The introduction of captive bred African lions (*Panthera leo*) to a private wildlife reserve in the Limpopo Province, South Africa

by

Paul Lodewyk Booyens

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Promoter: Prof. H.O. de Waal

Department of Animal, Wildlife and Grassland Sciences and the African Large Predator Research Unit (ALPRU), UFS, Bloemfontein, South Africa

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Declaration

I declare that this thesis, hereby handed in for the qualification Doctor of Philosophy in Wildlife Management in the Faculty of Natural and Agricultural Sciences at the University of the Free State, is my own independent work and that I have not previously submitted the same work for a qualification at another university/faculty. I cede copyright of the thesis in favour of the University of the Free State.

Paul Lodewyk Booyens


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Abstract

The introduction of captive bred African lions (*Panthera leo*) to a private wildlife reserve in the Limpopo Province, South Africa

The objective was to utilise an unique opportunity to monitor and explore the social and feeding behaviour, and the reproductive ability of captive bred, and reared African lions (*Panthera leo*) when reintroduced as a founder population on a large private wildlife reserve (hereafter, the Reserve).

The study did not aim to justify the captive breeding of lions, but the potential value of such lions was assessed, when recently introduced to a free-roaming scenario, to augment the conservation status of this iconic African predator species.

It was hypothesised that the reintroduction of such African lions in a free-roaming scenario would be deemed successful if the following five criteria were met: (i) The ability to form social groups in an extensive wild habitat; (ii) The ability to become self-sustaining with no interference or supplementation by management; (iii) The ability to reproduce by raising offspring to maturity/female sexual maturity and/or dispersal of males from natal prides; (iv) The ability to teach offspring to hunt effectively, interact socially, reproduce, and secure a healthy and viable F2-generation, characteristic of wild managed lions; and (v) Be regarded as suitable potential founders for reintroduction programmes where wild populations have disappeared or need to be augmented.

The Reserve was established in the Limpopo Province, South Africa with a vision to include the Big Five of Africa. Therefore, five African lions, bred and reared in captive facilities, were introduced in 2017 to the Reserve. The five lions comprised an adult male (10 years old and previously used for breeding at a captive facility in the Free State Province, South Africa) and four large female cubs (two years old, sourced from a captive facility in the Limpopo Province, South Africa).

In preparation for the envisaged introduction of lions, the adult male was moved from the Free State Province in November 2016 and joined with the four large female cubs in a 1-ha camp at their natal captive facility in the Limpopo Province. Four weeks after being joined, the five lions were relocated, and in December 2016 they were released in a boma (4-ha holding facility) on the Reserve to acclimatise. While the five lions were in the boma for a 6-week period, they were fed twice a week blue wildebeest (*Connochaetes taurinus*) or zebra (*Equus quagga*) carcasses. Without pre-release training, the five lions were released from the boma on 27 January 2017, when the gates of the boma were simply opened.

The spatial utilisation of the Reserve by the lions were monitored with satellite GPS collars, fitted to a few selected individuals. The ultra-high frequency (UHF) capabilities of the satellite GPS collars also allowed for real-time locating of the lions. The information was used to determine their temporal and spatial utilisation, home range selection, possible group formations, birthing incidences, and successful hunting sites. The ArcGIS Desktop (V. 10.8.1) was used to analyse the data.

In addition, visual observations of lions and detected kill sites were done from vehicles and electronically submitted via a WhatsApp group, whereafter it was chronologically logged for analysis. Social behaviour, prey killed, attempted hunts, and body condition of the lions were recorded via the WhatsApp group. Photographs and videos of the events were used to confirm activities.

Timelines of temporal activities and incidences were created for the lions, showing important occurrences such as social interaction, mating, births of known litters and hunting. When appropriate, the timelines of different individuals were linked to provide better insight of the social interaction of the lions on the Reserve.

When deemed necessary, excess lions were removed from the Reserve to comply with Provincial and National legislation and ensure ecological sustainability of the Reserve. Inbreeding of the lion population was prevented by vasectomising some males and by introducing an unrelated adult male to the Reserve in 2020.

The lions showed varying degrees of social bonding and possible reasons for the grouping behaviour are provided. During the study, only two stable groups of more than two adult lions were recorded.

The hunting success of the lions could not be accurately determined, because of large areas of dense vegetation and the few access roads, limiting the recovery of the remains of kills before being scattered by scavengers. Furthermore, the dense vegetation of some areas on the Reserve prevented the visual sighting of hunting attempts. Therefore, the hunting success of the lions was determined indirectly by the continuous evaluation of body conditions and the changes in the density of suitable prey species on the Reserve. Since the lions were released from the boma, they were self-sustaining.

The cub survival rate was high and comparable to that on small wildlife reserves (<1 000 km^2). Population growth was high, as was expected for a wild managed population. In the study, most cubs brought from hiding by their mothers, comprising 2, 3 or 4 cubs when first sighted, survived. Subsequently, some young lions dispersed from their natal prides, and became self-sustaining.

Two of the lionesses born on the Reserve, namely F1-generation lions, later gave birth to their own litters, namely F2-generation lions.

In conclusion, when introduced in a free-roaming scenario on the Reserve, the captive bred, and reared African lions, as well as their offspring (i) formed social groups, albeit it often a single lactating female with cubs; (ii) became self-sustaining by hunting successfully, with no interference or supplementation by management; (iii) reproduced and raised offspring to reach female sexual maturity and dispersal of sub-adult males from natal prides; (iv) taught their offspring to hunt effectively and interact socially, enabling reproduction of the species, thereby securing a healthy and viable F2-generation, characteristic of wild managed lions; and (v) suggested that similar lions may be considered as founders for reintroduction programmes, where wild populations have disappeared or need to be augmented in specific circumstances.

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List of acronyms

ALPRU	African Large Predator Research Unit
AWT	Africa Wildlife Tracking
AZA	Association for Zoos and Aquariums
bTB	Bovine tuberculosis
CSV	comma separated values
ESA	Endangered Species Act
GPS	Global Positioning System
GSM	Global System for Mobile Telecommunications
HiP	Hluhluwe-iMfolozi Park
IUCN	International Union for the Conservation of Nature
KNP	Kruger National Park
KTP	Kalahari Transfrontier Park
LEDET	Limpopo Department for Economic Development, Environment and Tourism
LF	Lion, Female
LM	Lion, Male
MHz	Megahertz
MTCA	Mapungubwe Transfrontier Conservation Area
SANBI	South African National Biodiversity Institute
UHF	Ultra-high frequency
USA	United States of America
USFWS	United States Fish and Wildlife Services

1 Introduction

1.1 Background

Historically, lions occurred in parts of Eurasia, southern regions of North America, and large parts of Africa (Henschel *et al.,* 2014). Lions were extirpated from most of these regions and fragmentation of populations were caused by the expansion of the human population and subsequent conversion of wild areas to urban and agricultural land uses (Bauer *et al.,* 2016; Peterson *et al.*, 2014). Today, African lions are found in only 8% of its historical range (Bauer *et al*., 2016). The numbers of free ranging African lions (*Panthera leo*) have decreased by almost 50% in the last four decades (Bertola *et al*., 2011; Bauer *et al.,* 2016).

It is acknowledged that competition with humans for suitable habitat is a major contributing factor to the decline in predator numbers (Everatt *et al*., 2015). Riggio *et al*. (2013) estimated that only 3.5 million km^2 of the potentially suitable 13.5 million km^2 savannah habitats in Africa is currently utilised by lions. Protection of human lives, retaliatory killings of livestock raiding lions and poor management of trophy hunting seem to be the major threats to the survival of the species (Henschel, 2014; Bauer *et al.,* 2016). Everatt *et al*. (2015) concur that lion populations can be limited by top-down anthropogenic influences, but also adds that bottom-up prey-based limitations have a negative effect on lion population densities.

It is important to distinguish between the two subspecies of lion: (i) the African lion (*P. leo leo*) which is present in large parts of sub-Saharan Africa, excluding the densely forested regions with an extant estimated population of less than 40 000 (Bauer *et al.,* 2016); and (ii) the Asiatic lion (*P. leo persica*) found only in one isolated (but protected) population in the Gir Forest National Park, India (Bertola, 2015) with an estimated population of 670 (Goswami *et al.,* 2021).

This study focused on the subspecies of the African continent, *P. leo leo*. Although the official IUCN status of African lions is Vulnerable, a breakdown of the different subpopulations shows that stable subpopulations exist in southern African countries (specifically Botswana, Namibia, South Africa, and Zimbabwe) (Bauer *et al.,* 2016).

Whilst in recent years wild lion numbers increased in South Africa and thus have been granted the status of Least Concern (EWT, 2016), the lion is critically endangered in West Africa (Henschel *et al*., 2014). Only 33% of the African countries hold more than 1 000 free roaming individuals and one country, namely Tanzania holds more than 40% of the wild lions on the continent (Riggio *et al*., 2013).

The lion subpopulations in West and Central African countries are impacted most (Bertola *et al*., 2011; Riggio *et al*., 2013; Bauer *et al*., 2010) by fragmentation of suitable habitat and currently occur in low densities of 1-3/100 km^2 (Bauer *et al*., 2010). Lion populations in West Africa have subsequently been given Critically Endangered status by the IUCN (Henschel *et al*., 2014; Bauer *et al.,* 2016). Furthermore, the African lion (*P. leo*) subpopulations of West and Central Africa are now believed to be genetically more like the Asiatic lions (*P. leo persica)* than the subpopulations in East and Southern Africa (Bertola *et al*., 2016), which may add constraints and provisions to conservation efforts.

Given the current situation of African lion populations, it requires investigation and implementation of alternative conservation methods (Hayward *et al*., 2007a). Therefore, when a few captive bred African lions were used to introduce the species to a privately owned reserve in the Limpopo Province of South Africa, an opportunity presented itself to scientifically determine the validity of using such founder animals.

In South Africa the free ranging African lion population is restricted to national parks and provincial reserves (Funston & Levendal, 2015). In addition, a substantial number of African lions are found on private properties and are regarded as wild managed populations. So-called captive lion facilities and zoological gardens holds a larger population than the free roaming and/or wild managed populations (Hutchinson & Roberts, 2020; Funston & Levendal, 2015; Van der Vyver, 2017). The actual number of these lions in captive facilities remains in doubt.

It is important to view the specific terminology pertaining to the lion populations in South Africa as they are dealt with separately in the legislation. Funston & Levendal (2015) developed the objectives for lion conservation in South Africa and drew

important and clear distinctions between the objectives for three defined lion populations, namely:

> "*1. **Wild lions** completely fulfil their role in biodiversity processes and are largely unmanaged, and exist only in formally proclaimed national parks and game reserves. Conservationists do not actively manipulate vital rates and lion demographics.*
>
> *2. **Wild managed lions** include all lions that have been re-introduced into smaller fenced reserves (<1 000km^2), and are managed to limit population growth and maintain genetic diversity. Managers actively manipulate some vital rates and demographics.*
>
> *3. **Captive bred lions** are bred exclusively to generate money. Managers actively manipulate all vital rates and demographics.*"

Van der Vyver (2017) suggested another population, namely ***Ranch lions*** which are bred for consumptive sustainable utilisation purposes. These lions are not exposed to so-called human imprinting activities such as cub petting and lion walks.

Given the definitions by Funston & Levendal (2015), as well as varied views and strong opposition to the practice of captive lion breeding, there is for all practical purposes an impenetrable barrier preventing captive bred lions from being reintroduced in the wild as free ranging lions (Funston, 2012; Lindsey *et al*., 2012; Hunter *et al*., 2012).

Founders sourced from captive bred lion facilities have been used in reintroductions, but with either low success rates, or little recorded post release data available (Abell *et al*., 2013). Rahbek (1993) expressed the usefulness of captive breeding for the conservation of species and explained the role that zoological gardens have in the survival of a species. However, most zoological gardens lack sufficient funding.

The use of captive bred lions for reintroduction have been widely criticised by scientists and animal right's organisations (Funston, 2012; Hunter *et al*., 2012; Lindsey *et al*., 2012). In this regard, Funston (2012) elaborated on the dangers and implications of using captive bred lions in reintroduction (or supplementation) programmes. Funston (2012) explained that captive bred lions would not be able to

adopt new foraging requirements, could not contribute to genetic diversity if released into an existing population, and would unquestionably become a threat to human livelihoods. However, no data is presented to support this hypothesis.

Guidelines for the release of captive bred wildlife have been provided by the IUCN and AZA (The Association for Zoos and Aquariums) (Abell *et al*., 2013), albeit not specifically for the African lion. Furthermore, Turner *et al.* (2016) focused on the hunting abilities of white lions and found no significant difference in the hunting ability of two groups of white lions which were captive bred to that of a group of wild and free roaming tawny lions under similar conditions. However, the ability of lions to forage successfully may on its own not be sufficient evidence to conclude on the success of a reintroduction venture.

Wild caught lion founders have also been reintroduced with apparent success, but the reporting was limited and then discontinued (Kilian & Bothma, 2003; Hayward *et al*., 2007b).

In South Africa, the genetic stock of wild free roaming African lions originates mainly from three populations, namely the Kruger National Park (KNP), Greater Mapungubwe Trans frontier Conservation Area (GMTCA) and Kgalagadi Trans frontier Park (KTP). These are the only populations of African lions, along with a supposedly inbred population in Hluhluwe-iMfolozi Park (HiP), to have survived extirpation in South Africa in the 1900's (Miller *et al.,* 2013).

The lion population in the KNP (South Africa) cannot be considered for reintroductions because of the potential rapid spread of bovine tuberculosis (bTB) by a large portion of its prides (Maas *et al.,* 2008). Sadly, the KNP contains most of the free roaming lions in South Africa (~1 700) (Miller *et al.,* 2013). The GMTCA population is believed to contain less than 50 lions (Funston, 2010) and the KTP approximately 125 (Funston, 2011). Thus, large reintroductions with good genetic integrity from wild stock of African lions from South Africa would be very complex and difficult to incorporate.

The remainder of the free roaming (so-called wild managed) population of African lions in South Africa is found in some 44 small, fenced reserves (Miller *et al.,* 2013). Collectively, the national and provincial reserves, as well as the privately owned reserves in South Africa contain a large part (~ 3490; 17%) of the current free roaming lions on the continent (Hutchinson & Roberts, 2020).

The captive lion industry in South Africa is lucrative, allegedly comprising more than 6 000 lions (Funston & Levendal, 2015). According to Van der Vyver (2017) an estimated 8 000 lions are in captive facilities. The captive lion facilities came under scrutiny because allegedly the breeding activities are for financial gain only (Funston, 2012; Funston & Levendal, 2015). Furthermore, Funston (2012) said that the majority of lions bred in captivity are used in the tourism industry (lion walks), culled and sold for body parts (bones) in Asian markets and/or hunted as trophies by paying clients. Consequently, a debate on the suitability of captive bred lions to contribute towards the conservation of the species ensued between scientists and captive lion breeders (Funston, 2012; Lindsey *et al*., 2012).

The hunt of a collared lion “Cecil” in Zimbabwe (2015) caused international public outcry (Nelson *et al*., 2016; The Humane Society of the United States, 2016). Therefore, the United States Fish and Wildlife Service (USFWS) listed the African lion under the Endangered Species Act (ESA). Essentially no hunted African lion trophies may be imported into the US without proving that the specific hunt contributed to the conservation of the species (Nelson *et al*., 2016; The Humane Society of the United States, 2016). No trophies of captive bred African lions would thus qualify and the decision severely affected the lion breeding and hunting industries in South Africa. From 2005 to 2014, almost 4 000 lion trophies were exported from South Africa to the United States of which nearly 40% were of captive bred origin (The Humane Society of the United States, 2016).

Since 2008, the export of lion bones to East Asian buyers is legal in South Africa, with an unprecedented spike in exports between 2013-2015, namely 4 000 between 2013 and 2015 compared to 1 500 between 2008 and 2012 (Williams *et al*., 2017). With a massive loss of income caused by the absence of trophy hunters, the spike in lion bone exports may be linked to the decline in hunted lion trophy exports.

On 10 October 2019, the Honourable Me. Barbary Creecy, the Minister of Forestry, Fisheries and Environment, announced the establishment of a High-Level Panel (HLP) of experts to review policies, legislation and practices on matters of elephant, lion, leopard, and rhinoceros management, breeding, hunting, trade and handling. The assessment focussed on five iconic species in South Africa, namely elephants, white and black rhinoceros, lions, and leopards.

The HLP Report (High-level Panel Report, 2020) was released on 2 May 2021 and in the media release the Honourable Minister Creecy stated "*The Panel identified that the captive lion industry poses risks to the sustainability of wild lion conservation resulting from the negative impact on ecotourism which funds lion conservation and conservation more broadly, the negative impact on the authentic wild hunting industry, and the risk that trade in lion parts poses to stimulating poaching and illegal trade. The panel recommends that South Africa does not captive-breed lions, keep lions in captivity, or use captive lions or their derivatives commercially. I have requested the department to action this accordingly and ensure that the necessary consultation in implementation is conducted*."

Essentially the captive breeding of lions in South Africa was to be terminated. However, the report did not elaborate on how this termination was to be implemented, but the matter was considered urgent.

The African lion is under threat across its range, as well as in captivity where the captive lion industry is at risk to be terminated. If the latter realises, the lack of an appropriate exit management plan for the estimated 8 000 lions currently in captivity would inevitably lead to the killing (but, euphemistically called euthanising) of the large population.

1.2 Characteristics of the African lion (*Panthera leo*)

African lions are gregarious and typically form fission-fusion groups/prides (Packer *et al.,* 1990). Prides typically consist of 2-18 related females and their young (Hunter, 1998b; Packer *et al.,* 1990), with an unrelated male, or cohort of males, holding mating rights over the females (Packer & Pusey, 1982). The social tendency of lions

is not necessarily a strategy to increase their success rates during hunts, but rather a defence tactic for their young against strange males and/or other prides (Packer *et al.,* 1990). Maruping-Mzileni (2009) found that the ability of African lions to form social groups is positively correlated to the survival rate of the cubs. Therefore, if the released captive bred founders can form social groups, it will increase the survival rate of their young and show their ability to contribute to positive population growth.

The African lion is a well-known, large carnivorous species (Schaller, 1972; Smuts, 1978; Funston *et al.,* 2001*;* Eloff, 2016; DeSantis & Patterson, 2017) with a diversity of preferred prey (Funston *et al.,* 2001; Hayward & Kerley, 2008; Eloff, 2016; Stander *et al*., 2018). The preference for specific prey species is influenced by home ranges (Everatt *et al.,* 2015). Even though, African lions hunt ungulates of all sizes (Funston *et al.,* 2001), they probably hunt the most abundant species available within their home range (Stander *et al*., 2018).

Generally, African lions are not fussy regarding prey preference and, although in small quantities, lions do prey on non-mammalian species (Hayward *et al.,* 2011; Stander *et al*., 2018).

The foraging behaviour of the African lion is well documented, suggesting that many hunts are carried out by groups of females hunting co-operatively (Stander, 1992) and co-ordinately (Funston *et al.,* 2001). Male lion coalitions hunt together and are less successful when hunting medium sized prey than large prey such as buffalo (*Syncerus caffer*) (Funston *et al*., 2001).

According to Packer *et al.* (1990) hunting success might not be the most important driver for the grouping behaviour in African lions, but rather the protection of individuals within the group (specifically the young). Access to food is thus sacrificed for the safety provided by larger groups. However, a self-sustaining wild population is only one criterium regarded as a measure of a successful reintroduction (Jule *et al.,* 2007).

Lionesses become reproductively active between two years (Rudnai, 1973a) and 40 months (Maruping-Mzileni, 2009). After giving birth to 2-6 cubs, a lioness keeps

herself and the cubs separate from the pride for up to 8 weeks (Packer & Pusey, 1983b).

Birthing intervals range from 24 months (Packer & Pusey, 1983b) to 40 months (Funston *et al.,* 2003), however, shorter intervals may occur in smaller, closed systems (Hunter, 1998b; Lehman *et al.,* 2008; Kilian & Bothma, 2003).

Young females generally remain in their natal pride, but they can be forced to leave the group if a new male (or males) takes over pride tenure and the females are still too young to conceive (Funston *et al.,* 2003), or if the group exceeds 10 females (Packer & Pusey, 1987). The erratic timing of male take-overs causes a large variation in sub-adult dispersal from prides (Borrego *et al.,* 2018) and is often accompanied by the killing of dependent younger individuals not related to the new male, namely infanticide (Funston *et al.*, 2003; Packer & Pusey, 1984).

Young male lions will disperse before the age of three years from their natal pride because of pressure from a resident pride male, or a cohort of unrelated males, taking over pride tenure from the resident pride male(s). The dispersing young males (usually related) form groups (cohorts or coalitions) consisting of 2-7 related individuals (Packer & Pusey, 1982), adopting a nomadic lifestyle until they themselves are able to gain tenure over a pride of sexually mature females (Funston *et al.,* 2003).

Large cohorts of males often gain simultaneously tenure over several adjacent prides (Packer & Pusey, 1982) and will lose control only by death, being evicted by a stronger male/cohort of males, or when his offspring is about 17 months old, or if the cubs would normally not be killed by incoming males any more (Funston *et al.,* 2003).

The natural process of African lion population growth thus depends on availability of sexually mature females, a male/coalition of males mating with these females, and the dispersal of young males from natal prides to another pride or prides.

Sub-adult offspring are taught hunting skills by lionesses, namely the mothers and other related females in the pride (Funston *et al.,* 2001). However, it presupposes that the lionesses themselves have mastered the skill to hunt successfully.

Because lions hunt co-operatively and co-ordinately; hunting success increases with group size (Funston *et al.,* 2001) and the addition of more members to a hunt benefits the entire pride. However, the cost of having more individuals present at a kill is a smaller share of available food per kill for each member (Funston *et al.,* 2001). Schaller (1972) suggested that all individuals in a group will not contribute equally to the hunt without having an influence on their access to the carcass. The ability of an individual lion to learn to hunt is important for the hunting success of the pride, specifically in the case of females which would normally remain in the pride, but also to its own chances of survival (Funston *et al.,* 2001). It could thus be reasoned that sociality, and more specifically social learning, contributes to the survival of the offspring in African lions.

Therefore, if an individual lion originating from a captive facility would affect the ability of a lion, or a group of lions to interact socially, it would theoretically impede the lion's chances of survival in an *ex situ* reintroduction programme.

Dunston *et al.* (2016) assessed the *ex situ* reintroduction of two prides of lions and noted that the social cohesiveness of the prides was vital to the success of the venture.

1.3 Objective

The objective of this study was to utilise, monitor, and explore the social and feeding behaviour and reproductive ability of a founder population of captive bred lions when released in a reintroduction programme on a large private wildlife reserve (here after, the Reserve).

There is no consensus yet on the definition of a successful reintroduction. However, according to Jule *et al.* (2007), at least one of the following criteria must be met: (i) successful breeding by F1-generation of wild-born individuals, (ii) population growth

exceeding adult death rate within three years of breeding, (iii) a self-sustaining wild population exceeding 500 individuals, or (iv) a self-sustained wild population.

In this study it was hypothesised that reintroducing captive bred, and reared African lions in a free-roaming scenario would be deemed successful if the following five criteria were met:

1.3.1 The ability to form social groups in an extensive wild habitat.

1.3.2 The ability to become self-sustaining with no interference or supplementation by management.

1.3.3 The ability to reproduce and raise offspring to maturity/female sexual maturity and dispersal of males from natal prides.

1.3.4 The ability to teach offspring to hunt effectively, interact socially, reproduce, and secure a healthy and viable F2-generation characteristic of wild managed lions.

1.3.5 Regarded as suitable potential founders for reintroduction programmes where wild populations have disappeared or need to be augmented.

The study was not intended to justify the breeding of lions in captivity, but an opportunity presented itself when a group of five captive bred African lions were released on an extensive system to fend for themselves. If the African lion is under threat across its range individuals of the captive bred population could contribute to the alleviate the situation. It would be a sad situation if said population would have to be terminated without proper scientific investigation.

Captive bred African lions do not forage for their own food (Funston & Levendal, 2015), therefore, it is assumed that they have not acquired the skills to hunt and would not be able to self-sustain. If an individual lion is unable to successfully hunt and feed, it would certainly not be able to thrive, conceive, or care for its offspring. Therefore, the key adaptive characteristic of founder lions to be deemed suitable for reintroduction would be the ability to obtain sufficient food sources for a sufficiently long period to reproduce and raise its offspring to adulthood/sexual maturity.

Therefore, given the five criteria of the hypothesis, it was important to explore whether captive bred, and reared founder lions could establish social groups for survival and establish a viable free roaming lion population.

2 Study area

2.1 Background on the Reserve

The first of the properties, previously used for cattle and/or wildlife farming, were purchased in 2014 to establish a large private wilderness area in the Waterberg Biosphere and eventually 14 title deeds of properties were acquired. The 14 properties were consolidated by taking down most of the inner camp fences, allowing the remaining wildlife to roam freely on an area of approximately 29 000 ha.

The livestock were removed from the properties before the fences were taken down and other unnecessary infrastructure such as cattle crushes, storerooms and most of the brick and mortar buildings were demolished. During the period 2014-2015 the perimeter fences of the consolidated properties were upgraded to contain wildlife. A wildlife fence with a height of 2.4 m and electrified offsets to the inside (Slide 2.1) and 90 mm mesh wire at the bottom, was set as the standard for the perimeter fence. The specifications of the wildlife fence set for the Reserve exceeded the requirements of the Limpopo Department of Economic Development, Environment and Tourism (LEDET) for the keeping of dangerous large African wildlife.

In 2016, a 27 km wildlife fence was erected along a river as a barrier between the area where it was planned to release dangerous wildlife such as African lion (*P. leo*) and elephant (*L. africana*). The fence was erected as a safety precaution to keep dangerous wildlife from roaming close to accommodation areas, which were already built close to the river. The area designated for the release of the dangerous African wildlife was about 22 000 ha. Lions were released in that portion of the Reserve in 2016, where leopard (*P. pardus*), African buffalo (*S. caffer*) and white rhinoceros (*C. simum*) were already present, albeit in small numbers.

A wildlife survey was conducted in September 2015 to establish the numbers of the wildlife species present on the consolidated property to serve as baseline for the ecological management plan of the Reserve. An ecological resource analysis was conducted in 2016 to determine the biological condition and potential of the grazing and browsing resources. Soon afterwards, it was decided to mechanically clear the

areas which were heavily encroached by bush because of lack of appropriate livestock grazing management. The mechanical clearing was done with two mulching machines and the remaining tree stumps were chemically treated to prevent regrowth of the undesired plants. About 4 000 ha have been cleared, creating large areas of open savannah-type habitat (Slide 2.2).

Slide 2.1. The electrified perimeter wildlife fence of the Reserve.

2.2 Location and climate

The Reserve is in the Waterberg region of Limpopo Province, South Africa. The area is in the Savannah biome (Mucina & Rutherford, 2006). Due to the presence of high-risk wildlife species specifically targeted during poaching, the specific location of the Reserve could not be disclosed.

Slide 2.2. An area that was mechanically cleared, showing the marked contrast with an area (top left) which have not yet been cleared.

The rainfall pattern in the area is unimodal, with an expected rainy season from October to April, with a distinct peak in January and a long-term mean annual rainfall of 531 mm. The highest mean monthly rainfall is 103 mm in January and the lowest mean monthly rainfall is 2 mm during July (Fig. 2.1).

Here, the hotter periods of higher rainfall (October to April) are referred to as the wet seasons and the cooler, dryer months (May to September) as the dry seasons.

The summers are hot, and winters are relatively mild without frost (Fig. 2.2). The hottest months are January and February, with an average temperature of 23.4°C and the coldest time of the year is during July (13.3°C).

The ecological resource analysis conducted for the study area followed the description by Low & Rebello (1996) and distinguishes two main veld types, namely Moist Mountain Bushveld and Mixed Bushveld (Orban & Van Hoven, 2016). A third veld type, Sweet Bushveld, covers a very small area in the south western part of the study area (Fig 2.3).

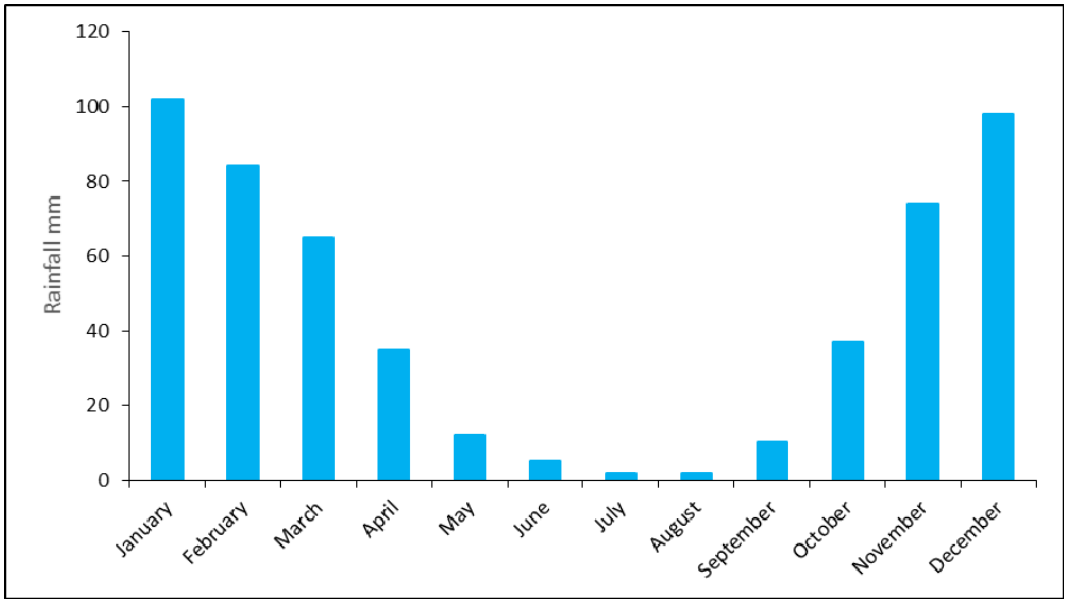


Figure 2.1. The mean monthly average rainfall on the Reserve for the period 1999 to 2019[1].

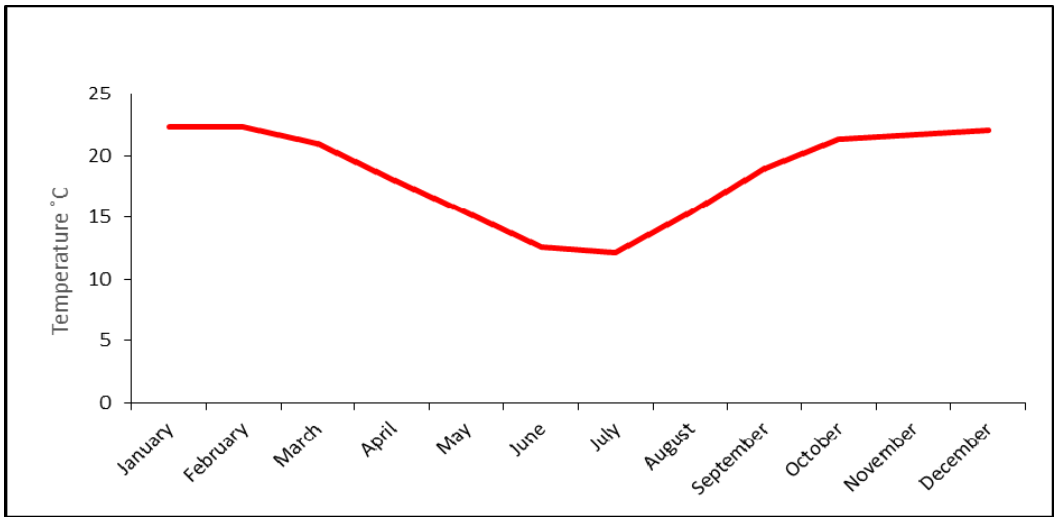


Figure 2.2. The mean monthly average temperature on the Reserve for the period 1999 to 2019[2].

2.3 Ecological resource analysis

In conclusion, the ecological resource analysis of the Reserve was used to determine the ecological capacity of the available natural resources. This was done by determining the available Grazer and Browser Units.

[1] Information on rainfall was obtained from a weather station close to the Reserve at an altitude of 1 293 m above sea level. Accessed 2021.
[2] Information on temperature was obtained from a weather station close to the Reserve at an altitude of 1 293 m above sea level. Accessed 2021.

According to Bothma & du Toit (2010), Grazer Units are determined by using the condition of available grazing resources and comparing the metabolic requirements of different wildlife to that of a blue wildebeest (*C. taurinus*) of 180 kg. The Browsing Units are divided into the available foliage below 2 m and that between 2 and 5 m. The BECVOL method (Smit, 1996) is used to determine the available leaf biomass and with a comparison of the metabolic requirements of a female greater kudu (*T. strepsiceros*), the Browser Unit is determined. Essentially, each wildlife species is assigned a Grazer and Browser Unit according to their dietary requirements and their body weight (Bothma & du Toit, 2010).

In this way the stocking rate of the Reserve can be kept at a sustainable level, while sufficient provision is made for the predators, hunters and non-consumptive ecotourists.

2.4 Habitat

The Moist Mountain Bushveld is at a higher altitude and dominates the northern part of the Reserve by covering most of the mountainous terrain (Fig. 2.4). The Mixed Bushveld dominates most of the central and southern region of the Reserve (Fig. 2.3).

The ecological resource analysis of the Reserve involved a structured dissection and the vegetation was classified in 12 distinct habitat units (Fig. 2.5).

The scientific and common names of the grasses, shrubs and trees are presented in Table 2.1.

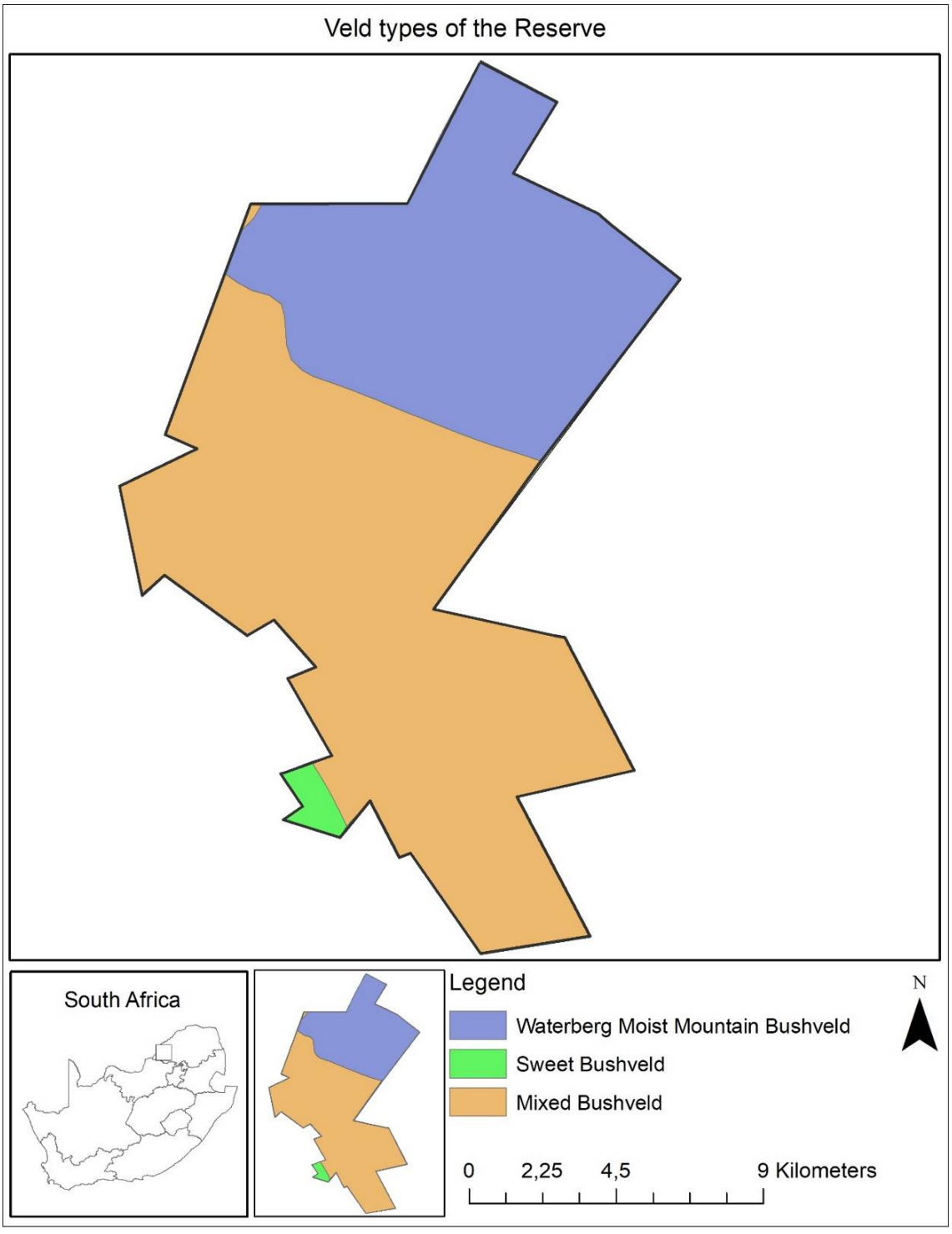


Figure 2.3. The three main veld types on the Reserve[3].

[3] Maps of vegetation were adopted after Orban & van Hoven, 2016.

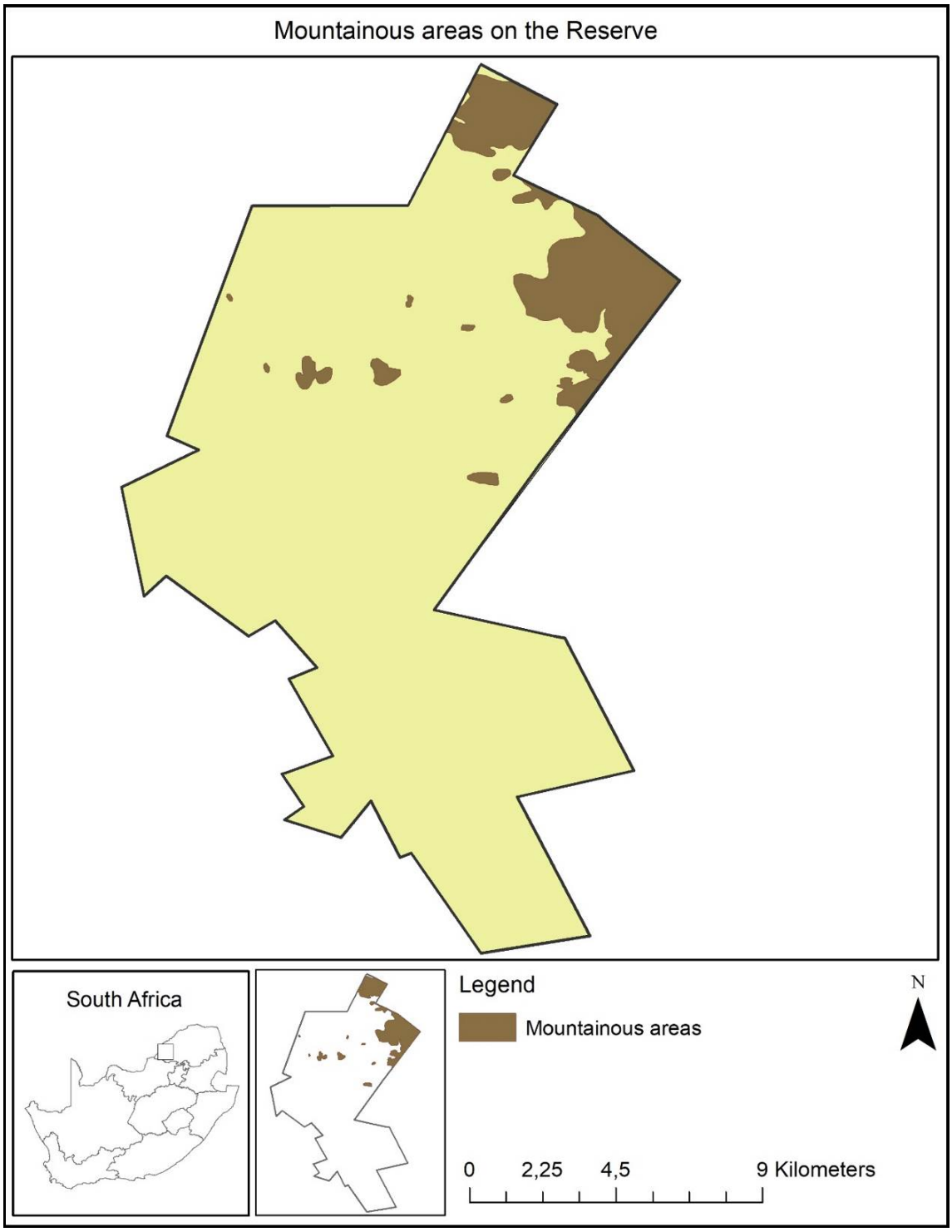


Figure 2.4. The mountainous areas, namely a rocky mountain and small rocky outcrops are found in the north and north eastern parts of the Reserve but covers only a small part of the total surface area.

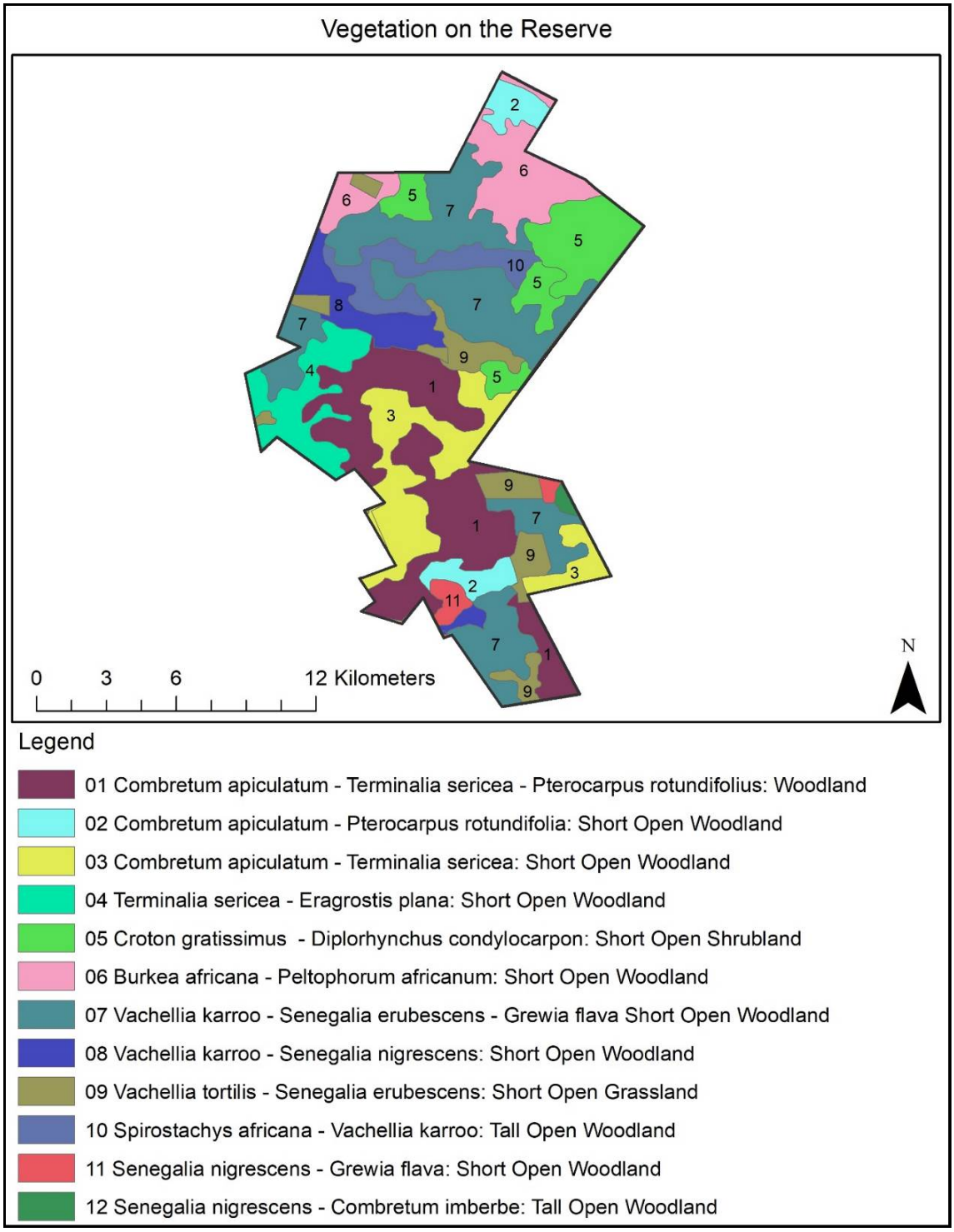


Figure 2.5. The 12 different habitat units identified on the Reserve[4].

[4] Maps of vegetation were adopted after Orban & van Hoven, 2016.

Table 2.1. Dominant plant species on the Reserve, providing the scientific names, as well as common English and Afrikaans names (Van Oudtshoorn, 2012; Coates-Palgrave, 2002; SANBI, 2012).

Scientific name	English name	Afrikaans name
Grasses		
Aristida congesta	Wire grass	Lossteekgras
Aristida stipitata	Long-awned grass	Langnaaldsteekgras
Bothriochloa insculpta	Pinhole grass	Stippelgras
Digitaria eriantha	Common finger grass	Smuts vingergras
Enneapogon scoparius	Bottlebrush grass	Borseltjiegras
Eragrostis lehmanniana	Lehman love grass	Knietjiesgras
Eragrostis pallens	Broom love grass	Besemgras
Eragrostis patentipilosa	Footpath love grass	Voetpadgras
Panicum maximum	Guinea grass	Buffelsgras
Schmidtia pappophoroides	Sand quick	Sandkweek
Stipagrostis uniplumis	Silky bushman grass	Beesgras
Tragus berteronianus	Carrot-seed grass	Kousklitsgras
Trees and shrubs		
Bauhinia galpinii	Pride-of-de Kaap	Vlam-van-die-vlakte
Burkea africana	Wild seringa	Wildesering
Combretum apiculatum	Red Bushwillow	Rooiboswilg
Combretum imberbe	Leadwood	Hardekool
Combretum zeyheri	Large fruit bushwillow	Raasblaar
Commiphora glandulosa	Tall Firethorn corkwood	Groot gewone kanniedood
Croton gratissimus	Lavender fever berry	Laventelkoorsbessie
Dichrostachys cinerea	Sickle-bush	Sekelbos
Diplorhynchus condylocarpon	Horn-pod tree	Horingpeultjieboom
Grewia bicolor	White-leaved raisin	Witblaarrosyntjie
Grewia flava	Velvet raisin	Brandewynbos
Grewia flavescens	Sandpaper raisin	Skurwerosyntjie
Gymnosporia buxifolia	Common spike thorn	Gewone pendoring
Mundulea sericea	Cork-bush	Kurkbos
Ozoroa sphaerocarpa	Currant resin-tree	Korenteharpuisboom
Peltophorum africanum	African wattle	Huilboom
Pterocarpus rutondifolius	Round-leaved Bloodwood	Dopperkiaat
Senegalia erubescens	Blue thorn	Blouhaak
Senegalia mellifera	Black thorn	Swarthaak
Senegalia nigrescens	Knob thorn	Knoppiesdoring
Spirostachys africana	Tamboti	Tambotie
Terminalia sericea	Silver cluster-leaf	Vaalboom
Vachellia karroo	Sweet thorn	Soetdoring
Vachellia nilotica	Scented-pod thorn	Lekkerruikpeul
Vachellia tortilis	Umbrella thorn	Haak-en-steek

2.4.1 *Combretum apiculatum - Terminalia sericea - Pterocarpus rotundifolius*: Woodland

This habitat unit is most widespread in the Mixed Bushveld region and dominates the lower altitudes of the Reserve. The most common grasses are long-awned grass (*A. stipitata*), broom love grass (*E. pallens*) and sand quick grass (*S. pappophoroides*). The most common trees are silver cluster-leaf (*T. sericea*), sickle-bush (*D. cinerea*) and velvet raisin (*G. flava*) with an estimated 21% of the potential browse available below 2 m and 43% available to giraffe (*G. camelopardalis*) and elephant (*L. africana*). Round-leaved bloodwood (*P. rotundifolius*) and red bushwillow (*C. apiculatum*) are also abundant in clusters. An average density of 1 860 trees/ha was calculated. This habitat unit is not present in the Moist Mountain Bushveld region of the Reserve.

2.4.2 *Combretum apiculatum - Pterocarpus rotundifolius:* Short Open Woodland

This habitat unit is scattered across both veld types on the Reserve. The dominant grasses are bottlebrush grass (*E. scoparius*) and Lehman love grass (*E. lehmanniana*). The tree density in this habitat is 2 080 trees/ha with velvet raisin (*G. flava*) dominating the woody composition and contributing the most to an estimated 31% of possible browse being available below 2 m and 61% available to large browser species. Other abundant trees in this habitat unit are red bushwillow (*C. apiculatum*), cork-bush (*M. sericea*), horn-pod tree (*D. condylocarpon*), and sandpaper raisin (*G. flavescens*).

2.4.3 *Combretum apiculatum - Terminalia sericea*: Short Open Woodland

This habitat unit is found only in the central parts of the Mixed Bushveld veld type on the Reserve with guinea grass (*P. maximum*) the most abundant grass species, being the most valuable grazed species in its distribution range (Van Oudtshoorn, 2012), and sand quick grass (*S. pappophoroides*). Consequently, this unit showed signs of selective patch overgrazing, possibly due to the restriction of movement of grazing ungulates, specifically cattle prior to the consolidation of the properties. The tree density was estimated at 2 440 trees/ha. Available browsing is mostly

contributed by velvet raisin (*G. flava*) and sickle-bush (*D. cinerea*). Only 10% of the potential browse is available below 2 m, with 56% being available to large browsers (*i.e.* giraffe and elephant).

2.4.4 *Terminalia sericea - Eragrostis pallens*: Short Open Woodland

Guinea grass (*P. maximum*), long-awned grass (*A. stipitata*), sand quick grass (*S. pappophoroides*) and silky bushman grass (*S. uniplumis*) are the dominant species in the herbaceous layer of this habitat unit which is also only found in the central part of the Mixed Bushveld region of the Reserve. Like habitat unit type 3, this habitat unit showed signs of selective overgrazing but demonstrated a moderate utilisation of available natural foraging resources. Tree density was also similar to that of habitat unit type 3 at 2 467 trees/ha and 23% of available browse resources available below 2 m, whilst 63% is available at between 2 and 5 m. Dominant shrub is velvet raisin (*G. flava*) and trees are silver cluster-leaf (*T. sericea*), sickle-bush (*D. cinerea*), scented pod-thorn (*V. nilotica*) and black thorn (*S. mellifera*).

2.4.5 *Croton gratissimus - Diplorhynchus condylocarpon:* Short Open Shrubland

The mountainous regions of the Reserve (Fig. 2.4) constitute most of the Moist Mountain Bushveld veld type and consists of high mountains (up to 1 337 m above sea level), rocky outcrops and flat mountain plateaus. Habitat unit type 5 dominates these mountainous areas and contains predominantly bottlebrush grass (*E. scoparius*), broom love grass (*E. pallens*), long-awned grass (*A. stipitata*), common finger grass (*D. eriantha*) and guinea grass (*P. maximum*) as herbaceous cover. Tree density is estimated at 2 733 trees/ha and dominated by lavender fever berry (*C. gratissimus*), sickle-bush (*D. cinerea*), white-leaved raisin (*G. bicolor*) and sandpaper raisin (*G. flavescens*). Silver cluster-leaf (*T. sericea*), currant raisin-tree (*O. sphaerocarpa*), large-fruit bushwillow (*C. zeyheri*), red bushwillow (*C. apiculatum*), pride-of-de Kaap (*B. galpinii*), knob thorn (*S. nigrescens*) and black thorn (*S. mellifera*) are present to a lesser extent but contribute to the available browse to a large extent. Consequently, 28% of the potential browse is available below 2 m and a further 54% of the dry leaf mass is potentially available to the larger browsers.

2.4.6 *Burkea Africana - Peltophorum africanum*: Short Open Woodland

This habitat unit is found only in the Moist Mountain Bushveld region of the Reserve and is associated with the plateau areas of higher altitudes. The dominant grass species is guinea grass (*P. maximum*). These areas are most densely populated by trees with 3 489 trees/ha. The most important contributors to available potential browse resources are sweet thorn (*V. karroo*), and the shrubs velvet raisin (*G. flava*) and sandpaper raisin (*G. flavescens*). Only 16% of the potential browse resources are available below 2 m and 47% between 2 and 5 m.

2.4.7 *Vachellia karroo - Senegalia erubescens - Grewia flava:* Short Open Woodland

This habitat unit is fragmented across both veld types found on the Reserve. Although grass species from most ecological categories are present, guinea grass (*P. maximum*) is the dominant grass species contributing most to the available graze potential. The density of trees is moderate in this habitat unit at 2 729 trees/ha. Blue thorn (*S. erubescens*) *and* velvet raisin (*G. flava*) contribute to most of the available potential browse resources. Common spike thorn (*G. buxifolia*), umbrella thorn (*V. tortilis*), red bushwillow (*C. apiculatum*), sickle-bush (*D. cinerea*) and white-leaved raisin (*G. bicolor*) are also found in moderate abundance. An estimated 28% of the potential available browse resources are available below 2 m and 45% between 2 and 5 m.

2.4.8 *Vachellia karroo - Senegalia nigrescens*: Short Open Woodland

This habitat unit is found in both veld types on the Reserve. Although guinea grass (*P. maximum*) is a dominant grass in this habitat unit, the prevalence of wire grass (*A. congesta*) and carrot-seed grass (*T. berteronianus*) and a high frequency of bare ground is indicative of vegetative degradation. The tree density of the habitat unit is moderate at 2 680 trees/ha and although sickle-bush (*D. cinerea*) dominates, velvet raisin (*G. flava*) contributes most to the available potential browse. Even though most trees in this habitat unit have grown above the potential browse height for ungulates found on the Reserve, an acceptable amount is available. Sweet thorn (*V. karroo*)

and knob thorn (*S. nigrescens*) are also found in abundance, contributing to the available browse.

2.4.9 *Vachellia tortilis - Senegalia erubescens*: Short Open Grassland

This habitat unit shows the most deteriorated habitat of all the units found on the Reserve in both veld types where the habitat was historically disrupted (i.e., abandoned cultivated fields, old air strips). The herbaceous layer is dominated by wire grass (*A. congesta*), footpath love grass (*E. patentipilosa*) and carrot-seed grass (*T. berteronianus*). The woody component of the habitat unit is described as short woodland and 46% of the potential browse resources are available below 2 m. Velvet raisin (*G. flava*), blue thorn (*S. erubescens*), umbrella thorn (*V. tortilis*), fire thorn corkwood (*C. glandulosa*), sickle-bush (*D. cinerea*), red bushwillow (*C. apiculatum*) and white-leaved raisin (*G. bicolor*) are all abundantly available at 1 680 trees/ha.

2.4.10 *Spirostachys Africana - Vachellia karroo*: Tall Open Woodland

This habitat unit is typically found along drainage lines in the Moist Mountain Bushveld on the Reserve. Guinea grass (*P. maximum*), long-awned grass (*A. stipitata*) and broom love grass (*E. pallens*) are the dominant grass species. The habitat unit is associated with a lower density of trees (1 100 trees/ha) with more than 36% of the potential available browse resource unreachable to most of the antelopes present on the Reserve. The most common shrub is the velvet raisin (*G. flava*) and trees are sickle-bush (*D. cinerea*), sweet thorn (*V. karroo*), tamboti (*S. africana*) and silver cluster-leaf (*T. sericea*).

2.4.11 *Senegalia nigrescens - Grewia flava*: Short Open Woodland

Found only in the Mixed Bushveld vegetation type within the study area, this habitat unit is associated with short trees and shrubs making most of the potential browse resources available to the antelope species present. The dominant grass species are pinhole grass (*B. insculpta*) and guinea grass (*P. maximum*). Tree density is

estimated at 2 200 trees/ha and, as with most other habitat units on the Reserve, the velvet raisin (*G. flava*) is the most abundant potential browse resource available.

2.4.12 *Senegalia nigrescens* - *Combretum imberbe*: Tall Open Woodland

This habitat unit is found only on a very small portion at the eastern tip of the Mixed Bushveld vegetation type within the study area. It is associated with areas which suffers from severe historic habitat manipulation and have consequently degraded in the past few years. The herbaceous layer is dominated by broom love grass (*E. pallens*) and bottlebrush grass (*E. scoparius*). Trees and shrubs occur at a lower density of 1 650 trees/ha and more than 50% of the potential browse resources have grown beyond a reachable height for most of the ungulates present on the Reserve.

2.5 Wildlife fauna

An abundance of wildlife was already present at the inception of this study because most of the acquired properties contained wildlife. The ecological resource analysis conducted in 2016 showed that some species were overrepresented, and the management of the Reserve tried to rectify this systematically over time. The results of the wildlife surveys conducted in 2016-2021 (excluding 2020) are shown in Table 2.2. A total of 24 species were counted, most of which are suitable potential prey for African lion (Funston *et al.,* 2001; Hayward & Kerley, 2008; Eloff, 2016; Stander *et al*., 2018).

