Department of Geography, University of Zurich

GEO 511

Master's Thesis

Spatio-temporal variation of lion and leopard home ranges in Botswana

How do predators react to changing prey availability?

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Summary

The numbers of free living lions and leopards have been declining rapidly over the past few decades. Habitat loss due to the irresistible expansion of human settlements and livestock farming are among the major reasons and this development inevitably led to conflicts between humans and predators, often with a deadly outcome for the large cats. These types of conflicts are well known around the Khutse Game Reserve and the adjacent Central Kalahari Game Reserve in Botswana. In order to better protect predators and livestock and prevent conflicts from happening, a deeper knowledge about the space use of these large predators is necessary.

In the first part, GPS data of 4 leopards and 10 lions was analysed to estimate the home ranges and core areas for these predators. The analysis was conducted for 4 different time intervals (entire observation period, year, wet season and dry season), with a special focus on the seasonality. Kernel Density Estimation with a reference bandwidth h calculated for every time interval was used for the analysis. Datasets for each individual covered at least two consecutive years of sampling. A second approach of home range estimation using Biased Random Bridges turned out to be not feasible due to high discrepancies of the results. The results confirmed the hypothesis that the home ranges of lions and leopards living in this semi-arid environment are among the largest worldwide. Leopard home ranges covered areas between 58 km^2 and 2411 km^2 and lion home ranges between 285 km^2 to 5991 km^2. A tendency of leopard home ranges being smaller during the wet season was detected. Lion home ranges, on the other hand, are smaller during the dry season. Furthermore, it was possible to determine the affiliation of lions to prides and which individuals live as nomads. A distinct pattern of predators leaving the game reserves was not evident.

The second part focussed on the habitat quality, especially the potential access to prey animals. Datasets of prey availability covered the 2014 wet- and dry season and prey numbers were recorded using the transect method. A previously conducted analysis by Zucchini (2016) suggested that prey densities around KGR and CKGR are higher during the dry season. As there is a distinct seasonality in the study area, a correlation between precipitation and prey densities is likely. Using a point in polygon approach, the absolute and relative prey numbers within the 95%- and 50% home range of 2 leopards and 7 lions were calculated for the 2014 wet- and dry season. The results suggested that lions and leopards potentially have access to more prey animals during the dry season which could be related to higher prey densities. Additionally, dominant prides seem to be able to successfully defend the highest quality habitats against conspecifics and they have access to more prey animals within their core area than nomadic lions.

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Abbreviations and definitions

BM	Brownian motion
BRB	Biased Random Bridge
CA	Core area
CI	Compactness Index
CKGR	Central Kalahari Game Reserve
DOP	Dilution of precision
GIScience	Geographic information science
GPS	Global positioning system
HR	Home range
IUCN	International Union for Conservation of Nature
KDE	Kernel Density Estimation
KGR	Khutse Game Reserve
LEC	Leopard Ecology & Conservation
LSCV	Least-square cross validation
MCP	Minimum convex polygon
NDVI	Normalized differenced vegetation index
PA	Protected area
REF	Reference bandwidth
SI	Sampling interval
t-LCH	Time local convex hull
UD	Utilization distribution
VHR	Very high frequency
VI	Volume of intersection
95% HR	Home range, 95% isopleth
50% HR	Core area, 50% isopleth
LF00_Name	Lion female
LM00_Name	Lion male
PF00_Name	Leopard female
PM00_Name	Leopard male
D2010	Dry season 2010, June 1st 2010 to September 30th 2010
W2010	Wet season 2010, November 1st 2009 to April 30th 2010
Y2010	Year 2010, June 1st 2009 to May 31st 2010

I General Introduction

1. Context and Motivation

The number of lions (*Panthera leo*) living on the African continent has declined massively over the last few decades (Bauer & Van der Merwe 2004) and therefore the lion is classified as a vulnerable species by the International Union for Conservation of Nature (IUCN). For leopards (*Panthera pardus*), a vulnerable species as well, the same development has been observed (Winterbach et al. 2013). Although there are several factors responsible for the declining number of large carnivores, conflicts with humans are the main reason (Kissui 2008; Ogutu et al. 2005; Woodroffe & Frank 2005). Lions and leopards lose their natural habitats because of the rapid expansion of livestock farming across Southern Africa. As a result, attacks on livestock are increasing as well as the number of predators killed in retaliation by farmers (Bauer et al. 2014; Kissui 2008; Ogutu et al. 2005). These problems are well known around the Khutse Game Reserve (KGR) and the adjacent Central Kalahari Game Reserve (CKGR) in Botswana (Schiess-Meier et al. 2010). Among the possible solutions to reduce conflicts and prevent predator numbers from further declining is the use of modern technology. Recent advances in Geographic Information Science (GIScience) and the development of radio-collars using GPS (Global Positioning System) have facilitated the study of wild animals (Tomkiewicz et al. 2010). More sophisticated analysis of their space use and interaction with the environment are possible, which are both key factors for successful animal protection (Shamoun-Baranes et al. 2012).

2. Research gaps

Since the late 1990s and the advance of GPS technology many studies have been carried out in the field of estimating animal home ranges, a concept originally introduced by (Burt 1943). Predator home ranges are believed to be influenced by ecological factors such as prey abundance, precipitation and the presence of conspecifics (Bothma et al. 1997; Nash et al. 2012). Harsh, arid environments with few natural resources, such as the Kalahari, force predators to maintain extremely large home ranges compared to their conspecifics in richer environments, for example in the South African Kruger National Park (Bothma et al. 1997). Especially in environments with distinct seasonal variations, it is likely that predators move around and use different areas of their home range. A better understanding of the predator's space use is one key element for successful conservation (Winterbach et al. 2013). Up to date, many studies focus on the estimation of the total home range using all tracking data available. Seasonal patterns are usually neglected, although there is evidence (Tuqa et al. 2014) that seasonal changes do have an influence on an animal's home range. The next step is then to determine which factors do affect home ranges, to quantify their impact and observe the predator's reaction. These questions are widely discussed among researchers. However, there is disagreement about the main factors responsible for changes in home range size. Hopcraft et al. (2005) claimed beneficial hunting spots to be the main driver. Loveridge et al. (2009) and Celesia et al. (2010) on the other hand identified prey abundance or climatic variables, such as rainfall, to be more important. However, as lions and leopards inhabit many different environments, it is crucial to take the local conditions and specifics into account. To my knowledge, most studies focussed either on the home range estimation or the determination of driving factors. The combined approach is particularly interesting as it provides vital information for both predator and livestock protection.

3. Research Questions

Based on the last section on research gaps, I derived the following research questions for my thesis.

1. *Home ranges and the core areas of lions and leopards are dynamic. Can these variations of size and location be characterised? Are patterns of temporal variation identifiable?*
2. *How do predators react to changing environmental conditions such as precipitation or the abundance of native prey?*

4. Study area

The study area of Leopard Ecology & Conservation (LEC) is the Khutse Game Reserve (KGR) and the Central Kalahari Game Reserve (CKGR) in central Botswana. KGR (2590 km^2) and CKGR (52'800 km^2) together form Botswana's largest protected area (Figure 1). To the south, KGR is surrounded by the Kweneng District, an area intensely used for livestock farming. In order to better protect livestock from raiding predators, a fence was erected along the eastern and southern border of the CKGR and KGR in 2009. As described in Schiess-Meier (2013: 9 -10) its benefits could not match the expectations, however, for several reasons. First, resources for fence maintenance are limited; second, large animals such as elephants destroyed parts of the fence; and third, predators started to dig holes beneath it. Large natural barriers like rivers, lakes or mountain ranges are missing and therefore animals can move freely. In this area topography is very little pronounced and the average altitude above sea level is roughly 1000 meters.

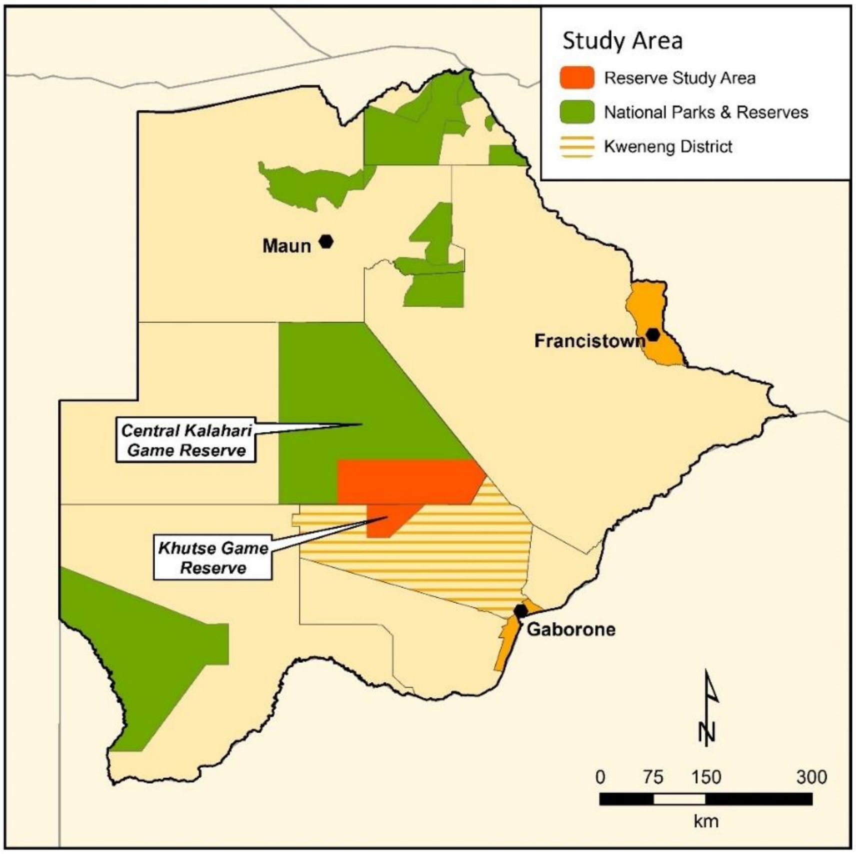

Figure 1: Location of the study area in Botswana, Southern Africa (LEC 2016).

4.1. Climate

The proximity of the Kalahari Desert leads to a semi-arid climate in the study area, characterised by low annual rainfalls (~350 mm/y) and a pronounced seasonality (Mishra et al. 2015). One distinguishes between the wet season (November – April) and the dry season (June – September). May and October are transition periods between the two main seasons (Henley 2014). In the hemispherical winter months there is very little precipitation (< 5%) and the daily mean temperature drops below 10°C. During the summer months the area receives most of its annual precipitation (> 90%) and daily mean temperatures can rise as high as 30°C. Over the course of the year, extreme temperatures ranging from below 0°C to over 45°C are possible (Henley 2014: 3). Figure 2 shows the temperatures and precipitation over the course of one year starting in July 2013. Exceptional rainfalls in December and February resulted in an above-average annual precipitation of 566 mm (Schiess-Meier 2014: 4).

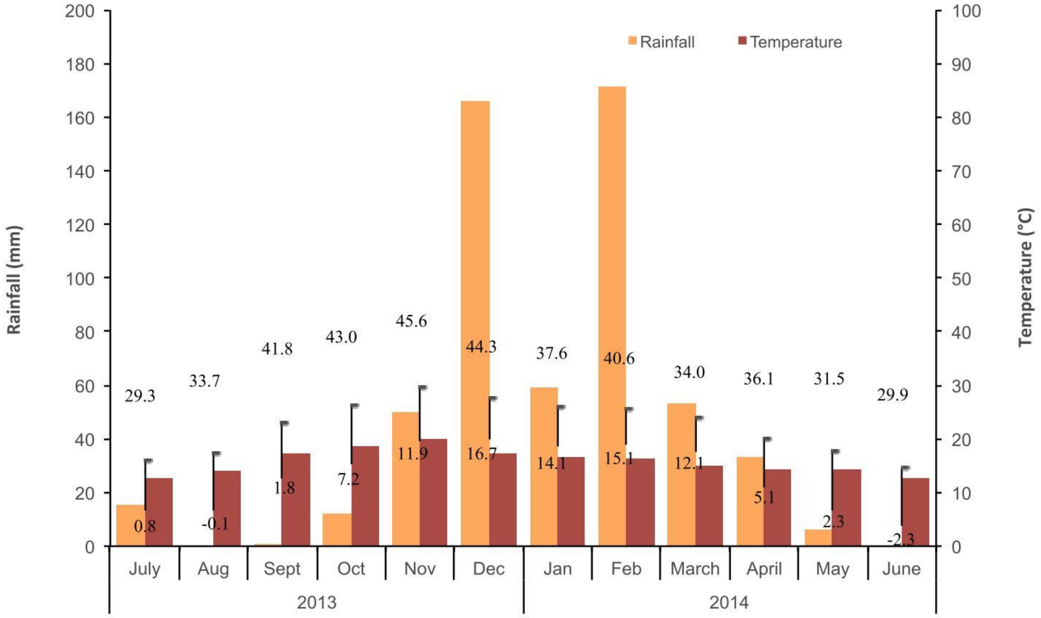

Figure 2: This figure shows the rainfall and temperature measured at the Khutse Base Camp from July 2013 – June 2014. The average median daily temperature is shown as a point, with the average daily maximum and minimum as bars. The figures represent the lowest and highest temperatures measured during the period (Schiess-Meier 2014: 5).

4.2. Vegetation & Fauna

Based on the climatic conditions and its geographic location the study area is classified as semi-arid savannah with rainfall as the main growth limiting factor. Mishra et al. (2015: 200) developed a vegetation morphology map for the study area using the MODIS MOD13Q1 16-day composite 250-m NDVI product, which was acquired from NASA. NDVI data used covered a time span of 14 years, starting in July 2000. The remotely sensed data were than validated by extensive field trips and an overall classification accuracy of 91.9% was achieved (Mishra et al. 2015: 206). Six predominant vegetation types were identified across the whole area, with some regional differences caused by variations of the annual rainfall. As shown in Figure 3, the landscape is dominated by bare areas and salt pans as well as grasslands and short shrub lands. This is particularly true for the main study area of LEC, which is located at the southern tip of the map. High grown vegetation is limited to the more humid northeast and covers less than 10% of the total area. A characteristic species for the Kalahari region is the family of the *acacia* (Weilenmann et al. 2010). The Kalahari region is also home to a large variety of wildlife. Ungulates such as steenbok, springbok or gemsbok as well as the greater kudu, red hartebeest and the common duiker are characteristic species for central Botswana. Giraffes, ostriches and the African elephant are other species frequently found in the area. Besides lions and leopards there are other predators like cheetahs, spotted hyenas, caracals or bat eared foxes (Bauer et al. 2014; Bothma & Le Riche 1984; Schiess-Meier & Mills 2007).

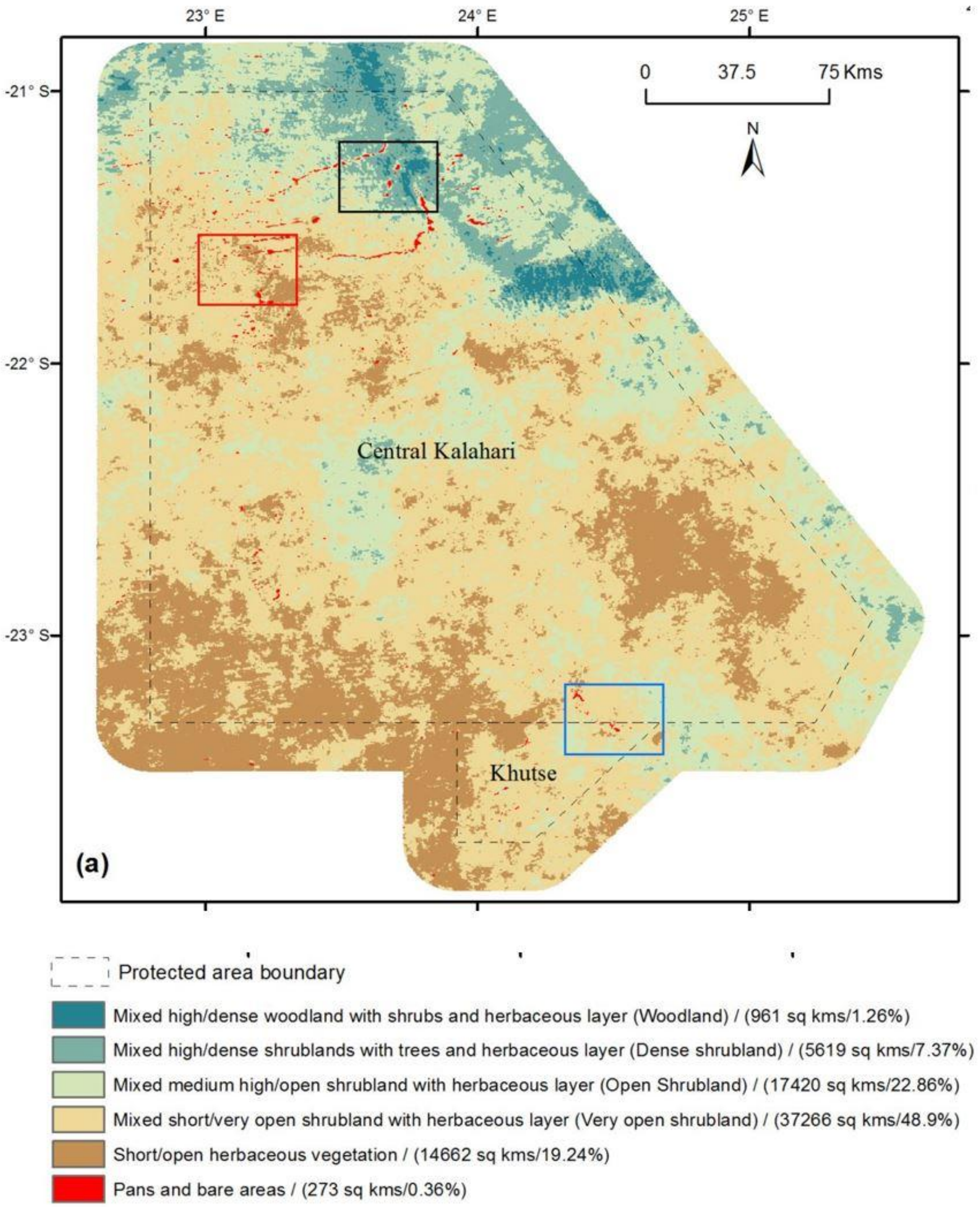

Figure 3: Vegetation Morphology Map (Mishra et al. 2015).

5. Biology

5.1. The leopard

The leopard *panthera pardus* is one of the most widespread members of the large felids, occurring throughout sub-Saharan Africa, India and southern Asia (Hayward et al. 2006: 298). They are highly adaptive and inhabit a wide range of habitats like rainforests, grasslands, mountain ranges and even human-dominated areas (Marker & Dickman 2005; Swanepoel et al. 2015). The body size of adult leopards is highly variable and closely related to their natural environment and prey abundance. In regions with high prey densities they tend to grow larger. Male leopards, with a body length of 1.16 – 1.83 m and a weight of 34 – 69 kg, rarely up to 90 kg, are bigger than females, which measure from 1.05 – 1.27m and weigh 20.5 – 42 kg (Macdonald & Loveridge 2010: 22).

Numbers of free living leopards have been declining over the past few decades. The IUCN (2008, cit. in: Macdonald & Loveridge 2010: 22) sees habitat loss and fragmentation, persecution and poaching among the major reasons for this development. Swanepoel et al. (2015) concluded that survival rates of leopards are strongly dependent on whether they live inside or outside protected areas. Outside protected areas leopards are more likely to be killed by humans than dying by a natural cause. Consequently, the leopard is classified as a vulnerable species, with somewhat over 50’000 individuals left (Hayward & Kerley 2008). Being one of the largest predator in Africa, lions and groups of hyenas are the only natural enemies of an adult leopard. Therefore, leopards actively avoid lions and in case of an accidental contact try to escape into a tree (Palomares & Caro 1999). Cubs and juvenile leopards are more vulnerable and occasionally killed by adult male leopards as they are seen as competitors (Macdonald & Loveridge 2010; Stein & Hayssen 2013).

As most felids, leopards are solitary, with the exception of females rearing cubs or during the mating season (Eisenberg and Lockhart 1972, cit. in: Stein & Hayssen 2013: 40). Cubs are raised by their mother and stay with her for about 18 months (Stein & Hayssen 2013). Having excellent night vision, leopards are most active during the night (Macdonald & Loveridge 2010, Stein & Hayssen 2013).

Leopards have the broadest diet of all large predators, ranging from small birds or rodents up to larger ungulates such as the eland (Hayward et al. 2006: 298). Medium sized prey such as impalas, duikers, gazelles or steenboks are preferred where they occur. However, their morphology and their solitary hunting strategy impose limitations on the prey they can capture. Adult wildebeest, buffalos or zebras are usually out of range. Another factor is the risk of injury. For a solitary predator even a small injury can have fatal consequences (Hayward et al. 2006). Leopards are ambushing predators and rely on dense vegetation providing sufficient cover. Other hunting strategies are less common. According to Balme et al. (2007) leopards tend to avoid open grassland as a hunting spot. Once being within striking distance (~10 m), they initiate a short, powerful sprint to tackle their prey. Large prey is killed by a forceful bite in their throat (Stein & Hayssen 2013). Only around 5% - 38% of the attempts are successful (Balme et al. 2007). Due to the risk of kleptoparasitism by lions or hyenas, leopards cache larger kills or drag it into the treetop (Hayward et al. 2006).

Figure 4: A collared leopard resting on a tree in the study area. Photo by Monika Schiess-Meier.

Home range sizes of leopards show a great variation but are directly influenced by the availability of prey animals. In the Kalahari region with very low prey densities leopards maintain the largest home ranges recorded, covering an area of over 2000 km^2, whereas in richer environment like northern Namibia or Thailand, they can be as small as 8 – 50 km^2 (Macdonald & Loveridge 2010; Stein & Hayssen 2013; Zehnder 2015). Male home ranges are usually larger and often cover several female home ranges. The main reason is to have access to as many females as possible. Core areas, on the other hand, are exclusively used by one individual and defended against intruders. Scent markings and scratches on trees are used to mark the territory (Stein & Hayssen 2013). Direct contact between individuals is usually avoided but fights among leopards occur, especially after the arrival of a newcomer (Stein & Hayssen 2013). However, in areas with vast leopard home ranges, overlapping home ranges are very likely, as it is impossible for a single individual to defend such a large area (Bothma et al. 1997; Zehnder 2015). Females are known to share parts of their home range with their last offspring (Stein & Hayssen 2013).

5.2. The lion

The lion *panthera leo* is the largest member of the family of large cats in Africa and just second overall to the tiger *panthera tigris* (Haas et al. 2005). Extinct in the Middle-East and Asia, free ranging lions are limited to sub-Saharan Africa (Bauer & Van Der Merwe 2004). Their primary habitat are the savannas of Eastern Africa but there are also populations in Southern Africa as well as the semi-arid Kalahari Region (Macdonald & Loveridge 2010). The preferred habitat consists of open woodland, grasslands and thick bush for protection (Haas et al. 2005). Male lions are substantially larger than females, measuring 1.84 – 2.09 m and weighing between 145 – 225 kg. Females reach a body length of 1.42 – 1.85 m and weigh around 90 – 160 kg. Similar to leopards, their body size is related to their natural environment, with the largest lions living in Eastern Africa (Macdonald & Loveridge 2010: 20). Besides their size, the characteristic dark mane differentiates males from females. The population of free ranging lions has been declining over the past decades. Researchers estimate that from over 200’000 individuals in 1975 only about 22’000 – 38’000 animals are left. Thus, the lion is classified as a vulnerable species (Bauer et al. 2014). The reasons for the rapid decline are similar to the ones threatening leopards and other predators (Haas et al. 2005; Kissui 2008; Patterson et al. 2004).

The lion is the only exception among all felids to live in prides with highly complex social structures, rather than living solitary (Macdonald & Loveridge 2010). Hunting strategies, home range size and reproduction are influenced significantly by a life in prides. Pride sizes are highly variable ranging from only 3 – 5 animals in areas with few natural resources to up to 15 – 20 individuals in rich environments such as the Ngoro Ngoro Crater (Celesia et al. 2010; Haas et al. 2005; Macdonald & Loveridge 2010). Being strongly hierarchical, prides are led by matriarchs and one or more dominant male (Eloff 1998; Haas et al. 2005). Lions are very protective of their young and all females within a pride are involved in raising the cubs. The biggest threat for lion cubs is the arrival of a new dominant male, as he will usually kill them to be able to mate (Haas et al. 2005; Macdonald & Loveridge 2010). Other threats are hyenas or adult leopards. Although the latter are known to actively avoid lions they will kill any unprotected lion cub (Palomares & Caro 1999). Adult lions have no natural enemies but can be killed during hunting or fighting with conspecifics.

Lions have several hunting strategies depending on their environment and the prey chosen. Mostly, they act as ambushing predators and therefore rely on appropriate cover to get close enough for the attack (Hopcraft et al. 2005). After a short sprint lions try to tear down their prey, and kill it with a bite in their throat (Haas et al. 2005). To increase their chance for prey lions usually hunt in groups and under the screen of night. Against earlier beliefs, male lions are very skilled hunters and regularly accompany their female pride members (Loarie et al. 2013). Hunting in groups allows lions to attack large animals, including buffalos and even young elephants. However, due to the risk of injury or death these hunts are very rare (Loveridge et al. 2009). Their preferred prey are large ungulates such as blue wildebeests, gemsboks or zebras. After a successful kill prey is consumed on location or dragged into the thicket (Haas et al. 2005). Lions quite frequently act as scavengers, stealing prey from other predators such as hyenas, leopards or cheetahs. Inversely, they seldom suffer kleptoparasitism. The only exception are individuals or small groups being outnumbered by hyenas (Haas et al. 2005; Macdonald & Loveridge 2010).

Figure 5: A male lion in the study area. Photo by Monika Schiess-Meier.

The home range size of lions is dependent on several factors including habitat quality, pride size and the presence of conspecifics. Tuqa et al. (2014) found a negative correlation between home range size and prey availability. Home ranges are highly variable even within the same region and can cover areas between 20 - 500 km^2 in the Serengeti and 266 – 4532 km^2 in Kgalagadi Transfrontier Park in South Africa (Macdonald & Loveridge 2010). Stephen Henley, field coordinator and leading researcher at LEC in Botswana, expected home range sizes of lions around KGR and CKGR to be among the largest worldwide covering similar areas as in South Africa. This assumption was confirmed by Zehnder (2015). Beside scent and scratch markings lions show their presence by roaring. Unlike leopards, lions and their prides are regularly involved in fights for territory, pride leadership and access to females. A deadly outcome is not uncommon (Haas et al. 2005; Macdonald & Loveridge 2010). Overlapping home ranges are possible but the core areas are exclusively used by the resident pride (Haas et al. 2005). While young males are forced to leave their native pride after a couple of years, female offspring usually stay (Haas et al. 2005).

6. Livestock predation in Southern Africa

Over the past few decades, the human population across southern Africa increased massively and therefore food production is ever-growing. Livestock farming expands fast and into territories occupied by large predators, such as lions and leopards. Conflicts between farmers and predators are inevitable (Kissui 2008; Kolowski & Holekamp 2006; Ogutu et al. 2005).

Researchers found that predators prefer natural over livestock prey whenever it is present (Schiess-Meier et al. 2007; Valeix et al. 2012). However, the fast expansion of human activity also negatively affected local densities of native prey and therefore predators search for alternative prey (Marker & Dickman 2005; Patterson et al. 2004). General statements about the timeframe of increased livestock predation are difficult. In the Maasai Mara attacks on livestock were significantly more frequent during the wet season compared to the dry season, while in the Khutse region more attacks were registered during the dry season (Kissui 2008; Ogutu et al. 2005; Schiess-Meier et al. 2007). Despite different seasons the increased number of attacks could be related to low natural prey densities in the area. Predators, especially leopards, usually attack during the night when farmers are not with their livestock (Kolowski & Holekamp 2006; Patterson et al. 2004). There is a negative correlation between the distance of cattle posts to protected areas and the number of attacks (Kolowski & Holekamp 2006; Schiess-Meier et al. 2007). Following their preferences, lions attacked larger animals such as cattle, steers or donkeys. Leopards on the other hand killed more sheep, goats or calves (Kolowski & Holekamp 2006; Schiess-Meier et al. 2007).

Livestock predation leads to economic losses for farmers and consequently, they often react fiercely (Ogutu et al. 2005; Schiess-Meier et al. 2007). This usually means killing the predators responsible for the attacks (Kissui 2008; Patterson et al. 2004). In some countries, for example Kenya, lethal control of so called problem animals, often young male lions, is legal (Patterson et al. 2004; Woodroffe & Frank 2005). However, the vast majority of lions and leopards are killed illegally using snares, traps or being shot or poisoned (Kolowski & Holekamp 2006; Macdonald & Loveridge 2010; Ogutu et al. 2005). Lions were killed more often than leopards and researchers see the following reasons. First, lions kill larger animals which are more valuable; and second, leopards are more difficult to track down; and third, in some cultures killing a lion is seen as heroic (Kissui 2008). Nevertheless, compared to other reasons for livestock losses, diseases for example, killings by lions and leopards are only a minor factor (Kissui 2008; Schiess-Meier et al. 2007).

In order to better protect large predators as well as livestock, several key factors must be fulfilled. First, it is essential to have a deeper knowledge of the wild animals and an understanding of how they are influenced by other factors such as prey availability, seasonality or conspecifics. Second, farmers must better protect their livestock in order to reduce or even prevent losses to predators. Improved fencing, teaching of locals and active guarding have proven to be effective measures (Kolowski & Holekamp 2006; Schiess-Meier et al. 2007; Schiess-Meier & Mills 2008; Shamoun-Baranes et al. 2012).

II Data

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7. Telemetry data

The organisation Leopard Ecology & Conservation (LEC), active in Botswana since the year 2000, recorded and provided telemetry data for 18 leopards and 27 lions. Datasets always contain coordinate pairs (latitude and longitude), date and time as well as an unique ID for each pair. More recently sampled datasets further contain information about temperature, height above sea level, dilution of precision (DOP) and for some lions even accelerometer data. The coordinates were recorded using the WGS84 (EPSG: 4326) coordinate system. Prior to the analysis all coordinates were converted to the local Cape / UTM 36S (EPSG: 22236) reference system.

7.1. Criteria for animal selection

Among all datasets available there is a large heterogeneity in terms of sampling duration, sampling intervals and data quality. On the basis of my research questions I defined the following criterion to be fulfilled by a dataset in order to be selected for further analysis:

- A dataset must cover a timespan of at least two consecutive years

It is essential for my first research question to be able to calculate at least 2 home ranges and core areas per time interval (wet season, dry season, year) and animal. This criterion guarantees a certain degree of comparability between consecutive wet- and dry seasons as well as between years. The leopard PM08_Bogarigka has been selected despite not fulfilling the criterion. This step was necessary to add a second male leopard. However, following this criterion, four leopards and ten lions were selected to be analysed (shown in Table 1 and Table 2). With the exception of one female leopard (PF12_Salome) and one lioness (LF12_Verity) the starting date was set to be 1st of June. It is a trade-off but the only way to assure two years of sampling. Longer time periods are preferred but it would mean to reduce the number of selected lions and leopards even further. The determined minimum sampling duration is also relevant for my second research question but not to the same degree, as it is also dependent on the availability of other data such as precipitation or prey availability.

Table 1: Overall sampling duration of all selected leopards. PM stands for “pardus male” and PF for “pardus female”. The “start_date” and the “end_date” is indicated on the x-axis.

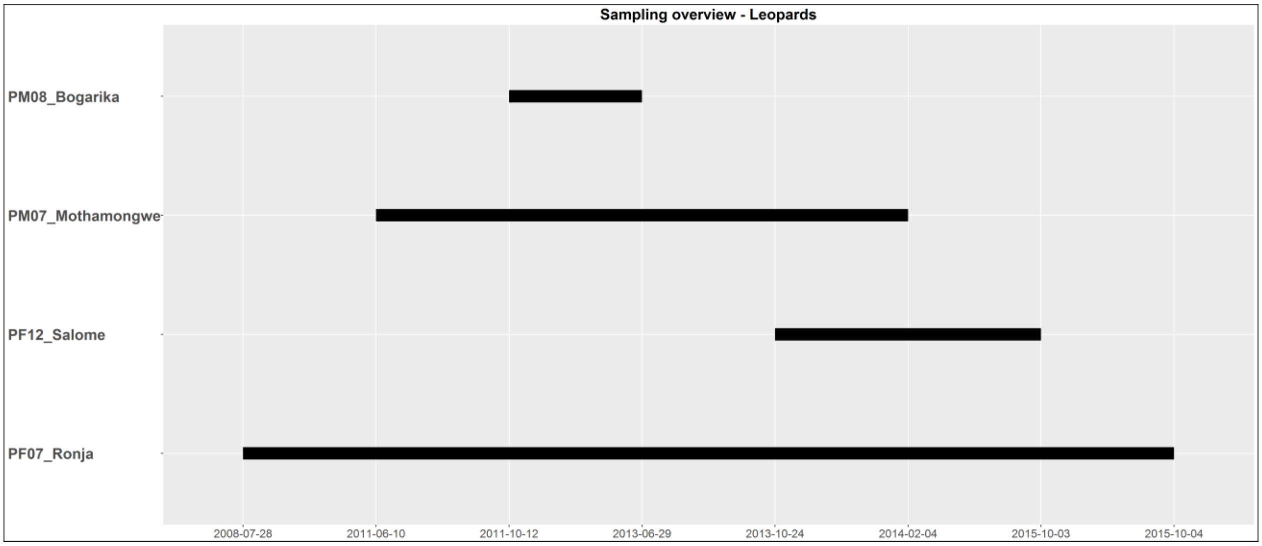
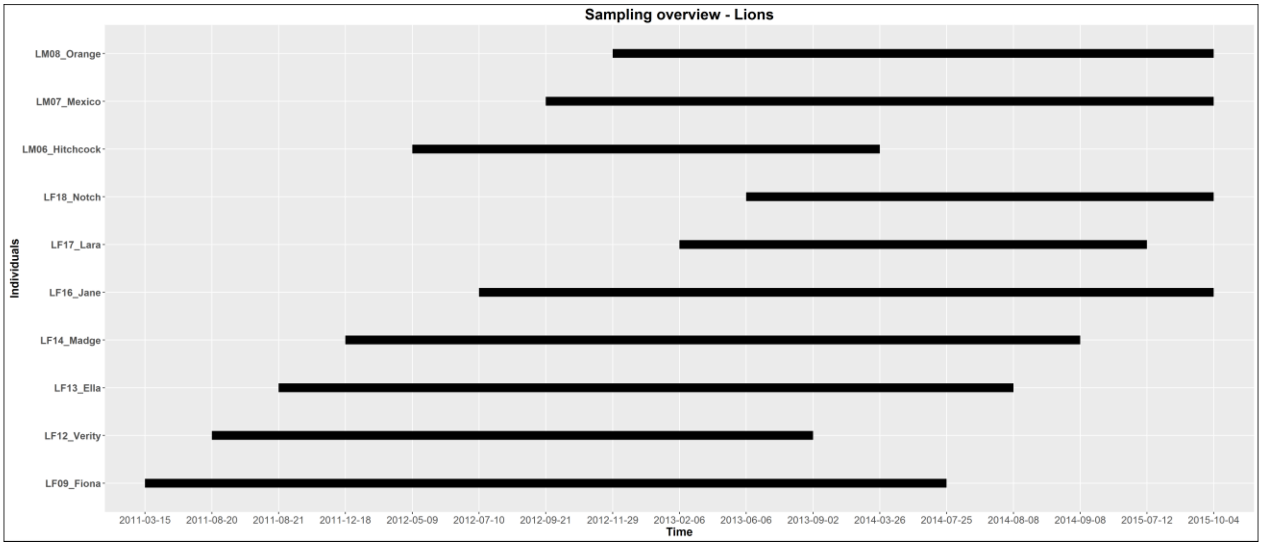


Table 2: Overall sampling duration of all selected lions. LM stands for “leo male” and LF for “leo female”. The “start_date” and the “end_date” is indicated on the x-axis.



7.2. Pre-processing

In order to guarantee consistency across all datasets several pre-processing steps were necessary. First, time (HH.MM.SS, 24h format) and date (YYYY.MM.DD) were standardised. The second step included the removal of empty and erroneous cells (e.g. missing time, date or coordinate values). Outliers were identified using a minimum bounding rectangle around the study area. A buffer of several kilometres was added as lions and leopards are known to leave the protected areas. These steps were conducted with all selected datasets.

The last pre-processing step included, where possible, the removal of large dilution of precision (DOP) values. In order to precisely determine an animal's position, the signal of the collar must be received by at least three satellites. DOP is a measurement used to indicate how well the spatial constellation of the satellites is suited to determine the position of a GPS transmitting device (Frair et al. 2010; Lewis et al. 2007). A small DOP value stands for less scattering of the measured values and indicates a suitable satellite constellation. DOP values ranging from 1 to 10 are regarded as suitable in animal ecology and therefore GPS-fixes exceeding this range were deleted (Lewis et al. 2007). All pre-processing steps combined resulted in an average data-loss of 1.35% for leopards and 0.47% for lions. Considering the fact that all datasets contain at least 4000+ fixes these data losses are tolerable.

Table 3: Selected datasets, PP1 = Number of fixes after the first pre-processing steps (outliers, erroneous fixes, DOP > 10 removed). Time_Filter = Number of fixes lost due to sampling interval harmonization (further explanations see respective section XX). Nr.of records = number of fixes used for extensive analysis. Per_remain (%) = Percentage of fixes left compared to fixes prior to time filter application. Collar_type (1 = Argos, 2 = Sirtrack Argos, 3 = Vectronics Global Star, 4 = Vectronics GPS Plus, 5 = Vectronics Irdium Survey, 6 = Vectronics Vertex Plus).

Name	Species	Sex	PP1	Time_Filter	Nr. of Records	Per_remain	Collar_type
PF07_Ronja	Leopard	F	13856	0	13 856	100	1, 2, 5, 6
PF12_Salome	Leopard	F	4091	0	4 091	100	5,6
PM07_Mothamongwe	Leopard	M	7180	0	7 180	100	3
PM08_Bogarigka	Leopard	M	7467	0	7 467	100	3
LF09_Fiona	Lion	F	49 086	24 322	24 764	50.5	4
LF12_Verity	Lion	F	28 887	17 580	11 307	39.1	4
LF13_Ella	Lion	F	36 578	19 748	16 830	46.0	4
LF14_Madge	Lion	F	32 590	14 941	17 649	54.2	4
LF16_Jane	Lion	F	34 164	9 883	24 281	71.1	4
LF17_Lara	Lion	F	21 611	4 001	17 610	81.5	4
LF18_Notch	Lion	F	18 798	2 086	16 712	88.9	4
LM06_Hitchcock	Lion	M	22 199	10 153	12 046	54.3	4
LM07_Mexico	Lion	M	31 866	11 504	20 362	63.9	4
LM08_Orange	Lion	M	25 367	4 929	20 438	80.6	4

7.3. Uncertainty

Technological advances over the past few decades facilitated and replaced traditional VHF (very high frequency) radio telemetry animal tracking. Modern GPS transmitting collars have several advantages such as a higher positional precision. GPS can achieve a precision of less than 3m, usually between 10-28 m compared to 200-600 m of VHF radio telemetry (Frair et al. 2010; Lewis et al. 2007). Further, 24-hour coverage, remote data access and animal tracking on ground and in air are possible (Bacon et al. 2011; Swanepoel et al. 2010; Tomkiewicz et al. 2010).

Yet, limited battery supply, location errors or connection failures are among the most relevant drawbacks of GPS technology. As GPS collars must not exceed 4% of an animal's bodyweight, battery lifespan is the main limiting factor for sampling duration. Usually, batteries need to be changed after one year (Girard et al. 2006; Tomkiewicz et al. 2010). Connection failures between GPS collar and satellite lead to incomplete tracking and potentially add bias to the results. The main source of connection failures are dense canopy cover or complex terrain (Lewis et al. 2007; Swanepoel et al. 2010). As most parts of the LEC study area are flat without complex topography, the latter factor is only of minor importance. Nevertheless, explorative analysis of the datasets revealed a higher number of missed fixes in leopard datasets. This is in line with the expectations as leopards are known to spend a lot of time resting in trees or under bushes. However, the number of missed fixes has not been quantified. Location errors, expressed by the difference (distance) of the recorded position and the true position of an animal, are caused by the same conditions (Lewis et al. 2007).

7.4. Sampling Intervals

Lions and leopards were sampled at different sampling intervals. As shown in Table 4, there is not only a variation between individuals but also within a single dataset. This is mainly due to the use of different collar or experiments. Lions were sampled at rates between 5 minutes and 60 minutes. Coarser sampling intervals, ranging from 60 minutes to 300 minutes, were used to track leopards. A major reason is the smaller body-size of a leopard. In view of the smaller battery used, tracking at high frequency is too energy-consuming. Further, lion collars are fitted with accelerometers which are used for kill site detection. This research question requires a shorter sampling interval. Between 08:00h and 17:00h, most predators were sampled at a 4.5h interval. This is due to the inactivity of lions and leopards during daytime and mainly to save battery power.

Sampling at different time intervals can introduce bias into the results as areas sampled at higher frequency receive more weight (Katajisto & Moilanen 2006). Even datasets with a regular sampling schedule can be affected as connection failures with the satellite lead to irregular sampled datasets (Downs et al. 2011; Katajisto & Moilanen 2006; Kranstauber et al. 2012). Two solutions are currently used in literature to deal with irregular sampling intervals. The first consists of adjusting all datasets to the one with the coarsest sampling interval. The second uses interpolation to estimate an animal's position between two coarsely sampled fixes. However, the latter approach can introduce even more uncertainty and lead to biased results, depending strongly on the interpolation method chosen (Lonergan et al. 2009). Defining the best choice is difficult, as other factors such as purpose of the study or sampling technique must be considered as well.

Table 4: Sampling intervals used to track lions and leopards. Most animals were sampled at different time intervals ranging from 5-minute to 60-minute intervals for lions and 60-minute to 300-minute intervals for leopards.

Name	**5min_SI**	**30min_SI**	**60min_SI**	**90min_SI**	**120min_SI**	**180min_SI**	**300min_SI**
PF07_Ronja					x	x	x
PF12_Salome						x	
PM07_Mothamongwe				x			x
PM08_Bogarigka			x	x			
LF09_Fiona	x	x	x				
LF12_Verity	x	x					
LF13_Ella	x	x	x				
LF14_Madge	x	x	x				
LF16_Jane	x	x	x				
LF17_Lara		x	x				
LF18_Notch		x	x				
LM06_Hitchcock	x	x	x				
LM07_Mexico		x	x				
LM08_Orange		x	x				

In agreement with Stephen Henley[1], the first strategy was chosen to synchronise all ten lion datasets to 60-minute time intervals. As shown in Table 3, this resulted in a data loss of 11.1 – 60.9%. Yet, these losses must not be overrated as several datasets (LF09_Fiona, LF12_Verity, LF13_Ella, LF14_Madge, LF16_Jane, LM06_Hitchcock), were partially sampled at 5-minute time intervals. Therefore, a large number of fixes were recorded covering only a short period of time. Considering only datasets sampled at 30- and 60-minute intervals, data losses range between 11.1% and 37.1%. It should also be noted that sampling at very high frequency, such as 5 minutes, is not beneficial for seasonal or annual home range estimation. Leopard datasets were not synchronised as data losses would have been quite significant, and the sampling interval is already rather coarse, alleviating effects of uneven weighting.

7.5. Temporal autocorrelation

The challenge of dealing with temporal autocorrelation in animal ecology has been discussed at length over the past decades. There is a disagreement about the severity and the solutions to deal with temporal autocorrelation. Tracking data sampled at high frequency are often autocorrelated, thus biasing home range estimates (Hansteen et al. 1997; Swihart & Slade 1985). Swihart & Slade (1985) suggested to track animals at sampling intervals where temporal autocorrelation is negligible or to remove records afterwards. Yet, removing records in order to avoid temporal autocorrelation can lead to unacceptable data losses which prevents meaningful statements about an animal's behaviour (Fieberg et al. 2010). Other scientists (De Solla et al. 1999: 221; Katajisto & Moilanen 2006) state behavioural data are autocorrelated by nature as animals

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[1] Personal Communication with Stephen Henley, April 2016

move in non-random fashion. Valuable information about an animal's biology is lost by the removal of tracking records (Boyce et al. 2010; De Solla et al. 1999). Consequently, more recent studies suggest including temporal autocorrelation and trying to better understand its effects on home range estimations rather than eliminating it (De Solla et al. 1999; Otis & White 1999). On the other hand the negative correlation between sampling interval and temporal autocorrelation is uncontested (Hansteen et al. 1997; Swihart & Slade 1985). Meaning the shorter the time span between two consecutive fixes the stronger the temporal correlation.

7.5.1. Measurement of temporal autocorrelation

The most common measurement for temporal autocorrelation is the so-called Schoener's ratio (t^2/r^2) developed by Thomas W. Schoener in 1981 (De Solla et al. 1999). "*t^2/r^2 is the ratio of the mean squared distance between successive observations (t^2) and the mean squared distance from the center of activity (r^2)*" (Swihart & Slade 1997: 49). While values > 2 stand for a negative correlation between two consecutive observations, values < 2 implicate a positive temporal autocorrelation. The value for independent observations is 2 (De Solla et al. 1999).

The Schoener's ratio has been calculated for all lion and leopard datasets (Table 5). Due to memory constraints of the computer lion datasets had to be split in half and an averaged ratio is displayed. Leopard datasets were split as well to account for irregular sampling intervals.In line with the expectations, all 4 leopard and 10 lion datasets show a positive temporal autocorrelation having. All values for the Schoener's ratio are below the threshold of 2 and range between 0.00202 (LM06_Hitchcock) and 0.08395 (PF12_Salome). Therefore, the data of all 14 datasets is temporally autocorrelated. While Biased Random Bridges rely on sufficient autocorrelation, Kernel Density Estimation expects the input data to be free of temporal autocorrelation. Leopard datasets are slightly less autocorrelated due to their coarser sampling intervals. The constant 3-hour sampling interval used for the leopard PF12_Salome resulted in the highest value for the Schoener's ratio.

Table 5: The average Schoener's ratio (t2/r2) calculated for all selected datasets.

Name	**Schoener's ratio (t2/r2)**
PF07_Ronja	0.02666
PF12_Salome	0.08395
PM07_Mothamongwe	0.06454
PM08_Bogarigka	0.01102
LF09_Fiona	0.00428
LF12_Verity	0.00388
LF13_Ella	0.00388
LF14_Madge	0.00230
LF16_Jane	0.00504
LF17_Lara	0.00377
LF18_Notch	0.00668
LM06_Hitchcock	0.00202
LM07_Mexico	0.00668
LM08_Orange	0.00755

III Home range analysis

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8. Concepts of animal space use

8.1. Home range and territory

Home range and territory are the two most widely used concepts in animal ecology to describe their space use. These concepts are important in determining habitat preferences, carrying capacities or aspects of species-extinction susceptibility (Hemson et al. 2005). The origin of these concepts lies in the 1860s when Charles Darwin first attempted to describe animal space use:

"(...) it may be here remarked that most animals and plants keep to their proper homes, and do not needlessly wander about; we see this even with migratory birds, which almost always return to the same spot" (Darwin 1861, cit. in: Börger et al. 2008: 637).

Darwin's statement provided the basis for William H. Burt, whose definition of home range and territory are, despite some criticism and debates (Bothma et al. 1997; Seaman & Powell 1996), still broadly accepted. Home range is defined as:

"that area traversed by the individual in its normal activities of food gathering, mating and carrying for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range" (Burt 1943, cit. in: Powell 2000: 65).

The main weak point of Burt's definition is its vague wording and not primarily its content. As a clear guidance is missing, it remains unclear what to include in "normal activities" or how "occasional sallies" should be differentiated from regular space use (Powell 2000). The home range is hence the resultant patterns of dynamic processes (Börger et al. 2008: 638). The time frame used for its calculation, the sex and age of the studied animal as well as environmental circumstances such as climatic factors, food availability or presence of conspecifics do all affect the result of a home range estimation (Börger et al. 2008; Loveridge et al. 2009). Per definition, home ranges are neither defended against conspecifics nor for an animal's exclusive use (Börger et al. 2008). In contrast, territories are actively defended and described as follows:

"A territory is an area within an animal's home range over which the animal has exclusive use, or perhaps priority use. A territory may be the animal's entire home range or it may be only part of the animal's home range (its core, for example)" (Powell 2000: 70).

