

Movements and home ranges of translocated and resident lions (*Panthera leo melanochaita*) in relation to the translocation potential in Meru National Park, Kenya.

Master Project submitted to obtain the degree of Master in Biology,
specialisation Biodiversity: conservation and restoration.

Gert-Jan Goeminne

Promotor: Prof. Dr. Ir. Hans H. de Iongh

Supervisor: Msc. Luka Narisha

University of Antwerp

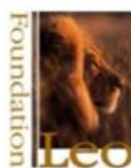
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Department of Biology

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Abstract

The number of human-wildlife conflicts has steadily increased in recent years, due to habitat loss and growing human populations. Translocation of problem animals has often been suggested as a possible solution, because of its non-lethal character and relative cost-efficiency. The location of release and pre-release handling (soft vs. hard release) are considered to be the most important factors for translocations to be successful. In this thesis, differences in behaviour between resident lions and translocated lions were examined for Meru National Park (MNP) in Kenya, a park regularly used by Kenyan Wildlife Services (KWS) as a translocation site for problem lions. Additionally, an ecological translocation suitability analysis for lion translocations was performed. Both the movements and home ranges of resident and translocated lions were compared, based on the data of five satellite collared lions. For the home ranges both the home range size and the time of establishment were compared. The ecological suitability analysis was performed using different ecological variables to quantify the ecological suitability of different areas in the park. The weight of each variable was adapted from literature and later optimized with Bayesian statistics. Home ranges and movements differed strongly between resident and translocated lions with the exception of one translocated male, which showed similar behaviour to resident lions. This male was observed to have joined a local resident pride. The two other problem lions showed large movements outside the park and both died within a few months. The developed method for the optimization of the ecological suitability analysis seemed to be useful and could be a possible tool to determine the translocation potential of a park. However, to give more reliable results, a more extensive data set would be needed, in order to improve the outcome of the method for the future.

Summary

The translocation of carnivores has often been proposed as a possible strategy to prevent human-wildlife conflicts. However, very limited data is available to determine the success of this strategy in the case of problem lions. In this research, the difference in behavior between resident and translocated problem lions in Meru National Park (MNP) has been determined. Movements and home range of a total of five satellite collared lions were available, two being resident lions and three being translocated problem lions. Firstly, movements, home range size and establishment of a new territory by the lions were analyzed. Secondly, an ecological translocation suitability analysis was performed based on literature and optimized using Bayesian statistics.

The analysis showed that resident and translocated problem lions move differently, barring one translocated problem lion. This individual (MTL1) was the only successful translocation, joining an existing pride territory, surviving for more than a year and even reproducing in the same pride. Not only was there a difference in the average potential minimum distance traveled in a day (24h) but also in the standard deviation of the distance translocated problem lions traveled, indicating more variation. However, none of the differences were found to be significant which could be due to the lack of data. The difference in movements also resulted in larger home ranges for unsuccessfully translocated problem lions, compared to the resident lions and MTL1. The same trend can be found in the home range establishment. Again the unsuccessfully translocated problem lions were never able to establish a new territory while MTL1 only needed two months to establish his home range, resident lions took only one month to do so.

The performed ecological translocation suitability analysis for lion translocation, based on literature, was able to give a prediction on the translocation potential of MNP. Later, this analysis was optimized using Bayesian statistics. The analysis showed that all the ecological variables found in the literature were significant in predicting the translocation potential of an area. However, there was a difference in the importance of the different ecological variables compared to the analysis based on literature. Since only limited data were available for this analysis, more research needs to be done to make accurate predictions on the translocation potential of the park.

This research contributes to the PhD thesis of Luka Narisha and was supervised by the University of Antwerp, the University of Leiden and the Kenya Wildlife Service.

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Chapter 1

Introduction

1.1 Conservations status

Large carnivores, like the African lion (*Panthera leo*) L., Leopard (*Panthera pardus*) and Cheetah (*Acinonyx jubatus*) are in decline worldwide (Inskip & Zimmermann, 2009). However, trends differ geographically (Chapron *et al.*, 2014). The decline in carnivore populations has many causes like prey depletion (Craigie *et al.*, 2010; Lindsey *et al.*, 2013), habitat destruction (Björklund, 2003), demand for traditional African and Chinese medicines (Williams, 2015), illegal trade and poorly regulated sport hunting (Becker *et al.*, 2013). However, the biggest threat to large carnivores is suggested to be the growth of human populations, the consequential habitat loss for many predator species and the increase in human-wildlife conflicts (Bales *et al.*, 2005). Human-wildlife conflicts often include the predation on livestock, which causes economic damage and elicits a negative attitude of the local inhabitants towards wildlife. This often results in the retaliatory killing of the predators (Mills, 1998; Nowell *et al.*, 1996). As human populations are expected to increase further in the coming years, especially in developing countries, competition for natural resources and the associated human-wildlife conflicts are expected to increase (Messmer, 2000). Muntifering *et al.* (2006) found that large carnivores are the most vulnerable to extinction caused by human influences. Apart from human-wildlife conflicts, biological factors like low densities, small population sizes and large home ranges cause large carnivores to suffer first when human populations expand into their habitat (Cardillo *et al.*, 2005). Since large carnivores are at the top of the food chain, their population size will always be smaller than the population size of their prey (Sillero-Zubiri & Laurenson, 2001).

The historical distribution of the lion covered Africa, Europe, the Middle East and Southwest Asia, in all habitats except very dry deserts and very moist forests (Nowell *et al.*, 1996). During the first century AD, lions disappeared from Europe and between 1800 and 1950 they disappeared from North Africa, the Middle East and most of Asia

(Fig. 1.1) (Nowell *et al.*, 1996). Nowadays, lions can only be found in savannah habitats across sub-Saharan Africa as well as a small population in the Gir Reserve India and are mostly associated with protected areas and managed hunting areas (Nowell *et al.*, 1996; Dolrenry *et al.*, 2014; Riggio *et al.*, 2013). Currently, 27 countries have a free-ranging lion population in Africa, of which only nine countries have a lion population exceeding 1,000 individuals (Riggio *et al.*, 2013). Riggio *et al.* (2013) estimates the global lion population at 32,000 lions divided over 67 Lion Conservation Units. However, the exact number of lions is not known since lions are difficult to count and population estimates are essentially imprecise (Bauer, 2008).

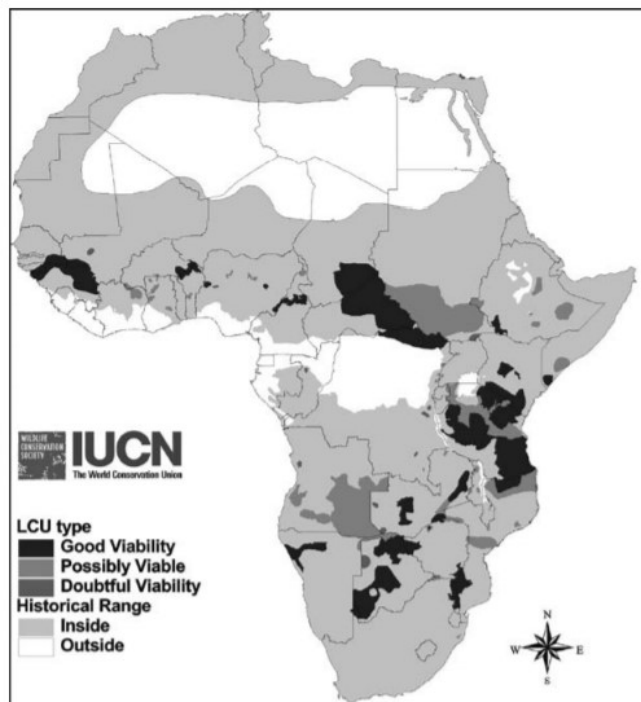


Figure 1.1: The historical and recent distribution of lions (*Panthera Leo*) in Africa (Bauer, 2008).

Previously, lions were split into two subspecies, namely the African lion (*Panthera leo leo*) and the Asian lion *Panthera leo persica*), however, this taxonomy has been recently adapted (Kitchener *et al.*, 2017). Recent studies implicate that lion populations of Western and Central Africa are more related to the Asiatic lion than populations of Eastern and Southern Africa. Therefore, a new taxonomy has been accepted for the African lion, two subspecies are now recognized by the IUCN Cat Specialist Group, *Panthera leo leo*, in Western, Central Africa and India and *Panthera leo melanochaita*, in Eastern and Southern Africa (Kitchener *et al.*, 2017).

The lion is globally still classified as vulnerable on the global IUCN Red List. Depending on the region considered, lions range from being classified as Regionally Critically Endangered to Least Concerned. For example, in West Africa, the lion population meets the criteria for Regionally Critically Endangered and in India, lions are classified as

Regionally Endangered while they are also considered Regionally Endangered in East Africa (Bauer *et al.*, 2015; Henschel *et al.*, 2014). Nonetheless, in South Africa, lions are considered to be of Least Concern (Bauer *et al.*, 2015; Miller *et al.*, 2016). The variation in regional Red List status is the result of different trends in different regions, like in West, East and Central Africa, with decreasing trends, in contrast to the populations in India and South Africa where trends are increasing (Bauer *et al.*, 2015).

1.2 Home range and movements

A home range can be described as: “The area transversed by an individual in its normal activities of food gathering, mating and caring for the young” (Burt, 1943). Generally, the home range of carnivores is as large as necessary but as small as possible to contain enough resources to satisfy the energy needs of the pride, therefore, larger prides need a larger home range (Gittleman & Harvey, 1982; Macdonald, 1983; Kruuk & Macdonald, 1985). The upper limit is often determined by the energy cost of protecting the home range against other lions, while the lower limit is set by the availability of resources (Bertram, 1973). However, anthropogenic effects and geographical boundaries also shape home ranges (Davidson *et al.*, 2012; Oriol-Cotterill *et al.*, 2015). The core of the home range is often protected more forcefully against rivals and is often defined as the lions’ territory (Schaller, 2009). Males can protect their pride by chasing away rivals and scent marking their territory with urine (Funston *et al.*, 1998; Packer *et al.*, 1991). The security of the territory is maintained by patrolling the borders, scent-marking with urine by the pride males and roaring, the latter by both males and females (Bertram, 1973; Funston *et al.*, 1998).

Lions are opportunistic predators, therefore, seasonal shifts in prey preference have been observed, causing home range size changes at different time scales (Loveridge *et al.*, 2009; Owen-Smith, 2008; Lesilau *et al.*, 2019). Apart from shifts in prey diversity, seasonal shifts in prey density can also cause the expansion or contraction of home ranges. Where prey is more concentrated around water sources in the dry season, densities decrease in the wet season, causing lion home ranges to increase, in order to contain sufficient resources (Bauer & De Jongh, 2005; Loveridge *et al.*, 2009; Tuqa *et al.*, 2014; Gittleman & Harvey, 1982; Ogutu & Dublin, 2002; Patterson *et al.*, 2004). Lion home ranges vary considerably in size, between different study areas and can range from 20-45 km² in, for example, Lake Manyara National Park and the Ngorongoro Crater in Tanzania (Schaller, 2009; Hanby & Bygott, 1987) to as much as 2,075 km² in arid ecosystems as Etosha National Park in Namibia (Stander, 1991). Even inside a national park home range sizes can differ between prides, in Makalali reserve, home range sizes vary between 24.9 km² and 106.8 km² (Druce *et al.*, 2004). Furthermore, intraspecific differences in home range sizes are also found. While the home range size

of male lions depends on both resources and access to females. Female home ranges depend almost solely on the available resources and the presence of cubs (Schaller, 2009). Therefore, it is possible for a male lions' home range to cover the home range of two or more female prides (Orsdol *et al.*, 1985; Funston *et al.*, 2003). Additionally, nomad males generally have larger home ranges due to the fact that they avoid the territories of pride males and move over longer distances (Loveridge *et al.*, 2009).