The wildlife surveys focused on small to large ungulates, elephant (*L. africana*) and ostrich (*S. camelus*) and did not include other potential prey species such as porcupine (*H. africaeaustralis*) and chacma baboon (*P. ursinus*), also present on the Reserve. Population densities of predators such as African lion are dependent on the available biomass of preferred prey species (Hayward *et al.,* 2007b), therefore the stocking densities (*i.e.,* lion) must be managed in small, fenced reserves (Miller *et al.,* 2013; 2015).

Several indigenous predators, other than lions, are also present on the Reserve. The leopard (*P. pardus*) is widespread in the region (Skinner & Chimimba, 2005) and

have been informally monitored on the Reserve since 2018. The Reserve falls in the natural distribution range of cheetah (*A. jubatus*) (Marnewick & Somers, 2015) and a viable population was observed from the inception of the project. Despite the presence of the African lions on the Reserve, the cheetah population (*A. jubatus*) increased to the extent that the reserve management decided to relocate several individuals to other reserves in southern Africa. Isolated sightings of spotted hyaena (*C. crocuta*) have been observed, but their permanent residence could not be confirmed in the study area. Other larger African predators present are brown hyaena (*H. brunnea*), black-backed jackal (*Lupulella mesomelas*) [previously known as *Canis mesomelas* (Hilzheimer, 1906; Atickem, *et al.* 2018; Alvares *et al*., 2019)] and caracal (*C. caracal*).

At the inception of the study, white rhinoceros (*C. simum*) and African buffalo (*S. caffer*) were present and completed the full complement of the Big Five of Africa. More African buffalo (*S. caffer*) were released on the Reserve and in 2017 a small herd of elephant (*L. africana*) was also released.

Table 2.2. The annual wildlife surveys of the Reserve for 2016 to 2021 (see Figure. 6.2 for illustration of data for 2021).

Scientific name	Common name	2016	2017	2018	2019	2021
Aepyceros melampus	Impala	1 823	1 328	2 297	2 291	1031
Alcelaphus buselaphus	Red hartebeest	185	140	93	95	97
Ceratothorium simum	Rhinoceros, White	25	18	27	30	25
Connochaetes taurinus	Blue wildebeest	1 184	1 003	365	270	314
Damaliscus lunatus	Tsessebe	16	12	11	2	5
Damaliscus pygargus phillipsi	Blesbok	38	26	20	10	1
Equus quagga	Zebra	598	798	588	546	477
Giraffa camelopardalis	Giraffe	91	102	130	130	122
Hippotragus equinus	Roan	8	12	3	3	8
Hippotragus niger	Sable	66	72	47	31	31
Kobus ellipsiprymnus	Waterbuck	588	425	322	301	133
Loxodonta africana	Elephant	-	-	-	7	9
Oreotragus oreotragus	Klipspringer	7	1	15	3	4
Orycteropus afer	Aardvark	-	-	-	-	-
Oryx gazella	Gemsbuck	145	116	97	165	97
Pacochoerus africanus	Warthog	-	-	-	416	241
Panthera leo	Lion	-	-	-	15	15
Raphicerus campestris	Steenbok	38	-	62	36	19
Redunca fulvorufula	Mountain reedbuck	3	-	-	-	-
Struthio camelus	Ostrich	33	54	40	32	21
Sylvicapra grimmia	Duiker	30	-	40	26	2
Syncerus caffer	Buffalo	67	65	248	377	409
Tragelaphus angasii	Nyala	44	42	40	21	13
Tragelaphus oryx	Eland	166	167	223	233	178
Tragelaphus scriptus	Bushbuck	20	6	10	3	2
Tragelaphus strepsiceros	Kudu	848	547	724	693	355
Prey density (animals/km^2)		28.68	23.50	25.72	27.31	17.14

3 Research methodology

3.1 Data collection

The five founder lions were released on the Reserve in December 2016. Towards the end of 2018 the importance and value to collect very important data in this introduction initiative only became apparent when the potential of a scientific study was realised and discussed with colleagues.

Detail about the origins and release of the five founder lions are presented and discussed in Chapter 4.1. Therefore, this chapter focuses on the general research methodologies used in the study.

Initially, post-release sightings of the lions were recorded by only noting information of importance (*i.e.,* location, number of lions, general body condition, etc.). No formal scoring was done for the body condition of the lions, but a general appraisal was made during the visual sighting of individuals (see the different slides). Reserve managers were asked to routinely report all sightings of lions via the official two-way radio system. Some managers were provided with sighting report cards to record the information and submit it monthly.

In January 2019, the incidental type of reporting described previously evolved to a digital format when a dedicated WhatsApp group was established with some managers. Critical information such as numbers, sex, overall condition, possible kills, Global Positioning System (GPS) locations, photographs and videos were posted electronically on an internal WhatsApp group. If an observation was recorded by staff other than the author, specific behavioural analysis was disregarded unless it could be substantiated by photographic or video evidence. The information was organised and tabulated chronologically. Available data was used to create maps of the spatial and temporal distribution of all the lions on the reserve.

3.1.1 Immobilisation

A registered private wildlife veterinarian (hereafter, the Veterinarian) immobilised/sedated the lions on all occasions. A mixture of Zoletil 100 (Tiletamine

hydrochloride + Zolazepam hydrochloride) and medetomidine (compounded by V-Tech to 20 mg/ml) was administered intra-muscular by a single projectile fired from a Pneu-Dart Model 136, cartridge-fired projector. Atipamezole (compounded by V-Tech to 50 mg/ml) was administered at 5 times the medetomidine dose (measured in mg) to reverse the effect of the medetomidine once the procedure was completed with the lion/s. To prevent infections at the dart wound, Duplocilin (procaine benzylpenicillin, 300 mg/ml) was administered sub-cutaneous at 12.5 mg/kg body weight, whilst a lion was immobilised. Kyroligo (Vitamins A, D3, B1, B2, B6, B12 and E, calcium pantothenate and methionine) was administered to every immobilised lion as a multi-vitamin booster and as a measure to counter the stressful effects of immobilisation.

The first attempts to immobilise lions on the Reserve was conducted from a helicopter. After consultation with the Veterinarian, it was decided that this method was too intrusive and possibly stressful to the animals. The effects of the drugs used for immobilisation were also believed to be countered by the adrenaline presumably being released while being chased for extended distances by the helicopter. It was observed that the time for the drugs to take effect was extended when the lions ran long distances when approached with a helicopter.

A manager from another wildlife reserve with lions suggested the use of a carcass of a dead animal to lure/bait the lions which had to be immobilised. A suitable ungulate [*i.e*., blue wildebeest (*C. taurinus*), zebra (*E. quagga*), impala (*A. melampus*)] was shot and secured with a chain to a tree close to where the desired lions were keeping at the time. The Veterinarian would then immobilise the lions from the safety of a vehicle. However, for the safety of the team, all the lions present in a group were immobilised, even if only one of them had to be inspected, removed, or undergo a medical procedure. Animals were mostly immobilised late in the afternoon or at night.

When a lion was immobilised/sedated for removal or fitting of satellite collars, medical procedures and/or translocations, body measurements (**Appendix I**) were taken according to the method described by De Waal *et al*. (2004a).

3.1.2 Tracking of the lions

The adult male lion (later designated Lion LM1) and one of the lionesses (at the time still a large female cub and later designated Lioness LF1) of the initial group of five founder lions were fitted with iridium satellite collars[5] on 17 January 2017, whilst they were still in the holding boma on the Reserve. The male lion and one female lion were sedated to fit the collars as described in section 3.1.3. The satellite GPS collars are manufactured by Africa Wildlife Tracking (AWT) and allowed two-way traffic ("over the air settings") and automatically sent information to a cloud server accessible by the user. The data was downloaded in csv table format for conversion into graphic illustrations. The satellite GPS collars were chosen because the signals are received by satellite and thus suitable for terrain where a Global System for Mobile Telecommunications (GSM) network proved to be unreliable. Every GPS log contained the tag ID, GPS position, date, time, temperature, accelerometer, and speed (movement).

The satellite GPS collars also contain a UHF (ultra-high frequency) tag (operating in the 148 MHz to 152 MHz range) which could be tracked with a UHF transceiver unit connected to a Yagi antenna. Depending on the terrain, the range over which the UHF tag could be tracked varied from a few hundred meters up to a few kilometres. Primarily, the AWT mobile tracker application was used to identify the latest position of the collared lions, whereafter their precise location was tracked using the UHF transceiver and Yagi antenna.

The satellite GPS collars are supported by two D cells and one C cell which could last up to 24 months depending on the volume and/or frequency of data sent. Although the satellite GPS collars were mostly set to transmit information on a 4-hourly frequency, specific situations cropped up during the study, requiring alteration of the setting for shorter periods of time.

In July 2018, it was decided to increase the capability of monitoring the lions and a second lioness (later designated Lioness LF2) was fitted with a satellite GPS collar.

[5] The iridium satellite collars provided accurate GPS data; hereafter referred to as satellite GPS collars.

During the study, nine lions were fitted with 11 different satellite GPS collars (Table 3.1).

Lions were mostly observed from the safety of official vehicles, although lions were several times successfully located on foot. However, because of the dense vegetation, approaches on foot usually led to very close encounters with the lions before a visual sighting could be established. Isolated incidents occurred where data of lions could be collected while approaching on foot. After several aggressive responses by a lioness[6] towards people on foot, this method of data collection was stopped.

A pair of Zeiss 10x50 binoculars were used during observations when necessary. Photographs were taken with a Canon EOS 7D and a 75-300 mm digital lens. When the camera was not available, the onboard cameras of various types of smart phones were used to capture photographs and make video recordings of the lions.

Using satellite GPS collars was the least intrusive means of near real time tracking (Stabach *et al.,* 2020). However, fitting a lion with a collar required sedation of the individual animal, which could have adversely affected the health of the animal (Kock & Burroughs, 2012).

[6] The lioness was later designated LF2 (see Chapter 4.4).

Table 3.1. Information of the satellite GPS collars fitted to individual lions between 2017 and 2021. The asterisks (*) indicate the collars which were utilised consecutively on more than one lion.

Index	Lion ID	Tag ID	Date of fitment	Type	Frequency	Battery	Colour
1	Lioness LF1	2105	2017/01/16	IR-SAT Tag (IR-SAT (3))	149.990	2 x D and 1 x C	Brown
2	Lion LM1	2104	2017/01/16	IR-SAT Tag (IR-SAT (3))	149.690	2 x D and 1 x C	Brown
3	Lioness LF1	2774	2018/06/12	IR-SAT Tag (IR-SAT (3))	149.140	2 x D and 1 x C	Brown
4	Lion LM1	2873*	2018/07/18	IR-SAT Tag (IR-SAT (3))	149.440	2 x D and 1 x C	Brown
5	Lioness LF2	2874	2018/07/18	IR-SAT Tag (IR-SAT (3))	149.940	2 x D and 1 x C	Green
6	Lion LM2	2873*	2019/09/12	IR-SAT Tag (IR-SAT (3))	149.440	3 x D and 1 x C	Brown
7	Lion LM6	3615	2019/12/01	IR-SAT Tag (IR-SAT (3))	149.500	2 x D and 1 x C	Blue
8	Lioness LF5	3772	2019/12/01	IR-SAT Tag (IR-SAT (3))	149.540	2 x D and 1 x C	Orange
9	Lion LM5	3844*	2020/02/15	IR-SAT Tag (IR-SAT (3))	149.610	2 x D and 1 x C	Blue
10	Lioness LF1	3988	2020/05/25	IR-SAT Tag (IR-SAT (3))	149.140	2 x D and 1 x C	Brown
11	Lioness LF2	3844*	2020/09/03	IR-SAT Tag (IR-SAT (3))	149.610	2 x D and 1 x C	Blue
12	Lioness LF1	4666	2021/05/20	IR-SAT Tag (IR-SAT (3))	149.190	2 x D and 1 x C	Brown
13	Lioness LF7	4606	2021/04/02	IR-SAT Tag (IR-SAT (3))	149.170	2 x D and 1 x C	Orange
14	Lioness LF8	3844*	2021/06/25	IR-SAT Tag (IR-SAT (3))	149.610	2 x D and 1 x C	Blue

3.1.3 Identification of individual lions

By the end of 2018 it was decided to identify the lions individually on the Reserve to improve the scientific correctness of the recorded observations. The specific method of identification of the lions was adopted from Hunter (1998b) by assigning everyone with a unique number according to its sex and chronological order of arrival on the Reserve. The unique number for individual lions started with 'L', indicating the species (lion). This was followed by the letter 'F' (female) or 'M' (male), indicating the sex of the animal. A number followed next, starting at '1' for both sexes. Thus, the first male lion was assigned the number Lion LM1 and the first female was Lioness LF1; these were the first two lions on the Reserve to be fitted with satellite collars (see section 3.1.1).

The prefixes Lion or Lioness used to indicate sexes were allocated to individuals, regardless whether the individual was at the time still a cub, a large cub, a sub-adult, or a mature lion.

The identification numbers of the other three founder lionesses which were released on the Reserve in 2016, together with Lion LM1 and Lioness LF1, were assigned unique numbers at random, namely LF2, LF3 and LF4.

As the study progressed, the lions were also identified by the unique spot patterns of their vibrissae (Pennycuick & Rudnai, 1970). In chronological order of arrival and when their vibrissae spot patterns were photographed, the lion cubs born on the Reserve were each sequentially assigned their unique identification numbers.

In addition, other obvious markings found on lions (*i.e.,* cuts in ears, permanent scars elsewhere on the bodies, etc.) were also used to easily distinguish between individuals during visual sightings.

An additional measure to simplify visual identification was also used by dying the acrylic covers of some of the satellite GPS collars different colours (Table 3.1).

Identification records (cards) were constructed for each lion to which a unique number was assigned (**Appendix II**).

3.1.4 Recording of hunting and feeding behaviour

Prey killed by the lions were documented mainly by two methods: (i) accidentally coming across the lions while they were feeding, (ii) or establishing a possible feeding sight (using data from the satellite collars) and approaching later on foot, after the lions had left the area and it was safe (Tambling *et al.,* 2010).

It was very difficult to obtain photographic evidence of the lions while in the process of actually hunting, mainly due to the density of the vegetation, the tendency of lions to hunt at night (Funston *et al.,* 2001) and the fact that the lions did not hunt in open, savannah-like areas where visual observation and photographing would have been easier.

Possible preferences for prey were established by comparing all available kill data. The GPS positions of confirmed prey kills were used to establish possible preferences of hunting areas, vegetation type and proximity to fences and permanent water holes on the Reserve.

3.2 Assessing and presenting the data in timelines and figures

As discussed previously, successful reproduction and rearing of cubs by lionesses was an integral part of the information base to establish the viability and sustainability of captive bred lions being able to adapt, hunt and socialise in free ranging conditions. Therefore, the physical condition and social behaviour of the lions became the focus during data collection, rather than the hunting statistics of the lions.

Detailed timelines were created for each individual lion, showing recorded incidences of social interaction, mating, births of known litters of cubs, hunting, etc. Where appropriate, the timelines of different individuals were linked to form a broader view and insight of the social interaction of the lions on the Reserve.

Initially recording of data was not scientifically structured and only two of the five founder lions released were fitted with satellite collars, therefore dispersal after being released from the boma could only be established from the positions received from the two collared lions.

Using the kernel density estimator model of the Home Range Tool in ArcGIS Desktop (V. 10.8.1), the spatial utilisation of the available habitat by each lion was determined and graphically illustrated for specific time periods. The GPS fixes of the collars were delineated in the home range analysis to illustrate the areas normally occupied by each lion. A 50% isopleth contour illustrated the area most often utilised, whilst the 95% isopleth is a broader indication of the overall movement of the lion for the selected period (Lehmann *et al.,* 2015; Rodgers & Carr, 1998).

The isopleth contours extending outside the perimeter fences of the Reserve were manually excluded from all figures. The difference between the actual (A) and potential (B) spatial utilisation of the enclosed area of the Reserve by Lioness LF1 is illustrated in Figure 3.1, thus showing the limiting effect imposed by the perimeter fence. By comparing the spatial and temporal utilisation of specific areas by the lions, important behavioural adaptations were assessed and discussed.

Data gathered via the satellite GPS collars was used to analyse the time and frequency which certain individual lions spent in the presence and/or away from each other. By using the available data from the satellite GPS collars, a sudden decrease in spatial utilisation of the Reserve by adult females was linked with a possible mating incidence. The average gestation period (about 110 days) for African lions (Schaller, 1972) was used to estimate the possibility of the birth of a litter of cubs. If an imminent birthing was suspected, every attempt was made to verify as soon as possible the presence of cubs by means of visual observation. The data was used to determine the inter-birthing interval and reproductive rates for each lioness.

Figure 3.1 Comparative illustration of the actual (A) and potential (B) spatial utilisation by Lioness LF1 of the Reserve showing the restrictions of her movement imposed by the perimeter fence.

The survival rate of cubs could only be determined for those cubs physically observed and/or photographed. This was mostly 6-8 weeks after birth (Packer & Pusey, 1983b) when the cubs emerged from hiding and started moving around with their mothers. It should be noted that the actual number of cubs born to each lioness during the study could not be determined, only those present at the first visual sighting of the cubs.

Furthermore, the GPS data was used to hypothesise on other possible reasons for a reduction in spatial utilisation, distance of a female from a group, dispersal of cubs from their natal pride and other behavioural deviances. The results for each lion are discussed in Chapter 4.

The hunting and feeding behaviour of each lion is presented in Chapter 4 and comparisons were made as to the possible prey preferences and preferred hunting habitat. Not all kills could be discovered, especially because of the inaccessibility of the densely vegetated areas, thus obscuring the results for hunting habitat.

Utilisation of the different habitat types (section 2.1, namely open savannah-like and dense vegetated areas) was graphically compared by using the available GPS data.

The focus of the observations in this study was aimed at providing sufficient information to determine whether the captive bred founder lions could successfully adapt to an extensive system and being able to interact socially, hunt and feed successfully, reproduce, raise cubs, and the cubs successfully reproduce themselves.

4 Lion demography and the spatial and temporal use of the Reserve

4.1 Introduction to the results

The four large female cubs used as founders in this study were born at a captive facility in the Limpopo Province. According to Smuts *et al* (1978) lions in this study are broadly categorised as large cubs – 2 to 3 years, sub-adults – 3 to 4 years, and adults – over 4 years. The four large female cubs were the progeny of two lionesses and both litters consisted of four cubs, two males and two females. The eight cubs were weaned at the age of about four months and moved on the same property to a smaller holding facility of approximately 0.2 ha.

The four large female cubs were sired by the same male lion with two lionesses (breeder provided the information by telephone). This was confirmed by DNA profiles of Lionesses LF1 and LF2, showing they were indeed sired by the same male lion but with different mothers. The exact birth dates of the cubs are unknown; however, information from the owner indicated the four large female cubs were approximately two years old when they were moved from the captive facility to the Reserve. Therefore, 1 December 2014 was assumed as common birth date of the four founder lionesses.

At the age of one year the owner separated the four large female and four large male cubs. The four large female cubs were moved into a 20 m wide enclosure (corridor camp) which surrounded a 35-ha camp to act as deterrent against poaching of white rhinoceros (*C. simum*) kept in the 35-ha camp.

The large female cubs were fed fresh meat twice a week after weaning. Carcasses of horses, cattle and various wildlife species were fed in quantities as recommended by a private veterinarian. The animal carcasses or pieces of carcasses were not weighed before being provided to the lions. When possible, the intestines were left in the unskinned carcasses as part of the diet for the lions.

At the age of two years, the four large female cubs were introduced to an adult male lion (later designated Lion LM1) originating from a captive facility in the Free State Province, South Africa. The precise birth date of the adult male lion is also not known. Information obtained from the owner indicated 2006 as an approximate year of birth. When he was three days old, the male lion cub was separated from its mother and hand-reared along with other cubs of a similar age. At the age of 18 months, he was moved to a larger 4 ha camp and joined with male lions of the same age. He remained there until, at the age of five years, he was joined as breeding male lion with four lionesses in a camp of 4 ha, where he remained as a breeding male for approximately four years.

After being weaned from the formula milk, the young male cub (later designated Lion LM1) was fed fresh carcasses of cattle, horses and/or wildlife species. The size of the daily rations was adapted according to the requirements of the number of lions at the time in a specific camp at the captive lion facility. Again, the rations were not weighed before being provided to the lions in a camp.

The adult male Lion LM1 was relocated from the Free State Province, and in preparation for their joint relocation to the Reserve, the lion was joined early in November 2016 by the four large female cubs (2 years old) in an enclosure of approximately 1 ha on the property where the four females were bred and reared.

On 14 December 2016, the four large female cubs and the adult male lion were relocated to the Reserve and released in a 4 ha boma and while acclimatising, monitored. One large female cub and the adult male lion were fitted with satellite GPS collars to monitor their movements after being released from the boma.

The gates of the boma were opened on 30 January 2017. The movement of vehicles and/or the presence of people near the boma were limited. No pre-release training was conducted during the adaptation period of the five lions in the boma. Abell *et al.* (2013) referred to this method as a hard release.

Slide 4.1. One of the four large female cubs cautiously exiting from the transport trailer in the 4 ha boma on the Reserve, while another large female cub lies in the shrub watching her exit. The author took the photograph when the four large female cubs and adult male lion were released in the boma on the Reserve in December 2016.

Starting with the release of the five captive bred lions in the boma on the Reserve, subsequent important events for all the lions are illustrated as timelines in different sections of Chapter 4.

In 2019, about two years after the release of the five lions, it was decided to identify the lions individually: the male lion was easily identifiable as the only male on the Reserve at the time and was designated as Lion LM1; the lioness with the satellite GPS collar was designated Lioness LF1 and the other three females were randomly designated as Lionesses LF2, LF3 and LF4 (see section 3.1.3). The three lionesses without satellite GPS collars could be distinguished by their unique patterns of their vibrissae (Pennycuick & Rudnai, 1970) (see section 3.1.3). Hereafter, the lionesses will be referred to as Lionesses LF1, LF2, LF3 and LF4.

It is important to note that prior to the study being formally registered at the university, the behaviour of the lions was not specifically monitored and recorded other than noting their reaction to approaching vehicles at different times of the day and night.

To remain compliant with the relevant National and Provincial legislation and subsequent Nature Conservation permits, Lionesses LF3 and LF4 were darted in April 2019 and relocated from the Reserve. The relocation of lions from the Reserve was continuously managed throughout the study period by the management of the Reserve. The specifics of the relocations are discussed in subsequent sections of Chapter 4.

By the end of 2019, Lion LM1 was becoming very old and his body condition deteriorated. The management of the Reserve decided to intervene and replace Lion LM1 with another unrelated adult captive bred male lion.

On 12 December 2019 the new adult male, Lion LM6 was released in the boma on the Reserve and supplied every 3-4 days with fresh impala (*A. melampus*) carcasses. After acclimatising in the boma for about 6 weeks, Lion LM6 was released from the boma on 26 January 2020. Lion LM6 was also released without any pre-release training (Abell *et al.,* 2013) or “rewilding”.

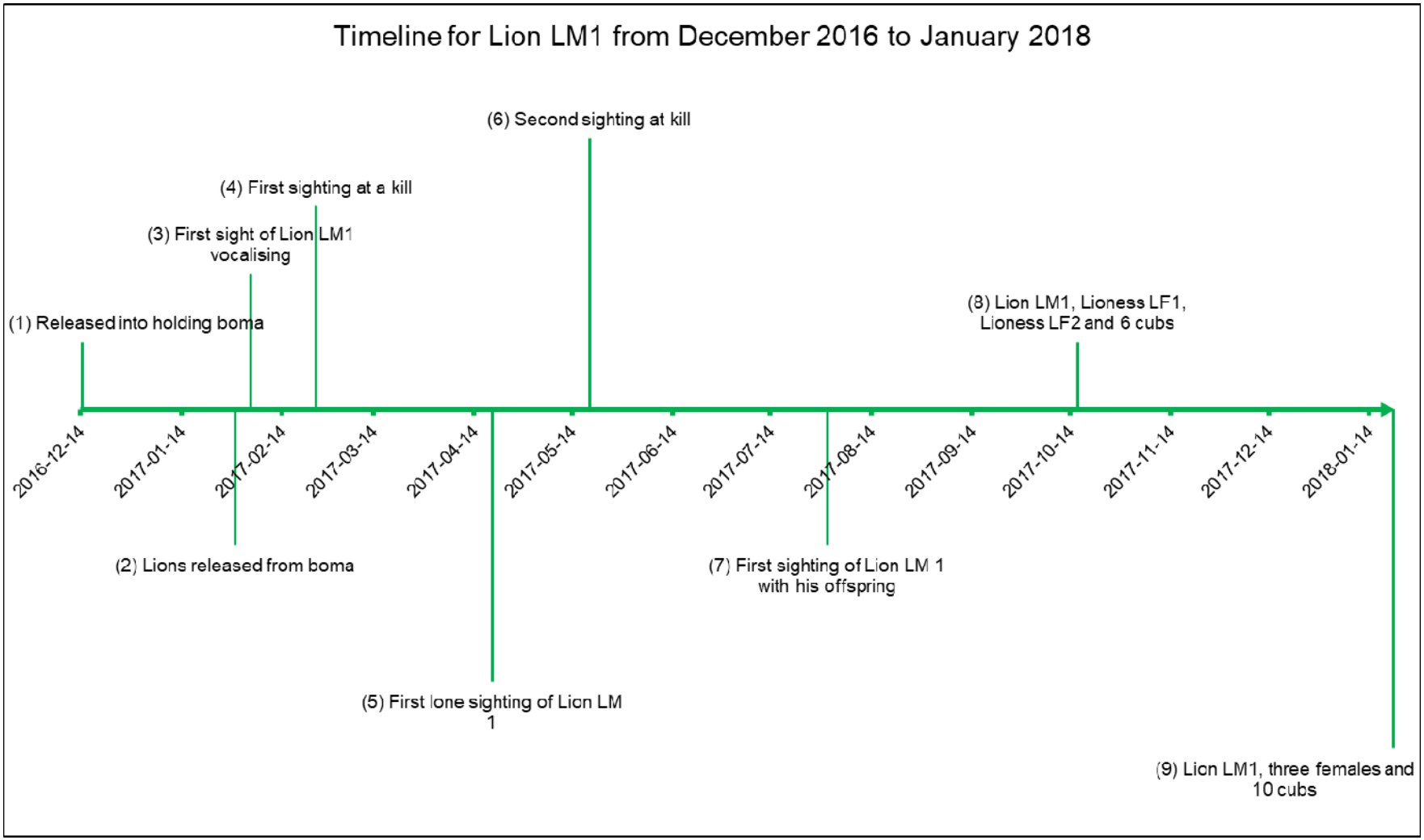
4.2. Timeline of important events for Lion LM1 on the Reserve

4.2.1 Timeline for Lion LM1 from December 2016 to January 2018

The adult male Lion LM1 exhibited specific exceptional phenotypic traits, such as a large head, strong limbs and a well-developed mane extending to the groin area (Slide 4.2); therefore, Lion LM1 was selected to be released with the four large female cubs (Lionesses LF1, LF2, LF3 and LF4) as the founding lion population on the Reserve.

Slide 4.2. Lion LM1 (about 10 years old at the time), exhibiting the exceptional phenotypical traits which was considered in selecting him as a founder lion male.

In preparation for their relocation to the Reserve, the adult Lion LM1 was relocated and released early in November 2016 in an enclosure of approximately 1 ha with the four large female cubs (2 years old) on the property where the four lionesses had been bred and reared. The Lion LM1 was approximately 10 years old.



Timeline 1. Illustrating a timeline of important events (numbered in chronological order) for Lion LM1 on the Reserve from December 2016 to January 2018.

Timeline 1; event (1): A month after being released in the small introduction enclosure, Lion LM1 and the four large female cubs were sedated and transported in appropriate crates (see Slide 4.1) to the boma (a small holding facility) on the Reserve where they were monitored for a six-week period.

Timeline 1; event (2): In the first six weeks after being released from the boma on 30 January 2017, Lion LM1 remained within 300 m of the boma along with the four large female cubs (designated Lionesses LF1, LF2, LF3 and LF4). During this period, Lion LM1 was regularly observed near the four large female cubs. Hunter (1998b) recorded similar behaviour in a reintroduction programme of lion in the Phinda Resource Reserve, KwaZulu-Natal Province, South Africa, where most of the lions released remained relatively close to the holding boma within the first month.

Timeline 1; event (4): On 24 February 2017, Lion LM1 was sighted at the carcass of an adult kudu bull (*T. strepsiceros*) that one of the large female cubs had killed (at the time the female was still unidentified). In prides, male lions seldom contribute to hunting activities (Scheel & Packer, 1991; Funston *et al.,* 2001). Shortly after released, the unidentified large female cub broke away from the group and thereafter was regularly seen alone. Hunter (1998) and Kilian (2003) observed similar early dispersal behaviour in reintroduced African lions.

Lions require about 5-7 kg meat daily to survive, although lions rarely eat every day (Schaller, 1972). More than six weeks passed since Lion LM1 was last provided food in the boma, therefore it is unlikely that this was the first time that Lion LM1 had eaten since released from the boma. However, this observation at the kudu (*T. strepsiceros*) carcass was the first sighting of Lion LM1 feeding on a carcass, which had not been provided to him by humans.

The temperament of Lion LM1 towards approaching vehicles was generally non-aggressive, although he tended to avoid open areas and moved into brush when approached by a vehicle.

Timeline 1; event (5): On 19 April 2017, the first sighting of Lion LM1 without any females was recorded. At the time, the sighting reports may still not have been very

exact. Therefore, several factors could have influenced the sighting of a single lion (Lion LM1): (i) dense brush concealing other lions; (ii) the time spent by the observer looking for other lions, although, thereafter Lion LM1 was recorded to be temporarily separated several times from the group (n = 14; 19 April 2017 to 12 May 2019).

Although early sighting reports were not scientifically structured or designed, observations suggested the social structure of the group of lions did not conform to typical descriptions of fission-fusion social groups (Schaller, 1972; Packer & Pusey, 1982; Kilian & Bothma, 2003). At that stage (26 September 2017) it was uncertain whether the group of five lions (Lion LM1 and the four large female cubs) had formed a cohesive unit. Kilian (2003) recorded similar observations in a group of lions released in 1998 on Welgevonden Private Game Reserve, Limpopo, South Africa, when after being held in a boma for an extended period, the reintroduced group of lions did not form a cohesive unit or pride (as described by Packer & Pusey, 1987) after being released.

The records of sightings also suggested that Lion LM1 did not prefer a particular female but was mostly seen with at least one of the females. This was especially the case for the first post-release year.

Timeline 1; event (6): In mid-May 2017, the second recording was made of Lion LM1 at a confirmed lion kill. It appeared to be only Lion LM1 and one other female, which at the time had not been identified yet. A zebra (*E. quagga*) carcass was dragged under a *P. rotundifolius* (round-leaved bloodwood). The estimated consumption of the carcass was about 50% (Kilian & Bothma, 2003).

Two weeks later (24 May 2017), Lion LM1 was with a lioness next to a boundary fence. Their tracks led past a male waterbuck (*K. ellipsiprymnus*), which had apparently been killed during a fight with another male waterbuck. No signs of consumption of the waterbuck were visible. Although lions are known to scavenge (Scheel & Packer, 1991) and waterbuck have been found to be hunted by African lion (Hunter, 1997b; Kilian, 2003), they did not consume the waterbuck. Instead, the two lions were laying close to a fresh zebra (*E. quagga*) carcass, presumably killed by the two lions close to the dead waterbuck (*K. ellipsiprymnus*).

At an earlier sighting (March 2017) of Lion LM1 and an unidentified lioness at a blue wildebeest (*C. taurinus*) carcass, which ostensibly had also been killed in a dominance fight; very little utilisation of the carcass had taken place. However, the next day the carcass was pulled to a nearby waterhole with a single lioness visible.

Timeline 1; event (7): On 31 July 2017, Lion LM1 was seen with one of the unidentified lionesses and three cubs. The five lions were laying next to the fresh carcass of a young male waterbuck (*K. ellipsiprymnus*). Notes kept by the author indicated that this lioness was later designated as Lioness LF2. At this time Lioness LF1 was easily identifiable with the satellite GPS collar and Lionesses LF3 and LF4 had two and four cubs respectively. In October 2017, Lion LM1 was seen with Lioness LF1 (with three cubs) and Lioness LF2 with her three cubs [Timeline 1; event (8)].

Timeline 1; event (9): The largest grouping of the lions was recorded on 21 January 2018; Lion LM1, three lionesses (including Lioness LF1) and 10 cubs were seen resting at one place. Calculating the cubs born to each young lioness, indicated that it had to be Lionesses LF1 (with three cubs), Lioness LF2 (with three cubs) and Lioness LF4 (with four cubs). A sighting of Lioness LF3 with her two cubs on 3 February 2018 confirmed the conclusion. This assembling of the 14 lions was recorded only once during the study and by 13 February 2018 the remainder of the group was seen without Lioness LF4 and her four cubs being present.

From February 2018 to February 2019, Lion LM1 was regularly seen with Lioness LF1 and Lioness LF2 and their two litters of six cubs, although not all members of the group were present every time. Of the 13 times Lion LM1 was observed during this period, Lioness LF1 was observed with Lion LM1 only on two occasions, even though their spatial utilisation of the Reserve overlapped almost entirely (Fig. 4.1). On one occasion only Lioness LF2 was observed. In all three instances, all six cubs of Lioness LF1 and Lioness LF2 were present.

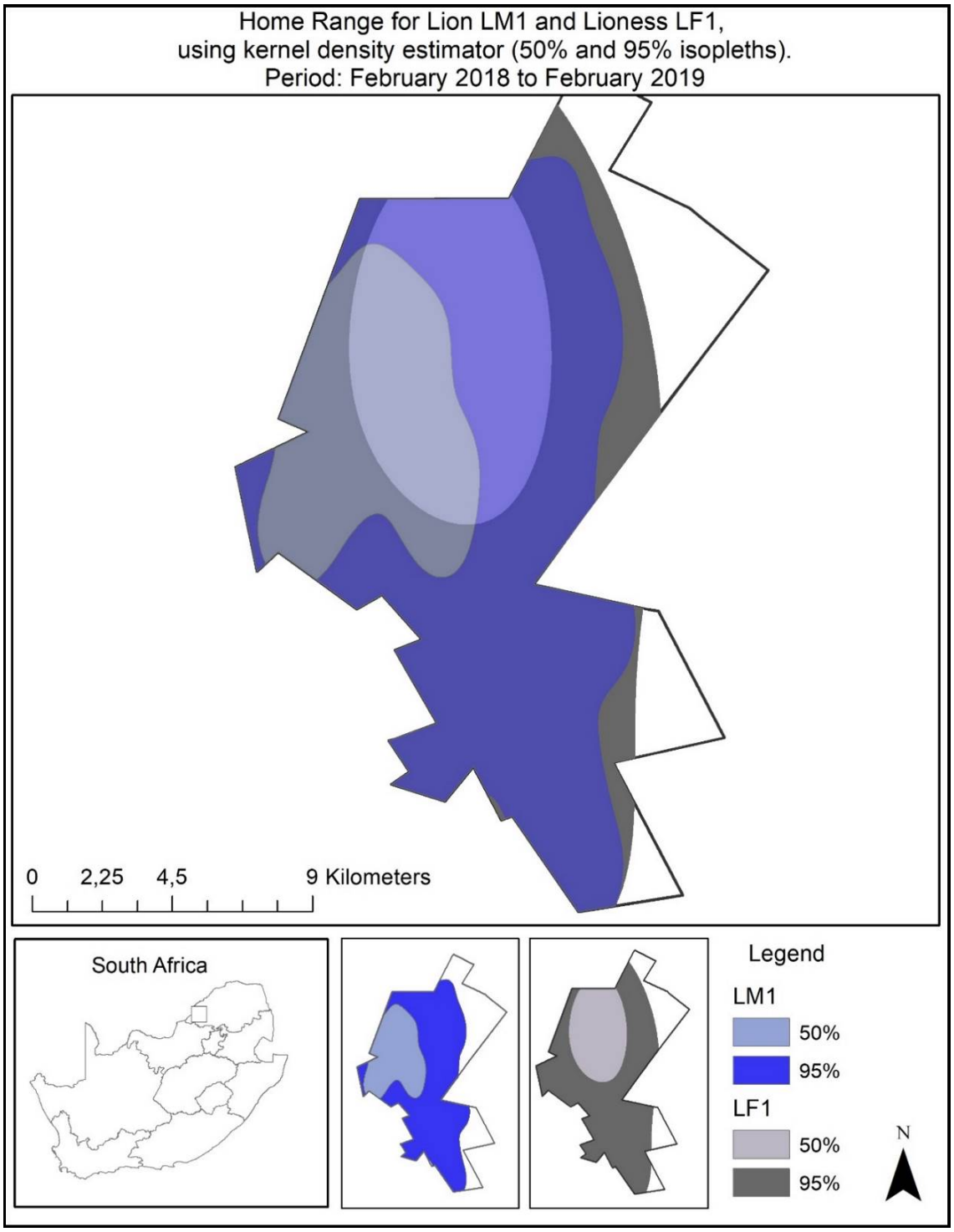


Figure 4.1. Home range comparison for Lion LM1 and Lioness LF1 from February 2018 to February 2019. Lioness LF2 was fitted with a satellite GPS collar in July 2018 and was thus not included in this comparison.

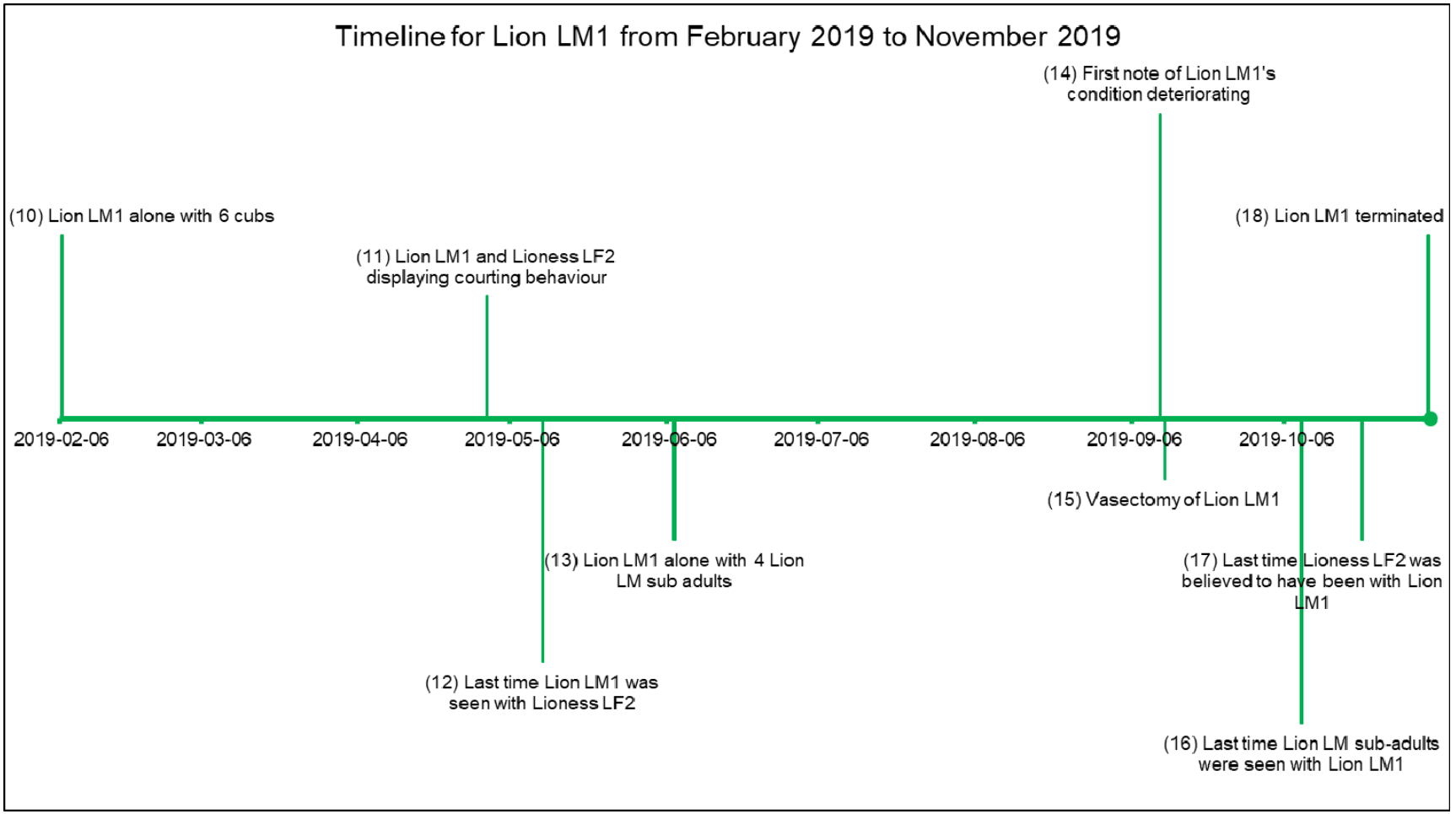
4.2.2 Timeline for Lion LM1 from February 2019 to November 2019

Timeline 2; event (10): According to Funston *et al.* (2001) when lionesses hunt in pairs, they are more likely to succeed when not accompanied by their young. This may be a possible reason why Lion LM1 was recorded being alone with the six large cubs of Lioness LF1 and Lioness LF2 on 6 February 2019.

Slide 4.3. Lion LM1 and Lioness LF2 with the six large cubs (four males and two females) of Lioness LF1 and Lioness LF2.

Timeline 2; event (11): By May 2019, Lioness LF1 had already permanently left the main group (section 4.3) and left her three cubs [Litter 1 (LF1)] with Lioness LF2 and Lion LM1. On 1 May 2019, Lioness LF2 and Lion LM1 were seen displaying behaviour suggesting a courtship cycle (Skinner & Chimimba, 2005). This behaviour was recorded again on 5 May 2019. The observations regarding possible mating were confirmed on 13 September 2019 when Lioness LF2 was found at a den site with an unknown number of cubs; her second litter. African lions have a mean gestation period of 110 days (Schaller, 1972) and by using the estimated age of the cubs of Lioness LF2 at the first sighting, the courting behaviour of Lion LM1 and Lioness LF2 observed on 1 May 2019 was confirmed.

Timeline 2; event (12): Seven days after Lion LM1 was seen displaying courtship behaviour with Lioness LF2 (5 May 2019), Lion LM1 was seen for the last time in the presence of Lioness LF2 (see section 4.4).



Timeline 2. Illustrating a timeline of important events (numbered in chronological order) for Lion LM1 on the Reserve from February 2019 to November 2019.

Timeline 2; event (13): The separation of Lioness LF2 from the remaining group [Lion LM1 and the sub-adult lions of Litter 1 (LF1) and Litter 1 (LF2)] resulted in a further break-up of the group. However, the spatial utilisation of the Reserve by Lion LM1 and Lionesses LF1 and LF2 were similar in the following months (Fig. 4.2).

On 7 June 2019, Lion LM1 was seen with the four sub-adult males (Lions LM2[LF1][7], LM3[LF1], LM4[LF2] and LM5[LF2]) only. This grouping (coalition of males) adopted a nomadic lifestyle [a common feature when related male lions disperse from their natal prides (Packer & Pusey, 1982)] and they remained together until 9 October 2019 [Timeline 2; event (16)] when they were seen for the last time in a group.

Slide 4.4. Lion LM1 (standing) and the coalition of sub-adult lion males LM2, LM3, LM4 and LM5 after separating from the females in June 2019.

Timeline 2; event (15): There was concern that the four sub-adult males were approaching sexual maturity (Brown *et al.,* 1991; Bothma & Du Toit, 2010) and could start mating with siblings. Therefore, the management of the Reserve decided to request the Veterinarian to vasectomise all five males, namely the old founder Lion LM1 and the young Lions LM2, LM3, LM4 and LM5, to prevent inbreeding of the lion population. Several methods for population control may be considered (Miller *et al.,*

[7] The smaller text font in square brackets [e.g. LF1] indicate the respective mother lionesses.

2013), but vasectomising the resident male lions was deemed least intrusive and most effective by the management of the Reserve.

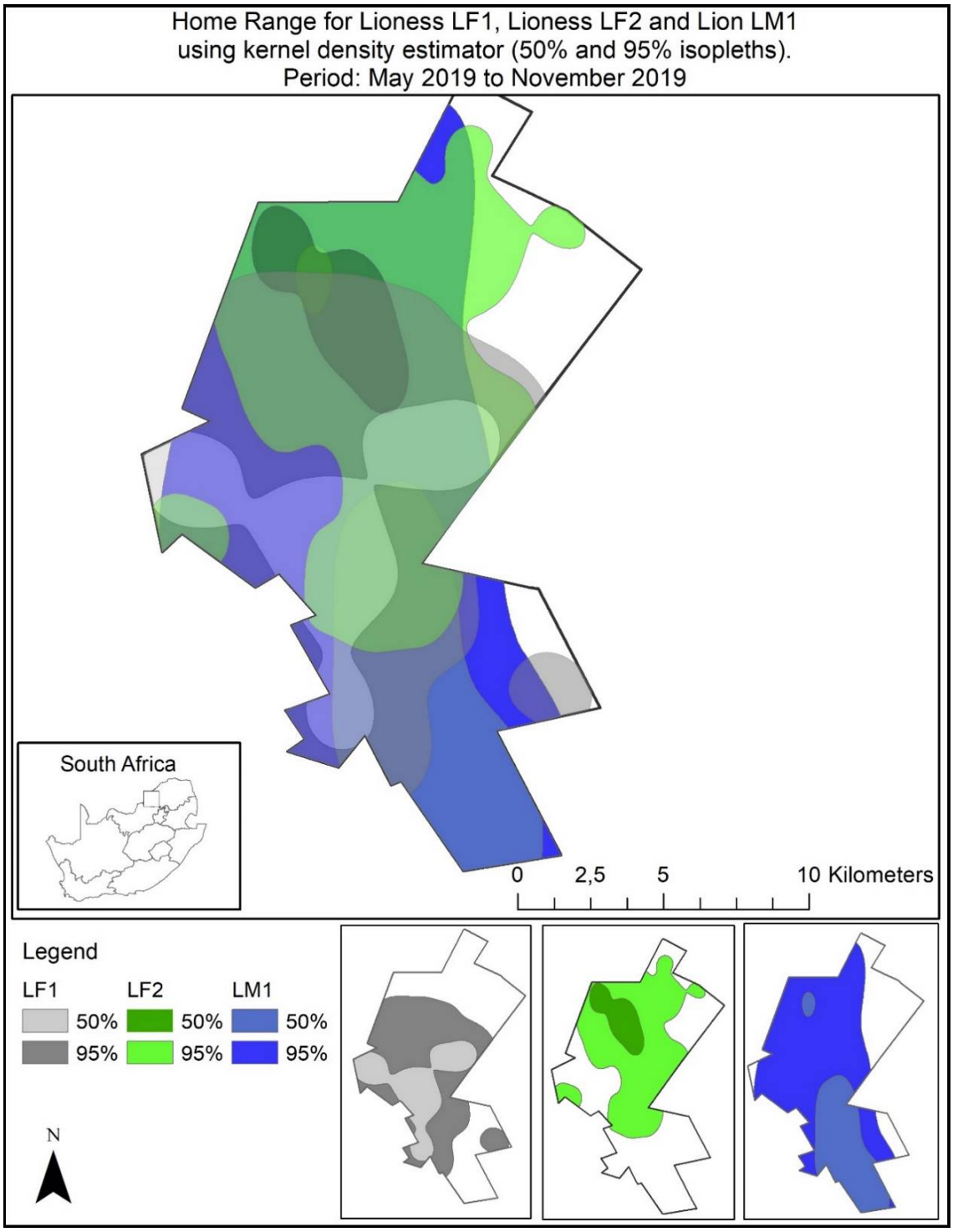


Figure 4.2. Home range comparison for Lion LM1, Lioness LF1 and Lioness LF2 from May 2019 to November 2019, showing the overlapping in spatial utilisation of the Reserve, without spending much time in the presence of one another.

The first three Lions LM1, LM2 and LM3 were vasectomised on 12 September 2019 and the last two sub-adult males (Lions LM4 and LM5) were vasectomised on 19 September 2019. While sedated, the body dimensions of the five male lions (De Waal *et al.,* 2004a) were recorded (**Appendix I**, Table 1).

While the lions were sedated, the satellite GPS collar of Lion LM1 was removed and fitted to Lion LM2. The day before this procedure on Lion LM1 it was the first time that the decline in his body condition was recorded [Timeline 2; event (14)].

On 21 October 2019, the position of Lioness LF1's satellite GPS collar indicated that she had been stationary at the same site (spatial) in the same period (temporal) like Lion LM1. This is believed to have been Lion LM1's last encounter with Lioness LF1. On 22 October 2019, the GPS position of Lioness LF2 placed her within 1 km of Lion LM1's position; however, no physical evidence was found of an encounter between the two lions, namely Lion LM1 and Lioness LF2 [Timeline 2; event (17)].

From 9 October 2019, Lion LM1 remained in an area of about 100 m in diameter [Timeline 2; event (16)] until he was terminated (shot) with a hunting rifle (3 November 2019) [Timeline 2; event (18)].

The method of terminating Lion LM1 with a single shot from a hunting rifle was preferred instead of darting and then euthanising. The lack of mobility was probably an indication of his progressively weakening condition because of advancing age (Slide 4.5). Consultation with the Veterinarian engaged in the project justified the management's decision that Lion LM1 would not recover from his weakened state.

During the time Lion LM1 spent on the Reserve (1 058 days post release from the boma on 30 January 2017), 16 records were made of him at a kill. However, all sightings of Lion LM1 at a kill was in the presence of other lions. During his tenure, Lion LM1 sired 19 cubs on the Reserve between 2017 and 2019.

Slide 4.5. At the end of October 2019, the old Lion LM1 was showing definite signs of a deteriorating emaciated body condition.

The reason why Lion LM1 stayed with his sons (sub-adult males Lions LM2, LM3, LM4 and LM5) is unusual, because one would have expected him to retain tenure of the pride, and the young sub-adult males to disperse as competition for breeding with available females increased (Miller *et al.,* 2013). However, the dynamics of the lion population most likely forced Lion LM1 into a nomadic lifestyle with his sons; after the birth of Lioness LF1's second litter she did not return to the main pride (section 4.3), leaving Lioness LF2 with all six large cubs and Lion LM1.

Furthermore, when Lioness LF2 left the group to give birth to her second litter (section 4.4), Lion LM1 remained with four young (approximately 24 months old) large male cubs and two large female cubs of the same age [Litter 1 (LF1) and Litter1 LF2)]. At that age, the large male cubs were turning into sub-adult males, (Lions LM2, LM3, LM4 and LM5) and dispersal from the natal pride is common (Packer & Pusey, 1987). The reason why Lion LM1 did not to stay with his female offspring is not clear, but Packer & Pusey (1987) found that a third of young females dispersed from their natal prides to form new prides. Interestingly, females would be more likely to disperse from their natal prides when the group size became too large (Packer & Pusey, 1987), which was not the case in this study.

4.3 Timeline of important events for Lioness LF1 on the Reserve

Synopsis: Lioness LF1 produced six cubs from 2017 and 2019, sired by Lion LM1 (Figure 4.3). Her first Litter 1 (LF1) comprised two males (Lions LM2 and LM3) and a female (Lioness LF5), and the second Litter 2 (LF1) comprised two females (Lionesses LF7 and LF8) and a male (Lion LM7). The third litter of Lioness LF1 [Litter 3 (LF1)] was born in February 2021, comprised two cubs (Lioness LF11 and Lion LM10), sired by another Lion LM6. The litter sizes reported were only when the cubs were observed, and it is not necessarily the number of cubs born. The birth intervals were in line with that reported for lions on small reserves (Kilian & Bothma, 2003, Lehman *et al.,* 2008).

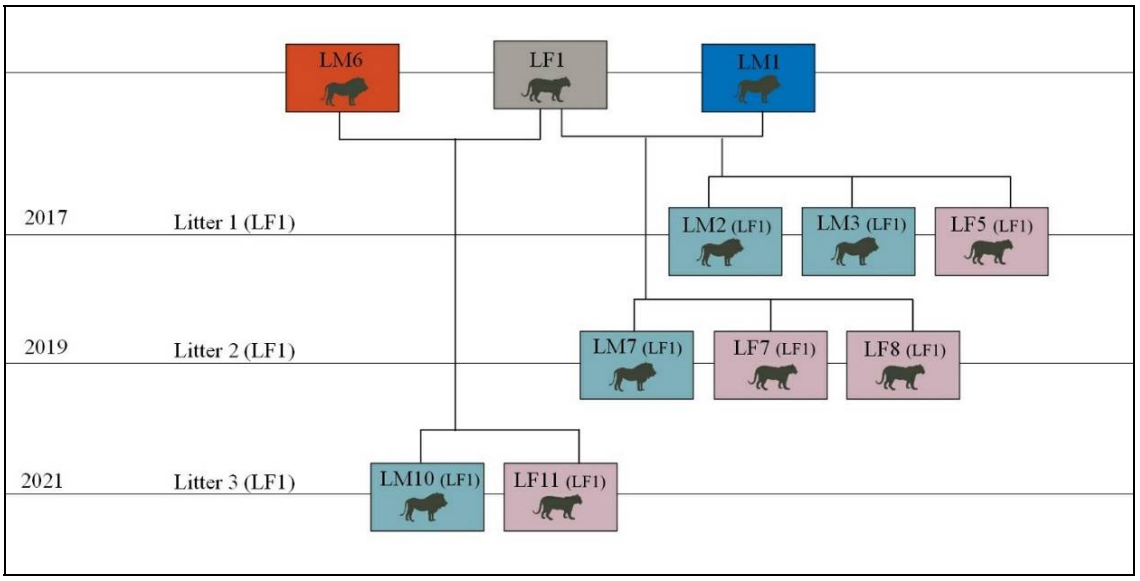


Figure 4.3. Schematic illustration of the offspring of Lioness LF1 during this study (December 2016 to December 2021).

4.3.1 Timeline for Lioness LF1 from December 2016 to December 2018

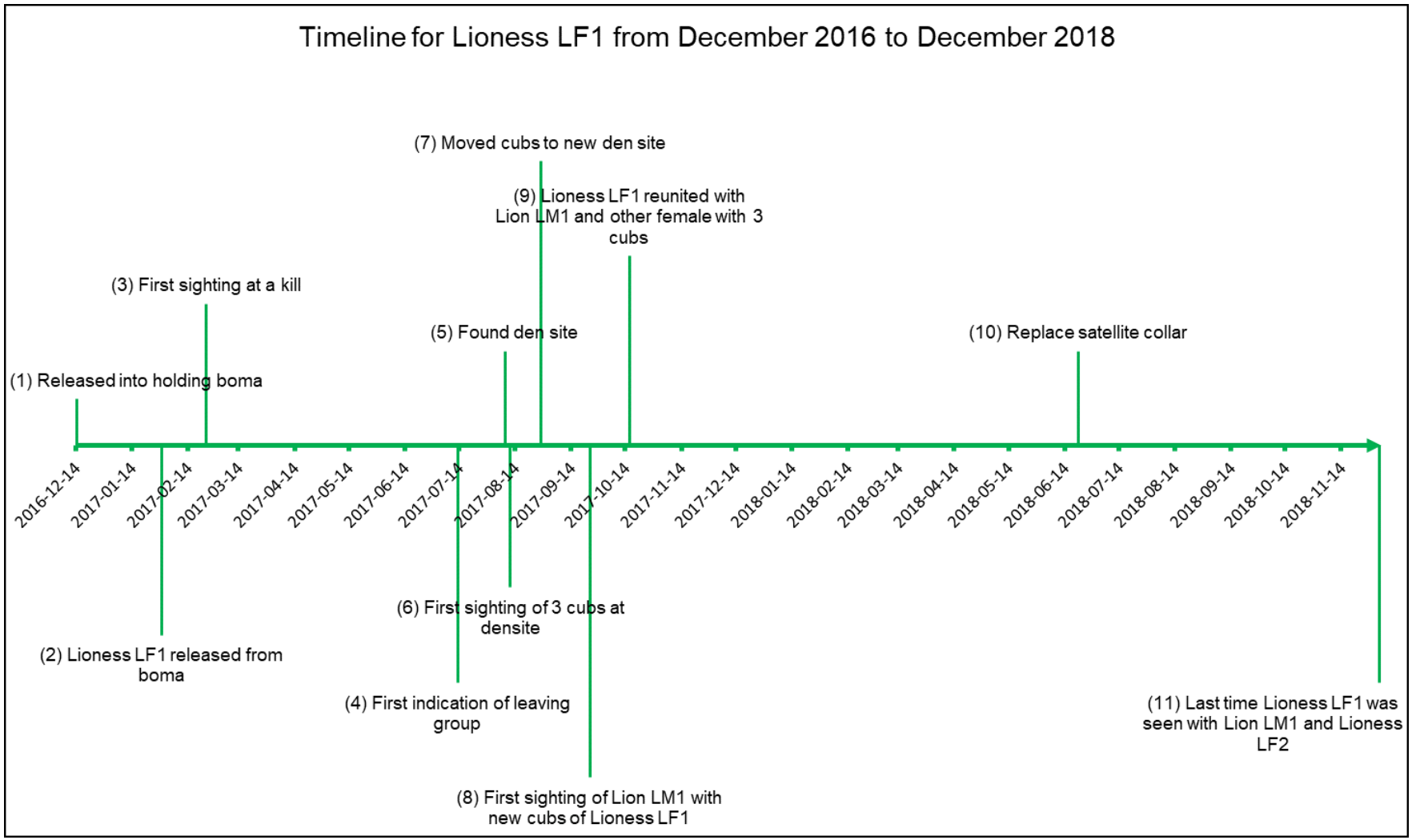
Timeline 3; event (1): Lioness LF1 was released with the other four lions (Lion LM1 and Lionesses LF2, LF3 and LF4) in the holding facility (boma) in December 2016.

