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Social structure, movements and home ranges of lions *(Panthera leo)* in relation to lion-livestock conflicts around Nairobi National Park, Kenya

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Abstract

Nairobi National Park is a small reserve which is located 7 km south of the capital city of Kenya. I studied social structure, movements and home ranges of lions (*Panthera leo*) in relation to human-lion conflicts. Five lions had satellite collars with GPS and VHF functions. Results show a high lion density with a lion population size of 37 individuals. The pride structure seems to be disturbed as a consequence of high human pressures in and around the national park and by retaliatory killings of pride males. Home ranges were small and showed aberrant patterns. Contrary to other studies, female lions have larger home ranges compared to males, and home ranges of rival males showed large overlap in my study.

Human-lion conflicts mainly occur in the south, because this part is not fenced. Lions in this part of the park include a considerable part outside the park in their home range. Livestock raiding behavior seems therefore mainly to be influenced by the lion's location in the park, but also by its social status and by the seasons. Effective livestock husbandry practices, such as flashlights and a good boma (livestock enclosure) construction, reduces livestock depredation, although habituation to flashlights may occur in the near future.

Summary

The last decades have shown a dramatic increase in the number of conflicts between humans and wildlife in Africa. Because of expanding human populations, borders of National Parks become more and more densely inhabited and conflicts between wildlife and humans occur more frequently. Nairobi National Park is the only protected nature reserve in Kenya neighbouring a major city; Kenya's capital is located at the northern borders of the park. Consequently the borders of the park are densely inhabited, increasing conflicts between humans and wildlife. The southern border of the park is not fenced, enabling herbivore migration. But it also makes it possible for lions and other carnivores to go outside of the park borders and to come in close contact with livestock, which then are attracted and killed by lions. Because most local farmers are financially dependent on their livestock, the killings have a severe economic impact. In recent years, several lions have therefore already been killed in retaliation by the local population, to protect their own lives and their economically important livestock.

The aim of this research is to study social structure, home ranges and livestock predation of the African lion, in relation to increasing human-lion conflicts around Nairobi National Park in Kenya. Insight in the lion home ranges and movements can help in indicating conflict points and to warn and inform local people.

This research contributes to the PhD thesis of Francis Lesilau and is supervised by the University of Antwerp, the University of Leiden and the Kenya Wildlife Service.

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Introduction

Lion conservation and population status

Large carnivores, like the African lion (*Panthera leo)*, Cheetah (*Acinonyx jubatus)*, Leopard (*Panhtera pardus*) and the African wild dog (*Lycaon pictus*), have declined in Africa (Woodroffe *et al.,* 2005). Land use change, resulting in fragmentation and loss of habitats is considered as the greatest immediate threat to their survival (Jetz *et al*., 2007; Riggio *et al*., 2012; Vitousek *et al*., 1997). They are particularly vulnerable because they have large home ranges and require extensive, intact habitats to survive (Sillero-Zubiri & Laurenson, 2001). Hunting, depletion of prey, diseases, conflicts and trade in body parts are other major reasons for their global declines (Novaro *et al*., 2000; Sillero-Zubiri & Laurenson, 2001). These declines are also accelerated by inherent biological factors that make carnivores more vulnerable to environmental change, such as their low densities and large home ranges (Cardillo *et al*., 2004; Cardillo *et al*., 2005). Large carnivores are usually at the top of the food chain, which means that they will always be less abundant compared to their herbivore prey. Therefore, they have a smaller population size and are more vulnerable to extinction (Nosse *et al*., 1996; Sillero-Zubiri & Laurenson, 2001). This makes that large carnivores tend to suffer first when human populations expand into natural habitats (Muntifering *et al*., 2006). A strong correlation was found between high human density and the loss of carnivore populations from a region (Woodroffe, 2000).

Riggio *et al* (2012) estimate the entire lion population size at 32,000 individuals in 67 lion areas, with evidence of strong declines and even extirpation of lions in some range countries. To date, these lion populations inhabit only 17% of their historical range and are restricted to Sub-Saharan Africa and to one small endemic population in the Gir Forest in India (Schaller, 1972; Nowell & Jackson, 1996; Riggio *et al*., 2012). Most lions (30,000) live in East and South Africa, while numbers in West and Central Africa (< 3,000) have greatly declined (Nowell & Jackson, 1996; Bauer & Van der Merwe, 2004; Riggio *et al*., 2012).

Currently 27 countries across Africa contain resident populations of free-ranging lions, where only nine countries, including Kenya, contain at least 1,000 lions (Riggio *et al*., 2012). However in Kenya, lions have suffered dramatic reductions in population size over the past decades, from 7,000 in the 1990s to 2,000 in recent years (Patterson *et al*., 2004; Bauer & Van der Merwe, 2004). Nowadays, the lion's permanent range in Kenya is 18% of the total area of the country (see Appendix I; Kenya Wildlife Service, 2008). Table 1 gives the estimates of lion numbers in Kenya, according to different surveys. Some of the areas are cross-border areas; Masai Mara NP connects to Serengeti NP, and Tsavo NP to Mkomazi NP, which are both situated in Tanzania. Arawale connects to Bush Bush National Park which is part of Somalia. Serengeti-Mara and Tsavo-Mkomazi are considered as lion strongholds and are therefore of major importance for lion conservation (Riggio *et al.*, 2012). In Africa, only ten lion areas qualify as lion strongholds, containing 24,000 lions (Riggio *et al*., 2012). Lion populations are able to recover quickly when offered enough protection and space, but this is rarely possible when surrounded by human settlements, because of the constant threat lions pose to the local communities and their livestock (Patterson *et al*., 2004).

Table 1: Estimates of lion numbers in different areas in Kenya, based on Chardonnet (2002), Bauer & Van der Merwe (2004) and Riggio *et al.* (2012). Lion areas in bold are considered as lions strongholds. *refers to estimates of cross-border areas, e.g. Serengeti-Mara. The total estimate by Riggio *et al.* (2012) is therefore an overestimation of the lion population size in Kenya.

Area	**Chardonnet *et al.*, 2002**	**Bauer & Van der Merwe, 2004**	**Riggio *et al.*, 2012**
Aberdares NP	162	7	
Amboseli NP	130	20	
Arawale			750*
South, East of Rift Valley		20	
North, East of Rift Valley	271	650	
Galana Game Ranch		150	
Nairobi NP	22		
Hells Gate & Kedong	9		
Lake Nakuru NP	37		
Laikipia plateau	362	120	271
Masai Mara NP	547	558	3673*
Surrounds of Masai Mara	394		
Meru Complex	65	80	40
Tsavo NPs	750	675	880*
Total	**2749**	**2280**	**5614***

Based on the latest published phylogeographical study of lions, the traditional split between Asian and African Lions as distinct subspecies is no longer acceptable (Barnett *et al*. 2014; Bertola *et al*., 2016). Studies on analyses of mtDNA and nuclear DNA sequences suggested that the western and central populations of the African lion are genetically more related to the Asiatic lion than the eastern and southern populations (Barnett *et al*. 2014; Bertola *et al*., 2016; Henschel *et al.*, 2014). A different split into two subspecies, *Panthera leo leo* (Asia and West and Central Africa), and *Panthera leo melanochaita* (South and East Africa) is recently accepted by the IUCN Cat Specialist Group (Kitchener *et al.*, 2016).

Lions are considered Vulnerable on the IUCN Red List (IUCN, 2016); however trends differ across their range: there is an increase in the number of lions in southern Africa and in India, but a decline in West, East and Central Africa (Bauer, 2016 IUCN). This dichotomy is reflected in listings of the species in different Red Lists of threatened species. On the regional level, the lion is recognized as Least Concern in South Africa (Bauer *et al.* 2015a; Miller *et al.*, 2016), whereas it is Regionally Endangered in Central and East Africa (Bauer *et al.* 2015a). In India, the lion is considered Endangered (Breitenmoser *et al.* 2008) and in the region of West Africa, it meets the criteria for Critically Endangered (Bauer *et al.*, 2015a; Henschel *et al.* 2014).

Social structure

Lions live in so called fission-fusion social units (prides). Prides engage in group foraging and defend their territory and young collectively (Packer, 1990). They can be subdivided in 'semi-permanent sub prides' dispersed throughout the pride range, possibly because this may increase hunting success and decrease competition for food (Schaller, 1972; Bauer, 2003). This fission-fusion results in different home ranges for the individual pride members (Schaller, 1972). A pride of lions consists of 2-35 animals, with 2-18 related females and 1-7 males, and their offspring. The males can either be related or unrelated (Schaller, 1972; Van Orsdol *et al.* 1985). The composition of a pride is usually more or less stable for several years and is primarily affected by birth, death, emigration of sub-adults and take-over by non-resident coalitions of males (Pusey & Packer, 1983; 1987). In contrast to females, males never stay with the same pride throughout their lives. Males associate with a pride to reproduce and protect their offspring, typically staying in charge of a pride for about 2-2.5 years (Schaller, 1972); the time a generation of cubs needs to reach sub-adulthood. During male takeovers, the new male may kill or evict all cubs and juveniles in a pride to increase their own reproductive output (Van Orsdol *et al.*, 1985; Hanby & Bygott, 1987). Lions evicted from a pride may become nomadic (Grinell *et al.*, 1995).

Several factors influence groups and prides composition. Van Orsdol *et al*. (1985) pointed out that pride structure is correlated to food availability especially during the period of lowest prey availabilty, usually the wet season. Besides environmental factors, anthropogenic activities inside and outside protected areas affect the social structure as well (Loveridge *et al*., 2007; Loveridge *et al*., 2009). This may be one explanation for the disturbed social structure observed in Nairobi National Park (Lattuada, 2012; Kral, 2014; Gatta, 2016).

Home range and movements

A lion's home range is defined as "the area transversed by the individual in its normal activities of food gathering, mating and caring for the young" (Burt, 1943). The core of its home range is defined as the most intensely used area within the animal's home range (Powell, 2000). That part of a home range that is avoided by other lions or where other lions are driven away by the owner is called a territory (Schaller, 1972). Sizes of pride home ranges vary greatly but mostly fit within the values of 20 to 400 km² (95% KDE) found by several studies in eastern and southern Africa (Loveridge *et al*., 2009; Schaller, 1972; Tuqa *et al*., 2015; Van Orsdol *et al*., 1985). Home ranges in West Africa are generally larger (Stander, 1991), varying between 256 km² in Pendjari Biosphere reserve, Benin (Sogbohossou, 2011) and 641 km² (95% KDE) in Waza National Park, Cameroon (Tumenta *et al,* 2013a)). Home ranges can be very large in arid and hyper-arid areas (4500 km² (95% KDE) in the Kgalagadi Transfrontier Park, Botswana (Funston, 2001); 7337 km² (95% KDE) in the Kunene Region, Namibia (Stander, 2006)). Large home ranges overlap extensively with those of adjacent prides, while small ranges tend to have little overlap (Van Orsdol *et al*., 1985).

