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

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Issue Date: 2019-12-04

3

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

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Abstract

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

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

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

Submitted to Oryx Journal (under review)

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

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

3.1 Introduction

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

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

Lions generally occur in prides. A pride is defined as a "fission–fusion" social unit. The home range of individual lions may be defined by the pride's territory. A pride territory is the area that is avoided by other lions or from which other lions are actively excluded (Schaller 1972). Sub-adults that have been forced to become nomadic, usually remain close to the natal territory and may establish a new home range near the natal pride's territory (Elliot et al. 2014; Funston et al. 2003). Valeix et al. (2011) have suggested that lion movements within the pride territory is based on the patch-disturbance theory, where lions leave an area, even if they could hunt successfully, due to behavioral changes, i.e. prey becoming more vigilant. Of all the ecological variables, prey density is the core determinant influencing home range (Gittleman & Harvey 1982).

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

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

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

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

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

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

3.2 Material and methods

3.2.1 Study area[1]

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

1 This section is partly based on section 2.2.1.

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

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

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

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

The park is home to four species of the so-called Big Five: lion (*Panthera leo)*, leopard *(Panthera pardus)*, African buffalo *(Syncerus caffer caffer)*, and eastern black rhinoceros (*Diceros bicornis*). The blue wildebeest (*Connochaetus taurinus)*, Burchell's zebra (*Equus quagga burchelli)* and associated smaller ungulates such as Grant gazelle (*Gazella granti)*, Thompson's gazelle (*Eudorcas thomsoni)* and warthog (*Phacochoerus africanus*) tend to range into community land during the wet season (Gichohi 1996). Other resident ungulate species include: White rhinoceros (*Ceratotherium simum),* Common eland *(Tragelaphus oryx)*; hartebeest *(Alcephalus buselaphus*); giraffe *(Giraffa Camelopardalis)*; impala (*Aepyceros melampus),* waterbuck (*Kobus ellipsiprymnus),* Bohor *reedbuck (Redunca redunca) and Common reedbuck (Redunca arundinum)* (Owino et al. 2011). The park is an important bird area with a high diversity of bird species (see www.naturekenya.org/content/important-bird-areas). In Amboseli, the cut-off point between the wet and the dry season was 28.3 mm a month (Tuqa 2015). We considered the high altitude of NNP and relatively higher rainfall and determined our cut-off point to be a mean of 30 mm of rainfall per month.

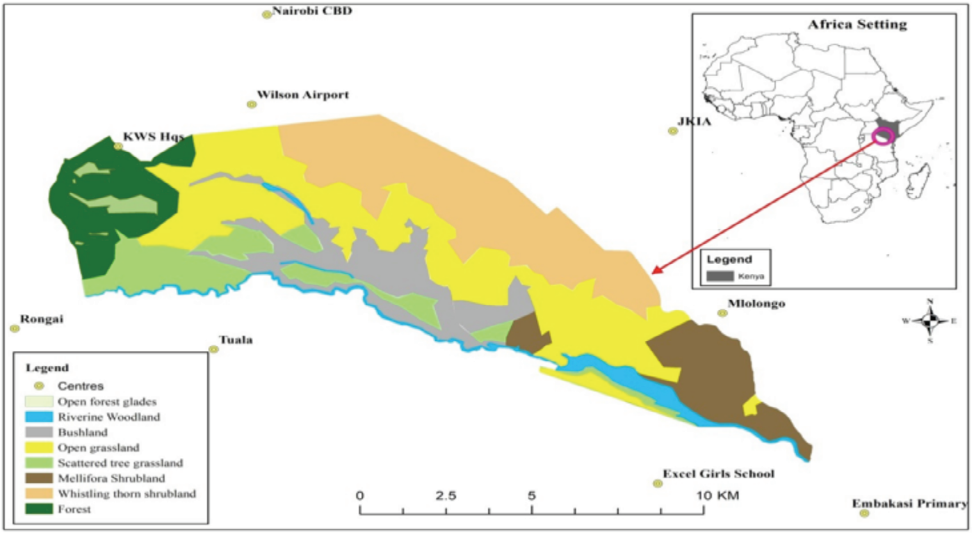


Figure 3.1
Map of Nairobi National Park showing habitat classification

3.2.2 Data collection[2]

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

2 This section is partly from section 2.2.2.

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

Table 3.1
Summary data for collared lions during the study period (2014 - 2017).