Timeline 3; event (2): The release of Lioness LF1 from the boma on 30 January 2017 is discussed in section 4.1.

Timeline 3; event (3): On 24 February 2017, Lioness LF1 was observed feeding on the carcass of a kudu bull (*T. strepsiceros*) next to a water hole, approximately 2 km from the boma. Only Lioness LF1 was seen at the carcass. The previous day another young lioness (a large female cub and at that stage still unidentified) caught the kudu bull. At the time of the kill, the most recent GPS position of Lioness LF1 was approximately 500 m to the west of the kill site. Along with Lion LM1, two of the other (also still unidentified) large female cubs were spotted at an old livestock water trough near the boma, while Lioness LF1 was feeding on the kudu carcass. The large female cub that killed the kudu bull was not observed near the carcass, nor was she seen with the other group of lions. Lioness LF1 was feeding alone on the carcass.

Timeline 3; event (4): In mid-July 2017, it was clear that Lioness LF1 had moved away from the rest of the group of five lions. The positions provided by the satellite GPS collar indicated her prolonged absence from the group. Several attempts were made to get a visual of Lioness LF1. Using the last known GPS location received via the satellite GPS collar, a group of three staff members would drive as close as possible, thereafter the search was continued on foot. A handheld Yagi antenna and VHF transceiver was used to pin the exact location of Lioness LF1; however, the accuracy of the VHF frequency was influenced by the high iron ore content of the rocky outcrop and yielded poor results in the area that Lioness LF1 frequented. Several crevasses and caves formed part of the rocky outcrop and this complicated the search for Lioness LF1 and increased the risk of fatal confrontation at close range for people on foot.

Timeline 3; event (5): In early August 2017, a possible den site was discovered while patrolling the rocky outcrop on foot. Lioness LF1 was observed at the entrance to one of the many crevasses. The presence of small cubs could not be confirmed; however, she had been returning to the same area for more than three weeks and only the presence of cubs would have explained her lengthy absence from the group (Lehmann *et al*., 2008) and a smaller core range size (Maruping-Mzileni *et al.,* 2019) (Fig 4.4).



Timeline 3. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF1 on the Reserve from December 2016 to December 2018.

Slide 4.6. Lioness LF1 (1 August 2019), approximately five years old at the time, walking towards the author.

Timeline 3; event (6): Three days after discovering the potential den site on 11 August 2017, a camera trap that was set close to the trail thought to have been used by Lioness LF1, recorded the first sighting of three cubs[8]. The presence of numerous tracks approaching and leading away from the den site indicated that it was a route frequently used by Lioness LF1.

Timeline 3; event (7): Two weeks later (end of August 2017), Lioness LF1 moved her cubs approximately 2 km away to a new den site, which was closer to a waterhole. The new den site also consisted of rock piles, forming safe crevasses to hide her cubs from possible threats and the natural elements, as well as providing good lookout points from which to scan the surroundings.

Very little is available on the preference of den sites by African lions. In this study, personal observations suggested that no lioness returned to a den site after it was abandoned. Furthermore, the four young lionesses (Lionesses LF1, LF2, LF3 and LF4) did not use the same den sites even though they gave birth at different times, suggesting that the choice of den site may be an individual preference. Lioness LF1

[8] This was the first litter for Lioness LF1 and designated Litter 1 (LF1) when referred to in a group.

occupied seven den sites between 6 July and 22 September 2017. The longest occupation of a den site was 11 days and the shortest was three days. The furthest distance between two serial den sites was 2.2 km and the shortest less than 100 m.

Slide 4.7. Lioness LF1 nursing the three cubs [Litter 1 (LF1)] at one of the den sites in a rocky outcrop in August 2017.

Timeline 3; event (8): At the end of September 2017, Lioness LF1 and Litter 1 (LF1) were seen with Lion LM1. According to Monks (2008), lionesses introduce their cubs to their natal prides when the cubs are several weeks old. In this study, it was not certain how old the cubs were at the time of the first sighting, but they must have been at least four weeks when first photographed at the first den site early in August 2017.

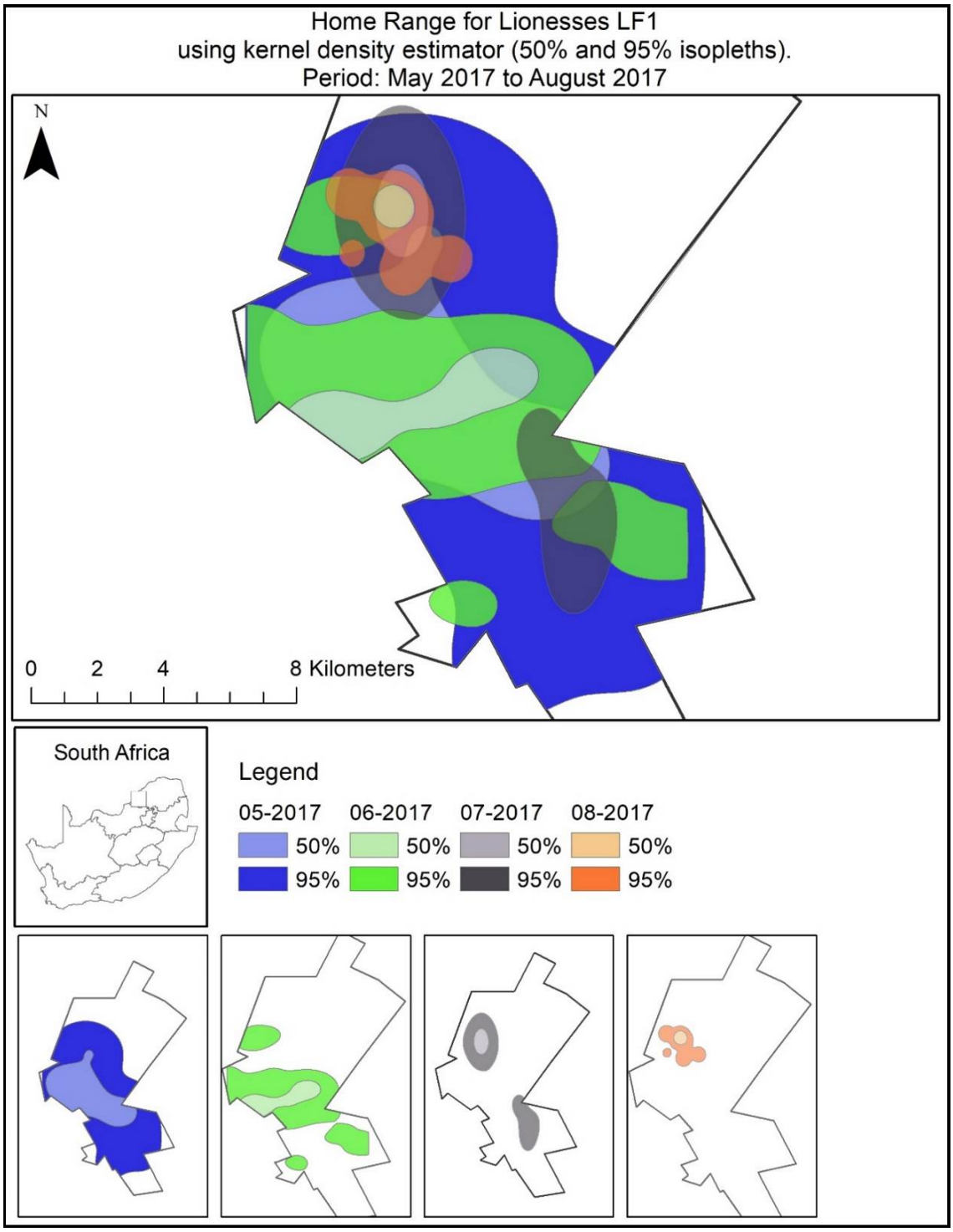


Figure 4.4. Home range size comparison for Lioness LF1 from May 2017 to August 2017.

Timeline 3; event (9): From mid-October 2017, Lioness LF1 was regularly seen with Lion LM1 and another lioness (still unidentified at the time) who also had three cubs. Shortly after this sighting, these nine lions collectively became known as the main

pride, namely Lion LM1, Lioness LF1, Lioness LF2 and their six cubs [Litter 1 (LF1) and Litter 1 (LF2)].

During the following months, Lioness LF1 was seen with Lioness LF2 and Lion LM1 and the two litters of cubs [Litter 1 (LF1) and Litter 1 (LF2)]. A report received from several staff members indicated the presence of yet another lioness (and her four cubs) in the main pride. This sighting of a group of 14 lions (Lion LM1, Lioness LF1 and her three cubs, Lioness LF2 and her three cubs and the unidentified lioness and her four cubs) was reported together only once, on 21 January 2018.

It was reported that on several occasions not all nine lions of the main pride (Lion LM1, Lioness LF1, Lioness LF2 and six cubs) were seen together. This was attributed to the following factors: (i) dense cover making it difficult to locate and see all the lions; (ii) the time spent by the staff member at the sight to establish the exact number of lions present; and (iii) poor visibility and sightings after dark.

It was also possible that Lioness LF1 and Lioness LF2 had left their cubs with Lion LM1, while they were out hunting. According to Funston *et al.* (2001) pairs of lionesses are less likely to succeed in a hunt when accompanied by their young cubs.

Timeline 3; event (10): In June 2018, the satellite GPS collar of Lioness LF1 was replaced before a loss of battery power disabled its ability to transmit GPS locations. At that time, LF1 was still part of the main pride; therefore, on 21 June 2018, the Veterinarian had to sedate both Lioness LF1 and Lion LM1. To facilitate locating the lions easier, the two satellite GPS collars (Lioness LF1 and Lion LM1) were set remotely by satellite the previous day to transmit coordinates every 30 min and provide the most recent locations of the lions at sunrise. A Robinson 44 helicopter flew in the direction of the most recent GPS location and the exact position of the lions was confirmed with the Yagi antenna and VHF transceiver. The author disembarked on the ground from the helicopter, allowing the pilot to manoeuvre to a favourable position for the veterinarian to dart the two lions. While the old the satellite GPS collar (with its depleted battery) of Lioness LF1 was replaced with the new satellite GPS collar and a fresh battery, the helicopter pilot kept visual sightings

on the rest of the lions from a height of about 60 m. After the new satellite GPS collar had been fitted, Lioness LF1 was administered an antidote for the tranquiliser drugs (Chapter 3) and the ground crew stayed within visual distance while she recovered. In the meantime, the veterinarian was airlifted to dart and sedate Lion LM1 with a dart to replace his old satellite GPS collar, with its depleted battery.

The two lions (Lioness LF1 and Lion LM1) were not removed from the location where they were sedated, and the removal and fitting of satellite GPS collars were done on site. The veterinarian constantly checked the vital signs of both animals during the handling process. The process lasted approximately 15 minutes per lion and each lion was not sedated for longer than 30 minutes in total.

Timeline 3; event (11): The last positive visual sighting of Lioness LF1 with the main pride was on 5 December 2018. Her three cubs [Litter 1 (LF1)], however, remained with the main pride (Lions LM4, LM5 and Lioness LF5). At the time the large cubs of Lioness LF1 were approximately 17 months old. Although the nine lions were not seen together again, their spatial utilisation of the reserve overlapped (Fig. 4.5).

4.3.2 Timeline for Lioness LF1 from January 2019 to October 2020

Timeline 4; event (12): After leaving the main pride in December 2018, Lioness LF1 was seen for the first time again on 10 January 2019. During several attempts to get a visual sighting of Lioness LF1 (mostly on foot using the telemetry to pinpoint her location), she evaded the staff by constantly moving and staying in thick brush. The evasive behaviour of Lioness LF1 suggested that she had separated herself from the group again to give birth, because her behaviour resembled that when she gave birth for the first time in 2017.

Timeline 4; event (13): During the time that Lioness LF1 spent isolated from the group, it was recorded that she had killed several medium and small sized species. In one instance, Lioness LF1 killed an adult blue wildebeest female (*C. taurinus*) and without removing the intestines the carcass was dragged into the shade of a nearby tree. By the time the carcass was discovered, the estimated utilisation was less than 10%, because only parts of the inner groin area had been consumed (Slide 4.8).

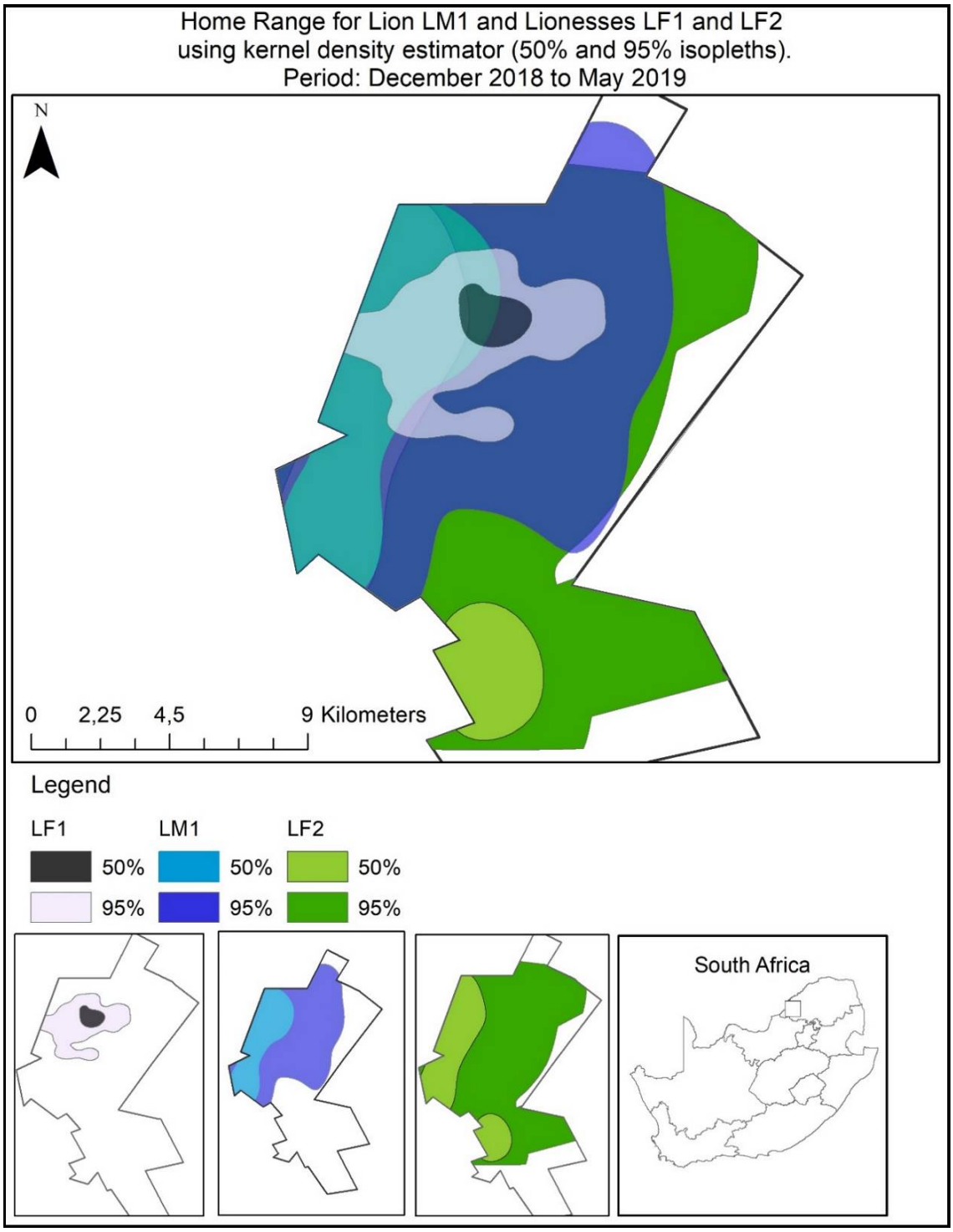


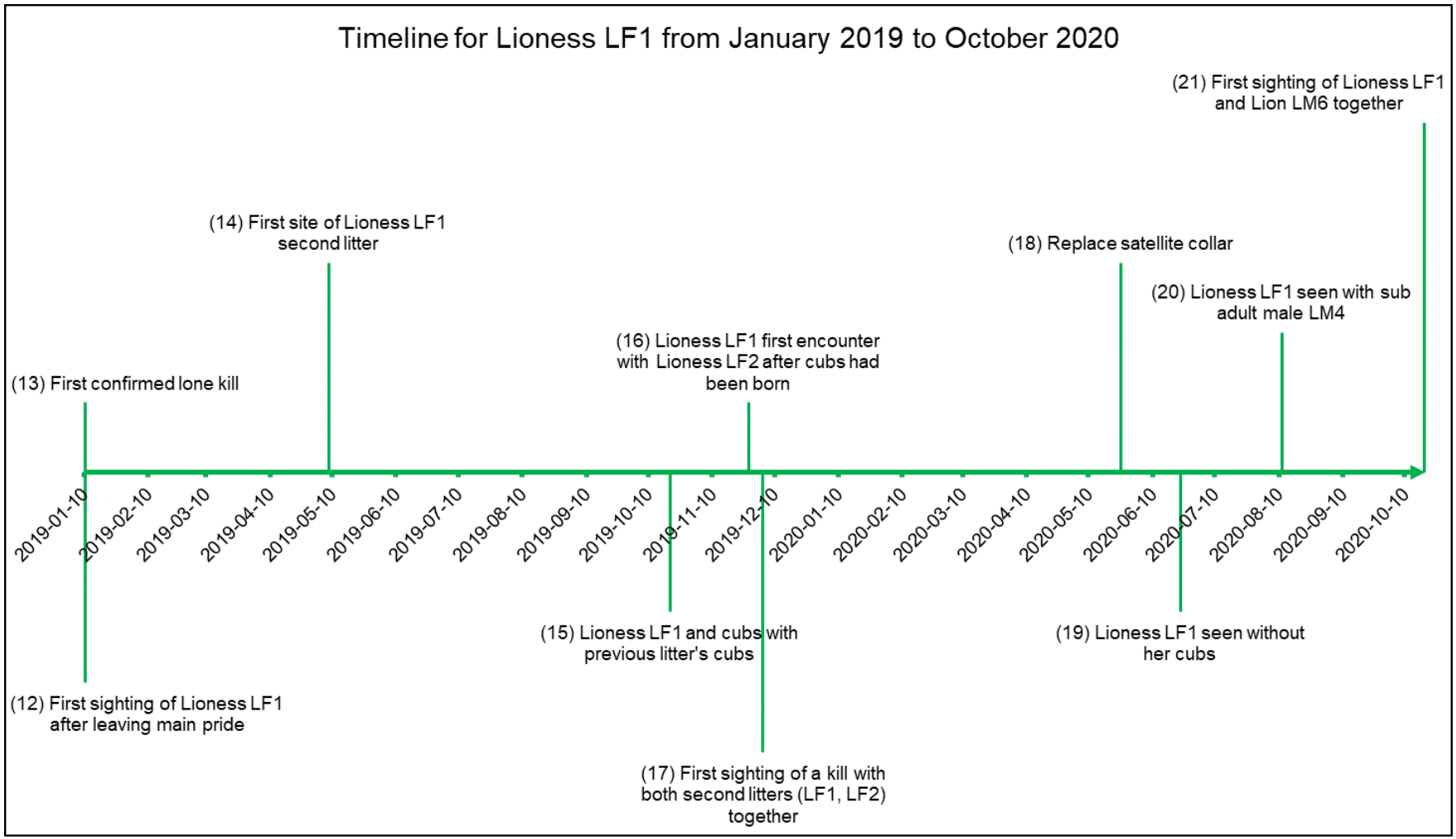
Figure 4.5. Comparison of home ranges of Lioness LF1, Lioness LF2 and Lion LM1 from December 2018 to May 2019 using kernel density estimator (50% and 95%). The map shows definite overlapping of spatial utilisation by Lioness LF1 and Lion LM1, even though Lioness LF1 was separated from the main pride during this time. Lion LM1 and Lioness LF2 were last seen together on 12 May 2019.

Slide 4.8. Blue wildebeest (*C. taurinus*) female killed by Lioness LF1 in May 2019, whilst separated from the rest of the pride. By this time, her second litter was already born.

The percentage utilisation of the carcass was estimated according to the method described by Kilian (2003). No tracks or other signs indicated the possible presence of cubs nearby.

Timeline 4; event (14): In May 2019, the birth of a second litter by Lioness LF1 [Litter 2 (LF1)] was confirmed with a trail camera, which was set up next to another blue wildebeest (*C. taurinus*) carcass; it was suspected to have been killed by Lioness LF1. The three cubs (Lion LM7 and Lionesses LF7 and LF8) were approximately 4-6 weeks old when first sighted with the trail camera (Slide 4.9). During a long-term study of 15 lion prides (Serengeti National Park and Ngorongoro Crater, Tanzania), Packer & Pusey (1983) reported the difficulties to observe lion cubs earlier than 4 to 8 weeks after birth. Lehman *et al.* (2008) reported similar results when lions were reintroduced in Karongwe Game Reserve, South Africa.

Data from Lioness LF1's satellite GPS collar indicated a small home range size from early January 2019. Such behaviour was usually associated with lionesses giving birth (Maruping-Mzileni *et al.*, 2019). From May 2019, Lioness LF1 gradually expanded her home range again (Fig. 4.6).



Timeline 4. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF1 on the Reserve from January 2019 to October 2020.

Slide 4.9. First photograph of the second litter of Lioness LF1 captured with a trail camera on 3 May 2019 at a blue wildebeest (*C. taurinus*) kill (The camera date shown is set to the American format of Month-Day-Year).

Timeline 4; event (15): Five months passed before it was observed that Lioness LF1 had introduced her three cubs [Litter 2 (LF1)] to the other lions; the introduction might have occurred earlier based on data from the satellite GPS collars of the lions. By 20 October 2019, the structure of the group had completely changed. The main pride was no longer a cohesive unit, because (i) Lioness LF2 had broken away from the group; (ii) the two female sub-adults (Lioness LF5[LF1], Lioness LF6[LF2]) (Lioness LF1 and Lioness LF2's first litters) were keeping to the northern border of the reserve; and (iii) the four sub-adult males (Lions LM2[LF1], LM3[LF1], LM4[LF2] and LM5[LF2]) developed a nomadic lifestyle, occasionally meeting with Lion LM1. At this stage Lion LM1 was in a very poor state (old age) and did not move much. On 20 October 2019, Lioness LF1 and the three cubs of Litter 2 (LF1) were seen with two of the LM sub-adult males. No aggression was noted by the LM sub-adult males toward the new cubs. It was assumed the two LM sub-adult males were from Litter 1 (LF1), although at that time no attempt was made to identify the LM sub-adult males.

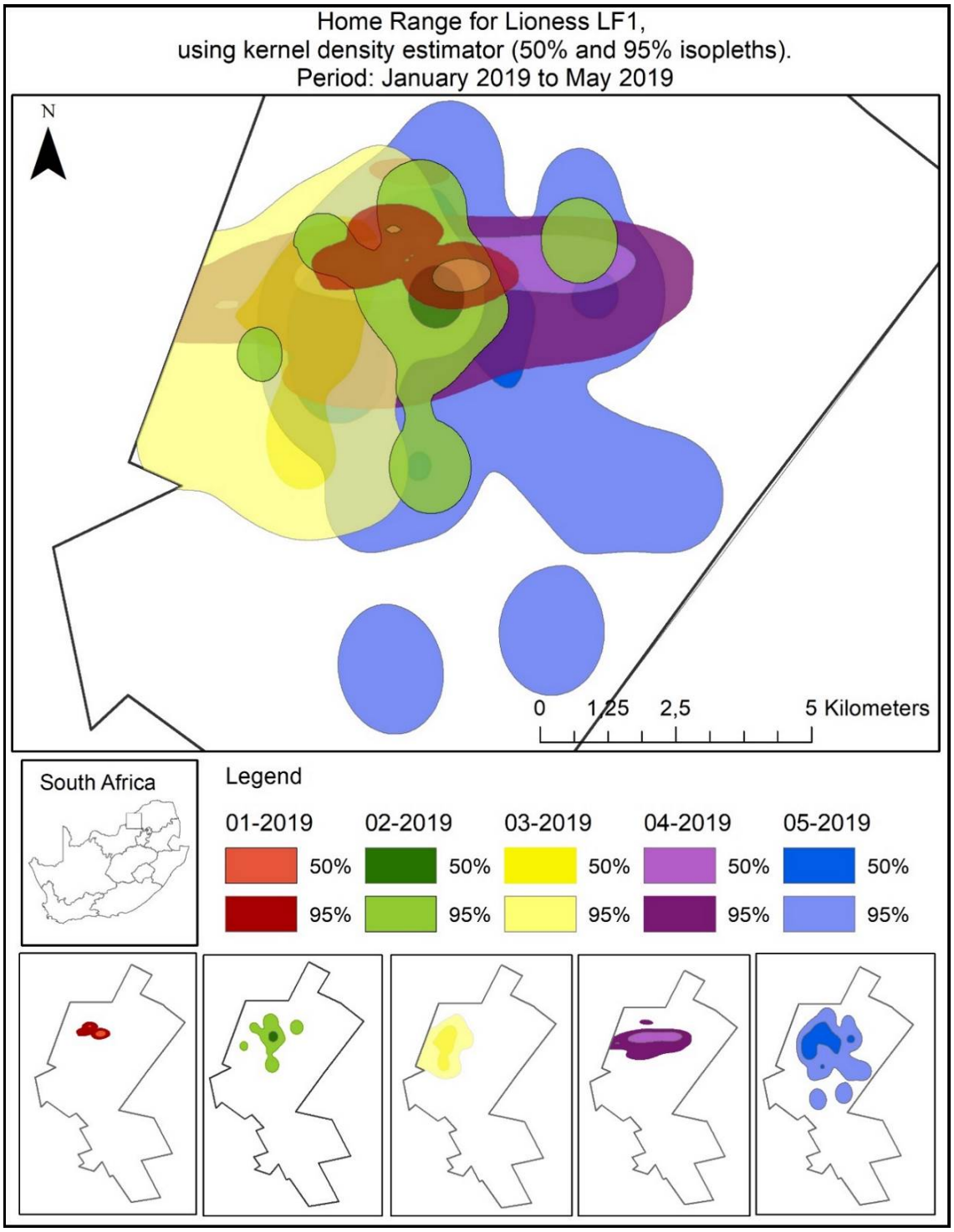


Figure 4.6. Comparison of home range size for Lioness LF1 from January 2019 to May 2019 showing a gradual extension of her spatial utilisation from January 2019 when her second litter of cubs [Litter 2 (LF1)] were born.

Timeline 4, event (16): The first sighting of Lioness LF1 and Litter 2 (LF1) with Lioness LF2 was near the end of November 2019. Some altercation occurred

between Lioness LF1 and Lioness LF2, but Lioness LF2 showed no aggression towards the cubs of Lioness LF1. The aggression of Lioness LF2 toward Lioness LF1 could have been due to an injury that Lioness LF2 had sustained; she limped badly on her front left leg. Lioness LF1 and her cubs slowly moved off into the thicket, leaving Lioness LF2 at the site of the incident. The introduction took place at the same old livestock water trough where the very first kill of the lions was recorded shortly after being released from the holding boma in 2017.

Four days later (1 December 2019), Lioness LF1 and Lioness LF2 were again recorded together, this time Lioness LF2 had brought her four new cubs [Litter 2 (LF2)] along. No aggression from either lion was recorded and after a short interaction, they moved off again in different directions.

Timeline 4; event (17): On 4 December 2019, Lioness LF1 and Lioness LF2 and their two litters [Litter 2 (LF1) and Litter 2 (LF2)] were seen at a kill of a male waterbuck (*K. ellipsiprymnus*). The kill must have been made shortly before the author arrived, because only the intestines had been removed, with no visible consumption yet and the two lionesses were still breathing heavily from apparent exhaustion after the chase.

This was the first recorded shared hunt by Lionesses LF1 and LF2 since the birth of both their second litters. Lioness LF2 allowed her cubs to play with and over the carcass but did not tolerate the older and larger cubs of Lioness LF1 to come closer. Lioness LF1 was laying approximately 5 m from the carcass.

On 12 December 2019, Lioness LF1 and her three cubs of Litter 2 (LF1) were seen again, without Lioness LF2 and her four cubs of Litter 2 (LF2). On 8 January 2020, the nine lions were recorded together again. This fission-fusion behaviour by Lioness LF1 and Lioness LF2 and their cubs were recorded several times during the study.

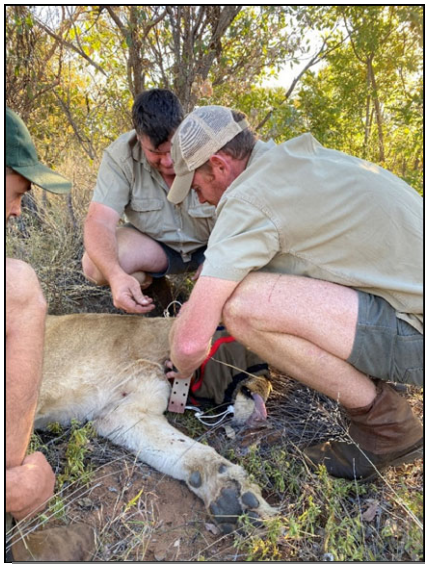
On 14 January 2020, a sighting of Lioness LF2 and Litter 2 (LF2) confirmed the group had split up again. The first sighting that confirmed re-grouping of the lions was three months later (13 April 2020) at a kill of an adult male waterbuck (*K. ellipsiprymnus*).

Slide 4.10. Lioness LF1 (lying right, with collar), Lioness LF2 (standing left, with collar) and their seven cubs eating on a male waterbuck (*K. ellipsiprymnus*) killed by the two lionesses on 13 April 2020. One cub is not visible in the photograph.

Timeline 4; event (18): On 25 May 2020, Lioness LF1 and the three cubs of Litter 2 (LF1) were sedated by the Veterinarian to replace her satellite collar. The four lions were located with the telemetry, because the battery of Lioness LF1's satellite GPS collar had already lost all power. The lions were resting next to the carcass of an adult female eland (*T. oryx*) on which they had fed. As a safety precaution, the cubs were also sedated and while sedated, their body measurements recorded (De Waal *et al*., 2004b) (See **Appendix I**, Table 2 and 3 for measurements).

Timeline 4; event (19): From 23 June to 22 July 2020, the three cubs of Litter 2 (LF1) were seen without their mother Lioness LF1 on three occasions. During the same period, Lioness LF1 was seen without her cubs on two separate occasions, confirming the separation. The reason for the separation is unclear, although Lioness LF1 may have been coming into oestrous and was seeking a male lion on the Reserve. The cubs of Litter 2 (LF1) were 15-16 months old and it would thus seem normal for Lioness LF1 to be ready to conceive again (Hunter, 1998b; Lehmann *et al.,* 2008).

This contrasts with findings of Maruping-Mzileni *et al.* (2019) where lionesses in the Kruger National Park, South Africa were more likely to conceive during the wet season (October – February) when prey abundance was high. It must be emphasised that a high density of suitable prey species was present on the Reserve (Chapter 2), and abundant artificial water points further allows for a more even distribution of prey across the Reserve.



Slides 4.11 & 4.12. Fitting the sedated Lioness LF1 with a new satellite GPS collar (left) and Lioness LF1 with the newly fitted satellite GPS collar.

Timeline 4; event (20): One more sighting of Lioness LF1 with Litter 2 (LF1) was recorded on 27 July 2020, before she was seen with a sub-adult male (in the absence of her three cubs) on 11 August 2020. On 5 August 2020, the three cubs of Litter 2 (LF1) were seen with Lioness LF2 and Litter 2 (LF2). Lioness LF1 was seen again with Lioness LF2 and all seven cubs on 1 September 2020, although the sub-adult male with which Lioness LF1 was seen with previously, was recorded to have joined his three brothers seven days prior to that sighting. The four sub-adult males Lions LM2[LF1][9], LM3[LF1], LM4[LF2], and LM5[LF2]) were sedated on 26 August 2020 and permanently translocated to another reserve.

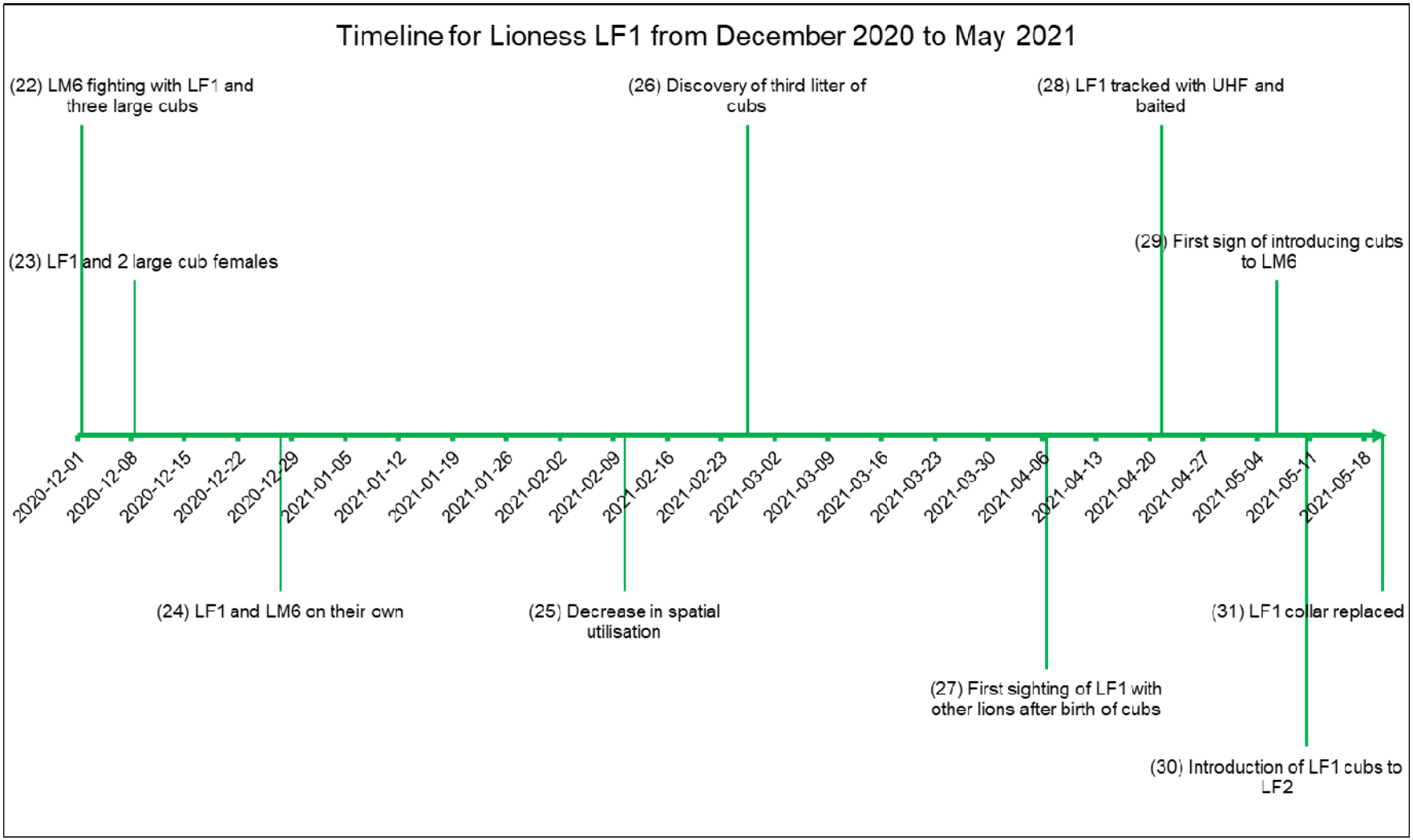
On 19 October 2020, Lioness LF1 was seen with the new adult male Lion LM6 that

[9] The smaller text font used in the square brackets [e.g. LF1] indicate the respective mother lionesses.

was released on 26 January 2020. Again, the individuals of Litter 2 (LF1) were seen with Lioness LF2 during this time. On two more occasions (26 and 30 October 2020), Lioness LF1 and Lion LM6 were seen together and although courting behaviour was not observed, it is reasonable to assume that they engaged in such behaviour because no aggression was recorded and no influencing factors could have prevented Lioness LF1 from leaving the company of Lion LM6. Data received from the satellite GPS collars, showed that Lion LM6 and Lioness LF1 stayed together from 18 October 2020 to 4 November 2020, with a slight pause in their grouping between 21 and 24 October 2020 (Fig. 4.7). During November 2020, Lioness LF1 was regularly seen with Lioness LF2 and the seven cubs of Litter 2 (LF1) and Litter 2 (LF2). Lioness LF1 was seen with only Litter 2 (LF1) on only one occasion (23 November 2020) during this time.

4.3.3 Timeline for Lioness LF1 from December 2020 to May 2021

Timeline 5; event (22): On 1 December 2020 Lioness LF1 and the three large cubs of Litter 2 (LF1) were seen in one of the open areas on the Reserve. At the same time Lion LM6 was seen approaching from approximately 500 m away. Lioness LF1 started walking towards Lion LM6 as soon as she saw him and submissively laid down at his feet whilst making soft noises. Lion LM7 (the large male cub of Lioness LF1) ran towards Lion LM6 and the latter retreated hastily. Lion LM6 ran for approximately 1 km, whilst the other four lions were following, whereafter he stopped and laid down. Lion LM7 displayed possessive behaviour by scent-marking a nearby brush and positioned himself between the lionesses (LF1, LF7 and LF8) and Lion LM6. Then Lion LM6 approached Lion LM7 slowly in a circular pattern before scent-marking several bushes close to Lion LM7, who had by then adopted aggressive behaviour. When Lion LM6 came within 2 m of Lion LM7, a physical fight of claw-strikes, biting and growling erupted between the two males. The three females (Lionesses LF1, LF7 and LF8) joined the fight by simultaneously attacking Lion LM6. Lion LM7 ran off whilst Lion LM6 physically overpowered the three females. The three females submitted to Lion LM6 who continued to challenge them by loud growling and aggressive swipes of his front paws towards them. One of the large female cubs attempted to run away but was followed by Lion LM6 (Slides 4.13 to 4.20).



Timeline 5. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF1 on the Reserve from December 2020 to May 2021.

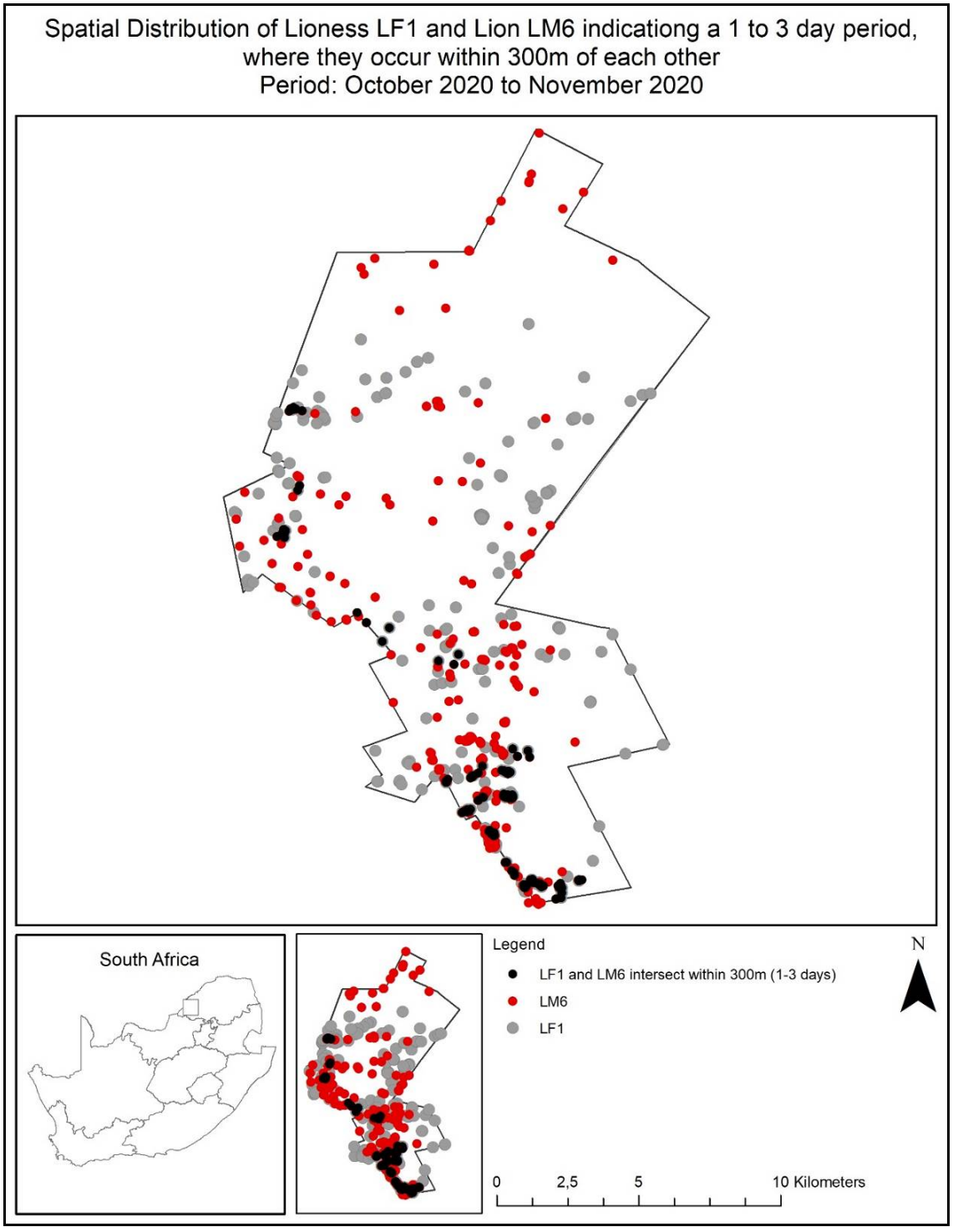


Figure 4.7. Illustration of spatial distribution of Lioness LF1 and Lion LM6 for October 2020 to November 2020. The black markers indicate where the GPS locations of Lioness LF1 and Lion LM6 intersected within 300 m within a three-day period, indicating their time spent together.

Slides 4.13 to 4.20. Sequence of events as described in Timeline 5; event (22) between Lion LM6, Lioness LF1 and her three large cubs (Lion LM7 and Lionesses LF7 and LF8).

The altercation between the loins lasted approximately 2 minutes, whereafter a herd of buffalo (*S. caffer)* appeared from the nearby thickets and, in a group formation, chased all the lions for more than 500 m. Visual sighting of the lions was lost when they ran into the thick brush.

The lions were seen again 10 min later, approximately 2 km from the scene of the altercation where Lion LM7 had adopted a submissive attitude towards Lion LM6 who came to lie down next to him. Lioness LF1 and one of the large female cubs arrived minutes later and kept approximately 10 m from the two males. All the lions were breathing heavily from apparent exhaustion. The other large female cub was only seen again the next day.

That night at approximately 20h15, Lion LM6 was recorded walking north, stopping frequently to smell the air and scent-marking nearby brush. Lioness LF1 and her three large cubs were not seen, but their tracks were noted heading in a northern direction.

Timeline 5; event (23): One week later, Lioness LF1 and her two large female cubs (Lionesses LF7 and LF8) were seen in the absence of Lion LM7 who had not been witnessed to be in their presence since the altercation on 1 December 2020. It was only on 15 December 2020 that Lion LM7 was seen again. He was joined by Lion LM6 and two adult females, Lionesses LF5 and LF6 in the central part of the Reserve (section 4.8). Lion LM7 was seen with his mother (Lioness LF1) only once after this, on 20 January 2021.

Timeline 5; event (24): Lion LM6 and Lioness LF1 was again seen together on 27 December 2020 at a small pan in the south-eastern part of the Reserve where they rested approximately 50 m apart, softly vocalising. After this event, Lioness LF1 was frequently observed in the presence of Lion LM6.

Timeline 5; event (25): By 10 February 2021 a definite reduction in spatial utilisation of the Reserve by Lioness LF1 was observed from GPS data (Figure 4.8). The birth of a third litter of cubs was suspected and would have confirmed a successful mating

with Lion LM6 (the only resident adult male on the Reserve at the time) during their interactions in October and November 2020. On 26 February 2021, a litter of two cubs [Litter 3 (LF1)] were indeed confirmed when the author investigated a possible den site [Timeline 5; event (26)] (Slide 4.21).

The cubs were presumed to be only a few days old and the date of birth was estimated at between 10 and 20 February 2021. By 28 February 2021, Lioness LF1 moved the cubs of Litter 3 (LF1) to a new den site approximately 1 km away. The chosen den sites were inconsistent to those previously utilised by Lioness LF1 and consisted of dense growths of sweet prickly-pear (*Opuntia ficus-indica*) and a fallen-over shepherd's tree (*B. albitrunca*). Lioness LF1 remained at the second den site until 7 March 2021 when her satellite GPS collar unexpectedly ceased to work.

Slide 4.21. The two cubs of Lioness LF1, born in early February 2021.

On 6 April 2021, Lioness LF1 was seen at a zebra (*E. quagga*) bait used to lure Lioness LF7 for sedation. The two cubs of Litter 3 (LF1) was not present and Lioness LF1 only remained at the carcass for a short time before retreating into the thick brush.

Timeline 5; event (28): On 21 April 2021, Lioness LF1 was tracked using the UHF

transponder on her satellite GPS collar which was still working at the time. She and presumably Litter 3 (LF1) were hidden in dense brush and not visible. A zebra (*E. quagga*) carcass was used as bait to lure Lioness LF1 to a nearby clearer area where she could be sedated to fit a new satellite GPS collar. Lioness LF1 was skittish and did not allow any vehicles close to her or to her two cubs.

Timeline 5; event (29): On 6 May 2021, Lioness LF1 and Litter 3 (LF1) were found at a waterhole in the central part of the Reserve. Upon the arrival of the vehicle, Lioness LF1 and the two cubs fled into nearby dense brush. When inspecting the point of entry into the dense brush, the author found Lion LM6 laying next to the road. Lioness LF1 had clearly passed him. It could not be confirmed whether this was the first introduction of Litter 3 (LF1) to Lion LM6 because Lioness LF1 had not yet been fitted with a new satellite GPS collar.

Timeline 5; event (30): On 10 May 2021, Lioness LF1 and Litter 3 (LF1) were at the carcass of a blue wildebeest (*C. taurinus*) which she had caught in an open area of the Reserve. Upon the author's arrival, Lioness LF1 and the two cubs retreated to the cover of the nearby dense brush. Lioness LF2 was laying approximately 10 m from the carcass. Presumably this was the first introduction of Litter 3 (LF1) to Lioness LF2. Lion LM6 appeared and claimed the carcass and dragged it into the dense brush. Lioness LF2 followed Lion LM6 with the blue wildebeest carcass.

On 19 May 2021, Lioness LF1 was found, by chance, in a road in the central part of the Reserve with Litter 3 (LF1). Lioness LF1 appeared uneasy with the presence of the vehicle but the two cubs were curios and approached to within 1 m of the vehicle. Lioness LF1 tolerated this behaviour for a very short while, whereafter she nudged the cubs into the dense brush using her head and making soft vocalisations.

The next day Lioness LF1 was found at the same location. The Veterinarian sedated her from the vehicle and the satellite GPS collar was replaced with a new collar and its fresh battery [Timeline 5; event (31)]. During the sedation, Lion LM6 and Lionesses LF7 and LF8 were also present. All the lions were feeding on the carcass of an adult ostrich (*S. camelus*) which was presumably caught by Lioness LF1 the previous day.

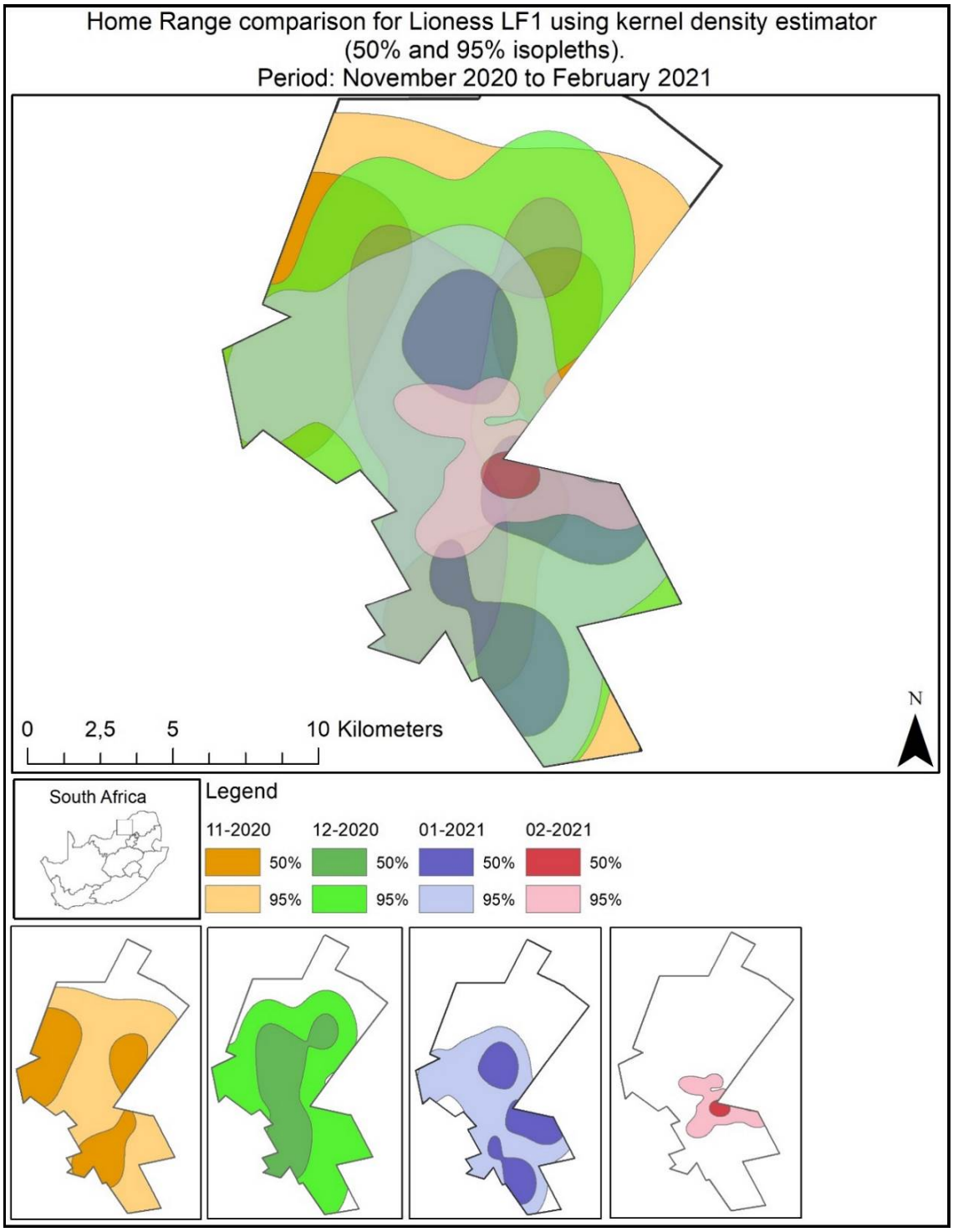


Figure 4.8. Comparison of home range size for Lioness LF1 from November 2020 to February 2021 showing a gradual reduction of her spatial utilisation to February 2021 when her third litter of cubs were born.

During the study, Lioness LF1 was positively identified with 35 prey kills, comprising nine species. Apparently, Lioness LF1 was more successful at killing blue wildebeest

(*C. taurinus*) (25%; n= 9), followed by eland (*T. oryx*) (14%; n = 5) and waterbuck (*K. ellipsiprymnus*) (11%; n = 4). The prey species least killed by Lioness LF1 were ostrich (*S. camelus*) (5%; n = 2) and giraffe (*G. camelopardalis*) (5%; n = 2). Other species recorded to have been preyed on by Lioness LF1 are gemsbuck (*O. gazella*), zebra (*E. quagga*), kudu (*T. strepsiceros*) and warthog (*P. africanus*).

4.4 Timeline of important events for Lioness LF2 on the Reserve

Synopsis: Lioness LF2 produced seven cubs whilst on the Reserve (Fig. 4.9). The progeny produced from 2017 to 2019 comprised two males (Lions LM4 and LM5) and a female (Lioness LF6) in the first litter [Litter 1 (LF2)], and two males (Lions LM8 and LM9) and two females (Lionesses LF9 and LF10) in the second litter [Litter 2 (LF2)], all sired by Lion LM1. The birth intervals were in line with that reported for lions on small reserves (Kilian & Bothma, 2003, Lehman *et al.,* 2008).

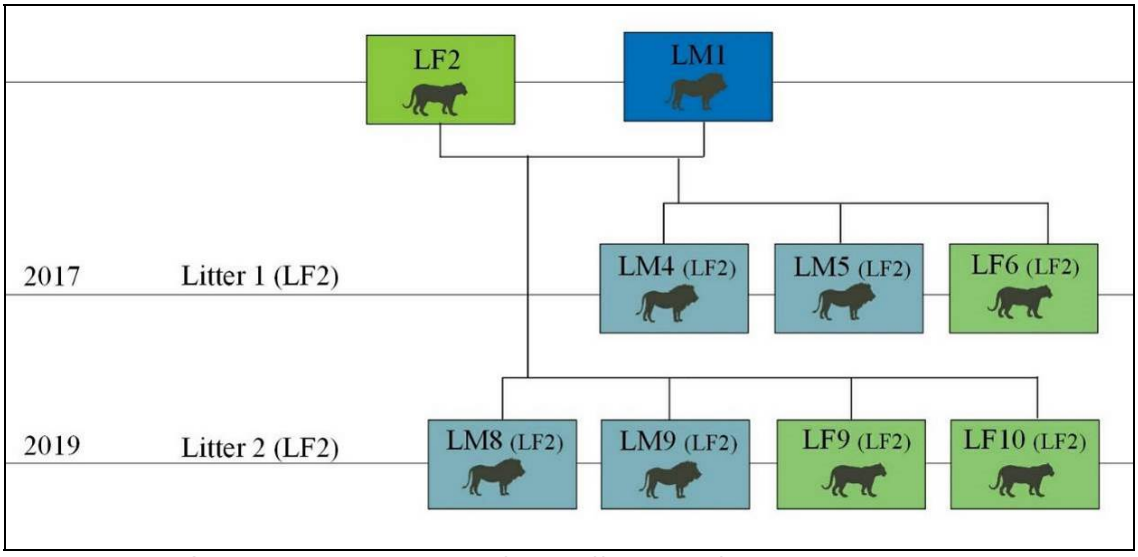


Figure 4.9. Schematic illustration of the offspring of Lioness LF2 during this study (December 2016 to December 2021).

4.4.1 Timeline for Lioness LF2 from December 2016 to April 2019

The chain of events for Lioness LF2 leading to her release in December 2016 in the boma on the Reserve was the same as that described for Lionesses LF1, LF3 and LF4 (see section 4.1) [Timeline 6; event (1)].

Lioness LF2 was kept for six weeks in the boma along with the other four founder lions (Lion LM1 and Lionesses LF1, LF3 and LF4) until they were released in the Reserve on 30 January 2017 [Timeline 6; event (2)].

