing of park sections and installing flashlights at bomas (Lesilau et al. 2018; Manoa & Mwaura, 2016; Woodroffe & Frank, 2005) largely through conflict with people. Here, we quantify the impact of lethal control, associated with livestock depredation, on a population of African lions (Panthera leo.

5.4.3 Impact of fencing and rainfall

We found that complete or partial fencing of the protected areas is not a guarantee solution to address human–lion conflict. Our analysis shows that the partial fencing of NNP allows lions to access livestock in the surrounding rangelands through the southern corridor or to make a detour at end of the

fence (Figs. 5.2 and S4). For complete fencing, Massey, King, & Foufopoulos, (2014) showed a temporal change in wildlife population numbers, biomass, and species richness decline after the complete fencing of the Aberdare N. Park.

Although our data show minimal human-lion interaction in the fenced section compared to that in the partially fenced section of NNP (Fig. S4), interaction is intensified and affects locals neighboring partially fenced section. Evidence suggests that the welfare of local communities and wildlife conservation status are threatened when fences are erected because access to common resources and other facilities such as water bodies and roads are also restricted (Redpath et al. 2013).

Although fencing has become a quick-fix therapy to human–wildlife conflict and to parks with high surrounding human population numbers, high livestock densities, bushmeat hunting and logging activities (Packer et al. 2013; Redpath et al. 2013); it cause a decline in wildlife species as it limits the migration of some species to breeding and grazing grounds (Harris et al. 2009; Poor et al. 2014) and burden human communities by denying access to resources and disrupt ecological processes (Massey et al. 2014; Pekor et al. 2019; Redpath et al. 2013). By contrast, the community around NNP did not suggest fencing as an option in resolving the human-lion conflict situation (Lesilau et al. 2018). This imply that the community around NNP are pro-conservation of wildlife.

As areas near fences are often avoided by wildlife, it causes species "bunch-up" against resources, which ultimately alters the ecological processes in the park (Loarie et al. 2009; Vanak et al. 2010). By contrast, in partially fenced areas, the species adopt a more directional movement towards open corridors, thus only intensifying interactions with surrounding communities. In NNP most lions reside in the park, also during the wet season, and only make small trips via the SW to feed on livestock (Figs. 5.5 & S4). Due to the availability of livestock in close proximity to the NNP borders (Lesilau et al. 2018), there is no need for the lions to continue following their migratory prey during the wet season, as livestock is a perfect substitute with minimal travelling costs (Valeix et al. 2012).

The significant correlation between the amount of rainfall and the number of incidences of lions being outside the park and subsequent levels of livestock depredation demonstrates that when an area receives more rainfall, the intensity of livestock depredation and the incidences of lions leaving the park may increase (Fig. 5.4). This is also confirmed in other parks, such as Tsavo NP (Patterson et al. 2004), Amboseli NP (Tuqa et al. 2014), Waza NP (Tumenta et al. 2013), and Nairobi National Park (Lesilau et al. 2018).

5.4.4 Costs of lion attacks

The number of predated heads of livestock and the market price may not be a good indicator of the magnitude of livestock depredation and conflicts in an area. A better indicator is the monetary value and the social impact on human livelihoods. A compensation scheme for livestock owners around NNP was implemented for a limited period (2008-2012) but as a result of rapid urbanization and the difficulties of sustaining such a program it was not considered a success (Matiko 2014). Although, in terms of numbers, most of the depredated species are shoats, in terms of economic losses, livestock farmers bear the socio-economic burden when cattle are killed (Table 2). The market price and the cultural value of cattle in the community tradition contribute to a vengeful attitude of herders towards lions after a kill (Hazzah et al. 2014). Groom & Harris (2006) suggest that, this is especially the case in the absence of wildlife benefits to livestock owners. To share and spare some land, land scarcity and commodity production, intellectual value must be accommodated in the debate (Fischer et al. 2014).

5.4.5 Added value of scats and predation records

Our comparison of different livestock prey hair items in each scat and the numbers of livestock actually predated revealed a relationship between the number of predated livestock and proportion of livestock prey hair items from the scats (Fig. S1). Consequently, the category of livestock prey hair items from the scat was higher than the category of depredation incidents reported. This is not unexpected because a pride of lions could share one livestock prey and pride members or hunt alone, and may subsequently defecate at different locations within their territory.

It also demonstrated that non-herded livestock, such as domestic dogs, pigs, and donkeys, are least reported after depredation by lions or other predators (Fig. 5.3). They are found in lion scat but are not included in the official depredation records. Traditionally, these non-herded livestock are more vulnerable to attacks as they are not held in bomas and are free to stray into the park during the day as well as at night (Fig. S3). The results of our research demonstrate that cultural and economic values to certain domestic species by local residents. We suggest that livestock species without guardians are easy prey for lions and hence function as a "predator magnet". Once lions discover the ease of depredating dogs, pigs and donkeys, they may be more inclined to attack nearby bomas.

5.5 Conclusion

Our study demonstrated partial fencing of parks intensifies human-wildlife interaction in one part of the park, causing higher losses for communities in that section compared than the other sections. We recommend that NNP management improve the park perimeter fence to decrease the losses of livestock depredation by lions and compensate livestock farmers for depredated animals.

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Supporting information

Table S1

Lengths of fenced and unfenced sections of Nairobi National Park in km (%)

No.	Type of Fence	NW section	SW section	Total length in NNP
1	KWS Official Fence	21.5 (0.33)	14.8 (0.23)	36.3 (0.56)
2	Other fences (Plot)	4.1 (0.06)	0.6 (0.01)	4.7 (0.07)
3	Completely unfenced	5.6 (0.09)	18.1 (0.28)	23.7 (0.37)
	Total	**31.2 (0.48)**	**33.5 (0.52)**	**64.7**

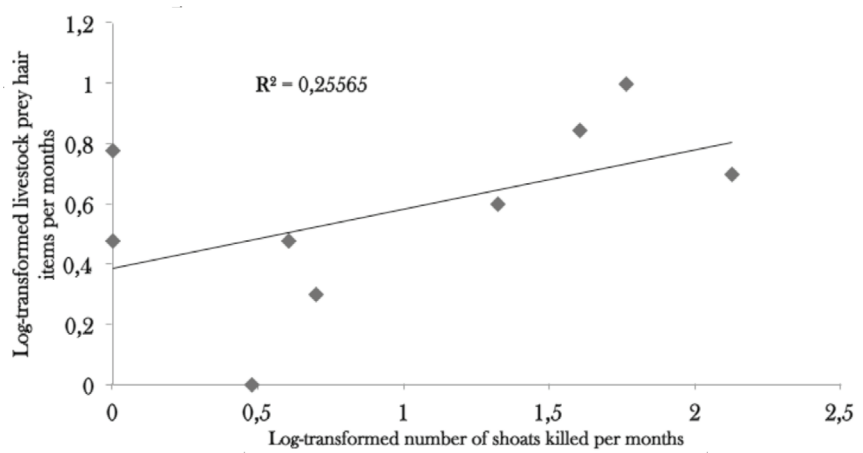

Figure 5.5

The number of confirmed reported cases of lions sighted in the community land, either by community members or the wildlife authority. In some cases, the lions attacked *bomas*; in others, they were chased into the park or sedated by veterinary personnel and released in the park.

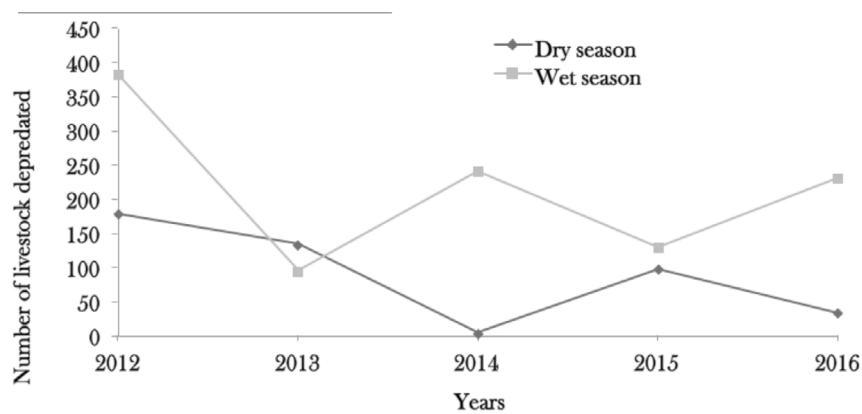

Figure S2

Seasons and level of depredation around NNP based on depredation data of 2012-2016

Figure S3
A domestic dog scavenging on a male impala carcass killed by a lion in Nairobi National Park (14 July 2015).

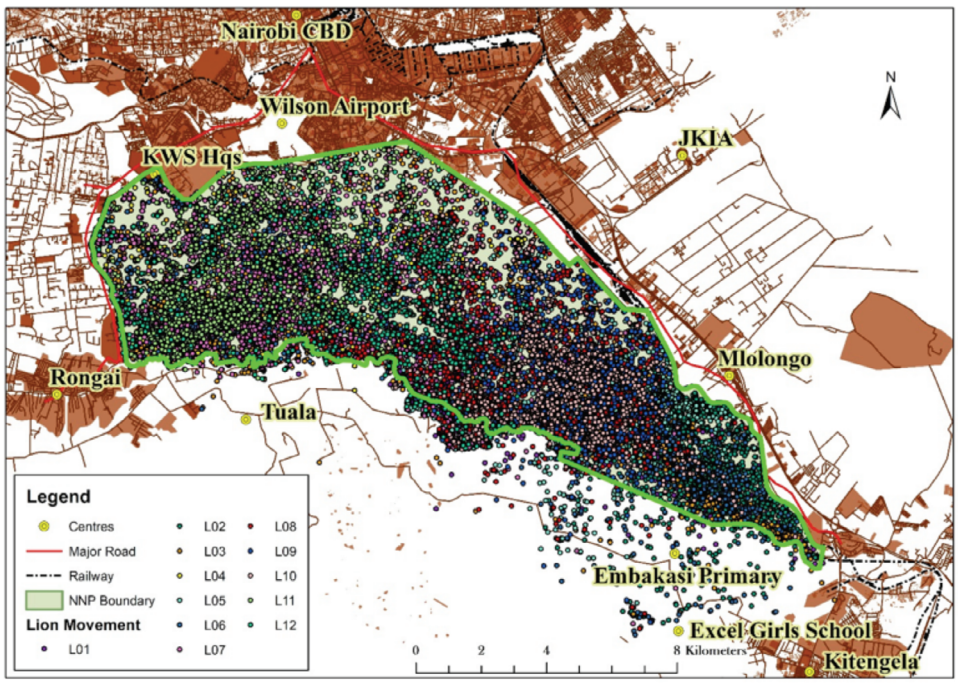

Figure S4
Movement of collared lions in NNP, 2014-2017 based on GPS locations from the satellites collars. L01-L12 signifies the code of the collared lions

6

Effectiveness of LED Flashlight Technique in Reducing Livestock Depredation by Lion (*Panthera leo melanochaita*) around Nairobi National Park, Kenya

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Conflict of Interests
The authors confirmed that they have no conflict of interests.

Abstract

The global lion (*Panthera leo*) population decline is partly a result of retaliatory killing in response to livestock depredation. Nairobi National Park (NNP) is a small protected area in Kenya surrounded by a human-dominated land-

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scape. Communities around the park use flashlights to deter lions from their livestock bomas. We investigated the response by lions to the installation of LED flashlight technology during 2007-2016. We interviewed 80 owners of livestock bomas in the surroundings of NNP with flashlights (n=43) and without flashlights (n=37) and verified reported attacks on bomas against depredation data over 10 years. The frequency of attacks on bomas equipped with flashlights was significantly lower compared to bomas without flashlights. We also found that after flashlights were installed on livestock bomas, lion attacks took place further away from the park edge, towards areas where the bomas had no flashlights. Furthermore, with increased numbers of flashlight installations at bomas in recent years, we noticed a shift from nocturnal to more diurnal depredation incidences. Our study shows that LED flashlight technology is effective in reducing nocturnal livestock depredation at bomas by lions. Long-term studies on the effects and expansion of this technique into other communities around NNP are recommended.

6.1 Introduction

The global decline in lion (*Panthera leo*) populations has largely been attributed to habitat fragmentation, diminished large prey populations in some areas and retaliatory killing over livestock losses (Bauer & Van der Merwe 2004; Tumenta et al. 2010; Riggio et al. 2013). Retaliatory killing of lions has serious repercussions in terms of both declining population densities and disturbed social structures (Bertola et al. 2011; Tumenta et al. 2013). Especially in areas where natural habitat is encroached on by expanding settlements and land-use practices, retaliatory killing ranks amongst the greatest threats for lions. Several studies in Kenya as well as in e.g. Namibia and Botswana have reported retaliatory killing of lions by local farmers after livestock attacks due to economic losses (Linnell et al. 2001; Patterson et al. 2004). In West and Central Africa, lion mortality due to retaliatory killing is a major concern as the few remaining lion populations have reached critically low densities (De Iongh et al. 2009; Bauer et al. 2010; Sogbohossou et al. 2011; Tumenta et al. 2013). For conservationists working in these areas, conflict retaliation has therefore, become a main priority (Patterson et al. 2004; Bauer et al. 2010; Tumenta et al. 2013; Henschel et al. 2014).

