THE MANAGEMENT OF LIONS (*PANTHERA LEO*) IN SMALL, FENCED WILDLIFE RESERVES

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ABSTRACT

Reintroduced lion (*Panthera leo*) populations pose several ecological and management challenges in small (< 1,000 km^2), fenced wildlife reserves. Changes in the natural social-ecological conditions of reintroduced lion populations may lead to rapid population growth and a breakdown of natural predator-prey relationships. Reduced competition with other lions also likely reduces the potential for reintroduced lions to naturally form groups. My study used a combination of questionnaire surveys with tourists, existing lion demographic data from 16 wildlife reserves across South Africa and a controlled lion social experiment to address these ecological and management issues. Tourism was the primary reason for lion reintroductions. Tourists scored lions highly in terms of preference for viewing on safari, in particular, lions in larger, natural groups and adult males. Viewing lions also enhanced a tourists' overall safari experience. The breakdown of natural social behaviour may likely therefore reduce tourist satisfaction related to lions. The number of resident prides and male coalitions in a reserve affected lion vital rates. Lion population growth rate was highest in reserves that contained a single resident pride, and the presence of unknown adult males significantly reduced cub survival and lioness birth intervals. The ratio of male cubs born also increased in reserves with a higher density of unknown adult males. Fertility control measures (deslorelin implants and unilateral hysterectomy) were effective at limiting lion population growth. Deslorelin treatment increased the age of first reproduction or the birth interval and decreased the subsequent litter size of treated lionesses to closer reflect natural vital rates in larger (> 10, 000 km^2) systems. However, there was variability in infertility response between lionesses including adverse reactions in a small proportion of treated individuals. The number of resident prides and male coalitions in a reserve affected lion social behaviour. Lionesses formed larger groups in reserves with a higher density of unknown adult female neighbours, likely driven by territory defence. Lion prides with resident cubs were generally more fragmented, likely in response to reduced competition from unknown adult males. However, in areas with a high density of unknown adult female neighbours, prides with cubs formed larger groups likely in response to heightened territory defence. Therefore, with smaller foraging group sizes, predation rate was increased in reserves with reduced competition from unknown lions. My study supports a metapopulation approach for the management of lions in small, fenced reserves, and the standardisation of lion management procedures and database management. Endorsed by the Biodiversity Management Plan for lions in South Africa, this will enhance the long-term conservation potential of isolated populations.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. History of lion reintroduction in South Africa

Lions (*Panthera leo*) went extinct throughout much of their former range in South Africa during the early 20th century (Nowell and Jackson, 1996). Reduced to fragmented populations, lion strongholds in South Africa persisted only in the Kruger National Park (NP) and the Kgalagadi Transfrontier Park (TP) (Miller *et al.* 2015). Lions have since been reintroduced to 49 small (1,000 km²), fenced reserves nationwide (Hayward *et al.* 2007a; Hunter *et al.* 2007; Miller *et al.* 2015; see Chapter 7). Fence-line removals with the Kruger NP and the adjoining private reserves have since reduced this number to 48 small, isolated populations. Lions were reintroduced to Hluhluwe-iMfolozi Park (HiP) from the Kruger NP in the 1960's. However, the next lion reintroduction in South Africa took place in the early 1990's, with the rapid expansion of the tourism industry in privately-owned, fenced reserves (Miller *et al.* 2015; Slotow and Hunter, 2009). A small proportion of the reintroduced lions were sourced directly from wild populations throughout southern Africa and the remaining populations have been sourced from other fenced reserves in South Africa (Miller *et al.* 2015; Slotow and Hunter, 2009). The process of lion reintroduction into small, fenced reserves has been reviewed in detail, documenting successful establishment and high population growth rates (Hayward *et al.* 2007; Hunter, 1998; Kettles and Slotow, 2009; Miller and Funston, 2014).

1.2. History of lion management in South Africa

Lion reintroduction across fenced reserves in South Africa led to several management concerns including population control, disease and genetic integrity (*reviewed in* Miller *et al.* 2013). Best-practise tools for the management of lion populations in small, fenced reserves include fertility control, lion removals (translocation, hunting, euthanasia) and prey supplementation (Kettles and Slotow, 2009; Miller *et al.* 2013). Lion removals have typically been carried out through translocation however, lethal control measures have become more relied upon with the regional saturation of fenced lion populations (Kettles and Slotow, 2009; Miller *et al.* 2013). Although hunting has been an available technique for lion population control, many reserves with reintroduced populations are tourism-driven and have not typically relied on hunting as a lion management tool (Sims-Castley *et al.* 2005). Increased media awareness and international regulation with respect to trade in lion body parts has led to the ban on lion trophy importation/exportation in certain international countries and commercial airlines (Bouché *et al.* 2016), limiting the use of hunting as a lion management tool.

Due to ethical considerations linked with more reactive lethal control methods, fertility control can represent a more desirable management option (Miller *et al.* 2013). However, potential side-effects on natural behaviour, physiology and ecology are an important consideration (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013). Fertility control has been practised in small, fenced lion populations across South Africa over the past two decades, in the form of deslorelin implants (Peptech Animal Health, Sydney) (Bertschinger *et al.* 2001). Deslorelin treatment is effective at hormonally inhibiting oestrus activity in lionesses for approximately 2.5 years after a single implant (Bertschinger *et al.* 2008). Unilateral hysterectomy is a more recently developed experimental technique in lions, in which litter capacity is physically reduced through the surgical removal of a single uterine horn. First performed on a lioness in South Africa in 2011, this procedure should in theory halve the average litter size born to treated lionesses (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013). However, it is important to evaluate the relative efficacy of contraceptive treatments in mimicking population growth compared to more open systems and to evaluate for potential side-effects (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013). Many small, fenced reserves have also historically supplemented prey species to counter the impact of higher lion densities (Louw *et al.* 2012; O'Brien, 2012). In addition, disease-risk management has also been an important factor in small, isolated reserves, with limited opportunities for immigration (Kissui and Packer, 2004; Trinkel *et al.* 2011).

Translocations have been used to remove excess lions that are introduced to establish new founder populations or for genetic refreshment into established populations (Miller *et al.* 2015). Little consideration has previously been given to the preservation of long-term genetic integrity and management decisions were primarily based on more imminent factors including disease and lion availability (Miller *et al.* 2015). A primary example of this was the reintroduction of lions from Etosha NP (geographically separated from South Africa's lion populations) to fenced reserves in South Africa during the 1990's, the progeny of which have since been widely translocated nationwide (Miller *et al.* 2015). This has resulted in an unnaturally high representation of lions with a genetic provenance from Etosha NP across South Africa's fenced reserves (Miller *et al.* 2015). If unmanaged, this may lead to degradation of the three distinct evolutionary significant units identified in southern Africa (Miller *et al.* 2015).

Likely due to their small size and isolation, most individual lion populations across fenced reserves in South Africa were not identified as viable conservation units in the IUCN's regional conservation strategy for eastern and southern Africa (IUCN SSC Cat Specialist Group, 2006). In South Africa, the regions containing viable lion populations were identified as the Kruger NP, the Kgalagadi TP and HiP, the conservation of which is a primary goal (IUCN SSC Cat Specialist Group, 2006). To date, lion management protocols across small, fenced reserves in South Africa have largely been carried out on an *ad hoc* basis, dependent on individual reserve management requirements (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013). However, metapopulation theory has been suggested as a mechanism to maintain long-term genetic viability and enhance the conservation potential of small, isolated lion populations (Funston and Levendal, 2015; Miller *et al.* 2015). The translocation of lions between fenced reserves in South Africa has resulted in a level of genetic diversity and gene flow that is comparable the lion population in the Kruger NP (Miller *et al.* 2015). This is particularly important given the increasing role that small, intensively-managed reserves have been playing in species protection (Packer *et al.* 2013, Bauer *et al.* 2015). In some circumstances these fenced systems may be a more feasible and financially viable method of conserving lion populations compared to unfenced counterparts (Packer *et al.* 2013).

The first Biodiversity Management Plan (BMP; 2015 - 2019) for lions in South Africa (Funston and Levendal, 2015) was developed under the jurisdiction of the Department of Environmental Affairs (DEA) and in compliance with the IUCN's regional conservation strategy for eastern and southern Africa (IUCN SSC Cat Specialist Group, 2006). A key component of the BMP has been the designation of the three distinct lion population structures in South Africa, each associated with discrete socio-ecological roles and characteristics (Table 1.1). The driver behind defining the relative roles of lion populations in South Africa is to clarify and coordinate lion management objectives and procedures across the three population structures. Lion populations that have been reintroduced into small, fenced reserves constitute managed wild lions (Funston and Levendal, 2015). These populations are managed in terms of population limitation and for genetic integrity. Key national objectives for managed wild lions include the development and implementation of metapopulation management and the expansion of norms and standards for the reintroduction of lions (Funston and Levendal, 2015). Through metapopulation planning, geographically-isolated lion populations can be managed as socially distinct groups, with translocation between reserves mimicking natural dispersal and gene flow (Ferreira and Hofmeyr, 2014; Miller *et al.* 2015). Part of the BMP 5-year plan sought the incorporation of at least 80% of managed wild populations in South Africa into a shared metapopulation planning database. This will further support the role that managed wild lions play as important social, economic and ecological drivers in South Africa (Funston and Levendal, 2015).

Table 1.1. Breakdown of the three lion population categories defined in the Biodiversity Management Plan for lions in South Africa (Funston and Levendal, 2015).

Category	**Definition**
1. Wild	Largely unmanaged lion populations residing within formally gazetted national parks. Vital rates and lion demographics are not manipulated by managers. Populations fulfil their role in terms of biodiversity processes and are stable and viable (e.g. Kruger NP).
2. Managed wild	Lion populations are managed primarily to limit population growth and maintain genetic integrity. Managers actively manipulate vital rates to achieve this. Occur in a range of small, fenced reserves (<1,000 km²).
3. Captive	Lion populations which are used exclusively to generate income with limited conservation value. Managers manipulate all vital rates.

1.3 Social-ecological conditions of lion populations in small, fenced reserves

In open systems, lions form group sizes of 2 – 18 adult lionesses, that actively defend their territory from neighbouring prides (Smuts, 1976; Stander, 1991; Funston, 2011; VanderWaal *et al.* 2009). Male lions also group, with larger coalitions outcompeting smaller coalitions in terms of tenure of female prides (Bygott *et al.* 1979; Packer and Pusey, 1982). The driver behind group formation in lionesses has therefore been suggested to be intraspecific competition from unknown lions in response to territory and cub defence (Packer *et al.* 1990). Lionesses in larger groups have better success at protecting a territory and defending their cubs from unknown lions (Mosser and Packer, 2009; Packer and Pusey, 1983; Packer *et al.* 1990).

Many small, fenced reserves reintroduced one or only a few prides and/or adult male/coalitions, to delay the effects of subsequent population increase (Druce *et al.* 2004; Slotow and Hunter, 2009). In these circumstances, intraspecific competition between unknown lion groups is likely reduced. Furthermore, most small, fenced reserves sequentially remove subadult dispersers (Bissett, 2007; Druce *et al.* 2004; Kettles and Slotow, 2009; Lehmann *et al.* 2008a), limiting the formation of unknown lions. The drivers for social behaviour may therefore break down in small, isolated lion populations, leading to fragmented lion groups and posing potential management and ecological concerns.

Although capture success can increase with lion group size (Stander, 1992), lions are effective solitary hunters (Caraco and Wolf 1975) and generally opportunistic in prey selection (Hayward and Kerley, 2005). Therefore, reduced cohesion among lion pride members may lead to degraded predator-prey dynamics. Many small, fenced reserves have experienced reductions in prey species subsequent to their lion reintroduction (Lehmann *et al.* 2008b; Hayward *et al.* 2007b; Power, 2002; Tambling and Du Toit, 2005). Lions in small, fenced reserves generally have higher reproductive and survival rates and reduced opportunities for natural dispersal, compared to lions in more open systems (Miller and Funston, 2014). Lion management interventions can therefore be targeted to mimic these natural ecological processes that have been degraded (Ferreira and Hofmeyr, 2014; Miller and Funston, 2014). Intraspecific competition between unknown lions in open systems can lead to higher mortality rates (Mosser and Packer, 2009; Packer and Pusey, 1983). The number of resident prides and male coalitions in managed wild populations can therefore likely also have a significant effect on lion population growth, further interacting with the efficacy of lion management responses.

Tourism is a primary revenue-driver for many small, fenced reserves (Langholz and Kerley, 2006; Sims-Castley *et al.* 2005). However, research indicates that tourists generally show preference for viewing social species like lions in natural groups (Di Minin *et al.* 2013). Therefore, reduced cohesion among lion pride members may also impact tourist experiences in reserves with managed wild lions, with potential economic implications for those reserves. This necessitates further research evaluating the interactions between lion population structure, lion management interventions and tourism outcomes in small, fenced reserves. Together with enhanced database management and standardised procedures, this understanding will facilitate decision-making processes when it comes to the management of managed wild lion populations and the ongoing development of the BMP for lions in South Africa (Miller *et al.* 2013; Funston and Levendal, 2015).

1.4. Research objectives

My study had four primary objectives linked with the social-ecological conditions of lion populations in small, fenced reserves. Broadly, I wanted to investigate how the number of resident prides and male coalitions in a reserve can affect tourism (Chapter 3), lion population management (Chapter 4 and 5) and lion social behaviour (Chapter 6). Specifically, I wanted to evaluate if a reduced number of unknown lions in small, fenced reserves can reduce group formation in lions and the associated levels of lion-tourist satisfaction. I also wanted to evaluate best-practice lion management interventions in terms of their efficacy in achieving desired management outcomes and mimicking or restoring the natural ecological processes that have been degraded. I introduce the study area and populations in Chapter 2 and end with a chapter on the conservation and management implications of my research (Chapter 7).

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CHAPTER 2

STUDY SITES, LION (*PANTHERA LEO*) POPULATIONS AND GENERAL METHODOLOGY

2.1. Introduction to study sites

My study incorporated four national parks and 24 provincial or private reserves, across six provinces and covering eight biomes in South Africa (Figure 2.1; see Supplementary Material Table S2.1). This included 25 managed wild lion (*Panthera leo*) populations in fenced areas ranging from 20 km^2 to 910 km^2 and one wild population in the Kruger National Park (NP) and two adjoining private reserves. The latter reserves formed part of the Great Limpopo Transfrontier Park (TP), a semi-open system (> 35,000 km^2). Many small (< 1,000 km^2), fenced reserves had a fenced sub-section(s) that excluded the resident lion population for game-breeding purposes. The longest established reserve was proclaimed in 1912/1913 (reserves 11 and 18; see Figure 2.1 and Supplementary Material Table S2.1) but most reserves were established after 1990 (1991 – 2011) and were reclaimed from previous land-usages including livestock pastoralism, game-breeding and agriculture (Bissett, 2007; Brooks *et al.* 2011; Govender, 2010; Hunter, 1998). Consequently, many reserves have been actively involved in restoration processes, including soil erosion control and invasive plant species removal. The primary reserve management goals were conservation and tourism.

2.2. Climate, topography, soils and vegetation

South Africa is situated within the sub-tropics and consists of varied climatic zones (Conradie, 2012) and topographical features that drive differential vegetation types (Mucina and Rutherford, 2006). The contrasting cold (Benguela: west) and warm (Agulhas: east) coastal currents play a driving role in precipitation levels and patterns (Walker, 1990). Coastal and eastern regions have higher rainfall than inland (Schulze, 1997). Rainfall can be non-seasonal or with bimodal peaks in the southern coastal regions (Schulze, 1997). In addition, rainfall season occurs during the winter months in the west and during the summer months in the remaining regions (Mucina and Rutherford, 2006; Schulze, 1997). Topography varies from a high central plateau (1,200 - 3,450 m) to the low-lying regions towards the coast and north-east of the country (Schulze, 1997). In total, 73 soil forms have been identified nationwide and placed into 14 soil groups (Fey, 2010). The range of climatic, topographical and edaphic features affects the local biomass available to herbivores (Ellery *et al.* 1995). Historically, this has also driven land-use patterns in South Africa, and cultivation practices have been concentrated in the higher rainfall (Hoffman *et al.* 1999) and higher productivity areas (Kemper *et al.* 2000). Nine vegetation biomes have been identified across South Africa (Mucina and Rutherford, 2006; Figure 2.2). Many reserves incorporated several vegetation biomes. The reserves used in my study can be divided into four broad geographical areas: North West, Lowveld, KwaZulu-Natal and Frontier (Figure 2.1).

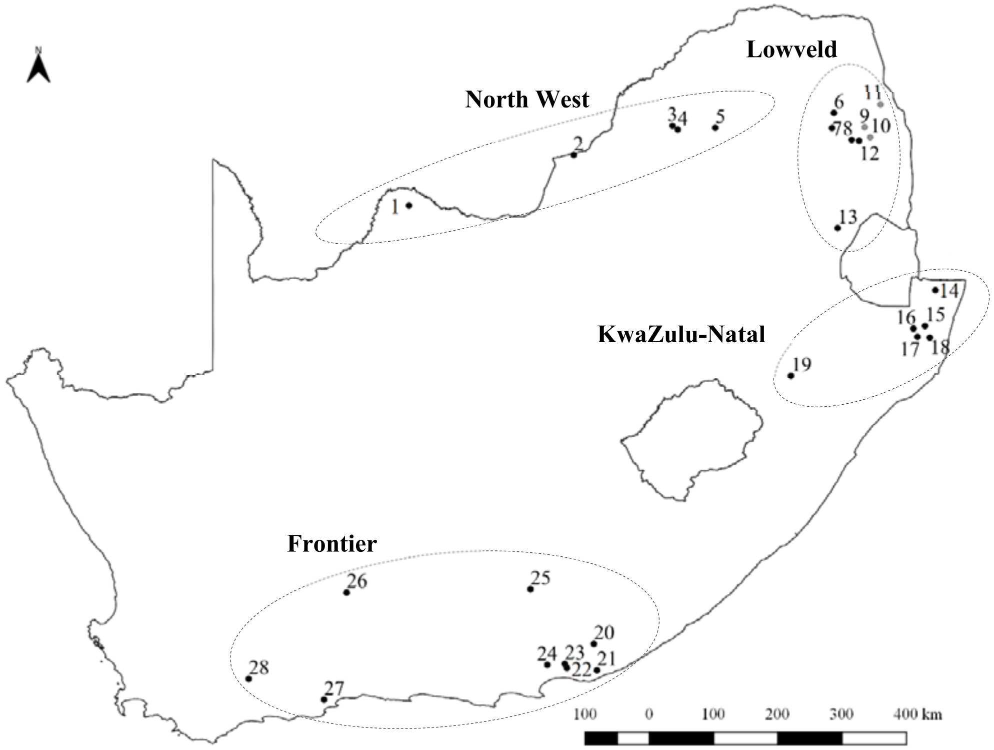

Figure 2.1. The 28 study reserves with wild (grey circle) or managed wild (black circle) lions across four regional nodes in South Africa. The number corresponds to Supplementary Material Table S2.1.

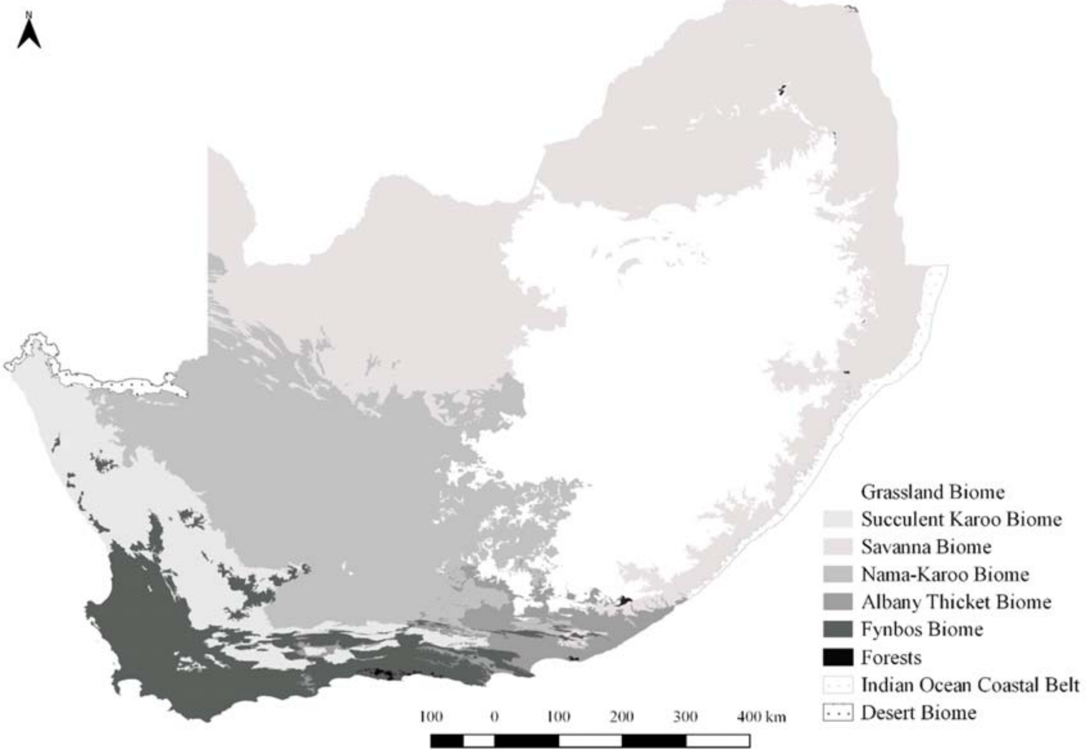

Figure 2.2. The relative distribution of the nine biomes across South Africa.

2.2.1. North West

The five reserves located in the North West are dominated by the Savanna Biome. There is limited variation between reserves 3, 4 and 5 in terms of mean seasonal temperature (4 - 33Cº), annual rainfall (530 – 589 mm) and rain season (summer). Reserve 2 and 1 are each more successively arid by comparison (Mucina and Rutherford, 2006). Reserves 3, 4 and 5 are associated with higher rainfall levels and cooler temperatures than reserves in the Lowveld, driving nutrient-poor soils and high leaching levels (Mucina and Rutherford, 2006). The mountainous terrain across these reserves primarily includes Waterberg Mountain Bushveld vegetation communities, ranging from bushveld on higher slopes to open savanna on the lower slopes (Mucina and Rutherford, 2006). Central Sandy Bushveld is located on deep, sandy soils in lower-lying areas and patches of grass-dominated Waterberg-Magaliesberg Summit Sourveld is located on the highest plateaus (Mucina and Rutherford, 2006). Reserve 2 is dominated by more open plains of Dwaalboom Thornveld which support a well-developed grass layer. The clay soils in this reserve also support scattered trees (e.g. *Vachellia* species) and shrubs. Madikwe Dolomite Bushveld vegetation communities are located on a high-lying ridge to the south of this reserve (2), composed of a grass-dominated herbaceous layer and scattered deciduous species (Mucina and Rutherford, 2006). Patchy outcrops of Dwarsberg-Swartruggens Mountain Bushveld can also be found extruding from the surrounding plains (Mucina and Rutherford, 2006). The final reserve (1) is dominated by Molopo Bushveld vegetation and is characterised by very low winter rain (annual rainfall ~ 330 mm), closed to open shrublands and a well-developed grass layer (Mucina and Rutherford, 2006).

2.2.2. Lowveld

Seven out of the eight reserves in this region are dominated by the Savanna Biome, and there is limited variation between reserves in terms of mean seasonal temperature (7 - 38C°), annual rainfall (450 – 600 mm) and rain season (summer) (Mucina and Rutherford, 2006). Compared to reserves in KwaZulu-Natal, the temperatures are more extreme as they are not regulated by the coastal climate (Schulze, 1997). Reserves 7, 8, 9, 10 and 12 are dominated by Granite Lowveld, (Mucina and Rutherford, 2006), which is associated with low quality soil and a dense herbaceous layer (Environomics and MetroGIS, 2009). The vegetation structure varies from tall shrublands with a few trees (upland areas) to open savanna and dense thickets in lower-lying areas (Mucina and Rutherford, 2006). Lowveld Rugged Mopaneveld occurs on rocky outcrops in the northern section of reserve 9 (Mucina and Rutherford, 2006). Phalaborwa-Timbavati Mopaneveld, associated with a higher tree density, occurs in undulating plains in reserves 9 and 10 and dominates reserve 6 (Environomics and MetroGIS, 2009; Mucina and Rutherford, 2006). Small sections of Gravelotte Rocky Bushveld are located throughout rocky outcrops in reserves 6 and 7. The Kruger NP (11) includes approximately 21 vegetation communities. The vegetation communities are underlaid by coarse granite soils in the west (south: Granite Lowveld and north: Tsende Mopaneveld) and more fertile basalt soils in the east (south: Tshokwane-Hlane Basalt Lowveld and north: Tshokwane-Hlane Basalt Lowveld) (Mucina and Rutherford, 2006). Furthermore, mean annual rainfall increases from the north (~ 450 mm) to the south (~ 750 mm) of the reserve.

Reserve 13 is associated with divergent climatic variables. This reserve is positioned within a transition zone between the Savanna and Grassland Biomes and contains both high plateau grasslands and more low-lying savannas (Mucina and Rutherford, 2006). Mean temperatures are generally lower (5 - 25 C°) and rainfall is generally higher than other reserves in this region

(Mucina and Rutherford, 2006). Vegetation communities in this reserve are consequently dominated by Swaziland Sour Bushveld, regions of Barberton Montane Grassland at higher altitudes and small ultramafic outcrops of Barberton Serpentine Sourveld (Mucina and Rutherford, 2006).

2.2.3. KwaZulu-Natal

The six reserves in the KwaZulu-Natal (KZN) region are dominated by the Savanna Biome, and are characterised by moist, hot summer periods and dry, cooler winter periods (Mucina and Rutherford, 2006). The Grassland, Thicket and small patches of Forest Biome are also represented within these reserves. There is limited climatic variation between reserves in terms of mean seasonal temperatures (25 - 35ºC), annual rainfall (550 - 750 mm) and rainfall season (summer) (Mucina and Rutherford, 2006). Reserves 16 and 17 are dominated by Zululand Lowveld vegetation communities, which includes *Vachellia sieberiana var. woodii* and other tree species, shrubs and grasses (Mucina and Rutherford, 2006). Structure varies from open Savanna Thornveld to more closed thickets (Mucina and Rutherford, 2006). Reserves 15 and 18 are dominated by a combination of vegetation communities including Makatini Clay Thicket, Southern Lebombo Bushveld and vegetation communities adapted to more sandy soils towards the coast (e.g. Tembe Sandy Bushveld) (Mucina and Rutherford, 2006). Lowveld Riverine Forest vegetation is located along waterways and highly restricted Sand Forest vegetation communities occur in small patches (15 and 18) (Mucina and Rutherford, 2006). Reserve 14 encompasses large sections of Sand Forest and is characterised by dense thickets of trees in a matrix of more open Tembe Sandy Bushveld (Mucina and Rutherford, 2006). Reserve 19 is in proximity to the central high plateau of South Africa and as such is dominated by more open grassland (e.g. Northern KwaZulu-Natal Moist Grassland), and areas of *Vachellia*-dominated Thukela Thornveld (Mucina and Rutherford, 2006). Highveld alluvial vegetation is located along waterways in this reserve (Mucina and Rutherford, 2006).

2.2.4. Frontier

The Frontier region is a transition zone of different climates (Mucina and Rutherford, 2006), with variations in localised vegetation increased by changing topography (Cowling *et al.* 1996). As such, the nine participating reserves in this region incorporate seven biomes: Grassland, Nama-Karoo, Succulent-Karoo, Thicket, Savanna, Forest and Fynbos (Mucina and Rutherford, 2006). The relative representation of each biome within these reserves varies from Thicket dominance in the east to Fynbos in the west and Nama-Karoo in the north. The region is typically characterised by relatively low annual rainfall (245 - 700 mm), with rainfall generally increasing in the east and with increasing proximity to the coast (Mucina and Rutherford, 2006). The reserves in the more arid, western and inland regions receive sporadic rain, with peaks in March (25, 26) and winter (28) (Mucina and Rutherford, 2006). The remaining reserves are dominated by either non-seasonal or bimodal rainfall patterns with optima in October/November and March (Mucina and Rutherford, 2006). Temperature fluctuations are more exaggerated inland (0 - 40ºC) compared to the more moderate coastal climate (10 - 35ºC).

Reserves 20 to 24 are dominated by a diversity of thicket vegetation types (e.g. Kowie Thicket, Sundays Thicket) that are interspersed with sections of more open Bhisho Thornveld (Mucina and Rutherford, 2006) and old farmlands (Parker and Bernard, 2005). Small sections of Karoo and Fynbos shrubland are also present in reserves 22 and 24 (Mucina and Rutherford, 2006). Thicket structure is characterised by medium to tall dense vegetation, dominated by succulent and woody components (Mucina and Rutherford, 2006). Perennial plant cover displays little annual variation, providing a high biomass of good quality forage (Mucina and Rutherford, 2006). Dominant species include euphorbias, aloes, small trees and grasses of medium to high grazing value (Mucina and Rutherford, 2006; Van Oudtshoorn, 2012). Albany Coastal Belt vegetation dominates small regions towards the coast (22, 23, 24) and is characterised by graminoids with dispersed *Vachellia natalitia* trees.

The reserves to the west (27, 28) are dominated by Fynbos and Renosterveld vegetation (higher fertility soils) that are interspersed by sections of Thicket towards the coast (27) and Succulent-Karoo in the more arid inland region (28) (Mucina and Rutherford, 2006). Dominant Fynbos (Swellendam Silcrete Fynbos, Montagu Shale Fynbos) and Renosterveld (Mossel Bay Shale Renosterveld, Montagu Shale Renosterveld) vegetation in these reserves include ericoid shrubs and to a lesser extent proteoids (Mucina and Rutherford, 2006). The drier Karoo-shrubland region (28) is dominated by both succulent (e.g. *Euphorbia mauritanica*) and non-succulent species (e.g. *Chrysocoma ciliata*) (Mucina and Rutherford, 2006). Reserves 25 and 26 lie within the summer rainfall region (March optima) and are dominated by more open vegetation structures (Mucina and Rutherford, 2006). Reserve 25 is dominated by dry Nama-Karoo grassland, low-level shrubland and a small amount of Thicket (Karoo Escarpment Grassland, Eastern Upper Karoo, Eastern Cape Escarpment Thicket) at altitudes between 1,000 and 1,600 m a.s.l. (Mucina and Rutherford, 2006). Dominant species include members of the Asteraceae and Poaceae families (Pond *et al.* 2002). Reserve 26 is dominated by Nama-Karoo vegetation communities at varying elevations and localised Karoo grassland communities (850 – 1,300 metres) (Gamka Karoo, Upper Karoo Hardeveld, Karoo Escarpment Grassland) (Mucina and Rutherford, 2006). Predominant species include Karoo shrubs (e.g. *C. ciliata*) and drought resistant, lower grazing-value, grasses (e.g. *Aristida congesta*) (Mucina and Rutherford, 2006).

2.3. Lion populations

A small proportion of the managed wild lion populations was established from lions translocated directly from the Kgalagadi TP (24; 2003), Etosha NP (2; 1995) or the Kruger NP and surrounding areas (7; 1995 and 18; 1992). A single managed wild population (12) was established from captive lions that had been "re-wilded" in association with the Global White Lion Protection Trust (GWLPT) (Turner *et al.* 2015). The population was successfully released into a confined (300 – 700 Ha) area without other lions in order to drive self-sufficient foraging (Turner *et al.* 2015). The remaining managed wild populations were established from other small, fenced reserves in South Africa (*reviewed in* Miller and Funston, 2014). All these managed wild populations were established between 1992 and 2013 (Supplementary Material Table S2.1) and their vital rates are manipulated by managers for ecological and genetic integrity (Miller *et al.* 2013; Miller *et al.* 2015). Active lion management interventions include translocation, contraception, trophy hunting, euthanasia and prey supplementation (*reviewed in* Miller *et al.* 2013; Chapter 4). Translocations are carried out through "soft-release" methods, whereby individuals are released after a period (2 - 16 weeks) of acclimatisation in a wildlife enclosure – known locally as a boma (Hunter, 1998; Killian and Bothma, 2003). The best-practice protocols for soft-release methods have been summarised in Miller *et al.* (2013).

The wild lion population in the Kruger NP and adjacent private reserves (9, 10, 11) is the only naturally persisting population in my study (i.e. not reintroduced) and the lions are not intensively managed (Funston and Levendal, 2015). The wild lion population also has a contrasting fencing history. First proclaimed a national park in 1926, the Kruger NP erected fences in response to disease control in 1959 and completed the final boundary in 1980 (Mabunda *et al.* 2003). In 2003, a project to remove the eastern boundary fence was initiated, forming the Great Limpopo TP (~ 35,000 km^2) (Whande and Suich, 2009). The adjoining private reserves were surveyed and purchased as private farms in the early 1900's (Bornman, 1995). The land was primarily purchased as hunting concessions and, to a lesser extent, for livestock pastoralism and agriculture (Bornman, 1995). The region was still unfenced at the time and lions naturally occurred in the area (Bornman, 1995). These private reserves were first fenced in 1961 (10) and 1971 (9), shortly after proclamation as private nature reserves (Bornman, 1995). The fences were erected in response to disease control however, there were significant reductions in certain species, including migrating zebra (*Equus quagga*) and wildebeest (*Connochaetes taurinus*), during the 1962 drought (Bornman, 1995).

Managed wild lion population structure varied across the study reserves. Some reserves had a single pride and single adult male/coalition and some reserves had multiple prides (2 to 5 prides) and/or multiple adult male coalitions (2 to 7 coalitions) (Supplementary Material Table S2.1). At the beginning of my study, the total number of lions in the managed wild population was 202 adult lions (> 3 years), 102 subadults (1 – 3 years) and 59 cubs (< 1 years) across 50 prides (including 11 solitary lionesses with/without dependent offspring). The smallest population had two adults (and two dependent offspring) and the largest population had 44 lions. Managed wild pride size ranged between one and eight adult lionesses and the mode was three lionesses. Thirteen small, fenced reserves contained a single adult (> 3 years) male lion. Three reserves contained a single coalition of two males and one reserve contained one coalition of three males. The remaining small, fenced reserves (*n* = 8) contained between two and nine male coalitions including 12 solitary males, 17 coalitions of two males, two coalitions of three and one coalition of four males. All lion populations were monitored on a regular basis by reserve staff (e.g. guided tourist vehicles, research groups, management teams). Several reserves also had lion ID kits constructed for their lion population.

2.5 General Methodology

Ethical approval to carry out my study was granted from the Rhodes University Ethical Standards Committee (project number: RU-HSD-15-02-0002). I had four primary research objectives (Table 2.1). My study initiated with the distribution of two questionnaires to wildlife managers (*n* = 61) across South Africa in association with the Lion Management Forum of South Africa (LiMF): 1) Lion Audit and Management Survey and 2) Lion Contraception Survey. These surveys were distributed and returned online between April 2015 and September 2015. The surveys gathered data on lion population structure at reserves, which management practices were in place and what, if any, other information was available regarding lion population demographics. The surveys also sought voluntary participation in a lion monitoring scheme that involved recording field observations of lions (Chapter 6). The relative participation of each reserve varied depending on information availability, lion management intervention and lion population structure (Supplementary Material Table S2.1).

Available data (e.g. lion sightings, lion population demographics, management interventions, game stock history and rainfall levels) were collected from the reserves through email and personal interview between October 2015 and September 2018. I evaluated lion management interventions through direct survey measures (contraception treatment) and database analyses (Chapter 4 and 5). I evaluated lion grouping through initiating a lion monitoring scheme at several study reserves to analyse predictions on lion grouping behaviour (Chapter 6). I also carried out a field experiment to test my research hypotheses on lion social behaviour (Chapter 6). In addition, I designed and carried out a tourist questionnaire to evaluate interactions between tourist experience and lion population structure (wild or managed wild lions) (Chapter 3).

Table 2.1. The four primary research objectives of my study and the corresponding methodology and chapter.

Objective	**General methods**	**Chapter**
1. Assess lion-related tourism outcomes in small, fenced reserves	- Questionnaires - Field observations	3
2. Assess the outcome of lion management interventions utilised in small, fenced reserves	- Questionnaires - Existing data	4 & 5
3. Assess the social behaviour of lions in small, fenced reserves	- Field observations - Social experiment	6
4. Derive best-practice management conclusions for managed wild lions	- Evaluation of outcomes from previous sections	7

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SUPPLEMENTARY MATERIAL

Table S2.1. The total area (km^2) of study reserves, the area (km^2) available to resident lion population, reintroduction year (year), the lion pride structure within each reserve (A – E), the relative involvement of each reserve in the study (Chapter), rainfall levels and lion population size (*n*).

No.	**Reserve**	**Region**	**Total area (km2)**	**Lion area (km2)**	**Year**	**Chapter**	**Structure**	**Rainfall season**	**Rainfall (mm)**	**Lions (*n*)**
1	Khamab Kalahari Reserve	North West	940	910	2010	4	B	Summer	330	29
2	Madikwe GR	North West	620	620	1995	3	D	Summer	490	39
3	Welgevonden GR	North West	348	336	1996	4*	D	Summer	775	13
4	Shambala PGR	North West	120	100	2001	5,6	A	Summer	530	4
5	Entabeni GR	North West	135	100	1998	5,6	A	Summer	590	4
6	Selati GR	Lowveld	275	270	2004	4,5,6	C / A	Summer	530	10
7	Greater Makalali PGR	Lowveld	220	220	1995	4,5,6	A / D	Summer	450	29
8	Blue Canyon Conservancy	Lowveld	150	150	2008	4,6	A	Summer	500	10
9	Klaserie PNR	Lowveld	600	35,000	NA	3,6	Wild	Summer	450	2000†
10	Timbavati PNR	Lowveld	534	35,000	NA	6	Wild	Summer	530	
11	Kruger NP	Lowveld	19,485	35,000	NA	3	Wild	Summer	375 - 830	
12	GWLPT	Lowveld	20	20	2005	5	A	Summer	530	7
13	Nkomazi GR	Lowveld	150	150	2009	6	A	Summer	680	9
14	Tembe Elephant Park	KZN	300	300	2002	4,5	A / D	Summer	720	44

15	uMkhuze GR	KZN	400	400	2013	4,5	C	Summer	660	10
16	Manyoni PGR	KZN	230	230	2011	4,5,6	A / B	Summer	600	19
17	Thanda GR	KZN	134	134	2004	4,5,6	C	Summer	555	13
18	Munyawana GR	KZN	233	233	1992	3,4,5,6	D	Summer	750	24
19	Nambiti PGR	KZN	100	100	2007	5	C	Bimodal	630	10
20	Kwandwe PGR	Frontier	250	190	2001	4,6	C	Bimodal	530	24
21	Kariega GR	Frontier	100	30	2004	5,6	A	Bimodal	700	5
22	Amakhala GR	Frontier	72	59	2004	4,5,6	A	Winter	570	4
23	Shamwari GR	Frontier	230	150	2000	4,5,6	C	Spring	585	4
24	Addo Elephant NP º	Frontier	1,640	270	2003	3,4,5,6	D	Winter	400	24
25	Mountain Zebra NP	Frontier	284	230	2013	5	A	Summer	400	6
26	Karoo NP	Frontier	768	880	2010	4,5	D	Autumn	260	15
27	Gondwana GR	Frontier	110	100	2009	4,5,6	A	Winter	380	8
28	Sanbona Wildlife Reserve	Frontier	540	240	2003	4,5,6	D / A	Winter	245	6

Population: **A:** single pride and single male lion/coalition **C:** more than one pride and a single male/ coalition **E:** open system (wild lions)

B: single pride and more than one male/coalition **D:** more than one pride and more than one male/coalition

º abiotic variables (size, rainfall, temperature) for Main Section of the park and the lioness population primarily consisted of solitary adult females

* lion population eradicated by a CDV outbreak during the study period (primary research contribution)

† lion population estimate derived from Funston and Levendal (2015) for the combined region of the Kruger NP and the adjacent private reserves

CHAPTER 3

TOURIST PREFERENCES AND SATISFACTION ACROSS RESERVES WITH LIONS (*PANTHERA LEO*) IN SOUTH AFRICA

3.1. INTRODUCTION

Current tourist opportunities for reserves with either wild or managed wild lions (*Panthera leo*) in South Africa include photographic safaris and trophy hunting (Alexander, 2012; Krug, 2001; Novelli *et al.* 2006). There are roughly 3,555 wild or managed wild lions in South Africa, with over 800 individuals residing in 48 small (< 1,000 km^2), fenced reserves (Funston and Levendal, 2015: Miller *et al.* 2013; Chapter 7). Most small, fenced wildlife reserves in South Africa rely on photographic tourism, with a small number utilising lion trophy hunting (Slotow and Hunter, 2009). This is likely due to the negative associations and ethical considerations linked with trophy hunting by photographic tourists from a reserve management perspective (Cousins *et al.* 2009; Kettles and Slotow, 2009; Miller *et al.* 2013). Trophy hunting of wild lions in South Africa has largely been restricted to the wild population in the Associated Private Nature Reserves and the managed wild population in small, fenced reserves (Funston and Levendal, 2015). Voluntourism (whereby tourists pay to participate in reserve management and/or research) is an additional, relatively new, form of revenue to both small and large private wildlife reserves in South Africa (Alexander, 2012; Cousins *et al.* 2009; Sin, 2009).