Home ranges are defined by resources and mainly influenced by prey availability (Bauer & de Iongh, 2005. Gittleman & Harvey, 1982). Other factors such as social status and structure, sex, age, season, habitat quality, disturbance and the presence of livestock influence their home range as well (Loveridge *et al*., 2007; Ogutu & Dublin, 2002; Schaller, 1972; Tumenta *et al*., 2013b). Contraction and expansion of home ranges occurs in response to prey availability to maintain a relative constant prey biomass within the home range (Bauer & de Iongh, 2005; Loveridge *et al*., 2009; Tumenta *et al*., 2013a; Tuqa *et al*., 2015; Van Orsdol *et al*., 1985). When the rainy season starts, water becomes more available and the native prey starts to disperse. This temporary change in prey densities causes an increase in lion's home range in the search for food, and this is when livestock attacks can occur in reaction to the reduced native prey density (Ogutu & Dublin, 2002; Patterson *et al.*, 2004). It is suggested that the size of the home range and distance travelled by lions negatively correlates with the density of native prey and available surface water (Ogutu & Dublin, 2002; Tuqa *et al.*, 2015). Home ranges of male lions are generally larger than those of females (Tumenta *et al.*, 2013a; Van Orsdol *et al.*, 1985). Males may defend a large home range that covers that of two or more female prides (Van Orsdol *et al.*, 1985). Reason for this is that lionesses defend the resources they need to sustain themselves and defend and raise their cubs. Their home range includes areas in which to conceal small cubs and access to areas frequented by prey animals, and can be defined as the pride's territory (Funston *et al.*, 2003). Territorial males, on the other hand, defend an area so as to have sole access to (a) group(s) of lionesses, and in so doing protect their cubs (Funston *et al.*, 2003).

Activity patterns of both nomads and pride members are similar. It peaks between 17.00 h and 8.00 h, although hunting, feeding and mating may occur at all times of the day (Schaller, 1972). On average, two hours a day is spent walking and 40 to 50 minutes of a day are spent eating (Schaller, 1972). The rest of the day, about 20 to 21 hours, the cats are largely inactive (Schaller, 1972). Of course, large variation between days exists where, for example, several days of not feeding may be followed by a night during which 5 to 6 hours may be spent on feeding after a kill (Visser, 2011).

Human – lion conflict

Where contacts with humans and livestock are frequent, lions regularly include livestock in their diet, causing human-lion conflicts. With the rapid growth of human populations, the protected areas to which most lion populations are confined are surrounded by human settlements and livestock areas (Tuqa *et al.*, 2015). The relatively small size of protected areas is not enough to contain the large home range of lions (Brashares *et al.*, 2001). The degradation of habitat, depletion of natural prey and the proximity of relative easy prey (livestock) favour a shift in the lion's diet towards livestock (Sogbohossou, 2011). Human-lion conflicts are not limited to livestock predation, but also imply attacks on humans and, in response, retaliatory killings of lions. This all may induce negative perceptions towards carnivores (Hemson *et al.*, 2009; Tuqa *et al.*, 2015). In Nairobi National Park for example, livestock represented 10 to 25% of the lion's diet (Beveridge, 2012; Fonk, 2014; Nooteboom, 2016; Tommissen, 2017) and in 44.73% of the attacks on cattle, lions were responsible (Gatta, 2016). In Tsavo East National Park, Kenya, livestock represented ca. 5.8% of the lion's diet and 85.9% of the attacks on cattle were caused by lions, resulting in high costs for local farmers (Patterson *et al*., 2004). Similar results were found in the Pendjari Biosphere Reserve in Northern Benin, where lions were the main predator of livestock (78.9% of all attacks) (Sogbohossou, 2011). Consequently, local farmers in the proximity of lions often suffer substantial losses to depredations, frequently followed by persecution and retaliatory killings, either by authorities (problem animal killings) or by locals (poaching) (Bauer & de Iongh, 2005; Van Bommel *et al*., 2007). In some areas, e.g. Nairobi National Park, local farmers receive a certain amount of money to compensate for the economic impact of their losses, to increase tolerance and prevent killings (Hemson, 2003). However, it has to be considered that increasing tolerance for a conflict is not a long term solution. Therefore, a strategy of prevention, mitigation and compensation based on an understanding of factors leading to these attacks is important.

Livestock attacks are more common during the rainy season, because water becomes available everywhere and native prey disperse, temporary depleting the local prey base (Ogutu & Dublin, 2002). The temporary reduction in prey causes an increase in lion home range and native prey may be replaced by livestock (Ogutu & Dublin, 2002; Patterson *et al*., 2004; Tumenta *et al*., 2013a; Woodroffe & Frank, 2005;). Livestock predation brings lions in direct conflict with humans. Predator density and the availability of wild prey are important factors influencing this livestock predation. However human activities, husbandry practices, seasons, distances to park boundaries, number of livestock in a village and attitudes of local livestock owners towards these livestock losses can be of influence as well (Van Bommel *et al*., 2007). Lions avoid bomas (livestock enclosures) with high levels of human activity at night (Ogada *et al*., 2003; Oriol-Cotterill *et al*., 2015; Woodroffe & Frank, 2005). Two studies based on GPS data (Oriol-Cotterill *et al*., 2015; Valeix *et al*., 2012) have found that lions modify their behavioural ecology and space use when in human-dominated landscapes, switching their movement patterns and activity peak times to avoid encounters with humans, due to the risk of injury or death.

In the boundaries of Nairobi National Park, a novel system imitating humans on watch around bomas was created by an 11 year old local schoolboy, Richard Turere. He observed that lions avoided flashing lights as they mimic human activity. These lights have now been installed on several bomas surrounding the park. Fonk (2014) and Gatta (2016) found that bomas with flashlights had almost no attacks after the installation of this system. In addition, geofencing of collared lions can help as well to prevent livestock attacks. This implies that if lions approach a livestock boma within 500 m, an SMS alert will be sent to the researchers so that rangers can chase the lions back to the park.

Research objectives

Lions have intrinsic value, are important (as a keystone species) in structuring terrestrial communities and form a crucial component of Africa's tourism industry (Woodroffe & Frank, 2005; Ogada *et al.*, 2003). Protecting lions from extirpation or total extinction is therefore crucial, and understanding lion-livestock conflicts and mitigating them is essential for the success of both social and conservation efforts (Patterson, 2004, Woodroffe, 2000; Woodroffe & Frank, 2005 and Van Bommel *et al.*, 2007).

My research contributes to a PhD study implemented by Francis Lesilau of Kenya Wildlife Services. It builds on the work of previous students in the Nairobi National Park (Lattuada, 2012; Beverigde, 2012; Kral, 2014; Fonk, 2014; Gatta, 2016; Nooteboom, 2016). My study focuses on the home range and movements of lions during the dry season. I aim to get insight in the factors influencing home range and the increase in frequency of livestock conflicts around the National Park. Geographical positioning data are useful in generating answers to important conservation questions, such as to what extent lion ranging is affected by human and livestock distribution around the Park (Visser, 2011). Because of the high human pressures in and around Nairobi National Park, I expect that this has its severe effects on the ecology of the lion population. Based on previous research, I expect to see a disturbed social structure of the lion population. The presence of livestock around the park will also influence the lion home ranges and their movements. Therefore I expect that human-lion conflicts in Nairobi National Park will increase in time and space, especially during the wet season. More knowledge about the daily lion movement patterns and how they are influenced by the present livestock can help in an early warning system for the local people.

I defined the following research questions:

1. Lion population size and structure in time and space

    1.1. What is the current lion population size?
    1.2. What is the male:female ratio?
    1.3. What is the adult:juvenile ratio?
    1.4. Is there any clear pride structure?

2. Lion movements and home range in time and space

    2.1. What are the home range estimators for the different lions?
    2.2. Which factors influence home ranges?
    2.3. Which factors influence movements?
    2.4. Which type of habitat do lions prefer?

3. Human-lion conflict

    3.1. How often, and when, do lions leave the park?
    3.2. Which factors influence livestock raiding behavior?
    3.3. Is there avoidance of flashlight's bomas?
    3.4. Is geofencing of collared lions an effective early warning system?

Material and methods

Study area

The Nairobi National Park (NNP), established in 1946, is situated in the Nairobi Province, Kenya. With a surface of 117 km², the park is small in comparison to most of Africa's national parks. Altitude ranges between 1533 meters and 1760 meters (Foster and Coe, 1968). Nairobi National Park has a subtropical highland climate: evenings may be cool, especially in the June/July season, when the temperature can drop to 9 °C (Foster and Coe, 1968). The sunniest and warmest part of the year is from December to March. Rainfall is bi-modal with a period of long rains from March until May, and another period of short rains from October until December (Foster and Coe, 1968). As the national park is situated close to the equator, the differences between the seasons are minimal (Foster and Coe, 1968).

Located only 7 km south of Nairobi city, the park is one of the very few protected areas with large mammals in the world close to a capital city. There is electric fencing around the park's northern, eastern and western boundaries (Fig. 1). Its southern boundary is formed by the Mbagathi River. This boundary is not fenced and is open to the Kitengela Conservation Area (located immediately south of the park) and the Athi-Kapiti plains. There is considerable movement of large ungulate species across this boundary. And in this area, lion-livestock conflicts occur. Livestock is prohibited in the park and legislation states that any domestic animal within the parks boundaries should be shot. But livestock still is around the park as they are the basic livelihood of the local inhabitants.

The savannah ecosystem comprises a variety of vegetation types (Table 2; Fig. 1), but open grass plains with scattered acacia bush are predominant. The western side has a highland dry forest and in the south is a permanent river with riverine woodland. Many wildlife species are present, including large predators like lion (*Panthera leo*), spotted hyeana (*Crocuta crocuta*) and leopard (*Panthera pardus*) and large herbivores such as Cape buffalo (*Syncerus caffer),* zebra (*Equus quagga*), wildebeest (*Connochaetes taurinus*), white and black rhinoceros (*Ceratotherium simum* & *Diceros bicornisand*) and giraffe (*Giraffa camelopardalis*).