Similar to the home range, the potential minimum distance travelled by lions is found to be negatively correlated with prey densities and surface water availability (Ogutu & Dublin, 2002; Tuqa *et al.*, 2014). Most activity peaks are found at dusk and at dawn (Lesilau *et al.*, 2019), where lions can be observed hunting, mating and feeding during all times of the day, depending on ambient temperatures (Schaller, 2009). Diurnal movements can also be the result of the location of their resting site. When they come in contact with large herbivores like African buffalos (*Syncerus caffer*) or elephants (*Loxodonta africanus*), the lions often get chased away (Hayward & Hayward, 2007). The same can happen when tourists harass the lions or drive too close (Hayward & Hayward, 2007). Large variations exist but, on average, lions spend two hours a day walking and 40 to 50 minutes a day eating, the rest of the day lions are largely inactive (Schaller, 2009). When multiple coalitions are present in an area, it is possible that both coalitions have a different activity pattern (Hayward & Hayward, 2007). In this case, the dominant coalition has first choice when to be active, while the subordinate coalition is active during other periods, to avoid competition with the dominant coalition (Hayward & Hayward, 2007).

1.3 Human-carnivore conflicts

1.3.1 Lion Translocation

Since many of the problem animals are considered endangered, non-lethal solutions for human-carnivore conflicts are often preferred by conservation organisations such as KWS (Bradley *et al.*, 2005). Translocation is a method where wild individuals are transferred from one place to another, both areas being part of the current or historic range of the species (Fontúrbel & Simonetti, 2011; Miller *et al.*, 1999). It is a possible solution for human-wildlife conflicts, but it is also used by wildlife managers to achieve enforcement or reintroduction of species populations (Fischer & Lindenmayer, 2000; Treves & Karanth, 2003). Apart from the clear potential advantages to translocations, there is no consensus about their effectiveness (Fischer & Lindenmayer, 2000; Bradley *et al.*, 2005; Goodrich & Miquelle, 2005). When animals are translocated to new territories, survival might be compromised due to homing behavior and having to establish a new territory in an environment often housing a resident population (Bradley *et al.*,

2005; Stamps & Swaisgood, 2007). Furthermore, translocations can often be ineffective since translocated problem animals often cause high rates of livestock attacks after their translocations (Treves & Karanth, 2003). However, Weise *et al.* (2015) found that translocated problem leopards and lions, do not cause more livestock attacks after their translocation but they found that translocating problem leopards and lions often causes other leopards and lions to replace these translocated animals and start preying on livestock, inducing local source-sink dynamics.

1.3.2 Ecological translocation suitability

Weise *et al.* (2015) found that the success of translocations of leopards in Namibia depends for a large part on the location of release and the method of release (soft versus hard release). They were able to develop an ecological translocation suitability analysis, determining the possible release sites for leopards. The ecological translocation suitability analysis was based on resident leopard densities in the area, where locations with zero leopards or with too high densities were considered unsuitable. A 50 km buffer around urban centers was constructed and finally, areas smaller than the square of the longest measured distance travelled by a translocated leopard, before settling in an area, were taken out of the ecological translocation suitability analysis. Based on this ecological translocation suitability analysis they predicted 87 suitable leopard translocation sites in Namibia, in total covering 117,613 km². They also found less homing behavior for animals translocated with a soft release, from an acclimatization pen, compared to hard-release, straight into the new environment.

Due to its remote character, Meru National Park (MNP) has often been used as a translocation site for problem animals in Kenya (Hans de Iongh, personal communication, January 2019). Since 2012, a total of 13 problem lions have been translocated to MNP (Appendix 3). Although it is known that not all translocations were successful, Kenyan Wildlife Service (KWS) is planning to continue this translocation policy (Narisha, 2018). Very few studies have been published on the subject of problem lion translocations and very little is known about the success of the translocations.

1.4 Research objectives

Species extinction and the resulted loss of biodiversity is a global environmental problem (Heywood *et al.*, 1995; Myers *et al.*, 1979; Pimm *et al.*, 2001). Even though there is some discussion about the rate of extinction, most authors agree that human development accelerates extinction between 1,000 to 10,000 times the 'background' extinction (May *et al.*, 1995). As a consequence, the ecological, spiritual and economical function of these species is lost forever (May *et al.*, 1995).

This research contributes to the PhD of Luka Narisha (Kenya Wildlife Services) assigned to CML, Leiden University. It is the first PhD performed in MNP, concerning lions. It is a collaboration between KWS, Born Free, Leo, CML and UA. Home ranges and movements have been studied before in other national parks like Nairobi National Park, however, MNP offers a very specific study area. Together with Tsavo National Park it is the main site in Kenya to which problem lions have been translocated. This makes it possible to study the effectiveness of problem lion translocations as a mitigation strategy for problem lions. This is different from the reintroduction of lions in areas where lions became extinct.

The goal of this research is to define the differences in both home ranges and movements between resident and translocated problem lions and their possible interaction. Furthermore, I intend to predict the potential of MNP as a translocation site, for future lion translocations. Firstly, I hypothesize that home ranges and movements differ between resident and translocated problem lions, in the first few months after the translocation. I expect translocated problem lions to have a larger home range than resident lions. Secondly, I hypothesize that MNP has a good potential as a translocation site for future translocations, due to the fact that it is still recovering from high degrees of poaching in the past and therefore the full carrying capacity has not been reached yet. Expanding our knowledge on the behavior of translocated problem lions and defining which factors influence the success or failure of translocation will be crucial for a sound translocation policy. I have defined the following research questions:

1. Lion movements and home range in time and space:
 - (a) What are the movements for the different lions?
 - (b) Which factors influence movements?
 - (c) What are the home range estimators for the different lions?
 - (d) How often do lions leave the park?
 - (e) How long does it take for the lions to establish a home range?
 - (f) Is there a difference in home range between resident and translocated problem lions?
2. Ecological translocation suitability for translocation in the park:
 - (a) What is the carrying capacity for lions in the park?
 - (b) Which factors influence the carrying capacity for lions?
 - (c) What is the potential of the park as a translocation site for problem lions?
 - (d) Which area in the park is still suitable for translocation?

Chapter 2

Material and Methods

2.1 Study site

The study site, MNP, offers a highly biodiverse ecosystem and is located at the base of the Nyambene Hills in the heart of Kenya, about 360 km north-east of Nairobi, close to the foothills of Mount Kenya. MNP was established in 1957 as a game reserve until it became a National Park in 1967 (Narisha, 2018). The Park covers 884 km² and is surrounded by Kora National Park, Bisanadi reserve and Rahole reserve, as well as community lands (Sitienei *et al.*, 2014). As a whole, MNP is part of a protected area covering around 4000 km², located in the Eastern Province from 37°59' 55" to 38°25' 22.76"E and 0°19' 8"N to 0°5' 24"S, hence crossing the equator (Narisha, 2018).

MNP is characterized by very high biodiversity, with different carnivore species including African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*) and African lion (*Panthera leo melanochaita*). Besides many species of carnivores, herbivores such as African elephants (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*) and Grevys zebra (*Equus grevvi*) appear in MNP (Narisha, 2018). Large conservation areas, such as the Meru Conservation Area (MCA), are important for the protection of large-scale processes that take place in nature, as well as for conserving important biodiversity corridors protecting migratory species and species with large home ranges (IUCN, 2009).

The climate in MNP is hot and arid with low humidity and, due to its position near the equator, the park experiences fairly uniform temperatures. Temperatures range from 32 °C during the day to 17 °C at night. Two rainy seasons can be differentiated, with the long rainy season taking place from March to May, and the short rainy season from October to December. Precipitation varies throughout the park and is the highest along the western border of the park, leading to zones that remain green throughout the year. Lowest precipitation is found in the southern part of the park giving rise

to a much drier area (Narisha, 2018). Broadly, three different vegetation types can be distinguished. First, *Acacia*-wooded grassland, which can be found in the eastern part of the park, dominated by *Acacia* species, along rivers and swampy areas other, mostly *Hyphaene coriacea* can be found (fig. 2.1f (Bekele *et al.*, 2006). The western part of the park is covered by *Combretum*-wooded grassland. Here, *Combretum* species dominate the upland parts, while the riverine vegetation is dominated by *Lawsonia inermis*. Some swampy areas in this part of the park are dominated by *Acacia* trees, while most of the swamp floor is covered by the grass *Chloris gayana*. Finally, the southern region consists of *Acacia-Commiphora* bushland. Appearing in small areas of the park are other habitat types, including riverine forests, inselbergs, groundwater forest and swamps (Bekele *et al.*, 2006).

2.2 Lion collaring

The study of the home ranges was done using four satellite-GPS/VHF collars of Savannah Tracking by Born Free and one iridium-satellite GPS collar of African Wildlife Tracking (Fig. 3.1). A total of five lions were collared, three of which were translocated problem lions from other areas (Table. 3.1). The collars were programmed to record the GPS position of each lion every hour. However, we experienced that for the collars of Savannah Tracking, when the lions were in thick bushes, the GPS location was not always recorded. Lions could also be located using the VHF-receiver and opportunistic encounters. However, this proved to be more challenging than expected due to the dense nature of the vegetation in MNP. During fieldwork we were not able to use the VHF receiver.

2.3 Movements and home ranges

Movements were analyzed using Microsoft Office Excel 2010 (Microsoft, U.S.A). The distance between two data points was calculated as a straight line between these data points. Distances were divided by the number of hours between the GPS fixes, hereby calculating the average potential minimum distance (m) per hour. In order to correct for the times no signal was emitted. Since the potential minimum distance uses a straight line it may be an underestimation of the actual travelled distance. In order to calculate the average potential minimum daily travelled distance, the sum of all the average potential minimum distance during 24 hours was taken.

Home ranges were constructed using RStudio v.1.1.447. Both Kernel Density Estimates and Minimum Convex Polygons were used to calculate the home range. The Kernel Density Estimator represents a surface area on an x-y plane and plots the GPS

fixes as a three-dimensional "hill", the kernel, on the x-y plane (Boitani & Fuller, 2000). The kernel is higher where the density of the GPS fixes is higher, the width of the kernel can be adjusted to prevent over smoothing and was calculated using the reference bandwidth parameter (h_{ref}) (Boitani & Fuller, 2000). Even though the Kernel Density Estimator is often considered the best method to calculate home ranges, this method is very sensitive to over smoothing (Powell *et al.*, 1997; Seaman & Powell, 1996; Worton, 1989). As a consequence, home ranges were also calculated using the Minimum Convex Polygon estimation. The Minimum Convex Polygon is defined as the smallest convex polygon that encompasses all lion locations (Boitani & Fuller, 2000). The Kernel Density estimator was calculated twice, once removing 5% of the outliers (95% Kernel Density Estimator) and once removing 50% of the outliers (50% Kernel Density Estimator) which is considered the core home range. The same was done for the Minimum Convex Polygon, however, here the 100% Minimum Convex Polygon was added where all of the data points were used in calculating the home range, hereby not correcting for exploratory behavior (Boitani & Fuller, 2000). After calculating the home ranges in RStudio v.1.1.447, they were plotted in ArcGIS v.10.3 to calculate the percentage outside the boundaries of MNP.

The establishment of the home ranges was calculated using the Minimum Convex Polygon. The home ranges were calculated starting with the first five GPS fixes, after which the same was done adding the following GPS fixes. This was repeated until the total amount of GPS fixes were used. Briers-Louw *et al.* (2019) defined the establishment of a home range as the time it takes a lion to reach a home range, within 10% of his home after one year. Since none of the collars of the lions in this research emitted a signal for over a year, the definition was set to the moment the 95% Minimum Convex Polygon reached a maximum.

2.4 Statistical analysis

Statistical analyses were carried out in RStudio v.1.1.447. Normal distribution of the data was calculated using the Shapiro-Wilk test. In order to calculate the differences in movements between males and females and between translocated and resident lions, a generalized linear mixed (GLM) effect ecological translocation suitability analysis was used (R package lmerTest). Both gender and origin were used as fixed factors and the different individuals were added as a random factor. However, because of the small sample size and the lack of males in the group of resident lions, it was not possible to test for an interaction between gender and origin. Results are considered statistically significant for $p < 0.05$. Differences in home ranges were not calculated due to the very limited sample size.