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

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

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

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

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

3.2.3 Data analysis and statistics

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

We analyzed the data using ArcGIS 10.2.2 and projected the results in the Universal Transverse Mercator (UTM) WGS-84, zone 37 ° S. The Spatial Analyst tool and the Geospatial Modelling Environment software (www.spatialecology.com/gme/) were used to analyze the GPS data. We determined the resolution bandwidth with least-squares cross (LSC) validation for fixed-kernel home ranges (Seaman & Powell 1996). We considered two seasons (dry and wet) based on the monthly rainfall (mm) with a cut-off point of 30 mm of rainfall per month.

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

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

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

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

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

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

Table 3.2
Average home range (km^2) size per annum and distance travelled by 12 collared lions in NNP, 2014-2017 and summary of maximum of potential minimum distance (km) travelled per 24hrs by collared lions. (Average and maximum calculated over number of collared days).

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

3.3 Results

3.3.1 Home range size

The annual MCP (100%) home ranges of males were significantly larger than those of females as in the Chi-square test was the result of a LRT: (LRT: χ^2 = 8.78, df = 1, p-value = 0.003) and home range sizes between prides also differ significantly (LRT: χ^2 = 7.41, df = 2, p-value = 0.025). However, there is no significant difference in home range size between different seasons (LRT: χ^2 = 0.17, df = 1, p-value = 0.680) or different age classes (Tables 3.2 & 3.3; LRT: χ^2 = 0.79, df = 1, p-value = 0.375). The 100% MCP annual mean home range size of males is 124.4±31.7 (range = 92.2–179.7 km^2) and of females is 70.2±35.0 (range = 18.7–153.9 km^2) for the whole study period (Table 3.4). L06 has the largest home range with 96.4 km^2 at KDE (95%) and 179.7 km^2 at MCP (100%). The annual mean of all the lions' home ranges, across sexes, pooled in MCP 100% is 93.4±43 (range = 18.7–179.7 km^2). Avoidance of the urban fringe section of the park is significant (Fig. 3.2 and S3; χ^2 = 5836, df = 1, p-value = 0.001).

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

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

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

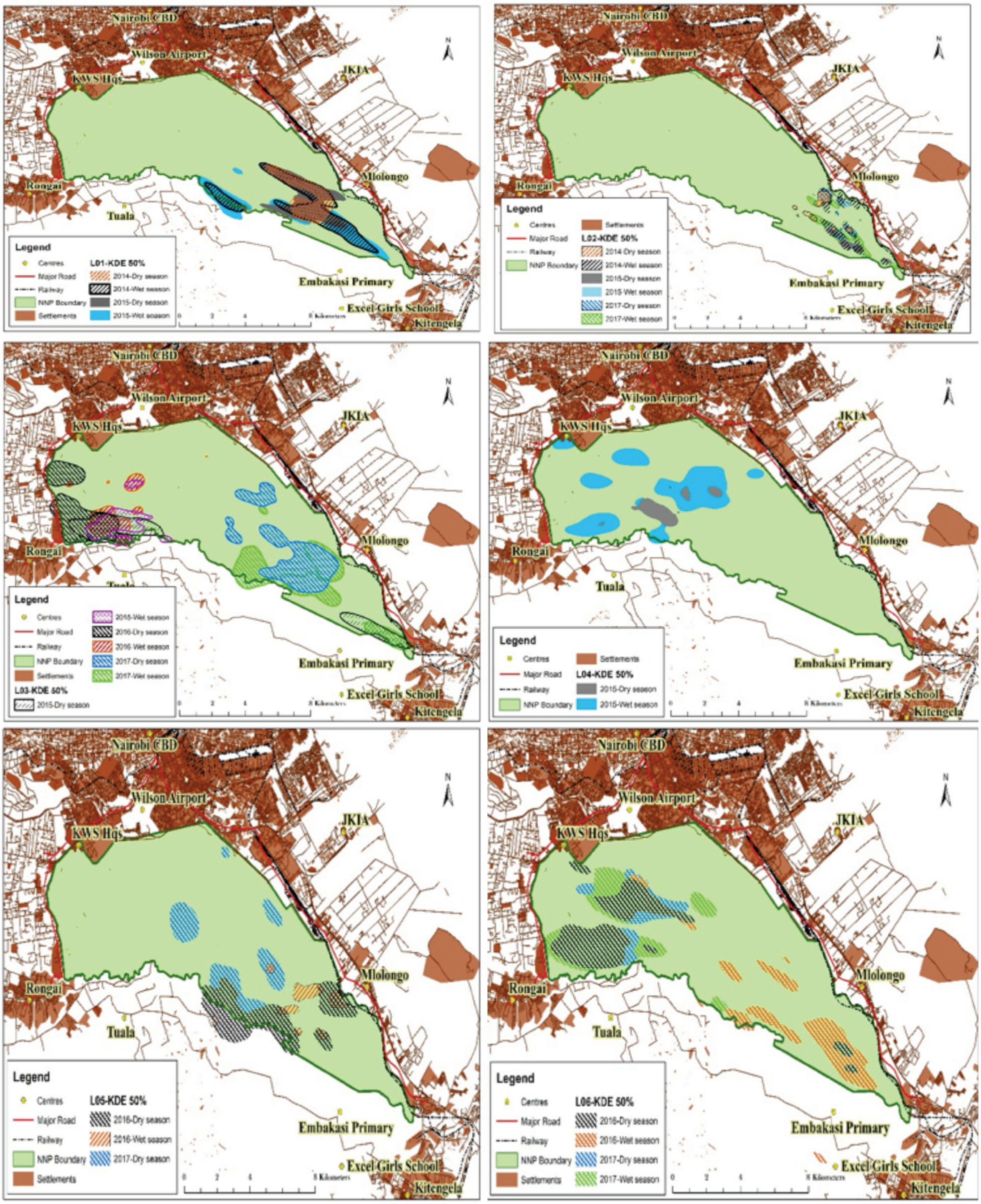
The mean seasonal core area estimate (50% of KDE), averaged across sexes, ranges between 0.4–18.1 km^2 (mean = 8.6±4.9) and the KDE 95% was 5.27–91.7 km^2 (mean = 43.72 ± 22.4). The NNP lion's avoidance of the eastern border of the park near urban fringe (Fig. 3.2). The mean home range size of males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