3.1.1. The role of wildlife tourism in South Africa

Over 10 million international visitors arrived in South Africa during 2017 (Statistics South Africa, 2017), a growing trend which supports a vast network of tourism-related employment and revenue opportunities (Bigg *et al.* 2011; Butler and Rogerson, 2016; Rogerson, 2013; Sims-Castley *et al.* 2005; Spenceley, 2003). Comparatively higher levels of visiting tourists in other countries (e.g. United Kingdom ~ 40 million tourists in 2017; British Tourist Authority, 2018), indicates the potential for tourism growth in South Africa. Wildlife tourism, through state and private reserves, can therefore play an important role in terms of the socio-economy of integrated landscapes in South Africa, with secondary benefits for biodiversity conservation

(Gallo *et al.* 2009; Langholz and Kerley, 2006). State-owned protected areas represent over 15% of South Africa's ecosystems in roughly 6% of the total land surface (Driver *et al.* 2005). Led by the Department of Environmental Affairs (DEA), SANParks envision the integration of conservation initiatives and sustainable socio-economic development of local communities through a robust network of initiatives, including responsible tourism (Spenceley, 2003; Swemmer and Taljaard, 2011). National parks and state protected areas are an important source of employment and regional economic revenue in South Africa (Saayman and Saayman, 2006; Saayman *et al.* 2009) and in other southern Africa countries (Snyman, 2012). There are also a growing number of sustainable-use programs between SANParks and local communities for access to raw materials including mopane worms (*Gonimbrasia belina*) and plant materials (Swemmer, 2018).

There has been a recent shift in private land-use practises in South Africa, from livestock pastoralism to more profitable wildlife-based tourism ventures (Langholz and Kerley, 2006; Sims-Castley *et al.* 2005). The economic benefits of this land-use are increased in regions otherwise unsuited to farming due to climate (Langholz and Kerley, 2006). Land transformation from farming to private, eco-tourism driven reserves in the Eastern Cape Province alone, increased overall revenue, regional employment numbers and average salary, among other socio-economic benefits (Langholz and Kerley, 2006; Sims-Castley *et al.* 2005). Due to the frequency of private ownership within areas of high productivity, such as lower elevations, privately owned protected areas can significantly contribute to biodiversity conservation in terms of endangered species and biome representation in the conservation estate (Gallo *et al.* 2009). The range of many endangered and threatened species, including lions, African wild dogs (*Lycaon pictus*) and white rhinoceros (*Ceratotherium simum*), have also been expanded through successful reintroductions to South Africa's private, fenced reserve network (Buk *et al.* 2018; Davies-Mostert *et al.* 2015; Miller and Funston, 2014).

Private wildlife reserves are often faced with challenges in terms of aligning tourism and conservation goals. For example, driven by tourism incentives, many private reserves stock high numbers of reintroduced, charismatic species that may be extralimital (introduced to regions outside of their natural historic range; Langholz and Kerley, 2006), or that may have otherwise questionable reintroduction value (Hayward and Kerley, 2009; Slotow and Hunter, 2009). In addition, most small, fenced reserves cannot maintain viable wildlife populations of large mammal species without long-term monitoring and intensive management (Hunter *et al.* 2007; Slotow *et al.* 2005; Slotow and Hunter, 2009). Limited competition for access to resources (e.g. food, water, safety) in small, fenced reserves can degrade the natural population control mechanisms for large mammal species (Ferreira and Hofmeyr, 2014). Wildlife tourism can also have negative ecological impacts, including changes to natural animal behaviour, habitat degradation and the loss of more rare or sensitive species (Green and Giese, 2004; Reynolds and Braithwaite, 2001). Moreover, the socio-economic benefits of both state- and privately-owned protected areas to surrounding communities are often limited and indirect, requiring careful planning and management to ensure that benefits are reached at the community scale (Adams and Hutton, 2007; Pelser *et al.* 2013; Spenceley and Goodwin, 2007; Stricklund-Munro *et al.* 2010).

3.1.2. Wildlife tourist preferences in South Africa

With the ecological and socio-economic benefits of well-managed and sustainable, nature-based tourism ventures understood, a wealth of research has focussed on ascertaining tourist preferences and satisfaction levels (Akama, and Kieti, 2003; Kruger and Saayman 2010; Lindsey *et al.* 2007; Meng *et al.* 2008; Okello and Yerian, 2009). Drivers of tourist visitation to a wildlife reserve may include a combination of push and pull elements. A case study comparing two national parks in South Africa revealed that tourists had both common and differential motivations for visiting the respective parks, providing capacity for enhanced, niche marketing (Kruger and Saayman 2010). Primary motivations shared between reserves included knowledge seeking, relaxation and park attributes, while key differential motivations included photography and overall nature experience (Kruger and Saayman 2010). The primary motivation for visiting the Kruger National Park (NP) among South African respondents was seeking to ‘escape’, exemplifying further potential niche marketing opportunities for wildlife areas (Van der Merwe and Saayman, 2008).

In a survey-based study extending across four fenced reserves in South Africa, tourists selected high mammal diversity followed by large predators, as the most important reasons for visiting a wildlife reserve (Lindsey *et al.* 2007). The top selected species for game-viewing among all tourists were leopard (*Panthera pardus*) followed by lion and both were selected significantly higher than ungulate species such as zebra (*Equus quagga*) and wildebeest (*Connochaetes taurinus*) (Lindsey *et al.* 2007). First-time and international visitors were more interested in seeing the larger, high-profile mammal species including the so-called ‘big five’ [elephant (*Loxodonta africana*), white rhinoceros; buffalo (*Syncerus caffer*), lion and leopard; Lindsey *et al.* 2007]. African visitors and more experienced international visitors showed preference for viewing lesser-seen and rarer mammals, birds, plants and scenery, indicating the capacity for holistic conservation approaches (Lindsey *et al.* 2007). In other studies, tourists have expressed highest preference for viewing carnivores and high-profile large mammals, with more experienced and local tourists tending towards broader biodiversity preferences (Di Minin *et al.* 2013; Hausmann *et al.* 2017). Differences have also been found between international and local tourists in terms of their willingness to pay for wildlife experiences (Barnes *et al.* 1999; Mmopelwa *et al.* 2007) and their views towards community engagement in wildlife tourism (Chaminuka *et al.* 2012). International tourists were generally willing to pay more for both wildlife and community engagement activities compared to local tourists (Barnes *et al.* 1999; Mmopelwa *et al.* 2007) and expressed increased support for tourism that promoted rural development projects (Chaminuka *et al.* 2012).

Tourist preferences have also been evaluated through indirect measures, during which tourist behaviour in a wildlife reserve has been monitored by trained researchers (Maciejewski and Kerley, 2014; Okello *et al.* 2008). Tourist vehicles generally stopped more frequently and for longer, building up a larger crowd, when viewing large carnivores and elephants, but also showed high preference for a diversity of large mammals including giraffe (*Giraffa camelopardalis*) and hippopotamus (*Hippopotamus amphibious*) (Okello *et al.* 2008). Importantly, lions are always amongst the top preferred species for game-viewing by tourists (Maciejewski and Kerley, 2014; Okello *et al.* 2008).

3.1.3. Wildlife tourist satisfaction

High tourist satisfaction has been linked with high destination loyalty, in terms of tourist return rate and destination recommendation (Assaker *et al.* 2011; Ramseook-Munhurrun *et al.* 2015; Valle *et al.* 2006). With the market importance of return visitors, a surplus of research has aimed to measure the level of satisfaction of tourists through direct survey analyses (Akama and Kieti, 2003; Alegre and Garau, 2010; Arabatzis and Grigoroudis, 2010; Meng *et al.* 2008; Okello and Yerian, 2009). A variety of theories have been developed to explain tourist satisfaction (Churchill and Surprenant, 1982; LaTour and Peat, 1979; Westbrook and Reilly 1983). Leading theories are disputed (Yüksel and Yüksel, 2001), but are largely based upon the disparity between a tourist's actual experience and a standard or pre-conceived concept about the experience (expectation) (Bowen and Clarke, 2002; Oliver, 1980; Swan and Martin, 1981; Yüksel and Yüksel, 2003). Destination image, or the collective thoughts/emotions about a destination, and its perceived value can therefore have a significant effect on tourist satisfaction (Assaker *et al.* 2011; Meng *et al.* 2008; Prayag and Ryan, 2012; Ramseook-Munhurrun *et al.* 2015). High levels of tourist satisfaction are generally linked with tourists that perceive a higher value for the experience than expected and have a higher destination image (Chi and Qu 2008; Ramseook-Munhurrun *et al.* 2015). Various destination attributes in the nature-based tourism industry can increase trip quality and perceived value, thereby affecting tourist satisfaction (Meng *et al.* 2008; Okello and Yerian, 2009). Examples include natural scenery, staff friendliness and food and lodging (Meng *et al.* 2008).

In Tsavo NP, Kenya, gap analyses revealed that tourists' expectations were significantly exceeded across several park attributes, which led to high overall satisfaction levels (Akama and Kieti, 2003). Attributes included natural attractions, staff knowledge and attention to tourists and accommodation (Akama and Kieti, 2003). By comparison, tourist satisfaction level varied among national parks in Tanzania, with largely no link between satisfaction and destination attributes, including the number of species seen and tour type (Okello and Yerian, 2009). There are limited published studies on tourist satisfaction within state or private reserves in South Africa. Studies in the region have mainly focused on visitor species preferences and observations (Boshoff *et al.* 2007; Maciejewski and Kerley, 2014) and their travel motivations (Kruger and Saayman, 2010).

3.1.4. Research hypotheses

The primary driver for natural grouping behaviour in lions is believed to be intraspecific competition with unknown lions (Packer *et al.* 1990; Chapter 6). Lion populations in small, fenced reserves are often limited in the number of prides and nomadic males, resulting in reduced interactions with unknown lions (Miller *et al.* 2013). This may result in a degraded social structure (Chapter 6) which may in turn affect lion sightings. Di Minin *et al.* (2013) theorised that tourists' preference for viewing wild dogs as part of a pack rather than individually could reflect a preference for viewing natural animal behaviour. I therefore hypothesised that tourist experience and satisfaction with game-viewing lions on wildlife reserves can be affected by the number of resident prides and male coalitions. Specifically, in reserves with fewer prides and/or adult male coalitions, degraded social dynamics would reduce tourist satisfaction. I also evaluated how lion sighting (group size, age class, sex) affected tourist satisfaction and experience.

3.2. METHODS

The primary approach was through the development and administration of a questionnaire for tourists visiting wildlife reserves with different lion population structures (see below). The secondary approach was an analysis of the time spent by tourists at lion sightings across some of the reserves (see Chapter 6).

3.2.1. Questionnaire development

I developed a tourist satisfaction questionnaire between September and December 2015 for administering to tourists visiting 'big five' reserves in South Africa between January 2016 and April 2018. The primary aim was to collect information on respondents' experience and satisfaction linked with their recent visit to a wildlife reserve. Specifically, I wanted to compare their experience and satisfaction across different lion sighting types and reserves with different lion population structures to test my hypotheses.

3.2.1. i) Pilot study

I designed a pilot questionnaire consisting of 26 questions that I carried out through personal interviews (Passamore *et al.* 2002) with tourists at two locations [November and December 2015; East Gate airport, Limpopo (n = 15) and Addo Elephant NP, Eastern Cape (n = 15)]. The location selections were based on access to a high number of tourists visiting wildlife reserves. East Gate airport is near to (< 80 km) several wildlife reserves, containing either wild or managed wild lion populations. Permission was granted at both locations prior to commencement of the questionnaire. The questionnaire first collected general respondent information including age, gender, group number, nationality, trip motivation and reserve(s) visited (Q.1-7). Following this, the questionnaire requested information on the respondent's expectations before arrival (Q.8), safari-viewing preferences (Q.9) and general experience (Q.10-17), including wildlife sightings and top features of their stay. The final section was lion-specific, starting with lion game-viewing preferences (Q.18-19). The questionnaire was then complete for respondents who had not seen lions. The final questions (Q.20-26) related specifically to the respondent's experience with lions, including which lion age/sex groups were sighted and the level of satisfaction with their experience.

3.2.1. ii) Questionnaire design

On completion of the pilot study, I streamlined the questionnaire with the removal (*n* = 6) adjustment (*n* = 13) and addition (*n* = 9) of questions. Superfluous questions were removed or reduced to minimise overall questionnaire time (Iarossi, 2006). The final questionnaire (Appendix I) began with simple, introductory questions (Q 1 – 11) (Iarossi, 2006; Passamore *et al.* 2002) that collected basic respondent information. This included respondent demographics and the particulars of the destination visited. The questionnaire covered three primary areas of respondent experience: i) sensory impressions (what wildlife was seen), ii) emotional responses to experience and iii) destination loyalty (Ballantyne *et al.* 2011; Ramseook-Munhurrun *et al.* 2015). The questionnaire also included two questions related to tourist's safari-game viewing preferences in terms of species and lion age/sex group. Most questions were closed-ended, with only four open-ended questions related to emotional response that provided respondents an opportunity to formulate answers in their own way and without answer bias (Iarossi, 2006).

The response to eight questions on experience was based on a Likert-type scale from low enjoyment (1) to high enjoyment (3, 4 or 5), being a widely-used technique that is thus familiar to most respondents (Passamore *et al.* 2002). Likert scales to the straightforward question "How satisfied were you with X" (*n* = 3), consisted of non-labelled answers from 1 (not satisfied) to 5 (very satisfied/exceeded expectations). The Likert scales to more complex questions (*n* = 5) were provided with labelled answer options to increase the reliability of respondent interpretation (Passamore *et al.* 2002). Three questions requested respondents to rank listed items according to preference. The answer layout to these questions was varied by using a selection of separate answer sheets (displayed on a Google Nexus) to minimise bias based on answer position (Iarossi, 2006). When referring to different species of animals and behaviours, separate answer sheets with photographs (Google Nexus) were used to assist language barrier issues. The questionnaire included the same question twice, with a slightly different layout (Q.10 and 14), asking the respondent to rank wildlife species in order of preference. Respondents who answered these questions inconsistently were removed from the analyses due to unreliability (Iarossi, 2006). To increase sample size, an online format of the questionnaire was designed through SurveyMonkey®. With granted permission, the website link was shared via email by in-house reserve staff to respondents visiting study reserves.

3.2.1. iii) Questionnaire response indices

The questionnaire was designed to generate two tourist experience indices: 1) overall experience satisfaction and 2) lion experience satisfaction. The indices each evaluated tourists' experience level (emotional response and destination loyalty) based on the additive response of several questions (see Supplementary Material Table S3.1). The answers were largely based on Likert scales, or transformed, which were then summed to calculate a respondent's response index for experience.

3.2.2. Questionnaire administration

I carried out the personal interviews between March 2016 and August 2017 at four sampling locations (East Gate airport, Addo Elephant NP Main Camp, Satara Rest Camp in the Kruger NP and Munyawana Conservancy). I first had to ask tourists at East Gate airport if they had visited a wildlife reserve. If respondents answered yes, and to all those approached at the other sampling locations, I then explained the purpose of the study as wildlife research and asked if they could participate in a questionnaire (up to five minutes). At East Gate airport, I interviewed respondents from approximately two hours prior to the departure of flights. At national parks, I sampled between peak game-drive hours (10:00 – 15:00). Answers were collected via pen and paper and later transcribed into Microsoft Excel (MS Excel 365 ProPlus). The online questionnaire format included a brief cover email explaining the purpose of the questionnaire (wildlife research) and the length of time required. There were limitations in achieving a desired sample size (> 25 respondents) from reserves with a known population of a single pride and single adult male lion. The online format of the questionnaire was designed to increase sample size in this area. However, most participating reserves were reluctant to carry out questionnaires with visiting tourists in all formats (personal interview, online, pen & paper in room).

3.2.3. Time spent at lion sightings

Time (minutes) spent at lion sightings was recorded by in-house teams at study reserves (see Chapter 6). For reserves in which these data were collected by field-guides (staff employed at reserves to guide tourist safari activities) with tourist groups, the data were extracted and used to analyse the time spent at sightings across different lion age/sex groups.

3.2.4. Data formatting analyses

I performed data formatting and analyses using MS Excel and RStudio (RStudio Team 2016) using R v3.4.4 (R Core Team, 2018). For the questionnaire analysis, I summarised respondents according to their first language and nationality, age-group, motivation for visit, reserve visited, length of stay and whether they had previously visited a wildlife reserve. I performed Mann-Whitney U-tests of independent samples comparing tourists' experience indices (overall experience and lion experience) across reserves that varied in lion population structure (wild or managed wild lions) and between national parks and private reserves. This was carried out using the *wilcox.test* command in the R programming language (R Core Team 2018). I used linear modelling to evaluate tourist experience (continuous) across reserve visited, lion population structure (categorical: wild or managed wild), reserve status (categorical: public or private), length of stay (continuous: nights), dominant biome (categorical: Savanna or Thicket), activities undertaken (categorical: guided, self-guided or both), respondent age (categorical: 18 – 30 or 31 – 60 or > 60 years), gender (categorical: male or female) and whether the respondent had seen lions during their recent visit (categorical: yes or no). I performed Kruskal-Wallis tests to compare the lion experience index between respondents which saw different lion age/sex groups (*kruskal.test* command in R programming language; R Core Team 2018). I then used linear modelling to analyse the lion experience index across lion population structure and other variables, including whether the respondent had seen a pride (≥ 2 lionesses), adult male/s or cubs (see Supplementary Material Table S3.2).) Linear mixed modelling was carried out using the *lmer* command in the R programming language (R Core Team 2018). In cases for which there was no random variable, the model was structured as a linear model (*lm* command; R Core Team 2018). Non-significant terms were removed throughout using a backward stepwise elimination approach (Kuznetsova *et al.* 2017). Maximal models, that contained all selected explanatory variables, were fitted to the data after which the explanatory variables were sequentially removed, and the explanatory power of the model was assessed.

For the analysis of time spent at lion sightings, I used linear modelling to analyse the length of time (continuous: log-transformed minutes) spent by tour guides with tourists across fixed predictor variables: lion group number (continuous), the presence/absence of; a pride (≥ 2 lionesses; categorical: yes or no), cubs (< 12 months; categorical: yes or no) or an adult male at the sighting (categorical: yes or no). The random effect of reserve was included to account for variance among tour-guiding protocols on the different reserves. Model simplification was used to remove non-significant terms (Kuznetsova *et al.* 2017).

3.3. RESULTS

In total, 82 questionnaires were completed (March 2016 - April 2018) either through personal interview (n = 57) or online (n = 25). The personal interviews were carried out at Addo Elephant NP (n = 11), East Gate airport (n = 25), Kruger NP (n = 18) and Munyawana Conservancy (n = 1). The online questionnaires were administered with the support of two participating lodges in the Klaserie Private Nature Reserve. Three online questionnaires were removed from the analyses due to incompletion. Six questionnaires were removed due to inconsistent answers (n = 4 online; n = 2 interviews), resulting in a final total of 73 completed questionnaires. The recorded lion sightings (time spent wildlife viewing) took place at Addo Elephant NP (n = 56), Blue Canyon Conservancy (n = 66) and Kwandwe Private Game Reserve (n = 189) (see Chapter 6).

3.3.1. Overview of respondents

Thirty-eight (52%) females and 35 males (47%) completed the questionnaires, that were national (RSA: n = 16) and international (n = 57) travellers (Supplementary Material Figure S3.1). Most respondents (51%) were aged between 31 and 60 years of age and English was the dominant first language (Supplementary Material Figure S3.1). The primary trip motivation for respondents (n = 71) was either “holiday” or “wildlife”. Other motivations provided by respondents included “volunteer work”, “photography” and “entertainment” and “work”. A total of 47 respondents (64%) had previously visited a “big five” wildlife reserve, compared to 26 respondents who were first-time visitors. Almost half (48%) of respondents took part in both guided (game drives, n = 55; bush walks, n = 21) and self-guided (n = 38) safari activities (Supplementary Material Figure S3.1). Fifty percent of respondents visiting a national park (n

= 17) did not take part in guided safari activities, whereas all safari activities within the private reserves were guided by professional staff. Six respondents visited a wildlife reserve for one day without staying overnight (see Supplementary Material Figure S3.2). The longest time spent by a respondent within a reserve was three months within the Kruger NP, while the modal duration of a respondent's stay at a wildlife reserve was two nights. There was a total of 15 wildlife reserves visited during the respondents' recent trips (see Supplementary Material Table S3.3). Twenty-eight (38%) and 45 (62%) respondents provided feedback from their stay at a reserve with a managed wild lion population and a wild lion population respectively (see Supplementary Material Table S3.4).

Leopard was most frequently selected by respondents (*n* = 35; 48%) as the 'big five' species most preferred to view on safari (elephant = 19%, rhino = 7%, buffalo = 1%). One-quarter (*n* = 18) of respondents selected lion as their first choice however, a further 42% (*n* = 31) of respondents selected lion as their second preference out of the 'big five'. Amongst the large cats, questionnaire respondents selected leopard (34%), lion (29%), cheetah (*Acinonyx jubatus*; 23.3%) and caracal (*Caracal caracal*; 14%) as the highest preference for viewing on safari. Most respondents (62%) selected "Lion pride with cubs" as the lion group they would most like to view [lion group including two or more adult lionesses, an adult male(s) and cub(s)]. A coalition of two males was the second highest lion group selected by tourists as a game-viewing preference (see Supplementary Material Figure S3.3). No respondents selected a single lioness as their most preferred lion group to view however 4% of respondents selected a single adult male (see Supplementary Material Figure S3.3).

3.3.2. Experience of respondents

All respondents saw at least one (elephant) of the "big five" species during their recent visit to a wildlife reserve (see Supplementary Material Figure S3.4), with 26 respondents (37%) seeing all "big five" species. A total of 52 respondents (71%) saw lions during their visit. The level of overall experience (lodging, service, food etc.) of respondents was generally high (Table 3.3.1), and 46 respondents (63%) said they were likely to return to the destination. Out of these respondents, 21 had previously visited a 'big five' reserve.

Table 3.3.1. Summary of the values provided in response to the four quantitative questions regarding a respondent's general experience at a wildlife reserve and the corresponding values for 'experience index'.

Questionnaire measure	**Median**	**Mean**	**SD (±)**	***n***
Overall experience satisfaction level (1-5)	5	4.5	0.82	73
Rating of destination compared to other trips (1-5)	5	4.5	0.75	73
Future recommendation of the destination (1-5)	5	4.8	0.57	73
Likelihood of returning to destination in future (-1,0,1)	1	0.5	0.77	73
Experience index	15	14.23	2.09	73

Experience index was lower for respondents visiting small, fenced reserves ($n = 28$; managed wild lions) compared to respondents that had visited the larger, Greater Kruger area ($n = 45$; wild lions) ($W = 441.5, p < 0.05$). However, there was variation in the distribution of experience index associated with different reserves (see Supplementary Material Figure S3.6), likely driving location-based bias. Experience index was higher for respondents that saw lions (mean = 14.75 ± 1.25) (model intercept = 1.10, estimate = 0.07, SE = 0.03, $p < 0.05$) and was generally lower in the Thicket Biome (mean = 12.45 ± 2.08) (estimate = -0.07, SE = 0.04, $p = 0.11$) (mean experience index in Savanna Biome = 14.55 ± 1.95, respondents that did not see lions = 12.95 ± 3.06). However, experience index in the Thicket Biome significantly increased with increased length of stay (estimate = 0.10, SE = 0.04, $p < 0.05$) (model intercept = 1.10, SE = 0.03, $p < 0.01$; $F_{(4,68)} = 4.18, p < 0.01$; $R^2 = 0.15$) (see Supplementary Material Table S3.5).

In response to the open-ended question "What did you enjoy most about your recent trip?", the most common answer was wildlife related ($n = 26$), either a sighting or general game-viewing. Twelve respondents provided answers that were related to the natural attributes of the visited reserve (colloquially referred to as the "bush"). Other responses included the quality of service (staff, communication etc.) ($n = 10$) or an activity undertaken (game drives, braai, bush walks etc.) ($n = 6$), while eight respondents provided "unknown". The remaining responses included "general experience", "everything" ($n = 5$), a lodge ($n = 3$), self-driving/accessibility ($n = 2$) and "nothing" ($n = 1$). The responses to "Any other general comments about your recent safari trip" were divided into four categories based on the quality (negative/positive) of the comment (see Supplementary Material Table S3.6). Most negative comments (89%) were provided by respondents visiting national parks, with these comments focused on the "need for further information" in relation to maps, road signage, brochures and game-drive routes/tips (n = 7). The experience index of visitors to national parks (median = 14, n = 33) was lower than those visiting private reserves (median = 15, n = 40) (W = 450, p = < 0.05). The remaining negative comments centred around the expense of the trip (n = 3), "speeding/reckless driving" of other drivers (n = 2), the wildlife experience (n = 2), poor restaurant/facilities/roads (n = 3) and poor guiding staff (n = 1). Positive comments were received by respondents visiting both national parks (n = 7) and private reserves (n = 7). Most positive comments were generalised such as "terrific stay" (n = 11), others were related to the quality of the "guide/tracker" (n = 5), the facilities/services (n = 4) and the wildlife experience (n = 3).

3.3.2. ii) Experience with lions

Fifty-two respondents (71%) saw lions during their recent visit to a wildlife reserve and provided information for 'lion experience index'. The level of experience with lions varied but was high overall (Table 3.3.2). A total of 35 respondents saw a lion group(s) consisting of two or more adult lionesses (lion pride), 39 respondents saw an adult male lion(s) and 22 respondents saw lion cubs. Thirty-two respondents recorded that they observed one of the listed lion behaviours (greet, lick, play, mate, call) while viewing lions.

Table 3.3.2. Summary of the values provided in response to the four quantitative questions regarding a respondent's wildlife experience with lions during their recent visit, along with the corresponding mean value for 'lion experience index'.

Questionnaire measure	**Median**	**Mean**	**SD (±)**	***n***
Wildlife experience satisfaction level (1-5)	5	4.8	0.5	52
Wildlife experience with lions satisfaction level (1-5)	5	4.5	0.7	52
Lion experience added value to trip (1-4)	3.5	3.4	0.86	52
Any disappointment about experience with lions (-1,0)	0	-0.2	0.41	5
Lion experience index	13	12.5	1.83	52

No statistically significant difference was found between respondents who had visited reserves with managed wild lions (median = 12.5, n = 18) and those that visited reserves with wild lions (median = 13, n = 34) (W = 299, p = 0.89). Similarly, no statistically significant difference was found between respondents who saw lions of different sex/age categories ($X^2 = 6.45$, d.f. = 4, $p = 0.17$) (Table 3.3.3). Lion experience was higher for respondents that viewed wild lions (intercept = 2.13, estimate = 0.04, SE = 0.06, $p = 0.56$) and for respondents that viewed listed lion behaviours (estimate = 0.06, SE = 0.05, $p = 0.16$). Nevertheless, these terms were not significant and were removed from the final model. Lion experience index was higher for visitors that saw adult male lions (all sightings with adult males) (intercept = 2.12, estimate = 0.36, SE = 0.08, $p < 0.001$) and was higher for male respondents (estimate = 0.31, SE = 0.09, $p < 0.001$) (see Supplementary Material Table S3.7). A significant interaction limited lion experience of male respondents when adult male lions were sighted (estimate = -0.31, SE = 0.10, $p < 0.01$, $R^2M = 0.34$, $R^2C = 0.35$).

Table 3.3.3. The mean values for lion experience index across respondents that experienced different lion sightings (lion sex/age categories) during their recent visit to wildlife reserve.

	Lion experience index		
Lion group(s) sighted during recent visit	**Mean**	**SD (±)**	***n***
All: Pride (>2 lionesses) and adult male lion(s) and cub(s)	12.9	1.1	17
Pride (two or more adult lionesses)	11.4	2.3	8
Adult male lion(s)	12.7	0.9	13
Cub(s)	14	0.0	2
Pride (two or more adult lionesses) and lion cubs	11	4.2	2
Pride (two or more adult lionesses) and adult male lion	13.1	0.8	8
Total			50

**Two samples not included due to (n = 1): Respondents that saw i) an adult male lion(s) and lion cubs and ii) single adult lioness*

Out of the 28 respondents visiting reserves with managed wild lion populations, 13 respondents (46%) replied that they were aware of lion management protocol(s) (i.e. monitoring, game introductions or wildlife contraception) being utilized within the reserve they recently visited. A single respondent replied that this knowledge detracted from their experience, whereas the remaining respondents replied that it added value to their experience within the reserve. The respondents that were unaware of any lion management protocols ($n = 15$) within the small, fenced reserve visited were either indifferent or unsure of the potential effect this would have on their experience (*n* = 9, 60%) or thought that this information would add to their experience (*n* = 6, 40%).

3.3.3. Time spent at lion sightings

The average time spent at lion sightings (*n* = 311) was 37 ± 26.42 minutes (range = 2 – 180) across three reserves from September 2015 to May 2017 (see Supplementary Material Table S3.8 for mean sighting interval across reserves). This amounted to 190.93 hours that guided tourist vehicles spent with lions. The log-transformed time spent at lion sightings increased with increasing lion group number across all reserves ($F_{(307,3)} = 8.54$, $p < 0.001$, $R^2 = 0.07$), although the linear model had low overall explanatory power (see Supplementary Material Table S3.9). There was an average increase of over three minutes spent at a lion sighting for each increase in lion number.

When reserve was included as a random variable, the amount of time spent at a lion sighting reduced when cubs were present at the sighting (intercept = 2.97, estimate = -0.25, SE = 0.13, $p = 0.06$) and increased for sightings in which lions were active (i.e. on kill, walk, stalk) (estimate = 0.14, SE = 0.08, $p = 0.09$) rather than inactive (static, sleep). However, these terms were not significant, and the amount of time spent at a lion sighting increased with increasing lion group number (intercept = 3.10, estimate = 0.09, SE = 0.03, $p < 0.001$) (Figure 3.3.1). The overall explanatory power of the model was higher however, most of the variation was associated with reserve ($R^2M = 0.03$; $R^2C = 0.13$).

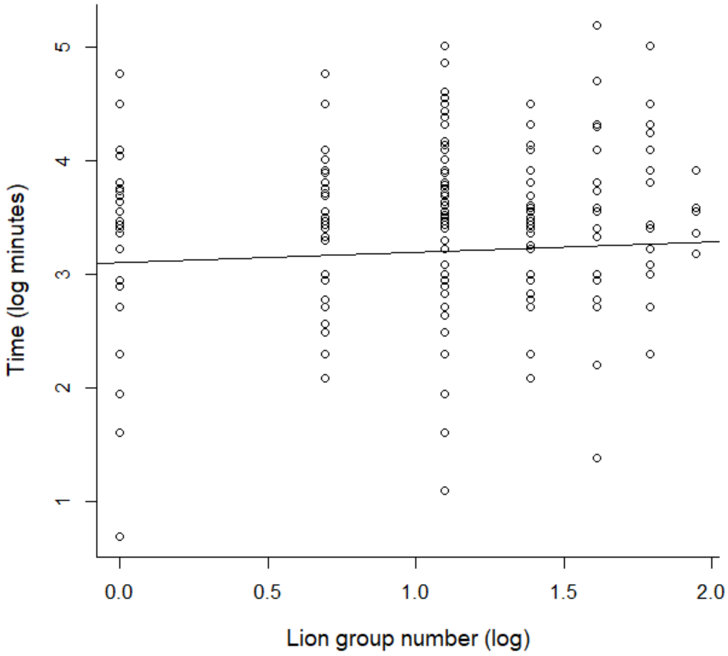

Figure 3.3.1. The amount of time (log: minutes) spent at lion sightings over increasing lion group size (log) across three reserves.

3.4. DISCUSSION

3.4.1. Tourist wildlife preferences on reserves in South Africa

Tourist preferences generally reflected previous findings from wildlife reserves, in that larger, charismatic carnivore species were ranked higher as a game viewing preference (Di Minin *et al.* 2013; Lindsey *et al.* 2007; Maciejewski and Kerley, 2014). Maciejewski and Kerley (2014) found that lions and leopards were species that tourists preferentially selected at Shamwari Private Game Reserve (PGR), with the largest monetary value linked with leopard, then lion, then cheetah. These higher-profile, flagship species provide an important role in terms of revenue generation, particularly regarding international and first-time visitors (Lindsey *et al.* 2007), which were a large proportion of respondents in my study. Tourists also showed lowest preference for buffalo compared to other 'big five' species, reflecting a previous evaluation of direct observation during tourist sightings (Okello *et al.* 2008). Not surprisingly, most respondents preferentially selected a full pride structure to view on safari. Novelty-seeking likely played a role in this, particularly for first-time visitors. Di Minin *et al.* (2013) also found that visitors to wildlife reserves preferentially valued a pack of wild dogs over an individual wild dog, postulating an appreciation for natural species behaviour. The second highest selected group in my study was a coalition of adult males (rather than a solitary male), and respondents rarely selected an individual lion. With lions being naturally social by nature, this further supports visitor's appreciation for natural behaviour.

3.4.2. Tourist experience on wildlife reserves in South Africa

Overall tourist experience was very high, reflecting previous findings for visitors to similar 'big five' wildlife areas (Akama and Kieti, 2003; Okello and Yerian, 2009). A large proportion (> 60%) of questionnaire respondents were repeat visitors to 'big five' wildlife areas. Similarly, Lindsey *et al.* (2007) found that a high volume of visitors to South Africa's wildlife reserves were experienced, return tourists, with up to 34% of respondents having visited a wildlife reserve more than five times within the last five years. There was significant variation between reserves visited, with previous research finding that lodge quality (including service) was a dominant factor in determining tourist experience (Torres-Sovero *et al.* 2012). Tourist experience was lower for respondents visiting a reserve in the Thicket Biome however, the experience significantly increased as the number of days per visit increased. The primary negative factors that respondents listed with regards to their overall experience related to information communication (game drive information and tips, signage, maps). Therefore, it is not surprising that as length of stay increased, respondents likely became more familiar with their surroundings and experience increased. The majority (77%) of respondents that were day and one-night visitors were also visiting this reserve. Furthermore, a large proportion of all positive comments reflected on wildlife experience and the level of personal service and guiding during a respondent's stay. The reserve within the Thicket Biome is a national park, and respondents from both national parks took a larger proportion of self-guided safaris. Therefore, an aspect of personal service was likely reduced.

Boshoff *et al.* (2007) found that increased education in Addo Elephant NP led to higher quality tourist experience. It is interesting that respondents both ranked lions higher as a game-viewing preference and that respondents who saw lions during their recent trip had a higher overall experience index. Clements *et al.* (2016) found that tourism revenue increased in regions with a higher lion density on small game reserves. However, over half of the respondents (62%) in my study that did not see lions took self-drive safari only, likely affecting their experience. Important destination attributes that were highlighted among respondents as enhancing the overall experience were wildlife and natural attributes, followed by the level of service provided, reflecting previous work (Akama and Kieti, 2003; Meng *et al.* 2008; Okello and Yerian, 2009).

Adult male lion/s were more frequently sighted by respondents than prides (≥ 2 lionesses) or cubs and overall lion experience was high. Although respondents that viewed wild lions had a slightly higher lion experience index, the difference was not significant. Similar to overall experience, this was likely affected by the level of service provided and other sensory impressions. Although most respondents preferentially selected a mixed lion pride group to view on safari, respondents that saw adult male lions (regardless of accompanying lions) generally had a higher lion experience. This reflects the importance of sensory impressions in determining wildlife tourist satisfaction (Agapito *et al.* 2017). Di Minin *et al.* (2013) also found that tourists preferred to view adult male lions compared to lion prides across all visitor types. Differences were also found between tourists' preference of viewing cheetahs and leopards of different age/sex groups, with cubs only being preferred in the case of leopards (Di Minin *et al.* 2013). Preference for viewing large carnivores, and adult males over cubs, may be linked with thrill-seeking if these species are perceived as imposing a higher danger level. Furthermore, tourists' preference of viewing various carnivore species was independent of whether they had already seen the species during their recent visit to a wildlife reserve (Lindsey *et al.* 2007). This independence was evident despite differences in terms of which carnivore species were more frequently seen by tourists (Lindsey *et al.* 2007). Therefore, although adult males were most often seen, experience index remained high. Furthermore, tourist sightings during which lions were mobile, were longer than sightings for which lions were static. This reflects that increased lion activity likely added to tourist sensory stimulus.

In my study, female respondents generally had a lower lion experience index than male respondents, which included two questions related to the value respondents placed on viewing lions. Previous research has indicated that female tourists visiting natural areas generally place higher importance on natural attributes and relaxation, compared to male tourists who generally place higher importance on action and thrill-seeking (Meng and Uysal, 2008), possibly driving the observed difference. The decrease in lion experience by female respondents may also have been the result of fewer sightings of prides and young cubs. With a large proportion of respondents in my study consisting of return-visitors, some respondents may have placed increased value on viewing intact breeding groups (Di Minin *et al.* 2013). With male tourists generally more interested in thrill-seeking, this reduction to experience may have been more pronounced in female respondents.

The amount of time spent by guided-tourist vehicles at lion sightings significantly increased with lion group size across all reserves, indicating tourist preference for larger lion groups. This may further indicate tourist preference for natural lion social behaviour (Di Minin *et al.* 2013). With more lions present at a sighting, there may also be increased opportunity for interactions between the lions and potential photographic opportunities. The average sighting interval was also likely dependent on reserve management guidelines, with each reserve having a unique intercept. Furthermore, lion sightings during which cubs were present were generally shorter than those for which cubs were not present. Many reserves have management guidelines and protocols in place (*pers. obs.,* Author), including sighting restrictions when lions (and other selected species) have young dependent offspring. The other possible factor was that lionesses with dependent offspring were more mobile or otherwise concealed in such a way as to reduce sightings. However, lionesses with/without cubs were either mobile or static for a similar proportion of sightings (with cubs = 66% sightings were mobile; without cubs = 68% of sightings were mobile).

3.4.3. Implications of lion-tourist satisfaction on fenced wildlife reserves

With tourism playing a major role in sustainable socio-economic development in South Africa (Rogerson, 2013; Sims-Castley *et al.* 2005; Spenceley, 2003), it is imperative to gain a clearer understanding on how reserve management and tourism objectives align in small, fenced wildlife reserves. Overall experience and lion experience indices were high, and respondents visiting wildlife reserve with managed wild lions did not score the lion experience index significantly lower than respondents visiting reserves with wild lions. However, tourists showed significantly lower preference for smaller lion groups, in particular, isolated adult lionesses. Therefore, degraded social dynamics and fragmented prides would likely impact negatively on tourist's experience with lions and reduce observations of natural lion behaviour (Di Minin *et al.* 2013). As male lions were preferentially selected as a priority for game-viewing by respondents, the effect of degraded pride dynamics on lion experience may likely have been reduced. Male respondents generally valued lion experiences higher and therefore are more likely to be more affected by a reduction in lion experience. However, all respondents that saw lions had higher quality experiences overall, indicating their important role in reserve tourism and revenue generation. According to respondent's open-ended responses, important factors determining satisfaction included sensory impressions and the service provided.

