The impact of climate variability on the ecology of a lion (Panthera leo Linnaeus 1758) population and lion livestock conflicts in the Amboseli ecosystem – Kenya

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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 analyse 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 strong positive correlation between the home range size and distance moved in 24 hours 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 the severe drought. We conclude that under fragmented habitats coupled with severe climate conditions create can new challenges for lion conservation due to its 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.

3.1 Introduction

African lions (Panthera *leo leo*) are threatened with extinction across their range, and have been classified as 'Vulnerable´ on the global IUCN Red List (Brooks et al., 2006). They are also currently under consideration for the Endangered Species Act, US Fissures and wildlife society (US-FWS) (Place et al., 2011). Several authors have described the declines in lion population due to factors related to human interference (trophy hunting, poaching, agricultural and urban development, habitat fragmentation and conflicts) while others relate it to natural factors related to environment-climate variability, cover, prey availability and topography (Bauer & 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 & 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 & Prasad, 1998; Ohlemuller et al., 2006). Knowledge of a species' ranging behaviour 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 & Jachmann, 2008; McNaughton et al., 1988) and can induce changes in habitat suitability, which is 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 (Hanby & Packer, 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 show a spatially heterogeneous pattern and may have already resulted in several recent local species extinctions (Parmesan 2006). These changes raise concerns about the effectiveness of existing species protection strategies (Halpin, 1997; Hannah et al., 2002; Peter & 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 & 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 neighbouring protected areas, where home ranges extend significantly into non-protected areas relative to the size of the neighbouring protected areas (Woodroffe & Ginsberg 1998; Woodroffe et al., 2001). Increased anthropogenic activities as a consequence of rapid human population growth has resulted in the reduction of natural habitats for lions (Riggio et al., 2013; Bauer et al., 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 & Harvey, 1982; Van Orsdol et al., 1985; Spong, 2002; Bauer & De Iongh, 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 & Harvey, 1982; MacDonald, 1983).

The home range area is used during an animal's normal activities of food gathering, mating and caring for its young. The core of its home range is defined as the most intensely 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 home range (Schaller, 1972; Loveridge et al., 2007; Tumenta, 2013).

Group size and territoriality are social factors that also influence home range size (Packer et al., 1990). Home-range size increase therefore lead to group size (Van Orsdol et al., 1985). Larger group require more prey and therefore larger areas corresponding to prey biomass and density. The most important factor that influences lion home range size (Van Orsdol et al., 1985; Bauer & De Iongh, 2005), with lion home range size being negatively correlated with prey abundance (Van Orsdol et al., 1985; Bauer & De Iongh, 2005; Loveridge et al., 2007). Maintaining a pride home range is of great importance, as evidenced by 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 & Grimm, 2007), habitat selection (Rhodes et al., 2005), community structure (Matias, 2013), as well as the management and conservation of ecosystems (Woodroffe & Ginsberg, 2000).

The present study is the first of its kind to analyse the effect of drought on lion movements, covering a period of three years before and during the drought period (2007-2009) as well as a three year period after the severe drought period (2010-2012). 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 abundance) before and during versus after a severe drought period.

3.2 Materials and methods

3.2.1 Study area

The Amboseli ecosystem is situated in the south-west of Kenya, bordering Tanzania. The ecosystem covers an area of approximately 5,700 km^2 stretching between Chyulu Hills and Tsavo West National Parks South to Mt. Kilimanjaro in Tanzania (Figure 3.1). Administratively, the Amboseli ecosystem consists of Amboseli National Park (ANP; 392 km^2) and the six surrounding communally-owned Maasai group ranches. These group ranches cover an area of about 5,063 km^2 in Kajiado County (Figure 3.1). In the centre 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 a long rain period in March-May (Altmann et al., 2002). An average of 340 mm rainfall per annum is expected (Moss et al., 2011), This rainfall deficiency makes 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 (Groom & Harris, 2010; Muthiani & 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 (Makonio et al., 2009), its future might be threatened by the increase of human development and livestock grazing- this is already indicated by increased human conflicts (Okello & Kioko, 2010). The development activities around the park have caused fragmentation of wildlife habitats, diminished the dispersal areas and limited the free movement of animals (Okello & Kioko, 2010, Moss et al., 2011).