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

A comparison of NNP prides shows that the southern pride has the smallest annual mean home range of 14.4± 5.9 (range = 6.2–19.7), the middle pride home range size is 45.5±11.1 (range = 29.4–59.5) and the northern pride has the largest home range, with 50.9±23.6 (range = 19.1–85.2) at 95% KDE) (Table 3.4c). In the South, home ranges extended outside NNP into the community land (Figs. 3.2, S 2 & S 3). The annual average is 34 km² (95% KDE).

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

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


Nairobi CBD
Wilson Airport
KWS Hqs
JKIA
Mlolongo
Rongai
Tuala
Embakasi Primary
Excel Girls School
Kitengela
N
8 Kilometers
Legend
Centres
Major Road
Railway
NNP Boundary
Settlements
L01-KDE 50%
2014-Dry season
2014-Wet season
2015-Dry season
2015-Wet season
L02-KDE 50%
2014-Dry season
2014-Wet season
2015-Dry season
2015-Wet season
2017-Dry season
2017-Wet season
L03-KDE 50%
2015-Dry season
2015-Wet season
2016-Dry season
2016-Wet season
2017-Dry season
2017-Wet season
L04-KDE 50%
2015-Dry season
2015-Wet season
L05-KDE 50%
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2017-Wet season

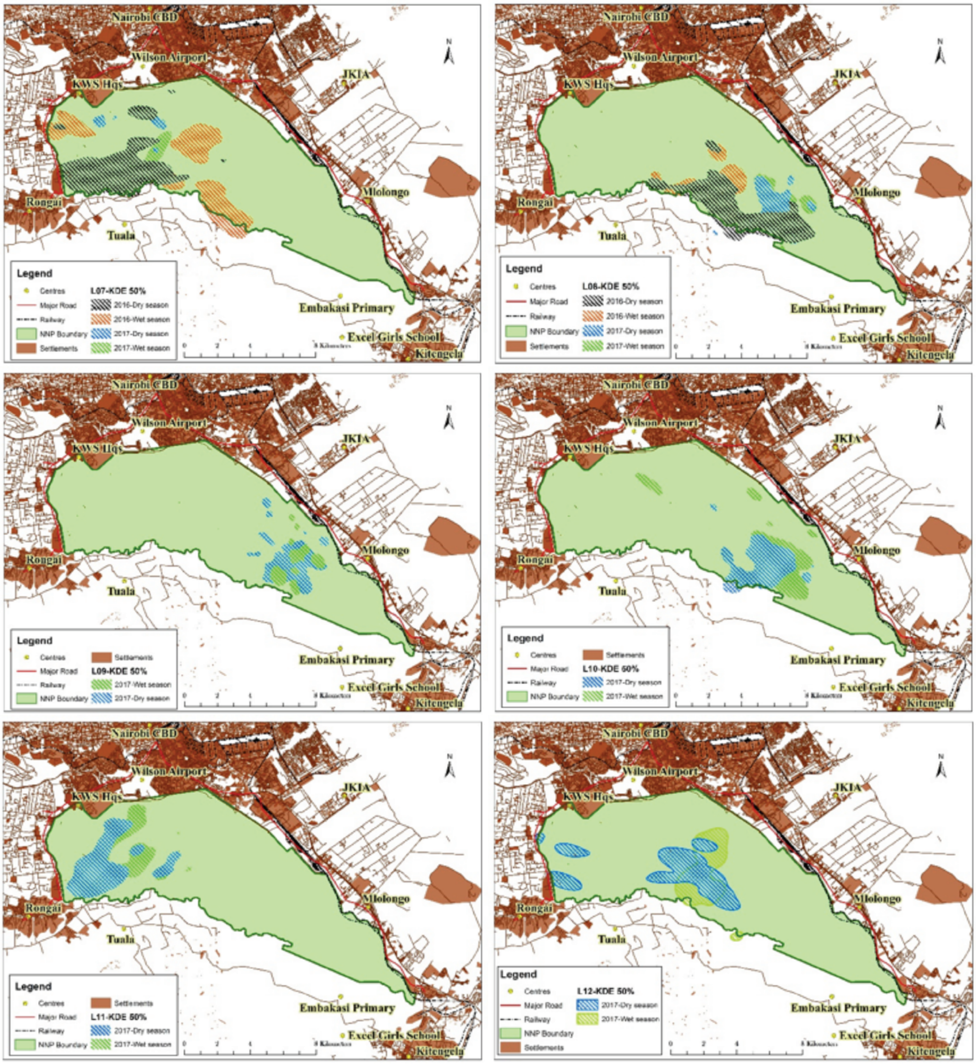

Figure 3.2

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

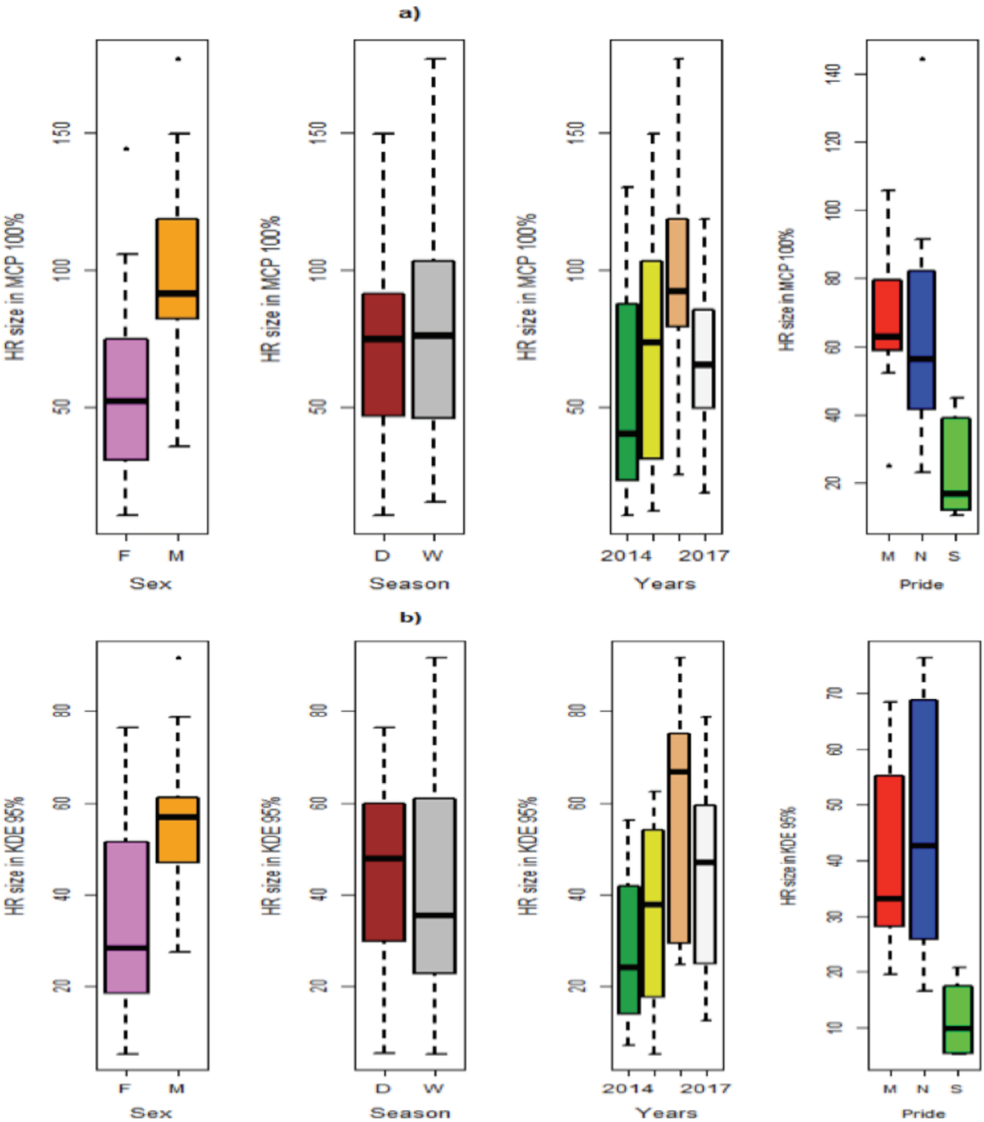

Figure 3.3

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

3.3.2 Seasonal movement, exit and re-entry

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

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

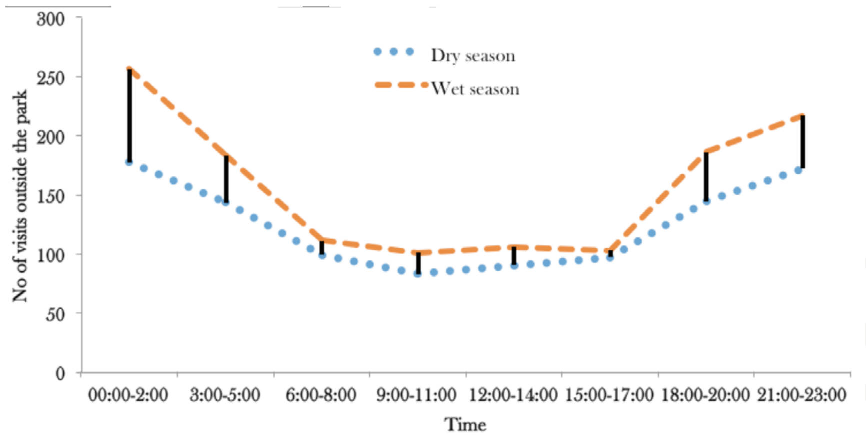

Figure 3.4
Number of collared lion visits outside the park during the dry and the wet season. (The black lines show the difference between the wet and dry season based on GPS data of all 12 collared lions during 2014-2017).