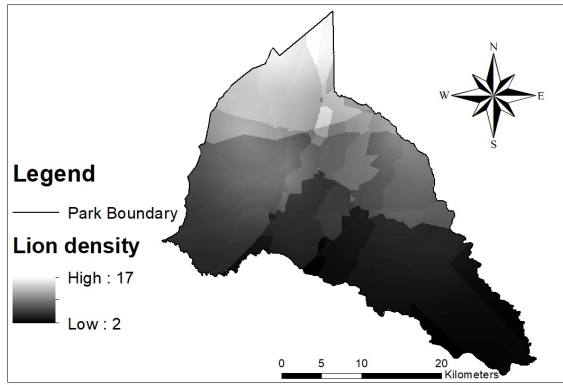
2.5 Ecological translocation suitability

In order to perform the ecological translocation suitability analysis, the park was divided into pixels, each having a surface area of 0.858 m². For each pixel, a value was determined for seven different ecological variables. Variations in each of the variables were scaled in terms of lion preference from 10-90 with increments of 10, assuming no conditions are perfect, and nothing is impossible (Appendix 1). The seven different ecological variables were given a weighted value depending on their importance in lion ecology. The weights were determined based on an ecological translocation suitability analysis constructed by Lemeris (2013) and adapted for lions based on literature. Using the Raster Calculator in ArcGIS v.10.3 a final map was constructed showing the weighted average of the ecological parameters for different locations in MNP. Three different scenarios are considered where different tolerances were assumed for lions. The scenario with the highest tolerance translocated problem lions would tolerate areas with an ecological translocation suitability score of 40 and above, while in the scenario with the lowest tolerance, lions would need areas with an ecological translocation suitability score of at least 60 to survive. When medium tolerance was assumed, the lions would stay in areas with an ecological translocation suitability score of 50 and above.

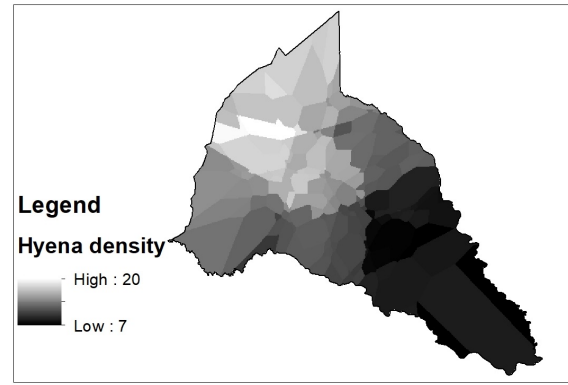
2.5.1 Ecological variables

The ecological variables altitude (Fig. 2.1c), precipitation (Fig. 2.1d), distance to rivers (Fig. 2.1e), vegetation (Fig. 2.1f) and prey diversity (Appendix 2) were included in the final ecological translocation suitability analysis for their obvious influence on the suitability of the area for lion translocations. Since the current ecological translocation suitability analysis was intended only for MNP, which is a protected area, only ecological variables were taken into account, assuming no human influences inside a protected area. More complex ecological variables, like the lion density factor (Fig. 2.1a) and the hyena density factor (Fig. 2.1b), were also used in the ecological translocation suitability analysis, following the method developed by Lemeris (2013).

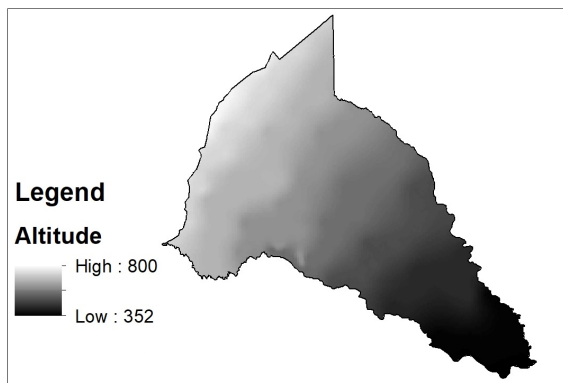
Prey species densities affect the ecological translocation suitability positively as higher prey densities can support higher lion densities (Hayward *et al.*, 2007). Therefore, both the prey densities and the lion densities were used to calculate the lion density factor, which was also included as one of the variables in the ecological translocation suitability analysis. In order to calculate the lion density factor, the carrying capacity for lions in the park was divided by the measured lion densities. Hence, the lion density factor can be defined as the rate up to which the carrying capacity has been reached. The carrying capacity is defined as the maximum number of lions that available resources in MNP can support and was calculated based on the prey species densities



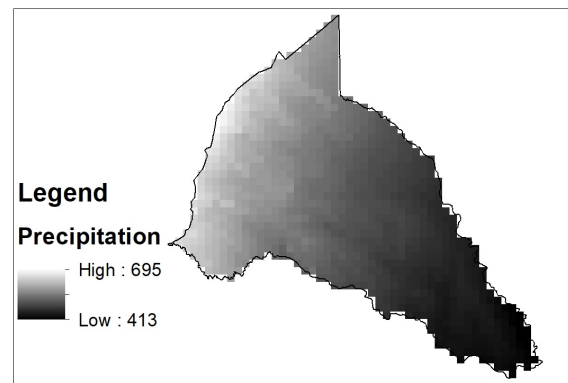
(a) Lion density in lion/100km² (Bundotich *et al.*, 2016)



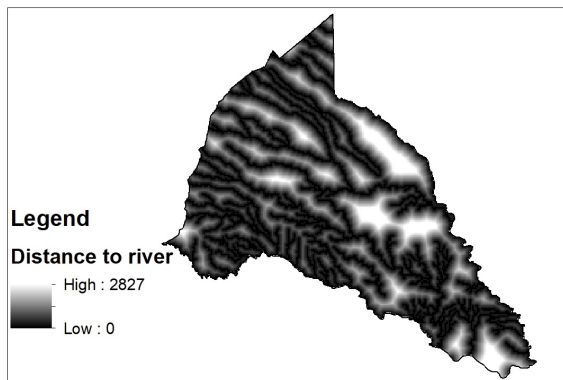
(b) Hyena density in hyenas/100km² (Bundotich *et al.*, 2016)



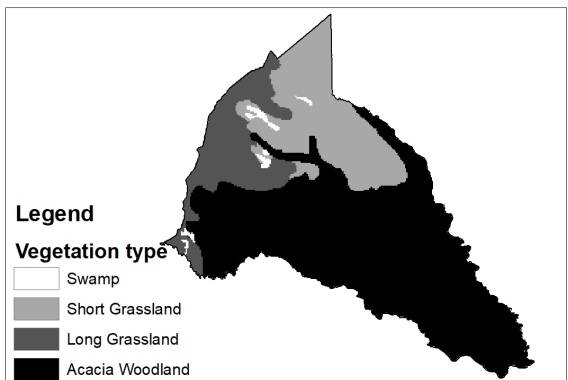
(c) Altitude in m (WRI, 2019)



(d) Precipitation in mm (WRI, 2019)



(e) Distance to rivers in m (Bundotich *et al.*, 2016)



(f) Vegetation (Bekele *et al.*, 2006)

Figure 2.1: Representation of variables used for the translocation ecological translocation suitability analysis for lions in MNP (Bekele *et al.*, 2006; WRI, 2019; Bundotich *et al.*, 2016)

(Fig. 2.2) (Hayward *et al.*, 2007). Lion densities in itself give little information about the competition in an area. Whenever carrying capacity is low, high lion densities will cause high competition, however when carrying capacity is high, high lion densities may not necessarily cause high competition. Therefore, it was decided to include the

carrying capacity in the ecological translocation suitability analysis. Carrying capacity, however, is hard to quantify since it is a very dynamic concept that can change from year to year (Byron *et al.*, 2011) and its estimation will always be partially theoretical. Despite this limitation, carrying capacity was added to the ecological translocation suitability analysis because of the important information it contains, which more than compensated for the slight decrease in ecological translocation suitability analysis robustness. Lion carrying capacity was calculated following the procedure of Hayward *et al.* (2007) with the formula:

$$y = 10^{(-2.158 + 0.377x)} \quad (2.1)$$

where y is the carrying capacity for lions (lion km^{-2}) and x is the \log_{10} of the prey biomass (kg km^{-2}), including giraffe (*Giraffa camelopardalis*), common zebra (*Equus quagga*), gemsbok (*Oryx gazelle*) and buffalo. Blue wildebeest (*Connochaetes taurinus*) was not included since it is not present in MNP. Data on prey densities (Fig. 2.2) were obtained from Bundotich *et al.* (2016).

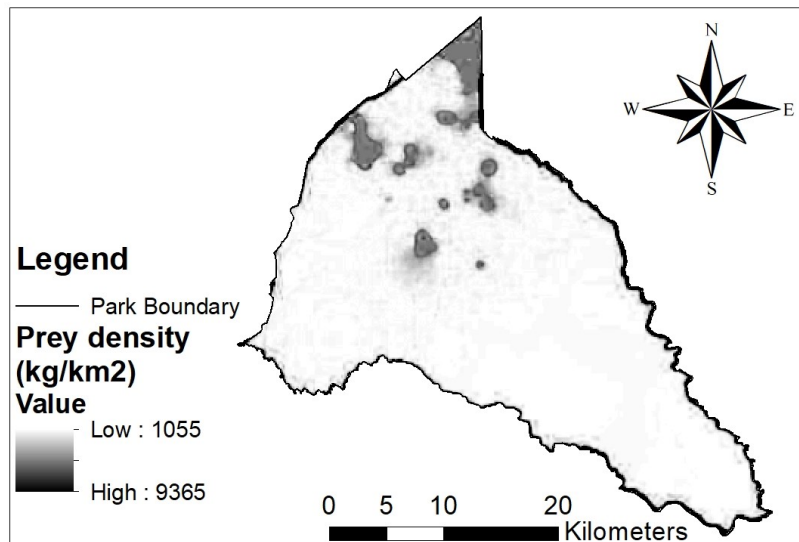


Figure 2.2: Prey density for lions in MNP, including giraffe, common zebra, gemsbok and buffalo (Bundotich *et al.*, 2016).

The effect of the lion and spotted hyena density factor is more complex to determine than the other ecological variables. On the one hand, a high lion or spotted hyena density factor has a negative effect on the ecological translocation suitability of the park as they increase competition. A low spotted hyena density factor, on the other hand, has very little effect on the translocation ecological translocation suitability analysis, while a low lion density factor would again have a negative effect due to the lack of possible mates. This may cause the translocated problem lion to move out of the area

in search of a potential mate. Medium lion and spotted hyena density factors were expected to have a positive effect on the ecological translocation suitability, since small groups of hyenas are not able to prevent getting their kills stolen by lions, in this way benefiting the lion population, while a medium lion density factor reduces competition, yet provide sufficient potential mates.

Some of the variables could be scored immediately, while others had to be adjusted before they contained the needed information for the ecological translocation suitability analysis. Prey diversity, for example, was calculated for the different vegetation types using transect counts. The number of recorded prey species was then divided by the total number of prey species in the park, following the procedure of Hayward *et al.* (2007), with the addition of dik-dik (*Madoqua*), gerenuk (*Litocranius walleri*) and Grevy-zebra, to determine which species are considered prey species. The distance to rivers (m) raster (Fig. 2.1e) was generated using the Euclidean Distance function in ArcGIS v. 10.3. Lion and hyena densities were calculated based on call back data found by Bundotich *et al.* (2016). The callback data were plotted on a map and using the kriging-tool in ArcGIS v. 10.3 the data were extrapolated over the whole park. The ratio of the measured hyena densities to lion densities in the park was calculated using the Raster Calculator function in ArcGIS v. 10.3, since the ratio gives more information about competition than plain densities. Measured lion densities were divided by the previously calculated carrying capacity, again using the Raster Calculator function in ArcGIS v. 10.3, to estimate the percentage of the carrying capacity that is reached.

Data on prey diversity in MNP were collected during a three-month period from the beginning of February to the end of April through prey counts in a total of seven transects of 2km each (Bal, 2020). A shapefile containing the river network was obtained from KWS. Altitude, as well as precipitation data, were abstracted from shapefiles, made available by the World Recourses Institute (WRI, 2019). Information about the different vegetation types was extracted from Bekele *et al.* (2006).

