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

Lesilau, F.L.

2

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

F. Lesilau*[a,b], C.J.M. Musters[a], G. R. De Snoo[a] and H. H. De Iongh[a]

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

(*Submitted to Mammalia Journal*)

a Institute of Environmental Sciences, Leiden University, PO Box 9518, 2300, RA Leiden, The Netherlands
b Kenya Wildlife Service, P.O. Box 40241-00100, Nairobi, Kenya

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.

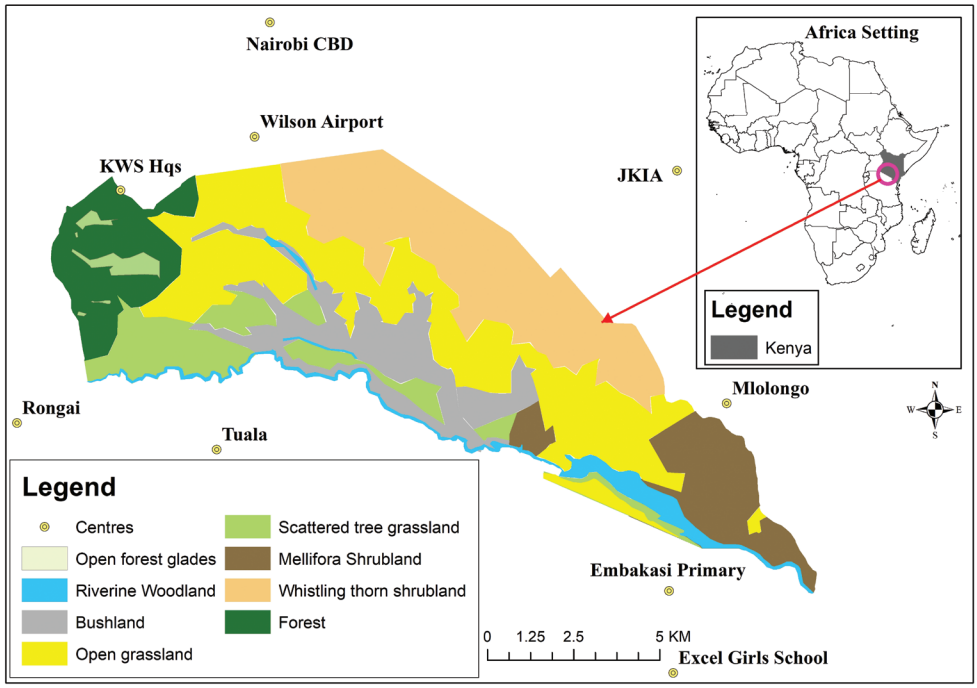

Figure 2.1
Map of Nairobi National Park showing habitat classification

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.

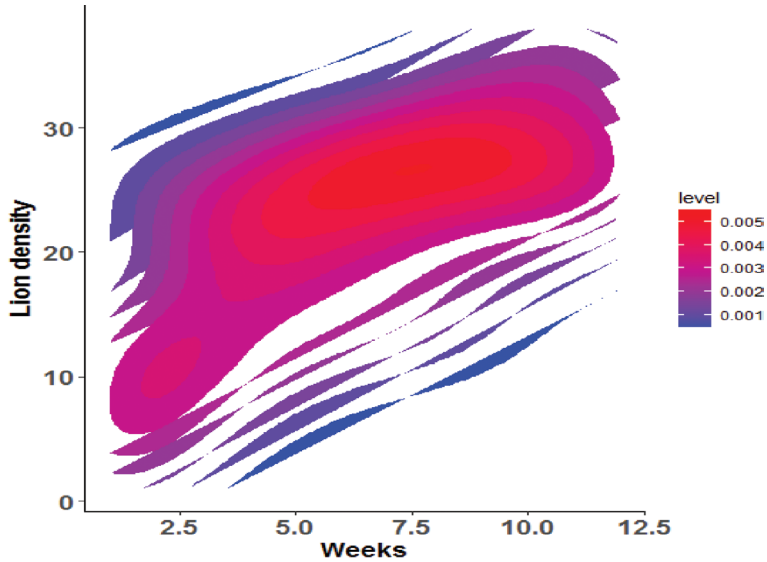

Figure 2.2
Lion density based on bi-annual lion survey during 2012, and 2014-2018