The results on geo-fencing of livestock bomas using an AWT option in order to alert the park management and research team when a collared lion had left the park showed that lions are mostly close to livestock bomas during the day while the collared is actually in the park. On 127 occasions delays have been reported in receiving the SMS when lions approached livestock bomas. In addition, in 53 cases a false alert was received during the day when the collared lion was still in the park.

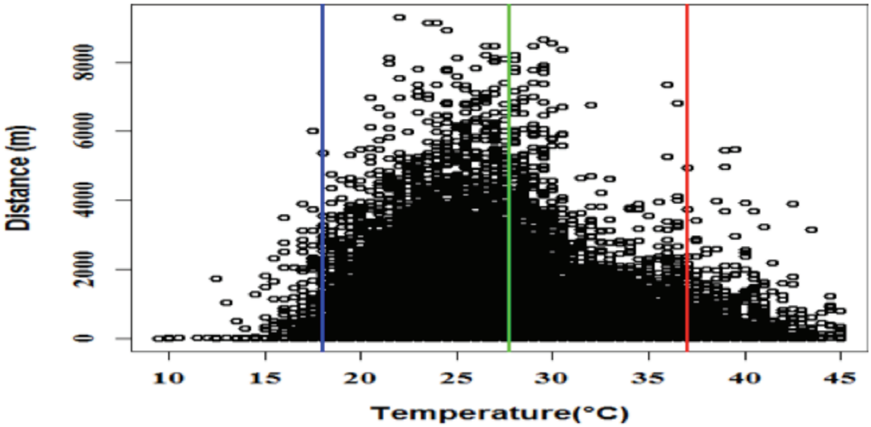

Figure 3.5
Relationship between the ambient temperature reading from the collars and the distance travelled by the lions between two points. (The blue vertical line = minimum, green = the mean and red = maximum. Between blue and red is the ambient temperature).