We explored a novel method for reducing human–lion conflict in Kenya. Kenya is a stronghold for lions, with an estimated population of 2,000 individuals in 2008 (Musyoki et al. 2012). With an estimated population of 35, including cubs, lions in Kenya's Nairobi National Park (NNP) are surviving despite their relative confinement inside the park and being surrounded by a

densely populated urban area. Although the park is largely fenced (Steinhart 1994), an unfenced connection between the southern border of the park and the Athi-Kapiti Plains (Ogutu et al. 2013) provides a wildlife migratory corridor and a possibility for lions to roam into surrounding communities. The intensified human demand for space around Nairobi City in recent decades has led to a spillover of human activities around NNP and the surrounding buffer zone, which has affected the availability of natural prey for lions (Rudnai 1974; Gichohi 2003; Owino et al. 2011). At the same time, livestock pressure has intensified, which has led to more livestock incursions into the park and significantly higher portions of livestock in the lions' diet (Patterson et al. 2004; Bauer et al. 2008, 2010; Tumenta et al. 2013). In 2011, six lions were killed in retaliation by the community south of NNP after livestock was lost to lions (KWS depredation records). Between 2012 and 2016, more frequent attacks by lions on livestock in bomas were reported and three more lions known to reside inside the park were killed in 2016 in the community land (KWS Predation Records).

Several factors are known to influence the frequency of lion attacks on bomas, including prey densities, season, distance to the park, time of day, livestock herd size, type of livestock and energy cost (Bauer & De Iongh 2005; Van Bommel et al. 2007; Woodroffe et al. 2007; Kissui 2008; Sogbohossou et al. 2011). Due to their large body size, lions need large prey to compensate for energy lost during hunting and handling (Carbone et al. 2007). To maximize the gain, they seek to take advantage of landscape and habitat elements with high prey catchability (Grant et al. 2005). In the Amboseli Ecosystem in Kenya, where severe climate conditions have changed and habitats are fragmented, there is evidence that large carnivores are increasingly ranging into communal land, resulting in more frequent reports of human–carnivore conflicts (Tuqa 2015). In other protected areas, e.g. Waza National Park, northern Cameroon (Van Bommel et al. 2007), Serengeti National Park, Tanzania (Holmerna et al. 2007), Pendjari Biosphere Reserve in north-west Benin (Sogbohossou et al. 2011), the distance of a community to the protected area boundary was found to be a determinant of depredation by lions. In Laikipia, Kenya, daytime depredation was lowest for small livestock herds with human herders in open fields, while depredation at night was lowest when livestock herds were held inside decently built enclosures (Ogada et al. 2003; Woodroffe et al. 2007). Studies conducted in India, Nepal and South Africa (Khorozyan et al. 2015) and in Laikipia, Northern Kenya (Ogada et al. 2003) further showed that depredation rates could depend on biomass of the domestic prey or on mitigation technique and type of predator and wild prey density, respectively.

Bomas around NNP generally consist of a nighttime livestock enclosure fenced with a ring of thorn bushes, wood, posts and chain-links and/or live vegetation. They are usually owned by one family or related family members with a single herd of cattle and a flock of shoats, herded together during the day. Some bomas keep shoats and cattle together in one large enclosure, separated by a small fence but sharing one flashlights unit.

In this study, we investigated if and how nocturnal attacks by lions on bomas around NNP could be controlled by using the so-called LED flashlight technique. This novel method was initially proposed by an 11-year old school pupil named Richard Turere as a measure to prevent nocturnal livestock depredation at his family's boma near NNP (see http://edition.cnn.com/2013/02/26/tech/richard-turere-lion-lights/). This technique has received international attention following its publication online as a TED talk (see www.youtube.com/watch?v=DdH6L5u2eMM).

In 2012-2013, the first 19 flashlights were installed in accordance with this technique at livestock bomas along the southern border of the park by Non-Governmental Organization (NGOs), including The Wildlife Foundation and FoNNaP. As soon as their effectiveness became apparent for some households, neighbouring livestock owners started to use the LED flashlight technique for their bomas. With approximately 30 additional bomas equipped with flashlights by NGOs, such as Friends of Nairobi National Park and KWS, the technique slowly became a standard practice for many pastoralists in the surroundings of NNP. As a result, a spatial gradient has become apparent; the closer a boma is located to the park's edge, the more likely it is to have flashlights installed. To date, the installation of flashlights in the study area has not been systematic and is not part of any official protection scheme.

Although similar techniques have been used in other areas to deter carnivores and birds, either from livestock, crops or other properties (see www.niteguard.com; http://predatorguard.com; www.foxlights.com), the application of lion deterrence lights is the first in Africa to our knowledge. The system uses a solar panel to power a series of LED flashlight bulbs connected by cable wire (Fig. 6.1). Depending on the size of the boma, a car battery supplies energy to between four and six bulbs mounted on several outward facing poles along the boma perimeter. The flashlights are set to continuously flicker at a rate that mimics a livestock guardian holding a flashlight and walking on foot around the boma. An investment of approximately $250 is required to equip one livestock boma with flashlights (Nickson Parmisa personal comm.).

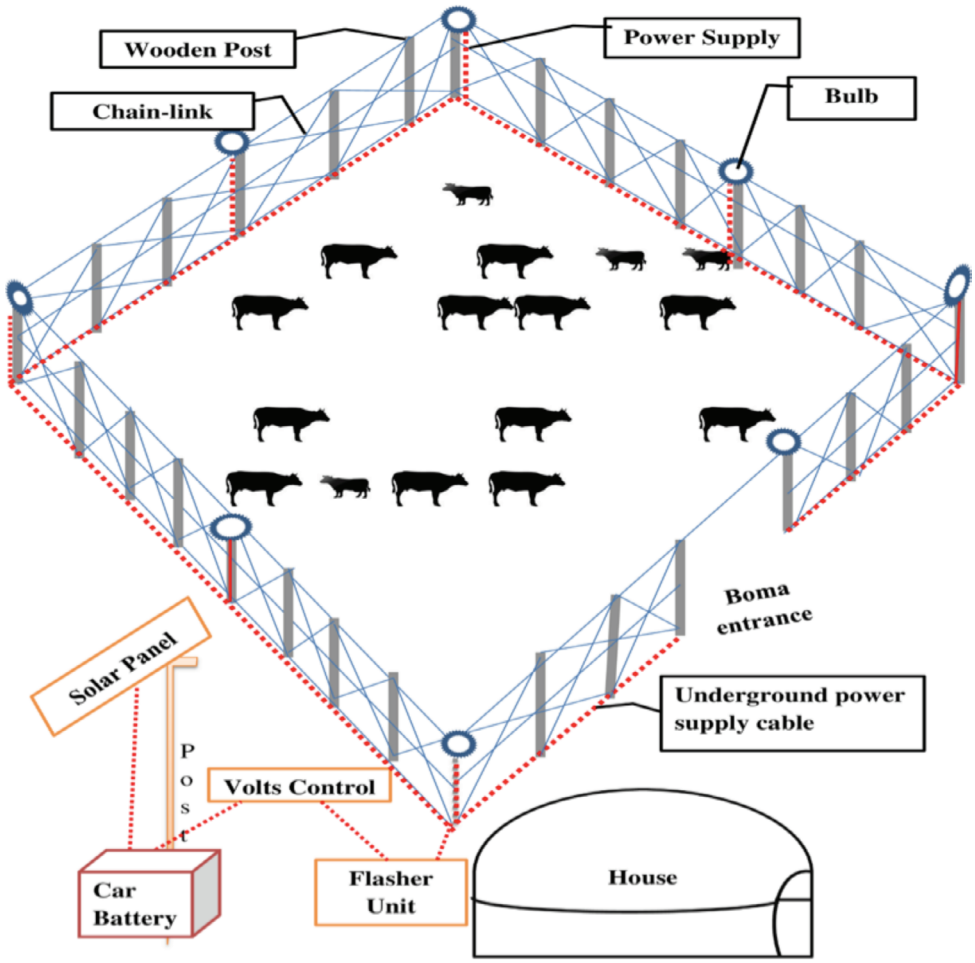

Figure 6.1
Diagram of a livestock boma with flashlights installed. The car battery is powered by a solar panel. The bulbs at the fence perimeter are connected by a wire from the flasher unit to flicker at night.

We hypothesize that the presence of flashlights would reduce the frequency of lion attacks on livestock bomas during the night and could lead to behavioural changes in livestock raiding lions. Such behavioural changes could include avoidance strategies, in which lions would move greater distances from the park boundary in search for bomas that are not equipped with flashlights, or a certain level of habituation to the flashlights. An attack is defined as a livestock depredation incident leading to either death or injury to one or more heads of livestock (cattle, donkeys, or shoats). A boma is a Kiswahili term for a livestock or household compound enclosing structure (Manoa &

Mwaura 2016) used for overnight livestock protection against predators constructed with tree branches, wood, poles and/or chain-link material. In this chapter, we use the term "shoats" to refer to a mixed flock of sheep and goats.

6.2 Materials and methods

6.2.1 Study area

Our study was conducted in the Kitengela triangle in Kenya, adjacent to the southern part of NNP. The study area is situated between latitudes S013.9054° to S01.15162° and longitudes E036.8251° to E036.9681° at an altitude ranging from 1495 m to 1684 m above sea level (see Fig. 6.2). The eastern part of the study area is defined by the Athi River export industries processing zone and the Kitengela River. The western part is characterized by two high density human settlement areas: Rongai and Twala.

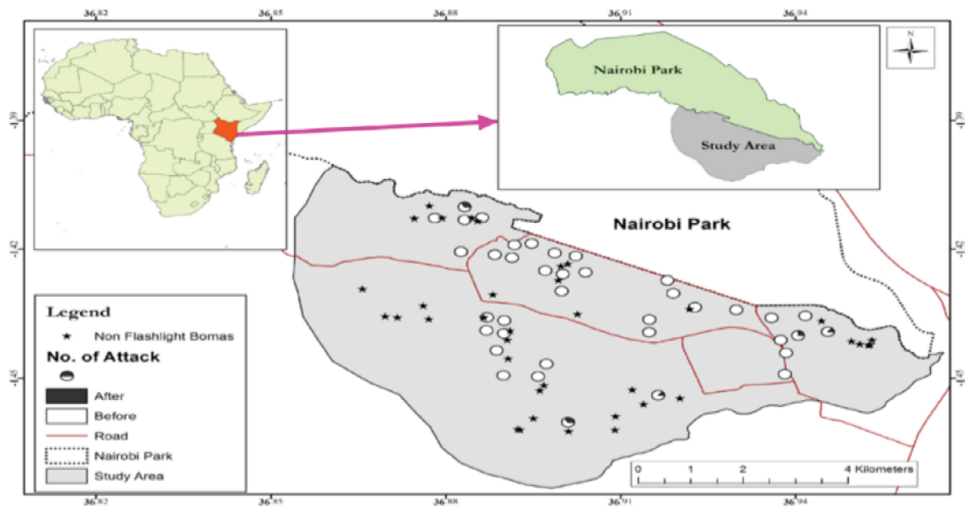

Figure 6.2
Map of the study area showing the proportion of boma attacks prior to and after installation of the flashlight technique. Empty circles (○) represent bomas where attacks had been reported before installation and none after installation. The partly filled circles (◔) represent bomas where attacks took place after flashlight installation. The stars (★) represent bomas of interview participants without flashlights.

The study area is rich in soil nutrients and receives a mean annual precipitation of 780mm (Rudnai 1974). The riverine vegetation is dominated by *Acacia xanthophloea* and *Acacia mellifera*, while plains are dominated by *Balanites* tree species and *Themeda* savanna grassland (Rudnai 1974; Gichohi 1996). The Mbagathi and Kiserian rivers are tributaries of the Athi River and both provide a permanent water source. The study area is a wildlife dispersal zone and is part of the Athi-Kaputiei plains. It covers a surface area of 2,200 km^2 (Matiko 2014). The Kitengela triangle, which consists of 390 km^2 of open grassland, is the first stop-over for annual migration of the blue wildebeest (*Connochaetus taurinus*), Burchell's zebra (*Equus burchelli*) and other ungulates such as common eland (*Tragelaphus oryx*), coke's hartebeest (*Alcephalus buselaphus*), Grant gazelle (*Gazella granti*) and giraffe (*Giraffa camelopardalis*) in the wet season (Gichohi 1996).

The local communities in the study area are mainly represented by traditional transhumance pastoralists, mostly of Maasai origin. Unlike the exclusive pastoralists in the Maasai Mara, described by Kolowski & Holekamp et al. (2006), the communities in our study area are sedentary; families or households stay in one location for an extended period of time. During the day, cattle and shoats from different households share communal grazing fields but do not share a boma at night. Each boma owner has a separate enclosure for shoats and cattle. Guided by a few male household members, they migrate to neighbouring counties in search of pastures and water. During this time, only a few shoats or cows are kept in bomas for milk.

6.2.2 Ethics statement

This research did not involve any invasive or intrusive methods. There was no financial inducement for information, personal data and no involvement of vulnerable groups (children, mentally disabled) from the society. Interviews were conducted in a transparent manner, voluntarily and with the participant's consent. The ethical conduct of the interviewers was verified and confirmed by the PhD supervisors during field visits. The research has been approved by the Graduate School of Leiden University, the Faculty of Science and the Directory Board of the Institute of Environmental Sciences in Leiden (Ref HDI/634/2014).

6.2.3 Data collection

Data were collected from 43 bomas where flashlights had been installed at the initiative of individual livestock owners or by NGOs such as Friends of NNP during 2012-2016 (Fig. 6.2). During the time of our research, the num-

ber of bomas with functional flashlights varied to some extent, as additional flashlights were installed while some flashlights broke down. We therefore only included bomas in our analyses that had functional flashlights during the entire period of our research.