2.5.2 Validation of literature based weights

In order to provide a rough validation of the accuracy of the ecological translocation suitability analysis based on literature, the output was compared to the data of the translocated problem lions. In total, 1,427 GPS locations of a translocated problem lions were obtained from KWS. A histogram was created, starting from an ecological translocation suitability score of 30 to an ecological translocation suitability score of 70, with increments of 5. The upper and lower limit of the analysis were defined based on the scores obtained from the ecological translocation suitability analysis adapted from literature. For each bar, the total number of GPS locations of translocated lions, recorded in these areas was divided by the calculated surface to estimate if the translocated lions

selected for areas with a higher ecological translocation suitability score.

2.5.3 Weight optimisation

Optimizing the weights of the ecological translocation suitability analysis was done by using Bayesian statistics (Van Oijen *et al.*, 2005). Firstly, an ideal histogram with eight bars was created, again starting with an ecological translocation suitability score 30 and ending with an ecological translocation suitability score of 70. The ideal histogram represents the density of GPS recordings, calculated by dividing the number of GPS recordings in each pixel by the number of pixels with a certain ecological suitability score. Ideal values for the histogram were calculated based on the available data. A linear increase of the density was expected starting from zero, with the same average density of GPS recordings as the actual data. This results in an ideal histogram starting from zero and ending at two times the average density of GPS recordings, with a step wise increase of $(2 * \text{the average density}) / (\text{number of bars} - 1)$.

Secondly, random weights were generated for the different ecological variables, each time calculating a histogram with the same axes as the ideal histogram. Thereafter, the difference between the ideal histogram and the newly generated histogram was calculated based on the log likelihood (Van Oijen *et al.*, 2005). This process was repeated with slightly different weights, however, when the last generated histogram differs more from the ideal histogram than the previous attempt the newly generated weights were no longer used and new weights were generated based on the best attempt. This loop was repeated 10,000 times, in this way optimizing the weights. Finally, the best fitting weights were used to do an ecological translocation suitability analysis.

2.5.4 Weight selection

Table 2.1: Estimates of ecological variables with their weighted value, contributing to the ecological suitability analysis for translocated lions.

Ecological variable	Weight (Literature)	Source	Weight (Bayesian)
Lion density factor	0.25	Lemeris (2013)	0.20
Hyena density factor	0.10	Trinkel & Kastberger (2005)	0.18
Prey diversity	0.05	Lemeris (2013)	0.20
Vegetation	0.15	Spong (2002)	0.10
Distance to the river	0.15	de Boer <i>et al.</i> (2010)	0.06
Precipitation	0.15	Celesia <i>et al.</i> (2010)	0.06
Altitude	0.15	Celesia <i>et al.</i> (2010)	0.17

For the weights based on literature the highest weight was assigned to the lion density (0.25) while prey diversity had the lowest importance for the ecological suitability analysis (0.05). Vegetation, distance to rivers, precipitation and altitude got assigned a

weight of 0.15 while hyena density was assigned a weight of 0.10. These weights give the following equation for our ecological suitability analysis (Table 2.1):

$$\begin{aligned} \text{Ecological suitability} = & 0.25 * \text{Lion density factor} + 0.15 * \text{Vegetation} + \\ & 0.15 * \text{Distance to the river} + 0.15 * \text{Altitude} + 0.15 * \text{Precipitation} + \\ & 0.10 * \text{Hyena density factor} + 0.05 * \text{Prey diversity} \end{aligned} \quad (2.2)$$

After using Bayesian statistics to optimize the weights based on the available data, all seven ecological variables were found to be significant. However, prey diversity was assigned a weight equal to the lion density factor (0.20), while both distance to the river and precipitation were assigned the lowest weight of 0.06. Vegetation was assigned a weight of 0.10, slightly lower than the weight adapted from literature. Hyena density factor on the other hand was assigned a weight slightly higher than the weights adapted from literature (0.18). Finally, altitude was assigned a weight of 0.17, similar to the weight adapted from literature. Resulting in the following equation:

$$\begin{aligned} \text{Ecological suitability} = & 0.20 * \text{Lion density factor} + 0.10 * \text{Vegetation} + \\ & 0.06 * \text{Distance to the river} + 0.17 * \text{Altitude} + 0.06 * \text{Precipitation} + \\ & 0.18 * \text{Hyena density factor} + 0.20 * \text{Prey diversity} \end{aligned} \quad (2.3)$$

with each parameter expressed in its assigned score (Appendix 1).

Chapter 3

Results

3.1 Lion collaring

As shown in table 3.1 the lions were not all collared during the same period. One lioness was collared in 2016, all other lions were collared in 2018. FRL1 (Virginia) was collared in 2016 but the collar stopped working in October of that year and started working again in September of 2017, therefore data of the full time period she was collared are not available. Of the three translocated problem lions, two lions died within a year after translocation, FTL1 (Sericho) was killed by farmers and FTL2 (Tall Boy) of unknown causes. Therefore, their translocation is considered unsuccessful. MTL1 (Solio) however, did survive more than a year after his translocation, after a few months he integrated with an existing pride by defeating the pride male and even got to reproduce. His translocation is therefore considered successful (Weise *et al.*, 2015; Briers-Louw *et al.*, 2019; Yiu *et al.*, 2015).

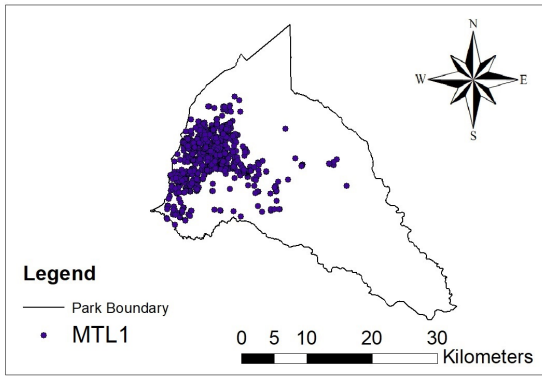
Table 3.1: Available data of lion collaring in Meru National Park with the number fixes representing the number of fixes used in this research.

Nickname	ID	Gender	Translocated	Origin	Collaring	End of collar	No. of fixes (n)
Solio	MTL1	m	yes	Mt. Kenya Holiday Homes	11/07/2018	(active)	1394
Sericho †	FTL1	f	yes	Sericho	28/02/2018	30/09/2018 †	2256
Tall boy †	FTL2	f	yes	Mutara ranch	13/07/2018	06/10/2018 †	615
Virginia	FRL1	f	no	MNP	12/05/2016	22/01/2018	5397
G-coy	FRL2	f	no	MNP	08/09/2018	10/03/2019	4352

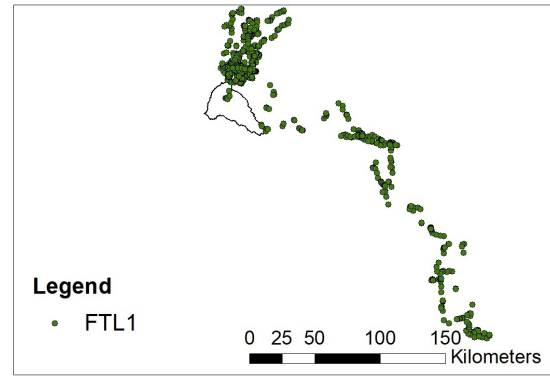
† Deceased lion

3.2 Movements

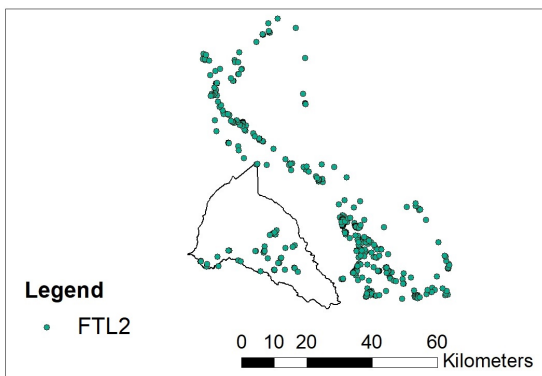
When analysing the average potential minimum distance travelled during a day (24h) it became clear that both FTL1 (Sericho) and FTL2 (Tall Boy) travelled greater distances than the three other lions (Table 3.2). Apart from travelling greater distances they also



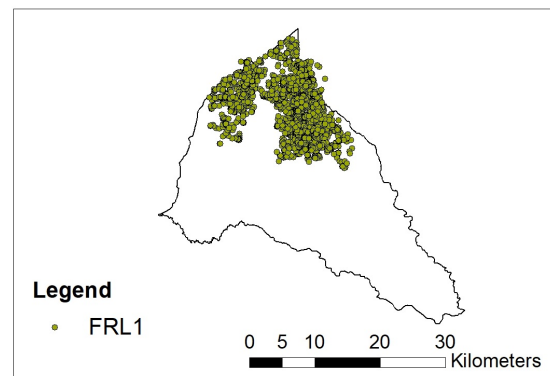
(a) GPS fixes for MTL1 (Solio) (translocated)



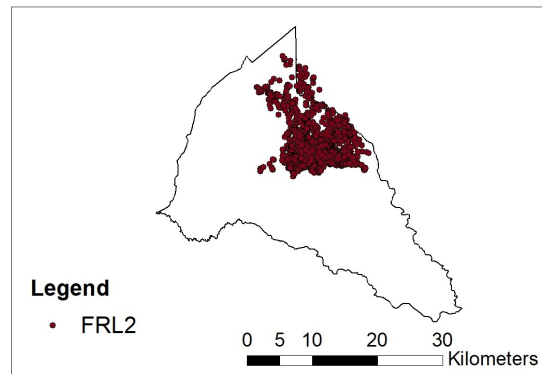
(b) GPS fixes for FTL1 (Sericho) (translocated)



(c) GPS fixes for FTL2 (Tall Boy) (translocated)



(d) GPS fixes for FRL1 (Virginia) (resident)



(e) GPS fixes for FRL2 (G-coy) (resident)

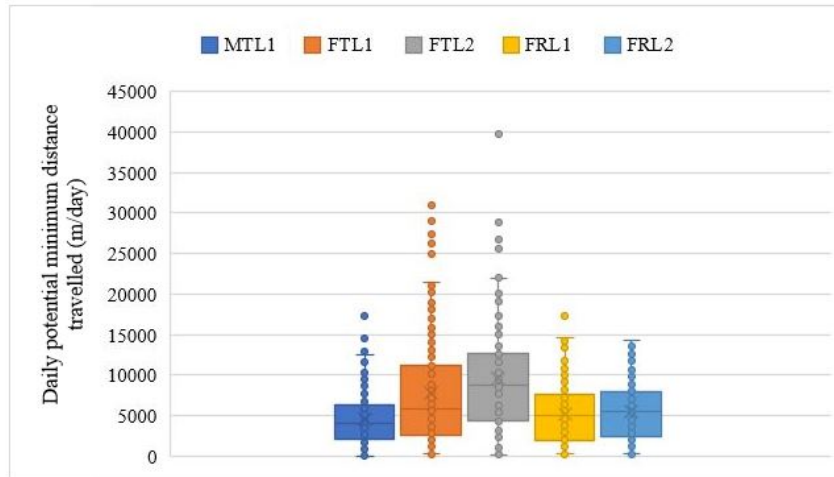
Figure 3.1: GPS fixes for the collared lions in MNP

had a greater standard deviation, indicating more variation in potential minimum distance they travelled.

Differences in average potential minimum distance travelled in 24h, between males and females were not significant (Fig. 3.2, $p = 0.0836$). Similarly, average potential minimum distance travelled (24h) between translocated and non-translocated individuals were not significant either (Fig. 3.2, $p = 0.0852$).

Table 3.2: Overview of average (\pm s.d.) in meters travelled per 24hr for the collared lions in Meru National Park.

Nickname	ID	Gender	Translocated	Average (\pm s.d.) (m)	No. of fixes (n)
Solio	MTL1	m	yes	4467 \pm 3029	1394
Sericho	FTL1	f	yes	7704 \pm 6892	2256
Tall boy	FTL2	f	yes	9569 \pm 7207	615
Virginia	FRL1	f	no	5242 \pm 3592	5397
G-coy	FRL2	f	no	5575 \pm 3635	4352

**Figure 3.2: Average potential minimum distance (m) travelled in a day (24h) \pm s.d.**

Similar to the average potential minimum distance travelled in 24h, differences in average potential minimum distance travelled during three hour intervals of the day, were analysed. Fig. 3.3 clearly shows that during day light, lions in MNP travelled less than during the night. Apart from MTL1 (Solio), the translocated problem lions travelled greater distances during the most active hours, compared to the resident lions. However, differences between translocated and resident lions were not significant ($p = 0.0814$) and neither were the differences between males and females ($p = 0.0661$).