Table 2: Habitat types in Nairobi National Park (KWS GIS and Biodiversity Office, 2011).

Type	area (km²)	area (%)
bushland	13.03	11.18%
open forest glades	1.38	1.18%
forest	10.92	9.37%
mellifora shrubland	13.44	11.53%
open grassland	33.12	28.41%
riverine woodland	5.05	4.33%
scattered tree grassland	12.48	10.70%
whistling thorn shrubland	27.17	23.30%
Total	116.57	100.00%

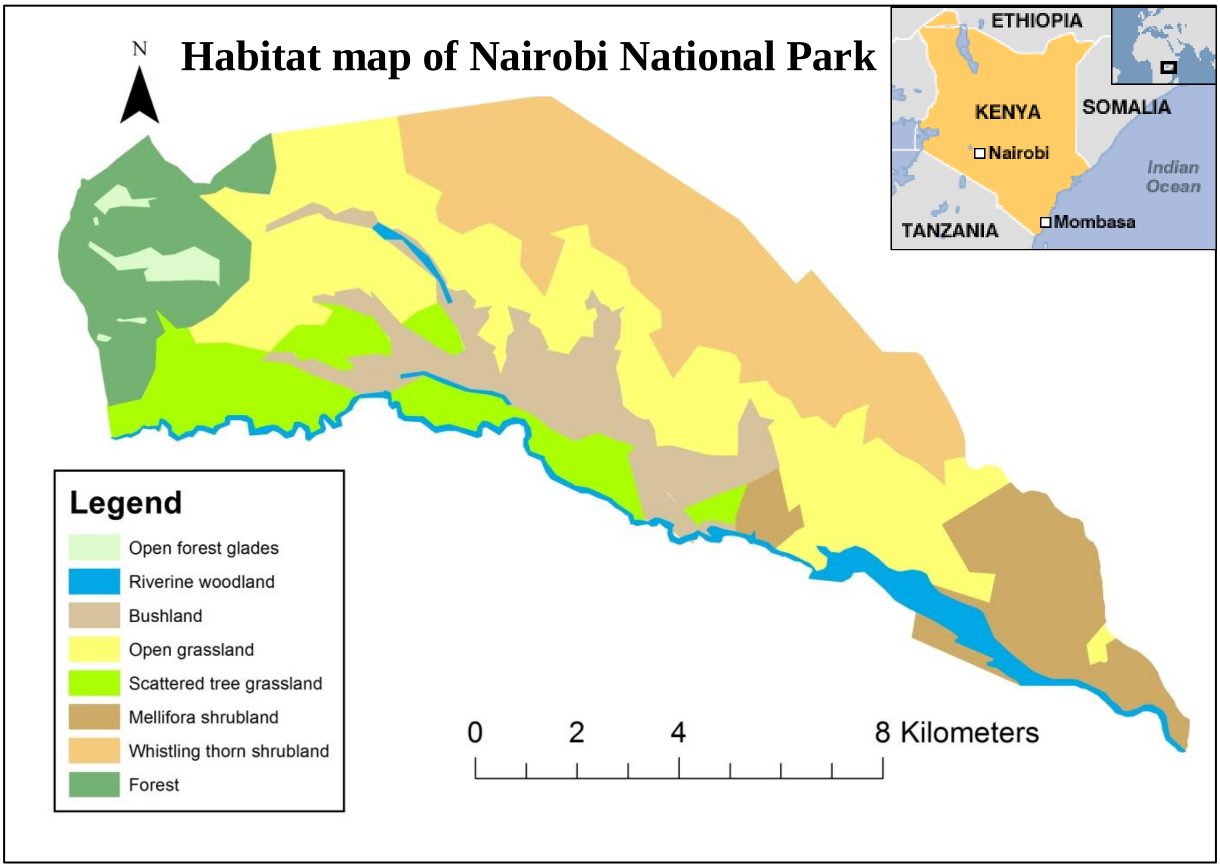

Fig. 1: Habitat map of Nairobi National Park, designed in Arcmap 10.3.1 (ESRI Software, U.S.A.). (Data from KWS GIS and Biodiversity Office, 2011).

Lion collaring

To study the lions' home ranges and movements, HAWK-VHF Iridium satellite collars with GPS and VHF functions were fitted onto lions resident in NNP (Table 3). The collars were programmed to collect the GPS location of animals at 3-hour intervals. The GPS collars recorded date, time, temperature, longitude and latitude of each lion. VHF radio techniques were used to make direct observations of individuals. Data was used from the 7th of July until the 6th of October 2016, during the dry season. During our research, the collar L1 had only the VHF function operative. L2 died in October 2015.

Table 3: Overview of lion collarings in Nairobi National Park. No. of GPS fixes represents the fixes during this research period.

Lion ID	**Collar Frequency**	**Gender**	**Start Collaring**	**End of Collar**	**Estimated birth year**	**No. of GPS fixes**
L1 **Nelly**	150.5692	F	25/01/2014	25/5/2015 (active in VHF)	2000/01	/
L2 (†7/10/2015) **Kiprono**	150.7701	M	26/01/2014	† 7/10/2015	unknown	/
L3 **Dirk**	150.6400	M	02/02/2015	30/12/2016	2009/10	722
L4 **Alex**	150.0500	M	02/02/2016	(active)	2005	721
L5 **Bertine**	150.6200	F	02/02/2016	(active)	2006/07	674
L6 **Mumbi**	150.2612	F	26/02/2016	(active)	2004/05	735
L7 **Nina**	150.7800	F	12/07/2016	(active)	2006/07	728

Lion population size and social structure

From the 7th of July until the 6th of October 2016, fieldwork was carried out in the Nairobi National Park, in order to investigate the current lion population. Direct observations of lions took place during the whole day, with a focus on the hours that lions are most active. Fieldwork was done mainly during weekdays. Methods used, covered both direct opportunistic observations in the field and homing in on collared lions, using their last recorded GPS position. In order to find lions, people situated in the park (tourists, rangers etc.) were asked about the locations of possible lion sightings.

When a lion was encountered, the latitude and the longitude of the location were noted making use of a GPS (Garmin eTrex 10). Lions were visually and approximately aged into the following categories: cubs (0 – 1 year), juveniles (1 - 2 year), subadults (2 - 4 year) and adults (> 4 year), following Schaller (1972). Additional notes were made on date, time, sex, health status, habitat, behavior, and if the lion was in a group, on the composition of that group. All lions were identified to the individual level by investigating typical characteristics such as marks, scars and ear notches. A database of all lions observed by Gatta (2016) was available for identification. When no clear marks were present, additional use was made of counting the whisker spots on both sides of the face, according to Pennycuick & Rudnai (1970). As the whiskerspot pattern can change with growth, this method was only used for adult and sub-adult lions (Pennycuick & Rudnai, 1970). Therefore, cubs could not always be identified to the individual level.

To examine the social structure, a similar method was used as in Gatta (2016), allowing comparisons. A dendrogram was created, based on a dissimilarity matrix for every group sighting. Data was slightly modified in order to create a dendrogram which is consistent with the observations during the fieldwork.

Lion movements, home range analysis and habitat use

GPS data were downloaded at the end of the study from the website "Africa Wildlife Tracking" (http://www.awt.co.za/). Movements were analyzed in Microsoft Office Excel 2010 (Microsoft, U.S.A). Distance between two fixes was calculated as a straight line between those two points; this was considered as the potential minimum distance (m) travelled in three hours, however this is an underestimation.

Data points were plotted and analyzed using Arcmap 10.3.1 (ESRI Software, U.S.A.). Home ranges were estimated using the 'Kernel Density Estimator' (KDE). This method considers the density of locations; the areas were defined as 95% (the boundary of the lion's home range), 50% (the core home range) and 5% (the heart of the core area) (Visser *et al*., 2011).

For the habitat use analysis, a vegetation map of Nairobi NP was designed (Fig. 1), using data available from KWS GIS and Biodiversity Office (2011). The map was used to assign a vegetation type to each fix. With the proportion of time spent in each type of vegetation, habitat preference can be assessed based on Manly's selection index (Manly *et al.*, 1993). The selection index is measured by the formula: $w_i = {}^{o_i}/_{p_i}$

where w_i = Ratio for vegetation type *i* (Table 2)

o_i = Proportion or percentage of time spent (corresponding to number of fixes) in vegetation *i*

p_i = Proportion or percentage of vegetation *i* available in the environment

Values above 1.0 indicate preference while values less than 1.0 indicate avoidance. The standardized index B_i allows comparisons: $B_i = {}^{w_i}/_{\sum_{i=1}^{n} \hat{w}_i}$

where B_i is the standardized selection index for vegetation *i* and $\hat{w}_i$ 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.

Human – lion conflict

Coordinates of boma locations with and without flashlight system were plotted and compared with the home range estimators to see if there is avoidance behavior of lions to flashlight bomas. Fixes outside the National Park were analyzed in detail and some characteristics were identified such as the number of fixes outside the park, the number of times a lion went outside the park (called an event), the duration of an event (<12h, 12h-24h, >24h), number of nights an event lasted (in case >24h), distance from the park boundary and the distance from a boma. An event was characterized by analyzing the consecutive GPS fixes outside the park, including the last data point in the park and the first data point back in the park.

Data analysis and statistics

Statistical tests were carried out using the software R version 3.0.2 (R Foundation, Vienna, Austria). For all tests, a significance level of ($p < 0.05$) was used. Normality was tested by using the Shapiro-Wilk test ($W > 0.9$). The Pearson correlation coefficient was used to test the correlation between distance travelled and temperature. The Kruskal-Wallis test was used as a non-parametric alternative for ANOVA, to test differences in home range size between months. The paired Wilcoxon test was used as a non-parametric alternative for the paired t-test to test differences in home range size between the wet and the dry seasons. All tests (except Pearson correlation test) were carried out using a very small sample size and have therefore little statistical power.

Results

Lion population size and social structure

In total, 107 lion observations were recorded during twelve weeks. Throughout this period, 37 lions were identified. During my research period, one lion cub (1 year old) was trapped in a snare around a boma on the 19th of July 2016. The total density of lions in the park was 32 lions per 100 km², when cubs (< 1 year) were removed; the density was 26 lions per 100 km².

