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Original research article

## Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya



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## ABSTRACT

In this study, we were interested in understanding if droughts influence the home range of predators such as lions, and if it does, in what ways the droughts influenced lions to adjust their home range, in response to prey availability. We monitored movements of ten lions fitted with GPS-GSM collars in order to analyze their home range and movement patterns over a six year period (2007–2012). We assessed the impact of a severe drought on the lion home range and movement patterns in the Amboseli ecosystem. There was a strong positive correlation between the home range size and distance moved in 24 h before and during the drought (2007–2009), while after the drought there was a significant negative correlation. A weak positive correlation was evident between the lion home range and rainfall amounts (2010–2012). The male and female home ranges varied over the study period. The home range size and movement patterns coincided with permanent swamps and areas of high prey density inside the protected area. Over the course of the dry season and following the drought, the ranges initially shrank and then expanded in response to decreasing prey densities. The lions spent considerable time outside the park boundaries, particularly after severe the drought. We conclude that under conditions of fragmented habitats, severe climate conditions create new challenges for lion conservation due to effects on prey availability and subsequent influences on carnivore species ranging patterns. Stochastic weather patterns can force wide-ranging species beyond current reserve boundaries, into areas where there will be greater conflicts with humans.

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## 1. Introduction

African lions (*Panthera leo leo*) are threatened to extinction across their range, and have been classified as 'vulnerable' on the global IUCN Red List (IUCN, 2013). They are also currently under consideration for the Endangered Species List, US Fish and Wildlife Society (US-FWS) (Place et al., 2011). Several authors have described the decline in lion population due to factors related to human interference (trophy hunting, poaching, agricultural and urban development, habitat fragmentation and conflicts) or due to natural factors related to the environment—climate variability, cover, prey availability and topography (Bauer and Van Der Merwe, 2004). There is however paucity of research on the impacts of stochastic drought on a lion population and their home ranges.

Conservation policy and habitat management based on scientific information is important for managing protected areas for large carnivores (Karanth and Chellam, 2009). However, climatic changes may modify the distribution and abundance of species and include some key variables that may have severe impact on ecosystems that adversely influence lions' natural habitat selections (Iverson and Prasad, 1998; Ohlemüller et al., 2006). Knowledge of a species' ranging behavior is both fundamental to understanding its behavioral ecology and a prerequisite to planning its management. Rainfall determines habitat quality and structure through its influence on vegetation health, mediated through edaphic and topographic/catenary gradients (Bell, 1982; McNaughton, 1983) and can induce changes in habitat suitability, which are capable of substantially modifying predator–prey relations (Smuts, 1978; Whyte et al., 1995). Besides prey availability and vegetation cover, rainfall also affects the distribution of drinking water, thereby modulating the spatial–temporal distribution of water-dependent herbivores and carnivores (Western, 1975; Hanby et al., 1995; Krebs & Dominique, 2006), "similarly, climate affects the distribution and abundance of mammals (Krebs & Dominique, 2006)"; Moreover, the impact of climate change and climatic variability shows a spatially heterogeneous pattern and may have already resulted in several recent local species extinctions (Pounds et al., 2006). These changes raise concerns about the effectiveness of existing species protection strategies (Halpin, 1997; Hannah et al., 2002; Peter and Darling, 1985).

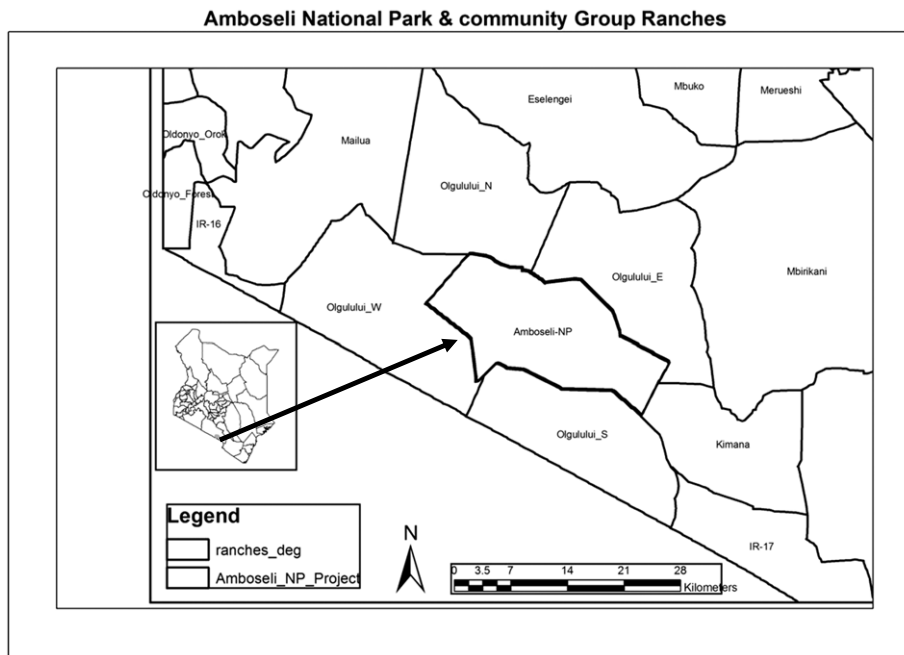
Species conservation relies predominately on fixed systems of protected areas. Furthermore, the mandated goals of many conservation agencies and institutions are to protect particular species assemblages and ecosystems within these systems (Lemieux and Scott, 2005). Of particular importance are the challenges associated with conservation of carnivores outside protected areas, including both anthropogenic and ecological factors (Dolrenry et al., 2014). The home range size of large carnivores is a good predictor of its extinction probability relative to the size of the neighboring protected areas where home ranges extend significantly into non-protected areas relative to the size of the neighboring protected areas (Woodroffe and Ginsberg, 1998; Woodroffe et al., 2001). Increased anthropogenic activity as a consequence of rapid human population growth has resulted in the reduction of natural habitats for lions (Riggio et al., 2013, Bauer and Nowell, 2004) and increasing persecution (Tumenta et al., 2010).

