

## Original study

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# Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: the case study of Nairobi National Park, Kenya

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**Abstract:** Human population growth near protected areas often results in detrimental edge effects for apex carnivores, such as the African lion. Urbanization leads to new scenarios of the human–lion conflict, thus understanding ranging patterns close to urban environments is crucial to inform future management strategies. We collected GPS data from 12 collared lions between 2014 and 2018 in Nairobi National Park, which borders the capital city of Kenya, Nairobi city. We estimated home ranges, calculated daily distance traveled and tested for differences between sex, season and pride. Additionally, we investigated how disturbance from Nairobi and surrounding human settlements affected space-use of lions, and tested for differences between sex, season and time of day. Lions showed restricted movements (4.5 km/day) and had small home ranges (49 km<sup>2</sup>). Male lions had larger ranges than females, but avoidance behavior of disturbed areas was similar. Lions took advantage during times of low human activity, i.e., during the night, to extend ranging behavior in search for resources. Risk for livestock depredation also increased during the wet season when lions roamed longer, more frequently, and deeper into the community lands. We recommend the establishment of buffer zones to maintain a viable lion population and reduced risk for conflict.

## 1 Introduction

Apex carnivores, such as the African lion (*Panthera leo* Linnaeus, 1758), cheetah (*Acinonyx jubatus* Schreber, 1775), leopard (*Panthera pardus* Linnaeus, 1758), and the African wild dog (*Lycaon pictus* Temminck 1820) show global declines in population numbers (Bauer and Van Der Merwe 2004; Riggio et al. 2013; Woodroffe 2000). The main threats have been defined as habitat destruction, decline of prey populations, and human–carnivore interactions (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-Zubiri and 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). Lions generally live in prides, and the home range of an individual may be confined by the pride's territory (Schaller 1972). Lion home ranges mostly range between 50 and 600 km<sup>2</sup> (Loveridge et al. 2009; Tumenta et al. 2013; Tuqa et al. 2014), but can be as large as 2000 km<sup>2</sup> in arid environments (Stander 1991). Home range size is mainly dependent on prey density, thus on factors reflecting prey availability, such as environment, season and human presence (Bauer and Iongh 2005; Davidson et al. 2012; Loveridge et al. 2009; Spong 2002; Tuqa et al. 2014). Home ranges of male lions are often larger than those of females and may encompass two or more female prides (Funston et al. 2003; Orsdol et al. 2009). Nomadic males may roam over extensive ranges due to the fact that they avoid the territories of pride males (Funston et al. 2003; Loveridge et al. 2009). 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).

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The expansion of home ranges outside protected areas increases the likelihood of contact with people, which may ultimately result in livestock depredation conflicts (Bauer and Iongh 2005; Loveridge et al. 2009; Ogutu and Dublin 2002; Patterson et al. 2004; Tumenta et al. 2013). When native prey migrates away, lions may switch to livestock as an alternative prey source (Valeix et al. 2012). Furthermore, it has been found that lions in pastoralist areas show fine-scale, spatiotemporal avoidance strategies to reduce the risk of encounter humans: Lion spatial distribution and habitat selection shifted in relation to seasonal movements of people and livestock (Schuette et al. 2013), and lions have been observed to approach settlements at times when human activity was lowest (Oriol-Cotterill et al. 2015).

Urbanization has led to new scenarios of human–wildlife interactions and affected predator behavior and distributions (Braczkowski et al. 2015; Hölker et al. 2010; Magle et al. 2014). An understanding of lion ranging patterns in such systems is a requirement for future management strategies of protected areas threatened by urban development. Therefore, we focused our study on lion home ranges and movements in and around the Nairobi National Park (NNP) in Kenya. NNP is a small, partially fenced protected area, surrounded by dense urban and communal settlements from Nairobi city, which is located only 7 km north of NNP. South of NNP are community lands where livestock is abundant. Lions have little space to roam and reports of livestock attacks, retaliatory lion killings, and lions wandering in the city are presently occurring frequently (Kushner 2016; Smith 2012).

We intended to address the following research questions: (i) What is the average home range size of lions in

NNP and which factors influence this? (ii) What is the average daily distance traveled by lions in NNP and which factors influence this? (iii) Which habitat is preferred by lions in NNP? (iv) How is the spatial ecology of lions in NNP influenced by disturbance from Nairobi city? (v) How is the spatial ecology of lions in NNP influenced by access to the community lands?

## 2 Material and methods

### 2.1 Study area

NNP is located to the south-west of Nairobi city in Kenya (Figure 1). The park was gazetted in 1946 with a surface area of 117 km<sup>2</sup> (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 within an altitude ranging between 1533 and 1760 m above sea level (Owino et al. 2011). Annual temperature range is between 13.6 and 25.3 °C (Deshmukh 1985; Muya and Ouge 2000). Kenya has two periods of rainfall, one long wet season from March to May with a mean of 150 mm of rainfall and a short wet season from November to December with a mean of 90 mm of rainfall (Deshmukh 1985).