As lion experience was only marginally (and not significantly) reduced in reserves with managed wild prides compared to wild prides, it appears that the relative effects of the sightings and service provided likely outweighed the degradation to natural lion behaviour. However, a major drawback of my study was the inability to access a substantial sample size of respondents visiting reserves with known, isolated lion populations. Most respondents that visited reserves with managed wild lion populations visited reserves with multiple lion groups, or a lion population that was not otherwise part of this study and the population structure was unknown. Therefore, increased intraspecific competition from neighbouring lion groups may have increased natural social behaviour (Mosser and Packer, 2009; Chapter 6) and subsequent lion experience on these reserves. Further research is required to quantify the direct extent to which degraded population structure can affect lion-tourist satisfaction and related revenue. The different lion population structures provide niche-marketing opportunities across national parks and private reserves in South Africa, with regards to the activities offered and services provided (Kruger and Saayman 2010). This is further enhanced by the two primary visitor types to wildlife areas in South Africa – less experienced tourists with a higher cash flow and preference for 'big five' species and more experienced tourists with a lower cash flow and preference for a wider range of wildlife (Di Minin *et al.* 2013). Interpretation is a key driver that can increase tourist engagement and satisfaction in wildlife reserves (Moscardo *et al.* 2004), also exemplified by my study. The interpretation of wildlife-related activities and management structure among tourists is heavily reliant on effective communication (Moscardo *et al.* 2004).

3.4.4. Concluding remarks

The benefits of tourism, from revenue generation to biodiversity conservation, propel this industry forward in South Africa (Marnewick *et al.* 2014; Sims-Castley *et al.* 2005; Spenceley, 2003). My study suggests that tourists visiting wildlife areas in South Africa showed preference for viewing lions in relatively large natural social groups (consisting of adults and dependent offspring), and that adult male lions and lion behaviour were two important factors in driving lion experience and tourist satisfaction. Therefore, it is likely that reduced sociality and pride fragmentation in reserves with a limited lion population structure could negatively impact on tourist satisfaction. However, the levels of service at visited wildlife reserves and information communication were also key factors affecting overall satisfaction. Furthermore, sightings of large, adult males may contribute to off-setting the reduced tourist satisfaction that is likely associated with degraded lion social dynamics in small, fenced reserves.

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SUPPLEMENTARY MATERIAL

Table S3.1. Two response indices designed to evaluate tourist's satisfaction level. Individual question responses were summed for each respondent.

Question	**Measurement**		
Overall experience index	**Min**	**Max**	
Q. How satisfied were you with your overall experience this trip? (lodge, activities, transport, food etc.)? Please rate from 1 (not satisfied / very disappointed) to 5 (very satisfied / exceeded expectations).	+1	+5	
Q. How would you rate your recent destination compared to other trips you have taken? From 1 (much worse) to 5 (much better).	+1	+5	
Q. How strongly would you recommend this destination to your family and friends? From 1 (strongly recommend against) to 5 (strongly recommend).	+1	+5	
Q. Will you return to this destination again for another trip in the future?	No: -1	Unsure: 0	Yes: +1
Experience index	3	16	
Lion experience index			
Q. How satisfied were you with your wildlife experience? Please rate from 1 (not satisfied / very disappointed) to 5 (very satisfied / exceeded expectations)	+1	+5	
Q. How satisfied were you with your wildlife experience with lions? Please rate from 1 (not satisfied / very disappointed) to 5 (very satisfied / exceeded expectations)	+1	+5	
Q. Did your experience add value to your trip?	+1	+4	
1 – It detracted value from my trip			
2 – It made no difference to the value of my trip			
3 – It added value to my trip			
4 – It added great value to my trip			
Q. Is there anything about your lion experience that you were disappointed about?	Answer 'no' = '0'. If answered any other response the output was '-1'		
Lion experience index	2	14	

Table S3.2. The independent variables analysed in association with lion experience index.

Variable	**Unit**
Visited reserve management structure	Wild, or wild, manage lions
Visited reserve status	National park or private reserve
Visited reserve	Identity
Activities	Guided, self-guided or both
First time visitor	Yes/No
Respondent age-group	18 – 30; 30 – 60; >60 years
Respondent gender	Male/Female
Sighted a pride (≥ 2 lionesses) during visit	Yes/No
Sighted an adult male during visit	Yes/No
Sighted cubs during visit	Yes/No
Sighted lion behaviour/interactions	Yes/No

Table S3.3. The number of respondents (*n*) visiting 15 different wildlife reserves.

Reserve	***n***	**Reserve**	***n***
Addo Elephant National Park*	11	Balule Game Reserve+	2
Blue Canyon Conservancy	4	Kgalagadi Transfrontier Park*	2
Kapama Game Reserve	8	Mabula Game Reserve	1
Karongwe Game Reserve	2	uMhkuze Game Reserve	1
Klaserie Private Nature Reserve+	19	Pilanesberg National Park	1
Kruger National Park*+	26	Hluhluwe-Imfolozi Park	1
Greater Makalali Private Game Reserve	2	Munyawana Conservancy	1
Timbavati Private Nature Reserve+	10		

**National park*

+ Greater Kruger area

Table S3.4. The number of respondents that provided feedback regarding nine reserves, and the corresponding lion population status within each reserve (Funston and Levendal, 2015).

Reserve	Count	Lion Population
Addo Elephant National Park* (AENP)	11	Managed wild
Blue Canyon Conservancy	4	Managed wild
Kapama Game Reserve	8	Managed wild
Karongwe Game Reserve	2	Managed wild
Greater Makalali Private Game Reserve	2	Managed wild
Munyawana Conservancy	1	Managed wild
Klaserie Private Nature Reserve$^+$	15	Wild
Kruger National Park (KNP) *$^+$	22	Wild
Timbavati Private Nature Reserve$^+$	8	Wild
Total	73	

**National park*

$^+$*Greater Kruger area*

Table S3.5. Linear model coefficients associated with $\log_{10}$-transformed tourist experience index, dependent on whether the tourists saw lions during their recent trip, biome region visited (Savanna or Thicket) and length of stay (nights) ($F_{(4,68)} = 4.18$, $p < 0.01$; $R^2 = 0.15$).

Reserve	Estimate	SE	***p***
Model intercept	1.10	0.03	
Tourist saw lions	0.07	0.03	<0.05*
Thicket Biome	-0.07	0.04	0.11
Length of stay (Savanna Biome)	0.00	0.00	0.99
Length of stay (Thicket Biome)	0.10	0.04	< 0.05*

Table S3.6. Summary of respondents' answers to the open-ended question "Any other general comments about your trip"

Comment	**n**
Provided a positive comment about their recent visit	23
Provided a negative comment about their recent visit	16
Provided a both a positive and negative comment about their recent visit	2
Comment provided was neither negative nor positive about their recent visit	3
No comment was provided	29

Table S3.7. Linear mixed model coefficients associated with lion experience index across respondents that either saw or did not see adult males ($R^2M = 0.34$, $R^2C = 0.35$).

Reserve	**Estimate**	**SE**	***p***
Model intercept (female respondents that did not see male lion/s)	2.18	0.07	
Female respondents that did see male lion/s	0.36	0.07	< 0.001***
Male respondents that did not see male lion/s	0.32	0.09	< 0.001***
Male respondents that did see male lion/s	-0.31	0.10	< 0.01**
Random: reserve	**SD** ± 0.02		

Table S3.8. The number of sightings and the hours spent at lion sightings across three wildlife reserves in South Africa between September 2015 and May 2017. The mean sighting interval (minutes) is indicated for each reserve.

	Total		**Sighting duration**	
Reserve	**Sightings (*n*)**	**Hours**	**Mean (mins)**	**SD (±)**
Addo Elephant National Park	56	46.48	49.80	37.69
Blue Canyon Conservancy	66	29.28	26.62	12.18
Kwandwe Private Game Reserve	189	115.17	36.56	24.45
Total	311	190.93	36.84	19.97

Table S3.9. Linear model coefficients associated with the time (minutes) spent at lion sightings over increasing lion group size in three reserves ($F_{(3,307)} = 8.54$, $p < 0.001$, $R^2 = 0.07$)

Reserve	**Estimate**	**SE**	***p***
Intercept (Addo Elephant NP)	3.34	0.12	
Blue Canyon Conservancy	-0.49	0.12	< 0.001***
Kwandwe Private Game Reserve	-0.23	0.10	< 0.05*
Increasing lion group size	0.09	0.03	< 0.001***

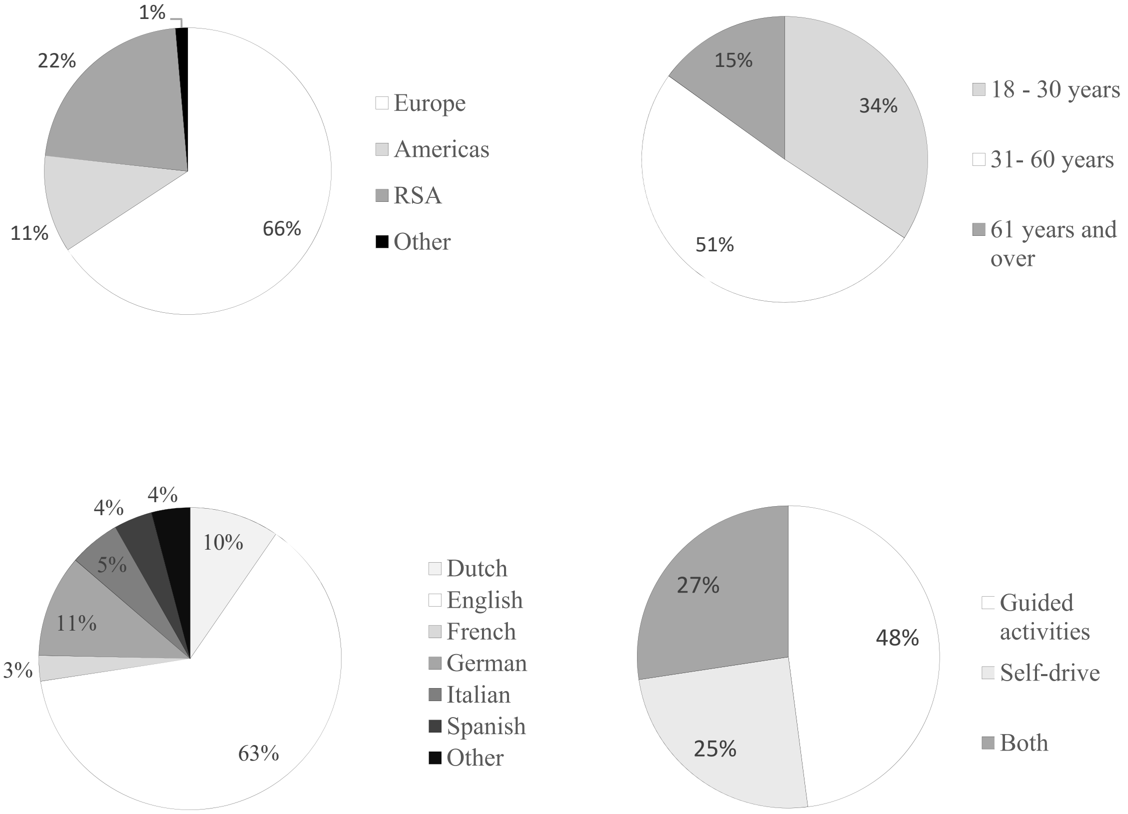

Figure S3.1. The nationality (Top, LHS), age group (Top, RHS), first language (Bottom: LHS) and the safari activities (Bottom, RHS) undertaken across 73 questionnaire respondents. The percentage value for each group is displayed.

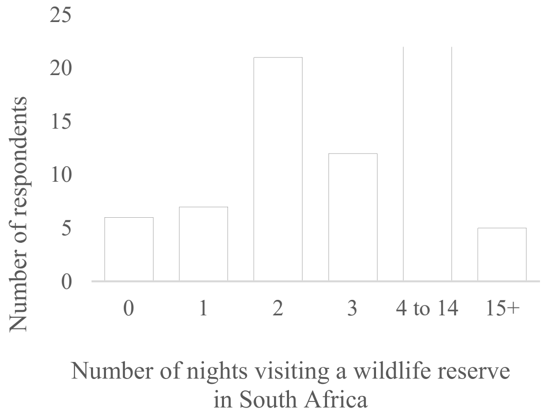

Figure S3.2. The length of stay (nights) within a wildlife reserve across all respondents (n =73), from day visitors (0 nights) to respondents spending over two weeks (15 nights or longer) within a wildlife reserve (mode = 2 nights).

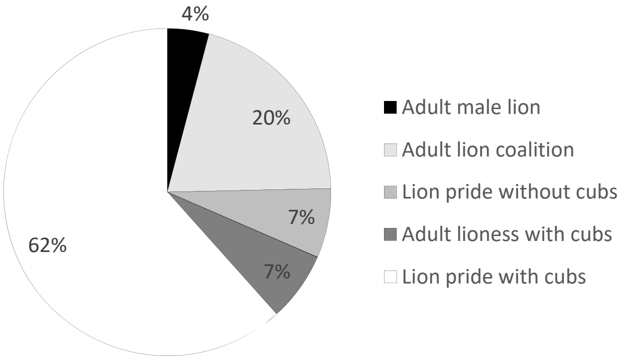

Figure S3.3. The relative proportion that different lion groups were selected by respondents (*n* = 73) as the lion group they most wanted to see on safari.

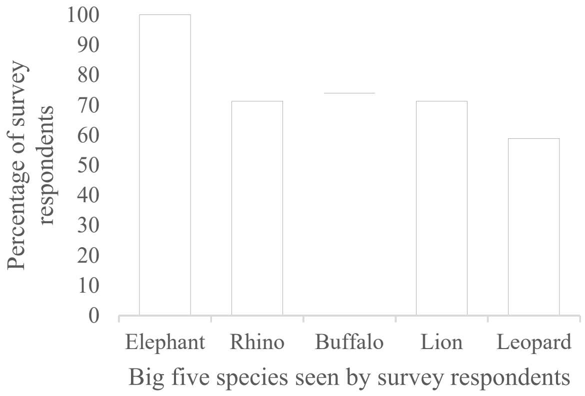

Figure S3.4. The percentage of respondents who saw the respective "big five" species during their visit to a wildlife reserve

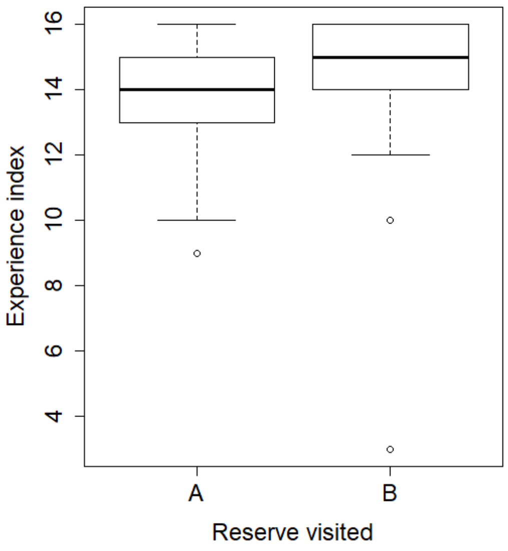

Figure S3.5. The median values and interquartile ranges of respondent's Experience index across small (< 1,000 km^2), fenced reserves (A; n= 6 reserves, *n* = 28 respondents) and larger reserves within the Greater Kruger (B: *n* = 3 reserves, *n* = 45 respondents).

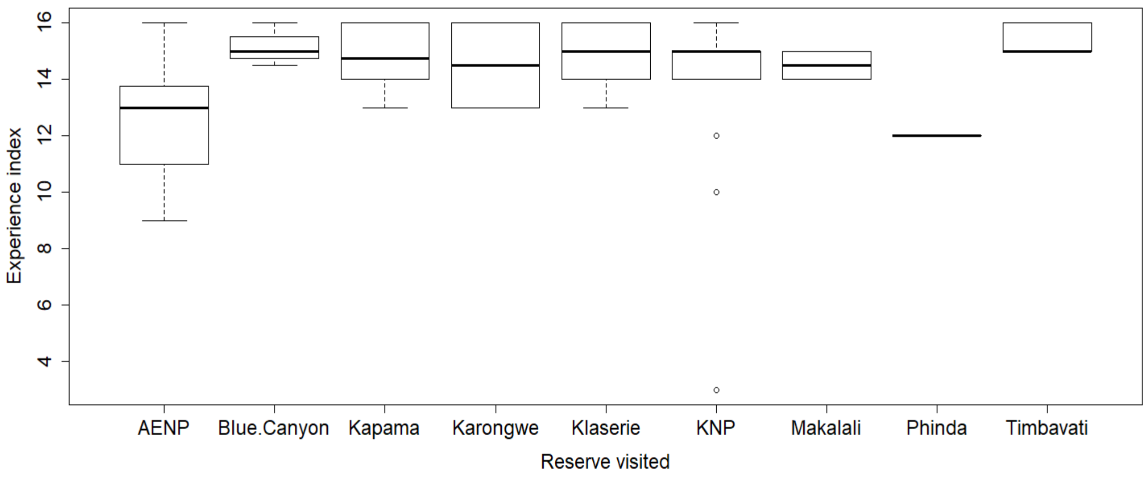

Figure S3.6. The median values and interquartile ranges of respondent's overall 'experience index' recorded across nine reserves (see Supplementary Table S3.4 for full names), displaying the variation within each reserve.

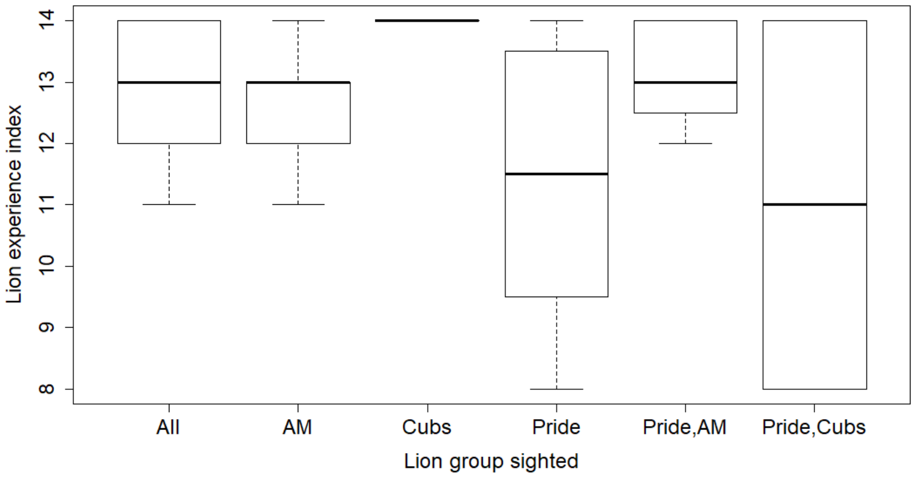

Figure S3.7. The distribution of lion experience across respondents that saw different lion groups (age/sex categories) during their recent visit to a wildlife reserve in South Africa (AM = adult male; Pride = ≥ 2 adult lionesses; cubs = < 12 months).

APPENDIX I

The 29 questions asked of survey respondents visiting wildlife reserves.

1. What is your nationality: Open-ended

2. What is your first language: Open-ended

3. Please select your gender from the list below: (Male / Female)

4. Please select your age group from the list below: (18 – 30 / 31 – 60/ > 60 years)

5. What was your primary motivation to recently visit to a wildlife reserve in South Africa:
Holiday / Wildlife / Work / Other (please specify)

6. Name of reserve visited: Open-ended

6a. What was the total length of your recent stay at X Reserve? (how many nights?): Open-ended

7. Had you visited this reserve or other Big 5 game reserves before your recent trip?: Yes / No

8. Which of the following activities did you take part in:
Self-guided safari / Guided safari / Walking trail

9. Which of the following animals would you most like to see on a wildlife safari:
Please rank in order of preference from 1 (most preferred) to 5 (least preferred)
Elephant / White rhinoceros / Buffalo / Lion / Leopard

10. Did you see any of the following animals on your recent wildlife safari trip:
Elephant / White rhinoceros / Buffalo / Lion / Leopard

11. How satisfied were you with your wildlife experience during your recent trip:
Please rate from 1 (not satisfied / very disappointed) to 5 (very satisfied / exceeded expectations)

12. How satisfied were you with your overall experience this trip? (lodge, activities, transport, food etc.)
Please rate from 1 (not satisfied / very disappointed) to 5 (very satisfied / exceeded expectations)

13. Which of the following animals would you most like to see on a wildlife safari:
Please rank in order of preference from 1 (most preferred) to 4 (least preferred).
Lion / Leopard / Cheetah / Caracal

14. Which of the following animals would you most like to see on a wildlife safari:
Please rank in order of preference with 1 being the animal(s) you would most like to see.
Lion pride group with cubs (≥ 2 lionesses and adult male) / Lion pride group (≥ 2 lionesses and adult male) without cubs / Single lioness with cubs / Single lioness without cubs / Coalition of two males / Single male

15. How many times did you see lions during your recent trip: Open-ended

16. During your recent trip, did you see any of the following lion groups:
Lion pride group (≥ 2 lionesses) / Adult male / Lion cubs

17. During you recent trip, did you see any of the following lion behaviours:
Greet / Groom / Call / Play / Mate

18. How satisfied were you with your wildlife experience with lions during your recent trip:

Please rate from 1 (not satisfied / very disappointed) to 5 (very satisfied / exceeded expectations).

19. Is there anything you were disappointed about with your wildlife experience with lions: Open
20. Did your wildlife experience with lions add value to your recent safari trip:
It detracted from the trip / It made no difference to the trip / It increased the value of the trip / It greatly increased the value of the trip
21. How would you rate your recent destination compared to other trips you have taken: From 1 (much worse) to 5 (much better)
22. What did you enjoy most about your recent safari trip at the reserve visited: Open-ended
24. How strongly would you recommend this destination to your family and friends: From 1 (strongly recommend against) to 5 (strongly recommend in favour)
25. Will you return to this destination again for another trip in the future?
Likely not / Unsure / Like will return
26. Any other general comments about your recent wildlife safari trip? Open
27. Are you aware of any lion management protocols on the reserve you recently visited?
28. Would/did this alter your experience in any way: Open
29. Please briefly explain your reasoning for this: Open

CHAPTER 4

THE MANAGEMENT OF LIONS (*PANTHERA LEO*) IN SMALL, FENCED WILDLIFE RESERVES

4.1. INTRODUCTION

With successful reintroduction and subsequent population growth of lions (*Panthera leo*) in small (< 1,000 km^2), fenced reserves across South Africa (Bissett, 2007; Hayward *et al.* 2007a; Hunter, 1998; Hunter *et al.* 2007), research focus has turned towards the effective management of managed wild lion populations (Kettles and Slotow, 2009; Miller *et al.* 2013; Miller *et al.* 2015; Slotow and Hunter, 2009). Throughout their range, lions are currently only increasing in small, intensively managed reserves (Bauer *et al.* 2015). Key management concerns for reserves with managed wild lions include population control, genetic viability and disease control (Miller *et al.* 2013). For the long-term viability of these managed wild lion populations, it is also essential to consider the evolutionary consequences of potential management interventions (Hayward and Kerley, 2009; Miller *et al.* 2015; Slotow and Hunter, 2009). Many small, fenced wildlife reserves are also heavily reliant upon tourism as a primary revenue source (Sims-Castley *et al.* 2005). Therefore, tourism factors, and the marketing thereof, are usually a core management consideration (Clements *et al.* 2016; Slotow and Hunter, 2009). When managed as a secondary conservation outcome of tourism, lions in small, fenced reserves can also play an important role in terms of the socio-economy and ecology of integrated landscapes. This situation drives a multi-level construct for lion management priorities.

4.1.1. Lion population growth in small, fenced reserves

There are 48 reserves across South Africa with managed wild lions (Miller *et al.* 2015; see Chapter 7). Many small, fenced wildlife reserves in South Africa have experienced high lion population growth rates after reintroduction (Hunter *et al.* 2007; Miller and Funston, 2014). Initially, a small number of reserves introduced relatively large founder populations (range = 16 – 19 lions), consisting of multiple lion groups (Slotow and Hunter, 2009). The trend has since decreased to introducing fewer lions, to delay the inevitable effects of lion population growth (Slotow and Hunter, 2009). Pride fragmentation and dispersal have increased the number of prides since reintroduction in some small founder populations (Bissett, 2007). However, lion population structure in many small, fenced reserves has been managed through lion removal (Bissett, 2007; Druce *et al.* 2004; Kettles and Slotow, 2009; Lehmann *et al.* 2008a), limiting pride formation. Lion population growth rate has been highest in years immediately post-reintroduction (Miller and Funston, 2014). Management protocols initiated the regular removal of excess lions, within two to five years after reintroduction (Miller and Funston, 2014). After this period, population growth rates stabilise at just over zero (Miller and Funston, 2014).

Lioness reproductive output and cub survival are both higher in small, fenced reserves compared to various larger systems (Miller and Funston, 2014). Lionesses in small, fenced reserves reproduce larger, average litter sizes (3 cubs), that have a higher survival rate (87%) than lion populations in the Serengeti National Park (NP) (2.5 cubs with associated 38 – 54% survival) (Bertram, 1975; Hanby and Bygott, 1979; Miller and Funston, 2014). Lion cubs in the Kgalagadi Transfrontier Park (TP), have a similarly low survival rate of 59% (Funston, 2011), and only 30% of cubs born in Nairobi NP reached the age of 2 years (Rudnai, 1973). Compared to the Kruger NP, lionesses in small reserves reproduce for the first time at a younger age (3.30 years versus 3.83 – 5.40) (Miller and Funston, 2014). Birth interval (time between successful litters) was similar between small, fenced reserves (2.17 years), the Serengeti NP (2.03 years) and Nairobi NP (1.96 years), compared to significantly longer intervals in the Kruger NP (3.33 years) (Miller and Funston, 2014).

Lions in the Serengeti NP have been recorded to encounter rival lion prides on average once every five days (Packer *et al.* 1990). Such intraspecific competition can pose considerable energetic constraints on individual fitness, affecting lioness reproductive and mortality rates (Mosser and Packer, 2009). In large systems, lions may be forced beyond the limits of their normal territory during times of drought, which can increase the chances of encountering unknown lions (Mosser and Packer, 2009). Up to 20% of lion cub mortalities have been attributed to infanticide from unknown males in wild populations (Packer *et al.* 1988), with lionesses also suffering fatal wounds in the defence of cubs (Druce *et al.* 2004; Mosser and Packer, 2009; Pusey and Packer, 1994). Small, fenced reserves without nomadic or unknown male lions do not have this mortality factor. Vital rate differences between lions in small, fenced reserves and larger systems can therefore be partly attributed to differences in intraspecific competition levels between unknown lions. In addition, many small, fenced wildlife reserves stock high numbers of prey to align with their tourism objectives (Clements *et al.* 2016; Louw *et al.* 2012). This reduces the need for lions to forage outside of their normal territories and risk encountering unknown prides (Mosser *et al.* 2009; Mosser and Packer, 2009). Furthermore, lioness body condition and consequential reproductive rate will likely be higher in areas with higher prey biomass (Ferreira and Hofmeyr, 2014). Another limiting factor that is absent in small, fenced reserves is starvation. Starvation is a leading driver of cub mortality in large systems (Eloff, 1980), accounting for up to 25% of lion cub mortalities in the Serengeti NP (Bertram, 1975).

4.1.2. Lion population management in small, fenced reserves

Management techniques for reducing lion population growth currently include pre-emptive, contraceptive measures to limit birth rate, and reactive measures to limit recruitment and survival (Kettles and Slotow, 2009; Miller *et al.* 2013). Contraception can be utilised to alter birth schedules and reduce litter size in small, fenced reserves, to closer reflect natural lion vital rates in the Kruger NP and the Serengeti NP respectively (Miller *et al.* 2013; Miller and Funston, 2014). There are two primary contraceptive treatments currently utilised across managed wild lion populations in South Africa, deslorelin implants and unilateral hysterectomy (see Chapter 5). Cub recruitment can be manipulated through direct lion removals or through the introduction of unknown adult male lions (Bissett, 2007; Druce *et al.* 2004; Kettles and Slotow, 2009; Miller *et al.* 2013). Lion removals have been utilised to mimic natural dispersal and mortality, while adult male introduction can drive natural infanticide (Kettles and Slotow, 2009).

Lions were historically removed through translocation (Druce *et al.* 2004; Kettles and Slotow, 2009; Miller *et al.* 2013). However, with a more saturated regional availability, the demand for founder lion populations has reduced over the past 10 years (Kettles and Slotow, 2009; Slotow and Hunter, 2009). Euthanasia has since become an increasingly used management option for lion removal, and a small number of removals have been carried out through trophy hunting (Kettles and Slotow, 2009; Miller and Funston, 2014). Lions have usually been removed when they are away from the pride to minimise pride disturbance (Kettles and Slotow, 2009). Lion removals have primarily been carried out on an *ad hoc* basis (Kettles and Slotow, 2009; Lehmann *et al.* 2008b) through an average removal of 0.2 to 7.5 lions annually (Miller and Funston, 2014). Some reserves have prioritised the removal of subadult males over females

(Bissett, 2007). In translocation, lions are usually removed in same-sex groups (1 – 4 lions) of subadult (1.25 – 2.25 years) lions for genetic purposes (Kettles and Slotow, 2009; Miller *et al.* 2015). Founder populations have sometimes included non-related individuals which were bonded together prior to release (Killian and Bothma, 2003; Tambling *et al.* 2013; Trinkel *et al.* 2008).

Natural male tenure lasts roughly two years in wild lion populations (Funston *et al.* 1998; Funston *et al.* 2003; Packer *et al.* 1988), and up to three years for larger coalitions (Bertram, 1975). Male tenure for longer periods in small, fenced reserves increases the risk of inbreeding (Druce *et al.* 2004; Trinkel *et al.* 2010). Adult male lions have therefore been introduced into established managed wild lion populations for genetic refreshment (Kettles and Slotow, 2009; O'Brien, 2012; Miller and Funston, 2014), creating a higher demand for translocated adult males. Introduced male coalitions have tended towards forming an independent hunting group, removing larger prey species including buffalo (*Syncerus caffer*), compared to solitary males (Lehmann *et al.* 2008b; Tambling *et al.* 2013). Adult males have therefore often been translocated as solitaries, or coalitions have been reduced (O'Brien, 2012; Lehmann *et al.* 2008b). The timing of a small number of hunted lions has been managed to coincide with the introduction of new adult males and genetic refreshment (Kettles and Slotow, 2009). Between 1999 and 2006, the average income for a translocated lion/lioness was USD 827.0 ± 261.17, excluding donated lions, while the income derived from hunting an adult male was higher, at over USD 14,000 in 2006 (Kettles and Slotow, 2009).

The effect of lion population increase has also been reactively mitigated through the supplementation of prey (Louw *et al.* 2012; O'Brien, 2012). Several small, fenced reserves have recorded substantial declines in prey populations following lion reintroduction (Lehmann *et al.* 2008b; Hayward *et al.* 2007b; Power, 2002; Tambling and Du Toit, 2005). Species which would normally migrate, such as blue wildebeest (*Connochaetes taurinus*), can be more affected due to the unnatural, sedentary constraints caused by fencing (Tambling and Du Toit, 2005). To counteract prey loss, lower value, preferred prey species have been supplemented in some small, fenced reserves (O'Brien, 2012). Prey supplementation can also be carried out to support rare or declining populations, such as eland (*Tragelaphus oryx*) (Louw *et al.* 2012). There are limited studies on the effect of such prey introductions on the long-term dynamics of either prey or predator populations (Louw *et al.* 2012; Owen-Smith, 2003). Newly introduced game populations have increased slowly at first, only showing significant population increase after about five years (Magome *et al.* 2008; Owen-Smith, 2003). The delay in population increase has been attributed to the time taken to establish an understanding of local food sources and territory attributes (Owen-Smith, 2003). Many prey species also often originate from other reserves or facilities without predators and are therefore “naïve” on introduction which may further impede subsequent survival rates (O’Brien, 2012).

4.1.3. Genetic viability in small, fenced reserves

Genetic management is essential to enhance the long-term viability of managed wild lion populations (Ferreira and Hofmeyr, 2014: Funston and Levendal, 2015; Miller *et al.* 2015). Inbreeding can lead to population depression and increased disease risk (Trinkel *et al.* 2008; Trinkel *et al.* 2011). The origin of reintroduced lion populations across South Africa has had an extensive effect on the current distribution of lion genetics regionally (Miller *et al.* 2015; Slotow and Hunter, 2009). A relatively small number of reintroduced lion populations have been sourced directly from wild populations in Etosha NP, Namibia (n = 2), the Kgalagadi TP (n = 4), the Kruger NP/surrounding areas (n = 7), and the Greater Mapungubwe Transfrontier Conservation Area (MTCA), Botswana (n = 2) (Miller *et al.* 2015). The remaining managed wild populations have been sourced from other fenced reserves in South Africa (Miller *et al.* 2015; Slotow and Hunter, 2009; Chapter 7).

Two wildlife reserves in the North West (Pilanesberg NP and Madikwe GR) introduced lions from Etosha NP in 1994 and 1995 respectively, the derivatives of which have since been extensively translocated to other fenced reserves across South Africa (Miller *et al.* 2015; Slotow and Hunter, 2009). This has resulted in a disproportionately high representation of Etosha-based lion genetics across regional fenced reserves (Miller *et al.* 2015). Comparatively few reserves (n = 13) have translocated lions from Kruger sources (between 1991 and 2005) or the Kgalagadi TP (between 2001 and 2007) (Miller *et al.* 2015). Introductions of lions from the MTCA were limited to two reserves in South Africa and formed a unique genetic grouping (Miller *et al.* 2015). Etosha NP was the only source for managed wild lion populations that did not occur naturally in wild lions in South Africa (Miller *et al.* 2015). Miller *et al.* (2013) demonstrated that the translocation of lions between fenced reserves effectively supported gene flow since reintroduction (Miller *et al.* 2015). Mixed genetics (combination of two wild sources) were found across multiple managed wild populations (Miller *et al.* 2015). Allelic diversity among small, fenced reserves was also comparable to that of the Kruger NP population (Miller *et al.* 2015). Miller *et al.* (2015) propose that the matrix of managed wild lion populations across South Africa represent adequate genetic diversity to support metapopulation planning.

4.1.4. Disease control in small, fenced reserves

Although many naturally occurring pathogens are linked with ecological processes including population control (Tompkins and Begon, 1999; Tompkins *et al.* 2011) and drivers of genetic diversity (Altizer *et al.* 2003), disease outbreak can significantly reduce fenced, isolated lion populations (Kissui and Packer, 2004; Trinkel *et al.* 2011). Up to 30% of inbred lions in Hluhluwe-Imfolozi Park (HiP) died from bovine tuberculosis (bTB) and associated malnutrition, attributed to reduced genetic resilience (Trinkel *et al.* 2011). The bTB was transmitted from infected buffalo (Trinkel *et al.* 2011), after multiple, unrelated introductions (Hlokwe *et al.* 2007). Buffalo have been identified as the key host responsible for the spread of bTB throughout the Kruger NP and HiP (De Vos *et al.* 2001; Michel *et al.* 2006). There were no population-level effects of bTB identified in lions in the Kruger NP (Ferreira and Funston, 2010). In the naturally isolated Ngorongoro Crater, Tanzania, lion populations significantly reduced since the outbreak of epidemic pathogens, including canine distemper virus (CDV) (Kissui and Packer, 2004). Domestic dogs were indicated as the disease reservoir (Harder *et al.* 1995; Kissui and Packer, 2004). Comparatively, the more expansive lion population in the Serengeti NP underwent relative population recovery after more frequent outbreaks (Kissui and Packer, 2004), highlighting the vulnerability of isolated populations Translocation can affect the epidemiology and spread of pathogens (Trinkel *et al.* 2011). Lions translocated to HiP to alleviate inbreeding depression inadvertently introduced feline immune-deficiency virus (FIV) (Trinkel *et al.* 2011).

Certain pathogens, including rabies and bTB, have historically required control in South African legislation (Anon, 1984). The primary pathogens of lion management concern in South Africa are the infectious pathogens rabies, bTB, and CDV (Miller *et al.* 2013). Evidence suggests that FIV is endemic to wild lions, as it has been found at consistently high prevalence across multiple populations (Antunes *et al.* 2008; Packer *et al.* 2001; Troyer *et al.* 2004). Miller *et al.* (2013) caution that the transmission and occurring serotypes of FIV in managed wild lion populations should be monitored for the potential effects of different strains (Troyer *et al.* 2004). Both rabies and CDV have been associated with substantial reductions in wild carnivores (Alexander and Appel, 1994; Murray *et al.* 1999; Sillero-Zubiri *et al.* 1996). Reoccurrent CDV outbreaks in lion populations in the Serengeti NP occurred during years with higher lion density (Packer *et al.* 2001). Both rabies and CDV have been identified in African wild dogs (*Lycaon pictus*) in fenced reserves in South Africa (Prager *et al.* 2012). Rabies vaccinations have been used to inoculate wild dog populations, including Tanzania (Gascoyne *et al.* 1993) and South Africa (Hofmeyr *et al.* 2004). The population in South Africa (Madikwe GR) was treated during a breakout with overall high mortality however, 50% (*n* = 3) of vaccinated wild dogs survived (Hofmeyr *et al.* 2000).

4.1.5. The Lion Management Forum of South Africa

The Lion Management Forum of South Africa (LiMF) is a Public Benefit Organisation comprised of wildlife reserve managers, researchers, veterinarians and government officials, formed in 2009 to address the issues surrounding managed wild lion populations. The LiMF published a peer-reviewed paper outlining the primary challenges to lion management in South Africa (Miller *et al.* 2013). Findings focused on lion management recommendations that would restore or mimic the degraded ecological processes that led to lion population increase (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013). Birth schedules can be manipulated through contraception however, caution was advised as empirical research on their efficacy and potential side-effects was lacking (Miller *et al.* 2013). There are also potential, negative population-level effects when using fertility control in small, isolated populations (Miller *et al.* 2013; Miller *et al.* 2015). It was recommended that adult male lions should be frequently replaced through translocation to more closely mimic the high turn-over rate of adult males in open systems (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013). Similarly, it was suggested that lion removals should mimic the natural dispersal of younger individuals or the death of older individuals (Miller *et al.* 2013).

It has been recommended to apply a standardised, regional strategy regarding lion translocation management, according to the four genetic sources of lions across South Africa (Ferreira and Hofmeyr, 2014; Miller and Funston, 2014; Miller *et al.* 2015). Similar metapopulation dispersal principles have been applied to wild dogs across fenced reserves in South Africa (Davies-Mostert *et al.* 2009; Davies-Mostert *et al.* 2015). Isolated lion populations would be managed as a single population separated into different social units (Ferreira and Hofmeyr, 2014). Linking spatially isolated lion populations through intensively managed translocations would support the restoration of degraded ecological processes in small, fenced reserves including genetic integrity and social dynamics (Ferreira and Hofmeyr, 2014). A Biodiversity Management Plan (BMP) for lions in South Africa was drafted for 2015 to 2019 (Funston and Levendal, 2015). The key focus of the BMP for managed wild lions was the development of metapopulation linkages between and standardised procedures among small, fenced reserves to support the socio-economic-ecological role of managed wild lion populations in South Africa (Funston and Levendal, 2015).