Of all subadult and adult lions (> 2 year), 11 females and 6 males were identified, resulting in a female:male sex ratio of 1.83:1. The adult to juvenile ratio was 1:1.18. (12 adults, 5 sub-adults, 20 juveniles).

Solitary adult lions (> 2 year) were observed 52 times (31 observations were solitary lionesses with juveniles). Groups of adult lions (≥ 2) were observed 50 times (Fig. 2). Juveniles alone were observed 5 times. The mean adult group size observed was 1.6 adult lions.

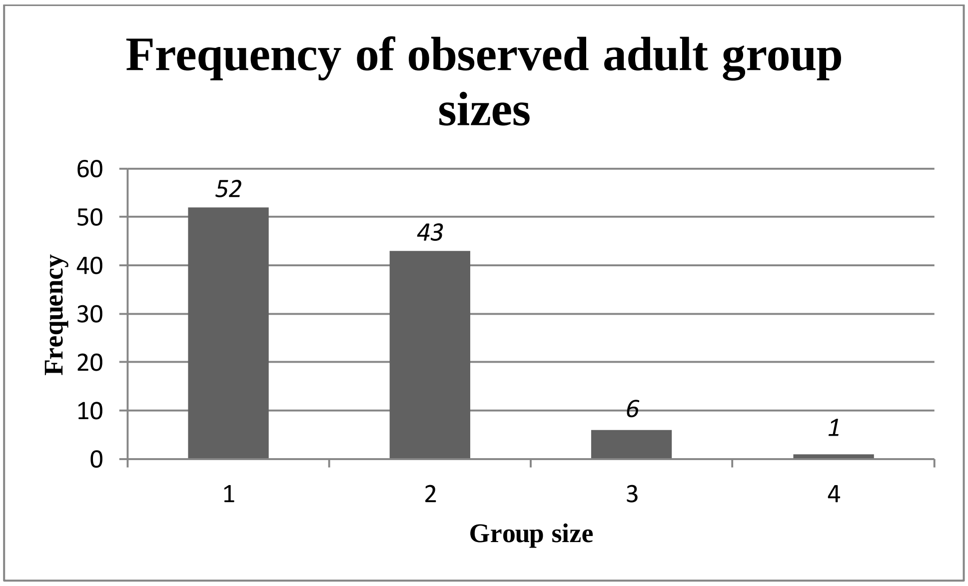

Fig. 2: Frequency of observed adult group sizes.

I identified three different prides in the park, situated in the western part (“Kingfisher pride”), the middle part (“middle pride”) and the southeastern part (“Athi pride”). The dendrogram in Fig. 3 confirms this, although a clear pride structure as described in literature is not present. All three pride males (L3 (Dirk), and the coalition L4 (Alex) and a male lion called Cheru) were part of Kingfisher pride, which consisted out of five lionesses, plus a coalition of two male subadults (Tall Boy and Pretty Boy). The grouping closest to the base is not entirely accurate as it contains a grouping of two lionesses (Neema and Elsie) which were never observed together. However, they were most often observed around the Kingfisher area, and thus believed to be part of this pride. The middle pride consisted of three lionesses (Nina, Bertine and Bertine's mom) with juveniles, but without a pride male. In the southern part, I observed during the first months of this research only one lioness (L1 - Nelly) with her grown up cubs. But near the end of the research period, a male sub-adult lion (MP1) was observed mating with this lioness. MP1 (middle pride sub-adult 1) previously wandered around with two subadult lionesses (MP2 and MP3) in the middle part of the park.

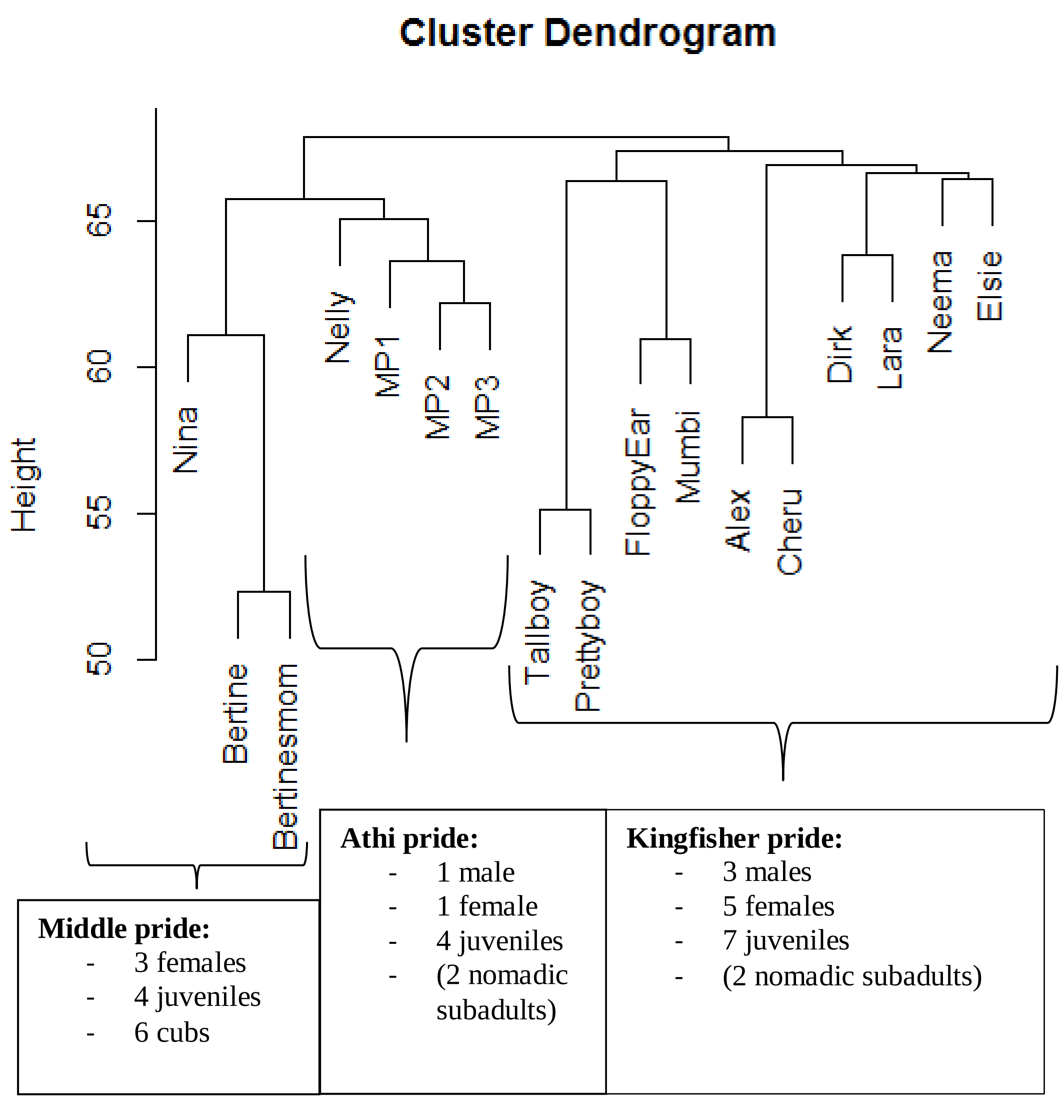

Fig. 3: Dendrogram of the social structure of lions in Nairobi National Park.

Lion movements, home range analysis and habitat use

When analyzing movements, it became apparent that L4 (Alex) travelled the largest distances (both average and maximum) in 24h (Table 4 and Fig. 4). This was also observed during fieldwork. Very often after sunset, L4 (Alex) started walking around and started with marking his territory. This was not observed with pride male L3 (Dirk), which traveled considerably shorter distances during 24h, equal to distances covered by L6 (Mumbi) and L7 (Nina). L5 (Bertine) was the lioness which travelled the least. An overview of distances travelled by the different lions is given in Table 4 and Fig. 4.

Table 4: Overview of average and maximum distance (± s.d.) in meters travelled per 24hr for the collared lions (n = 90).

Distance travelled per 24h (m)						
ID	L3 Dirk	L4 Alex	L5 Bertine	L6 Mumbi	L7 Nina	**Average**
Gender	M	M	F	F	F	
Average	4835 (± 2812)	8114 (± 4818)	3288 (± 2070)	5295 (± 3592)	4464 (± 2798)	5290 (± 1791)
Maximum	12119	23692	8813	20854	12310	16417

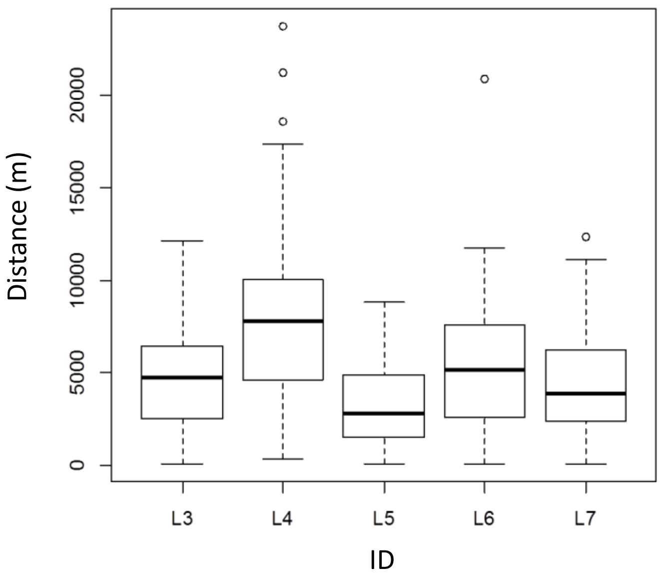

Fig. 4: Mean daily distances in meters travelled by the collared lions.

Activity patterns show peaks during night time and a dip during the heat of the day (Fig. 5). A significant difference between distances travelled by different temperatures was found to explain this observation ($F = 536.44$, $p < 0.001$).