Since no official records are kept on the number of bomas with flashlights installed in the study area, this information was collected during a survey by car and on foot, which we conducted prior to the start of the interviews. We used Arc GIS v.10.2.2 (ESRI, Redlands, USA) to plot the GPS locations of all bomas with or without flashlights in the study area. Households were then selected semi-randomly from this group, ensuring that the entire buffer zone was covered equally. The interviews covered 12% of livestock owners in the Kitengela corridor, who kept livestock in a boma within a distance of 5 km from the park boundary (Fig. 6.2). We interviewed only one person in case different families shared one boma protected by flashlights to avoid bias.

During April 2014, we interviewed a total of 80 boma owner's south of NNP, including the 43 bomas with flashlights. All households interviewed in 2014 were interviewed again in 2016, though sometimes with different respondents. The questions were specifically aimed at techniques and measures used to deter predators or otherwise protect livestock from large carnivore attacks. We used a known dataset of lion depredation cases that had been reported around NNP between 2007 and 2016 to KWS, FoNNaP and TWF, as part of the Wildlife Conservation and Management Act (2013), and the Wildlife Lease Conservation (2000-2012) and Consolation (2008-2012) program, respectively, to verify the results of our questionnaires.

Each interview consisted of a pre-structured questionnaire for which the questions had been translated from English to Maasai and Swahili language (S1 File) and which were posed by two native research assistants. The 2014 questionnaires were enhanced in 2016 with a few additional variables (S1 File). The number of livestock per boma, fence materials used (thorn branches, wood, chain-link, plant material and mix), fence height (0-1.5 m, above 1.5 m), transparency of the fence (visibility of livestock) (see Woodroffe et al. 2007) were only addressed in the questionnaires of 2016 (S1 File). We only interviewed owners of single livestock bomas (with and without flashlights). Bomas included in the depredation data that were not mentioned during the interviews were excluded from the analyses. The unit of analysis was "boma owner".

6.2.4 Data analysis and statistics

In order to isolate the effect of flashlights on the probability of a boma attack by a lion, we first identified confounding variables, possibly explaining the probability of a boma attack. These confounding variables were defined as:

(i) bomas with flashlights and without flashlights; (ii) distance of boma to the park boundary; (iii) timing of the lion attack (i.e. during the day or night); (iv) mean yearly rainfall; (v) fencing materials used; (vi) numbers of livestock in a boma; and (vii) year of flashlights installation. In all cases, our response variable was "the probability of attack per year", expressed as the number of bomas attacked in a year, divided by the number of all bomas present within a 5 km zone from the park boundary in that year. We made a distinction between boma with flashlights and boma without flashlights.

All data were tested for normal distribution with a Shapiro-Wilk test for normality. For bomas with flashlights installed, we calculated the mean number of attacks prior to and after flashlight installation by dividing the number of attacks by the number of years with and without flashlight. A Wilcox rank and paired test was used to test the significance. We tested the intensity of attacks between bomas with flashlights and those without flashlights using a Chi-square test.

To determine other factors that could affect the probability of an attack, we developed a case-specific general linear mixed model (GLMM). The dependent variable in this model was a binary variable indicating whether the boma was attacked at night during a certain year or not. Independent variables were defined as "presence of a flashlight", "year" (as a scale variable), "mean rainfall" and "distance to the park boundary". "Year" (as a factor) and "Boma code" were used as random factors. The model-family was binomial using a logit link. For testing the significance of the different stable factors, we applied a likelihood-ratio test (LRT). For fitting the model, we used glmer from the lme4-package (Bates and Maechler, 2010) in R (R Development Core Team 2017).

The distance of a boma to the park boundary was determined from coordinates obtained with a global positioning system (Garmin eTrex 20) and Arc View v.10.2.2 (ESRI, Redlands, USA). The bomas were classified into four distance categories: (i) near (at 0-1 km); (ii) intermediate (at 1-2 km); (iii) far (at 2-3 km); and (iv) the furthest (at more than 3-4 km from the park). For each of these categories, we calculated the average probability of attack over 10 years. The differences were tested with a Mann-Whitney U test (p-value 0.005) (Bates and Maechler, 2010) in R (R Development Core Team 2017).

We compared the average probability of attack during the night versus at daytime using a Mann-Whitney U test. The change in probability of diurnal versus nocturnal boma attacks over the years was studied by calculating the probability of diurnal and nocturnal attacks per year, thereby assuming that every boma has an equal chance of being attacked. Thus, we calculated the number of attacks per night by dividing the total number of yearly attacks by the number of days (365) in that year and multiplying it by the number of

bomas (80). The resulting probabilities were tested using a Chi-square test. We also tested diurnal livestock attacks prior to installation flashlights and diurnal attacks after installation using a Chi-square test.

Changes in probability of a boma attack over time in relation to distance to the park were calculated based on yearly mean distance to the park of the attacks. The trend in these distances was tested through a linear regression model using R statistics. Each boma was given a reference number (boma code), which ensured individual bomas could be recognized while protecting the boma owners' identities.

In the absence of accurate local density estimates for prey, we used annual rainfall as a proxy for the prey density, based on the assumption that in wet years, large prey species leave the park and move into community land, driven by access to more equally distributed water and grazing resources (Bauer & De Iongh 2005). The relationship between the amount of rainfall (mm) and the frequency of attacks was analyse using a Pearson correlation (p-value 0.05). We averaged the number of nocturnal attacks by fencing category and applied a Chi-square test.

For the analysis on livestock herd size (shoats and cattle), we used reported livestock herd sizes during the 2016 interviews to average herd size and classified these as "small" when below mean herd size and "large" when above mean herd size. We used a Kruskal test to test the significance.

6.3 Results

A total of 814 livestock were reported killed by lions between 2007 and 2016. Interview respondents reported a total of 413 depredation cases related to lions during this period, and these were confirmed against KWS depredation records. In the 413 reported cases, 308 (75%) cases occurred during the night and 105 (25%) during the day. Of the 43 bomas where flashlights had been installed during the course of this study, 184 (96%) attacks took place prior to flashlight installation and 7 (4%) after flashlight installation (Wilcox paired test W = 780, p-value <0.0001, Figs. 3 and S1). The probability of an attack on bomas without flashlights is significantly higher compared to bomas with flashlights (Fig. 6.4; $\chi^2 = 10.37$, df = 4, p-value = 0.035). Twenty-three percent (23 %) of the respondents who reported depredation after flashlight installation had not suffered any previous livestock losses at the bomas and 68% had no flashlights installed. Of the 105 diurnal depredation cases, 21 (20%) occurred prior to flashlight installation (2007-2011) and 84 (80%) after flashlight installation (2012-2016, (t = 2.47, df = 61.11, p-value = 0.016). Figure 6.5 shows the shift in time (nocturnal to diurnal) in livestock depredation prior

to and after cumulative installation of the flashlights. There appeared to be a pronounced peak in depredation during 2012 (55 cases).

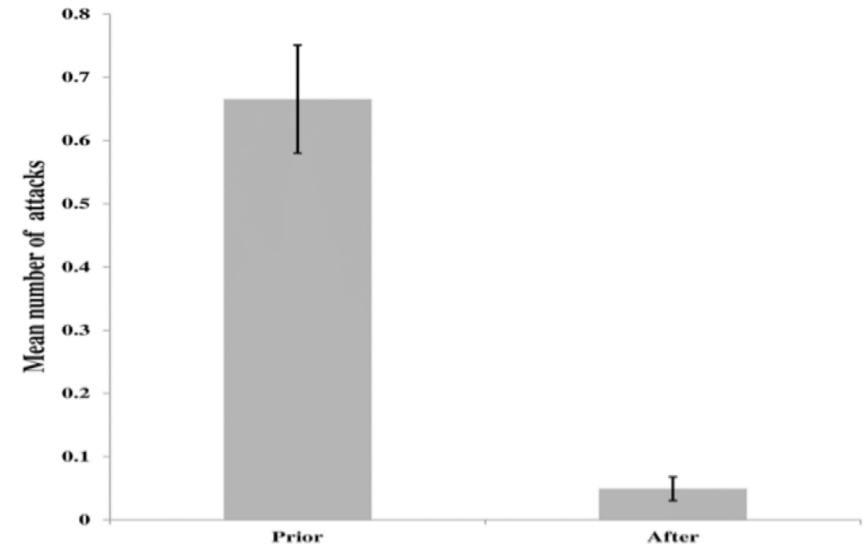

Figure 6.3
Mean number of attacks (±sd) by lions prior to and after installation of the LED flashlight technique based on 43 bomas with flashlights.

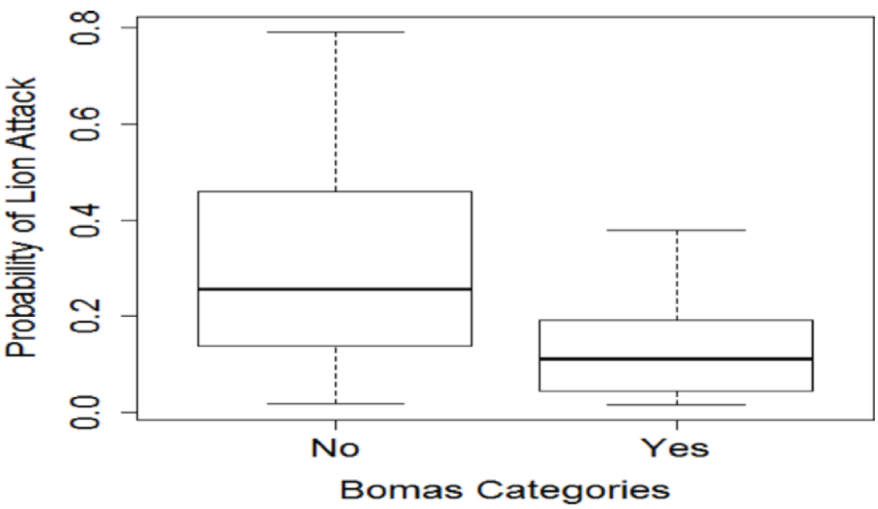

Figure 6.4
Difference in the probability of lion attacks between the two categories of livestock bomas, (Yes = with Flashlight, No. = without flashlight) between 2007 and 2016 based on GLMER model.

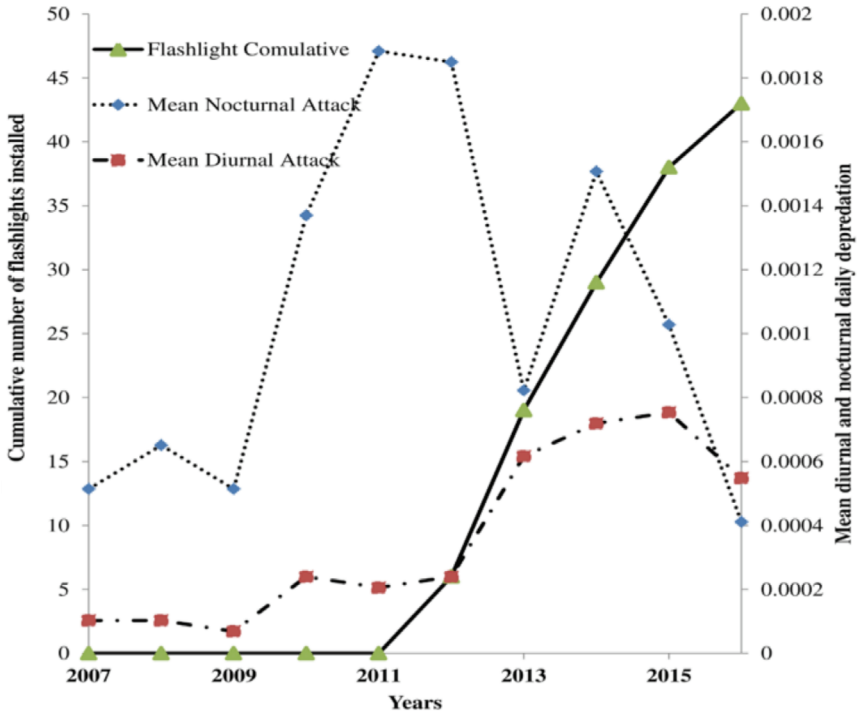

Figure 6.5
Cumulative flashlights installed and Mean nocturnal and diurnal livestock depredation during 2007-2016.

Table 6.1
GLMER showing the significance variables in relation to depredation around the park using likelihood ratio test.

Variables	Df	AIC	LRT	Pr (Chi)	Significance
Flashlight	1	743.92	14.303	0.0001556	***
Years	1	742.83	13.220	0.0002770	***
Mean Rainfall	1	741.64	12.029	0.0005237	***
Park Distance	1	743.95	14.333	0.0001532	***

Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05'.', 0.1 ' ', 1[***] represents the reference variable.
Model 1: Attnight ~ Flashlight + Year + Mean Rainfall + Park Distance+ (1 | Code) + (1 | Years)

The mean rainfall, distance of the boma from the park, years and flashlights were all significant (see Figs. 6.4, 6.5, 6.7, and S1) on each of the variables of attack (Table 6.1). Whereas the period of working flashlights in a boma has high probability of reducing nocturnal livestock attacks, the findings show

that the shorter the distance of the boma from the park border, the higher the intensity of attack. The yearly increase in the attacks is due to lions changing their behaviour and searching for bomas without flashlights. The number of boma attacks is related to the presence of flashlights ($\chi^2 = 12.98$, df = 1, p-value = 0.001).