For a given period of time and under stable conditions the area covered by a territory is fixed (Börger et al. 2008; Mizutani & Jewell 1998). Spatial equality of territory and home range is limited to areas where animals live under favourable conditions and where there is no need to maintain large areas. In poor environments such as the Kalahari with predator home ranges exceeding 1000 km^2 an active defence is impossible and therefore one of the key elements of territoriality is violated. The estimation of a territory comes at a high cost for researchers as one must prove its exclusive use through acts of defence or the location of competing neighbours (Börger et al. 2008). Consequently, the term “territory” is often avoided in animal ecology. Instead, “core area” is used to describe an area of intensified use within the total home range (Fieberg & Börger 2012; Hemson et al. 2005; Powell 2000). It can be seen as “territory light”.

8.2. Translation into home range analysis

In order to extract the home range and core areas one must first translate these terms into mathematical terms. Home range is defined as the 95% isopleth and core areas as the 50% isopleth. Depending on the home range estimator chosen, it is either referred to the percentage of utilization distribution density (UD) or points geometrically closest to the centroid (Benhamou & Cornélis 2010; Downs et al. 2011; Hemson et al. 2005; Loveridge et al. 2009; Tuqa et al. 2014). While the 95% isopleth has some biological relevance as it excludes exploratory strays and prevents an overestimation of the home range area, the 50% isopleth is just used by convention[2].

As described above home ranges can be seen as dynamic constructs which are highly dependent on other factors. A homogenous space use by an animal is rather unlikely given that resources are not distributed equally across the home range but are usually somewhat patchy (Girard et al. 2002; Katajisto & Moilanen 2006). Gautestad & Mysterud (2005) state even in a perfectly homogeneous environment complex habitat utilization patterns will emerge because of an individual’s preference and experience. In the case of lions and leopards, waterholes, favourable hunting spots or areas providing protection could be areas of intense use. Traditional home range estimators like Minimum Convex Polygon (MCP) are incapable of detecting complex activity patterns. Advances in technology provided more sophisticated home range estimation methods (e.g. Kernel Density Estimation, KDE), with which it is possible to identify these areas (Hemson et al. 2005). These approaches produce a utilisation density distribution instead of assuming uniform space use within the home range (Benhamou & Cornélis 2010; Katajisto & Moilanen 2006). The UD is directly related to the amount of time spent by the animal, meaning longer periods of time lead to more fixes and a higher UD (Seaman & Powell 1996).

In this thesis, the terms home range and core area are used as suggested in the section above. Home range is assumed to be equal to the 95% isopleth and core area to the 50% isopleth.

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[2] Personal conversation with Stephen Henley, November 2015

8.3. Kernel Density Estimation, KDE

Nowadays, KDE is the most popular home range estimator in animal ecology and has replaced the traditional MCP method. One of the main reasons is the capability of KDE to account for heterogeneous space use of an animal by assigning a UD at each point within an area (Hemson et al. 2005; Katajisto & Moilanen 2006; Lichti & Swihart 2011; Seaman & Powell 1996). The basic principle of KDE can be described as follows: First, a kernel is placed over each point of the sample. Second, a regular grid is superimposed on the data and an estimated density is obtained at each intersection using information of the entire sample. The density estimation at a certain point is the average of the densities of all overlapping kernels at that point (Seaman & Powell 1996). The bivariate kernel estimator of $f(x)$ can be described as follows:

$$\hat{f}(x) = \frac{1}{nh}\sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right) \quad (1)$$

The estimated density at point *x* is $\hat{f}(x)$, with a kernel function *K*, smoothing parameter h and n as the total number of fixes. X_i is a series of vectors whose coordinates describe the location of each observation *i* (Seaman & Powell 1996; Silverman 1986; Worton 1989). The resulting UD surface displays the animal's space use and its intensity. Using the UD surface one can extract the area covering 95% or 50% of the volume under the UD surface.

8.3.1. Parameter selection

Compared to other home range estimators, the number of parameters to be selected is quite small and only the soothing parameter h and the kernel type must be chosen prior to the analysis. Yet, their selection, especially the smoothing parameter, does largely influence the resulting home range sizes (Hemson et al. 2005; Silverman 1986; Worton 1989).

8.3.2. Smoothing parameter h

The smoothing parameter h or bandwidth determines the width of the kernels (Seaman & Powell 1996). While a small bandwidth allows nearby observations to have greater influence on the density estimation, wide kernels allow more influence of distant observations (Keating & Cherry 2009). Choosing h too small produces noisy estimates with spurious structure. On the other hand, bandwidths selected to wide tend to over smooth density estimates and obscure important structures (Keating & Cherry 2009). To avoid biased results one must choose the right bandwidth (Hemson et al. 2005; Keating & Cherry 2009; Seaman & Powell 1996). Both cases fail to determine the size of the home range accurately.

The key to determining the true home range is the choice of the best value for h (Worton 1989). The two most widely used bandwidth selection methods are the reference bandwidth (REF) and the least-squares cross-validation (LSCV) (Gitzen & Millspaugh 2003; Hemson et al. 2005; Kie et al. 2010; Lichti & Swihart 2011). The parameter REF is derived from the standard deviation of the input data and unimodal normal distribution is assumed (Seaman & Powell 1996). In reality, animal datasets often have multiple modes and therefore the assumption of a unimodal distribution is violated. Consequently, the REF chosen is too large and leads to an over smoothing (Seaman & Powell 1996). Nevertheless, it is possible to achieve reasonable home range estimates using REF (Worton 1989). A considerable advantage of REF over LSCV is its calculation, which is much less time consuming (Hemson et al. 2005; Lichti & Swihart 2011). LSCV on the other hand determines the bandwidth that leads to the smallest difference between the estimated and the true density distribution (Gitzen & Millspaugh 2003; Hemson et al. 2005; Seaman & Powell 1996). However, LSCV tends to be quite sensitive to sample size, and results are often under smoothed, especially when dealing with large sample sizes containing thousands of points (Kie et al. 2010).

Kernel choice

The second choice to be made is to use either fixed or adaptive kernels. Fixed kernels use the same bandwidth h to smooth all observations in a given dataset. The use of adaptive kernels is a more sophisticated approach, where the smoothing parameter h is variable. Areas with a low concentration of points receive a higher bandwidth value and are therefore more smoothed, whereas areas with high concentration get a small h values and therefore are less smoothed (Gitzen & Millspaugh 2003; Kie et al. 2010; Seaman & Powell 1996; Worton 1989). In practice, the fixed method is used more often, mainly because it produces reasonable results, is more stable and less likely to introduce bias (Gitzen & Millspaugh 2003; Kie et al. 2010; Seaman & Powell 1996).

Advantages and drawbacks

One of the biggest advantages of kernel density estimation is that it has now been used for roughly three decades. Its strengths and weaknesses have been studied extensively and clear guidance on how to select parameters is available. Results of a study are no longer experimental but can be compared to others (Downs et al. 2011; Hemson et al. 2005; Lichti & Swihart 2011; Seaman & Powell 1996). Unlike recently developed home range estimators such as Biased Random Bridges (BRB) or time Local Convex Hull (t-LCH), the number of parameters to be selected for KDE is quite small and their influence on the home range estimations has been described thoroughly. The most significant drawback of KDE is its high sensitivity to the bandwidth chosen and the assumption that input values are independent of each other. As shown in the section on temporal autocorrelation this is hardly the case when working with tracking data.

8.4. Biased Random Bridges (BRB)

Brownian Bridges, first introduced by Bullard (1991) and carried on by Horne et al. (2007), are based on the concept of Brownian Motion (BM). Unlike KDE, it incorporates temporal structure of the data and derives the UD from the animal's trajectory (Byrne et al. 2014; Kranstauber et al. 2012). The trajectory must be approximated as continuous tracking of an animal is impossible and thus only individual fixes are available (Horne et al. 2007; Kranstauber et al. 2012). It is assumed that an animal moves randomly (random walk) between two consecutive fixes (Horne et al. 2007).

The expected positions of an animal moving randomly between a and b can be estimated using a normal distribution (Horne et al. 2007), described by the following formula:

$$\varphi(z;\, \mu,\, \sigma^2) = \frac{1}{2\pi\sigma^2}\, exp\left(\frac{-(z-\mu)^2}{2\sigma^2}\right) \quad (2)$$

with $\mu(t) = a + \frac{t}{T}\,(b-a)$, and $\sigma^2(t) = \frac{t\,(T-t)}{T}\,{\sigma^2}_m$

Any position in $\mathbb{R}^2$ (a two-dimensional space spanned by two vectors) is denoted by z, the mean value by μ and the variance by σ^2. The starting point of a segment is a and the ending point is b. T is the total duration of the segment with $t \epsilon [0, T]$ as the time of evaluation. The variance of the Brownian Motion is described by ${\sigma^2}_m$. The density function of Brownian Bridges $h_{BB}(z)$ (Horne et al. 2007) at position z with T_{tot} as the total time span between all points and n as the total number of points is:

$$h_{BB}(z) = \frac{1}{T_{tot}} \sum_{i=0}^{n-1} \left\{ \int_0^{T_i} \varphi\,(z;\, \mu_i\,(t), \sigma_i^2\,(t))\, dt \right\} \quad (3)$$

According to Byrne et al. (2014: 2), the driving parameter is the Brownian Motion variance ${\sigma^2}_m$ which is a measure of how irregular the path of an animal between successive locations is. Similar to KDE, the calculated UD provides the basis for the extraction of the desired home ranges. An extensive description of how Brownian Bridges work exactly can be found in Bullard (1991) or Horne et al. (2007).

8.4.1. Accounting for preferences

A major weak spot of the above described Brownian Bridges is the assumption of random movement. It is in contrast to Burt's (1943) definition of animal space use where he clearly states an animal's behaviour is driven by the necessity to fulfil their needs. Especially when studying animals over longer periods of time it is hard to justify random movement (Byrne et al. 2014). For tracking data sampled at high frequency, simpler estimation methods might be more suitable (Byrne et al. 2014). A directional bias has been introduced by Benhamou (2011) to account for non-random animal movement and therefore the calculation method is called Biased Random Bridges (BRB).

The added bias leads to slightly different equations:

$$\varphi(z;\ \mu,\ \sigma^2) = \frac{1}{2\pi\sigma_{tot}^2}\ exp\left(\frac{-(z-\ \mu)^2}{2\sigma^2}\right) \quad (4)$$

With $\mu(t) = a + \frac{t}{T}\ (b - a)$, and $\sigma_{tot}^2\ (t) =\ \sigma_{min}^2 + \frac{4t\left(1-\frac{t}{T}\right)}{T_{max}} * \frac{D*T_{max}}{2}$

While the mean value μ did not change, the variance has become more complex compared to the classic Brownian Bridges with σ_{tot}^2 as the total variance and σ_{min}^2 as relocation variance. The diffusion coefficient is *D* and T_{max} is the upper time threshold and prevents exceptionally large time gaps between two segments from being entered into the calculation (Benhamou 2011). An extensive description on Biased Random Bridges can be found in Benhamou (2011). The adjusted density function is:

$$h_{BRB}(z) = \frac{1}{T_{tot}} \sum_{i=0}^{n-1} \left\{ \int_{0}^{T_i} \varphi\ (z;\ \mu_i\ (t), \sigma_{tot\ i}^2\ (t))\ dt \right\} \quad (5)$$

8.4.2. Parameter selection

Maximum duration Tmax

The time threshold *T_{max}* needs to be selected based on the sampling interval of the tracked animal. T_{max} ensures that only values with sufficient temporal autocorrelation, a key assumption of BRB, are included into the calculation of the UD (Benhamou 2011). Is T_{max} exceeded between two values these are no longer considered as they potentially lack temporal autocorrelation.

Smoothing parameter

The smoothing parameter is based on the moving capability of the tracked animal as well as on the precision of the tracking device used. By moving capability one means the potential distance an animal can travel during the timespan between two fixes. Usually, an average speed is taken as reference to calculate the potential distance (Benhamou & Cornélis 2010; Benhamou 2011).

Advantages and drawbacks

The most significant advantage of BRB compared to KDE is the approach to estimate the trajectories rather than the loose points. Second, BRB make use of the temporal autocorrelation of animal tracking data and are less sensitive to changing sampling intervals (Byrne et al. 2014; Horne et al. 2007). Drawbacks are the higher complexity and the inability to deal with tracking data sampled at high frequency (Byrne et al. 2014).

IV Methodology

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9. Home range estimation

This section gives an overview of the selected home range estimators, time intervals, the calculations performed and all parameter settings. The primary home range estimator (HRE) chosen is the Kernel Density Estimation (KDE) and the secondary HRE are Biased Random Bridges (BRB). Using KDE, all possible home ranges were calculated for every individual. For the BRB control group, consisting of two leopards and four lions, the same calculations were done. Yet, for these calculations only a timespan covering two consecutive years was used. Home ranges were characterised and described using the following attributes:

- Absolute size [km^2]
- Compactness Index (CI)
- centroid (coordinates)
- centroid-shift [km] between two time intervals
- bearing of the centroid shift [degrees]
- overlap of home ranges and core areas [%]
- Volume of Intersection (VI)
- number of peaks
- number of holes and polygons

The KDE results are analysed in four parts. Part one characterises the home ranges and core areas using the above presented home range descriptors. The second part includes the analysis of how the home range of a single individual changes over time. Is it possible to detect certain patterns and can variations be characterised? The focus of the third part is on the comparison of several individuals (intra-specific) within a defined time interval but also whether the same patterns, e.g. an extension, are identifiable over a longer period of time. An extensive cross-species analysis is not intended, as this has been done extensively by Zehnder (2015) . In the fourth part the results of KDE and BRB are compared and potential differences analysed. All calculations were performed in the freely available *statistics software R* (version 3.2.2). Additional packages were necessary in order to be able to do all analysis. *R*-Code developed by André Zehnder (Zehnder 2015) during his Master's Thesis was used as a framework and adjusted to my needs.

9.1. Kernel Density Estimation

9.1.1. Smoothing parameter h

The reference bandwidth REF was used for all calculations. It was derived directly during the home range estimation using the *R*- package *adehabitatHR*. The choice of REF was based on the following considerations. First, it can produce reasonable home ranges estimations. Second, unlike LSCV the computational effort is smaller and REF is insensitive to sample size. Third, the main drawback of over smoothing is well known. For each individual the bandwidth was calculated for every single time interval analysed. This means, for instance, for the female leopard Ronja (LF07_Ronja) 21 different values for REF were derived from the input data (1 for the entire observation period, 6 for annual time intervals and 7 per wet- and 7 per dry-season).

9.1.2. Kernel selection

Using the *kernelUD* function of the *R*-package *adehabitatHR* the Gaussian kernel was chosen to perform all calculations. The second choice to be made was to use either a fixed or an adaptive kernel. The fixed kernel was selected following the recommendation in the literature (Gitzen & Millspaugh 2003; Kie et al. 2010; Seaman & Powell 1996). Further, the fixed kernel produces more stable results and is less likely to introduce bias into the results.

9.1.3. Grid and extent

The 700 cells grid and the extent-factor of 0.3 chosen are identical to the ones described in Zehnder (2015) and applied for all individuals, in order to make the two results comparable. While the grid parameter determines the size of the grid on which the UD is calculated, the extend-factor controls how much larger the area is compared to the minimum-bounding rectangle of all points included for the UD.

9.2. Biased Random Bridges

The direct home range estimation using Biased Random Bridges is not yet possible in *R* but it is approximated using movement-based KDE (Benhamou 2011).

9.2.1. Smoothing parameter hmin

According to Benhamou & Cornélis (2010) the appropriate value of h_{min} must fulfil the two following criteria. First, the location uncertainty must be incorporated and second, the potential distance covered by the animal between two fixes must be considered (Benhamou & Cornélis 2010; Benhamou 2011). The value for the location uncertainty was set to 30m as this precision must be achieved by modern GPS collars, second component of h_{min} was calculated using the recommendation of Benhamou & Cornélis (2010). The maximum velocity an animal can maintain for a longer period of time is derived by using the 99% percentile of all speeds recorded in a dataset. The main sampling interval was set to be equal to a longer period of time.

Consequently, for lions it is 60 minutes and for the two selected leopards it is 90 minutes, 180 minutes or 300 minutes, depending on the time interval selected for calculation. Table 4 provides an overview of all selected animals as well as the sampling rates. As shown by Zehnder (2015) the value of h_{min} has a huge influence on the home range estimation. Therefore, the derived value for h_{min} was multiplied by a factor ranging from 0.25 – 2.00 using increments of 0.25 in-between. This step was done for every individual using the same factors. After comparing all outputs, the best one was selected for further analysis. The best one, neither over smoothed nor under smoothed, was identified by visual comparison.

9.2.2. Maximum time difference t_{max}

The maximum time difference allowed between two fixes was set to 120*60 seconds for all lions and to 120*60 and 330*60 seconds for leopards. T_{max} ensures that fixes being temporally further apart are not considered for the BRB. Furthermore, the parameter should ensure temporal autocorrelation between consecutive fixes. In section xx, the calculation of the Schoener's ratio clearly indicated that even the coarsest datasets (300-minute main sampling interval) are well within the threshold of temporal autocorrelation.

9.2.3. Minimum moving distance l_{min}

This parameter defines the minimum distance an animal must move between two consecutive fixes in order to be counted as movement. If the distance is below the distance threshold it is classified as resting. Dürr & Ward (2014) suggested to set the minimum distance as twice the uncertainty of the GPS collar. In this case with an estimated uncertainty of 15 meters (Zehnder 2015), the recommendation leads to a minimum moving distance of 30 meters.

9.2.4. Number of sub-bridges parameter tau

Up to date, it is not possible to calculate BRB directly but with an approximation based on movement-based KDE. Therefore, a single bridge between two fixes is subdivided into several smaller bridges. The duration of each segment is determined by the parameter *tau*. Unfortunately, there is no guidance on how to select this parameter and thus its selection is rather ambiguous. Zehnder (2015) conducted a brief analysis on the influence of *tau* on the home range estimation. The conclusion was that there is only a minor influence of *tau* on the HRE and it is therefore negligible. His recommendation to set *tau* to 10% of the main sampling interval was implemented.

9.2.5. Grid and extent

In order to be able to compare the results of BRB to the ones of KDE the same values were taken. This means a grid of 700 cells and an extent factor of 0.3.

9.3. Time intervals

The main goal of the first research question is to determine whether it is possible to characterise home range dynamics over time. Therefore, four different ecologically meaningful time intervals were defined in agreement with Stephen Henley[3]:

- entire observation period
- annual (June – May)
- wet season (November – April),
- dry season (June – September)

The annual time interval and the wet season interval cover two calendar years. Therefore, the following definitions were applied:

Year 2010 = June 2009 – May 2010
Wet Season 2010 = November 2009 – April 2010
Dry Season 2010 = June 2010 – September 2010

Table 6 (KDE) and Table 7 (BRB) give an overview of all selected animals and the time intervals covered.

9.4. Home range descriptors

9.4.1. Area

The total area [km^2] of the home range (95% isopleth) and the core area (50% isopleth) are extracted for each time interval. All polygons, also disjoint polygons, associated with home range or core area are summed up to the total area. Holes are excluded. Zehnder (2015) suggested an area must exceed a threshold of 0.25 km^2 to be classified as a hole. Disjoint polygons must exceed 1 km^2 to be counted as part of the home range or core area. These thresholds should prevent artefacts from being included.

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[3] Personal communication with Stephen Henley, February 2016

Table 6: Overview of all time intervals used for the calculation of KDE. The following abbreviations have been used: Mothamongwe = Motha, Bogarigka = Boga, Hitchcock = Hitch. Ronja – Bogarikga are leopards, all others are lions. Male animals are represented using a bold “X”. all_time includes all fixes available for an individual, Year 2013 (June 2012 – May 2013) = Y2013, wet season 2013 (November 2012 – April 2013) = W2013, dry season 2013 (June 2013 – September 2013) = D2013.

Interval	**Ronja**	**Salome**	**Motha**	**Boga**	**Fiona**	**Verity**	**Ella**	**Madge**	**Jane**	**Lara**	**Notch**	**Hitch**	**Mexico**	**Orange**
all_time	X	X	**X**	**X**	X	X	X	X	X	X	X	**X**	**X**	**X**
Y2009	X													
Y2010	X													
Y2011	X													
Y2012	X		**X**		X	X								
Y2013	X		**X**	**X**	X	X	X	X				**X**		
Y2014	X	X			X		X	X	X	X	X	**X**	**X**	**X**
Y2015	X	X			X				X	X	X		**X**	**X**
W2009	X													
W2010	X													
W2011	X													
W2012	X		**X**	**X**	X	X	X	X						
W2013	X		**X**	**X**	X	X	X	X	X			**X**	**X**	**X**
W2014	X	X			X		X	X	X	X	X		**X**	**X**
W2015	X	X			X				X	X	X		**X**	**X**
D2009	X													
D2010	X													
D2011	X				X									
D2012	X		**X**	**X**	X	X	X	X				**X**		
D2013	X		**X**		X		X	X	X	X		**X**	**X**	**X**
D2014	X	X			X			X	X	X	X		**X**	**X**
D2015	X	X							X		X		**X**	**X**

Table 7: Overview of all time intervals used for the calculation of BRB. The following abbreviations have been used: Mothamongwe = Motha, Bogarigka = Boga, Hitchcock = Hitch. Ronja – Bogarikga are leopards, all others are lions. Male animals are represented using a bold “X”. all_time includes all fixes available for an individual, Year 2013 (June 2012 – May 2013) = Y2013, wet season 2013 (November 2012 – April 2013) = W2013, dry season 2013 (June 2013 – September 2013) = D2013.

Interval	**Ronja**	**Salome**	**Motha**	**Boga**	**Fiona**	**Verity**	**Ella**	**Madge**	**Jane**	**Lara**	**Notch**	**Hitch**	**Mexico**	**Orange**
all_time	X		**X**					X	X				**X**	**X**
Y2012	X		**X**											
Y2013	X		**X**					X						
Y2014								X	X				**X**	**X**
Y2015									X				**X**	**X**
W2012	X		**X**					X						
W2013	X		**X**					X	X				**X**	**X**
W2014								X	X				**X**	**X**
W2015									X				**X**	**X**
D2012	X		**X**					X						
D2013	X		**X**					X	X				**X**	**X**
D2014								X	X				**X**	**X**
D2015									X				**X**	**X**

9.4.2. Compactness Index

The Compactness Index is defined by Li et al. (2013: 1227) as a numerical quantity representing the degree to which a shape is compact. A perfect circle would achieve the highest value. CI is an important parameter to describe an animal's home range or territory as it is closely related to defensive costs. At least in theory a round area is seen as optimal as defensive costs are minimal. In reality, this is rarely the case as a homogenous distribution of resources is unlikely (Eason 1992). Nevertheless, a very small or high CI values could be an indicator whether the resource distribution is rather heterogeneous or homogeneous, respectively. Up to date there are many different approaches to calculate a CI (Li et al. 2013). The method presented by Ebdon (1985), also used by Zehnder (2015), was implemented.

$$CI = \frac{4\,A}{\pi\,D^2}$$

A is defined as the area of the isopleth (e.g. 95% - isopleth of the 2014 wet season) and *D* represents the diameter of the smallest circumscribing circle around the isopleth area (Ebdon 1985). *S* is the ratio of the isopleth area to the smallest circumscribing circle. The higher the value for S, the more compact the isopleth area.

9.4.3. Centroid

The centroid for all 95% isopleth polygons was calculated. A centroid consists of a coordinate pair given in the local Cape / UTM 36S (EPSG: 22236) reference system. The function *gCentroid* of the *R*-package *rgeos* was used to determine the centroids.

9.4.4. Centroid – Shift

The straight-line distances [km] between all centroid pairs have been calculated for every individual and all time intervals using the *gDistance* function of the *R*-Package *rgeos*. A shift between two consecutive time intervals (e.g. Y2014 and Y2015) could be an indication of a home range variation.

Additionally, the bearing of the centroid shift is indicated. The *bearing* function of the *R*-Package *geosphere* was used to calculate the bearing between a centroid pair (Table 8). The result consist of a single number consists of a single number between -180° and +180° with North [0°] as reference. A potential centroid shift between two consecutive time intervals can be characterised as follows: e.g. the 2015 wet season centroid of the 95% home range is located 20 km northeast of the 2014 wet season 95% home range centroid. The comparison of several individuals at the same time interval could indicate an alteration on the larger scale. In order to the reduce the number of centroid shifts, only shifts exceeding 10 kilometres were considered.

Table 8: Translation of angles into cardinal directions.

CARDINAL DIRECTION	ANGLE [° DEGREES]
SOUTH	- 180.0 to - 157.5
SOUTH-WEST	- 157.5 to - 112.5
WEST	- 112.5 to - 67.5
NORTH-WEST	- 67.5 to -22.5
NORTH	-22.5 to 22.5
NORTH-EAST	22.5 to 67.5
EAST	67.5 to 112.5
SOUTH-EAST	112.5 to 157.5
SOUTH	157.5 to 180

9.4.5. Home range and core area overlap

The percentage of overlap of home ranges and core areas at different time intervals are calculated. A small or large, respectively, value could indicate a significant change in size or location. Here, it is important to be able to compare not only different areas of a single individual but also between different animals of the same species. Certainly, an intraspecific comparison is only feasible for identical time intervals. The *gIntersection* function of the *R*-package *rgeos* was used.

9.4.6. Volume of Intersection (VI)

Kernel Density Estimation and Biased Random Bridges are both based on a UD. As described in the respective chapters on KDE and BRB, the UD is an indicator of how intensely a certain area within an animal's home range is used. The use of VI has been proposed by several researchers (Gitzen & Millspaugh 2003; Jay et al. 2012; Kochanny 2005; Kranstauber et al. 2012; Lichti & Swihart 2011) as an additional measurement of home range and core area comparison. A value of 0 indicates no overlap and 1 stands for a total overlap. The *kerneloverlaphr* function of the *R*-Package *adehabitatHR* package was used.

9.4.7. Home Range Peaks

A brief analysis of the estimated home ranges and core areas showed that in many cases multiple polygons jointly build up the home ranges or core area. Especially the number of peaks within the core area is interesting as this measure an indicator which space is used most intensely by an animal. In addition to the 95%- and 50% isopleths the 20% isopleth was calculated and defined as peak. The threshold of 20% was defined by myself and not by recommendation of a scientific study. Post-calculation analysis revealed that the 20% home range is in many cases a reasonable approximation to detect peaks within the core area. Multiple peaks could be an indicator of a heterogeneous environment.

9.4.8. Holes and polygons

Based on the parameter settings described in the section on absolute area, the number of holes and polygons were captured. This was done for both, the home range and the core area. A large number of holes and polygons could be an indicator of a heterogeneous environment. The second possibility would be a quite significant over smoothing or under smoothing, respectively.

9.4.9. Movements outside the CKGR and KGR

All calculated 95%- and 50% home ranges (annual and seasonal) were intersected with the border of the CKGR and KGR. Based on the findings animals are then classified into a group with and a group without parts outside the protected area. If parts of an animal's home range and/ or core area are located outside the protected area, a sub-classification into "very low", "low", "moderate", "high" and "entire" follows. It should be seen as a qualitative rather than a quantitative analysis.

9.5. KDE vs. BRB

A brief comparison between the results of KDE and BRB should enhance the overall home range analysis. Table 7 shows the two leopards and four lions as well as the corresponding time frames selected for comparison. As mentioned earlier, the same parameters used to describe KDE-based home ranges and core areas are available for BRB.

V Results

The result section concerning the first research question is subdivided into four sections. In the first section the results of the KDE are generally described using the home range descriptors presented in the previous chapter on methodology. The second and the third section focus on the home range developments of individual animals and the comparison of several individuals at the same time interval. The result comparison of KDE and BRB follows in the fourth section. In general, for every individual a plot is included in this chapter. However, additional plots can be found in the appendix.

10. Home range descriptors

10.1. Absolute area

The absolute area of the 95%- and 50% home ranges is highly variable across all four leopard and ten lion datasets. Although the home range size using data of the entire observation period is displayed, it should not be overrated as it is biologically not as meaningful as are annual or seasonal home range estimations. Further, some individuals (e.g. the leopard PF07_Ronja) cover a time span of 7 years while others (e.g. the leopard PM08_Bogarika or the LF12_Verity) cover only 2 years. This leads to quite significant differences in the number of fixes available and based on how KDE works, small datasets are more vulnerable to outliers than larger datasets. Keeping this in mind one can explain the fact that certain annual home ranges (e.g. PF12_Salome, PM08_Bogarika, LF17_Lara or LM08_Orange) cover a larger area than the ones calculated using all data available. In the following two tables (Table 9 and Table 10), the absolute area for all 14 predators is shown:

Table 9: Overview of the area [km^2] of the 95% HR for leopards and lions. The ID is an indicator for the species (P = pardus/leopard, L = leo/lion) and the sex (F = female, m= Male) of an animal. Abbreviations used: PM07_Motha = PM07_Mothamongwe, PM08_Boga = PM08_Bogarikga and LM06_Hitch = LM06_Hitchcock. For each time interval (all data, year, wet season, dry season) the largest, the smallest and the average home range size are displayed.

ID	all_data	year_max	year_min	year_avg	wet_max	wet_min	wet_avg	dry_max	dry_min	dry_avg
PF07_Ronja	1202.6	1176.6	547.1	750.9	1246.9	221.0	485.0	1078.6	271.7	720.0
PF12_Salome	976.9	2410.7	98.9	1254.8	1820.3	58.1	939.2	2415.7	105.3	1260.5
PM07_Motha	720.3	682.2	621.0	651.6	696.5	499.4	597.9	748.4	613.7	681.0
PM08_Boga	2425.4	2553.6	2553.6	2553.6	2705.8	1187.5	1946.7	2411.6	2411.6	2411.6
LF09_Fiona	4133.9	4312.9	692.6	2641.9	2445.6	406.4	1865.8	5991.3	892.3	2787.8
LF12_Verity	3482.8	3586.8	1559.0	2572.9	3192.2	1006.1	2099.2	1374.8	1374.8	1374.8
LF13_Ella	2360.2	1444.5	1216.0	1330.3	3184.8	880.0	1717.8	1324.8	959.0	1141.9
LF14_Madge	3757.0	3941.1	804.3	2372.7	3634.5	798.6	2033.2	3285.2	285.0	1742.2
LF16_Jane	3714.5	2727.1	2248.1	2487.6	2357.9	2144.8	1836.9	2824.5	1372.2	1548.5
LF17_Lara	3474.1	4624.8	1349.9	2987.4	4558.0	1050.9	2804.5	3319.4	1300.3	2309.9
LF18_Notch	1242.6	1456.3	980.4	1218.3	1277.3	882.0	1079.7	1263.8	755.9	1009.8
LM06_Hitch	4392.2	4444.8	3060.5	3752.7	4040.6	4040.6	4040.6	3427.1	1355.3	2391.2
LM07_Mexico	2259.5	2438.9	867.7	1653.3	2588.9	827.0	1901.6	1713.1	627.6	1297.9
LM08_Orange	1325.3	1503.1	1112.5	1307.8	1402.0	1222.2	1218.1	1207.5	67.6	941.9

Table 10: Overview of the area [km^2] of the 50% HR (core area) for leopards and lions. The ID is an indicator for the species (P = pardus/leopard, L = leo/lion) and the sex (F = female, m= Male) of an animal. Abbreviations used: PM07_Motha = PM07_Mothamongwe, PM08_Boga = PM08_Bogarikga and LM06_Hitch = LM06_Hitchcock. For each time interval (all data, year, wet season, dry season) the largest, the smallest and the average home range size are displayed.

ID	**all_data**	**year_max**	**year_min**	**year_avg**	**wet_max**	**wet_min**	**wet_avg**	**dry_max**	**dry_min**	**dry_avg**
PF07_Ronja	174.4	191.1	106.8	147.9	259.9	34.8	103.7	282.2	77.0	191.3
PF12_Salome	56.4	232.1	19.5	125.8	342.5	11.3	176.9	217.9	25.9	121.9
PM07_Motha	190.5	213.8	164.2	189.0	195.8	157.4	176.6	174.9	171.1	173.0
PM08_Boga	495.8	646.0	646.0	646.0	690.1	245.9	468.0	616.8	616.8	616.8
LF09_Fiona	685.9	854.3	692.6	773.5	588.8	469.5	426.4	1346.4	144.1	630.8
LF12_Verity	728.5	998.9	391.4	695.2	994.7	242.5	618.6	454.7	454.7	454.7
LF13_Ella	426.6	242.9	232.0	237.4	939.5	157.1	423.3	364.1	206.3	285.2
LF14_Madge	619.0	967.8	155.0	561.4	911.3	149.2	416.1	630.4	63.2	342.1
LF16_Jane	968.6	767.5	539.3	653.4	617.0	467.4	434.2	806.9	264.8	365.0
LF17_Lara	640.7	872.0	333.2	602.6	827.1	218.8	523.0	781.8	350.7	566.2
LF18_Notch	306.1	349.4	252.5	301.0	284.9	216.6	250.7	402.1	177.5	289.8
LM06_Hitch	1122.5	1083.4	714.8	899.1	1083.4	1009.1	1046.3	1030.0	250.6	640.3
LM07_Mexico	345.5	552.3	101.8	327.1	693.8	132.8	400.1	446.1	88.3	298.0
LM08_Orange	325.1	340.1	275.8	308.0	394.1	265.3	321.1	272.8	112.4	195.1

As shown in Table 9 above, lions usually maintain larger average annual home ranges than leopards as they do live in prides rather than solitary. The only exception is the male leopard PM08_Bogarika, with an exceptionally large home range. PF07_Ronja and PM07_Bogarika maintained significantly larger annual home ranges than the remaining leopard PF12_Salome. Looking at PM07_Mothamongwe one can clearly see that its home ranges are fairly stable across all categories.

Similar to the leopards, the average annual lion home range sizes show quite a variation ranging from only 1218.5 km^2 (LF18_Notch) up to 3752.7 km^2 (LM06_Hitchcock). A clear trend for males maintaining larger home ranges than females is not apparent. The comparison of the average dry season and wet season home ranges reveals the following pattern. While for all four leopards the average dry season home range is larger than during the wet season, this is only true for the lioness LF09_Fiona. All remaining nine lions inhabit significantly larger home ranges during the wet season.

The average annual core areas follow the same pattern. For the seasonal core areas there are some distinct changes compared to the 95% seasonal home ranges. Only two leopards (PF07_Ronja and PM08_Bogarika) maintain a larger average dry season core area while the average core area size for PF12_Salome is larger during the wet season. For the remaining leopard PM07_Mothamongwe a classification is impossible as the difference between the wet- and dry season is only 3.6 km^2. For all lions, with the exception of three females (PF09_Fiona, PF17_Lara and PF18_Notch), the core areas cover a larger area during the wet season than during the dry season. Table 9 and Table 10 revealed that there is a big difference between the size of the core area and the home range. This circumstance is not surprising as the predators live in a semi-arid environment with few natural resources. Table 11 gives information about the core area to home range ratio (percentage of the home range covered by the core area) for all time intervals analysed.

Table 11: Average percentage [%] of the 95% home range covered by the core area (50% home range) for each time interval. The values for avg_year, avg_wet and avg_dry were calculated for each individual by taking the average of all values available per time interval. The avg_overall has been calculated by taking the average of the previous four averages per individual.

ID	avg_all	avg_year	avg_wet	avg_dry	avg_overall
PF07_Ronja	14.51	20.26	20.61	26.76	20.53
PF12_Salome	5.77	14.67	19.09	16.81	14.09
PM07_Mothamongwe	26.44	28.89	29.81	25.62	27.69
PM08_Bogarigka	20.44	25.30	23.11	25.58	23.61
LF09_Fiona	16.59	21.06	22.96	21.78	20.60
LF12_Verity	20.92	26.48	26.85	33.07	26.83
LF13_Ella	18.08	18.02	21.09	24.49	20.42
LF14_Madge	16.47	21.91	18.34	20.49	19.30
LF16_Jane	26.08	26.07	25.31	22.82	25.07
LF17_Lara	18.44	21.77	19.48	25.26	21.24
LF18_Notch	24.63	24.88	23.43	27.65	25.15
LM06_Hitchcock	25.56	23.87	21.73	24.28	23.86
LM07_Mexico	15.29	17.19	19.73	21.09	18.32
LM08_Orange	24.53	23.71	27.15	20.58	23.99

Looking at the average overall values one can see that in most cases the core area covered between roughly 20 – 25% of the home range with a lower limit of 14.09% (PF12_Salome) and an upper limit of 27.69% (PM07_Mothamongwe). The other extreme values are 5.77% (PF12_Salome) for the interval using all data available and 33.97% (LF12_Verity) for the dry season. There is a slight trend towards a higher percentage of the home range covered by the core area during the dry season. In 9 out of 14 cases (2 leopards, 7 lions). the dry season core areas covered a larger percentage of the 95% than during the wet season. Yet, big differences were not identifiable as they only range between 1.18% and 6.57%. Comparing the values of the overall average there is neither an apparent difference between lions and leopards nor between males and females within the same species.

10.2. Compactness Index

With potential values ranging from 0.01 to 1, the CI is an indicator for the shape of a polygon. The higher the CI the more compact the polygon and the closer it is to a circle. Comparing the core areas of lions and leopards one can determine that leopards have slightly more compact core areas. Lions on the other hand have somewhat more compact home ranges with a CI of 0.51. At the individual level, the leopard PF12_Salome achieved the highest overall CI for the core area (0.72) and the smallest overall for the home range (0.33). PM07_Mothamongwe has both, the least compact core area (0.36, together with PM08_Bogarigka) and the most compact home range (0.61). The lioness LF17_Lara with a CI value of 0.17 has the least compact core area while the most compact home range is maintained by LF18_Notch (0.57) and LF12_Verity, LF13_Ella and LM07_Mexico (each 0.56) with an almost identical CI.

Table 12: The compactness index for the core area and the home range are displayed for each individual and per species. Average CI were calculated by taking the average of every single CI for each core area or home range per time interval.

ID	core area					home range				
	avg_all	avg_year	avg_wet	avg_dry	avg_overall	avg_all	avg_year	avg_wet	avg_dry	avg_overall
PF07_Ronja	0.45	0.42	0.40	0.35	0.41	0.31	0.44	0.50	0.53	0.44
PF12_Salome	0.83	0.66	0.70	0.70	0.72	0.15	0.41	0.41	0.37	0.33
PM07_Mothamongwe	0.38	0.41	0.33	0.30	0.36	0.55	0.60	0.66	0.64	0.61
PM08_Bogarika	0.51	0.29	0.39	0.27	0.36	0.37	0.40	0.47	0.36	0.40
all_leopards	0.54	0.45	0.45	0.41	0.46	0.34	0.46	0.51	0.48	0.45
LF09_Fiona	0.22	0.34	0.33	0.29	0.29	0.40	0.35	0.38	0.40	0.38
LF12_Verity	0.65	0.48	0.41	0.31	0.46	0.53	0.55	0.64	0.52	0.56
LF13_Ella	0.60	0.46	0.41	0.39	0.46	0.72	0.49	0.51	0.53	0.56
LF14_Madge	0.13	0.30	0.51	0.23	0.29	0.56	0.52	0.44	0.55	0.52
LF16_Jane	0.29	0.25	0.25	0.21	0.25	0.51	0.54	0.55	0.47	0.52
LF17_Lara	0.12	0.20	0.17	0.20	0.17	0.41	0.45	0.32	0.43	0.40
LF18_Notch	0.41	0.52	0.43	0.34	0.43	0.51	0.58	0.63	0.57	0.57
LM06_Hitchcock	0.38	0.28	0.16	0.40	0.30	0.56	0.57	0.44	0.50	0.52
LM07_Mexico	0.69	0.49	0.51	0.48	0.54	0.62	0.60	0.47	0.56	0.56
LM08_Orange	0.44	0.39	0.34	0.34	0.38	0.50	0.59	0.58	0.51	0.55
all_lions	0.39	0.37	0.35	0.32	0.36	0.53	0.52	0.50	0.50	0.51

Between the dry- and the wet season there is no significant difference regarding the CI values, neither for the core area nor the home range. The same pattern can be observed for the average annual leopard CI, while there is a difference of 0.15 for the lion CI. A 2-tailed Spearman's test with a p-value of 0.05 was conducted to determine whether there is a correlation between the size of the core area or home range and the CI. In 50% of the cases (PF07_Ronja, PM08_Bogarikga, LF09_Fiona, LF12_Verity, LF13_Ella, LF14_Madge, LM07_Mexico) there was no significant correlation between area and CI. While PM07_Mothamongwe, LF16_Jane, LF17_Lara, LM07_Hitchcock and LM08_Orange showed a moderate to strong positive correlation, PF12_Salome showed a strong negative correlation between CI and size. Yet, due to the lack of samples it is not possible to make a conclusive statement about this correlation.

10.3. Centroids

The straight line distances between all centroid pairs were calculated for every individual. 9 out of 14 lions and leopards show at least one centroid shift of more than 10 kilometres between two consecutive time intervals (either seasons or years). The leopards PF12_Salome and PM07_Mothamongwe and the lions LF18_Notch, LM07_Mexico and LM08_Orange lack a distinct centroid shift. A visual analysis of the home range plots revealed that in most cases a distinct centroid between two consecutive time intervals is indeed an indicator for an actual change in location and size as well. A good example is the lioness LF09_Fiona (Figure 6) with a centroid shift between the Y2012 – Y2013 (27.59 km towards southeast) and the Y2013 – Y2014 (15.08 km towards southwest).

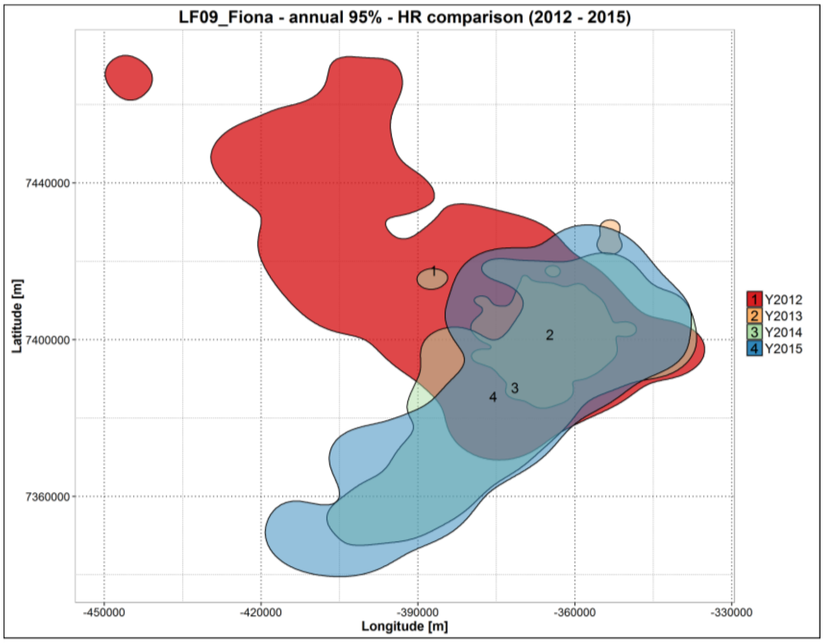


Figure 6: Size and location change of the 95% home range of the lioness LF09_Fiona. The numbers indicate the centroid position of the respective 95% home range polygon.

During this period, the area of the 95% home range shrunk from 4312.9 km^2 in 2012 to 692.6 km^2 in 2013 before expanding again to 2381.3 km^2 in the year 2014. For the majority of the cases the same pattern could be observed for the core areas but changes are pronounced to a lesser extent. The analysis covered a total of 106 time intervals across all lions and leopards resulting in 78 centroid shifts. 27 out of the 78 shifts or 34.6% covered a distance of more than 10 kilometres. Shifts of more than 25 kilometres were identified for PF07_Ronja and the lionesses LF09_Fiona, LF12_Verity and LF14_Madge.

10.4. Overlap measurements

A detailed analysis of the overlapping home ranges and core areas (including VI) is presented in the following section where the core area and home range transformation of individuals over time and between individuals for the same time intervals are investigated.

10.5. Home range peaks

The 20% isopleth was used to determine the number of peaks within an animal's home range. The vast majority of home ranges (72.5%) contain a maximum of 2 peaks, while the other 27.5% show 3 or more peaks. LF12_Verity (D2012 = 4 peaks) and LF16_Jane (D2015 = 5 peaks, Y2015 = 4 peaks) are the lions with the most peaks within their annual or seasonal home range.

Table 13: Overview of all home range peaks (20% home range) of home ranges calculated using KDE. The following abbreviations have been used: Mothamongwe = Motha, Bogarigka = Boga, Hitchcock = Hitch. Ronja – Bogarikga are leopards, all others are lions. Male animals are represented using bold letters. all_time includes all fixes available for an individual, Year 2013 (June 2012 – May 2013) = Y2013, wet season 2013 (November 2012 – April 2013) = W2013, dry season 2013 (June 2013 – September 2013) = D2013.

Interval	Ronja	Salome	Motha	Boga	Fiona	Verity	Ella	Madge	Jane	Lara	Notch	Hitch	Mexico	Orange
all_time	2	1	**3**	**1**	1	2	1	1	4	2	3	**1**	**1**	**4**
Y2009	1													
Y2010	1													
Y2011	1													
Y2012	1		**3**		1	2								
Y2013	1		**2**	**2**	1	3	1	2				**3**		
Y2014	1	1			3		2	2	3	1	3	**1**	**1**	**3**
Y2015	1	1			2				4	2	1		**2**	**2**
W2009	1													
W2010	1													
W2011	2													
W2012	2		**2**	**2**	2	4	3	1						
W2013	1		**3**	**1**	3	3	2	1	1			**3**	**1**	**2**
W2014	1	1			1		1	3	3	1	1		**1**	**3**
W2015	1	1			3				2	2	3		**2**	**3**
D2009	3													
D2010	2													
D2011	3				2									
D2012	2		**1**	**3**	1	4	2	2				**3**		
D2013	3		**2**		1		2	2	1	2		**3**	**1**	**2**
D2014	3	1			2			1	1	1	2		**2**	**2**
D2015	2	2							5		1		**2**	**1**

One must be careful with the interpretation as the high numbers of peaks are likely to be introduced by the KDE calculation method and the selection of the smoothing parameter *h*. As Figure 7 below shows, there are several regions within the home range which are used more intensely than others. The example in Figure 7a contains a high number of potential peaks. Yet, due to the small size, some peaks could be an artefact of the calculation method. The larger circles in Figure 7b are more likely to represent actual peaks rather than artefacts. Therefore, it is possible to use this approach in a first brief analysis as an indicator for multiple peaks within an animal's home range. Home ranges with a maximum of only two or fewer peaks were identified for the following individuals: PF12_Salome, LF14_Lara and LM08_Orange.

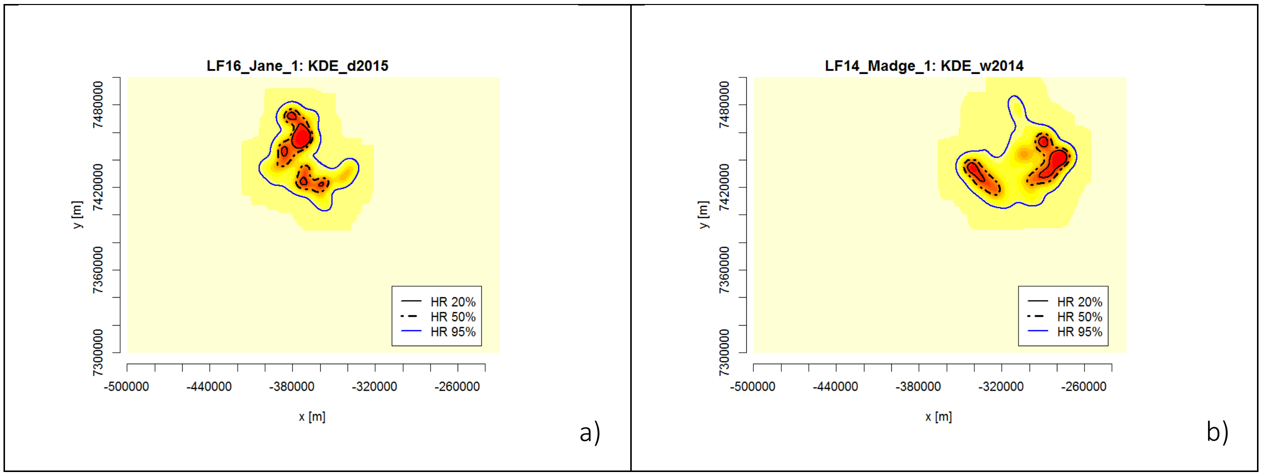


Figure 7: 2015 dry season HR of LF16_Jane (5 peaks) and the 2014 wet season home range of LF14_Madge (3 peaks).

10.6. Holes and polygons

LF18_Notch during the 2015 wet season is the only example of a home range featuring of two holes. While all leopards and the lions LF09_Fiona, LF17_Lara and LM06_Hitchcock have no holes, the home ranges and core areas of the remaining seven lions contain a maximum of 1 hole. 22 core areas and 10 home ranges consist of at least 3 polygons. The combined 32 polygons are equal to 15.09% of all polygons.