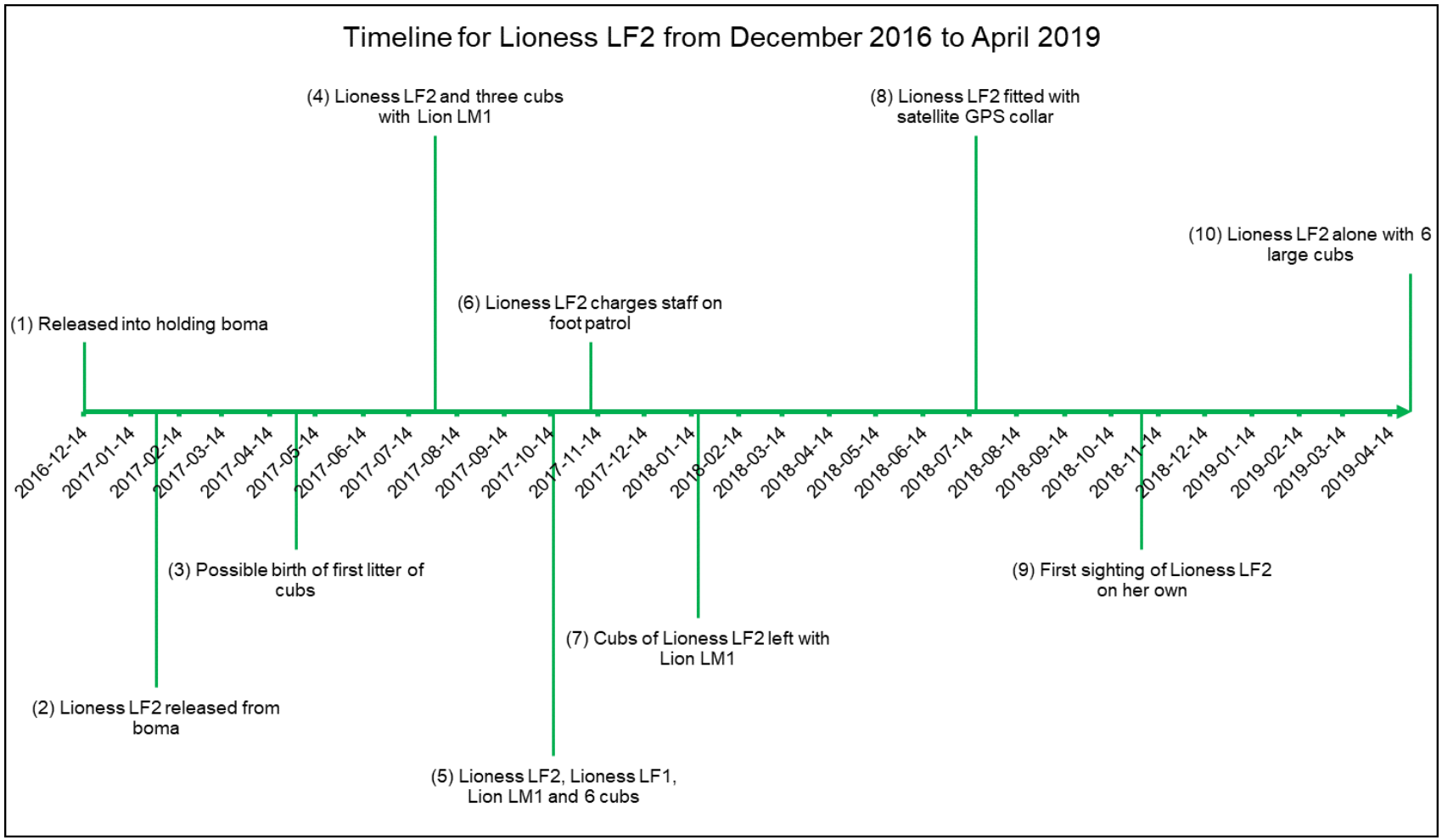
No attempt was made to individually identify Lioness LF2 after being released from the boma, until 18 July 2018 when she was fitted with a satellite GPS collar [Timeline 6; event (8)] (see Chapter 3 for fitting of satellite GPS collars).

Timeline 6; event (4): However, the records kept since the release of the five founder lions in January 2017, made it possible to backdate the first identification of Lioness LF2 at a visual sighting of a possible kill on 31 July 2017. On this occasion, Lioness LF2 and her three cubs as well as Lion LM1 were at the carcass of a young male waterbuck (*K. ellipsiprymnus*).

This was also the first time that Lion LM1 was seen with the cubs of Lioness LF2. The date of birth of the cubs of Lioness LF2 was not known precisely, but Lehmann *et al.* (2008) and Packer & Pusey (1983b) have indicated that lionesses are hiding their cubs for the first 4 to 8 weeks. Considering this behaviour and comparing the size of the cubs of Lioness LF2 with those of Lioness LF1, as well as notes kept by the author, it was calculated that the first litter of Lioness LF2 (namely Lions LM4 and LM5, and Lioness LF6)[10] were born early in May 2017 [Timeline 6; event (3)].

Timeline 6; event (5): On 16 October 2017, Lioness LF2 with her three cubs, Lioness LF1 with her three cubs, and Lion LM1 were seen together for the first time.

[10] Subsequently referred to as Litter 1 (LF2) when referred to in a group.



Timeline 6. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF2 on the Reserve from December 2016 to April 2019.

The nine lions were resting around an abandoned old farm building after feeding on the carcass of a blue wildebeest (*C. taurinus*). Some lions were resting in the shade of the veranda roof of the building. Lioness LF2 made an aggressive charge towards the vehicle. This was the first documented sign of aggression shown by lioness LF2. Thereafter, several incidences were recorded of aggressive behaviour by Lioness LF2 towards people and vehicles. On one occasion, Lioness LF2 charged at a group of security scouts on a foot patrol [Timeline 6; event (6)].

Shortly after this reported incidence, Lion LM1, Lionesses LF1 and LF2 and their six cubs [Litter 1 (LF1) and Litter 1 (LF2)] collectively became known as the main pride on the Reserve.

The cohesion of this group of lions (Lion LM1, Lionesses LF1 and LF2 and their six cubs) lasted for almost two years. On several occasions during this time (specifically October 2017 to August 2019), it was observed that the dynamics of this group of lions deviated from what is to be expected from literature, discussed hereafter in the text.

Timeline 6; event (7): On 18 January 2018, the three cubs of Lioness LF2 [Litter 1 (LF2)] were seen with Lion LM1 along with the three cubs of Lioness LF1 [Litter 1 (LF1)]. The two lionesses were not present. The three cubs in Litter 1 (LF2) were approximately eight months old. It is not uncommon for lionesses to leave their young cubs with the pride when they are out hunting (Funston *et al.,* 2001).

A few days later, 21 January 2018, another founder lioness and her four cubs temporarily joined the group. This unidentified lioness was later designated as Lioness LF4. Later that same year, Lionesses LF1 and LF2 and their six cubs were observed at the kill of a zebra foal (*E. quagga*) without Lion LM1 being present.

It is assumed that the apparent absence of some members in the group could be attributed to (i) dense cover making it difficult to locate and see all the lions; (ii) the time spent by the staff member at the sight to establish the exact number of lions present; and (iii) poor visibility and sightings after dark limiting the observer's chances of seeing all the lions present.

Slide 4.22. Lioness LF2 (with two of her cubs) showing clear signs of aggression. Lioness LF2 often showed signs of aggression towards vehicles and people on the Reserve.

Because of the changing dynamics of the group, Lioness LF2 was also fitted with a satellite GPS collar on 18 July 2018 [Timeline 6; event (8)].

These lions remained together as a group until December 2018 when Lioness LF1 left, leaving Lioness LF2 with the two litters of six large cubs [Litter 1 (LF1) and Litter 1 (LF2)]. According to Smuts *et al.* (1978), the cubs of about 17-18 months old were classified as large cubs. The reports of sightings between November 2018 and July 2019 confirmed the unstable dynamics of the remaining group of lions. Lioness LF2 was seen on her own on several occasions during this time [Timeline 6; event (9)]. This was confirmed by sightings of Lion LM1 with the six large cubs [Litter 1 (LF1) and Litter 1 (LF2)] in the absence of Lioness LF2. In other instances, Lioness LF2 was seen with the six large cubs in the absence of Lion LM1 [Timeline 6; event (10)].

On 12 May 2019, Lioness LF2 was seen the last time with Lion LM1. Soon after this event, there was a total scattering of the main pride (see section 4.2).

4.4.2 Timeline for Lioness LF2 from July 2019 to September 2020

Timeline 7; event (11): By the end of July 2019, Lioness LF2 completely separated from the remainder of the main pride, namely Lion LM1 and the six sub-adult lions of Litter 1 (LF1) and Litter 1 (LF2). The six sub-adult lions were identified respectively as Lions LM2[LF1], LM3[LF1], LM4[LF2], LM5[LF2] and Lionesses LF5[LF1] and LF6[LF2]. The spatial use of the Reserve by Lion LM1 and Lionesses LF1 and LF2 were largely overlapping, even though they were not recorded to have spent time together (Fig. 4.5, section 4.3.2).

Timeline 7; event (12): A reduction in home range size for Lioness LF2 from June 2019 (Fig.4.10) could be explained by the birth of her second litter (Maruping-Mzileni *et al.,* 2019), which was positively confirmed on 13 September 2019. See Figure 4.9 for a graphic illustration of the progeny of Lioness LF2 during this study.

Timeline 7; event (13): By the end of September 2019, Lioness LF2 moved her new cubs approximately 2 km further away to a new den site. It was confirmed that her Litter 2 (LF2) comprised four cubs (two females designated Lionesses LF9 and LF10 and two males designated Lions LM8 and LM9). The den site/s of Litter 1 (LF2) was not located, because at the time (about May 2017) Lioness LF2 had not yet been fitted with a satellite GPS collar. However, the birth of her second litter on the Reserve indicated that Lioness LF2 (apparently like Lioness LF1) also chose the safety of the rocky outcrops on the northern section of the Reserve (Slide 4.23).

For the first 30 days after suspected of giving birth, Lioness LF2 moved her cubs of Litter 2 (LF2) only once and a very short distance of about 100 m. Thereafter, Lioness LF2 moved her cubs southeast to another rocky outcrop about 2 km away. The information logged by the satellite GPS collar, indicated that Lioness LF2 had moved Litter 2 (LF2) only twice during the first eight weeks, thus utilising only three confirmed den sites. The shortest period spent at one den site was about six days, and the longest up to 28 days.

Timeline 7; event (14): On 1 December 2019, Lioness LF2 joined Lioness LF1 at a popular water trough in the centre of the Reserve. All seven their new cubs [Litter 2 (LF2) and Litter 2 (LF1)] were also present. The introduction was peaceful and after a short interaction, the females moved off again in different directions with their cubs.

Slide 4.23. Two of the small cubs from Litter 2 (LF2). Based on the size of the cubs, their age was estimated to be less than four weeks (13 September 2019). Initially only three cubs of Lioness LF2 could be identified at this den site.

Timeline 7; event (15): On 4 December 2019, both lionesses LF1 and LF2 and their seven cubs [Litter 2 (LF1) and Litter 2 (LF2)] were seen at the carcass of an adult male waterbuck (*K. ellipsiprymnus*). Although it seemed to be a joint hunt by Lionesses LF1 and LF2, the Lioness LF2 was clearly dominant at the carcass. Attempts by the older cubs of Lioness LF1 (approximately 6 months older than the cubs of Lioness LF2) to approach the carcass were met with aggression from Lioness LF2. Lioness LF1 showed little interest in the carcass and rested about 5 m away.

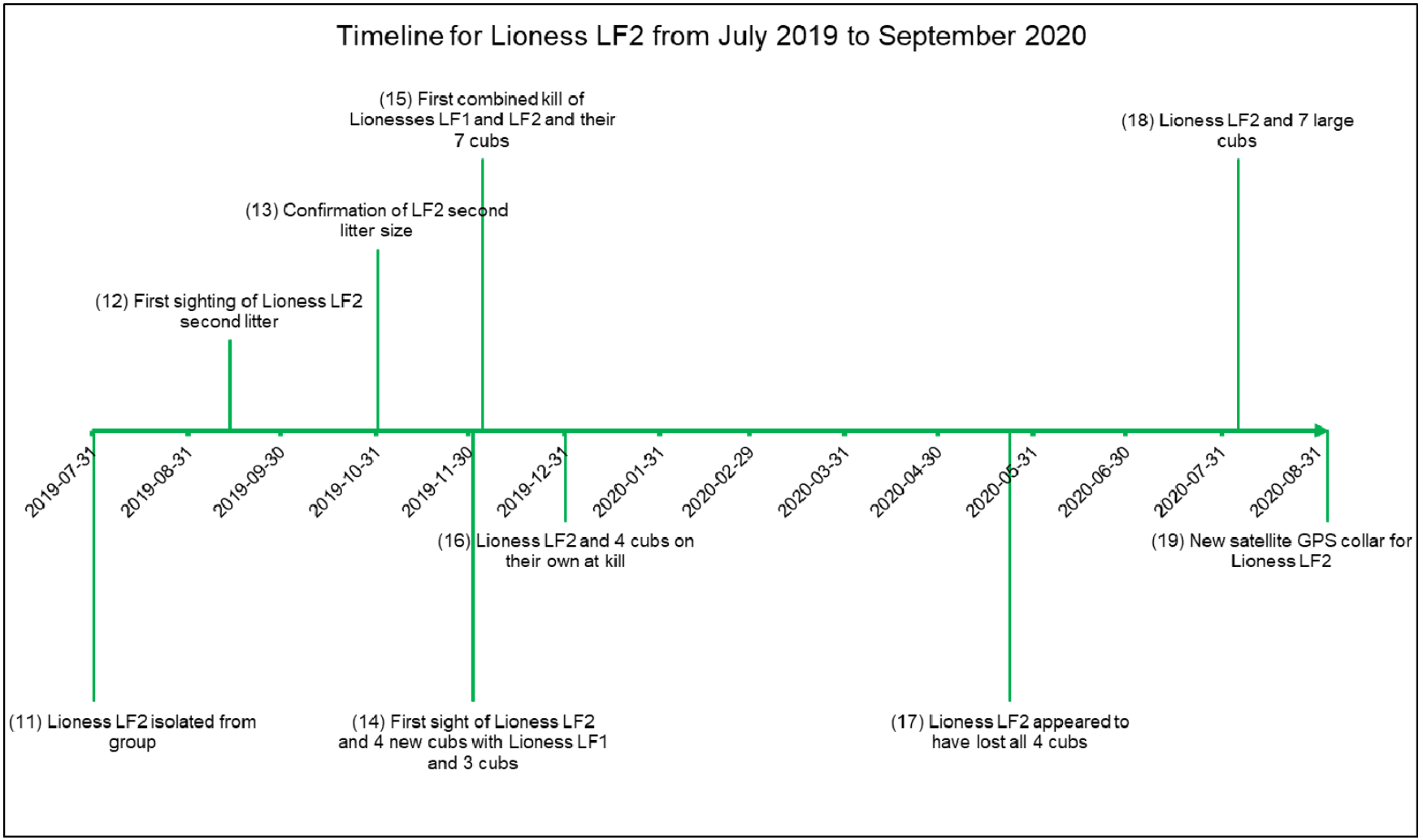
The vehicle was stopped approximately 15 m from the carcass and the engine switched off. Lioness LF2 showed clear signs of unease toward the author's presence by pulling her upper lip to expose the canines. This action was accompanied with loud growling. After several warnings from Lioness LF2, she

charged the vehicle and came to a halt approximately 5 m from the closed window. She immediately returned to the carcass where her cubs were still playing. Lioness LF2 repeated this show of aggression twice before the author increased the distance to approximately 30 m and she did not charge at the vehicle again.

Timeline 7; event (16): Shortly afterwards, Lioness LF2 and Litter 2 (LF2) were seen on their own at a kill of a blue wildebeest (*C. taurinus*). During this study, Lioness LF2 joined on several occasions with Lioness LF1 and Litter 2 (LF1), only to separate again after a short period of time (see section 4.3).

Timeline 7; event (17): On 23 May 2020, Lioness LF2 was found alone. No signs of Litter 2 (LF2) were found nearby and Lioness LF2 was making soft sounds, while running up and down the same road. Tracks in the road indicated that Lioness LF2 had been there for an extended period. After following Lioness LF2 for most of the morning the conclusion was made that she was looking for her cubs. The satellite GPS collar fitted to Lion LM5 also indicated the presence of the four sub-adult male lions (Lions LM2, LM3, LM4 and LM5) in the same general area as Lioness LF2 and her four cubs the previous night (22 May 2020). After she had left the area, a thorough inspection of the tracks indicated that an altercation had occurred between Lioness LF2 and the four sub-adult male lions. Apparently, Lioness LF2 and her cubs separated during her altercation with the four sub-adult male lions.

The next day (24 May 2020), Lioness LF2 was recorded feeding on the carcass of a warthog (*P. africanus*) accompanied by only two of the cubs of Litter 2 (LF2). Three days later, 27 May 2020 it was confirmed that Lioness LF2 had reunited with all four her cubs of Litter 2 (LF2). Lioness LF2's satellite GPS collar showed that while searching for the cubs, she had repeatedly returned to the site where the altercation had taken place.



Timeline 7. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF2 on the Reserve from July 2019 September 2020.

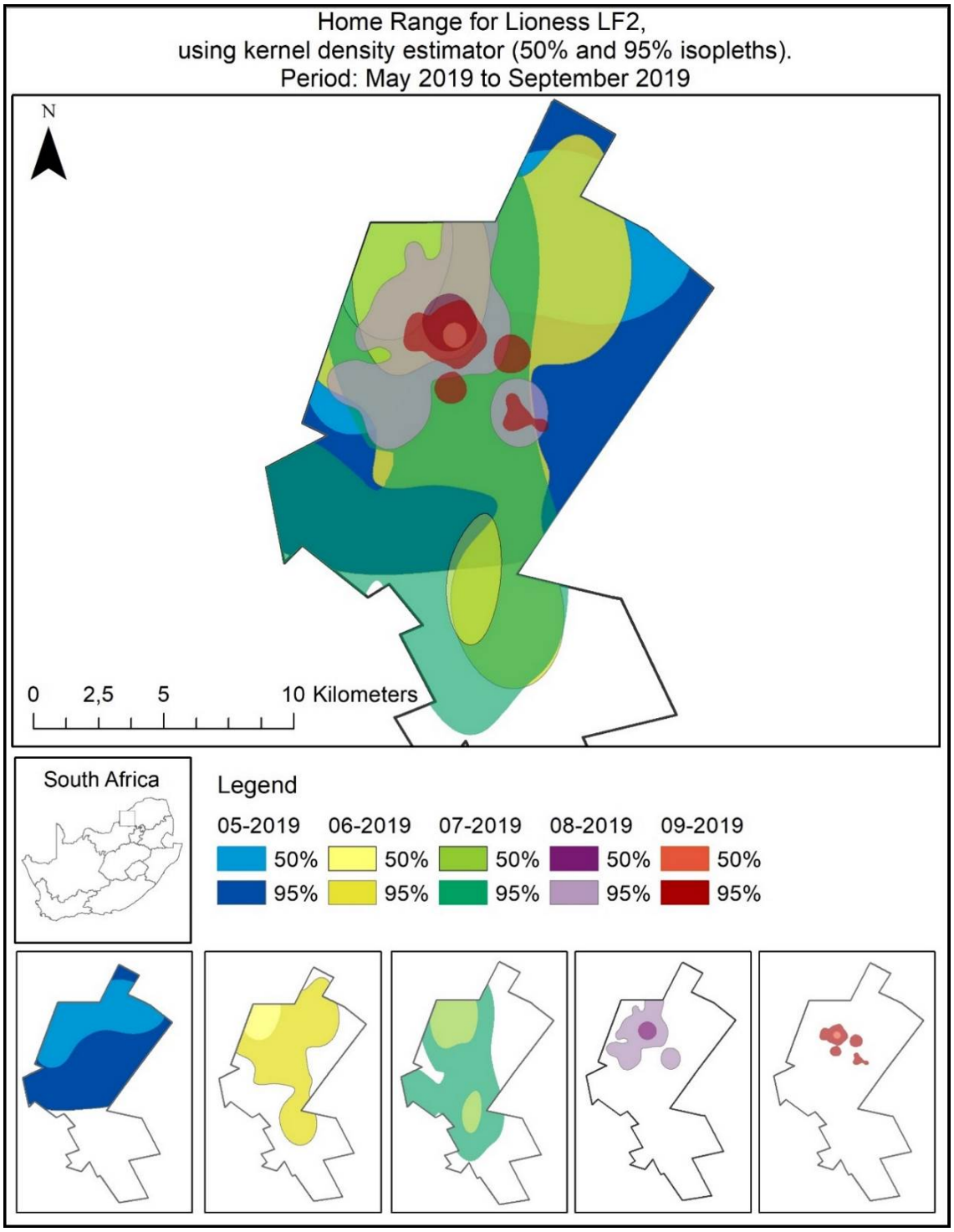


Figure 4.10. Comparison of home range size over time for Lioness LF2 using kernels density estimator 50% and 95% isopleths. A gradual reduction in spatial utilisation from May 2019 to September 2019 is clearly illustrated.

The four sub-adult male lions (Lions LM2, LM3, LM4 and LM5)[11] formed a coalition and adopted a nomadic lifestyle on the Reserve. Except for Lioness LF2, several lionesses were occasionally recorded as being present with one or more of the sub-adult males.

Timeline 7; event (18): On several occasions during the study, the three cubs from Litter 2 (LF1) were seen in a group with Lioness LF2 and her four cubs Litter 2 (LF2)] but without Lioness LF1. The three large cubs of Litter 2 (LF1) were approximately 18 months old at the first documented occurrence on 5 August 2020.

Timeline 7; event (19): On 3 September 2020, the satellite GPS collar of Lioness LF2 was replaced once again. The nine lions (Lionesses LF2 and LF1 and Litter 2 from both Lionesses) were all present when Lioness LF2 was sedated. While the satellite GPS collar was replaced, staff members noisily chased the other lions to keep them at bay. Lioness LF2 was regularly recorded to have all seven cubs (Lions LM7[LF1], LM8[LF2] and LM9[LF2] and Lioness L7[LF1], LF8[LF1], LF9LF2] and LF10[LF2]) in her presence, because Lioness LF1 started spending time with Lion LM6 (see section 4.3).

Slide 4.24. Lioness LF2 and the cubs of Litter 2 (LF2) and Litter 2 (LF1) at a giraffe (*G. camelopardalis*) killed by the group on 9 November 2020. One larger female cub of Litter 2 (LF1) is not shown in the photograph and Lioness LF1 was not present at the carcass.

[11] The sub-adult males were from Litter 1 (LF1) and Litter 1 (LF2).

4.4.3 Timeline for Lioness LF2 from January 2021 to June 2021

Timeline 8; event (20): On 18 January 2021 Lionesses LF7 and LF8 had separated from the group of nine lions, whilst Lion LM7 [also a large cub from Litter 2 (LF1)] remained with the group. Lionesses LF7 and LF8 were only approximately 24 months old at the time. The next month these two large female cubs engaged regularly with the resident adult male Lion LM6.

A single mating incident was recorded between Lion LM6 and Lioness LF8 on 17 February 2021. The mating was successful because Lioness LF8 gave birth to her first litter of cubs in June 2021 [Litter 1 (LF8)].

The cubs of Lioness LF8 [Litter 1 (LF8)] was a F2-generation of wild born cubs, because she was born in Litter 2 (LF1) and sired by Lion LM1 (see section 4.3.2).

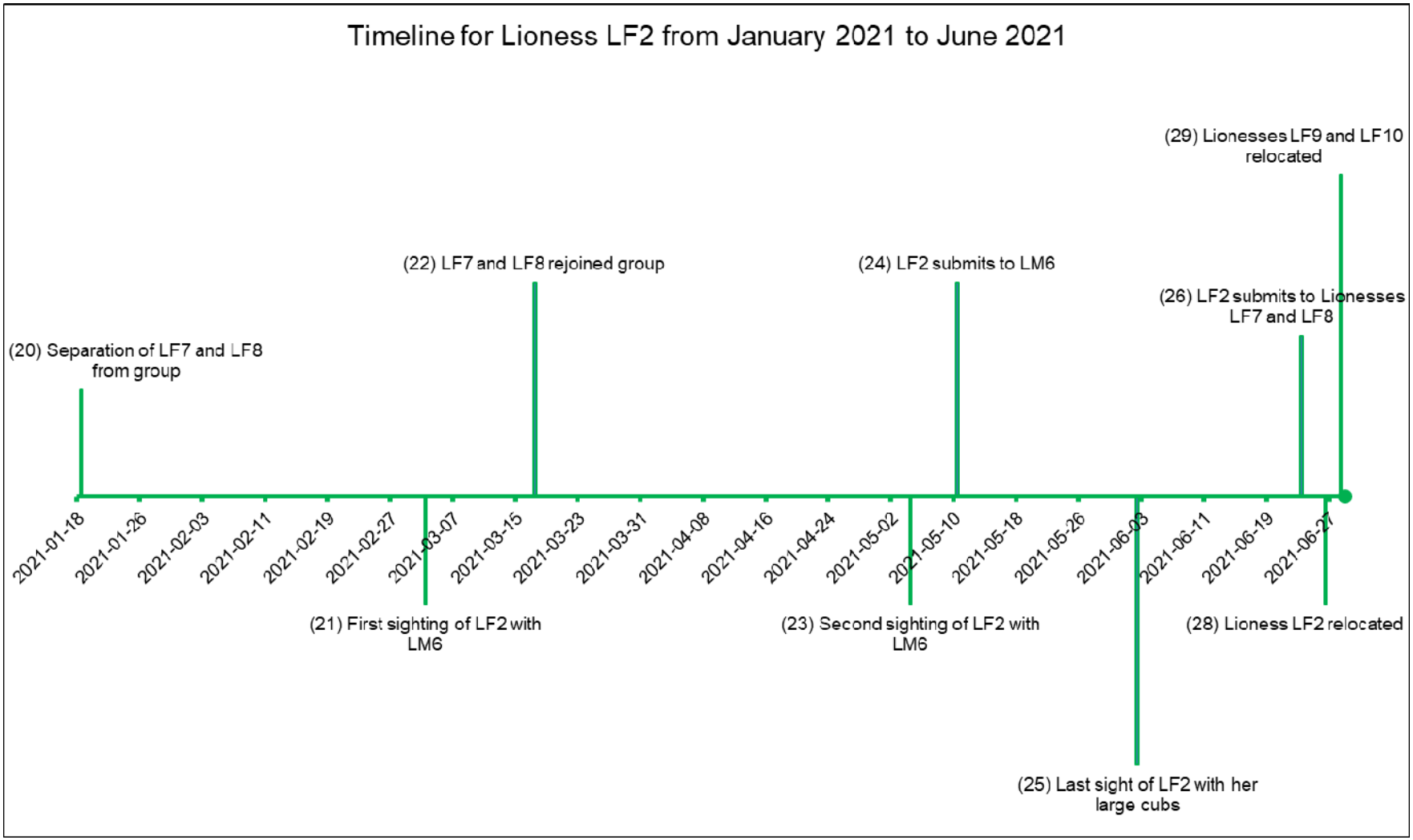
The actual number of cubs born could not be confirmed, but four cubs of Lioness LF8 were photographed for the first time on 11 August 2021 when they were approximately six weeks old (Slide 4.25). By the end of 2021, Lioness LF7 had not yet given birth to any cubs. Even though courting behaviour between Lioness LF7 and Lion LM6 was recorded on several occasions, copulation could never be confirmed.

Timeline 8; event (21): A physical altercation between Lion LM6 and Lioness LF2 was recorded on 3 March 2021. This was the first time the two lions were seen together, which was later confirmed by the data from the satellite GPS collar. Both Lion LM6 and Lioness LF2 were injured during the fight with cuts to the faces and abdominal areas. Lioness LF2 retreated by walking away from Lion LM6 whilst he vocalised loudly in her direction. After Lioness LF2 had disappeared into the thicket, Lion LM6 was seen laying down next to Lionesses LF7 and LF8, close to where the altercation had taken place. The large cubs of Litter 2 (LF2) and Lion LM7 were not present.

Slide 4.25. Lioness LF8 (standing in front with blue satellite GPS collar) and her four cubs shortly after they were born. Lioness LF7 (orange satellite GPS collar) is sitting at the back.

Lioness LF2 was seen on her own until 13 March 2021 when she was joined again by her four large cubs. On 17 March 2021, Lionesses LF7 and LF8 were seen with Lioness LF2 and her four large cubs [Timeline 8: event (22)], before Lioness LF2 left the group for the final time the next day. The large cubs of Litter 2 (LF2) were approximately 18-19 months old at the time.

Lioness LF2 was seen with Lion LM6 again on 4 May 2021 [Timeline 8; event (23)]. It was later confirmed by the data from the satellite GPS collars that the two lions had not been together since their interaction on 3 March 2021. Lioness LF2, the four large cubs of Litter 2 (LF2) and Lion LM7 were seen on a road of the Reserve. Lion LM6 was approximately 300 m away when the author arrived. Lion LM6 was jogging towards Lioness LF2 whilst vocalising in her direction. Lioness LF2 retreated in the direction of her four large cubs and Lion LM7, who had also adopted a faster pace than before. It was clear that Lion LM6 was in pursuit of them.



Timeline 8. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF2 on the Reserve from January 2021 to June 2021.

When considering the inter-birth intervals of African lions (Lehmann *et al.,* 2008), it is reasonable to believe that Lioness LF2 was ready to conceive again and that Lion LM6 was seeking to engage in courting behaviour with her. Lion LM6 frequently stopped and scent-marked brushes. Later that morning the four large cubs of Litter 2 (LF2) and Lion LM7 were spotted at a waterhole approximately 3 km from where the interaction had taken place. Lioness LF2 was not present. Later that same day (at 17h38), Lioness LF2 was seen on her own, not far from where the interaction took place the same morning.

Five days later (10 May 2021), Lioness LF2 was seen reacting submissively to Lion LM6 [Timeline 8; event (24)]. The interaction took place at the carcass of a blue wildebeest (*C. taurinus*) which Lioness LF1 had presumably caught. She and her two small cubs [Litter 3 (LF1)] were resting next to the carcass when the author arrived. Lioness LF1 took cover in the thickets with her two small cubs, whereafter Lion LM6 approached the carcass from approximately 400 m away. Lioness LF2, who had been laying 30 m from the carcass moved towards Lion LM6 and submissively laid down on her back in front of him. Lion LM6 softly vocalised at Lioness LF2 and then continued towards the blue wildebeest (*C. taurinus*) carcass. He then carried the entire carcass approximately 250 m to the thick brush (Slide 4.26). Lioness LF2 followed and laid down next to the carcass with Lion LM6. No aggression was observed from either lion.

Timeline 8; event (25): On 2 June 2021, Lioness LF2 reunited with her Litter 2 (LF2) and Lion LM7. Lioness LF2 was seen with Lion LM6 again on 23 June 2021 [Timeline 8; event 26)]. On this occasion it appeared that lioness LF2 and Lion LM6 was feeding on the carcass of a gemsbuck (*O. gazella*), which they had presumably caught. Shortly after the kill had been made, Lionesses LF7 and LF8 arrived and aggressively took control of the carcass from Lioness LF2. Whilst Lioness LF8 was feeding on the carcass, Lioness LF7 kept Lioness LF2 away with loud vocalisations and aggressive body language. Lioness LF2 remained within 40 m of the carcass. After feeding for approximately 20 min, Lioness LF8 joined Lioness LF2 and LF7 where they rested together without any further aggressive behaviour. Both Lioness LF2 and Lioness LF8 were visibly pregnant (enlarged abdominal areas and swollen nipples).

Slide 4.26. Lion LM6 carrying the blue wildebeest (*C. taurinus*) carcass, which Lioness LF1 and her two small cubs had abandoned, towards the thickets.

Timeline 8; event (27): On the evening of 23 June 2021, Lions LM7[LF1], LM8[LF2] and LM9[LF2] were lured to the carcass of a blue wildebeest (*C. taurinus*), sedated by the Veterinarian and then relocated from the Reserve.

Timeline 8; event (28): On 26 June 2021, Lioness LF2 was sedated and relocated. During sedation, her satellite GPS collar was removed and transferred to Lioness LF8 who was also sedated later that same day. Two days later (28 June 2021) the two large cub lionesses of Litter 2 (LF2) (Lionesses LF9 and LF10) were also sedated by the Veterinarian and removed from the Reserve [Timeline 8; event (29)]. Body dimensions of Lionesses LF2, LF9 and LF10 were not recorded. Lioness LF2 had been separated from the two large female cubs since 2 June 2021. Approximately one month after being removed from the Reserve, Lioness LF2 gave birth to four cubs. This was her first litter sired by Lion LM6.

During this study, Lioness LF2 was recorded to be present at 39 kills, which comprised 12 species and included blue wildebeest (*C. taurinus*) (31 %, n = 12), waterbuck (*K. ellipsiprymnus*) (15%, n = 6) and eland (*T. oryx*) (17%, n = 5), and in smaller numbers kudu (*T. strepsiceros*) (n = 2), giraffe (*G. camelopardalis*) (n = 2),

tsessebe (*D. lunatus*) (n = 1), impala (*A. melampus*) (n = 1), gemsbuck (*O. gazella*) (n = 1), and Red hartebeest (*A. buselaphus*) (n = 1). Other species utilised by Lioness LF2 are zebra (*E. quagga*) and warthog (*P. africanus*).

Lioness LF2, her four cubs [Litter 2 (LF2) and the three cubs of Lioness LF1 [Litter 2 (LF1)] were once seen scavenging on the remains of a female impala (*A. melampus*) which was shot the previous day because of serious injuries. The next morning (20 August 2020) some limbs of the impala were found in a tree, presumably dragged into the tree by a leopard (*P. pardus*). The eight lions were found feeding on the remains of the carcass under the tree. Lioness LF2 only allowed one of the younger lionesses to feed with her, whilst reacting aggressively towards any other cubs that approached.

4.5 Timeline of important events for Lioness LF3 on the Reserve

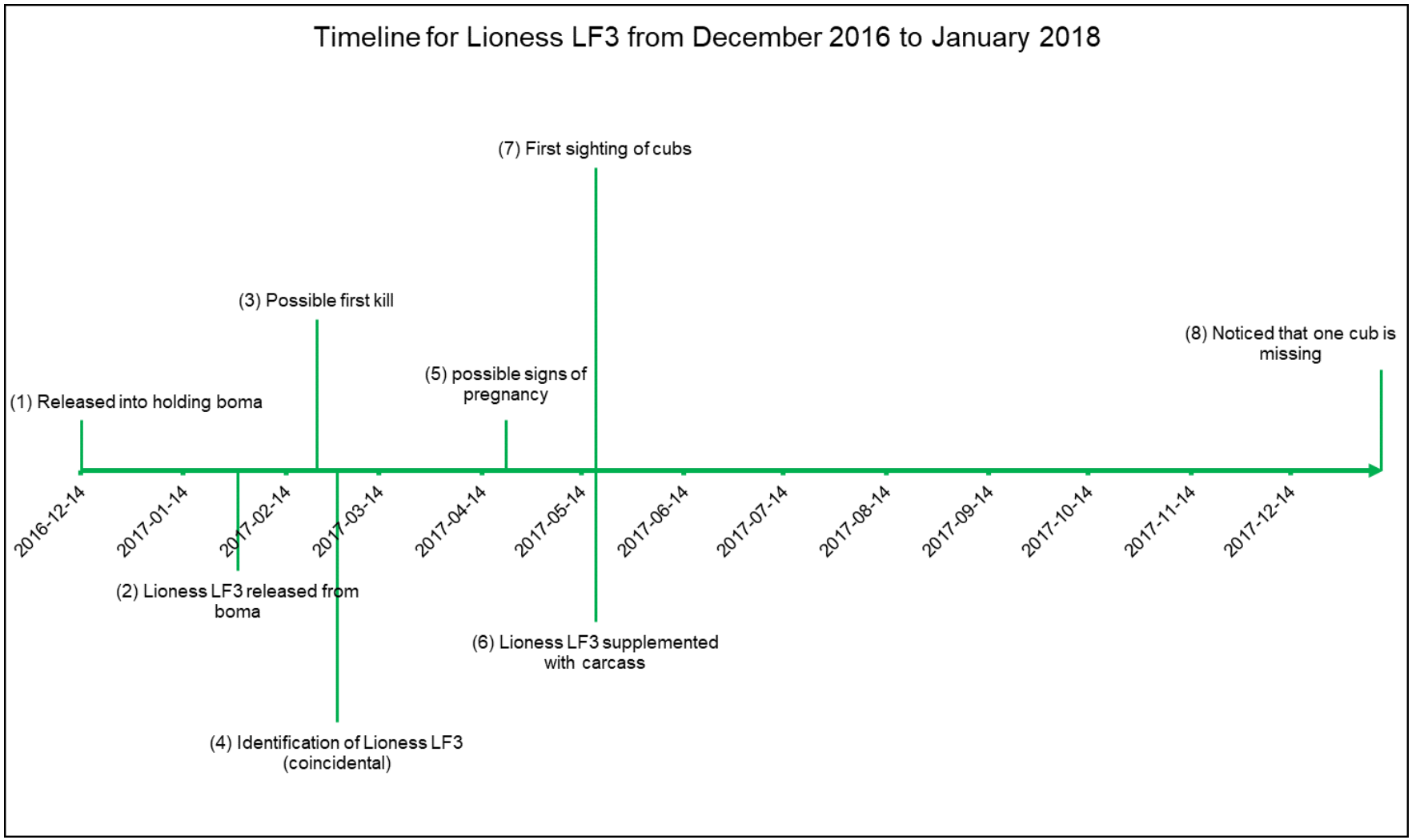
4.5.1 Timeline for Lioness LF3 from December 2016 to January 2018

The events for Lioness LF3 leading up to her release on 30 January 2017 from the boma on the Reserve [Timeline 9; event (1)], were similar to that of the other three founder lionesses (Lionesses LF1, LF2 and LF4). The four lionesses and Lion LM1 were released on the Reserve when the gates of the boma were opened on 30 January 2017 [Timeline 9; event (2)]. The first six weeks post release, the five lions were often seen at a water trough about 300 m from the boma.

Initially, Lioness LF3 was not individually marked or identified. It was observed that a lioness left the group on several occasions during the first couple of weeks. This lioness was the first to be observed hunting and on 23 February 2017 a male kudu (*T. strepsiceros*) [Timeline 9; event (3)] was killed. By referring to the notes kept at that time, it was concluded to have been Lioness LF3.

Timeline 9; event (4): By 1 March 2017, a lone lioness was recorded with Lion LM1 at another kudu (*T. strepsiceros*) kill at the water trough close to the boma. The lioness had visible scratch marks on her left shoulder. The scars remained visible long enough to identify the lioness later in the study. The lioness became known as “scar shoulder” because at that time it was not attempted to distinguish between the unmarked lionesses. The method described by Pennycuick & Rudnai (1970) to identify lions by the spot patterns of the vibrissae was only incorporated in the study during 2019.

On a separate occasion, Lioness LF3 sustained injuries to her left abdominal area, which also left visible marks (Slide 4.27) and allowed easy identification. Using the photographs taken during the study, it was also noticed that Lioness LF3 (at that time she had already been uniquely identified with a number) had unique colour patterns in her left eye (Slide 4.28).



Timeline 9. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF3 on the Reserve from December 2016 to January 2018.

Slide 4.27. Lioness LF3 and three cubs on 20 May 2017. Note the scars on the ventral part of the body, the abdomen, and the thorax. The causes of the injuries were unknown.

Timeline 9; event (5): On 21 April 2017, Lioness LF3 was seen with Lion LM1 and Lioness LF1 (identifiable by the colour coded satellite GPS collar around her neck). All three lions visibly had lost body condition since being released from the boma. The nipples of Lioness LF3 were also noticeably swollen and she was believed to be lactating.

Timeline 9; event (6): On 16 May 2017, it was noted that the body condition of Lioness LF3 had further deteriorated: she had lost more weight, her hair appeared curly and her movements were slow and stiff. It was decided to provide Lioness LF3 with two impala (*A. melampus*) carcasses as it was believed that she had given birth to cubs. Consumption of the carcasses was slow.

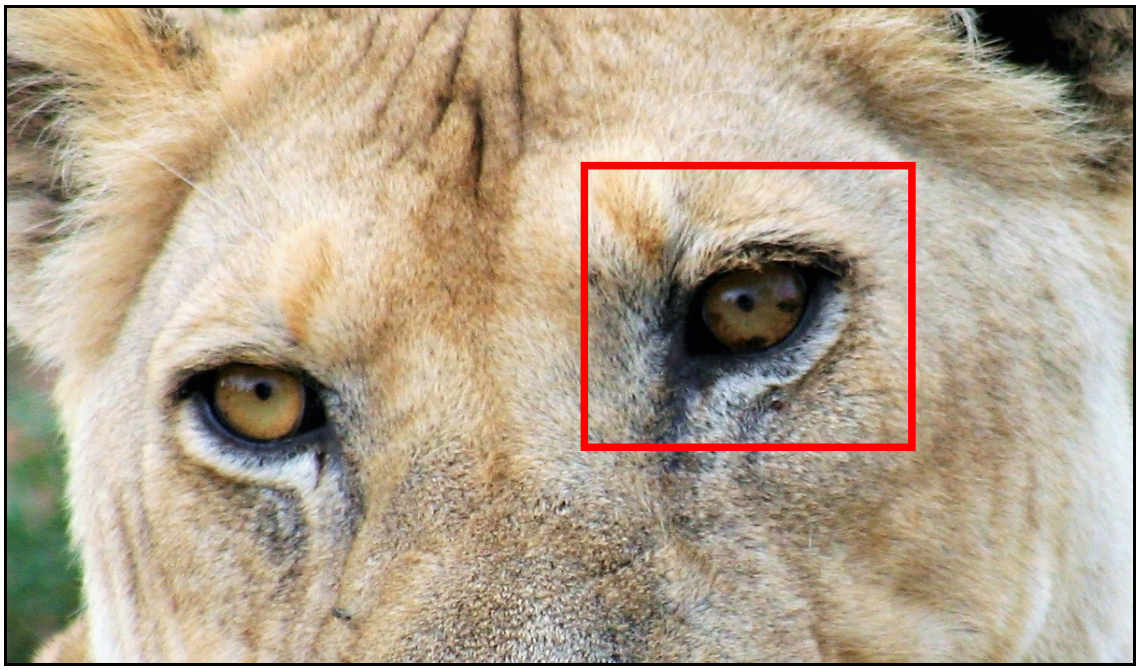
[Timeline 9; event (7): The next morning the presence of her cubs was confirmed [Litter 1 (LF3)].

One of the cubs fell into an unfenced water reservoir and could not get out. A senior staff member of the Reserve arrived while the cub was still alive and removed it from the water. Upon placing the cub on the ground, Lioness LF3 came to collect her cub.

The cub was recovered and was observed with its mother and two other siblings several times thereafter.

At the time of the first sighting, the cubs were believed to be approximately four weeks old. A possible birth date of late April 2017 was assumed for the cubs of Lioness LF3 for the purpose of this study.

All the den sites used by Lioness LF3 were not detected. However, one site that Lioness LF3 used to hide her cubs was a small brick building, which covered a bore hole. The building was approximately 1.5 by 2 m and two sides were partially open. A roof covered the entire building. Lioness LF3 was seen with her cubs both inside and outside the building on several occasions.



Slide 4.28. Lioness LF3 showing the unique eye colouration in the left eye. Even though this photograph was taken on 15 February 2019, it could be used to identify Lioness LF3 in scenes photographed as early as May 2017, as the eye colouration had already occurred.

Keeping track of Lioness LF3 became extremely difficult as her spatial utilisation of the property increased over time (Fig. 4.11) and she remained without a satellite GPS collar for her entire stay on the Reserve. Records of sightings of Lioness LF3 were recorded when possible and on 10 January 2018, Lioness LF3 was seen with

only two of the three cubs [Timeline 9; event (8)]. The missing cub was never found and Lioness LF3 remained with the two cubs. The disappearance of the cub was never solved. Packer & Pusey (1983a) reported that the survival rate of lion cubs to the age of one year was less than 50%. In a study of 11 lion prides at Mana Pools National Park, Zimbabwe, Monks (2008) reported an average cub survival rate of 66%.

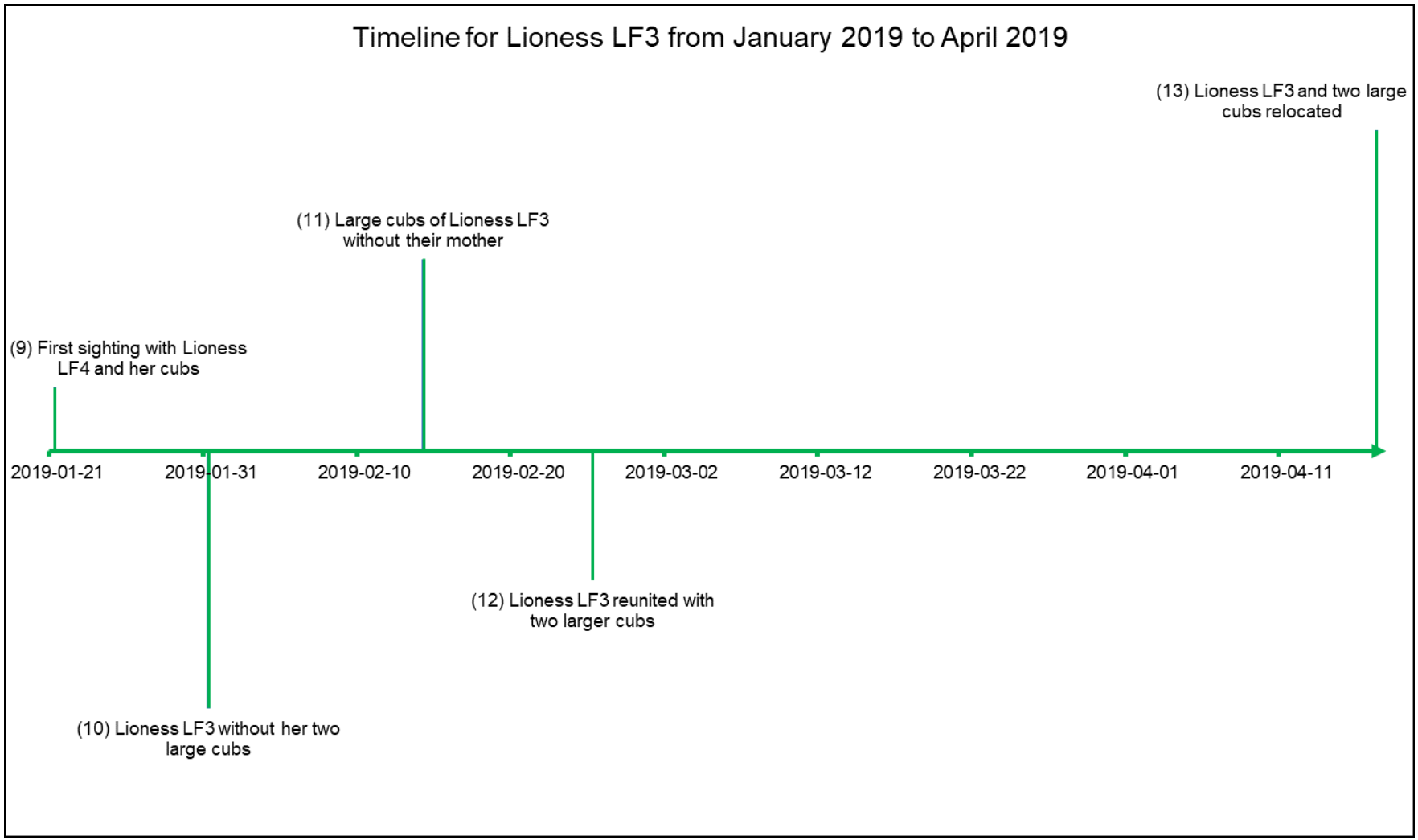
Lioness LF3 remained largely out of sight and with no tracking device, her spatial and temporal utilisation could not be accurately determined.

4.5.2 Timeline for Lioness LF3 from January 2019 to April 2019

Timeline 10; event (9): On 21 January 2019, Lioness LF3 and her two remaining cubs were observed in the presence of Lioness LF4 and her four cubs. A staff member of the Reserve spotted the lions first and reported that a minor scuffle took place between Lionesses LF3 and LF4, after which the two groups rested approximately 30 m apart.

Lionesses LF3 and her remaining two cubs of her Litter 1 (LF3) and Lioness LF4 and her four cubs were recorded together on several occasions. This grouping was not permanent, and the two lionesses and their respective cubs were also recorded to be on their own for several days at a time. Monks (2008) described similar behaviour in lion prides, where the members of a pride would split up only to re-join later. Monks (2008) did not state the duration of the split and the occasional grouping behaviour by Lioness LF3 with Lioness LF4 remains pure speculation.

The Lionesses LF1 and LF2 were recorded to behave in a similar manner during this study (see sections 4.3 and 4.4). Lioness LF3 did not interact with Lioness LF1 or Lioness LF2 after giving birth to her cubs in April 2017. Dunston *et al.* (2016) and Killian (2003) both described incidences where females and their cubs did not form part of groups of prides and remained solitary.



Timeline 10. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF3 on the Reserve from January 2019 to April 2019.

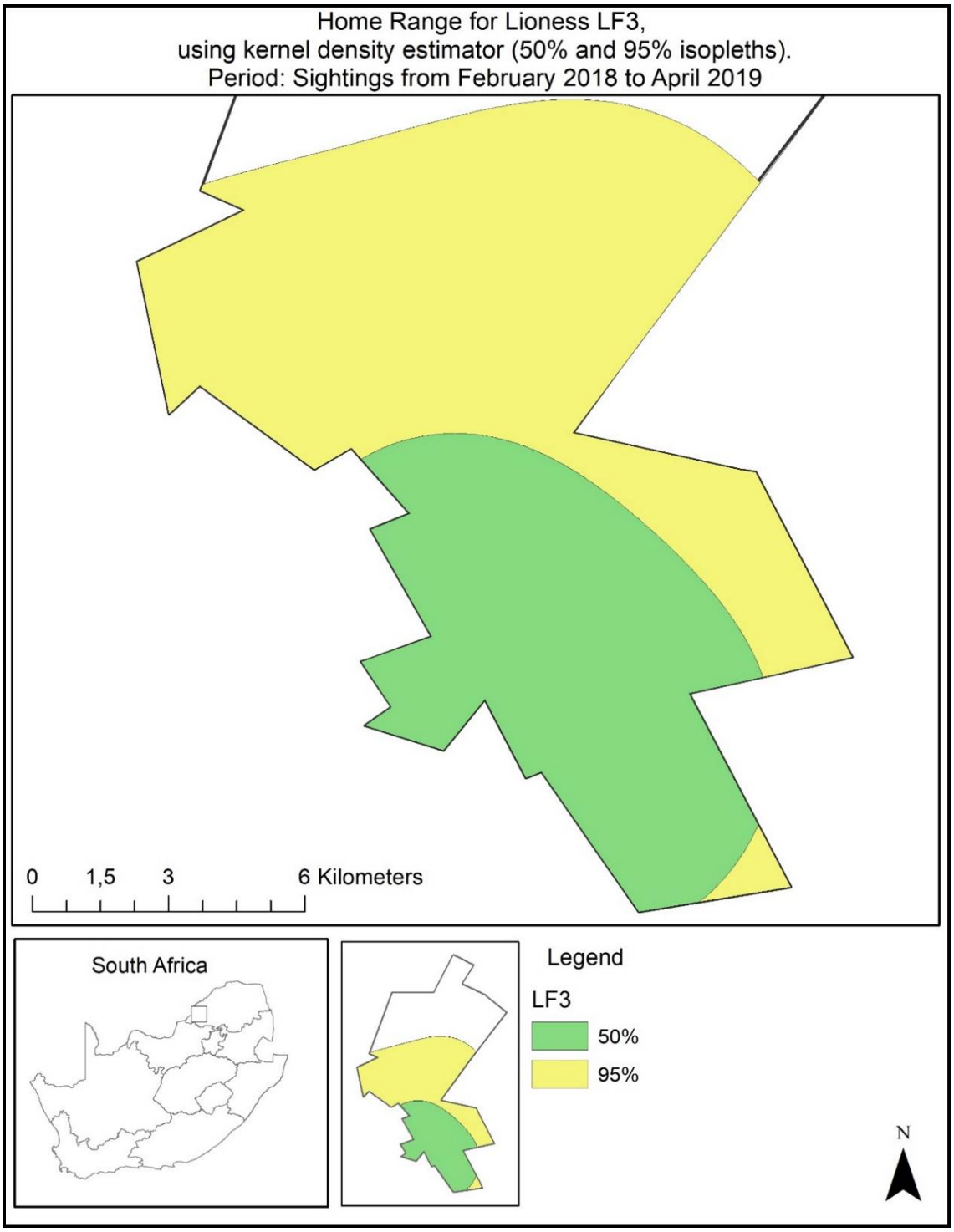


Figure 4.11. Home range of Lioness LF3 for the period February 2018 to April 2019 using kernel density estimator (50% and 95% isopleths). The data in the map was gathered at visual sightings of Lioness LF3, as she was not fitted with a GPS satellite collar. Lioness LF3 was spending time most often in the south-western part of the Reserve.

Timeline 10; event (10): On 31 January 2019, Lioness LF3 was observed without her two large cubs. As alluded to previously, the accuracy of the report could have been influenced by the following factors: (i) the dense cover of the bush could have concealed the large cubs if they were present, (ii) the willingness of the observer to remain at the sight for an extended period to ensure the quantity of lions in the area; (iii) Lioness LF3 could have left her large cubs behind to go hunting without them as that would increase her probability of success (Funston *et al.,* 2001). Lehmann *et al.* (2008) found that lions spent an increasing amount of time on their own from the age of 10–18 months and even started hunting themselves.

Slide 4.29. The large male cub (left) and female cub (right in the tree) of Litter 1 (LF3) in March 2019, shortly before these large cubs and their mother were relocated from the Reserve.

The cubs of Lioness LF3 were approximately 22 months old at the time. Dispersal from prides by sub-adult lions usually occur at the age of about 30 months (Funston, 2001; Schaller, 1972) and mostly include only males (Pusey & Packer, 1986). Monks (2008) found social pressure to be the deciding influence for male dispersal, while Funston (2003) argued that habitat type might be the strongest deciding factor. Although dispersal generally includes only young males, females do temporarily leave their natal prides to form smaller sub-groups (Monks, 2008). The large cubs of Lioness LF3 were a male and a female, too young to leave their mother's group and with no known social pressures observed, dispersal would seem unlikely.

However, it is possible that Lioness LF3 came into oestrous and was looking for an adult male lion to mate (Miller & Funston, 2014). Actual courtship was unlikely, as the only resident adult male lion was still in the presence of Lioness LF2 and the six large cubs of the main pride (see section 4.2).

Fourteen days later (14 February 2019), the large cubs of Lioness LF3 were observed without their mother [Timeline 10, event (11)]. Three days later Lioness LF3 was seen reunited with her cubs [Timeline 10, event: (12)]. This process repeated itself from 18 to 25 February 2019.

Timeline 10; event (13): On 17 April 2019, Lioness LF3 and her two large cubs were sedated together and all three relocated to another reserve.

While on the Reserve, Lioness LF3 raised only the two cubs (a male and a female). Neither of the cubs were assigned an individual identification before being removed from the Reserve. The two cubs were sired by Lion LM1.

4.6 Timeline of important events for Lioness LF4 on the Reserve

4.6.1 Timeline for Lioness LF4 from December 2016 to January 2018

Lioness LF4 was one of four founder lionesses in the project and subjected to the same treatment as Lionesses LF1, LF2 and LF3 until they were released in the boma on the Reserve [Timeline 11; event (1)]. After six weeks in the boma, Lioness LF4 was released on 30 January 2017 in the Reserve with the other three females and the male Lion LM1 [Timeline 11; event (2)][12].

Lioness LF4 was not identified by any markings, therefore it was difficult to individually identify her in the group of lions. However, a medical issue with the left eye, and which was treated while she was in the boma, remained visible long enough post-release for the author to be able to identify Lioness LF4 from photographs (Slide 4.30) taken much later during the study.

Unfortunately, very few scientifically based notes of Lioness LF4 were recorded while she was on the Reserve. However, occasional sightings were recorded, and are explained in chronological order below.