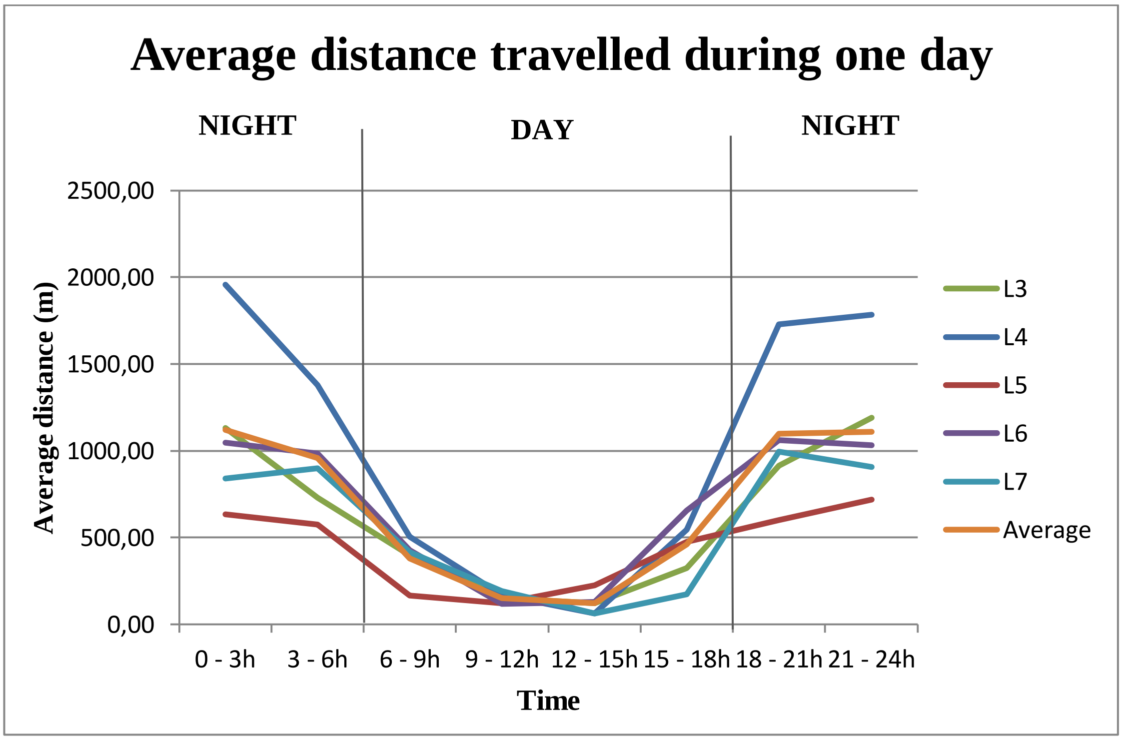

Fig. 5: Average distance travelled over 24h. The graph shows increased activity at night.

An overview of the Kernel Home range Estimators (95%, 50%, 5%) is given in Table 5 and Fig. 6. Male lions tend to have smaller home ranges compared to the lionesses in Nairobi National Park. However when analyzed per month (Table 6), this difference is not significant (χ^2 = 5.9667, p = 0.2017). Remarkable is the overlap of home range between L3 and L4, two rival males. This was also already suggested by the dendrogram (Fig. 3).The overlapping area of their home ranges is no less than 13.92 km², which is almost half of the home range of L3, and even more than half of the home range of L4. L6 is also part of the same pride and has a big overlap with these two male lions. L5 and L7, part of middle pride, show also a large overlap in home range. These two lionesses have a considerable part of their home range outside the park, respectively 26.36% for L5 and 14.45% for L7. L3 and L6 also include an area outside the park in their 95% KDE. However, these areas do not seem to be used often, given the low amount of GPS fixes in that area.

Table 5: Home range estimates for the collared lions, using Kernel Density Estimations.

ID	Gender	KDE 95%	KDE 50%	KDE 5%	Number of fixes
L3 (Dirk)	M	28.73 km²	1.06 km²	0.05 km²	722
L4 (Alex)	M	22.94 km²	1.86 km²	0.10 km²	721
L5 (Bertine)	F	32.29 km²	1.17 km²	0.06 km²	674
L6 (Mumbi)	F	60.94 km²	7.46 km²	0.12 km²	735
L7 (Nina)	F	43.86 km²	2.13 km²	0.08 km²	728

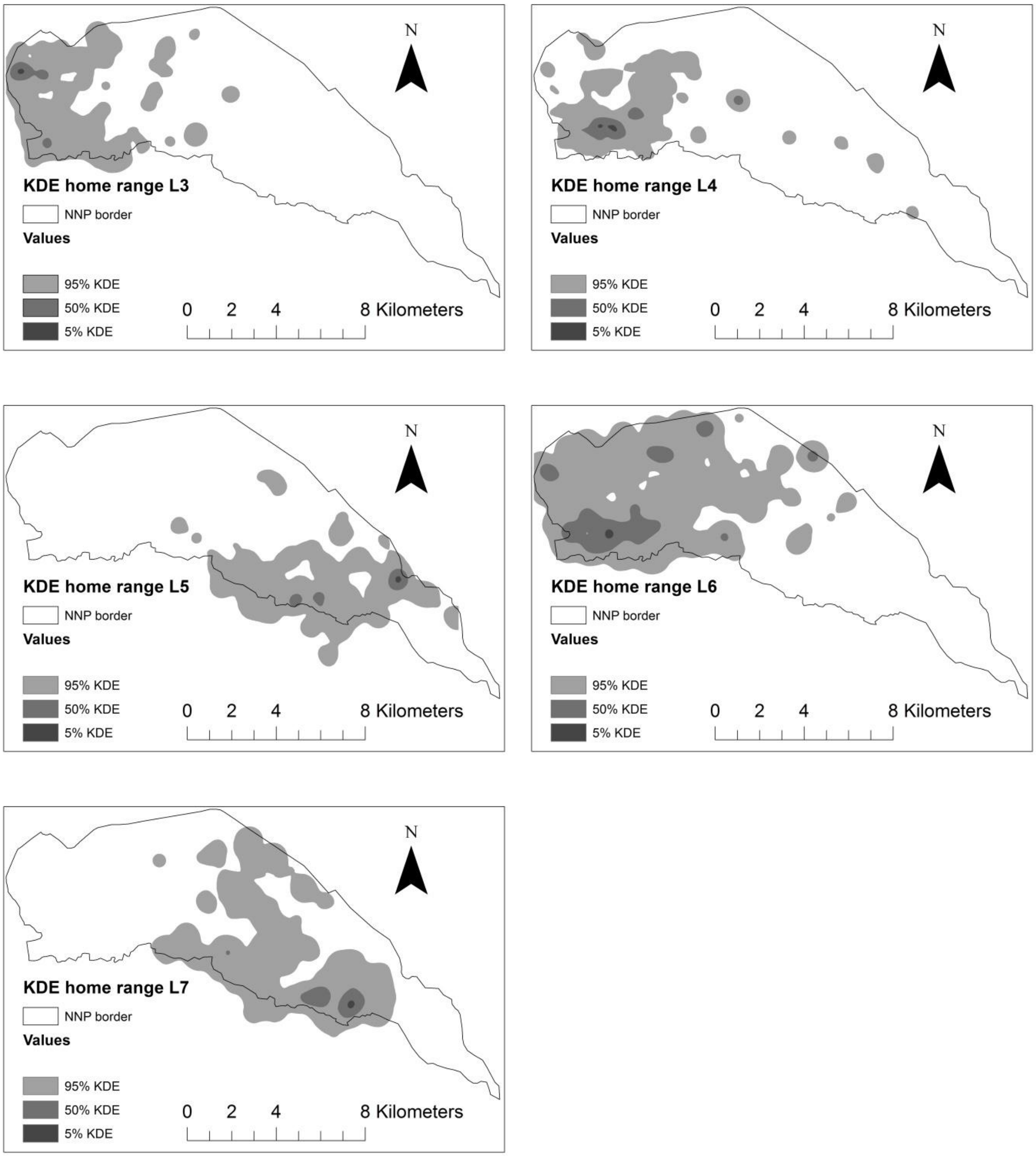

Fig. 6: Kernel Density Home Range Estimators for the different collared lions.

Home range sizes between months do not differ significantly ($\chi^2 = 0.38$, $p = 0.827$). Differences in rainfall between these months are small compared to rainfall during the wet season (monthly peaks up to 160 mm and above). However, compared with home range sizes during the wet season (Gatta, 2016), there is also no significant difference found ($p = 0.625$). Note that sample size was very small (n=4).

Table 6: KDE 95% home range size between months.

ID	KDE 95%		
	July	August	September
L3	34.57 km²	30.88 km²	11.57 km²
L4	17.78 km²	24.84 km²	15.73 km²
L5	12.82 km²	22.51 km²	24.04 km²
L6	57.66 km²	50.87 km²	31.08 km²
L7	22.40 km²	22.62 km²	57.19 km²
Average	29.05 km²	30.34 km²	27.92 km²
Monthly rainfall (mm)	0	8	2

Lions in Nairobi National Park preferred mainly 'Scattered tree grasslands', followed by 'Open forest glades' and 'Forest' (Table 7). 'Mellifora shrubland', 'Whistling thorn shrubland' and 'Outside' have the lowest values in general, indicating avoidance of these habitats. However, habitat preference differs strongly between individuals. Note that 'Outside' is not a real habitat type, but contains the area outside the park.

Table 7: Habitat selection indices. w_i selection index: Values above 1.0 indicate preference while 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) indicated relative avoidance while values above indicate relative preference. Indices in bold show habitat preferences, grey boxes show the highest index per lion. 'Outside' is in italic as it is not a real habitat type.