Table 14: Overview of 95%- and 50% home ranges consisting of 3 or more polygons. The following abbreviations have been used: Home range = HR, Core area = CA, Mothamongwe = Motha, Bogarigka = Boga, Hitchcock = Hitch. Ronja – Bogarikga are leopards, all others are lions. Male animals are represented with bold letters. all_time includes all fixes available for an individual, Year 2013 (June 2012 – May 2013) = Y2013, wet season 2013 (November 2012 – April 2013) = W2013, dry season 2013 (June 2013 – September 2013) = D2013. Time intervals containing no entry (3+ polygons) were omitted.

Interval	Ronja	Salome	Motha	Boga	Fiona	Verity	Ella	Madge	Jane	Lara	Notch	Hitch	Mexico	Orange
all_time	5 (HR)	8 (HR)	**3 (HR)**	-	-	-	-	-	5 (CA)	-	3 (HR)	-	-	**3 (CA)**
Y2012	-	-	-	-	-	3 (CA)	-	-	-	-	-	-	-	-
Y2013	-	-	-	-	-	-	-	3 (HR)	-	-	-	-	-	-
Y2014	-	3 (HR)	-	-	-	-	-	-	4 (CA)	3 (CA)	-	**7 (CA)**	-	-
Y2015	-	-	-	-	-	-	-	-	6 (CA)	-	-	-	-	-
W2013	-	-	-	-	3 (CA)	-	-	-	3 (CA)	-	-	-	-	**3 (CA)**
W2014	-	-	-	-	-	-	-	-	-	-	-	-	-	**5 (CA)**
W2015	-	-	-	-	-	-	-	-	3 (CA)	-	-	-	-	**3 (CA)**
D2012	-	-	-	-	-	-	-	3 (CA)	-	-	-	-	-	-
D2013	-	-	-	-	3 (CA)	-	3 (CA)	3 (HR)	-	4 (CA)	-	**4 (HR)**	-	-
D2014	-	-	-	-	3 (CA)	-	-	-	3 (CA)	3 (CA)	3 (CA)	-	**3 (HR)**	-
D2015	-	-	-	-	-	-	-	-	-	-	3 (HR)	-	**3 (CA)**	-

In five cases polygons, either 95%- or 50% home ranges, consisting of 5 or more polygons are present (PF07_Ronja, PF12_Salome, LF16_Jane, LM06_Hitchcock and LM08_Orange). The all data home range of PF12_Salome (Figure 8a) and the Y2014 core area of LM06_Hitchcock (Figure 8b) are the most fragmented polygons of all 212. Similar to the number of peaks, some of these small polygons are likely to be artefacts introduced by the KDE calculation method and therefore one must be careful not to overrate these numbers.

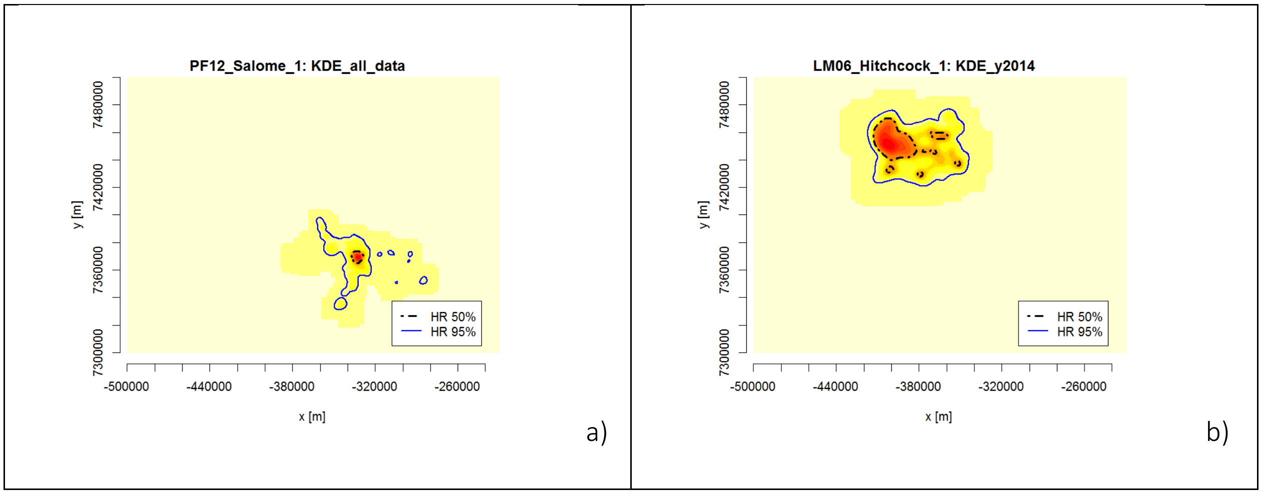


Figure 8: Example of potential artefacts introduced by the calculation method KDE.

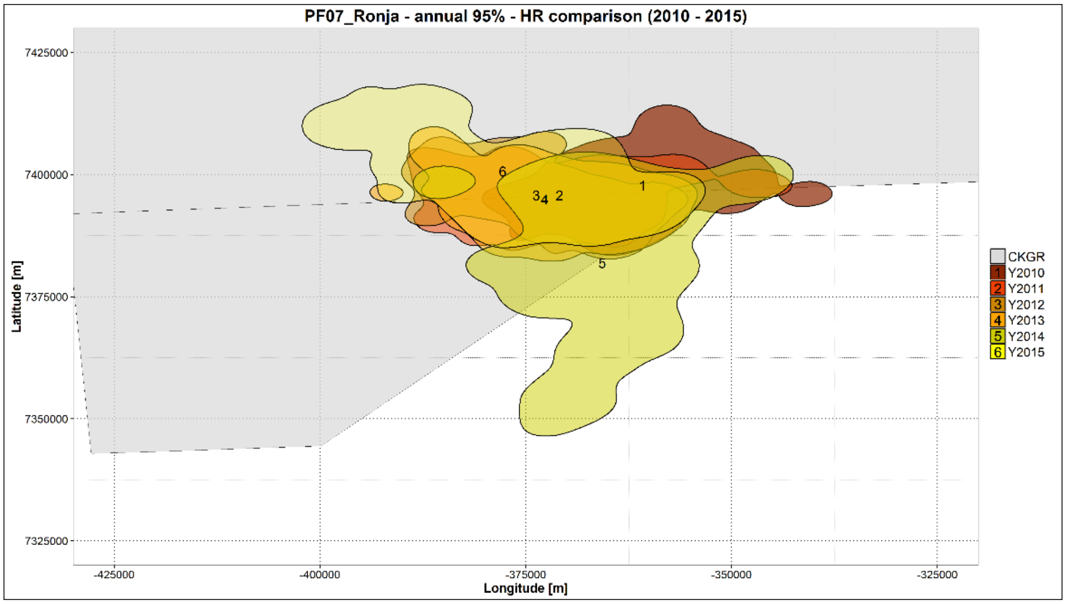
10.7. Home range outside CKGR and KGR

Table 15 shows which collared animals have parts of their home range and/or core area outside the protected areas CKGR and KGR. The lions LF16_Jane and LM06_Hitchcock are the only two animals having their entire annual and seasonal home ranges and core areas inside the protected areas. Other leopards (PM07_Mothamongwe and PM08_Bogarigka) and lions (LF12_Verity, LF13_Ella, LF18_Notch, LM07_Mexico and LM08_Orange) spent some time outside the game reserves but remained fairly close to its borders.

Table 15: This table shows all 4 leopards and 10 lions and whether parts of their annual/ seasonal home range (ann_95/ sea_95) and/ or annual/ seasonal core area (ann_50/ sea_50) are outside the CKGR and KGR. The columns parts_os_PA (parts outside protected area) indicates to what extent (very low, low, moderate, high, entire) a home range and/ or core area is located outside. The periods during which the respective core area lies outside are indicated in the column time_interval.

ID	**ann_95**	**part_os_PA**	**ann_50**	**part_os_PA**	**time_interval**	**sea_95**	**part_os_PA**	**sea_50**	part_os_PA	**time_interval**
PF07_Ronja	yes	moderate	yes	low	Y2014	yes	moderate	yes	low	D2009, W2014
PF12_Salome	yes	high	yes	entire	Y2014, Y2015	yes	high	yes	entire	W2014 - D2015
PM07_Mothamongwe	yes	very low	no	-	-	yes	very low	yes	very low	D2013
PM08_Bogarigka	no	-	no	-	-	yes	very low	no	-	-
LF09_Fiona	yes	moderate	yes	low	Y2012 - Y2015	yes	moderate	yes	low	D2011 - W2015 without D2012
LF12_Verity	yes	low	yes	very low	Y2012	yes	low	no	-	-
LF13_Ella	no	-	no	-	-	yes	very low	no	-	-
LF14_Madge	yes	moderate	yes	moderate	Y2014	yes	moderate	yes	moderate	W2014 - D2014
LF16_Jane	no	-	no	-	-	no	-	no	-	-
LF17_Lara	yes	moderate	yes	high	Y2015	yes	moderate	yes	high	D2013, W2015
LF18_Notch	yes	very low	no	-	-	yes	very low	no	-	-
LM06_Hitchcock	no	-	no	-	-	no	-	no	-	-
LM07_Mexico	yes	low	yes	very low	Y2015	yes	moderate	yes	very low	W2015
LM08_Orange	yes	very low	no	-	-	yes	very low	no	-	-

PF07_Ronja, LF09_Fiona, LF14_Madge, LF17_Lara and LM07_Mexico are among the predators maintaining a moderate part of their home range and core area outside the protected areas (Figure 9).



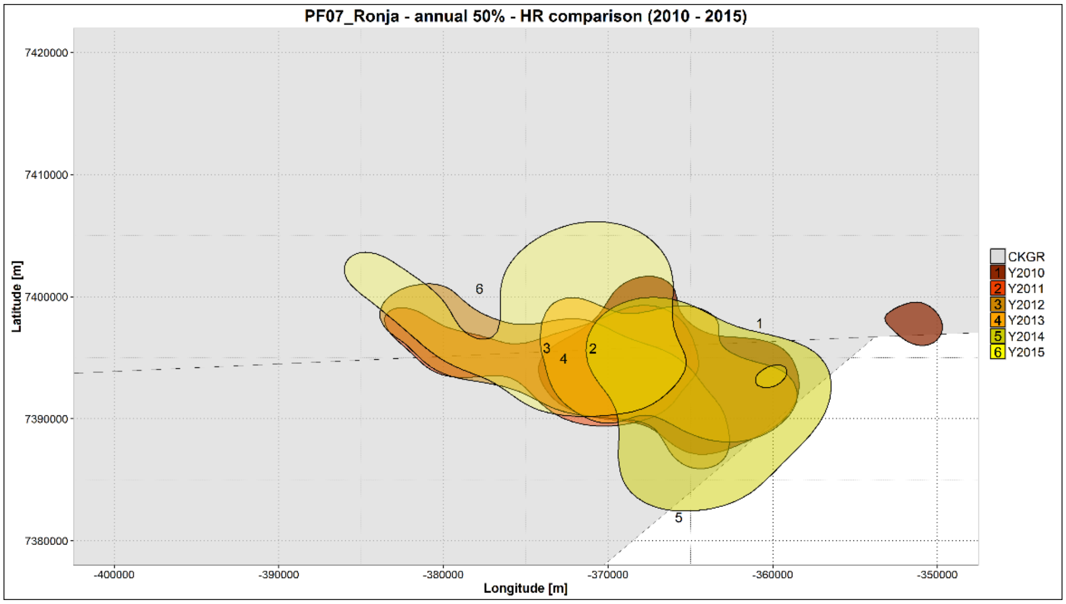


Figure 9: Comparison of 95% home range (top) and 50% home range (bottom) for PF07_Ronja. Note that compared to the 95% home range of Y2014, only a small part of the Y2014 50% home range is actually located outside of the protected area.

The examples of PF07_Ronja and LM07_Mexico are particularly interesting as the fraction located outside is significantly different between the 95% home range and the core area (Figure 9 and Figure 10). PF07_Ronja's 2014 annual home range reaches far out into the southern farmlands, while the respective core area hardly transgresses the reserve border.

A similar development can be observed by comparing the seasonal home ranges and core areas of LM07_Mexico (Figure 10). While parts of the 95% home ranges of the W2013, W2015 and D2015 are located outside, only a fraction of the W2015 core area is located outside as well. In other words, PF07_Ronja and LM07_Mexico spent much more time inside the protected area than one could assume by just looking at their 95% home range. Nevertheless, these plots clearly indicate their potential of being a problem animal as their wanderings take them outside the CKGR and the KGR. The remaining female leopard PF12_Salome is the only animal maintaining her entire core area outside the reserve borders. Consequently, the better part of her 95% home ranges is outside the borders as well and there is a high risk for her to be classified as problem animal.

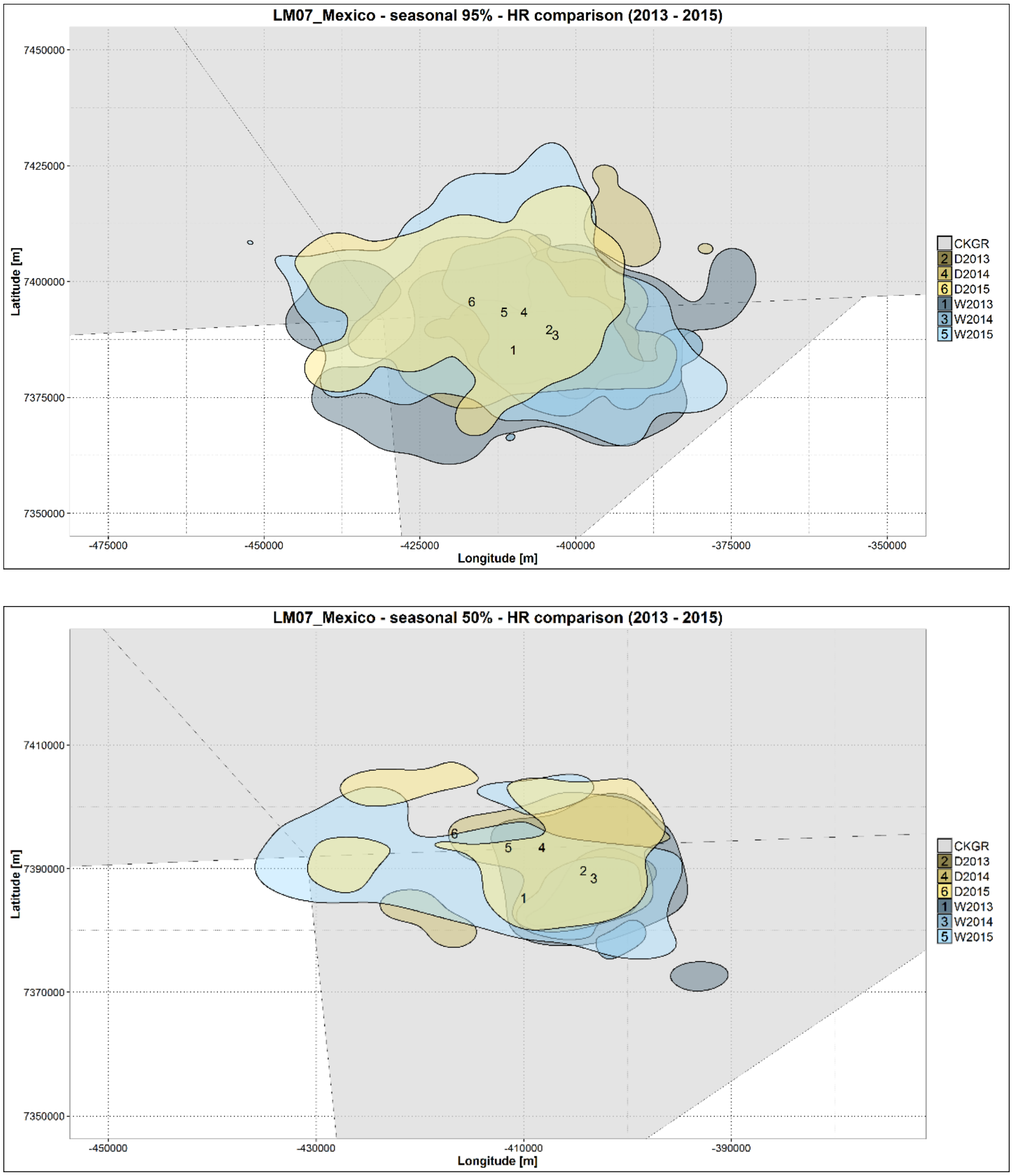


Figure 10: Comparison of 95% home range (top) and 50% home range (bottom) for PM07_Mexico. Note that compared to the 95% home range of W2013, W2015 & D2015, only a small part of the W2015 50% home range is actually located outside of the protected area.

11. Individual home ranges over time

11.1. Leopards

In this section, the development in size and location of the leopard home ranges and core areas is presented. This consists of an extensive analysis for every individual leopard underlined with plots showing the most important features. Datasets covered a timespan between the Y2010 – Y2015 and W2009 – D2015, respectively. Figure 25 and Figure 26 in the section 12.1. give an overall impression of the development in size (km^2) of leopard 95% annual- and seasonal home ranges. Additional plots for every individual can be found in the appendix 1.

The female leopard PF07_Ronja has been tracked for more than 6 years and therefore it is possible to make the most meaningful statements about the temporal variation of home ranges and core areas (Figure 25 and Figure 26). PF07_Ronja is known to occasionally leave the CKGR and KGR but maintains most of her 50% home ranges within the reserve borders. Every year, with the exception of 2013, she gave birth to cubs in November or December during the early stage of the wet season. On an annual level she maintained a fairly stable home range during the period between 2010 and 2013, followed by massive increase in 2014 from 622 km^2 to 1176 km^2 (Figure 11). Core areas followed the same pattern, though the increase in 2014 is not as distinctive. Simultaneously, there is a pronounced centroid shift of 14.8 km in south-easterly direction transgressing the reserve borders into the adjoining farmlands. Already in the following year 2015, PF07_Ronja moved back towards the northeast to her initial area. A shift of 22.3 km has been measured and the home range slightly decreased to 901 km^2.

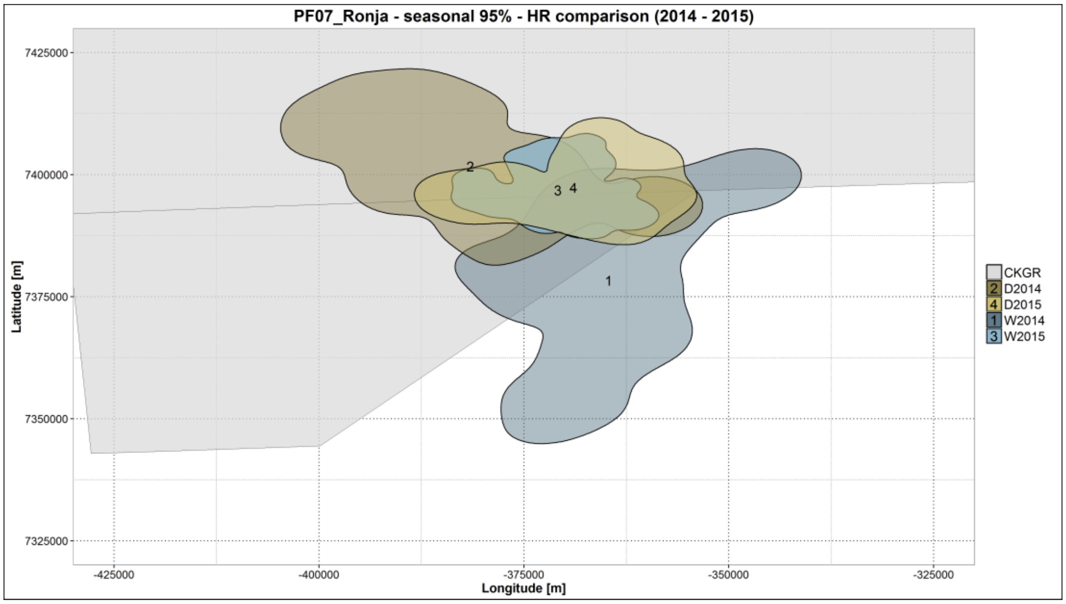


Figure 11: Development of the 95% home range of PF07_Ronja between the 2014 wet – and the 2015 dry season.

Yet, on a seasonal level the home ranges and core areas are less stable (Figure 11, Figure 26) and show a distinct pattern between 2009 and 2012. Throughout this period, the dry season home ranges are significantly larger than the respective wet season home ranges. While wet season home ranges cover only an area of 201 km^2 to 483 km^2 the ones of the dry season are as large as 472 km^2 to 1019 km^2. The location of her home range is fairly stable, as the 95%- and 50% home range overlap measurements as well as the VI indicate. Due to the distinct difference in size, dry season home ranges and core areas overlap the respective wet season areas by 86.3% to 100%. Starting with the 2013 dry season, PF07_Ronja's home range is characterised by distinct shifts in size and location (Figure 11). The migration to the South is accompanied by an increase in home range size from 271 km^2 to 1247 km^2 followed by another shift by 28.9 km back to the Northwest. Before returning to her main area, a shift in south-easterly direction and a decrease in size by about 65% can be observed. Again, the core areas show a comparable pattern.

PF12_Salome has been translocated from the Motsetsanamontle Ranch in Eastern Botswana to the KGR on February 24th 2014[4] because of livestock predation. She gave birth to cubs in November 2014. The initial annual home range and core area with 2410 km^2 and 232 km^2 are extraordinarily large for a female leopard. While the seasonal home range still increased towards the 2014 dry season, the core area already started its decline. The following wet season 2015 is characterised by a massive decline of both, the home range and core area, reaching a minimum of 58.1 km^2 and 11.3 km^2. These are by far the smallest values calculated for any leopard. An increase of about 50% can be observed through the next dry season.

Figure 12 shows PF12_Salome leaving the protected area right after being translocated into KGR. Another indicator is the absence of a distinct centroid shift between two seasons although there is a significant distance between the point of release and the actual centroid of her first home range. Only small fractions of the 2014 wet- and dry season reached into the game reserve. Due to the tiny size, the 2015 wet season areas only overlap by a fraction (2.40% home range, 5.18% core area) of the 2014 dry season. At an annual scale the massive decrease in size between 2014 and 2015 is evident.

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[4] Personal Communication with Stephen Henley, July 2016

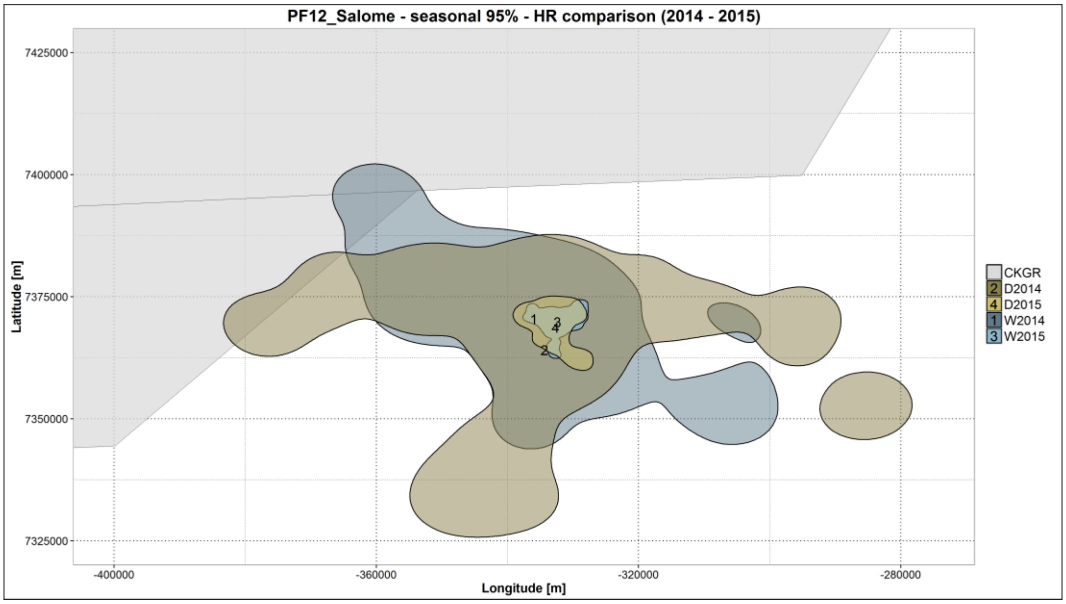


Figure 12: Size and location of all seasonal 95% home ranges of PF12_Salome. The CKGR the KGR (southern tip of CKGR) are displayed in grey.

PM07_Mothamongwe is a resident male leopard inside KGR and CKGR which shows occasional sallies into the neighbouring farmlands. With the exception of the decrease (748 km^2 to 499 km^2) throughout the transition period from the 2012 dry season towards the subsequent 2013 wet season his home ranges and core areas are fairly stable regarding their size (Figure 13). This is confirmed by steady overlap measurements of about 90% for the 2012 and 2013 dry season and 62% for the 2013 wet season home ranges. For the core area values of 45% and 41% (D2012 and D2013) and 52% (W2013) were measured. The VI values are higher than 60% for all periods. A distinct centroid shift is not present. At an annual scale the same characteristics can be observed.

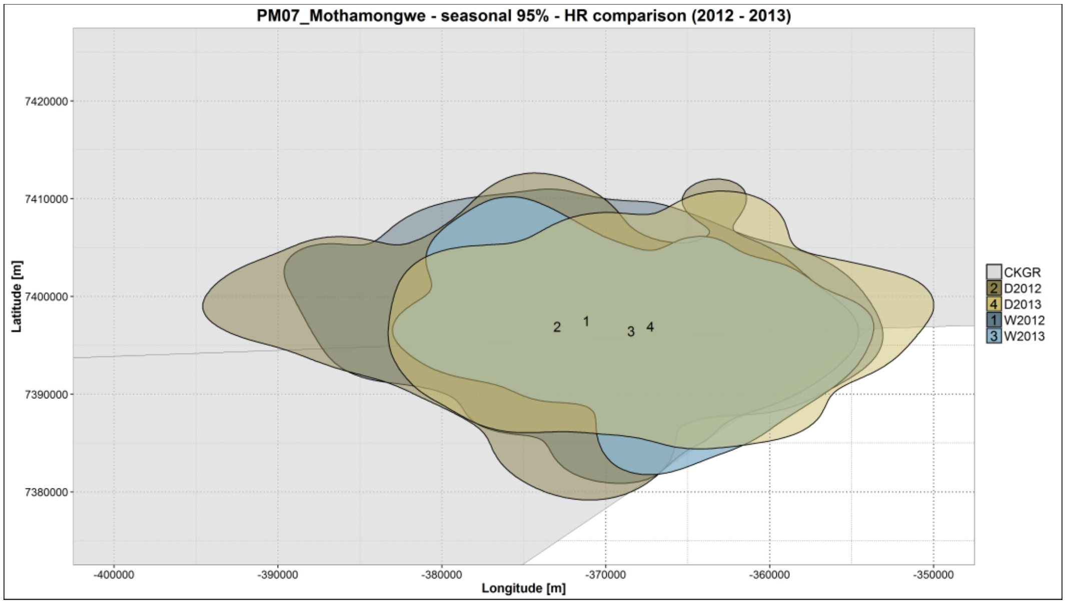


Figure 13: Development of the seasonal 95% home ranges of PM07_Mothamongwe.

Similar to PM07_Mothamongwe, PM08_Bogarigka is a male leopard resident within the borders of CKGR and KGR. Only a tiny fraction of the wet season home ranges is located outside the reserve. An analysis at an annual level is not possible due to lack of data.

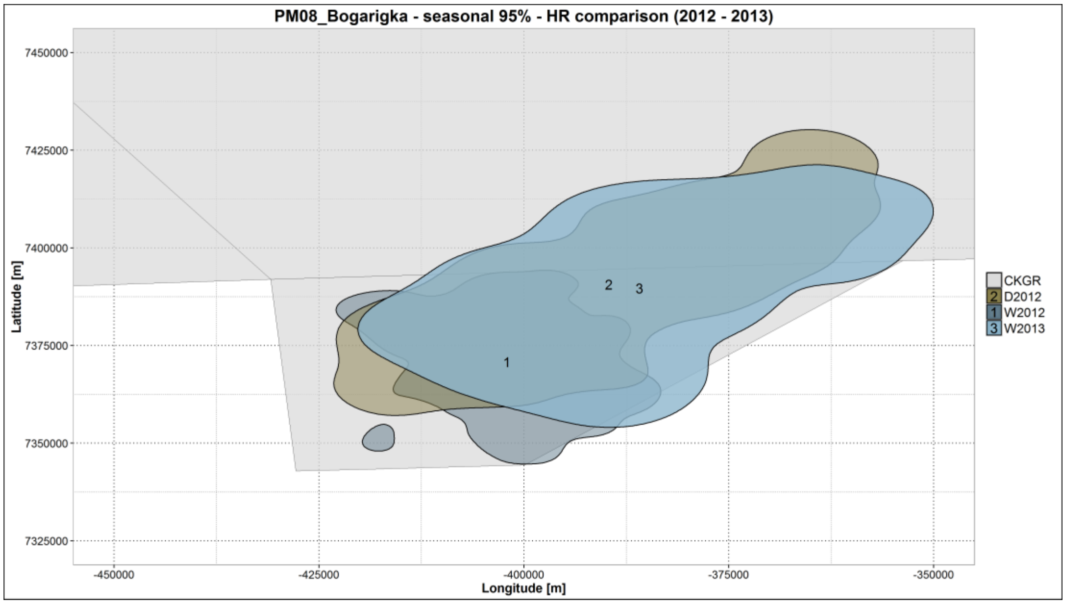


Figure 14: Seasonal development of the 95%- and 50% home ranges of PM08_Bogarigka.

Between the 2012 wet season and the 2013 wet season a sharp increase of both the 95%- and the 50% home range is apparent. Starting at 1188 km^2 (home range) and 246 km^2 (core area) sizes reach a maximum of 2705 km^2 and 690 km^2 and are by far the largest observed for all leopards. A significant centroid shift of 23.4 km towards the northeast happens simultaneously to the increase in size. Afterwards, the centroid location remains stable. Due to the vast expansion in terms of size, there is still a quite large overlap of the 2012 dry season home range (72.63%) and core area (44.81%) over the 2012 wet season areas. Yet, the VI of 43% is markedly lower.

11.2. Lions

In this section, the development in size and location of the lion home ranges and core areas is presented. This consists of an extensive analysis for every individual lion underlined with plots showing the most important features. Datasets covered a timespan between the year 2012 – 2015 and the wet season 2011 – dry season 2015, respectively. Figure 30and Figure 31 (section 12.2.) give an overall impression of the development in size (km^2) of lion 95% annual- and seasonal home ranges. Additional plots for every individual can be found in the appendix 0.

The datasets of seven female and three male lions covered a period of about 4.5 years starting with the 2011 dry season. After leaving a small group of lions LF09_Fiona was living as a nomad female and gave birth to cubs in June 2012. She spent quite some time along the south-eastern border of KGR and occasionally left the protected area.

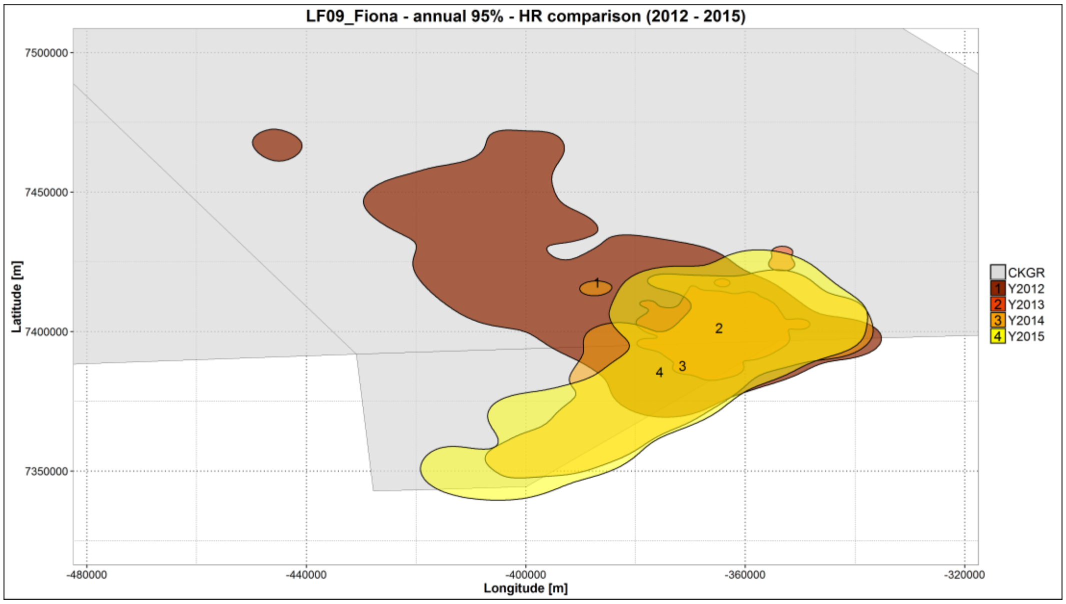


Figure 15: Annual 95% home ranges of LF09_Fiona from Y2012 to Y2015.

Her initial home range in 2012 was extremely large with 4313 km^2 and a core area of 684 km^2. The following year is characterised by a massive decrease in size to 692 km^2 and 126 km^2, paired with a distinct centroid shift of 27.6 km in south-easterly direction. Consequently, the overlap of the 2013 95%- and 50% home range is rather small with 15.3% and 18.4%. VI declined as well, reaching average values of 20% to 30%. Throughout the years 2014 and 2015 with a shift towards southwest, her home range and core area were expanding continuously, reaching a maximum of 3180.8 km^2 and 854.3 km^2. On a seasonal level, (Figure 31), the differences in size are even more striking. The 2011 dry season home range and core area are exceptionally large covering an area of 5991 km^2 and 1346 km^2. A minimum is reached during the 2013 wet season with only 406.4 km^2 and 95.3 km^2 before expanding again until the 2015 dry season and the second decrease is size. Similar to the annual analysis there are several distinct shifts toward southeast and later changing direction towards southwest. Due to the decrease in size and change in location, overlaps are rather small between the dry seasons 2012 and 2013 (35% to 38%). Core areas follow these patterns, with the exception of the wet season 2014 overlapping the dry season core area only by 7.9% despite a significant expansion.

LF12_Verity is a member of the East Khutse pride, gave birth to cubs in late 2010 and rarely left the reserves. Between the 2012 and 2013 wet season there are two significant shifts in north-easterly direction (Figure 16). The new centre is now at the CKGR – KGR border. Simultaneously, the 95%- as well as the 50% home range are steadily decreasing by roughly 75% from 3192.2 km^2 and 944.7 km^2 to 1006.1 km^2 and 242.5 km^2.

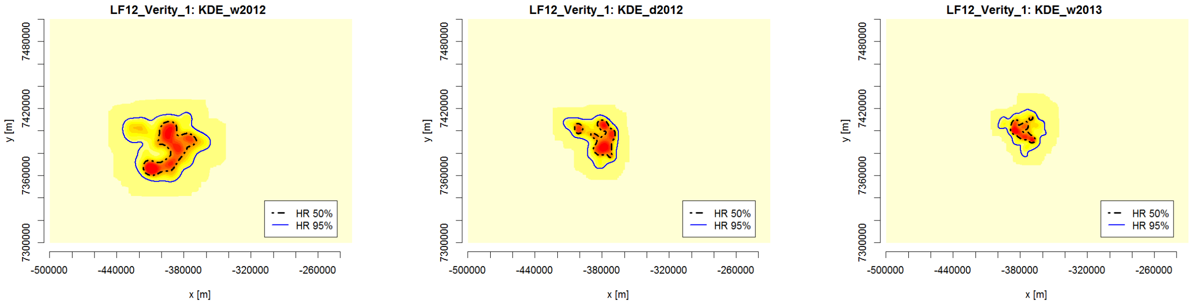


Figure 16: Seasonal home range development of LF12_Verity between W2012 and W2013.

PF13_Ella has been a member of the East Khutse pride bevor she left in September/ October 2012 and gave birth to cubs in late 2013. Her movements are almost entirely within the protected areas (Figure 17).

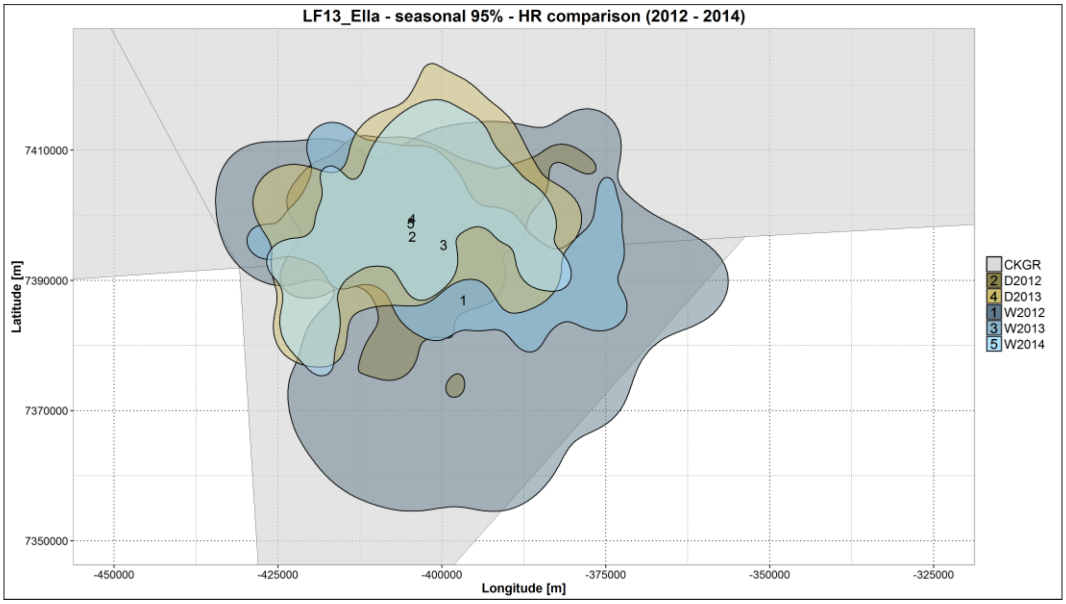


Figure 17: Development of the 95% seasonal home range of LF13_Ella.

A shift of 12.5 km to the northwest could represent her departure. The enormous decline of her home range was induced during the same period. Over the course of the 2012 dry season the home range and core area shrunk by 71.5% and 78.5%, respectively, reaching a lower limit of 939 km^2 and 206 km^2. Throughout the next 18 months, only minor changes are detectable, which is also underlined by stable overlap measurements. At the core area scale, the differences in size are somewhat more pronounced.

LF14_Madge is a female regularly leaving the eastern part of the reserves entering the adjoining farmlands (Figure 18). As a member of a small group of lionesses she gave birth to cubs in mid-2012. After a decrease in the 2012 dry season and the movement (22.8 km) to the west, the expansion of her home range started immediately afterwards. The lower limit of her 95%- and 50% home range in 2012 was 285 km^2 and 63 km^2 and the upper limit in 2014 (3634 km^2, 911 km^2). While the location of her home range was stable through the year 2013, she started to move east (25.5 km) in 2014. Stable measure for the overlap were achieved. VI values of over 50% confirm the trend. Especially during the 2014 wet- and dry season, LF14_Madge frequently crossed the eastern reserve borders.

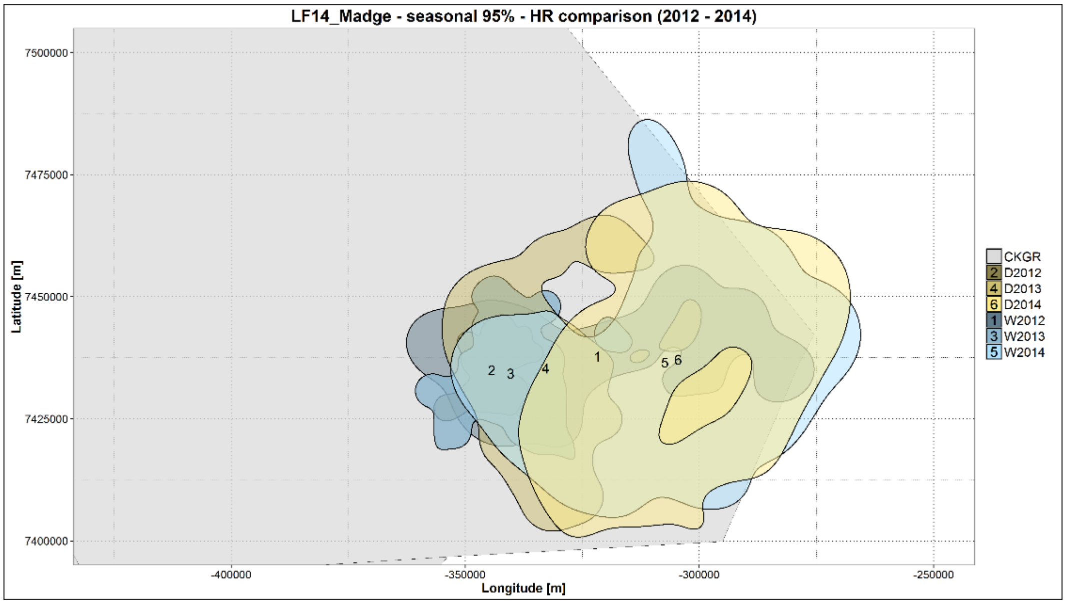


Figure 18: Transition of the seasonal 95% home range of LF14_Madge between W2012 and D2014.

PF16_Jane is a member of a small group of female lions without a pride male. During the whole period of tracking she always maintained a home range entirely inside the game reserves and she gave birth to cubs in mid- 2011 and August 2013. Until the 2014 wet season the size of her home range and core area were fairly stable at around 2000 km^2 to 2350 km^2 and 410 km^2 to 600 km^2, respectively. A short period of decline of roughly 800 km^2 through the 2014 wet season was then followed by a period of steady expansion, accompanied by a shift 16.7 km to the west.

The spatio-temporal development of the seasonal 95%- and 50% home ranges of LF16_Jane is shown above (Figure 19). Unlike other animals, LF16_Jane core areas consist of multiple centres of activity. Between the

2014 dry season and the 2015 wet season one can clearly see a shift of the activity centre towards the west. Through the whole period of monitoring, her 95% home ranges show quite high values for the spatial overlap (58% to 80%). Similar to other individuals, the core areas show the same developments. Yet, the VI does only reach values between 31% to 54%. At an annual scale the size of the 95%- and 50% home ranges increased by 21% and 42%.

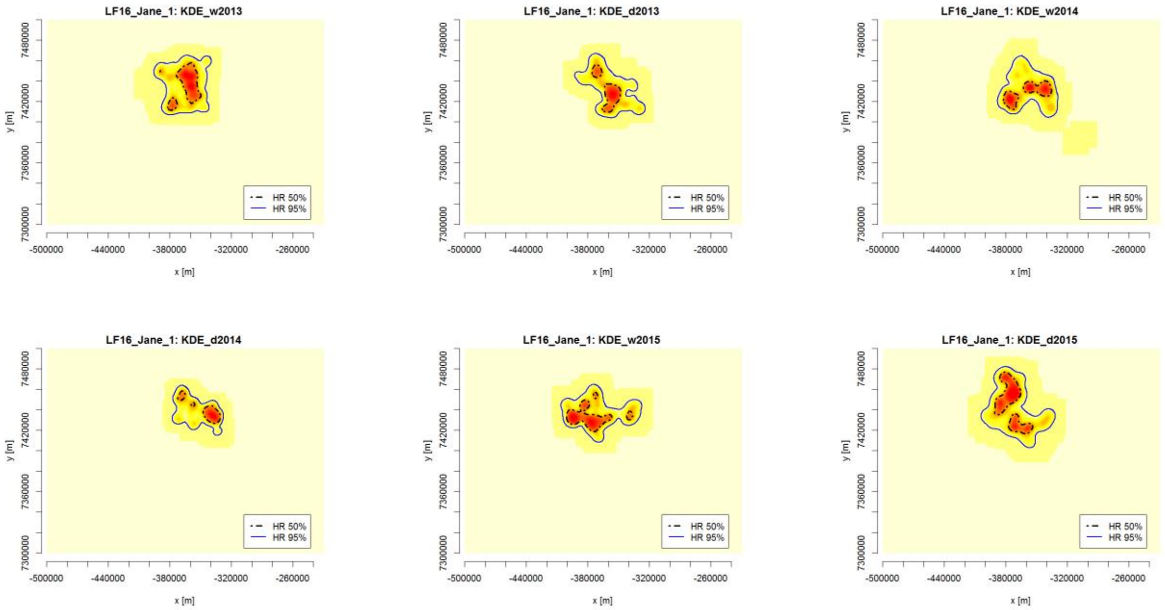
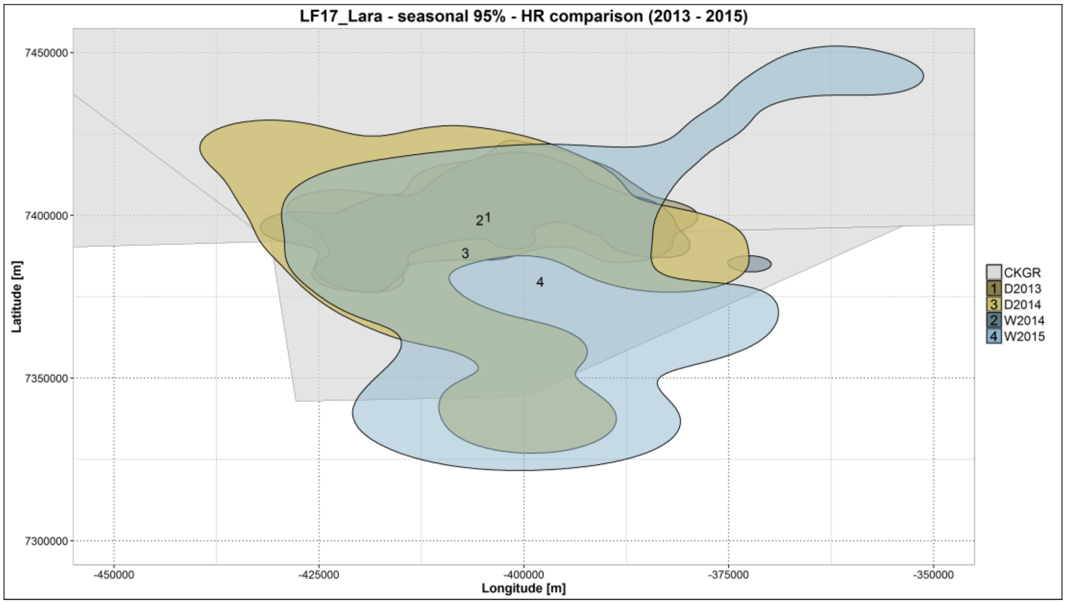


Figure 19: Spatio-temporal variation of the 95% and 50% seasonal home ranges of LF16_Jane between the 2013 wet season and the 2015 dry season.

PF17_Lara is another female known to be associated with LF13_Ella. She gave birth to cubs in February 2013. After LF13_Ella's death in August 2014, LF17_Lara started to move south, later in south-eastern direction and crossed the reserve border into the adjoining farmlands (Figure 20).



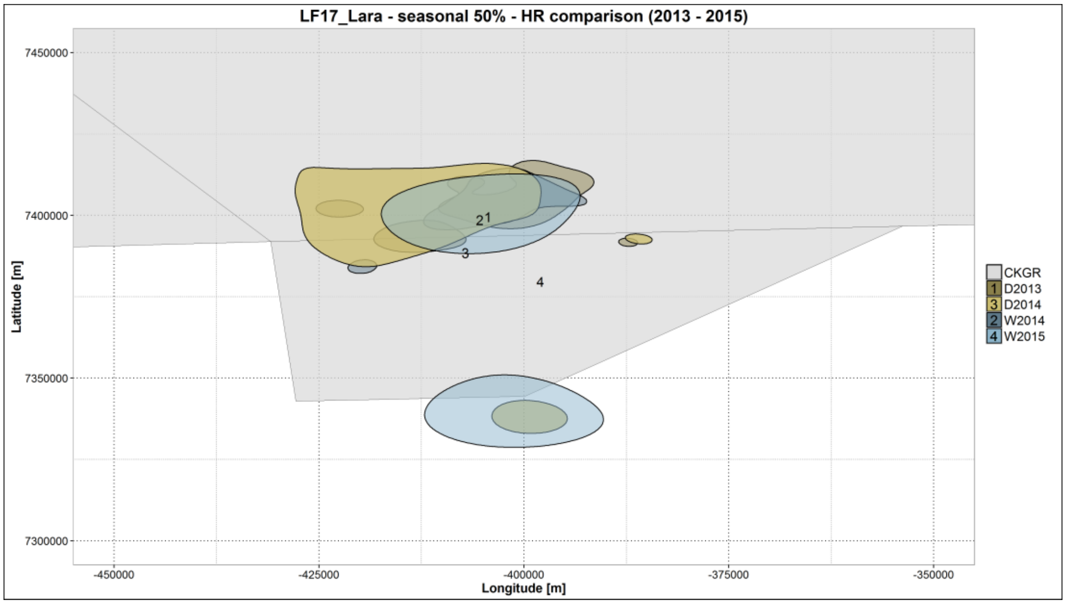


Figure 20: The seasonal 95% home ranges (top), the seasonal 50% home ranges (bottom) of LF17_Lara. For the 2014 dry season and the 2015 wet season one can clearly see the activity centres outside the borders of KGR.