Analyses showed a significant positive relationship between rainfall and the number of attacks on livestock per year (Pearson's correlation test; t = 157.11, df = 725, p-value < 0.001; Fig. S1), with a significantly lower probability of attacks in 2009, which had extremely low rainfall (59.2 mm) compared to 2012, when rainfall was relatively high (102.6 mm).

Bomas at a distance of 3 km or more from the southern park border were attacked significantly less often compared to bomas located closer to the park (Fig. 6.6). The percentage of attacked bomas ranged from 54% (at 0-1 km); 31% (at 1-2 km); 11% (at 2-3 km) to 4% (at >3 km from the park boundary). We also found a significant yearly increase in mean distance of attacks from the park boundary following the application of flashlights in 2012 (Mann-Whitney U test t = 11.291, df = 79.002, p-value = 0.001; Fig. 6.7). The yearly regression with intercept of 2.001+03 and slope of 0.008 shows that every three years, there is 300metres increase in distance of attack.

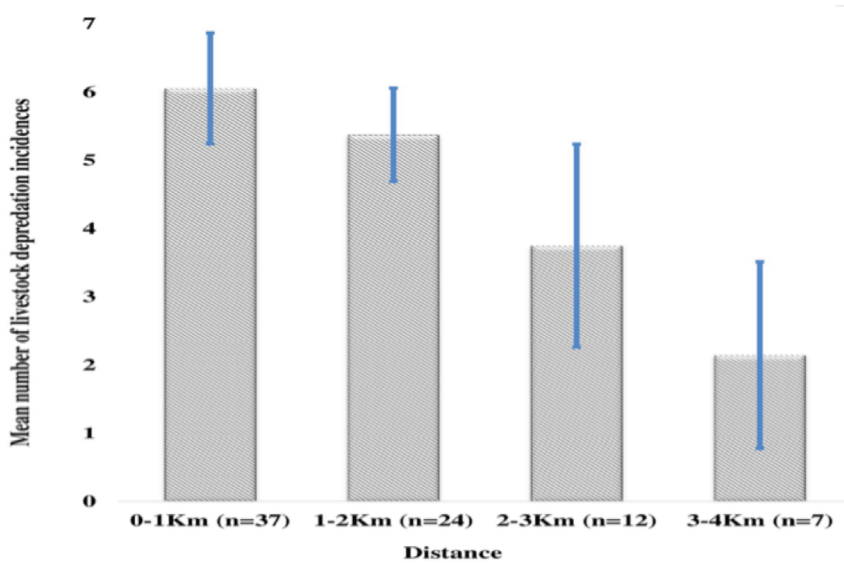

Figure 6.6
Mean number of nocturnal and diurnal boma attacks around NNP between 2007 and 2016 at different distances from the park boundary.

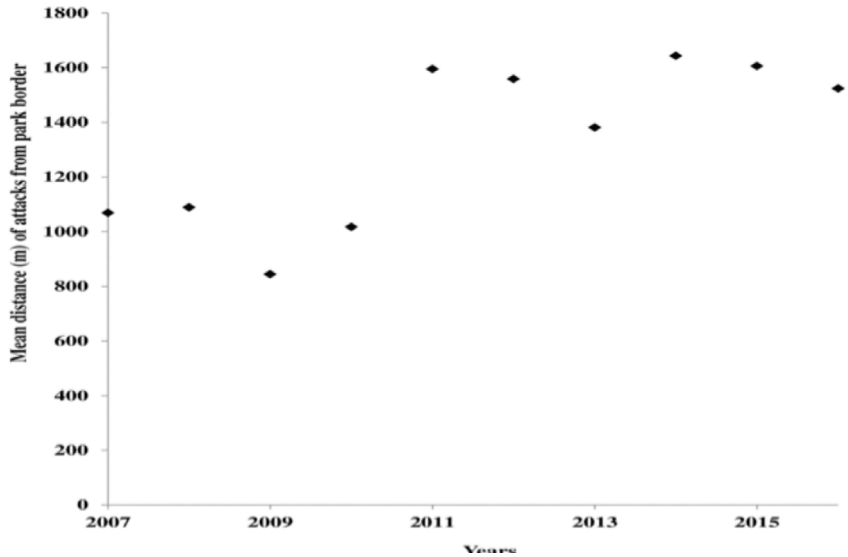

Figure 6.7
Annual mean distance of boma attack from the park boundary since the introduction of the flashlight technique south of NNP.

The fence height in relation to percentages of attack is significant (high = 12%, medium 23%, short = 71% and $\chi^2 = 8.09$, df = 2, p-value = 0.017). This shows that bomas without flashlights and those with short-medium fences are more likely to be attacked by lions than those with flashlights and higher fences. The data normality distribution test was W = 0.87567, p-value < 0.00001.

Bomas constructed with high wooden posts supported by chain-link ($\chi^2 = 8.11$, df = 1, p-value < 0.005) and barbed wire were attacked less frequently than the other categories ($p < 0.05$, Fig. 6.8). None of the other deterrence variables (scarecrow, dogs, spotlight, radio, fire and noise) were significant in depredation prevention (see Table S1). Herd size did not affect nocturnal depredation of shoats (Kruskal test, $\chi^2 = 21.76$, p-value = 0.7) and cattle ($\chi^2 = 25$, p-value = 0.6) (see Table S1).

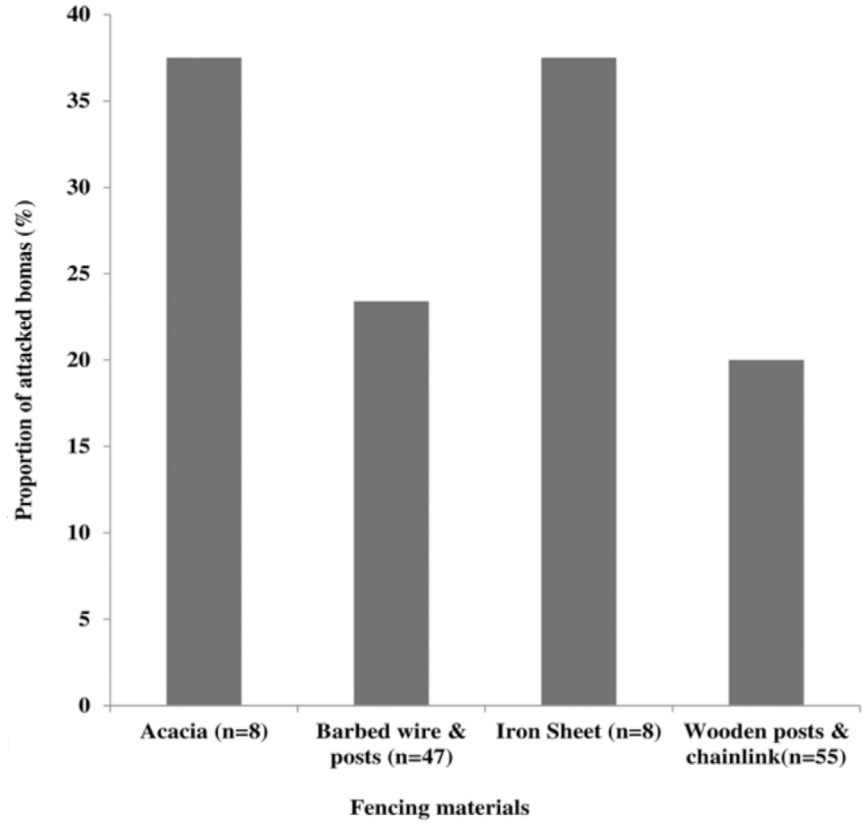

Figure 6.8
Proportion of reported attacks on bomas at night for each type of livestock fencing materials.

When respondents were asked an open question about what they believed should be done to resolve human–lion conflicts around NNP, (Appendix I, question 13), most respondents (92%) had one or more suggestions (Table S3): "flashlight installation" and "some form of compensation" were by far the most mentioned suggestions, followed by measures that would prevent lions from roaming outside the park boundaries. Although "fencing the park" was sometimes mentioned, 62% of the respondents did not believe that complete fencing of the park would resolve the human–lion conflict. Further suggestions included measures that could rapidly detect and relocate freely roaming lions back into the park, which, according to some, will become an even more important strategy when the announced plans for the construction of a railway through NNP (in the northern area) eventually take effect.

6.4 Discussion

The highly significant decline (96%, Figs. 6.3 and 6.4) in lion attacks on bomas with flashlights installed, confirmed by positive experiences from the majority of interviewed owners of such bomas (92%), support the hypothesis that flashlights reduce the probability of nocturnal lion attacks at livestock bomas. Secondly, we found a change in lion behaviour, which shifted their attacks to attacking non-flashlight bomas or a shift from nocturnal attacks to diurnal attacks (Fig. 6.5)

At the same time, lions covered greater distances from the park boundary, towards areas where bomas had no flashlights installed (Fig. 6.7). This, in combination with the shift in timing from nocturnal to diurnal attacks (Fig. 6.5), suggests that lions in the study area actively search for livestock bomas with no flashlights installed, thereby avoiding those with flashlights. Our findings have great implications for livestock owners in the region, especially for those who have no flashlights installed at their bomas. The losses suffered as a result of the shift from nocturnal to diurnal attacks, however, are generally small and could be addressed by relatively simple changes in herding strategies during the day by avoiding livestock grazing close promixity to protected area and use of mature human guardian (Woodroffe et al. 2007; Kuiper et al. 2015; Miller et al. 2016).

Similar to results from other studies (Van Bommel et al. 2007; Tumenta et al. 2013; Abade et al. 2014), our findings show that increased rainfall is related to higher livestock depredation frequencies. This is a common phenomenon that is associated with a greater dispersal by both lions and their natural wild prey species during the wet season due to an increased and more widespread availability of both water and pasture after the rains (Bauer & De Iongh 2005). Rainfall in the study area was highest during the 2011-2012 season, which was also the peak for livestock depredation.

Despite the great variation in reports on the importance of boma characteristics and construction materials (Ogada et al. 2003; Woodroffe et al. 2007; Abade et al. 2014) in the prevention of attacks on livestock by large carnivores, it is generally agreed that improved enclosures as well as both nighttime and daytime vigilance reduces the rate of livestock depredation (Patterson et al. 2004; Woodroffe et al. 2007; Bauer et al. 2010; Sogbohossou et al. 2011). The improved fencing techniques used in studies such as "Living walls bomas" (Abade et al. 2014; Lichtenfeld et al. 2015) and "predator-proof bomas" (Manoa & Mwaura 2016) demonstrated success rates similar to those found after flashlight installation: a 90% to 99.9% decrease in nocturnal lion attacks. However, the outcome of the use of dogs by the community around NNP contradicts the findings of Van Eeden et al. (2018), who found that use

of animal guidance to prevent livestock attack. Our study further demonstrated that boma attacks by lions could, to a certain extent, be prevented by using wooden fencing materials, reinforced with chain-link perimeter fencing material, provided that these were constructed at a height of at least 2.5 meters and when livestock visibility from outside was poor. Respondents with few shoats (<20) used iron sheets, or concrete walls and roof covered bomas to minimize the chances of lions climbing over.

In individual cases, replacing traditional thorn-bush fencing with high concrete or chain-link materials has been reported to actually increase the losses of livestock. During the course of our study, a lion was observed by the principal author climbing over a chain-link fence of 2.5 meters surrounding a boma where no flashlights had been installed to predate on the livestock that was kept inside. Several additional reports of attacks on bomas that were covered by roofs of chain-link material described cases in which a lion would climb the chain-link roof and then fall through the chain-link barrier into the boma, where the livestock was trapped. While livestock would still be able to escape from a boma that is built with thorn fencing, thereby minimizing catchability and number of casualties, the chain-link fence and roof offer no escape route. A lion trying to escape a death trap like this is likely to kill and injure even more livestock in the boma.

Whereas in our study livestock herd size did not influence nocturnal boma attacks by lions, the findings of Van Bommel et al. (2007) suggest that the number of livestock present in a village is directly related to the number of lion attacks. Woodroffe et al. (2007) also found that a large livestock herd is associated with a higher risk of diurnal depredation. Although the frequency of attacks on livestock is generally higher closer to the park boundary (as was found for e.g. Waza National Park in Cameroon (Van Bommel et al. 2007), Serengeti National Park (Holmerna, Tomas, Julius Nyahongoa, Røskafta 2007) in Tanzania and Kweneng in Botswana (Schiess-Meier et al. 2007), lions would cover up to 20 km per day in search of prey (Tuqa 2015), thereby entering high-risk, human-dominated areas to kill livestock (Ogada et al. 2003; Oriol-Cotterill et al. 2015).

The ability of NNP lions to adapt their behavior to the installation of flashlight bomas, by targeting non-flashlight bomas futher away from the park boundary and shifting from nocturnal to diurnal attacks, could eventually lead to a decrease in the damage suffered by livestock owners. This positive effect is expected to also promote a further increase in the number of flashlight bomas.

6.5 Conclusion and recommendations

Despite the effectiveness of our proposed LED flashlight technique in deterring lions from livestock bomas around NNP, its successful implemenation in a different situation is not guaranteed. Conflict mitigation techniques that are effective in one place could fail in another and, even at a local scale, measures could become less effective over time, due to changes in e.g. environmental or social factors (Miller et al. 2016). Eklund et al. (2017) suggested that a single intervention is usually not a long-term solution to human–wildlife conflicts. Livestock owners should be aware of this and ensure they have multiple anti-predation techniques in place at any given time (Miller et al. 2016; Treves et al. 2016). Working together with local authorities in managing such techniques, but also the implementation of rapid response mechanisms and simply ensuring that faulty flashlights are serviced, are all additional aspects that can be crucial for any mitigation measure to be effective (Miller et al. 2016). Whereas evidence-based lethal control measures to ban lions from villages have historically been recommended (Treves et al. 2016; Van Eeden et al. 2018), for the pastoralist communities around NNP this certainly has no preference. The majority of livestock owners we interviewed suggested non-lethal techniques could and should be used to effectively reduce livestock depredation rates in the area.