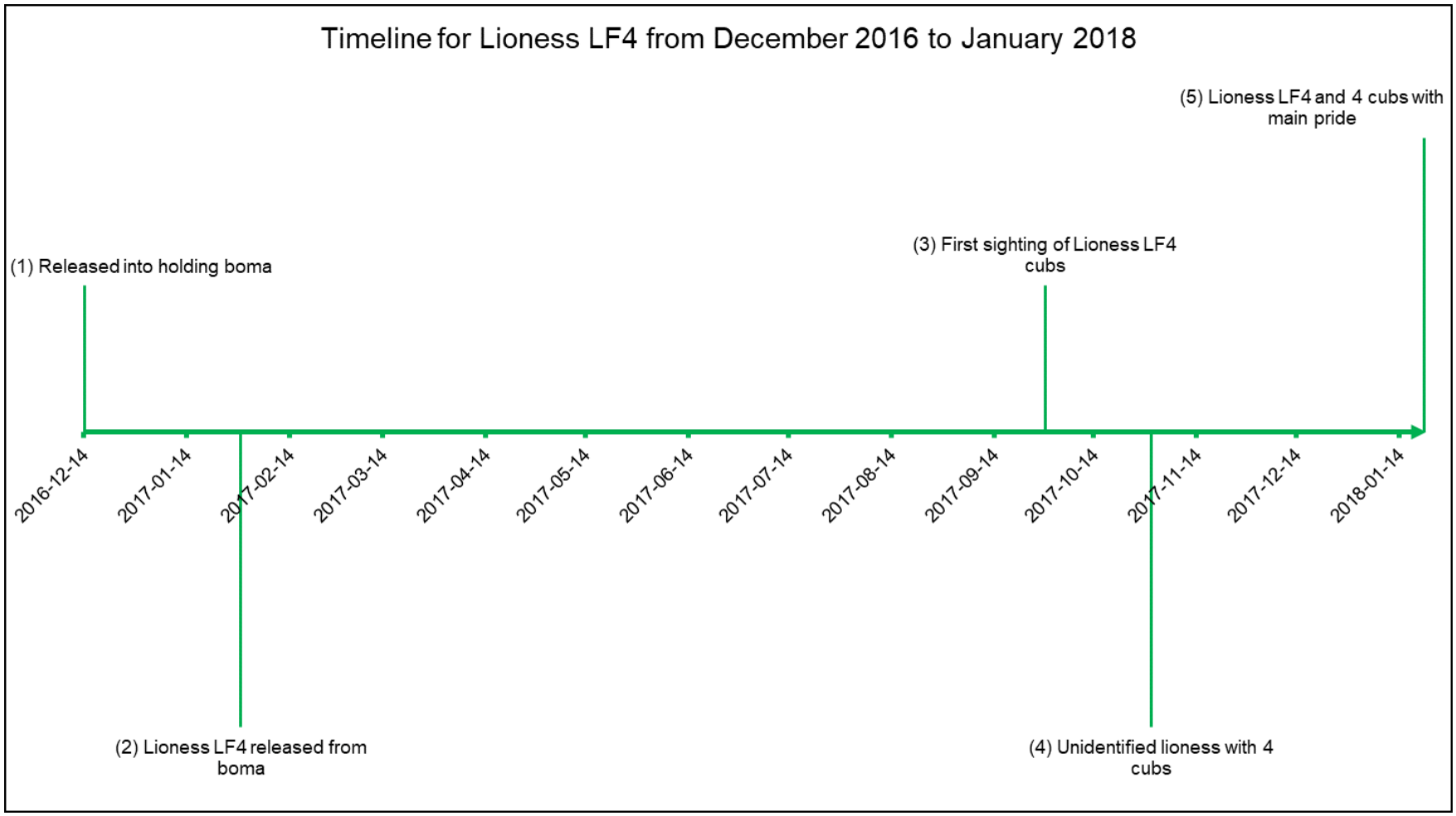
Timeline 11; event (3): On 29 September 2017, a manager reported a sighting of a female with five cubs. This sighting was questioned because it was the only sighting of a lioness with five cubs during that period. However, many factors could have influenced the soundness of the sighting. It is also possible that Lioness LF4 could have given birth to five cubs (Miller & Funston, 2014) and one of the cubs could have died without being noticed. The survival of African lion cubs (up to the age of one year) may be as low as 50% (Packer & Pusey, 1983a) in open systems compared to as high as 86.9% in small managed reserves (Miller & Funston, 2014).

[12] See section 4.1 for a description of the life of Lioness LF4 leading to her release from the boma.

Slide 4.30. Lioness LF4, a large female cub photographed whilst still in the boma in December 2016. The female had an obvious irregularity in her left eye and could be identified on photographs and notes taken while she was on the Reserve.

Timeline 11; event (4): Only four cubs were later seen with Lioness LF4 [Litter 1 (LF4)] and the original observation that five cubs were born in 2017 could not be confirmed. The date of birth of the cubs of Lioness LF4 could not be determined exactly because detailed notes were not yet kept and Lioness LF4 was not fitted with a satellite GPS collar and physically not easily identifiable. However, the size of her cubs compared to those of two other founder lionesses (Lionesses LF1 and LF3)[13], suggested that Lioness LF4 must have given birth to her cubs between April and July 2017.

[13] See **Appendix I**, Table 2 and Table 3 for comparative data.



Timeline 11. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF4 on the Reserve from December 2016 to January 2018.

Usually, lionesses in the same group exhibit synchronised oestrous, specifically after a male take-over and (usually subsequent) infanticide when the cubs of the females are all killed (Packer & Pusey, 1983a). Synchronised oestrous would also be advantageous for the survival of the cubs of a pride of lionesses (Pusey & Packer, 1994). It was assumed that infanticide was not the influencing factor inducing synchronised births, therefore it is more likely that the oestrus cycle of females was synchronised by age and reproductive development (see section 4.1). It could also be argued that the synchrony of oestrous was a result of the simultaneous joining of the four large female cub with the adult male before they were relocated and released in the boma on the Reserve. A combination of these factors could have triggered a synchronised oestrus among some of the four founder large cub lionesses.

Infrequent and unpredictable groupings of different lions were recorded in the first year following release. On 21 January 2018 [Timeline 11; event (5)], Lioness LF4 and her four cubs were found with Lionesses LF1 and LF2 and their cubs [Litter 1 (LF1) and Litter 1 (LF2)], as well as Lion LM1. The 14 lions were resting peacefully close to a frequently visited waterhole in the central part of the Reserve. This specific large grouping of lions was observed only once during this study.

4.6.2 Timeline for Lioness LF4 from January 2019 to April 2019

Timeline 12; event (6): As discussed previously (see section 4.5, Timeline for Lioness LF3 on the Reserve), Lioness LF4 with her four large cubs and Lioness LF3 and her two large cubs were seen together in a group on 21 January 2019.

Timeline 12; event (7): The four large cubs [Litter 1 (LF4)] were seen without their mother (Lioness LF4) for the first time on 14 February 2019. The large cubs were approximately 18 to 22 months old and would have been able to hunt by themselves (Lehmann *et al.,* 2008). The separation could have been due to a male takeover and consequential eviction of the cubs (Packer & Pusey, 1983b) because Lioness LF4 could have been coming into oestrus again (Miller & Funston, 2014). However, the only adult male Lion LM1 on the Reserve at the time had remained with Lioness LF2. Just two days before the separated large cubs of Lioness LF4 were seen, Lion LM1

was recorded to have been with Lioness LF2 about 12 km away from where the cubs of Litter 1 (LF4) were. Even though it would be possible for both Lion LM1 or Lioness LF4 to have covered that distance, Lioness LF4 and Lion LM1 were not seen together again after this event and a possible mating incident is thus ruled out.

As detailed in Figure 4.12, Lioness LF4 occupied a large area of the available habitat on the Reserve, but her spatial utilisation was focused to the central parts of the Reserve.

Timeline 12; event (8): The first sighting of Lioness LF4, reunited again with her four cubs was 10 days later when the group was seen at a kill of a sub-adult giraffe (*G. camelopardalis*). This was the largest species killed by Lioness LF4. On one occasion in August 2018, a young buffalo (*S. caffer*) heifer wandered from the herd and was killed by a group of lions. However, because of the lack of recorded notes at the time, the lions present at the kill could not be identified.

The lions present at the kill were not the main pride, namely Lion LM1, Lionesses LF1 and LF2, as well as Litter 1 (LF1) and Litter 1 (LF2), and therefore could only have been Lioness LF3 or Lioness LF4.

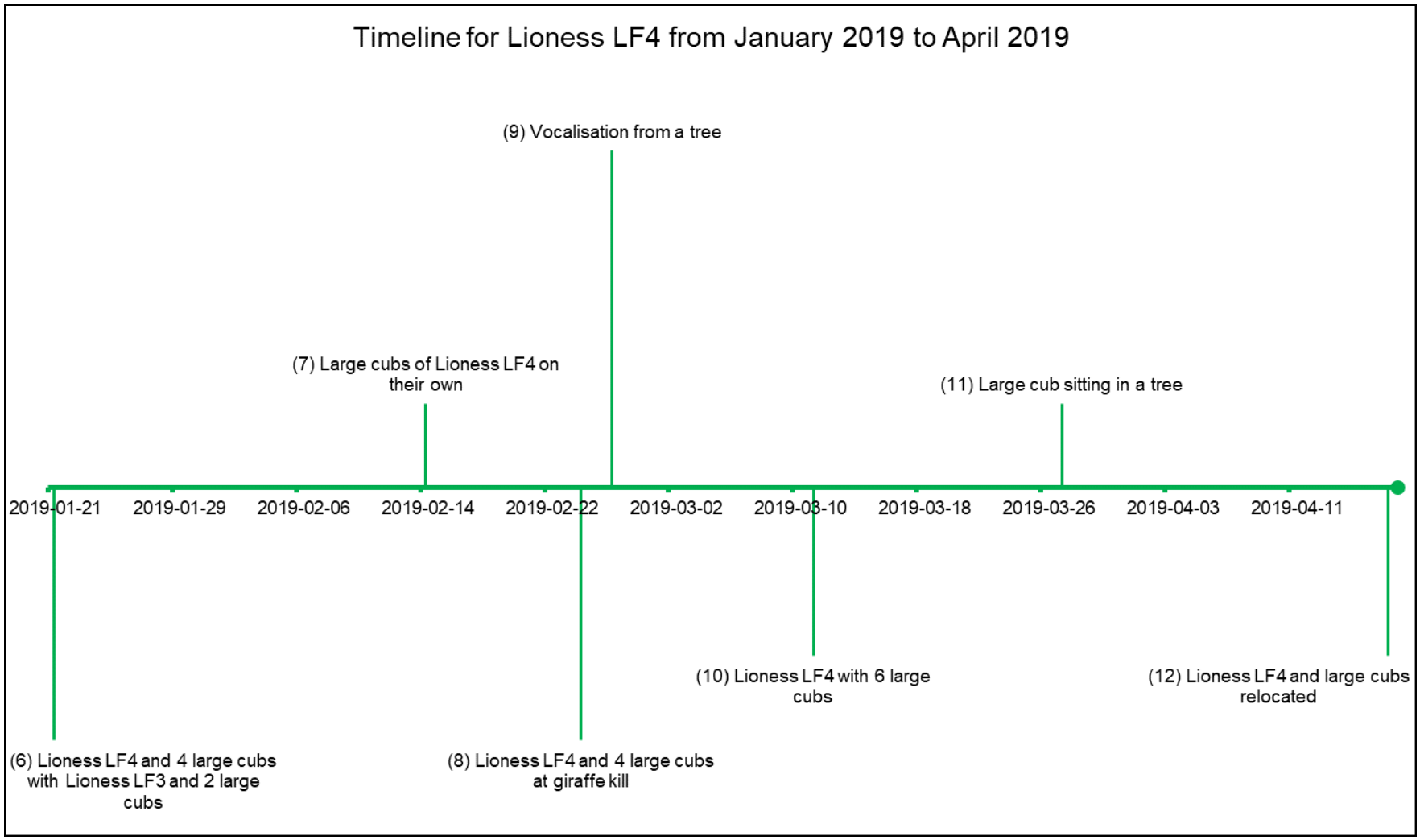
Timeline 12; event (9): Several days later (26 February 2019), Lioness LF4 was recorded sitting in a tree in an area that had been mechanically cleared of dense bush (see Chapter 2), vocalising softly towards her large cubs. They responded to her vocalisation and together started walking towards her.

On a separate occasion (26 March 2019), a large female cub of Litter 1 (LF4) was perched in a tree [Timeline 12; event (11)]. Tree climbing by lions are well documented and can be attributed to several reasons (Eloff, 2016). The head of one large female cub was stained with blood and she breathed fast and heavy. Upon inspection of the tracks nearby, the rest of the group (Lioness LF4 and the other three large cubs) was about 200 m from her position where a blue wildebeest (*C. taurinus*) had been killed.

During this study, only the cubs (specifically female cubs) of both Lionesses LF3 and LF4 were recorded to sit in a tree.

Once all six large cubs of Litter 1 (LF3) and Litter 1 (LF4) were seen together, but only with Lioness LF4 visible [Timeline 12; event (10)]. The dense bush cover could have blocked out sighting of Lioness LF3, especially if she laid down further away from the vehicle from where the sighting of the kill was recorded. From January to April 2019, Lioness LF3 and her two large cubs were often seen separated from each other (see section 4.5) and on two separate occasions, Lionesses LF4 was seen with five large cubs. The five large cubs could possibly have been miscounted for several reasons alluded to previously and could thus have been six cubs. If this was the case, the conclusion could be drawn that the large cubs were Litter 1 (LF3) and Litter 1 (LF4).

It is not uncommon for lionesses in stable prides to form crèches (Packer & Pusey, 1983b). The grouping of Lionesses LF3 and LF4 was not stable. However, the short duration of observation (less than 24 months) and the lack of sufficient detailed records of these lionesses and their offspring could have influenced the outcome.



Timeline 12. Illustrating a timeline of important events (numbered in chronological order) for Lioness LF4 on the Reserve from January 2019 to April 2019.

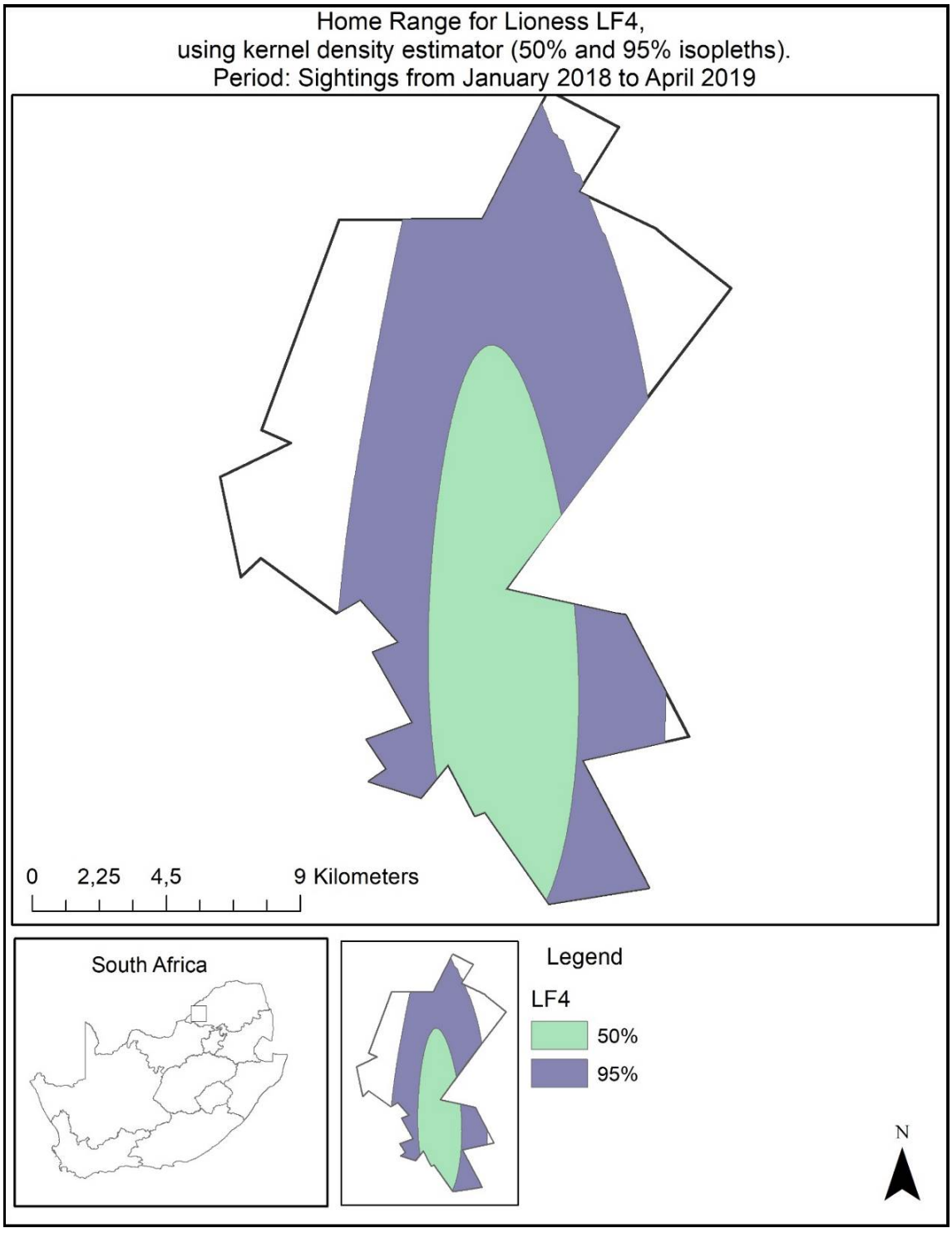


Figure 4.12. Home range of Lioness LF4 for the period of January 2018 to April 2019 using kernel density estimator 50% and 95% isopleths. The range of Lioness LF4 is based on visual sightings for the period mentioned, as she was not fitted with a satellite GPS collar. Lioness LF4 was observed spending time most often in the southern and central parts of the Reserve.

Slide 4.31. One of the large female cubs of Lioness LF4 feeding on the remains of a kill made by the group in March 2019.

Lioness LF4 and her four large cubs [Litter 1 (LF4)] were sedated on 17 April 2019 and relocated to another reserve [Timeline 12; event (12)].

Lioness LF4 raised only four cubs [Litter 1 (LF4)], all sired by Lion LM1, but they were not individually identified.

4.7 Timeline of important events for Lions LM2, LM3, LM4 and LM5 on the Reserve

4.7.1 Timeline for Lions LM2, LM3, LM4 and LM5 from June 2019 to September 2019

The births of Lions LM2[LF1], LM3[LF1], LM4[LF2] and LM5[LF2] were discussed in sections 4.3 and 4.4. These four young male lions were among the first generation of cubs born to the four founder lionesses [Litter 1 (LF1) and Litter 1 (LF2)], and thus the first generation of wild born lions on the Reserve.

The four males spent most of their time together and they formed part of the main pride (see sections 4.3 and 4.4). The Lions LM2, LM3, LM4 and LM5 are referred to in subsequent paragraphs as the four sub-adult males when referred to in a group.

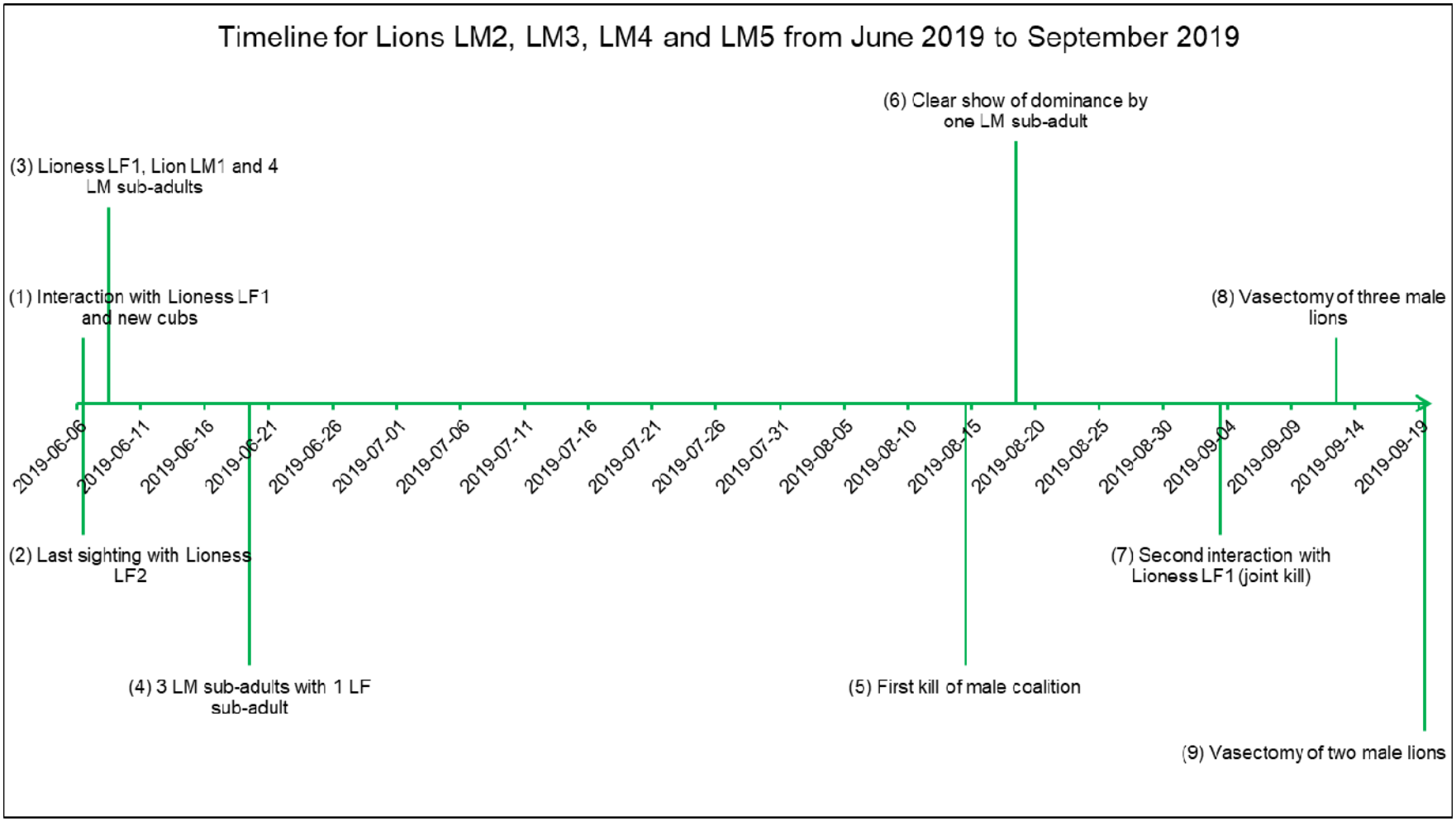
The dispersal of the only remaining adult female lion (Lioness LF2) from the main pride led to the total disintegration of the pride in mid-2019. The four sub-adult males were about 22-24 months old at the time. Their dispersal from the pride, however, was not caused by pressure from the adult male holding pride tenure at that time (Eloff, 2016), nor could it have been caused by a take-over of the pride from incoming alien males or a male (Borrego *et al.,* 2018) as there was no other adult male present on the Reserve. Instead, the adult male Lion LM1 joined the coalition with some offspring, the four sub-adult males.

Timeline 13; event (1): On 6 June 2019, the four sub-adult males were found laying in the middle of a road. When Lioness LF1 and her three cubs [Litter 2 (LF1)] crossed the same road about 300 m away they all got up and walked in her direction. Lioness LF1 adopted a submissive pose by laying on the ground when she noticed the four sub-adults. She then sought cover in the nearby thickets when the sub-adults started running towards her and the cubs. The interaction could not be observed, because the brush was too thick, although loud growling could be heard. The cubs [Litter 2 (LF1)] were not injured in the interaction.

On 8 June 2019, Lioness LF1 and her three cubs [Litter 2 (LF1)] were interacting peacefully with Lions LM1, LM2, LM3, LM4 and LM5 [Timeline 13; event (3)].

Timeline 13; event (4): The joining and interaction of the four sub-adult males and Lion LM1 remained volatile throughout the study, because they were not all present at all sightings recorded. The first such indication was on 19 June 2019 when only three sub-adult males were seen with one of the sub-adult females (originally from the main pride), which had last been seen with another sub-adult female. The two sub-adult females were Lionesses LF5[LF1] and LF6[LF2], also cubs from Litter 1 (LF1) and Litter 1 (LF2). The six sub-adults were not individually identified and at that time it was not possible to distinguish them from one another.

Slide 4.32. The four sub-adult males (Lions LM2, LM3, LM4 and LM5) at a permanent water hole on 13 March 2020 on the Reserve.



Timeline 13. Illustrating a timeline of important events (numbered in chronological order) for Lions LM2, LM3, LM4 and LM5 on the Reserve from June 2019 to September 2019.

Meetings or introductions of new cubs to their natal prides often occur in the presence of larger cubs/sub-adults (Lehman *et al.,* 2008). Later that same day (19 June 2019) all six sub-adults from the main pride (Lions LM1, LM2, LM3, LM4 and Lionesses LF5 and LF6) were seen interacting with Lioness LF2 [Timeline 13; event 2), not far from where the previous interaction with Lioness LF1 had occurred.

Timeline 13; event (5): The first record of the group of five males (adult Lion LM1 and sub-adult Lions LM2, LM3, LM4 and LM5) at their own kill was on 14 August 2019, when the remains of an ostrich (*S. camelus*) was found where the satellite GPS collar of Lion LM1 had positioned the lions. Inspection of the tracks indicated the presence of more than one lion, and it was assumed that the group of five lions had fed on the carcass. On 3 September 2019 the five male lions were again joined by Lioness LF1 and Litter 2 (LF1) at a kill of an adult zebra (*E. quagga*) [Timeline 13; event (7)].

By August 2019, the four sub-adult males (LM2, LM3, LM4 and LM5) started showing aggressive, challenging behaviour towards the old Lion LM1. An occasion was recorded where a sub-adult male (unidentified at the time) challenged Lion LM1 at a kill of a young giraffe (*G. camelopardalis*), which the group had presumably killed. On another occasion, Lion LM1 and a sub-adult male were found alone along the southern boundary of the Reserve. The sub-adult male mounted Lion LM1 for a few seconds until he was pushed off by Lion LM1 [Timeline 13; event (6)]. It is doubtful that this was an act of homosexuality by the sub-adult male, but rather a show of dominance and the sub-adult male's progression into sexual maturity.

Timeline 13; event (8): The four sub-adult males were believed approaching sexual maturity (Kilian, 2003), therefore the management of the Reserve decided to vasectomise them. There were also concerns that the sub-adult females (Lionesses LF5 and LF6) could soon reach sexual maturity, therefore it was decided to vasectomise Lion LM1 as well to prevent inbreeding with his daughters.

Finding and sedating the lions on the Reserve was difficult and only three of the five males were located and vasectomised on 12 September 2019. The procedures were conducted in the field (Slide 4.33) with Lions LM1, LM2 and LM3. While still sedated,

Lions LM2 and LM3 were identified by means of the spot patterns of their vibrissae (Pennycuick & Rudnai, 1970). The satellite GPS collar of Lion LM1 was removed and fitted to Lion LM2. Body measurements were taken of the sedated lions (**Appendix I**, Table 1). All three males recovered safely from the sedation.

Slide 4.33. The Veterinarian preparing one of the sub-adult males for a bi-lateral vasectomy on 12 September 2019 on the back of one of the vehicles used to recover the lions after being sedated.

Timeline 13; event (9): The remaining two intact sub-adult males (Lions LM4 and LM5) were vasectomised one week later, 19 September 2019. The next day the four sub-adult males regrouped, but Lion LM1 was absent from the group. Lion LM1 was only seen back with the group on 23 September 2019.

4.7.2 Timeline for Lions LM2, LM3, LM4 and LM5 from October 2019 to August 2020

Lion LM1 remained with the four sub-adult males until 9 October 2019 when seen with them for the last time [Timeline 13; event (10)]. The body condition of the old Lion LM1 deteriorated fast and he would ultimately spend most of his last days at a waterhole in the central part of the Reserve (see section 4.2).

The cohort of four vasectomised sub-adult males remained nomadic without the old Lion LM1, because there was no stable pride for them to join or possible females to consort. There was no marked difference in spatial utilisation of the Reserve by the

four sub-adult males in the absence of Lion LM1 (Fig. 4.13), neither did the presence of Lion LM1 influence the spatial utilisation of the Reserve by the sub-adult males.

Although the notes kept by the author indicated that the bellies of the sub-adult males were large (and thus they have probably eaten prior to the observation); the first record of the sub-adult males catching their own prey was on 29 October 2019 [Timeline 14; event (11)] when they brought down a sub-adult male eland (*T. oryx*). The four sub-adult males were not present at the carcass, but data from the satellite GPS collar linked them to the scene. The following day, all four sub-adult males were found still feeding on the carcass.

Timeline 14; event (12): On 12 December 2019, a new adult breeding male Lion LM6 was transferred to the Reserve and released in the boma to adapt (see section 4.1). At 20h33 on 14 December 2019, the four sub-adult males were approximately 5.9 km from the boma. The next morning at 05h10, they were resting next to the boma where new adult Lion LM6 was held. The four sub-adult males spent the following three days circling the boma and resting next to the fence. By 17 December 2019 they had left that spot at the boma.

Timeline 14; event (13): In February 2020, the satellite GPS collar of Lion LM2 lost battery power and had to be replaced. When the Veterinarian arrived at the Reserve, the four sub-adult males had split up again and only two were located. Lion LM2 could not be found that day, therefore it was decided to fit the new satellite GPS collar to Lion LM5 instead so that Lion LM2 could be relocated when he re-joined the group. A zebra (*E. quagga*) carcass was used to lure the two sub-adults with bait from a nearby waterhole where they were resting, to an open area where they could be sedated from the vehicle by the Veterinarian.

On 23 February 2020, Lion LM2 was located with the aid of the new satellite GPS collar which was fitted to Lion LM5, because the four sub-adult males had regrouped at a waterhole in the centre of the Reserve. Another zebra (*E. quagga*) carcass was used to keep the lions in the same area until the Veterinarian could arrive the next day. All four sub-adult males were sedated to remove the satellite GPS collar with

the depleted battery from Lion LM2, because the other three lions would not allow the team a safe working space [Timeline 14; event (14)].

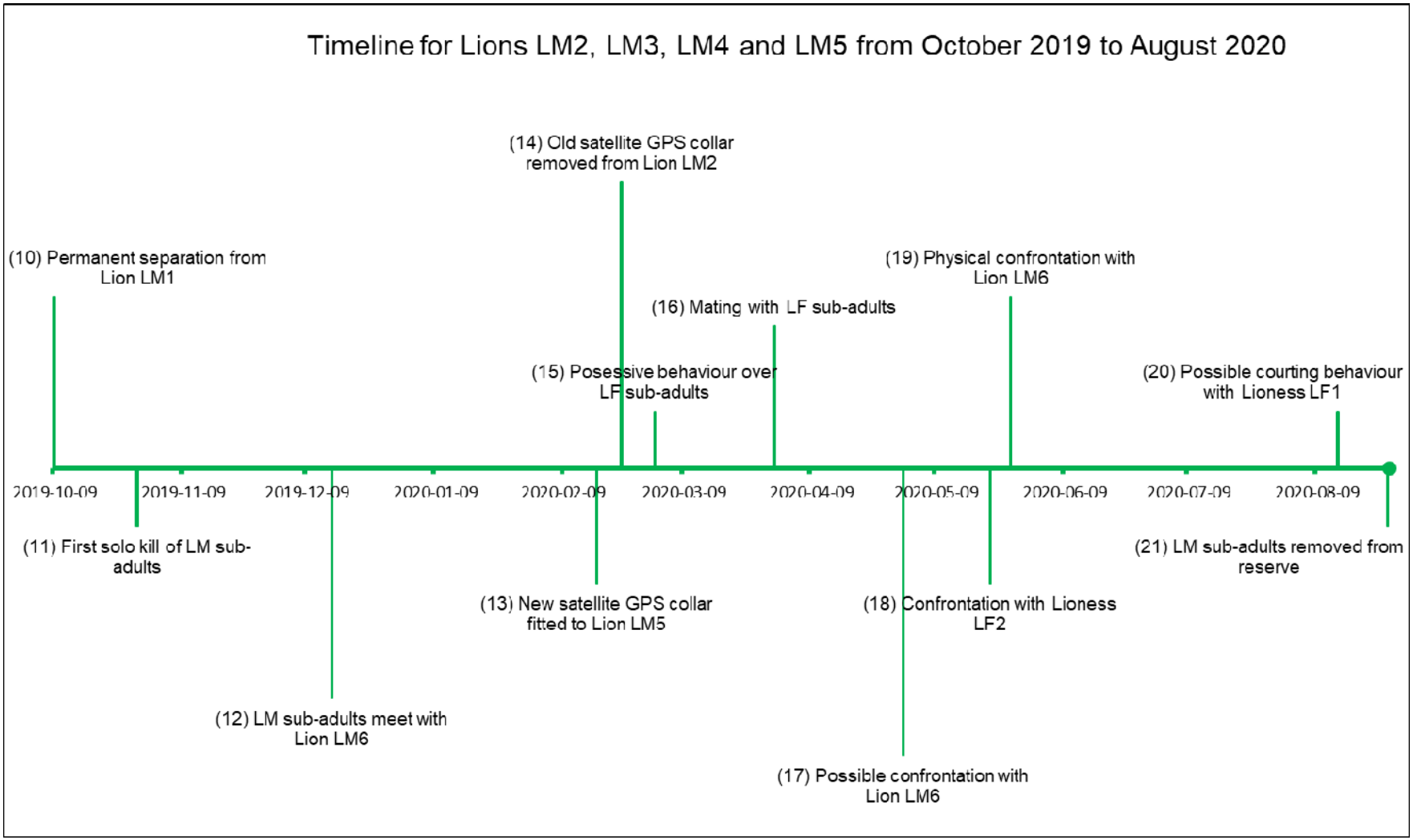
The unpredictability of the group of sub-adult male cohesion continued and lonely individuals from the group were often seen or in alternate unions.

Timeline 14; event (15): On 2 March 2020, Lion LM4[LF2] was seen with Lioness LF5[LF1]. The other three sub-adult males were approximately 400 m away. When the other sub-adult males approached, Lion LM4 moved between them and Lioness LF5. Lion LM4 also marked nearby shrubs with urine as a sign of possession (presumably) over Lioness LF5 (Packer & Pusey, 1982). Lioness LF5 showed no signs of soliciting courtship or visibly being in an oestrous cycle. She was approximately 32 months old at the time.

On 20 March 2020, two of the sub-adult males were again seen with Lioness LF5, and both showed interest in Lioness LF5. Dense cover made it difficult to assess the behaviour of the lions and identify the specific sub-adult males.

Timeline 14; event (16): On 31 March 2020, the four sub-adult males were seen with both sub-adult females (Lionesses LF5 and LF6) at a pan on the northern border of the Reserve. Two sub-adult males were each guarding a female by keeping the other two sub-adult males away. The movement of the females influenced the movements of the males. Lioness LF5[LF1] allowed Lion LM4[LF2] (Slide 4.35) to copulate four times in 90 minutes. The sub-adult males were approximately 33 months old and thus sexually mature (Rudnai, 1973a; Smuts, 1978a). Lioness LF5 could not conceive because all the sub-adult males were vasectomised.

On 19 April 2020, Lioness LF5[LF1] was seen with a different male, Lion LM5[LF2], while the other sub-adult males were resting about 700 m away. No courting behaviour was observed on this occasion.



Timeline 14. Illustrating a timeline of important events (numbered in chronological order) for Lions LM2, LM3, LM4 and LM5 on the Reserve from October 2019 to August 2020.

Slide 4.34. Two of the four sub-adult males after being administered with the sedative on 23 February 2020.

Slide 4.35. Lion LM4 copulating with Lioness LF5 next to a pan on 31 March 2020.

Timeline 14, event (17): On 1 May 2020, while checking the positions of the satellite GPS collars, it was noticed that the new adult Lion LM6 had escaped from the fenced area of the Reserve. Upon inspection of the fence, it was observed that at

least three pairs of large lion tracks had followed Lion LM6 to a customised cattle grid (Slides 4.36 & 4.37), which gave access to a safe fenced area where staff were housed. Analysis of the tracks by expert trackers of the Reserve, and the last known location of the sub-adult male (Lion LM5), indicated that Lion LM6 had been cornered against the fence by at least three sub-adult males. It was clear from the tracks that Lion LM6 tried to avoid the sub-adult male lions and when he got to the cattle grid, managed to cross the electrified access point. A sheer survival instinct must have kicked in, helping him to cross the barrier.

Slides 4.36 & 4.37. The custom steel cattlegrid gate used to keep dangerous wildlife from entering the safe area where staff is housed on the Reserve.

The customised steel cattlegrid gate consisted of railroad tracks, spaced 10 cm apart over a 1 m deep trench constructed from brick and cement. Electrified wire strands were installed between every railroad track. The total distance of the cattle grid crossing was 5 m across and 4.5 m wide. This was the only recorded incident of a wild animal crossing the custom cattlegrid from one side to another.

Later that day (1 May 2020), Lion LM6 was sedated approximately 7 km from where he had escaped over the customised cattlegrid and released again on the northern border of the Reserve, close to a waterhole and approximately 25 km from the cattlegrid. He had sustained minor wounds to his paws, thorax, groin area and face, and was medically treated while he was sedated (Slide 4.38).

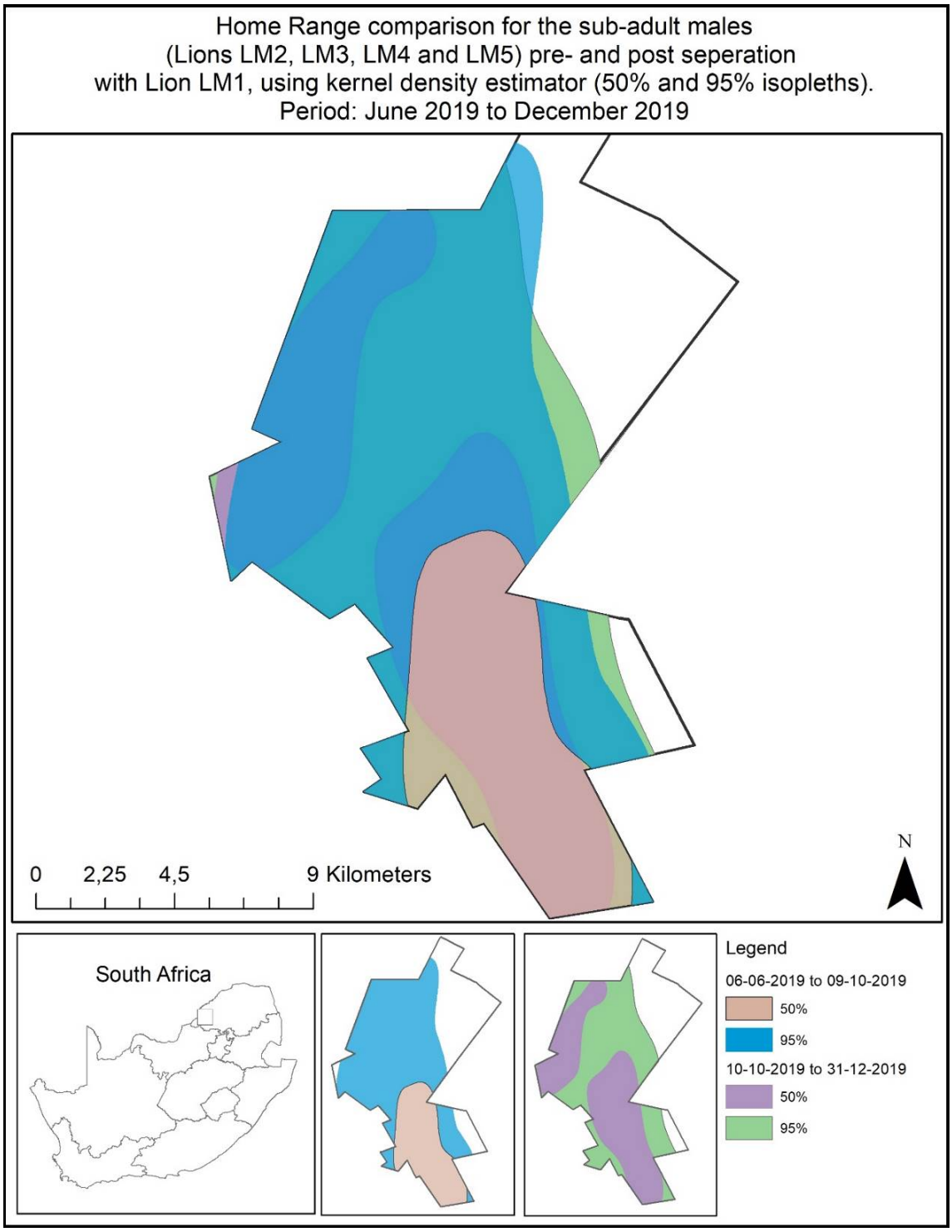


Figure 4.13. Spatial utilisation by the sub-adult males (Lions LM2, LM3, LM4 and LM5) four months before separating from Lion LM1 (6 June 2019 to 9 October 2019) compared to the spatial utilisation after their separation from Lion LM1 (10 October 2019 to 31 December 2019). There is no visible difference in the utilisation of the Reserve by the sub-adult males.

Timeline 14; event (18): On 22 May 2020, the four sub-adult males were believed to have been in a skirmish with Lioness LF2 and her second litter of cubs [Litter 2 (LF2)]. Upon inspection of the tracks on the site where the satellite GPS collars of Lioness LF2 and Lion LM5 had positioned them together, it was clear that there had been an altercation between the four sub-adult males and Lioness LF2. She was separated from the cubs, but all four cubs survived. The interaction is discussed in section 4.4.

Timeline 14, event (19): On 27 May 2020, three of the sub-adult males were found laying in a circle around Lion LM6. When one of the sub-adults approached Lion LM6, he was met with loud vocalisation by Lion LM6 who remained lying down facing the sub-adult males. The other two sub-adults got up and engaged in scent marking the brush around Lion LM6, who kept vocalising. All three sub-adults took turns in approaching Lion LM6, which resulted in a short fight of paw strikes and loud vocalisations. The sub-adult males then left, walking away from Lion LM6 who started walking up and down the border fence of the Reserve. Lion LM6 sustained only minor injuries and no intervention from the Veterinarian was necessary.

Slide 4.38. Lion LM6 being treated for minor wounds with an anti-bacterial spray while sedated on 1 May 2020.

It was noted that the sub-adult males were regularly interacting with the new adult Lion LM6, even though his presence did not affect their spatial utilisation of the Reserve (Fig 4.14). However, it is possible that Lion LM6 restricted his movement because of the presence of the four sub-adult males (section 4.9).

After this incident, the four sub-adult males were seen in alternating pairings and in solitude across the Reserve again.

Timeline 14; event (20): On one occasion (14 August 2020), Lions LM4[LF2] and LM5[LF2] were seen with Lioness LF1. Both sub-adult males showed interest in Lioness LF1 who could have come into oestrous (Kilian, 2003), because her cubs were already 15 months old. However, Packer & Pusey (1982) reported that males in the Serengeti, Tanzania were guarding females even if they were not in oestrus. Lion LM4 stayed close to Lioness LF1 who tolerated his presence but did not solicit or allow courtship. Lion LM5 remained at a close distance and eventually got up and scent marked a nearby bush, after which he went to lie down again. This grouping of Lioness LF1 and Lion LM4 was recorded again on 18 August 2020.

The first time the four sub-adult males were noted together again was on 25 August 2020. That night a blue wildebeest (*C. taurinus*) was shot as bait to lure the four sub-adult males to an open area where they could be sedated the next day.

The blue wildebeest had to be dragged past them to ensure that they would find the carcass tied to a tree, about 700 m from their resting position and with a clear view for the Veterinarian to dart them.

While trying to lure them, the vocalisation of other lions was heard. The satellite GPS collars confirmed that it was Lioness LF5 and possibly Lioness LF6, which were about 2 km away. This caused one of the sub-adult males (Lion LM3) to leave the group and attend to the two approaching sub-adult females.

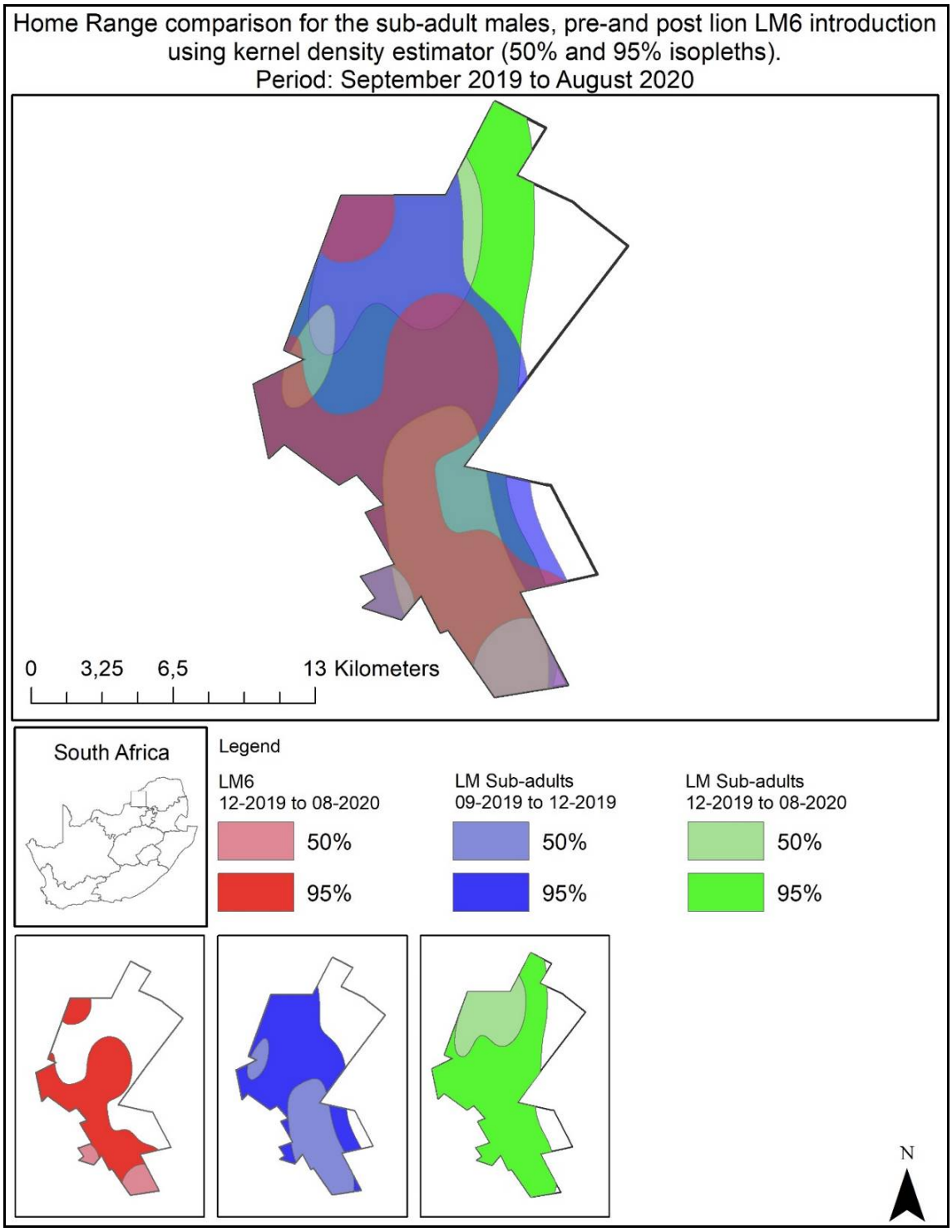


Figure 4.14. Comparison of the spatial utilisation of the four sub-adult males before and after the release of Lion LM6 on the Reserve. The sub-adult males left Lion LM1 in September 2019 and therefore the data pre-release of Lion LM6 was chosen accordingly.

The three remaining sub-adult males (Lions LM2, LM4 and LM5) were successfully lured to the blue wildebeest (*C. taurinus*) carcass and successfully sedated the following day (26 August 2020). Later that same day, Lion LM3 (who had left the group and joined the two sub-adult females the previous night) was found approximately 5 km from where the other three sub-adult males were sedated. The carcass of a female waterbuck (*K. ellipsiprymnus*) was tied to a tree to keep Lion LM3 at that position so he could also be sedated.

The Veterinarian sedated all four sub-adult males on 26 August 2020, and they were loaded on an appropriate wildlife transport trailer and moved to another reserve [Timeline 14; event (21)].

4.8 Timeline of important events for sub-adult Lionesses LF5 and LF6 and interactions with sub-adult Lions LM2, LM3, LM4 and LM5 on the Reserve

By the end of November 2021, Lioness LF5 had given birth to three cubs (Figure 4.15). The sex of the cubs Litter 1 (LF5) was not determined but they were sired by Lion LM6.

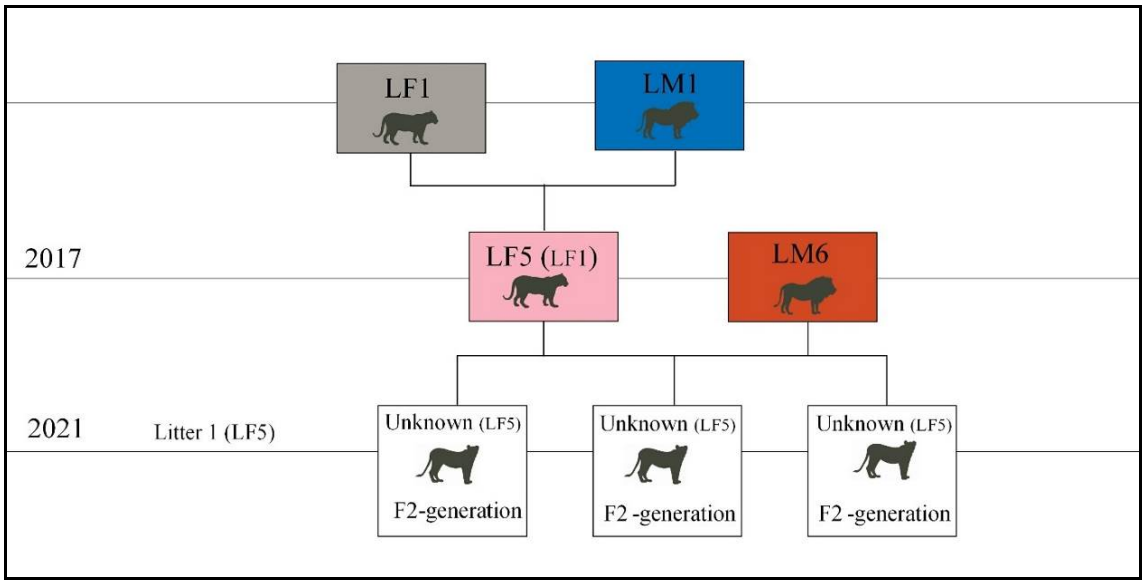


Figure 4.15. Schematic illustration of the offspring of Lioness LF5 and Lion LM6, indicating that the three cubs born to Lioness LF5 in 2021 was the first F_2-generation of lion cubs born on the Reserve.

4.8.1 Timeline for Lionesses LF5 and LF6 from June 2019 to August 2021

The births of Lionesses LF5[LF1] and LF6[LF2] were discussed in sections 4.3 and 4.4. Lionesses LF5 and LF6 were respectively born in Litter 1 (LF1) (July 2017) and Litter 1 (LF2) (May 2017) and was thus members of the first generation (F1) of lions born on the Reserve.

Lionesses LF5 and LF6 were members of the main pride (see section 4.2) and remained in that group until the age of about 22-24 months. After separating from the main pride in June 2019 [Timeline 15; event (1)], Lionesses LF5 and LF6 spent most of their time in the company of each other in the northern part of the Reserve (Fig.

4.16). When referring to these lionesses (Slide 4.39) in subsequent paragraphs, Lionesses LF5 and LF6 are referred to as the two sub-adult females.

After leaving the main pride, it was very difficult to track the two sub-adult females because they were not fitted with tracking devices. Visual observations were recorded opportunistically, therefore their data are limited.

Timeline 15; event (2): The first sighting of the two sub-adult females after leaving the main pride was on 11 June 2019. The condition of both lions was acceptable and previous concerns about their ability to self-provide was removed. Eight days later (19 June 2019) only one of the sub-adult females (still unidentified at the time) was seen with three of the sub-adult males [Litter 1 (LF1) and Litter 1 (LF2)]. It is accepted that the observation could have been influenced by several factors (alluded to in other chapters), however, the occurrence of only one of the sub-adult females and not all of the sub-adult males were regularly observed in the following months.

Even though the sub-adult females spent time in the presence of their siblings (sub-adult males), no sighting of the old adult Lion LM1 with the sub-adult females was recorded after the separation of the female and male lions of the main pride in June 2019.

As indicated previously (see section 4.7), the four sub-adult males had formed a coalition with the old Lion LM1. It implied that the sub-adult males left the company of Lion LM1 to start interacting with the two sub-adult females (Lionesses LF5 and LF6).

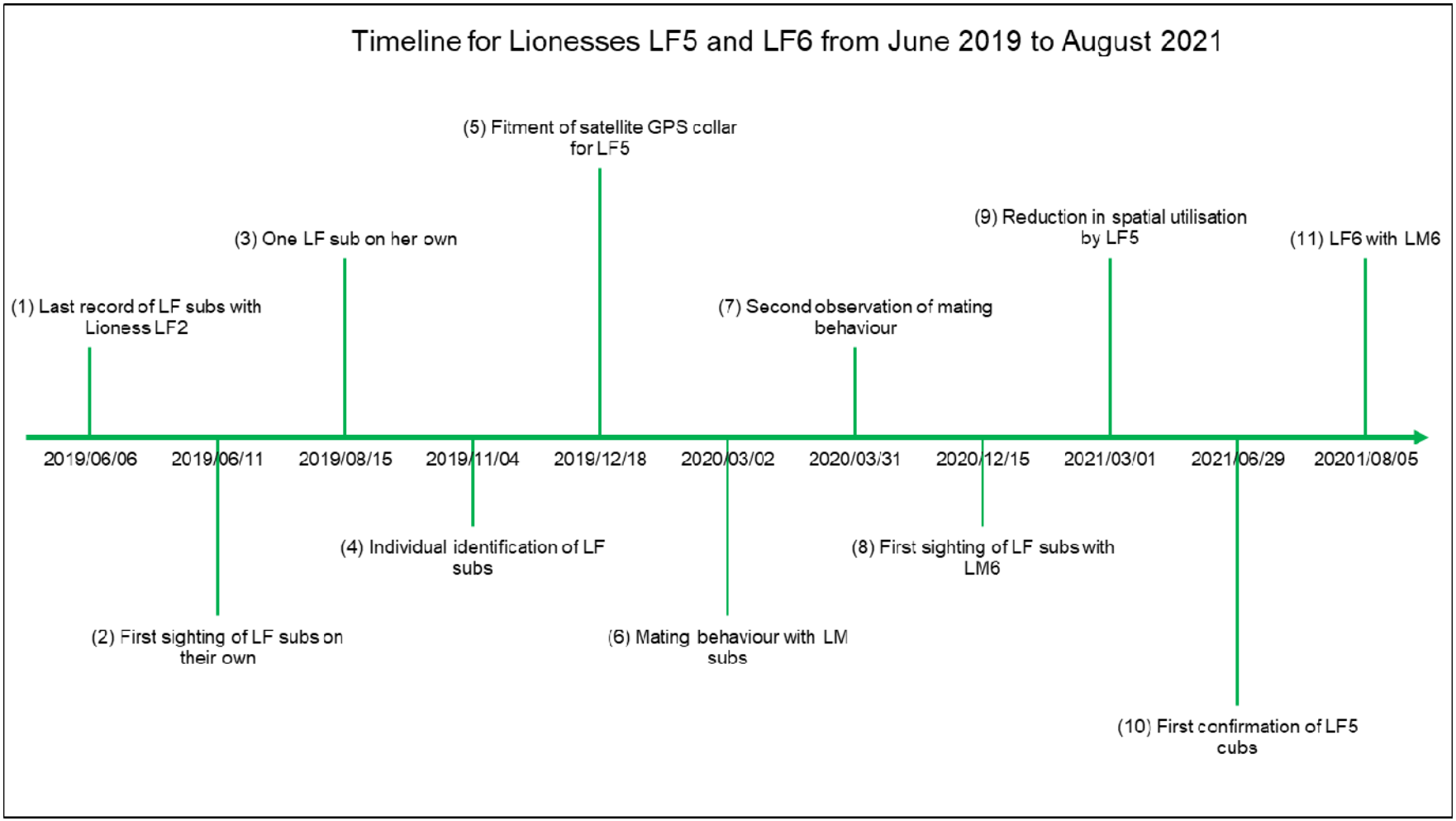
Timeline 15; event (3): On 15 August 2019 one sub-adult female was found on her own. She was in a good body condition. A similar observation was made on 27 August 2019. Individual identification of the two sub-adult females had not yet been completed and it could not be ascertained if it was the same sub-adult female which was recorded to be on her own. The two sub-adult females were recorded in each other's company again on 10 September 2019.

Slide 4.39. The two sub-adult females (Lionesses LF5 and LF6) shortly after separating from the main pride in June 2019.

Timeline 15; event (4): The first sighting of the two sub-adult females at a kill was on 4 November 2019. During the observation, the author was able to record individual identity cards of the sub-adult females (**Appendix II**) according to the method of vibrissae identification described by Pennycuick & Rudnai (1970).

On 18 December 2019, Lioness LF5 was sedated by the Veterinarian and to fit her with a satellite GPS collar [Timeline 15; event (5)]. Once the general location of the two sub-adult females was known, an impala (*A. melampus*) carcass was tied to a tree to lure them to an open area where they could be sedated. The effort to lure the two sub-adult females was not successful, but they were located later that night in the road approximately 2 km from the bait site. Both sub-adult females were not alarmed by the presence of the vehicle and they were successfully sedated by darting. Again, both sub-adult females had to be sedated as a precautionary measure for the team's safety while fitting the satellite GPS collar to Lioness LF5. After successfully fitting the satellite GPS collar (see Table 3.1 for detail on the collar), both sub-adult females were administered with the antidote to reverse the action of the sedative (Slide 4.40).

Figure 4.16. Graphic illustration of the home range of Lioness LF5 on the Reserve from December 2019 to August 2021. Lioness LF6 was not fitted with any tracking devices but was mostly close to Lioness LF5.



Timeline 15. Illustrating a timeline of important events (numbered in chronological order) for Lionesses LF5 and LF6 on the Reserve from June 2019 to August 2021.