3.3 Home ranges

Table 3.3 shows the home range (100% Minimum Convex Polygon, 95% Minimum Convex Polygon and 95% Kernel Density Estimation) and core home range (50% Minimum Convex Polygon and 50% Kernel Density Estimation) of the five collared lions in MNP. The average home range of the unsuccessfully translocated problem lions, using the 95% Minimum Convex Polygon estimate, equaled $10,735 \pm 9,788 \text{ km}^2$ while the average home range for resident lions was $199 \pm 76 \text{ km}^2$. When using the 95% Kernel Density Estimation home ranges of translocated problem lions were found to be $13,208 \pm 11,968 \text{ km}^2$ and $187 \pm 71 \text{ km}^2$ for resident lions. Average home ranges

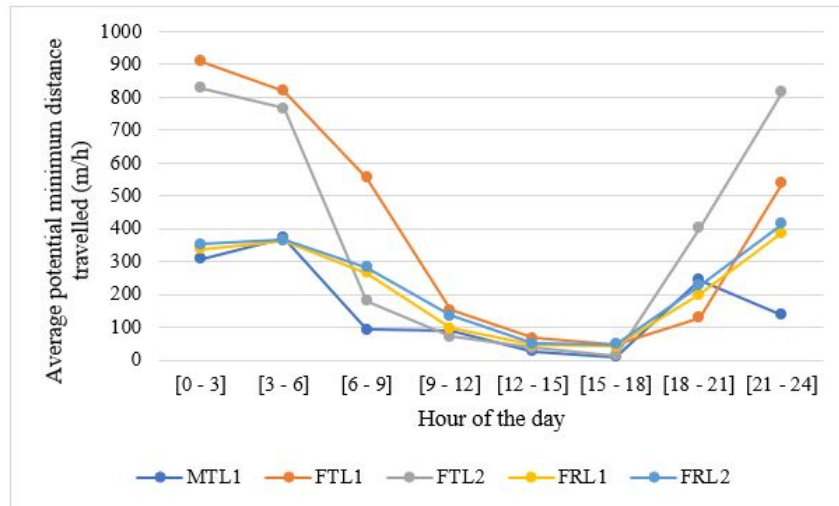


Figure 3.3: Average potential minimum distances (m) per hour travelled during 3-hour time periods.

differed clearly between translocated and resident lions, except for MTL1 (Solio). For example, the 95% Kernel Density Estimation home range of the translocated problem lion FTL1 (Sericho) was found to be 158 times bigger than the 95% Kernel Density Estimation home range of FRL2 (G-coy), a resident lion. Similarly, core home ranges of two translocated problem lions, FTL2 (Tall Boy) and FTL1 (Sericho), were found to be much larger compared to the other three lions. In the same way as the home range, the 50% Kernel Density Estimation core home range of FTL1 (Sericho) was found to be 105 times larger compared to the 50% Kernel Density Estimation core home range of FRL2 (G-coy). Despite being translocated, MTL1's (Solio) home range and core home range had around the same size as the home range and core home range of resident lions. The home ranges and core home range are shown in figure 3.4.

Table 3.3: Home range and core home range estimates for the collared lions in Meru National Park, using Minimum Convex Polygon and Kernel Density Estimations.

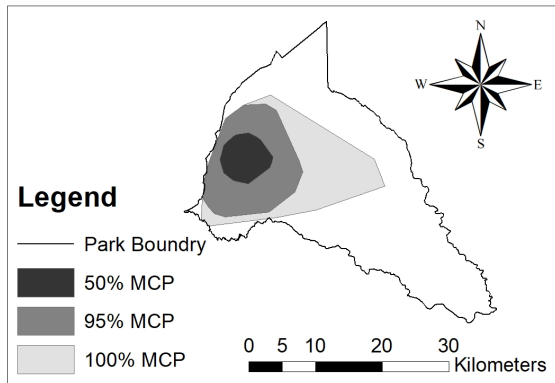
Nickname	ID	Gender	Translocated	MCP100 (km ²)	MCP95 (km ²)	MCP50 (km ²)	KDE95 (km ²)	KDE50 (km ²)
Solio	MTL1	m	yes	344.44	184.53	43.43	193.49	33.72
Sericho	FTL1	f	yes	18214.88	17655.77	4752.07	21670.33	2503.72
Tall Boy	FTL2	f	yes	4317.43	3813.81	1091.97	4744.73	981.06
Virginia	FRL1	f	no	293.42	253.19	124.35	236.86	46.15
G-coy	FRL2	f	no	213.57	145.11	34.18	136.88	24.19

As shown in Table 3.4 and Fig. 3.4 parts of the lions home ranges and core home ranges surpasses the boundaries of the park (Fig. 3.4). For the translocated problem lions FTL1 (Sericho) and FTL2 (Tall Boy) the proportions outside of the park were found to be larger than for the other lions, with FTL1 (Sericho) with 96.07% of its 95% Kernel Density Estimation outside the park. In comparison, for the resident lions

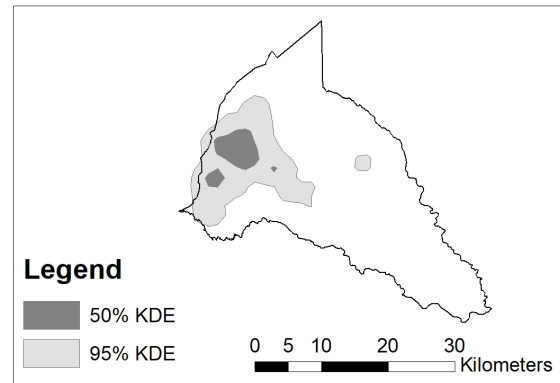
FRL1 (Virginia) had the highest proportion of its home range outside the boundaries of the park, 13.52% of its 95% Kernel Density Estimation surpasses the park boundaries. Similarly, for the core home range estimates both FTL2 (Tall Boy) and FTL1 (Sericho) were found to have 95.58% and 93.62% of their 50% Kernel Density Estimation core home range outside of the Park respectively. Again, with 12.55%, FRL1 (Virginia) was the resident lion with the largest proportion of its 50% Kernel Density Estimation core home range outside the park. Conversely to the other translocated problem lions, MTL1 (Solio) was found to only have 5.34% of its 95% Kernel Density Estimation outside of the park and 0% of its 50% Kernel Density Estimation core home range.

Table 3.4: Proportion of the home range and core home range estimates for the collared lions, using Minimum Convex Polygon and Kernel Density Estimations, outside Meru National Park.

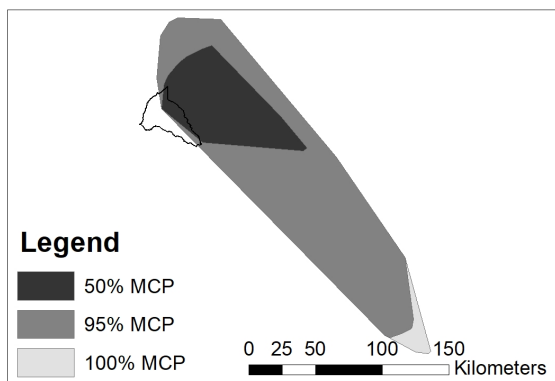
Nickname	ID	Gender	Translocated	MCP100	MCP95	MCP50	KDE95	KDE50
Solio	MTL1	m	yes	0.11%	0.10%	0.00%	5.34%	0.00%
Sericho	FTL1	f	yes	97.97%	97.91%	94.34%	96.07%	93.62%
Tall boy	FTL2	f	yes	81.72%	79.40%	74.94%	85.18%	95.58%
Virginia	FRL1	f	no	12.24%	13.52%	8.52%	16.91%	12.55%
G-coy	FRL2	f	no	9.46%	5.87%	0.00%	5.36%	0.00%



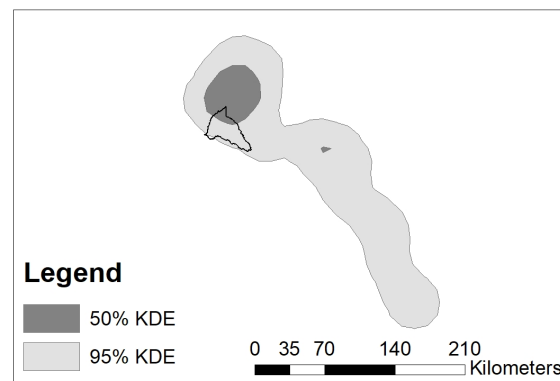
(a) Minimum Convex Polygons for MTL1 (Solio) (translocated)



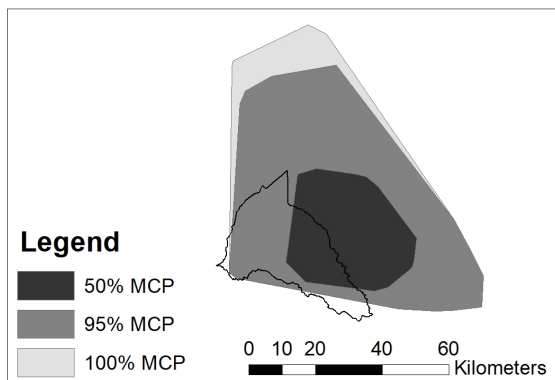
(b) Kernel Density Estimates for MTL1 (Solio) (translocated)



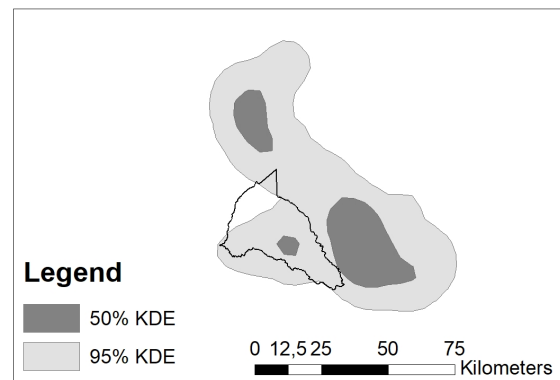
(c) Minimum Convex Polygons for FTL1 (Sericho) (translocated)



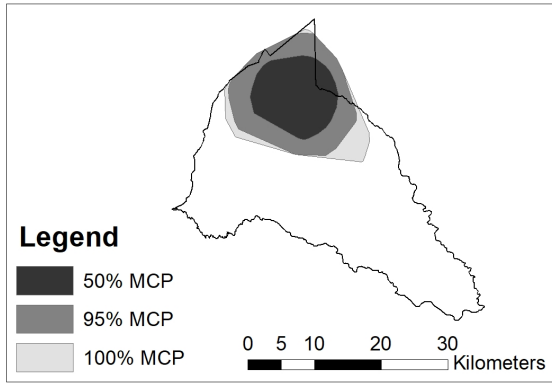
(d) Kernel Density Estimates for FTL1 (Sericho) (translocated)



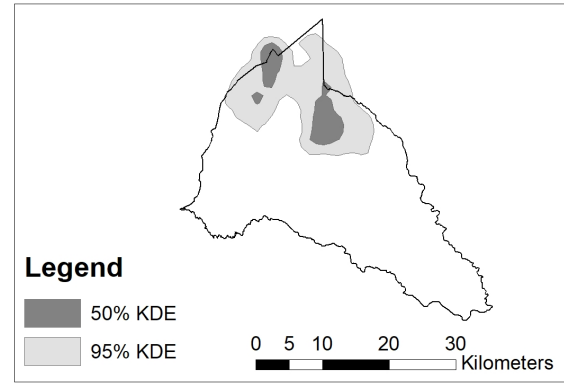
(e) Minimum Convex Polygons for FTL2 (Tall Boy) (translocated)