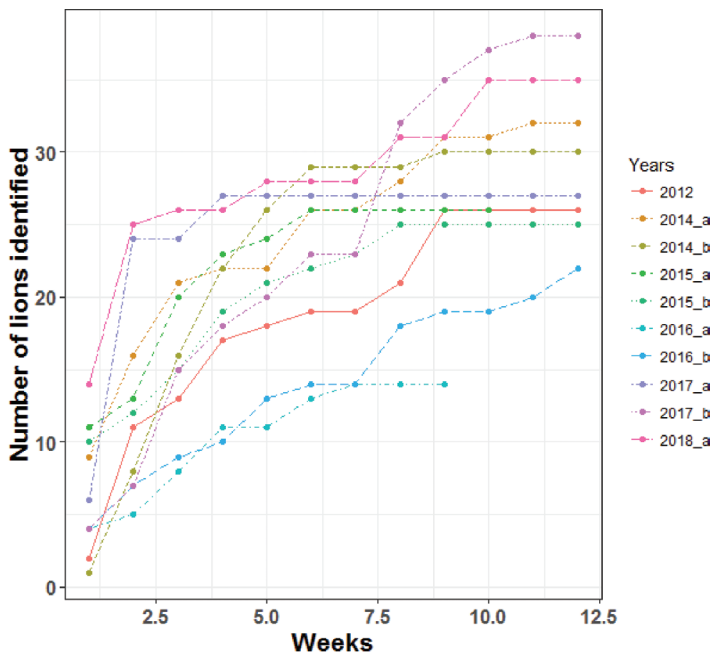

Figure 2.3
Total number of identified individuals (2 years and older) during lion survey from 2012-2018. In 2012, only one survey was carried out, during 2014-2018 two surveys per annum (a) = first survey and (b) = is second survey.

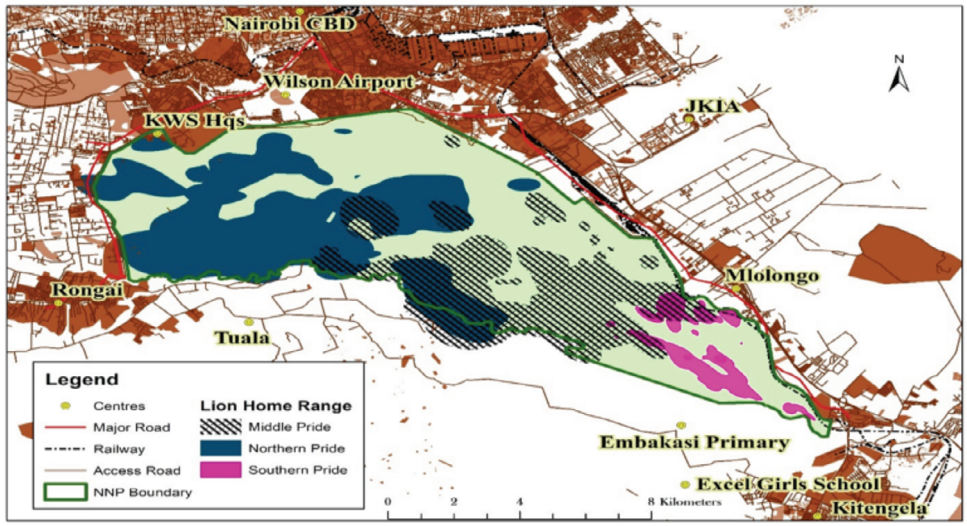

Figure 2.4
The home ranges of the three prides of Nairobi National Park prides (KDE 50%) based on collared females during 2014-2017.

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.