4.1.6. Research objectives and hypotheses

There were two primary aims for this chapter. The first aim was to test predictions of lion vital rates (reproductive output and population growth) across reserves that varied in the number of prides and adult males/coalitions present (intraspecific competition levels). I predicted that lion vital rates in small, fenced reserves could be affected by population structure. Specifically, I predicted that lionesses would have higher reproductive rates (e.g. age of first reproduction, birth interval) and cub survival in reserves that contained fewer resident prides and adult males/coalitions, leading to higher population growth rates. The second aim was to review lion management protocols and their associated outcomes across small, fenced reserves in South Africa. With contraceptive techniques analysed in depth in Chapter 5, this chapter focusses on lion removal (translocation, culling, hunting), prey supplementation and adult male lion introduction and tenure. Other management outcomes evaluated include disease control and metapopulation planning across the LiMF.

4.2. METHODS

I collected records on lion demographic history across study reserves (see Supplementary Material Table S4.1). Demographic history included available details regarding all lion introductions, removals, births and mortalities (see Supplementary Table S4.2). Details of contraceptive use at participating reserves were collected via questionnaire (see Chapter 5). I evaluated the genetic provenance of introduced lions according to Miller and Funston (2014). I collected available records on the numbers and dates of key prey species (annual census, removals and introductions), annual rainfall levels and annual census of other carnivores during the study period, relative to each reserve since lion reintroduction (1992 to 2018).

4.2.1. Data formatting and analyses

All data were formatted using MS Excel (Microsoft Office 365 Pro Plus). All statistical tests and models were carried out in RStudio (RStudio Team 2016) using R v3.4.4 (R Core Team 2018). I categorised participating reserves according to their lion population structure (Table 4.2.1). For populations that fluctuated over time, the reserves were categorised accordingly. For example, if a reserve introduced a second pride, the population structure category was adjusted temporally. Prides were defined as groups of adult (≥ 3 years) lionesses that were maternally related (*n* = 28 prides), unrelated lionesses that had been bonded together (*n* = 4 prides) or solitary lionesses (with offspring) that maintained a territory (*n* = 4). Fragmented prides were accounted as separate prides after more than five years had passed since the time of pride fissure (VanderWaal *et al.* 2009). I calculated lion density (lions/100 km^2), as the number of lions present in each reserve at the end of every calendar year.

Table 4.2.1. Lion population structure categories across participating reserves (*n* = 16)

Lion population structure on reserve	
A	One pride and a single adult male lion/coalition
B	One pride and more than one adult male/coalition
C	More than one pride and a single adult male lion/coalition
D	More than one pride and more than one adult male/coalition

I listed the total number of lion introductions, mean founder population size and the origin of introduced lions. I then listed the total number of lions born to study reserves and the total number of lions alive at the time of data collection according to sex, age and genetic provenance (Miller *et al.* 2015).

4.2.1.i) Reproductive vital rates

I calculated the age of first reproduction (years) for each lioness, as lioness age when her first litter was recorded to emerge from the den (Miller and Funston, 2014). I removed any first litters that were produced after a contraceptive treatment from this dataset. I next calculated the birth interval (years) between each recorded litter across all lionesses (Miller and Funston, 2014; Packer *et al.* 1988). I removed birth intervals for which lionesses were treated with contraception between litters. Birth intervals following a failed litter (i.e. no cubs survived to 12 months), were also removed to analyse the full birth interval when cubs were raised to near-independence (Miller and Funston, 2014). I also calculated the known litter size and sex ratio for all recorded litters (according to first emergence from the den) after removing litters that were produced subsequent to a contraceptive treatment and for which the litter size was unknown due to young cub mortality or creche formation. I then calculated the percentage of cubs surviving from date of first emergence from den until 12 months of age across all litters (Funston, 2011; Miller and Funston, 2014). I removed litters for which survival to 12 months was affected by a lion management intervention, and that had not yet reached 12 months of age at the time of data collection, from the analyses. I then used linear mixed modelling (using the *lmer* command in the R programming language; R Core Team 2018) to compare the following independent variables;

1. lioness age of first reproduction (years) – no random variable
2. lioness birth interval (years)
3. litter size
4. sex ratio of cubs born
5. cub survival (%) to 12 months

across i) lion population structure categories (A – D), ii) presence/absence of more than one resident pride, iii) presence/absence of more than one resident adult male/coalition and iv) annual lion density (lions/100 km^2), with v) lioness ID as a repeated, random variable. Non-significant terms were removed from models through stepwise backwards model simplification (Kuznetsova *et al.* 2017). In cases for which there was no random variable, the model was structured as a linear model (using the *lm* command in the R; R Core Team 2018). I also summarised the causes of lion cub mortalities according to natural and unnatural causes.

4.2.1.ii) Lion population growth

I calculated annual lion population growth (λ) for each reserve, based on the number of lions present at the end of each consecutive year (Miller and Funston, 2014). The finite rate of growth (λ) formula was used:

$$N_{t+1} = \lambda(N_t) \text{ or } \lambda = N_t / N_{t+1},$$

where, N_{t+1} is the number of individuals after one time unit and N_t is the original population size. I calculated the mean annual growth rate across all reserves, since the time of lion reintroduction. I also calculated the mean annual growth rate particular to each reserve, summarising the highest and lowest values. I carried out a Kruskal-Wallis test to compare the mean annual population growth between reserves that introduced one or more than one founder pride. I then used a Kruskal-Wallis test to compare the mean annual population growth between reserves that introduced one or more than one founder adult male/coalition.

I calculated the total number of lions and the percentage of populations that were introduced, born, removed and died annually across each reserve. I also calculated the number of lions contracepted annually for each treatment across all reserves, tabulating deslorelin implants as current for two years subsequent to treatment (conservative estimate based on findings from Chapter 5), and unilateral hysterectomy and sterilisation as life-long treatments for individuals. I then calculated the annual percentage cover of contraception for each reserve, according to the total number of resident adult females, for each deslorelin, unilateral hysterectomy and sterilisation treatments. I also then added the contracepted individuals together for each reserve and divided by the total lioness population number for that year to calculate a percentage cover of contraception – 'contraception cover'.

To investigate the role of lion removal rate (percentage of each lion population removed annually), I used linear modelling to analyse lion removal rate over; time since lion reintroduction (continuous: years), lion population category (categorical: A – D), lion density (continuous: lions/100 km^2), and 'contraception cover'. I then used linear modelling to analyse lion birth rate (percentage of each population born annually) over the same listed variables and the additional dependent variable, lion removal rate from the previous year. Following this, I evaluated annual lion population growth rate (λ) across lion population categories (A – D) using linear modelling. Other variables included in the model were the number of years since lion reintroduction, lion density (lions/100 km^2), biome, founder population size, the proportion of each respective population that was treated annually i) deslorelin or ii) contraception (contraception cover), and that was i) removed or ii) introduced annually by reserve management subsequent to population establishment.

4.2.1.iii) Lion removals

I calculated the total number of lions removed across participating reserves and the mean value for the first year during which lions were removed from participating reserves. I calculated the mean percentage of lion populations that were removed during the first year of removal and during subsequent years. I used Spearman's Rank Correlation to test for a relationship between the percentage of annual births and the percentage of populations removed in the previous year. I then summarised the sex and the mean and standard deviations of lion-age at time of removal. The method of lion removal was categorised according to; translocation, euthanasia, hunt, other or unknown. I then listed all records of lions that broke out from reserves and the relevant management response.

4.2.1.iv) Introduction of adult male lions and male tenure

I calculated the number of adult males/coalitions that were introduced to existing lion populations and summarised according to age at time of introduction and coalition size. I then summarised all records of cub infanticide and lion mortalities within i) six months and ii) 12 months of adult male release. I also calculated the age (years; at date of first litter) and coalition size of adult males in tenure of prides. I calculated the known tenure interval of adult males, from the date of first recorded litter until the date of i) pride take-over, ii) male death or iii) male removal. I then analysed tenure i) age (years) and ii) interval (years) across population categories (A – D) and coalition size using linear modelling. In the analysis on tenure age, I also included whether the lions were introduced or born to the study reserve.

4.2.1.v) Key prey species – supplementation, removal and biomass trends

I listed all key prey species recorded across study reserves, along with their relevant biomass weight (kg) (Coe *et al.* 1976; Hockey *et al.* 2005) and calculated the mean annual percentage change in prey population sizes across all reserves. I outlined the game stocking history (supplementations and removals) across reserves and details on game census interval. To evaluate the effect of prey supplementation, I calculated the population growth rate (λ) of key prey species for one year prior and one year subsequent to each supplementation. I also calculated the population growth rate at five years subsequent to prey supplementation, or the latest year for which data was available (follow-up species introduction or date of data collection). To evaluate the management effort of prey species removal over time, I displayed the rate of prey species removal across reserves, according to i) total prey density (kg/km^2) and ii) the percentage of reserve prey biomass that the removed species represented annually.

There was a single reserve from a drier biome (Succulent-Karoo) and I therefore calculated the proportion (%) of prey biomass introduced or removed annually relative to the overall reserve biomass for that year (to eliminate biome-based differences in biomass density). I then used linear modelling to analyse the proportion of overall prey biomass A) introduced and B) removed annually across reserves according to i) total annual prey biomass in the reserve, ii) number of years since lion reintroduction and iii) reserve. I next used linear mixed modelling to analyse total prey biomass (kg/km^2) across reserves according to: i) years since lion reintroduction, ii) lion density (lion/100 km^2), iii) lion population category (A – D), iv) biome and v) reserve (random variable: repeated). I then eliminated the single reserve dominated by a biome other than Savanna (limited sample size) and limited the dataset to years (since lion reintroduction) for which there was a minimum reserve sample size of two. There was a single reserve in the sample with each lion population categories C and D respectively, and no reserve with lion population category B. I next analysed the effect of lion population structure according the number of resident prides alone. I used linear mixed modelling to analyse prey biomass (kg/km^2) according to: i) years since lion reintroduction, ii) lion density, iii) presence of singular or multiple resident prides, iv) rainfall and v) reserve (random). Rainfall was tested both directly, as the average level of annual rainfall for the corresponding year and categorised as low (> 100 ml less than average rainfall for reserve), medium (within 100 ml of average rainfall) or high (> 100 ml above average rainfall for reserve).

4.2.1.vi) Lion mortalities and disease control

I tabulated the total number of lion mortalities across reserves. I then summarised the sex, mean and standard deviations of lion-age at time of death. I categorised the cause of lion mortality according to; intraspecific competition, natural (old-age, disease, injury), unknown or anthropogenic. I calculated annual lion mortality rate (percentage of lion mortalities) for each reserve and used linear mixed modelling to analyse for a difference in mortality rate across: i) lion population structure (A – D), ii) years since reintroduction iii) lion density and iv) reserve (random). The total number of disease management interventions and occurrences that were provided from participating reserves were summarised.

4.2.1.vii) The Lion Management Forum of South Africa

A 'Lion Audit and Management Questionnaire' was distributed via email correspondence to reserve managers in association with the LiMF. The questionnaire included two questions relating to management goals within the reserve:

1. Please rank the overall goals of your reserve (up to 4, but you can have less)
2. Please rank the motivation for having lions on your reserve (up to 4, but you can have less)

The rank-answer options provided were: Tourism, Conservation, Hunting, Other (please specify). I summarised and compared the results from survey respondents participating otherwise in the current chapter. I next summarised the total number of email correspondences between the LiMF members, from 2015 to 2018, that pertained to the translocation of lions between reserves, according to the type of request (available lions or lions sought) and the time interval between the correspondences.

4.3. RESULTS

Historic lion demographic information was obtained from 16 reserves with managed wild lions in South Africa, dating from 1992 to 2018. The data pertained to 890 lions. The reserve area available to lions varied from 58 to 910 km² (mean = 287.9 ± 246.4). There were 146 lion introductions recorded, of which, 55 were born on other study reserves. A total of 100 lions were introduced as part of a founder-population. This included one lioness that was introduced to two study reserves as a founder lion. One reserve removed all lionesses and re-initiated with new founders twice during the study period. Founder populations ranged in size from 2 – 13 lions (mean = 5.7 ± 2.6, n = 18). The remaining introductions were into existing lion populations (established a minimum of 12 months prior). There were also three records for lions that immigrated through the fence on separate occasions (n = 2 reserves). Introduced lions originated from the Kruger NP region (n = 12), the Kgalagadi TP (n = 8), fenced reserves within South Africa (n = 123) or of unknown origin (n = 3). The remaining lions were born within the participating reserves (*n* = 276 litters; 799 cubs). Annual lion density varied from 0.9 – 19.3 lions/100 km^2 in reserves (*n* = 14) dominated by the Savanna and Thicket Biomes (mean = 7.1 ± 4.3). In reserves (*n* = 2) dominated by the Nama and Succulent-Karoo Biomes, lion density varied from 0.9 – 3.7 lions/100 km^2 (mean = 2.1 ± 0.7).

There were 293 lions across the participating reserves at the time of data collection, including 59 cubs (< 1 year), 79 subadults (1 – 2.9 years) and 155 adults (see Supplementary Material Table S4.3). Adult lions ranged in age from 3 – 18.8 years (mean = 7.1 ± 3.5) and included 97 lionesses and 58 lions. Nine males were over the age of 10 years. The genetic provenance of the lions included Etosha (*n* = 93), Kgalagadi (*n* = 36) and mixes of; Etosha/Kruger (*n* = 101), Etosha/Kgalagadi (*n* = 37), Etosha/Kruger/Kgalagadi (*n* = 24) and two reintroduced lions of unrecorded origin. Lions with genetic provenance from Etosha were present in all four regional nodes across South Africa (Lowveld, North West, Frontier and KwaZulu-Natal), with only Etosha-mixes present in the North West. Lion populations with genetic provenance from the Kgalagadi were present only in reserves of the Frontier region, with the Kgalagadi-mixes also present in North West (*n* = 29) and KwaZulu-Natal (*n* = 24). Lions with a Kruger-mix provenance were present in the Lowveld (*n* = 39), KwaZulu-Natal (*n* = 56) and the Frontier (*n* = 30).

4.3.1. Age of first reproduction

Out of 114 lionesses, 20 received either deslorelin implants or unilateral hysterectomy before producing their first litter and were removed from analyses. An additional lioness produced her first litter prior to translocation to a study reserve and was also removed. The average age of first reproduction across remaining lionesses (*n* = 93) was 3.3 ± 0.8 years (range: 1.8 - 6.0). Lionesses produced their first litter at an older age in reserves with a single pride and single adult male (A) compared to reserves with other lion populations structures (Table 4.3.1). This difference was only statistically significant compared to reserves with both multiple prides and adult males (D) (see Supplementary Material Table S4.4). Age of first reproduction decreased with increasing lion density (lions/100 km^2), except in reserves containing both multiple prides and adult males (see Supplementary Material Table S4.4). However, lionesses on reserves with more than one pride reproduced on average three months earlier (estimate = -0.33, SE = 0.16, $p < 0.05$) than lionesses on reserves with a single pride (intercept/estimate = 3.89, SE = 0.28, $p < 0.001$; $F_{(1,92)} = 4.39$, $p < 0.05$, $R^2 = 0.04$). Similarly, lionesses on reserves with more than one resident male/coalition reproduced at a younger age (estimate = -0.88, SE = 0.35, $p < 0.05$) than lionesses in reserves with a single adult male (intercept/estimate = 4.80, SE = 0.59, $p < 0.001$). In the same model, age of first reproduction declined in regions with higher lion density (estimate = -0.11, SE = 0.55, $p = 0.05$), but significantly less so in reserves with more than one resident male/coalition (estimate = 0.06, SE = 0.03, $p = 0.06$; $F_{(3,90)} = 2.46$, $p = 0.09$, $R^2 = 0.04$). There was a single lioness that appeared to be naturally sterile. The lioness was 12.68 years of age at the time of data collection and had not produced a litter or showed signs of reproductive activity, during her lifespan.

Table 4.3.1. Mean age (years) of first reproduction, across 93 lionesses (*n*).

Lion population structure on reserve		**Mean**	**SD (±)**	***n***
A	One pride and a single adult male lion/coalition	3.67	0.94	25
B	One pride and more than one adult male/coalition	3.28	0.63	10
C	More than one pride and a single adult male lion/coalition	3.17	0.45	12
D	More than one pride and more than one adult male/coalition	3.22	0.72	46

4.3.2. Lioness birth interval

Sixty-nine lionesses produced more than one litter (*n* = 220 litters; *n* = 152 birth intervals). Intervals between litters during which lionesses were contracepted or translocated were removed (*n* = 21 intervals). The average length of time between all remaining litters was 1.76 ± 0.55 years (*n* = 131 litters). Birth intervals after failed litters (*n* = 9) were removed from further analyses and average birth interval increased by three weeks (mean = 1.82 ± 0.51; range = 0.67 – 4.08 years, *n* = 122 intervals). The longest average birth interval was recorded across reserves with more than one pride and a single adult male (C; Table 4.3.3). This was almost three months longer than average birth interval in reserves with a single lion pride and adult male/coalition (A). The presence/absence of neighbouring adult males was significant, with a significant interaction dependent on lion density (see Supplementary Material Table S4.5). Lioness birth intervals in reserves that contained more than one pride (intercept = 2.62, estimate = 0.16, SE = 0.12, $p = 0.18$) were significantly longer than their respective counterparts in reserves that had a single lion pride (one pride/one coalition estimate = 2.62, SE = 0.47, $p <$

0.001). In the same model, birth interval generally decreased with increasing lion density (estimate = -0.08, SE = 0.04, $p = 0.07$), but to a lesser extent in reserves with more than one adult male/coalition (interaction estimate = 0.05, SE = 0.02, $p < 0.05$). Birth interval was generally shorter in reserves with more than one adult male/coalition (estimate = -0.69, SE = 0.26, $p < 0.01$).

Table 4.3.3. Mean birth interval (years), across 61 lionesses and 122 intervals (*n*).

Lion population structure on reserve		**Mean**	**SD (±)**	***n***
A	One pride and a single adult male lion/coalition	1.77	0.43	23
B	One pride and more than one adult male/coalition	1.64	0.42	10
C	More than one pride and a single adult male lion/coalition	2.01	0.66	25
D	More than one pride and more than one adult male/coalition	1.78	0.47	64

4.3.3. Lion litter size and sex

Across 109 lionesses, the average size of 264 litters counted at first emergence from the den was 2.93 ± 0.98 cubs. This included a total of 360 male cubs, 302 female cubs and 111 unsexed cubs (*n* = 773 total). When restricted to litters prior to contraceptive treatment, litter size increased to 3.03 ± 0.99 (range = 1 – 7; mode = 3, *n* = 190 litters). Lionesses (*n* = 90) were aged between 1.76 and 14.59 years (mean = 5.32 ± 2.75 years) at the time of birth. Litters included the first (*n* = 91), second (*n* = 44), third (*n* = 23), fourth (*n* = 15), fifth (*n* = 7), sixth (*n* = 5), seventh (*n* = 2) and eighth (*n* = 3) litters born to lionesses. Litter size did not vary significantly between reserves with different lion population structures and increased marginally with lion density (see Supplementary Material Table S4.6). When the dataset was restricted to litters (*n* = 158) for which the sex was confirmed, the proportion of male cubs born was over 20% higher in reserves with a single pride and more than one adult male/coalition (B) compared to other reserves (see Table 6.3.4; see Supplementary Material Table S4.7).

Table 4.3.4. The mean proportion (%) of male cubs born across 158 litters (*n*) and 81 lionesses, between reserves that varied in lion population structure (A – D).

Lion population structure on reserve		**Mean**	**SD (±)**	***n***
A	One pride and a single adult male lion/coalition	50.53	36.71	41
B	One pride and more than one adult male/coalition	73.72	28.43	13
C	More than one pride and a single adult male lion/coalition	44.25	31.35	29
D	More than one pride and more than one adult male/coalition	59.98	29.27	75

4.3.4. Cub Survival

There were 27 litters affected by reserve management interventions (i.e. lion removals, translocations) or that had not reached 12 months of age by the time of data collection and were removed from cub survival models. Mean cub survival was 88% across all remaining litters (*n* = 238 litters; 681 cubs), while a total of 607 cubs (89%) survived to 12 months. Cubs born in reserves with more than one pride and more than one adult male lion/coalition (D) had significantly lower survival rates than cubs born in reserves with a single pride and one adult male/coalition (Table 6.3.5; see Supplementary Material Table S4.8). In a separate model, while the presence of more than one pride was not a predictor variable, reserves with more than one adult male/coalition (B and D) had lower cub survival rates (estimate = -11.68, SE = 3.84, $p < 0.01$) than reserves with a single adult male/coalition (A and C) (intercept / estimate = 105.73, SE = 6.30, $p < 0.001$; lion SD = 2.59, $R^2M = 0.04$, $R^2C = 0.05$).

Table 4.3.5. The mean survival rate (%) of lion cubs born across 238 litters (*n*) across wildlife reserves that varied in lion population structure (A – D).

Lion population structure on reserve		**Mean**	**SD (±)**	***n***
A	One pride and a single adult male lion/coalition	94.69	21.75	64
B	One pride and more than more one adult male/coalition	83.25	33.34	19
C	More than one pride and a single adult male lion/coalition	93.12	16.55	40
D	More than one pride and more than one adult male/coalition	82.22	35.18	115

There were 21 litters, across 19 lionesses, for which all cubs were deceased or unaccounted for, due to natural causes, within 12 months of birth. The majority (*n* = 18) of these litters were born on reserves with multiple prides and multiple adult males/coalitions (D). The remainder were born on reserves with a single pride and multiple adult males/coalitions (B; *n* = 2 litters), and those with a single pride and adult male (A; *n* = 1 litters). In reserves with a single pride and adult male lion, the mortality was caused by a recently translocated male. There were 74 cubs in total that died before 12 months of age across 41 litters, and an additional four litters that died before litter size was established (counted as *n* = 1 cub each). The cause of death was unknown for more than half of the cubs (58%). Unknown cub deaths were largely attributed to natural causes, including one suspected case of rickets. Infanticide was the second leading cause of death, recorded for 25 cubs (31%) across 14 litters. Infanticide was recorded across six reserves, four of which had more than one pride and/or more than one adult male/coalition. Lion cubs were killed by male lions (*n* = 8 litters), female lions (*n* = 1 litter) or unknown lions (*n* = 5 litters). The remaining causes of natural cub mortalities included a leopard (*Panthera pardus*) attack (*n* = 1 cub), a lioness that died during birth and cub exposure (*n* = 1 litter). Three cubs were euthanised by reserve management due to mortal injuries, including a broken back and a broken leg. There were an additional five cubs that were euthanised by reserve management due to suspected illness, including bTB (*n* = 3) and haemophilia (*n* = 2).

4.3.5. Lion population growth rate

Lion population growth rate (λ) varied annually from 0.43 to 3.3, across 16 reserves (mean = 1.16 ± 0.43, *n* = 182), over a 5 – 23 year period (Figure 6.3.1). Across all reserves, mean growth rate was 1.12 ± 0.09 since the time of lion reintroduction. The lowest overall growth rate in a reserve was an average of 1.04 ± 0.36 over 13 years, in the Nama-Karoo Biome and 1.07 ± 0.33 in a reserve in the Savanna Biome (*n* = 23 years). The highest overall growth rate was 1.36 ± 0.71 over 14 years (Savanna Biome). Since the time of reintroduction, mean annual lion population growth was higher in reserves that initiated with a single pride (1.24 ± 0.08, *n* = 7 reserves), compared to reserves that initiated with more than one founder pride (1.11 ± 0.04, *n* = 9) ($X^2 = 8.51$, d.f. = 1, $p < 0.01$). Mean annual population growth was also lower in reserves that initiated with more than one founding adult male/coalition (1.14 ± 0.09, *n* = 8), compared to reserves that initiated with a single adult male/coalition (1.22 ± 0.08, *n* = 8) ($X^2 = 4.21$, d.f.

= 1, $p < 0.05$). For the total number of lion introductions, removals, births, mortalities and contraceptive treatments since lion reintroduction see Supplementary Material Figure S4.1.

Lion density generally increased over time however, population growth rate reduced after the first year and began to level out after roughly nine years (Figure 4.3.1). The percentage of a lion population removed from reserves annually, increased over time since lion reintroduction (year estimate = 0.84, SE = 0.19, $p < 0.001$) and decreased with increasing annual contraception cover (contraception estimate = -0.06, SE = 0.03, $p = 0.06$) (model intercept = 5.07, SE = 1.66; $F_{(2,195)} = 10.29$, $p < 0.001$, $R^2 = 0.09$). Birth rate reduced with increasing contraception cover (intercept = 10.00, estimate = -0.06, $p = 0.15$) however, this term was not significant and was removed from the final model. Birth rate was higher in reserves with a single lion pride and more than one adult male/coalition (population B estimate = 14.43, SE = 5.69, $p < 0.05$) compared to other reserves (population A / intercept = 8.82, SE = 2.85; population C estimate = -4.28, SE = 4.00, $p = 0.28$; population D estimate = 0.78, SE = 3.39, $p = 0.82$) and increased with lion density (lions/100 km^2) (lion density estimate = 2.03, SE = 0.34, $p < 0.001$) (model intercept = 8.82, $F_{(4,193)} = 10.76$, $p < 0.001$, $R^2 = 0.17$).

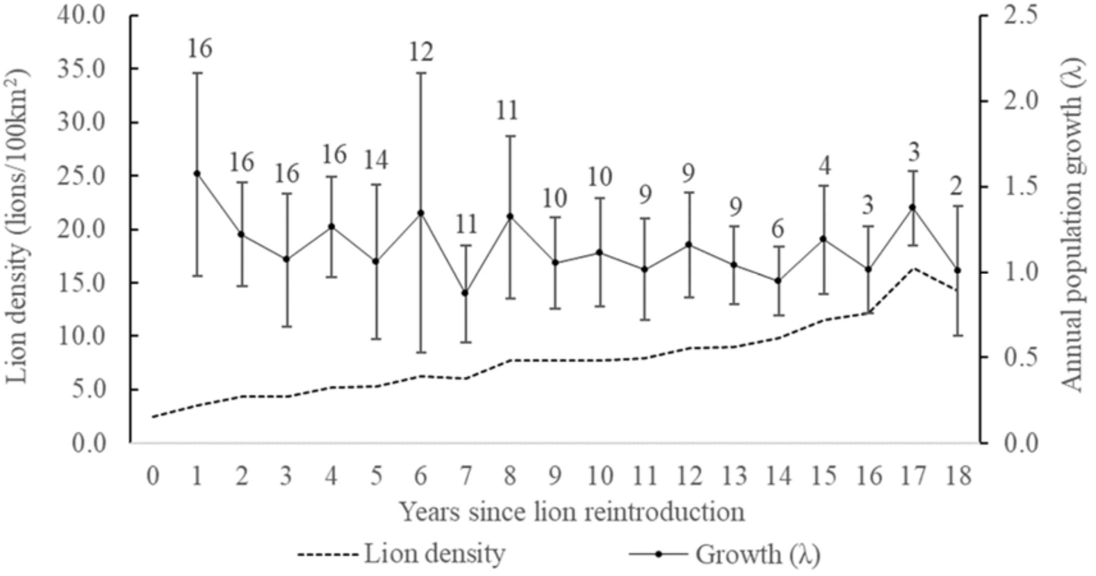

Figure 4.3.1. Mean lion density (lions/100 km^2) since the first year of lion reintroduction (year 0) across 16 wildlife reserves. Mean annual lion population growth rate (λ), and associated standard error, are displayed on the secondary axis. Reserve sample size for each year is displayed above the respective bar. As the sample size reduced over time, the final study years ($n = 5$) are not included in figure.

Lion population growth (λ) generally decreased over years since lion reintroduction (intercept = 1.27, estimate = -0.02, SE = 0.01, $p < 0.05$). When time (years) since reintroduction was accounted as a random effect, lion population growth had a positive relationship with lion density (lions/100 km^2) in reserves with a single pride and adult male/coalition (intercept = 0.96; density estimate = 0.06, SE = 0.01, $p < 0.001$). However, there was a significant reduction in this relationship in reserves with more than one pride (population C estimate = 0.15; density estimate = -0.05, SE = 0.02, $p < 0.05$) (population D estimate = 0.05; estimate = -0.04, SE = 0.02, $p < 0.05$). As a result, mean annual population growth was lower in reserves with more than one pride compared to reserves with a single pride (see Supplementary Material Tables S4.9 and S4.10 for mean annual lion population density and growth, across reserves that varied in lion population structure). This relationship accounted for 5% of the model variation. In the same model, population growth rate decreased with increased lion removals (estimate = -0.01, SE = 0.002, $p < 0.001$), accounting for roughly 10% of the model variation (see Supplementary Material Table S4.11 for model summary). Population growth decreased with increasing contraception cover (all treatments) (estimate = -0.001, SE = 0.001, $p = 0.31$) however this term was not significant accounting for less than 1% of the model's variation and was not included in the final model.

4.3.6. Lion removals

There was a total of 449 lions removed from 14 participating reserves during the study period (including translocations between study reserves). The first year in which lions were removed from reserves was 4 ± 2.27 years post lion reintroduction (range = 2 - 11), when an average of 25 ± 15% of the population was removed. Annual removal rate ranged from 0 to 59% of the total population (mean = 10.0 ± 14%). There was a significant positive correlation between annual birth rate and the proportion of lions removed from a reserve the previous year (Spearman's rho = 0.18, d.f. = 182, $p < 0.01$). Lion removals included 268 males, 175 females and six individuals for which sex was unrecorded, aged between 0.25 and 16.10 years (mean = 2.69 ± 2.37). Most lions ($n = 337$) were removed at the age of three years or younger. Five lions (aged between 1.33 and 6.59 years) were euthanised by reserve management due to injuries that included general poor condition/injury, a damaged eye and a bacterial infection. Four of these lions were male. One lioness was removed to a rehabilitation centre in response to poaching injuries. Two reserves removed no lions during the study period over five years since reintroduction, with an average annual growth rate of 1.11 and 1.25 respectively.

A small number of lions were euthanised as problem animals (*n* = 5) or in response to displays of aggression/dangerous behaviour towards reserve staff or tourists (*n* = 4). These lions had been introduced (*n* = 5) or were born on the reserve (*n* = 4). One lioness, LF1, was translocated between small, fenced reserves for the first time at eight months, when she was introduced (with her mother and littermates) to source a founder population. LF1 was translocated for a second time (at 3.42 years of age) to a reserve containing only a coalition of two males (~ 2 years of age), to initiate a second founder population. Reserve staff recorded displays of aggression from the males towards LF1. LF1 also charged tourist vehicles in the new reserve on several occasions and was removed by reserve management within 10 months. LF1 was relocated back to the second reserve, where she re-joined her pride and there was no further aggression towards vehicles noted. Two lionesses (~ 2 years of age) were next introduced (1.5 years later) to the reserve with the two males. Similarly, no further aggression was recorded between the males and new females, and cubs were produced within eight months.

Eighteen lions were confirmed to have naturally emigrated out of reserve fences across eight lion groups (*n* = 7 reserves). One a nomadic male lion (~ 3.5 years of age) had also immigrated to the reserve over preceding months by natural means and is not discussed further. The remaining lions that broke-out of reserves were all born within their residing reserves except for two lionesses, aged 3.67 and 4.75 years at the time of their escapes (translocated to the respective reserves 1.5 and 2.75 years prior to escape). Escapes from reserves occurred during years in which lion density was above average relative to each reserve's lion population history and more than half of cases were lionesses (see Supplementary Material Table S4.12). In three out of six cases, the lions broke out again after being returned by reserve management. The escaped lions were ultimately euthanised (*n* = 4) or translocated (*n* = 1) by reserve management, destroyed on neighbouring properties after escape (*n* = 10) or had no intervention recorded (*n* = 2). One nomadic, rogue lioness was euthanised as a potential disease threat. The remainder of lion removals were carried out to reduce inbreeding risk and for population management.

Nineteen lions were translocated internationally to Rwanda (*n* = 7), Mozambique (*n* = 10) and Dubai (*n* = 2) between 2009 and 2015. A further 23 lions were translocated to the Kalahari region. In the remaining translocations, lions were moved to other small, fenced reserves in

South Africa (*n* = 235) or locations were not provided (*n* = 42). The unrecorded locations extended across eight reserves (50%) between 2010 and 2018. Eleven lions, born between 1999 and 2012, were translocated from four reserves with no accurate removal date recorded. Five of which also had no translocation destination recorded. There were a further 100 lions removed through euthanasia during the study period. A small number of lions (*n* = 6) were removed through hunting, between 2006 and 2015 across three reserves. Five of these lions were male, aged between 7.25 and 11.43 years of age. Four males had sired confirmed litters raised to independence and were removed to prevent inbreeding, followed by introduction of new males. The single lioness was younger at 3.33 years.

4.3.7. Lion mortalities

There were 11 lions for which there was no record of death or further status update and that are not discussed further. After removing lions affected by escapes or management intervention, the mean annual mortality rate (over 4 – 23 years since lion reintroduction) was 0.8 – 12% (mean = 3.9 ± 2.8%) across all lion age-groups (cub/subadult/adult). A total of 81% (*n* = 120) of known adult females that were born on study reserves survived to 36 months (see Supplementary Material Table S4.13). The lowest mortality rate was recorded across two reserves, in which no lions died over four and five years since reintroduction. Both reserves reintroduced a single pride and adult male/coalition (A). The next lowest mortality rate was recorded in a reserve with two prides and generally one resident adult male, in which an average of 1.7% of the population died annually, or a loss of 7.1% (*n* = 6) of the total lion population over 17 years. The highest annual mortality rate was an average of 8.3% per year, or 38.7% (*n* = 12) of the total population over a 13-year period. However, a significant proportion of mortalities (*n* = 4) at this reserve were attributable to poaching. The second highest mortality rate was an average of 7.2% per year, or 37.5% (*n* = 12) of the total lion population over 13 years. Over half of the deaths were cubs (*n* = 7), six of which died due to infanticide by recently introduced lions, and two lions died due to poaching. The total reserve mortality across all sites was 16.44 ± 11.80% over 4 – 23 years since lion reintroduction (*n* = 16 reserves).

There were 101 records for mortalities or disappearances of lions over one year in age (1.08 – 18.85 years). This represents 13.8% of the total lion population that reached over the age of 12 months during the study period (*n* = 731). Forty percent (*n* = 40) of mortalities were lions aged 1 – 3 years, and 42% (*n* = 42) were 3 – 10 years of age. There were only 11 mortalities (10.7%)

recorded for lions older than 10 years. Mortality age was not accurately recorded for eight lions. Approximately half of the recorded mortalities were each female (*n* = 49) and male lions (*n* = 52). Most lion mortalities (*n* = 11) occurred in reserves that contained both more than one pride and more than one adult male/coalition (D). Mortality rate was highest in these reserves (D: estimate = 5.21, SE = 1.52, *p* = 0.30) however, the differences between population categories (A – D) were not significant. Mortality rate significantly increased in reserves with multiple prides and a single resident male/coalition (C) during years when lions were introduced (see Supplementary Material Table S4.14).

There were 31 cases (31% of all adult and subadult lion mortalities) of confirmed natural lion mortalities, of which 15 (*n* = 6 females; *n* = 9 males) were directly related to conflict with other lions. The cause of lion-related mortalities were adult male lions (*n* = 10), prides (*n* = 2), a subadult group (*n* = 1) and unknown lions (*n* = 2). There were two further mortalities suspected to be linked with the recent introduction of new males. All lionesses were killed by male lions, except for one lioness that was killed by unknown lions. Only three natural lion mortalities were recorded across reserves with a single pride and single adult male/coalition. Two of these mortalities were recently introduced lions that died within eight and five months of release. The remaining lioness died of natural causes (diagnosed as peritonitis ~ 12 years in age). Of the remaining natural mortalities (*n* = 14); five lionesses died of old-age symptoms (12.0 – 18.3 years in age), three lionesses died in circumstances linked with birthing, two mortalities were linked with suspected snake bites and the remainder were recorded as unknown (*n* = 4).

Poaching was a leading cause of death, with 29 confirmed subadult and adult lion mortalities (29% of mortalities), and four further cases of suspected poaching. Poaching was confirmed across six reserves and three provinces (between 1993 and 2017), and an additional reserve recorded two of the suspected incidents. Four reserves were based in KwaZulu-Natal (*n* = 22 lions), two in Limpopo (*n* = 5 lions) and one in the Western Cape (*n* = 2 lions). Most confirmed poaching incidents (*n* = 19) took place since 2009, across all three provinces. Confirmed poaching incidents were carried out through snaring (*n* = 20), poisoning (*n* = 2), shooting (*n* = 1) or unrecorded methods (*n* = 6). The collars from poached lions were found hanging on a tree on separate incidents within one reserve (*n* = 2 lions). There were 10 other lion mortalities that were anthropogenically-linked, four of which occurred during each translocation periods (heat capture, call-up injury, fight in boma) and veterinary intervention complications. The remaining anthropogenically linked mortalities (*n* = 2) occurred when lions interfered with power cables on a reserve. There were a further 27 lion (> 1 year in age) mortalities (*n* = 27%) for which the mortality cause was unknown.

4.3.8. i) Introduction of adult male lions

There were 20 records of adult male lions (*n* = 33) introduced across 11 reserves with an existing lion population. The translocated lions were either individual males (*n* = 8), or coalitions of two (*n* = 11) or three males (*n* = 1), aged between 2.6 and 16.1 years (4.01 ± 2.69). Two adult male introductions were carried out within one month of data collection and are not discussed further. One introduced coalition was older than the remaining males, at 11.18 and 16.10 years respectively. The average age at male introduction without these males was 3.4 ± 0.7 years (*n* = 26), including nine lions below the age of three years. In the process of six introductions, the previous resident males were removed within six months either side of male release. Eleven introductions (61%) were associated with at least one lion (cub/subadult/adult) mortality over the 12-month period after adult male release. At the time of three introductions, there were no cubs below the age of 12 months on the reserve or born within three months subsequent to introduction (sired by a previous male). At the time of the remaining introductions (and within three months of male release) there was a total of 114 resident cubs below the age of 12 months.

Only two introductions (11%) were associated with confirmed infanticide by introduced males within six months of male release (*n* = 4 cubs; 3 litters). The introduced males (solitary) were aged 3.5 – 3.7 years. The cubs were below six months in age (1 - 6 months) at the time of mortality and were killed by reintroduced males within one and four months of release. In both cases, the previous resident adult males were removed at roughly the same time the new males were introduced. In one case, a deceased cub was survived by three cubs from another litter within the pride, that were 12 months of age at the time of male introduction. The reserve had a single pride and no other adult males. In the second case of infanticide within six months, the reserve had multiple prides. A further two reserves recorded cub infanticide within 6 – 11 months of male introduction (*n* = 5 cubs; 3 litters). This included a pride take-over (*n* = 2 cubs; 3 months in age), carried out 11 months after introduction by a coalition of two males that were 2.7 years of age at release. There was only one unrelated resident pride on the reserve at the time of take-over and the previous resident male was not removed (3.5 years in age at the time of take-over). The final recorded case of infanticide within 6 – 11 months of male introduction was carried out by an adult male already resident on the reserve. The resident male killed cubs (*n* = 3; 1 – 5 months in age) from the first two litters sired by a newly introduced male. There were a further seven cub mortalities within 12 months of four separate male introductions for which the cause was unknown and all cubs were below the age of six months.

Five adult male introductions were associated with the mortality of either a subadult/s or adult lion within six months of male release (*n* = 6 mortalities). In one case, the newly introduced male (part of a coalition of two) was killed by a resident lioness and her dependent subadult male (*n* = 1) offspring. In another case, the newly introduced male was snared within six months. In the remaining three cases, the mortalities were lions already resident on the reserve prior to male introduction. One dominant lioness (10.8 years) was killed by the newly introduced males in the month of their release. Another dominant lioness died of suspected old age (17.4 years) and the cause of death was unknown for two subadults (2.2 years in age).