Home range analysis of large carnivores provides answers to many biological questions related to population dynamics, social interactions, and spacing patterns. Lions' home range size varies in relation to a wide range of factors, including prey availability, social interactions, habitat quality and reproductive status (Gittleman and Harvey, 1982; Van Orsdol et al., 1985; Viljoen, 1993; Spong, 2002; Bauer and De longh, 2005). Abundant food and high quality habitat allow an animal to meet its biological requirements in a relatively small home range and vice versa (Gittleman and Harvey, 1982; MacDonald, 1983).

The home range area is used during its normal activities of food gathering, mating and caring for its young. The core of an animal's home range is defined as the most intensively used area within that animal's home range (Powell, 2000). In the case of lions, their home range is directly related to prey abundance and the presence of water, thus lower prey densities and low availability of water correspond with larger home ranges and vice versa (Celesia et al., 2009; Van Orsdol et al., 1985; Tumenta et al., 2013). However, other factors, such as social status, sex, age, season, disturbance and the presence of livestock may influence the home range (Schaller, 1972; Loveridge et al., 2009; Tumenta et al., 2012).

Group size and territoriality are social factors that also influence home range size (Packer et al., 2005), with home range size increasing with group size (Van Orsdol et al., 1985). Larger prides require more prey and therefore larger areas corresponding to prey biomass and density. Lion home range size being negatively correlated with prey abundance (Van Orsdol et al., 1985; Bauer and De longh, 2005; Loveridge et al., 2009). Maintaining a pride home range is of great importance, evident from the fact that fatalities are relatively common during intergroup encounters (McComb et al., 1994). Understanding the variation in animal home range size, and identifying the factors that underlie this variation, are fundamental to understanding the distribution and abundance of animals, and ultimately their population regulation (Wang and Grimm, 2007), habitat selection (Rhodes et al., 2005), community structure (Matias, 2013), as well as the management and conservation of ecosystems (Woodroffe and Ginsberg, 2000).

The present study is the first of its kind to analyze the effect of drought on lion movements, covering a period of three years before and during the drought period (2007–2009) as well as three year period after the severe drought period. Our study investigated the impact of a severe drought on lion's home ranges size and movement patterns, in relation to variation in food resources (prey biomass) before and during versus after a severe drought period.



**Fig. 1.** Amboseli National Park and surrounding group ranches which together form Amboseli ecosystem.

## 2. Materials and methods

### 2.1. Study area

The Amboseli ecosystem is situated in the south-west of Kenya, bordering Tanzania. The ecosystem covers an area of approximately 5700 km<sup>2</sup> stretching between Chyulu Hills and Tsavo West National Parks South to Mt. Kilimanjaro in Tanzania (Fig. 1). Administratively, the Amboseli ecosystem consists of Amboseli National Park (ANP; 392 km<sup>2</sup>) and the six surrounding communally-owned Maasai group ranches. These group ranches cover an area of about 5063 km<sup>2</sup> in Kajiado County (Fig. 1). In the center of the ecosystem, lies the Amboseli Basin, a Pleistocene lake bed. The basin provides a permanent source of water from Mt. Kilimanjaro that attracts high concentrations of migratory animals during the dry season.

The area is generally arid to semi-arid. Rainfall is bi-modal with short rains coming in November and long rain period starts in March–May (Altmann et al., 2002). An average of 340 mm rainfall per annum is expected (Moss et al., 2011), while droughts are common when rainfall falls below average, making the area suitable for conservation and tourism enterprises (Moss et al., 2011). The ANP is a dry season grazing area for wildlife that disperses widely to the adjacent group ranches during the wet season, when water and forage is plentiful (Western, 1987; Groom, 2010; Muthiani and Wandera, 2000; Ntiati, 2002). Although ANP is one of the leading tourist destinations in the country with an average of 150,000 visitors per annum due to high congregation of wildlife (Okello et al., 2009), its future might be threatened by the increase of human developments and livestock grazing—this is already indicated by increased human conflicts (Okello and Kioko, 2010). The development activities around the park have caused fragmentation of wildlife habitats, diminished the dispersal areas and limited free movement of animals (Okello et al., 2009, Western et al., 1987, Moss et al., 2011).