4.8.2 Social and sexual interaction by Lionesses LF5 and LF6 with vasectomised sub-adult males (LM2, LM3, LM4 & LM5)

Timeline 15; event (6): Even though Lioness LF5 was fitted with a satellite GPS collar, observing the two sub-adult females remained very difficult because the northern territory of the Reserve is mostly mountainous terrain with few access roads. Therefore, the two sub-adult females were visually sighted the first time on 2 March 2020. Only Lioness LF5 was visible while Lion LM4 [Litter 1 (LF2)] was laying next to her and the other three sub-adult males (Lions LM2, LM3 and LM5) were resting 400 m from them. Lion LM4 did not allow the other three sub-adult males close to Lioness LF5 and scent-marked a bush with urine next to her.

The competition for a lioness in oestrous is common in coalitions (Packer & Pusey, 1982) and Lioness LF5 as well as the four sub-adult males were already sexually mature (Rudnai, 1973a; Smuts, 1978a). Although the four sub-adult males were vasectomised (12 and 19 September 2019) (see section 4.7), they still exhibited male sexual behaviour, including copulation.

Slide 4.40. The sedated Lioness LF5 whilst the team was fitting a satellite GPS collar on 18 December 2019.

Timeline15; event (7): More sexual and mating behaviour between the sub-adult females and sub-adult males were recorded in the following months (see section 4.7). However, the two sub-adult females failed to conceive because the four sub-

adult males have been vasectomised on 12 and 19 September 2019 (see section 4.7).

Comparing the spatial utilisation of the four sub-adult males with that of the two sub-adult females (Fig. 4.14 & Fig 4.16), it can be concluded that the sub-adult males' spatial utilisation of the Reserve was possibly influenced by the home range of the sub-adult females. A change in the core home range of the sub-adult males from the southern to the northern regions of the Reserve is supporting the theory (Fig 4.14). The change in their home range by the sub-adult males coincided with the introduction of a new adult male lion (Lion LM6) to the Reserve. The spatial utilisation of the new adult male lion was concentrated in the southern regions of the Reserve, but the four sub-adult males increasingly spent time within the home range of the two sub-adult females (Fig. 4.18).

It is acknowledged that the physical barrier caused by the electrified outer perimeter wildlife fence of the Reserve may have played a marked role in limiting the movement of the lions and thus their spatial utilisation of habitat (see section 3.2).

Slide 4.41. Lion LM2 consorting with Lioness LF6 on 31 March 2019, whilst one of the sub-adult males (not in the picture) rested nearby, watching the two. Lion LM2 was scent-marking the ground and did not allow the other three sub-adult males closer.

According to the information gathered from the satellite GPS collars, the two sub-adult females and four sub-adult males interacted frequently. The interactions took place in the inaccessible terrain where the two sub-adult females spent most of their time (Fig. 4.16). The sub-adult females did not utilise the southern regions of the

Reserve and therefore the interactions occurred in their home range and not in the extended home range of the nomadic coalition of four sub-adult males (Fig. 4.17 & Fig. 4.18). It is believed that the spatial utilisation of the Reserve by the sub-adult males was influenced by the home range of the sub-adult females, because once the sub-adult males became sexually mature their movements were mostly concentrated in the home range of the sub-adult females (Fig. 4.18).

When the four sub-adult males were relocated from the Reserve on 26 August 2020, a sub-adult male was accompanied by the two sub-adult females. All six sub-adult lions were located close to the most northern boundary of the Reserve and on the edge of the home range of the two sub-adult females.

4.8.3 Sexual interaction by Lionesses LF5 and LF6 with intact adult Lion LM6

Timeline 15; event (8): On 15 December 2020, the two sub-adult females were seen the first time with Lion LM6; the new adult male had been released on 26 January 2020 on the Reserve (section 4.9). That night the two sub-adult females were accompanied by adult Lion LM6 and sub-adult Lion LM7 [Litter 2 (LF1)].

The observation was short as the lions quickly disappeared into the thick brush, but no aggression or other behavioural activity could be assessed.

The following two days, Lion LM6 and Lioness LF5 were seen engaging in mating behaviour. Lioness LF6 and Lion LM7 were not seen in the area.

4.8.4 Birth of the first F2-litter from Lionesses LF5 on the Reserve

Timeline 15; event (9): At the beginning of April 2021, Lioness LF5 showed a marked reduction in home range size (Fig. 4.19). This was possibly because of the birth of her first litter of cubs. The birth of cubs would confirm that the mating with Lion LM6 witnessed in December 2020 had been successful. Attempts to confirm the birth of the first litter of a second-generation cubs (F2) on the Reserve was fruitless as the inaccessibility of the terrain made it difficult to get close enough to Lioness LF5. According to the data from the satellite GPS collar, Lioness LF5 chose a den site

very close to the one used by Lioness LF2 in 2019 when she gave birth to her Litter 2 (LF2).

Timeline 15; event (10): On 29 June 2021 the birth of three cubs was confirmed. Lioness LF5 started expanding her spatial utilisation again and caught an eland (*T. oryx*) in an open area. The following day a trail camera was set at the site (Slide 4.42). This was the first lions of a F2-generation born on the Reserve (Fig. 4.15). However, Lioness LF5 succeeded to keep her cubs [Litter 1 (LF5)] from visual sightings by humans and at the end of 2021, her cubs had not been photographed or seen yet during the day.

During the period that Lioness LF5 was believed to have been suckling her cubs, Lioness LF6 was often seen in her presence. However, Lioness LF5 was more often seen on her own with her cubs [Litter 1 (LF5)], but the latter were hidden from plain sight, than with Lioness LF6.

Timeline 15; event (11): After being observed on her own on several occasion after the birth of Litter 1 (LF5), Lioness LF6 was seen in the presence of Lion LM6 on 5 August 2021. The two lions rested next to the road. Although no courting behaviour was witnessed, it was assumed that mating did occur. By November it had not been observed or detected that Lioness LF6 had given birth to cubs.

Slide 4.42. Lioness LF5 and her three cubs [Litter 1 (LF5)] photographed by a trail camera that was set at the carcass of an eland (*T. Oryx*), which was presumably caught by Lioness LF5.

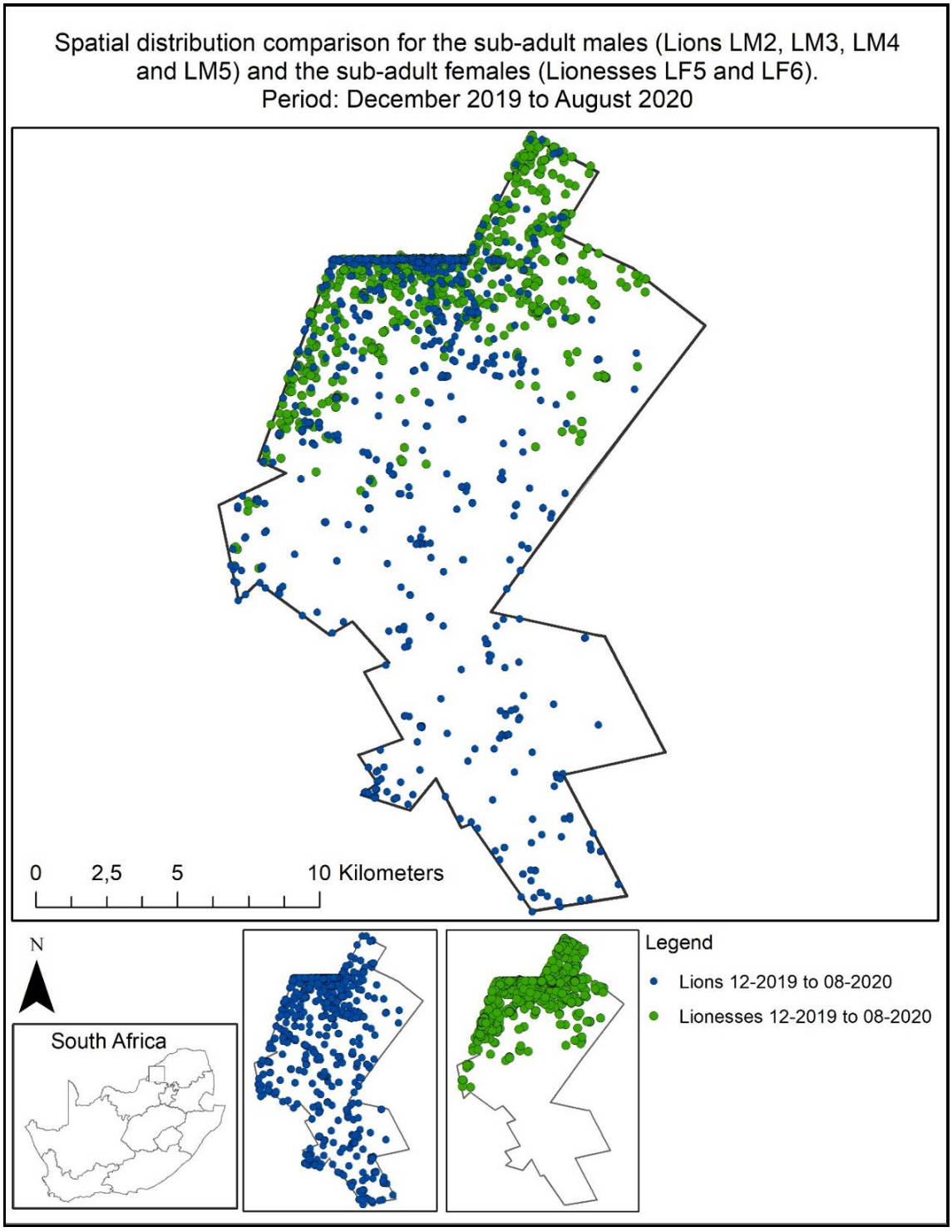


Figure 4.17. The spatial utilisation of the Reserve by the four sub-adult males (Lions LM2, LM3, LM4 and LM5) and the two sub-adult females (Lionesses LF5 and LF6).

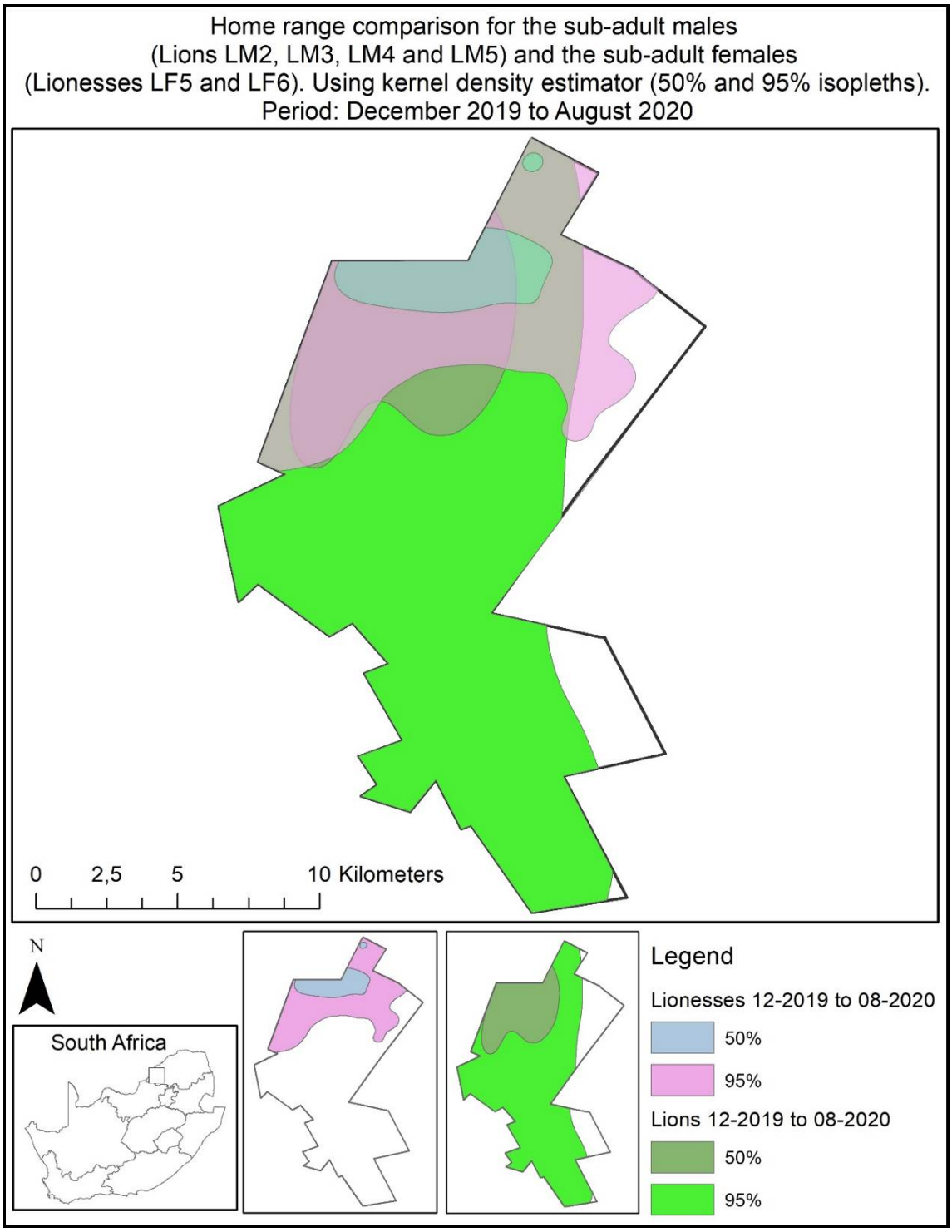


Figure 4.18. Comparison of the home ranges of the four sub-adult males (Lions LM2, LM3, LM4 and LM5) and two sub-adult females (Lionesses LF5 and LF6) from December 2019 to August 2020.

It was difficult to observe the two sub-adult females, therefore very little data is available on the possible kills they might have made. However, it was noted that

species such as eland (*T. oryx*), warthog (*P. africanus*) and zebra (*E. quagga*) were successfully hunted.

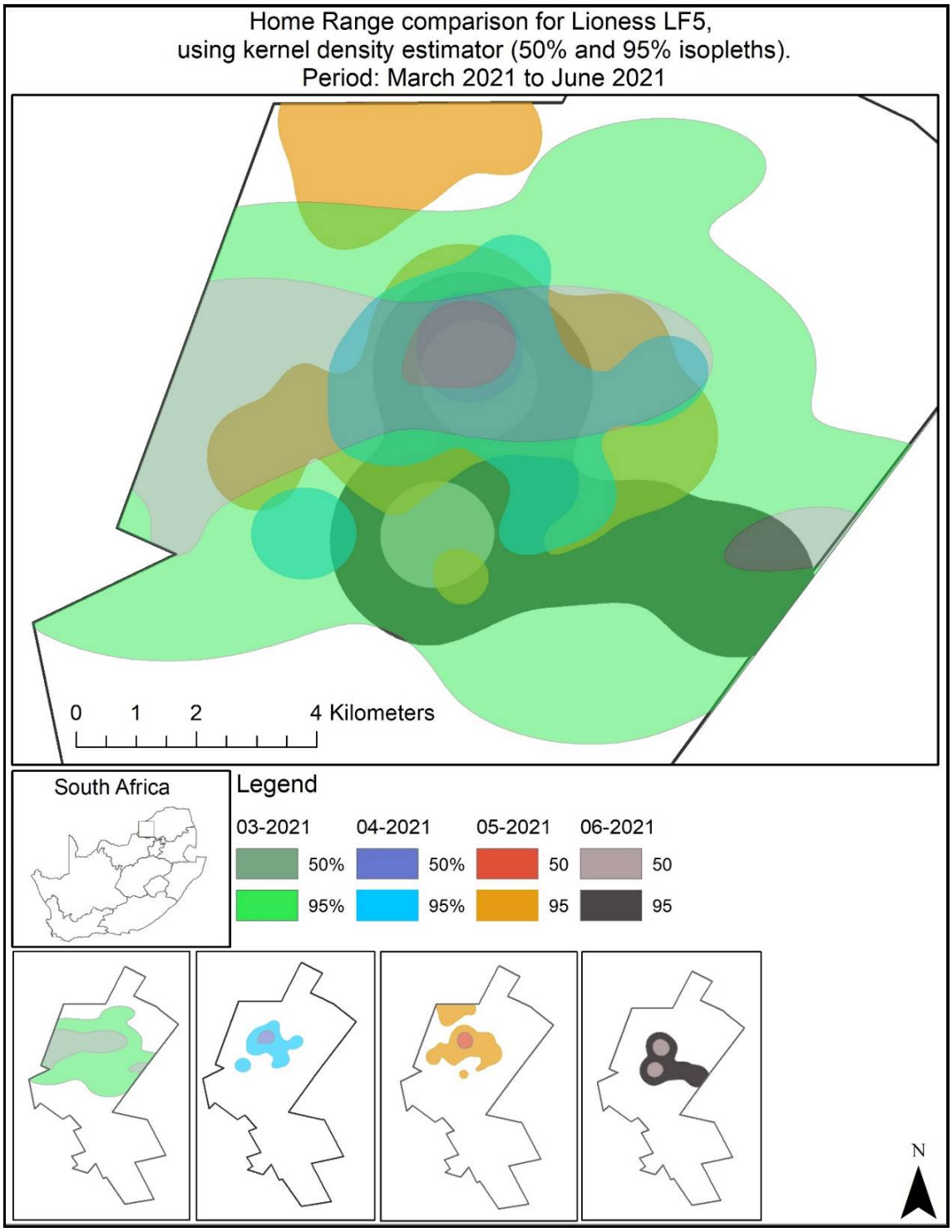


Figure 4.19. A graphic illustration of the marked reduction in home range size by Lioness LF5 in April 2021 when her first litter of cubs were presumably born.

4.9 Timeline of important events for Lion LM6 on the Reserve

4.9.1 Events leading up to the release of Lion LM6 on the Reserve

First some background on the origin of this new adult Lion LM6, which was born at a captive breeding facility in the Free State Province, South Africa. When he was three days old, the male cub (later designated Lion LM6) was removed with his siblings from their mother and reared by hand in a holding facility with cubs of both sexes and similar age. Up to the age of four months the cubs were bottle fed formula milk, specifically intended for African predators, whereafter they received chunks of fresh meat.

At the age of 18 months the large female and male cubs were separated from each other and placed in separate 4 ha holding camps. Until the age of 4.5 years, this individual (Lion LM6) remained with five other males, when relocated to the Reserve (see section 4.1).

Like the founder Lion LM1 (see section 4.2.1), the management of the Reserve selected Lion LM6 because of specific phenotypical traits, namely a large head, large body, dark and well-developed mane. It was important to prevent inbreeding of the lions on the Reserve, therefore blood samples were collected from Lion LM6 and three other suitable male lions considered for possible release to determine possible relatedness to the five founder lions (*i.e*., Lion LM1 and Lionesses LF1, LF2, LF3 and LF4) that were released in 2016. The blood samples were collected by the Veterinarian whilst the lions were sedated. Comparison of the DNA profiles showed that Lion LM6 was not related to any of the five founder lions and was thus a genetically suitable candidate for release on the Reserve.

On 4 September 2019 when the biological samples were taken, the body dimensions of Lion LM6 and the three other lions were recorded according to the method described by De Waal *et al*. (2004a) (**Appendix I**, Table 4).

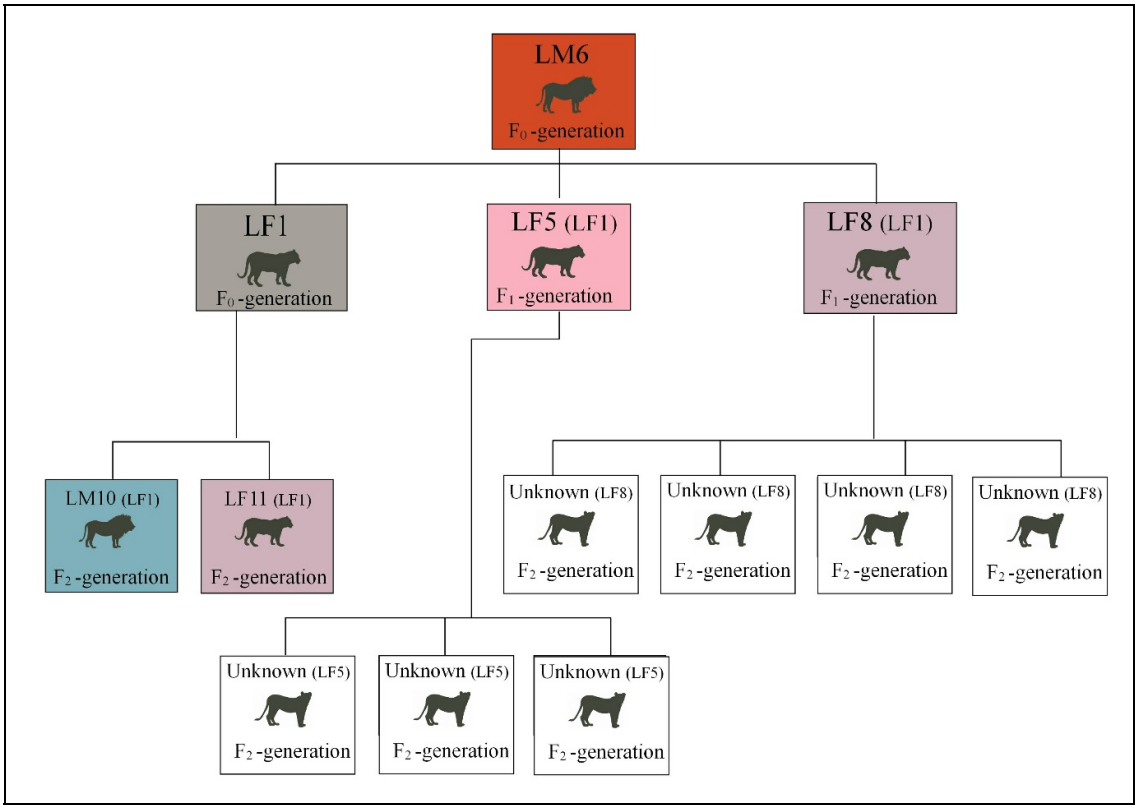
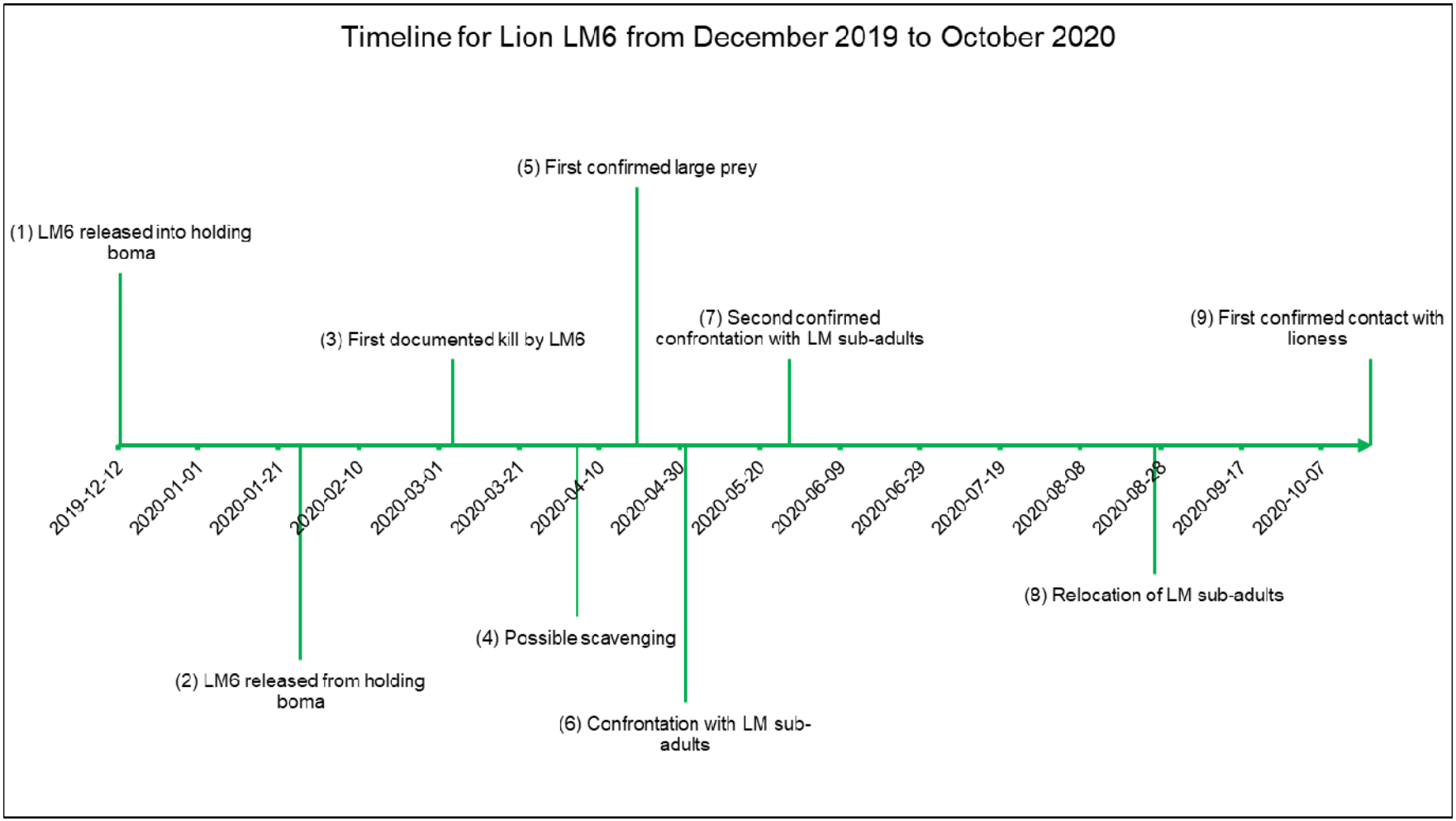


Figure 4.20. Schematic illustration of the offspring of Lion LM6 from January 2020 to August 2021.

By October 2021, Lion LM6 had sired nine cubs with three lionesses, namely Lionesses LF1, LF5 and LF8 (Fig. 4.21).

4.9.2 Timeline for Lion LM6 from December 2019 to October 2020

Timeline 16; event (1): On 12 December 2019, Lion LM6 was sedated by the Veterinarian, loaded onto an appropriate wildlife transport trailer and, later that same day, released in the boma on the Reserve. While sedated, Lion LM6 was fitted with a satellite GPS collar (see section 3.1) to track his movements after being released on the Reserve. Fitting Lion LM6 with a satellite GPS collar before being released in the boma avoided the need to sedate him again before being released on 26 January 2020 from the boma [Timeline 16; event (2)].



Timeline 16. Illustrating a timeline of important events (numbered in chronological order) for Lion LM6 on the Reserve from December 2019 to October 2020.

Within the first week of being released from the boma, Lion LM6 had travelled 14 km in a southern direction, mostly along the boundary fence of the Reserve. Lion LM6 settled at a large dam for approximately two weeks before returning to the area where the boma is. During this time, Lion LM6 spent a lot of time walking along the south western boundary of the Reserve. No signs of possible kills could be confirmed, however, his condition remained fair.

Slide 4.43. Lion LM6 walking along the boundary of the Reserve shortly after being released from the holding boma.

Timeline 16: event (3): On 3 March 2020, the first kill by Lion LM6 was confirmed when he killed an adult warthog (*P. africanus*) male and was seen feeding on it. On 10 March 2020 the remains of an aardvark (*Orycteropus afer*), presumably killed by Lion LM6, was found close to where he was resting. Only the one hind leg was missing from the carcass and very little consumption was noted (Slide 4.44).

In the second month of Lion LM6 being on the Reserve, he extended his home range further south (Fig. 4.22). Lion LM6 still spent most of the time along the southern boundary fence of the Reserve, occasionally returning to the area of the boma.

Another successful warthog (*P. africanus*) kill by Lion LM6 was documented on 30 March 2020. Lion LM6 confined his spatial utilisation between the southern boundary fence and a large dam, 500 m from the western boundary, which he had discovered during his first week of free roaming. On 4 April 2020, Lion LM6 was recorded scavenging on the carcass of an eland (*T. oryx*) which Lioness LF2 had caught on 1 April 2020 [Timeline 16; event (4)]. There was no indication that Lioness LF2 and Lion LM6 interacted, even though they were less than 500 m apart during a 24-hour period. The data from the satellite GPS collars indicated that Lioness LF2 had left shortly after the arrival of Lion LM6. The cubs of Lioness LF 2 [Litter 2 (LF2)] was about nine months old and thus she would have been wary to introduce them to an alien adult male (Packer & Pusey, 1983b).

Slide 4.44. The aardvark (*Orycteropus afer*) which Lion LM6 had presumably killed and partially eaten on 10 March 2020.

Timeline 16; event (5): On 19 April 2020, Lion LM6 killed a prey of substantial size when an adult male waterbuck (*K. ellipsiprymnus*) was presumably brought down. The hunt occurred within 20 m of the boundary fence, where Lion LM6 had been staying since his release from the holding boma on 26 January 2020. Lion LM6 left the carcass two days later, having consumed approximately 60% of the edible parts.

From 26 March to 26 April 2020, Lion LM6 gradually started moving away more from the fences than during the previous months, however, most of his spatial utilisation was still confined to the western and southern boundaries of the Reserve (Fig. 4.22).

Timeline 16; event (6): On 1 May 2020, Lion LM6 was in a skirmish with at least three sub-adult males of Litter 1 (LF1) and Litter 1 (LF2). This caused Lion LM6 to flee and cross the boundary of the Reserve into a safe area used to house staff (see section 4.7). Immediately, precautionary action was taken and within one day of escaping, Lion LM6 was sedated and safely released again in the northern section of the Reserve.

Within seven days of being released again, Lion LM6 returned to the southern boundary. Therefore, it was assumed the spatial utilisation of Lion LM6 was influenced (and limited) by the presence of the nomadic coalition of four sub-adult males (Lions LM2, LM3, LM4, and LM5). A small exploratory area in the early stages of post-translocation, and lions tending to explore in the general direction of their capture site (home) is not uncommon (Hunter, 1998a), although the behaviour of the sub-adult males might have greatly influenced the basic behaviour of Lion LM6.

On 27 May 2020, a second altercation occurred between Lion LM6 and the sub-adult males [Timeline 16; event (7)]. On this occasion Lion LM6 was, again, laying next to the southern boundary of the Reserve with three of the sub-adult males lying around him. The sub-adult males displayed aggressive and dominant behaviour to which Lion LM6 reacted aggressively defensively. No physical confrontation occurred and after the sub-adult males displayed possessive behaviour by scent-marking the brush around Lion LM6, they left the scene. Lion LM6 was visibly nervous and walked up and down along the boundary fence after the sub-adult males had left (see section 4.7).

Timeline 16; event (8): As described previously, the four sub-adult males of Litter 1 (LF1) and Litter 1 (LF2) were sedated on 26 August 2020 and removed from the Reserve. As was suspected, this relocation of the sub-adult males would have a marked influence on the spatial utilisation of the Reserve and social behaviour of Lion LM6 (Fig. 4.22).

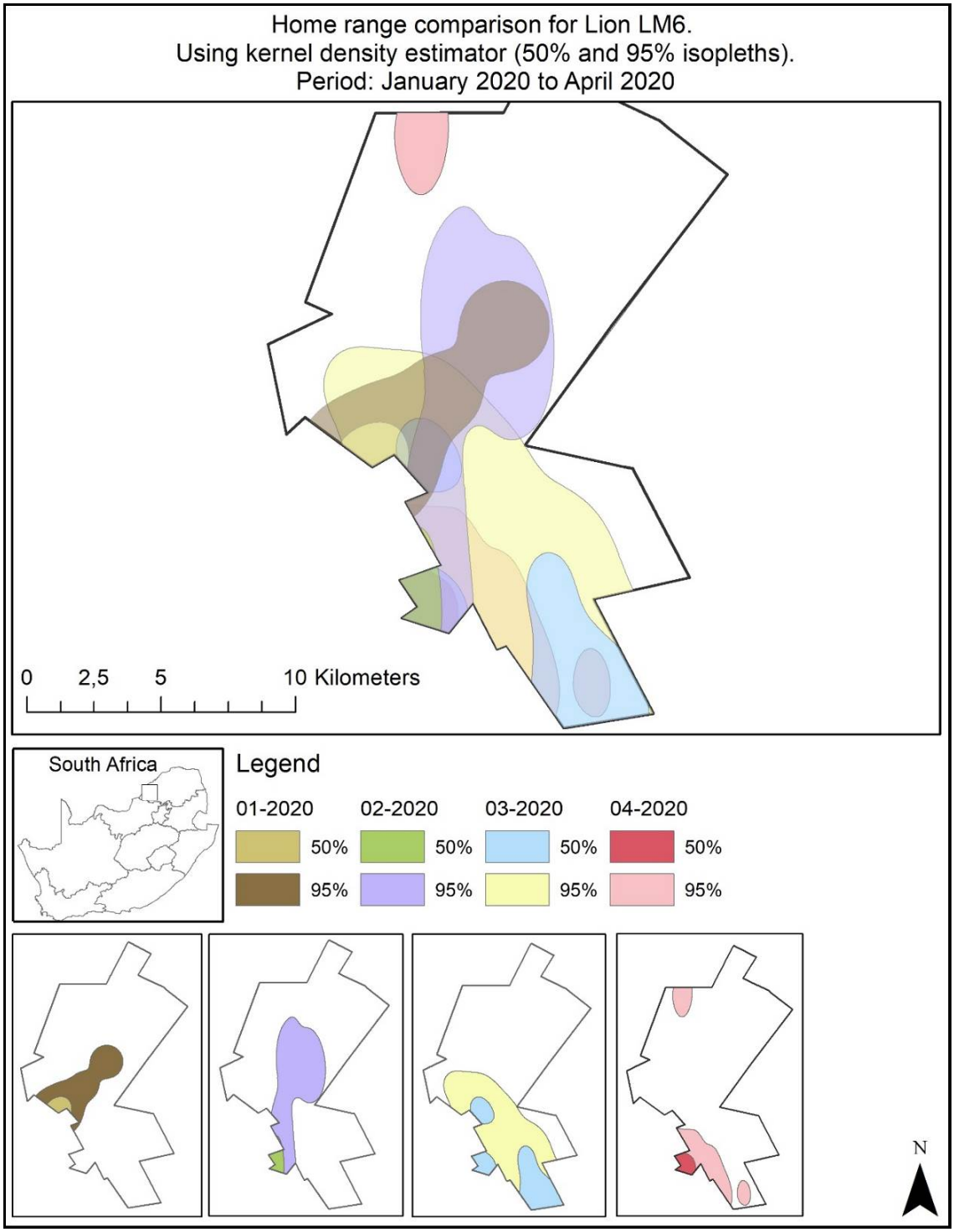


Figure 4.21. Graphic illustration of the gradual extension of the spatial utilisation by Lion LM6 for the first four months after being released from the boma on 26 January 2020. The spatial utilisation for January was from 27 to 31 January 2020.

Lion LM6 gradually started expanding his home range and by 19 October 2020 he was observed in the presence of Lioness LF1 [Timeline 16; event (9)] (see section 4.3). On this first encounter, Lion LM6 and Lioness LF1 spent 14 days together with a slight break in their engagement between 21 and 24 October 2020. It is reasonable to believe that mating occurred, however it could not be confirmed.

4.9.3 Timeline of events for Lion LM6 from December 2020 to October 2021

Timeline 17; event (10): Almost one month after the first encounter between Lion LM6 and Lioness LF1, an altercation occurred between Lion LM6, Lioness LF1 and her three large cubs [Litter 2 (LF1)]. The interaction became violent and Lion LM6 asserted his dominance over the other four lions (Lioness LF1, and three large cubs, Lion LM7 and Lionesses LF7 and LF8). The interaction is described in detail in section 4.3.

Shortly after this event, Lion LM6 was observed in the central part of the Reserve where he interacted with Lionesses LF5 and LF6 [Litter 1 (LF1) and Litter 1 (LF2)] and Lion LM7 [Litter 2 (LF1)]. The interaction between the four lions could only be observed for a short while before the lions moved into thick brush; however, the interaction seemed peaceful.

One day later, 16 December 2020, Lion LM6 and Lioness LF5 were recorded engaging in mating behaviour [Timeline 17; event (11)]. This grouping of the two lions lasted four days whereafter Lioness LF5 was observed to be on her own again and Lion LM6 returned to the southern region of the Reserve Timeline 17; event (12): After returning to the southern region of the Reserve, Lion LM6 was often accompanied by Lioness LF1. On 5 February 2021 the two lions were joined by Lioness LF8.

Lion LM6 clearly showed interest in consorting Lioness LF8 but was rejected by the lioness. Lioness LF1 layed close to Lioness LF8 and vocalised toward Lion LM6 when he presumably attempted to consort with Lioness LF8 (Slides 4.45 – 4.52).

Lion LM6 clearly asserted dominance over the two lionesses. On 17 February 2021 Lion LM6 was observed mating with Lioness LF8.

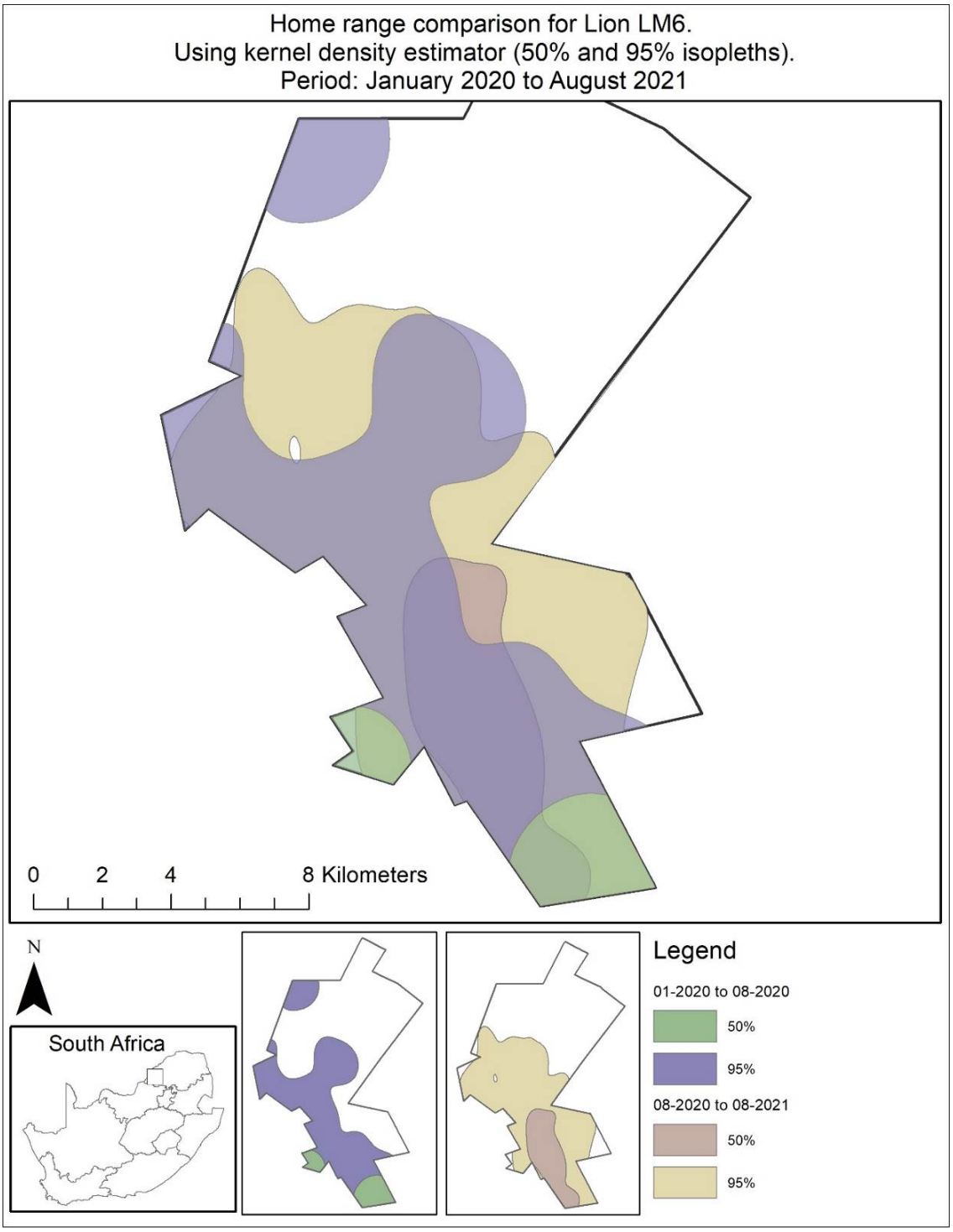


Figure 4.22. Graphic illustration of the change in spatial utilisation of the Reserve by Lion LM6 after the sub-adult males were relocated on 26 August 2020. The blue area in the northern corner is the area where Lion LM6 was relocated to after he escaped from the part of the Reserve that is enclosed with an electrified fence.

Timeline 17; event (13): In mid-February 2021, the data from the satellite GPS collars indicated a significant reduction in spatial utilisation by Lioness LF1. By 26 February 2021, the birth of a litter of cubs [Litter 3 (LF1)] was confirmed. This was the first litter of cubs sired by Lion LM6 on the Reserve (section 4.3).

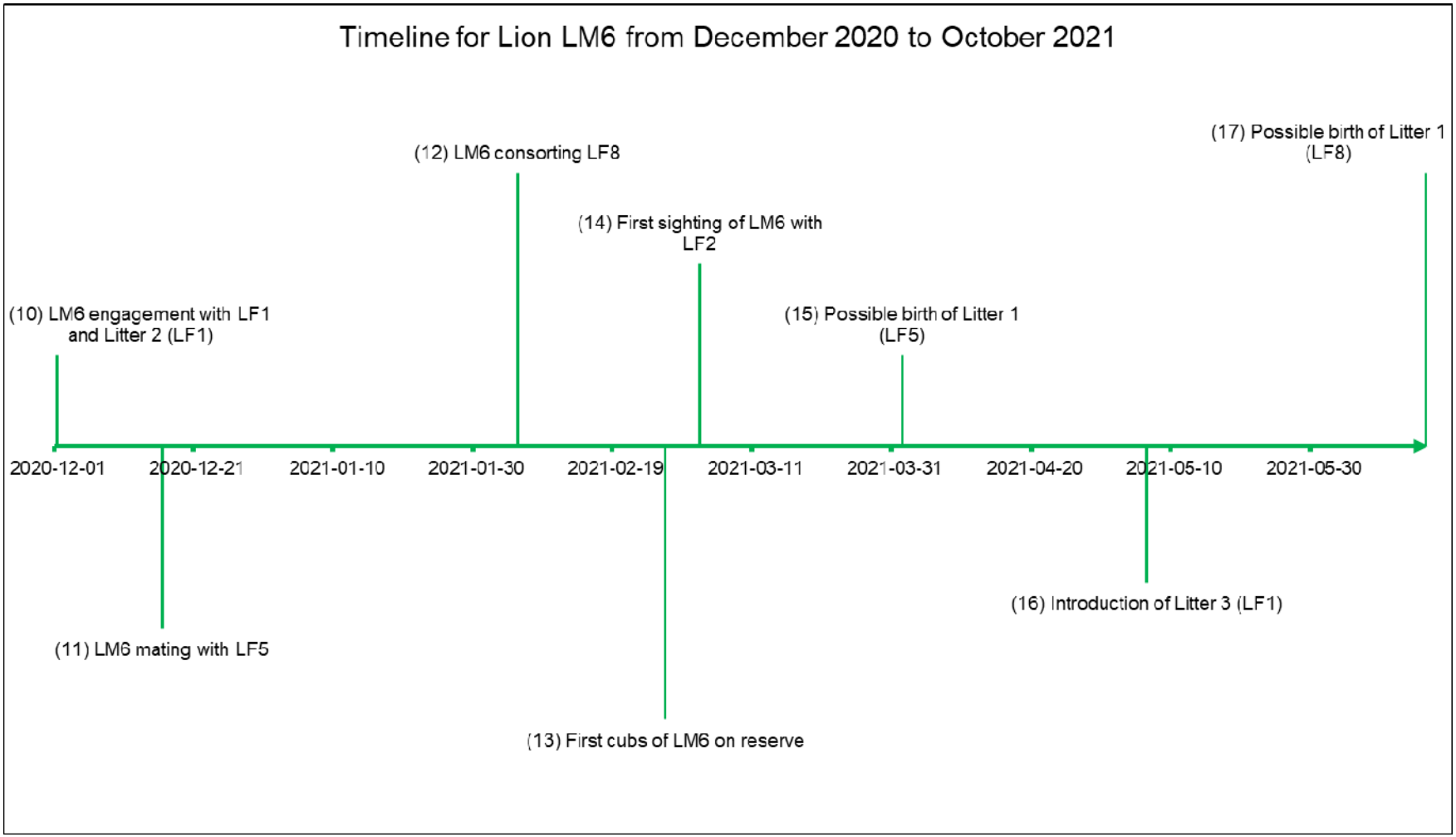
By that time, Lion LM6 had been in the presence of all the resident lionesses on the Reserve, except for Lioness LF2. The latter was still in a group with her four cubs [Litter 2 (LF2)] and the large male cub (Lion LM7) of Litter 2 (LF1).

Timeline 17; event (14): On 3 March 2021, the first record of Lion LM6 with Lioness LF2 was observed. The interaction was not peaceful and resulted in several injuries to both Lion LM6 and Lioness LF2 (see section 4.4). A second interaction between the two lions was observed on 4 May 2021. This time Lioness LF2 was accompanied by her four large cubs [Litter 2 (LF2)] and Lion LM7. The group of lions avoided physical contact with Lion LM6. It was only on 10 May 2021 that Lioness LF2 was observed voluntarily staying in the presence of Lion LM6. No mating was observed, but Lioness LF2 adopted submissive behaviour towards Lion LM6 (see section 4.4).

Timeline 17; event (15): Following the mating observed between Lion LM6 and Lioness LF5, the latter gave birth to a litter of cubs in April 2021. As explained in section 4.8, this was the first litter of a second-generation (F2-generation) cubs born on the Reserve. The first evidence of the birth of the cubs was confirmed in June 2021, however, considering the noted reduction in spatial utilisation by Lioness LF5, and the observed physical size of the cubs the estimated date of birth was assumed being in April 2021.

Timeline 17; event (16): The first introduction of Lion LM6's first litter of cubs [Litter 3 (LF1)] was not recorded, however on 6 May 2021 Lion LM6 was seen in the presence of Lioness LF1 and her two cubs. No interaction could be recorded because of the dense vegetation. On 20 May 2021, when Lioness LF1 was sedated to replace her satellite GPS collar with its depleted battery, Lion LM6 was interacting with the two small cubs of Litter 3 (LF1). The interaction was peaceful and Lion LM6

appeared tolerant towards the two small cubs who were engaging in playful behaviour with him.



Timeline 17. Illustrating a timeline of important events (numbered in chronological order) for Lion LM6 on the Reserve from December 2020 to October 2021.

Slides 4.45 – 4.52. The interaction between Lion LM6 and Lionesses LF1 and LF8, showing Lion LM6's interest in Lioness LF8 and his dominance over both females.

Timeline 17; event (17): Lioness LF8 [Litter 2 (LF1)] was the next female to give birth to cubs sired by Lion LM6. Even though the first sighting of the cubs occurred on 11 August 2021 it is believed that the cubs were born in early July 2021.

Lion LM6 continued to move between the different females/groups of females on the Reserve. On 5 August 2021, Lion LM6 moved to the northern region of the Reserve where he joined with Lioness LF6. This was the first recorded interaction between these two lions since their short interaction on 15 December 2020.

Since being released on the Reserve, Lion LM6 was positively identified with 16 prey kills, mostly warthog (*P. africanus*); n =8 (50%). The notes showed a high incidence of warthog (*P. africanus*), especially during the early periods after being released from the boma on 26 January 2020, when Lion LM6 was keeping to himself. On several occasions it was recorded that Lion LM6 layed next to an active warthog (*P. africanus*) burrow and/or digging at the opening of the burrow. Other species associated with killings by Lion LM6 included aardvark (*O. afer*), blue wildebeest (*C. taurinus*), gemsbok (*O. gazella*), impala (*A. melampus*), ostrich (*S. camelus*), waterbuck (*K. ellipsiprymnus*) and zebra (*E. quagga*).

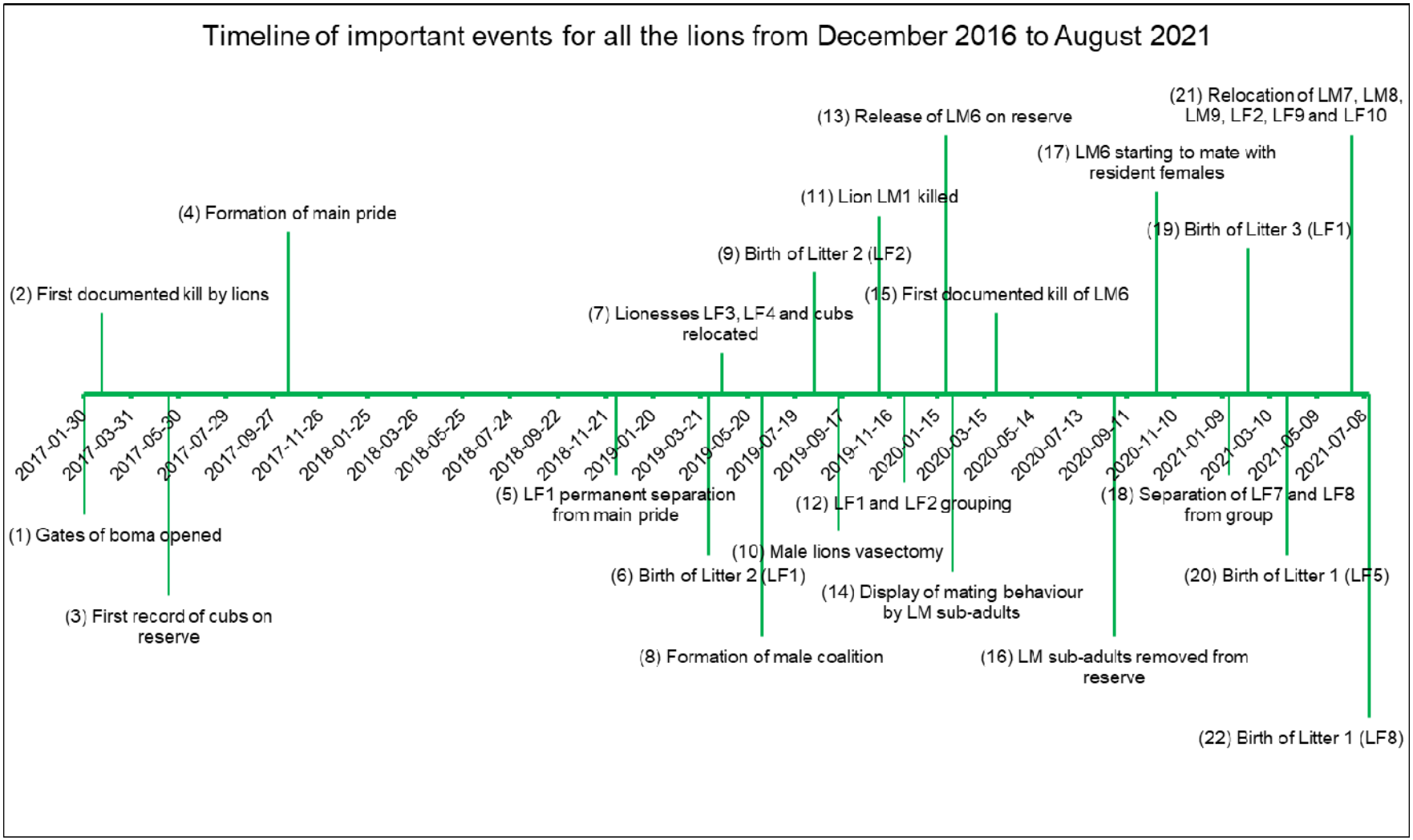
4.10 Summary of important events for the lion population on the Reserve

Given the detailed discussions in sections 4.1 to 4.9, a synopsis of events is presented in Timeline 18.

Timeline 18; event (1): On 30 January 2017 the gates of the boma were opened and the five founding African lions (adult Lion LM1 and the large female cubs, Lionesses LF1, LF2, LF3 and LF4) released on the Reserve. The five lions were all bred and reared in captivity. During their six weeks stay in the boma, one of the large female cubs (later designated Lioness LF1) and the adult male (Lion LM1) were fitted with satellite GPS collars to track their movements once released from the holding boma. For at least the first month after being released, the five lions remained within a 2 km radius from the boma.

Timeline 18; event (2): The lions were not provided with any food after being released from the boma. On 23 February 2017, one month after being released from the boma, one of the lionesses was seen killing an adult male kudu (*T. strepsiceros*) at a waterhole approximately 2 km from the boma. The female was unidentified at the time and the only lion present at the kill. The following day, one of the other lionesses (Lioness LF1) and the adult male (Lion LM1) was found at the carcass. This was the first documented occurrence of any of the lions providing for themselves for the entirety of their existence.

Timeline 18; event (3): Shortly after the release of the lions it was clear that this group did not conform to the grouping behaviour commonly associated with African lions (*P. leo*) (Packer & Pusey, 1983b). Alternate groupings of different females and the adult male was observed. As alluded to in previous sections, the notes kept at that point were not scientifically structured and could have led to inaccurate assessments of the behaviour. Another explanation could be that the lionesses had separated from the group to give birth to litters of cubs (Packer & Pusey, 1983b). The first litter of cubs born on the Reserve was recorded on 18 May 2017. The cubs (initially three) were already several weeks old at the time of the discovery. By the end of July 2017 all four the lionesses had given birth to their first litter of cubs.



Timeline 18. Illustrating a timeline of important events (numbered in chronological order) for the lion population on the Reserve from December 2016 to August 2021.

Timeline 18; event (4): Shortly after the birth of the cubs (October 2017), the lionesses and male lion began to form grouping patterns; Lionesses LF1 and LF2, each with three cubs [Litter 1 (LF1) and Litter 1 (LF2)] were regularly observed in a group with Lion LM1, whilst Lionesses LF3 and LF4 largely remained solitary with their two cubs and four cubs respectively. Similar results were observed by Kilian (2003) when a group of lions was released on Welgevonden Private Game Reserve, South Africa. The large group of lions (Lion LM1, Lioness LF1, Lioness LF2 and their cubs) became known as the main pride on the Reserve. The group remained intact until December 2018 when Lioness LF1 permanently separated from the group, leaving her three large cubs with Lioness LF2, Lion LM1 and the three large cubs of Lioness LF2 [Timeline 18; event (5)].

Timeline 18; event (6): Lioness LF1 left the group sooner than expected, as the first sighting of her second litter of cubs (and possibly the reason for leaving the group) was in May 2019. The cubs [Litter 2 (LF1)] were estimated to be 4-6 weeks old at the time of the sighting and thus born between March and April 2019.

All six the large cubs from the first litters of Lionesses LF1 and LF2 remained in a group (main pride) with Lioness LF2 and Lion LM1. Lionesses LF3 and LF4 (and their cubs) remained solitary, only occasionally pairing up with each other for short periods of time. Both lionesses remained in the central and southern regions of the Reserve with their home ranges overlapping considerably (Figures 4.11 & 4.12). In April 2019 the lions on the Reserve exceeded the carrying capacity and management decided to relocate Lioness LF3, with her two large cubs and Lioness LF4, with her four large cubs [Timeline 18; event (7)].

Timeline 18; event (8): When Lioness LF2 also left the main pride on 31 July 2019 it caused the remaining members (two large female cubs, four large male cubs and Lion LM1) to split up according to their sexes. The four large cub males (later designated Lions LM2, LM3, LM4 and LM5) and their father (Lion LM1) formed a coalition with a nomadic tendency. At this time the two large female cubs (Lionesses LF5 and LF6) preferred the northern region of the Reserve as their home range.

The dispersal of Lioness LF2 from the main pride in July 2019 was explained by the birth of her second litter of cubs [Litter 2 (LF2)] in September 2019 [Timeline 18; event (9)].

The nomadic coalition of male lions (adult male Lion LM1 and sub-adult males Lions LM2, LM3, LM4 and LM5) utilised almost the entire surface of the Reserve, only avoiding the mountainous areas to the north-east (Fig. 4.13).

The sub-adult males and the sub-adult females were approaching the age of sexual maturity (Smuts *et al.,* 1978). Therefore, On 12 September 2019 all five males (old adult male Lions LM1, and the four sub-adult males Lions LM2, LM3, LM4 and LM5) were bi-laterally vasectomised to eliminate any risk of inbreeding within the existing lion population [Timeline 18: event (10)]. The procedure would prove to be vital when, on 3 February 2020, the sub-adult male lions engaged in mating behaviour with their female siblings (Lionesses LF5 and LF6) [Timeline 18; event (14).

Timeline 18; event (11): Six weeks later, on 3 November 2019, Lion LM1 was shot with a hunting rifle (see section 4.2). His body condition had deteriorated to an extant where it was believed he would not recover. Lion LM1 was 13 years old at the time. The four sub-adult males (Lions LM2, LM3, LM4 and LM5) continued with their nomadic lifestyle and had proven to be completely self-sufficient.