As a consequence of killing livestock she has been relocated twice in October and November 2014 before dying one year later. Her migration into the Southern farmlands and the relocation is responsible for a massive expansion of her territory. The home range increased from 1050 km^2 to 4558 km^2 and the 218 km^2 to 827 km^2.Her migration south where she has been raiding livestock is clearly visible in Figure **20**. During the time when LF17_Lara was together with LF13_Ella, her home range and core area were rather small but constant. At an annual scale, the same increase in size is detectable and therefore the 2015 annual home range and core area cover the respective areas of 2014 by 97.4% and 78.3%.

LF18_Notch is another member East Khutse group, and rarely leaves the game reserves (Figure 21).

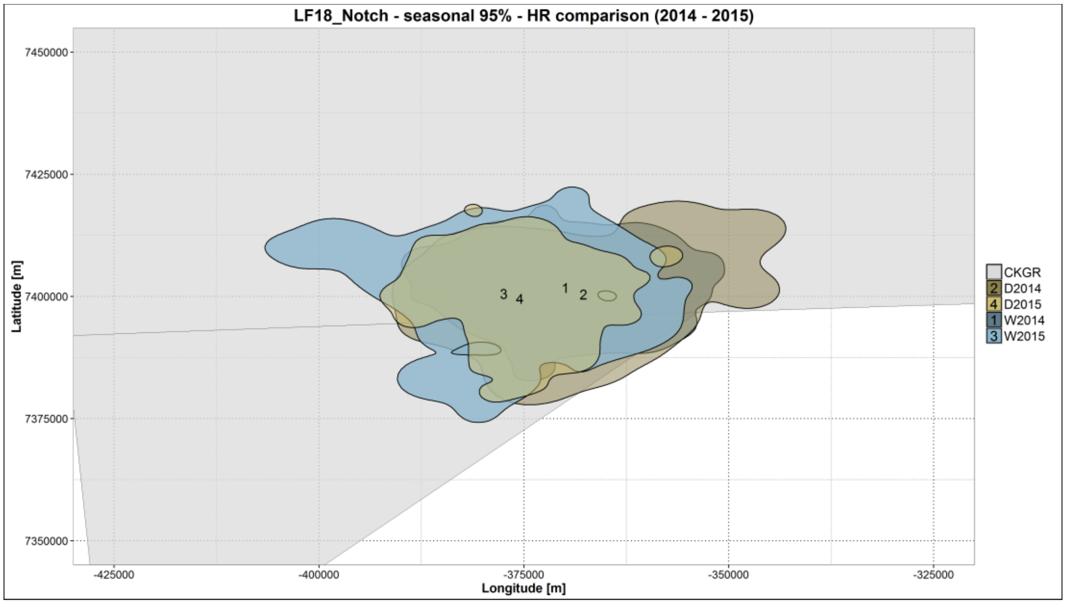


Figure 21: Season 95% home ranges of LF18_Notch between W2014 and D2015.

There are no records of her having cubs. Her core area and home range, respectively, are characterised by their relatively small size (177 km^2 to 402 km^2 and 755 km^2 to 1277 km^2). Thus, there is an expansion of the 95% home range after the 2014 wet season by 42%. Throughout the next year, the size remained very stable at about 1260 km^2 before declining again by 41%. At the same time, the core area shows more variation in size, expanding by 86% to 402 km^2 and later declining again by 65%. Due to the expansion without shift in the dry season 2014, the overlap with the 2014 wet season is very high for both the 95%- and 50% home range (94.5% and 70.6%). A VI of 65% underlines the lack of spatial variation.

LM06_Hitchcock is a nomad male lion in association with another male. Despite being a nomad his entire home range is within the reserve borders (Figure 22).

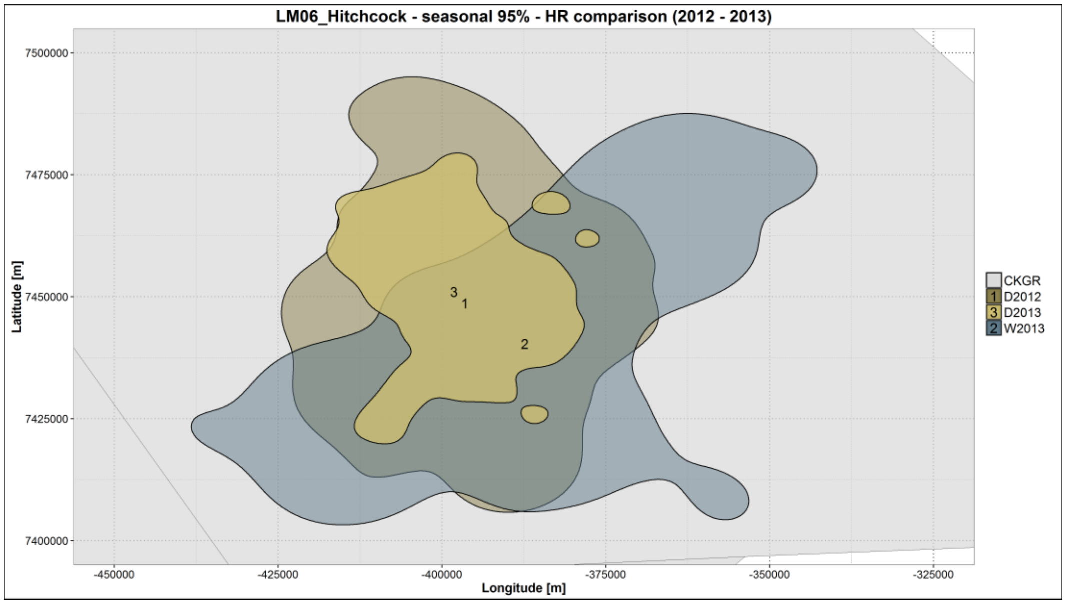


Figure 22: Annual 95% home range of LM06_Hitchcock between 2013 and 2014.

Unlike other lions, LM06_Hitchcock established his home range entirely in the North of KGR. Compared to other lions, his home ranges and core areas are extremely large, reaching a maximum of 4040 km^2 and 1009 km^2, respectively, in the 2013 wet season. Prior this maximum, a shift by 12.4 km towards the southeast was detected. The transition into the following 2013 dry season is characterised by a migration back (northeast) into the area of the 2012 wet season, accompanied by significant decline in size by 3085 km^2 to only 1355 km^2. Simultaneously, the core area shrunk by 780 km^2 to 250 km^2.

LM07_Mexico is the pride male of the Moloso group. At an annual scale an expansion in home range size from 867 km^2 to 2438 km^2 and from 101 km^2 to 552 km^2 for the core area are eminent. LM07_Mexico has a moderate part of his seasonal home ranges outside the protected areas, but only very small fractions of the respective core areas are located on the outside as well (Figure 23).

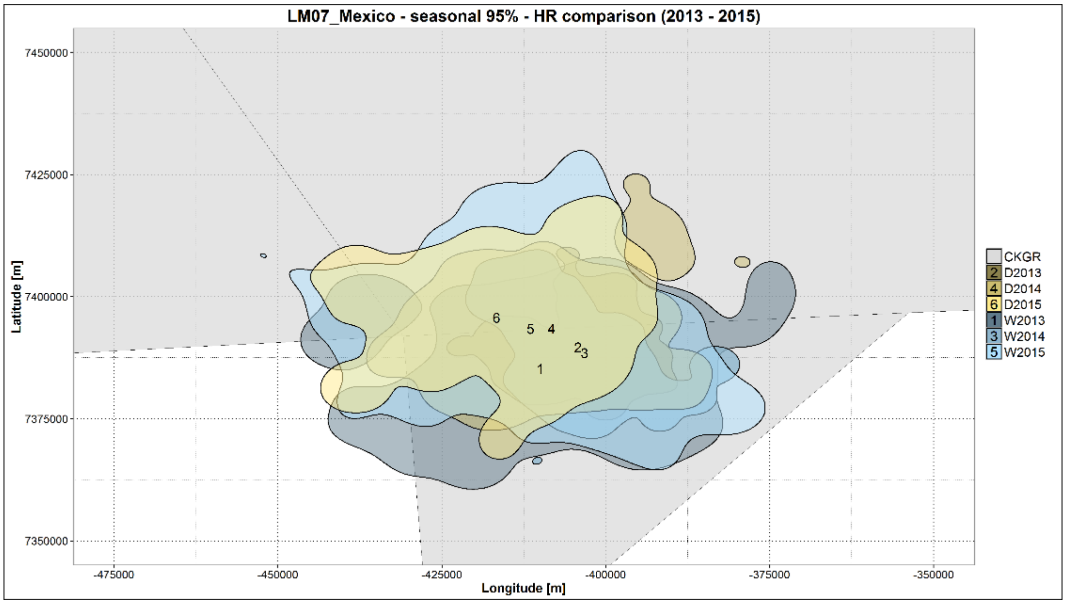


Figure 23: The seasonal 95% home ranges of LM07_Mexico. The small spatial variation in location of the home range centroids is an indicator for a stable home range and missing extensive wanderings.

Despite the expansion, there is no significant shift in location. At a seasonal scale much more variation in size and location is detectable. However, a pronounced shift is missing. The large initial area during the 2013 wet season is not maintained over the course of the following year, but decreased from 2289 km^2 to only 627 km^2. Already the following wet season 2014 showed a slight expansion in size, followed by a steady increase until the 2015 wet season. An upper limit of 693 km^2 for the core area and 2589 km^2 for the home range is reached. The 2015 dry season showed a decline to 1713 km^2 and 446 km^2. Throughout the period between the 2013 dry season and the 2015 wet season are characterised by large overlaps for both the core area and the 95% home range.

LM08_Orange is one of two pride males of the large East Khutse group. Despite the relatively large size of the pride, quite small 95%- and 50% home ranges were estimated, with lower limits (671 km^2 and 112 km^2) and upper limits (1402 km^2 and 394 km^2). LM08_Orange occasionally left the CKGR and KGR but no part of his core area is actually located on the outside (Figure 24). During this period between 2013 and 2015, one can see small ups and downs without major changes. After reaching the maximum during the 2015 wet season there is another decline in size, very similar to the one after the 2013 wet season. Again, the developments of the core area are more pronounced than the ones of the 95% home range.

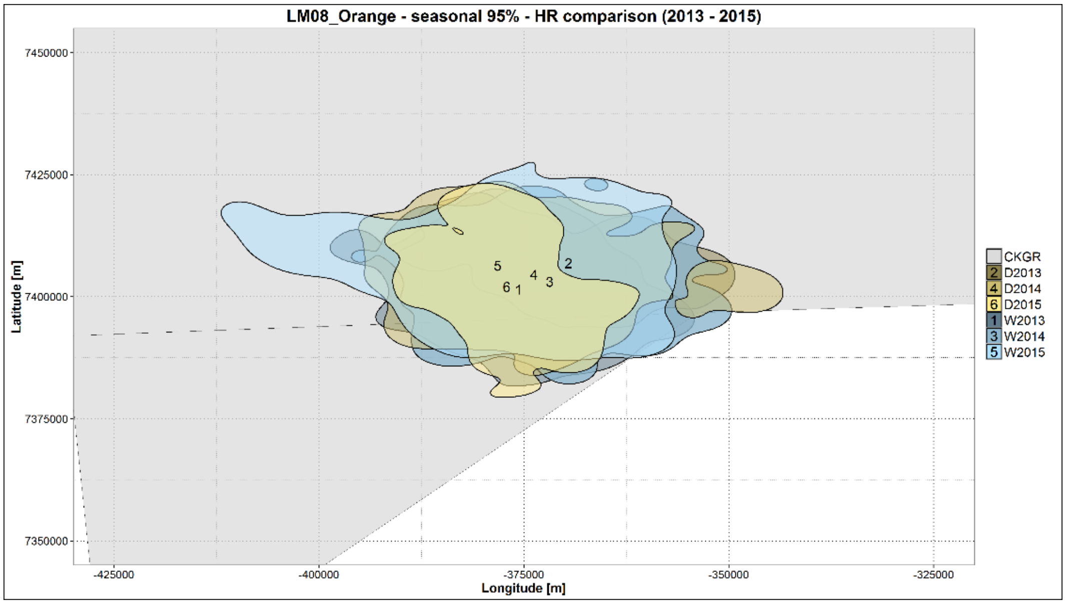


Figure 24: The seasonal 95% home ranges of LM08_Orange. The small spatial variation in location of the home range centroids is an indicator for a stable home range and missing extensive wanderings.

All centroids are located within close distance and therefore no distinct shifts of more than 10 km are evident. While the overlap measures of the 95% home range are fairly stable at 81% to 94% between the 2014 and 2015 wet season, there is a significant variation at the core area level (75% to 38% and up to 80%). Therefore, a pronounced shift in location of the core area is evident, as a significant decline in size is absent. Another striking feature of his core areas are the multiple centres of activity.

12. Comparison between individuals

12.1. Leopards

Figure 25 and Figure 26 below give an overall impression of the development in size (km^2) of the 95% annual- and seasonal leopard home ranges. The respective plots showing the development of the 50% home ranges can be found in the appendix 1.

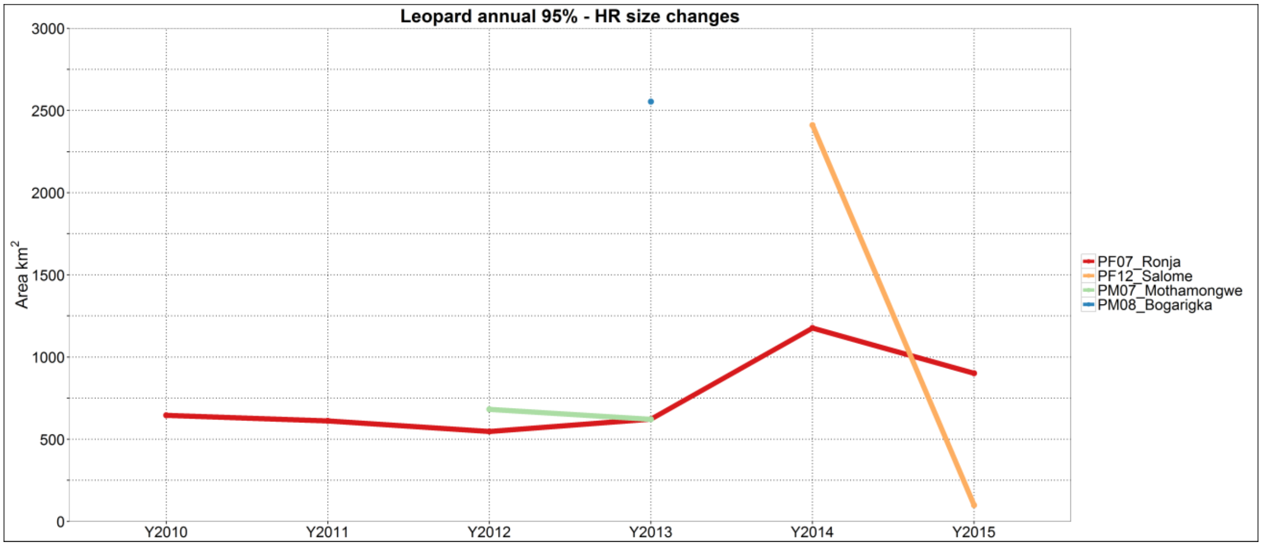


Figure 25: Development in size [km^2] of the 95% annual leopard home ranges from 2010 to 2015. Note that for the male leopard PM08_Bogarigka only one measurement (Y2013) is available and therefore displayed as point.

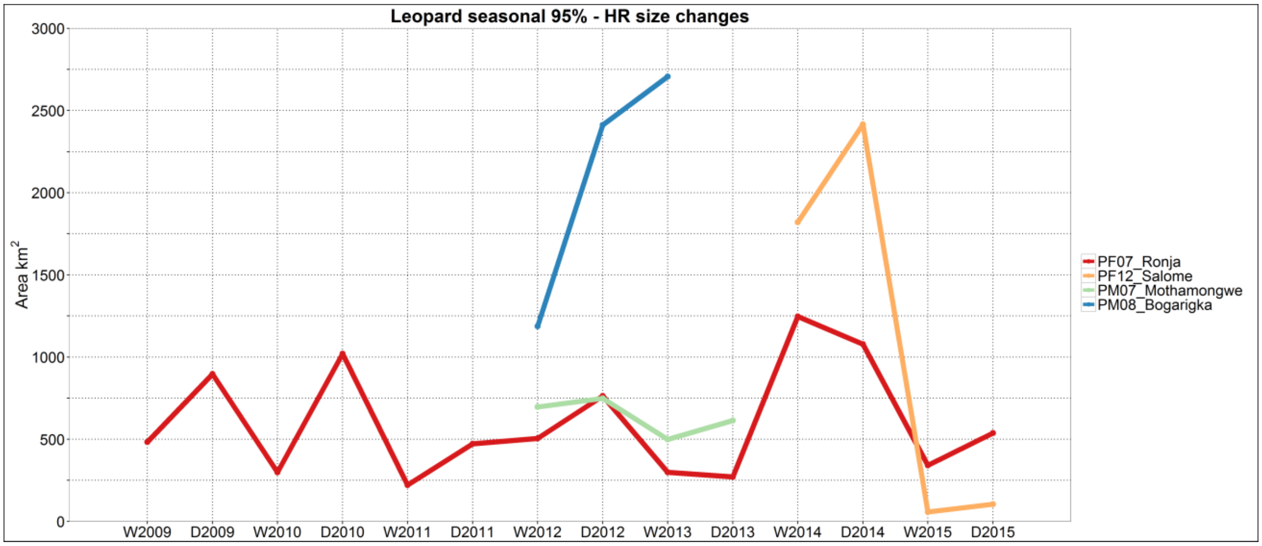
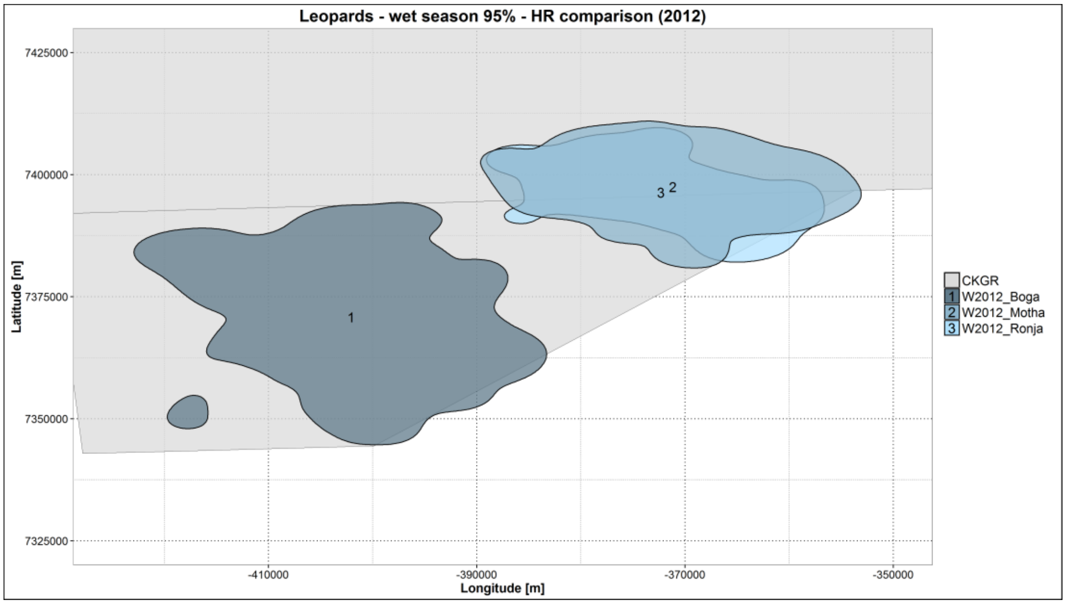


Figure 26: Development in size [km^2] of the 95% seasonal leopard home ranges from W2009 to D2015.

An extended analysis and trend detection is difficult due to the small number of tracked leopards. Figure 25 and Figure 26 revealed that for PF07_Ronja as well as PM07_Mothamongwe the dry season home ranges were usually larger than the respective wet season home ranges of the same year. For PF07_Ronja this is true in 5 out of 7 cases and for PM07_Mothamongwe both cases.

Over the entire sampling period of PM07_Mothamongwe, his 95%- and 50% home ranges show a significant overlap with the ones of PF07_Ronja (Figure 27).



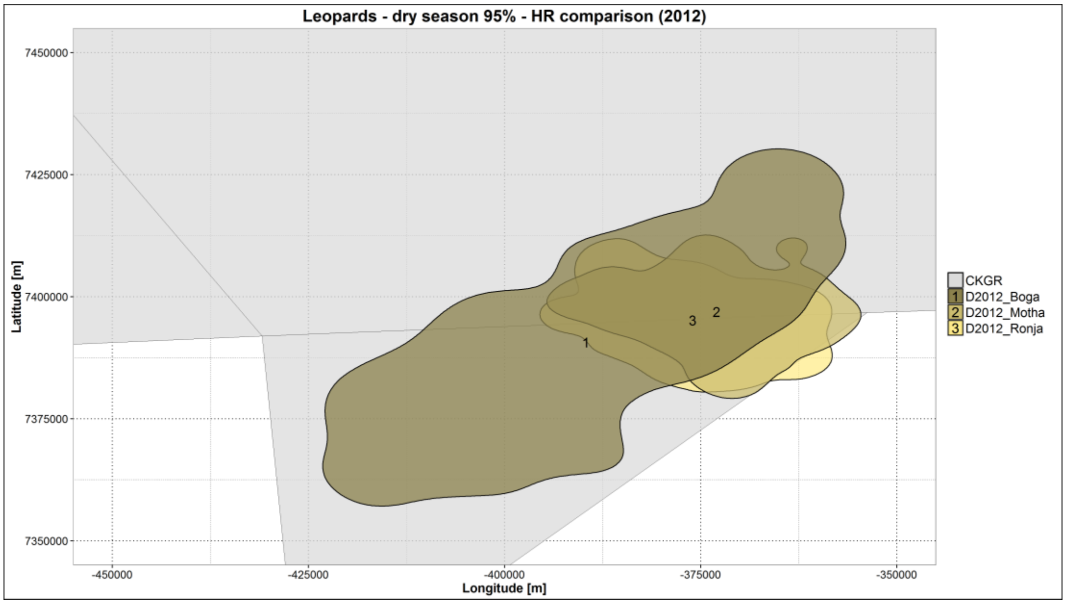


Figure 27: Comparison of the 2012 95%- wet season (top) and dry season (bottom) home ranges of PF07_Ronja, PM07_Mothamongwe and PM08_Bogarika. The expansion of PM08_Bogarigka to the northeast is evident and there is a striking overlap between PM07_Mothamongwe and PF07_Ronja.

At an annual scale, overlaps of 85% and 79% for the home range and 54% and 64% for the core area were calculated. Seasonal home range overlaps were even higher, reaching values over 97% (W2013, D2013). Core area overlaps are stable for the dry season at about 50%; for the wet season there is a significant increase from 37% to 76% between 2012 and 2013. The VI values between 39% and 66% underline the detected overlaps. With the exception of the 2012 dry season PM07_Mothamongwe's home ranges were considerably larger than the ones of PF07_Ronja. The expansion towards the northeast of PM08_Bogarigka is shown in Figure 27. His home range overlaps PM07_Mothamongwe by 76% (D2012, CA = 38%) and 83% (W2013, CA = 20%) and PF07_Ronja by 79% (D2012, CA =33%) and 82% (W2013, CA = 1%).

During the years 2014 and 2015 the only possible comparison is PF07_Ronja and PF12_Salome. How PF07_Ronja and PF12_Salome use their space differently is illustrated in Figure 28.

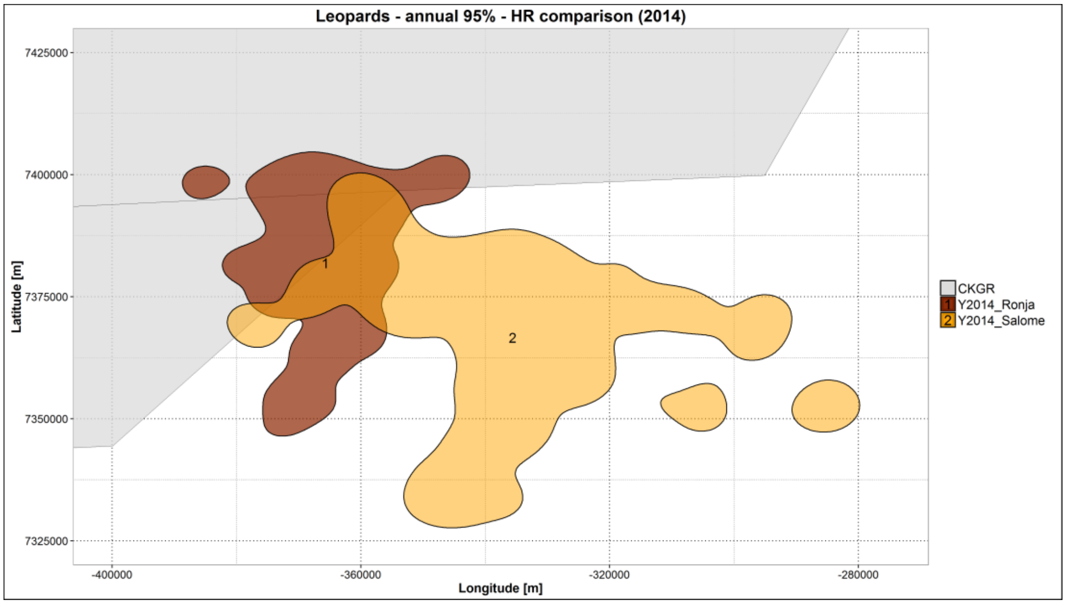


Figure 28: Annual 95% home ranges of PF07_Ronja and PF12_Salome in 2014. The only home range overlap is during the 2014 wet season where PF07_Ronja overlapped PF12_Salome by 18%. Additionally, the VI was less than 10%. Consequently, this overlap is noticeable for the annual comparison of 2014. There is no overlap of their core areas for the entire period.

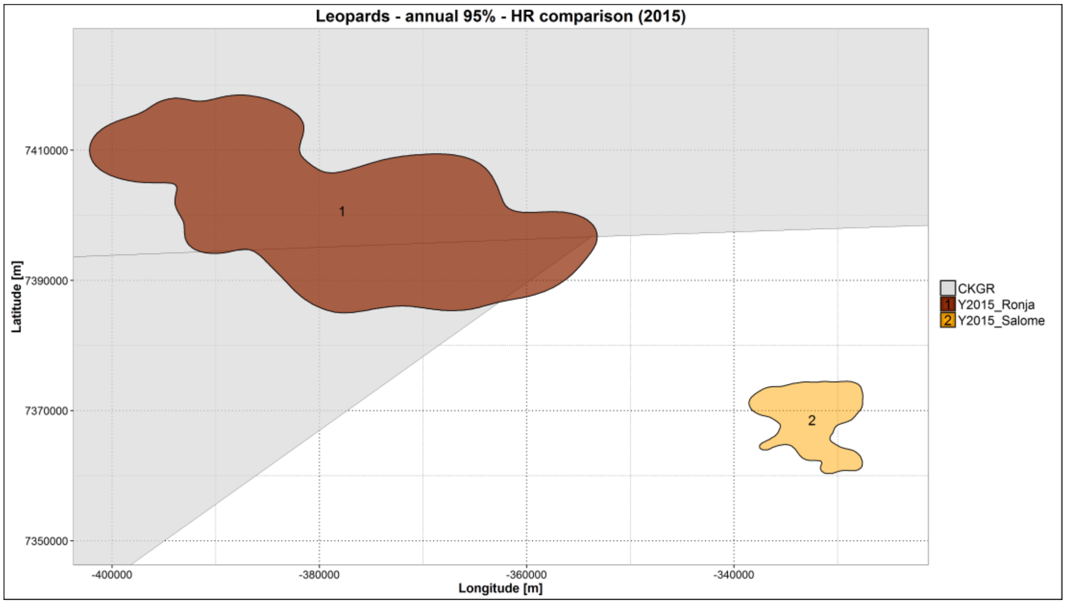


Figure 29: Annual 95% home ranges of PF07_Ronja and PF12_Salome in 2015.

12.2. Lions

In a first part of this section the focus is on the different time intervals regarding overlap, size development and shifts and at towards the end some general findings are presented. Figure 25 and Figure 26 below give an overall impression of the development in size [km^2] of the 95% annual- and seasonal leopard home ranges. The respective plots showing the development of the 50% home ranges can be found in the appendix.

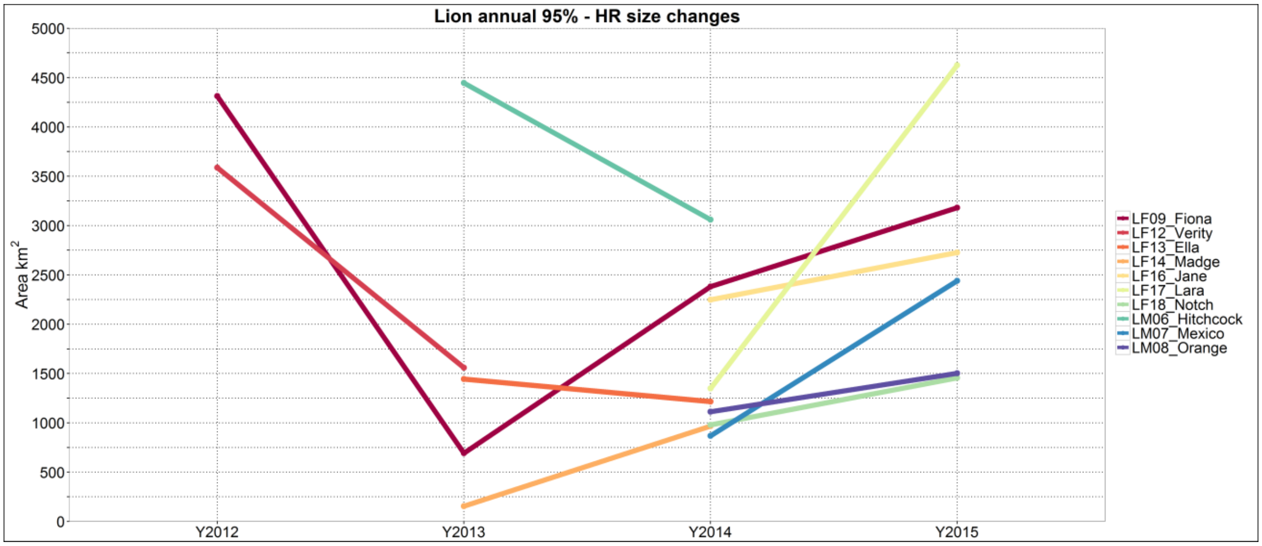


Figure 30: Development in size [km^2] of the 95% annual lion home ranges from 2012 to 2015.

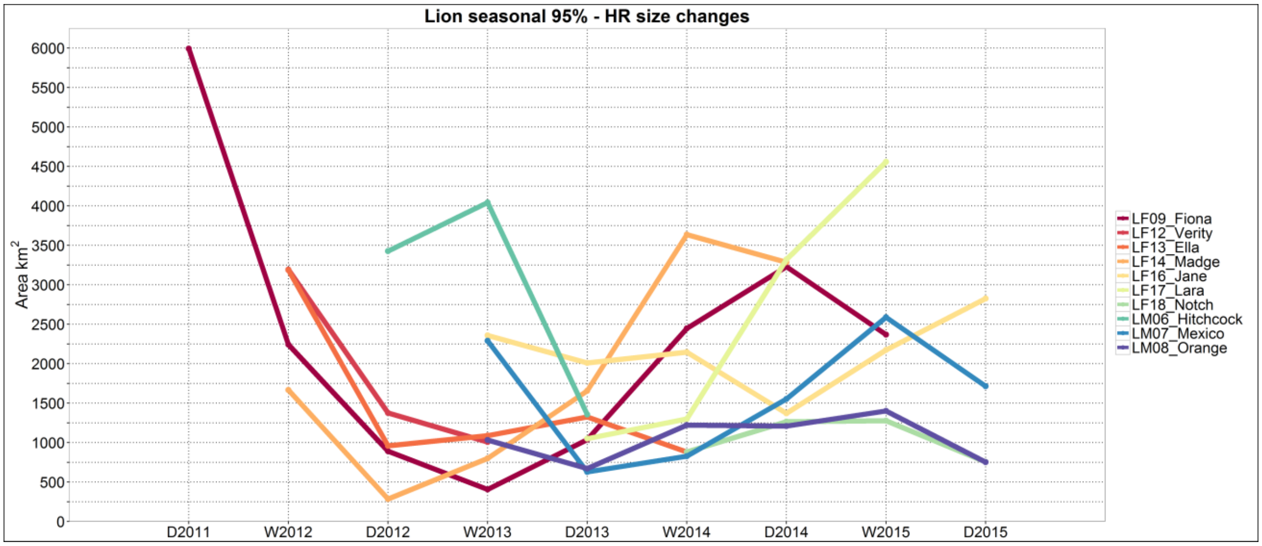


Figure 31: Development in size [km^2] of the 95% seasonal lion home ranges from D2011 to D2015.

The first possible analysis is during the year 2012, with data available of LF09_Fiona, LF12_Vertiy, LF13_Ella and LF14_Madge. The 95% seasonal home ranges of the 2012 wet season are presented in Figure 32 below. There is a striking overlap of 99.4% of LF12_Verity's and LF13_Ella's 95% home range. For the respective core area an overlap of 98.3% was calculated and a VI of 99%. Despite both being members of the East Khutse pride, these numbers are unusually high.

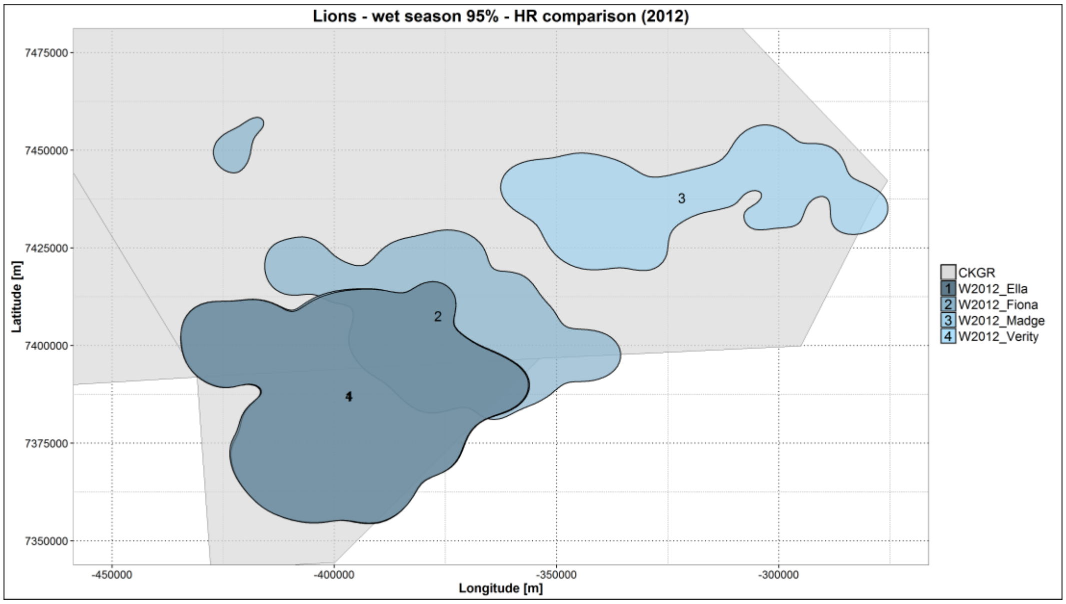


Figure 32: 95% home ranges of LF09_Fiona, LF12_Verity, LF13_Ella and LF14_Madge.

However, already in the following dry season the values dropped to 32% for the home range and only 4% for the core area (VI = 23%). During the same period there is a significant overlap of LF12_Verity's and LF09_Fiona's home range of 42% and 28% core area. LM06_Hitchcock established his home range just north of LF12_Verity and LF13_Ella, overlapping only a minor part of their territories.

In the year 2013 data is available for eight lions (Figure 33 & Figure 34). There is a striking overlap (84% HR, 62% CA, 76% VI) of LM08_Orange with LF12_Verity as they are both members of the East Khutse pride. Further, one can clearly see the home ranges of the three nomadic individuals and small groups, LM06_Hitchcock, LF14_Madge and LF16_Jane, north of the lions living in prides. While the 95% home ranges do overlap to a certain degree, there is no overlap among all three core areas.

Further, VI values are usually lower than 10%. In the southwestern part of the area, the home ranges and core of LF13_Ella and LF17_Lara do overlap by 97.8% and 92.5% as the two females are known to be closely associated. The VI of 96.5% reaches similar dimensions. In September or early October 2012, LF13_Ella left the East Khutse pride and therefore during the following wet season 2013, the overlap between her and LF12_Verity declined.

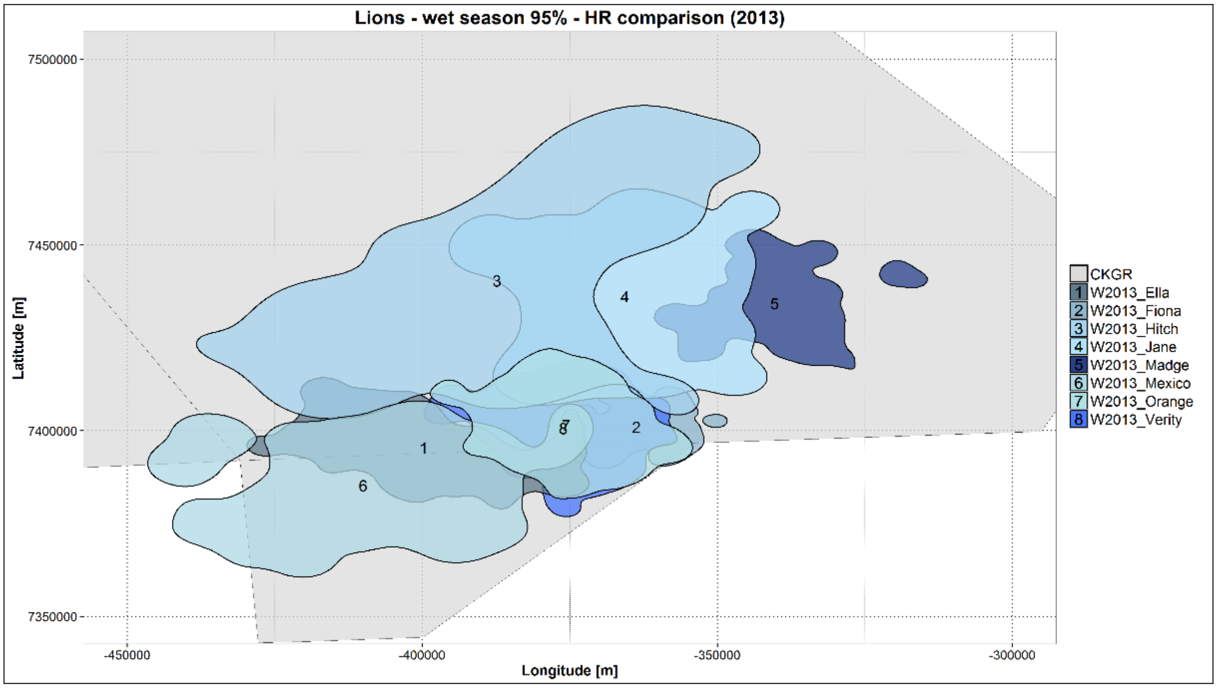


Figure 33: 95% home ranges during the 2013 wet season.

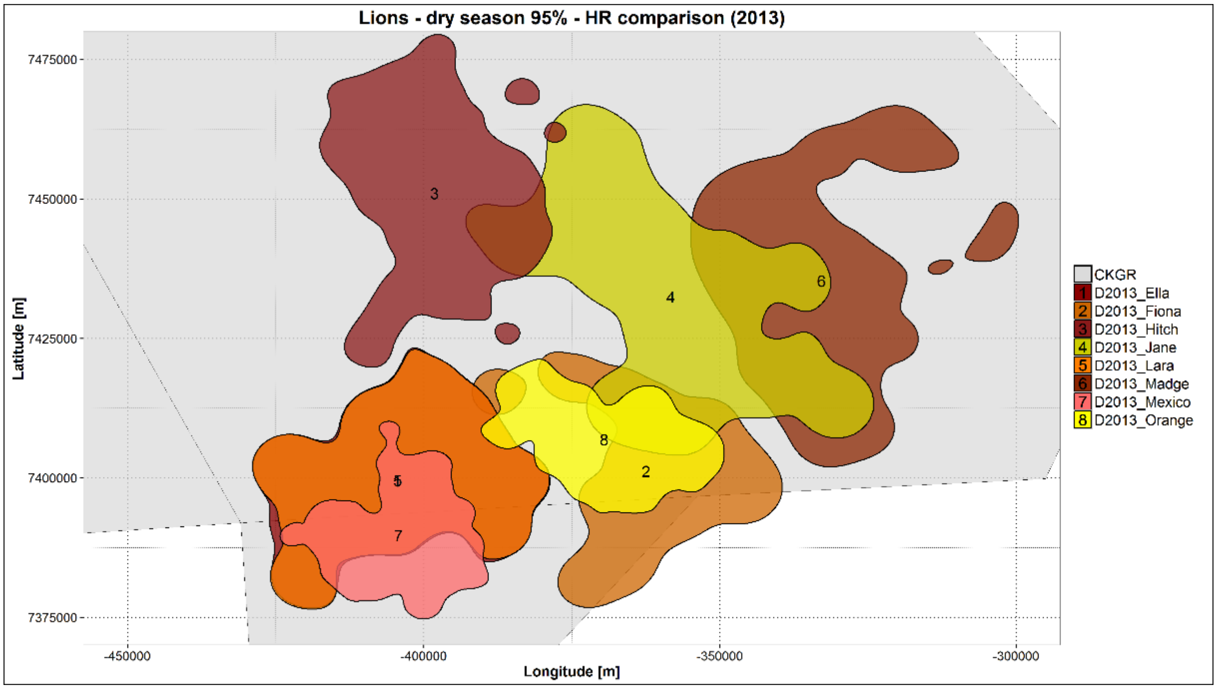


Figure 34: 95% home ranges of the 2013 dry season.

The home range decrease between the 2013 wet- and dry season (Figure 33 and Figure 34) of LM06_Hitchcock and LM07_Mexico as well as the expansion of LF09_Fiona and LF14_Madge are evident. Pronounced centroid shifts are missing. Similar to 2013, the three nomadic lions kept their territory north of all other lions and low values for the overlaps were calculated. The addition of LF18_Notch, another member of the East Khutse group resulted in very high overlap values (97% and 72%) between her and LM08_Orange's home range and core area. Between LF13_Ella and LF17_Lara there are no changes regarding the high overlaps.

In 2014 (Figure 35), LF09_Fiona clearly showed an expanding trend south. At the core area level one can clearly see the nomadic lions avoiding other resident lions, with hardly any overlap and low VI values. Simultaneously, LF09_Fiona and LF14_Madge significantly expanded and shifted their home range compared to 2013. During this process, they both crossed the southern and eastern border of CKGR and KGR. Resident lions, living in prides such as LF18_Notch, LM07_Mexico and LM08_Orange as well as the two associated females LF13_Ella and LF14_Lara maintained the location of their home ranges. Although the lionesses are not members of the Moloso pride lead by LM07_Mexico, the 95% home ranges of all three lions do clearly overlap by 50% to 67%. However, their core areas do not or only marginally intersect.

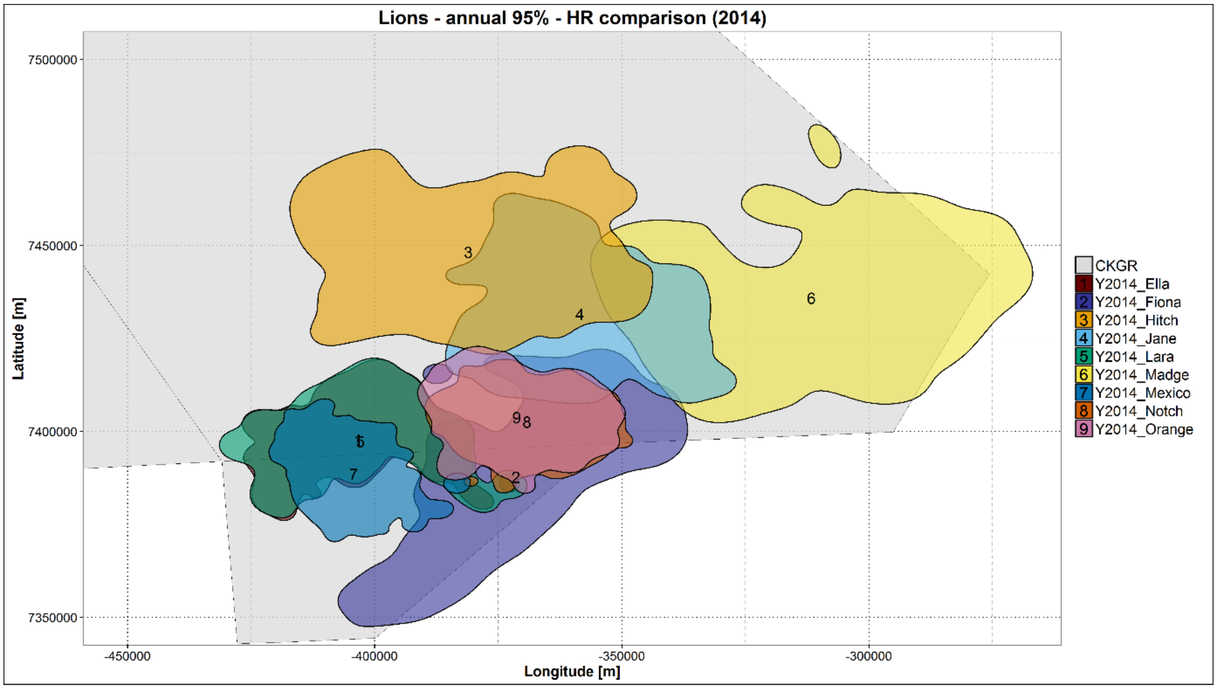


Figure 35: 95% home ranges of the year 2014.

In 2015 (Figure 36), LF16_Jane expanded her home range to the east, while LF17_Lare migrated south leaving the game reserve. In both cases distinct shifts of their centroids are noticed. The situation between LF18_Notch and LM08_Orange remains unchanged and their home ranges are usually about the same size. Members of the Moloso group and the East Khutse pride show to a certain degree overlapping 95% home ranges, but maintain their core area exclusively. By looking at Figure 30 and Figure 31 at the beginning of section 12.2, one can see some trends in home range size developments. Between the wet season 2012 and the following dry season all tracked animals (LF09_Fiona, LF12_Verity, LF13_Ella and LF14_Madge) showed a pronounced downwards tendency of their home range and core area sizes. For all these lions it took a couple of months before expanding their range again. Another noticeable trend is between the 2013 dry season and the 2014 wet season where six out of seven tracked lions showed a moderate to strong expansion. LF13_Ella was the only animal to show a negative trend.