To separate wildlife from Nairobi city, NNP was partly fenced in 1955 with a chain-link fence and galvanized wire powered by electricity (6 kV) (Foster and Coe 1968; Reid et al. 2008). The southern border is formed by the Mbagathi river and provides open access to the Athi-Kaputiei Plains (AKP), an area of 2200 km<sup>2</sup> pastoralist rangeland, hereafter named ‘community lands’ (Reid et al. 2008). This open access is necessary to maintain herbivore migrations during the wet season for feeding and calving. In the dry season, herbivores concentrate around water sources in NNP as the community lands contain no permanent water sources (Reid et al. 2008).

NNP has three distinct vegetation zones (Foster and Coe 1968): (i) The western part of NNP is covered by semi-evergreen forest patches of

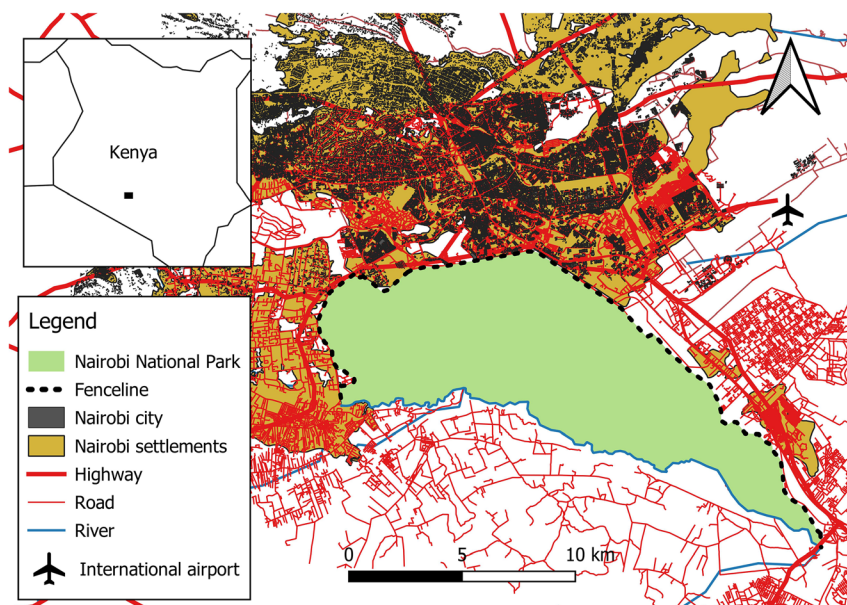
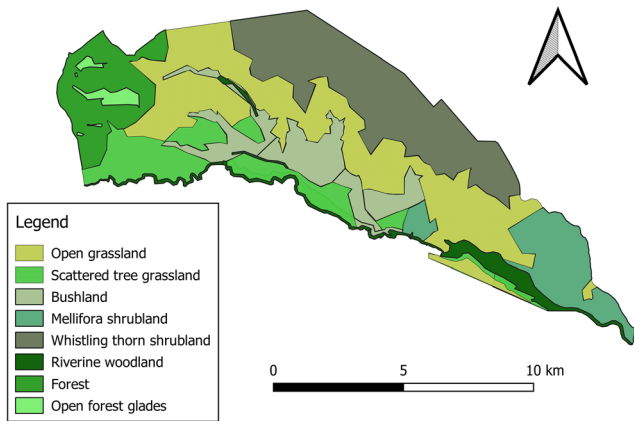


Figure 1: Study area map.



**Figure 2:** Habitat map of Nairobi National Park.

*Croton macrostachys* (Hochstetter and Rich, 1850) and *Olea africana* (Green, 1979) with an open grass glade, occupying 10 km<sup>2</sup>; (ii) The Athi Basin area is an open grass savannah with monocots like *Pennisetum meszianum* (Rich, 1805), *Themeda triandra* (Forssk, 1775) and *Balanites* spp (Delile, 1813) trees and egg-shaped *Acacia mellifera* (Benth, 1842) due to giraffe herbivory. (iii) The Mbagathi River is covered with riverine vegetation dominated by *Acacia xanthophloea* (Benth, 1842) and *A. mellifera*. Dwarf woody plants are a result of controlled burning by park management. The different habitat types are presented in Figure 2.

The park is home to four species of the so-called Big Five: lion, leopard, African buffalo (*Syncerus caffer* (Sparman, 1779)), and black rhinoceros (*Diceros bicornis* (Linnaeus 1758)). The blue wildebeest (*Connochaetes mearnsi* (Heller, 1913)), plains zebra (*Equus quagga* (Boddaert, 1785)) and associated smaller ungulates, such as Grant's gazelle (*granti* (Brooke, 1872)), Thomson's gazelle (*Eudorcas thomsonii* (Günther, 1884)) and common warthog (*Phacochoerus africanus* (Gmelin, 1788)) are abundant throughout the park and tend to range into community land during the wet season (Gichohi 1996). Other resident ungulate species include: southern white rhinoceros

(*Ceratotherium simum simum* Burchell, 1817; introduced), common eland (*Taurotragus oryx* (Pallas, 1766)), kongoni (*Alcephalus buselaphus cokii* (Günther, 1884)), giraffe (*Giraffa camelopardalis* (Linnaeus, 1758)), impala (*Aepyceros melampus* (Lichtenstein, 1812)), waterbuck (*Kobus ellipsiprymnus* (Ogilby, 1833)) and Bohor reedbuck (*Redunca bohr* Rüppell, 1842)) (Owino et al. 2011). The park is also an important bird area with a high diversity of species.