Timeline 18; event (12): On 1 December 2019 Lionesses LF1 and LF2 had re-grouped. Both lionesses were joined by their second litter of cubs (three and four cubs respectively). Again, the grouping was a-typical in terms of consistency (Packer & Pusey, 1983b) and both lionesses and their respective cubs were recorded in separate groups on several occasions throughout the rest of the study. Neither of the lionesses joined with the two sub-adult females (Lionesses LF5 and LF6) after separation from the main pride and only Lioness LF1 was recorded to allow the company of the nomadic sub-adult males for a brief period of time (see section 4.3).

Further to the management of the genetic stock of the African lion (*P. leo*) population on the Reserve, an unrelated, captive-bred, adult male lion (Lion LM6) was released on 26 January 2020 [Timeline 18; event (13)]. Like the release of the five founder

lions in 2017, no pre-release training/"re-wildling" (Abell *et al.,* 2013) was practised with Lion LM6. Shortly after being released, the male displayed signs of homing behaviour (Hunter, 1998a); however, the presence of the sub-adult male coalition was presumably also affecting the spatial utilisation of Lion LM6 (see section 4.9).

Even though Lion LM6 maintained a satisfactory body condition in the first couple of weeks post-release, his first documented kill was made on 3 March 2020 [Timeline 18; event (15)]. The need to supply Lion LM6 with food post-release never arose.

In August 2020, it became apparent that Lion LM6 would not gain access to available lionesses in the presence of the sub-adult male coalition. On 26 August 2020 all four sub-adult males [from Litter 1 (LF1) and Litter 1 (LF2)] were relocated from the Reserve [Timeline 18; event (16)]. The males were aged between 36 and 40 months.

Timeline 18; event (17): By October 2020 the grouping of Lionesses LF1, LF2 and their second litters of cubs [Litter 2 (LF1) and Litter 2 (LF2)] had become more disrupted as Lioness LF1 regularly left her two large cubs with Lioness LF2 (and her four large cubs) for extended periods. From 23 October 2020 Lioness LF1 interacted with Lion LM6, perhaps explaining the separation from her cubs. Suspected mating behaviour was confirmed on 26 February 2021 with the discovery of the third litter of cubs from Lioness LF1 [Litter 3 (LF1)]. This was the first litter of cubs sired by Lion LM6 [Timeline 18; event (19)].

Lion LM6 had extended his spatial utilisation considerably by October 2020 (Fig. 4.21) and in December 2020 he was recorded engaging in mating behaviour with one of the lionesses in the northern region of the Reserve (Lioness LF5). Lion LM6 appeared to have assumed a nomadic lifestyle and was observed in the presence of various lionesses across the Reserve.

Timeline 18; event (18): By mid-January 2021 the two sub-adult lionesses from Litter 2 (LF1), Lionesses L7 and LF8, separated from the group of Lioness LF2, her four large cubs and Lion LM7 [the large cub male from Litter 2 (LF1)]. By the end of March 2021, Lioness LF8 and Lion LM6 had been recorded in several mating

incidences. The mating incidences involving Lion LM6 and the three lionesses referred to above, appeared to be in the absence of any other lions.

Once again, the resident African lion (*P. leo*) population became too large and deemed unsustainable for the prey population of the Reserve and the management of the Reserve decided to relocate certain individuals. In the last week of June 2021, Lions LM7, LM8, LM9 and Lionesses LF2, LF9 and LF10 were sedated by the Veterinarian and relocated to another reserve [Timeline 18; event (21)].

Timeline 18; event (20 & 22): In addition to Litter 3 (LF1), the new adult Lion LM6 had sired two other litters by August 2021 (Fig. 4.20), namely: (i) Litter 1 (LF5) was born to Lioness LF5 in April 2021, and consisted of three cubs of unknown sex, and (ii) Litter 1 (LF8) was born to Lioness LF8 in July 2021, and consisted of four cubs of unknown sex. Both litters were F2-generation wild managed cubs, because Lionesses LF5 and LF8 were born on the Reserve (F1-generation lions) in two separate litters to Lioness LF1 (Fig. 4.3; Timeline 19).

5 Timeline of introductions, births, and relocation of the lionesses (LF1 to LF8) and the breeding males (LM1 and LM6) on the Reserve

The detailed chain of important events (shown in previous chapters as Timelines 1 to 18, supported with appriopriate information provided in the text) is summarised below to accentuate the most important findings in this study.

The introduction on 27 January 2017 of the four founder lionesses (LF1, LF2, LF3 and LF4) is shown in Timeline 19. The births of successive litters of offspring, and relocation of some individuals, are also shown during different years.

The introduction of the founder male (Lion LM1) on 27 January 2017 and his termination on 3 November 2019, as well as the introduction of the new adult breeding male Lion LM6 on 26 January 2020, are also shown in Timeline 19.

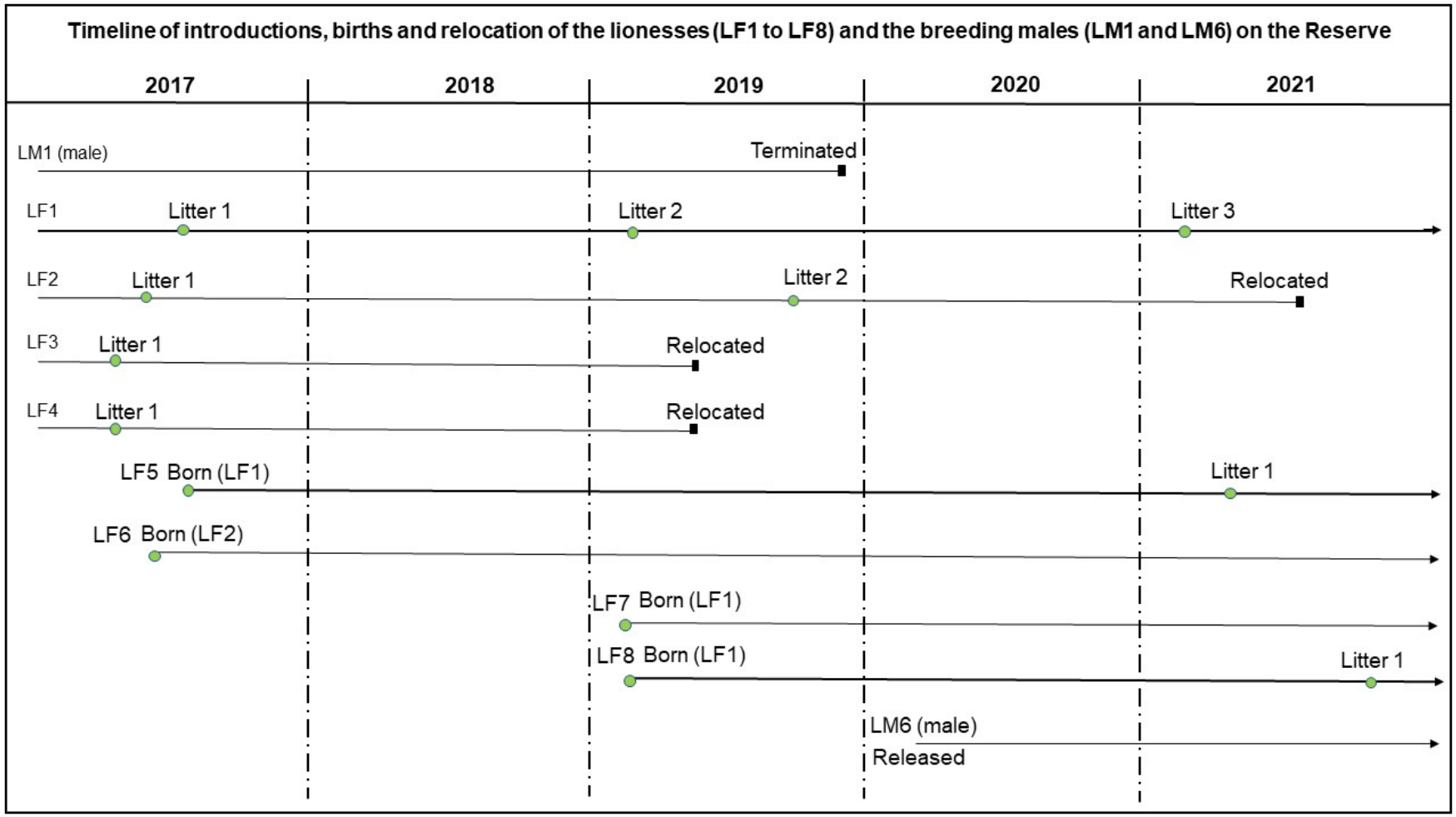
Note the following (indicated with darker lines in Timeline 19) for founder **Lioness LF1** and her offspring:

(i) **Lioness LF5** (an F1-generation lion) was born in Litter 1 (LF1) in July 2017 [see section 4.3];

(ii) **Litter 1 (LF5)** (F2-generation of lions) was born in April 2021 [see section 4.8.4];

(iii) **Lioness LF8** (an F1-generation lion) was born in Litter 2 (LF1) in April 2019; and

(iv) **Litter 1 (LF8)** (F2-generation of lions) was born in August 2021 [see section 4.4.3].



Timeline 19: Illustration of the introduction of the four founder lionesses (LF1, LF2, LF3 and LF4) and the founder male (Lion LM1), as well as the births of offspring in successive years, focusing on the female offspring and the introduction of the breeding male (Lion LM6). Lioness LF2 and her Litter 2 were relocated, as well as Lionesses LF3 and LF4 and both their litters.

6 Home range selection and the utilisation of resources

The size of home ranges for African lions varies greatly across its distribution range. Stander *et al.* (2018) found that in arid regions such as the Namib Desert, male lions could dominate areas of 40 000 km^2, whilst females used considerably smaller home ranges of up to 12 500 km^2. In areas with higher prey densities, such as the semi-arid Lowveld in the Savannah Biome of South Africa, home ranges tend to be considerably smaller, namely 195 km^2 for males and 84 to 172 km^2 for females (Turner, 2005).

The distribution of resources like water and food, and social factors are the most important factors influencing the home range sizes of large carnivores such as lions (Macdonald, 1983; Stander *et al.,* 2018; Spong, 2002). The size of the pride can be an additional factor influencing home range size (Eloff, 2016).

Overlapping of home ranges between different prides of lions are not uncommon (Eloff, 2016), although the simultaneous utilisation of the same space is less likely, especially in arid environments where home ranges are larger (Stander *et al.,* 2018).

6.1 Utilisation of the available resources on the Reserve

The permanent water resources on the Reserve, mostly old livestock water points, are evenly distributed and water is available throughout the year (Fig. 6.1). Consequently, the large number of suitable prey species present (see Chapter 2; Table 2.2) was regarded as readily available in most parts of the Reserve (Fig. 6.2).

According to Funston *et al.* (2001), the hunting success of lions are affected by (i) lion-related factors (*i.e.,* sex and group size), (ii) environmental factors (*i.e.,* suitable cover, moon light, and wind direction), and (iii) prey-related factors (*i.e*., herd size and species).

From January 2017 to November 2021, 110 kills by the lions were confirmed. The positions of the confirmed kills in relation to the areas which were mechanically cleared and transformed into open savannah-like habitat (see section 2.1) are shown in Figure 6.3.

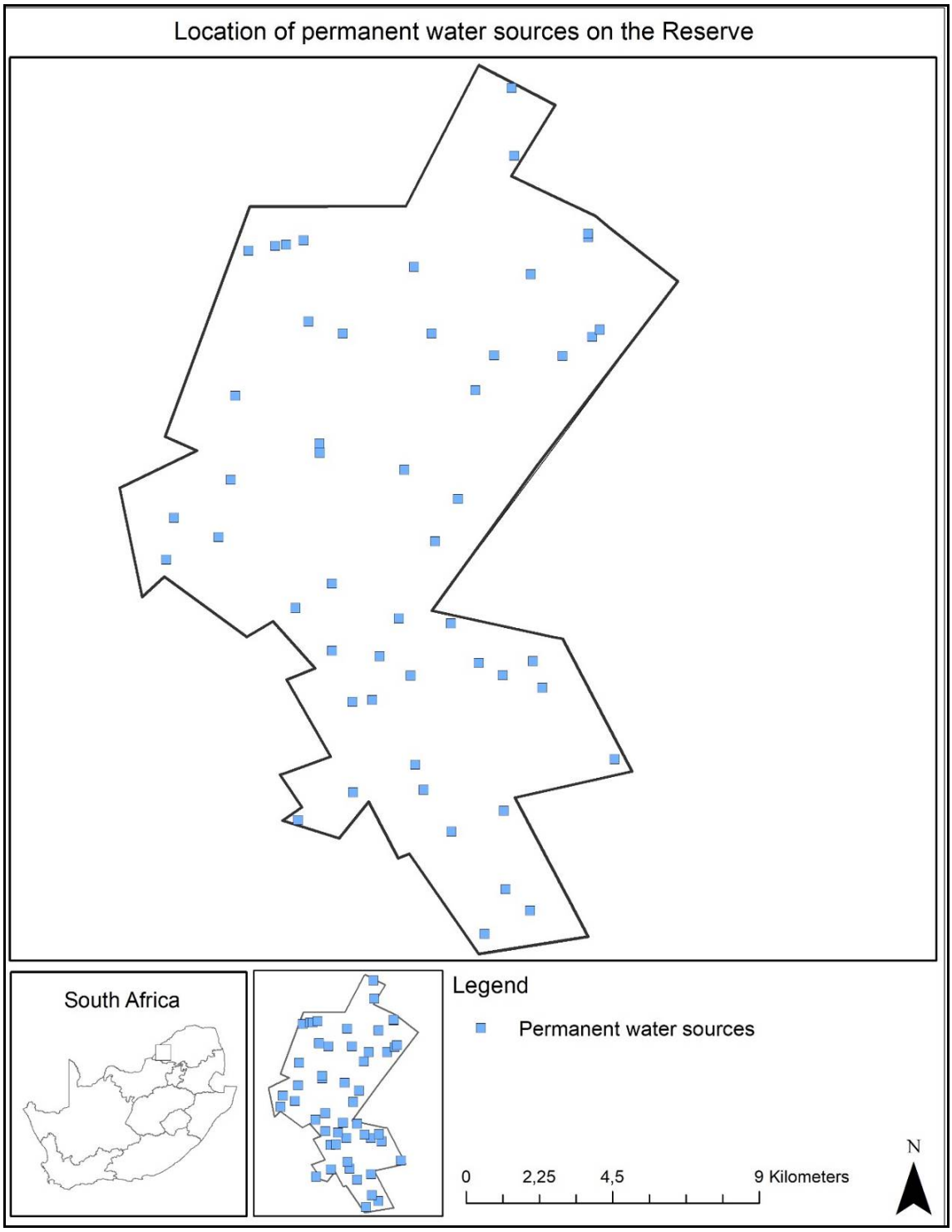


Figure 6.1. Schematic illustration of the location of permanent water sources on the Reserve; the vast majority are man-made livestock water points (troughs).

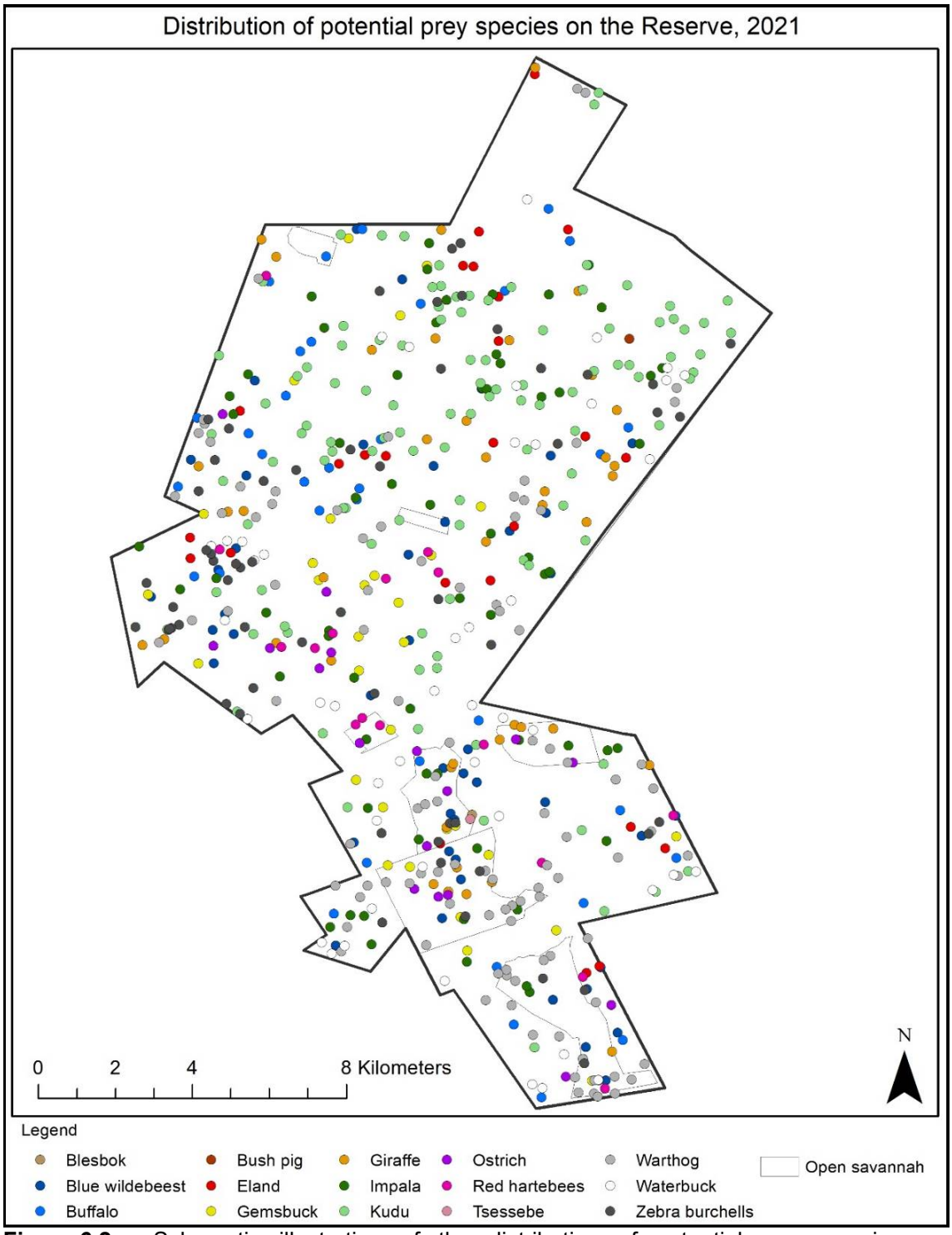


Figure 6.2. Schematic illustration of the distribution of potential prey species as determined during the annual aerial wildlife survey in September 2021.

Only 23% (n = 26) of the kills could be confirmed in these cleared open areas, while the rest of the confirmed kills occurred in more densely vegetated areas. However, it is acknowledged that many kills could not be confirmed due to inaccessibility of kill

sites and, therefore, a bias was introduced towards kills in the open areas. Furthermore, the road network on the southern parts of the Reserve is more developed, allowing easier access by human patrols to kill sites. This exacerbated inaccuracies in collecting data of successful hunts and kills by the lions. Furthermore, a bias may have been created towards larger prey species, because the lions did not remain long at the kill sites of smaller prey species (Tambling *et al.,* 2010). It caused difficulty in identifying kill sites with the satellite GPS collars (clusters of GPS fixes), because the specific time intervals between transmitting locations were longer than the stay at the kill; the satellite GPS collars were mostly set to report GPS locations at 4-hourly intervals (see section 3.1.2). Successful kill sites of smaller prey species, such as warthog (*P. africanus*) and impala (*A. melampus*), were mostly discovered by chance.

If African lions require approximately 5-7 kg of meat per lion per day to survive (Schaller, 1972), it is accepted that a very small percentage of the actual kills made by the lions were recorded. It must be remembered that lions are feast and famine feeders and do not eat daily (Schaller, 1972). The lions on the Reserve were not provided food by management, and those remaining are still self-maintaining.

Furthermore, when considering the decrease in prey species on the Reserve (Table 2.2, Chapter 2), the lion population had a markedly larger impact on the ungulate population than what was deduced from the actual kill sites.

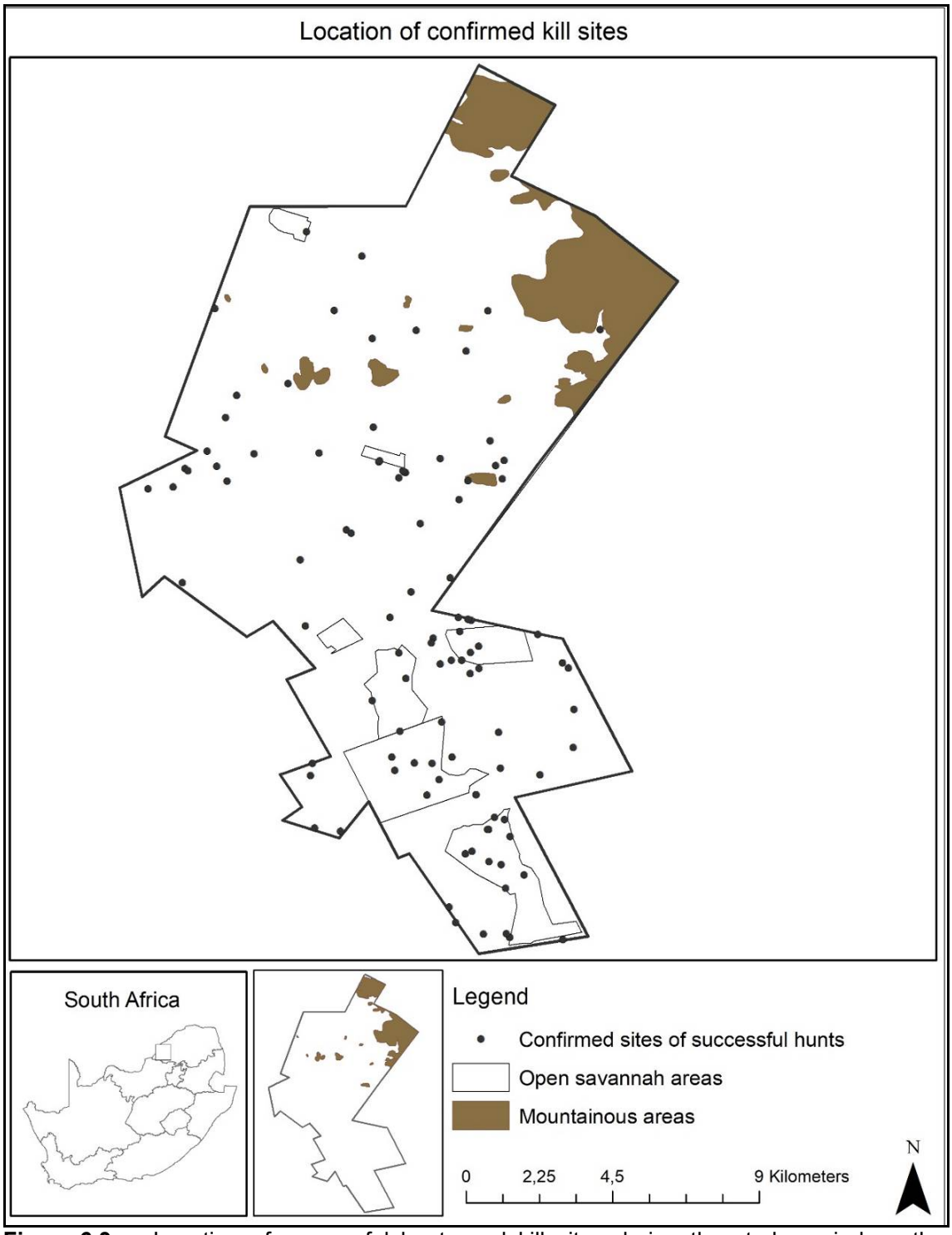


Figure 6.3. Location of successful hunts and kill sites during the study period on the Reserve in relation to open savannah-like areas and mountainous regions.

6.2 Utilisation and home range selection by specific lions on the Reserve

The home range selections for specific lions (LM1, LF1, LF2, LF3, LF4, LM sub-adults, LF5 and LM6) on the Reserve from January 2017 to August 2021 are illustrated in Figure 6.4. Except for Lionesses LF3 and LF4, which were never fitted with satellite GPS collars, the data was provided by the satellite GPS collars fitted to the lions and is thus relevant to those specific time periods (Chapter 3; Table 3.1). Comparisons of home range selections during wet and dry seasons (see section 2.2)[14] are shown in Figure 6.5 for specific lionesses, and in Figure 6.6 for specific males.

The home range sizes of specific lions in this study were comparable to that of lions in a similar habitat (Turner, 2005). It should be noted that the selected home ranges for all lions would have been larger had they not been contained (restricted) by the perimeter fences of the Reserve. Analysing the home ranges (see section 3.2), the areas extending beyond the perimeter fences of the Reserve were eliminated. It was obvious that all lions avoided the more mountainous area in the north-eastern part of the Reserve (Fig. 6.4).

6.2.1 Spatial utilisation by Lioness LF1

Lioness LF1 utilised a large percentage (78%) of the available habitat (see section 3.2 for description of the technique) on the Reserve (95% = 164 km^2; 50% = 45.98 km^2). The 50% core range of Lioness LF1 is most likely linked with the three sites where she gave birth to her cubs (Figures 4.4, 4.6 & 4.8) and thus spent long periods of time in the vicinity. The home range selection for Lioness LF1 during wet and dry seasons did not vary considerably (Fig. 6.5). However, the 50% core range areas for Lioness LF1 during the dry season (Fig. 6.5) was slightly larger and more centralised on the Reserve.

[14] The criteria for defining wet and dry seasons were based on the long-term data gathered from nearby weather stations as explained in section 2.2.

6.2.2 Spatial utilisation by Lioness LF2

Lioness LF2 utilised the largest available area on the Reserve (95% = 188.69 km^2; 50% = 70.92 km^2) for all females/groups of females. A small portion of her 50% core range in the northern region of the Reserve (Fig. 6.4) can be attributed to the birth of her second litter, and a subsequent reduction in spatial utilisation for an extended period (Fig. 4.10). Lioness LF2 mostly utilised the southern region of the Reserve after the birth of her second litter and remained there until she was removed from the Reserve (26 June 2021; see section 4.4). As with Lioness LF1, the differences in wet and dry season home range selection for Lioness LF2 was influenced by the birth of cubs more than it was by seasonal changes in resource availability (Fig. 6.5).

6.2.3 Spatial utilisation by Lionesses LF3 and LF4

As indicated previously, Lionesses LF3 and LF4 were never fitted with satellite GPS collars and therefore, limited amounts of spatial utilisation data are available from visual observations only. However, both these females were seen only within the central and southern regions of the Reserve (Fig. 6.4). Their total home range size was markedly smaller compared to the other lionesses. The period for data collection was shorter than for the other lions, because Lionesses LF3 and LF4 were sedated and relocated in early 2019 (see sections 4.5 & 4.6). Therefore, because of the limited available data, the differences in wet and dry season home range selection could not be calculated for Lionesses LF3 and LF4.

6.2.4 Spatial utilisation by Lionesses LF5 and LF6

Lionesses LF5 and LF6 spent a large part of the time on the Reserve together, separating permanently after the birth of Lioness LF5's first litter of cubs in June 2021 (see section 4.8). Lionesses LF5 and LF6 remained in the northern region of the Reserve after separating from the main pride in June 2019 (see section 4.8).

Only Lioness LF5 was fitted with a satellite GPS collar (as a matter of convenience because Lionesses LF5 and LF6 largely remained together), therefore the following discussion will refer to Lioness LF5 only. Lioness LF5 utilised the smallest portion (41.8%) of all lions of the available habitat on the Reserve (**Appendix II**, Table 1). There was no marked difference in the home range size during wet and dry seasons

for Lioness LF5 (Fig. 6.5). The difference in core range (50% isopleth) location between wet and dry season (Fig. 6.5) could possibly be attributed to the birth of Lioness LF5's first litter in June 2021 (see section 4.8).

Figure 6.4. The selected home ranges for specific lions (LM1, LF1, LF2, LF3, LF4, LM sub-adults, LF5 and LM6) on the Reserve.

Figure 6.5. Graphic comparison of the wet and dry season home range selection for specific lionesses on the Reserve.

6.2.5 Spatial utilisation by Lion LM1

Lion LM1 mostly remained in the company of other lions on the Reserve (see section 4.2). Therefore, it is expected that his home range would overlap largely with that of

the other lions, especially in the case of Lionesses LF1 and LF2, and the sub-adult males, Lions LM2, LM3, LM4 and LM5. There is a noticeable difference in the home range size and selection during wet and dry seasons by Lion LM1 (Fig. 6.6). However, this difference was more likely due to his sudden change to a nomadic lifestyle with the sub-adult males (Lions LM2, LM3, LM4 and LM5) after the separation of the main pride on 7 June 2019, than to seasonal changes and resource availability. There is a clear change in home range and core range selection by Lion LM1 after the dispersal from the main pride on 7 June 2019 (Figures 4.1 & 4.2).

6.2.6 Spatial utilisation by Lions LM2, LM3, LM4 and LM5

The total home range size for the group of sub-adult males (Lions LM2, LM3, LM4 and LM5) was the largest for all lions on the Reserve (95% = 198.7 km^2 and 50% = 98.44 km^2). This is most likely due to their adoption of a nomadic lifestyle (see section 4.7). The group of sub-adult males utilised 94.6% of the available habitat, only avoiding the high-altitude mountainous areas in the north east (Fig. 6.4). The difference in home range selection during wet and dry seasons was not marked. However, the difference in the locations of the core range (50% isopleth) is noticeable (Fig 6.6). The core range location of the sub-adult males was believed to have been influenced by (i) the release of an adult male lion (Lion LM6) in January 2020; (ii) the availability of sexually mature lionesses in the northern region of the Reserve; and (iii) the sub-adult males becoming sexually mature (see section 4.7).

6.2.7 Spatial utilisation by Lion LM6

Lion LM6 gradually increased his home range after being released from the boma in January 2020 (Fig. 4.21). Initially, Lion LM6 spent most of the time along the southern border of the Reserve and displayed a degree of homing behaviour (see section 4.9). It is believed that the selection of home range was influenced by the presence of the group of sub-adult males (Lions LM2, LM3, LM4 and LM5) because his home range expanded soon after the removal of the sub-adult males (26 August 2020; see sections 4.7 & 4.9). Until August 2021, Lion LM6 utilised 56.1% of the available habitat on the Reserve (**Appendix II**, Table 1). The small portion of spatial utilisation in the north western corner of the Reserve (Fig 6.4) was coincidental,

because Lion LM6 was released there again after he had escaped from the electrified boundaries of the Reserve in May 2020 (see section 4.7). There is a marked difference in home range size between wet and dry seasons for Lion LM6 (Fig. 6.6), although this is most likely attributable to Lion LM6's gradual shift to a nomadic lifestyle moving between the sexually available lionesses on the Reserve after the removal of the group of sub-adult males just before the start of the wet season of 2020-2021.

It is interesting to note that the home range sizes during the dry season for all the lions, except Lion LM6, was larger than the home range sizes during the wet season (**Appendix II**, Table 1). Possible reasons have been alluded to previously.

6.3 Habitat selection and prey utilisation

There was no evidence that the lions preferred any habitat type (resource availability) (Fig. 2.5 & 6.4), but rather that their home range and core range selections were influenced by the presence (or absence) of the other lions on the Reserve (social influences). The evenly distributed permanent water points most likely influenced the distribution of the prey species on the Reserve accordingly (Fig. 6.1 & 6.2), which in turn could have caused the extended and overlapping home ranges of the lions.

The acquaintance of the five founder lions (Lion LM1 and Lionesses LF1, LF2, LF3 and LF4) with each other (see section 4.1) could have played a role in the sharing of home ranges, even though the lions did not remain in a group after being released from the boma in January 2017 (Kilian, 2003). There were several interactions between the lions during the study period (Chapter 4) attesting to their overlapping home ranges on the Reserve. Most of these interactions were peaceful.

Figure 6.6. Graphic comparison of the wet and dry season home range selection for specific lions on the Reserve.

The effect of the lions on the prey populations of the Reserve is clear from Table 2.2 (Chapter 2). It should be considered, however, that the presence of the lions was not the only possible cause for decreases in prey population numbers, because the prey

population sizes were actively managed by the management of the Reserve. Prey selection by the lions on the Reserve can be concluded by looking at the reduction of population sizes for warthog (*P. africanus*), waterbuck (*K. ellipsiprymnus*), gemsbuck (*O. gazella*), eland (*T. oryx*) and kudu (*T. strepsiceros*) from 2019 to 2021 (Table 2.2). The population sizes of these species were not synthetically altered by the management of the Reserve during this time. However, considering the presence of other large predators on the Reserve (see section 2.5), it is acknowledged that the reduction in prey population sizes cannot be attributed to the lions alone.

It is important to note that the density of suitable prey species (see section 2.5) was controlled by the management of the Reserve by supplementing (buying and offloading) populations below a certain quantity and removing (selling or culling) from populations which increased undesirably. Furthermore, the dietary requirements of the ungulate populations were augmented by supplementary feeding during the dry seasons (May-September). This could have caused animals to concentrate at specific areas on the Reserve, and consequently influenced the home range selection and hunting behaviour of the lions. However, ungulates in the northern region of the Reserve did not receive supplementary feeding and yet permanently sustained Lionesses LF5 and LF6, and some of the other lions temporarily.

7 Conclusions

The results obtained in this study are assessed against the five objectives set for the study (see Chapter 1, sections 1.1 to 1.5) and presented, discussed, and appropriately concluded.

7.1 The ability to form social groups in an extensive wild habitat

Social grouping of African lions (*P. leo*) in captivity is actively managed and manipulated along with "all vital rates and demographics" (Funston & Levendal, 2015). Therefore, the generally accepted scenario of lions forming groups or prides comprising related females (Packer *et al.,* 1990) is ignored and not allowed. No territory can be established, sufficient food is provided, no hierarchy exist at a carcass (Packer *et al.,* 1990), therefore competition and confrontation between individuals would theoretically seem unlikely in captivity.

The primary functions for formation of groups in wild African lions is (i) protection of territory and (ii) protection (survival) of young (Packer *et al.,* 1990). In captive situations the major threats to cub survival (infanticide and starvation) are not present and access to food (foraging success) is manipulated, therefore it is reasonable to accept that it is not necessary for lions in captivity to form social groups.

At the age of one year, four female cubs born in two separate litters (same father, but two different mothers) at a captive facility, were placed together in an enclosure of about 4 ha (see section 4.1). When they were released from the boma on the Reserve in January 2017 (Chapter 4), despite having spent more than a year together in the small enclosure at the captive facility, the large female cubs split up shortly afterwards.

The break-up could have been caused by several factors, namely (i) between April and June 2017 the young lionesses all gave birth to their first litters of cubs, and typical of pregnant lionesses nearing term they separated from other lions to give birth and nurse the new born cubs (Lehmann *et al.,* 2008; Packer & Pusey, 1983), (ii) the abundance of prey on the Reserve did not necessitate a need to form a large

group (Packer *et al.,* 1990), (iii) the absence of systematic close observations and recordings of the five founder lions during the initial period of post-release (Chapter 3), (iv) there was no real need for the lionesses to collectively protect their cubs from other lions and/or larger predators, (v) the genetic source of the large female cubs forced them into related sub-groups (Kilian & Bothma, 2003), and (vi) the tendency of lions to form small sub-groups spread over a common territory (Kilian & Bothma, 2003).

Lionesses tend to leave their prides when nearing term to give birth to cubs and usually return when the cubs are 4–8 weeks old (Packer & Pusey, 1983). Only Lionesses LF1 and LF2 were observed raising their cubs collectively, whilst Lionesses LF3 and LF4 largely remained solitary, only joining up with each other for short periods. It should be noted that Lionesses LF1 and LF2 were half-sisters from two different litters, having different mothers but a common father.

This initial grouping (see section 4.3) remained stable for almost two years until Lioness LF1 left the so-called main pride in 2019 to give birth to her second litter of cubs. Lioness LF1 did not return to the pride with her second litter of cubs, possibly because the pride had broken up after Lioness LF2 had also left to give birth to her second litter of cubs in June 2019. However, Lioness LF1 and LF2 temporarily joined up again after the birth of Lioness LF2's second litter. The rest of the initial so-called main pride comprised a nomadic coalition of four sub-adult males (Lions LM2, LM3, LM4 and LM5) and their father, the old adult Lion LM1, and then separated from the other the two sub-adult Lionesses LF5 and LF6, who had moved away from the nomadic coalition of five males.

The size of the Reserve might have influenced the way in which the lions structured groups, because the removal of the nomadic four sub-adult males (like what happens when sub-adult males are pushed out of natal prides) could have produced different results. Therefore, the management of a "wild managed" African lion population (Funston & Levendal, 2015), and specifically the way it is managed (Miller *et al*., 2013; 2015), can influence the social structure and formation of groups (prides).

Lioness LF5, the daughter of Lioness LF1, remained solitary after giving birth to her own first cubs in April 2021 and did not reunite with Lioness LF6, with whom she spent two years after leaving their natal pride at the age of two years in 2019.

Lioness LF8, the daughter of Lioness LF1, gave birth to her first litter of cubs at the age of 30 months and shortly afterwards reunited with Lioness LF7. In this study, the formation of so-called fission-fusion groups (Packer & Pusey, 1983b) was thus not consistent across all prides. This challenged the prerequisite to use a stable pride for *ex situ* reintroductions of lions as suggested by Bertram (1998).

The need for the lionesses to remain in groups or prides would not have been pressing because (i) the size of lion hunting groups is influenced by prey size (Packer & Pusey, 1990; Funston *et al.,* 2001) and (ii) the Reserve has a high density and diverse population of suitable prey of variable sizes (Table 2.2).

The grouping behaviour of the founder populations on the Reserve may seem abnormal but grouping of unrelated lionesses have been recorded in reintroduction studies (Hunter, 1998). In contrast, Kilian & Bothma (2003) found that reintroduced lions formed groups in accordance to their relatedness. If reintroduced lions can successfully forage and protect their young (thus protecting the home range which seems to be the primary function of grouping behaviour) without forming groups, the necessity of the formation of social groups is questioned.

It is important to revisit the objective of the lion reintroduction. If the primary objective is conservation, then the formation of social groups seems to be unnecessary for the survival of African lions in wild managed areas. However, if the primary objective is ecotourism, stable social groups of African lions would be of greater benefit.

7.2 The ability to become self-sustaining with no interference or supplementation by management

Since being released from the boma on the Reserve on 27 January 2017, the five founder lions were not provided with food except for Lioness LF3, who was provided food once, shortly after the release (see section 4.5). Lioness LF3 only partially

utilised one of the two impala (*A. melampus*) carcasses provided to her. The first recorded kill of a large prey by the five founder lions was one month (23 February 2017) after being released from the boma (see section 4.5).

In this study a hard release method was followed (Abell *et al.,* 2013), therefore the lions received no rewilding training. The founder lions (Lion LM1 and Lionesses LF1, LF2, LF3 and LF4) were released in January 2017 with no previous experience in hunting because they originated from captive facilities and was fed regularly.

In January 2020 the new breeding Lion LM6 was released and the same method of release was used. Again, once Lion LM6 was released from the boma he was not provided any food by management. The first recorded kill by Lion LM6 was an impala (*A. melampus*) lamb, after which his prey size gradually increased to include zebra (*E. quagga*).

As alluded to previously, not all the kills made by the lions on the Reserve were detected and recorded, however, the lions were clearly able to sustain body conditions enabling them to successfully breed. This implies that the lionesses had to obtain at least 5–7 kg of meat per lion per day (Schaller, 1972) for a period long enough to interact socially, engage in mating behaviour, carry the foetuses for at least 110 days (Rudnai, 1973; Packer, 1983a), nurse and protect their young until they reached adulthood themselves and disperse from the group, and eventually repeat this process after two years (Rudnai, 1973; Packer, 1983a). It must be remembered that lions are feast and famine feeders and do not eat daily (Schaller, 1972). Considering the variation in prey densities on the Reserve (see Table 2.2), it is concluded that the lions procured enough food for survival and reproduction.

Analysis of the wildlife surveys on the Reserve (Table 2.2) indicated a higher preference for some prey species: blue wildebeest (*C. taurinus*), kudu (*T. strepsiceros*), gemsbok (*T. oryx*), waterbuck (*K. ellipsiprymnus*) and warthog (*P. africanus*) were utilised the most. The species are in abundance on the Reserve and would thus naturally be preyed on most by the lions (Stander *et al.,* 2018).

Successful foraging by reintroduced lions have been documented (Abell *et al.,* 2013; Turner *et al.,* 2016), but this study produced tangible evidence on the ability of captive bred lions to successfully forage after being released in a relatively large open system.

The high density of prey on the Reserve (Table 2.2) would have simplified foraging efforts because the lions did not have to travel long distances to find prey. Furthermore, an abundance of permanent water holes (old livestock water troughs and/or small dams) (Fig. 6.2) aided a wider distribution of prey species favoured by lions. This is different from a harsh environment such as the Namib Desert, Namibia, with much lower prey densities (Stander *et al.,* 2018). However, being bred and reared in captive facilities the skills of hunting, namely locating, stalking, catching, and killing prey, is an acquired set of skills, which the founder lions (Lion LM1 and Lionesses LF1, LF2, LF3 and LF4) may have been lacking. According to Funston (2012) the captive bred lions must have been at a disadvantage because they had been deprived the opportunity to acquire knowledge and hunting skills from older lions.

Both male and female lions successfully hunted small to medium sized prey (see Chapter 4). Recorded kills were made by groups of females, solitary females, coalitions of males and solitary males. The association between prey selection and the lions participating (sex, numbers) in hunting activities were comparable to other studies (Funston *et al.,* 2001; Kilian, 2003). Only two incidences of buffalo (*S. caffer*) falling prey to the lions were recorded, although in all these cases, it was young females which wandered from the herds. Four incidences were recorded of giraffe (*G. camelopardalis*) being caught by the lions. Of those, only one giraffe was a young calf, whilst the others were sub-adult or adult females. Incredibly, an adult giraffe cow was brought down by Lioness LF1 while her attending cubs were only six months old. In a post-mortem evaluation it was clear it was a very old giraffe cow.

Lioness LF2 was present when two other giraffes (a sub-adult and an adult) were killed. In both these incidents Lioness LF2 was the only adult lion, accompanied only by sub-adult lions aged 15–18 months old. This was impressive as larger prey such

as buffalo (*S. caffer*) and giraffe (*G. camelopardalis*) are usually killed by larger groups of lions and/or groups of male lions (Funston *et al.,* 2001).

7.3 The ability to raise offspring to maturity/female sexual maturity and dispersal of males from natal prides

The four founder females (Lionesses LF1, LF2, LF3 and LF4) might have become sexually active sooner than the expected sexual maturity age for African lions (Rudnai, 1973; Maruping-Mzileni, 2009). However, they only conceived after being released on the Reserve. This first generation of wild managed lions produced by the founder lionesses consisted of 14 cubs, of which 12 survived to sub-adulthood. Only two of these cubs remained on the Reserve and later one of them had her own cubs, whilst the rest of the first-born cubs were relocated from the Reserve before reaching adulthood (see Chapter 4).

The four sub-adult males of Lionesses LF3 and LF4 were not individually identified and removed on 17 April 2019 from the Reserve. They were relocated before the expected age at which sub-adult males would be pushed from their natal prides and disperse (Funston *et al.,* 2003).

Because of the social dynamics of the remaining pride of lions (Lion LM1, Lionesses LF1 and LF2 and dependant young), the dispersal of the sub-adults (Lions LM2, LM3, LM4, LM5 and Lionesses LF5 and LF6) from this pride was earlier than what would be expected. Lioness LF1 left the group earlier in 2019, therefore Lioness LF2 was the only adult lioness in the pride. It is suspected that the dispersal of Lioness LF2 from the group or pride led to its breakup, rather than a dispersal of young sub-adult males. These sub-adult males and females were approximately 24-26 months old and thus becoming sexually mature (Rudnai, 1973).

The sub-adult males and their father (Lion LM1) formed a nomadic coalition. The reason why Lion LM1 remained with the four sub-adult males (his sons) was possibly because of the lack of sexually active females (other than his own daughters Lionesses LF5 and LF6). It is not clear why Lion LM1 chose not to remain solitary,

however his age (approximately 13 years) and thus an inability to sustain himself might have played a major role.

The coalition of four sub-adult males kept to their nomadic lifestyle well after the death of Lion LM1 and, even though they were vasectomised, they collectively retained tenure over all available lionesses, except Lioness LF2, until the four sub-adult males were translocated from the Reserve.

Prior to their removal, a new adult male lion (Lion LM6) was introduced to the Reserve. The sub-adult males were 30-32 months old, but the presence and number of young males of the coalition must have overwhelmed Lion LM6 to such an extent that his spatial utilisation of the Reserve remained limited. It is not clear if the coalition of four sub-adult males held tenure over the females and territory at their young age, or if their numbers (four to one) was simply the overriding and decisive factor to keep the newly introduced adult Lion LM6 at bay.

The second litters of Lioness LF1 [Litter 2 (LF1)] and LF2 [Litter 2 (LF2)] were removed from the Reserve prior to reaching sexual maturity, however their apparent ability to self-sustain in a pride formation was noted and similar to that of Litter 1 (LF1) and Litter 1 (LF2) (see sections 4.3 & 4.4).

7.4 The ability to teach offspring to hunt effectively, interact socially, reproduce, and secure a healthy and viable F2-generation, characteristic of wild managed lions

According to Funston (2012) and Funston & Levendal (2015), captive bred, and reared lions cannot provide for itself. Thus, introducing a captive bred lion to an extensive, open system such as the Reserve, without any prior rewilding to teach its young to hunt would seem impossible because the founder lion itself have not acquired these necessary skills.

However, if the drive to obtain sufficient food is an instinct of predators, it is reasonable to assume that the same requirement would apply to captive bred lions. The difference being that a captive bred, and reared individual does not have access

to a suitable habitat, hosting potentially suitable prey species. This does not imply that the lions do not have the necessary skills required to hunt, it simply implies that they cannot hunt due to the constraints of their previous limited “home range” imposed on them.

To hunt effectively as a social felid in an extensive system, a lion requires the skills necessary for hunting, but it would also have to interact socially because hunting is performed co-operatively when lions are found in groups (Stander *et al.,* 2018). However, solitary lions have been as successful in hunting as groups of lions (Funston *et al.,* 2001) and a lion would not have to share the resources obtained during a hunt when being on its own. If lions in groups (prides) and solitary lions were to obtain prey of similar size, the solitary lion’s costs (energy expenditure, risks, etc.) over benefit (obtaining enough food) would be much lower. Thus, theoretically, foraging alone would be more beneficial to African lions.

The five founder lions introduced on the Reserve in January 2017 did not learn to hunt from any relative or older lions, because they were removed from their mothers when only a few days old and hand reared. However, at the age of about two years, Lionesses LF1, LF2, LF3 and LF4 successfully hunted their first prey (see section 4.3). It is thus reasonable to deduce that the instinct to survive superseded any shortcomings in social learning of the founder lion population. Whether these four lionesses taught their offspring to hunt could not be physically recorded, but by 2021 they have raised a total of 19 cubs successfully to adulthood. The cubs of these four founder lionesses were all able to provide for themselves (some in groups, others in solitary) after separation from their natal prides. Another nine lion cubs were born in 2021 to Lionesses LF1, LF5 and LF8 of which seven cubs were F2-generation wild born cubs (see sections 4.4 & 4.8).

Again, the need for lions in wild managed areas to form social groups for any other purpose than breeding, is questioned. It is accepted, however, that an extensive, wild, and unfenced habitat with lower prey densities and intra-species competition cannot be compared to this scenario and should be investigated. However, if the captive bred founder lions could be self-sufficient, protect themselves and their

young and secure a home range, their ability to survive a large (>1 000 km^2) open system is hopeful.

For a lioness to produce healthy cubs, it would require sufficient food to obtain a state of health required for conception, growth of the foetuses and feeding and protection of the young, until the cubs reach an age to become self-sufficient. Hunting and social learning by an individual lion is thus important for the growth of a lion population. This study showed that the importance of any social interactions other than those displayed during copulation are questionable for wild managed African lion populations.

7.5 Regarded as suitable potential founders for reintroduction programmes where wild populations have disappeared or need to be augmented

Apparently, there is no consensus on the definition of a successful reintroduction. However, according to Jule *et al.* (2008) at least one of the following criteria must be met: (i) successful breeding by F1-generation of wild-born individuals, (ii) population growth exceeding adult death rate within three years of breeding, (iii) a self-sustaining wild population exceeding 500 individuals, or (iv) a self-sustained wild population.

Let us view and discuss the findings of this study against the four criteria proposed by Jule *et al.* (2008) for a successful reintroduction:

(i) The Reserve is fenced; therefore, limitations are placed on the number of lions which can ecologically be sustained. Furthermore, limitations on the number of lions are determined externally by the Department of Economic Development, Environment and Tourism in Limpopo Province, South Africa (LEDET). Therefore, to comply with this externally set quota, the management of the Reserve continuously had to remove excess lions throughout this study. However, the four F1-generation Lionesses LF5, LF6, LF7 and LF8 stayed long enough for them to reproduce. Lionesses LF5 and LF8 successfully gave birth to three and four cubs respectively in 2021. By November 2021 the seven cubs were still alive and in good condition. According to the first criteria this reintroduction programme was deemed successful.

(ii) For a population to grow, the survival rate of young to adulthood would have to exceed the rate of fatalities. Thus, a population growth rate exceeding adult death rate would equal population growth. The number of adult lions allowed on the Reserve (as set out in the approved management plan) was 10. With a founder population of only five individuals (Lion LM1 and Lionesses LF1, LF2, LF3 and LF4) this limitation would have been exceeded fairly quickly with 12 cubs born to the four lionesses within the first year of release and no fatalities of adult lions. If the cubs of Lionesses LF3 and LF4 had not been removed from the Reserve in 2019 (see sections 4.5 & 4.6), they would have (by reasonable expectation) reached adulthood. This assumption is based on the six cubs of Lionesses LF1 and LF2 (born in the same year as the cubs from Lionesses LF3 and LF4) surviving to adulthood whilst on the Reserve (see sections 4.7 & 4.8) and the assessment of the condition of the relocated lions. Similarly, the cubs from Litter 2 (LF2) could have survived to adulthood on the Reserve had they not been removed in 2021 (see section 4.4). However, if the African lion population on the Reserve was not artificially manipulated by removal of some members, the population would have grown to 24 adult lions and nine cubs by November 2021. Considering that only the very old Lion LM1 had died (see section 4.2) during the period 2017 to 2021, the total population growth of 28 (total of 33 lions by November 2021, minus the five founder lions released in January 2017) in only five years far exceeded the minimum requirements set for a successful reintroduction.

(iii) Restrictions are impeded on the carrying capacity of African lions of most of the wildlife reserves in South Africa due to the size of their fenced in natural habitat. Sustaining a population of more than 500 African lions would thus not be ecologically, nor financially, viable for most of the reserves. According to Funston & Levendal (2015) the only wildlife area in South Africa holding more than 500 African lions is the KNP. Only 30% of the African countries holding African lions have populations of 1 000 individuals and more (Abell *et al.,* 2013). Furthermore, considering the average growth rate for free roaming African lions (Miller & Funston, 2013), reintroduction of a large founder population would be required to exceed the minimum requirements set for a successful reintroduction. Time constraints, financial viability, research limitations and overall feasibility of such a project seems unlikely within the borders of South Africa. The Reserve consisted of only 220 km^2 and thus

fell short of being able to sustainably contain such a large population of free roaming African lion. Therefore, this criteria for a successful reintroduction could not be considered for this study.

(iv) A self-sustaining wild lion population implies that the individuals are not provided for in terms of foraging and/or food, whilst they are free to roam a large enough area where vital rates and demographics do not have to be managed or manipulated (Funston & Levendal, 2015). The introduction of fences is constraining the movement of an African lion population and thus automatically relegates its identification to “wild managed”. Funston & Levendal (2015) specifically noted that any lion population contained by fences within an area smaller than 1000 km^2 cannot be regarded as wild. For this reason, the reintroduction of African lion on the Reserve cannot be regarded as successful. However, considering the reduction of suitable habitat for African lion on a continental scale (Riggio *et al*., 2013; Everatt *et al*., 2015), the validity of this criteria for a successful reintroduction should be questioned for the African lion.

The concerns to use captive bred founders in reintroduction programmes are realistic (Jule *et al.,* 2008; Abell *et al.,* 2013) and the disapproval of using captive bred African lion for *ex-situ* reintroductions is wide spread (Funston, 2012; Born Free, 2018). However, the emotional attachment to animals, specifically certain wildlife species, should not be allowed to obscure scientific judgement and ultimately deter possible conservation methods.

The *ex-situ* release of African lions should not be attempted without duly considering the list of recommended criteria set by the IUCN and AZA. The successful release of handreared African lion cubs were documented as early as the 1960s, however very few attempts were ever scientifically documented and published (Abell *et al.,* 2013).

In conclusion, the evidence provided in this study and literature clearly shows that the successful reintroduction of captive bred African lions to wild managed areas is plausible. It is therefore believed that captive bred African lions can contribute to the conservation of the species on a global scale.The outcome of the reintroduction will undoubtly be influenced by the approach.

It is therefore advised that the following factors be taken into consideration when attempting an *ex situ* reintroduction of African lions:

- A suitable habitat with sufficient resources comparable to wild environments are imperative;

- The protection of the introduced population from retaliatory killings (removal of original cause of decline) should be implemented before the release of a population is attempted;

- The safety of potential surrounding human settlements needs to be considered. No incidences of intentional attacks on humans were documented in this study, but such incidences have occurred (Hunter, 1998b) and African lions have been documented to kill and prey on innocent humans (DeSantis & Patterson, 2017);

- Continuous research and monitoring of the success of the introduction will provide important data necessary for the long-term management of the population. A continuous monitoring of the habitat and available prey base should be integrated into the overall monitoring of the reintroduction;

- The genetic integrity of possible existing populations at the proposed reintroduction sight must be predetermined. Genetic fragmentation of the African lion has been documented (Bertola *et al.,* 2011; Bertola *et al.,* 2016);

- The demographics of existing populations can severely impact the outcome of a reintroduction. It would be illogical and counter-productive to introduce a population of African lions in an area where a healthy population already exists and would inevitably impose risks on the survival of the reintroduced population, at least for the first couple of months. However, this does not imply that a reintroduced lion or group of lions are inferior to a wild managed or wild population. The outcome of reintroductions with groups of lions that would theoretically be superior/inferior to the inhabited group of lions was not explored in this study and requires more investigation;

- Introducing a population of African lions to a wild and/or wild managed area unable to financially sustain such large predators would be detrimental. As shown in this study, the impact of African lions can have a significant effect on the available

prey species. In the South African conservation model, where wildlife carries considerable financial value, the potential of generating income from the keeping of African lion must be weighed against the cost of containing a self-sustaining population;

- Even though captive breeding programmes can be a useful tool for the conservation of species (Rahbek, 1993), the breeding of endangered species in captivity should not be used as an excuse for the preservation of natural habitat; and

- The source of the captive bred founders and how likely they will be to succeed in *ex situ* introductions is important. As captive breeding can impede on an individual's abilities to learn social and feeding behaviour from its parents (Funston, 2012), it presupposes a risk that the reintroduced founders will not be able to adapt to extensive living circumstances. This was not the case in this study, however, not all captive facilities implement the same management plan and the behaviour of the lions can be influenced by management. Furthermore, the increased population density synonymous with captive facilities could heighten the risk for infectious pathogens (Green *et al.,* 2020) rendering infected possible founders as useless like the lion population of the KNP, carrying the risk of spreading bovine tuberculosis (bTB) (Maas *et al.,* 2008), for relocations and/or reintroductions. However, captive facilities can identify and treat animals in time because the lions are constantly monitored. Founder lions identified for *ex situ* reintroduction should be sourced from reputable captive facilities following high standards of caring, rearing and health protocols.

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9 Appendices

Appendix I

Table 1. Body dimensions of Lions LM1, LM2, LM3, LM4 and LM5 in September 2019 while sedated to undergo bi-lateral vasectomies. Ages of the sub-adult males (Lions LM2, LM3, LM4 and LM5) were calculated from the estimated time of birth.