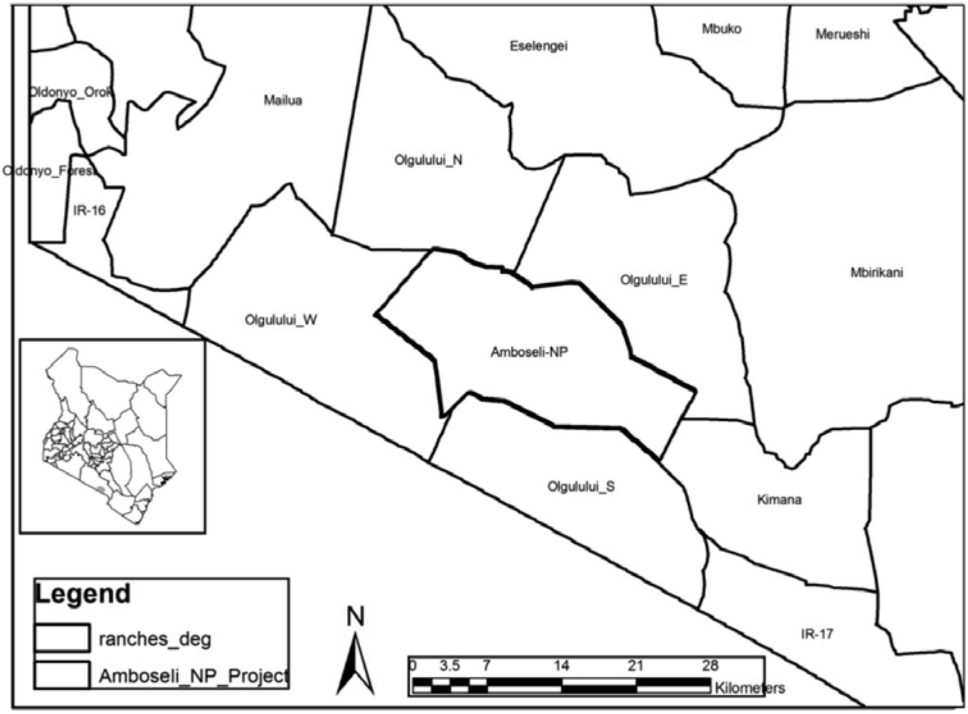

Figure 3.1
Amboseli National Park and surrounding group ranches which together from the Amboseli ecosystem.

3.2.2 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 & De Iongh, 2005), after being attracted using a calling station set-up adapted from Ogutu & Dublin (1998). We used GPS-GSM collars from African Wildlife Tracking with an integrated VHF radio transmitter (Pretoria, SA). Characteristics of these collars have been described previously (Tomkiewicz et al., 2010; Schwartz & Arthur, 1999). The collars were programmed to attempt location of animals at either 3-hour or 30-minute intervals. The collars recorded date, time, latitude, longitude, and general cause of successful location fixes. Direct observations of individuals were made periodically using VHF radio tracking techniques, following White & Otis (1999). Table 3.1 presents details of the collared lions. The GPS coordinates of scheduled lion locations were downloaded from the Yrless website (www.yrless.co.za). The lion locations were subsequently processed in ArcMap (ArcGIS 9.3.1, ESRI, Redwood, CA, USA), using the 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. We only used the functioning GPS/GSM continuously for more than one month (Table 3.1). A large number of fixes, 17,333 before and during the 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 GPS points per day.

3.2.3 Home 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), being the smallest convex polygon that encompasses all lion locations, either using all the locations (MCP 100%) or by first removing 5% of the outliers in the dataset (MCP 95%) (Powell, 2000). Some authors suggest that MCP is inefficient and highly sensitive to sample size and outliers (Börger et al., 2006), hence important to compare with KDE for accuracy. 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 (KDE 95%), the core home range (KDE 50%) and the heart of the core area (KDE 5%). We used the KDE method to calculate home range metrics. We set the outer boundary at 95% and the core area at 50% (White & Otis, 1999). The smoothing factor was chosen using the least square cross validation (Garton & Horne 2006) of 0.02 for all our calculations. Ranges were analysed for each year during the study period. Home ranges, both MCP and KDE, for the different seasons were calculated and compared with other studies.