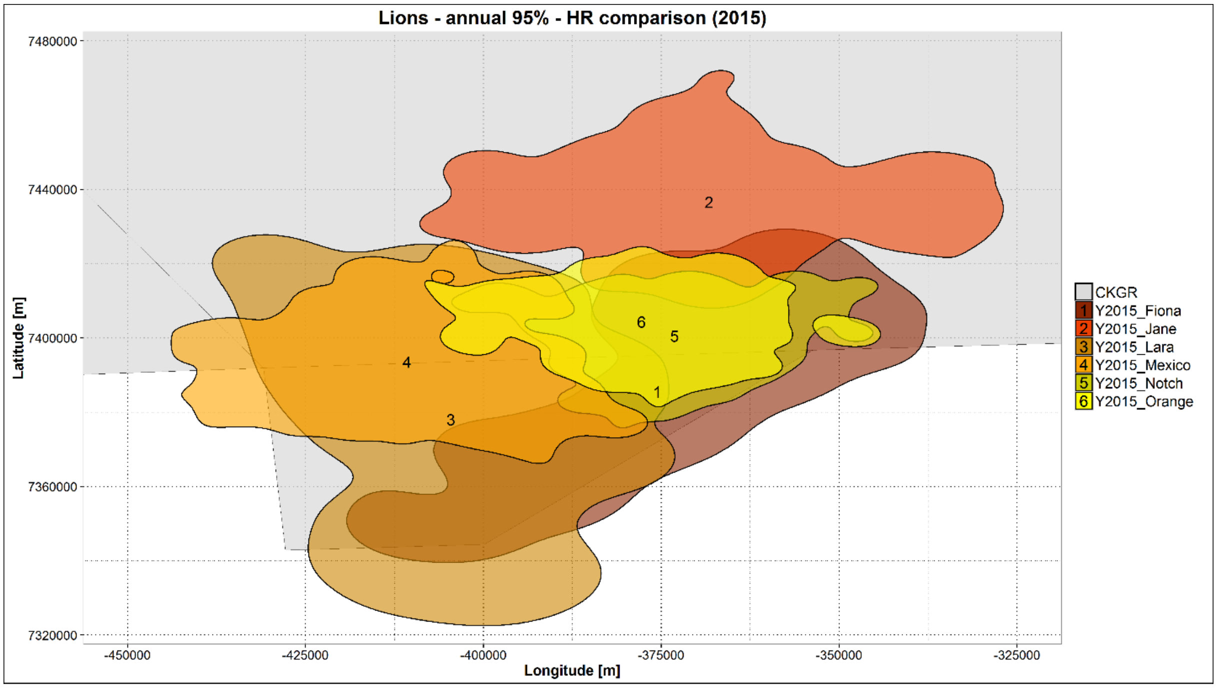


Figure 36: 95% home ranges of the year 2015.

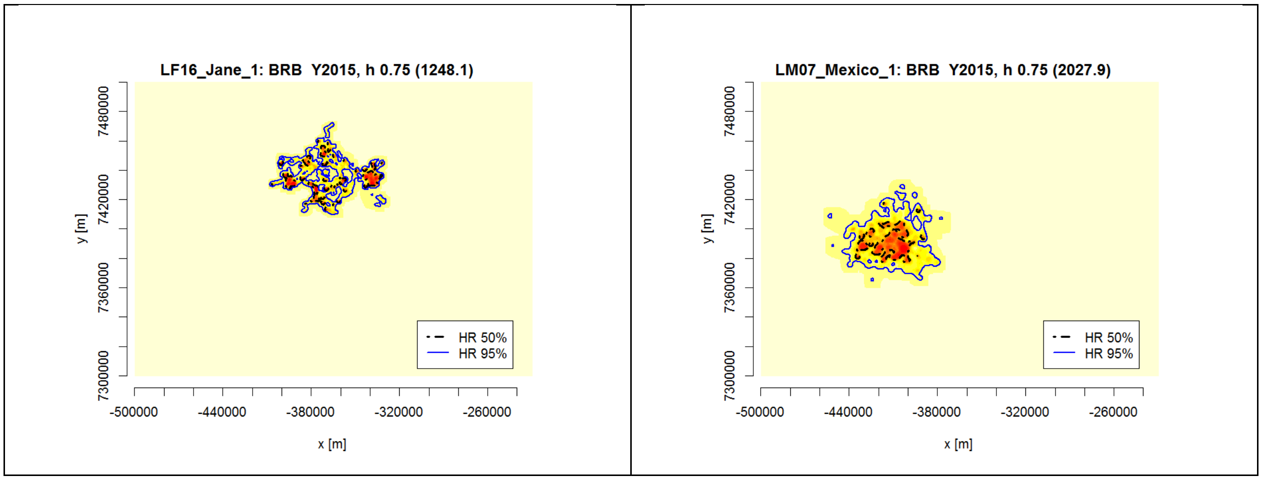
The situation after the 2014 dry season is very similar, with 5 out of 6 animals significantly expanding their home range. LF09_Fiona was the exception. For the period of the 2015 wet- and dry seasons 3 out of 4 lions exhibit a declining tendency. Due to the relocations of LF17_Lara her home range did not follow the common pattern. While there is no trend detectable for the size comparison between the wet and dry season for 2012 and 2013, wet season home ranges in 2014 and 2015 tend to be slightly larger than the respective dry season home ranges. Yet, in 2015 the differences in size are more pronounced. Core areas followed the patterns of the home ranges.

At an annual level, there is a significant declining tendency between 2012 and 2013 as well as an expanding tendency between 2014 and 2015. In 2014, 6 out of 9 tracked lions had their smallest home range in that period. During the wet season 2015, 4 out of 5 lions maintained their largest home range. After the 2014 dry season three distinct centroid shifts were detected, all belonging to nomadic lions (LF09_Fiona, LF16_Jane and LF17_Lara) which were moving towards the south. Between the 2013 wet season and 2014 wet season home ranges were fairly stable concerning their location as there was only one single shift per period. Again, the three nomadic females and the lone male LM06_Hitchcock were responsible for these shifts.

13. Comparison of KDE and BRB

The results of the home range estimations using BRB were not satisfying and therefore an extensive comparison of the two home range estimators is not warranted. Setting the right parameters, especially the smoothing parameter *h* as well as choosing the right number of steps between two consecutive fixes proved to be very difficult. Already a minor variation in *h* resulted in a significant size change and therefore a reasonable comparison was not possible. For the two leopards it was even more unpredictable as their datasets were not harmonized. Even a step-wise calculation using tailored settings did not produce reasonable results. The results calculated for PM07_Mothamongwe for the 2012 wet season and the year 2012 were significantly different from using KDE. Sizes of 2224 km^2 (W2012) and 1938 km^2 (Y2012) for the 95% home ranges were calculated. Compared to the 696 km^2 (W2012) and 682 km^2 (Y2012) using KDE these results are equal to 320% and 284% of the KDE results. The results for LF14_Madge and LF16_Jane were susceptible to graining. For LM07_Mexico and LM08_Orange, the results were quite reasonable and there were only minor issues regarding graining and over-smoothing.

As the of Figure 37 below should illustrate, over-smoothing and extremely patchy home range estimates were other serious problems. The approach of multiplying the parameter *h* by a factor to reduce over-smoothing or graining suggested by Zehnder (2015) was applied as well. Yet, the choice of the right home range estimation remained unclear and somehow arbitrary. At this point one must note that this is not primarily the weakness of BRB in general. The main reason behind these challenges is the fact that up to date it is not possible to directly implement BRB in the R-Software to estimate home ranges. An indirect approach with kernels is used instead. LF14_Madge and LM07_Mexico are good examples to illustrate the difficulties, especially the graining, of the home range estimation using BRB. For all home range estimates, the smoothing parameter in brackets was multiplied by several factors indicated just in front of the brackets (Figure 37). A factor of 1 is the default setting.



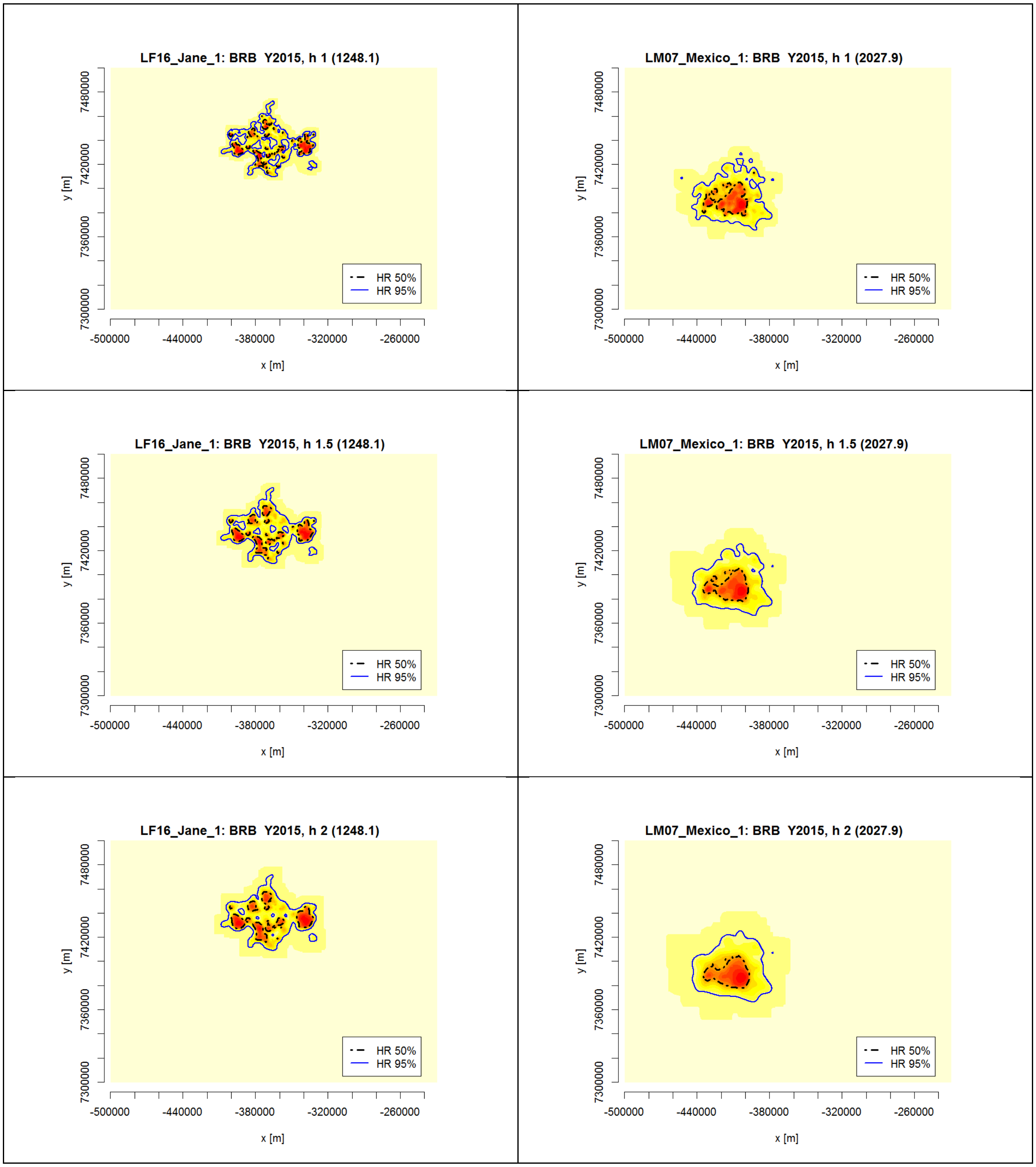


Figure 37: Results of the home range estimation using BRB and the associated problems of over-smoothing and graining. In brackets the used smoothing parameter is indicated as well as the factor (number following h) by which the smoothing parameter was multiplied.

VI Discussion

14. Home range descriptors[5]

Absolute area - leopards: The extensive analysis of the 95%- the 50% home ranges calculated for the leopards PF07_Ronja, PF12_Salome, PM07_Mothamongwe and PM08_Bogarigka revealed that their home ranges are exceptionally large. These findings are perfectly in line with the literature. In semi-arid to arid environments with limited natural resources, leopards must maintain large home ranges in order to fulfil their needs (Bothma et al. 1997; Macdonald & Loveridge 2010; Stein & Hayssen 2013). For leopards living in the Kalahari Desert, home ranges of male leopards covering areas as large as 2182 km^2 were calculated by Bothma & Le Riche (1984; cit. in: Stein & Hayssen 2013: 37). The results using the entire dataset are in a similar dimension as the ones presented by Zehnder (2015). Female leopards reached sizes between 196 km^2 and 780 km^2. The annual average home ranges of the 4 leopards PF07_Ronja (751 km^2), PF12_Salome (1255 km^2), PM07_Mothamongwe (652 km^2) and PM08_Bogarigka (2709 km^2) reached, with the exception of PF12_Salome, similar sizes. The calculation of the core area to home range ratio revealed that core areas on average cover between 14% to 27.7% of an animal's 95% home range. Values calculated for the two males (PM07_Mothamongwe = 27.7%, PM08_Bogarigka = 23.6%) were slightly higher than for the two females (PF07_Ronja = 20.5%, PF12_Salome = 14.1%). A seasonal variation of the ratios is not evident.

In the case of PF12_Salome one must keep in mind that she has been classified as problem animal (potential livestock killer) and has been translocated from the Motsetanamontle Ranch into KGR. In the area of release there was a resident leopard population. Exploratory wanderings were necessary in order to be able to establish her own home range. This background knowledge explains the sheer size of her initial home range during the 2014 wet season and the following dry season. Shortly after her release PF12_Salome left KGR again and moved south into the adjoining farmlands where she established her tiny home range in the thicket. The size of her seasonal home ranges (W2015 = 58 km^2, D2015 = 105 km^2) are in line with the results of Marker & Dickman (2005) who investigated the space use of leopards on Namibian farmlands. Home range sizes between 52 km^2 and 394 km^2 were calculated using minimum convex polygons (MCP). Keeping in mind that MCP overestimates the actual size of a home range one can assume that the results are similar.

The calculated home range and core area sizes showed a strong tendency for home ranges being larger during the dry season. For the core area it is true in 2 out of 4 cases. Yet, to my knowledge there are no direct hints in the literature regarding the seasonal variation of leopard home ranges in Southern Africa. Thus, there are indirect hints as several authors (Kissui 2008; Macdonald & Loveridge 2010; Stein & Hayssen 2013) argued that there is a direct link between prey availability and space use. A seasonal variation

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[5] All biological background information about the studied animals was obtained by personal communication with Stephen Henley, July 2016

in prey availability should then be visible through size changes of leopard home ranges. Hayward et al. (2009), Marker & Dickman (2005) and Norton & Henley (1987) did not find any evidence of leopard home ranges showing a distinct seasonality. Odden & Wegge (2005) investigated the space use of leopards in Nepal and there was tendency towards smaller home ranges during the wet season. Due to the very different location and habitat composition it would be unsafe to adopt their findings, however.

Bothma et al. (1997), Mizutani & Jewell (1998) and Stein & Hayssen (2013) argued that male leopards maintain larger home ranges than females. In this case, the results do not fully support this hypothesis. The average annual and wet season home range of PF07_Ronja (750 km^2 and 720 km^2) are larger than the ones of PM07_Mothamongwe (651 km^2 and 681 km^2). Only during the wet season, he maintained a larger home range (598 km^2) than PF07_Ronja (485 km^2). If one only takes the period of simultaneous sampling between the 2012 wet season and the 2013 dry season into account, then PM07_Mothamongwe's 95% home range covers a larger area in 75% of the cases. The results of PM08_Bogarika on the other hand do fully support the hypothesis. PF12_Salome is excluded due to her relocation.

Absolute area - lions: The average annual home range size of the seven female and three male lions ranges between 1218 km^2 and 2987 km^2, with an upper limit of 4624 km^2 and a lower limit of 692 km^2. Results calculated by using the entire dataset (Table 9) are quite similar to the ones described by Zehnder (2015). Home ranges and core areas maintained by these lions belong to the largest worldwide. Only lions in the South African Kgalagadi Transfrontier Park are known to maintain such enormous home ranges (Macdonald & Loveridge 2010).

Similar to leopards, the quality of an environment is a key determinant for the size of the home range maintained. The high quality environment allows the Serengeti lions to maintain home ranges as small as 20 km^2 to 500 km^2 (Celesia et al. 2010; Haas et al. 2005; Macdonald & Loveridge 2010). A tendency towards male home ranges being larger is not evident in our results. Female home ranges range between 1218 km^2 and 2987 km^2. For male lions, home range sizes of 1307 km^2 to 3752 km^2 were calculated. These findings are in contrast to the study of Loveridge et al. (2009) where male home ranges were larger. Further, a distinct size difference between the 95%- and 50% home ranges is also present, which is typical for a semi-arid environment. Core area to home range ratios calculations resulted in values ranging from 18.3% (PM07_Mexico) to 26.8% (LF12_Verity). Neither a seasonal variation nor a tendency towards males or females is evident, however.

Similar to leopards, lions must increase their range with decreasing habitat quality (Eloff 1998; Haas et al. 2005; Tuqa et al. 2014). Therefore, the results are in line with the literature (Loveridge et al. 2009; Macdonald & Loveridge 2010). In contrast to the leopards, which show a strong tendency towards larger dry season home ranges, lions show a distinct tendency towards larger wet season home ranges. In 9 out of 10 cases home ranges are significantly larger during the wet season. The only exception is LF09_Fiona. On a core area level this is true for 70% of the cases. Similar to the leopards, concrete statements about the seasonality of home ranges are rare, but there are indirect answers. Loveridge et al. (2009) for example stated that there is no constant seasonal variation in size but there is a positive correlation between rainfall and home range size. Nash et al. (2012) found a correlation between home range size and prey availability considering the pride size as well. The results of Tuqa et al. (2014) support the findings of lion home ranges being larger during the wet season. A reason is the lower prey density, which is related to a more evenly distributed food supply.

Five lions (LF09_Fiona, LF14_Madge, LF16_Jane, LF17_Lara and LM06_Hitchcock) maintained significantly larger home ranges and core areas than the remaining 5 lions. While they average an annual size of 2372 km^2 to 3753 km^2 (CA between 561 km^2 and 899 km^2) the resident lions only reach 1218 km^2 to 2572 km^2 (CA between 237 km^2 to 695 km^2). The main reason behind the huge home range of LF17_Lara is her migration to the Southern farmlands in the second half of 2014. In October and December, she was caught and translocated back into KGR after killing livestock. However, soon thereafter she left again and therefore her home range is exceptionally large. The other mentioned individuals either live solitarily (LF09_Fiona) or in small groups of female or male lions. Therefore, these lions are unable to maintain a stable home range and are forced to move more frequently. This behaviour explains the increased size of their territories (Haas et al. 2005).

Interestingly, the members of the large East Khutse pride (LF12_Verity, LF13_Ella, LF18_Notch and the pride male LM08_Orange) maintained a quite small home range despite the size of the pride and the need for more resources. Spong (2002) provides a plausible explanation as from his point of view larger prides should be more successful in defending an area with high quality resources and there is no need for a huge home range.

Compactness: Compactness measurements presented in Table 12 did not support the hypothesis that core areas are more compact than the 95% home ranges. For leopards, the average compactness indices are almost identical for the core areas and the home ranges. While there is a difference of 0.20 between the two average all data CIs, a maximum of 0.07 is reached for the remaining four categories. There is only a minor difference between the overall average core area CI (0.46) and the overall average home range CI (0.45).

Compactness indices for lions show more variation with differences between the average core area CI and the average home range CI ranging from 0.14 to 0.18. There is a difference of 0.15 between the overall average core area CI (0.36) and the overall average home range CI (0.51). A statistically significant correlation between area and CI could not be demonstrated.

Centroid shift: Determining the centroid shift between two consecutive 95% isopleth polygons was shown to be a good indicator of significant changes in home range size. A total of 27 (7 for leopards, 20 for lions) centroid shifts exceeding 10 kilometres were identified and in 23 or 85.2% of the cases either a substantial increase or decrease was present. For the other 4 cases the actual size remained similar to the previous season. However, the knowledge of a shift alone is not sufficient to determine the kind of size change. Likewise, the reverse argument that a missing centroid shift is an indicator for a stable home range size is similarly invalid. For example, the decrease of LM07_Mexico's home range after the 2013 and 2015 wet season as well as the increase after the 2014 dry season are not captured in the centroid shift, despite home range size changes in the dimension of 800 km^2 to 1500 km^2. Nevertheless, it is a helpful measure to characterize the space use of lions and leopards, especially for detecting nomadic predators (e.g. LF09_Fiona) or exceptional migrations (e.g. LF07_Ronja) of usually resident predators.

Space use outside CKGR and KGR: The intersection of all home ranges and core areas with the borders of CKGR and KGR revealed that LF16_Jane and LM06_Hitchcock were the only individuals to remain inside the reserve borders for the entire period of analysis. All others had at least a fraction of their home range or core area outside the protected area. On the annual and seasonal level LF14_Madge and LF17_Lara have moderate parts of their 50% home range outside the reserve borders. PF12_Salome's core areas are located entirely outside the reserve. In their extensive analysis of livestock predation around the CKGR and KGR, Schiess-Meier et al. (2007) concluded that more livestock was lost during the dry season. Therefore, one could assume that predators left the game reserves more frequently during the dry season than the wet season. The findings presented in Table 15 do not support the findings of Schiess-Meier et al. (2007), however. A total of 8 dry seasons and 9 wet seasons were identified where predators had significant parts of their 95%- and 50% home ranges located outside the game reserve. Nevertheless, as the number of tracked animals is very low it might well be the case that predators leave the game reserves more frequently during the dry season. The fact that all three predators are females might just be a coincidence.

15. Temporal variation of leopard space use

Between 2009 and 2011, as well as in 2012 and 2015, the female leopard PF07_Ronja showed an oscillation between dry season and wet season home range size. Average dry season home ranges were significantly larger. This development could be related to the raising and nursing of cubs. Leopards usually give birth during the wet season and in the first couple of weeks, cubs are hidden (Hayward et al. 2006; Balme et al. 2007; Balme et al. 2013). Therefore, the potential range use of the mother is limited as she has to return to her litter frequently until they are able to join her after about 3 months. PF07_Ronja gave birth to cubs every year with the exception of 2013 (equals W2014). With the exception of the 2011 dry season, the oscillation and the cycle of her giving birth match perfectly with significantly smaller home range sizes in these periods. The UD underlines these assumptions as the area of most intense space use is very small.

In the wet season 2014 she did not have any cubs with her. This is plausible as she was migrating south into the adjoining farmlands. Already in the following year the pattern of small wet season home ranges and giving birth is evident. To know the cause of her singular migration would be very interesting but at this point one can only speculate about the reason. The arrival of a conspecific or poor prey availability are among the most likely reasons for her migration (Balme et al. 2007; Marker & Dickman 2005; Stein & Hayssen 2013). Despite the migration south, the 2013 dry season and 2014 wet season core area overlapped by 57% and 40% of the VI was shared. This is not surprising as her core area consists of 2 disjoint polygons, one in the South and one in the North. The seasonal plot (Figure 11) demonstrates that she was able to regain her initial home range for the wet season 2015 when she raised cubs again. Additionally, the sizes of her 95%- and her 50% home range levelled off at earlier dimensions.

PM08_Bogarigka migrated northeast between the 2012 wet- and dry season expanding his home range by a factor of 2.5. Again, determining the driving factor is difficult. As the ranges of PM07_Ronja and PM07_Mothamongwe were stable during PM08_Bogarigka's migration, it could be possible that he either conquered an existing home range of an uncollared leopard or has been displaced by a contender (Norton & Henley 1987).

PM07_Mothamongwe remained in the same area for the entire period of tracking. PM07_Mothamonge can be characterised as a resident male leopard. Interestingly, his 95% home range overlapped the one of Ronja by 77.7% to 97.4%, the 50% home range by 37.2% to 76.5% and a VI of 43.5% to 66.3%. This situation is in contrast to Stein & Hayssen (2013) and also the original definition of core areas by Burt (1943) according to whom the core area is maintained exclusively. A possible explanation is the sheer size of the core areas (125 km^2 to 646 km^2) and therefore it is impossible for an individual leopard to prevent conspecifics from entering. An overlap not necessarily means a direct contact. Further, a direct contact could also be wanted for the purpose of mating, which is assumed to be the case for PF07_Ronja and PM07_Mothamongwe (Schiess-Meier et al. 2011).

Due to his expansion PM08_Bogarigka showed a core area overlap with PM07_Mothamongwe (from 19.7% to 37.5%) and a VI of (22.9% and 27.9%). Compared to his arrival in the 2012 dry season, both values declined in the following wet season. Further, his 95% home range overlaps the one of PF07_Ronja by about 80%. Thus, the core areas only overlap in the 2012 dry season (33.4%, VI = 28.7%) but not in the subsequent wet season. These adjustments of space could have been a result of direct or indirect defence strategies (e.g. scent markings, scratches, fights) of the individuals (Stein & Hayssen 2013).

PF12_Salome left KGR shortly after her release. Only during the 2014 wet season there is a home range overlap (18%) between her and PF07_Ronja. Core area overlaps do not exist and also the VI (9.5%) is extremely low. They probably never met. The area of release was known to be a place with a resident leopard population. Conspecifics are probably the main reason why PF12_Salome was wandering around and soon after she left the KGR because she was unable to establish her own home range. Her home range, especially the core area is by far the smallest for any leopard but also by far the most compact and thus defensive costs are the lowest. The absence of conspecific competitors and a stable source of non-natural prey are potential explanations.

An extensive statistical analysis of leopard space use or the detection of correlations between several individuals over time was not possible due to the lack of data.

16. Temporal variation of lion space use

LF09_Fiona can be characterised as a nomadic lioness, which is unable to maintain a stable home range. Her dry season 95% home range 2011 (5991 km^2) is by far the largest maintained by any lion. This sheer size could be an indicator that she was constantly on the move and there was no niche for her to settle in. In the following seasons (W2012 – D2013) she was able to occupy a niche. Consequently, her own home range and its location were fairly stable. Although during this period her 95% home range significantly overlapped (40% to 75%) with several other lions, especially LF12_Verity and LM08_Orange, their core area hardly overlapped by less than 20%. The exception is the 2013 wet season with values as high as 33%. Additionally, the volume of intersection supports the findings of her actively avoiding other conspecifics.

At a seasonal level, PF09_Fiona has the highest VI (20% to 35%) with the four members of the East Khutse group LF12_Verity, LF13_Ella, LF18_Notch and LM08_Orange. For all remaining lions the VI is smaller than 5%. After the 2013 dry season she left the area and migrated southwest. This change of behaviour resulted in markedly higher home range and core area sizes and there is a high probability for conspecifics forcing her to leave.

LF13_Ella was a member of the East Khutse group until she left in September or October 2012 (late D2012, but before W2013). The splitting of prides is not uncommon for lions, especially in harsh environments such as the Kalahari (Eloff 1998; Macdonald & Loveridge 2010; Spong 2002). The fact of LF13_Ella and LF12_Verity being members of the same pride explains the simultaneous home range decline after the 2012 wet season. The reason for the decline, however, remains unclear. During the time that LF13_Ella was tracked as a member of the East Khutse group she showed very high core area overlaps with LF12_Verity (up to 98%). Values for the VI reached similar dimensions. The emergence in 2012 is clearly visible as the core area overlap and VI were declining quite significantly (CA = 4%, VI = 23%). Higher overlap measurements for all three indicators with LM07_Mexico were evident during her migration to the northwest, crossing the area of the Moloso group.

The newly formed association with LF17_Lara is visible through an extremely high VI of over 96%. Remarkably, she and LF17_Lara were able to maintain a fairly stable home range despite being just a pair of females. After LF13_Ella's death in August 2014 LF17_Lara became a nomad lioness avoiding conspecifics and migrating to the Southern farmlands. The proportion she shared with LM07_Mexico is rather small, with a maximum VI of 42% in the 2014 dry season. As a known livestock killer she was relocated twice but immediately returned. Because of the small VI with LM07_Mexico one could assume she quickly passed the Moloso group when wandering south.

The other three nomadic lions (LF14_Madge, LF16_Jane and LM06_Hitchcock) chose a different strategy than constantly looking for niches within the range of resident lions. They all established their home range north of the resident Moloso and East Khutse prides and occupied quite large areas. During the dry season 2012 and 2013, LM06_Hitchcock's home range did hardly overlap with another lion. For the 2013 wet season however, his home range overlapped the one of LF16_Jane by more than 50%, yet at the core area level there was no overlap at all and also the VI is only 26%. LF16_Jane and LM06_Hitchock shared parts of their home range but actively avoided each other. Similar to LF09_Fiona VI values for LM06_Hitchock hardly exceeded 10%. An interpretation of the significant decline of this home range after the 2013 wet season is difficult. Based on the 95% home range and 50% home range plots other collared lions showed no expansion towards his territory. Therefore, other uncollared conspecifics are likely to be the cause of the decline. Maybe he was displaced by a competitor.

LF16_Jane showed a similar pattern to LM06_Hitchchock, maintaining her home range north of the East Khutse group. Overlaps of the 95% home range with other nomads were frequent but core areas did never overlap and VI was low. LF14_Madge was located even further to the east at the very edge of CKGR. Due to her remote location there are hardly any overlaps with other collared lions, even at the 95% level. Unlike LF16_Jane and LM06_Hitchcock she maintained a fair part of her home range and core area outside the reserve border. Her settlement in the East was the result of a migration by more than 25 kilometres after the 2013 dry season. During this period none of the collared conspecifics showed movement towards her home range. Again, the arrival of a competitor is likely to be the driver. The 50% home range of the 2014 wet season clearly had two peaks of intense use. Thus, her migration must have started in the mid dry season or even later. There is a high probability for her being a potential livestock killer as hunting is more difficult for a solitary lion (Haas et al. 2005; Macdonald & Loveridge 2010).

The lions of the East Khutse group, namely LF18_Notch and LM08_Orange unsurprisingly shared a high VI (55% to 75%) and the other overlap measurements are equally high. Yet, these values are significantly lower than the ones achieved by lions living in small groups of only 2 individuals. LF13_Ella and LF17_Lara reached VI of over 90% while they were associated with each other. Also in the 2012 wet season when LF13_Ella and LF12_Verity were both members of the East Khutse group, they almost shared 100% of their VI.

As the East Khutse group is known to be quite large with two pride males, it could be that LF18_Notch and LM08_Orange were not that closely engaged. Further, LF12_Verity and LF13_Ella were both females and spent much time together while hunting and nursing cubs. Pride males on the other hand do less frequently join the hunts and are more engaged in defending their pride. Further, they mate with several lionesses which also has an influence on their space use (Haas et al. 2005; Loarie et al. 2013; Macdonald & Loveridge 2010; Woodroffe & Frank 2005). The plots indicated that the East Khutse pride was able to maintain their home range over the course of several seasons. Although LF12_Verity and LF18_Notch and LM08_Orange were not all tracked at similar time intervals, their VI is valuable in highlighting that the location of their home range has not changed significantly since the decline in 2012. In other words, their space of activity is still very similar as the following example shows: LF12_Verity shared a VI of 55% to 75% over all seasons sampled, for LM08_Orange values ranged from 29% to 76% with 5 out of 6 values over 62%.

With the adjoining Moloso group, led by LM07_Mexico, the members of the East Khutse group shared hardly any VI although some overlaps at the 95% home range level were evident. Yet, these overlaps were predominantly along the borders of their home ranges. Therefore, the defensive strategies such as scent markings, roaring or scratching were successful. LM07_Mexico did not show distinct overlaps with other conspecifics. The only exceptions were the two associated females LF13_Ella and LF17_Lara. As discussed earlier, their common space use is likely due to the wandering of the females as the core area is maintained exclusively (Haas et al. 2005). Similar to the East Khutse pride the Moloso group was able to maintain their home range after the massive decline after the 2013 wet season. Of course only the data of LM07_Mexico is available but as pride male his space use is to a certain degree representative for the entire pride. By just looking at the data available an interpretation of the decline is not possible. The same is true for the expansion which started after the 2014 wet season.

The higher number of tracked lions allowed a comparison of the lions' space use over time. At an annual scale the most evident feature was the collective expansion of all 6 lions tracked between 2014 and 2015. The dimension of their expansion ranged from about 200 km^2 for LM08_Orange and LF18_Notch up to about 1500 km^2 for LM07_Mexico. Simultaneously, the nomadic lions LF09_Fiona, LF16_Jane and LF17_Lara expanded their home range as well. One could conclude that changes in food supply, either positive or negative, allowed or forced the Moloso and East Khutse group to adjust their home range. As the above discussion revealed, the nomadic lions actively avoided the proximity of resident prides. Therefore, one could argue that the pride movements directly affected the space use of the nomads. Across all sampled animals, the core areas followed the same pattern.

At the seasonal scale other patterns were detectable across several individuals. After the 2012 wet season all four tracked lions showed a massive decline of their home range. This was not only true for the nomadic lions LF09_Fiona and LF14_Madge, but also for the two members of the East Khutse group (LF12_Vertiy and LF13_Ella). A potential explanation could be a sudden change in prey densities. Several researchers (Loveridge et al. 2009; Macdonald & Loveridge 2010; Patterson et al. 2004; Tuqa et al. 2014) described that lion home ranges decrease with higher prey densities during the dry season. Prey, mostly herbivores, need to stay close to steady water sources and therefore densities increase. Meteorological data recorded by LEC revealed that between November 2011 and March 2012 (wet season 2012) an unusual high amount of precipitation (528 mm) was received and prey animals were likely dispersed over the area. Predators were then forced to increase their home range. The decrease in home range size during 2012 dry season could indicate the transition back to normal state.

Interestingly, throughout the following two seasons the home ranges of the prides as well as the nomadic lions were fairly stable at a low level. These findings support the above mentioned hypothesis of a correlation between pride movements and the movement of small groups or solitary lions. After the 2013 dry season there was another collective expansion in terms of home range size. Again, the 2014 wet season was fairly wet (532.4 mm) which and the above mentioned explanation could be applied as well. Unlike the other two events of expansion and decline, a potential correlation between pride space use and individual space use is less pronounced.

On the other hand one must bear in mind that other factors do have a significant influence on space use and the majority of lions in the Khutse area was not tracked (Hopcraft et al. 2005; Haas et al. 2005; Loveridge et al. 2009). Despite an increase in home range size for 80% before and decrease for 75% of the lions tracked over the 2015 wet and dry season, the above mentioned explanation is not suitable here as 2015 wet season was unusually dry (105 mm). The lack of rainfall led to an increased risk of bushfires which have a major impact on the environment. Yet, the extensive analysis and comparison did not reveal distinct seasonal changes in size and location of lions’ home ranges and core areas. As presented above there is a weak tendency towards lion home ranges being larger during the wet- compared to the dry season.

VII Habitat Quality

17. Related work

Determining all factors influencing the habitat quality and consequently the space use of large predators is very difficult. Statements are often only valid for a specific region as environmental factors, e.g. precipitation or prey availability, are highly variable. Recalling the definition of home ranges by Burt (1943), that animals do not wander around randomly but with the purpose to fulfil their needs.

"Home range configuration is affected by overall resource abundance with increases in abundance leading to smaller ranging areas (...)" (Nash et al. 2012: 2490).

The above citation of Nash et al. (2012) briefly summarises how animals are influenced in their space use. Nash et al. (2012) stressed the importance of the temporal and spatial variability of resources. Complexity is further increased as most factors are dependent on or determined by each other as the following example underlines: "Biomass of prey species is determined by the primary production which is dependent on the availability of water, light and nutrition. Prey biomass then determines the carrying capacity of predators in a given area" (Macdonald & Loveridge 2010: 6). The focus of this section is on the most often mentioned factors associated with habitat quality and range use of predators, namely water availability, vegetation and prey abundance (Celesia et al. 2010; Hopcraft et al. 2005; Macdonald & Loveridge 2010; Tuqa et al. 2014).

Precipitation is seen as the most important factor affecting the home range size of lions and leopards across Southern Africa (Balme et al. 2007; Celesia et al. 2010; Tuqa et al. 2014). In the semi-arid Kalahari with very low annual rainfall and a distinctive water shortage during the dry season, precipitation is even more crucial, as it directly influences several other factors. In the KGR and CKGR surface water is scarce for much of the year, with the exception of the wet season peak (Winterbach et al. 2014). During the dry season, surface water is restricted to a few waterholes. Most prey animals and predators are dependent on a steady water supply and do therefore search the proximity of waterholes (Balme et al. 2007; Celesia et al. 2010; Nash et al. 2012; Valeix et al. 2012).

Additionally, precipitation is the main growth limiting factor for all plants in the study area. Its availability determines when, and which types of, vegetation are growing. Consequently, precipitation directly affects the food supply of herbivores, the main prey of lions and leopards (Balme et al. 2007; Loarie et al. 2013; Valeix et al. 2012). Around the KGR and CKGR, the landscape is dominated by open pans, grasslands and short- to medium grown shrub- and bushlands. As Mishra et al. (2015) point out in their study on the vegetation composition in the Central Kalahari, the vegetation follows a particular pattern. At the micro scale it is highly variable with grassland, bushes and short trees within close distance. On the macro scale, however, the landscape is very homogeneous due to the water shortage. Yet, vegetation growth does only not have an influence on the nutrition supply of herbivores, but also on the hunting behaviour of lions and leopards, especially as they are ambushing predators, relying on sufficient cover (Balme et al. 2007; Haas et al. 2005; Macdonald & Loveridge 2010; Stein & Hayssen 2013; Valeix et al. 2012).

Prey abundance is the third very important factor affecting the range of lions and leopards. Basically, there is a negative correlation between prey abundance and home range size (Macdonald & Loveridge 2010; Tambling et al. 2010; Tuqa et al. 2014). As described above, prey and predators are highly dependent on steady water supply. In the Hwange National Park in Zimbabwe, an area with comparable conditions to the KGR and CKGR, a trend towards prey densities being higher towards the peak of the dry season was described (Macdonald & Loveridge 2010; Nash et al. 2012). On the other hand, their results indicated that more precipitation leads to lower prey densities and therefore lions were forced to increase their home range. The same tendency was described by Patterson et al. (2004) in the Tsavo National Park in Kenya. Herbivores gathered around the few remaining water sources and thus attracted predators, especially lions. Despite the rich food supply, leopards tended to avoid such areas due to the potential of lethal conflicts with lions (Balme et al. 2007).

In high-quality environments it takes predators less time to fulfil their needs and consequently such areas are preferred to establish the home range. Gautestad & Mysterud (2005) suggested that high-quality habitats are used most intensively. Following Darwin’s theory of the survival of the fittest, the highest quality habitat should be occupied by dominant leopards or lion prides. In the literature, there are several examples underlining this hypothesis (Mosser & Packer 2009; Spong 2002; Tuqa et al. 2014). Dominant prides can be characterised by their relatively large number of members and the successful defence of their home range (Haas et al. 2005; Mosser & Packer 2009; Spong 2002). Despite their size there is no need to maintain extremely large home ranges. Nomadic animals and smaller groups of lions on the other hand, have to look for niches to fulfil their needs.

18. Data

The analysis period for the second research question covers the time between the beginning of the 2014 wet season (November 2013 – April 2014) and the end of the 2014 dry season (June 2014 – September 2014). May 2014 and October 2014 are defined as transition months and excluded.

18.1. Selected animals

The above mentioned timespan is covered by the 2 leopards PF07_Ronja and PF12_Salome, the 5 lionesses LF09_Fiona, LF14_Madge, LF16_Jane, LF17_Lara, LF18_Notch and the 2 pride males LM07_Mexico and LM08_Orange. The results of the extensive home range analysis of the first research question are used as a basis for the following analysis regarding changing environmental conditions.

18.2. Meteorological data

Meteorological data is recorded by LEC at several spots within the study area (Figure 38). With a total precipitation of 541.6 mm, the period between November 2013 and October 2013 was unusually and well above average (~350 mm/y). The wet season received a total of 532.4 mm and the transition months May and October 5.8 mm and 3.4 mm, respectively. No precipitation was recorded for the dry season between June and September.

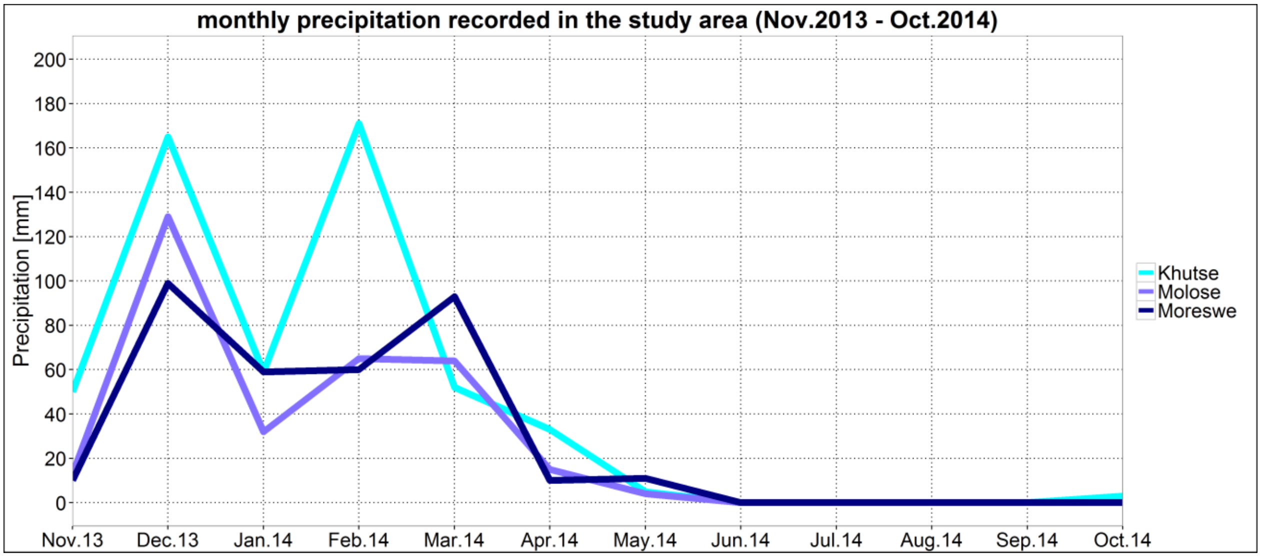

Figure 38: Monthly precipitation [mm] recorded at three stations in the study area for the period between November 2013 and October 2014.

18.3. Waterholes

There are 4 waterholes in the study area, which offer a steady water supply throughout the entire year.

Table 16: Waterholes in the study area given in the local UTM36S reference system.

Name	Longitude	Latitude
Khutse 1	-370470.0650	7393244.1000
Molose	-403361.6521	7386924.7510
Moreswe	-410598.1064	7366211.4820
Sekaka	-325647.9633	7427469.8640

18.4. Vegetation data

The only available information about vegetation in the study area is the map (Figure 3) developed by Mishra et al. (2015). As the analysis has shown, the vegetation around Khutse is very homogeneous at the large scale and very heterogeneous at the small scale. Therefore, it is not taken into account.

18.5. Prey data

Prey animals around the study area are recorded on a monthly basis by LEC, using the so-called transect method (Figure 39).

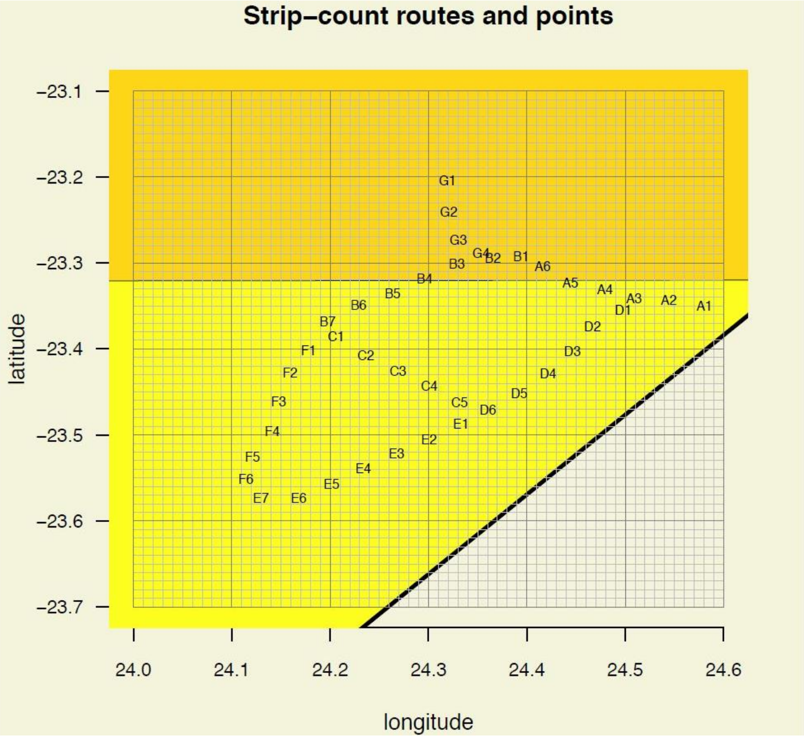

Figure 39: Routes and sampling points used by LEC to estimate prey animals in the study area. Points with similar letters define one route. Note that coordinates are given in WGS84 instead of the usual UTM36S. Plot by Zucchini (2016).

A car is used to drive along predefined routes and all animals spotted within a certain distance to the road are taken into account (Bankert et al. 2003; Fewster et al. 2005; Keith et al. 1980; Stephens et al. 2006). The number of animals counted is then used for an extrapolation in order to estimate the total population in the study area. Results can vary significantly based on the extrapolation method chosen (Bankert et al. 2003; Fewster et al. 2005; Stephens et al. 2006). In case of LEC[6], they drive along 7 predefined routes (A-G) and use a buffer of 200 m on each side of the road (Figure 39).

19 different species were classified as potential prey, of which 14 species are native prey (baboon, blue wildebeest, duiker, eland, gemsbok, giraffe, greater kudu, hartebeest, kori bustard, ostrich, scrub hare, springbok, steenbok, warthog) and 5 species are domestic animals (cow, donkey, goat, horse, sheep). Over the course of the whole sampling period, gemsbok, giraffes, hartebeest, kudus, ostriches and steenbok were by far the most seen (details: Appendix 3 & 4). No baboons, scrub hares or warthogs and no domestic animals were recorded in either season. Yet, the average number of prey animals seen per visit (Table 17) per point are very low for both seasons. The different number of visits is plausible as the wet season includes 6 months while the dry season only includes 4 months.

Table 17: Overview of the number of visits, number of prey encountered, relative prey score and average number of prey animals seen per point and visit. Numbers from Zucchini (2016).

SEASON	VISITS	PREY_ABS	REL_PREY_SCORE	AVG. NUM. PER VISIT
WET 2014	239	230	51.5	0.96
DRY 2014	195	244	66	1.25

As shown in Figure 40 a & b, each point is located on or between two isopleths with a certain value for the relative prey density. The relative prey score was calculated by assigning a value for the relative prey density (Figure 40 a & b) to every sampling point A1 to G4 (Figure 39).

A point located between the 1- and 1.5 isopleth was given a value of 1.5 for the relative prey density. Points lying on an isopleth were given the higher of both values. All sampling points per season were then summed up to estimate the REL_PREY_SCORE (Table 17). Details about the calculation of the relative prey densities can be found in Zucchini (2016).

There is a distinct variation in prey densities with higher prey densities calculated for the dry season. However, higher prey densities during the wet- and dry seasons occur in the same areas in the north-eastern and north-western part of the study area. The large areas between two transects show very low prey densities. One must be careful, however, as prey densities in the plots above might be significantly underestimated due to their distance to the closest transect.

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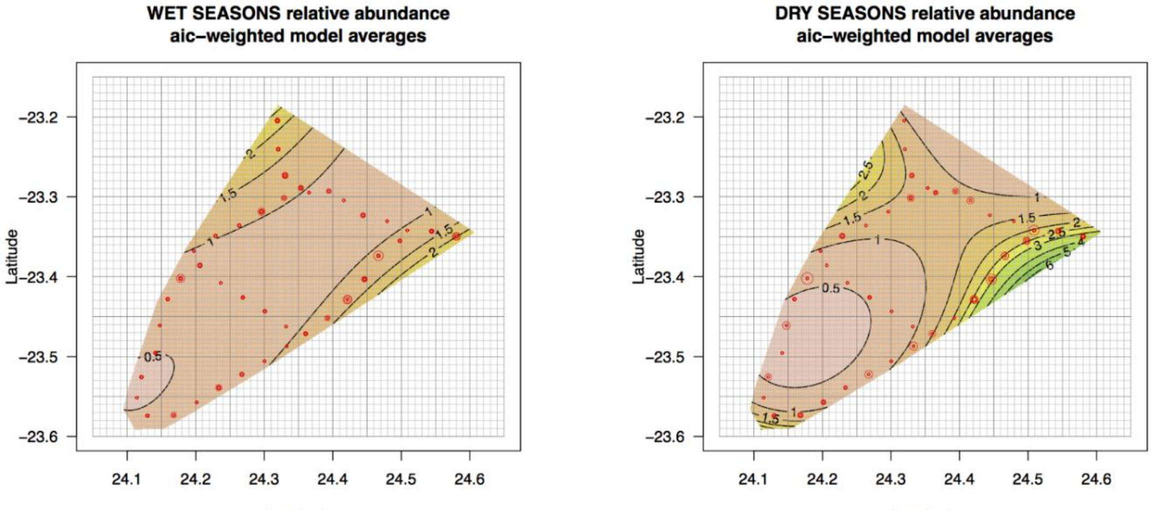
[6] Personal communication with Stephen Henley, May 2016



a) b)

Figure 40: Relative prey densities in the study area given in the local UTM36S reference system. A distinct variation of prey densities between the wet season a) and the dry season b) is visible. The points represent the 7 transects illustrated in Figure 39. Plots by Zucchini (2016).

19. Methodology

This section gives an overview of the methods used to test how predators do react to changing environmental conditions using the data described in Section 18 as well as the results obtained in the first research question on home range analysis.