4.3.8 ii) Adult male tenure

Tenure age and interval (years) were calculated for 47 male lions across 33 coalitions. This included 33 reintroduced males (*n* = 12 reserves) and 14 males born within six study reserves. Most adult males held tenure as a solitary male (*n* = 22) however, there were also coalitions of two males (*n* = 8) and three males (*n* = 3). Adults males attained pride tenure at the age of 3.9 ± 1.3 years of (1.9 – 7.3 years). The youngest male to attain pride tenure was 1.9 years of age, introduced as a founder population. The youngest male to attain tenure within a reserve they were born to was 2.7 years, and the average age was 4.5 ± 1.0 years.

Average tenure interval was 4.1 ± 1.9 years (0.1 – 7.4), subsequent to the birth of their first associated litter. Twenty-five lions (48% of tenures) were removed by reserve management at the end of their tenure, through translocation (*n* = 14), hunting (*n* = 7) or euthanasia (*n* = 4). Nine males died at the end of their tenure, including a single coalition (*n* = 2 males). Cause of death included poaching (*n* = 3), other male lions (*n* = 2) and unknown (*n* = 4). The remaining males (*n* = 13) were still alive at the time of data collection. Four tenures were held for less than two years, until the adult males died (*n* = 2) or were translocated (*n* = 2). When these males were excluded, mean tenure increased by almost six months (4.5 ± 1.6 years). Male tenure was shortest in reserves (*n* = 2) with a single pride and multiple adult males/coalitions (B; 3.36 ± 1.45 years) however, the sample size was limited (*n* = 3 coalitions). Male tenure was also less than four years in reserves (*n* = 3) with multiple prides and multiple adult male coalitions (D; 3.9 ± 2.6 years; *n* = 9 males/coalitions). Across reserves with a single male/coalition and one pride (A; 4.3 ± 1.4 years, *n* = 7 reserves) or multiple prides (C; 4.3 ± 1.9, *n* = 5 reserves), male tenure was similar (see Supplementary Material Table S4.15). Male tenure held by solitary males (4.4 ± 1.4 years) was slightly longer than that held by coalitions (3.50 ± 1.83 years; see Supplementary Material Table S4.15). There were no significant differences in tenure age or interval between reserves with different population structures or across coalition sizes (see Supplementary Material Tables S4.16 and S4.17).

4.3.9. Key prey species

Full stocking history (introductions, removals and census) of key prey species was obtained from six reserves. Game census information alone was obtained from a further five reserves. For a full list of key prey species (*n* = 25), their scientific names, relative biomass weight (kg) and overall percentage change in study reserves see Supplementary Material Table S4.18. There was an average of 13.8 ± 3.34 various key prey species resident across reserves (range = 9 – 20). Most reserves both stocked (*n* = 5) and removed (*n* = 6) prey species since their lion reintroduction. Ten reserves provided at least three separate years of game census data, enabling trend analyses. Census dates extended intervals of 3 – 17 years (mean = 7.3 ± 5.4 years). The time between consecutive census dates varied from one (*n* = 45 intervals) to four years (*n* = 1) (two years, *n* = 7; three years, *n* = 2). Across all reserves (*n* = 10), individual prey species had a mean annual increase in 71% (*n* = 96) of cases. However, only two reserves contained prey populations for which all species had a mean annual increase, over 9 and 15 years. One of these reserves stocked six prey species during this time, while the stocking history of the remaining reserve was unknown. Both reserves contained more than one pride. Nine prey species decreased over time across more than 50% of reserves in which they were resident.

4.3.9. i) Prey species supplementation

Out of the reserves that stocked prey species during the study period (*n* = 5), detailed prey supplementation information (date, species and size) was available from four. Roughly half of all prey supplementations were made into a population that was already decreasing (see Supplementary Material Table S4.19). Three reserves carried out only one (*n* = 1 reserve) or two (*n* = 2 reserves) prey species supplementations, over 6 – 17 years since lion reintroduction. The supplemented species were springbok (*Antidorcas marsupialis*) (*n* = 649), mountain reedbuck (*Redunca fulvorufula*) (*n* = 13), buffalo (*n* = 16), waterbuck (*Kobus ellipsiprymnus*) (*n* = 130) and blue wildebeest (*n* = 155) (see Supplementary Material Table S4.19). The springbok were introduced during the last year of data collection, therefore no population trend data were available. Reliable game census information pertaining to the mountain reedbuck population was unavailable and is not discussed further. The waterbuck and blue wildebeest were introduced to the same reserve one year apart. Both species decreased in overall population size during the years after the supplementation (waterbuck $\lambda = 0.45$; blue wildebeest $\lambda = 0.95$). The buffalo population that was supplemented, was increasing prior to supplementation and continued to increase over three years post-supplement ($\lambda = 1.12$).

The final reserve that stocked prey species (with reliable dates), stocked six species [buffalo, giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), wildebeest, zebra (*Equus quagga*)] and a total of 2,224 individuals across 13 years (see Supplementary Material Table S4.19). The buffalo and wildebeest were introduced during a single year, whereas all other species were introduced more than once (2 – 6 introductions). The wildebeest, and one introduction of each impala, zebra and kudu, were released during the last year of data collection therefore no trend was obtained. Out of the remaining introductions (*n* = 15), giraffe and buffalo both increased one-year post introduction (giraffe $\lambda = 1.05$; buffalo $\lambda = 1.36$). However, both rates reduced over subsequent years (giraffe $\lambda = 0.75$ after 4 years; buffalo $\lambda = 1.3$ after 3 years). The impala population largely declined before ($\lambda = 0.74 – 1.18$) and after ($\lambda = 0.69$) supplementation. The zebra population was supplemented six times over 13 years (*n* = 435 zebra) and generally increased over the first year after supplementation ($\lambda = 0 .83 – 2.21$) however, the rate of growth reduced over time ($\lambda = 0.75 – 2.29$). The population growth rate of the kudu population generally declined after introductions ($\lambda = 0.36 – 0.76$).

4.3.9. ii) Prey species removals

All reserves for which stocking history was available (*n* = 6) removed key prey species (over 5 – 17 years; mean = 10.0 ± 5.6). Reliable dates for the animal removals were not available for one reserve which is not discussed further. A total of 16 prey species were removed through live captures (*n* = 4,198 individuals), commercial or private hunts (*n* = 2,201), culling protocols (*n* = 2,176) or undefined methods (*n* = 10,564). The undefined methods were recorded from a single reserve. The remaining four reserves all conducted culls of prey species, whereas only three reserves used live captures and a single reserve carried out all three methods. Culled species were predominantly impala (*n* = 53%), warthog (*Phacochoerus africanus*) (*n* = 20%) and nyala (*Tragelaphus angasii*) (*n* = 18%), the latter culled in a single reserve. The predominant species that were hunted were also impala (58%) and warthog (18%). Nyala was the predominant species removed through live removal (*n* = 78%), followed by impala (8%) and common reedbuck (*Redunca arundinum*) (8%). Three reserves removed prey species on an annual basis, and two reserves removed species on only a single occasion, totalling three removals. One of the latter reserves was the same reserve with the highest stocking rate of prey species. An average of 242.3 ± 279.6 kg/km^2 of prey biomass was annually removed from reserves, across 34 years during which prey was removed (range = 1.5 – 969.5 kg/km^2). The density (kg/km^2) of prey removed annually increased in only one reserve throughout the study period (see Supplementary Material Figure S4.2). The reserve contained more than one pride and adult males/coalition (D) and only supplemented two prey species (wildebeest and waterbuck). The proportion of prey biomass removed annually varied from 0.1 – 24.1% of the total reserve biomass (mean = 6.9 ± 6.2%) and increased in the same reserve over time and in an additional reserve (see Supplementary Material Figure S4.2). The latter reserve contained a single pride and adult male/coalition.

4.3.9. iii) Prey species and biomass trends

Across reserves for which full prey supplementation and removal data were available, there were larger oscillations in the relative abundance of prey species over longer time periods (see Supplementary Material Figure S4.3). A preferred prey species (Hayward and Kerley, 2005) was the most abundant available throughout the study period in only one reserve. Wildebeest were the most abundant preferred prey species across four reserves. The remaining reserve was within the Nama-Karoo Biome, and the most abundant preferred prey species was gemsbok. The overall abundance of each prey species was similar at the beginning and end of the study period, except for one reserve, which had the highest removal rate (Supplementary Material Figures S4.2 and S4.3). The relative proportion (%) of prey biomass introduced decreased with increasing reserve biomass (kg/km^2) (estimate: -0.002, SE = 0.001, p = 0.18) (n = 4 reserves). This trend was not significant, and the term was removed from the model. The proportion of reserve biomass supplemented annually increased over year of study (see Supplementary Material Table S4.20). Not surprisingly, this increase was only significant in the reserve that introduced an extensive number of prey species (*n* = 2,224). The relative proportion (%) of prey biomass removed decreased with increasing reserve biomass (kg/km^2) (estimate = -0.001, SE = 0.001, *p* = 0.15) however, this difference was not significant. The proportion of prey biomass removed annually significantly varied between reserves (see Supplementary Material Table S4.21). Two reserves removed a higher proportion of prey biomass than remaining reserves. In one reserve the proportion of prey biomass removed significantly increased over time.

The density of prey biomass (kg/km^2) across all reserves, increased over time since lion reintroduction and, not surprisingly, was lowest in the reserve dominated by the Succulent-Karoo Biome (see Supplementary Material Table S4.22). In the same model, prey biomass density was lower in reserves with more than one pride (C and D) compared to reserves with a single pride. When the analysis was restricted to reserves dominated by the Savanna Biome (*n* = 4), prey biomass density was lower in reserves with more than one pride (B: reserves 4 and 5) and had a positive relationship with lion density (see Supplementary Material Table S4.23). Conversely, the higher level of prey biomass in reserves with a single resident pride (A: reserves 1 and 3) decreased with increasing lion density (Figure 4.3.2). The latter were the two reserves with the highest biomass removal rates (see Supplementary Figure S4.2). The model had high explanatory power ($R^2M = 0.86$, $R^2C = 0.94$).

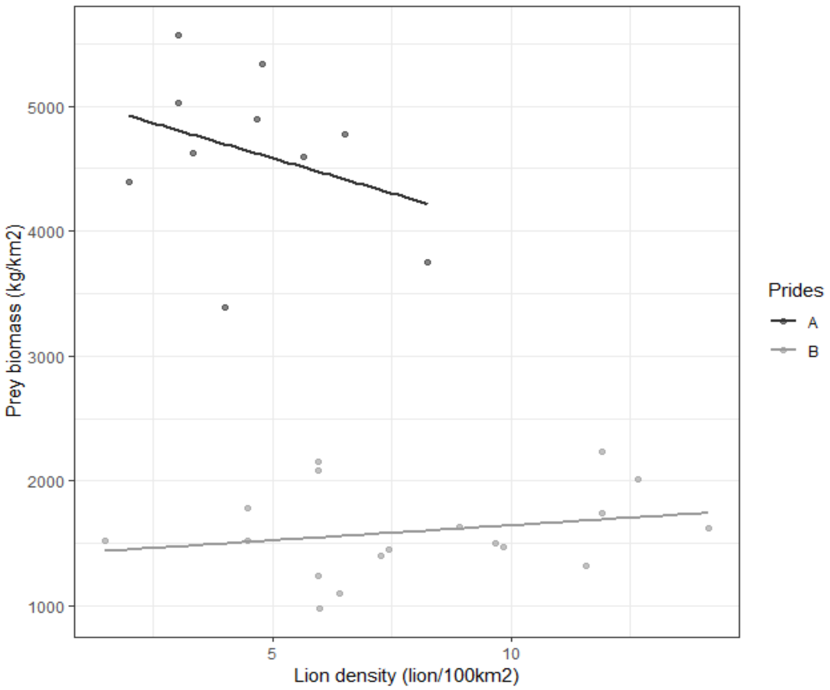

Figure 4.3.2. The average change in annual prey biomass (kg/km^2) over increasing lion density (lion/100 km^2) across four reserves with either a single pride (A) or more than one pride (B).

The four reserves represented in Figure 4.3.2 (A: 1, 3 and B: 4, 5) also housed populations of other large carnivores. Other resident carnivores included cheetah (*Acinonyx jubatus*), African wild dog, leopard and spotted hyena (*Crocuta crocuta*) (see Supplementary Material Table S4.24). All reserves contained each of the four other large carnivores, except for one reserve that did not contain a resident wild dog population. All leopard and spotted hyena populations were established from vagrant populations, whereas only one wild dog pack was endemic within a reserve. This pack died of a rabies outbreak during the study period and was replaced with another translocated pack within six months.

4.3.10. Disease control

Records were obtained for 20 lions treated with rabies vaccinations between 2003 and 2016, across two fenced reserves. Most vaccinations (n = 15) occurred between 2003 and 2006, with a further seven lions treated in 2016. Two of the lions were treated at separate intervals, three years apart. At one reserve, the vaccinations were applied during a known rabies breakout [pack of wild dogs and other species including black-backed jackal (*Canis mesomelas*), died from infection]. No lions showed visible signs of clinical rabies. There were three lions treated successfully for mange, one subadult lioness in 2005 and two cubs in 2015. There were 28 lions tested for bTB across a single reserve. Most lions (*n* = 18) were tested before translocation to another reserve. No positive test results were reported. There were a further three cubs euthanised due to suspected bTB. The mother of the cubs had recently died in a snare. There was an outbreak of CDV at a single reserve during the study period (E2015/B2016), that resulted in the death of the entire lion population (*n* = 15), except for a single young lioness, within roughly a 12-week period. Undiagnosed symptoms were noted in October 2015. The first confirmed clinical symptoms were reported to management in December 2015 followed by localised population extinction in January 2016. The majority (53%) of the lions died or were euthanised (40%; *n* = 5 positive test results). The single lioness that survived never showed clinical signs and did not test positive. A time lag was reported in the availability of lion-specific CDV vaccination, that was required to be ordered from abroad.

4.3.11. The Lion Management Forum of South Africa

Completed management surveys were returned from 12 reserves. Fifty-eight percent of reserve managers (*n* = 7) ranked “Conservation”, as the primary goal of their reserve, with the remaining reserve managers ranking “Tourism” (33%) and other (8%). The secondary overall reserve goals were tourism (58%), conservation (33%) and the sustainable use of resources (8%). By contrast, tourism was the primary goal for having lions on a reserve across a higher number of reserve managers (75%), with conservation the primary goal for only three reserves (25%). Reference was made to ‘big five status’ by two survey respondents. Only eight managers provided a secondary goal for having lions on the reserve, of which five (63%) answered conservation.

Between December 2014 and December 2018, the LiMF facilitated emails through their membership database regarding 55 requests to translocate managed wild lions. During February 2018, the LiMF used another method, whereby a summary of all reserve’s translocation requirements, submitted during a LiMF workshop, were emailed to members. This method was used three times throughout February, during which the translocation summary was updated by the LiMF and re-issued members. After this point, reserve translocation requirements returned to single requests. Translocation requests pertained to 29 reserves and four requests for which the reserve location was not provided/relevant. There were 30 notifications regarding lions that were available for outgoing translocation (*n* = 98 lions) across 17 reserves, one unspecified reserve and a rogue lion(/s). There were 20 requests (*n* = 68 lions) for incoming translocated lions (*n* = 15 reserves and 2 unspecified locations). Five requests sought a swap of lions (*n* = 17 lions outgoing; *n* = 9 lions incoming). When excluding notifications that were received on the same day as the previous (*n* = 9), the LiMF issued translocation emails on average once every 4.6 ± 5.2 weeks (0.1 – 19.2 weeks). There were 12 reserves that submitted more than one email request (*n* = 34 emails). The mean time interval between successive requests from reserves was 10.6 ± 8.7 months (range = 0.4 – 32.8). This included 18 emails that were sent successively about the same lions, with one pair submitted within two weeks of each other. Excluding the latter, the shortest time interval between reserve translocation requests was 1.6 months. Nine reserves issued follow-up requests regarding the same lions (available lions, *n* = 6 reserves; seeking lions, *n* = 2 reserves).

There were 70 male lions available for translocation out from reserves (direct and swap) and 45 lionesses, according to age-groups listed in Supplementary Material Table S4.25. This included a group of either one or two rogue male lions found outside of a protected area. Thirty-five male lions were sought through translocation, and 42 lionesses. There was a single further request for adult male and female lions to re-source a population (CDV outbreak), for which the group number was not provided. Almost half (49.6%) of lions available through translocation were between the ages of 1 – 3 years (range = <1 – 10, mean = 3.59, SD = 2.42 years), whereas 61% of lions sought through translocation were between the ages of 3 – 6 years (range = 2.5 – 10, mean = 4.28, SD = 1.53 years). All requests were placed at an immediate to short-term basis, except for one request placed over 18 months prior to the potential establishment of a lion population. In total, there were four requests (47% of sought lions) to establish a new founder population. The remaining lions were sought for genetic refreshment. Two founder populations were sought for fenced reserves within South Africa, while further founders were requested from reserves in Mozambique and Malawi. Any further communications were taken up directly between interested LiMF members.

4.4. DISSCUSSION

4.4.1. Lion population growth in small, fenced reserves

Lion population growth was similar to that reported in Miller and Funston (2014), with a high mean growth rate of 1.6 (60%) in the first-year post-reintroduction. Although variable, growth rate reduced in subsequent years, stabilising at close to 1.0 after nine years. However, the proportion of lion populations removed annually from reserves also increased over time which significantly reduced population growth. Ten percent of lion populations were removed annually (SD = 14, range = 0 – 60%). Birth rate and overall growth rate were higher in years following those during which a higher proportion of the population was removed however, this does not indicate density-dependence. Furthermore, growth rate generally increased with lion density in isolated populations. The increase in birth rate was likely linked with lioness birth interval. As excess lions were primarily removed as subadults (< 3 years), lionesses were likely reproductive again close to the time when lions were removed. Lioness age of first reproduction (3.34 years), litter size (*n* = 3) and cub survival (87.5%) reflected previous findings for managed wild lions (Miller and Funston, 2014) however, birth interval (1.82 years) was shorter by four months. These estimates place age of first reproduction younger and birth interval shorter than in lion populations in the Kruger NP, while litter sizes were larger and cub survival was higher compared to lion populations in the Serengeti NP (Miller and Funston, 2014).

Age of first reproduction was similar across lionesses, except for reserves with multiple prides and adult males, where age of first reproduction was significantly younger. Conversely, lionesses reproduced four months later in reserves with a single pride and adult male/coalition compared to other sites. Furthermore, age of first reproduction declined with increasing lion density in all sites, except for reserves with multiple prides and adult males. In Nairobi NP, age of first reproduction of adult lionesses was closer to the younger age observed in managed wild prides (B – D) (Rudnai, 1973), and was significantly younger than lionesses in the Kruger NP (Funston *et al.* 2003) or the Serengeti NP (Packer *et al.* 1988). Lions populations persisted at higher densities in the Nairobi NP (Rudnai, 1973), comparable to maximum densities recorded in the current study. The Nairobi lion population also persisted at high prey availability and lion emigration rates (Rudnai, 1973), both of which are mimicked in small, fenced reserves and likely further increased lioness reproductive parameters. Both populations had high reproductive rates, indicating that they did not exceed optima (Rudnai, 1973). Furthermore, reproductive parameters in the current sample generally increased with lion density.

In the Kruger NP, the extended age of first reproduction in lionesses was associated with female avoidance and aggressive defence towards roaming adult males, after the resident adult male has left the pride (Funston *et al.* 2003). The lion population in the Kruger NP included multiple territorial and non-territorial male coalitions (Funston *et al.* 2003), compared to Nairobi NP that largely had a single territorial male coalition (Rudnai, 1973) and compared to the current managed wild populations with minimal territorial males. Lionesses have been recorded to mate with multiple males during a reproductive cycle (Packer and Pusey, 1983; Rudnai, 1973). Therefore, it is likely that lionesses in managed wild prides within reserves containing more than one territorial adult male/coalition, also mated with the small number of extra-pride males during oestrus. Lioness avoidance and aggressive defence from unknown adult males was therefore likely lower in managed wild prides and likely also contributed to the younger age of first reproduction. Although all prides included reproductive females that were unrelated to the resident adult male(s), the extended age of first reproduction in reserves with a single pride and adult male may have been driven by inbreeding avoidance (Hanby and Bygott, 1987). Subadult lionesses have also been shown to disperse from their prides in order to avoid paternal mating (Pusey and Packer, 1987).

Lioness birth interval was shorter in reserves with a single pride, and inherently reduced competition from other females, compared to reserves with multiple prides. With minimal associated mortalities, this indicates that cubs may have reached independence at a younger age in these reserves. After the loss of a dependent litter, lionesses normally become reproductive again within six months (Packer and Pusey, 1983). Within the reserves that contained either one pride (A, B) or more than one pride (C, D), lionesses in reserves with more than one adult male/coalition (B, D) had shorter birth intervals than their counterparts in reserves containing a single resident male/coalition (A, C). Pride-take overs in open systems can be associated with longer birth intervals due to temporary lioness infertility (Packer and Pusey, 1983). Furthermore, the presence of unknown adult males would increase infanticidal threat for dependent offspring (Borrego *et al.* 2018), potentially increasing the age at which independence is reached. Therefore, longer birth intervals in reserves with multiple adult males/coalitions could be expected. The shorter birth intervals may therefore indicate increased subadult (1 – 2 years) mortalities due to infanticide from unknown males (birth intervals following litters lost below the age of 12 months were excluded in the analyses). In reserves with unknown resident males, birth interval was also significantly lower than other reserves. In the Serengeti NP and Nairobi NP, birth interval is shorter, and offspring survival is lower than in the Kruger NP (reviewed by Miller and Funston, 2014).

Cub survival (to 12 months) was 11% lower in reserves with more than one adult male/coalition (B, D), compared to reserves with a single resident male (A, C). This reflects the significant role that infanticide from non-resident males plays in cub survival of managed wild populations. Infanticide was the leading cause of all known lion cub mortalities (~30%) and most failed litters occurred on reserves with multiple adult males/coalitions. Significantly, the ratio of male cubs born was higher in reserves with a single pride and more than one adult/male coalition. The primary sample population in this category (B) included only coalitions of males, and with a single pride, the level of intraspecific competition between coalitions was high. The male-biased sex ratio reflects a high rate of natural coalition turn-over in these reserves (Beukes, 2016; Funston, 2011; Packer and Pusey, 1987).

Differences in birth interval and cub survival reflect that the lowest overall lion population growth was recorded in reserves with multiple prides and multiple adult males/coalitions (D). Similarly, in open systems, prides with increased unknown adult male and female neighbours had lower reproductive output due to intraspecific competition (Mosser and Packer, 2009). With competition between prides highest in densely populated regions in which access to resources are limited (Mosser and Packer, 2009; Grinnell, 2002), lion population growth was expectedly lowest in fenced reserves with more than one pride. Lion population growth in fenced reserves was further reduced by male infanticide, the significant effects of which have also been recorded in open systems (Pusey and Packer, 1987). Regardless of pride fracturing, lion introductions or removals subsequent to reintroduction, annual lion population growth was significantly higher in reserves that introduced one founder pride, and to a lesser extent, one founder adult male/coalition. This reflects the high breeding success and cub recruitment recorded for an isolated pride that had survived a disease epidemic in the Ngorongoro Crater (Packer *et al.* 1991). Within the Ngorongoro Crater, population growth similarly stabilised within 10 years after a population crash, after which point there were no further prides formed (Packer *et al.* 1991). Therefore, population growth stabilised with an increased number of neighbouring prides, reflected by the current data.

4.4.2. Management interventions

4.4.2.i) Lion removals

The first year during which lions were removed after reintroduction (*n* = 4) reflected previous findings (*n* = 3; Miller and Funston, 2014). Lion removal rate varied extensively (based on reserve management guidelines) and increased over time after lion reintroduction. Not surprisingly, increased removal rate was associated with lower annual population growth and was likely partially responsible for the reduction in population growth over time. Most lions were removed for genetic/ecological purposes. In translocations, most lions were relocated nationally to other fenced reserves within South Africa, while a small number were translocated internationally. There were several translocations for which destination and/or translocation date were not accurately recorded. These incidents generally occurred within more recent years when lion densities and removal rates were comparatively high. Therefore, record keeping was likely less accurate. This poses potential concerns regarding metapopulation planning, for which a thorough understanding of lion population demographics and record keeping will be imperative, for example to limit inbreeding-risk and to identify demographic trends. This also poses concern regarding the recent increase lion poaching (Williams *et al.* 2017a), as some of these individuals may not have been translocated. There were further lions for which the status was unrecorded, highlighting the need for consistent monitoring and accurate record keeping.

A small number of lions (*n* = 6) were hunted over the study period. Most were older, adult males that had sired independent offspring (replaced for genetic refreshment). Being part of a finite, well-documented population, the lions were relatively easy to locate and identify for hunting purposes (Kettles and Slotow, 2009). Extensive research has been directed towards the effect of trophy hunting on wild lion populations (Groom *et al.* 2014; Loveridge *et al.* 2007; Loveridge *et al.* 2016; Packer *et al.* 2011). Unsustainable harvest rate of adult male lions in open systems can lead to more frequent pride take-overs and lion mortalities (Loveridge *et al.* 2016; Whitman *et al.* 2004). However, if managed sustainably (minimum tenure of two years) trophy hunting can have negligible population-level effects (Loveridge *et al.* 2016; Whitman *et al.* 2004; Snyman *et al.* 2015). With the ability to accurately age and identify lions in managed wild populations, the primary population-level threats of trophy hunting can be managed (Miller *et al.* 2016) to remove expended males. However, hunting played a negligible overall role in lion management, likely associated with the tourism-driver for lion reintroduction

4.4.2.ii) Supplementation of adult male lions

In two cases of adult male supplementation, an introduced coalition member died shortly after release. With a small number of other lion mortalities recorded during routine management procedures (darting/translocation etc.), translocating males in coalitions may increase the survival chances of at least one coalition member and subsequent gene flow. The effect of lion introduction on mortality rate was most extensive in reserves with multiple prides and a single adult male (no male competition). Only 5.3% (n = 6) of all resident cubs died due to confirmed infanticide within 12 months of male release. There were a small number of other cub mortalities within the same timeframe for which the cause was unknown. In all cases of cub infanticide, the cubs were below the age of six months at the time of mortality, with no reported cases for cubs aged 6 – 12 months (n = 65). This reflects findings from the Serengeti NP (Packer and Pusey, 1983), where cubs born at least six months prior to a male take-over were more likely to survive than younger cubs. However, most cubs below the age of 12 months were killed during a take-over, with dependent offspring above this age often forced to disperse (Bertram, 1975; Packer and Pusey, 1983). In the current sample, the introduction of adult males did not induce the level of pride take-over and cub mortality as expected from open systems.

In both cases of resident cub infanticide within six months of male release, reserve management removed the previous resident adult male(s), which may have left the pride more vulnerable to pride take-over (Pusey and Packer, 1994). The males were also older in age (3.5 and 3.7 years) at the time of introduction. Therefore, younger males (< 3 years) were less effective at disrupting pride dynamics than older males (Kettles and Slotow, 2009). The delayed pride take-over by a coalition of young introduced males (2.67 years at introduction), that occurred almost one year after the introduction, further supports this. The introduced males reached 3.57 years of age before they proceeded to take over the pride. However, the previous resident adult male was not removed in this case, which may also have delayed tenure take-over. In the Kruger NP, male lions often take up territories within proximity to their natal territory (Funston *et al.* 2003), therefore the delay in pride take-over could also be attributed to the introduced male's lack of experience in the new territory.

4.4.2.iii) Adult male lion tenure

Two-thirds all males/coalition groups that achieved pride tenure were introduced by reserve management. Two coalitions (n = 2 males) bonded naturally as a combination of introduced and natal lions, reflecting previous findings on unrelated coalitions (Packer and Pusey, 1982). Tenure age (3.95 years) and tenure interval (4.08 years) reflected previous findings for managed wild populations (Miller and Funston, 2014). Tenure age was over one year younger than that reported for the Kruger NP (Funston *et al.* 2003), particularly considering that the youngest age was below two years. However, tenure attained by males within the reserve they were born to was six months older. Tenure interval was significantly longer than natural male tenure recorded in open systems, of 17 – 24 months (Bertram, 1975; Funston *et al.* 2003), posing inbreeding concerns (Miller *et al.* 2013). The longest tenure interval recorded was over seven years. Nearly half of all tenures were artificially terminated. In the Kruger NP, male tenure generally ceased through natural emigration of dominant males in search of other reproductive opportunities, once their sired offspring reached 6 – 12 months in age (Funston *et al.* 2003).

As male tenure was largely manipulated based on reserve management protocols, tenure parameters were not heavily influenced by natural drivers and did not vary significantly between lion population structures or coalition sizes. Consequently, single male lions held tenure for longer intervals (mean = 4.37, SD = 1.83 years) than coalitions of two or more males (mean = 3.50, SD = 1.83 years). In open systems, larger coalitions naturally outcompete smaller coalitions, retaining tenure for longer periods (Bygott *et al.* 1979; Packer and Pusey, 1982). A likely driver behind the management of longer tenure intervals is linked with the photographic safari industry and the affiliation of tourists towards large adult males from the perspective of reserve management (Miller *et al.* 2013). Secondly, administrative and financial challenges linked with retrieving a new adult male, with tourism industry-friendly traits, may impede processes (Miller *et al.* 2013). Across the LiMF, most male lions available for translocation, were below the age of three years. Male tenure was generally longer across reserves with a single adult male/coalition compared to reserves with multiple adult males, which may indicate some degree of tenure competition. Most male tenures were held by solitary males, indicating reserve management preference for solitary dominant males (O'Brien, 2012; Lehmann *et al.* 2008b).

4.4.2. iv) Prey species biomass trends

Most key prey species displayed an average annual population increase over time. Species generally not selected by lions, including eland, roan antelope (*Hippotragus equinus*), sable (*Hippotragus niger*) and common tsessebe (*Damaliscus lunatus lunatus*) (Hayward and Kerley, 2005) generally decreased across more reserves. Eland, roan and sable are relatively slower antelope (Estes, 1997), making them more susceptible to lion predation. However, equipped with protective horns and largely occurring at lower densities, they have generally been selected by lions in relation to their population density and therefore at a lower level (Hayward and Kerley, 2005). Comparatively, species generally selected by lions, including buffalo, blue wildebeest, giraffe and zebra (Hayward and Kerley, 2005) generally increased across reserves. Louw *et al.* (2012) demonstrated that lions in small, fenced reserves showed preference for blue wildebeest, but also for prey species including eland, that were generally not selected by lions in previous literature (Hayward and Kerley, 2005). One of the key drivers indicated was unnatural assemblages of prey species and high stocking densities of typically rarer species compared to open systems (Louw *et al.* 2012). Tourism is likely the primary driver behind unnatural herbivore stocking levels in small, fenced reserves. However, due to the constraints caused by the size of fenced reserves with no natural immigration, maintaining low density populations of certain herbivore species may violate the minimum viable population size and lead to increased risk of local extinction (Stanley-Price, 2016).

The prey preferences of lions in small, fenced reserves vary temporally based on both individual and overall prey species abundance (Louw *et al.* 2012, O'Brien, 2012). Therefore, the supplementation or removal of prey species may drive differences in lion prey selection between small, fenced reserves (Louw *et al.* 2012; O'Brien, 2012). Being opportunistic hunters, lions generally select more abundant prey species within their preferred weight class (Louw *et al.* 2012). However, lions have also selected warthog as a key prey species, which lie below the generally preferred weight class (Hayward and Kerley, 2005). This has been attributed to the inferior evasive capabilities and high densities of warthog populations (Hayward and Kerley, 2005), highlighting the vulnerability of lesser predator-adapted prey species. The population growth of reintroduced herbivores is initially hampered by the time required for introduced herds to learn how to access resources in the new territory (Magome *et al.* 2008; Owen-Smith, 2003). This time-lag of low population growth is likely further impeded by high levels of predation.

Prey naivete also increases lion predation-risk (Hayward *et al.* 2009). Research suggests that preferred lion-prey species, including blue wildebeest and zebra, display higher levels of anti-predator behaviour towards lions than non-selected species such as red hartebeest (Makin, 2016). This factor may have further reduced the resilience of some supplemented species, as prey supplementation was generally followed by a population decline, reflecting previous research (Lehmann *et al.* 2008b; Power, 2002; Tambling and Du Toit, 2005). Hayward and Kerley (2005) evaluated that Ostrich (*Struthio camelus*) was not a selected lion-prey species. However, in personal communication with reserve managers, at least three predator-naïve Ostrich populations were depleted shortly after reintroduction with lions and selection for Ostrich has also been recorded in one study reserve (O'Brien, 2012). This further supports a combination of naïve and non-preferred prey species as less resilient to lion predation in small, fenced reserves. Slotow and Hunter (2009) also recorded at least one local species extinction after the reintroduction of lions in 13% of reserves surveyed.

Although most prey populations increased on average over time, the overall biomass stocked, and the proportion of prey biomass introduced annually varied significantly between sites. Reserves (1 and 3) had higher annual prey biomass and contained a single resident pride and adult male/coalition at lower mean lion density. In these reserves, increasing lion density was associated with decreasing prey biomass, which may indicate degraded social ecological conditions and predator-prey dynamics (Ferreira and Hofmeyr, 2014). However, these reserves also had the highest prey removal rate and the lowest prey supplementation rate. The reduction in overall biomass was therefore likely amplified by unnaturally high prey populations combined with management removals (Louw *et al.* 2012; Peel and Montagu, 1999; Tambling and Du Toit, 2005).

Reserves (4 and 5), with more than one pride, were associated with lower overall prey biomass that increased with lion density. Management input varied between the two reserves, with one reserve supplementing a large biomass of prey combined with minimal removals. The second reserve introduced prey species in the last years of data collection only and removed a higher prey biomass particularly towards the end of my study and the onset of a drought period. There was no significant difference in overall reserve biomass between the two reserves however, there was a higher density of other large carnivores, including an African wild dog population, in the reserve that supplemented more prey. The relationship between prey biomass and lion density was inconsistent between reserves and there was no significant effect of rainfall levels on annual prey biomass. This indicates the influential role that management intervention and the matrix of other carnivores can play as prey population drivers in small, fenced reserves. The matrix of the overall carnivore guild requires careful consideration. The presence of lions in a fenced reserve may temporally or spatially displace smaller carnivores, including cheetah (Durant, 1998; Swanson *et al.* 2016). This displacement may affect prey selection in smaller carnivores, which would have a feedback mechanism in determining prey availability and subsequent lion-prey selection. Furthermore, although individual carnivore species may select certain prey species according to their availability (i.e. not preferentially selected or avoided), the combined effect of multiple carnivores on these prey species may have a compounded effect (O'Brien, 2012). Further research is required to elucidate the relationship between lion population structure, the density of other carnivores and prey species selection in small, fenced reserves.

4.4.3. Lion mortalities

Less than 15% of all lions that reached the age of 12 months were deceased at the time of data collection due to natural or anthropogenic causes, compared to 36% that had been translocated. High lion removal rates likely reduced natural mortality, particularly given that lions were largely removed below the age of three years. Over one-third of all subadult and adult lion mortalities were lions aged between 1 – 2.9 years, with a similar proportion dying between the longer interval of 3 – 9.9 years. This reflects findings of reduced natural survivorship in younger lions (Bertram, 1975; Funston, 2011). Lion mortalities in open systems have largely been associated with intraspecific competition, starvation and other natural causes, with times of subadult dispersal associated with higher mortality rates (Bertram, 1975; Funston, 2011; VanderWaal *et al.* 2009). Subadult and adult mortality rate was highest in reserves with unknown lion groups, particularly unknown adult males. This reflects previous findings (Mosser and Packer, 2009) and is not surprising given that nearly all documented natural mortalities in the current study were caused by other lions.

Although mortality was generally low, it is concerning that anthropogenic causes were a leading mortality factor. Close to one-third of all subadult and adult lion mortalities were attributable to each poaching, natural causes and unknown causes, with a small number of other anthropogenically linked mortalities. Confirmed poaching incidents were recorded across more than 50% of study reserves and three provinces between 1993 and 2017. Most lion poaching incidents were recorded in KwaZulu-Natal (*n* = 75.7% of lions), where high poaching levels have previously been reported within one study reserve (Hunter, 1998). A large proportion of the unknown deaths may be attributable to natural causes however, the already high number of poached lions may likely have been underreported and the carcasses never found.

Poaching, and the recent surge in lion bone trade, have both become increasing concerns regarding threatened lion populations (Bauer, 2003; Becker *et al.* 2013; Williams *et al.* 2017a). Lion poaching has been traditionally carried out through snare by-catch (Becker *et al.* 2013) while poisoning has been one of the methods used in East Africa in response to predator conflict (Hazzah *et al.* 2009). Most confirmed poaching incidents (65.6%) occurred since 2009, while only three study populations were established since this point indicating an increase in poaching frequency. Most lions poached in the current study were snared, supporting by-catch as the primary historical driver. However, two poisoning and several unknown causes were also reported. The inaccessibility of diminished lion populations in other parts of Africa may increase the poaching risk of South Africa's managed wild populations, fuelling illegal bone trade (Williams *et al.* 2017b). It is imperative to maintain effective monitoring of lion populations to enable appropriate response to poaching incidents and tactile research, including rapid response to wildlife poisoning incidents or to limit the impact of damage (Murn and Botha, 2018).

4.4.4. Genetic viability in small, fenced reserves

The study populations represented three of the four genetic nodes (Kruger, Kgalagadi, Etosha) found in managed wild lion populations in South Africa (Miller and Funston, 2014). The genetic provenance of lion populations across reserves is a management concern. As reported by Miller *et al.* (2015), lions originating from Etosha NP would have limited natural ability to interbreed with lions within South Africa due to geographic separation. Miller *et al.* (2015) recommend limited lion translocations between populations that vary in genetically-distinct provenance, in order to conserve the local evolutionary significant units (ESU's). However, the genetic provenance of most populations was either Etosha or Etosha-mix derivatives, indicating a thorough level of population mixing and gene flow through translocations (Miller *et al.* 2015). On the one hand, this has provided allelic richness and genetic diversity across isolated lion populations however, this mixing may also degrade ESU longevity (Miller *et al.* 2015). With the market saturated with potentially non-preferable populations, management options to limit ESU degradation are restricted. The extended tenure intervals increased the likelihood of inbreeding within reserves. However, the average tenure of four years has generally been the upper limit recorded for open systems (Pusey and Packer, 1984). Furthermore, the effect of inbreeding can be ‘outbred’ relatively quickly through the introduction of new lions (Trinkel *et al.* 2008) however, the genetic provenance of introduced lions would require strategic consideration.

4.4.5. Disease control in small, fenced reserves

There was limited information available on disease control measures, which has likely been underreported. This is a management concern, particularly regarding metapopulation management, the translocation of lions and the potential spread of pathogens (Trinkel *et al.* 2011). Most disease testing (bTB) was carried out prior to translocation and no positive tests were reported. Buffalo were present in only half of the reserves in this study, reducing the likelihood of bTB transmission to lions (Keet *et al.* 1996). However, being a multi-host pathogen, bTB has also been identified in other wildlife species in South Africa, including kudu and warthog (Michel *et al.* 2006). Although the pathology of bTB in lions has been associated with relatively low impact on population parameters, it can reduce individual fitness (Ferreira and Funston, 2010; Trinkel *et al.* 2011), transmits between species (Renwick *et al.* 2007) and requires control as part of the Animal Diseases Act (Anon, 1984).