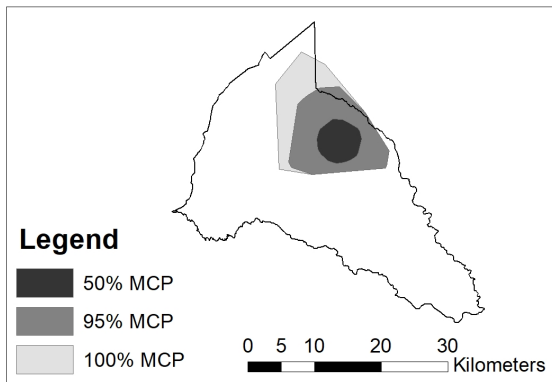
(f) Kernel Density Estimates for FTL2 (Tall Boy) (translocated)



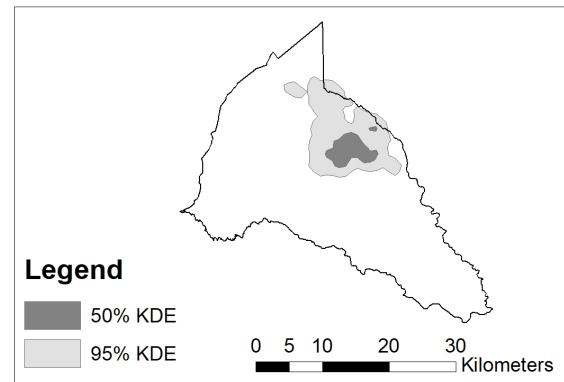
(g) Minimum Convex Polygons for FRL1 (Virginia) (resident)



(h) Kernel Density Estimates for FRL1 (Virginia) (resident)



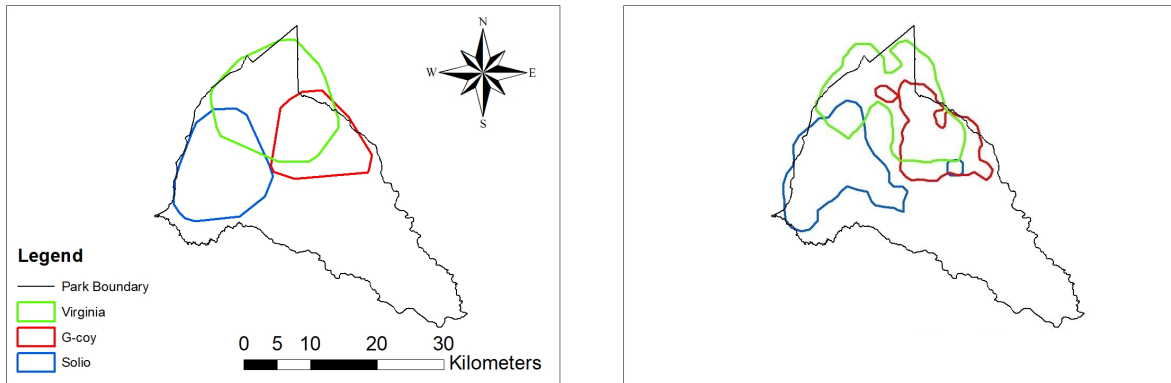
(i) Minimum Convex Polygons for FRL2 (G-coy) (resident)



(j) Kernel Density Estimates for Frl2 (G-coy) (resident)

Figure 3.4: Home ranges and core home ranges (95% and 50% Kernel Density Estimates (KDE) and 100%, 95% and 50% Minimum Convex Polygons (MCP)).

Between the home ranges of the lions that did not move outside of the park boundaries there was overlap of home range (Fig.3.5). Both the 95% Minimum Convex Polygon (Fig. 3.5a) and 95% Kernel Density Estimate (Fig. 3.5b) home range show the same trend. Most of the overlap was between both resident lions FRL2 (G-coy) and FRL1 (Virginia), while there was some overlap between the successfully translocated problem lion MTL1 (Solio) and FRL1 (Virginia), home ranges of MTL1 (Solio) and FRL2 (G-coy) did not overlap.

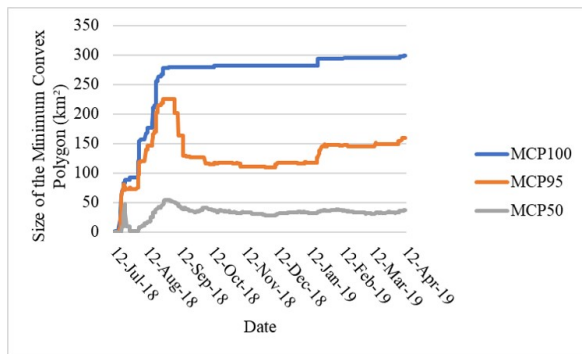


(a) Overlap in 95% Minimum Convex Polygons home range (b) Overlap in 95% Kernel Density Estimate home range

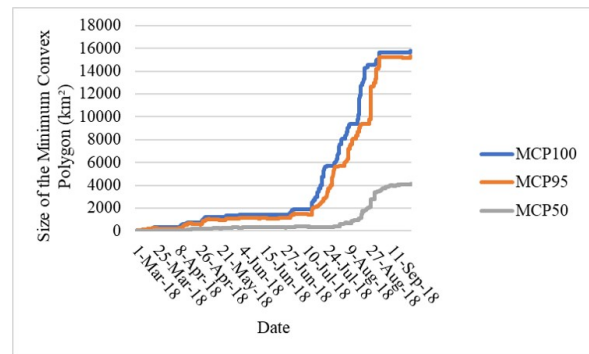
Figure 3.5: Home ranges overlap in the form of 95% Minimum Convex Polygons (a) and 95% Kernel Density Estimates (b) for the lions that stayed inside the park, namely, resident lions FRL2 (G-coy) and FRL1 (Virginia) and successfully translocated problem lion MTL1 (Solio).

3.4 Home range establishment

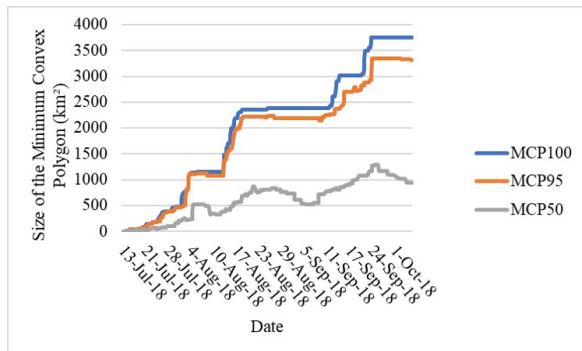
Both FTL1 (Sericho) (Fig. 3.6b) and FTL2 (Tall Boy) (Fig. 3.6c) had a constantly increasing home range (95% Minimum Convex Polygon), in contrast to MTL1 (Solio) (Fig. 3.6a). This lion is the only translocated problem lion, who's home range started to decline after two months. The home range of resident lion FRL2 (G-coy) (Fig. 3.6d) started declining one month after release. The same trend was found for the core home range (50% Minimum Convex Polygon). However, FTL2's (Tall Boy) core home range seems to become smaller from time to time. Due to the missing data on FRL1 (Virginia) (Fig. 3.1d) both the home range and core home range will not be discussed.



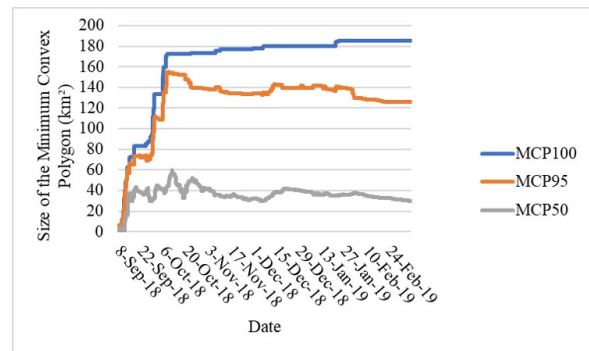
(a) Home range asymptote for MTL1 (Solio) (translocated)



(b) Home range asymptote for FTL1 (Sericho) (translocated)



(c) Home range asymptote for FTL2 (Tall Boy) (translocated)



(d) Home range asymptote for FRL2 (G-coy) (resident)

Figure 3.6: Home range and core home range asymptotes in the form of 100%, 95% and 50% Minimum Convex Polygons (MCP).

3.5 Ecological translocation suitability

A total carrying capacity of 80 lions was calculated for the entire MNP, based on prey biomass. Local carrying capacities ranged from 10 lions per 100km² to 22 lions per 100km². The highest carrying capacity was found in the southern part of the park, where small patches with higher prey densities were available (Fig. 3.7). Apart from

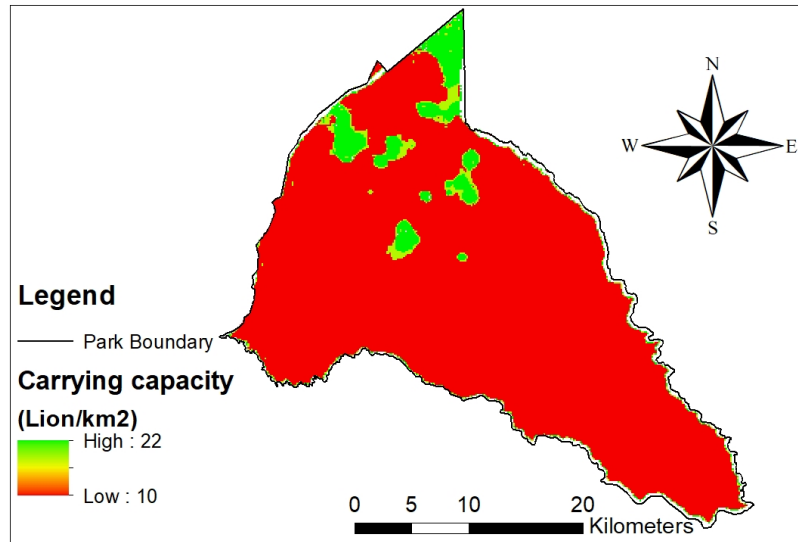
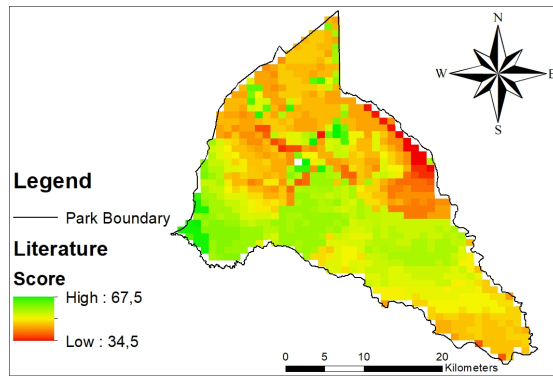


Figure 3.7: Carrying capacity for lions (lions/100km²) in MNP based on the prey densities of giraffe, gemsbok, common zebra and buffalo.

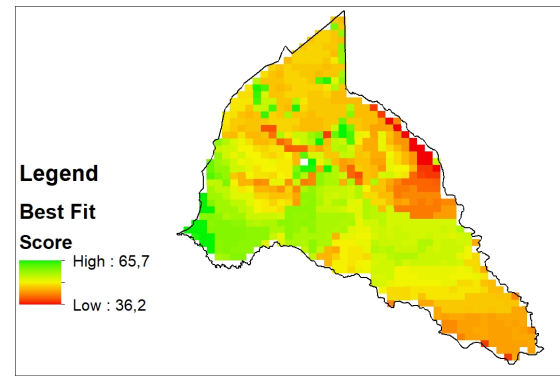
these local maxima, carrying capacity was rather low in the rest of the park.

Ecological translocation suitability scores in MNP varied between 34.5 and 67.5 for the analysis adapted from literature and between 36.2 and 65.7 for the best fit ecological translocation suitability analysis. The constructed ecological translocation suitability analyses (Fig. 3.8a,b) showed a low score for lion translocation suitability in both the northern and southern part of the park, whereas the central part of the park showed a higher translocation suitability score. Highest translocation suitability scores were found in the western part of the park and lowest scores were found in the north-eastern side of the park. As shown in figure 3.8c,d the histogram calculated with the best fit weights differed less from the ideal histogram than the histogram based on the weights adapted from literature.