### 2.2. Methods

To understand lion ranging patterns and seasonal movements, we immobilized and radio-collared ten lions between 2007 and 2009. The lions were captured by free darting (Bauer and De longh, 2005), after being attracted using a calling station set-up adapted from Ogutu and Dublin (1998). We used GPS-GSM collars from African Wildlife Tracking with an integrated VHF radio transmitter (Hawk collar Pretoria, SA). Characteristics of these collars have been described previously (Tomkiewicz, 1996, Schwartz and Arthur, 1999). The collars were programmed to attempt locations of animals at either 3 h or 30 min intervals. The collars recorded date, time, latitude, longitude, and general cause of unsuccessful location fixes. Direct observations of individuals were made periodically using VHF radio tracking techniques, following White and Garrot (1999). Table 1 presents details of the collared lions. The GPS coordinates of scheduled lion locations were downloaded from the Yrless website ([www.yrless.co.za](http://www.yrless.co.za)). The lion locations were subsequently processed in ArcMap (ArcGIS 9.3.1, ESRI, Redwood, CA, USA), using Hawth's Tools extension packages Spatial Analyst and Animal Movement (Gitzen et al., 2006) to determine the home ranges, movement path parameter, and step length. A large number of fixes, 17,333 before and during

**Table 1**

Summary of mean dry–wet seasonal variation of lion home ranges for MCP100, KDE95 and KDE50, also indicating periods before/during and after the drought, for both the male and female lions.

Home range (km <sup>2</sup> )	Sex	Period before and during drought		Period after drought	
		Dry season	Wet season	Dry season	Wet season
Mean range size MCP100	Female	121.6970	34.90731	262.4299	187.9834
	Male	177.1273	57.03124	373.6114	272.2590
Mean range size KDE95	Female	23.92670	46.15006	63.98443	73.28422
	Male	26.01459	52.76172	74.15555	91.24822
Mean core range size KDE50	Female	4.845110	9.219601	11.96629	14.06204
	Male	9.562454	4.522554	11.59452	14.94625

drought and 26,309 after the drought were obtained during the study period. To facilitate analysis and reduce the probability of autocorrelation, a three-hour selection was carried out on the data reducing the data size to six points per day.

### 2.3. Range analysis

Home ranges were estimated using two methods, the minimum convex polygon (MCP) and the kernel density estimator (KDE). The MCP method is the oldest one used among home range analysis methods (Burt, 1943; Mohr, 1947), being the smallest convex polygon that encompasses all the lion locations, either using all the locations (MCP100%) or by first removing 5% of the outliers in the dataset (MCP95%) (Powell, 2000). Some authors suggest that MCP is inefficient and highly sensitive to sample size and outliers (Börger et al., 2006). In contrast, the KDE method is remarkably efficient, robust and unbiased (Worton, 1989; Börger et al., 2006). This method uses the harmonic mean of the locations to assess the core density areas, with the areas defined as the boundaries of the lion's home range (KDE95%), the core home range (KDE50%) and the heart of the core area (KDE5%). We used the KDE method to calculate home range metrics. We set the outer boundary at 95% and the core area at 50% (White and Garrot, 1990). The smoothing factor was chosen using the least square cross validation (Kernohan et al., 2001) and was 0.02 for all calculations. Range was analyzed for each year during the study period. Home ranges, both MCP and KDE, for the different seasons were calculated and compared with other studies.

We use potential minimum distance, defined as the minimum distance traveled by a lion in a straight line, measured in kilometers, either in a 12 h period, night (18.00 p.m. until 6.00 a.m.) or day (6.00 a.m. until 18.00 p.m.) or average potential minimum movement, measured over a 24 h period. All were measured for the period before, during, and after the drought to assess the impact of severe drought on the lion movement pattern.

We also assessed use of protected area versus non-protected areas by lions in relation to the drought by assessing the number of days that the lions were exclusively inside the park, the number of days the lions were both inside and outside the park and number of days the lions were exclusively outside the park. We determined overlap in home range and movement inside and outside ANP using ARC-GIS (ESRI, Redwood, CA, USA).

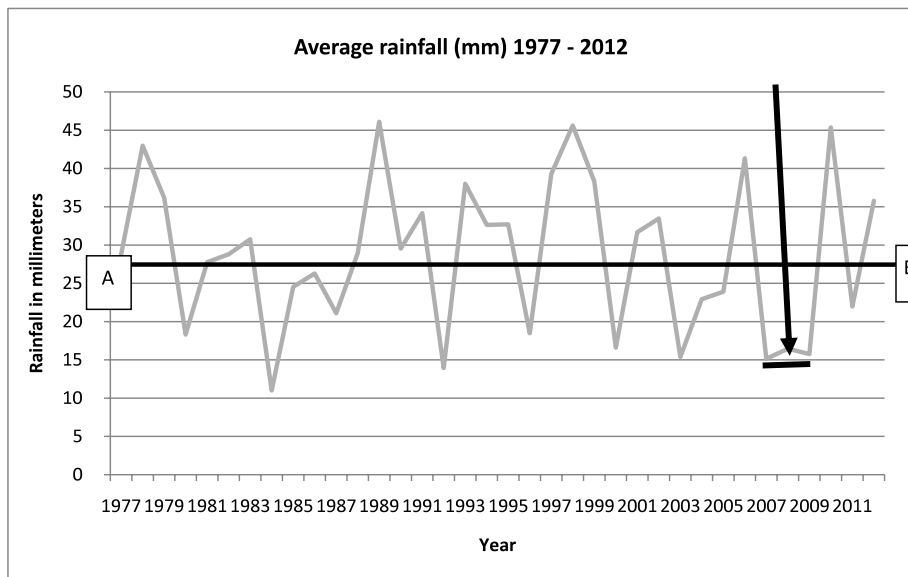
We analyzed rainfall statistics during 1977–2012 obtained by the Amboseli Baboon Research Project following Altmann et al. (2002). We then determined the effect of rainfall variability and severe drought on lion home range by relating seasonal rainfall and lion home range in square kilometers and daily distance moved, in kilometers. We described rainfall of 28.3 mm (Fig. 2, line A–B) as cutoff point between the drought and wet period.