Having a catastrophic effect, one reserve lost an entire population with the exception of a single lioness within six weeks of a CDV break-out. The break-out occurred over the summer months during an extended drought period in South Africa. Similar CDV outbreaks have been recorded in open systems following droughts, with lion mortalities linked with an increase in *Babesia* infections (Munson *et al.* 2008). The unavailability of lion-specific vaccinations (required from abroad) impeded the ability of management response and poses a concern. Management intervention through vaccination could therefore focus on vulnerable lion populations after drought periods. However, precaution is advised as vaccinations themselves have in rare cases been associated with subsequent clinical symptoms in other species (Sutherland-Smith *et al.* 1997; Van Heerden *et al.* 1989). If identified before widespread transmission, it may be also feasible to quarantine uninfected individuals until the disease threat has subsided however, there are no reports of this. With no specific antivirals currently available to treat CDV, infected wildlife is euthanised (*reviewed in* Leisewitz *et al.* 2001). Treatments have been investigated in-vitro (Carvalho *et al.* 2014; Gallina *et al.* 2011) and in-vivo in dogs (Bogdanchikova *et al.*

2016). Therefore, a CDV treatment may be developed for wildlife species over coming years. Research is required into the epidemiology of CDV in African wildlife populations, to identify potential reservoir hosts and transmission routes (Gowtage-Sequeira, 2009; Viana *et al.* 2015).

A single rabies outbreak was reported across one reserve, during which lions were treated with vaccinations and no cases of clinical signs or lion mortalities were recorded. The vaccinations supplied to wild dogs during a rabies outbreak in Madikwe GR were associated with lower success (Hofmeyr *et al.* 2000) and success rate increased with repeated vaccinations (Hofmeyr *et al.* 2004). The repeated outbreaks at Madikwe GR highlight the exposure risk from domestic and potentially wild animals from outside of the park (Sabeta *et al.* 2018), a common risk factor for fenced reserves (Prager *et al.* 2012; Westerberg *et al.* 2008). There were several other lions treated with precautionary rabies vaccinations. There are limited records for rabies affecting lion populations however, an outbreak in kudu populations led to clinical symptoms and morbidity in lions in Etosha NP (Berry, 1993). This conflicts with a report of non-clinical rabies in a lion population in Zambia (Berentsen *et al.* 2013), highlighting the importance of further epidemiological research on the transmission of rabies to lions in southern-Africa.

No other diseases were controlled for or recorded during the study period. It is likely that FIV, naturally occurring in other lion populations (Packer *et al.* 2001; Spencer *et al.* 1992) and introduced to HiP (Trinkel *et al.* 2011) may be present in some populations. Research has documented clinical symptoms in wild lions (Roelke *et al.* 2009). Further research on the pathology of FIV in managed wild populations is required, particularly given that varying strains are linked with differential levels of disease (Troyer *et al.* 2011). This requires consideration before lion translocation for example, it may not be desirable for populations to host more than one FIV strain. When lion samples are being taken, it is recommended to test for the presence and strain of FIV antibodies. Infectious diseases can spread rapidly among social carnivore species (Guiserix *et al.* 2007), with population-level effects heightened in isolated populations. Therefore, management interventions relative to disease-risk need to be weighed against the benefits of natural ecological processes (Miller *et al.* 2013), with wildlife populations in small, fenced reserves prone to a higher risk of disease transmission and prevalence compared to larger systems (Ezenwa, 2004; Lebarbenchon *et al.* 2006). Successful disease management requires vigilant monitoring and an effective response action plan.

4.4.6. The Lion Management Forum of South Africa

Although conservation was generally ranked as the primary overall reserve goal, the primary goal for the reintroduction of lions was tourism. This affects lion management protocols, for example, the extended lion tenure recorded. Furthermore, most reserves introduced a minimal founder-population of lions in order to delay the effects of population increase while gaining the benefits of 'Big Five' status. However, lion population growth was highest in the years immediately following reintroduction, particularly among reserves with a single pride and adult male/coalition. The LiMF served as an effective conduit for members to discuss options regarding lion translocation requirements, with correspondence on lion availability sent on a regular basis. The high instance of lionesses sought through translocation was due to a single request from a reserve in Mozambique (n = 20 lionesses). The average interval between all LiMF correspondences on translocation requirements (4.59 weeks) was substantially shorter than the interval between successive translocation requests issued by individual reserves (10.61 months). There were also several instances of repeated requests regarding the same lion individuals available for translocation, and a smaller number of repeated requests seeking available lions, indicating the low demand for lions. Recommendations regarding lion translocation planning, supported through the LiMF, are provided in Chapter 7. Effective metapopulation management for managed wild lions will be critically reliant on accurate record-keeping, database management and standardised procedures. The databases developed with the current study can be expanded to support the standardisation of data collection methods facilitated through the LiMF.

4.4.7. Conclusions

The major drawback associated with research based on retrospective analyses is the ability to test formulated hypotheses regarding sample size and stratification. Reserve selection was based on the availability of reliable historic data, which limited sample size within the lion population categories (A - D) and other variables tested. Furthermore, conducting analyses across multiple reserves that used variable data collection methods and sampling efforts, likely introduced variability to the dataset. To counteract this, I increased the study sample size as much as I could. Although population growth and reproductive vital rates of managed wild lions have previously been evaluated from a reserve management perspective, this research took the additional approach to investigate how lion pride structure and dynamics can affect these vitals in fenced reserves. The primary factors leading to increased lion population growth in small, fenced reserves were increased survivorship (all age-classes), young age of first reproduction and short birth intervals. This was largely driven by reduced intraspecific competition from unknown lions. With high prey availability, starvation also likely played a negligible role in lion mortality and actually increased lioness reproductive fitness. Cub survival was most affected by the presence of adult males, while overall population growth rate was lowest in reserves that also contained more than one pride. The introduction of adult males was relatively infrequent, with longer tenure periods than open systems. The supplementation of prey species had minimal long-term impact on prey species population growth, with prey species generally increasing in reserves with lower overall prey biomass. Incidents of poaching were high, and together with infectious diseases, require careful monitoring and further research to ensure effective planning and mitigation. Lion management record-keeping has been considerable across study reserves, and while some gaps were identified, standardised database management and procedures will enhance planning and decision-making capabilities. These results allow more informed decision-making processes when it comes to the management of managed wild lion populations (see Chapter 7). Management protocols require adaptation based on reserve management objectives and can be adapted to address a combination of reproductive output, pride cohesion and immigration/emigration to best reflect natural lion population dynamics in open systems (Ferreira and Hofmeyr, 2014).

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SUPPLEMENTARY MATERIAL

Table S4.1. Participating study reserves according to Supplementary Table S2.1 (Chapter 2).

Reserve number
4, 5, 6, 7, 8, 9, 10, 13, 14, 15, 16, 17, 18, 20, 21, 22, 23, 24, 26, 27, 28

Table S4.2. The information on lion demographic history collected across all study reserves.

Collected across:	**Data collected:**
All lions	Date of introduction, removal, birth*, mortality on reserve
	Lion ID
	Sex
	Pride ID
Lion introductions	Origin reserve
	Date of birth*
	Boma interval (weeks)
Lion births	Maternity
	Paternity
Lion removals	Method
Lion mortalities	Cause

* Date of birth recorded as date of first emergence from the den

Table S4.3. The age and sex distribution of managed wild lions at the time of data collection, across 16 wildlife reserves in South Africa.

	Cub (< 1 year)	**Subadult (1 – 3 years)**	**Adult (3 – 10 years)**	**Adult (> 10 years)**	**Total**
Female	18	32	74	23	147
Male	15	32	49	9	105
Unknown	26	15	-	-	41
Total	59	79	122	32	293

Table S4.4. Linear model coefficients linked with lioness age of first reproduction, across reserves that varied in lion population structure (A – D) and lion density (lions/100 km^2) ($F_{(84,7)} = 2.08$, $p = 0.05$, $R^2 = 0.08$).

Variable	Estimate	SE	*p*
Population A	3.89	0.29	
:Lion density (slope)	-0.03	0.03	0.37
Population B	0.18	0.56	0.76
:Lion density (interaction)	-0.12	0.08	0.16
Population C	-0.19	0.82	0.81
:Lion density (interaction)	-0.02	0.07	0.81
Population D	-1.11	0.40	<0.01**
:Lion density (interaction)	0.07	0.04	0.08

Table S4.5. Linear model coefficients linked with lioness birth interval across reserves that varied according to i) lion density (lions/100 km^2), the presence/absence of more than ii) one pride and iii) more than one adult male/coalition ($F_{(4,117)} = 2.43$, $p = 0.05$, $R^2 = 0.05$).

Variable	Estimate	SE	*p*
Single pride/single adult male coalition / intercept	2.62	0.47	
Lion density	-0.08	0.04	0.07
More than one pride	0.16	0.12	0.18
More than one adult male/coalition	-0.69	0.26	< 0.01**
:Lion density (interaction)	0.05	0.02	< 0.05*

Table S4.6. Linear mixed model coefficients linked with lioness litter size, across reserves that varied in lion population structure (A – D) and lion density (lions/100 km^2) ($R^2M = 0.03$, $R^2C = 0.24$).

Variable	Estimate	SE	*p*
Population A / intercept	2.58	0.24	
Population B	0.42	0.31	0.17
Population C	-0.21	0.26	0.93
Population D	0.09	0.20	0.63

Lion density: slope	0.03	0.02	0.08▪
Random variable – lioness ID	**SD:** ± 0.47		

Table S4.7. Linear model coefficients linked with the percentage of cubs born that were male, across reserves that varied in lion population structure (A – D) ($F_{(154,3)} = 3.49$, $p < 0.05$, $R^2 = 0.05$).

Variable	**Estimate**	**SE**	***p***
Population A / intercept	50.53	4.95	
Population B	23.19	10.08	<0.05
Population C	-6.28	7.69	0.42
Population D	9.46	6.15	0.13

Table S4.8. Linear mixed model coefficients linked with cub survival rate (percentage of litter that survived to 12 months) across reserves that varied in lion population structure (A – D) ($R^2M = 0.04$, $R^2C = 0.05$).

Variable	**Estimate**	**SE**	***p***
Population A	94.68	3.71	< 0.001***
Population B	-11.63	7.51	0.14
Population C	-1.64	5.98	0.78
Population D	-12.39	4.63	< 0.01**
Random variable – lioness ID	**SD:** ± 3.40		

Table S4.9. Mean annual (*n*) lion population density (lions/100 km^2) rate across in 16 wildlife reserves that varied in lion population structure (A – D).

Lion population structure on reserve	**Mean**	**SD**	**Min**	**Max**	***n***
A) One pride: Single adult male lion/coalition	4.96	3.22	1.33	17.67	73
B) One pride and > one adult male/coalition	4.80	3.42	0.88	12.63	14
C) > One pride and a single adult male lion/coalition	8.09	4.66	1.49	19.33	41
D) > One pride and > one adult male/coalition	7.59	4.62	0.91	18.00	70

Table S4.10. Mean annual (*n*) lion population growth (λ) rate across in 16 wildlife reserves that varied in lion population structure (A – D), and the maximum and minimum values.

Lion population structure on reserve	**Mean**	**SD**	**Min**	**Max**	***n***
A) One pride: Single adult male lion/coalition	1.23	0.56	0.43	3.33	66
B) One pride and > one adult male/coalition	1.35	0.42	0.69	2.25	12
C) > One pride and a single adult male lion/coalition	1.13	0.33	0.62	2.00	40
D) > One pride and > one adult male/coalition	1.07	0.33	0.00	1.86	65

Table S4.11. Linear mixed model coefficients associated with lion population growth rate (λ) across reserves that varied in i) lion population structure (A – D), ii) lion density and the proportion (%) of a population iii) removed annually. Time (years) since reintroduction was isolated as a random effect ($R^2M = 0.22$, $R^2C = 0.30$).

Variable	**Estimate**	**SE**	***p***	**CI-**	**CI+**
Population A / intercept	0.96	0.10		0.76	1.16
Lion density (slope)	0.06	0.01	< 0.001***	0.03	0.09
Population B	0.33	0.23	0.21	-0.10	0.77
Lion density (slope)	-0.05	0.04	0.18	-0.12	0.02
Population C	0.15	0.15	0.23	-0.14	0.44
Lion density (slope)	-0.05	0.02	< 0.05*	-0.09	-0.01
Population D	0.05	0.13	0.89	-0.20	0.30
Lion density (slope)	-0.04	0.02	< 0.05*	-0.08	-0.01
Removed (%)	-0.01	0.002	< 0.001***	-0.01	-0.01
Random: time (years)	**SD:** ± 0.13				

Table S4.12. Summary of the lions that escaped from six different fenced reserves between 2001 and 2016, and lion density (lions/100 km^2) details for the respective reserves.

	Annual reserve lion density (number of lions per 100 km^2)				
Lion group (*n* = group size)	**Mean (SD)**	**Min**	**Max**	**(n) years**	**During year of break-out**
1. Pride - two adult females (sisters: 6.09 years) with seven sub-adults aged between 1.0 and 1.75 years (*n* = 9)	7.63 ± 3.92	2.27	17.27	19	15.00
2. Pride - two adult females (sisters: 5.34 and 7.68 years) (*n* = 2)	8.14 ± 3.66	1.49	14.14	14	10.42
3. Solitary female (3.67 years) (*n* = 1)	3.15 ± 1.19	2.08	5.83	14	5.42
4. Solitary female (4.75 years) (*n* = 1)	4.89 ± 1.83	3.00	8.00	9	7.00
5. Two adult males (3.08 years) (*n* = 2)	2.96 ± 0.85	1.48	5.19	15	5.19
6. Solitary adult male (3.5 years) (*n* = 1)	1.58 ± 0.43	1.04	2.21	7	2.21
7. Solitary adult male (2.51 years) (*n* = 1)	10.42 ± 5.7	1.33	18.00	15	17.67

Table S4.13. The number of lionesses that were born and that survived to 36 months across reserves that varied in lion population structure (A – D).

Lion population structure on reserve	**Births**	**Survival (%)**
A) One pride: Single adult male lion/coalition	41	80.49
B) One pride and > one adult male/coalition	9	100.00
C) > One pride and a single adult male lion/coalition	33	90.91
D) > One pride and > one adult male/coalition	65	73.85

Table S4.14. Linear mixed model coefficients linked with annual lion mortality rate (%), across reserves that varied i) in lion population structure (A – D) and ii) increasing introduction rate (% of lions introduced annually) ($R^2M = 0.16$, $R^2C = 0.21$).

Variable	**Estimate**	**SE**	***p***
Population A	3.60	1.09	< 0.01**
:Lions introduced (slope)	-0.01	0.03	0.79
Population B	4.79	2.63	0.65
:Lions introduced (slope)	0.00	0.07	0.91
Population C	2.26	1.73	0.44
:Lions introduced (slope)	0.21	0.04	< 0.001***
Population D	5.21	1.52	0.30
:Lions introduced (slope)	0.00	0.42	0.92
Random variable: reserve	**SD:** ± 1.75		

Table S4.15. The average length of adult male lion tenure (years), along with standard deviation, range and sample size across study reserves, according to reserve lion population structure (A – D) and lion coalition size (1 – 3 lions).

Variable	**Mean**	**SD (±)**	**Min**	**Max**	***n***
Population A	3.73	1.50	1.83	7.26	13
Population B	3.20	2.42	0.75	5.58	3
Population C	4.76	1.85	2.25	7.42	9
Population D	4.21	2.24	0.08	6.51	8
Coalition $n = 1$	4.37	1.38	1.92	7.34	22
Coalition $n = 2$	3.50	1.27	2.08	5.84	8
Coalition $n = 3$	3.50	0.88	3.00	4.75	3

Table S4.16. Linear model coefficients linked with adult male tenure age (years) across reserves that varied in i) lion population structure (A – D), ii) increasing coalition size and iii) whether the lion/s were born or introduced to the reserves ($F_{(5,27)} = 0.84$, $p = 0.53$, $R^2 = -0.03$).

Variable	**Estimate**	**SE**	***p***
Population A / intercept	4.18	0.75	
Population B	0.36	0.85	0.64
Population C	0.47	0.60	0.43
Population D	-0.31	0.59	0.61
Coalition size	0.15	0.37	0.69
Introduced lions	-0.78	0.50	0.13

Table S4.17. Linear model coefficients linked with adult male tenure interval (years) across reserves that varied in i) lion population structure (A – D) and ii) increasing coalition size ($F_{(4,28)} = 0.49$, $p = 0.74$, $R^2 = -0.07$).

Variable	**Estimate**	**SE**	***p***
Population A	5.23	1.02	
Population B	-0.86	1.23	0.49
Population C	-0.29	0.87	0.75
Population D	-0.54	0.87	0.54
Coalition size	-0.60	0.54	0.27

Table S4.18. The list of prey species recorded across 10 participating reserves for which census data over multiple years was available. The unit weight (kg) of each species and the number of reserves (*n*) where each species was recorded is listed. The mean annual population change (% increase/decrease), and standard deviation, for each species across the participating reserves is provided. The percentage of reserves for which each species decreased in population (decreasing populations) is also listed.

Species	**Weight (kg)**	**Reserves (*n*)**	**Population change (%)**	**SD (±)**	**Decreasing populations (%)**
Blesbok (*Damaliscus pygargus phillipsi*)	53	2	-9.60	54.49	50.00
Buffalo (*Syncerus caffer*)	450	8	9.77	11.60	12.50
Bushbuck (*Tragelaphus scriptus*)	30	7	34.39	52.98	14.29
Duiker, Common (*Sylvicapra grimmia*)	10	8	30.04	48.20	25.00
Duiker, Red (*Cephalophus natalensis*)	10	3	45.87	50.04	33.33
Eland (*Tragelaphus oryx*)	340	7	-2.72	20.38	57.14
Gemsbok (*Oryx gazella*)	150	3	5.39	4.37	0.00
Giraffe (*Giraffa camelopardalis*)	750	9	9.79	14.32	22.22
Impala (*Aepyceros melampus*)	40	8	55.31	114.72	12.50
Kudu, Greater (*Tragelaphus strepsiceros*)	136	10	44.83	81.60	30.00
Nyala (*Tragelaphus angasii*)	73	6	47.55	54.27	16.67
Ostrich (*Struthio camelus*)	95^{+}	5	10.49	37.80	40.00
Red hartebeest (*Alcelaphus buselaphus caama*)	125	4	19.88	42.60	50.00
Reedbuck, Common (*Redunca arundinum*)	40	2	18.47	15.00	0.00
Reedbuck, Mountain (*Redunca fulvorufula*)	40	4	55.55	64.79	0.00
Roan Antelope (*Hippotragus equinus*)	220	1	-63.89	NA	100.00
Sable (*Hippotragus niger*)	185	1	-33.33	NA	100.00
Springbok (*Antidorcas marsupialis*)	26	3	-27.00	24.85	66.67
Steenbok (*Raphicerus campestris*)	10	6	29.96	72.24	50.00
Tsessebe, Common (*Damaliscus lunatus lunatus*)	91	1	-41.85	NA	100.00
Warthog (*Phacochoerus africanus*)	45	9	52.32	99.49	11.11
Waterbuck (*Kobus ellipsiprymnus*)	160	8	9.82	19.21	37.50
Wildebeest, Black (*Connochaetes gnou*)	120	3	-4.56	-4.56	66.67
Wildebeest, Blue (*Connochaetes taurinus*)	123	7	0.57	28.73	28.57
Zebra, Burchell's (*Equus quagga*)	200	10	20.47	38.89	20.00
Mountain zebra (*Equus zebra*)	200	1	*Introduced during last year of study*		
Bushpig (*Potamochoerus larvatus*)	54	2	*Reliable population estimate unknown*		

Unit weight for species except ostrich attained from Coe *et al.* (1976);
+ unit weight attained from Hockey *et al.* (2005)

Table S4.19. The species, population size (*n*) and annual growth rate (λ) of supplemented prey populations in the year before supplement, across four reserves over 5 – 17 years. The number of animals introduced (*n*) and the relative proportion (%) of total prey species biomass for that year, that the introduced individuals represent is displayed. The population growth rate one year after release (Year ^{1}) is indicated, along with the growth rate in the last year (^{x}) that data follow-up was available, relative to population size before the supplement. The total reserve area is also displayed.

	Pre-supplement		**Supplement**		**Post-supplement**		
Species	λ	Population size (*n*)	Introduced (*n*)	% Reserve biomass	λ Year ^{1}	λ Year ^{x}	Reserve area
Blue wildebeest	0.99	467	155	2.97	0.94	0.95 ^{4}	233.33
Blue wildebeest*	0.82	82	239	12.16	-	-	134.34
Buffalo	1.17	463	16 $^{+}$	0.59	1.40	1.30 ^{2}	230.00
Buffalo	1.26	110	16	3.05	1.36	1.12 ^{3}	134.34
Giraffe	0.95	57	13 $^{+}$	4.51	1.05	0.75 ^{4}	134.34
Impala	0.77	1359	403 $^{+}$	9.10	0.78	-	134.34
Impala	1.18	1057	478	8.11	0.93	0.69 ^{2}	134.34
Impala*	0.74	272	497	8.23	-	-	134.34
Kudu	1.18	59	14	0.91	1.12	0.76 ^{5}	134.34
Kudu	2.42	160	47	2.71	0.71	0.36 ^{2}	134.34
Kudu*	0.51	58	82	4.61	-	-	134.34
Springbok*	0.48	57	649	10.27	-	-	240.00
Waterbuck	1.33	20	130	4.78	0.90	0.45 ^{3}	233.33
Zebra	1.56	56	44	5.29	2.21	2.29 ^{4}	134.34
Zebra	1.32	155	12	0.80	0.83	0.75 ^{3}	134.34
Zebra	0.91	116	284 $^{\wedge}$	26.30	1.72	1.03 ^{2}	134.34
Zebra*	0.60	119	95	7.86	-	-	134.34

* introduced during last year of data collection therefore no trend available

\+ introduced over two or three ^ consecutive years

Table S4.20. Linear model regression coefficients associated with the proportion (%) of overall annual prey biomass introduced over increasing years (slope), across four reserves. The reserve number corresponds with Figure 6.3.2 and Figure 4.2, on the relative introductions and removals ($F_{(32,7)} = 4.87$, $p < 0.001$, $R^2 = 0.41$).

Variable	**Intercept**	**SE**	***p***	**Slope**	**SE**	***p***
Reserve 2	-4.12	4.64	0.42	2.05	1.27	0.13
Reserve 3	0.08	3.53	0.93	0.01	0.97	0.93
Reserve 4	-0.31	2.02	0.88	0.09	0.20	0.66
Reserve 5	-1.73	3.09	0.65	1.11	0.35	<0.05*

Table S4.21. Linear model regression coefficients associated with the proportion (%) of overall annual prey biomass removed over time (slope), across five reserves. The reserve number corresponds with Figure 6.3.2 and Figure 4.2, on the relative introductions and removals ($F_{(34,9)} = 22.90$, $p < 0.001$, $R^2 = 0.82$).

Variable	**Intercept**	**SE**	***p***	**Slope**	**SE**	***p***
Reserve 1	9.31**	2.61	<0.001	-0.83	0.57	0.16
Reserve 2	-1.46**	3.74	<0.01	0.73	0.99	0.12
Reserve 3	15.84	3.53	0.07	0.15	0.84	0.25
Reserve 4	-1.09**	2.92	<0.01	0.65*	0.58	<0.05
Reserve 5	1.13*	3.01	<0.05	-0.11	0.60	0.24

Table S4.22. Linear mixed model coefficients linked with prey biomass density (kg/km^2) according to: i) time (years) since lion reintroduction, ii) lion population structure (A – D) and iii) Savanna or Succulent-Karoo Biome. There were no reserves with a single pride and multiple adult males/coalitions (B) present in the dataset ($R^2M = 0.83$, $R^2C = 0.89$).

Variable	**Estimate**	**SE**	***p***
Lion population A / intercept	4,420.83		
Lion population C	-2,988.07	475.91	0.14
Lion population D	-3,173.79	526.98	0.08
Years since lion reintroduction / slope	42.69	18.79	< 0.05
Succulent-Karoo Biome	-4,253.85	522.39	0.06
Reserve	**SD:** ± 349.50		

Table S4.23. Mixed linear model regression coefficients linked with the change in prey biomass density (kg/km^2) according to i) increasing lion density (slope) and ii) the number of prides (intercept) across four reserves ($R^2M = 0.86$, $R^2C = 0.94$).

Variable	**Estimate**	**SE**	***p***
Reserve with one pride: intercept	5,525.50	487.72	< 0.001
Reserve with one pride: slope	-213.16	75.73	<0.01
Reserves with more than one pride: intercept	-4,230.60	640.30	< 0.001
Reserves with more than one pride: slope	238.601	80.50	< 0.01
Reserve	**SD:** ± 474.90		

Table S4.24. Other large carnivores present across the four reserves (1, 3, 4, 5) in the Savanna Biome, the relative year of establishment of each population (according to the year of lion reintroduction: 0) and the approximate population density (individuals/100 km^2) at the end of the study period.

	Reserve			
Species	**1**	**3**	**4**	**5**
Cheetah				
Lion year	0	-1	0	-2
Density	4.67	8.26	10.73	3.72
African wild dog				
Lion year	endemic	3	absent	0 to 9 * removed
Density	6.67	2.17	-	4.47
Leopard				
Lion year	endemic	endemic	endemic	endemic
Density	4.67	4.35	unknown	14.89
Spotted hyena				
Lion year	endemic	endemic	endemic	endemic
Density (/100 km^2)	9.33	3.48	5.91 - 11.82	26.05

* pack was translocated from reserve nine years after the introduction of lions and the density is recorded from their last resident year

Table S4.25. The age-group and sex of lions sought for translocation, either from (Out) or to (In) wildlife reserves between December 2014 and December 2018. The lion populations were pertained to 25 reserves in South Africa, two international reserves, three non-specified locations and one unknown location (rogue lions).

		Lion age group (years)					
Sex	**Translocation required**	**< 1**	**1 - 3**	**3 – 6**	**> 6**	**Unknown**	**Total**
Male	Out	2	38	13	8	9	70
Female	Out	2	19	11	9	4	45
Male	In	0	0	26	1	8	35
Female	In	0	7	21	1	13	42

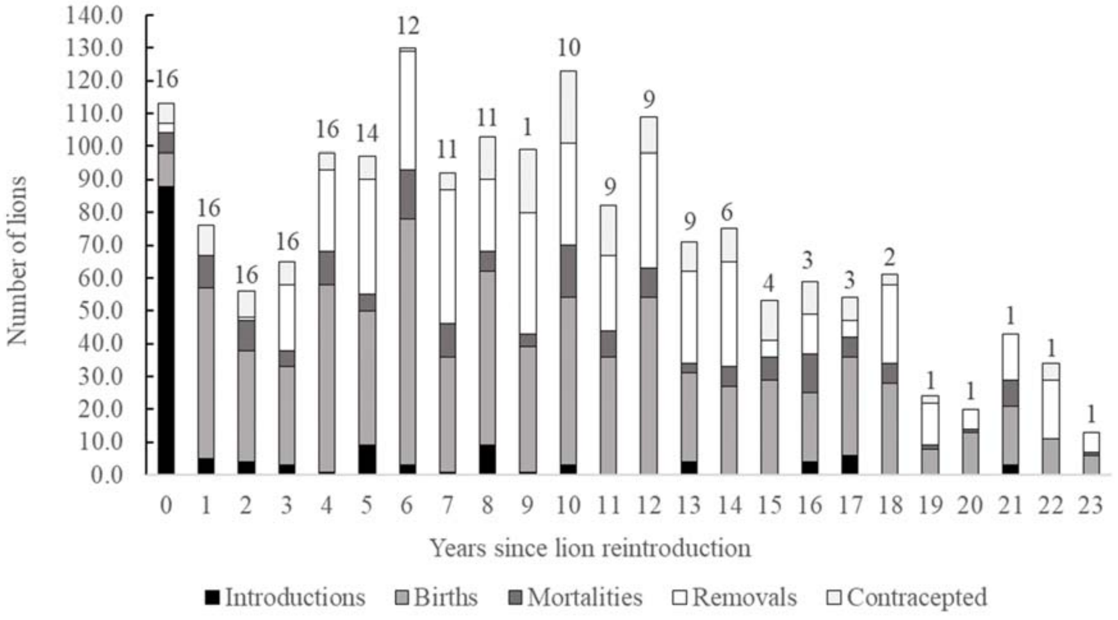


Figure S4.1. The total number of lions that were introduced, born, deceased, removed and contracepted since the first year in lion reintroduction across 16 reserve4.The reserve sample size for each year is displayed above the respective bar.

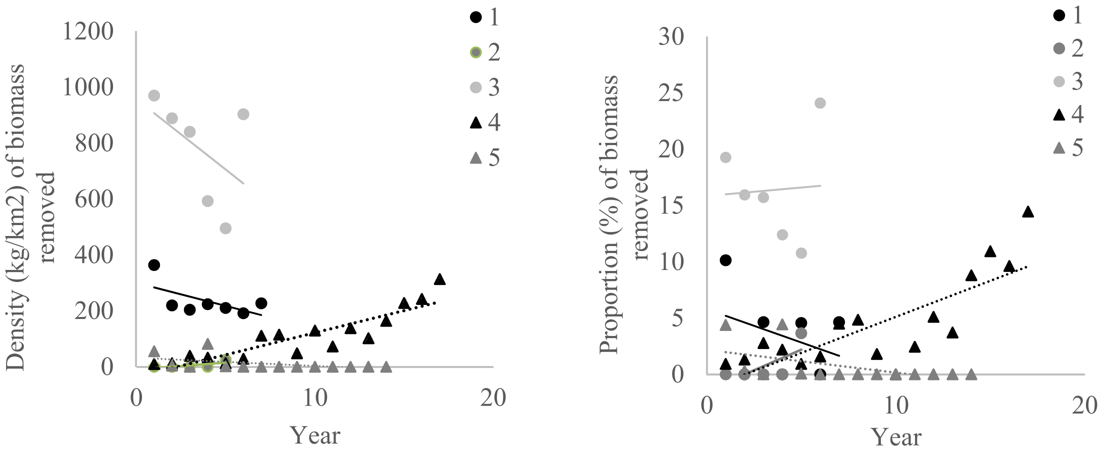
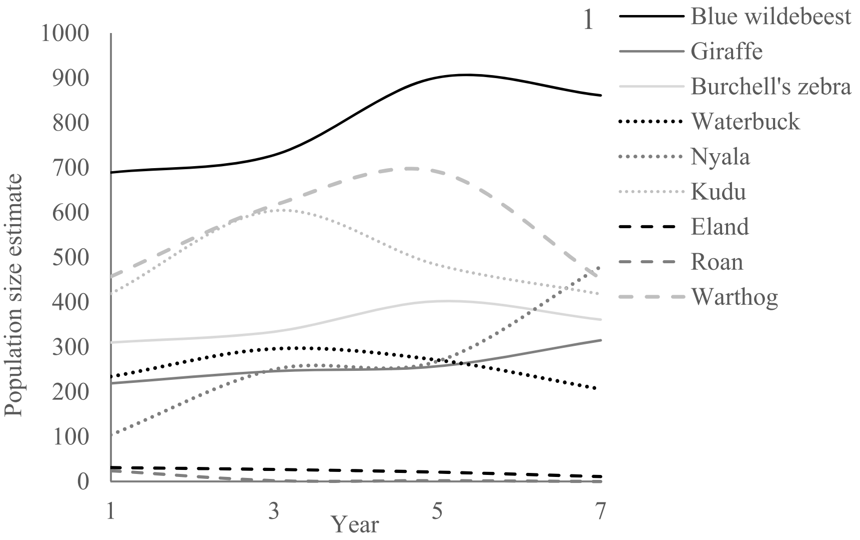
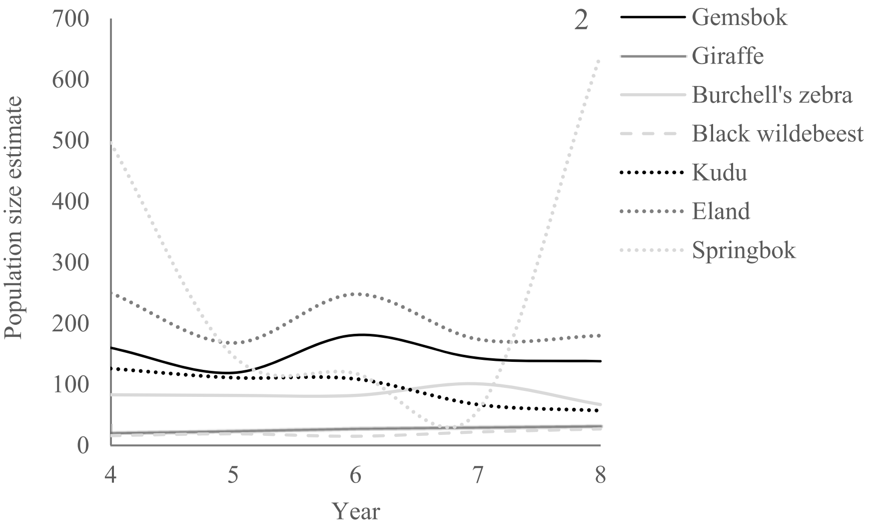


Figure S4.2. The density (kg/km2) (LHS) and the relative proportion (%) of prey biomass (RHS), according to overall reserve biomass in the same year, removed annually across five reserves (1 – 5) from the first year that data was available (year). The circles represent reserves with a single pride and the triangles represent reserves with more than one pride. The solid lines display linear trends for reserves with a single pride and the dashed lines display linear trends for reserves with more than one pride.



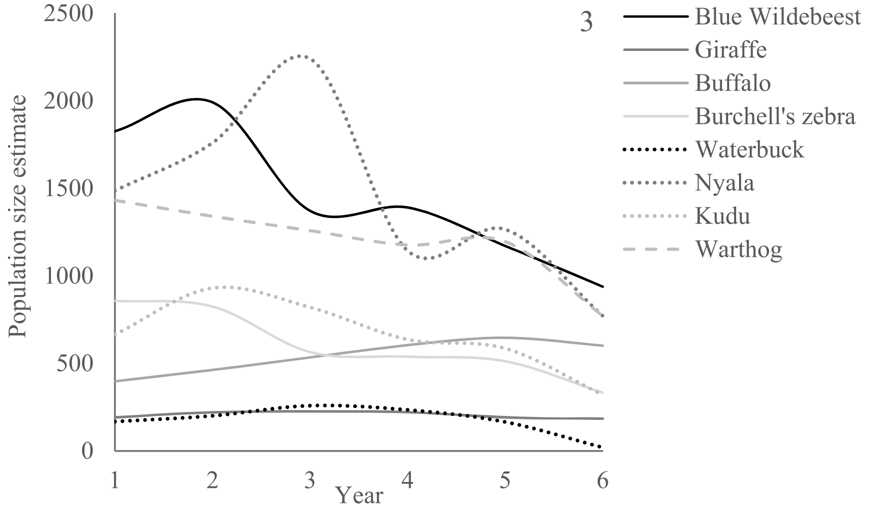
No supplements

Area = 150 km^2



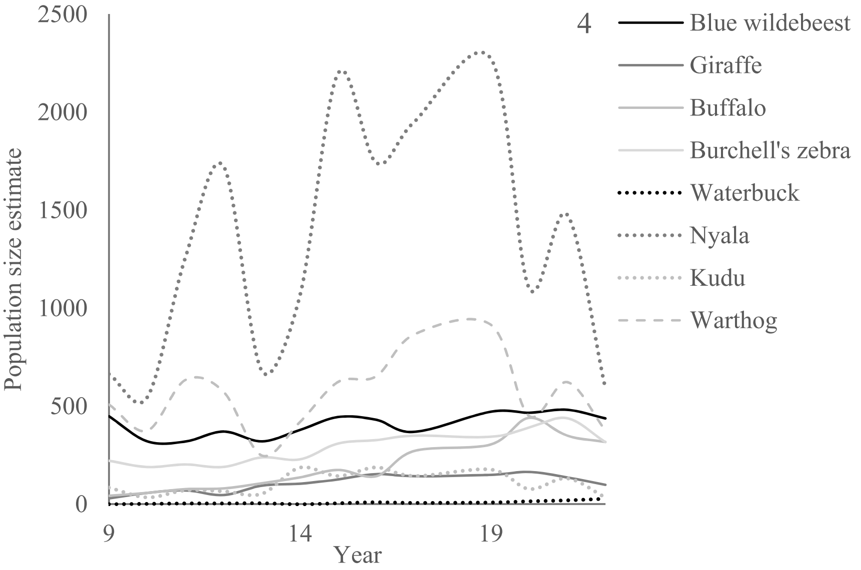
649 springbok (8)

Area = 240 km^2



16 buffalo (3,4)

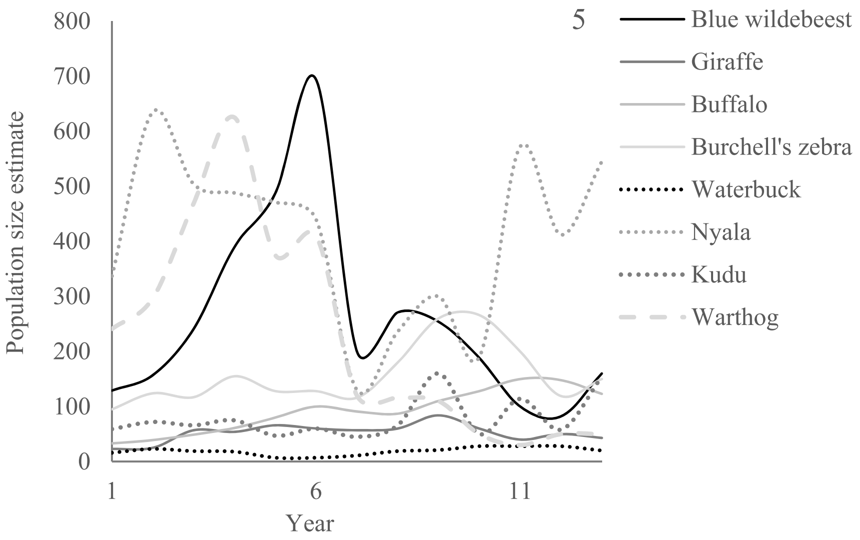
Area = 230 km^2



155 wildebeest (21)

130 waterbuck (22)

Area = 233.48 km^2



239 wildebeest
(13)
13 giraffe (8,9)
16 buffalo (10)
435 zebra
(5,8,9,10,13)
143 kudu (2,10,13)
Area = 134.34 km^2

*1,378 impala
(7,8,10,13)

Figure S4.3. The number of different prey species according to reserve census data over years since lion reintroduction, across five reserves from which full herbivore stocking and removal data was available. The number beside the legend corresponds to the reserves in Figure 6.3.2. The number of prey species introduced are indicated to the right of plot, with the corresponding year of supplement/s in bracket4.The solid lines represent species that lions have shown selection for in previous research (Hayward and Kerley, 2005). The dashed lines represent species previously indicated as not selected for by lions (Hayward and Kerley, 2005). Total reserve area is also displayed to the right of the figure.

CHAPTER 5

THE USE OF CONTRACEPTIVE TECHNIQUES IN MANAGED WILD AFRICAN LION (PANTHERA LEO) POPULATIONS TO MIMIC OPEN SYSTEM CUB RECRUITMENT

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Running head: Contraception of managed wild African lions

Table of Contents Summary:

African lion growth rates in smaller fenced protected areas are managed to prevent overpopulation. Using historical data, we found that deslorelin implants were more effective at reducing reproductive output than unilateral hysterectomy surgery. However, there were some undesirable side-effects associated with the implants. These findings advance the lion management practices on small fenced reserves; habitats that are becoming more valuable as larger lion populations are threatened across Africa.

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ABSTRACT

Context: Managed wild lions (*Panthera leo*) are lions found in smaller (<1,000 km^2), fenced protected areas and hold a substantial portion of South Africa's wild lion population. Managers must actively control population growth rates within these properties as the natural population control mechanisms are compromised. Fecundity control is used by wildlife managers, but long-term, empirical data on the impact and consequences of such interventions in lions are lacking.

Aims: We assess the effectiveness of two methods of contraception (deslorelin implant and unilateral hysterectomy) in reducing cub recruitment of managed wild lions.

Methods: Survey data spanning 14 years from 94 managed wild lions on 19 protected areas were used to evaluate the effectiveness of deslorelin implant treatments and unilateral hysterectomies on population growth rates through mimicking open system cub recruitment.