## 2.2 Data collection

Between 2014 and 2017, we collared 12 lions (five males and seven females) in NNP, following Tuqa et al. (2014), with Africa Wildlife Tracking (AWT, Pretoria, South Africa), Very High Frequency (VHF) iridium satellite collars (Table 1). The collars recorded date, time, longitude, latitude, altitude, temperature and distance to previous location. We programmed all the collars to record one fix per three hours and data were accessible and downloaded via the AWT website (<http://www.awt.co.za>). When lions moved outside NNP or when they were suspected to do so, we modified the GPS collars to collect data every 30 min for the analysis of roaming events of lions outside the park.

The collar weight was 1.5 kg which was less than 1% of the animal's weight. We removed collars at the end of battery life or when the animal had an injury. We collared four sub-adult lions from three different prides in January 2017. We monitored sub-adult lions and adjusted collars in November 2017.

## 2.3 Data analysis and statistics

For our first research question, we estimated annual and seasonal home range size of each collared lion by calculating Minimum Convex Polygons (MCP) and Kernel Density Estimation (KDE) home ranges. MCP creates a polygon by connecting the outer GPS locations, while KDE takes into account density estimations of GPS locations (Powell 2000). We determined the resolution bandwidth with least-squares cross validation for fixed-kernel home ranges (Seaman and Powell 1996). The boundaries of the home range areas were defined as 100%

**Table 1:** Summary data for collared lions in Nairobi National Park between 2014 and 2018.

ID	Sex	Pride	Start	End	Fixes	Status
L01	M		2014.01.25	2015.10.07	4669	Dead
L02	F	Southern	2014.01.26	2015.05.25	7386	Neck injury
			2015.08.20	2015.11.14		End of battery power
			2017.01.25	2018.05.17		Dead
L03	M		2015.02.02	2016.12.30	7706	End of battery power
			2017.01.26			Active
L04	F	Northern	2015.02.03	2015.10.10	1744	Dead
L05	F	Middle	2016.02.02	2017.03.16	3709	End of battery power
L06	M		2016.02.02	2017.08.09	4959	End of battery power
L07	F	Northern	2016.02.26	2017.09.13	5088	Dead
L08	F	Middle	2016.07.12		4153	Active
L09	F	Middle	2017.01.23		2486	Active
L10	M		2017.01.23	2018.03.28	2444	Dead
L11	F	Northern	2017.01.30		2518	Active
L12	M		2017.06.30	2018.04.11	1682	Dead

MCP and 95% of KDE, and the core home range as 50% of KDE (Hemson 2003; Powell 2000). We built for each home range estimator (i.e., 50% KDE, 95% KDE and 100% MCP) a mixed effect model (model 1–3), with sex (male/female), season (wet/dry) and pride (northern/middle/southern) as explanatory categorical variables. Bi-annual lion survey sightings were used to allocate lions to the three prides present in NNP. We excluded males from pride home range estimations due to their frequent involvement in pride takeovers.

For our second research question, we calculated the minimum potential daily distance traveled as the Euclidean distance between following GPS fixes within 24 h (Hunter 1998). We build a mixed effect model with daily distance traveled as response variable, and with sex and season as explanatory categorical variables (model 4).

For our third research question, we assigned a vegetation class to each GPS fix to determine the proportion of fixes spent in each habitat type. We determined different habitat types based on vegetation data from the Kenya Wildlife Service's GIS and Biodiversity Office (2011) (Figure 2). All GPS locations outside the park were excluded since there was no habitat classification available. We used the Manly's selection index to assess lion habitat preference (Manly et al. 2002). The selection index was measured using the formula:  $w_i = o_i/p_i$ , where  $w_i$  = selection index for vegetation type  $i$ ;  $o_i$  = proportion (number) of fixes in vegetation type  $i$ ; and  $p_i$  = proportion of vegetation  $i$  available in the park. Values above 1.0 indicated preference, while values less than 1.0 indicated avoidance. The standardized index  $B_i$  allowed comparisons between habitat types:  $B_i = w_i/(\sum n_i \cdot \hat{w}_i)$ . Values below 0.125 (corresponding to 1/number of vegetation types) indicated relative avoidance, while values above indicate relative preference.

For our fourth research question, we investigated how lion space use was affected by human disturbance from Nairobi city and surrounding settlements. We investigated the potential impact of the urban fringe, i.e. the urbanized area along the fence-line, by calculating the nearest distance from each GPS fix inside NNP to the fence-line. We then built a mixed effects model with the lion's relative distance to the fence-line as response variable, and sex and time of day (Day (05:00 h–23:00 h)/Night (23:00 h–05:00 h)) as explanatory categorical variables (model 5). Levels within the factor time of day were based on hours of high and low human activity, instead of daylight hours (Oriol-Cotterill et al. 2015).