### 2.4. Statistical analysis

All statistical analysis was carried out in R 3.0 programme (R Development Team, Austria). The dependent factors are home range and potential minimum movement per day; the independent factors are monthly rainfall and sex of lion. The regression of covariates on MCP was done using a generalized linear mixed effects model (GLM) with the Poisson link function. For the problem of fit of distribution to the KDE data, we did a linear mixed effects model for both KDE50 and KDE95 response variables.

The lions' home range and daily movements were compared to one another to test for significant differences according to social status and sex differences. A test on normal distribution was done with the Shapiro–Wilkes test. We found the distribution of home range data was non-normal, thus we log-transformed the data and applied *t*-test. Furthermore, each lion's day and night movements were compared using one-sided Wilcoxon signed rank tests ( $p < 0.05$ ) since the samples were not normally distributed and the subsamples were paired. In order to test whether the lion's traveled distance changed between 2010 and 2011, a paired *t*-test ( $p < 0.05$ ) or a Wilcoxon signed rank test ( $p < 0.05$ ) was run. Difficulties with data analysis were attributable to unbalanced structures, nesting versus crossed structure, size of data and negativity of variance, as well as residual analysis and diagnostics due to assumptions on the residuals, among others. Restricted/Residual Maximum Likelihood Estimation (REML) is well-suited to handle the negativity of variance estimates, unlike ANOVA or Maximum Likelihood Estimation (MLE).

We compared several models before we ended up with an optimal model for all home ranges and KDE on parameter interpretation. We considered a fixed effect factor as opposed to a random effect factor whose levels in the study are just



**Fig. 2.** Mean rainfall for years 1977–2012 and severe drought period 2008–2009 in Amboseli Ecosystem (Source: Amboseli Baboon research). The arrow indicates drought which was comparable to 1984 and 1992 droughts and drought period which indicate worse in 35 years (2009).

a sample of all the other possible choices. In the mixed model the multilevel structure contains factors that are considered fixed and others random. In such a mixed model scenario, the key steps of mixed model analysis involve estimating variance component parameters using Restricted Maximum Likelihood (REML), then estimating fixed effects parameters using Bayesian Information Criterion (Sclove 1987), for lion home range. We carried out ANOVA on (models 1, 2 and 3) as follows:

Model 1, had the response variable as home range areas MCP in  $\text{km}^2$  while the explanatory variables were: fixed effects of season, period of drought, sex, interactions between season and drought period and the interaction between period of drought and sex. Random effect was the individual lion.

Thus, Model 1 was constructed as follows:

$$\text{Area of MCP, KDE 95 and KDE 50 in km}^2 \sim \text{season} * \text{drought period}_ * \text{sex} + (1 | \text{LION\_ID}).$$

Model 2, had the response variable as home range area MCP in  $\text{km}^2$  while the explanatory variables were: fixed effects of season, period of drought, sex, interactions between season and drought period, interaction between season and sex and the interaction between period of drought and sex. Random effect was the individual lion.

Model 2:

$$\begin{aligned} \text{Area of MCP, KDE95 and KDE50 in km}^2 &\sim \text{season} + \text{drought period} + \text{sex} \\ &+ (1 | \text{LION\_ID}) + \text{season} : \text{drought period} + \text{season} : \text{sex} + \text{drought period} : \text{sex}. \end{aligned}$$

Model 3, the response variable was the area of the MCPs, KDE95 and KDE50 in  $\text{km}^2$ . The explanatory variables were the: fixed effects main effects of season, period of drought, sex, and up to three way interactions between season, drought period and sex. Again, the random effect was the individual lion.

Model 3:

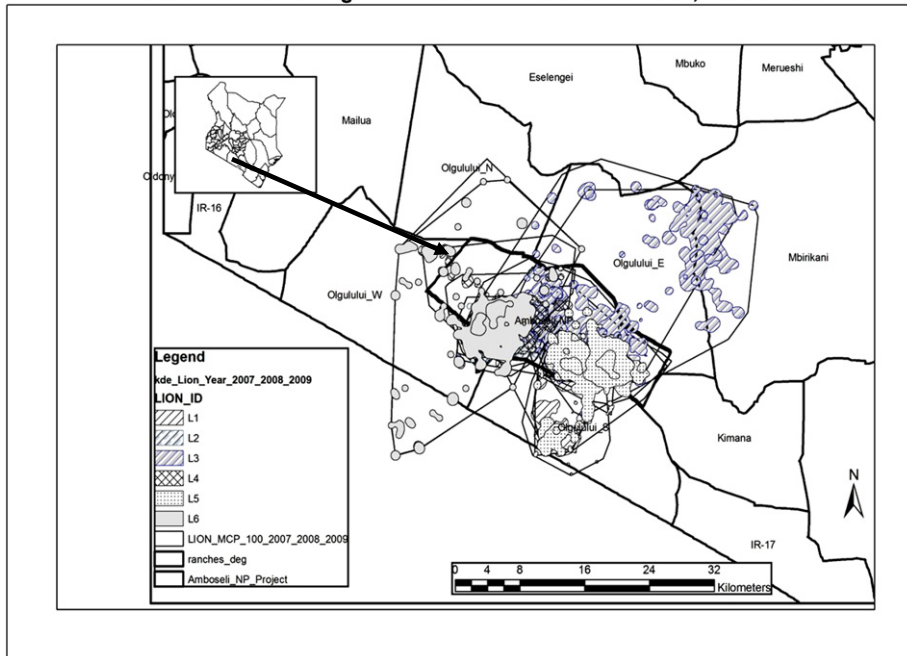
$$\begin{aligned} \text{Area of MCP, KDE95 and KDE50 in km}^2 &\sim \text{season} + \text{drought period} + \text{sex} \\ &+ (1 | \text{LION\_ID}) + \text{season} : \text{drought period} + \text{drought period} : \text{sex}. \end{aligned}$$