3.3.3 Travel distance

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

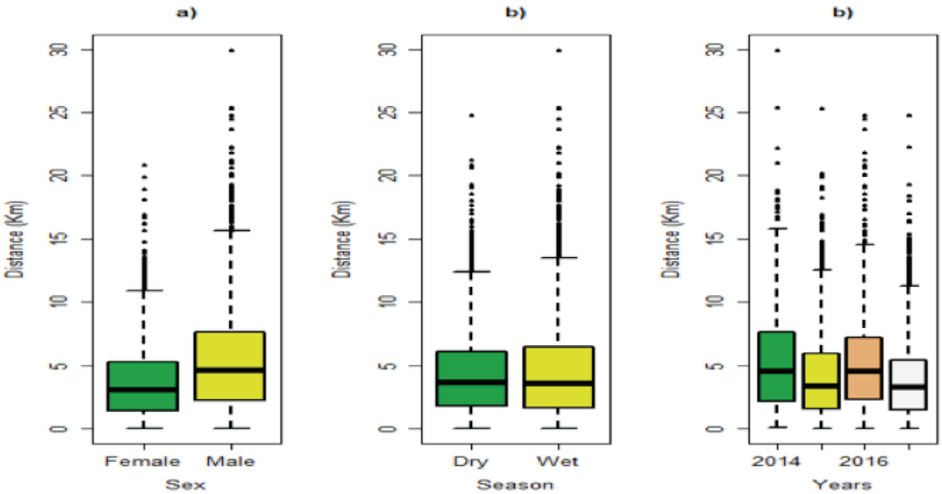

Figure 3.6
Differences in distances travelled by collared lions during 2014-2017 based on a) sex, b) season, c) year.

3.3.4 Habitat factors

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

Table 3.5
Habitat selection indices.

Type area		bush-land	open forest glades	forest	mellifera shrubland	open grass-land	riverine wood-land	scattered tree grassland	whistling thorn shrubland
(km^2) area(%)		**13.030 (11.18%)**	**1.380 (1.18%)**	**10.920 9.37%)**	**13.440 (11.53%)**	**33.120 (28.41%)**	**5.050 (4.33%)**	**12.480 (10.70%)**	**27.170 (23.30%)**
L01	wi Bi	**1.081** **0.125**	0.000 0.000	0.086 0.010	**2.014** **0.233**	**1.402** **0.162**	**3.226** **0.374**	0.729 0.084	0.099 0.011
L02	wi Bi	0.000 0.000	0.000 0.000	0.000 0.000	**5.186** **0.522**	0.016 0.002	**4.612** **0.464**	0.093 0.009	0.030 0.003
L03	wi Bi	1.086 0.082	**1.746** **0.131**	1.017 0.076	0.453 0.034	0.818 0.061	1.524 0.114	**3.070** **0.230**	**3.609** **0.271**
L04	wi Bi	**1.260** **0.214**	0.398 0.068	0.300 0.051	0.000 0.000	0.289 0.049	0.185 0.031	0.564 0.096	**2.900** **0.492**
L05	wi Bi	**1.106** **0.158**	0.000 0.000	0.014 0.002	**1.058** **0.151**	**1.780** **0.255**	**1.975** **0.283**	0.662 0.095	0.391 0.056
L06	wi Bi	**1.682** **0.184**	0.517 0.056	0.782 0.085	0.000 0.000	**1.141** **0.125**	**2.323** **0.254**	**2.568** **0.280**	0.141 0.015
L07	wi Bi	**2.493** **0.246**	**1.856** **0.183**	**1.286** **0.127**	0.036 0.004	0.693 0.068	0.866 0.085	**2.680** **0.264**	0.231 0.023
L08	wi Bi	**2.153** **0.279**	0.000 0.000	0.000 0.000	0.914 0.119	**1.243** **0.161**	**2.171** **0.282**	0.632 0.082	0.597 0.077
L09	wi Bi	0.555 0.093	0.000 0.000	0.000 0.000	**1.358** **0.226**	**1.737** **0.290**	**1.166** **0.194**	0.302 0.050	0.880 0.147
L10	wi Bi	**1.897** **0.270**	0.000 0.000	0.000 0.000	**1.004** **0.143**	**1.468** **0.209**	**1.818** **0.258**	0.165 0.024	0.681 0.097
L11	wi Bi	0.083 0.011	**1.314** **0.179**	0.830 0.113	0.000 0.000	**1.004** **0.137**	0.367 0.050	**3.392** **0.463**	0.334 0.046
L12	wi Bi	**3.356** **0.432**	0.110 0.014	**1.479** **0.190**	0.000 0.000	**1.005** **0.129**	0.564 0.072	0.941 0.121	0.319 0.041
Average of all lions	wi Bi	**1.396** **0.174**	0.495 0.053	0.483 0.055	1.002 0.119	1.050 0.137	**1.733** **0.205**	**1.316** **0.150**	0.851 0.107