19.1. Meteorological aspect

Although precipitation data would cover a timespan of more than just the 2014 wet- and dry seasons, the analysis is limited to this timespan due to the lack of prey data. It is not possible to carry out a statistical analysis, e.g. a correlation test, as the sample size is too small for the results to be robust. However, this is only a minor issue as the extensive statistical analysis of Zucchini (2016) revealed that dry season prey densities are significantly higher than wet season densities for the year 2014.

19.2. Waterholes

Waterholes with the given coordinates were plotted to determine whether there is a correlation between prey densities and the availability of a steady water source. Statistical tests were not possible due to the small sample size.

19.3. Access to prey

The first step included the modification of the original prey datasets by adding a variable for the relative abundance. Based on the relative abundance value, each point (A1 to G4) was then allocated to an ordinal category. Categories (Table 18) range between 1-6, as the highest relative abundance for either the wet- or dry season 2014 is 6. The actual determination of the potential access to prey animals was done in two steps. First, for each of the 9 selected individuals a point-in-polygon test was conducted to determine which points of the 7 transects are located within the 95%- and 50% polygon, respectively. Second, the sum of the absolute number of prey animals as well as the total score for the relative prey densities were calculated for each animal and both polygons. Consequently, 8 figures represent the potential access to prey for each predator. In order to be able to properly analyse the result, a plot was created for each animal including the transect points, waterholes, the KDE 95%- and 50% home range polygons as well as the outline of KGR and CKGR.

Table 18: Overview of the prey density classes for the 2014 wet- and dry season.

Category	**Category 1**	**Category 2**	**Category 3**	**Category 4**	**Category 5**	**Category 6**
Value	$x < 1$	$1 \leq x \leq 2$	$2 < x \leq 3$	$3 < x \leq 4$	$4 < x \leq 5$	$x > 5$
Description	very low	low	med low	med upp	high	very high

20. Results

The results of the estimation of the potential access to prey for the 2014 wet- and dry seasons are presented in Table 19 below. In the following Sections 20.1. and 20.2, dry season plots show the potential access to prey of all selected predators. The wet season plots can be found in the Appendix. For the 2014 wet season, a total of 230 prey animals were counted along the 7 transects which resulted in a total score of 51.5 for the relative prey density. During the 2014 dry season, a total of 244 prey animals was recorded and this led to a total score of 66.0 for the relative prey density.

Table 19: Overview of the potential prey access for W2014 & D2014. The following abbreviations have been used: W14_95_absl = absolute number of prey animals within the 95% HR polygon for the W2014. D14_50_rel = sum of the relative abundances of prey within 50% HR polygon for the D2014. W14_tot_abs/rel = total number (absolute/relative) of prey potentially available per season (all points A1 to G4 considered). W14_%_abs_acc = percentage of the total of prey (absolute/relative) within the 95% HR of an animal. Ronja & Salome = female leopards, Mexico & Orange = male lions, the rest are lionesses.

prey_access	Ronja	Salome	Fiona	Madge	Jane	Lara	Notch	Mexico	Orange
W14_95_abs	75	17	148	0	0	50	80	52	93
W14_95_rel	14.0	2.5	29.5	0.0	0.0	11.0	16.6	17.0	19.0
W14_50_abs	23	0	27	0	0	0	39	24	19
W14_50_rel	4.0	0.0	3.0	0.0	0.0	0.0	10.0	4.0	6.5
D14_95_abs	148	0	190	0	0	148	144	59	98
D14_95_rel	39.5	0.0	47.5	0.0	0.0	42.0	36.5	17.5	31.0
D14_50_abs	28	0	26	0	0	0	64	31	30
D14_50_rel	10.5	0.0	5.5	0.0	0.0	0.0	22.0	5.5	9.0
W14_%_abs_acc	32.6	7.4	64.3	0.0	0.0	21.7	34.8	22.6	40.4
W14_%_rel_acc	27.2	4.9	57.3	0.0	0.0	21.4	32.2	33.0	36.9
D14_%_abs_acc	60.7	0.0	77.9	0.0	0.0	60.7	59.0	24.2	40.2
D14_%_rel_acc	59.8	0.0	72.0	0.0	0.0	63.6	55.3	26.5	47.0
W14_tot_abs	230	230	230	230	230	230	230	230	230
W14_tot_rel	51.5	51.5	51.5	51.5	51.5	51.5	51.5	51.5	51.5
D14_tot_abs	244	244	244	244	244	244	244	244	244
D14_tot_rel	66.0	66.0	66.0	66.0	66.0	66.0	66.0	66.0	66.0

Most values for the female leopard PF12_Salome and the lionesses LF14_Madge and LF16_Jane are equal to zero, and therefore, they do not have access to prey recorded along the 7 transects. This is plausible as the extensive home range analysis of the first research question revealed that PF12_Salome left KGR shortly after her release and LF14_Madge and LF16_Jane are known to have their home ranges further north. Consequently, these animals are excluded of any further analysis and a comparison between leopards is no longer possible. Values for LF17_Lara are only available for the 95% home range, but not for the 50% home range.

Of the remaining 5 lions, LF09_Fiona recorded the highest values for all 4 percentage calculations. She potentially had access to 57.3% to 77.9% of all prey animals recorded during this period. While the two pride males LM07_Mexico (22.6% to 33.0%) and LM08_Orange (36.9% to 47.0%) show fairly stable percentages over the course of the year, the two females LF17_Lara (21.4% to 63.6%) and LF18_Notch (32.2%

to 59.0%) exhibit a significant increase between the wet and the subsequent dry season. At the 95% home range level, LF09_Fiona had access to most prey animals, with absolute values of 148 (W2014) to 190 (D2014) and relative values of 29.5 (W2014) to 47.5 (D2014). At the core area level, the highest values were calculated for LF18_Notch. Absolute values ranging from 39 (W2014) to 64 (D2014) and relative values from 10.0 (W2014) to 22.0 (D2014).

20.1. Leopards

Compared to the 2014 wet season (75 animals), PF07_Ronja had access to almost twice as many prey animals in the 2014 dry season (148 animals). Simultaneously, the relative prey score almost tripled from 14.0 to 39.5 (95% HR), and 4.0 to 10.5 (50% HR), respectively. The increase in prey access can be explained with her migration from the Southern farmlands back into CKGR and KGR (Figure 41).

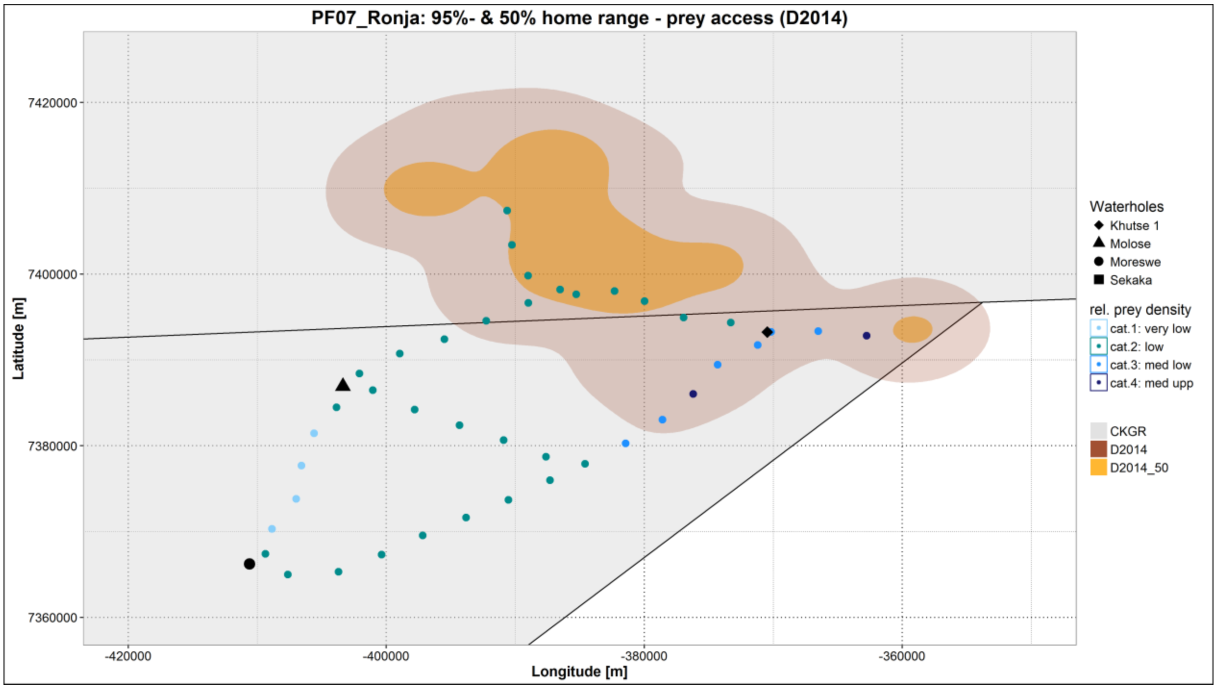


Figure 41: Potential prey access of PF07_Ronja during the 2014 dry season.

20.2. Lions

LF09_Fiona's prey access figures show a distinct pattern, especially when comparing them with other lions. While the absolute and relative figures for the 95% home range are significantly larger than the ones of other individuals, the numbers for the 50% home range are smaller. This can be observed for both, the wet- and the dry season. As shown in Figure 42, LF09_Fiona had two main areas for her core area during the 2014 dry season. The one at the border between, CKGR and KGR is located in an area with high prey densities, the other one further south in a scarce environment Figure 40b.

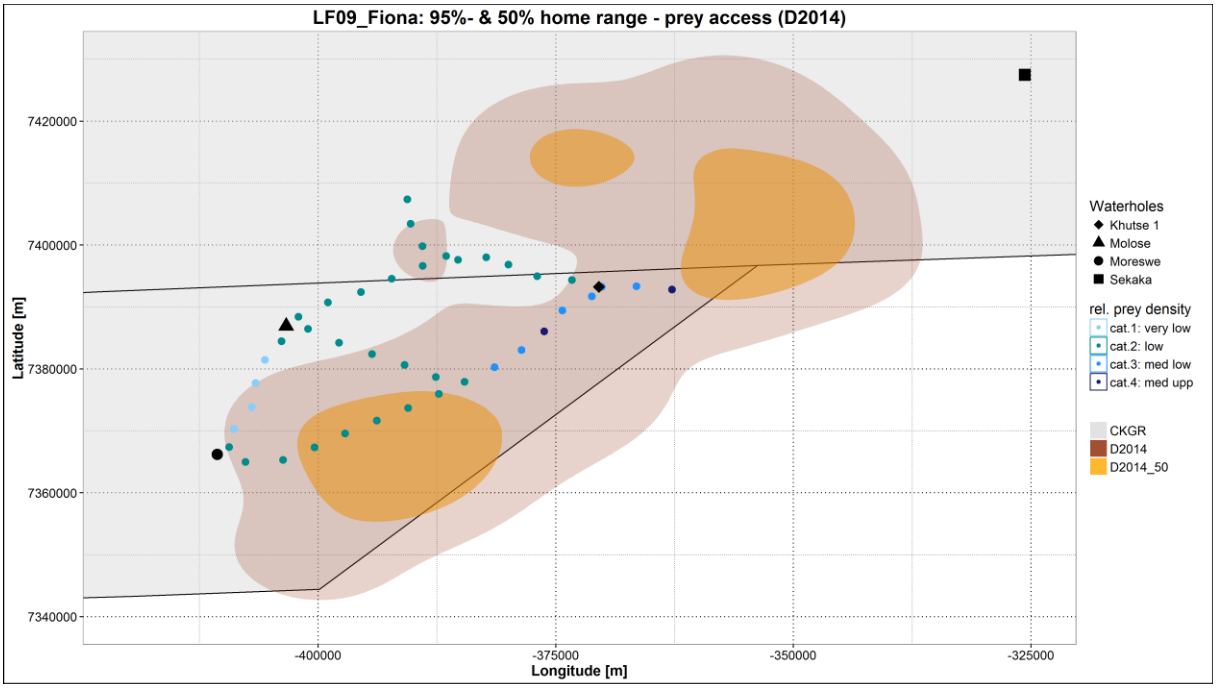


Figure 42: Potential prey access of LF09_Fiona during the 2014 dry season.

While the absolute and relative prey numbers remained fairly stable at the core area level during the year 2014 (27 and 3, W2014 and 26 and 5.5, D2014), LF09_Fiona managed to raise the numbers at the 95% home range level. Absolute numbers increased from 148 to 190 (+28.4%) and the relative prey score from 29.5 to 47.5 (+61.0%). As noted above, no prey counting point is located within the core area of LF17_Lara, but several ones within her 95% home range (Figure 43).

During the 2014 dry season, LF17_Lara started her migration south (Figure 43), crossing KGR, into the farmlands. The plot further reveals an expansion of her 95% home range to the East. These migrations were the main reason for a massive increase of the potential prey access during the 2014 dry season. The movement to the East led her into an area with high prey densities, close to the Khutse 1 waterhole.

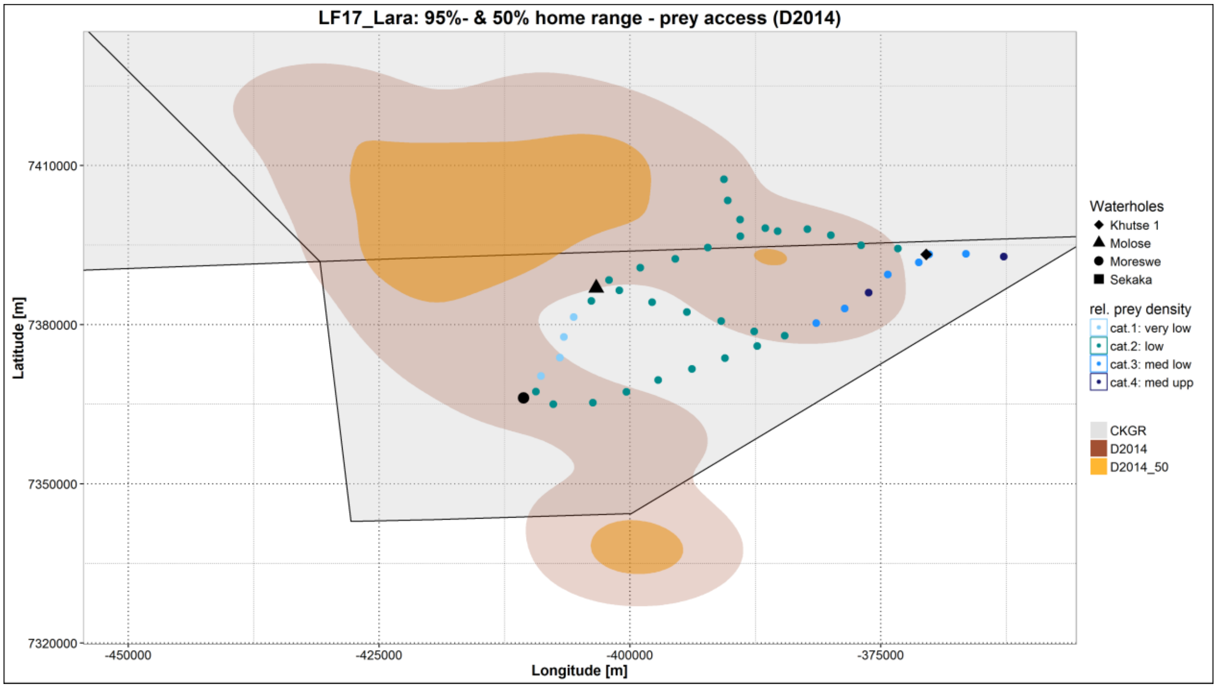


Figure 43: Potential prey access of LF17_Lara during the 2014 dry season.

For LF18_Notch, the highest values for the core area were recorded. Between the 2014 wet- and dry seasons, absolute numbers increased by 80% (95% HR) and 64% (50% HR) and relative numbers by 120% for both, the 95% home range and the core area.

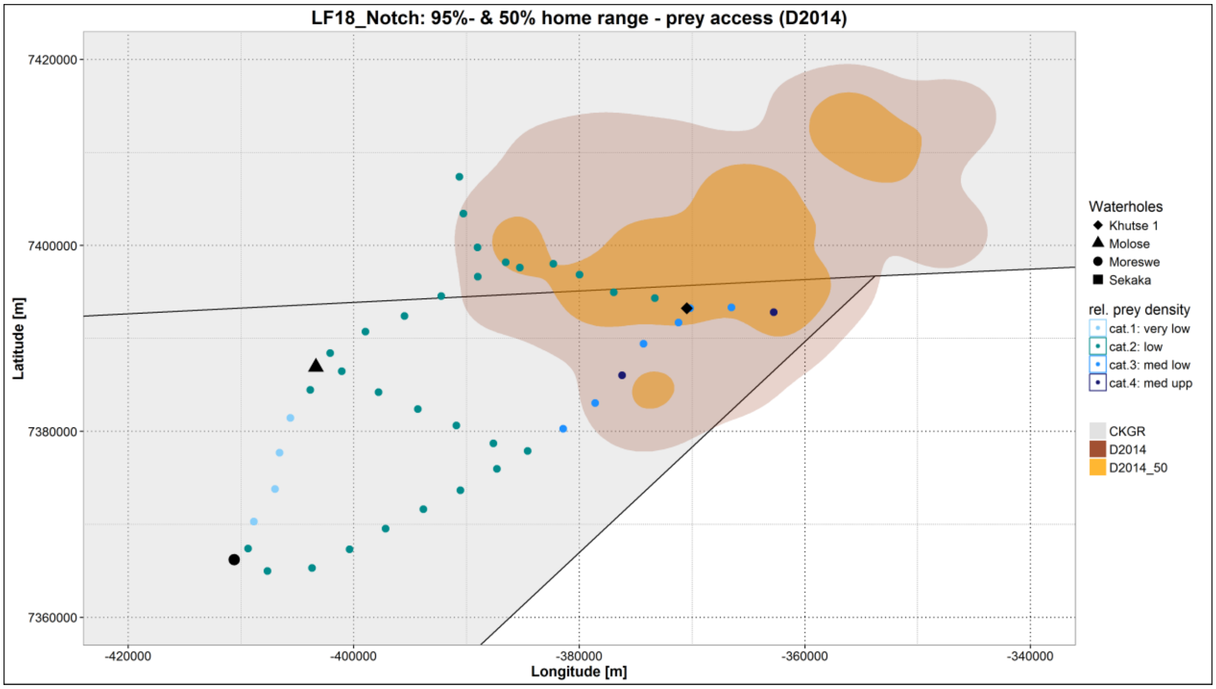


Figure 44: Potential prey access of LF18_Notch during the 2014 dry season.

Unlike the lionesses LF09_Fiona or LF17_Lara, LF18_Notch maintained a stable home range without major changes in location. As illustrated in Figure 44, LF18_Notch maintained her core area along the border of

CKGR and KGR and had access to the Khutse 1 waterhole. Further one can see a slight movement towards the eastern border of KGR during the dry season where prey densities were highest.

LM07_Mexico, pride male of the Moloso group, had his home range and core area established around the Molose waterhole in the centre of KGR (Figure 45). In contrast to the other lions, the number of potential prey within his home range remained fairly stable between the 2014 wet- and dry seasons.

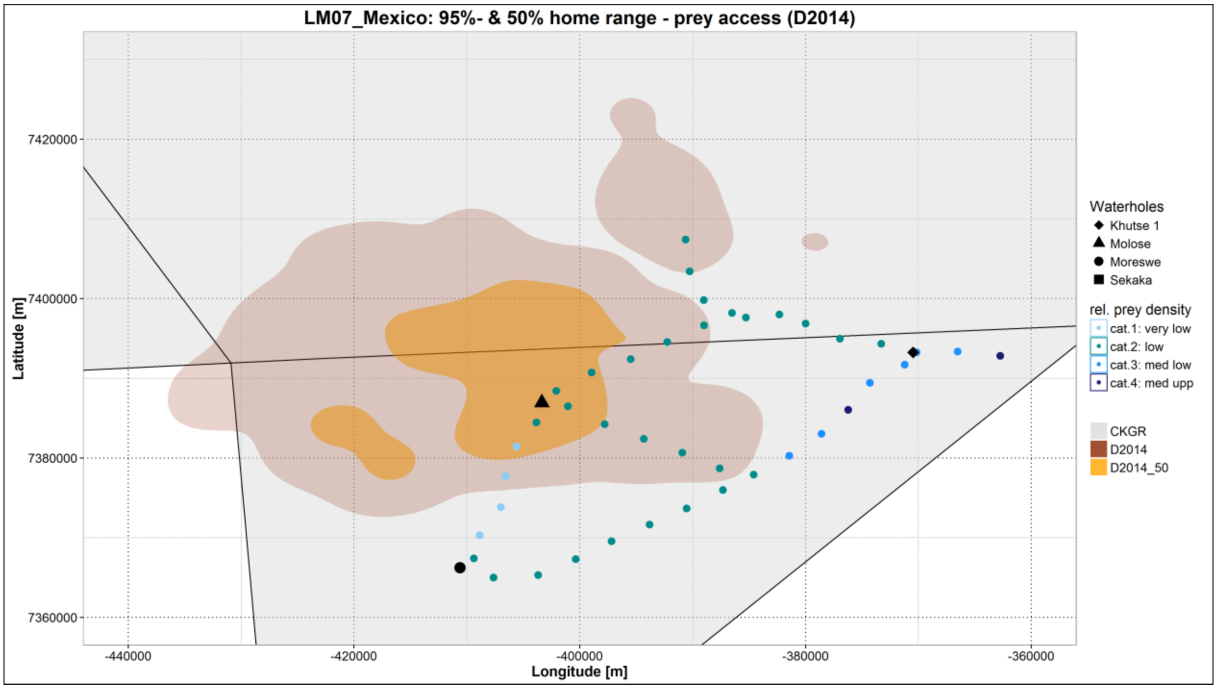


Figure 45: Potential prey access of LM07_Mexico during the 2014 dry season.

While absolute numbers increased from 52 to 59 (+13.5%, 95% HR) and from 24 to 31 (+29.2%, 50% HR), the relative prey density score increased from 17.0 to 17.5 (+2.9%, 95% HR) and from 4.0 to 5.5 (+37.5%, 50% HR). Therefore, the differences at the core area level are more pronounced than at the 95% home range level. Despite these increases, the percentage of prey animals within the range of LM07_Mexico remains fairly low compared to other resident lions, for example LF18_Notch or LM08_Orange.

The pride male of the East Khutse group, LM08_Orange, shows the same pattern as all other lions with increasing numbers for both, the absolute and the relative number of potential prey access. Over the course of the year 2014, the absolute numbers increased by 5.4% (from 93 to 98, 95% HR) and 57.9% (from 19 to 30, 50% HR). The relative prey score rose by 63.2% (from 19.0 to 31.0, 95% HR) and 38.5% (from 6.5 to 9, 50% HR). Similar to LF18_Notch, LM08_Orange's core area is located at the border of CKGR and KGR including the Khutse 1 waterhole (Figure 46). Despite being members of the same pride, LF18_Notch's numbers are significantly higher than those of LM08_Orange. The only exception is at the 95% home range level during the 2014 wet season.

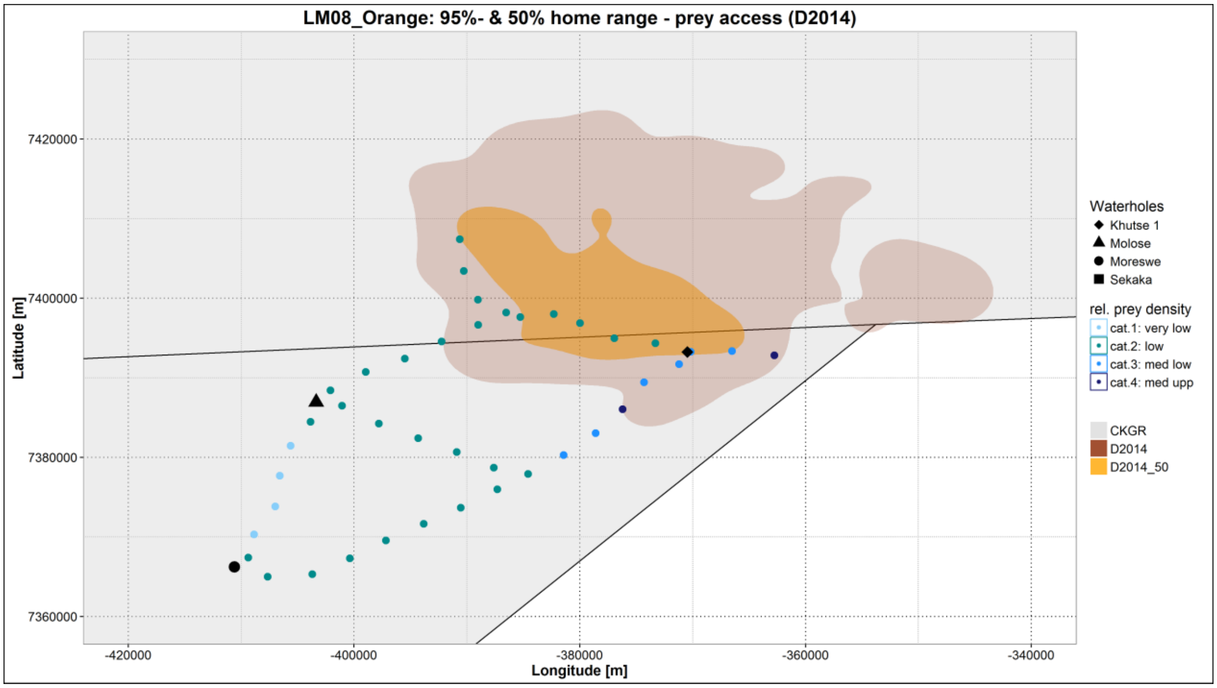


Figure 46: Potential prey access of LM08_Orange during the 2014 dry season.

21. Discussion

The discussion is subdivided into two parts. In the first part, the methodology of estimating the potential prey availability is discussed, while in the second part the focus is on how predators reacted to environmental factors.

21.1. Methodology

As the dataset, especially the prey counts data, are not yet available for several consecutive years, the possibilities for an extensive analysis were limited. This has an influence on the significance of the results, as a cross comparison between two consecutive time intervals, e.g. dry seasons, is not possible. As described in Keith et al. (1980), the transect method itself can potentially bias the results just based on how it works. The detection of all animals within the defined perimeter, disturbances by the researcher or the interpolation method of prey numbers are potential sources of bias. Yet, the simplicity of the data acquisition and the low costs are among the main advantages of the transect method (Fewster et al. 2005; Keith et al. 1980). As usually one sample per month is recorded, an extraordinarily high or low number of animals could have a significant effect on the overall result. Nevertheless, the line transect method is a decent method to estimate the number of free-living animals within a certain area (Bankert et al. 2003; Fewster et al. 2005; Keith et al. 1980; Stephens et al. 2006).

The point-in-polygon method was useful to a certain degree to get a first information about the potential numbers of prey animals within the home range of a predator. However, the consideration of the relative prey densities proved difficult, especially along contiguous isopleths. As illustrated in Figure 47, the distance between two isopleths is sometimes very small and thus the gradient of the interpolated is very steep. However, no point is located within the 5- or 6-isopleth. Based on the point-in-polygon test this would mean that the respective animal has no access to these areas. In reality however, this assumption is hardly justifiable as the prey animals move around. The same problem occurred with the borders of the MCP around all sampling points. In this case, the MCP was extended by 10% (Zucchini 2016), which is somewhat arbitrary, and there is no information about the prey densities beyond the MCP. Consequently, the point-in-polygon test was useful to get a feeling of the potential number of prey animals within a predator's home range, but there is still a high uncertainty. Furthermore, the method chosen for the interpolation and its characteristics do have an influence on the calculated prey densities (Keith et al. 1980; Lonergan et al. 2009). Different parameter settings for the could lead to different prey densities, which then have a direct influence on the statements about the potential access to prey for several predators.

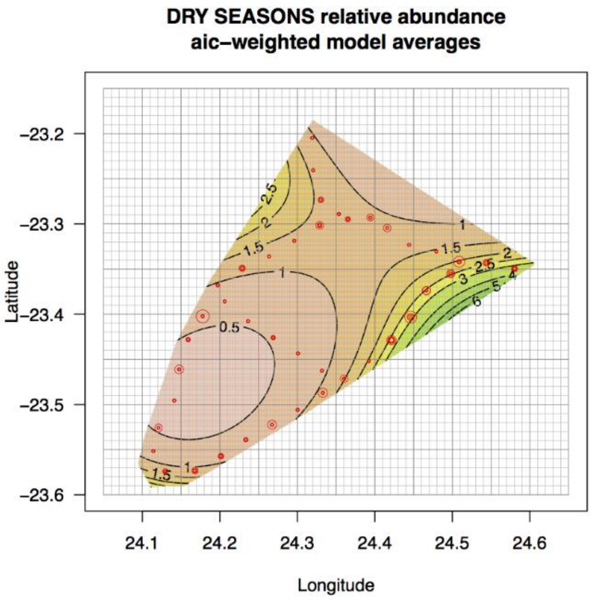


Figure 47: Relative prey densities in the study area. Note the high density of isopleths in the eastern part of the plot. Plot by Zucchini (2016).

21.2. Environmental factors

Precipitation: Precipitation seems to be a key driver behind the spatial distribution of prey animals in CKGR and KGR. The total amount of precipitation, especially the 532.4 mm recorded at Khutse Camp, underlined that the 2014 wet season was extraordinarily wet. The 2014 dry season on the other hand was extremely dry and no precipitation was recorded for the whole period between the start of June and end of September. The findings of Zucchini (2016) indicated that prey densities were significantly higher during the 2014 dry season than the 2014 wet season (Figure 40 a & b). Consequently, there is a high probability that the amount of precipitation had an influence on the spatial distribution of prey animals. Loveridge et al. (2009), Macdonald & Loveridge (2010), Patterson et al. (2014) and Tuqa et al. (2014) support these findings of prey densities being higher in the dry season. Nevertheless, a detailed analysis over several years would be necessary to confirm this hypothesis.

Waterholes: Based on the prey density plots of Zucchini (2016), it is likely the case that waterholes are more important for prey animals during the dry season than the wet season. While there is no obvious difference of prey densities between areas with steady waterholes and areas without during the wet season, there is a potential correlation in the dry season. As illustrated in Figure 47, the proximity to a waterhole seems to be beneficial for higher prey densities. This trend is detectable for the Khutse 1 waterhole in the East but also to a certain degree for the Moreswe waterhole in the Southwest. No such trend was detectable for the Moloso waterhole, and analysis for the Sekaka waterhole was not possible as it is located outside the prey sampling area. Several researchers (Balme et al. 2007; Celesia et al. 2010; Nash et al. 2012; Valeix et al. 2012) stressed the importance of steady water sources for herbivores as they must drink frequently.

Predators on the other hand are less dependent on water as they, to a certain degree, are able to cover their need for water by consuming prey[7].

Access to prey: The absolute as well as the relative number of prey animals recorded was higher for the 2014 dry season than for the wet season. Therefore, the predators potentially had access to more prey during this period. The calculated relative and absolute numbers calculated for all analysed lions, LF09_Fiona, LF17_Lara, LF18_Notch, LM07_Mexico and LM08_Orange, and the remaining leopard PF07_Ronja confirmed, that prey availability within their home range and core area was higher during the 2014 dry season.

Nevertheless, one must keep in mind that not all individuals of the tracked species were recorded and the actual availability of prey potentially could have been lower or higher. Among the recorded animals there are several species, such as hartebeest, kudus or wildebeest, which are out of range for a leopard. On the other hand, leopards are known to have a very broad diet, which includes many small animals such as birds or rodents that are not included in the analysis (Hayward et al. 2006). Consequently, the results PF07_Ronja could be different from the reality.

The comparison of the prey access of the nomadic lioness LF09_Fiona to the three resident lions LF18_Notch, LM07_Mexico and LM08_Orange revealed that LF09_Fiona had access to more prey animals within her home range than the other lions. They on the other hand had more prey within their core area. The first finding is not surprising as LF09_Fiona's home range for the two time intervals was more than twice the size than the ones of LF18_Notch, LM07_Mexico or LM08_Orange. Yet, at the core area level, the three resident lions, especially the female LF18_Notch, had access to more prey animals. Further, they all had permanent water sources within their core area, which seems to be beneficial during the dry season. Consequently, the resident lions were able to maintain a high quality habitat with high prey numbers within their core area. LF09_Fiona on the other hand was not able to establish her core area in a high quality environment. These findings are in line with the hypothesis of several researchers (Mosser & Packer 2009; Spong 2002; Tuqa et al. 2014), who stated that dominant prides should be able to defend the best habitats. Further, a negative correlation between home range size and habitat quality was described by Haas et al. (2005) and Taylor & Victoria (2010).

The analysis of the home range estimation in Chapter 16 revealed that the volume of intersection of LF18_Notch and LM08_Orange is considerably smaller than one would expect by just looking at the overlap measure. A similar development is evident regarding access to prey animals. While the absolute and relative numbers of LM08_Orange were only bigger at the 95% home range level during the 2014 wet season, in the other three cases values for LF18_Notch were significantly higher. A potential reason could be the different interests and duties of male and female lions within the same pride. As one of two pride

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[7] Personal communication with Stephen Henley, August 2016

males, LM08_Orange is responsible for the defence of their home range against other male conspecifics. Additionally, he is interested in mating with as many females as possible to secure his lineage (Haas et al. 2005; Macdonald & Loveridge 2010). Female lions collectively care for all cubs within a pride and while male lions only occasionally join the hunts, female lions always take part (Celesia et al. 2010; Haas et al. 2005; Loarie et al. 2013; Loveridge et al. 2009; Macdonald & Loveridge 2010). This behaviour of male and female lions could be one reason for the pronounced difference in prey access.

However, one must keep in mind that the whole ecosystem and the interaction between several species is highly complex, with numerous contributing factors (Celesia et al. 2010). The above mentioned differences in behaviour are only one potential explanation and there are many other factors which might be stronger. Vegetation cover, the presence of conspecifics or the actual abundance of prey at a certain time close to the pride do have an influence as well.

21.3. Home range size

After an enormous expansion after the 2013 dry season, the home range size during the 2014 wet- and dry seasons were among the largest maintained by PF07_Ronja. During this period, PF07_Ronja left her inherent home range and migrated south. Consequently, the size of her home range increased massively. Changing prey abundance could be among the reasons for the expansion but also the presence of conspecifics or other predators. A conclusive statement is not possible. Analogical, it would be unsafe to declare the expansions of lion home range sizes after the 2013 dry season as a reaction to variations in precipitation and prey densities of the subsequent 2014 wet season, especially as LF17_Lara, LM07_Mexico or LM08_Orange did not show very distinct changes in their home range or core area size. Intraspecific competition could just as well be the driver behind these adaptions. Again, changes in prey availability could be among the drivers for increases or decreases in home range size but other factors are likely to contribute as well. In order to be able to make meaningful statements about a potential correlation it would be essential to have data of several consecutive years.

VIII Conclusion

22. Major findings

The extensive analysis of lion and leopard home ranges in the CKGR and KGR revealed that spatio-temporal variations in size and location frequently occurred. Yet, the determination of factors contributing to or triggering these variations proved to be difficult. With home range sizes ranging from 58 km^2 to 2411 km^2 it was confirmed that leopard home ranges in the Central Kalahari belong to the largest worldwide (Bothma et al. 1997; Zehnder 2015). Based on the results of the four analysed leopards, a tendency towards home ranges being smaller during the wet season was detected. Raising cubs might be the main factor for home ranges of females being smaller during the wet season. These findings are in contrast to the literature, where no distinct seasonality is described. Home ranges of male leopards frequently overlapped the home ranges of females, which is in line with the literature (Bothma et al. 1997; Stein & Hayssen 2013; Zehnder 2015). All tracked leopards predominantly inhabited an area within the borders of KGR and CKGR and escapes were an exception.

The analysis of the 10 lions revealed that their home ranges from 285 km^2 to 5991 km^2 belong to the largest recorded worldwide and the results are in line with the literature (Macdonald & Loveridge 2010; Zehnder 2015). However, one must distinguish between resident lions living in stable prides and nomadic lions in search for niches. Unusually large or small home ranges were calculated for lions that are known to live either solitarily or in a small group unable to establish an own home range. Unlike in the study of Loveridge et al. (2009), home ranges of male lions were not larger than the ones of females. In contrast to leopards, a slight tendency for lion home ranges being larger during the wet season was found. Nomadic lions could be characterised by changing the location of their home range frequently and often over distances of 10 to 30 km. Volume of intersection measures suggested that these lions do actively avoid the proximity of resident prides. While LF17_Lara was known to have her home range established outside the protected areas, no seasonal trend of escapes was detected for the other lions.

The analysis of the precipitation, waterholes and prey access revealed that in this arid environment rain is among the most important factors influencing prey densities and therefore also the spatial distribution of predators. Based on the data of the year 2014, there is a negative correlation between prey densities and precipitation and therefore higher prey densities were recorded for the 2014 dry season. Further, waterholes seem to be a beneficial element within a predator's home range or core area, as water dependent prey animals gather around these spots during the peak of the dry season. The overall prey access appears to be different for resident or nomadic lions, respectively, as well as between males and females. While relative and absolute prey numbers were higher for the core area of resident lions, they were higher for the 95% home range of nomadic lions. These findings support the hypothesis in the literature (Mosser & Packer 2009; Spong 2002; Tuqa et al. 2014) that dominant prides should be able to defend the highest quality habitat.

There is a chance of home range and core area sizes being related to the availability of prey animals, but due to the limited data available no conclusive statement was possible. However, all these findings are based on datasets covering only a single year, and consequently, the are not robust and should not be overrated.

Summarising the results for the 10 lions and 4 leopards analysed, one can conclude that their home ranges are among the largest worldwide, and size and location change frequently. However, a pronounced seasonality is not evident. Of all factors influencing the space use of lions and leopards, the proximity of conspecifics, precipitation and the abundance of prey are likely among the most important. Yet, a quantification is difficult as these factors are either difficult to measure and/ or are highly interdependent.

23. Limitations

The choice of KDE as primary home range estimator was based on the considerations that it is an approved method and strengths and weaknesses are known. Yet, the size of the calculated home ranges is potentially larger than in reality as KDE, dependent on the bandwidth *h* chosen, is vulnerable to over-smoothing. Further, one must keep in mind that the choice of the reference bandwidth, *h* REF in this case, has significant influence on the results. Using LSCV instead of REF could have produced different results. The approach of using the more sophisticated method of BRB for the estimation of home ranges proved to be very difficult, as there was an extremely high variation in the results. A small adjustment of the smoothing parameter, which must be chosen based on the sampling interval, led to significantly different results for the size of home ranges. Over-smoothing and graining were identified as the two major issues. However, many of the difficulties were a result of the indirect approach necessary for the calculation of BRB and not due to the method per se.

The calculation of centroid shifts (> 10 km) using the 95% polygons of KDE proved to be a good indicator to detect significant changes in size and/ or location of a predator's home range. However, the type of change, increase or decrease, could not be determined. Further, one must be careful as the reverse argument is not valid. Overlap measures of the 95%- and 50% home range were sometimes unreliable as their values sometimes suggested a higher potential common space use of two predators than it might be the case in reality. In several cases, e.g. the comparison of LF18_Notch and LM08_Orange, the volume of intersection revealed that the common space use is less significant than one assumed based on the overlap measures. Additionally, the VI proved valuable to describe potential associations or avoidance of two animals.

The determination of the habitat quality with the potential access to prey animals proved to be difficult as only very limited data were available. Conducting a simple point-in-polygon was useful to get a first idea of the absolute and relative number of prey within the border of a predator's home range and core area. In reality, however, the distribution of prey animals is characterized by a higher complexity as prey is not static but mobile. An unsolved problem is how to deal with prey animals, within or just outside the MCP projected around the 7 transects (Figure 40 a & b), which are not allocated to a sampling point. At the moment, these animals are only qualitatively but not quantitatively included into the model. Another concern is the reliability of the results, as sampling sizes are too small for statistical testing. Consequently, no statements about the significance of the results are possible. The whole approach can be classified as experimental method to determine the quality of a predator's environment.

24. Future work

The two most important aspects of future work on the estimation of lion and leopard home ranges and the identification of potential factors affecting their space use are the availability of sufficient data as well as a deeper knowledge of the home range estimator and its implications on the results. Many results of the two research questions remain somehow speculative, as the available datasets were too small for statistical testing.

Tracking more lions and leopards would help to increase the reliability of the results and potential patterns, e.g. seasonality, could then be identified or one could conclude whether and why such patterns are not present. More meteorological datasets, a higher resolution vegetation cover map and more prey data are needed to increase the reliability of the results. Extending the area of sampling prey abundance and the use of different methods for the interpolation could be beneficial for further analyses and therefore to gain deeper knowledge and understanding of the space use of lions and leopard in and around CKGR and KGR.

References

Bacon, M.M. et al., 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildlife Society Bulletin*, 35(4), pp.409–415.

Balme, G.A. et al., 2013. Reproductive success of female leopards Panthera pardus: The importance of top-down processes. *Mammal Review*, 43(3), pp.221–237.

Balme, G., Hunter, L. & Slotow, R., 2007. Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, 74(3), pp.589–598.

Bankert, D., in ’t Groen, K.C.G. & van Wieren, S.E., 2003. A review of the transect method by comparing it with three other counting methods to estimate rabbit (Oryctolagus cuniculus) density. *Lutra*, 46(1), pp.27–34.

Bauer, D. et al., 2014. Using spoor and prey counts to determine temporal and spatial variation in lion (Panthera leo) density. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 92(2), pp.97–104.

Bauer, H. & Van Der Merwe, S., 2004. Inventory of free-ranging lions Panthera leo in Africa. *Oryx*, 38(1), pp.26–31.

Benhamou, S., 2011. Dynamic approach to space and habitat use based on biased random bridges. *PLoS ONE*, 6(1), p.e14592.

Benhamou, S. & Cornélis, D., 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. *Journal of Wildlife Management*, 74(6), pp.1353–1360.

Börger, L., Dalziel, B.D. & Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, 11(6), pp.637–650.

Bothma, J. d. P. et al., 1997. Range size of southern Kalahari leopards. *South African Journal of Wildlife Research*, 3, pp.94–99.

Bothma, J. du P. & Le Riche, E. a. N., 1984. Aspects of the ecology and the behavior of the leopard in the kalahari desert. *Koedoe*, Supplement, pp.259–279.

Boyce, M.S. et al., 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550), pp.2213–2219.

Burt, W.H., 1943. American Society of Mammalogists American Society of Mammalogists. *Journal of Mammalogy*, 24(3), pp.346–352.

Bullard, F., 1991. Estimating the Home Range of an Animal: A Brownian Bridge Approach. Department of Statistics. Chapel Hill, North Carolina, USA.

Byrne, M.E. et al., 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. *Journal of Animal Ecology*, 83(5), pp.1234–1243.

Celesia, G.G. et al., 2010. Climate and landscape correlates of African lion (Panthera leo) demography. *African Journal of Ecology*, 48, pp.58–71.

Downs, J.A., Horner, M.W. & Tucker, A.D., 2011. Time-geographic density estimation for home range analysis. *Annals of GIS*, 17(3), pp.163–171.

Dürr, S. & Ward, M.P., 2014. Roaming behaviour and home range estimation of domestic dogs in Aboriginal and Torres Strait Islander communities in northern Australia using four different methods. *Preventive Veterinary Medicine*, 117(2), pp.340–357.

Eason, P., 1992. Optimization of Territory Shape in Heterogeneous Habitats : A Field Study of the Red-Capped Cardinal (Paroaria gularis). *Journal of Animal Ecology*, 61(2), pp.411–424.

Ebdon, D., 1985. Statistics In Geography: A Practical Approach. Oxford, New York, USA: Wiley-Blackwell.

Eloff, F.C., 1998. The Life of the Kalahari Lion (Panthera Leo Vernayi). *Transactions of the Royal Society of South Africa*, 53(2), pp.267–269.

Fewster, R.M., Laake, J.L. & Buckland, S.T., 2005. Line Transect Sampling in Small and Large Regions Problems with the “ Buckland ” estimator Data truncation. *Biometrics*, 61(ii), pp.856–859.

Fieberg, J. et al., 2010. Correlation and Studies of Habitat Selection: Problem, Red Herring or opportunity? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, pp.2233–2244.

Fieberg, J. & Börger, L., 2012. Could you please phrase “home range” as a question? *Journal of Mammalogy*, 93(4), pp.890–902.

Frair, J.L. et al., 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550), pp.2187–200.

Gautestad, A.O. & Mysterud, I., 2005. Intrinsic scaling complexity in animal dispersion and abundance. *The American naturalist*, 165(1), pp.44–55.

Girard, I. et al., 2006. Balancing Number of Locations with Number of Individuals in Telemetry Studies. *The Journal of Wildlife Management*, 70(5), pp.1249–1256.

Girard, I. et al., 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management*, 66(4), pp.1290–1300.

Gitzen, R. a. & Millspaugh, J.J., 2003. Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. *Wildlife Society Bulletin*, 31(3), pp.823–831.

Haas, B.S.K. et al., 2005. Panthera leo. *Mammalian Species*, (762), pp.1–11.

Hansteen, T.L., Andreassen, H.P. & Ims, R.A., 1997. Effects of Spatiotemporal Scale on Autocorrelation and Home Range Estimators. *The Journal of Wildlife Management*, 61(2), pp.280-290.

Hayward, M.W. et al., 2009. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo elephant national park, South Africa. *Biodiversity and Conservation*, 18(4), pp.887–904.

Hayward, M.W. et al., 2006. Prey preferences of the leopard (Panthera pardus). *Journal of Zoology*, 270(2), pp.298–313.

Hayward, M.W. & Kerley, G.I.H., 2008. Prey preferences and dietary overlap amongst Africa’s large predators. *South African Journal of Wildlife Research*, 38(2), pp.93–108.

Hemson, G. et al., 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology*, 74(3), pp.455–463.

Henley, S., 2014. *Khutse Game Reserve - Seasons defined.*

Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C., 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74(3), pp.559–566.

Horne, J.S. et al., 2007. Analyzing animal movements using Brownian bridges. *Ecology*, 88(9), pp.2354–2363.

Jay, C. V., Fischbach, A.S. & Kochnev, A.A., 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Marine Ecology Progress Series*, 468, pp.1–13.

Katajisto, J. & Moilanen, A., 2006. Kernel-based home range method for data with irregular sampling intervals. *Ecological Modelling*, 194(4), pp.405–413.

Keating, K.A. & Cherry, S., 2009. Modeling utilization distributions in space and time. *Ecology*, 90(7), pp.1971–1980.

Keith, L.B. et al., 1980. Extimation of Density from Line Transect Sampling of Biological Populations. *Wildlife Monographs*, 72, pp.3–202.

Kerth, G. et al., 2013. Genetic sexing of stock-raiding leopards: not only males to blame. *Conservation Genetics Resources*, 5(4), pp.1101–1105.

Kie, J.G. et al., 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550), pp.2221–2231.

Kissui, B.M., 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Animal Conservation*, 11(5), pp.422–432.

Kochanny, C.O., 2005. Quantifying Home-Range Overlap : the Importance of the Utilization Distribution. *Journal of Wildlife Management*, 69(4), pp.1346–1359.

Kolowski, J.M. & Holekamp, K.E., 2006. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation*, 128(4), pp.529–541.

Kranstauber, B. et al., 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, 81(4), pp.738–746.

Lewis, J., Rachlow, J.L. & Vierling, L.A., 2007. Effects of habitat on GPS collar performance : using data screening to reduce location error. *Journal of Applied Ecology*, 44, pp.663–671.

Li, W., Goodchild, M.F. & Church, R., 2013. An efficient measure of compactness for two-dimensional shapes and its application in regionalization problems. *International Journal of Geographical Information Science*, 27(6), pp.1227–1250.

Lichti, N.I. & Swihart, R.K., 2011. Estimating utilization distributions with kernel versus local convex hull methods. *The Journal of Wildlife Management*, 75(2), pp.413–422.

Loarie, S.R., Tambling, C.J. & Asner, G.P., 2013. Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour*, 85(5), pp.899–906.

Lonergan, M., Fedak, M. & McConnell, B., 2009. The effects of interpolation error and location quality on animal track reconstruction. *Marine Mammal Science*, 25(2), pp.275–282.

Loveridge, A.J. et al., 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, 32, pp.953–962.

Macdonald, D.W. & Loveridge, A.J., 2010. *Biology and conservation of wild felids* D. W. MacDonald & A. J. Loveridge, eds., New York, New York, USA: Oxford University Press.

Marker, L.L. & Dickman, A.J., 2005. Factors affecting leopard (Panthera pardus) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research*, 35, pp.105–115.

Mishra, N. et al., 2015. Mapping Vegetation Morphology Types in Southern Africa Savanna Using MODIS Time-Series Metrics: A Case Study of Central Kalahari, Botswana. *Land*, 4, pp.197–215.

Mizutani, F. & Jewell, P., 1998. Home-range and movements of leopards (Panthera pardus) on a livestock ranch in Kenya. *Journal of Zoology*, 244, pp.269–286.