### 3. Results

#### 3.1. Relationship between rainfall, home range and movement patterns

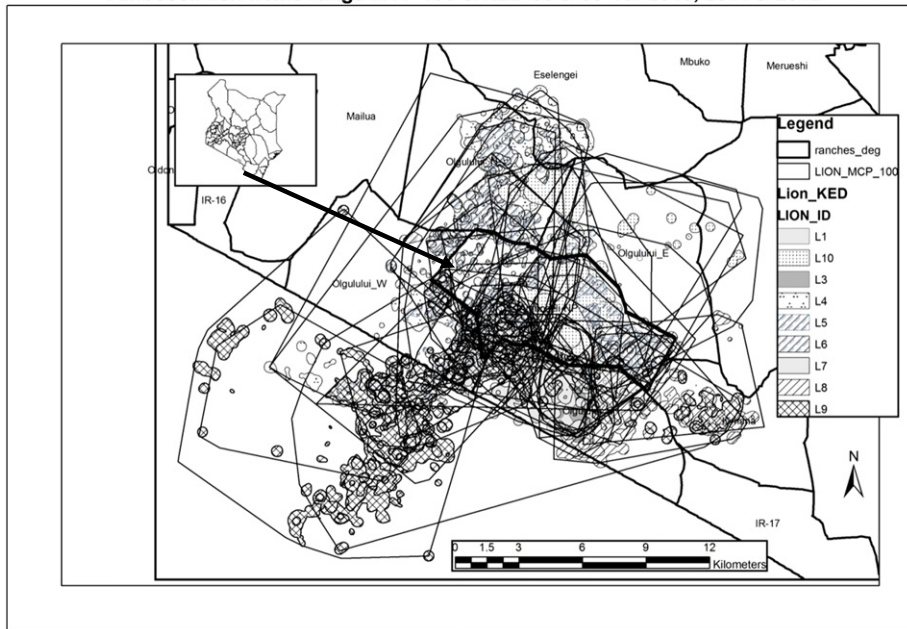
Our analysis of rainfall data during 1977–2012 showed high rainfall variability and severe recurrent droughts at varying annual intervals (Fig. 2). For example, severe droughts occurred during 1984, 1992, 1999, 2003, and 2009. The lion home range data during 2007–2012 showed strong correlation between home range sizes and lion daily distance moved in 24 h before (2007 and 2008;  $r^2 = 0.401$ ) and during (2009;  $r^2 = 0.359$ ) the drought. During the period that followed the drought (2010–2012) there was a non-significant correlation ( $r^2 = 0.285$ ) between home range size and average daily distance movement by lions. There was also a significant negative correlation ( $r^2 = 0.030$ ) between the amount of rainfall and the average potential minimum distance moved in 24 h after the severe drought.

### Amboseli lion home range MCP 100 & KED 95 & 50 for 2007, 2008 & 2009



**Fig. 3.** Lion home range sizes before and during the severe drought (2007–2009) measured in squared kilometer for MCP100, KDE95 and KDE50.

### Amboseli lion home range MCP 100 & KED 95 & 50 for 2010, 2011 & 2012



**Fig. 4.** Lion home range sizes for the period after the drought (2010–2012) measured in squared kilometer for MCP100, KDE95 and KDE50.

We found a high mean seasonal (wet and dry) lion home range variability before and during (2008–2009) and after the drought (2010–2012) (Table 1). The mean home range seasonal variability was greater during post-drought. Our results showed expanded ranges even during the dry season of the post-drought period, from the dry seasons of the pre-drought and drought period (Table 1). The mean overall home range was not significantly different for the male and female lions.

There was high variation of lion home range sizes for the period after the drought (2010–2012) as compared to period before and during the drought (2007–2009; Figs. 3 and 4). Lions expanded their home range during the period after the drought seeking new territories not covered before/during the drought.

**Table 2**

Output of fixed effects of mixed modeling for lion home range indicating seasonal home range variation, before/during and after the drought, male and female and their interactions showing estimate standard error, Z-values and level of significance  $P < 0.005$  for MCP100, KDE95 and KDE50.

	Period	Estimated	Std. error	Z-value	Pr(> z )
Model 2: Home range MCP100	(Intercept)	5.26893	0.15954	33.03	<2e–16***
	Dry season	–0.38578	0.01470	–26.25	<2e–16***
	Before drought	–0.61415	0.02347	–26.16	<2e–16***
	Sex: Male	0.88742	0.29099	3.05	0.00229**
	Dry Season: Before drought	–0.78875	0.02492	–31.65	<2e–16***
	Dry Season: Sex: Male	0.08383	0.01950	4.69	1.72e–05***
	Before drought sex: Male	–0.65428	0.04373	–14.96	<2e–16***
Model 3. Home range KDE95	(Intercept)	4.22476	0.06506	64.94	<2e–16***
	Dry Season	–0.17830	0.02053	–8.68	<2e–16***
	Before drought	–0.36607	0.03952	–9.26	<2e–16***
	Sex: Male	0.30873	0.11609	2.66	0.00783**
	Dry Season: Before drought	–0.48331	0.03967	–12.18	<2e–16***
Before drought sex: Male	–0.28064	0.05881	–4.77	1.82e–06***	
Model 2: Home range core KDE50	(Intercept)	2.55628	0.09153	27.927	<2e–16***
	Dry Season	–0.22355	0.04886	–4.576	4.758e–06***
	Before drought	–0.25082	0.08782	–2.856	0.00429**
	Sex: Male	0.07837	0.15118	0.518	0.604
	Seasondry: Before drought	–0.44136	0.09131	–4.833	1.34e–06***
	Before drought Sex: Male	0.35531	0.08014	–4.434	9.26e–06***

Significance: \* 0.05.