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

3.4 Discussion

3.4.1 Home range

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

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

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

Male lions that joined other prides following takeovers demonstrated adaptation to the new pride territory (Fig. 3.2). This pride takeover increased the home ranges of incoming pride male when moving from their pride to a new pride and to females that have large home ranges because avoidance of infanticide during a pride takeover (Table 3.2). This is similar to observation by Bygott & Hanby, (1987) where sub-adults stay at periphery of natal home range. Life stage, such as reproductive status of males and females, is an important factor in shaping lions' home range size (Bauer & De Iongh 2005; De Iongh et al. 2009; Loveridge et al. 2009). Other studies have also confirmed that season, prey and reproductive status of a lion influence their home range size (Lehmann et al. 2008; Loveridge et al. 2009). We conclude that landscape features and the small size of the semi-fenced park determine the movement patterns of lions in and outside the park.

3.4.2 Activity patterns

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

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

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

3.4.3 Distance travelled

The maximum of potential minimum travel distance of each collared lion as shown in Table 3.2 is much larger than the average potential minimum travel distance (Table 3.2). The 24 hrs distance is just a one-day travel distance which might have been either a result of avoidance behavior in response to a particular situation (e.g. males fighting or female avoidance of infanticide during a pride takeover). We observed three cases (Mumbi & Bertine) in which lions left the park into community, thereby increasing their maximum (potential minimum) distance.

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

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

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

3.4.4 Habitat factors

Although the location of lion scat with prey hair items (Fig. S1) and some carcasses show incidental lion presence in NNP (Lesilau et al. in prep), there is no single collared lion with its core home range (50% KDE) inside the park along the eastern border neighbouring Wilson Airport, the southern bypass and Mulolongo (Figs. 2, S 2 & S 3). Our results show that lions tend to avoid the urban fringe section of the park. Figs 2 & S 3 show the average annual home ranges of all collared lions at 50% KDE and this figure also shows the spatial avoidance by lions of the eastern border of the park which represents the urban fringe. It is our assumption that the increased artificial lights from the city, in combination with the smell and noise pollution from the road and airport in this region of the park is scaring the lions. Avoidance of high human densities and human disturbance was also demonstrated by Oriol-Cotterill et al. (2015). Furthermore, Rich and Longcore (2005) showed that artificial lights that have a similar intensity to moonlight and may disrupt nocturnal activity patterns, such as foraging behavior. NNP lions only utilized the urban fringe zone in order to transit to other parts of the park to stay, rest and hunt. Hölker et al. (2010) showed that, a change in nocturnal habits due to light pollution threatens biodiversity. In an open habitat with few barriers to block artificial lights from urban settlements, this light pollution may influence the distribution and behavior of predators (Longcore et al. 2016). In addition, Longcore et al. (2005) found that species tend to disperse away from the urban glow towards the darkest horizon. Moreover, species adjust their nocturnal hunting activities to coincide with darkness hours in order to increase hunting success (Van Orsdol 1985; Funston et al. 2001).

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

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

Acknowledgements

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

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Supporting information

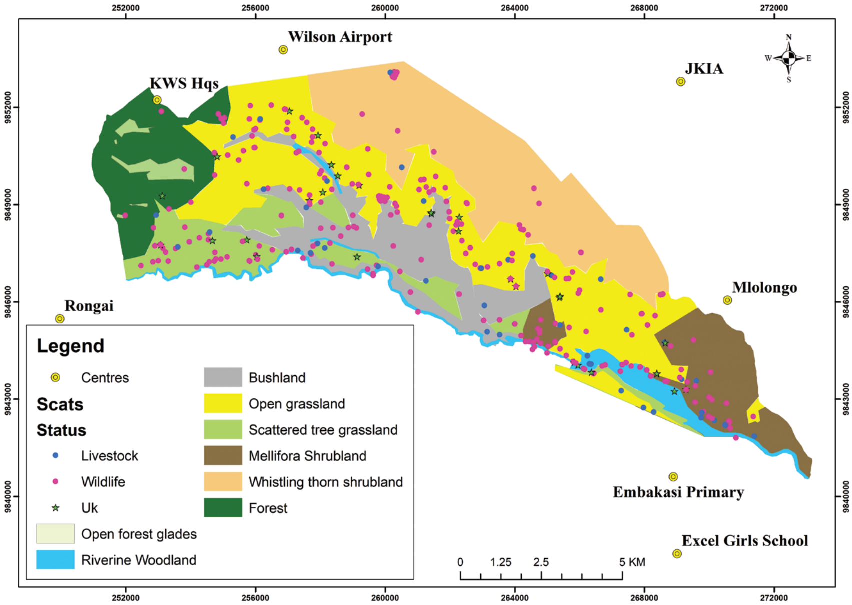

Figure S1
Map of NNP showing location of lion scats with different prey items.