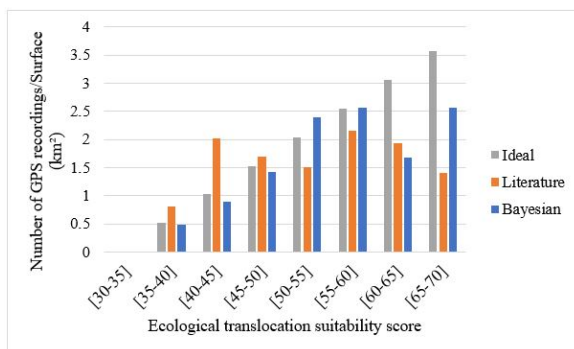
In the ecological translocation suitability analysis adapted from literature the high tolerance scenario (Fig. 3.9a) a total area of 800 km² was found to be suitable for translocation, while the low tolerance scenario (Fig. 3.9e) yielded a total area of only 33 km² as suitable. The medium tolerance scenario (Fig. 3.9c) gave a total suitable area of 429 km², with the largest patch being 335 km² and some other small patches divided over the park. The best fit ecological translocation suitability analysis yielded a favourable area of 807 km² for the high tolerance scenario (Fig. 3.9b), an area of 380 km² for the medium tolerance scenario (Fig. 3.9f). Finally, in the medium tolerance scenario (Fig. 3.9d) an area of 30 km² was found to be favourable.



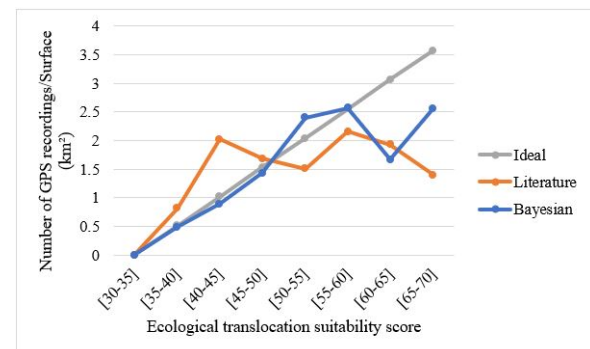
(a) Calculated ecological translocation suitability for MNP adapted from literature.



(b) Calculated ecological translocation suitability for MNP optimized with Bayesian statistics (Best fit).

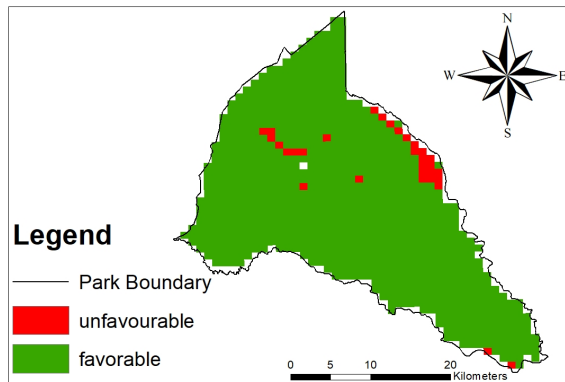


(c) The number of recorded GPS locations divided by the surface area for eight increments of five, between a calculated ecological translocation suitability score of 30 to 70 for the ideal, literature and best fit.

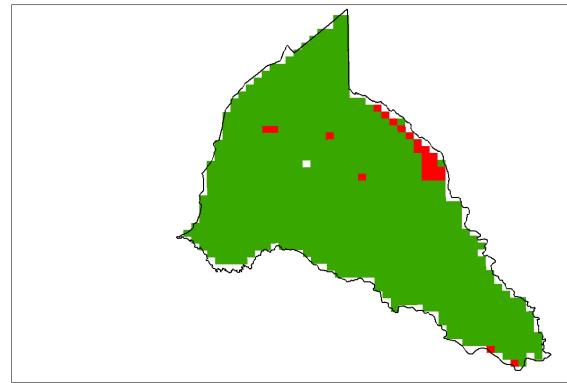


(d) The frequency polygon for the ideal, literature and best fit histograms.

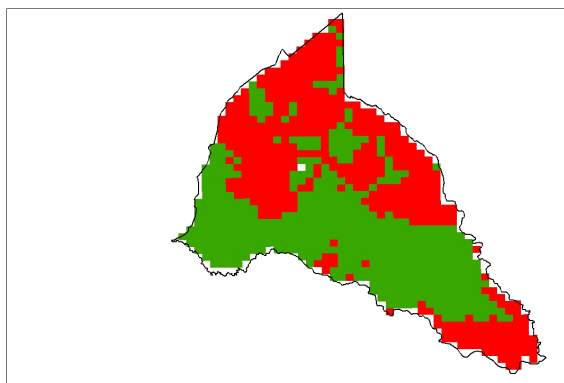
Figure 3.8: The final ecological translocation suitability analysis for MNP based on seven different ecological variables. (a) the ecological translocation suitability of MNP, (b) ecological translocation suitability of MNP with GPS locations of the surviving translocated problem lion. (c) The division of the GPS locations between different increments of the ecological translocation suitability score, divided by the surface area covered by these increments.



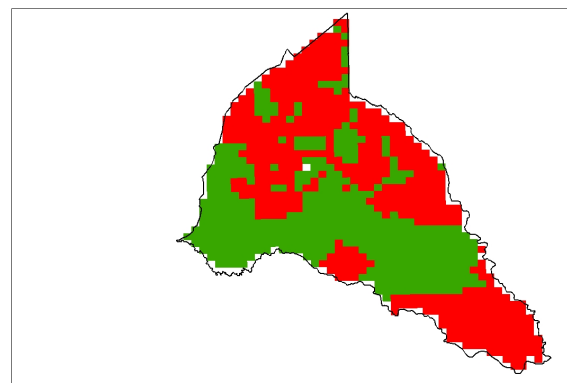
(a) High tolerance scenario where a score of 40 and above is suitable (literature).



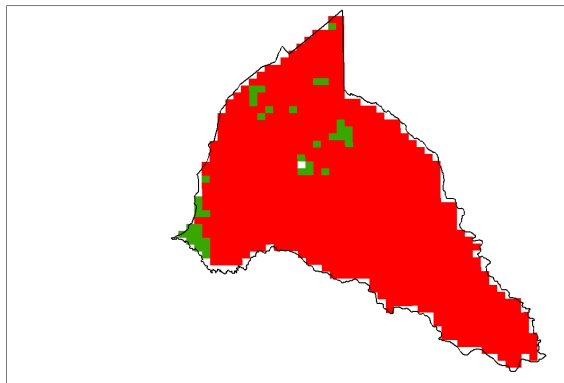
(b) High tolerance scenario where a score of 40 and above is suitable (best fit).



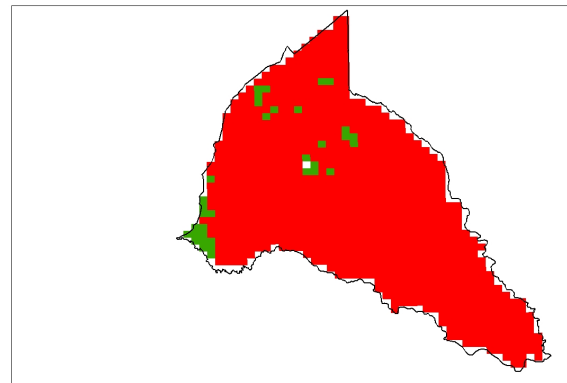
(c) Medium tolerance scenario where a score of 50 and above is suitable (literature).



(d) Medium tolerance scenario where a score of 50 and above is suitable (best fit).



(e) High tolerance scenario where a score of 60 and above is suitable (literature).



(f) High tolerance scenario where a score of 60 and above is suitable (best fit).

Figure 3.9: Three different scenarios for lion translocation, based on the calculated translocation score, assuming different tolerances of lions for both the ecological translocation suitability analysis adapted from literature and the best fit determined with Bayesian statistics.

Chapter 4

Discussion

4.1 Movements and home ranges

Based on the data of the collared lions in MNP a few conclusions can be drawn. Firstly, translocated problem lions travelled greater distances than resident lions. However, differences were not found to be significant for average potential minimum travelled distances in a day (Fig. 3.2, $p = 0.0852$) and neither for average potential minimum distance travelled per three hour interval (Fig. 3.3, $p = 0.0814$). Similarly, differences between males and females were not found to be significant for average potential minimum daily (24h) travelled distance (Fig. 3.2, $p = 0.0852$) or for average potential minimum distance travelled per three hour interval (Fig. 3.2, $p = 0.0661$). Nevertheless, differences between translocated and resident lions as well as between males and females all showed a trend, indicating that with a larger sample size differences could become significant. MTL1 (Solio), the successfully translocated problem lion, which integrated with a local pride, showed similar movements to those of the resident lions.

Secondly, the average home range of resident lions, calculated with the 95% Minimum Convex Polygon estimate, was found to be $199 \pm 76 \text{ km}^2$, while the home range of unsuccessfully translocated problem lions (FTL1 (Sericho) and FTL2 (Tall Boy)) was found to be much larger and respectively $17,656 \text{ km}^2$ and $3,814 \text{ km}^2$ (Table. 3.3). Using the 95% Kernel Density Estimation the average home range was found to be $13,208 \pm 11,968 \text{ km}^2$ for unsuccessfully translocated problem lions and $187 \pm 71 \text{ km}^2$ for resident lions (Table. 3.3). Of the calculated home ranges, for the unsuccessfully translocated lions FTL1 (Sericho) and FTL2 (Tall Boy), over 90% was located outside MNP, while resident lions had maximum 12.55% of their 95% Kernel Density Estimation home range surpassing the park boundaries (Table. 3.4). Contrary to the other translocated problem lions, MTL1 (Solio), the only translocated problem lion that could be considered successful in settling in an existing pride, had a 95% Kernel Density Estimate home range of only 193 km^2 , which was similar to the home range of resident lions (Table.

3.3). Almost his full home range was located within the boundaries of the park. When looking at the different home ranges (Fig. 3.4) there is a clear overlap between the home ranges of the different lions inside MNP (Fig. 3.5).

Finally, unsuccessfully translocated problem lions were not able to establish a stable home range (territory) before they died. However, the successfully translocated problem lion MTL1 (Solio) and resident lion FRL2 (G-coy), were able to establish a stable home range after a few months (Fig. 3.8). Due to the missing data, FRL2 (Virginia) will not be considered here. Apart from having a smaller home range than the other translocated problem lions, it took MTL1 (Solio) only two months to establish a home range (territory), his movements were similar to the movements of resident lions, probably because he settled in an existing pride (Table. 3.4).

The clear difference in size and location of the home ranges, as well as between the movements, between resident and unsuccessfully translocated problem lions, could be explained by multiple factors. Firstly, since the hard release method, which implies direct release after translocation, is used in MNP it is expected that the lions have more trouble selecting suitable habitats and establishing a home range (Moehrenschrager & Somers, 2004; Hunter, 1998; Hunter *et al.*, 2007). Secondly, translocated problem lions often show homing behavior, which would cause them to move outside the park boundaries. Therefore, they show an increase in home range as well as in the percentage of their home range outside of the park (Weise *et al.*, 2015). Thirdly, the unsuccessfully translocated problem lions might leave the park due to a high degree of competition inside the park. Lastly, unsuccessfully translocated problem lions are often found to continue their problem behavior after being translocated, therefore moving towards areas with higher cattle concentrations (Treves & Karanth, 2003). This way they have a high risk of conflict. As a consequence of the large movements and leaving the park, survival of translocated problem lions is often poor (Linnell *et al.*, 1997). Furthermore, overlap between the different home ranges could indicate a lack of pride structure in MNP. However, since overlap is more common between females than males and four out of the five collared lions were female, a certain degree of overlap between the home ranges could be expected (Loveridge *et al.*, 2009). Besides differences in behavior, it is important to note that home ranges are not static and the data used, to calculate the home ranges, do not all come from the same period, which could give a biased measure of overlap (Loveridge *et al.*, 2009; Orsdol *et al.*, 1985; Bauer & De Iongh, 2005). For example, G-coy and Solio were collared around the same period which may explain the lack of overlap between these lions, while Virginia was collared more than a year earlier (Table. 3.1).