The recent increase in the number of lion attacks at unprotected bomas has a great impact on the livelihoods of local communities. In fact, six recent reports of lions sighted in the suburbs of Nairobi City prove that today's challenges associated with human encroachment around NNP are greater than ever. In the current situation, the pressure on bomas without flashlights, further away from the park boundary or in new areas that have experienced very few or no lion attacks to date, is likely to further intensify, unless the proposed LED flashlight technique is implemented and reinforced throughout the lions' dispersal range by national and county governments. Future studies on the effectiveness of our technique should take this behavioral adaptation of lions into account and ideally should include a control sample of bomas with no flashlights installed.

The usefulness and applicability of the LED flashlight technique in other parts of the world, and thus to other species of large carnivores, is worth exploring. Although differences in behavior, habitat and range use must be considered, we believe this technique, after location-specific adaptations, has the potential to effectively reduce attacks on livestock by other conflict-prone carnivores, such as spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), tigers (*Panthera tigris*) or even coyotes (*Canis latrans*) and foxes (*Vulpes vulpes*). The loss of these apex predators would have a cascading

effect on ecosystem functioning, economic services and an intrinsic value, which they either contribute to directly or indirectly (Ripple et al. 2014).

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Author Contributions

Concept and design of field work: FL, CM, GDS, and HDI. Fieldwork: FL, MF, MG. Data analysis: FL, MF, and MG, KM. Materials/analysis tools: MZ, *C. J. M*, GAP, GDS and HDI. Author of paper: FL

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Supporting information

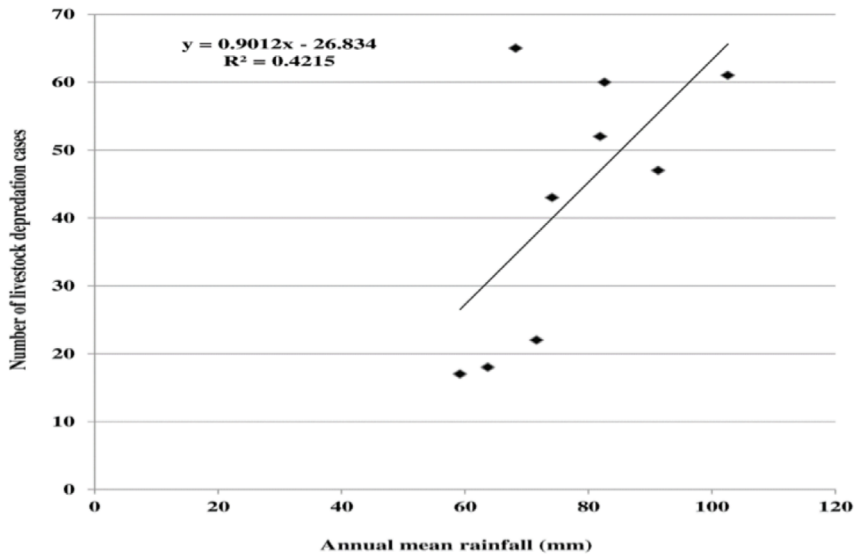

Figure S1

Annual mean rainfall (mm) correlation with total number of annual livestock depredation cases by lions from 2007-2015 in the southern part of NNP.

Table S1

Complementary depredation defense deployed by livestock owners at night, based on 2016 interviews.

	Attacked	Not Attacked	X2	Df	P -value
Radio	2	5	0.01	1	0.920
Fire	7	12	0	1	1
Prayers	16	36	1.2	1	0.27
Flashlight	1	28	12.975	1	0.0003
Scare Crow	3	7	1.205	1	0.2723
Noise	15	35	0.499	1	0.479
Spotlight	2	6	2.26e-31	1	1
Wood	11	55	8.113	1	0.00439
Wire	11	47	0.5996	1	0.4406
Acacia	3	8	0.0846	1	0.7711
Sheet	3	5	0.8463	1	0.7711

Table S2
Livestock herd size, number of attacks and cases without attack.

Categories	Shoats	Attacked	No Attack	Total	Cattle	Attacked	No Attack	Total
Below average	>100	13	27	40	>35	11	31	42
Above Average	<101	4	19	23	<36	6	15	21

Table S3
Participants' opinions on how to resolve human–lion conflicts.

S/n	Measures to be taken to resolve human–lion conflicts in NNP	% on opinion
	Flashlights installation	26.1
	Compensation	22.8
	Keep lions in park	12.0
	Prompt response by KWS	7.6
	Stop construction in NNP	6.5
	Proper fencing of bomas	4.3
	Cooperation between community and KWS	3.3
	Keep wild prey in park	2.2
	Herding	2.2
	Watch cattle at night	2.2
	KWS to patrol at night in the community land	2.2
	Translocation of problem animals	2.2
	KWS to monitor lions	2.2
	Reduce lion numbers in NNP	1.1
	Monitor collared lions and bring them back to NNP	1.1
	Train people from the community and let them monitor lions	1.1
	Feed lions if hungry	1.1

S1 File
Questionnaire

Additional questions of 2014 in italic

Name:

Age:

Sex: m/f

Education level: none/ school/ high-school/ college/ other:

Ethnicity:

Date:

GPS Coordinates:

1 *Do you keep all your livestock in bomas at night, or only part of it?*
All livestock/ part of it (_____ %) / none

2 *If none at night, where do you keep your livestock at night?*

3 *Do you keep all livestock in one boma or in several bomas?*

4 Could you describe the boma(s) construction materials and properties?

3a Is livestock visible through the boma structure?	Yes visible
	Partially visible
	Not visible
3b How high is the boma structure?	0 – 1 meters
	1 – 2 meters
	more than 2 meters
3c What is the thickness of the boma?	0 – 0.25 meters
	0.25 – 0.5 meters
	More than 0.5 meters
3d From which material is the boma constructed?	Bush (acacia)
	Fence (chain-link/barbed)
	Stone (stones/bricks/cement)
	Sheets (metal/wood)
	Wood (offcuts/posts/poles)
	House (inside house)
	Mixture of the above (specify which)

5 Has your boma(s) suffered any attack in the past two years? (to be filled in Appendix II)
- When (dates and time of the day)?
- Which predator was responsible for the attack?
- Who witnessed the predator?
- Which animals and how many did the predator kill?
- Did you report the attack? To whom (KWS, Area Chief, FONNAP, Game Scout)?

6 Do you think the attacks could have been prevented? How?

7 Do you have flashlights installed in your boma(s)? y/n

8 If yes, when was the flashlight installed?

9 Has there been any depredation since the flashlight was installed? y/n

10 If yes to Q7, are you happy with the functioning of the flashlights? y/n

11 *Could you name what other preventive methods against livestock depredation do you use at day/night?*

	Preventive method	Day	Night
1	Radio		
	Dogs		
	Fire		
	Human guards		
	Scarecrows		
	Herding		
	Noise		
	Prayers		
	Flashlights		
	Others		

1 Do you think fencing the southern border of the park could help prevent lion attacks? y/n

2 In your opinion, what do you think can be done to resolve human-lion conflict in this area?

3 *Are you aware of the satellite collaring of lions by the Nairobi lion project? y/n*

4 *What is your opinion on the satellite collaring of lions?*

very good/ good/ no opinion/ bad/very bad

5 What is your main source of income?

(livestock/ farmer/ employed/ business (e.g. grocery)/ other _____)

6 *How many livestock do you intend to keep?*

7 How many livestock do you currently have?

7

Synthesis and General Discussion

7.1 Background

Lions have been extensively studied as a top predator and as an indicator of healthy ecosystems and as a flagship species in the tourism industry (Schaller 1972; Macdonald 1983; De Iongh et al. 2009). Before the 1980s, research on lions focused on social status, population dynamics and interactions with prey and habitat. However, in the past two decades, lion research has become more focused on human–wildlife interaction (Ogada et al. 2003; Patterson et al. 2004; Woodroffe et al. 2007; Inskip & Zimmermann 2009). The African lion (*Panthera leo)* has declined as a result of habitat fragmentation, retaliatory killing and prey depletion (Woodroffe et al. 2007; Riggio et al. 2013; Tuqa et al. 2014). The African lion (*Panthera leo*) is listed as Vulnerable on the global "Red List" of the International Union for the Conservation of Nature (IUCN), based on criterion A2abcd (Bauer et al. 2016). The lions in West and Central Africa and India (*Panthera leo leo* Linnaeus, 1758) are classified as Regionally Critically Endangered while lions in East Africa (*Panthera leo melanochaita* Hamilton Smith 1842) are Regionally Endangered (Bauer et al. 2016). This has become a global concern (Riggio et al. 2013).

As a country, 8% of Kenya's land area has been declared as national park, national reserve or as government-managed sanctuaries (KWS 2015). This land mass excludes the private ranches and community conservancies that also host wildlife and cover some 11% of land area (KWCA 2016). This large land area, still holds a population of 2,000 (6.2% of the global population) lions. The problems facing lions in Kenya are similar to those lions are facing in Africa as a whole, including habitat destruction and fragmentation; prey depletion; and retaliatory killing as a result of human–carnivore conflict (Ogutu & Dublin 2002; Woodroffe et al. 2007; Riggio et al. 2013). To address these threats facing the lion population, Kenya has developed a number of policies and strategies (KWS 2008, 2011). Among the strategies is a long-term re-

search program on lion ecology within specific lion conservation units (KWS 2008). Lion research in Nairobi National Park is part of this strategy. My research addresses specific research objectives and questions aimed at finding possible solutions and recommendations for enhancing the conservation of lions. The main objective of my PhD research is to analyze factors influencing livestock depredation by lions around Nairobi National Park, impact of climate variability on lion movements and to investigate mitigation measures used by livestock farmers to prevent livestock depredation. To address the main objective of this study, we used the following research questions:

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

7.2 Population size, social structure and pride takeovers in Nairobi National Park

The results of my study show that Nairobi National Park has a relatively high lion density of 26 lions/100km^2 (including adult and sub-adults). In Africa, lion density is only higher in the Ngorongoro Crater, Tanzania (38.8 lions/100km^2 (Hanby et al. 1995) and in Maasai Mara National park, Kenya (37 lions/100km^2) (Ogutu et al. 2005). The high density of lions is an indicator of prey abundance and lack of competition with other predators (Ogutu & Dublin 2002; Bauer et al. 2008). During my research period, from 2012 to 2018, the lion population of NNP has fluctuated between 34 and 43 lions, including cubs (<1 year). We have established that NNP has three prides (Northern, Middle and Southern) during 2012 and 2014-2018. Despite human-induced causes are suggested to contribute significantly to lion mortality in NNP, my findings show that the current reproductive rate has sustained the lion population in the park. The transition of 5 newborn cubs annually into reproductive stage confirms that this lion population is relatively stable, despite its small size and "hard edges".

7.3 Home range sizes, dynamics and movements of Nairobi National Park lions

I found that there is no difference in home range size between the wet and the dry seasons. The only change observed in my study is a shift in the position of the lion range. Most of the pride home ranges shift longitudinally towards the southern section of the park into the open corridor. The NNP home range sizes were very small with an annual average of 34 km^2 (95% KDE). This is smaller compared to Waza National Park in Cameroon with an annual average of 641 km^2 (95% KDE) (Tumenta et al. 2013) and Amboseli National in Kenya with an annual average of 56.4 km^2 (95% KDE) (Tuqa 2015). As a consequence, some prides have extended their home range into relatively unoccupied and secure habitats in the community land at AKP. This high vigilance to protect the small home ranges and resources (females, food, cubs) has resulted in the death of three males during my study period (2012-2018) and it resulted in injuries to some females.

In NNP, male choice of habitat and home range size is influenced by their tenure status in relation to whether the pride has been taken over or not. I found that the southern part of the park has fewer compared to the northern part and when a pride male moves to the southern part of the park, he settles in the same pride home range without expansion of the territory size. This suggests that in such areas prey is probably equally distributed and access to preferred habitat (riverine) is secured.

My research indicates that lions mostly roam into pastoral land during the hours of low human activity (mainly at night). A study by Oriol-Cotterill et al. (2015) on lion home ranges and movements in a human-dominated landscape using satellite collars found that lions adapt their movements to human disturbance. Similar findings were reported by Tumenta (2012) for lions being nocturnal in the community land.

Overall, the Nairobi National Park lions avoid the urban fringe of Nairobi City. They prefer the riverine zone, despite its proximity to a zone with low human density. In this zone, lions have the advantage of accessing wildlife in the park and to both dispersing wild prey in the community area and to livestock during the wet season. I conclude that lions in NNP are partly dependent for their survival on community land for hunting livestock despite the relatively high densities of wild prey.

7.4 Feeding ecology and climate variability

I found that lions in the southern part of the park substitute the preferred weight class of wild prey with livestock during the wet season when there is a low density of wildlife in the park. The larger prey, such as African buffaloes, are consumed during the dry season when they are vulnerable to drought. These results reflect those of Bauer & De Iongh (2005) and Tuqa et al. (2014), who also found that lions feed on medium (50-200 kg body mass) to large prey (>200 kg body mass). Several studies have shown that lions are opportunistic feeders (Schaller 1972; Funston et al. 2003; Hayward & Kerley 2005; Davidson et al. 2013). According to these results, I can infer that selection of different prey in different seasons of the year is an important factor for lion survival and being adaptive to changing condition.