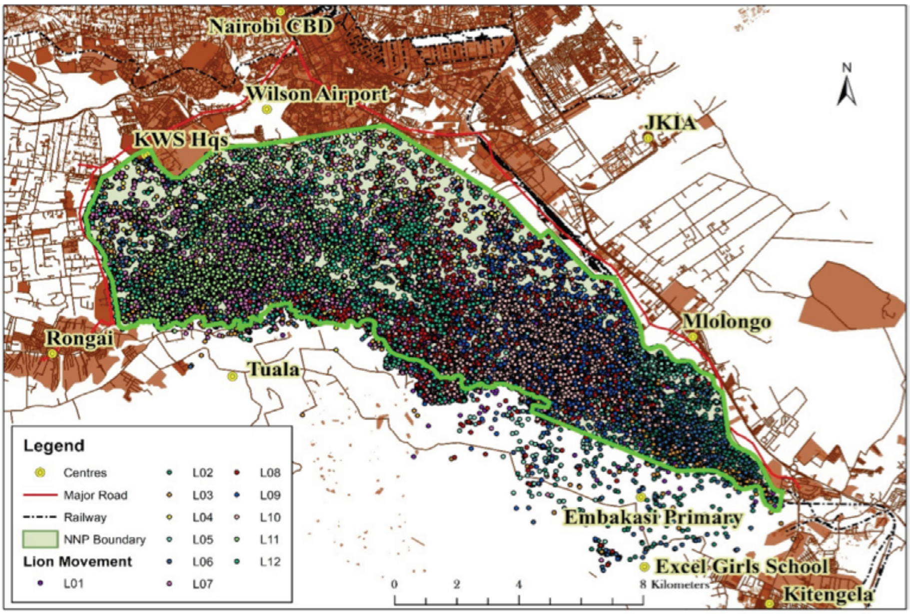

Figure S2
The GPS locations of collared lions inside the park and dispersal areas outside the park into the community land during 2014 – 2017.

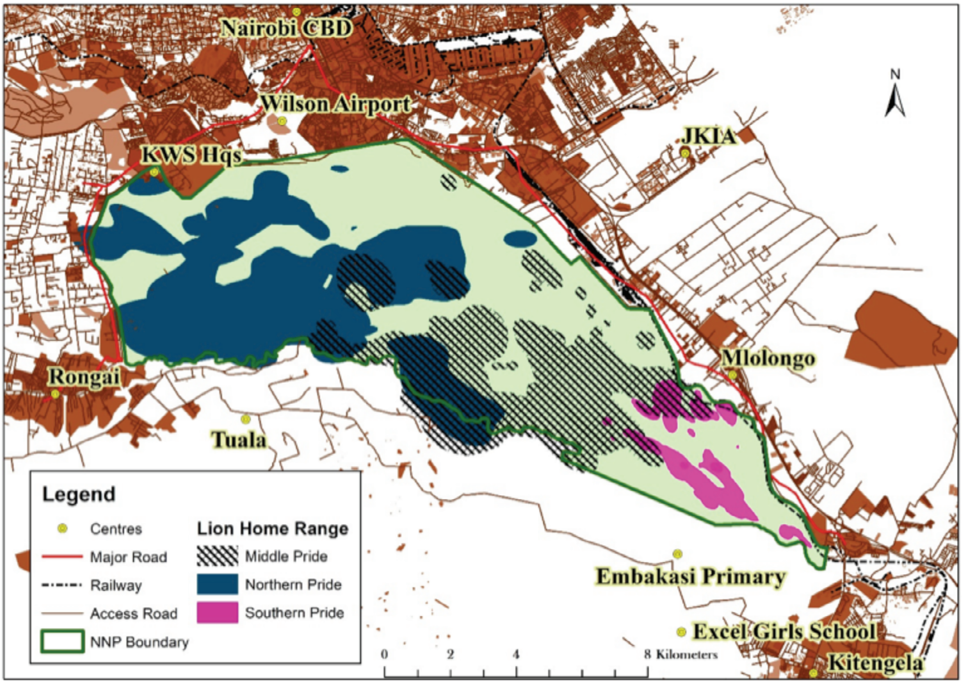

Figure S3

Pride home ranges at KDE 50%.