Celesia *et al.* (2010) found that the average home range for lions in Africa is about $219 \pm 233 \text{ km}^2$, meaning that the home ranges of the resident lions in MNP are close to average. Home ranges of different parks in Kenya are shown in table 4.1. Home

ranges in MNP are larger than the home ranges found in Amboseli National Park and Nairobi National Park. Very little research has been done on the difference in home range between translocated and resident lions and often the research covers reintroduction of lions, where there is no resident population. Briers-Louw *et al.* (2019) for example found that it takes lions about four months to establish a stable home range after reintroduction. However, they set the time to establish a home range as the time needed, for the lion to get a home range with a size 10% smaller, than the home range established after one year. Since none of the collared lions emitted GPS fixes for a year or more it was not possible to use the same definition in this research.

Table 4.1: Home range and core home range estimates for lions in different national parks, using Minimum Convex Polygon and Kernel Density Estimations.

Park	Gender	Translocated	MCP100 (km ²)	MCP95 (km ²)	KDE95 (km ²)	KDE50 (km ²)	Source
Meru	m	yes	344.44	184.53	193.49	33.72	This study
Meru	f	yes	11266.16	10734.79	13207.53	1742.39	This study
Meru	f	no	253.50	199.15	186.87	35.17	This study
Nairobi	m	no	92.95	72.73	74.545	12.885	Lesilau <i>et al.</i> (2019)
Nairobi	f	no	57.57	44.645	57.145	13.71	Lesilau <i>et al.</i> (2019)
Amboseli	m	no	177.13	\	26.01	9.56	Tuqa <i>et al.</i> (2014)
Amboseli	f	no	121.70	\	23.93	4.85	Tuqa <i>et al.</i> (2014)

My hypothesis of differences between translocated and resident lions in the first few months after translocation is not supported by my results. This research showed a non-significant difference in movements, home ranges and home range establishment, between individual lions, for two out of the three (FTL1,FTL2) translocated problem lions, compared to resident lions. The third translocated problem lion MTL1 (Solio) showed very little difference compared to the resident lions in its movements and home range. However, due to the small sample size it was impossible to conclude if differences were significant. In addition to the small sample size, there was also a bias since all the resident lion were females while male and female lions may behave differently when it comes to home ranges and only one translocated problem lion was male (Loveridge *et al.*, 2009). Therefore, it would be ideal to collar more lions in MNP, both translocated and resident lions, preferably during the same period, in this way increasing the sample size and getting more robust results. Besides giving more information on the difference in behavior between translocated and resident lions, this might also help us understand why some translocations are successful and others are not.

4.2 Ecological translocation suitability

The carrying capacity of MNP, meaning the number of lions MNP can possibly support, based on prey densities obtained for Bundotich *et al.* (2016) was found to be 80 lions, which is rather low for a park the size of MNP. Bundotich *et al.* (2016) estimated a total of 58 ± 21 lions in 2016, which means that the carrying capacity may already have been reached in the park. Table 4.2 shows the available prey biomass for lions in different national parks in Kenya. Only Tsavo West NP has a higher available prey biomass compared to MNP. However, since MNP is still recovering from extensive poaching, prey densities are expected to increase over time, thereby also increasing the carrying capacity for lions.

Table 4.2: Estimates of the available amount of prey biomass for lions, in different national parks across Kenya.

Park	Prey Biomass (kg \km ²)	Lion Density (lions \km ²)	Prey per lion (kg \lion)	Source
Amboseli	1225	0.051	24020	Celesia <i>et al.</i> (2010)
Nairobi	13215	0.240	55063	Celesia <i>et al.</i> (2010)
Tsavo East	1140	0.019	60000	Celesia <i>et al.</i> (2010)
Tsavo West	1476	0.016	92250	Celesia <i>et al.</i> (2010)
Meru	5075	0.066	77350	Bal (2020)

The constructed ecological translocation suitability analysis based on literature (Fig. 3.8a) proved effective in giving a useful indication of the translocation potential of the park. The area with the lowest ecological translocation suitability score had the lowest number of recorded GPS locations proportionate to its surface (Fig. 3.8c). Nonetheless, the increase in the number of GPS recordings per surface area was not always graduate and areas with a high score had a rather low density of GPS recordings. When looking at the best fit analysis, a graduate increase in the density of GPS recordings was visible, close to the ideal linear increase. However, for the highest scores only lower densities of GPS recordings were found. The latter could be explained by the limited amount of GPS recordings available. Nevertheless, we concluded that the best fit analysis is an improvement of the literature analysis.

As previously defined, the 95% Kernel Density Estimation home range for resident lions in MNP was 187 ± 71 km². Therefore, in both the analyses, translocations of problem lions to MNP are still a favorable solution for human-wildlife conflicts, if lions tolerate scores of 40 and above (Fig. 3.9). However, when lions only tolerate scores above 60, the available area is not suitable for lion translocations. Since GPS recordings were found in areas with a score below 40, I hypothesize that lions have a high tolerance and therefore MNP is still suitable for lion translocations. Nevertheless, it is important to note that the model was based on a limited data set and could be improved with

more GPS recordings.

Lemeris (2013) uses a very similar approach to construct an ecological suitability analysis for leopards and cheetahs in Namibia but it has never been used for lions. Lemeris ecological translocation suitability analysis, however, was made for an entire country, whereas the ecological translocation suitability analysis used in this study was developed for a relatively small area, in this case, the MNP. Abade *et al.* (2014) estimated lion distribution using landscape and bioclimatic features in Ruaha (Tanzania). They found that lion distribution was mostly influenced by distance to water and precipitation (Celesia *et al.*, 2010). However, their ecological translocation suitability analysis was constructed to estimate lion distributions of resident lion populations and not to predict translocation success, even though there is some overlap between both research questions.

Our ecological translocation suitability analysis output is considered a useful indication of the translocation potential of MNP. Nonetheless, caution is required when interpreting the results. Due to the open character of the northern side of the park, this side is better monitored compared to the southern part, and bias might therefore arise in the used data. This might cause a higher ecological translocation suitability score in the center and the southern part of the park, due to an underestimated lion density. Carrying capacity for the lion population is a very dynamic concept which may show huge fluctuations between dry years and wet years (Caughley & Sinclair, 1994). Also, the quality of the available data for MNP concerning the different ecological variables that were used was not always reliable. The ecological translocation suitability analysis could profit from more recent and improved data sets. Data sets used in this ecological translocation suitability analysis were all collected before 2016 and ever since a total of nine problem lions have been translocated to the park, probably significantly reducing the remaining ecological translocation suitability. The use of data on translocated problem lions is a good way to validate the ecological translocation suitability analysis, especially when the translocations happened after the period during which data was collected. However, due to the limited data on translocated problem lions, a conclusion based on these data, cannot be considered robust.

As translocation success depends for a major part on the location of release, the ecological translocation suitability analysis developed here could be a useful tool to quantify the suitability of a location. In this way, the ecological translocation suitability analysis could contribute to resolving human-wildlife conflicts in a non-lethal way, as well as help with the preservation of biodiversity. However, in its current state, the ecological translocation suitability analysis should not yet be used as the only tool to determine the suitability of a location for translocation, due to the small data set it is based on and the associated possible lack of robustness. To determine the exact potential of the ecological translocation suitability analysis it is thus very important to repeat

this methodology, as well as increasing our knowledge on lion ecology, to make the ecological translocation suitability analysis as accurate as possible. Nevertheless, it is important to mention that pre-release management and post-release monitoring in MNP, might also increase translocation success.

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Appendix 1

Table 4.3: Input for the translocation model with the source they were adapted from.

Ecological variable	Calculation	Variation	Score	Adapted from
Lion density	Lion density (Lion/km ²) / Carrying capacity (Lions/km ²)	0 - 0.05 & 0.95 - ∞ 0.05 - 0.10 & 0.90 - 0.95 0.10 - 0.15 & 0.85 - 0.90 0.15 - 0.20 & 0.80 - 0.85 0.20 - 0.25 & 0.75 - 0.80 0.25 - 0.30 & 0.70 - 0.75 0.30 - 0.35 & 0.65 - 0.70 0.35 - 0.40 & 0.60 - 0.65 0.40 - 0.60	10 20 30 40 50 60 70 80 90	Lemeris (2013) Lemeris (2013) Lemeris (2013) Lemeris (2013) Lemeris (2013) Lemeris (2013) Lemeris (2013) Lemeris (2013) Lemeris (2013)
Hyena density	Hyena density (Hyena/km ²) / Lion density (Lion/km ²)	0 - 2 2 - 3 3 - 4 4 - 5 5 - 6	90 80 70 60 50	Trinkel & Kastberger (2005) Trinkel & Kastberger (2005) Trinkel & Kastberger (2005) Trinkel & Kastberger (2005) Trinkel & Kastberger (2005)
Prey diversity	Observed species / Species present	0.30 - 0.40 0.50 - 0.60 0.60 - 0.70	40 60 70	Lemeris (2013) Lemeris (2013) Lemeris (2013)
Distance to rivers	/	500 m - 5000 m	80	de Boer <i>et al.</i> (2010)
Precipitation	/	0 m - 500 mm 0 mm - 500 mm 500 mm - 572 mm 572 mm - 644 mm 644 mm - 716 mm	90 10 20 30 40	de Boer <i>et al.</i> (2010) Celestia <i>et al.</i> (2010) Celestia <i>et al.</i> (2010) Celestia <i>et al.</i> (2010) Celestia <i>et al.</i> (2010)
Altitude	/	0 m - 450 m 450 m - 600 m 600 m - 750 m 750 m - 900 m	10 20 30 40	Celestia <i>et al.</i> (2010) Celestia <i>et al.</i> (2010) Celestia <i>et al.</i> (2010) Celestia <i>et al.</i> (2010)
Vegetation	/	Acacia Woodland Long Grassland Swamp Short Grassland	30 40 50 70	Spong (2002) Spong (2002) Spong (2002) Spong (2002)

Appendix 2

Table 4.4: Different species observed on the transects.

Species (Hayward <i>et al.</i> , 2007)	Transect 1	Transect 2	Transect 3	Transect 4
1. Babboon	no	yes	yes	yes
2. Buffalo	yes	yes	yes	yes
3. Bushbuck	no	no	no	no
4. Dik-dik	no	no	no	yes
5. Duiker, common	no	no	no	no
6. Eland	yes	yes	yes	no
7. Elephant	no	no	yes	no
8. Gazelle, grant's	yes	yes	yes	no
9. Gemsbok	yes	yes	yes	no
10. Gerenuk	yes	yes	yes	yes
11. Giraffe	yes	yes	yes	yes
12. Hartbeestyes	yes	yes	yes	no
13. Hippopotamus	no	no	no	no
14. Impala	no	yes	no	yes
15. Klipspringer	no	no	no	no
16 Kudu, lesser	no	yes	yes	yes
17. Ostrich	yes	yes	yes	no
18. Reedbuck, bohor	no	no	no	no
19. Vervet monkey	no	no	no	no
20. Warthog	yes	yes	yes	no
21. Waterbuck	yes	yes	yes	yes
22. Zebra, plains	yes	yes	yes	yes
23. Zebra, grevy	yes	no	no	no
Total (yes)	12	14	14	9

Appendix 3

Table 4.5: Table showing lions translocated into Meru National Park since 2012 (Narisha, 2018)

Name of collared lion	Pride	Age	Group composition	Sex	Origin	Collar type	Frequency	Date of fitting
Mutara female	Mutara lions	Adult (4-5 yrs)	1 Adult female (Collared) 1 Old male (not collared, small mark on the ears) 1 SA male (not collared, small mark on the ears)	F	Mutara Ranch	GPS-VHF	149.570	12/07/2018
Solio boy	Mt. Kenya homes pride	Adult (3yrs)	1 Adult male (Collared) 1 Adult female (not collared, small mark on the ears) 1 SA female (not collared, small mark on the ears) 1 SA male (not collared, small mark on the ears)	M	Mt. Kenya Holiday Homes	GPS-VHF	160.230	09/07/2018
Sericho females	Sericho females	Adult (4-5yrs)	1 adult female (Collared) 1 adult female(not collared, small mark on the ears)	F	Sericho	GPS-UHF	433.400	26/02/2018
Hugo		Adult (4-5 yrs)	Sub adult (1-2yrs)	M	Garissa	GPS-VHF	160.179	21/11/2015
Not collared (but identifiable)	Nairobi	Adult females	2 Adult females	F	Nairobi	Not Collared	\	2012