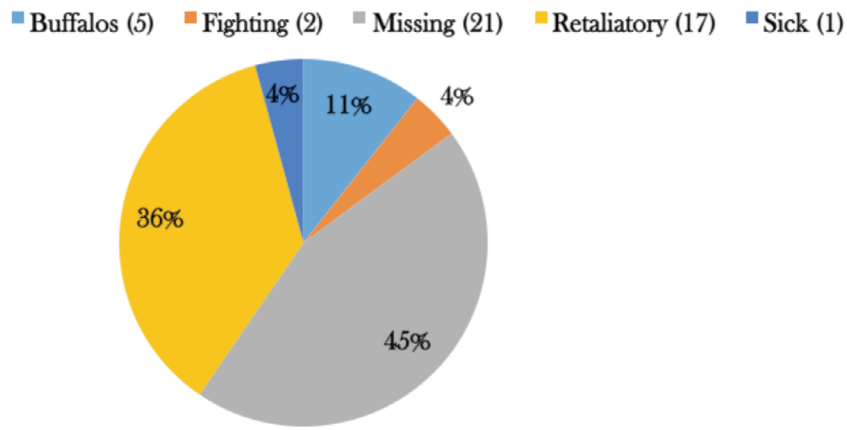

Figure 2.5
Causes of mortality and number of missing lions during 2012-2018.

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.

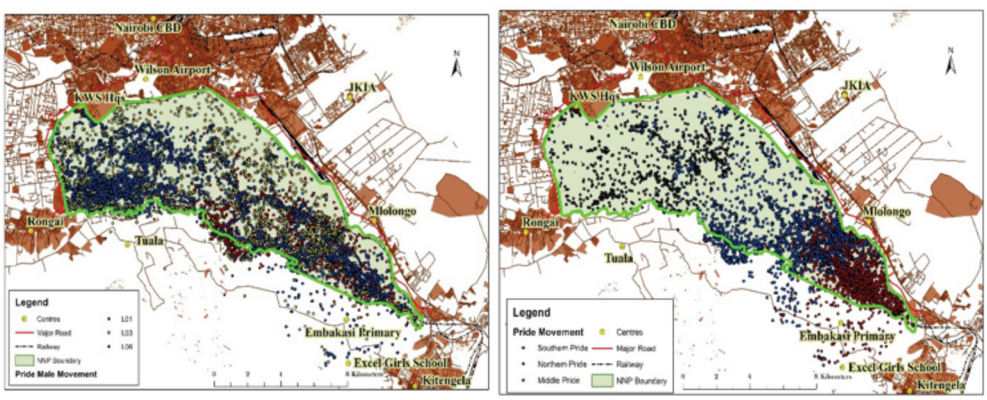

Figure 2.6

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.

Acknowledgements

We thank the Kenya Wildlife Service (KWS) for granting us permission to conduct research in NNP. The Louwes Fund for Water and Food, through Leiden University (CML) and the Leo Foundation providing financial support. This research would not have been possible without the assistance of KWS Rangers, Atif Chughtai and MSc students enrolled in the NNP lion project.

References

Barnett R, Yamaguchi N, Shapiro B, Ho YW, Barnes I, Sabin R, Lars W, Cuisin J, Larson G. 2014. Revealing the maternal demographic history of Panthera leo using ancient DNA and a spatially explicit genealogical analysis. Evolutionary Biology **14:** 1471-2148.

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

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

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

Bauer H, Vanherle N, Di Silvestre, De Iongh HH. 2008. Lion - prey relations in West and Central Africa. Mammalian Biology **73**: 70–73.

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

Breitenmoser U, Mallon DP, Ahmad KJ, Driscoll C. 2008. *Panthera leo ssp. persica.* The IUCN Red List of Threatened Species 2008: e.T15952A5327221.

De Iongh HH, Tumenta PN, Croes B, Funston PJ, Bauer H, De Haes HU. 2009. Threat of a lion population extinction in Waza National Park, North Cameroon. Cat News **50**:26–27. Available from https://openaccess.leidenuniv.nl/handle/1887/15071 (Accessed on 20th Septemebr, 2015)

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

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

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

Funston PJ, Mills MGL, Richardson PRK, Van Jaarsveld AS. 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). Journal of Zoology **259**: 131–142.