Table 3.1
Overview of Lion collarings in Amboseli NP during 2007-2012. Dates are in dd/mm/yy. Estimated year of birth is based on morphometrics and examination of nose pigmentation and canines during collaring. GPS fixes represent all fixes received from start of collaring until end of collaring or collar

Lion ID	Collar ID	Collar Frequency	Gender	Date collaring	End data-transmitter	Estimated year of birth	No. of months monitored	No. of GPS fixes
L1 **Amy Jane**	AS69, AS71	149.820 149.7067	F	9/7/2007 12/7//2008	12/7/2008 12/6/2010	2001	34	7134
L2 **Tato**	AS70 AS129	149.860 149.8607	F	10/7/2007 19/8//2009	2/2/2009 30/3/2010	1998	26	4514
L3 **Kip**	AS71 AS129 AG174 AG452	149.7067 149.8607 149.390 149.130	M	11/7//2007 11/7//2008 17/8/2009 3/7//2010	11/7/2008 17/8/2009 3/7/2010 24/8/2010	2004	37	5178
L4 **Shangiki**	AS72 AG513	149.7289 151.530	F	11/7//2007 9/11/2010	31/5/2010 8/3/2013	2003	63	16557
L5 **Ambogga**	AS73 AS128 AG369	149.9509 149.070 150.580	M	12/7//2007 13/7//2008 5/7//2010	23/3/2008 5/7/2010 29/11/2012	2004	60	12730
L6 **Willy**	AG175	149.620	F	17/8//2009	24/1/2012	2004	29	3456
L7 **Belta**	AG370	150.710	F	6/7//2010	25/5/2011	2006	10	2327
L8 **Amy**	AG451	149.050	F	6/7//2010	22/8/2012	2005	25	7730
L9 **Shaka**	AG452	149.130	M	12/10/2010	16/2/2013	2004	28	11023
L10 **Nane**	AG514	151.380	F	9/11/2011	28/9/2012	2004	22	5756

We used potential minimum distance, defined as the minimum distance travelled by a lion in a straight line, measured in kilometers, either in a 12-hour period, night (18:00 hours until 06:00 hours) or day (06:00 hours until 18:00 hours) or average potential minimum movement, measured over a 24-hour 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 by lions of protected areas versus non-protected areas in relation to the drought by assessing the number of days that the lions spent exclusively inside the park, the number of days the lions they were both inside and outside the park, and number of days the lions spent exclusively outside the park. We determined overlap in home range and movement inside and outside ANP using ARC-GIS (ESRI, Redwood, CA, USA).

We analysed 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 set annual mean monthly rainfall of 28.3 mm (Figure 3.2) as a cutoff point between the drought and wet period.

3.2.4 Statistical analysis

All statistical analysis were carried out in R 3.0 programme (R Development Team, Vienna, Austria). The dependent factors were home range and potential minimum movement per day. The independent factors were 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 were non-normal, thus we log-transformed the data and applied a 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 travelled distance changed between 2010 and 2011, a paired t-test ($p<0.05$) or a Wilcoxon signed rank test ($p<0.05$) were run. Difficulties with data analysis were attributable to unbalanced structures, nesting verses 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 decided on an optimal model for all home ranges MCPs 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 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 (model 1, 2 and 3) as follows:

Model 1, had the response variable as home range areas MCP in 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:

> Area of MCP, KDE 95 and KDE 50 in km^2 ~ season * drought period_ * sex +
> (1 | LION_ID)

Model 2, had the response variable as home range area MCP in 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:

> Area of MCP, KDE 95 and KDE 50 in km^2 ~ season + drought period + sex +
> (1 | LION_ID) +; season: drought period + season: sex + drought period: sex

Model 3, the response variable was the area of the MCPs, KDE 95 and KDE 50 in 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:

Area of MCP, KDE 95 and KDE 50 in km^2 ~ season + drought period + sex + (1 | LION_ID) + season: drought period + drought period: sex

3.3 Results

3.3.1 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 3.2). 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 hours 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 hours after the severe drought.