Key results: Deslorelin implants were effective at increasing the age of first reproduction and lengthening inter-birth intervals. There was also an unexpected decrease in litter size. Behavioural side-effects were recorded in some individuals, and the more successive deslorelin implants a lioness had, the more likely it was that weight gain was reported. Unilateral hysterectomy resulted in a decrease in litter size post-surgery, but this was not statistically significant. No behavioural or physiological side-effects were noted after unilateral hysterectomy.

Conclusions: Deslorelin treatment was more effective in reducing the reproductive output of managed wild lionesses than unilateral hysterectomy surgery. While more side-effects were associated with deslorelin implants than unilateral hysterectomies, a single deslorelin treatment is currently a good option for fecundity reduction. More research is required on unilateral hysterectomy surgery.

Implications: Neither deslorelin implants nor unilateral hysterectomies offer a 'silver bullet' solution for reducing rapid population growth in managed wild lions by mimicking cub recruitment rates in open systems. Reproductive control should be integrated with other best-practice approaches.

5.1. INTRODUCTION

Regulation of fecundity schedules has been widely used for the management of wildlife populations for several decades (reviewed by Fagerstone *et al.* 2002), and to mitigate the impacts of human-wildlife conflicts (reviewed by Massei and Cowan 2014). The management of various free-ranging wildlife species using contraceptive measures is well documented in South Africa (reviewed by Bertschinger and Caldwell 2016). African lion (*Panthera leo*) populations in small, fenced reserves, known as "managed wild lions" (Funston and Levendal 2015) are a prime example.

An absence of natural control mechanisms within managed wild lion populations results in artificially high growth rates (Miller *et al.* 2013; Miller and Funston 2014). Specifically, increased reproductive output of breeding females (both frequency and size of litters) and high cub survival due to social familiarity, minimal male infanticide and high prey numbers contribute to higher growth rates than those recorded in open systems (Miller and Funston 2014). This rapid population growth puts pressure on natural systems and can cause the degradation of predator-prey relationships, and financial strain on operating budgets (Miller *et al.* 2013). In response, active management, including the use of contraceptives, has been used to reduce growth rates of these populations (Lehmann *et al.* 2008b; Kettles and Slotow 2009; Slotow and Hunter 2009; Miller *et al.* 2013). Hormonal contraception, with deslorelin, is aimed at either increasing the age of first reproduction and/or inter-birth intervals to mimic those observed for lionesses in open systems such as Kruger National Park (NP) (Miller *et al*. 2013). Unilateral hysterectomy surgery aims to reduce litter sizes to mimic the lower post-parturition cub survival rates observed in open systems, such as the Serengeti NP (Miller *et al*. 2013). Implementing both strategies at once is not recommended (Miller *et al*. 2015).

A slow-release formula of deslorelin, a gonadotrophin-releasing hormone agonist, (Suprelorin®, Virbac, Sydney) was developed for domestic cats (*Felis catus*) (Munson *et al.* 2001) and dogs (*Canis familiaris*) (Trigg *et al.* 2001) and has been widely used in free-ranging carnivores (reviewed by Bertschinger and Caldwell 2016), including lions (Bertschinger *et al.* 2002; Bertschinger *et al.* 2008; Slotow and Hunter 2009; Kettles and Slotow 2009). The treatment down-regulates the production of follicle stimulating hormone (FSH) and luteinising hormone (LH) from the pituitary gland, subsequently inhibiting the reproductive hypothalamo-pituitary gonadal pathway (Bertschinger and Caldwell 2016). Theoretically, the treatment could be used on either male or female lions. However, due to the undesirable effects on androgen-dependant manes and dominance behaviour in males, female lions have been the focus of this method (Bertschinger and Sills 2013). A relatively simple veterinary procedure inserts deslorelin implants subcutaneously in immobilised lionesses (Trigg *et al.* 2001; Bertschinger *et al.* 2008).

Deslorelin implants were first used to reduce the fecundity of managed wild lions in South Africa in the late 1990's (Bertschinger *et al.* 2001; Bertschinger *et al.* 2008; Slotow and Hunter 2009; Kettles and Slotow 2009). The results from three relatively small studies (*n* = 40 and covering less than nine years), including a variety of doses (1 x 12mg, 3 x 4.7mg, 1 x 9.4mg, 1 x 4.7mg + 1 x 9.4mg), indicated that the implants generally inhibited oestrous activity, both biologically and behaviourally, for approximately 2.5 years (Bertschinger *et al.* 2001; Bertschinger *et al.* 2008; Kettles and Slotow 2009). Dosage selection was largely dependent on pharmaceutical availability at the time of treatment (Bertschinger *et al.* 2008). The 9.4mg implant was formulated to work over a longer period than the 4.7mg implants (pers. comm. Dr H. Bertschinger, September 2018). No apparent side-effects have been reported after successive treatments of deslorelin in lionesses, with the exception of weight gain in some individuals (Bertschinger *et al.* 2008). However, anecdotal data suggests that lionesses treated with successive implants, or those which have not previously reproduced prior to an implant treatment, may not return to normal oestrous activity (Miller *et al.* 2013). Field observations by managers also point towards possible behavioural changes, in the form of pride fragmentation, and additional reports of physiological changes in the form of weight gain (Miller *et al.* 2013). These *ad hoc* observations have led to concerns regarding the long-term use of deslorelin in managed wild lions, particularly given the long breeding lifespan of a lioness in managed wild populations (~10 years; Miller *et al.* 2013).

Unilateral hysterectomy is a more recent experimental technique for fecundity control in lions, and was first performed in South Africa in 2011 (reported in Miller *et al.* 2013). One horn of the normal bicornuate uterus is surgically removed from an immobilised lioness, leaving behind the ipsilateral ovary, severed at the level of the fallopian tube. The rest of the uterine horn is removed on the same side, down to the level of the bifurcation (pers. comm. Dr M. Toft January 2019). This theoretically reduces the space for implantation and decreases the reproductive capacity of the lioness to one to two cubs rather than two to four cubs. This reduction is aimed at mimicking the lower cub recruitment to adulthood that has been observed in relatively stable lion populations, such as those in the Serengeti NP (Schaller 1972; Bertram 1975; Miller *et al.* 2013). Unilateral hysterectomy has been successfully performed on dogs

(Seyrek-Intas *et al.* 2004), with no apparent side-effects and a reduction in litter size was observed.

In this study, we distributed a structured questionnaire to wildlife reserve managers to collect data on the use of both deslorelin implants and unilateral hysterectomies in managed wild lionesses across South Africa. We then explored the effectiveness of both treatments and evaluated the changes in the reproductive output of these lionesses. Specific effects that we explored were:

1. The duration of efficacy of deslorelin implants and the effects of dosage and consecutive implants.
2. Age effects and the impact of previous reproductive events on the duration of efficacy of deslorelin implants.
3. The impact of deslorelin implants on the age of first reproduction and inter-birth interval.
4. Consequence for litter size or cub survival following deslorelin implants.
5. The impact of unilateral hysterectomies on litter size and cub survival.
6. Behavioural and physiological impacts of either treatments post implantation/surgery.

5.2. MATERIALS AND METHODS

Between June 2015 and August 2016, the Lion Management Forum (LiMF), a Public Benefit Organisation comprised of wildlife managers, veterinarians, researchers and government officials, emailed a structured questionnaire to 61 wildlife reserve managers across South Africa. The questionnaire was partitioned into three sections regarding the outcome of the GnRH analogue deslorelin implants (22 questions), unilateral hysterectomy surgery (20 questions), in lions on their properties (Supplementary Material). Additional data regarding litters pre- and post-treatments were obtained from LiMF databases with permission from the data owners (unpublished data; Miller and Funston 2014). All data reported here are retrospective, and thus, we did not directly handle any animals or influence their course of treatment. Ethical clearance for the questionnaire was obtained through the Rhodes University Ethical Standards Committee (RU-HSD-15-02-0002). All data from the respondents were treated confidentially.

Respondents completed the questionnaire using historical data they had collected through direct observations and, in two cases, augmented with camera trap data. All participating reserves were ecotourism ventures, and lions were observed on a regular basis either from open safari-type vehicles and/or by reserve staff during the course of their duties, making this an appropriate data collection instrument (Radloff and Du Toit 2004). Physical measures, including weight gain and behavioural changes, were based on the observers' expert knowledge of individual lions over time, and were thus subjective observations.

Supplementary Material Table S5.1 summarises the parameters gathered during the survey, the assessments and statistical tests applied to these data for both deslorelin treatment and unilateral hysterectomy surgeries. All statistical tests were carried out in RStudio (RStudio Team 2016) using R v3.4.2 (R Core Team 2017). The generalised linear model for pair-wise comparison between pre- and post-treatment litter sizes, for deslorelin and unilateral hysterctomy treatments was setup as follows: Litter size was the 'response', ± treatment the 'term', and lioness ID was the random effect, using the *glmer* command in the *lme4* package (Bates *et al.* 2015). A power analysis for the unilateral hysterectomy model was performed using the *pwr* package (Champely 2018) using the following parameters: u = 2, v = to be calculated, f2 = 0.02, sig. level = 0.1 and power = 0.8. As the costs reported were highly variable, we also asked an experienced wildlife veterinarian (Dr Peter Caldwell from Old Chapel Veterinary Clinic) who has performed both deslorelin implants and unilateral hysterectomy surgery to provide us with quotations for both procedures that excluded travel time and other potentially highly variable costs.

5.3. RESULTS

Twenty completed questionnaires were returned that included data for 94 free-ranging lionesses across 19 protected areas in South Africa. One reserve returned two completed questionnaires, one for each of two separate sections of their reserve. Fourteen reserves only used deslorelin, two reserves only used unilateral hysterectomy, and three reserves used both treatments

5.3.1. Deslorelin implants

Between 2005 and 2016, a total of 76 lionesses were treated with deslorelin implants across 17 wildlife reserves in South Africa. Females ranged in age from 1.25 to 15.5 years at the time of treatment. Eight of these lionesses were fully or partially removed from our analyses for the following reasons: Four lionesses died of natural causes or were translocated within six months of their last treatment; two lionesses produced cubs within two and four weeks of their implant dates respectively; and two females had their implants removed after 12 and 10 months respectively. The former produced a litter nine months later, and the latter produced a litter 26 months after implant removal. The first of these lionesses was subsequently implanted again, which was not removed, so only her first treatment was eliminated from the analysis. Of the 69 individuals used in the analyses, 20 lionesses had more than one deslorelin treatment (including three lionesses that had litters in between treatments), bringing the total deslorelin treatments to 102. The doses of deslorelin used were: 2 x 4.7mg (*n* = 29), 1 x 9.4mg (*n* = 47), 3 x 4.7mg (*n* = 9) or an unrecorded dose (*n* = 17).

5.3.2. Effect of dosage

Twenty-one lionesses received one deslorelin treatment *and* had a litter post-treatment. Of these, ten received a 1 x 9.4mg dose, three received a 2 x 4.7mg dose, five received a 3 x 4.7mg dose, and three received an unknown dose. There was no difference between the mean duration of efficacy for the three doses (Figure 1; Kruskal-Wallis: $\chi^2 = 1.31$, df = 2, $p = 0.52$). Eighteen lionesses that had been treated with 1 x 9.4mg or 2 x 4.7mg doses of deslorelin were still alive and had not reproduced post-treatment. The average ongoing time post-treatment for 1 x 9.4mg was 6.69 ± 1.61 years (*n* = 6, range: 4.75 – 9.34) and for 2 x 4.7mg was 3.11 ± 0.78 years (*n* = 12, range: 2.42 – 4.92). Dosage has therefore not been used as a factor in the rest of our analyses.

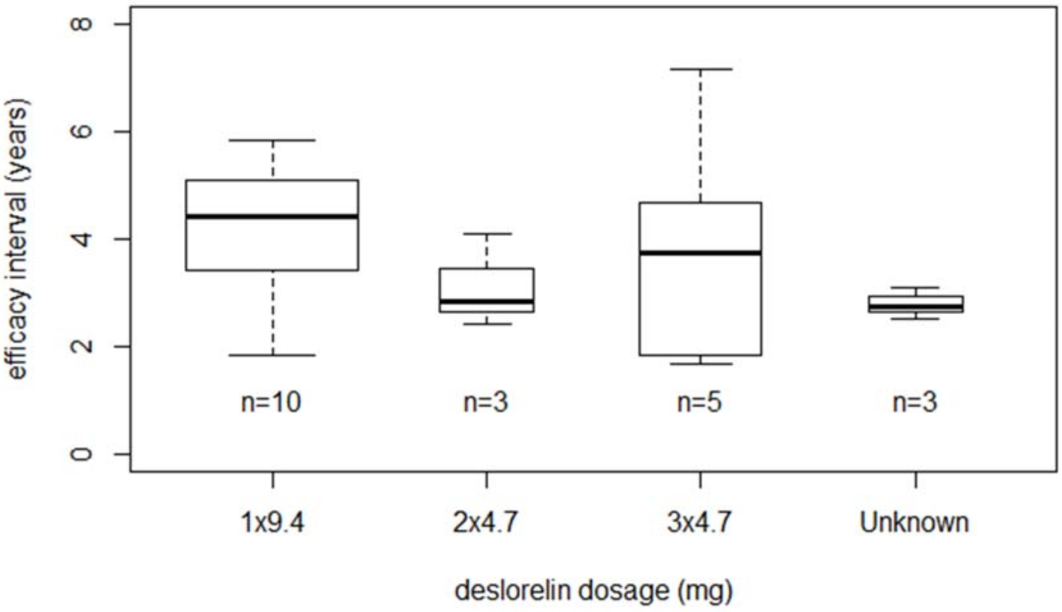

Figure 5.1. Effect of deslorelin dosage (mg) on duration of efficacy in 21 lionesses that received one dose and had a litter post-treatment. Tukey Boxplot: solid line represents the median, box represents 25 – 75 percentile and dotted lines extend to the maximum and minimum.

5.3.3. Deslorelin duration of efficacy

Sixty-seven lionesses received deslorelin implants. Three lionesses received a second single treatment after producing a litter (range: 8.08 – 8.58 years since first implant), resulting in the reporting of 70 deslorelin implants. Fifty single deslorelin treatments were reported (Figure 2a). This included a lioness that received a second single treatment after producing a litter subsequent to the removal of a previous implant (3 years since first implant). Eleven lionesses received two consecutive implants; seven lionesses received three consecutive implants; one received four consecutive implants; and one received five consecutive implants (Figure 2a). The average time interval between consecutive implants was 1.65 ± 0.55 years ($n = 52$ treatments, range: 0.56 – 3.00). The duration of efficacy of the deslorelin increased with increasing numbers of successive treatments (from one to five; Fig. 5.2a; Supplementary Material Table S5.2). Only lionesses with one, two or three successive treatments reproduced post-treatment within the timeframe of this study (Figure 5.2b; Supplementary Material Table S5.2).

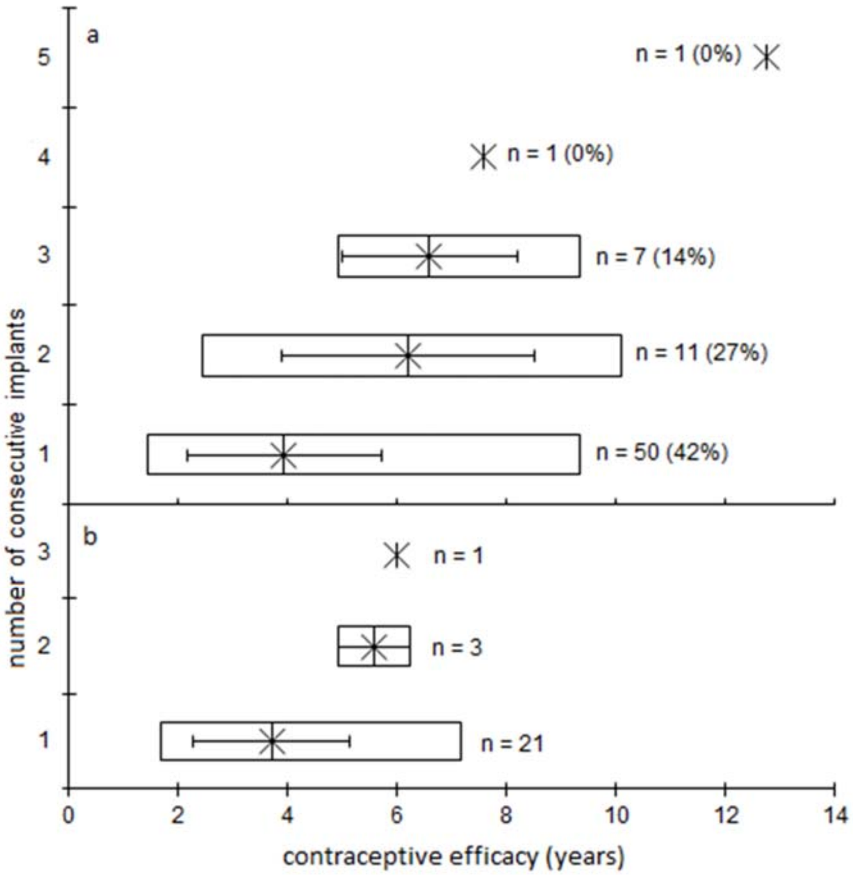

Figure 5.2. Duration of efficacy of deslorelin implants in lionesses (a) including lionesses that were yet to reproduce post-treatment and (b) that reproduced post-treatment. Bars represent the range of duration of efficacy, error bars represent standard deviation around the mean (×). The number of treatments is displayed (n) as well as the percentage of lionesses that reproduced post-treatment.

5.3.4. Effect of litter pre-treatment and lioness age on deslorelin duration of efficacy

Eleven out of 22 lionesses without a litter pre-deslorelin treatment and 10 out of 30 with a litter pre-deslorelin treatment (one treatment only) produced a litter post-deslorelin treatment. The average duration of efficacy of deslorelin in lionesses without a litter pre-treatment was 4.15 ± 1.71 years (n = 22, range: 1.67 - 7.76) compared to 3.53 ± 1.76 years (n = 30, range: 1.42 - 9.34) for those with a litter pre-treatment. However, this was not significantly different (Mann-Whitney U = 410.5, p = 0.14). There was no obvious relationship between age at time of implant and duration of efficacy (Figure 3). No lionesses implanted with deslorelin for the first time after the age of 10 years old, that were still alive, had successfully reproduced at the time of data collection (*n* = 2, Fig. 5.3). Seven other lionesses were implanted for the first time over the age of 10, two of these were translocated after 2.3 years, and the remaining five died at an average age of 16.9 years (average 5.12 years post-treatment; range: 1.42 – 7.67 years post-treatment) without producing a litter.

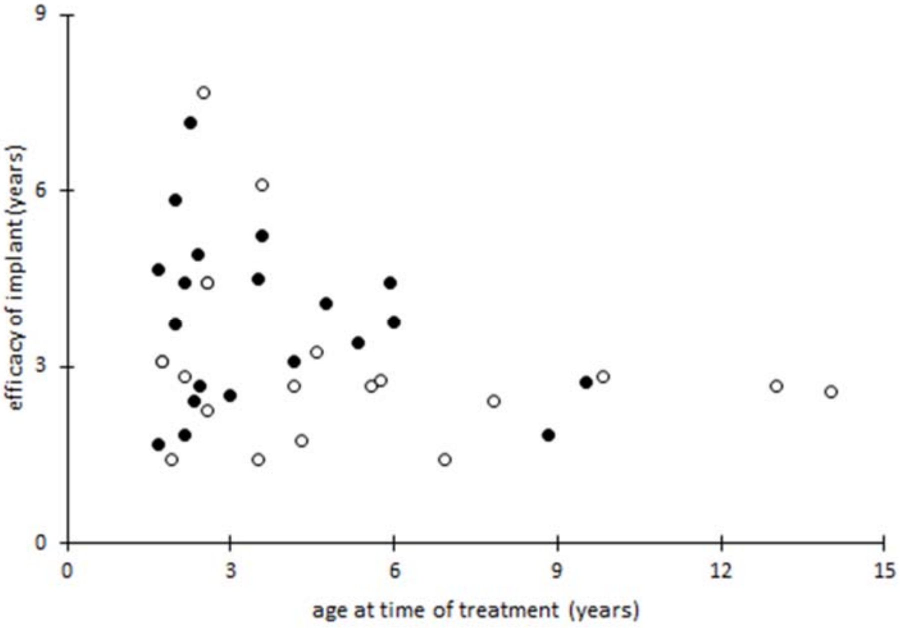

Figure 5.3. Age of lionesses at time of deslorelin implant compared to duration of efficacy of implants. Data from single treatment lionesses only (*n* = 42). Closed circles represent lionesses that have had a litter, while open circles indicate ongoing treatments.

5.3.5. Effect of deslorelin treatment on age of first reproduction

Twenty-two lionesses that had not reproduced pre-treatment received one deslorelin treatment. The average age at time of treatment was 2.25 years (Figure 5.4a). Of these, 11 reproduced post-treatment. Their average treatment age was 2.19 years, and their average age of first reproduction was 6.01 years (Figure 5.4a). The other 11 lionesses which had not reproduced post-treatment were treated at an average age of 2.30 years and their average age at time of data collection was 6.88 years (Figure 5.4a).

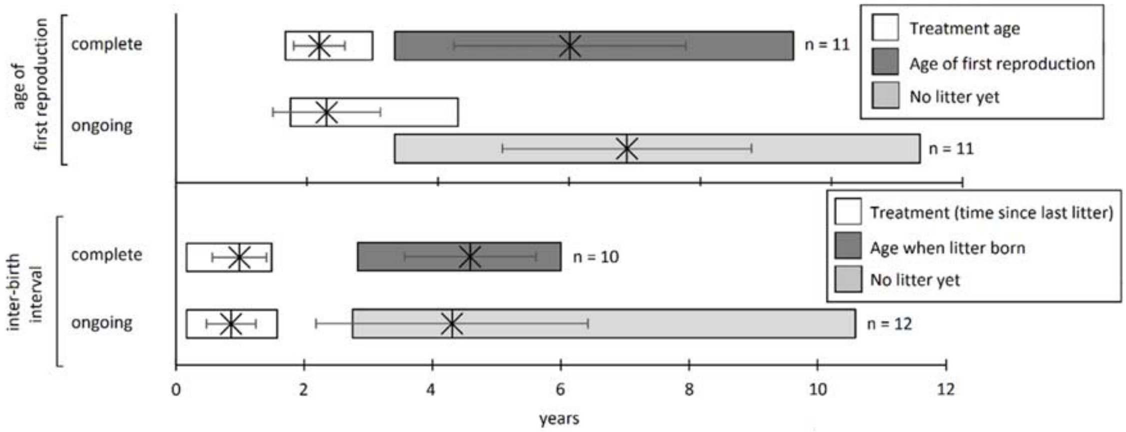

Figure 5.4. Effect of one deslorelin implant on the (a) age of first reproduction and (b) inter-birth interval in lionesses. 'Complete' refers to lionesses that have had a litter post-treatment while 'Ongoing' refers to those that have not. Bars represent the range of treatment (age or time post-litter)/duration of efficacy, error bars represent standard deviation around the mean (×).

5.4.6. Effect of deslorelin treatment on inter-birth interval

Thirty lionesses had litters pre-treatment followed by one treatment of deslorelin. The average time between their last litter and deslorelin treatment was 1.09 years (Figure 5.4b). Ten of these lionesses reproduced with an average inter-birth interval of 4.59 ± 1.02 years (Fig. 5.4b). Twelve lionesses had yet to reproduce at 4.30 ± 2.11 years post-treatment (Figure 5.4b). The remaining lionesses (*n* = 8), were either deceased or translocated at an average of 5.16 ± 1.91 years since their last litter.

5.3.7. Effect of deslorelin treatment on litter sizes

Twenty-five lionesses had litters post-treatment, 21 after one treatment, three after two successive treatments and one after three successive treatments with a mean litter size of 2.7 ± 0.9 cubs (range: 1 - 4). Thirty-five pre-treatment litters were reported with a mean litter size of 3.2 ± 0.8 cubs (range: 2 - 5). Twelve lionesses on six reserves had litters both pre- and post-deslorelin treatment, allowing for a matched comparison between pre- and post-treatment litter sizes. The mean litter size of pre-treatment litters (3.6 ± 0.79 cubs, *n* = 12) was significantly larger than the litter size post-treatment (2.5 ± 0.90 cubs, *n* = 12) (GLM results: post-deslorelin estimate = -1.08, CI: -1.76 – -0.40, z = 4.94, *p* = 7.66e-07).

5.3.8. Unilateral hysterectomy

Between 2012 and 2015, 19 lionesses on five wildlife reserves had a unilateral hysterectomy. The surgery was performed on lionesses aged between 1.25 and 9.35 years (mean = 3.14 ± 2.34 years). All of these surgeries, except two, were performed by the same veterinarian. Fifteen of these lionesses had recorded litters post-surgery, including the latter two which had not had any litters pre-surgery. Two lionesses were translocated immediately post-surgery and we could not follow-up; one died two years after the surgery, and one had yet to reproduce at the time of data collection. There were no observed complications following surgery.

Fifteen lionesses produced 21 litters post-surgery, with an average litter size of 2.5 cubs (mode = 2, n = 21 litters). There was one post-surgery litter with only one cub. The cub was only observed once, and it was assumed by management that this cub was killed by other lions soon after observation, or possibly abandoned by the mother. The average time interval between surgery and litters was 1.39 ± 0.81 years. The average inter-birth interval for lionesses that had a litter pre-surgery was 1.97 ± 0.58 years (n = 5). Five lionesses had at least one litter pre-surgery and post-surgery allowing for a direct, paired comparison. The average litter size pre-surgery (n = 9 from five lionesses) was 3.4 cubs (SD = 0.73) compared to post-surgery litter size of 2.9 cubs (SD = 0.90; n = 7 from five lionesses). Although the trend was for smaller litter sizes post-unilateral hysterectomy, the difference was not significant (GLM result: pre-surgery estimate = 0.22, CI: 0.33 – 0.79, z = 0.77; p = 0.44). Our power analysis revealed that, for a one-sided test (p = 0.1), we would need at least 381 litters in our dataset to detect a significant difference if the average litter sizes pre- and post-surgery were maintained.

A further comparison of the full dataset of post-treatment litters (n = 21) was performed to increase sample size. 'Control' lionesses (litters from lionesses before either a deslorelin treatment or unilateral hysterectomy) had significantly larger mean litter sizes (mean = 2.9 ± 0.94 cubs, n = 186 litters) than lionesses that underwent unilateral hysterectomy surgery (mean = 2.5 ± 0.68 cubs, n = 21 litters) (Mann-Whitney $U_{(1)}$ = 2540, p = 0.0086).

5.3.9. Effect of contraception on cub survival

One hundred and sixteen cubs were born in 41 litters to 25 lionesses post-deslorelin treatment. Of these, 105 survived to one year of age (91%). Fifty-two cubs were born in 21 litters to 14 lionesses post-unilateral hysterectomy. Of these, 47 survived to one year of age (90%). Compared to control data from lionesses not treated with deslorelin or unilateral hysterectomy

(549 cubs born in 186 litters to 75 lionesses with 473 cubs surviving to one year of age; 86% survival; Miller and Funston 2014), there were no significant differences in cub survival for either treatment ($\chi^2 = 0.145$; $p = 0.93$, df = 2).

5.3.10. Behavioural and physiological changes

There were no behavioural changes noted across 51% ($n = 35$) of the lionesses treated with deslorelin. Where behavioural changes were recorded, ($n = 28$; 40%) these were as follows: Pride fragmentation ($n = 13$; 19%), lack of receptiveness (antisocial behaviour) towards males ($n = 9$; 13%), pseudo-oestrus (with and without mating behaviour; $n = 2$; 2.9%), more relaxed behaviour around vehicles ($n = 2$; 2.9%), and unspecified changes ($n = 2$;2.9%). Pseudo-oestrus was described as lionesses that initiated courtship behaviour with male lions (2 - 5 days) with or without subsequent mating behaviour. No data were available for six ($n = 6$; 9%) lionesses. There was no obvious trend related to number of successive deslorelin treatments and behavioural changes [1 treatment: 50.1% no change ($n = 25$); 2 treatments: 58.3% no change ($n = 8$); 3+ treatments: 50% no change ($n = 4$)]. Pride fragmentation was observed on two reserves that contracepted multiple lionesses with between one and five successive treatments. Treatments were not synchronised, so this may have interrupted normal reproductive synchronisation of lionesses within a pride.

A single lioness was reported as undergoing repeated phases of pseudo-oestrus six months after her second implant, which involved courtship behaviour with an adult male lion, but no mating. This was recorded every three weeks throughout one year, after which there were no further signs of oestrus or reproduction. Another lioness was observed mating after two treatments but did not conceive.

Weight gain was the primary physiological change recorded for lionesses treated with deslorelin and was reported for 24 lionesses (34.3%). Increasing the number of successive treatments increased the incidence of weight gain (Figure 5.5). ‘Excessive weight gain’ was noted in two lionesses after three and five successive implants (Figure 5.5). The only other physiological change reported was an ovarian cyst recorded in one lioness after one implant; she also gained weight.

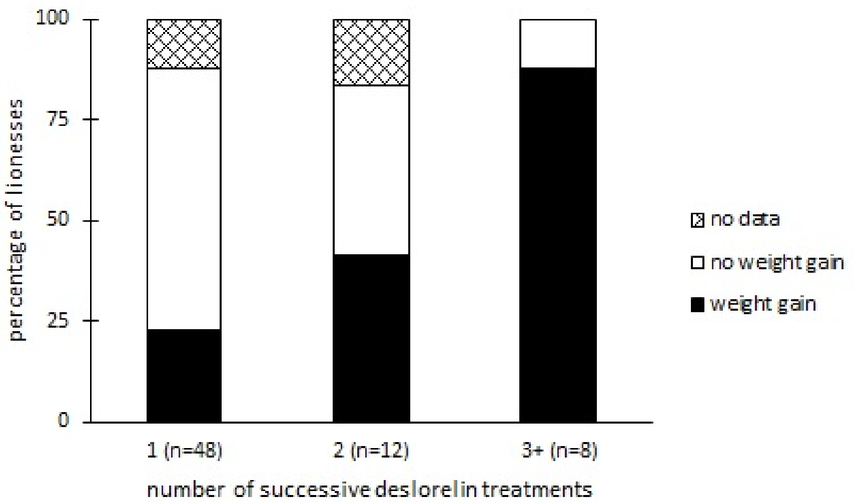

Figure 5.5. Subjective weight gain reported for lionesses following increasing number of deslorelin treatments.

There were no behavioural or physiological side-effects noted in the 14 lionesses that underwent unilateral hysterectomy and for which follow-up monitoring was possible. No clinical complications were recorded after unilateral hysterectomy, with no observations of dystocias or lost litters. Five lionesses were translocated immediately post-surgery and so lost to follow-up.

5.3.11. Costs

The average cost of treatment for a deslorelin implant between 2002 and 2016, was USD304 ± 160 (R3,300 ± R1,917, *n* = 32). The average cost of a unilateral hysterectomy between 2012 and 2015 was USD469 ± 274 (R5,552 ± R3,244, *n* = 5). These costs included all veterinary fees for each treatment, along with medication and the equipment required directly for the procedure. Direct costs from darting the animal until waking it up for both treatments, as provided by Dr Peter Caldwell in March 2018, were USD410.00 (R4,853) for a deslorelin implant and US411.00 (R4,867) for unilateral hysterectomy.

5.4. DISCUSSION

5.4.1. Deslorelin

All doses of deslorelin implant had an impact on reproductive rates in lionesses. The duration of efficacy of one implant was highly variable and the average was longer than the 30 months previously reported by Bertschinger and Sills (2013). Most of our data were from 9.4mg implants, and there was a general trend for shorter duration of efficacies associated with the 2 x 4.7mg and 3 x 4.7mg implants, supporting preliminary data in Bertschinger and Sills (2013) which suggested that 9.4mg implants resulted in longer duration of efficacies than 2 x 4.7mg implants.

While there was no specific age effect relating to the duration of efficacy for any deslorelin treatments, no lionesses in our study which were first treated after the age of 10 years had reproduced post-implant, indicating an increased time to return to normal reproductive activity in older lionesses. Successive implants, not surprisingly, resulted in increased duration of efficacy (more details below). Deslorelin did not appear to affect the pregnancy outcome of lionesses already pregnant when deslorelin implants were inserted. This is encouraging (although based on a very small sample size) as, ethically, managers do not want to cause abortions through implantation. Cub survival was not affected by deslorelin treatment. Behavioural changes were noted in less than half the lionesses treated with deslorelin, regardless of the number of treatments. These changes were subjective and based on observations and reporting of the survey respondents, and so must be interpreted with caution. The behaviours of concern to managers were pride fragmentation and changes in behaviour relating to pride males (unresponsiveness and pseudo-oestrus).

Managers are concerned with pride fragmentation as it disrupts natural social structure which can result in increased prey off-take by lions (e.g. Lehmann *et al.* 2008a). As only two reserves noted fragmentation of prides following deslorelin implants of multiple females, the link between deslorelin treatment and pride fragmentation is weak; however, worth exploring as it may be a real phenomenon in some cases. It is possible that the deslorelin treatments disrupted the synchronisation of related pride females' reproductive cycles as they were not applied at the same time. This could potentially increase the risk of pride fragmentation, as lionesses with new cubs have been known to split from their prides if older cubs are already present in the pride (Bertram 1975). Protection of cubs has been suggested as a primary driver of natural pride behaviour in wild lions (Packer *et al.* 1990; Ferreira and Hofmeyr 2014). If deslorelin treatment were to inhibit all reproduction from a pride over an extended period, this may reduce natural social integrity. Continued monitoring for any relationship between deslorelin treatment and pride fragmentation is recommended to determine if this phenomenon is real. Control prides, where no contraception has taken place, would also be required to determine causality.

Previous studies have indicated that male lions only groomed females during times of courtship, likely an important bonding mechanism between pride members (Rudnai, 1973). Thus, the loss of receptiveness to male lions, while an expected result of the treatment, could also contribute to pride fragmentation. More objective study of lion behaviour pre- and post-deslorelin implants is required to improve our understanding of the possible behavioural impacts of the treatment.

5.4.2. Application of deslorelin implants to mimic natural reproductive rates

More important for managers than the duration of efficacy values was the success of using deslorelin implants to mimic reproductive rates found in more open systems. Overall age of first reproduction (reported as age at parturition of litter) increased in lionesses or inter-birth intervals were lengthened by one deslorelin treatment, resulting in overall cub recruitment very similar to that observed in Kruger NP (Figure 5.6). There was, not unexpectedly, considerable variation in responses of individual lionesses as has also been observed in both African wild dogs (*Lycaon pictus*) and cheetahs (*Acinonyx jubatus*) (Bertschinger and Sills 2013).

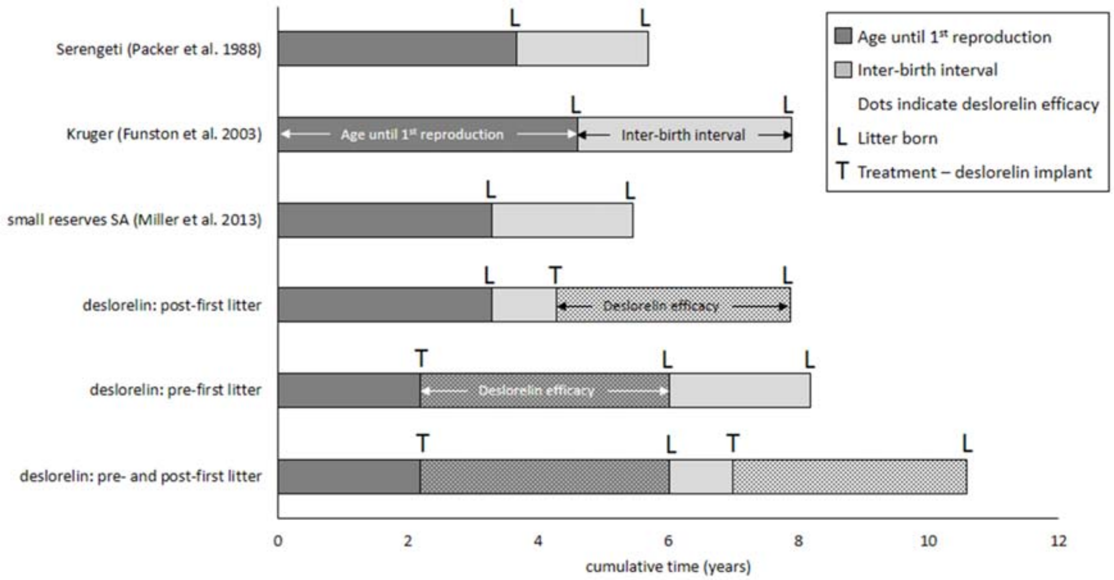

Figure 5.6. Effect of deslorelin treatment on age of first reproduction and/or inter-birth intervals of managed wild lionesses compared to open system data.

To increase the age of first reproduction, lionesses were treated at approximately 2.5 years of age. Miller and Funston (2014) reported a first litter in one 26-month-old lioness so this may not be effective in all cases. To increase inter-birth intervals, managers conservatively applied implants when existing cubs were on average 10.5 months old. The shortest inter-birth interval recorded by Miller and Funston (2014) was seven months, this was, however, an exceptionally short interval, so 10.5 months post-litter is appropriate. A surprising additional effect of the deslorelin implants was an apparent decrease in litter size. While based on a small subset of data, it was sufficiently dramatic (and based on matched-pair analysis) to warrant careful attention going forward. We do not have an explanation for this decrease in litter size. A study on the use of deslorelin in domestic cats did not find any difference in litter size post-treatment (Goericke-Pesch *et al.* 2013). Further research is required to establish the cause of the smaller litters.

Many lionesses underwent successive deslorelin treatments. Bertschinger and Sills (2013) recommended a treatment interval of 18 months for a second treatment and 24 months for successive treatments if continued contraceptive effect is required. Our study generally supports these findings, with the exception of three treated lionesses that reproduced within 19 months of their first treatment, each of which had recently undergone a change in pride structure. All other lionesses treated on a single occasion and that subsequently reproduced, produced a litter at least 2.5 years after treatment, therefore an interval of 18 to 24 months for a second successive implant would have provided ample time to prevent a further litter.

However, successive treatments of deslorelin implants (without a litter in between) are not recommended for a variety of reasons. Not only are they likely to artificially extend either the age of first reproduction or the inter-birth interval beyond that seen in more open systems, but there were increasing reports of weight gain following two or more successive treatments. We did not have enough data to determine if weight gain was more likely in lionesses that were treated, allowed to have a litter and then treated again. This requires further investigation.

Furthermore, there was some concern of permanent loss of reproductive function in older lionesses with successive treatments. Lionesses (without any deslorelin treatment) have been known to successfully raise cubs even at age 16 (Miller *et al.* 2013) and so it is possible that successive deslorelin treatments were responsible for the apparent sterility of some of these lionesses. However, it is likely that these lionesses have become naturally infertile as fecundity in lions decreases with age (Packer *et al.* 1998).

Due to concerns surrounding potential side-effects and also ethical concerns that lionesses be allowed to reproduce, and not contracepted for their entire reproductive life, lionesses should be allowed to reproduce at least once between deslorelin treatments. A staggered, or rotational, approach could be applied to reduce overall reproductive output of lionesses on a reserve and still allow all lionesses the chance to reproduce (Kettles and Slotow 2009). A similar approach has been successfully applied to elephants (*Loxodonta africana*) on small reserves in South Africa (Druce *et al.* 2011; Delsink *et al.* 2013). If managers are unable to control their lion population growth while still allowing their females to reproduce (at a reduced rate), they may need to reconsider the number of lionesses they are maintaining on their property. To this end, we recommend that managers make use of the population simulation model GrowLS (Miller *et al.* 2015). GrowLS is a simple, R-based model that can be used to simulate population growth rates with varying numbers of adult lionesses and assist managers with population planning (Miller *et al.* 2015). In the unlikely event that managers have a shortage of cubs, deslorelin implants can be removed and, at least in younger lionesses, a quick return to oestrus was observed. Bertschinger and Sills (2013) reported a similar reversibility following the removal of an implant 12 months post-implantation.