Gichohi HW. 1996. The Ecology of a Truncated Ecosystem - The Athi-Kapiti Plains. University of Leicester. Available from http://hdl.handle.net/2381/34356. (accessed on 14t March 2014)

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

Hanby JP, Bygott JD, Packer C. 1995. Ecology, Demography, and Behavior of Lions in Two Contrasting Habitats: Ngorongoro Crater and the Serengeti Plains. Pages 1-667. University of Chicago Press USA.

Hayward MW. 2006. Prey preferences of the spotted hyaena *(Crocuta crocuta*) and degree of dietary overlap with the lion (Panthera leo). Journal of Zoology **270**: 606–614.

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

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

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

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

KWS. 2008. Conservation and Management Strategy for Lion and Spotted Hyena in Kenya. Kenya Wildlife Conservancies Association, Nairobi Kenya. Pp 1-84.

Lehmann MB, Funston PJ, Owen CR & Slotow R. 2008. Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa, African Zoology **43**: 230–236.

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

Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biological Conservation **134**: 548–558.

Loveridge AJ, Valeix M, Davidson Z, Murindagomo F, Fritz H, MacDonald DW. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography **32**: 953–962.

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

Ogutu JO, 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.

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

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

Oriol-Cotterill A, Macdonald DW, Valeix M, Ekwanga S, Frank LG. 2015. Spatiotemporal patterns of lion space use in a human-dominated landscape. Animal Behaviour **101**: 27–39.

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

Packer C, Pusey AE. 1982. Cooperation and competation within coalitions of male lions: kin selection or game theory. *Nature* **296:** 740-742.

Patterson BD, Kays RW, Kasiki SM, Sebestyen VM. 2006. Develomental effects of climate on the lion's mane (*Panthera leo*). Biological Conservation **87**: 193–200.

Pennycuick C J, Rudnai J. 1970. A method of identifying individual lions (*Panthera leo)* with an analysis of the reliability of identification. Journal of Zoology London **160**: 497–508.

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

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

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

Rudnai J. 1979. Ecology of lions in Nairobi National Park and the adjoining Kitengela Conservation Unit in Kenya. African Journal of Ecology **17**: 85–95.

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

Singh AP. 2017. The Asiatic Lion (*Panthera leo persica*): 50 Years Journey for Conservation of an Endangered Carnivore and its Habitat in GIR Protected Area, Gujarat, India. Indian Forester **143**: 993–1003.

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

Trinkel M, Kastberger G. 2005. Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. African Journal of Ecology **43**: 220–224.

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

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

Tuqa JH, Funston P, Musyoki C, Ojwanga GO, Gichuki NN, Bauer H, Tamis W, Dolrenry S, Van't Zelfed M, De Snoo G, De Iognh HH. 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. Global Ecology and Conservation **2**: 1–10.

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

Whitman KL, Packer C. 2007. A Hunter's Guide to Aging Lions in Eastern and Southern Africa. Safari Press, Long Beach, California USA. Pages 1-50.

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

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													

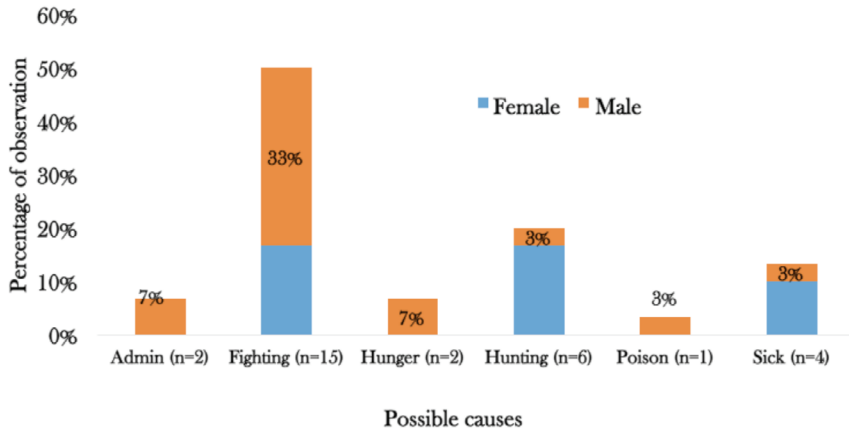

Figure S 1

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