Lion ID		**Lion LM1**	**Lion LM2(LF1)**	**Lion LM3(LF1)**	**Lion LM4(LF2)**	**Lion LM5(LF2)**
Sex		M	M	M	M	M
Date of measurement		12/9/2019	12/9/2019	12/9/2019	19/9/2019	19/9/2019
Age at measurement		13 years	26 months	26 months	25 months	25 months
Weight (kg)		201.6	194.2	202.4	182	183.9
Mane Measurements (mm)						
Top line		190	130	150	130	120
Between ears		160	120	120	130	120
Base of neck		205	190	190	165	160
Side of neck		220	140	160	130	140
Breast bone		220	190	175	140	150
Belly		200	0	0	0	0
Along the topline		340	220	270	190	220
Covering of front limbs		P340	0	0	0	0
Body measurements (cm)						
Total body length		311.5	293	306	285.5	287.5
Tail length:		103	90	104	89.5	92.5
Tail circum.		27	30.5	28	26	27
Heart girth		124.5	126	127	122.5	122
Abdominal girth		119	123	126	115.5	132.5
Head length		40.01	39.37	40.01	37.47	39.1
Head width		27.31	25.4	27.31	24.4	26.03
Rostrum width		10.153	9.351	9.681	9.359	9.134
Leg measurements (cm)						
Left:	Front legs length	64	65	66	64	62.5
	Front legs circumference	43	46	42.5	43	43.5
	Hind feet length	41	42	41.5	38.5	40
	Paws length front	12.5	13	13.5	12	12.5
	Paws width front	13	12.5	12.5	11	11.5
	Paws length back	13	13.5	14	12	12.5
	Paws width back	10	10.5	10.5	9.5	10.5
Right:	Front legs length	63.5	61.5	66	62.5	62
	Front legs circumference	43.5	42.5	43	44	44
	Hind feet length	41	41	41	38.5	40
	Paws length front	12.5	12	13.5	12	13
	Paws width front	11.5	12.5	12.5	11.5	12.5
	Paws length back	13	12.5	13	12.5	12.5
	Paws width back	10	10	10.5	9.5	10

Table 1 (cont.). Body dimensions of Lions LM1, LM2, LM3, LM4 and LM5 in September 2019 while sedated to undergo bi-lateral vasectomies. Ages of the sub-adult males (Lions LM2, LM3, LM4 and LM5) were calculated from the estimated time of birth.

Lion ID		**Lion LM1**	**Lion LM2(LF1)**	**Lion LM3(LF1)**	**Lion LM4(LF2)**	**Lion LM5(LF2)**
Canines (mm)						
Upper left:	Length	42.57	49.96	49.36	47.67	48.83
	Longer width	25.75	24.89	23.29	21.83	24.41
	Shorter width	19.78	17.32	16.35	16.76	16.97
Upper right:	Length	37.14	50.17	48.32	48.26	48.71
	Longer width	26.73	24.66	24.16	19.17	24.17
	Shorter width	20.24	19.5	17.47	23.76	19.97
Lower left:	Length	46.27	39.88	40	38.38	39.33
	Longer width	25.76	22.45	21.68	20.96	22.51
	Shorter width	18.33	16.94	16.28	15.27	15.45
Lower right:	Length	40.5	40.5	36.31	40.23	39.82
	Longer width	24.18	21.93	19.17	22.8	22.86
	Shorter width	17.21	16.63	14.87	16.02	17.16
Testis (mm)						
Left:	Length	41.96	43.16	41.29	35.25	43.61
	Width	37.64	28.98	28.73	35.36	31.71
Right:	Length	37.64	43.31	46.38	49.93	46.28
	Width	37.64	38.25	28.05	47.66	35

Table 2. Body dimensions of Lion LM7 [Litter 2 (LF1)] and unidentified Lions UM1, UM2, UM3[15] (offspring of Lionesses LF3 and LF4). The comparison shows the similarities in body dimensions of the large male cubs from different mothers at ages varying between 14 and 20 months.

Lion ID		**Lion LM7**	**Lion UM1**	**Lion UM2**	**Lion UM3**
Sex		M	M	M	M
Date of measurement		25/5/2020	17/4/2019	17/4/2019	17/4/2019
Age at measurement		14 months	20 months	20 months	20 months
Weight (kg)		143.0	146	175.8	132.2
Mane Measurements (mm)					
Top line		-	80	70	65
Between ears		-	60	65	70
Base of neck		-	100	160	90
Side of neck		-	81	110	80
Breast bone		-	95	155	70
Belly		-	-	-	-
Along the topline		-	47	47	47
Covering of front limbs		-	-	-	-
Body measurements (cm)					
Total body length		266	263	282	263
Tail length:		86	87	89	84
Tail circumference:		22.5	25	27.5	26
Heart girth		108	111	120	104.5
Abdominal girth		126	113	133	115.5
Head length		34.61	36.2	31.75	34.93
Head width		21.5	22.9	24	23.5
Rostrum width		8.47	8.328	8.756	8.322
Leg measurements (cm)					
Left:	Front legs length	59	60	65	58
	Front legs circumference	38.5	37	42.5	40
	Hind feet length	39	39	41.5	36.5
	Paws length front	13.5	12.5	12.5	11.5
	Paws width front	11.5	11	12.5	11.5
	Paws length back	13.5	11.5	13	12.5
	Paws width back	9.5	9.5	9.5	10
Right:	Front legs length	38	59	65.5	59.5
	Front legs circumference	38	40.5	41.5	39.5
	Hind feet length	38	39	39.5	36.5
	Paws length front	14	13	12.5	11.5
	Paws width front	11.5	12	12.5	11.5
	Paws length back	13	11.5	12.5	12
	Paws width back	9.5	9.5	10	10

[15] UM: unidentified male.

Table 2 (cont.). Body dimensions of Lion LM7 [Litter 2 (LF1)] and unidentified Lions UM1, UM2, UM3[16] (offspring of Lionesses LF3 and LF4). The comparison shows the similarities in body dimensions of the large male cubs from different mothers at ages varying between 14 and 20 months.

Lion ID		Lion LM7	Lion UM1	Lion UM2	Lion UM3
Canines (mm)					
Upper left:	Length	31.39	44.42	47.42	45.81
	Longer width	17.2	21.09	22.4	21.28
	Shorter width	12.98	16.08	21.58	18.3
Upper right:	Length	31.17	42.55	49.51	45.75
	Longer width	17.29	20.8	42.38	21.78
	Shorter width	12.54	15.42	17.4	16.75
Lower left:	Length	30.07	36.96	40.29	39.82
	Longer width	18.24	20.4	22.24	20.49
	Shorter width	13.03	14.71	14.77	16.13
Lower right:	Length	28.74	35.7	39.77	37.47
	Longer width	17.21	19.33	20.19	19.44
	Shorter width	13.65	14.88	14.07	15.32
Testis (mm)					
Left:	Length	33.38	31.33	-	41.46
	Width	22.97	31.45	-	34.64
Right:	Length	32.3	31.33	-	41.46
	Width	22.4	31.45	-	34.64

[16] UM: unidentified male.

Table 3. Body dimensions of Lioness LF7 and LF8 [Litter 2 (LF1)] and unidentified Lionesses UF1 and UF2[17] (offspring of Lionesses LF3 and LF4). The comparison shows the similarities in body dimensions of the large female cubs from different mothers at ages varying between 14 and 20 months.

Lion ID		**Lioness LF7**	**Lioness LF8**	**Lioness UF1**	**Lioness UF2**
Sex		F	F	F	F
Date of measurement		25/05/2020	25/05/2020	17/04/2019	17/04/2019
Age at measurement		14months	14months	20months	20months
Weight (kg)		112	103	109	-
Body measurements (cm)					
Total body length		255.5	230.5	237	250
Tail length:		82.5	76.5	79	79
Tail circumference:		20	20.5	21.5	21
Heart girth		94	96.5	98.5	91.5
Abdominal girth		127	124	99	99
Head length		30.8	30.48	32.5	34.5
Head width		20.5	18	20	20.5
Rostrum width		7.049	7.5	7.428	7.586
Leg measurements (cm)					
Left:	Front legs length	52.5	52	56	55
	Front legs circumference	34.5	35.5	36	34
	Hind feet length	35.5	32.5	33	35
	Paws length front	12.5	11.5	11	11
	Paws width front	10.5	9.5	10.5	11
	Paws length back	11	11.5	10	11
	Paws width back	9	8.5	9	9
Right:	Front legs length	53	54	55	55
	Front legs circumference	33.5	35.5	36.5	30.5
	Hind feet length	35.5	33.5	34	34
	Paws length front	12	11.5	10.5	11
	Paws width front	10	9.5	10.5	11
	Paws length back	11.5	11	11	11
	Paws width back	9	8	9	9

[17] UF: unidentified female

Table 3 (cont.). Body dimensions of Lioness LF7 and LF8 [Litter 2 (LF1)] and unidentified Lionesses UF1 and UF2[18] (offspring of Lionesses LF3 and LF4). The comparison shows the similarities in body dimensions of the large female cubs from different mothers at ages varying between 14 and 20 months.

Lion ID		**Lioness LF7**	**Lioness LF8**	**Lioness UF1**	**Lioness UF2**
Canines (mm)					
Upper left:	Length	31.49	34.87	40.08	37.05
	Longer width	15.89	17.45	19.37	17.43
	Shorter width	11.29	12.59	13.64	13.55
Upper right:	Length	28.72	32.92	41.6	37.05
	Longer width	16.13	16.96	18.83	15.17
	Shorter width	11.15	12.59	16.15	13.33
Lower left:	Length	28.72	30.71	34.38	30.39
	Longer width	15.04	17.77	17.13	14
	Shorter width	11.52	12.02	12.13	10.64
Lower right:	Length	30.22	32.09	34.2	29.89
	Longer width	16.67	16.63	17.95	13.92
	Shorter width	13.16	13.48	13.49	11.35

[18] UF: unidentified female

Table 4. Body dimensions of four adult male lions at a breeding facility in the Free State Province, South Africa, which were considered as potential candidates for introduction on the Reserve in 2019.

Lion ID[19]		***1654765**	***1654406**	***1388698**	***0506751**
Sex		M	M	M	M
Date of measurement		4/9/2019	4/9/2019	4/9/2019	4/9/2019
Age at measurement		4 years	4 years	6 years	7 years
Weight (kg)		239.2	219.4	208.8	210
Mane Measurements (mm)					
Top line		115	180	180	190
Between ears		180	190	210	180
Base of neck		260	260	260	290
Side of neck		225	200	190	220
Breast bone		190	210	180	220
Belly		0	0	0	80
Along the topline		705	660	725	680
Covering of front limbs		P205	-	-	P380
Body measurements (cm)					
Total body length		312.5	274	279.5	293
Tail length:		92	86	83.5	91.5
Tail circumference:		33.02	31.5	28	26.5
Heart girth		143.3	141.5	130.3	129.5
Abdominal girth		136.5	116.5	138	122.5
Head length		41.59	37.78	38.73	42.23
Head width		25.4	25.08	25.4	25.72
Rostrum width		9.415	10.097	87.89	99.62
Leg measurements (cm)					
Left:	Front legs length	66	64.6	63.5	66.5
	Front legs circumference	46	44.9	44.5	42.5
	Hind feet length	36.6	36	37	37
	Paws length front	12.6	12.5	13	12
	Paws width front	11.9	12	11.5	12
	Paws length back	11.5	11.5	11.5	12
	Paws width back	9.5	9.5	10	9
Right:	Front legs length	66	64.5	62	65.5
	Front legs circumference	46	45	42.5	45.5
	Hind feet length	36	37.5	37	37
	Paws length front	12.6	13	13	11.5
	Paws width front	11.5	12	11.5	11.5
	Paws length back	11.5	12.5	11.5	12
	Paws width back	9.7	9.5	10	9

[19] The identifications allocated to the lions were the electronic microchips inserted into them during sedation.

Table 4 (cont.). Body dimensions of four adult male lions at a breeding facility in the Free State Province, South Africa, which were considered as potential candidates for introduction on the Reserve in 2019.

Canines (mm)					
Upper left:	Length	51.17	-[20]	52.71	54.53
	Longer width	25.56	-	25.11	25.73
	Shorter width	18.21	-	18.29	19.29
Upper right:	Length	50.76	43.52	52.33	52.42
	Longer width	24.53	25.6	25.62	36.25
	Shorter width	18.02	17.72	18.49	23.08
Lower left:	Length	41.76	24.49	42.79	42.13
	Longer width	23.27	16.73	24.52	26.01
	Shorter width	15.86	16.53	16.96	17.69
Lower right:	Length	43.98	31.28	42.19	41.53
	Longer width	23.59	23.44	24.37	23.79
	Shorter width	16.40	16.36	21.22	18.89
Testis (mm)					
Left:	Length	44.12	49.11	44.72	48.59
	Width	36.48	39.31	28.70	43.59
Right:	Length	44.83	49.06	44.20	49.79
	Width	35.41	37.27	28.10	

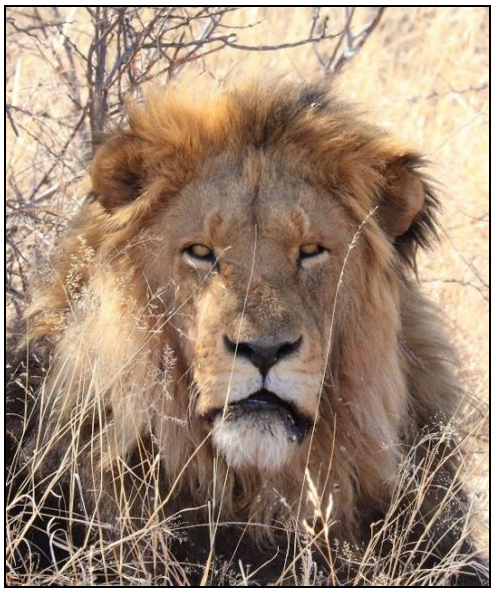
[20] The lion had a broken tooth and severe infection in his upper left canine.

Appendix II

Table 1. The home range sizes expressed in square kilometre (km^2) for specific lions.

	Total home range size		Wet season		Dry season	
Lion	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**
LM1	152.75	48.83	120.2	26.89	152.6	43.09
LF1	164.07	45.98	154.15	28.37	163.94	52.72
LF2	188.69	70.92	182.68	67.76	186.96	60.1
LF3	114.65	38.43	NA	NA	NA	NA
LF4	148.78	58.31	NA	NA	NA	NA
LF5	87.8	21.97	83.99	25.85	88.76	18.24
LM6	118.1	27.59	123.66	25	90.2	16.34
LM sub-adults	198.7	98.44	162.75	36.65	188.62	71.11

Appendix III A



Lion ID: LM1

Sex: Male

Date of Birth: 2000[21]

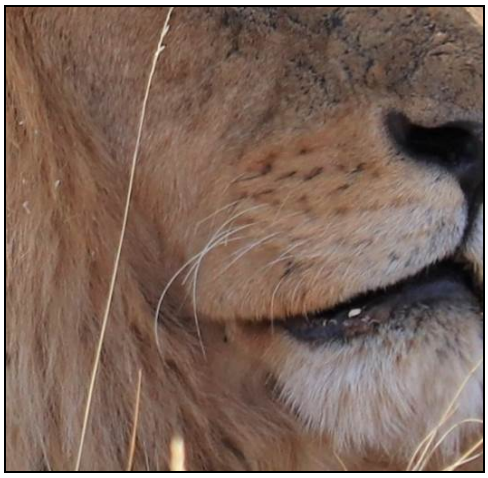
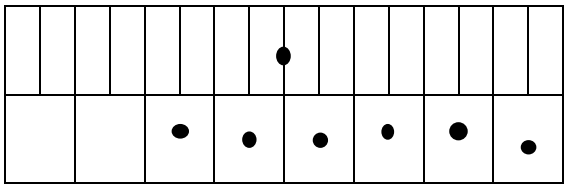
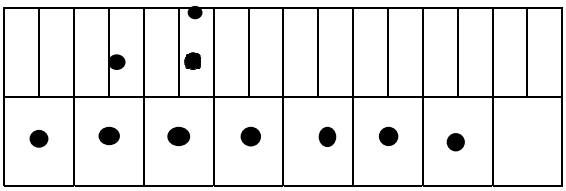
Collar ID: 2015/2873

Collar: Brown

Origin: Captive facility, Free State Province

Mother: N/A

Father: N/A

Right	Left
	
	

[21] The estimated date of birth was provided by the breeding facility.

Appendix III B

Lion ID: LF1

Sex: Female

Date of Birth: December 2014

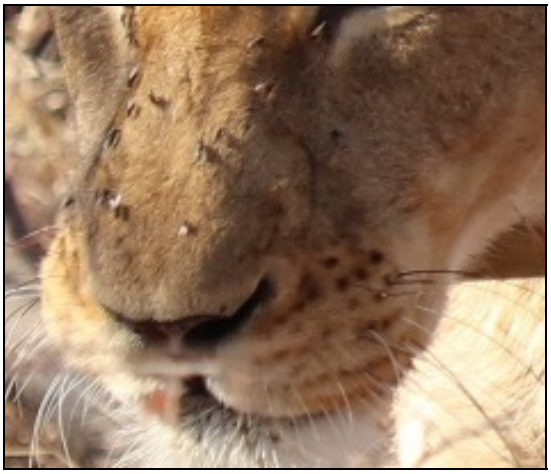
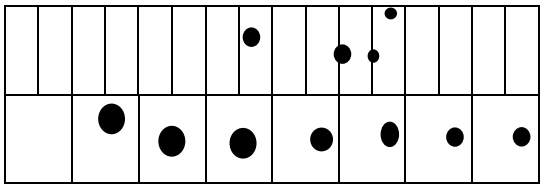
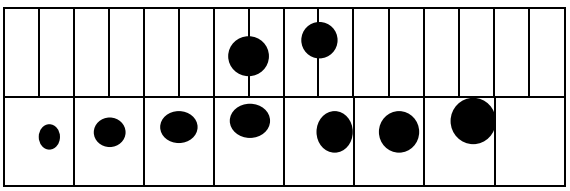
Collar ID: 2105/2774/3988/4666

Collar: Brown

Origin: Captive facility, Limpopo Province

Mother: Unidentified

Father: Unidentified

Right	Left
	
	

Appendix III C

Lion ID: LF2

Sex: Female

Date of Birth: December 2014

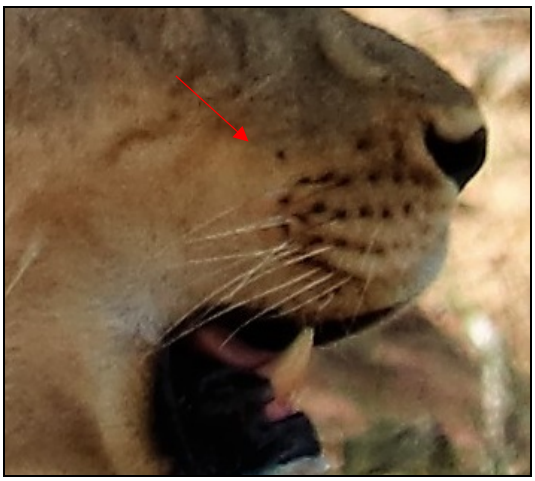
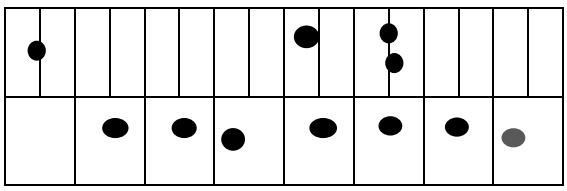
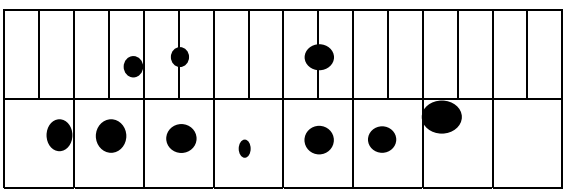
Collar ID: 2874/3844

Collar: Green/ blue

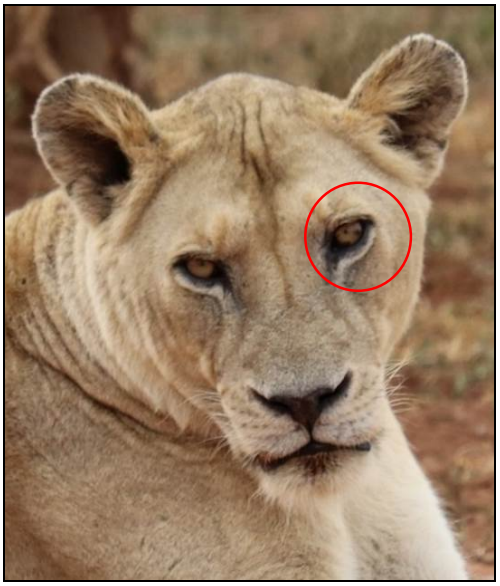
Origin: Captive facility, Limpopo Province

Mother: Unidentified

Father: Unidentified

Right	Left
	
	

Appendix III D



Lion ID: LF3

Sex: Female

Date of Birth: December 2014

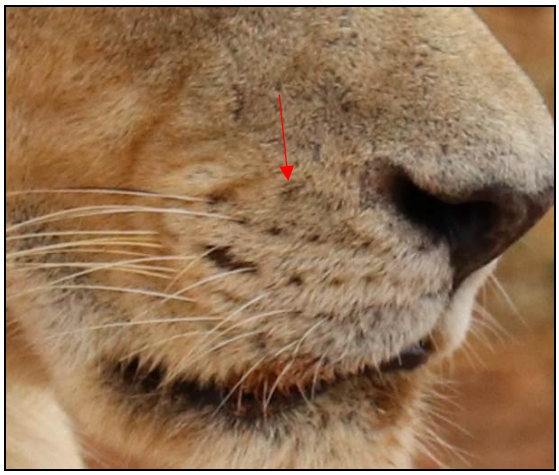
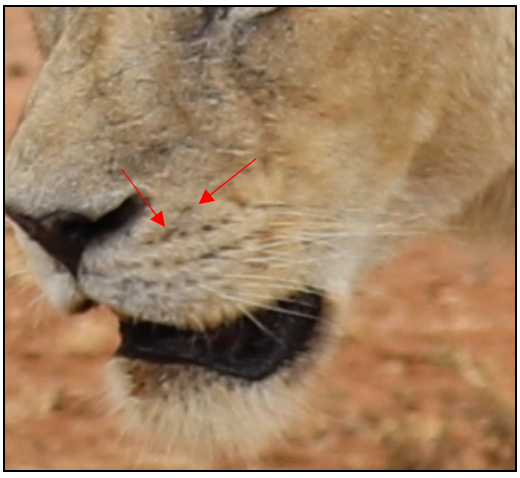
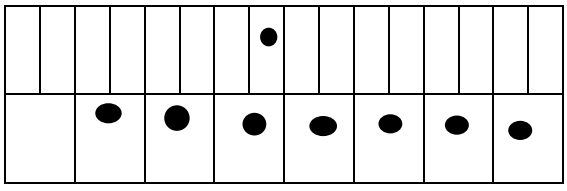
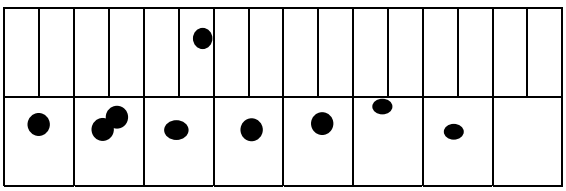
Collar ID: N/A

Collar: N/A

Origin: Captive facility, Limpopo Province

Mother: Unidentified

Father: Unidentified

Right	Left
	
	

Appendix III E

Lion ID: LM2

Sex: Male

Date of Birth: July 2017

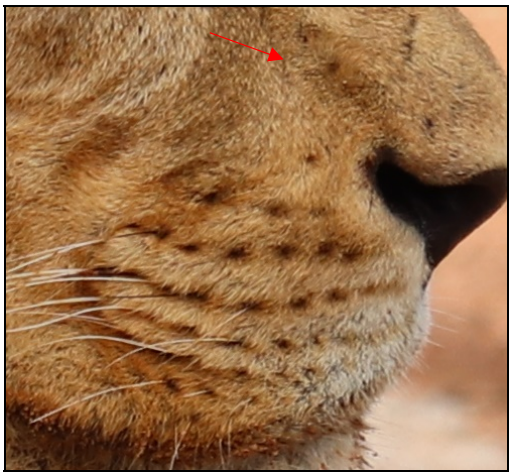
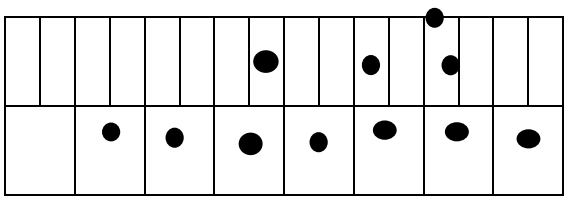
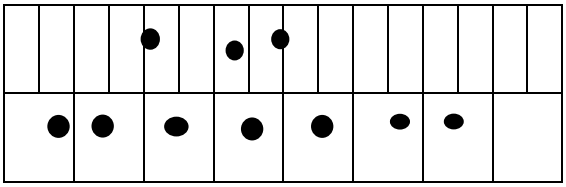
Collar ID: 2873

Collar: Yes (Brown) 2019/09/12-2020/02/24

Origin: The Reserve

Mother: LF1

Father: LM1

Right	Left
	
	

Appendix III F

Lion ID: LM3

Sex: Male

Date of Birth: July 2017

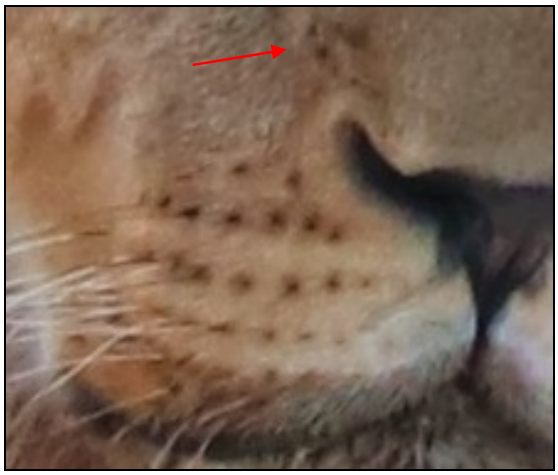
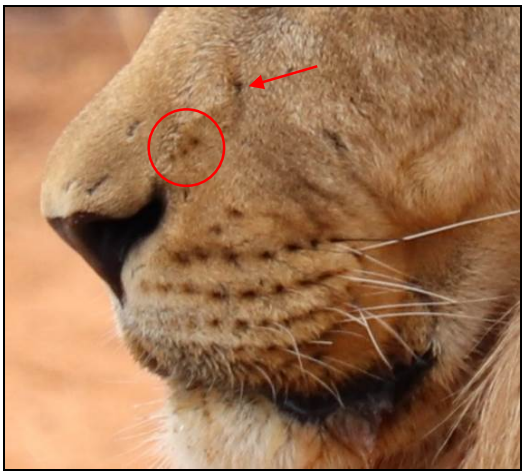
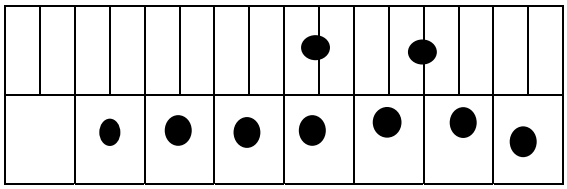
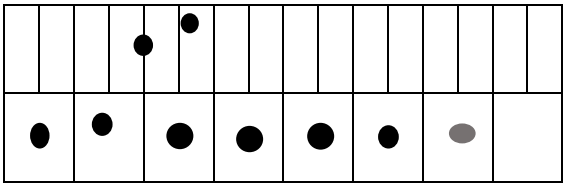
Collar ID: N/A

Collar: N/A

Origin: The Reserve

Mother: LF1

Father: LM1

Right	Left
	
	

Appendix III G

Lion ID: LM4

Sex: Male

Date of Birth: May 2017

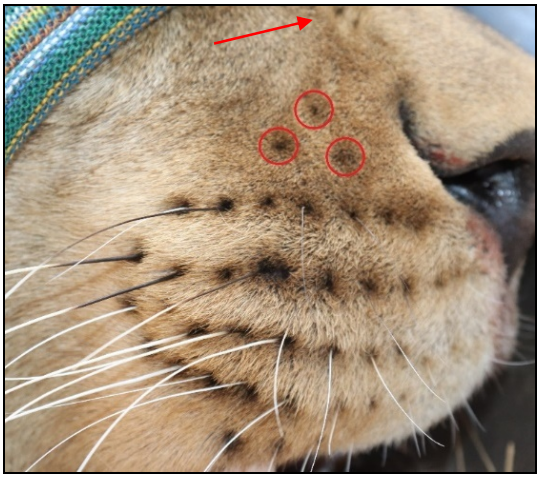
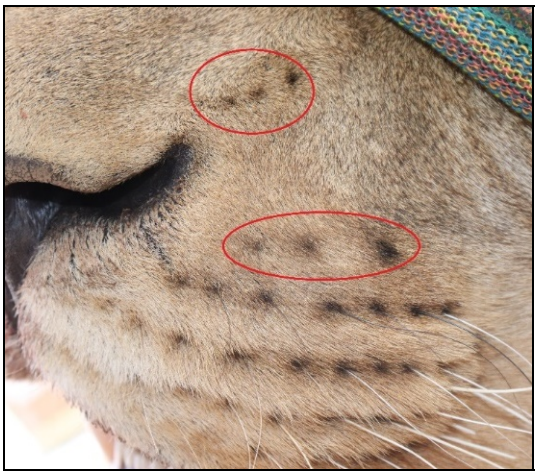
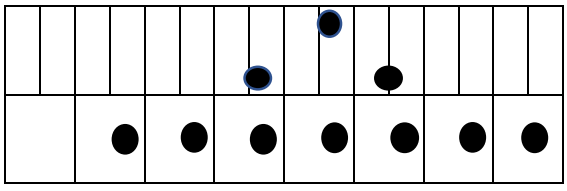
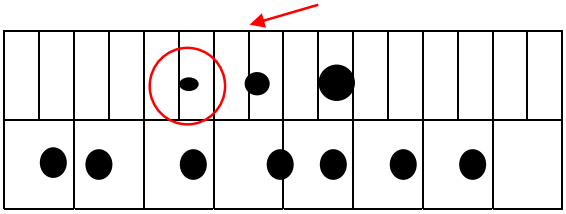
Collar ID: N/A

Collar: N/A

Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III H

Lion ID: LM5

Sex: Male

Date of Birth: May 2017

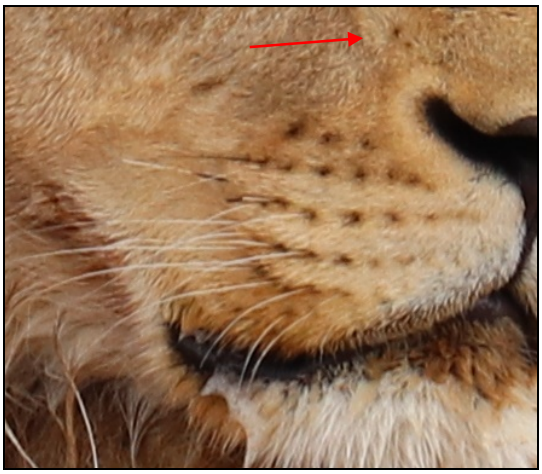
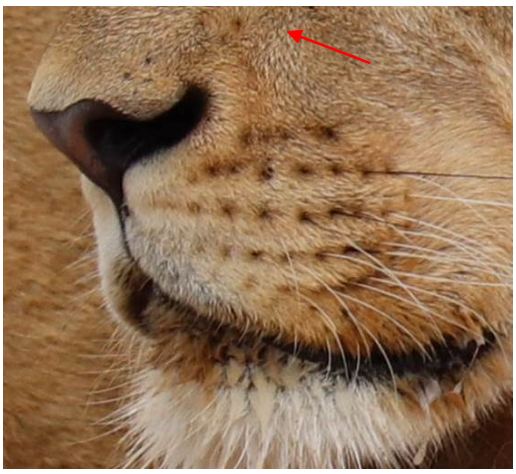
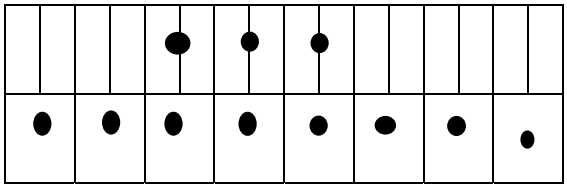
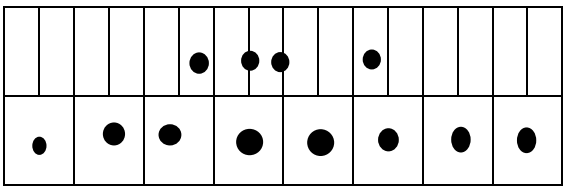
Collar ID: 3844

Collar: Blue 2020/02/15-2020/08/06

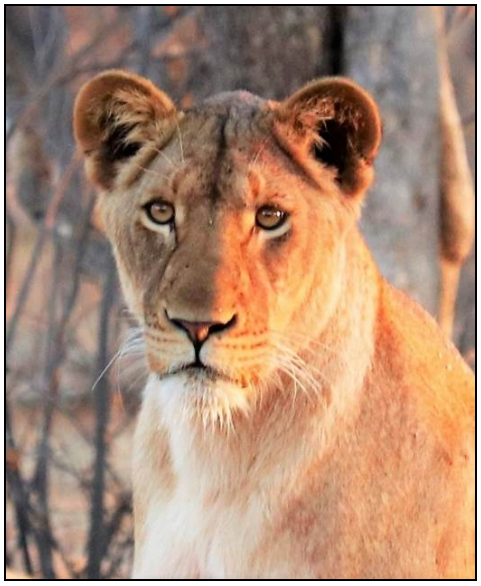
Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III I



Lion ID: LF5

Sex: Female

Date of Birth: July 2017

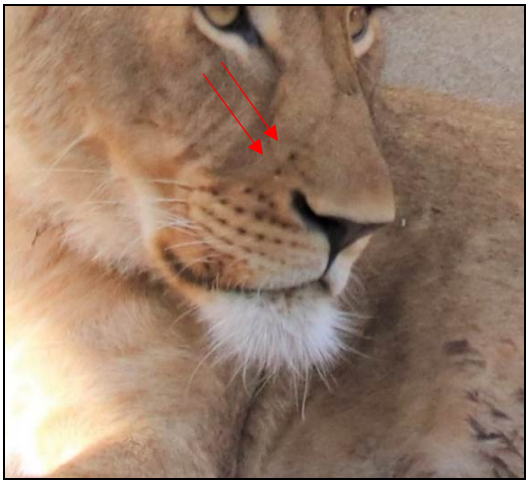
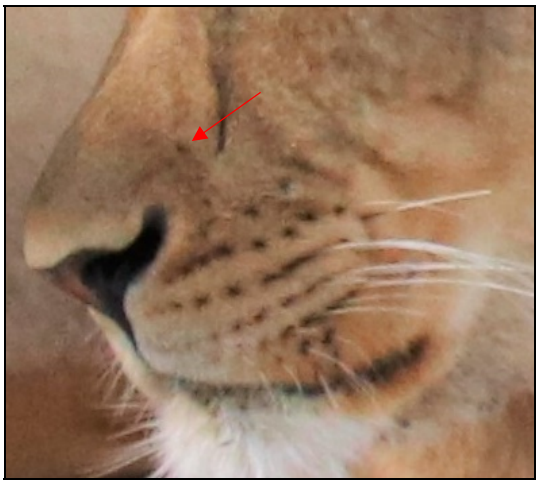
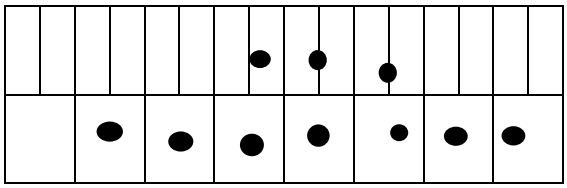
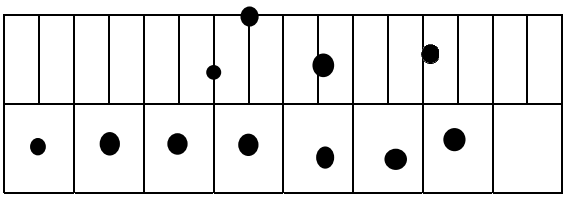
Collar ID: 3772

Collar:Orange

Origin: The Reserve

Mother: LF1

Father: LM1

Right	Left
	
	

Appendix III J

Lion ID: LF6

Sex: Female

Date of Birth: May 2017

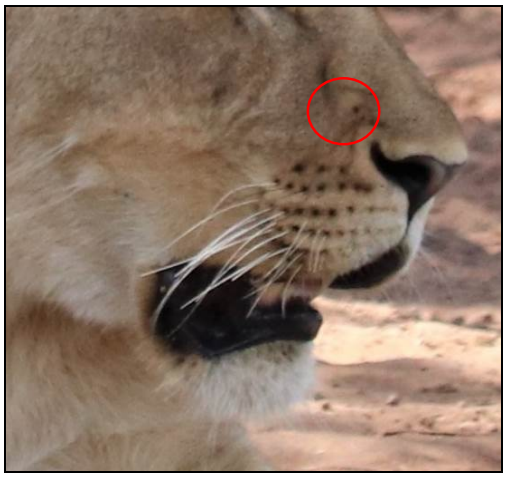
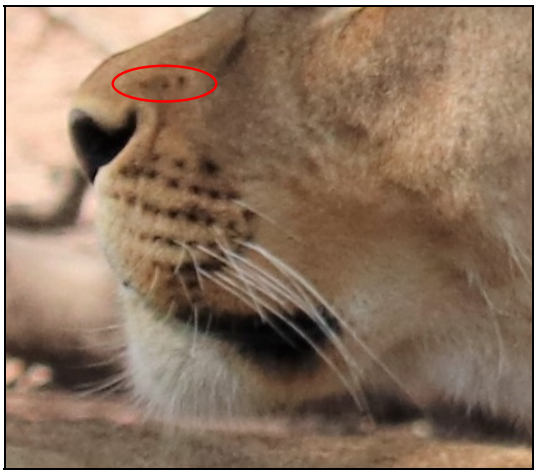
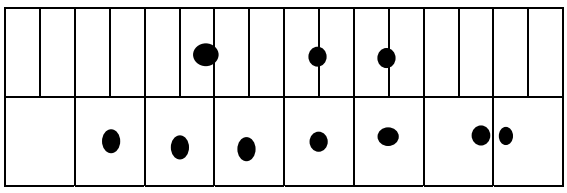
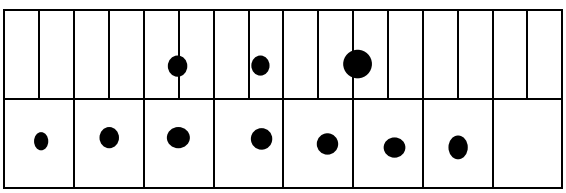
Collar ID: N/A

Collar: N/A

Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III K

Lion ID: LF7

Sex: Female

Date of Birth: April 2019

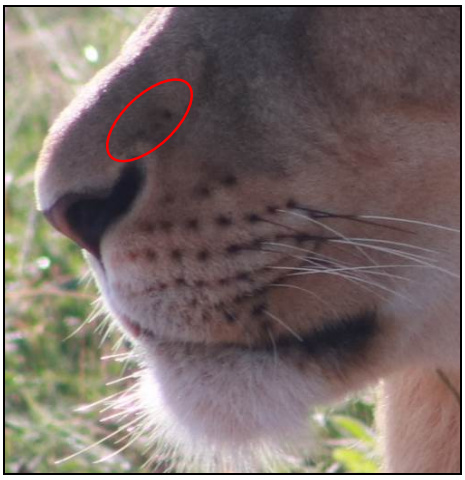
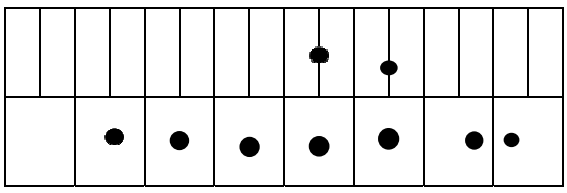
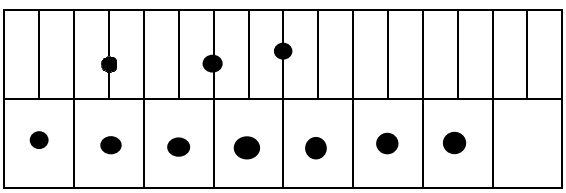
Collar ID: 4606

Collar: Orange (02/04/2021)

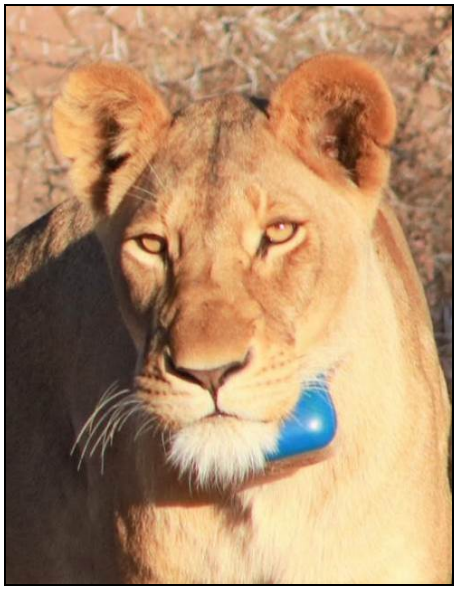
Origin: The Reserve

Mother: LF1

Father: LM1

Right	Left
	
	

Appendix III L



Lion ID: LF8

Sex: Female

Date of Birth: April 2019

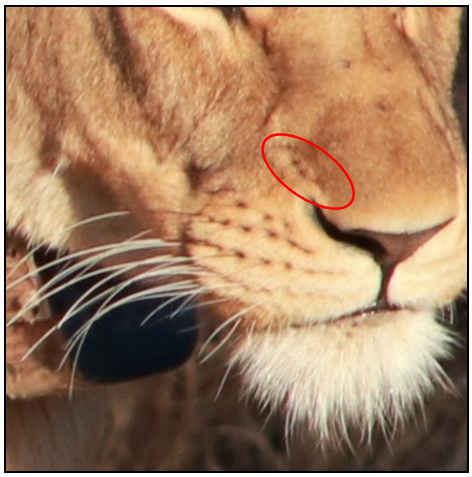
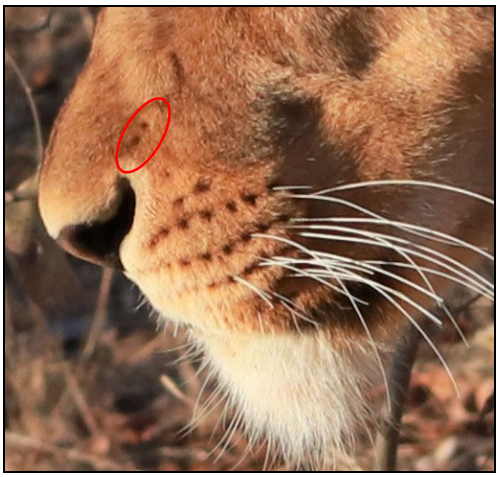
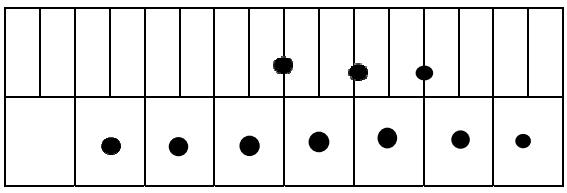
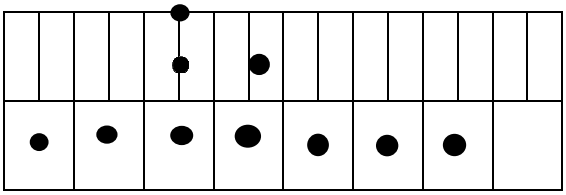
Collar ID: 3844

Collar: Blue (25/06/2021)

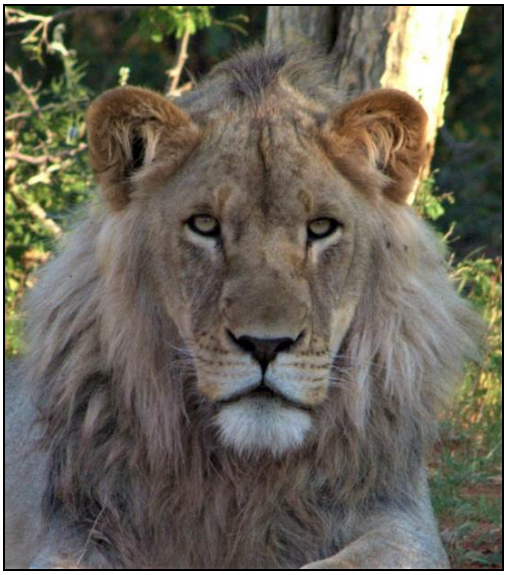
Origin: The Reserve

Mother: LF1

Father: LM1

Right	Left
	
	

Appendix III M



Lion ID: LM7

Sex: Male

Date of Birth: April 2019

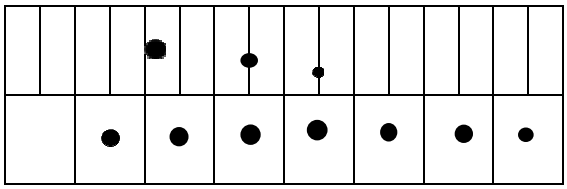
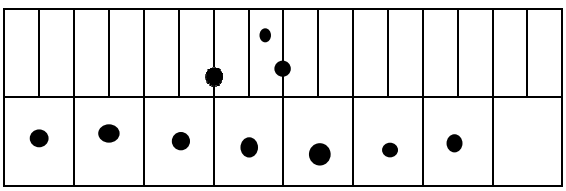
Collar ID: N/A

Collar: N/A

Origin: The Reserve

Mother: LF1

Father: LM1

Right	Left
	
	

Appendix III N

Lion ID: LF9

Sex: Female

Date of Birth: August 2019

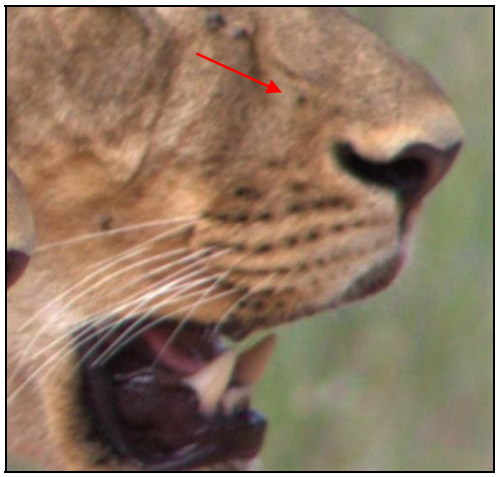
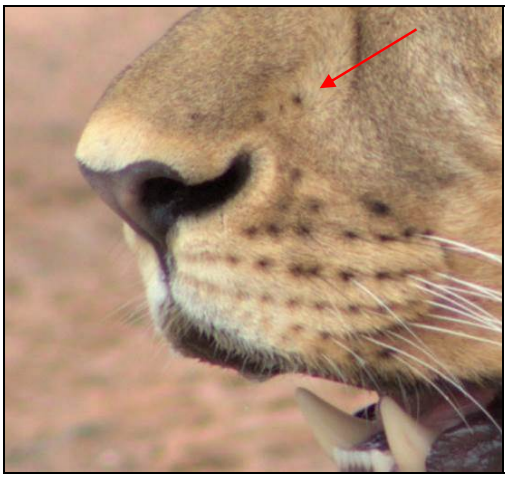
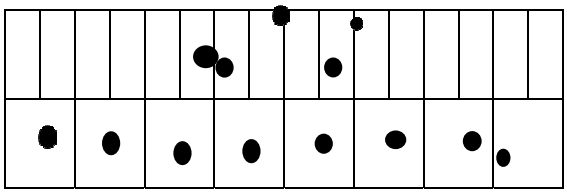
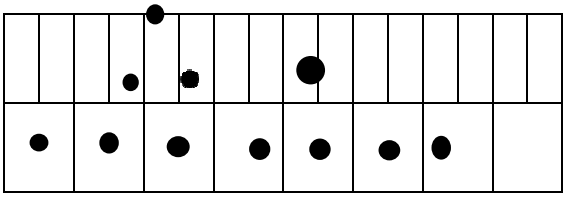
Collar ID: N/A

Collar: N/A

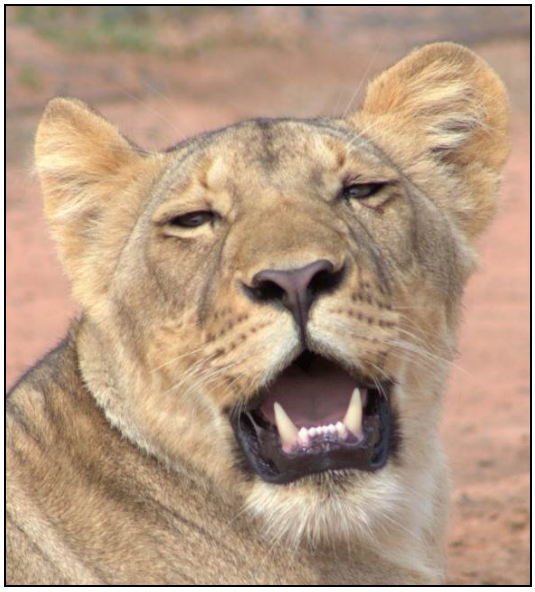
Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III O



Lion ID: LF10

Sex: Female

Date of Birth: August 2019

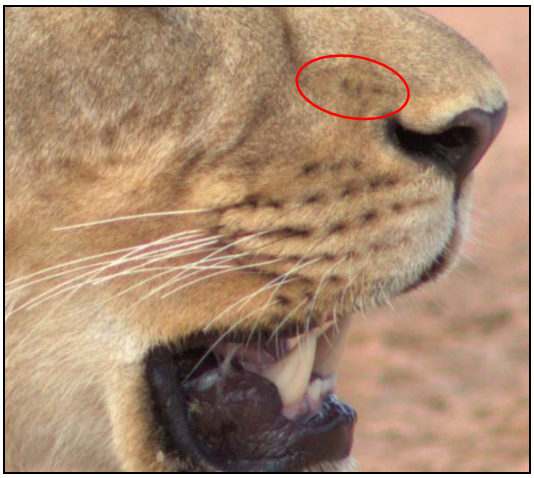
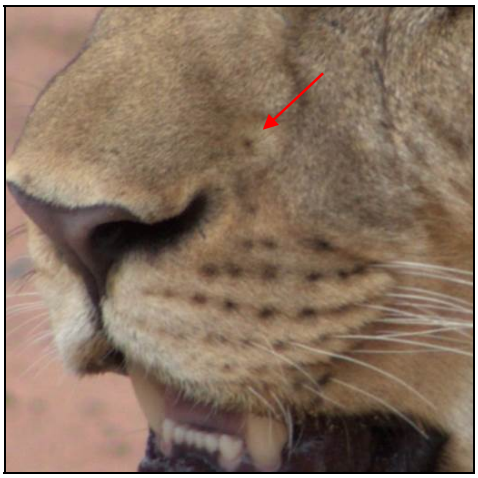
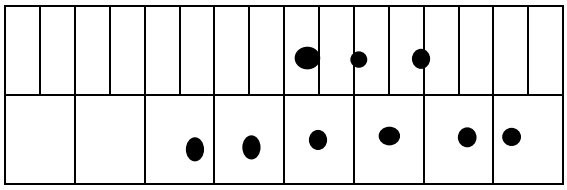
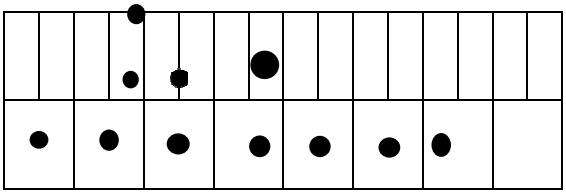
Collar ID: N/A

Collar: N/A

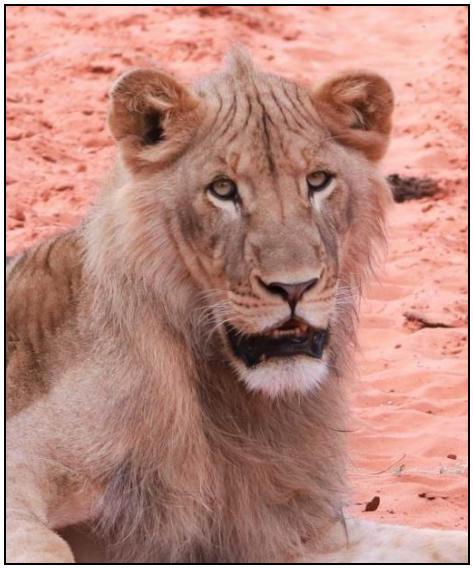
Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III P



Lion ID: LM9

Sex: Male

Date of Birth: August 2019

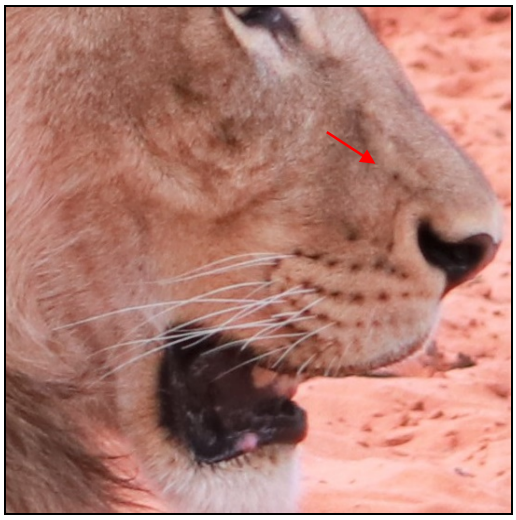
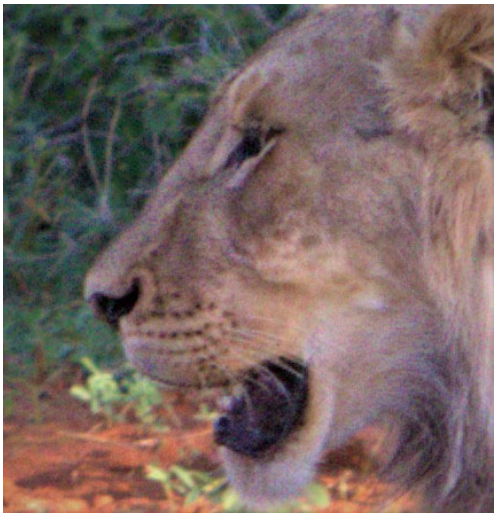
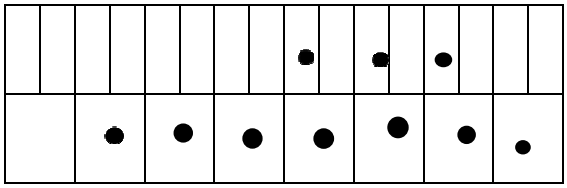
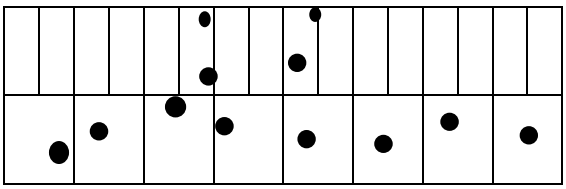
Collar ID: N/A

Collar: N/A

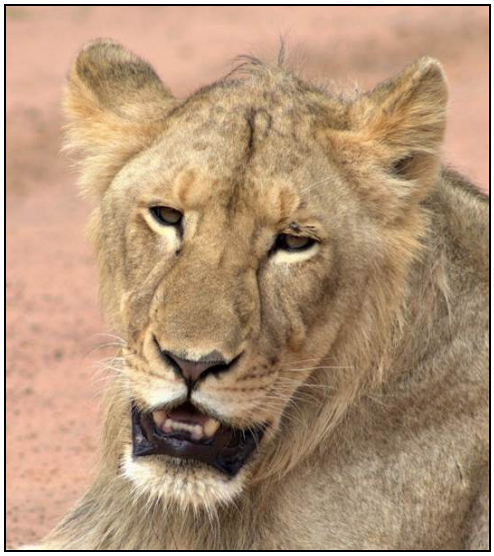
Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III Q



Lion ID: LM10

Sex: Male

Date of Birth: August 2019

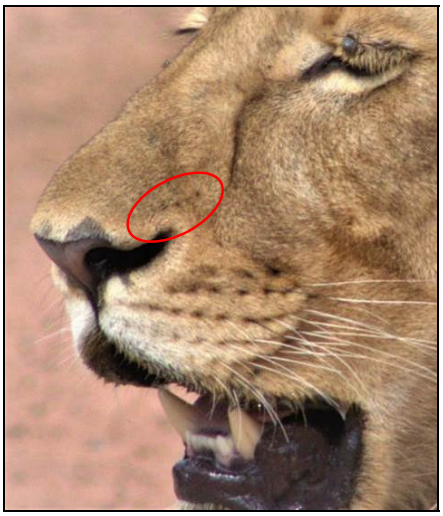
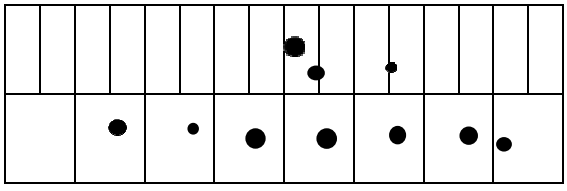
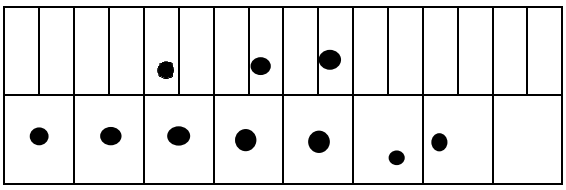
Collar ID: N/A

Collar: N/A

Origin: The Reserve

Mother: LF2

Father: LM1

Right	Left
	
	

Appendix III R

Lion ID: LM6

Sex: Male

Date of Birth: June 2015

Collar ID: 3615

Collar: Blue

Origin: Captive Facility, Free State Province

Mother: N/A

Father: N/A

Right	Left