For our last research question, we calculated the nearest distance from each GPS fix outside NNP to the southern park border, the Mbagathi river. We built a mixed effects model with lion's relative distance outside NNP to the southern park border, with sex, season, and time of day as explanatory categorical variables (model 6). We also analyzed the frequency and duration of roaming events of lions outside the park. Roaming events were defined as the trajectory of GPS fixes outside the park, including the last GPS fix inside the park and the first GPS fix back inside the park. This may represent an over-estimation of actual duration, but this was inherent to our study design. Different roaming events were separated by 12 h independence, thus multiple crossing of the southern park border by one individual within 12 h were considered as a single roaming event. We built a mixed effects model with respectively the duration (model 7) and frequency (model 8) of roaming events as response variable, and sex and season as explanatory categorical variables.

We implemented a 'geo-fence' around livestock bomas (i.e. livestock enclosures) close to NNP. Geofencing may warn park management and researchers when a lion is in the vicinity of a livestock boma. The collars were programmed such that a short message service (SMS) was received when a collared lion was 500 m from a livestock

boma. We counted the number of occasions when SMS notifications were received and the number of times the lion was located outside the park and no SMS notification was received.

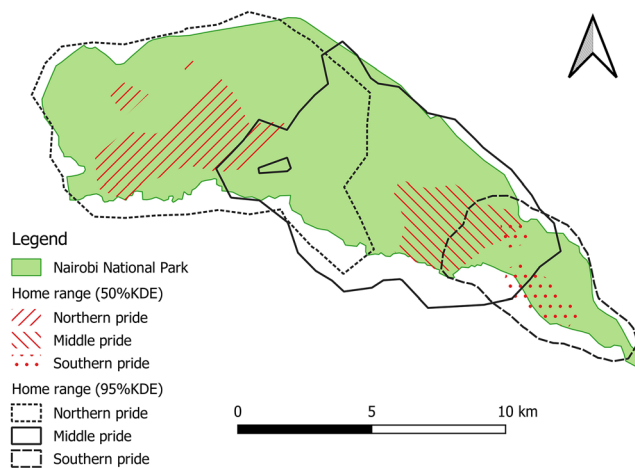
We analyzed the GPS data using the Spatial Analyst tool and the Geospatial Modelling Environment software in ArcGIS version 10.2.2 software (Esri, Redlands, CA, USA). We conducted statistical tests in R version 3.0.2 software and we used a significance level of  $p < 0.05$ . For the mixed effects models, we performed a Likelihood Ratio Test (LRT) with a Chi-squared test. We used the functions *lmer()* and *glmer()* from the package *lmerTest* (Kuznetsova et al. 2017) to build the mixed effect models and we used the function *drop1()* for the LRT-test. For each model, we included lion identity and year as random factors. Response variables of model 1–4 met model assumptions of normality and homoscedasticity. For model 5–7, response variables were right-skewed and non-negative continuous, so we assumed a gamma distribution with the negative inverse transformation as link function in order for the data to fit the model. For model 8, the response variable was count data, so we assumed a Poisson distribution with the log transformation as link function.

## 3 Results

### 3.1 Home ranges and movements

Mean annual home range size of lions in NNP was  $49.2 \pm 22.2 \text{ km}^2$  (95% KDE). Annual core home ranges were on average  $10.0 \pm 5.4 \text{ km}^2$  in size, which was around 20% of the 95% KDE home range. Including the 5% outer most GPS fixes resulted in a mean annual home range size of  $93.4 \pm 43.0 \text{ km}^2$  (100% MCP), covering almost 80% of NNP. Mean annual home range size did not differ significantly from seasonal home range size (95% KDE:  $\chi^2 = 1.93$ ,  $df = 1$ ,  $p$ -value = 0.165). Pride home ranges are presented in Figure 3.

Seasonal home ranges (95% KDE and 100% MCP) were significantly larger for males compared to females, and



**Figure 3:** Pride home ranges in Nairobi National Park between 2014 and 2018.

**Table 2:** Summary of test statistics of variables explaining lion home ranges and movements in and around Nairobi National Park between 2014 and 2018.

	Test statistic	Sex (df = 1)	Season (df = 1)	Pride (df = 1)	Time of day (df = 1)
Model 1	$\chi^2$	2.22	0.36	8.72	–
	<i>p</i>	0.136	0.546	0.128	–
Model 2	$\chi^2$	<b>5.31</b>	0.18	<b>9.31</b>	–
	<i>p</i>	<b>&lt;0.05</b>	0.678	<b>&lt;0.01</b>	–
Model 3	$\chi^2$	<b>8.78</b>	0.17	<b>7.41</b>	–
	<i>p</i>	<b>&lt;0.01</b>	0.678	<b>&lt;0.05</b>	–
Model 4	$\chi^2$	<b>4.28</b>	0.13	–	–
	<i>p</i>	<b>&lt;0.05</b>	0.72	–	–
Model 5	$\chi^2$	0.74	–	–	<b>9.36</b>
	<i>p</i>	0.39	–	–	<b>&lt;0.001</b>
Model 6	$\chi^2$	0.09	<b>26.84</b>	–	<b>146.57</b>
	<i>p</i>	0.76	<b>&lt;0.001</b>	–	<b>&lt;0.001</b>
Model 7	$\chi^2$	2.9	<b>31.36</b>	–	–
	<i>p</i>	0.089	<b>&lt;0.001</b>	–	–
Model 8	$\chi^2$	1.24	<b>78.23</b>	–	–
	<i>p</i>	0.265	<b>&lt;0.001</b>	–	–