Habitat type	L3 Dirk		L4 Alex		L5 Bertine		L6 Mumbi		L7 Nina		All lions	
	w_i	B_i	w_i	B_i	w_i	B_i	w_i	B_i	w_i	B_i	w_i	B_i
Bushland	0.421	0.037	0.372	0.040	0.836	**0.129**	0.596	0.068	**1.115**	**0.176**	0.666	0.079
Open forest glades	**3.042**	**0.268**	**1.758**	**0.190**	0.000	0.000	**1.839**	**0.211**	0.000	0.000	**1.347**	**0.159**
Forest	**4.540**	**0.400**	**1.496**	**0.162**	0.000	0.000	**2.063**	**0.236**	0.000	0.000	**1.643**	**0.194**
Mellifora shrubland	0.000	0.000	0.000	0.000	**1.107**	**0.171**	0.000	0.000	0.889	0.111	0.388	0.046
Open grassland	0.488	0.043	**1.055**	0.114	0.971	**0.150**	**1.020**	0.117	**1.399**	**0.175**	0.987	0.117
Riverine woodland	0.320	0.028	0.192	0.021	**2.022**	**0.312**	0.220	0.025	**1.248**	**0.156**	0.782	0.092
Scattered tree grassland	**2.381**	**0.210**	**4.329**	**0.467**	0.915	**0.141**	**2.416**	**0.277**	0.893	0.112	**2.204**	**0.261**
Whistling thorn shrubland	0.101	0.009	0.042	0.004	0.407	0.063	0.549	0.063	0.737	0.092	0.367	0.043
Outside	*0.061*	*0.005*	*0.017*	*0.002*	*0.223*	*0.034*	*0.033*	*0.004*	*0.054*	*0.007*	*0.075*	*0.009*

Human – lion conflict

Analyzing movements of lions in the area outside the national park showed some interesting aspects of their behavior (Table 8). The percentage of GPS fixes outside the park was calculated and events were categorized per timespan and per distance. On average, lions were 6.87% of their time outside the park, which is quite low. However, L5 had a much higher percentage outside the park (23.44%), while L2 was almost never outside the park (0.28%). In most cases, lions did not go further than 500m of the park boundary.

Table 8: Summary of details on the number of events lions leaving the park.

ID	Total no. of GPS fixes	No. of GPS fixes outside	% GPS fixes outside	No. of events	<12h	12h-24h	> 24h	No. of nights	> 500m park boundary	nights <250m boma
L3 Dirk	722	35	4.85%	6	1	3	2	**9**	3	0
L4 Alex	721	2	0.28%	1	1	0	0	1	0	0
L5 Bertine	674	158	**23.44%**	**17**	4	4	9	**32**	**12**	**6**
L6 Mumbi	735	17	2.31%	3	1	1	1	4	1	0
L7 Nina	728	34	4.67%	**10**	8	1	1	**11**	3	**2**
Total	3580	246	6.87%	37	15	9	13	57	19	8

From the analyses (Table 8) it became clear that L5 and L7 went much more outside than the other lions. As said before, they have also a considerable part of their home range outside the park (see Fig. 6 and Table 5). L5 and L7 always went outside in the area southeast of the park, where the community lands are. Both lionesses came several nights within 250m of a boma. The closest distance L5 came to a boma was 154 m and for L7, this was 61 m. However GPS fixes were only available every three hours and therefore there are strong possibilities that they went even closer or entered a boma, and during more nights. Remarkably, in the rare event when a lion came within 250 m distance of a boma, the boma was equipped with a flashlight (L5: 5 out of 6 bomas were equipped with a flashlight; L7: Both bomas she approached, had flashlights).

Another interesting observation is that L5 stayed more often longer times outside the park compared to L7. L7 mainly made short raids outside the park, lasting less than 12 hours, while L5 spend 9 out of 17 events more than 24 hours outside the park. The longest stay of L7 outside the park lasted from 08/07/2016 22:22h until 14/07/2016 4:23h. During this period, she approached a boma (< 250m) for four consecutive nights. L7 also went more times further than 500m of the park boundary, with a maximum of 2025m on 27/07/2016.

L3, L4 and L6 had few events outside the park. When they left the park, they went outside in the southwest of the park. The number of events L3 went out of the park may be alarming, because of the dense human population in this area.

Discussion

Lion population size and social structure

With 26 adult lions/100km², the lion density is well above the average density of lions in East Africa (16.2 lions/100km² - Woodroffe & Ginsberg , 1998), and is much higher than the mean lion density of West Africa (1 – 3 lions/100 km2 - Bauer & van Der Merwe, 2004). Higher estimates are found in Masai Mara National park, Kenya (37 lions/100km² - Ogutu *et al.*, 2005) and in the Ngorongoro Crater, Tanzania (38.8 lions/100km² - Hanby *et al.*, 1995). The high lion density is related to the high prey abundance and prey biomass present in Nairobi National park, compared to other lion areas (Beveridge, 2012; Fonck, 2014). High prey availability will have either a direct effect on the number of individuals a pride can maintain, or as an indirect effect on the number of prides that can occur in the same area (Ogutu and Dublin, 2002). In addition, the high density of lions can also be caused by the low density of competitors. The spotted hyena *(Crocuta crocuta)* is known to be a serious food competitor for lions, especially for middle-sized prey (Bauer *et al*, 2008; Trinkel *et al.*, 2005). When hyenas' clan sizes are small, they seem to be unable to recruit sufficient clan members to take over lion kills or deter lions from their own kills (Trinkel *et al.*, 2005).

The lion population size of Nairobi National Park fluctuated slightly over the years, yet the density of adult lions increased and the number of cubs per adult stayed more or less stable (Table 9). This indicates that the population is still capable to grow, which makes the occurrence of human – lion conflicts only more likely to happen. The observed sex ratio (0.55) in Nairobi National Park lies close to what is described in literature, which is around 0.3-0.5 male per female (Schaller, 1972; Ogutu & Dublin, 2002; Bauer, 2003, Tuqa *et al.*, 2015). Van Orsdol *et al.* (1985) suggested that the skewness towards females may be accentuated in small isolated reserves, where sub-adult males are driven away, and where immigration by new males is unlikely. This is not observed in Nairobi National Park.

Table 9: Comparison of estimates on the lion population of Nairobi National Park (Gatta, 2016; Kral, 2014; Lattuada, 2012).

Year	Season	Total population size	Density (>1yr)	Juveniles (<2yr) per adult	Males per female	Mean group size
2012	dry	35	19/100km²	0.89	0.9	1.98
2014	wet	30	22/100km²	0.67	0.7	1.8
2016	wet	34	24/100km²	0.9	0.6	1.6
2016	dry	37	26/100km²	0.85	0.55	1.6

From the observed population size (n=37), the dead lion cub was not taken into account for the population estimate, as well as one old lioness with two cubs, where I had indications for their presence (Gatta, 2016; personal communication with Francis Lesilau). However, the old lioness was observed again after my fieldwork period, but only with one cub. The dead lion cub is likely to be of this old lioness, as it was found around the area where she occurs. Therefore, the observed number of lions is a close representation, but still an underestimate of the true number of lions in the park. There is always the possibility that some lions have not been spotted, this is especially so with cubs.

In Nairobi National Park, three different prides have been identified by my research and this is confirmed by previous studies (Gatta, 2016; Lattuada, 2012). Pride structure differs from what is described in literature (Schaller, 1972), in the sense that, apart from the Kingfisher pride, the other two prides are rather small and without permanent pride males. This is a direct result of retaliatory killing of several pride males in 2015 and 2016. Anthropogenic activities around and within protected areas are known to affect the social structure (Loveridge *et al.*, 2007; Loveridge *et al.*, 2009). Mean adult group size is small. Bauer *et al.* (2003) suggested that a small group size of lions in West Africa may be a result of disturbance. The lack of a clear pride structure in Nairobi National Park can have an influence as well. In the Serengeti, where fully developed pride structures are present, an average group size of 2.8 lions is observed (Schaller, 1972), and in Kruger National Park, South Africa, the average group size is 4 (Funston, 2003). Recent changes in the population structure of Nairobi National Park have had their effects on the pride structure (Fig. 7). During the research period of Gatta (2016), there was a fourth pride male, called Mohawk. He was resident over the Kingfisher pride, but was chased away by L3 and ended up outside the park, where he eventually died as a result of a problem animal control action by KWS. The coalition L4-Cheru was then still resident to the Athi pride, but moved to the Kingfisher pride. As all three pride males were around the Kingfisher area, a sub-adult male (MP1) start mating with L1 (Athi pride) and took the opportunity to start his own pride. During my research period, L3 and L4 had several encounters, with visible wounds afterwards. After one encounter, L3 was chased outside the park into ‘Tuala Village’, which is situated southwest of the National Park and which is quite densely inhabited. After two days, L3 made it back safe to the park. Yet this scenario reminds us on what happened with Mohawk and therefore shows the importance of intensive monitoring and management of the lion population in the National Park.

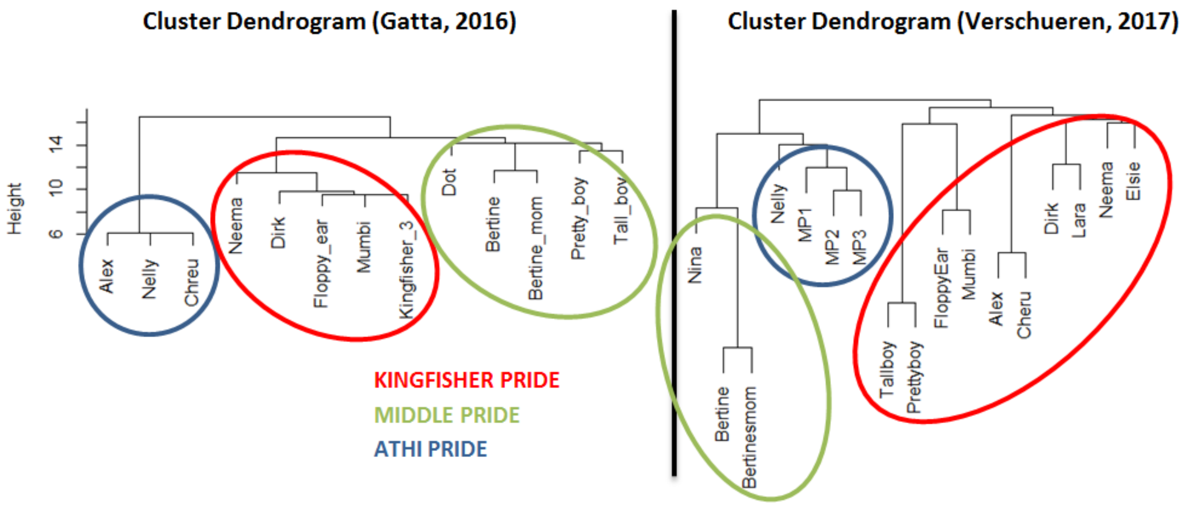

Fig. 7: Comparison of the lion social structure in Nairobi National Park during Gatta (2016) and during Verschueren (2017). L3 = Dirk; L4 = Alex; L5 = Bertine; L6 = Mumbi; L7 = Nina = Dot (Gatta, 2016); Kingfisher_3 (Gatta, 2016) = Lara (Verschueren, 2017).