· 0.1.

·· 1.

··· 0.01.

···· 0.001.

### 3.2. Mixed modeling and model comparisons

The result show that model 2 was the most optimal of the three models for MCP100 (smallest BIC = 19060), KDE95 (smallest BIC = 2511), and KDE50 (smallest BIC = 688.99). Similarly, the p-value shows that model 2 variables were significantly different ( $p = 1.718e - 05 < 0.05$ ), but model 1 was not significantly different from model 3 ( $p = 0.3756 > 0.05$ ). We therefore interpreted the output of model 2 for MCP100, KDE95 and KDE50.

The results show that all the variables considered in model 2 were significant (Table 2). We therefore did not need to remove any variables in the model before we ran the mixed model analysis. The intercept in this case represented the average area in km<sup>2</sup> for MCP100, KDE95 and 50 for the following conditions: dry season, period after drought, female lion.

#### Mixed model (main effects)

Holding other variables at their default, the mean MCP area in km<sup>2</sup> for male lions was greater by 0.88742 km<sup>2</sup> compared to the mean MCP for female lions. The difference is statistically significant ( $p = 0.00229 < 0.05$ ). The MCP area for the period before drought was lower by 0.61415 km<sup>2</sup> compared to the period after the drought. Similarly, the dry season MCP measurements were also lower by 0.38578 km<sup>2</sup> compared to the wet season. Conversely, holding other variables at their default, the mean KDE95 area in km<sup>2</sup> for male lions was greater by 0.30873 km<sup>2</sup> compared to the mean KDE95 for female lions. The difference was statistically significant ( $p = 0.00783 < 0.05$ ). The KDE95 area for the period before drought was lower by 0.36607 km<sup>2</sup> compared to the period after the drought while the dry season also had lower KDE95 areas by 0.17830 km<sup>2</sup> compared to the wet season. Similarly, holding other variables at their default, the mean KDE50 for male lions was higher by 0.07837 km<sup>2</sup> compared to the mean KDE50 for female lions. However, the difference was not statistically significant ( $p = 0.604 > 0.05$ ). The KDE50 area for the period before drought was lower by 0.25082 km<sup>2</sup> compared to the period after the drought while the dry season also had lower KDE50 by 0.22355 km<sup>2</sup> compared to the wet season.

#### Mixed effects (interaction terms)

Considering the interactions, the interaction between season and the period was significant ( $p < 0.0001$ ). We observed that the period before drought had a lower MCP compared to the period after drought by 0.78875 km<sup>2</sup> during dry season. The interaction between season and the period was significant ( $p < 0.0001$ ). We observed that the period before the drought had a lower KDE95 compared to the period after drought by 0.48331 km<sup>2</sup> during dry season. The interaction between season and the period was significant ( $p < 0.0001$ ). We observed that the period before the drought had a lower KDE50 compared to the period after drought by 0.44136 km<sup>2</sup>.

Table 3 shows that there was no significant difference by sex ( $W = 1680, p = 0.102$ ) in the number of days spent outside the park or by season ( $W = 2420, p = 0.114$ ), but there was a significant difference between males and females in the number of days spent outside the park for the period before and during the drought and after the drought ( $W = 1732.5, p = 0.033$ ). Clearly, the lions moved further outside of the protected area during drought when prey became scarce.

**Table 3**

Lion daily, seasonal and movement before/during and after the drought, Wilcoxon–Paired sample *t*-test values and level of significance  $P < 0.005$ .

Parameters	Wilcoxon (W) test	<i>P</i> = values
Days outside by sex	1680	0.1022–NS
Days outside by season	2420	0.1489–NS
Days outside by period before and after drought	1732.5	0.03394 <sup>†</sup>
Distance moved in 24 h	4972	1.873e–07 <sup>***</sup>
Distance moved in 24 h by season	8576	0.007838 <sup>***</sup>
Distance moved in 24 h by periods before and after drought	14717	<2.2e–16 <sup>***</sup>

Significance: \*\* 0.01.

† 0.1

\*\* 1.

\* 0.05.

\*\*\* 0.001.

## 4. Discussion

### 4.1. Home ranges and movement patterns

We found significant variation in lion home ranges, movement patterns by the lions before and during the drought versus after the drought. We also found variation in male and female home ranges over the study period (Table 1). This was not surprising since female lions defend smaller areas that provide good resources and are suitable for raising their cubs, male lions defend larger areas that may cover the ranges of two or more female prides (Funston et al., 2003). Interestingly, this variation was significantly different between the before/during period versus after the drought period (Table 1). Similar findings were reported for the lions in Cameroon by Tumenta et al. (2013), and Connor et al. (2001).