Model 1: 50% KDE ~ Sex + Season + Pride + (1 | ID) + (1 | Year). Model 2: 95% KDE ~ Sex + Season + Pride + (1 | ID) + (1 | Year). Model 3: 100% MCP ~ Sex + Season + Pride + (1 | ID) + (1 | Year). Model 4: Daily Distance ~ Sex + Season + (1 | ID) + (1 | Year). Model 5: Distance Fence ~ Sex + Time + (1 | ID) + (1 | Year), family = Gamma. Model 6: Distance South ~ Sex + Season + Time + (1 | ID) + (1 | Year), family = Gamma. Model 7: Duration Roaming ~ Sex + Season + (1 | ID) + (1 | Year), family = Gamma. Model 8: Frequency Roaming ~ Sex + Season + (1 | ID) + (1 | Year), family = Poisson. Bold face values: The bold values are most significance.

differed in size between the three prides (Table 2, Figure 4). In the southern part of NNP, home ranges were smallest and occasionally extended outside NNP into the community lands. No difference in size was found between wet season home ranges and dry season home ranges (Table 2). Core home ranges (50% KDE) remained stable and were not affected by sex, season or pride (Table 2).

The average daily potential minimum distance traveled by lions in NNP was  $4.5 \pm 1.3$  km. Males traveled significantly larger distances compared to females, with a maximum of 29.9 km traveled in one day by L01 (Table 2). All three pride males were observed to travel from the northern part of the park to the southern section in one day. Daily distance traveled was not affected by season (Table 2).

An overview of home range sizes and movements metrics is given in Figure 4 and Table 3.

### 3.2 Habitat factors

The analysis of habitat selection showed that lions in NNP preferred riverine woodland, followed by bushland and

scattered tree grassland. The largest habitat in the park, open grassland, was only slightly preferred by lions in NNP. The habitats that were avoided by lions in NNP were forest and open forest glades, and whistling thorn shrubland, which was the second largest habitat in NNP (Table 4).

### 3.3 Human disturbance

Lions inside NNP were located on average  $2.34 (\pm 1.38$  SD) km away from the fence-line. This distance did not differ between males and females, but lions moved closer to the fence-line at times of low human activity (Figure 4, Table 2).

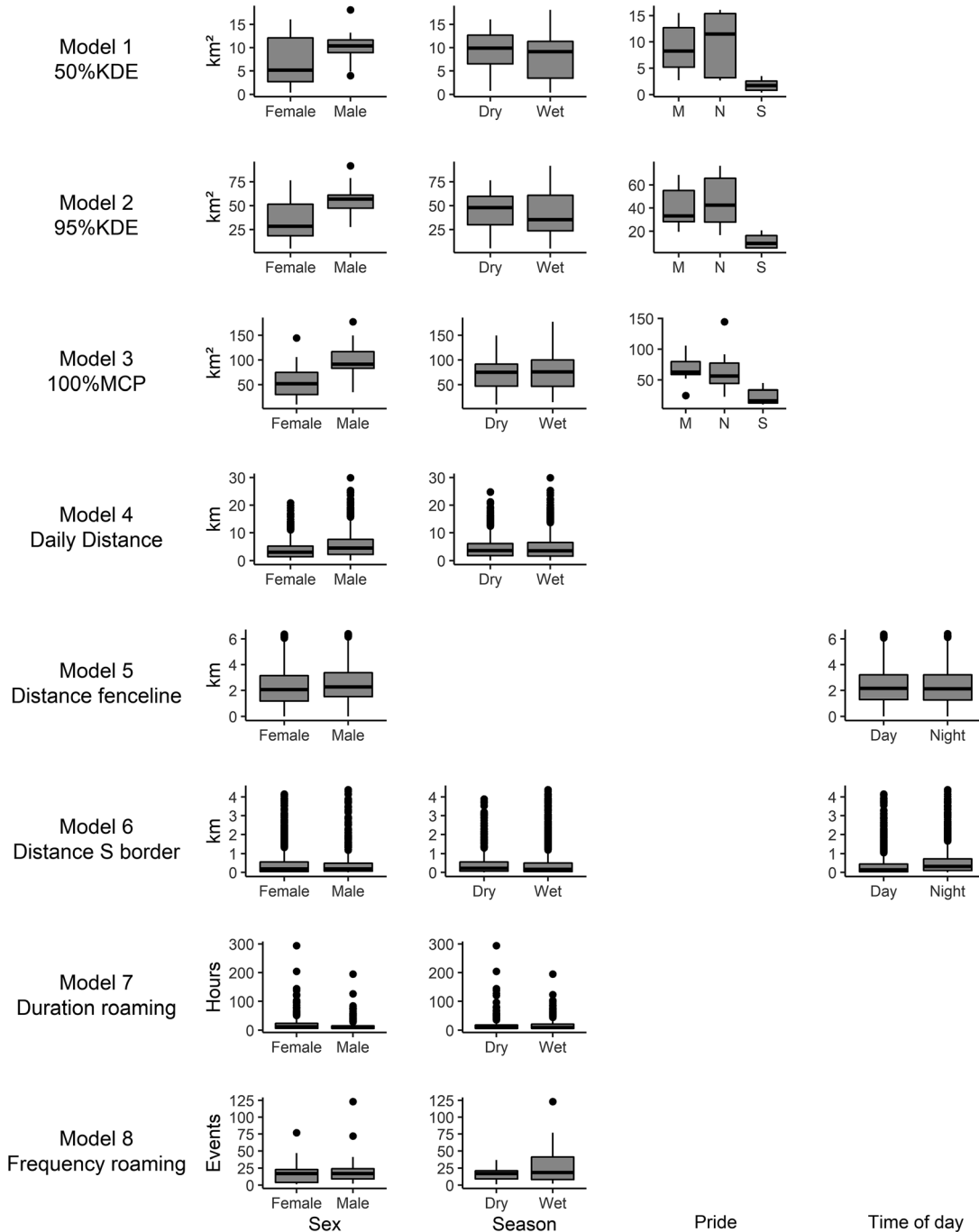
Between 2014 and 2018, collared lions made 864 roaming events into the community lands, lasting on average  $18 (\pm 22)$  hours per event. The median duration was 9 h. On eight occasions, roaming events lasted for more than five continuous days, with a maximum of 12 days by L05 (Figure 5). The average distance of lion locations outside NNP was  $0.47 (\pm 0.76$  SD) km away from the southern park border (Mbagathi river), with a maximum of 4.38 km by L06 (Figure 5). The median distance was 0.19 km. Lions roamed further into the community lands in the wet season compared to the dry season, and at night compared to daytime hours (Figure 6, Table 2). No difference in distance from the southern park border was found between males and females (Table 2). The south-eastern sector was found to be the main exit and entry point between NNP and the community lands (Figure 5).