Lion movements, home range analysis and habitat use

The lions of Nairobi National Park have one of the smallest home ranges throughout Africa. Similar lion home ranges were found in other national parks in East Africa, with an average home range size of 56 km² (KDE 95%) in Amboseli National Park, Kenya (Tuqa *et al.*, 2015) and 52 km² (KDE 95%) in the Seregenti, Tanzania (Schaller, 1972). Both are areas with high prey densities such as Nairobi National Park (Beveridge, 2012; Fonck, 2014). Therefore, prey availability is one important factor influencing home range size. Additional evidence comes from the difference in prey biomass between the dry and the wet season. The prey availability is considerably lower in the wet season and results in an expansion of the home range to maintain a relative constant prey biomass (Table 10). This has been extensively described in several other studies (Bauer & de Iongh, 2005; Loveridge *et al.*, 2009; Tumenta *et al.*, 2013a;

Tuqa *et al.*, 2015; Van Orsdol *et al.*, 1985). However in Nairobi National Park, there was no significant difference found in home range size between seasons. Note that sample size was very small. Another suggestion is that smaller prides, as found in Nairobi National park, would require fewer resources, and therefore are able to survive within smaller home ranges (Spong, 2002).

Table 10: Average home range sizes and prey biomass in Nairobi National Park. Home range size data from 2012 is based on direct observations (no collared lions) and is estimated by 100% Minimum Convex Polygons. Therefore this estimate is less accurate compared to home ranges based on GPS fixes and estimated by KDE 95%. (Beveridge, 2012; Fonck, 2014; Gatta, 2016; Kral, 2014; Lattuada, 2012).

Year	Home range size (km^2)	Prey biomass (kg/km^2)	Season
2012	18.93	9,162	dry
2014	55.04	4,165	wet
2016	65.85	N/A	wet
2016	37.75	6,138	dry

I found that male lions tend to have smaller home ranges than lionesses in Nairobi National Park. However, the difference in size is rather small and was not significant when analyzed per month (Table 6). This difference was not observed by Kral (2014) and by Gatta (2016) and is contradictory to what is described in literature (Schaller, 1972). There is also a remarkable large overlap between the two male lions (L3: 48%; L4: 61%), while small home ranges are expected to have little overlap (Van Orsdol *et al.*, 1985). I suggest that both lions are very territorial and neither one of them wants to give up its territory. Even with smaller home ranges, the male lions have travelled larger distances per 24h compared to the lionesses, especially L4. L4 was very active in marking his territory during the nights. There were several encounters between these lions resulting in fights with injuries afterwards. This strengthens my assumption.

I also observed that reproductive status of the lionesses had an influence on their movements and home range size. Lionesses with small cubs (e.g. L5) generally had smaller home ranges and travelled shorter distances per 24h compared to lionesses with larger cubs (e.g. L7) and lionesses without cubs (e.g. L6). Gatta (2016) suggested the same. Small cubs are not able to travel large distances and need safe places to shelter (Funston, 2003).

Other factors, such as the presence of livestock, influence home ranges as well (Ogutu *et al.*, 2002; Valeix *et al.*, 2012). When migratory herds move out the park during the wet season, lions are likely to switch to livestock, which are abundant and readily available (Valeix *et al.*, 2012). Some lions in Nairobi National Park have, even in the dry season, a considerably part of their home range outside the park. This indicates that in Nairobi National Park a vast percentage of their diets exists out of livestock (15% - Beveridge, 2012; 11% - Tommissen, 2017).

The preference for a certain habitat type differed strongly between individuals. This has probably to do with the distribution of these habitats and the location of an individual in the national park. For example, forest and open forest glades are only present in the western part of the park, and therefore never occupied by lions of the middle pride and the Athi pride. Shrubland habitat types seem to be avoided; however it could be that other lions occupy these areas. This is known for L1 and her cubs; she has her home range in the southeastern part of the park, where the 'Mellifora shrubland' is present. Therefore I conclude that home ranges of lions in Nairobi National Park are not much influenced by habitat type. Spong (2002) and Loveridge *et al.* (2009) found that during the dry season, lions focused their activities along watercourses and waterpoints where prey was most abundant. In the different habitat types in Nairobi National Park, several waterpoints and dams had still enough water in the dry season. The high lion density causes the lions to distribute all over the park, in all habitat types, which is possible because water stays available. The water availability outside the park does decrease more severely during the dry season and therefore I expected to see more avoidance of the area outside the park during the dry season compared with the wet season. This is confirmed by the observation that lions with a home range outside the park have generally a smaller part outside the park during the dry season (20.41%) compared to the wet season (44.48% - Gatta, 2016).

Human – lion conflict

I observed that human – lion conflicts mainly occur south of the park, because the southern border is not fenced. The livestock raiding behavior differs between lions and between the areas where they are situated. Stander (1990) described the existence of habitual, occasional and nonproblem animals, which is also applicable for the lions of Nairobi National Park. The area south of the national park can be divided in a western and an eastern part. The western part is a suburb of Nairobi and quite densely inhabited by humans. In this part, lions form a direct threat to humans. The eastern part consists mainly of community lands, where numerous bomas are situated and livestock raiding is a particular problem. L4 previously had his home range in the southeastern part of the park (Gatta, 2016). However, L4 moved in April 2016 to the western part of the park. During the study of Gatta (2016), the part of his home range outside the park made up 48% of the total home range (KDE 95%), while during my research, L4 had only 2 fixes outside the park. Nooteboom (2016) found also a significant difference in the contribution of livestock in scat between the prides. Kingfisher pride, occurring in the western part of the park, raids significantly less livestock compared to the Middle pride and Athi pride, which are situated much closer to the community lands (Nooteboom; 2016). The park in this southeastern part is rather narrow and therefore I suggest that there is not enough prey available for the lions in this part. As most areas in the park are occupied by other lions, lions from the middle and Athi pride are forced to feed in the community lands, where livestock is abundant and rather easy to catch. This is also observed in nomadic males that are not able to take over a pride. They live in the edges of the national park and feed on livestock (Woodroffe *et al.,* 2005).

Pride males generally have the best access to resources (Schaller, 1972) and therefore I suggest that they may feed less on livestock compared to nomadic males. L3's GPS fixes prior to his territory acquisition reveal that he used to venture out of the park. While being a pride male over the Kingfisher pride, he almost never went outside (Gatta, 2016), until L4 moved up to his territory. Bauer and de Iongh (2005) suggested that males contribute more to lion-livestock conflicts compared to females, because they have larger home ranges. During my research, the lionesses in Nairobi National Park had larger home ranges, but also spent more time outside the park.

The influence of seasons on the occurrence of livestock raiding is also of major importance (Valeix *et al.*, 2012). However differences in the proportion of livestock in the diets between the seasons is not very pronounced in Nairobi National Park. In the wet season proportions were 19% (Fonck, 2014) and 18.6% (Nooteboom, 2016) and in the dry season 15% (Beveridge, 2012) and 11% (Tommissen, 2017). Reproductive status seems to have minor influence on the time spent outside the park. I would expect that lionesses with cubs seek shelter in the safe surroundings of the park. L5, however, spent nearly 25% of her time outside the park. She was almost always seen together with another lioness and their six months old cubs. She went a couple of times quite far (> 500m) from the park boundary and she sometimes stayed outside for several days. I made no direct observations of the lioness wandering outside with their cubs, but the dead lion cub found around a boma indicates as well that lions, even with cubs, regularly roam in the area outside the park. An explanation could be that lionesses with cubs avoid pride males and their territory, so that their cubs aren't killed by infanticidal behavior (Van Orsdol *et al.*, 1985; Hanby & Bygott, 1987). Packer & Pussey (1983) observed lionesses with older cubs (1.5 - 2 yr) avoiding pride males and becoming temporarirly nomadic.

In Nairobi National Park, livestock losses due to predation are mainly caused by lions (Gatta, 2016). Cattle and donkeys, which are the most expensive livestock species, were reported to be the most attacked species (Gatta, 2016). Economic losses from diseases and theft are sometimes higher, nevertheless, predation is often considered as the most serious threat to livestock (Tumenta *et al.*, 2013b). There is financial compensation for damage to livestock by lions around the Nairobi National Park (personal communication with Francis Lesilau). This is known to be a useful conservation tool in situations where there is an imminent threat to biodiversity, and sustainable funding sources are available (Bauer *et al.*, 2015b). With such compensation scheme, there is of course the risk of a post-project collapse. It is possible that lions would decline or even disappear if compensation were to stop completely (Bauer *et al.*, 2015b). Geofencing with satellite collars to give an early warning when lions approach bomas is promising, although in practice, this is not yet effective. Communication between the researchers and the rangers should improve in order to undertake immediate action when a lion approaches a boma. Other actions, such as several husbandry practices (boma construction, high human activity, guard dogs, …) can reduce the number of livestock losses (Ogada *et al.*, 2003; Tumenta *et al.*, 2013b; Woodroffe, 2007). In Nairobi National Park, the height of the boma and the presence of flashlights are the best predictors to whether a boma will suffer an attack by a lion (Gatta, 2016). However during my research, bomas approached by lions were often equipped with flashlights. This can indicate that lions are becoming habituated by the system. Good husbandry may have the dual effect of reducing livestock losses in the short term and, in the long term, preventing predators from developing a "taste" for killing livestock (Ogada *et al.*, 2003).

The human population in Nairobi exploded in the last decades and is likely to grow even further (UN, 2016). New build highways and railways resulted recently in a loss of 300 acres of park land. Plans are now made to build a railway right through the middle of the park (personal communication with Francis Lesilau). The impact of this railroad needs further inverstigation, but it raises the debate on the coexistence between humans and wildlife.

Conclusion

Nairobi National Park and its surroundings are at high risk for human-lion conflicts. The high lion density causes lions to distribute all over the park, and even outside. The disturbed lion population structure is the consequence of high human pressures in and around the national park and recent retalioatry killings of pride males. The lions are able to survive by living in small prides within small home ranges. High prey availability and little competition from other predators in Nairobi National Park make this possible. Livestock raiding behavior seems to be influenced by a lion’s location, its social status and seasons. Effective livestock husbandry practices may reduce livestock depredation and are therefore recommended to be implemented by the herdsman around the Nairobi National Park. This would prevent new lions from learning how to hunt livestock enclosed in bomas, and would avoid lions relying on livestock as an alternative food source in the long term. Further investigation on avoidance or habituation of the flashlight system would be of high interest.