Mosser, A. & Packer, C., 2009. Group territoriality and the benefits of sociality in the African lion, Panthera leo. *Animal Behaviour*, 78(2), pp.359–370.

Nash, K., Goldberg, D.E. & Hartman, K.M., 2012. Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. *Ecology*, 93(11), pp.2490–2496.

Norton, P.M. & Henley, S.R., 1987. Home range and movement of male leopards in the Cederberg Wilderness area, cape province South Africa. *South African Journal of Wildlife Research*, 17(2), pp.41–48.

Odden, M. & Wegge, P., 2005. Spacing and activity patterns of leopards Panthera pardus in the Royal Bardia National Park, Nepal. *Wildlife Biology*, 11, pp.145–152.

Ogutu, J.O., Reid, R. & Bhola, N., 2005. The effects of pastoralism and protection on the density and distribution of carnivores and their prey in the Mara ecosystem of Kenya. *Journal of Zoology*, 265(3), pp.281–293.

Otis, D.L. & White, G.C., 1999. Autocorrelation of Location Estimates and the Analysis of Radiotracking. *The Journal of Wildlife Management*, 63(3), pp.1039–1044.

Palomares, F. & Caro, T.M., 1999. Interspecific Killing among Mammalian Carnivores. *The American Naturalist*, 153(5), pp.492–508.

Patterson, B.D. et al., 2004. Livestock predation by lions (Panthera leo) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation*, 119(4), pp.507–516.

Powell, R.A., 2000. Animal Home Ranges and Territories and Home Range Estimators Research Techniques in Animal Ecology. In New York, New York, USA: Columbia University Press, pp. 64–110.

Schiess-Meier, M. et al., 2010. *Leopard Ecology & Conservation - Annual Report 2010*.

Schiess-Meier, M., 2013. *Leopard Ecology & Conservation - Annual Report 2013*.

Schiess-Meier, M., 2014. *Leopard Ecology & Conservation - Annual Report 2014*.

Schiess-Meier, M. et al., 2007a. Livestock Predation—Insights From Problem Animal Control Registers in Botswana. *Journal of Wildlife Management*, 71(4), pp.1267–1274.

Schiess-Meier, M., Graf, J. & Graf, C., 2011. *Leopard Ecology & Conservation - Annual Report 2011*.

Schiess-Meier, M. & Mills, D., 2007. *Leopard Ecology & Conservation - Annual Report 2007*.

Schiess-Meier, M. & Mills, D., 2008. *Leopard Ecology & Conservation - Annual Report 2008*.

Seaman, D.E. & Powell, R.A., 1996. An Evaluation of the Accuracy of Kernel Density Estimators for Home Range. *Ecology*, 77(7), pp.2075–2085.

Shamoun-Baranes, J. et al., 2012. From Sensor Data to Animal Behaviour: An Oystercatcher Example. *PLoS ONE*, 7(5), p.e37997.

Silverman, B.W., 1986. Density estimation for statistics and data analysis. *Monographs on Statistics and Applied Probability*, 37(1), pp.1–22.

De Solla, S.R., Bonduriansky, R. & Brooks, R.J., 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, 68(2), pp.221–234.

Spong, G., 2002. Space use in lions, Panthera leo, in the Selous Game Reserve: Social and ecological factors. *Behavioral Ecology and Sociobiology*, 52(4), pp.303–307.

Stein, A.B. & Hayssen, V., 2013. Panthera pardus (Carnivora : Felidae). *Mammalian Species*, 45(900), pp.30–48.

Stephens, P.A. et al., 2006. Estimating population density from indirect sign: Track counts and the Formozov-Malyshev-Pereleshin formula. *Animal Conservation*, 9(3), pp.339–348.

Swanepoel, L.H. et al., 2015. Survival rates and causes of mortality of leopards Panthera pardus in southern Africa. *Oryx*, 49(4), pp.595–603.

Swanepoel, L.H., Dalerum, F. & van Hoven, W., 2010. Factors affecting location failure of GPS collars fitted to African leopards (Panthera pardus). *South African Journal of Wildlife Research*, 40(1), pp.10–15.

Swihart, R.K. & Slade, N.A., 1985. Influence of Sampling Interval on Estimates of Home-Range Size. *Journal of Wildlife Management*, 49(4), pp.1019–1025.

Swihart, R.K. & Slade, N.A., 1997. On Testing for Independence of Animal Movements. *Journal of Agricultural, Biological, and Environmental Statistics*, 2(1), pp.48–63.

Tambling, C.J. et al., 2010. Methods for locating African lion kills using global positioning system movement data. *Journal of Wildlife Management*, 74(3), pp.549–556.

Tomkiewicz, S.M. et al., 2010. Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 365(1550), pp.2163–2176.

Tuqa, J.H. et al., 2014. Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*, 2, pp.1–10.

Valeix, M. et al., 2012a. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology*, 49(1), pp.73–81.

Weilenmann, M. et al., 2010. Is translocation of stock-raiding leopards into a protected area with resident conspecifics an effective management tool? *Wildlife Research*, 37(8), pp.702–707.

Winterbach, H.E.K. et al., 2013. Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, 43(2), pp.89–110.

Winterbach, H.E.K., Winterbach, C.W. & Somers, M.J., 2014. Landscape Suitability in Botswana for the Conservation of Its Six Large African Carnivores. *PLoS ONE*, 9(6), pp.1–12.

Woodroffe, R. & Frank, L.G., 2005. Lethal control of African lions (Panthera leo): local and regional population impacts. *Animal Conservation*, 8(1), pp.91–98.

Worton, B.J., 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. , 70(1), pp.164–168.

Zehnder, A., 2015. *Home range analyses and kill site detection of lions and leopards in the Kalahari , Botswana.* Department of Geography. University of Zurich, Switzerland.

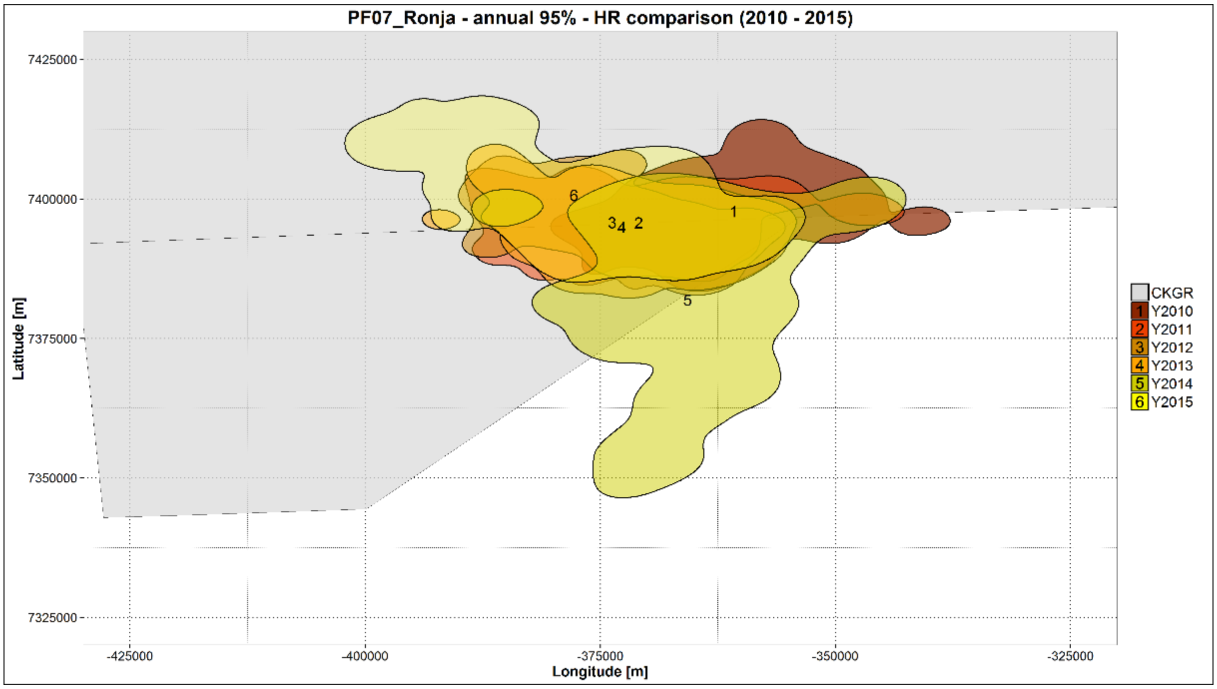
Zucchini, W., 2016. Notes on the maps of prey distribution. , pp.1–23.

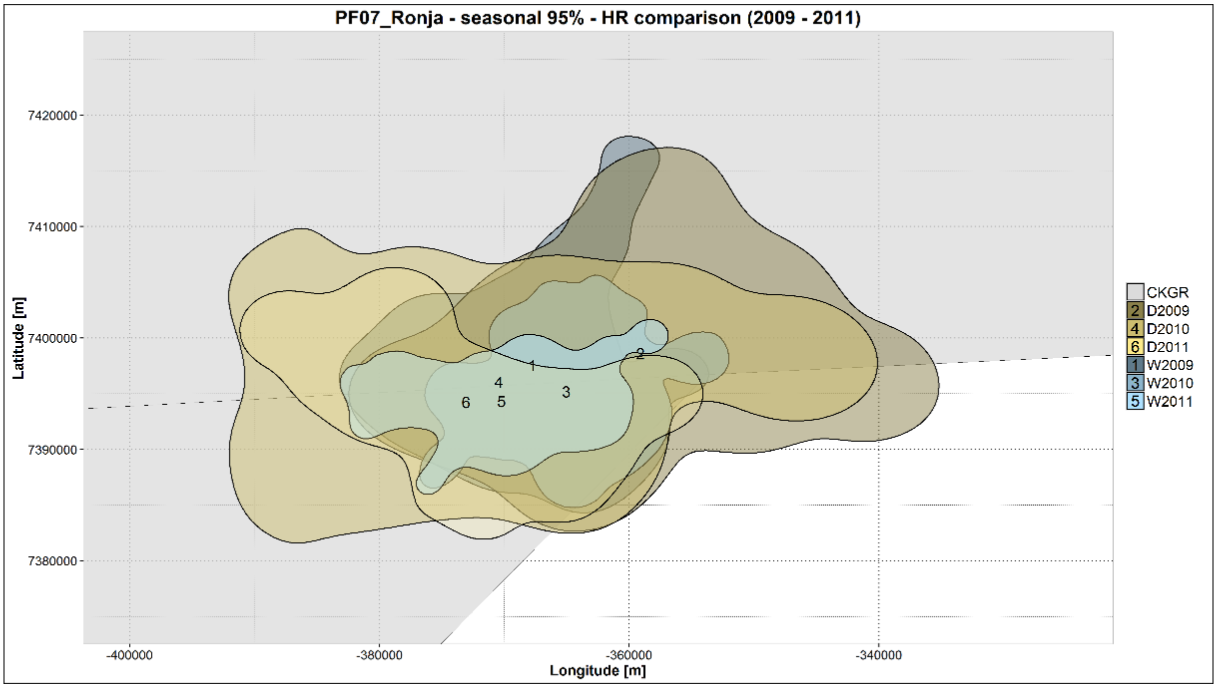
Appendix

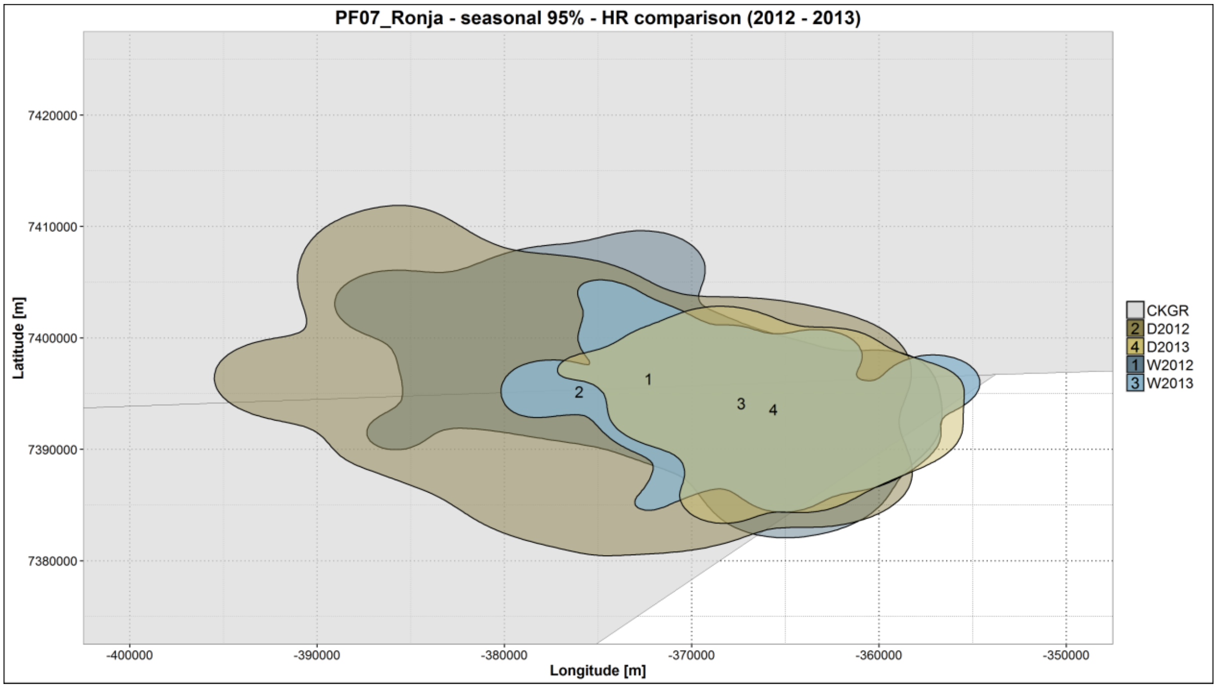
A1: Seasonal variation of lion and leopard home ranges

Leopards

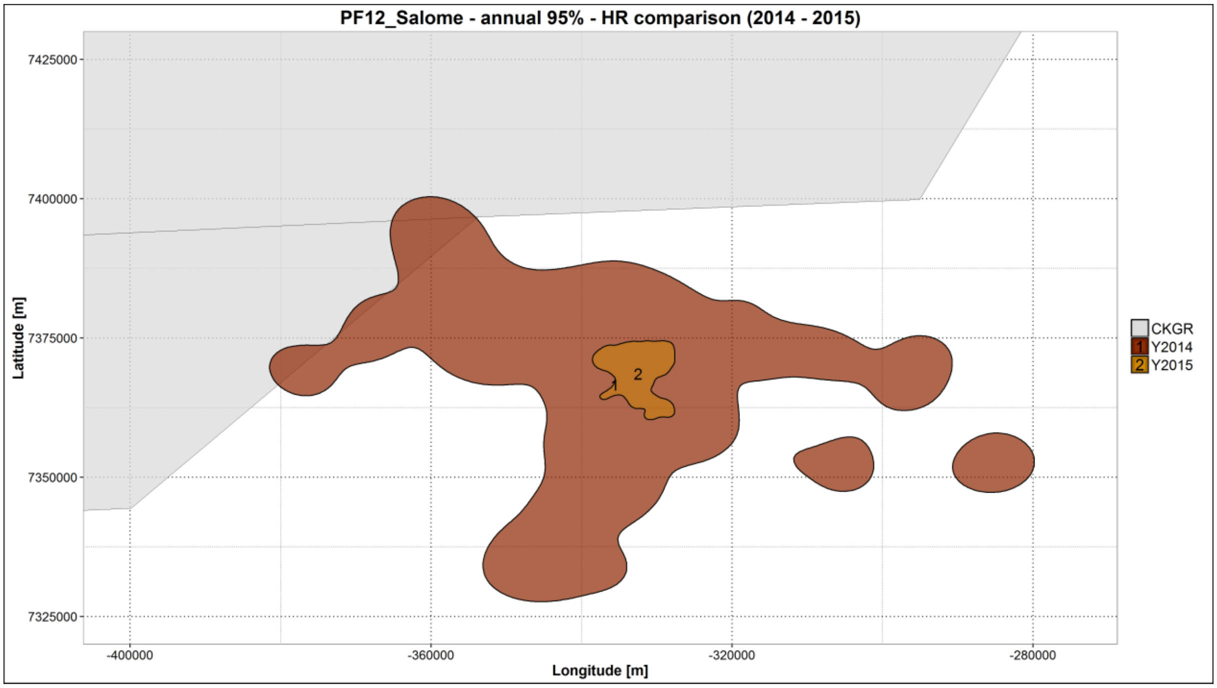
PF07_Ronja



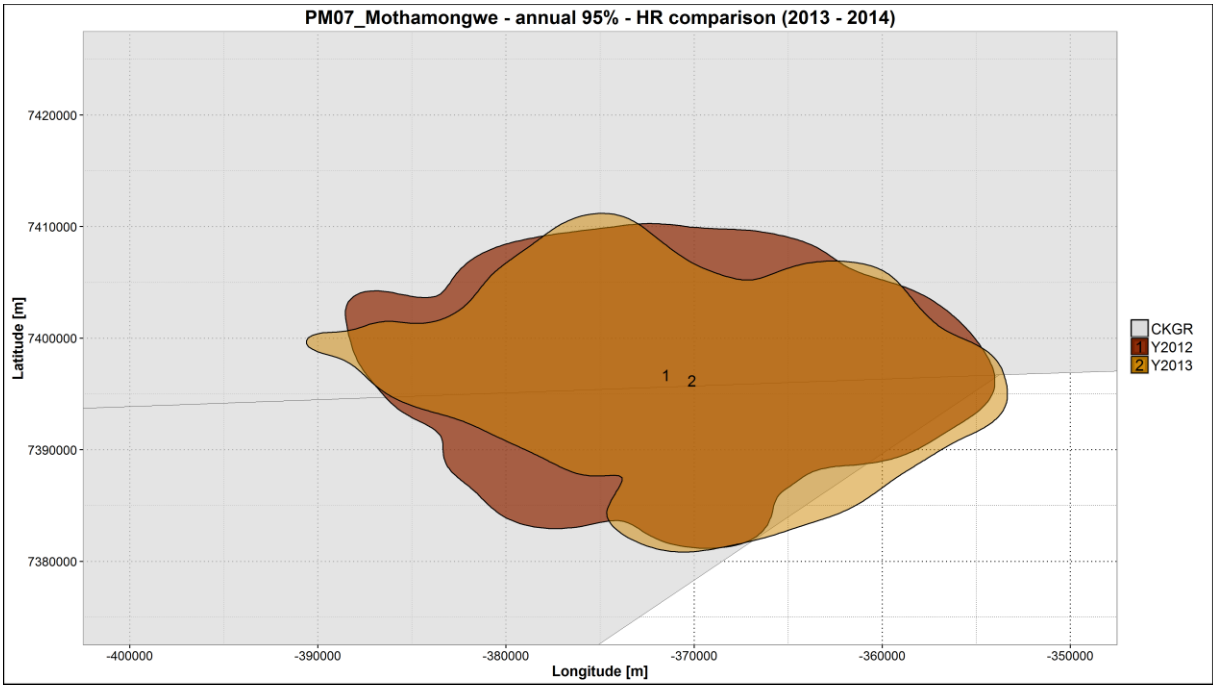



PF07_Ronja - seasonal 95% - HR comparison (2012 - 2013)
7420000
7410000
7400000
7390000
7380000
Latitude [m]
-400000
-390000
-380000
-370000
-360000
-350000
Longitude [m]
1
2
3
4
CKGR
2 D2012
4 D2013
1 W2012
3 W2013

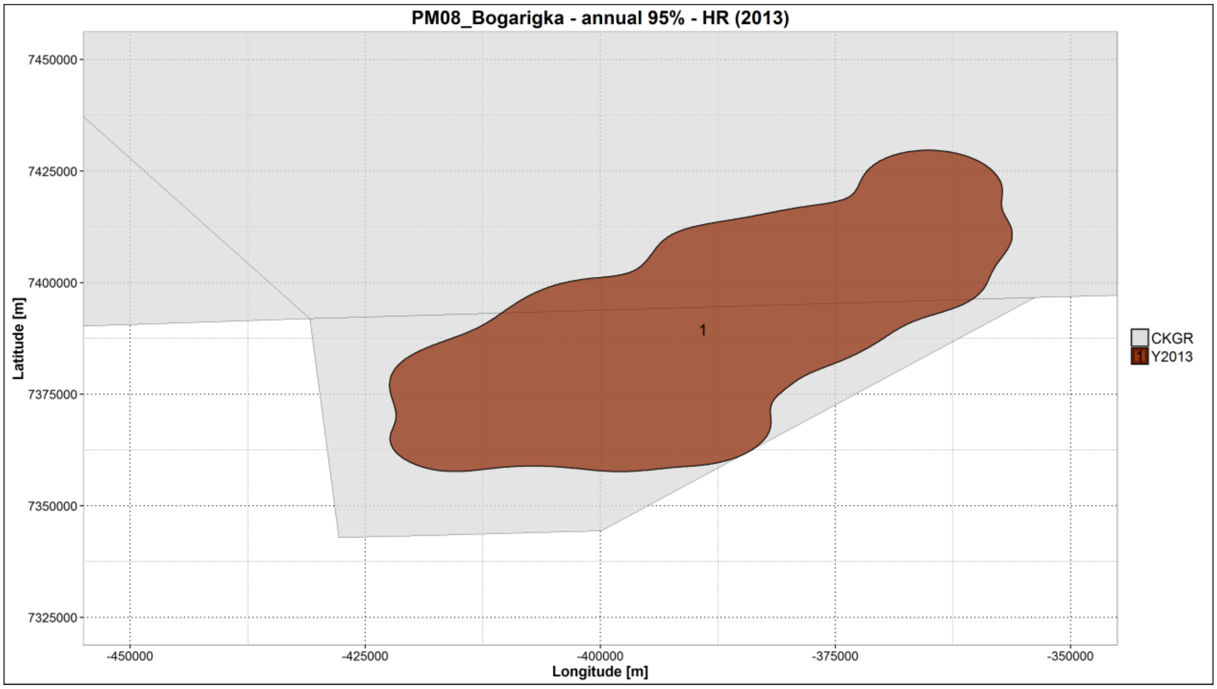
PF12_Salome


PF12_Salome - annual 95% - HR comparison (2014 - 2015)
7425000
7400000
7375000
7350000
7325000
Latitude [m]
-400000
-360000
-320000
-280000
Longitude [m]
1
2
CKGR
1 Y2014
2 Y2015

PM07_Mothamongwe

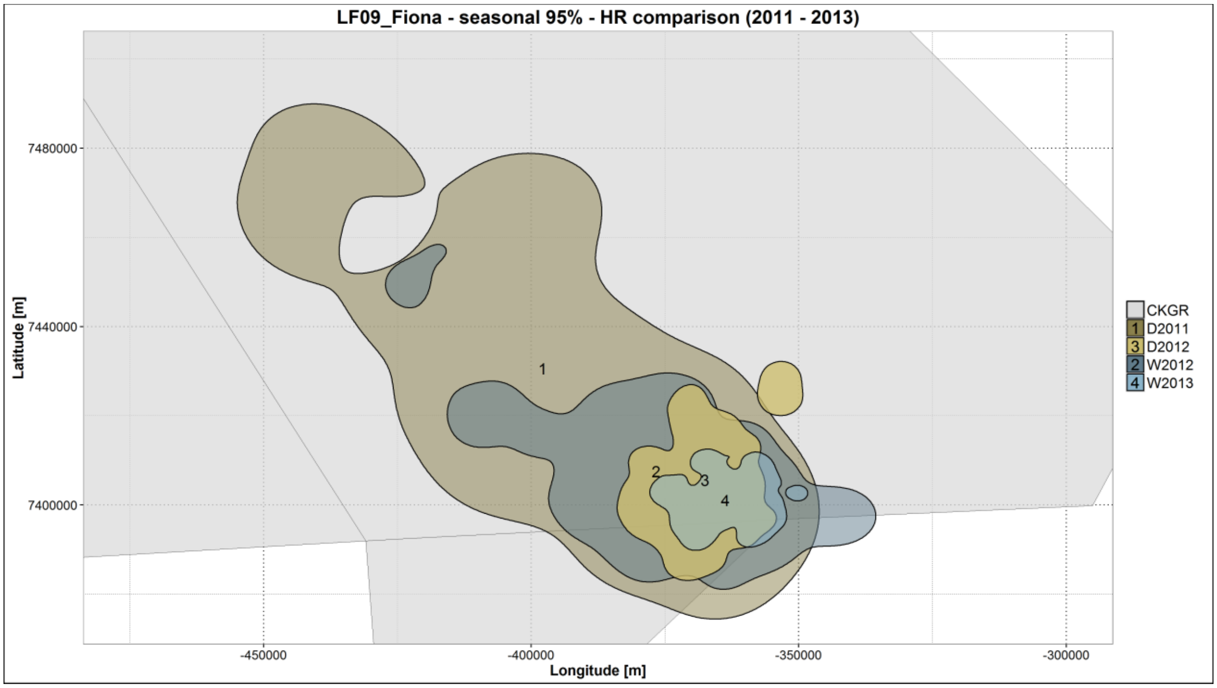


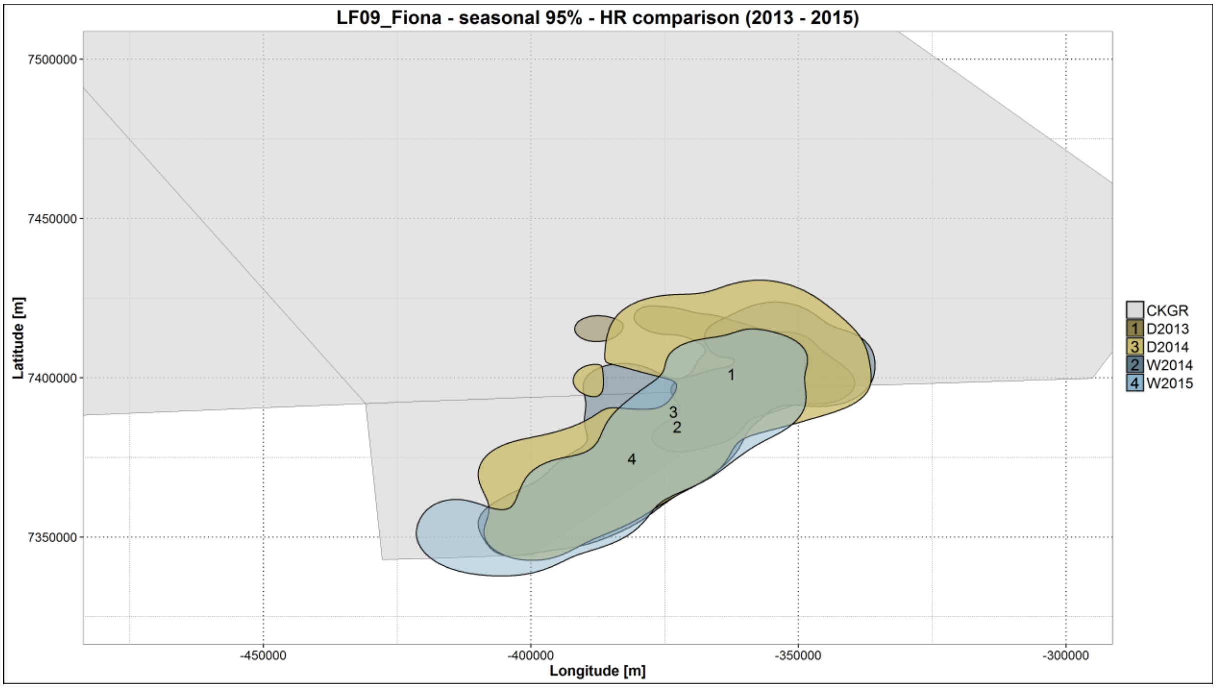
PM08_Bogarigka



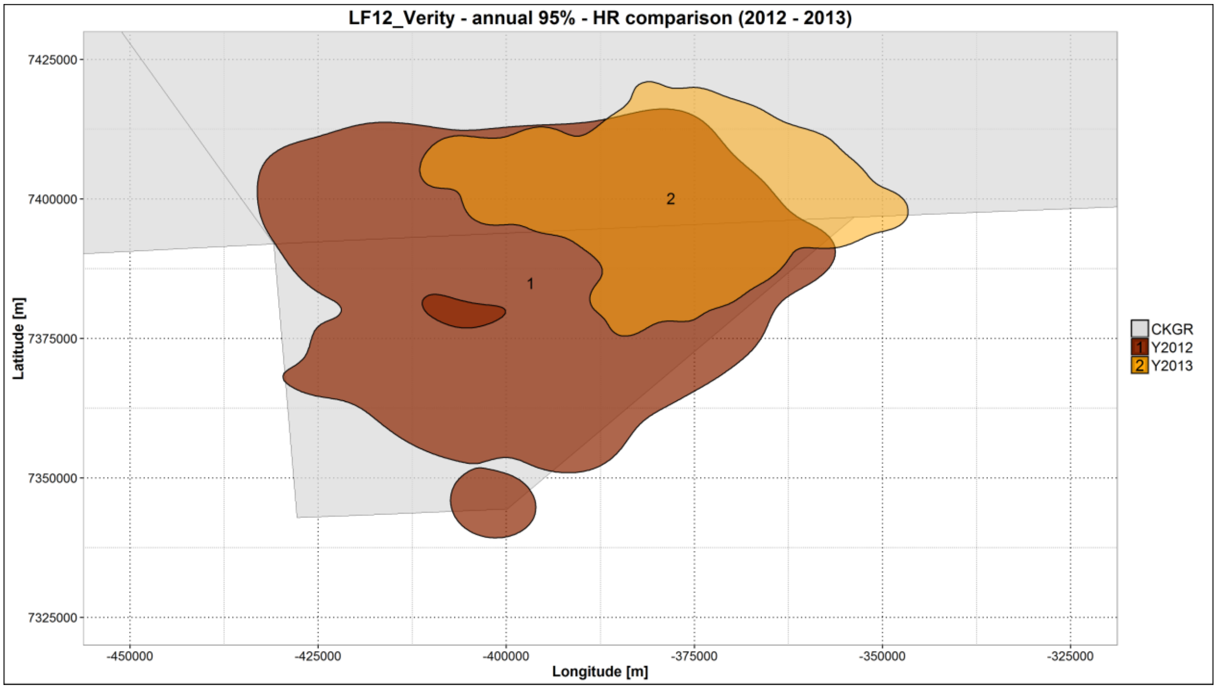
Lions

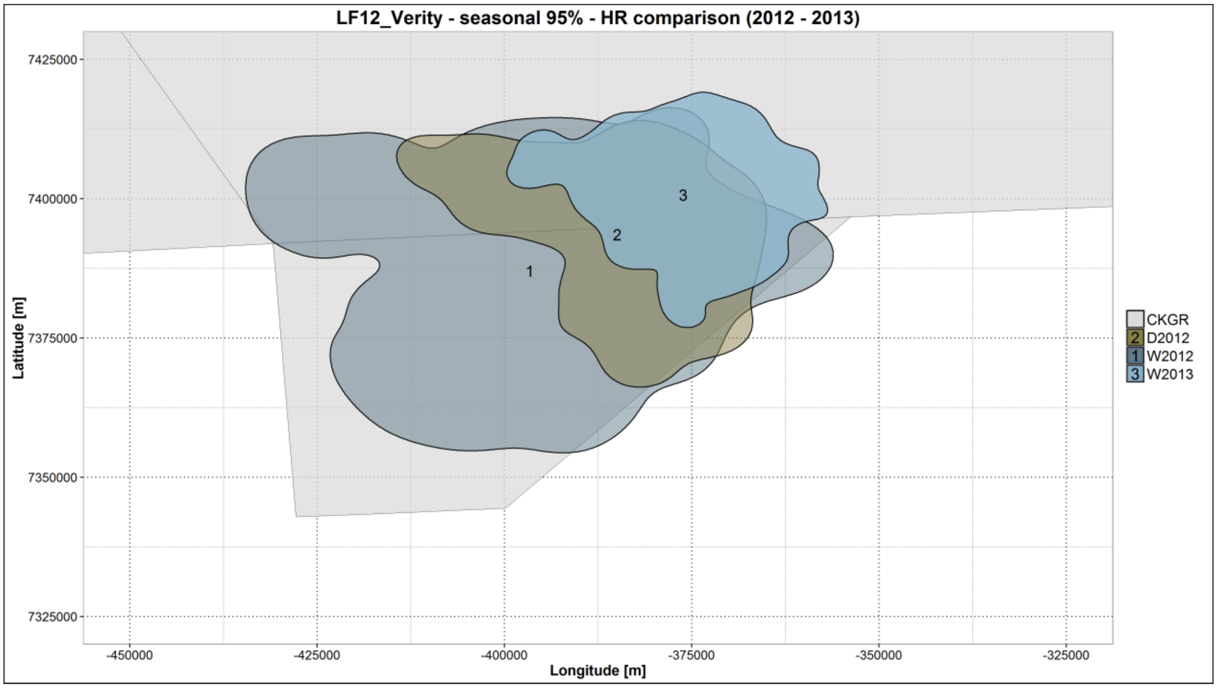
LF09_Fiona



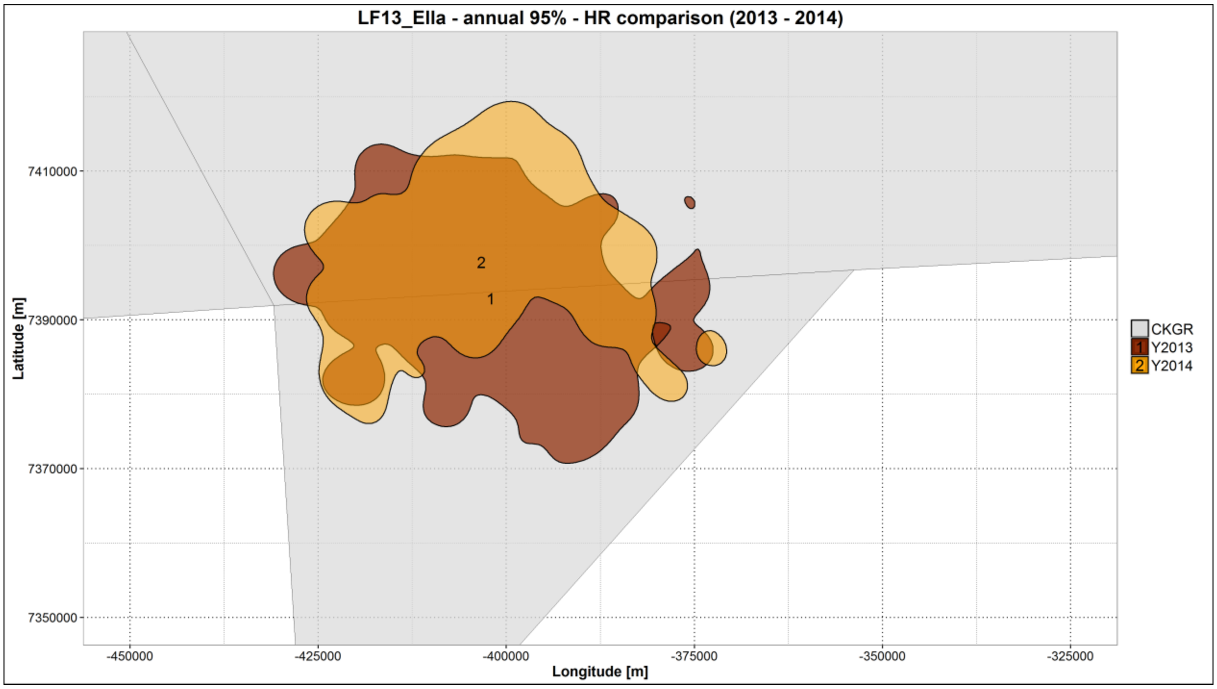


LF12_Verity

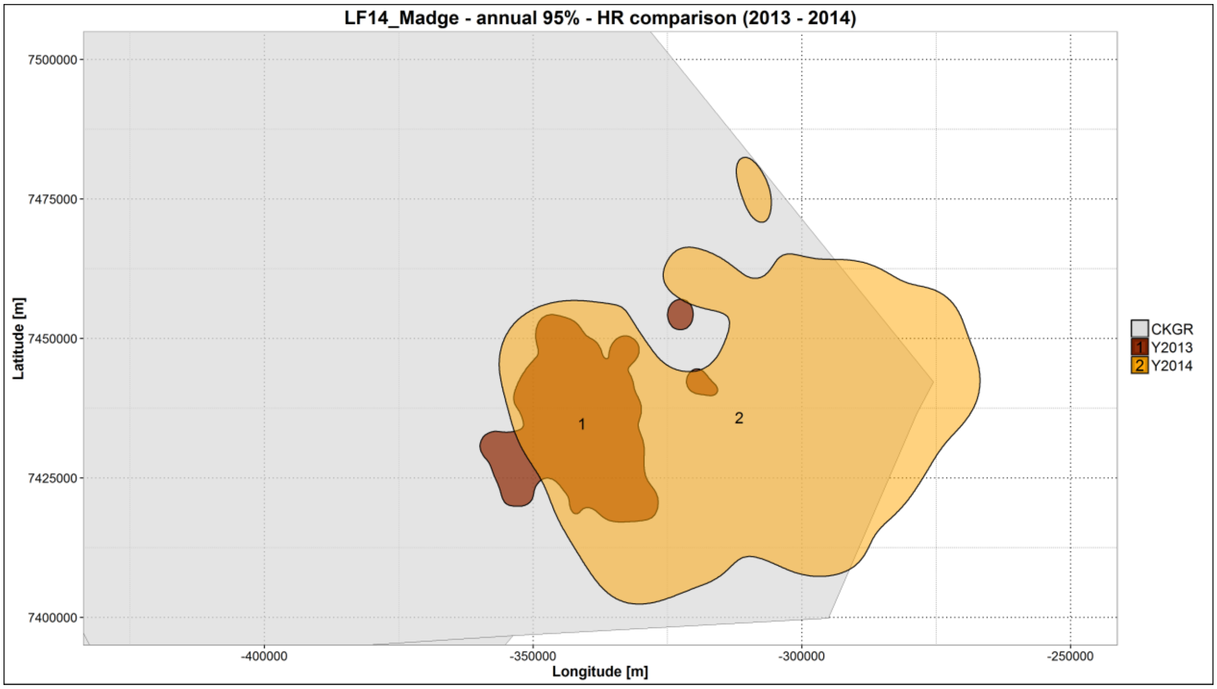

LF12_Verity - annual 95% - HR comparison (2012 - 2013)
7425000
7400000
7375000
7350000
7325000
Latitude [m]
-450000
-425000
-400000
-375000
-350000
-325000
Longitude [m]
1
2
CKGR
1 Y2012
2 Y2013


LF12_Verity - seasonal 95% - HR comparison (2012 - 2013)
7425000
7400000
7375000
7350000
7325000
Latitude [m]
-450000
-425000
-400000
-375000
-350000
-325000
Longitude [m]
1
2
3
CKGR
2 D2012
1 W2012
3 W2013

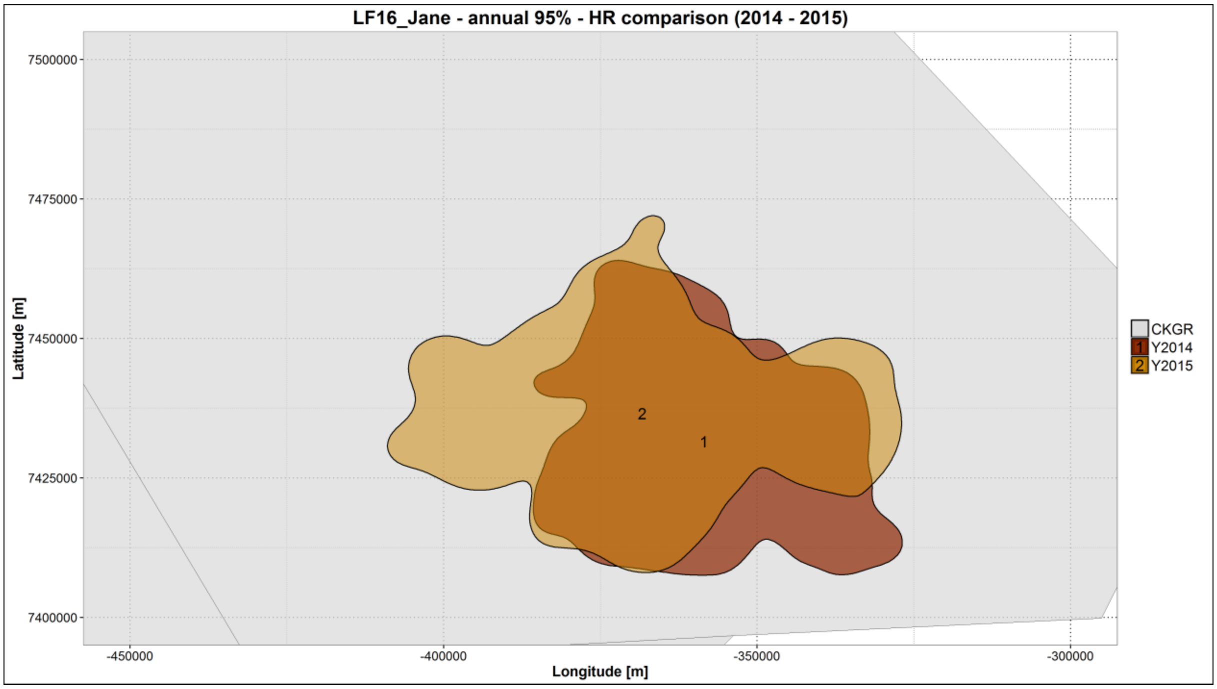
LF13_Ella

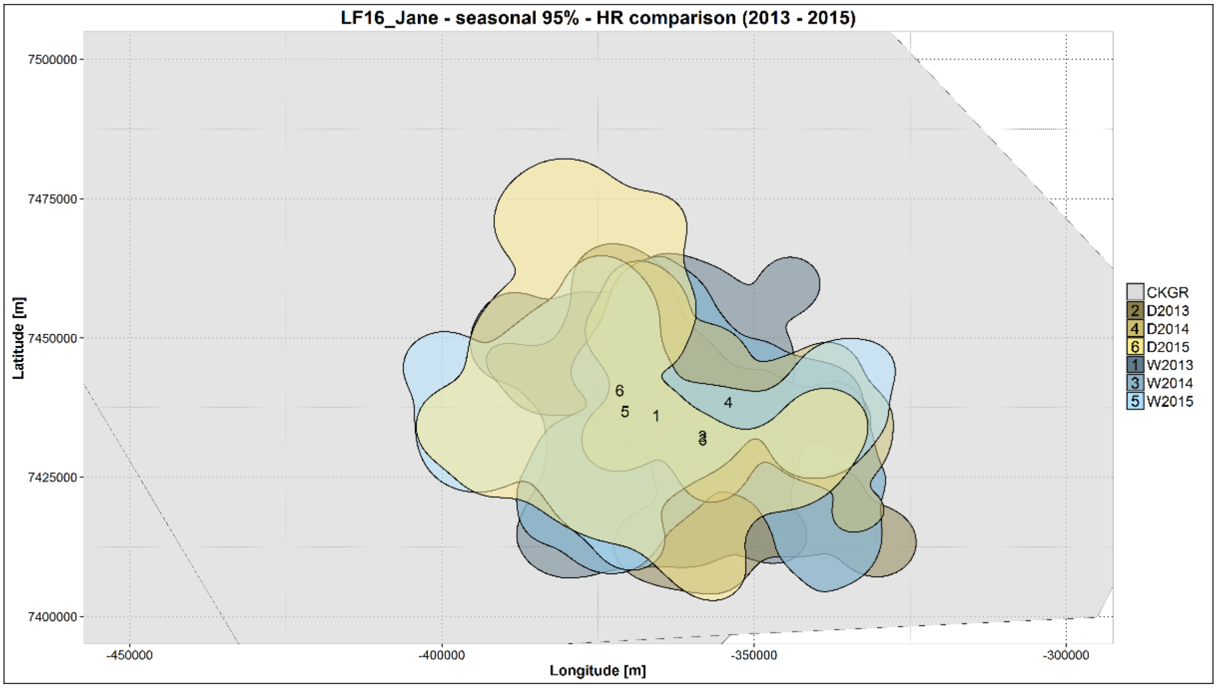


LF14_Madge

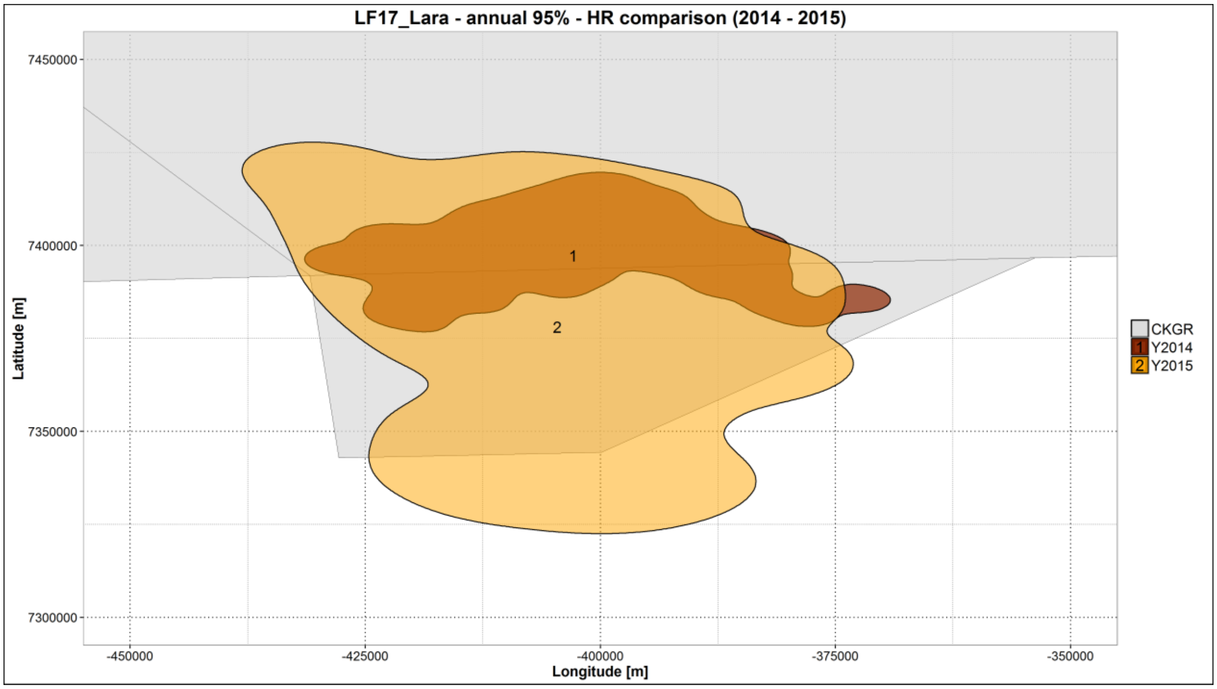


LF16_Jane

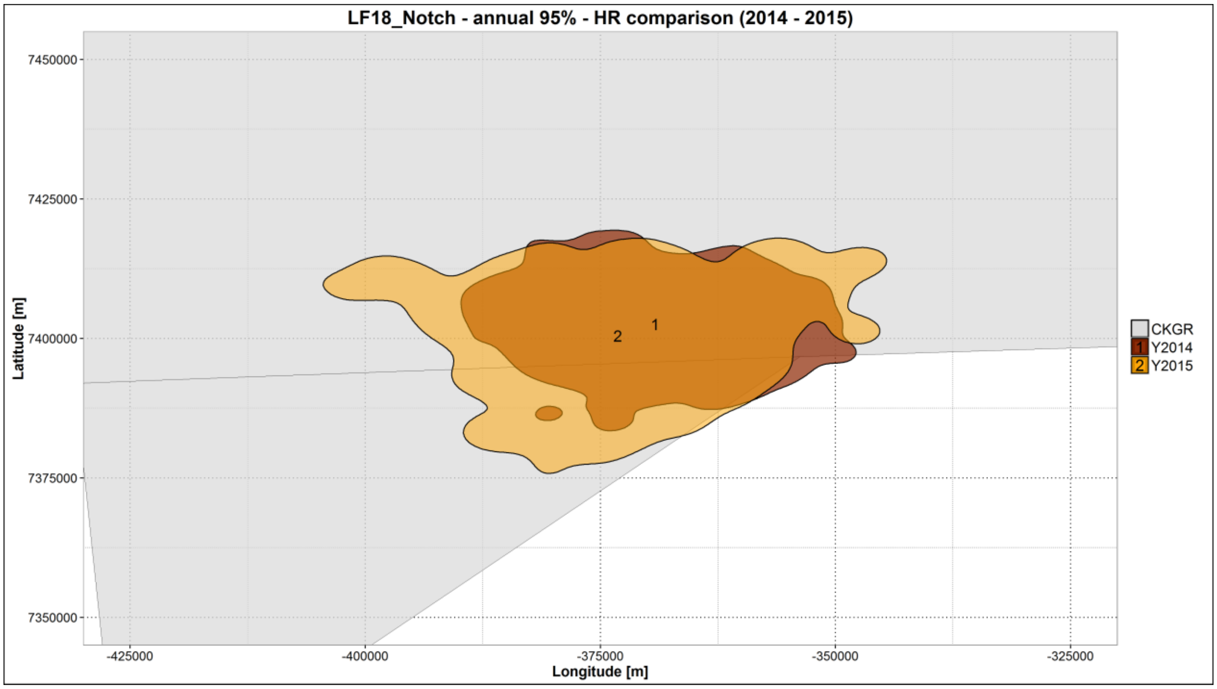

LF16_Jane - annual 95% - HR comparison (2014 - 2015)
7500000
7475000
7450000
7425000
7400000
Latitude [m]
-450000
-400000
-350000
-300000
Longitude [m]
2
1
CKGR
1 Y2014
2 Y2015