Visualizations of the differences in movement metrics outside NNP are presented in Figure 5.

The geo-fencing of livestock bomas resulted in 472 SMS notifications. On 127 occasions (27%) delays have been reported in receiving the SMS messages when lions approached livestock bomas, and in 53 cases (11%) a false alert was received during the day when the collared lion was still in the park.

## 4 Discussion

Home ranges of prides ranged between 14 and  $51 \text{ km}^2$  (95% KDE). Lion home ranges in NNP were amongst the smallest recorded for lions throughout Africa, but were comparable in size to lion home ranges in East Africa. In the Amboseli National Park, Kenya, for example, home ranges varied between 24 and  $91 \text{ km}^2$  95% KDE (Tuqa et al. 2014), and in the Serengeti National Park and the Selous Game Reserve in Tanzania, home ranges were on average  $52 \text{ km}^2$  (Schaller



**Figure 4:** Differences in home range size and movement metrics for the different variables tested for lions in and around Nairobi National Park between 2014 and 2018. Levels for the factor pride are: M = middle pride, N = Northern pride, S = Southern pride.

1972; Spong 2002). Daily distance traveled was short (4.5 km), which convenes with the small home ranges. For comparison, lions in the Waza National Park, Cameroon, traveled on average 7.5 km per day (Tumenta et al. 2013) and in the Serengeti National Park, Tanzania, lions traveled on average 14.5 km per day (Schaller 1972). The small home ranges and the short daily distances traveled by lions

in NNP may be sustained by high prey densities, especially during the dry season (Lesilau 2019). Additionally, neighboring prides and the small size of NNP and its surrounding settlements likely restrict lion movements. The different pride home ranges overlapped with the entirety of NNP, which may suggest insufficient coverage of NNP to sustain this lion population.

**Table 3:** Summary of home range size and movement metrics of lions in Nairobi National Park between 2014 and 2018 [mean  $\pm$  SD, range (min–max)].