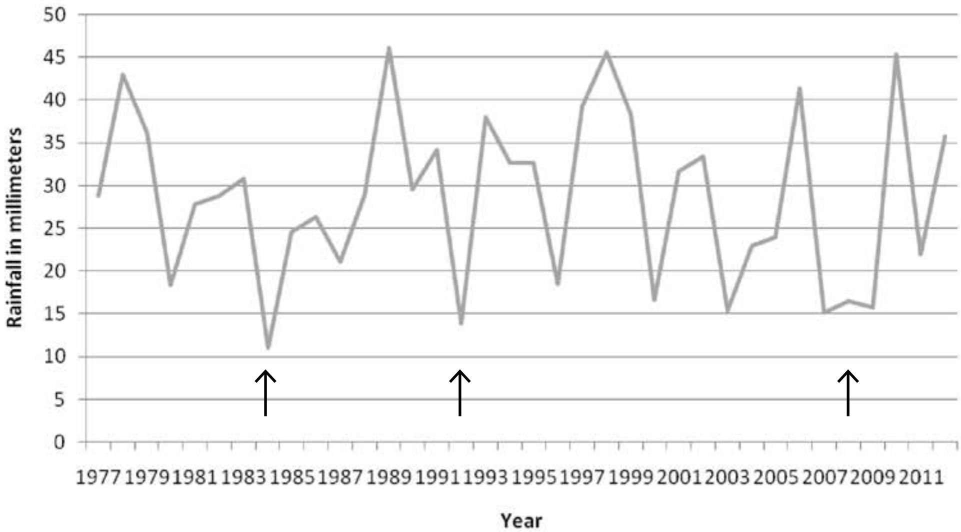

Figure 3.2
Mean annual monthly rainfall for the years 1977-2012 and severe drought period 2008-2009 in Amboseli Ecosystem (Source: Amboseli Baboon research). The arrow indicates drought which was comparable to 1984 and 1992 droughts and drought period which indicate worse drought in 35 years (2009).

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 3.2). The mean home range seasonal variability was greater during post-drought. Our results showed expanded home ranges even during the dry season for the post-drought period, as compared with that of dry seasons of the pre-drought and actual drought period (Table 3.2). The mean overall home range was not significantly different for male and female lions however.

Table 3.2
Summary of dry and wet seasonal variation of lion home ranges (km²) for MCP 100, KDE 95 and KDE 50, also indicating periods before/during and after the drought, for both male and female lions (T test, p>0.05).

Home range (km²)	Sex			Period before and during drought		Period after drought	
		Sample size	s.d.	Dry season	Wet season	Dry season	Wet season
Mean range size MCP100	Female	7	0.33	121.70	34.91	262.43	187.98
	Male	3	-1	177.10	57.03	373.61	272.26
Mean range size KDE95	Female	7	0.33	23.93	46.15	63.98	73.28
	Male	3	-1	26.01	52.76	74.16	91.252
Mean core range size KDE50	Female	7	0.33	4.85	9.22	11.97	14.06
	Male	3	-1	9.56	4.52	11.59	14.95

There was a high variation in lion home range sizes for the period after the drought (2010-2012) compared to the period before and during the drought (2007-2009; Figures 3.3 and 3.4). Lions expanded their home range during the period after the drought, seeking new territories not covered before/during the drought.