When I compared my results from microscopic prey hair morphology from lion scats and carcass counts with another method, i.e. analysis of DNA, I found that carcass counts underestimate the number of small (5-50 kg body mass) and cryptic prey. Carcasses of very small (<5 kg) prey are generally not found because they are entirely consumed by lions. Scat analysis through microscopic prey hair morphology analysis and DNA analysis have proven to be a better method for identifying very small (<5 kg), small (5-50 kg) as well as larger prey than carcass counts. I compared the results of scat analysis and carcass counts, and the results showed a broader spectrum of prey species in the scat than in the carcass counts.

I found some small (5-50 kg) and very small prey (<5 kg), such as Suni (*Neotragus moschatus)*, Mole rat (*Tachyoryctes sp*) and birds, both in eDNA and microscopic hair morphology analysis from the lion scats. The presence of very small prey confirms the opportunistic nature of lions, as suggested by Schaller (1972) and Hayward & Kerley (2005) and Davidson et al. (2013).

In my study, a cost-benefit analysis for lion prey choice provided more insight into the factors contributing to livestock raiding and human–lion interactions around Nairobi National Park. The wet and the dry seasons have been erratic, and this had an important impact on wildlife migration out of the park and the duration of stay in the community land. The lower the available natural prey biomass and density in the NNP during the wet season, the more difficult it becomes for lions to locate and catch natural prey species. According to Gichohi (1996); Owino et al. (2011) and Ogutu et al. (2013), the density of herbivores in Nairobi National Park is lower during the wet season compared to the dry season due to wild prey migration into community land. This could imply that the wild prey species base inside the park is not sufficient to sustain the current lion population during the wet season. Although non-migrating resident ungulate species such as hippo, rhinoceros

and giraffe contribute considerably to the available biomass, these species are not predated by lions, probably due to the risk of injury and energy costs involved in the hunt (Prins & Iason 1989; Hayward & Kerley 2005). This makes it necessary for the lions to follow common prey such as warthog, zebra and wildebeest outside NNP and to hunt outside the park borders, where they could encounter livestock. The abundance of livestock, in combination with their highly predictable distribution and inability to escape from the bomas, makes livestock an easy prey species for lions. Little energy is required to find livestock at night due to the fixed locations of the bomas, and once lions are in the boma, the tightly packed herds form an easy prey to catch. In other words, the benefits of livestock raiding in bomas are high and generally outweigh the costs. Therefore, with erratic climate variability, livestock attacks are very likely to continue and may even increase due to the ongoing process of sedentarization of pastoralists (Lesilau et al. 2018).

7.5 Impact of partial fencing of the park and costs of livestock depredation by lions

In my study, the communities neighboring the unfenced section of NNP suffer both significant social and economic costs of livestock attacks. Woodroffe et al. (2014) found that, although the construction of effective fencing systems around national parks requires intensive management of species, it could both resolve existing human-carnivore conflicts and increase the density of predators inside the park. The related risk of herbivore extinction through a "predator dip" should however not be underestimated.

My study shows that cultural and economic values of a particular livestock species determine the level of herding and protection. I found that unherded livestock such as donkeys, dogs and pigs also become a victim of lion depredation. This unherded livestock is more vulnerable to depredation by lions compared to herded livestock, such as cattle and shoats, especially at night when they enter the park unaccompanied by human guardians. Woodroffe et al. (2007) found that livestock with a child herder is more vulnerable to depredation as opposed to guards that are of adult age or operate in teams. Thus, our data show that when we look for a solution to address human-lion conflict in the importance of unherded livestock and age of herder must be given consideration.

Livestock is a major source of livelihood to all pastoral communities in Kenya (Tuqa 2015). Livestock with a high economic value are herded by mature persons (warriors). I found evidence of depredation of livestock species through microscopic prey hair morphology and DNA analysis. Live-

stock farmers around NNP incur 39,820 USD of costs to lion attacks annually compared to 22,498 USD at Tsavo National Park in Kenya (Patterson et al. 2004) and 610 USD annually at Gokwe in Zimbabwe (Butler 2000) (Table 7.1). These differences can be largely explained by the regional livestock price differences. In my study, lions predate more shoats due to less energy expenditure and high density in the area compared to cattle and donkeys. In West Africa, Bauer & De Iongh (2005) also found that lions prefer cattle and donkeys.

Table 7.1
Economic cost incurred by livestock farmers neighbouring protected areas to lion.

No.	Protected area/Ecosystem	Country	Economic cost (USD) annually	Source
1	Gokwe	Zimbabwe	610	Butler 2000
2	Tsavo National Park	Kenya	22,498	Patterson et al. 2004)
3	Waza National Park	Cameroon	113,366	Van Bommel et al; 2007
4	Makgadikgadi Pan N. P.	Botswana	24,385	Hemson et al, 2009
5	Nairobi N. Park	Kenya	39,820	Lesilau 2018*

* The source of data is from this study

The pastoral communities around NNP are rapidly becoming sedentary and pastoralist activities around the park (Lesilau et al. 2018) are gradually declining. With less livestock available around NNP, the future challenge could be to tackle problems arising from lion–urban conflicts.

I found that partial fencing of the protected areas is not a solution to human–lion conflict and complete fencing is not always a solution. In the case of NNP, the Athi-Kaputei corridor in the south-west of NNP could be crucial to sustain the lion population. Complete fencing would block the access for both the NNP lions and present prey populations to this corridor, and although lion numbers could increase in the short term, the dip in prey numbers would eventually make this a less sustainable option. In addition, after complete fencing, lions will no longer have access to suitable habitat in the buffer zone to hide cubs and escape from pride male(s) during pride takeover, while roaming for nomadic males will be difficult (Lesilau inprep). Wildlife authorities could prevent this development by securing the available space through land acquisition and the purchase of land from land owners for wildlife.

7.6 Response of lions to flashlights

I compared different livestock husbandry techniques with a modern technique of preventing nocturnal livestock depredation, i.e. flashlight equipped bomas. I found that the frequency of attacks on bomas equipped with flashlights was significantly lower compared to bomas without flashlights. I found that after the installation of flashlights at livestock bomas, lion attacks took place further away from the park edge, towards areas where bomas without flashlights were still present. I also found a shift in timing of attacks by lions, with more diurnal attacks than nocturnal attacks after 5 years of flashlight installation.

A predator's feeding strategy always serves to maximize energy intake and minimize risk (Schaller 1972; Nathan et al. 2008; Valeix et al. 2012). To optimize energy and maximize profitability, lions often prefer wild prey species of medium (50-200 kg) or large (>200 kg) weight class (Cowie 1977; Hayward & Kerley 2005; Carbone et al. 2007) over smaller prey. Prey profitability can be defined as "the quotient of a prey type's net energy value divided by the amount of time required to catch and handle it" (Scheel & Packer 1991). This is dependent on prey density, prey distribution, biomass and the defense strategy of prey (Scheel & Packer 1991; Hayward & Kerley 2005; Valeix et al. 2012).

In relation to aforementioned, I found that costs of livestock raiding include the risk of encountering humans, travel distance and entering well protected bomas. Evidence to this is shown in the hunting behaviour of lions. Around NNP, lions usually hunt at night when human activity and visibility are low. This is confirmed in other studies (Van Bommel et al. 2007; Valeix et al. 2012). The avoidance of bomas equipped with flashlight systems by NNP lions, could indicate that these lions perceive the cost of encounters with humans as too high, outweighing the benefits of livestock raiding. Livestock protection measures implemented by livestock owners around NNP include the use of barbed wire and an extra outer fence of Acacia branches and wood for bomas. These materials however appeared to be much less effective compared to the presence of flashlights. Lions are known to jump over three meters high fences, despite the presence of barbed wire on top (Lesilau et al. 2018).

Distance to the park boundary seems to be another important factor determining attack rate, with bomas further than three km away from the park boundary experiencing significantly less attacks compared to bomas closer to the park. The question is whether livestock raiding is still attractive when all accessible bomas are located further than three km from the park. The use of geo-fencing in the AWT iridium satellite collars as a means of tracking li-

ons that would venture large distances from the park, did not work well, due to the proximity of bomas to the park boundary.

Currently, the benefits of livestock raiding around the Nairobi National Park still seem to be higher than the costs, given the large contribution of livestock to the lions' diet found in scats (15%). This is comparable to the 22% of livestock in the diet of lions in Waza National Park, Cameroon (Tumenta 2012), but higher than 9% in the diet of lions in Amboseli National Park, Kenya (Tuqa 2015) (Table 7.2). Due to the availability of livestock in close proximity to the park borders, there is no need for the lions to follow their migratory prey during the wet season, as livestock is a perfect substitution and the energy costs associated with travelling are minimized. Consequently, most lions are able to reside inside the park, also during the wet season, and only make short trips outside the park at night to the areas where livestock is held. The application of flashlights seems to be an effective method in preventing nocturnal livestock attacks by lions as the lights mimic risky human activity, which is rather avoided by lions. Despite its success, the LED flashlight technique also has a downside: lions adjust their behavior by attacking livestock during the day and further away from the park border, although the damage suffered during such diurnal attacks is relatively small.

Table 7.2
Livestock depredation analysis from various parks in Africa

Country	Protected Area	Livestock Contribution to lion diet (%)	Source
Botswana	Makgadikgadi Pans	10-26	Hemson 2003.
Kenya	Tsavo N. Park	5.8	Patterson et al. 2004
Kenya	Samburu N. Reserve	6.2	Ogara et al. 2010
Benin	Pendjari Biosphere Reserve	18	Sogbohossou et al. 2011
Cameroon	Waza N. Park	21.6	Tumenta et al. 2013
Kenya	Mbirikani group Ranch	7	Maclennan et al. 2009
Kenya	Amboseli N. Park	6-9	Tuqa 2015
Kenya	Nairobi N. park	15	Lesilau 2018*

* The source of data is from this study

If livestock raiding is only favorable when natural prey availability is low, a decrease in the number of livestock attacks would be expected during the dry season (when natural prey density is highest) according to e.g. Patterson et al. (2004), Van Bommel et al. (2007) and Valeix et al. (2012). During my study, increased livestock attacks during the wet season was confirmed. Once

livestock raiding has proven to be an efficient and beneficial hunting strategy, lions are more likely to stick to this strategy, even in periods when wild prey is abundant, e.g. during dry season. This means that adapting the lion population or prey population numbers to the predicted carrying capacity of the park will not automatically solve the livestock depredation problem. Proximity of livestock to the park and illegal grazing by livestock inside the park may further encourage lions to select livestock over wild prey. The best solution seems to make the energy costs of livestock depredation higher than the energy benefits, thereby making the choice for livestock raiding less optimal and forcing lions to adapt their prey choice. This is achievable through proper fencing, presence of a proactive lion control team and an increase in the installation of flashlights at livestock bomas around the park. With effective livestock protection measures in place, the number of lions residing in the park during the wet season may eventually stabilize, as lions will again be forced to follow their natural migratory prey in order to survive.

7.7 Conclusions

In my study, I focused on lion population structure, home range and movement, feeding ecology, impact of partial fencing of parks and a comparison of modern and traditional protective measures. The following conclusions can be drawn from this study:

With respect to methodology, I have defined the following conclusion that I applied in my research:

1. Scat analysis focusing on microscopic prey hair morphology has proven to be a better methodology to identify very small (<5 kg), small (5 - 50 kg) and larger prey than carcass counts. It results in a broader spectrum of prey species in the diet than carcass counts.
2. The use of DNA has proven to be a potential method to identify an even broader spectrum of prey compared to scat analysis, but still needs further development and calibration.
3. The use of Irridium satellite collars in order to track movements and home ranges of lions has been successful in detecting conflict areas around the park but the use of geo-fencing in the collars for early warning has not functioned well due to the close proximity of livestock bomas to the park boundary.
4. Soco-economic surveys clearly complement empirical data gathered in my study and have added value to get more insight in the drivers of lion-livestock conflicts around Nairobi national park

I have also defined the following conclusion with respect to research results, that come from the five chapters of my research:

5 Nairobi National Park lions have small home ranges (among some of the smallest in Africa), due to high human disturbance from urban fringe (tourism, retaliatory killings, light, noise) but they are still able to survive in high densities by living in small prides, and high reproductive rates, in relation to relatively high prey densities.

6 Lions in Nairobi National Park are partially dependent on community land for their survival (hunting livestock and migrating wild prey) and as a refuge for males and females after pride takeovers.

7 Lions are opportunistic hunters, feeding on very small prey (<5 kg) such as Mole rat (*Tachyoryctes sp*) and birds to supplement their diet.

8 The localized high abundance of livestock, dependency on human guardians and their predictable distribution in combination with their inability to escape bomas, makes livestock a favorable prey species for lions in our study area.

9 Neither complete fencing, nor partial fencing of the Nairobi National Park areas is a solution to human–lion conflict. Complete fencing of NNP may cause herbivore extinction through a "predator-induced dip", which could eventually result in a drop in lion numbers below critical levels.

10 The Athi-Kapiti corridor in the south-west of NNP is crucial in providing suitable habitat for both lions and herbivores.