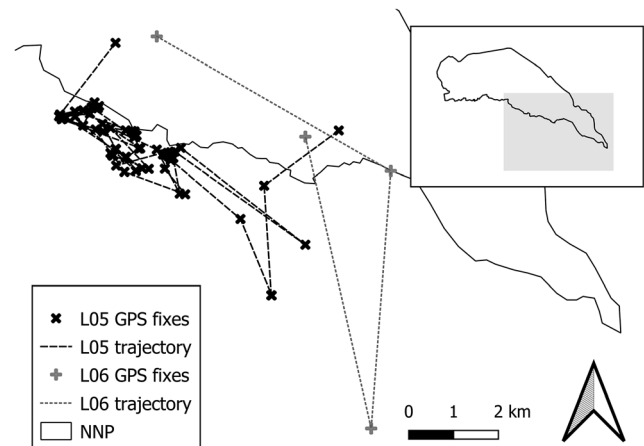
Annual home ranges and movements			
	All years	Males	Females
50% KDE (km <sup>2</sup> )	10.0 $\pm$ 5.4 (0.4–17.7)	11.9 $\pm$ 3.3 (6.4–17.7)	8.5 $\pm$ 6.1 (0.4–22.8)
95% KDE (km <sup>2</sup> )	49.2 $\pm$ 22.2 (6.2–96.4)	62.1 $\pm$ 15.6 (44.7–96.4)	39.5 $\pm$ 21.5 (6.2–85.2)
100% MCP (km <sup>2</sup> )	93.4 $\pm$ 43.0 (18.74–179.7)	124.4 $\pm$ 31.7 (92.2–179.7)	70.2 $\pm$ 35.0 (18.7–153.9)
Daily distance (km)	4.5 $\pm$ 3.6 (0.01–29.9)	5.4 $\pm$ 4.1 (0.01–29.9)	3.7 $\pm$ 2.9 (0.01–20.9)
Seasonal home ranges and movements			
	All seasons	Wet season	Dry season
50% KDE (km <sup>2</sup> )	8.6 $\pm$ 4.9 (0.4–18.1)	8.2 $\pm$ 5 (0.4–18.1)	9.0 $\pm$ 4.6 (0.74–16.1)
95% KDE (km <sup>2</sup> )	43.7 $\pm$ 22.4 (5.3–91.7)	42.6 $\pm$ 23.9 (5.3–91.7)	44.8 $\pm$ 20.3 (5.4–76.4)
100% MCP (km <sup>2</sup> )	74.4 $\pm$ 39.3 (10.4–177.2)	76.4 $\pm$ 43.1 (15.1–177.2)	72.5 $\pm$ 34.1 (10.4–149.1)
Daily distance (km)	4.4 $\pm$ 3.6 (0.01–29.9)	4.6 $\pm$ 3.8 (0.01–29.9)	4.3 $\pm$ 3.4 (0.01–24.8)
Pride home ranges			
	Northern	Middle	Southern
50% KDE (km <sup>2</sup> )	11.9 $\pm$ 7.1 (3.2–22.8)	9.8 $\pm$ 3.6 (6.2–14.9)	2.1 $\pm$ 1.2 (0.4–2.7)
95% KDE (km <sup>2</sup> )	50.9 $\pm$ 23.6 (19.1–85.2)	45.5 $\pm$ 11.1 (29.4–59.5)	14.4 $\pm$ 5.9 (6.2–19.7)
100% MCP (km <sup>2</sup> )	82.9 $\pm$ 43.5 (36.3–153.9)	81.4 $\pm$ 18.2 (62.9–113.8)	34.4 $\pm$ 11.3 (18.7–44.9)

Male lions had larger home ranges and traveled longer distances compared to females. Female ranging behavior is configured around the distribution of resources, while that of males is also influenced by the distribution of females (Loveridge et al. 2009). Additionally, females are restricted in movements when caring for their young (Bauer and Iongh 2005; Funston et al. 2003), while males may roam extensively during dispersal or after pride take-overs (Elliot et al. 2014; Loveridge et al. 2009). Despite differences in ranging behavior, no differences were found between males and females concerning roaming events in the community lands. Females with cubs may avoid the risk of infanticide by avoiding pride territories and may shift home ranges outside Protected Areas towards livestock feeding grounds (Bauer and Iongh 2005; Funston et al. 2003; Packer and Pusey 1983).

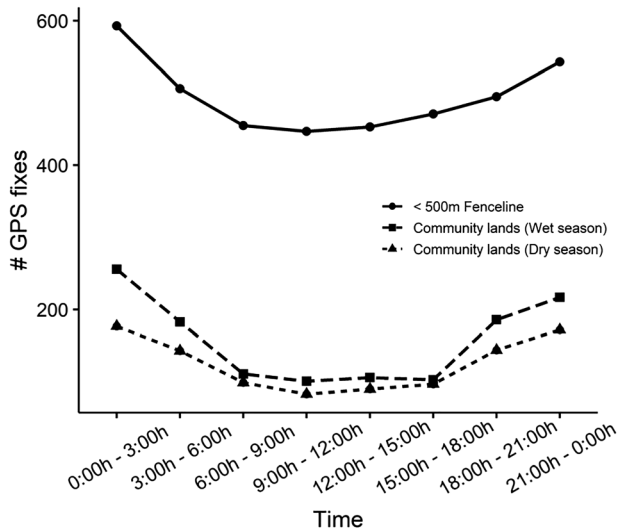
**Table 4:** Habitat selection by lions in Nairobi National Park (NNP).

Habitat type	Proportion of NNP	$w_i$	$B_i$
Bushland	11.18%	1.396	0.174
Open forest glades	1.18%	0.495	0.053
Forest	9.37%	0.483	0.055
Mellifora shrubland	11.53%	1.002	0.119
Open grassland	28.41%	1.05	0.137
Riverine woodland	4.33%	1.733	0.205
Scattered tree grassland	10.7%	1.316	0.15
Whistling thorn shrubland	23.3%	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, which allowing comparisons; values below 0.125 indicate relative avoidance; values above 0.125 indicate relative preference.