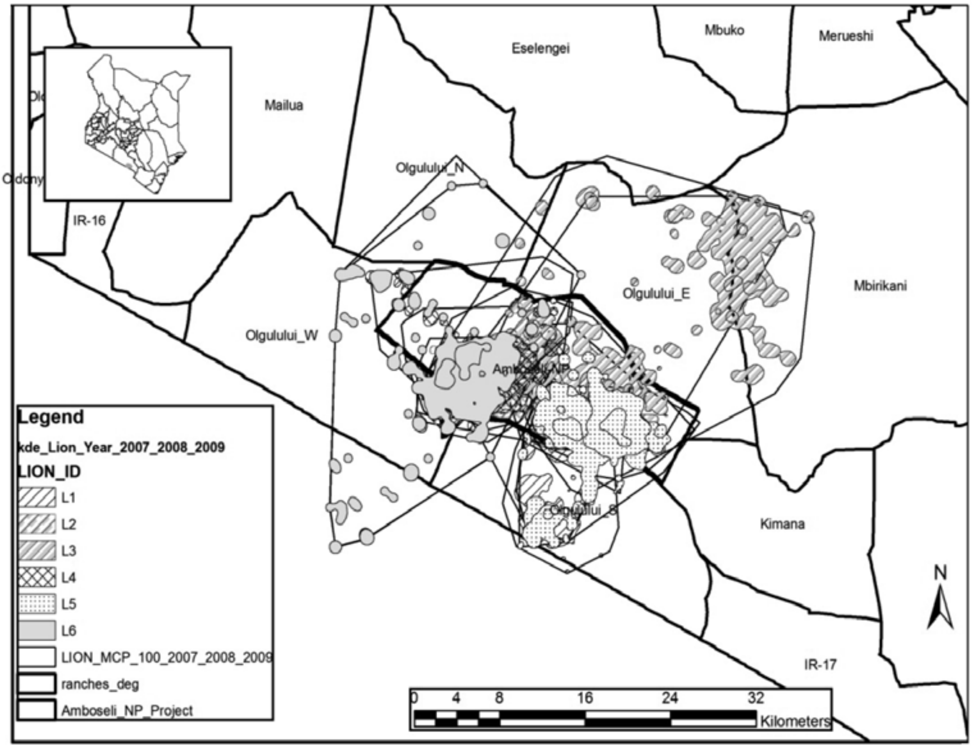

Figure 3.3
Lion home range sizes before and during the severe drought (2007-2009) measured in kilometer squared for MCP100, KDE95 and KDE50.

3.3.2 Mixed modeling and model comparisons

The results show that model 2 was the most optimal of the three models for MCP 100 (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=1.718), but model 1 was not significantly different from model 3 (p=0.375, >0.05). We therefore interpreted the output of model 2 for MCP100, KDE95 and KDE 50.

The results showed that all the variables considered in model 2 were significant (Table 3.3). 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^2 for MCP 100, KDE 95 and 50 for the following conditions: dry season, period after drought, female lion.

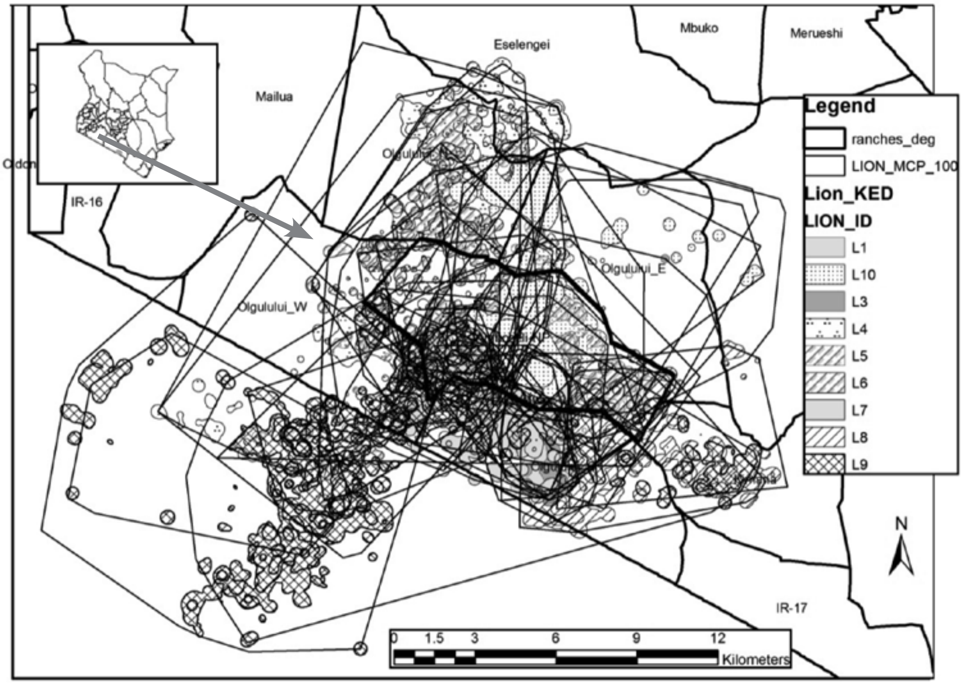

Figure 3.4
Lion home range sizes for the period after the drought (2010–2012) measured in km^2 for MCP100, KDE95 and KDE50.