During the wet season, when food is abundant due to the large herds of herbivores dispersing outside the park, the lions increased their home range. Permanent water sources in ANP would have drawn herds of prey animals into the ANP during the drought year, when the minimum observed lion home ranges varied between 28 and 37 km<sup>2</sup>. A similar situation was observed in Waza National Park in Cameroon with larger home ranges recorded during the wet seasons, probably because the prey species disperses more (Tumenta et al., 2011). Due to the expansion and contraction of home ranges in response to prey availability, the total prey biomass within the home range may remain relatively constant.

MacDonald (1983) suggested that resources and especially food dispersion are the main factors determining the home range size of large carnivores. According to their findings the home range size is mainly determined by how food is distributed in space, while the group size is determined by the prey size and quality of food patches (Bauer and De longh, 2005). An understanding of an animal's ranging patterns provides an important insight on how it uses its resources.

Climate events affected the habitat quality, food supply and access, which in turn, as our results show, influenced the lions' home-range and movement patterns.

Our study is the first extensive study on the impact of a severe drought on the movements and home ranges of lions as it has demonstrated dramatic changes before and after the drought that could be explained by changes in prey densities.

### 4.2. Lion movement and landscape connectivity

We found that the potential minimum distance traveled was significantly greater after the drought (2010–2012) compared to before or during the drought (2007–2009). The daily distance traveled represented a measure of space requirements that partly reflects the food resource needs and distribution (Carbone et al., 2005).

On several occasions, both the collared male and female lions moved far and wide from the ANP into the surrounding communal group ranches as also found by Dolrenry (2013). Furthermore, one of the males collared in this study spent a greater amount of time in the neighboring country of Tanzania located south of the park. This indicates the lion populations in ANP are not isolated as wildlife corridors exist between the park and group ranches (and maybe further away) (Dolrenry, 2013). This ability to disperse and survive in the surrounding landscapes and possibly connect to other lion populations serves an important function in endurance and cushioning the lion population inside the ANP (Dolrenry et al., 2014).

To improve lion conservation in a small National Park such as Amboseli we need to improve landscape connectivity so as to allow species movement for effective climate change adaptation. The expanded home ranges observed in this study depict that the wild prey populations are on the decline, due to severe climatic conditions such as the drought that caused the death of a large number of animals of a key lion prey, including wildebeest, zebra and buffaloes among others (Zwaagstra et al., 2010; ACC, 2009). When resource availability varies in both the short and long term periods, it poses difficult challenges for the long-lived, territorial species whose range persists longer than the periodicity of change in resource availability. To restore the populations of prey species and thus reduce the vulnerability of the lions, there is need for concerted efforts to implement measures such as establishing community conservancies, linkage and corridors to other protected areas within the region that will reverse existing trends and can cushion species vulnerabilities to climatic fluctuations.



We conclude that under conditions of fragmented habitats severe climate conditions create new challenges for lion conservation due to effects on prey availability and subsequent influences on carnivore species ranging patterns. Stochastic weather patterns can force wide-ranging species beyond current reserve boundaries, into areas where there will be greater conflicts with humans.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2014.07.006>.