**Figure 5:** Trajectory of two roaming events outside Nairobi National Park (NNP). L05 made the longest stay outside the park (13/12/2016 16h22–25/12/2016 22h22), while L06 moved furthest away from the southern park border (4.38 km). The gray area indicates the main exit and entry point between NNP and the community lands.

The absence of seasonal variation in home range size could be a reflection of abundant prey availability and accessibility year round (Bauer and Iongh 2005; Orsdal et al. 2009). Pride home ranges were smaller in the southern section of the park and may suggest higher prey densities in this part. This section also connects to the migratory corridor and some lions were observed to show a shift in home range southwards during the wet season. However, annual range size remained similar to seasonal range sizes, and core ranges did not fluctuate with environmental factors. This suggests relatively stable home ranges. Most lions concentrated their home range in grassland habitat and riverine woodlands, which coincides with their preference for open habitat nearby water sources with cover to ambush prey (Loveridge et al. 2009; Spong 2002). Denser habitats, such as forests and shrublands, were avoided as they may not contain the preferred prey



**Figure 6:** Number of GPS fixes per three-hour interval for lions in Nairobi National Park: (i) within 500 m of the fence-line; (ii) in the community lands during the wet season; and (iii) in the community lands during the dry season.

species (Spong 2002), or because of their location near the fence-line.

The urban fringe was generally avoided by lions, likely because of the light-, noise-, and air pollution from Nairobi city. This suggests that a considerable part of NNP is underused due to edge effects. Yet, we noticed that lions moved closer towards the fence-line at times when human disturbance was lower. At these times, lions actively search for resources and patrol territory boundaries (Schaller 1972).

Spatio-temporal avoidance of human activity was also identified along the southern park border. The community lands are privately owned and are progressively being partitioned into small fenced plots (Gichohi 1996). Due to human activity during the day, lions have little space to roam and may prefer to stay in the park. Roaming events mostly occurred at night because of low human disturbance, in combination with cover of darkness (Oriol-Cotterill et al. 2015). Most livestock returned to their bomas in the evening, which reduced depredation risk at night (Lesilau et al. 2018; Tumenta et al. 2013). Additionally, LED flashlights at these bomas work as an effective predator deterrent to protect livestock from predator attacks (Lesilau et al. 2018). Lions never roam far from the park border into the community lands and roaming events within the community land were mostly short distances. On the few occasions roaming events lasted multiple days, individuals were often located just beyond the park border, on the other side of the Mbagathi river, which may include part of their home range. Yet, pastoralists with grazing herds were

regularly observed close to the river, thus livestock here is readily accessible and available as an alternative prey source (Valeix et al. 2012).

Seasonal variation in roaming events suggested that, risk for human–lion conflict in the wet season is higher. Lions roamed further, more often, and longer into the community lands compared to the dry season. This observation coincides with previous studies and is likely a reflection of prey migration outside the national park (Tumenta et al. 2013; Valeix et al. 2012). The community lands contain important feeding grounds for both livestock and several large migratory herbivores during the wet season (Gichohi 2003). To fulfill their energetic requirements, lions may rely on roaming events, especially during the wet season, even when seasonal home ranges are similar in size and lie mostly within NNP.

Roaming events could not be identified when they were shorter than the specified GPS interval, which was mostly set at 3 h. Shorter events were likely to happen due to the closeness, proximity of livestock bomas to the park border. This issue could be overcome by the geo-fencing of these bomas. We found that this method was only partially successful. The observed delay in receiving SMS notifications may be due to cloud and/or vegetation cover, inhibiting signal transmission. While improvement of this technology might work as an innovative early-warning system, priority should be focused towards addressing the cause of human–lion conflict.

We conclude that lion spatial ecology in NNP is highly affected by human disturbance. High prey densities inside NNP may allow lions to survive in small home ranges with restricted movements. Urban development around NNP may have resulted in an isolated lion population with little to no gene flow. Lion home ranges are squeezed between the urban fringe in the north, and the community lands in the south. Lions show general avoidance of these areas, but take advantage during times of low human disturbance to extend their ranging behavior into these areas. Especially during the wet season, lions may become partially dependent on roaming events in search for resources. This highlights the importance to protect the migratory corridor in the community lands, but also indicates increased risks for human–lion conflict during the wet season.

Reducing detrimental edge effects could be facilitated by creating buffer zones in the southern border of NNP. Buffer zones may be defined as areas peripheral to a national park, where restrictions are placed upon resource use and where community development measures are undertaken to enhance the conservation value (Martino 2001). Buffer zones as defined above are difficult to



establish along the northern park border because of the permanent infrastructures of Nairobi city. However, an expansion of natural habitat may act as an embankment to filter noise-, air- and light pollution from the city and bordering highways. A buffer zone *sensu stricto* along the southern border would provide more space for lions to roam, while reducing risk for herders to lose livestock. Creating a buffer zone requires land reformation and implies involvement of stakeholders for successful establishment (Martino 2001). We deem this necessary around NNP to maintain a viable lion population in the near future and may restore connectivity with other conservation areas.

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