Mixed ***model (main effects)***

Holding other variables at their default, the mean MCP area in km^2 for male lions was greater by 0.89 km^2 compared to the mean MCP for female lions. The difference is statistically significant ($p=0.002$, <0.05). The MCP area for the period before drought was lower by 0.61 km^2 compared to the period after the drought. Similarly, the dry season MCP measurements were also lower by 0.385 km^2 compared to the wet season. Conversely, holding other variables at their default, the mean KDE95 area in km^2 for male lions was greater by 0.31 km^2 than the mean KDE95 for female lions. The difference was statistically significant ($p=0.017$, <0.05). The KDE95 area for the period before the drought was lower by 0.37 km^2 than the period after the drought, while the dry season also had lower KDE95 areas by 0.18 km^2 compared to the wet season. Similarly, holding other variables at their default, the mean KDE50 for male lions was higher by 0.08 km^2 than 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 the drought was lower by 0.25 km^2 compared to the period after the drought while the dry season also had lower KDE50 by 0.22 km^2 compared to the wet season.

Mixed *effects (interaction terms)*

The interaction between season and period was significant ($p < 0.0001$). We observed that the period before the drought had a lower MCP than the period after the drought by 0.79 km^2 during the dry season. The interaction between season and period was significant ($p < 0.0001$). We observed that the period before the drought had a lower KDE95 than the period after the drought by 0.48331 km^2 during the dry season. The interaction between season and period was significant ($p<0.0001$). We observed that the period before the drought had a lower KDE50 than the period after the drought, by 0.44 km^2.

Table 3.3
Output of Fixed Effects of Mixed Modeling for lion home range indicating seasonal home range variation, before/during and after the drought, sex, and their interactions showing estimated standard error, Z-values and level of significance P<0.005 for MCP100, KDE 095 and KDE 50.

	Period	Estimated	Std. Error	Z-value	Pr(>|z|)
Model 1: 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
	Season dry: Before drought	-0.44136	0.09131	-4.833	1.34e-06 ***
	Before drought Sex: Male	0.35531	0.08014	-4.434	9.26e-06 ***

Signifiance: *** p<0.001 ** p<0.01 '*' p<0.05 '.' P<0.1

Table 3.4 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 the drought when prey became scarce.

Table 3.4
Lion daily, and seasonal movement before/during and after the drought, Wilcoxon – Paired sample t-test values and level of significance.

Parameters	Wilcoxon (W) test	P=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*
Distance moved in 24hrs	4972	1.873e-07***
Distance moved in 24hrs by season	8576	0.007838***
Distance moved in 24hrs by periods before and after drought	14717	< 2.2e-16***

Significance: 0 '***' p<0.001 '**' p<0.01 '*' p<0.05 '.' P<0.1

3.4 Discussion

3.4.1 Home ranges and movement patterns

We found significant variation in lion home ranges and 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 3.2). This was not surprising, as female lions defend smaller areas that provide good resources and are suitable for raising their cubs, whereas 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 and the period after the drought (Table 3.2). Similar findings were reported for the lions in Cameroon by Tumenta et al. (2013).

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 28-37 km^2. 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 disperse more (Tumenta et al., 2010). 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 group size is determined by the prey size and quality of food patches (Bauer & De Iongh, 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.

3.4.2 Lion movement and landscape connectivity

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

On several occasions, both the male and female collared lions moved far 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 neighbouring country of Tanzania, located south of the park. This indicates that 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 of 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, which would allow species movement for effective adaptation to climate change. The expanded home ranges observed in this study depict that the wild prey populations are in decline, due to severe climatic conditions such as the drought that caused the death of a large number of key lion prey, including wildebeest, zebra and buffaloes (Zwaagstra et al., 2010). When resource availability varies in both the short and long term, 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 a need for concerted efforts to implement measures such as establishing community conservancies, and linkage and corridors to other protected areas within the region.

We conclude that under conditions of fragmented habitats, severe climate conditions create new challenges for lion conservation due to their 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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