LF16_Jane - seasonal 95% - HR comparison (2013 - 2015)
7500000
7475000
7450000
7425000
7400000
Latitude [m]
-450000
-400000
-350000
-300000
Longitude [m]
6
5
1
4
3
CKGR
2 D2013
4 D2014
6 D2015
1 W2013
3 W2014
5 W2015

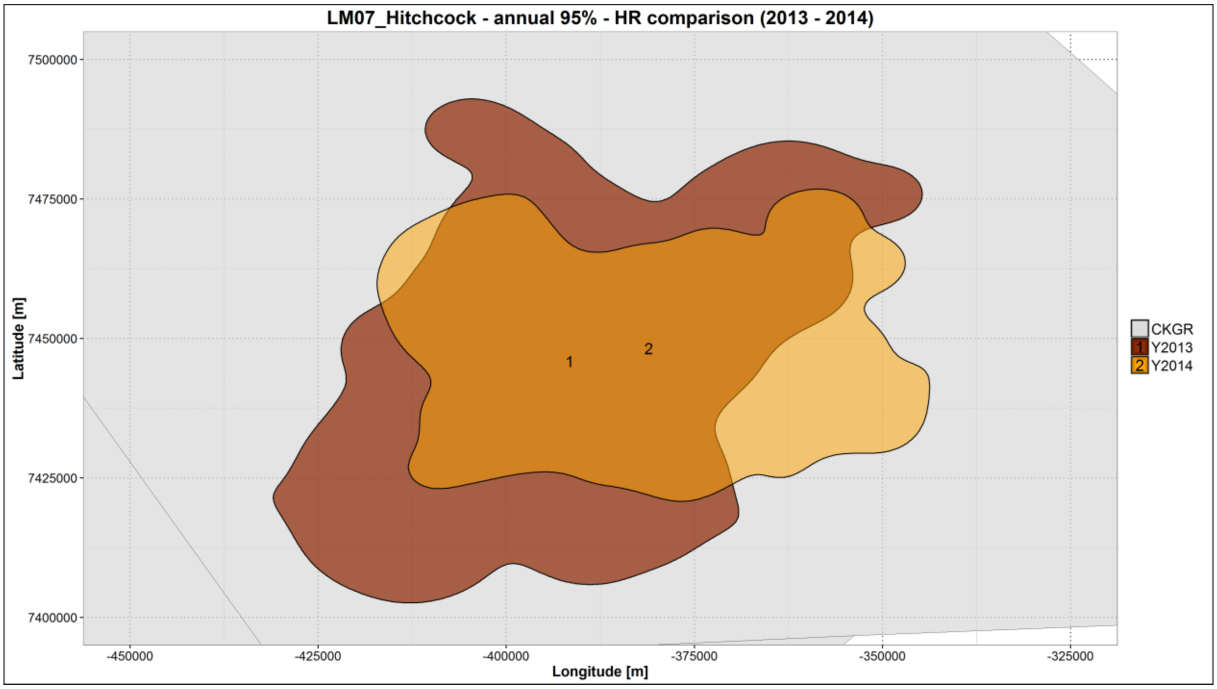
LF17_Lara



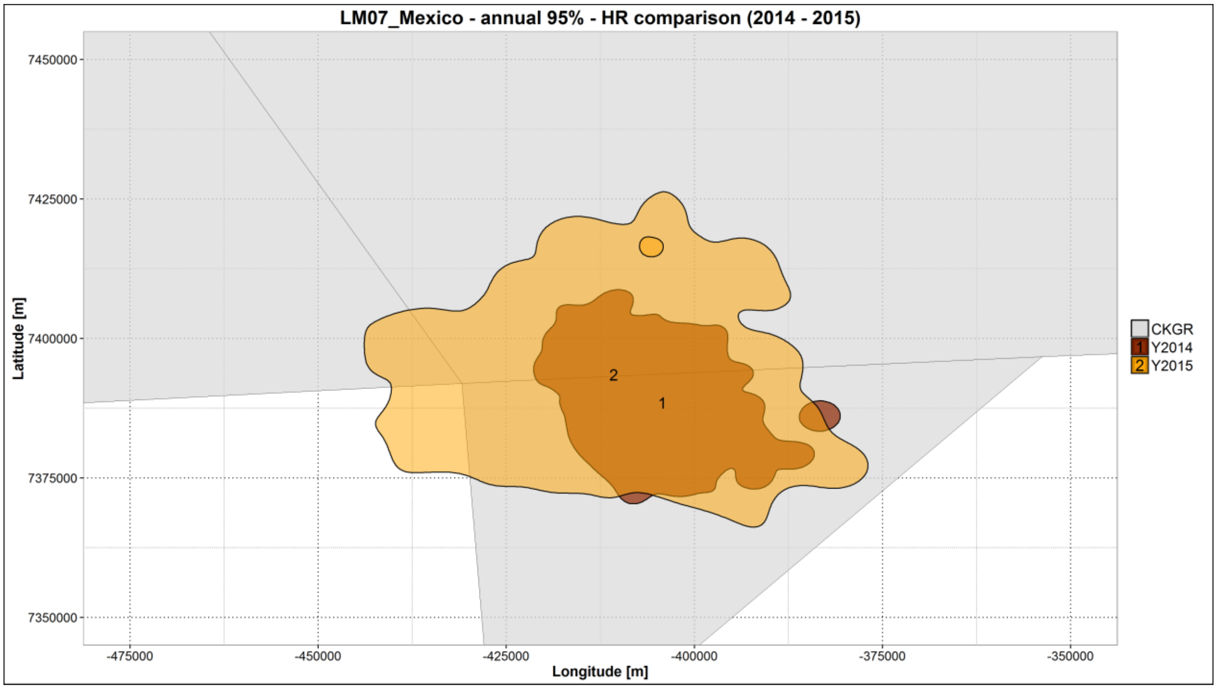
LF18_Notch



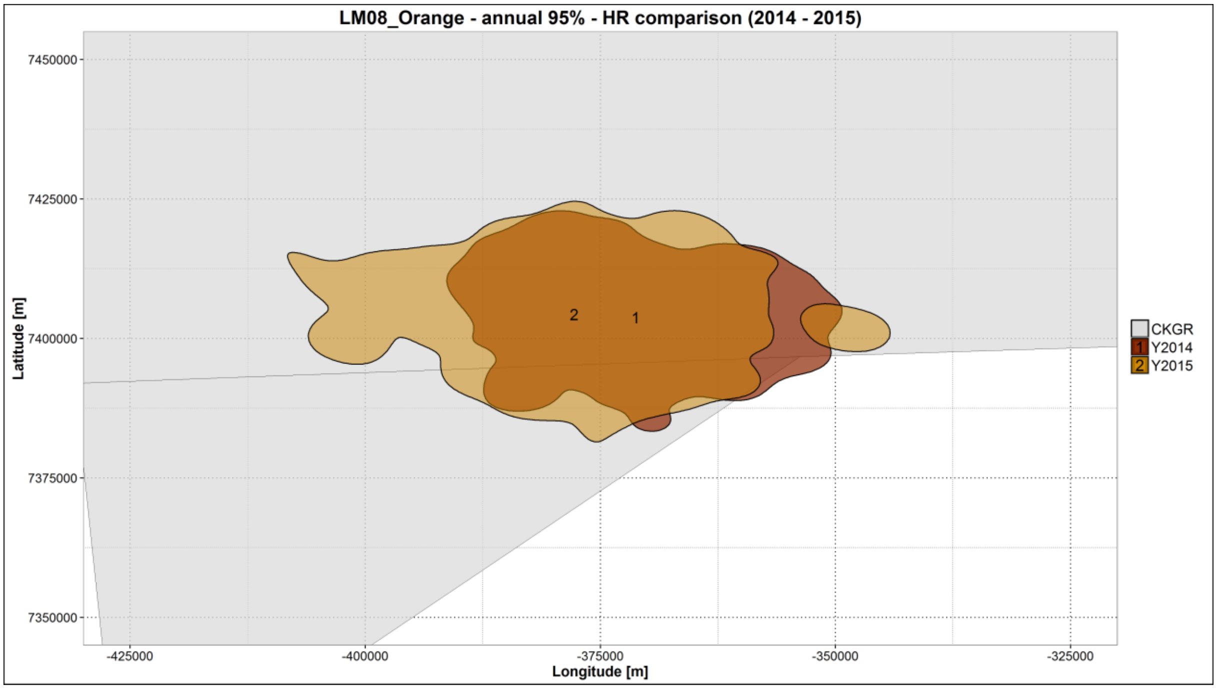
LM06_Hitchcock



LM07_Mexico

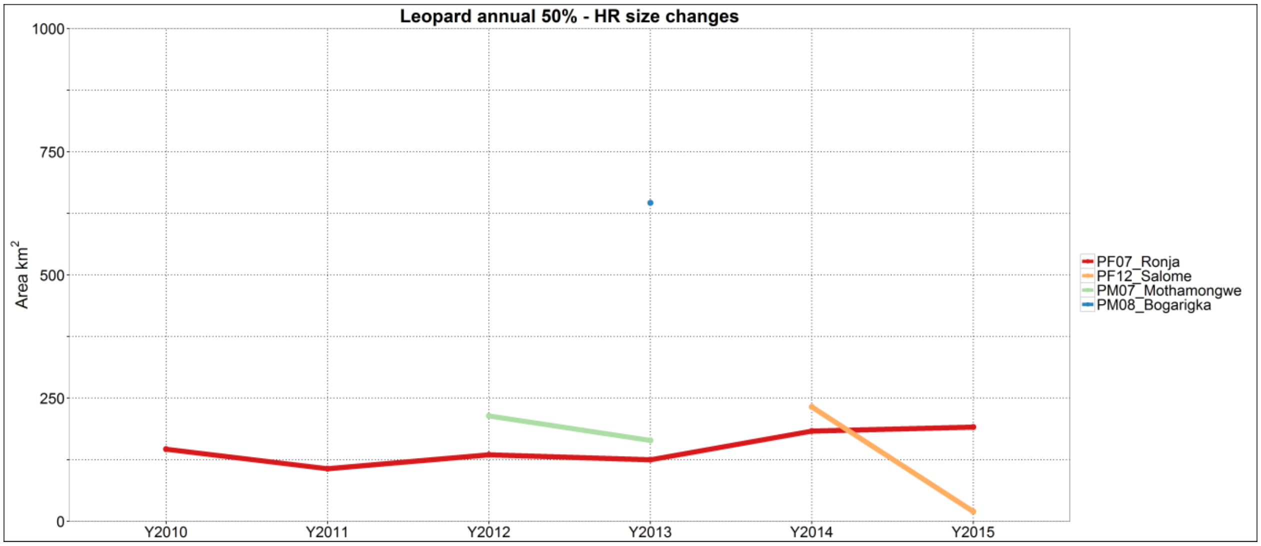


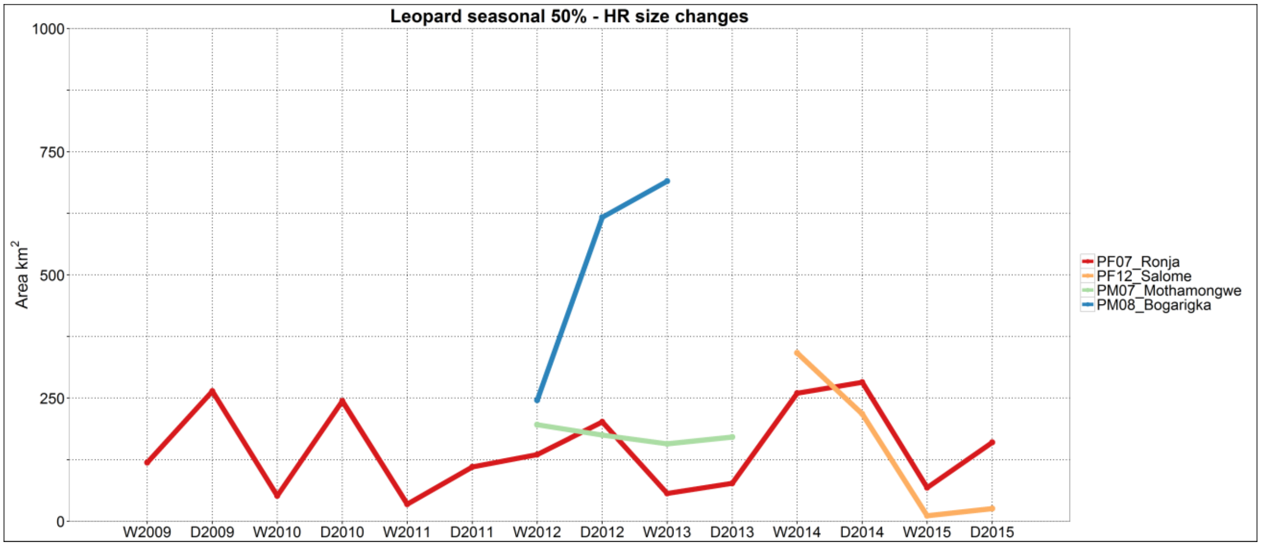
LM08_Orange


LM08_Orange - annual 95% - HR comparison (2014 - 2015)
7450000
7425000
7400000
7375000
7350000
Latitude [m]
-425000
-400000
-375000
-350000
-325000
Longitude [m]
2
1
CKGR
1 Y2014
2 Y2015

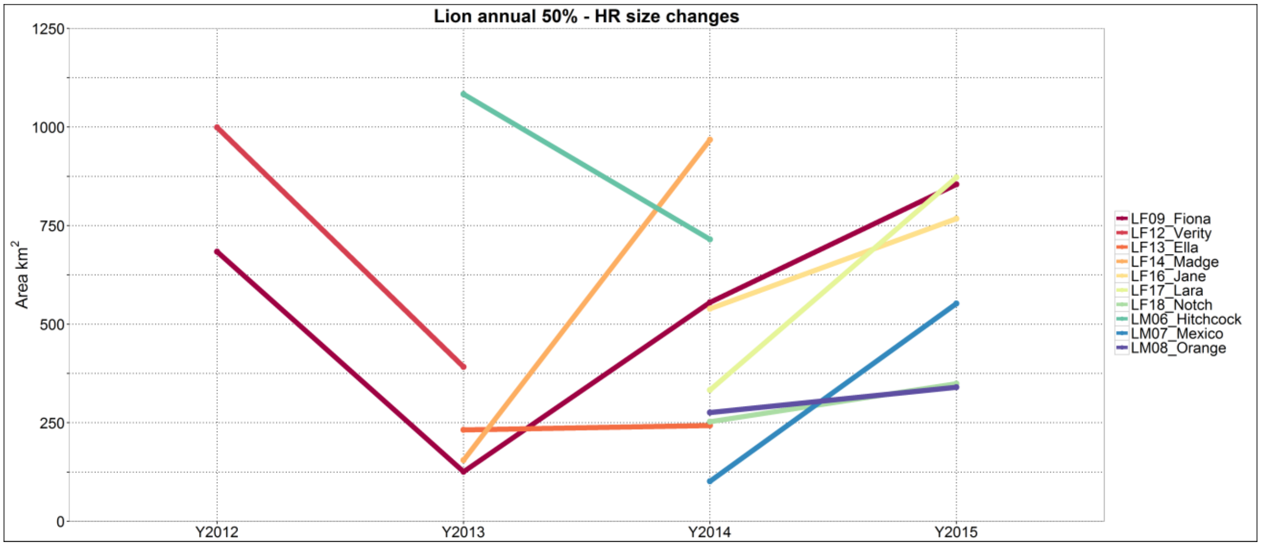
A2: Seasonal & annual variation of the 50% HR size

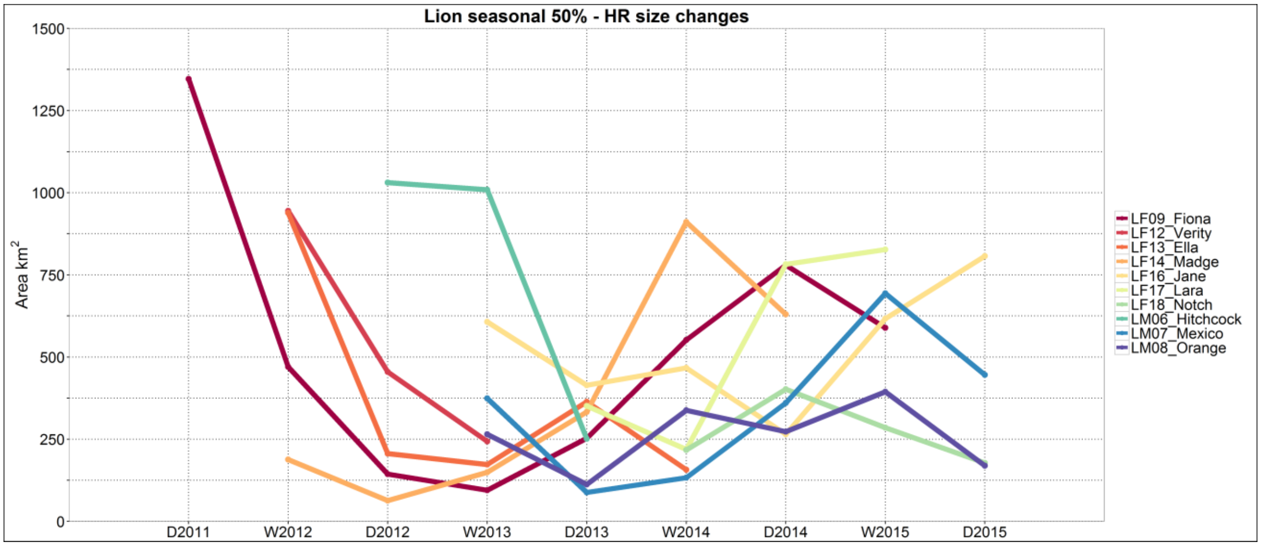
Leopards





Lions


Lion annual 50% - HR size changes
Area km^2
0
250
500
750
1000
1250
Y2012
Y2013
Y2014
Y2015
LF09_Fiona
LF12_Verity
LF13_Ella
LF14_Madge
LF16_Jane
LF17_Lara
LF18_Notch
LM06_Hitchcock
LM07_Mexico
LM08_Orange


Lion seasonal 50% - HR size changes
Area km^2
0
250
500
750
1000
1250
1500
D2011
W2012
D2012
W2013
D2013
W2014
D2014
W2015
D2015
LF09_Fiona
LF12_Verity
LF13_Ella
LF14_Madge
LF16_Jane
LF17_Lara
LF18_Notch
LM06_Hitchcock
LM07_Mexico
LM08_Orange

A3: Prey animals recorded by LEC for the 2014 Wet season

PointID	n	Tot	SPR	STE	WIL	GEM	HAR	WAR	DUI	KUD	ELA	GIR	BUS	OST	COW	SCR	DON	GOA	HOR	BAB	SHP	Long	Lat	rel_abun	abun
A1	6	17	0	3	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-362754.8152	7392823.9684	2.5	cat.3: med low
A2	6	6	0	2	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-366517.5267	7393339.7174	1.5	cat.2: low
A3	6	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-370170.3378	7393249.5858	1.5	cat.2: low
A4	6	2	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-373290.2965	7394330.8699	1	cat.2: low
A5	6	7	0	4	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	-376951.6471	7394945.9626	1	cat.2: low
A6	6	3	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-379986.7412	7396849.2438	1	cat.2: low
B1	5	4	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-382305.9229	7398013.0956	1	cat.2: low
B2	5	3	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-385274.7510	7397623.7777	1	cat.2: low
B3	5	5	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-388989.2348	7396647.2024	1.5	cat.2: low
B4	5	14	0	5	0	8	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-392245.1411	7394540.6568	1.5	cat.2: low
B5	5	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	-395489.0090	7392395.4977	1.5	cat.2: low
B6	5	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-398959.2998	7390717.4223	1.5	cat.2: low
B7	5	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-402079.8711	7388414.4416	1	cat.2: low
C1	6	7	0	4	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	-401052.1820	7386467.4158	1	cat.2: low
C2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-397791.9529	7384220.5496	1	cat.2: low
C3	6	3	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	-394321.5850	7382388.9093	1	cat.2: low
C4	6	3	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	-390906.3489	7380648.2307	1	cat.2: low
C5	6	4	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-387609.6812	7378702.9498	1	cat.2: low
D1	6	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	-371203.4903	7391716.1328	1.5	cat.2: low
D2	6	14	0	2	0	11	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-374304.4983	7389432.6995	1.5	cat.2: low
D3	6	10	0	4	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	-376206.6553	7386031.9968	1.5	cat.2: low
D4	6	17	0	6	0	10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-378591.5469	7383039.4778	1.5	cat.2: low
D5	6	5	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	-381440.4431	7380274.8985	1.5	cat.2: low
D6	6	7	0	5	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	-384586.1007	7377895.3299	1.5	cat.2: low
E1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-387308.2821	7375972.5940	1.5	cat.2: low
E2	6	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-390531.9908	7373677.1305	1	cat.2: low
E3	6	4	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	-393812.7914	7371627.3882	1	cat.2: low
E4	6	10	0	6	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	-397175.4405	7369552.7402	1	cat.2: low
E5	6	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-400361.2020	7367313.5877	1	cat.2: low
E6	6	6	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-403695.4025	7365304.1308	1	cat.2: low
E7	6	3	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-407636.4734	7364982.0639	1	cat.2: low
F1	6	13	2	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	-403851.0892	7384460.2366	1	cat.2: low
F2	6	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-405604.8107	7381452.5160	1	cat.2: low
F3	6	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-406574.8766	7377692.8176	1	cat.2: low
F4	6	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	-406986.6155	7373810.3523	1	cat.2: low
F5	6	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-408863.0754	7370311.8966	0.5	cat.1: very low
F6	6	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-409372.2922	7367389.8335	0.5	cat.1: very low
G1	6	10	0	7	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	-390622.1373	7407391.3938	2.5	cat.3: med low
G2	6	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-390263.0116	7403409.2803	2	cat.2: low
G3	6	13	0	6	0	0	0	0	0	5	0	2	0	0	0	0	0	0	0	0	0	-389014.1559	7399798.5800	1.5	cat.2: low
G4	6	10	0	5	0	0	0	0	1	1	0	3	0	0	0	0	0	0	0	0	0	-386519.2380	7398196.8073	1.5	cat.2: low
Total	239	230	2	103	0	39	24	0	7	11	4	25	3	10	0	0	0	0	0	0	0	NA	NA	51.5	NA

Prey codes

native prey				**domestic prey**	
BAB	baboon	BUS	kori bustard	COW	cow
DUI	grey duiker	ELA	eland	DON	donkey
GEM	gemsbok	GIR	giraffe	GOA	goat
HAR	hartebeest	KUD	greater kudu	HOR	horse
OST	ostrich	SCR	scrub hare	SHP	sheep
SPR	springbok	STE	steenbok		
WAR	common warthog	WIL	blue wildebeest		

A4: Prey animals recorded by LEC for the 2014 dry season

PointID	n	Tot	SPR	STE	WIL	GEM	HAR	WAR	DUI	KUD	ELA	GIR	BUS	OST	COW	SCR	DON	GOA	HOR	BAB	SHP	Long	Lat	rel_abun	abun
A1	4	8	1	2	0	0	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	-362754.8152	7392823.9680	4	cat.4: med upp
A2	4	8	1	0	0	0	5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	-366517.5267	7393339.7170	3	cat.3: med low
A3	4	15	0	0	0	0	11	0	0	4	0	0	0	0	0	0	0	0	0	0	0	-370170.3378	7393249.5860	2.5	cat.3: med low
A4	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-373290.2965	7394330.8700	2	cat.2: low
A5	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-376951.6471	7394945.9630	1.5	cat.2: low
A6	4	6	0	0	0	1	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	-379986.7412	7396849.2440	1.5	cat.2: low
B1	5	7	0	3	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	-382305.9229	7398013.0960	1.5	cat.2: low
B2	5	4	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-385274.7510	7397623.7780	1.5	cat.2: low
B3	5	10	0	4	0	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-388989.2348	7396647.2020	1.5	cat.2: low
B4	5	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-392245.1411	7394540.6570	1.5	cat.2: low
B5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-395489.0090	7392395.4980	1.5	cat.2: low
B6	5	9	0	4	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-398959.2998	7390717.4220	1.5	cat.2: low
B7	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-402079.8711	7388414.4420	1.5	cat.2: low
C1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-401052.1820	7386467.4160	1	cat.2: low
C2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-397791.9529	7384220.5500	1	cat.2: low
C3	5	3	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-394321.5850	7382388.9090	1	cat.2: low
C4	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-390906.3489	7380648.2310	1	cat.2: low
C5	5	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-387609.6812	7378702.9500	1	cat.2: low
D1	5	12	0	1	2	2	3	0	0	4	0	0	0	0	0	0	0	0	0	0	0	-371203.4903	7391716.1330	3	cat.3: med low
D2	5	15	0	8	0	0	0	0	0	0	0	5	0	2	0	0	0	0	0	0	0	-374304.4983	7389432.7000	3	cat.3: med low
D3	5	26	0	6	0	2	0	0	0	2	0	13	0	3	0	0	0	0	0	0	0	-376206.6553	7386031.9970	4	cat.4: med upp
D4	5	22	0	7	0	6	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	-378591.5469	7383039.4780	3	cat.3: med low
D5	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-381440.4431	7380274.8990	2.5	cat.3: med low
D6	5	6	0	0	5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-384586.1007	7377895.3300	2	cat.2: low
E1	5	9	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	-387308.2821	7375972.5940	1.5	cat.2: low
E2	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-390531.9908	7373677.1310	1	cat.2: low
E3	5	8	0	1	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-393812.7914	7371627.3880	1	cat.2: low
E4	5	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-397175.4405	7369552.7400	1	cat.2: low
E5	5	6	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	-400361.2020	7367313.5880	1	cat.2: low
E6	5	9	0	1	0	2	2	0	0	3	0	0	0	1	0	0	0	0	0	0	0	-403695.4025	7365304.1310	1.5	cat.2: low
E7	5	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	-407636.4734	7364982.0640	1.5	cat.2: low
F1	5	19	2	2	0	13	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	-403851.0892	7384460.2370	1	cat.2: low
F2	5	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-405604.8107	7381452.5160	0.5	cat.1: very low
F3	5	8	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	-406574.8766	7377692.8180	0.5	cat.1: very low
F4	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-406986.6155	7373810.3520	0.5	cat.1: very low
F5	5	6	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	-408863.0754	7370311.8970	0.5	cat.1: very low
F6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-409372.2922	7367389.8340	1	cat.2: low
G1	4	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-390622.1373	7407391.3940	1.5	cat.2: low
G2	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-390263.0116	7403409.2800	1.5	cat.2: low
G3	4	6	0	1	0	3	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	-389014.1559	7399798.5800	1.5	cat.2: low
G4	4	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-386519.2380	7398196.8070	1.5	cat.2: low
Total	195	244	4	61	7	50	30	0	5	24	0	29	0	34	0	0	0	0	0	0	0	NA	NA	66	NA

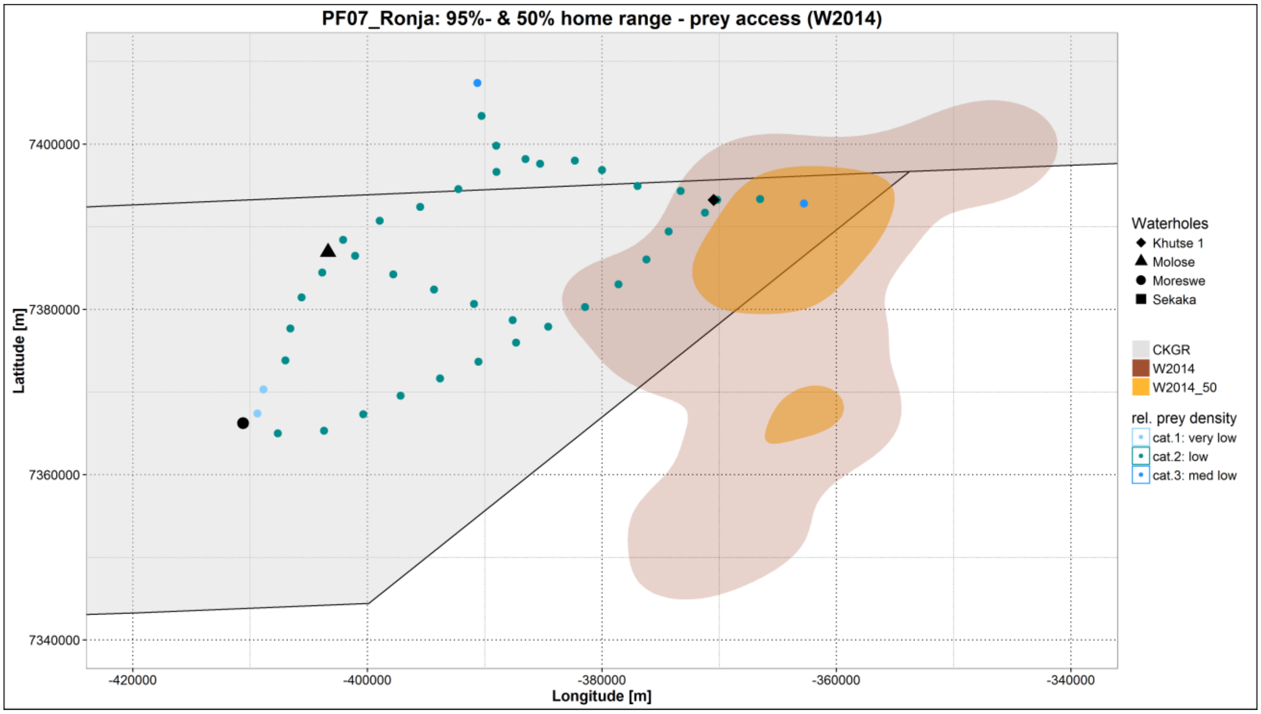
Prey codes

native prey				domestic prey	
BAB	baboon	BUS	kori bustard	COW	cow
DUI	grey duiker	ELA	eland	DON	donkey
GEM	gemsbok	GIR	giraffe	GOA	goat
HAR	hartebeest	KUD	greater kudu	HOR	horse
OST	ostrich	SCR	scrub hare	SHP	sheep
SPR	springbok	STE	steenbok		
WAR	common warthog	WIL	blue wildebeest		

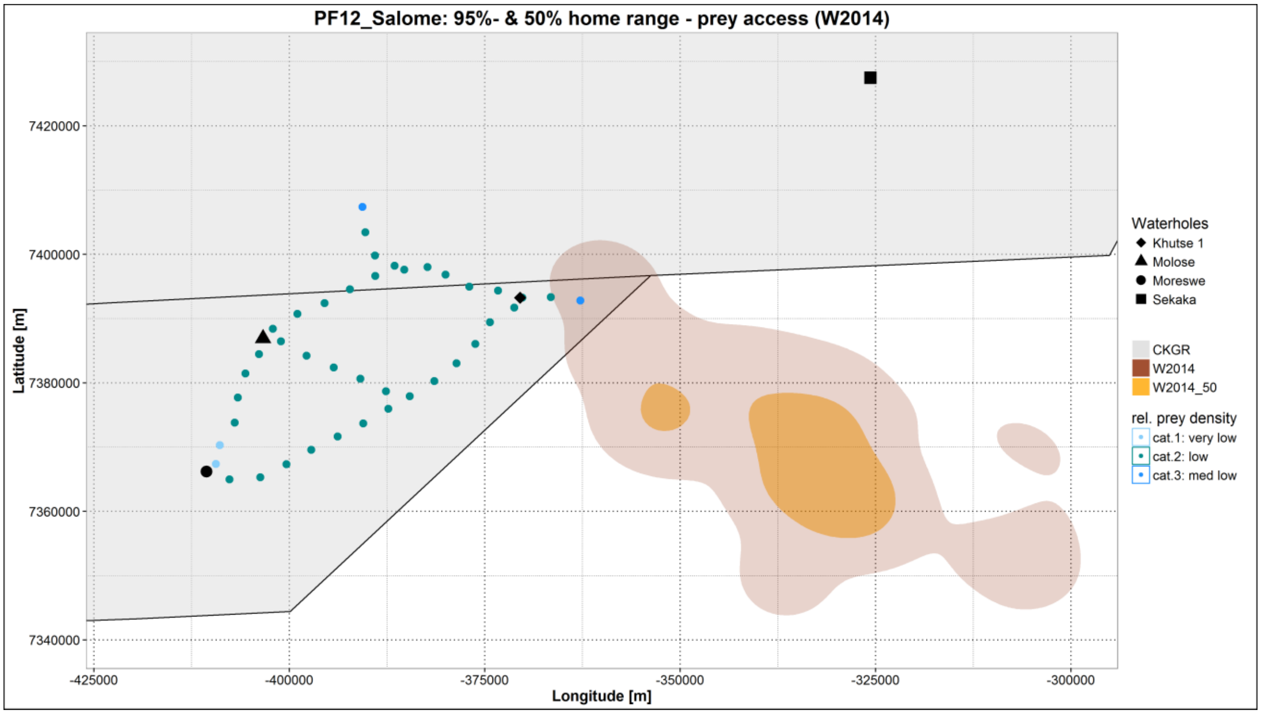
A5: Wet season prey access

Leopards

PF07_Ronja

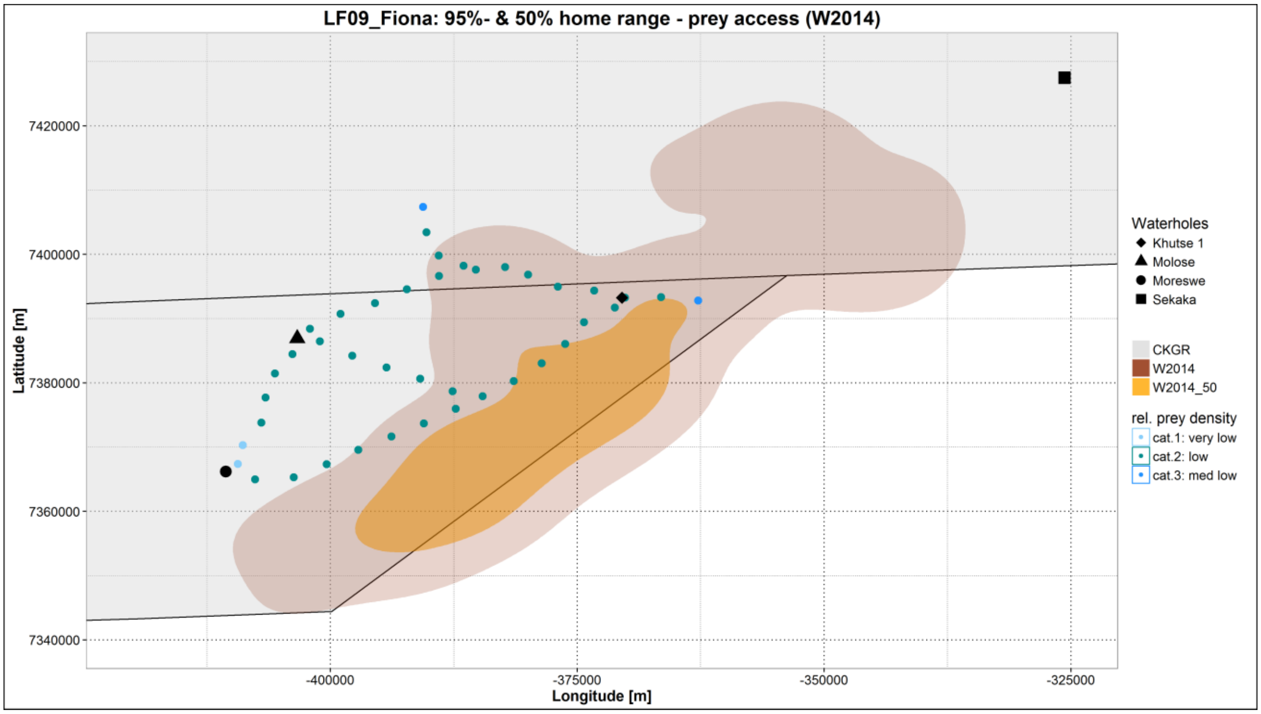


PF12_Salome

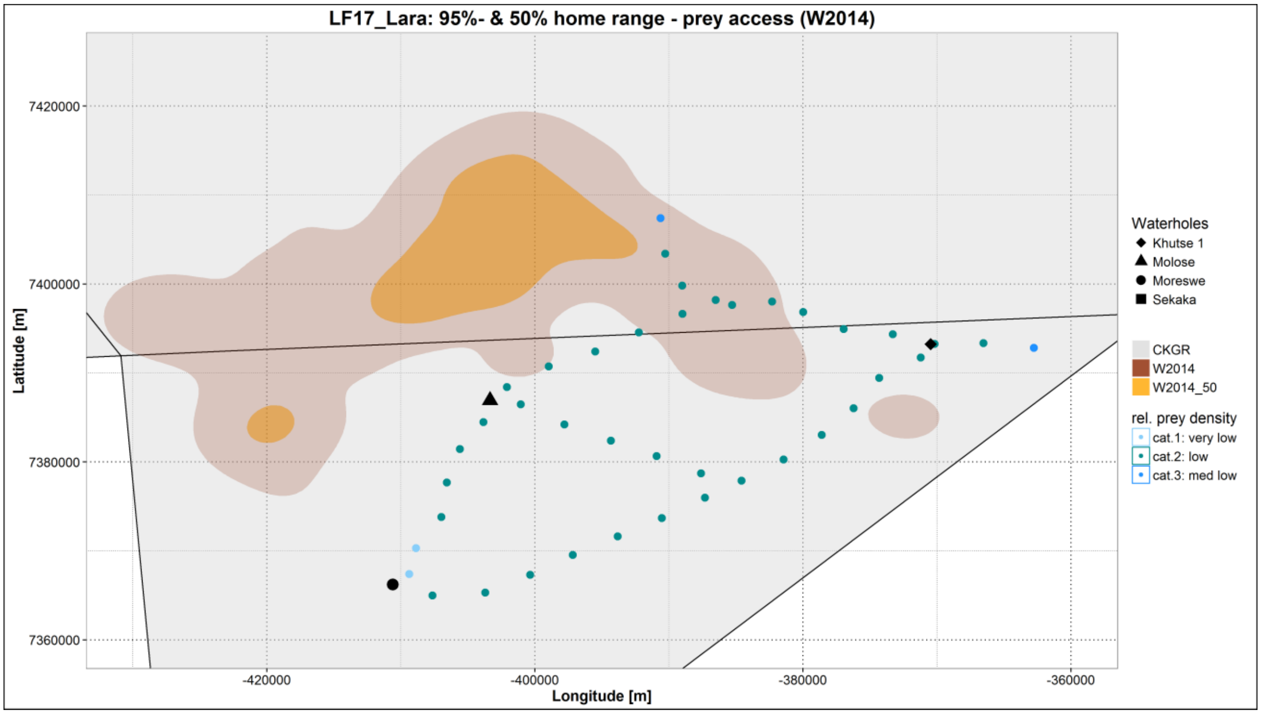


Lions

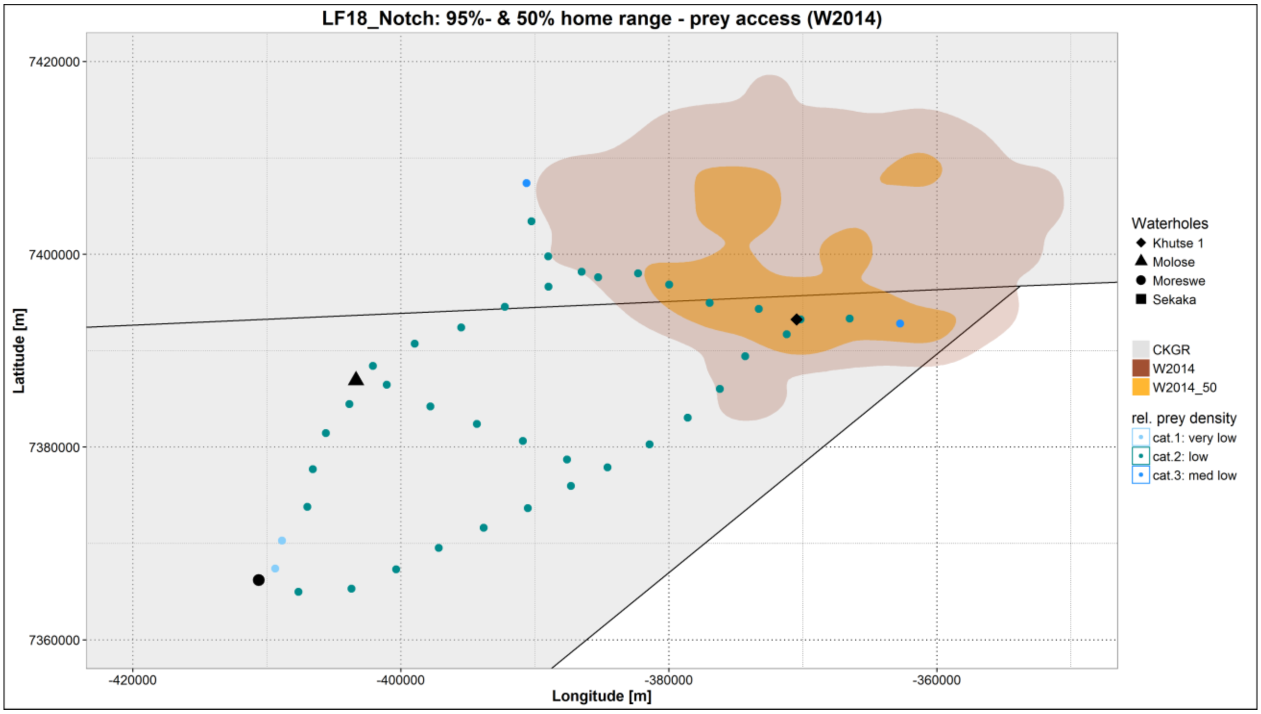
LF09_Fiona



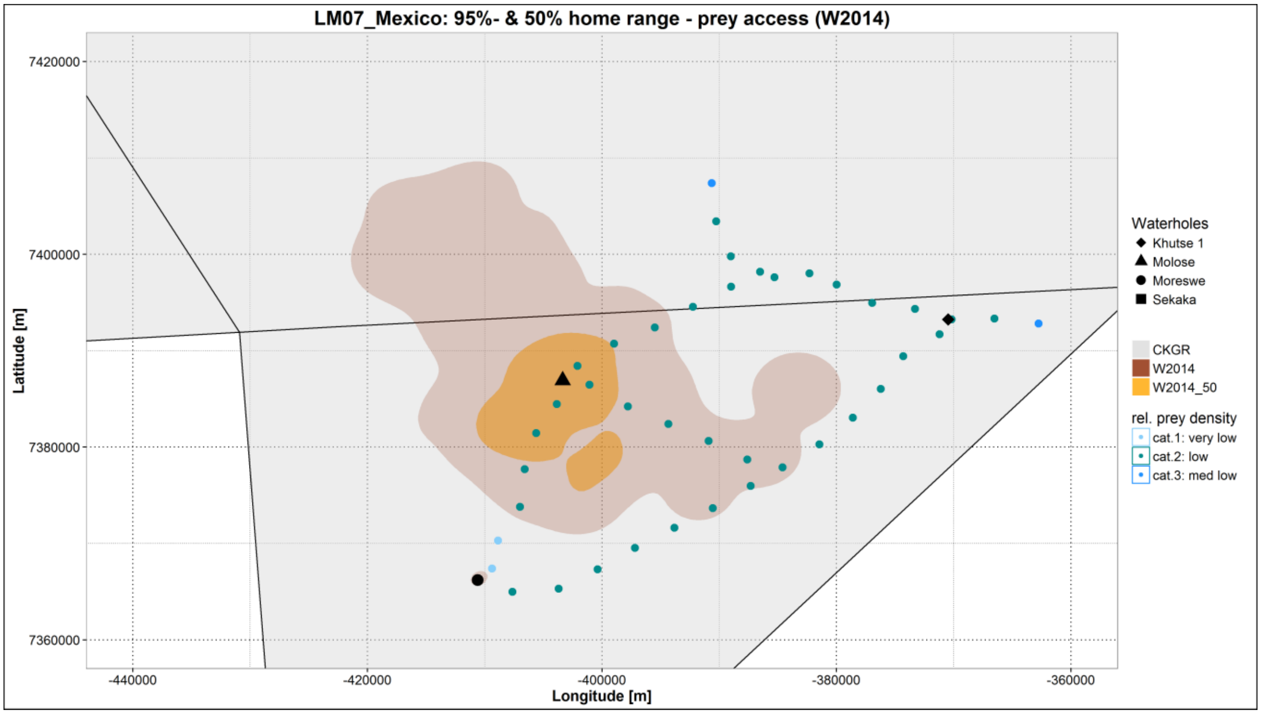
LF17_Lara



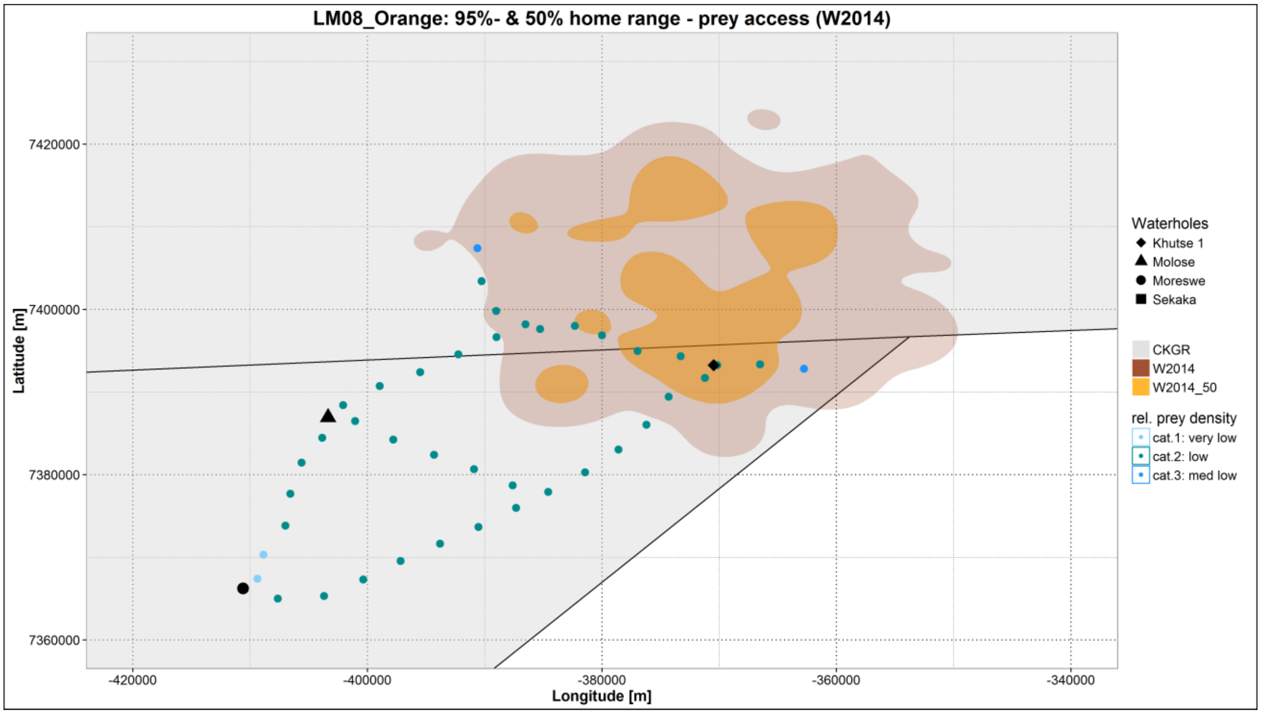
LF18_Notch



LM07_Mexico



LM08_Orange



A6: *R*-Code

The most important scripts as well as the documentation can be found on the attached CD.

A7: Personal Declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

Michael Matzig, ____ / ____ / 2016