11 Application of LED flashlights at livestock bomas is a more effective method for protecting livestock against nocturnal lion attacks compared to the traditional fencing materials (wood, post, barbed wire, and Acacia branches). The only problem is that lions adapt to flashlights by attacking livestock in the daytime and further away from the park border.

12 The communities around NNP incur both social and economic costs from lion interactions, related to their proximity to the park boundary, in particular to the unfenced section of the park.

13 The population numbers of waterbuck and reedbuck have been very low throughout our study period (2012 - 2018). They appeared in scats diet in wet seasons. They may experience local extinction in future.

14 As communities around NNP are becoming sedentary and pastoralism gradually disappears, the future threats in NNP will likely include a higher risk of conflicts related to urban development.

15 A zone of 25 km^2 along the northern urban fringe of NNP is not used by lions, probably due to urban disturbance (noise, smell and lights) arising from City, aircrafts, vehicles and trains.

7.8 Recommendations

A single intervention is not usually a long-term solution to human–wildlife conflicts. Human– carnivore conflict solutions that are effective in one region could fail in another, even at a local scale. Anti-conflict measures could become ineffective over time, due to changes in e.g. policies, politics, wildife administration, environmental or social factors. The implementation and enforcement of multiple anti-predation techniques by both livestock owners and wildlife authorities should take such changes into account. Based on my research I would recommend the following:

A Action by Kenya Widlife Service and Researchers

1. To understand the broader spectrum of the lion diet, the application of microscopic analysis of hair morphology and DNA-metabarcoding will provide a better result on lion feeding ecology and the role of very small prey. Therefore, I recommend further study of the role of very small prey through DNA from lion scats.
2. Based on knowledge from other re-introduction programs in the region, the current NNP lion population should be capable of contributing to lion repopulating schemes in other ecosystems, i.e. where lion populations have disappeared, provided that a wildlife migratory corridor is secured and lion retaliatory killing is controlled. It is advised to rapidly address the existing human–lion conflict situation, considering our suggested livestock protection measures and a compensation scheme for livestock, while securing the Athi-Kapiti Plains for habitat connectivity. This could be achievable through (i) land acquisition and compensation from private land owners (ii) land leasing from private land owners (iii) promotion of tourism activities on private farms which are part of lion home ranges.
3. Support is needed for the communities in the Athi-Kapiti corridor in order to develop ecotourism activities as an alternative form of land use.
4. To conduct a census and to monitor the reedbuck and waterbuck population in Nairobi National Park. The population of these species has been very low and they have been appearing in the lion diets in the wet season based on scat analysis. These shows their density is low and they are being consumed by lion. If urgent measures are not taken, they can go local extinct.
5. With current developments (Standard Gauge Railway, Southern bypass road, Oil pipiline and High Voltage Power cables) within and around NNP, continuous research and monitoring is necessary to understand

the impact of human development on the general biodiversity and especially the lion population in NNP.

6 A longer period of research in NNP is required to monitor human development, particularly regarding the predicted shift from pastoralism activities towards the expansion of urban activities around Nairobi National Park.

7 After de-collaring due to expiring batteries, the same lions could be recollared to understand long-term trends in movement, behavior and impact of collars on individual lions.

B Action by Kenya Widlife Service and Conservation NGO

8 Despite the effectiveness of the proposed LED flashlight technique in deterring lions from livestock bomas around NNP, its successful implemenation in a different situation is not guaranteed. We suggest long-term studies on the effects of LED flashlights on other large carnivores as well as expansion of this technique into other regions.

9 For wildlife authorities to effectively tackle the predicted increased urban development and related challenges, efforts should focus on securing suitable habitat through land acquisition.

10 Planting a buffer of trees border embankment and park counting embankment) to reduce light and noise pollution could be part of management efforts, especially along the urban fringe, where disturbance is highest.

11 Education and awareness programs focusing on lion conservation could contribute to a general positive attitude towards lions. The risks related to lion behavior (e.g. nocturnal vs. diurnal activities) and effective livestock protection techniques should be incorporated in such programs.

C Nairobi National Park Management

12 The proper and maintained park fence is effective than partial fencing, so the park management, should repaired and monitored park fence to reduce the number of lions that exit from the park in sections with fences into urban settlements.

13 For rapid response to a problem lion, a Problem Animal Management Unit (PAMU) should be stationed in the southern part of the park where lions exit into community land.

14 Software should be developed on reporting livestock depredation for easy follow-up of depredation cases.

D Communities

15 Communities around the park should be educated about avoiding grazing their livestock in the park as to avoid further habituation of lions to catching livestock.

16 Livestock should be escorted by an adult and not children when drinking water near the park border.

17 The communities around NNP are increasingly becoming sedentary and will become more dependent on modern livestock husbandry practices in a larger area comprising the Central and Part of Rift Valley.

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Summary

Human–Lion Conflict around Nairobi National Park

Lion (*Panthera leo melanochaita*) Population Structure, Landscape use and Diet in a Semi-Fenced Park

Keywords
Lion (*Panthera leo melanochaita*), population structure, lion diet, human–lion interactions, lion depredation mitigation, Nairobi National Park, Kenya

Apex predators like lions play an important ecological role in the African savannah ecosystem. Besides being a keystone species, the lion is also a flagship species and a symbol of power for both the government and business section, for the latter especially in the tourism industry. According to a population assessment in 2013, there are 32,260 remaining lions living in the wild in Africa. East Africa has the largest lion population (56.9% of the total) compared to other regions in Africa. Of the estimated 32,260 lions in Africa, only 6.2% are found in Kenya.

Kenya has declared 8 percent and 11 percent of the land area as national parks and conservancies for species conservation respectively. This land mass is assigned for the conservation of wildlife including large carnivores. Within this designated land for conservation of wildlife, there are six lion conservation units (LCU). The lion population in Kenya suffers from human-induced threats (habitat destruction and fragmentation, prey depletion and retaliatory killing) and climate variability (erratic and unpredictable seasons), which have caused lion numbers to decline.

In order to better understand the threats lion populations are facing, in support of better conservation and protection measures for the remaining lion populations in Kenya, continuous research on lion ecology and the subsequent monitoring of the lion populations within specific lion conservation units is required. The lion population in Nairobi National Park (NNP) has suffered from urban pressure, retaliatory killing and lack of habitat connectivity. This has resulted in intensified human–lion interactions around NNP in recent decades and the subsequent retaliatory killing of lions due to conflicts with livestock owners. During the years prior to the start of my research in 2012, the park has lost six lions as a result of retaliatory killing.

My research aims i) to analyze factors influencing livestock depredation by lions around Nairobi National Park, ii) to study the impact of climate variability on lion ecology and lion-livestock conflicts and iii) to investigate mit-

igation measures used by livestock farmers to prevent livestock depredation around NNP. My research covered lion population structure, lions home ranges, movements and landscape use, diet and prey choice and the effectiveness of administrative measures (park fence) and methods of communities' livestock husbandry practices to prevent and mitigate conflicts.

Reliable estimates of both prey and lion populations to sustain the lion population are important for management. My study revealed that despite considerable human-induced mortality, the NNP lion population has been fluctuating between 34 and 43 lions (including cubs) over the past decades. The lions in NNP have adapted to a high level of human disturbance by surviving in small prides and forming small groups with a high reproduction rate, to compensate for increased mortality.

Lion populations can recover quickly if retaliatory killing is mitigated and/or prevented. The park has an annual average mean male to female ratio of 1:1.56, which was stable during the years of my research (2012-2018). This ratio allows NNP lions to reproduce and compensate mortality, resulting in a relatively stable population. The mean pride size was 2.8±2.4 including cubs (< 1 year) during 2012-2018. The largest group size observed was 17 lions with cubs. The mean group size of adults and sub-adults (1-2 years, excluding cubs (< 1 year) was 1.6±0.17. This is smaller than the group size observed by other authors in the Serengeti, where a group size of 2.6 was observed. In NNP there was no difference between group size in the dry season and in the wet season. I also observed that the females in the northern and middle pride synchronized their denning seasons to the months of September and February.

A comparison of NNP pride male tenure with other parks revealed that Queen Elizabeth National park in Uganda had an average male tenure of 7.5 years (Van Orsdol. 1981), the Ngorongoro Crater 3 years (Hanby et al. 1987) and the Serengeti 2 years (Hanby et al 1987). I observed that NNP pride male tenure was long during 2012-2018 (up to 4.5 years) due to a stable coalition of two pride males. My results suggest that the long period of pride male tenure and synchronized female birth has increased cub survival, which compensates for enhanced mortality due to conflicts.

Most scientific literature suggests that lions require an extensive home range to survive, especially during the wet season. By contrast, my research shows that lions' home ranges in the semi-fenced NNP are very small compared to other protected areas and show no difference between wet and dry season.

The smaller size of lion home ranges in NNP could partly be explained by avoidance of the urban fringe of the park due to urban disturbance (noise, light, dust), which reduces their space even further. With high wild prey den-

sities and low natural mortality, lions are able to use a small home range of 34 km^2 and survive, in spite of the fences.

Previous studies have used microscopic prey hair morphology analysis from lion scats, in combination with prey transect counts and prey carcass counts to determine lion diet and prey choice. In my research, I was able to demonstrate the application of DNA-metabarcoding as an additional method to determine the diet and feeding ecology of lions. This novel technique has the capacity to reveal the wider feeding spectrum of lions, including cryptic small prey species like rodents and birds, which are often not observed in carcass counts, nor revealed by microscopic hair morphology.

In NNP, lions mostly depend on wild prey species and partly on livestock depredation. They depredate especially on livestock outside the park when there is low wild prey density in the park during the wet season. However, I observed that they also make excursions outside the park during the dry season.

Although NNP lions mostly depend on medium-sized (50-200 kg body mass) prey, I found that 2% and 9% of the diet consisted of very small prey (<5 kg), based on microscopic hair morphology analysis and DNA-metabarcoding respectively. This finding is probably a result of spatial-temporal fluctuation of herbivores in the park and extreme climate variability, forcing lions to switch their diet between prey species of different weight class, depending on availability. I found a correlation between extreme climate events caused by El Nino and the presence of very small prey in the lions' diet. Based on microscopic analysis of prey hair morphology, but also based on DNA analysis, I also found the presence of livestock prey hair items in lion scats. Despite reports of human fatalities as result of lion attacks, there was no evidence to support this either in hair morphology analysis or in DNA-metabarcoding.

My research revealed the role of the park fences and the livestock bomas equipped with flashlights in the buffer zone in reducing human–lion interactions and quantified the costs incurred by farmers through livestock depredation. The function of any fences either for the park, or for the livestock bomas is to prevent interaction between lions and livestock. Lions in NNP have more access to livestock through the unfenced section of the park as opposed to the fenced section and thus increase the cost to livestock farmers. I calculated that the livestock farmers incur an annual loss of 39,820 USD due to livestock depredation. Given the importance of the buffer zone for lions, I suggest that complete fencing of the park is not a viable option and instead we should look for alternative solutions such as habitat connectivity and compensation for livestock losses due to depredations. The Kitengela corridor in this respect remains of vital importance for the lion population in NNP.

My study revealed new insights into the effectiveness of construction materials for bomas (wood, chain-link, acacia branches and barbed wire). I compared the materials used in bomas installed with modern LED flashlights. The bomas with wooden fencing materials, reinforced with chain-link perimeter fencing of above 2.5 meters were less vulnerable to lion attacks compared to other fencing types. I also concluded that the farmers with roof-covered bomas are likely to incur more livestock losses and injuries during lion attacks than open roof bomas where livestock could escape from the boma during lion attacks. Roof-covered bomas suffer more to "mass-killing" of livestock than open roof bomas.

My study shows that the LED flashlight technique is very effective (96%) in reducing nocturnal livestock depredation at bomas by lions. However, I also found that lions adapt their behavior and engage more in diurnal attacks outside bomas after the installation of flashlight technology. My research has resulted in a number of recommendations for the management of Nairobi national Park, such as keeping the Southeastern border of the park non-fenced, building a green wall at the urban fringe of the park and investing in the Kitengela corridor.

Samenvatting

Conflicten tussen mensen en leeuwen rondom Nairobi National Park

Populatiestructuur, landschapsgebruik en dieet van leeuwen (*Panthera leo melanochaita*) in een gedeeltelijk omheind reservaat

Trefwoorden
Leeuw (*Panthera leo melanochaita*), populatiestructuur, dieet, mens-leeuw interacties, preventie van predatie van vee, Nairobi National Park, Kenia

Leeuwen zijn zogeheten apex-predatoren die een belangrijke rol spelen in de ecologie van Afrikaanse savannes. Maar de leeuw is ook een sleutelsoort, of 'flagship'-soort, die symbool staat voor kracht. Dit is door te voeren tot op het niveau van overheden en de commerciële sector, vooral het toerisme. Volgens een populatietelling die in 2013 plaatsvond, zijn er nog circa 32.260 in het wild levende leeuwen in Afrika. Daarbij herbergt Oost-Afrika de grootste populatie leeuwen (56,9% van het totaal) van alle leefgebieden in Afrika, waarvan 6,2% in Kenia te vinden is. De leeuwenpopulatie in Kenia staat onder druk als gevolg van menselijk toedoen bijvoorbeeld door degradatie en fragmentatie van het habitat, overbejaging van hun natuurlijke prooi of het gericht doden van leeuwen uit vergelding en het veranderlijke klimaat (grillige en onvoorspelbare seizoenen). Er zijn duidelijke aanwijzingen dat ook leeuwen in Kenia in aantal afnemen.