## References

- ACC, 2009. The Impact of the 2009 Drought on Wildlife, Livestock, and Tourism in the Amboseli Ecosystem. African Conservation Centre, Nairobi.
- Altmann, J., Alberts, S., Altmann, S., Roy, S., 2002. Dramatic change in local climate patterns in the Amboseli basin, Kenya. *Afr. J. Ecol.* 40, 248–251.
- Bauer, H., De longh, H.H., 2005. Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *Afr. J. Ecol.* 43, 208–214.
- Bauer, H., Van Der Merwe, S., 2004. Inventory of free-ranging lions (*Panthera leo*) in Africa. *Oryx* 38, 26–31.
- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., Coulson, T., 2006. Effects of sampling regime on the mean and variance of home range size estimates. *J. Anim. Ecol.* 75, 1393–1405.
- Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24, 346–352.
- Carbone, C., Cowlshaw, Isaac, G.N., J., Rowcliffe M., 2005. How far do animals go? Determinants of day range in mammals. *Amer. Nat.* 165 (2), 290–297.
- Celesia, G.G., Townsend Peterson, A., Kerbis Peterhans, J.C., Gnoske, T.P., 2009. Climate and landscape correlates of African lion (*Panthera leo*) demography. *Afr. J. Ecol.* 48, 58–71.
- Dolrenry, S., 2013. African lion (*Panthera leo*) behavior, monitoring, and survival in human-dominated landscapes. In: Ph.D. Nelson Institute for the Environment, University of Wisconsin, Madison.
- Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, R.S., Frank, L., 2014. A metapopulation approach to African Lion (*Panthera leo*) conservation. *PLoS* <http://dx.doi.org/10.1371>.
- Funston, P., Mills, M.G.L., Richardson, P.R.K., Van Jaarsveld, A.S., 2003. Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *J. Zool. (London)* 259, 131–142.
- Gittleman, J.L., Harvey, P.H., 1982. Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* 10 (1), 57–63.
- Gitzen, R., Millsbaugh, A., Kernohan, B.J., 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *J. Wildl. Manage.* 70 (5), 1334–1344.
- Halpin, P.N., 1997. Global climate change and natural-area protection: management responses and research directions. *Ecol. Appl.* 7, 828–843.
- Hanby, J.P., Bygott, J.D., Packer, C., 1995. Ecology, demography and behavior of lions in two contrasting habitats: Ngorongoro crater and Serengeti plains. In: Sinclair, A.R.E. (Ed.), *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. Peter Arcese, chap. 15.
- Hannah, L., Midgley, G.F., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Glob. Ecol. Biogeogr.* 11 (6), 445–451.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the Eastern United States. *Ecol. Monograph* 68 (4).
- Karanth, K., Chellam, R., 2009. Carnivore conservation at the crossroads. *Oryx* <http://journals.cambridge.org>.
- Lemieux, C.J., Scott, D.J., 2005. Climate change, biodiversity conservation and protected area planning in Canada. *Canad. Geogr.* 49 (4), 384–397.
- Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* 32, 953–962.
- MacDonald, D.W., 1983. The ecology of carnivore social behaviour. *Nature* 301, 379–384.
- Matias, M.G., 2013. Macrofaunal responses to structural complexity are mediated by environmental variability and surrounding habitats. *Mar. Biol.* 160 (3), 493–502.
- McComb, K., Packer, C., Pusey, A., 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Anim. Behav.* 47 (2), 379–387.
- Moss, C.J., Croze, H., Lee, P.C., 2011. The Amboseli Elephants; A long – Term Perspective on a Long – Lived Mammal. The University of Chicago Press, Chicago and London.
- Muthiani, E., Wandera, P., 2000. Feed preferences, optimal integrated stocking rates of selected browsers and grazers and economic viability of integrating wildlife and livestock in selected ASALs. 3.2.14.1. Kenya Agriculture Research Institute, Makindu.
- Ntiati, P., 2002. Group Ranches Subdivision Study in Loitokitok Division of Kajiado District, Kenya. African Wildlife Foundation, Nairobi, Kenya.
- Ohlemüller, R., Chen, C., Hill, J.K., Roy, D.B., Thomas, D., 2006. Rapid Range Shifts of Species Associated with High Levels of Climate Warming, vol. 333 (6045). pp. 1024–1026.
- Okello, M.M., Kioko, J.M., 2010. Contraction of wildlife dispersal area in Olgululul – Olololashi Group Ranch around Amboseli National Park, Kenya. *Open Conserv. Biol. J.* 4, 34–45.
- Okello, M., Makonjio, Simon, K. Ole Seno, Nthiga, R. Wairimu, 2009. Reconciling people's livelihoods and environmental conservation in the rural landscapes in Kenya: Opportunities and challenges in the Amboseli landscapes. *Nat. Resour. Forum* (2), 123–133.
- Peter, L.R., Darling, S.D., 1985. The Green house effect and Nature reserve, Global warming would diminish biological diversity by causing extinctions among reserves species. *BioScience* 35 (11).
- Place, J., Flocken, J., Travers, W., Waterland, S., Telecky, T., Kennedy, C., Goyenechea, A., 2011. Petition to list the African lion (*Panthera leo leo*) as endangered pursuant to the US Endangered Species Act. Petition before the Secretary of the Interior, by International Fund for Animal Welfare, Humane Society International, Human Society of the United States, Born Free and Defenders of Wildlife.
- Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In: Biotani, L., Fuller, T.K. (Eds.), *Research Techniques in Animal Ecology: Controversies And Consequences*. Columbia University Press, New York, pp. 65–110.
- Rhodes, J.R., McAlpine, Clive A., Lunney, D., Possingham, H.P., 2005. A spatially explicit habitat selection model incorporating home range behavior. *Ecology* 86, 1199–1205.
- Riggio, J.A., Dollar, Jacobson L., Pimm, S., Bauer, H., De longh, Hans, Dickman, A., Becker, M., Funston, P., Groom, R., Henschel, P., 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodiv. Conserv.* 22, 17–35.
- Schaller, G.B., 1972. *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago.
- Smuts, G.L., 1978. Interrelations between predators, prey, and their environment. In: *Biological Sciences*, vol. 28. Oxford University Press, No. 5, P. 316 of 316–320.

- Spong, G., 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behav. Ecol. Sociobiol.* 52, 303–307.
- Tumenta, P.N., Van 't Zelfde, M., Croes, B.M., Buij, R., Funston, P.J., Udo De Haes, H.A., De longh, H.H., 2010. Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mamm. Biol. - Z. Säuget.* 78 (6), 461–469. November 2013.
- Tumenta, P.N., Visser, H.D., van Rijssel, J., Müller, L., de longh, H.H., Funston, P.J., Udo de, H.H.A., 2012. Lion predation on livestock and native wildlife in Waza National Park, northern Cameroon. *Mammalia* 77 (3), 247–251.
- Van Orsdol, K.G., Hanby, J.P., Bygott, J.D., 1985. Ecological correlates of lion social-organization (*Panthera leo*). *J. Zool.* 206, 97–112.
- Whyte, I.J., Mills, M.G.L., Biggs, H.C., 1995. The relationship between rainfall, lion predation and population trends in African herbivores. *Wildl. Res.* 22 (1), 75–87.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280 (5372), 2126–2128.
- Woodroffe, R., Harcourt, A.H., Parks, S.A., 2001. Human density as an influence on species/area relationships: double jeopardy for small African reserves? *Biodiv. Conserv.* 10 (6), 1011–1026.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168.
- Zwaagstra, L., Sharif, Z., Wambile, A., Leeuw, J., Said, M., Johnson, N., Njuki, J., Ericksen, P., Herrero, M., 2010. An assessment of the response to the 2008–2009 drought in Kenya. A report to the European Union Delegation to the Republic of Kenya.