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References

Barnett, R., Yamaguchi, N., Shapiro, B., Ho, S.Y., Barnes, I., Sabin, R., Werdelin, L., Cuisin, J. and Larson, G. (2014). Revealing the maternal demographic history of Panthera leo using ancient DNA and a spatially explicit genealogical analysis. *BMC Evolutionary Biology*. 14: 70.

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

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

Bauer, H., Chardonnet, P., Nowell, K. (2005). Status and dirstibution of the lion *(Panthera leo)* in East and Southern Africa. *East and Southern African Lion Conservation Workshop*.

Bauer, H., & Iongh, H. H. (2005). Lion (Panthera leo) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*. 43(3), 208-214.

Bauer, H., Vanherle, N., Di Silvestre, I. & De Iongh, H. H. (2008). Lion – prey relations in West and Central Africa. *Mammalian Biology.* 73, 70–73.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., Macdonald, D. W., Packer, C. (2015a). Lion *(Panthera leo)* populations are declining rapidly across Africa, except in intensively managed areas. *PNAS*.

Bauer, H., Müller, L., Van Der Goes, D., Sillero-Zubiri, S. (2015b). Financial compensation for damage to livestock by lions *Panthera leo* on community rangelands in Kenya. *Oryx*. 51: 106-114.

Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K. 2015. Panthera leo. The IUCN Red List of Threatened Species (2016).

Bertola, L.D., van Hooft, W.F., Vrieling, K, Uit de Weerd, D.R., York, D.S., Bauer, H., Prins, H.H.T, Funston, P.J., Udo de Haes, H.A., Leirs, H., van Haeringen, W.A., Sogbohossou, E., Tumenta, P.N. and de Iongh, H.H. (2011). Genetic diversity, evolutionary history and implications for conservation of the lion (Panthera leo) in West and Central Africa. Journal of Biogeography 38: 1356-1367.

Beveridge, N. (2012). Analyzing factors contributing to lion-livestock conflicts: prey/biomass availability, lion diet and prey preference, lion population size and livestock losses. Msc. thesis, University of Leiden.

Brashares, J. (2001). Ecological, Behavioral, and Life-History Correlates of Mammal Extinctions in West Africa. *Conservation Biology*. 17: 733-743.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. Journal of mammalogy, 24(3), 346-352.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., Mace, G. M. (2004). Human Population Density and Extinction Risk in the World's Carnivores. *PloS Biology*. 2: 909-914.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., Purvis, A. (2005). Multiple Causes of High Extinction Risk in Large Mammal Species. *Science*. 309: 1239-1241.

Craigie, I. D., Baillie, J. E., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. Biological Conservation, 143(9), 2221-2228.

Fonck, M. (2014). Human-lion conflicts in the Nairobi National Park. Lion diet and factors influencing lion prey choice. Msc. thesis, University of Leiden.

Foster, J.B. & Coe, M.J. (1968). The biomass of game animals in Nairobi National Park, 1960-66. *Journal of Zoology London*. 155, 413-425.

Funston, P. J. (2001). Kalahari Transfrontier lion project: final report. Endangered Wildlife Trust.

Funston, P. J., Mills, M. G. L., Richardson, P. R. K., van Jaarsveld, A. S. (2003). Reduced dispersal and opportunistic territory acquisition in male lions *(Panthera leo)*. *Journal of Zoology*. 259: 131-142.

Gatta, M. (2016). Lion demography, home ranges and movement of Nairobi National Park lions in relation to livestock depredation. Msc. thesis, University of Leiden.

Grinnell, J., Packer, C., Pusey, A. E. (1995). Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour.* 49: 95-105.

Hemson, G. A. (2004). The Ecology of Conservation of Lions: Human Wildlife Conflict in Semi-arid Botswana (Doctoral dissertation, University of Oxford).

Hemson, G. A., Maclennan, S., Mills, G., Johnson, P, Macdonald, D. (2009). Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. *Biological Conservation.* 142: 2718-2725.

Henschel, P., Coad, L., Burton, C., Chataigner, B., Dunn, A., MacDonald, D. (2014). The Lion in West Africa Is Critically Endangered. *PLoS ONE*. 9(1).

Jetz, W., Wilcove, D. S., Dobson, A. P. (2007). Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. *PLoS*. 5(6).

Kenya Wildlife Service (2008). KWS Management Strategy for Lion and Spotted Hyena in Kenya.

Kitchener A. C., Breitemoser-Würsten Ch., Eizirik E., Gentry A., Werdelin L., Wilting A., Yamaguchi N., Abramov A., Christiansen P., Driscoll C., Duckworth W., Johnson W., Luo S.-J., Meijaard E., O'Donoghue P., Sanderson J., Seymour K., Bruford M., Groves C., Hoffmann M., Nowell K., Timmons Z. & Tobe S. (2016). A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. Cat News Special Issue 11, 80 pp.

Kral, M. (2014). Lion (Panthera leo leo) demography and home ranges relating to local husbandry and attacks on local livestock. MSc. thesis, University of Leiden

Lattuada, M.. (2012) Human-lion conflict around Nairobi National Park. MSc. thesis, University of Antwerp.

Loveridge, A. J., Searle, A. W., Murindagomo, F., and MacDonald, D. W. (2007). The impact of sport-hunting on the population dyamics of an African lion population in a protected area. *Biol. Conserv*. 134: 548-558.

Loveridge, A. J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. W. (2009). Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography,* 32(6), 953-962.

Miller, S., Riggio, J., Funston, P., Power, R. J., Williams, V., Child, M. F. (2016). A conservation assessment of Panthera leo. *The Red List of Mammals of South Africa, Swaziland and Lesotho.* South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Muntifering, J. R., Dickman, A. J., Perlow, L. M., Hruska, T., Ryan, P. G., Marker, L. L., Jeo, R. M. (2006). Managing the matrix for large carnivores: a novel approach and perspective fromcheetah *(Acinonyx jubatus)* habitat suitability modelling.

Nooteboom, N. (2016). Social structure, dietary preference and livestock raiding of the lions (*Panthera-leo leo*) in Nairobi National Park, Kenya. Msc. thesis, University of Leiden.

Ogada, M. O., Woodroffe, R., Oguge, N. O., & Frank, L. G. (2003). Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology*. 17(6), 1521-1530.

Ogutu, J. O., & Dublin, H. T. (2002). Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. African Journal of Ecology, 40(2), 120-129.

Ogutu, J. O., Bhola, N., Reid, R. (2005). The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology*. 265: 281-293.

Oriol-Cotterill, A., Macdonald, D. W., Valeix, M., Ekwanga, S., & Frank, L. G. (2015). Spatiotemporal patterns of lion space use in a human-dominated landscape. *Animal Behaviour*. 101, 27-39.

Packer, C. & Pusey, A. E. (1983). Adaptations of Female Lions to Infanticide by Incoming Males. *The American Naturalist.* 121(5).

Packer, C. (1987). Intrasexual Cooperation and the Sex ratio in African Lions. *The American Naturalist.* 130(4).

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: food is not enough. American Naturalist, 1-19.

Patterson, B. D., Kasiki, S. M., Selempo, E., & Kays, R. W. (2004). Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological conservation*, 119(4), 507-516.

Pennycuick, C. J., Rudnai, J. (1975). On the running of the gnu (Connochaetes taurinus) and other animals. *The Journal of Experimental Biology*, 63(3), 775-799.

Powell, R. A. (2000). Animal Home Ranges and Territories and Home Range Estimators. In *Animal Home Ranges and Territoires and Home Range Estimators.* North Carolina Agricultural and Technical State University.

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., ... & Pimm, S. (2012). The size of savannah Africa: a lion's (Panthera leo) view. *Biodiversity and Conservation.* 22(1), 17-35.

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

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

Spong, G. (2002). Space use in lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. *Behav. Ecol. Sociobiol.* 52: 303-307.

Sogbohossou, E. A. (2011). Ecology of lion *(Panthera leo Linnaeus 1975)* populations and human-lion conflicts in Pendjari Biosphere Reserve, North Benin. (Doctoral dissertation, University of Leiden)

Stander, P. (2006). Population ecology and demography of Kunene lions. Predator Conservation Trust research paper 2006/1, Namibia.

Tommissen, D. (2017). Lion diets in relation to prey dynamics and lionlivestock conflicts around Nairobi National Park in Kenya. MSc. thesis, University of Antwerp.

Trinkel, M. & Kasteberger, G. (2005). Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. African Journal of Ecology, 43, 220–224.

Tumenta, P. N., van't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., de Haes, H. A. U. & De Iongh H. H. (2013a). Changes in lion (Panthera leo) home range size in Waza National Park, Cameroon. Mammalian Biology, 78, 461–469.

Tumenta, P. N., de Iongh, H. H., Funston, P. J., de Haes, H. A. U. (2013b). Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. *Oryx.* 47(2): 237-242.

Tuqa, J. H., Funston, P. J., Musyoki, C., Ojwang, G. O., Gichuki, N. N., Bauer, H., Tamis, W., Dolreny, S., Van't Zelfde, M., de Snoo, G. R., de Iongh, H. H. (2015). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation.* 2: 1-10.

(2016). World Statistics Pocket Book. *United Nations, New York.*

Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*. 49: 73-81.

Van Bommel, L., Bij de Vaate, M. D., De Boer, W. F., & De Iongh, H. H. (2007). Factors affecting livestock predation by lions in Cameroon. African journal of ecology, 45(4), 490-498.

Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (Panthers, leo). Journal of Zoology, 206(1), 97-112.

Visser, R., de Iongh, H.H., Jirmo, T. 2011. Temporal and spatial dynamics of lions in Amboseli. The effects of drought on lion population size and structure, livestock depredation lion home ranges and movement. Master thesis

Vitousek, P. M., Mooney, H. A., Lubchenco, J., Melillo, J. M. (1997). Human Domination of Earth's Ecosystems. *Science.* 277: 494-499.

Woodroffe, R., Grinsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science.* 280: 2126-8.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. Animal conservation, 3(02), 165-173.

Woodroffe, R., & Frank, L. G. (2005). Lethal control of African lions (Panthera leo): local and regional population impacts. Animal Conservation, 8(1), 91-98.

Woodroffe, R., Frank, L.G., Lindsey, P.A. (2007). Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case–control study. *Biodivers. Conserv*. 16: 1245.

Appendix I

Current lion distribution across Kenya (Kenya Wildlife Service, 2008).