Om meer inzicht te krijgen in de factoren die een bedreiging vormen voor het voortbestaan van de resterende populatie leeuwen in Kenia, en deze op basis daarvan beter te kunnen beschermen, is het van essentieel belang om langdurig onderzoek te doen naar de ecologie van de leeuw en populaties te blijven volgen in aangewezen beschermde gebieden. De leeuwenpopulatie in Nairobi National Park (NNP) heeft veel te lijden gehad van stadsuitbreidingen, vergeldingsacties door veehouders en versnippering van het leefgebied. Dit heeft er in de afgelopen decennia toe geleid dat interacties tussen mensen en leeuwen rondom NNP steeds frequenter voorkomen met als gevolg dat leeuwen steeds vaker het doelwit zijn van vergeldingsacties door veehouders. Zo werden er in 2012, het jaar voorafgaand aan mijn onderzoek, zes leeuwen uit vergelding gedood door veehouders.

Mijn onderzoek is erop gericht om i) de factoren te analyseren die van invloed zijn op aanvallen op vee door leeuwen rondom Nairobi National Park, ii) de gevolgen te onderzoeken van het veranderende klimaat op de ecologie

van leeuwen en de conflicten die het gevolg zijn van veepredatie, en iii) de maatregelen in kaart te brengen die veeboeren rondom NNP hebben getroffen ter voorkoming van aanvallen op vee. Mijn onderzoek gaat in op de populatiestructuur, *home ranges*, bewegingen en landschapsgebruik van leeuwen, evenals het dieet en de prooiselectie van leeuwen. Daarnaast onderzoek ik in hoeverre de door lokale autoriteiten ingestelde maatregelen (zoals het hek rond het park) en door omwonenden ingezette methoden ter bescherming van hun vee, effectief zijn in het voorkomen en oplossen van conflicten.

Voor parkbeheerders is het van belang te beschikken over betrouwbare populatieschattingen van zowel de leeuwen als hun prooi om de populatie leeuwen effectief te kunnen beschermen. Mijn onderzoek heeft uitgewezen dat leeuwenaantallen in NNP in de afgelopen decennia varieerden tussen 34 en 43 (inclusief welpen), waarbij zowel natuurlijke als menselijke factoren bijdroegen aan de mortaliteit. Hoewel leeuwenpopulaties erom bekend staan snel te kunnen herstellen, mits vergeldingsacties en jacht op leeuwen tot een minimum worden beperkt, lijken deze leeuwen zich aangepast te hebben aan een sterke mate van verstoring door mensen, door zich ter compensatie van de toegenomen sterfgevallen, snel voort te planten in kleine troepen.

De verhouding van mannelijke en vrouwelijke leeuwen in het park bedraagt gemiddeld 1:1.56 op jaarbasis. Dit bleef gedurende mijn onderzoek (2012-2018) stabiel. In een dergelijke verhouding zijn leeuwen in staat zich met succes voort te planten en voor sterfgevallen te compenseren, wat in een relatief stabiele populatie heeft geresulteerd. Berekend over de periode 2012-2018 bestond een troep leeuwen gemiddeld uit 2,8±2,4 individuen, inclusief welpen (<1 jaar). De grootste groep die werd waargenomen bestond uit 17 leeuwen en welpen. Groepen met adulte en sub-adulte leeuwen (1-2 jaar, exclusief welpen (<1 jaar) hadden een gemiddelde grootte van 1,6±0,17. Dit is kleiner dan de groepen van gemiddeld 2,6 individuen die andere onderzoekers in de Serengeti hebben waargenomen. In NNP werd geen verschil in groepsgrootte gevonden tussen het droge seizoen en het regenseizoen. Uit mijn onderzoek blijkt dat de heerschappijperiode van mannetjesleeuwen in NNP relatief lang was gedurende 2012-2018 (tot wel 4,5 jaar), als gevolg van een stabiele coalitie tussen twee troepleiders. Bij vergelijking van de periode dat een mannetjesleeuw over een troep heerst tussen NNP en andere reservaten in de regio, kwam naar voren dat deze heerschappijperiode in Queen Elizabeth National park in Uganda gemiddeld 7,5 jaar was (Van Orsdol. 1981), in Ngorongoro Crater gemiddeld 3 jaar (Hanby et al. 1987) en in Serengeti 2 jaar (Hanby et al. 1987). Vrouwtjes in de noordelijke en de centrale troep bleken daarnaast hun werpcyclus op elkaar te hebben afgestemd; hun jongen werden in de maanden september en februari geboren. In combinatie met de relatief lange heerschappijperiode van de mannetjes uit mijn onderzoek is de

grotere overlevingskans van welpen als gevolg van deze synchronisatie van werpcycli mogelijk een strategie om te compenseren voor het hogere sterftecijfer dat het gevolg is van het conflictprobleem rondom NNP.

De meeste wetenschappelijke literatuur geeft aan dat leeuwen grote *home ranges* nodig hebben om te kunnen overleven, vooral in het regenseizoen. Uit mijn onderzoek komt echter naar voren dat leeuwen in het niet-geheel omheinde NNP een zeer kleine *home range* hebben vergeleken met andere beschermde gebieden en dat er geen verschil in omvang van de *home ranges* is tussen het droge seizoen en het regenseizoen. Deze beperkte omvang van de *home ranges* in NNP zou een gevolg kunnen zijn van het feit dat leeuwen het gebied dat aan de stad grenst actief ontwijken (vanwege het lawaai, licht en stof) waardoor hun leefgebied in werkelijkheid nog kleiner is dan gedacht. Aangezien de dichtheid aan wilde prooidieren hoog is en de sterfte ten gevolge van natuurlijke oorzaken laag, is het voor leeuwen in NNP toch mogelijk om in de kleine *home ranges* van gemiddeld slechts 34 km^2 te overleven, ondanks de parkomheining.

In eerdere onderzoeken werd al succesvol gebruikgemaakt van morfologische analyses van de vacht van prooidieren uit leeuwenuitwerpselen om de dieetsamenstelling en prooikeuze van leeuwen te bepalen. Dit werd meestal gecombineerd met het tellen van (karkassen van) prooidieren langs transectlijnen. In mijn onderzoek heb ik kunnen aantonen dat het gebruik van DNA-metabarcoding als methode hierop een goede aanvulling is. Dankzij deze innovatieve techniek is het nu mogelijk om een breder voedselspectrum van leeuwen in kaart te brengen, inclusief de kleinere, onopvallende prooidieren zoals knaagdieren en vogels. Dergelijke kleine prooidieren blijven meestal onzichtbaar tijdens transecttellingen en worden ook vrijwel niet opgemerkt in morfologische analyses van haren onder de microscoop, maar zijn dus wel op te sporen met DNA-metabarcoding van uitwerpselen.

In NNP leven leeuwen grotendeels van wilde prooisoorten maar tot op zekere hoogte ook van vee. Vooral wanneer de dichtheden aan prooidieren in het park laag zijn, zoals gedurende het regenseizoen, verlaten leeuwen het park om vee te doden. Hoewel dit ook in het droge seizoen werd waargenomen, was dat beduidend minder vaak. Leeuwen in NNP leven voor het overgrote deel van middelgrote prooidieren (gewicht van 50-200 kg), terwijl hun dieet op basis van de morfologische analyse van haren en de DNA-metabarcodingtechniek voor respectievelijk 2% en 9% bleek te bestaan uit zeer kleine prooidieren (<5 kg). Deze bevinding zou kunnen betekenen dat leeuwen hun prooikeuze kunnen aanpassen aan de beschikbaarheid van prooidieren, die afhankelijk is van variatie in tijd en ruimte en van extreme klimaatschommelingen. Dit laatste werd bevestigd door de relatie die ik vond tussen extreme, door El Nino veroorzaakte, klimaatgerelateerde omstandigheden en de aan-

wezigheid van zeer kleine prooidieren in leeuwenuitwerpselen. De microscopische morfologieanalyse van haren van prooidieren en de DNA-analyse lieten verder zien dat vee inderdaad deel uitmaakt van het dieet van leeuwen. En hoewel er in mijn onderzoek ook meldingen waren van fatale aanvallen door leeuwen op mensen, werd hiervan noch op basis van de morfologische analyse noch van de DNA-metabarcoding geen bewijs aangetroffen in de leeuwenuitwerpselen. Dat leeuwen in NNP jacht maken op mensen, kan op basis van mijn resultaten dan ook niet worden bewezen.

Tevens onderzocht ik welke rol de parkomheining en de verlichte veekralen in de bufferzone spelen in het terugdringen van conflicten tussen mensen en leeuwen. Een kwantitatieve analyse van de kosten die veehouders moesten maken als gevolg van aanvallen door leeuwen op hun vee wees uit dat zij hiervan jaarlijks gemiddeld 39.820 USD schade ondervonden. Deze hoge kosten zijn mogelijk het gevolg van de relatief ongehinderde toegang die leeuwen hebben tot het vee rondom NNP. Een hek dat het gehele park afsluit is mijns inziens echter geen haalbare oplossing voor dit probleem, aangezien de bufferzone een belangrijk deel uitmaakt van het leefgebied van de leeuwen. In plaats daarvan zou ik willen voorstellen de habitatconnectiviteit te verbeteren, waarbij het grote belang van de Kitengela-corridor voor de leeuwenpopulatie van NNP zeker in ogenschouw moet worden genomen.

Mijn onderzoek biedt nieuwe inzichten in de effectiviteit van verschillende soorten bouwmaterialen die voor veekralen worden gebruikt. Veekralen gemaakt van traditionele materialen (zoals hout, gaas, acaciatakken of prikkeldraad) werden vergeleken met veekralen uitgerust met moderne ledverlichting. Veekralen die een houten omheining hadden, verstevigd met een hekwerk van gaas van minimaal 2,5 meter hoog, bleken leeuwen beter te weren dan kralen van ander type materiaal. Daarnaast vond ik dat bij aanvallen door leeuwen op veekralen met een dak meer vee werd gedood en er ook ernstigere verwondingen optraden dan bij open veekralen zonder dak, waaruit het vee tijdens een aanval door een leeuw nog kan ontsnappen. De techniek met de ledverlichting blijkt uitzonderlijk effectief (96%) in het verminderen van nachtelijke aanvallen van leeuwen op veekralen waarbij vee wordt gedood. Een opmerkelijke bevinding ten aanzien van deze techniek was echter dat leeuwen hun gedrag, daar waar de ledverlichting was geïnstalleerd, leken aan te passen door het vee vaker overdag, wanneer het vee zich buiten de kralen bevond, aan te vallen.

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Finally, I would like to dedicate this work to daughters and sons of "*Mugur e-Serima*" and may this journey inspire many.

Curriculum Vitae

Francis Longory Lesilau (SS) was born on 9 September 1966 at the Laisamis sub-county in Marsabit County, Kenya. He attended the Laisamis primary school between 1977-1983 and Marsabit boys' secondary school between 1984-1987.

He worked with the Christian Children Fund (CCF) between 1988-1990 to monitor and evaluate children's education and sponsorship. This programme covered landscape restoration, planting trees and environmental advocacy. He briefly worked as a teacher with the Teachers Service Commission (TSC) during 1990-1991.

In 1992, he was employed as a cadet officer by the Kenya Wildlife Service (KWS). He was among the first cadet officers to attend and successfully complete paramilitary training at the Kenya Wildlife Law Enforcement Academy at Tsavo West National Park, Kenya. He was among the pioneer game wardens deployed to different protected areas in Kenya to combat escalating poaching of endangered species during 1992 to 1994.

He was awarded a scholarship by Internationalis Weiterbildung und Entwicklung (InWEnt), Germany to attend the College of African Wildlife Management-Mweka, Tanzania during 2001-2004 where he obtained a Diploma and Certificate in Conservation and Management of Wildlife. He also obtained several diplomas and certificates related to conservation, finances, human resources and general management. He was granted a Master of Science degree in Sustainable Management of Natural Resources from the University of Leicester in UK (2007-2008), which was sponsored by the East of England Agricultural Society (Marshal Papworth). In 2015 until 2019, he was awarded a scholarship by the Louwes Fund for Resources on Water and Food through Leiden University (CML) for a PhD on Human–Lion Conflict around Nairobi National Park Kenya at Leiden University (Institute of Environmental Sciences (CML) in The Netherlands.

In 1996, Mr. Lesilau was decorated with a Silver Star (SS) of Kenya by His Excellency the President of Republic of Kenya, in recognition of the outstanding and distinguished services he rendered in the Republic of Kenya for wildlife protection, conservation and management. He was also awarded a Wildlife Conservation Heroes Award in 2000 and a Clark R. Bavin Wildlife Law Enforcement Award by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) through the Species Survival Network (SSN) for extraordinary courage and commitment to wildlife protection, conservation and management.

Mr. Lesilau is a career wildlife conservationist with over 27 years' experience gained in diverse and dynamic work environments of wildlife protection, conservation and management. Currently, he works with the Kenya Wildlife Service as a Senior Assistant Director, Head of Wildlife Protection Department in Nairobi, Kenya. He has initiated and supported some of most successful wildlife conservation, park management and community work projects in Kenya. He is a member of Kenya's species introduction, re-introduction and translocation committee, which has developed a conservation, protection and management strategy for the most endangered species such as Black Rhino, Carnivores, Grevy Zebra, and Mountain Bongo among others.

He is also a member of the Chartered Management Institute (CMI) with a Level 6 Certificate in Management and Leadership (QCF) (UK) acquired in 2010. Lesilau is a member of Species Steering Committee in Kenya and the African Lion Working Group (ALWG) and World Congress on Protected Areas.