5.4.3 Unilateral hysterectomy surgery

A study on wild lions in Kruger NP found that average ovulation rates matched average implantation rates (embryos and foetuses) (Smuts *et al.* 1978) indicating that when conception was successful, all oocytes released by the ovaries were fertilised. Having left both ovaries intact, to prevent over-stimulation of the connected ovary, and reduced the implantation area by removal of one uterine horn, we therefore expected an approximate 50 percent reduction in the number of released oocytes and hence litter sizes following the unilateral hysterectomy surgery. We did not see this magnitude of effect, but rather a general trend for a slight reduction (20% smaller litters), with minimal statistical support. Thus, the remaining connected ovary must be producing more oocytes than normal. Similar results were seen in pigs and rabbits, however in these studies the ovary was removed along with the uterine horn and the resulting ovarian hypertrophy could be explained by this removal (Fenton *et al.* 1970; Webel and Dziuk 1974; Christenson *et al.* 1987; Blasco *et al.* 1994). We do not have an explanation for our results. Further investigation is required.

Regardless of the mechanism behind the slight reduction in litter size, our results most closely mimic average litter sizes in the Serengeti NP (Schaller 1972; Bertram 1975; Packer and Pusey 1995). This is smaller than the average in other lion populations which were: three to four cubs in 83% of litters (up to 1 year) observed in the Kruger NP (Smuts *et al.* 1978); three cubs in both Nairobi NP (Rudnai 1973), in captive populations (Bertschinger and Schulman 2013) and across South African small reserves (Miller and Funston 2014). Bertschinger and Schulman (2013) reported a slightly higher litter size (3.30 cubs) in South Africa.

All of the surgeries, except two, were performed by the same wildlife veterinarian using the same approach as outlined in the introduction. Since his pioneering work, other veterinarians within South Africa have tried a different approach to unilateral hysterectomy surgery. This modified approach involves removing the whole uterine horn, including the ovary, instead of just a portion of the horn, leaving the ovary intact as was done in the majority of cases reported on in this study (*pers. comm*. Dr Peter Caldwell). Further monitoring is required to determine if this second approach is more successful than the one reported on here.

A potential effect of smaller litter sizes is increased abandonment of litters by lionesses due to small litter size. Limited recorded evidence in open systems indicates that lionesses are more likely to abandon litters of a single cub rather than raise them in order to try again for another litter and optimise energy expenditure and reproductive output (Rudnai 1973; Packer and Pusey

1984). However, ten out of 13 single cub litters in managed wild populations included in Miller and Funston (2014) survived to at least one year of age suggesting that survival of small litter sizes may not be as big a concern in the managed wild lion populations.

5.4.4. Costs of treatments

Survey results suggested that deslorelin treatments were cheaper than unilateral hysterectomies. However, the level of variation was very high, presumably due to costs such as travel time and veterinary fees (some veterinarians performed procedures at reduced rates). Furthermore, the cost for a single deslorelin treatment was estimated using data that spanned several years, and inflation may well have influenced these data. A direct comparison in March 2018 from one experienced wildlife veterinarian revealed that the two procedures have almost identical costs.

5.4.5. Comparison of treatments and implications

Deslorelin implants were effective in reducing the reproductive output of managed wild lionesses through increasing age of first reproduction or increasing inter-birth interval. However, there were some undesirable side-effects in some individuals and an unexpected decrease in litter size. Unilateral hysterectomy surgery was less effective, resulting in only a slight decline in litter size, but with no noted side effects. Thus, based on our study, deslorelin treatment was more effective than the unilateral hysterectomy surgery in reducing cub recruitment to levels seen in open systems.

However, if the outcome of more recent unilateral hysterectomy surgeries results in a more dramatic decrease the litter size, it does have several benefits over deslorelin treatment. It does not have any impact on the number of litters born to a lioness, and thus there will be more litters on a reserve at any given time, which may improve pride cohesion this is thought to be linked to the protection of cubs (Packer *et al.* 1990; Ferreira and Hofmeyr 2014) and may be a tourism benefit. However, surveys have shown that tourists, especially international ones, favour adult males over prides with cubs (Di Minin *et al.* 2013), so it is possible that tourism would not suffer as much as managers think it might with a decline in the number of cubs. Another advantage of unilateral hysterectomy surgery is that there were no reported side-effects.

A potential drawback to unilateral hysterectomy surgery compared to deslorelin implants is that it is more invasive and requires an experienced veterinarian to perform it. Lionesses do, however, seem to recover quickly (Miller *et al.* 2013). The cost of the two procedures appears to be very similar. Deslorelin may need to be repeated within the lifetime of a lioness and if it were, would likely be more expensive than surgery. Currently, neither technique can be considered a 'silver bullet' for controlling population growth in managed wild lion populations. Managers must trade-off the risks and benefits of each approach when planning management interventions. Given the current decline of lion populations throughout much of their range, these smaller, fenced populations are becoming more important in the conservation of the species (Bauer *et al.* 2015). Therefore, analysis of currently applied techniques should continue in order to enhance management of small populations of lions and maintain their conservation value.

5.5.6. Funding

This research paper forms part of a larger project assessing the management of free-roaming lions in small reserves across South Africa. OKMcE was sponsored by the National Research Foundation, SATIB Conservation Trust and the Lion Management Forum of South Africa. SMM was supported by a Clancey Trust Postdoctoral Fellowship.

Conflict of interest

The authors declare no conflicts of interest.

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SUPPLEMENTARY MATERIAL

The following is the questionnaire distributed in this study. It was distributed as an excel spreadsheet, however it has been reformatted here as a PDF document.

Fertility-Control Programmes:

The Lion Management Forum (LiMF) is developing guidelines to assist with lion reproductive management. The goal of this survey is to accumulate knowledge on current fertility-control programmes in use across the country. The long term goal is to combine our collective knowledge to develop comprehensive guidelines for all managers to use. Participation in this process is completely voluntary. Please see separate sheets for each treatment type relative to your reserve: 1. Chemical-Deslorelin (this sheet), 2. Unilateral tube-tying (2nd sheet) and 3. Complete Sterilization (3rd sheet)

The information collected in this survey will only be accessible to LiMF members and will be used for LiMF planning and research purposes only. Any other use will only be approved with consent from individual participants.

Please fill in one column for each lioness on your reserve that has been treated - see example

Note that highlighted cells are automatically filled in by sheet and such cells have been formatted for relative data.

1. Chemical - Deslorelin implants

	Example
Reserve	AENP
Lioness ID	Aardlam
Date of birth	Jan-02
Age at first contraception	8.52
How many litters prior to contraception?	?
Date of last known litter (mmm-yy)	Feb-09

Size of last known litter	?
Date of implant (mmm-yy)	Jul-10
Effective period	2.07
How many times has this female been contracepted?	2
Date of first implantation	Jul-10
Date of follow up implantation (if applicable)	Nov-12
Date of follow up implantation (if applicable)	N/A
Date of first mating post-contraception (if applicable)	N/A
Date of first litter after contraception (if applicable)	Aug-12
How many litters post-contraception? (if applicable)	0
Size of first litter post-contraception (if applicable)	N/A
What was cub survival post-contraception? i.e. the % that survived to 1 year (if applicable)	N/A
Any behavioural changes (e.g. lack of receptiveness to males) observed post-contraception?	None
Any physiological changes (e.g. weight gain) observed post-contraception?	Weight gain
What was the average cost per treatment? (ZAR)	
Any additional comments	First Lioness to be contracepted at Addo

2. Unilateral Tube-tying

Please fill in one column for each lioness on your reserve that has been treated.

	Example
Reserve	AENP
Lioness ID	Carem
Date of Birth (mmm-yy)	Aug-06
How many times was this female contracepted prior to surgery?	0
Age at time of surgery	6.5
How many litters prior to surgery?	1
Date of last known litter	Mar-10
Size of last known litter	3
Date of surgery	Feb-13
How many uterine horns removed?	2
Date of first mating post-surgery (if applicable)	?

How many litters post-surgery? (if applicable)	none
Date of first litter after surgery (if applicable)	N/A
Size of first litter post-surgery (if applicable)	N/A
Size of subsequent litters post-surgery (if applicable)	N/A
What was cub survival post-surgery? i.e. the % that survived to 1 year (if applicable)	N/A
Any behavioural changes (e.g. lack of receptiveness to males) observed post-surgery?	increased time spent further from pride
Any physiological changes (e.g. weight gain) observed post-surgery?	none
Average cost of treatment? (ZAR)	
Any additional comments	

3. Complete sterilisation

Please fill in one column for each lioness on your reserve that has been treated.

	Example
Reserve	AENP
Lioness	L08
Date of Birth (mmm-yy)	Nov-06
How many times was this female contracepted prior to surgery?	1
Age at time of surgery	7.838356164
How many litters prior to surgery?	3
Date of last known litter (mmm-yy)	Nov-13
Size of last known litter	2
Date of surgery (mmm-yy)	Sep-14
Date of first mating post-surgery (if applicable)	none
Any litters post-surgery?	0
Date of first litter after surgery (if applicable)	NA
Size of first litter post-surgery (if applicable)	NA
Size of subsequent litters post-surgery (if applicable)	NA
What was cub survival post-surgery? i.e. the % that survived to 1 year (if applicable)	NA
Any behavioural changes (e.g. lack of receptiveness to males) observed post-surgery?	Minor decrease in activity
Any physiological changes (e.g. weight gain) observed post-surgery?	none
Average cost per treatment? (ZAR)	
Any additional comments	

Table S5.1. Summary of parameters recorded, assessment and statistical testing of the data

A. For each treatment of deslorelin or unilateral hysterectomy we recorded the following:		
Treatment method, date, cost, and dose (deslorelin only)		
Lioness: ID and date of birth		
Litters: date of birth*, size*, and survival[†] of associated pre-treatment and post-treatment litters		
Anecdotal behavioural or physiological changes post-treatment (e.g. pride fragmentation, weight gain, altered reproductive behaviour)		
Veterinarian involved		
B. The following parameters were assessed following deslorelin treatments:		
Duration of efficacy:		
Parameter	Assessment	Statistics
Single treatment across differing doses	Treatment date to date of first litter	Boxplot of efficacy interval by dose (*boxplot* command in R) Kruskal-Wallis test in R v3.4.2
Reproduction post-treatment for successive treatments (1-5)	Treatment date (first treatment for successive treatments) to date of first litter post-treatment.	Average, range and standard deviation
No reproduction post-treatment for successive treatments (1-3)	Treatment date (first treatment for successive treatments) to date of animal's death, translocation or data collection.	Average, range and standard deviation
Effect of lioness age (single treatment only)	Age plotted against duration of efficacy with and without litter post-treatment.	
Age of first reproduction:		
Parameter	Assessment	Statistics
With post-treatment litter (single treatment only)	Age of lioness at time of treatment and at parturition of first litter	Average, range and standard deviation

Without post-treatment litter (single treatment only)	Age of lioness at time of treatment and at time of data collection (dead and translocated individuals not included)	Average, range and standard deviation

Inter-birth interval:

Parameter	Assessment	Statistics
With post-treatment litter (single treatment only)	Age of lioness at time of treatment Date of parturition of pre-treatment litter to date of parturition of post-treatment litter	Average, range and standard deviation
Without post-treatment litter (single treatment only)	Age of lioness at time of treatment Date of parturition of pre-treatment litter to time of data collection (dead and translocated individuals not included)	Average, range and standard deviation

C. The following parameters were assessed for both deslorelin and unilateral hysterectomy treatments:

Parameter	Assessment	Statistics
Litter size	Pair-wise comparisons between pre-treatment and post-treatment litter sizes at first sighting, restricted to lionesses with both pre- and post-treatment litters.	Generalised linear mixed model and power of analysis (see text for details)
	Comparison of all the post-unilateral hysterectomy litters to litter size data of lionesses with no history of contraception	One-sided Mann-Whitney U-test (*wilcox.test* command in R); probability cut-off of 0.01
Cub survival	Cub survival to one year of age, calculated from estimated date of birth to either confirmed death or one year of age. With and without deslorelin implant compared to control data With and without unilateral hysterectomy compared to control data	Chi-squared test of independence in R v3.4.2

Behavioural/ Physiological changes	Observed behavioural and physiological changes were categorised.	As these data were subjective and anecdotal, no statistical tests were applied to these data.
Costs	The cost (converted to USD) of each treatment was documented.	

*date of litters was estimated from the first date the litter was observed; size was based on sightings

†Percentage of cubs surviving to twelve months from the estimated date of birth.

Table S5.2. Duration of efficacy of deslorelin with increasing number of implants.

Number of consecutive deslorelin implants	**All lionesses**			**Lionesses with litter post-treatment**			**Lionesses without litter post-treatment (ongoing)**		
	n	mean	range	n	mean	range	n	mean	range
1	50	3.92 ± 1.77	1.42 – 9.34	21	3.71 ± 1.43	1.67 – 7.17	19	4.18 ± 2.05	2.25 – 9.34
2	11	6.19 ± 2.32	2.42 – 10.09	3	5.59 ± 0.67	4.92 – 6.26	4	7.47 ± 3.10	3.42 – 10 .09
3	7	6.58 ± 1.61	4.92 – 9.34	1			1	9.34	
4	1[a]	7.59							
5	1[b]	7.34					1	7.34	

	Lionesses deceased post-treatment			**Lionesses lost to follow-up post-treatment**		
	n	mean	range	n	mean	range
1	10	3.88 ± 1.98	1.42 – 7.67			
2	4	5.38 ± 2.16	2.42 – 7.26			
3	2	4.92 ± 0.01	4.92 – 4.93	3	6.95 ± 0.90	5.92 – 7.59
4				1	7.59	

[a] Treated at 6.34, 7.60, 8.91 and 10.93 years. Translocated 3 years after her last treatment and lost to follow-up.

[b] Treated at 1.75, 2.84, 4.00, 5.25 and 7.17 years. Still alive at age 14.51 years with no cubs.

n = number of lionesses; mean = mean time in years between treatment and either a litter or the last available data with standard deviation; range = range of time in years between treatment and either a litter or the last available data.

CHAPTER 6

THE SOCIAL BEHAVIOUR OF LIONS (*PANTHERA LEO*) IN SMALL, FENCED WILDLIFE RESERVES

6.1. INTRODUCTION

The drivers behind sociality in lions (*Panthera leo*) have been the subject of much research. Initial work indicated that foraging efficiency played a role in driving the fusion-fission system of lion prides (Caraco and Wolf 1975). Another benefit of sociality is food protection. Studies have demonstrated losses of 10 – 20% of food to spotted hyenas (*Crocuta crocuta*), with lions in smaller groups suffering more frequent losses (Caraco and Wolf, 1975; Cooper, 1991). Lions are known to co-operate when dealing with more dangerous prey species (Scheel and Packer, 1991). However, based on the outcomes of cost-benefit analyses from Schaller's (1972) study in the Serengeti National Park (NP), lions did not typically forage in group sizes that optimised energy intake. Lions from smaller prides often foraged in maximal group sizes and foraging group size was unrelated to prey abundance (Packer *et al.* 1990). Caraco and Wolf (1975) listed the potential benefits of sociality that might outweigh this cost. In the Serengeti NP, lionesses in a pride had better success at protecting their cubs from nomadic males and defending their territory from other prides, compared to solitary lionesses (Packer *et al.* 1990).

Lion populations in open systems (e.g. Serengeti NP) consist of several neighbouring prides and multiple adult male groups that competitively interact (Packer *et al.* 1990). As much as 17% of lion populations can consist of non-territorial males (Funston *et al.* 2003). Consequently, the leading theories behind sociality in lion prides are cub defence from infanticidal males and territory defence. Lion populations in small (<1,000 km²), fenced reserves, have restricted opportunities for immigration (Miller *et al.* 2013). In these circumstances, natural competition between unknown lions would be negligible and in turn affect natural social drivers and predator-prey dynamics (Ferreira and Hofmeyr, 2014). Social network analyses identified that keystone individuals were important for maintaining pride integrity (Abell *et al.* 2013; Dunston *et al.* 2016). Therefore, the birth, death or management of lion populations (typical of most small reserves) can impact pride dynamics.

6.1.1. Cub defence theory

Infanticide is widely documented in mammals, occurring across numerous species including primates, rodents and carnivores (Ebensperger, 1998). Potential drivers of infanticide include predation, competition for resources and avoidance of surrogate parent responsibilities (Ebensperger, 1998; Hrdy, 1979). The effect of infanticide by unknown males on offspring survival has been documented in lions (Packer and Pusey 1983a; Packer and Pusey 1983b) and other large felids including leopards (*Panthera pardus*; Balme *et al.* 2012) and tigers (*Panthera tigris*; Bhattarai and Fischer, 2014: Goodrich *et al.* 2008). This behaviour is likely driven by sexual selection, with females becoming sexually receptive shortly after the loss of dependent offspring (Ebensperger, 1998; Packer and Pusey, 1983a). During a pride take-over, all resident lion cubs below the age of ~24 months are vulnerable to infanticide, with younger cubs (≤ 13 months) often killed and older cubs dispersing from the natal territory (Bertram, 1975; Packer and Pusey, 1983b). In response to infanticide, lionesses are usually defensive against and/or evasive of the new males, followed by a prolonged period of sexual activity that is thought to be coupled with lower fertility (Packer and Pusey, 1983b). Packer and Pusey (1983b) theorised that this increased sexual activity, paired with temporary infertility, evolved in response to a lionesses' requirement to safeguard a dominant breeding coalition. Thereby, enhancing the chances of subsequent tenure and offspring survival.

Accounting for up to 27% of lion cub mortalities (Pusey and Packer, 1987), infanticide can considerably decrease cub survival rates. The oestrus cycles, and subsequent birth cycles, of pride females are naturally synchronous (Packer and Pusey, 1983a), leading to lionesses collectively rearing young cubs from above the age of four to six weeks in 'creches' (Packer *et al.* 1990; Rudnai, 1973). There are no nutritional advantages evident from lion creche formation and mothers typically forage in groups larger than those predicted by the optimal foraging theory (Packer *et al.* 1990). Cubs born to synchronous litters do, however, have higher survival rates than cubs born asynchronously (Bertram, 1975; Packer *et al.* 1990). Lionesses can recognise whether an adult male lion is unknown based on its call alone and adjust their response accordingly (McComb *et al.* 1993). Lionesses in groups of two or more are better able to defend themselves from incoming males than solitary lionesses, with lionesses in groups undergoing significantly fewer pride take-overs (Packer and Pusey, 1983b; Packer *et al.* 1990). Furthermore, the formation of creches promotes increased protection from interspecific competitors (Packer *et al.* 1990). However, Funston *et al.* (2003) demonstrated that infanticide played a negligible role in overall cub survival in the Kruger NP, with 84% of cubs surviving to 12 months. Lionesses underwent a period of approximately 12 months between tenures by territorial males, during which the pride females avoided and aggressively defended their cubs from adult males (Funston *et al.* 2003).

The evolutionary pressure for male lions to group is also significant. Grinnell and McComb (1996) found that male lions were more likely to be prepared to encounter rival lions than females. In the Serengeti NP, males in larger coalitions had higher reproductive success in terms of pride tenure age, tenure length, mating females and offspring survival than smaller coalitions (Bygott *et al.* 1979). Coalitions of four or more males were significantly more likely to sire two generations of offspring than smaller coalitions, successfully holding tenure for over four years (Bygott *et al.* 1979). Similarly, during a 10-year study in the Kruger NP, all territory acquisitions were acquired by coalitions rather than solitary males (Funston *et al.* 2003). Male lions spent less time with a pride once their sired cubs reached 6 - 12 months in age, after which they acquired additional, neighbouring prides (Funston *et al.* 2003). Therefore, the key benefits of larger coalition formation appear to be linked with the acquisition of breeding lionesses. However, in the lower lion densities of the Kgalagadi Transfrontier Park (TP), there was no significant difference in cub survival between prides with a solitary male or a coalition (Funston, 2011). Higher cub survival rates among synchronous litters supports the cub-defence hypothesis as a key social driver in lions. However, in the Serengeti NP, most small prides (2 – 4 lionesses) consistently formed maximal group sizes regardless of the presence of cubs, and nearly all prides included female members without young cubs (Packer *et al.* 1990; Mosser and Packer, 2009), indicating that there may be alternative driving forces.

6.1.2. Territory defence theory

Lion territories typically extend between 15 and 219 km^2 in the Serengeti NP (Mosser and Packer, 2008) and an average of 200 km^2 (range 50 – 320 km^2) in the Tarangire NP, Tanzania (Laizer *et al.* 2014), while home ranges of between 150 km^2 and 2,075 km^2 have been recorded in Etosha NP (Stander, 1991). In the Kgalagadi TP, lion prides maintained significantly smaller home ranges (mean = 700 km^2) in the tree-savanna compared with the dune-savanna (mean = 2,823 km^2) (Funston, 2011). Similarly, lions living within the Ngorongoro Crater, Tanzania, with a year-round food supply, had smaller territory sizes (~ 45 km^2) than their counterparts in the Serengeti NP (seasonal food supply) (Hanby *et al.* 1995). Lion territories within fenced reserves in South Africa (dominated by the Savanna Biome) have been recorded between 56 km^2 and 60 km^2 (coalitions) and 64 km^2 (pride), and as low as 27 km^2 for a solitary lioness (Hunter, 1998; Lehmann *et al.* 2008a). The home range size of pride within a fenced reserve dominated by the drier Succulent-Karoo Biome was 146 km^2, with a core area of 19.6 km^2 (Vorster, 2011). Both male and female lions actively defend their territories through vocalisations, olfactory cues and tactile confrontations (Estes, 1997; Grinnell *et al.* 2002). Olfactory cues include scent-marking (spraying urine backwards onto an object) (Schaller, 1972) and scuffing (scraping the ground 2 – 30 times) (Estes, 1997). Male lions actively patrol and scent-mark their territories, whereas lionesses most often exhibit these behaviours after intra and interspecific confrontations and during times of increased sexual activity (Estes, 1997). Male lions have been known to inflict serious injury to lionesses (Mosser and Packer, 2009) but they have been theorised to provide extra strength that can support a positive outcome from inter-pride encounters (Mosser and Packer, 2009).

Resident lions are often forced to the limits of their territory during periods of prey scarcity, increasing the risk of encountering unknown lions (Mosser and Packer, 2009). During territorial encounters, lions can assess the number of individuals in a rival group from their vocalisation and gauge their response accordingly (McComb *et al.* 1994). Lions are less likely to approach larger, rival lion groups (McComb *et al.* 1994). Heinsohn (1997) found that lions in the densely populated Ngorongoro Crater were more likely to approach larger, rival groups than their counterparts in the Serengeti. The readiness to counter incursions was linked with the difficulty in maintaining territories in the more densely populated region (Heinsohn, 1997). Lions in Serengeti NP have been documented to encounter rival lions on average once every five days, with larger lion groups ousting smaller ones in over 50% of encounters (Packer *et al.* 1990). Such encounters can inflict fatal wounds and reduce overall lioness fitness (Mosser and Packer, 2009). In Serengeti NP, larger prides (≥ 4 lionesses) maintained higher quality habitats than smaller prides, in terms of prey abundance, vegetation and other resources (Mosser and Packer, 2009). Larger prides also had higher levels of reproductive success and lower levels of lioness mortality (Mosser and Packer, 2009). Lioness reproductive success reduced, and injury level increased with an increasing number of adult neighbours, demonstrating intraspecific competition (Mosser and Packer, 2009). Furthermore, lionesses from smaller prides (2 – 4 lionesses) that were surrounded by more neighbours were less often sighted alone than their counterparts with fewer neighbours and therefore had a lower risk of encountering a rival on their own (Packer *et al.* 1990). Heinsohn and Packer (1995) demonstrated the complex co-operative behaviour of lion prides in response to territorial conflict. Individuals utilise knowledge from past encounters to judge the reliability of other pride members and gauge their response accordingly. However, pride size and territory size have not been positively associated across all habitat types (Mosser and Packer, 2009; Spong, 2002). Further empirical evidence is required to differentiate the magnitude of cub and territory defence as the social drivers in lions.

6.1.3. Lion behaviour in small, fenced reserves

Many small, fenced reserves with reintroduced lions face challenges regarding genetic integrity, disease and population growth (Chapter 4; Druce *et al.* 2004a; Miller *et al.* 2013). Limited by space, many fenced reserves have lion populations consisting of one pride and one adult male/coalition. Therefore, all lions are “known” to one another and the natural mechanisms of population limitations collapse (Ferreira and Hofmeyr 2014; Miller and Funston, 2014). Without the motivation to protect territories from neighbouring prides (Mosser and Packer, 2009) or cubs from infanticidal males (Packer *et al.* 1990), I hypothesised that pride integrity in small, fenced reserves would be reduced. Solitary lions are effective hunters (Caraco and Wolf 1975), therefore, reduced cohesion among pride members can increase predation and degrade natural predator-prey dynamics in fenced reserves (Ferreira and Hofmeyr 2014). Prey availability naturally fluctuates throughout the wet/dry seasons across small, fenced reserves in South Africa (Druce *et al.* 2004b; Lehmann *et al.* 2008b). However, prey abundances remain generally high year-round (Lehmann *et al.* 2008c; Miller and Funston, 2014). The abundance of prey would reduce the need for lions to venture outside of their core territories and the risk of encountering rivals (*sensu* Heinsohn, 1997). However, intraspecific competition for the highest value territories in densely-populated areas should be intense when rival groups are present (Mosser and Packer, 2009).

6.1.4. Research hypotheses

The primary objective of this chapter was to investigate the grouping behaviour of resident lion prides in small, fenced reserves and assess the primary drivers thereof. Grouping behaviour was assessed in response to i) neighbouring prides and ii) unknown adult males in order to better protect territories and cubs. The range of fenced reserves across South Africa, with variable lion population structures, provided a unique “natural laboratory” to study this effect on lion social behaviour. I predicted that in reserves that contained a single resident pride, the drivers to protect a territory would degrade and lionesses would be less likely to group together than in reserves that contained unknown resident prides. I also predicted that in reserves that contained no unknown adult males, the drivers to protect cubs would degrade and that lionesses would be less likely to group together than in reserves that contained unknown adult males.

6.2. METHODS

Data were collected from October 2015 to March 2017 and originated from 18 reserves across seven provinces in South Africa. The reserves were categorized based on their resident lion populations (Table 6.2.1). Prides were defined as groups of lionesses (≥ 3 years) that were maternally related (*n* = 26 prides), unrelated lionesses that had been bonded (*n* = 1 pride) (Killian and Bothma, 2003) or solitary females (with offspring) that maintained a territory (*n* = 8 lionesses). Fragmented prides were defined as prides that had stayed separate for ≥ 5 years since a pride fissure/dispersal (VanderWaal *et al.* 2009). For populations that fluctuated during the study period, the reserve categorisations were adjusted accordingly. For example, if the number of coalitions was reduced to a single male/coalition, the population category was changed to either A or B respectively. The lion populations were either managed wild lions (see Funston and Levendal, 2015) within small, fenced reserves (Table 6.2.1), or wild lions within the Associated Private Nature Reserves (APNR), adjoining the Kruger NP (Table 6.2.1).

Table 6.2.1. Criteria used to categorize participating reserves according to their overall lion population structure at the time of study.

Reserve lion population structure	Population category
One pride, one adult male coalition	A
More than one pride, one adult male coalition	B
More than one pride and more than one adult male coalition	C
Wild lion population ^{*APNR}	D

6.2.1. Lion monitoring

I established a lion monitoring system whereby information was recorded every time lions were sighted by trained research volunteers. Research volunteer teams included staff already established on study reserves and who collected data during their daily schedule. I personally trained participating volunteers on data collection methods. I carried out a pilot period of four weeks (September 2015) at a single reserve whereby a team collected data at lion sightings (*n* = 34). The data entry sheet then was re-structured and streamlined for ease of use. Some information [i.e. distances (metres) between the lions and bearing (degrees) of the lion group from the observer] were removed after this trail-run as they were superfluous. Pen and paper were the selected collection method, being the most feasible across study reserves. For standardization, research volunteers were provided with a "Step by step guide" for data collection (see Appendix I). A key component of data collection was to record the lions that were sighted together (≤ 100 metres). The frequency of certain lion behaviours; greet, social lick, play, as described by Schaller (1972) and mate, fight, scent/scrape, as described by Estes (1997), were also recorded through a simple "check-box" system (see Appendix I and II). The behaviours greet, social lick and play have been identified as important indicators of natural cohesion in lion prides (Schaller, 1972). The time at the beginning and end of each sighting were recorded. All data were emailed to myself at four to eight-week intervals by reserve participants. I transcribed these data into Microsoft Excel (MS Excel 365 ProPlus), and hard-copies were retained by each reserve for later collection and storage. Historical and 'in-house' data from reliable databases held by some reserves were also collected when available and later combined for components of the analyses (see below). This dataset included a total of 1,424 additional sightings across 10 reserves from 2010 to 2017.

6.2.2. Social experiment

In addition to the sightings data, I also carried out a social test at some of my study reserves (*n* = 7) to evaluate my predictions of lion grouping behaviour in response to simulated, unknown lions. Collectively, these reserves had eight prides varying in size from two (*n* = 6) to three adult females (*n* = 2) and an additional pride consisting of one adult lioness and two subadult lionesses (> 2 years). Most reserves contained a single resident adult male (*n* = 5) and the remianing reserves contained a coalition of two males (*n* = 1) and two solitary resident males (*n* = 1). I played recorded territorial calls (playbacks) of unknown lions through four connected-loudspeakers amplified by a Sony GT530 amp in the vicinity of the resident lion prides (+/- 200m, as measured by a Garmin GPSMAP® 62s) (see McComb *et al.* 1994). I obtained the calls from the Lion Research Centre, University of Minnesota (*pers. comm.* Natalia Borrego) that were a) males lions and b) female lions. The aim was to test for a difference in social response of resident prides to recorded calls of a) unknown male lions and b) unknown female lions. The calls included a coalition of two males and two separate lionesses. I used computer software (iMovie) to edit the lion calls and created a chorus of two lionesses. Two lions per chorus were selected to maintain the simulated lion group as equal to or smaller in size to the response group. This was to avoid an overtly evasive response in tested prides due to numerical disadvantage (McComb *et al.* 1994). I designated each pride to undergo a call of both sexes (male and female) at a minimum of four-week intervals between test dates. Due to practical restrictions, six prides each underwent a call of a single sex, with random selection (stratified according to male/female call) assigning sex.

6.2.2. i) Experimental protocol

I adapted field procedural protocols from McComb *et al.* (1993) and McComb *et al.* (1994). The calls lasted 60 (male) and 55 (female) seconds. I edited them to repeat on a playback (1 hour) with a five-minute interval (empty noise) between calls. This provided freedom to monitor the resident lions from a research vehicle, without returning to the sound station. The sound station was set up approximately one hour before sunset, with the speakers erected on a three-metre steel pole connected to a cement base. An iPod Classic (playbacks) and amp were contained within a casing discretely located at the base of the speaker. The precise location of the sound station, relative to the resident lions, was maintained as consistent as possible (~ 200 metres upwind). The location was subject to several extrinsic factors including terrain and the presence of man-made structures (e.g. fence-lines). Depending on site-specific logistical restrictions (e.g. commercial game drive hours), the playback was initiated at 30 minutes before sunset to mimic a natural territorial encounter between unknown lions (Packer *et al.* 1990; McComb *et al.* 1994). Lasting for one hour, each playback emitted 10 territorial calls of the respective treatments. The area of the test site was zoned off from other vehicles for approximately 30 minutes either side of playback to minimise anthropogenic interference. The responses of the resident lions were recorded using field notes, a Canon SX530, a GoPro and with the support of a spotlight after dark.

I recorded the following variables for each playback: all lion individuals, lion GPS location, sound station GPS location, weather (temperature, cloud cover and wind direction), moon-phase and start-time. I recorded seven direct response measurements on the initiation of each call when possible (see Supplementary Material Table S6.1). Cubs below the age of 12 months were grouped together as a group response measure. Certain behaviours were recorded by noting the time and identity of lion(s) taking part: call, growl, groom, play. Lions were passively monitored by in-house research teams over the days preceding and following playbacks for lion movements, social behaviour and irregularities.

6.2.2. ii) Test parameters

The direct response measurements allowed for a comparison of resident lioness behaviour in response to unknown a) adult males and b) adult females respectively across six social parameters (see Supplementary Material Table S6.2). The null hypothesis was that prides would not vary in the outcome of social parameters between male and female lion simulated calls respectively. With no other pride members, the two subadults lionesses were treated as adults within the pride that only had a single adult female. They were above the minimum age of first reproduction recorded within small, fenced reserves (26 months) (Miller and Funston, 2014). For standardisation, I also included the single other subadult lioness between the age of two and three years as an adult in the associated analyses. Four prides were from reserves with more than one pride, which allowed for comparison of the above parameters between populations structures (*n* = 5 treatments in reserves with a single pride and adult male).

6.2.3. Data formatting and analyses

All data were formatted using MS Excel (Microsoft Office 365 Pro Plus) and all statistical tests were carried out in RStudio (RStudio Team 2016) using R3.4.4 (R Core Team 2018).

6.2.3. i) Lioness grouping behaviour – lion monitoring

I analysed sightings recorded at five-day intervals to ensure independent sightings (Packer *et al.* 1990). For each managed wild lion pride, I calculated the total number of adult (≥ 3 years) neighbours as the count of extra-pride individuals - in terms of females, males and total. Adult males were not counted as neighbours to prides that they were known to/had sired offspring. Lion sightings were categorised according to abiotic variables: a) reserve, b) biome, c) rain season (yes/no or N/A for non-seasonal areas) and d) date. Sightings were then categorised according biotic-linked variables: a) lion population category (A – D), b) group/pride identity, c) lion identity, d) number of adults/sub-adults/cubs of different sexes e) group size f) percentage of adult females from the pride present, g) overall lion density (lions/100 km^2) and the density (lions/100 km^2) of h) adult female and i) adult male neighbours. Lion prides were also categorised according to the presence/absence of the following variables associated with at least one pride member: a) deslorelin implants, b) sterilisation, c) unilateral hysterectomy, d) cubs (≤ 12 months in age), e) cubs from 3 – 12 months in age and f) subadults (12 – 36 months). Reserve lion density (lions/100 km^2) was accurately known for all managed wild prides and was taken from an estimation based in the adjacent region of the Kruger NP (Ferreira and Funston, 2010) for wild prides (D). The number of adult neighbours was only accurately known for managed wild prides and was encoded N/A for the wild prides. Prey biomass information was obtained from the closest available census dates (see Chapter 4) and reduced to (kg/km^2) for modelling purposes. Linear mixed-effect modelling was carried out using the *lmer* command in the R programming language (R Core Team 2018). In cases for which there was no random variable, the model was structured as a linear model (R Core Team 2018). Non-significant terms were removed through backwards stepwise model simplification (Kuznetsova *et al.* 2017).

I used linear mixed modelling to analyse the percentage of pride adult females sighted together based on a series of predictors (see Supplementary Material Table S6.3). Pride identity was a repeated random variable (pseudo-replication). I then used generalised linear modelling with a binomial distribution to analyse the presence/absence of adult males with prides across population structure (A – D) and the other predictor variables (see Supplementary Material Table S6.4).

I next used Spearman's Correlation to test for a relationship between the percentage of adult lionesses sighted together across managed wild prides and the density of i) adult female, ii) adult male and iii) total adult neighbours. Following this, I used linear mixed modelling to analyse the percentage of adult lionesses sighted together in managed wild prides against a series of predictors (see Supplementary Material Table S6.5). I also used a Chi-Square test of independence, to test for a difference in associations (number of sightings) of adult lionesses either in solitary or with the pride in respect to the presence of another lion population near (< 500 metres) the reserve fence-line. Following this, I re-ran the linear model, reducing the sample to prides within reserve categories (B and C), to test for any significant differences in the model predictions for managed wild prides with previous exposure unknown lions. To specifically investigate the interaction between the presence/absence of dependent cubs and pride fragmenting behaviour, I used Chi-Square tests of independence to test for differences in associations (number of sightings) between adult lionesses i) with/without adult males and ii) with/without other pride lionesses, in the presence and absence of dependent cubs respectively. I also conducted individual Chi-Square tests analysing the above associations over various pride sizes (1 to ≥4) and within lion population categories (A – D).

To further assess fragmenting, solitary behaviour in prides, I summarised the percentage of solitary lioness sightings across the total number of sightings and pride sizes. I then used Chi-Square tests to compare the frequency of sightings of solitary lionesses, between prides in which at least one member was treated with i) deslorelin, ii) sterilisation or iii) unilateral hysterectomy treatments and untreated prides. I also calculated the percentage of sightings for which known-aged lionesses were sighted away from their pride. I categorised lionesses according to 3 – 4.9 years, 5 – 9.9 years and > 10 years of age, at the time of data collection. I then used linear modelling to analyse the percentage of sightings in which a lioness was sighted away from her pride (fragmented) across a series of predictor variables particular to each lioness (see Supplementary Material Table S6.6).

6.2.3. ii) Frequency of social interactions

I calculated the total number of social interactions (greet, lick, play) between adult lionesses and other pride members and standardised this respective to adult lioness count and the length of time (minutes) spent with each pride. This produced a social index score for each pride. I then calculated an equivalent score as a territorial index, based on the frequency of scent/scraping behaviour. I carried out a student's t test to compare social index and territorial index of lion prides across reserves with a) one pride and one adult male lion and b) multiple prides and male lions.

6.2.3. iii) Social experiment analysis

Synchronicity in response prides was calculated from the reaction (look, approach, retreat) of pride lionesses to playbacks. The response was either synchronous or asynchronous depending on whether all lionesses were observed eliciting the same response within a one-minute interval after a call. I standardised the frequency of i) behavioural responses (scent/greet) during the playbacks and ii) the number of times that a lioness approached another lion (male/female) according to number of adult lionesses and minutes of observation, to produce respective behavioural indices. Times of visibility loss were subtracted from the respective hour-long playback. I then performed statistical tests (see Supplementary Material Table S6.7) to compare lioness responses between i) reserves varying in lion population structure (reserves with one pride or reserves with more than one pride) and ii) between treatments (male / female playback)

6.3. RESULTS

Thirty-four lion prides and 143 adult lions were included in this chapter. Lion population structure varied from managed wild populations containing i) one resident pride and adult male/coalition (*n* = 9), ii) multiple prides and one resident male/coalition (*n* = 4), iii) multiple prides and male coalitions (*n* = 3) and iv) a wild lion population (*n* = 2 reserves) (see Supplementary Material Table S6.8). Managed wild lion populations consisted of 1 – 3 prides and 1 – 3 adult males/coalitions. Managed wild populations comprised 33.26 ± 16.69 % adult females, 16.86 ± 12.04 % adult males, 24.15 ± 17.42% subadults and 25.72 ± 19.32% cubs annually (see Supplementary Material Table S6.9).

6.3.1. Lion grouping behaviour

A total of 6,642 lion sightings was collected across 16 reserves (2010 – 2017; see Supplementary Material Table S6.8). The reserves were dominated by Savanna (*n* = 10), Thicket (*n* = 5) or Succulent-Karoo (*n* = 1) and included information from 94 adult lionesses across 32 prides, and 43 adult male lions. Prides varied in size from solitary lionesses (*n* = 8) to prides with up to six adult females (see Supplementary Material Table S6.10). The group size of managed wild prides fluctuated during the study period with natal subadult recruitment (*n* = 18 lionesses) and the death (*n* = 10) and translocation (*n* = 4) of adult lionesses. There was one case of subadult (LF1) immigration from a non-natal pride. LF1 (2.8 years) was often sighted with a pride consisting of a mature lioness (> 16 years) and two younger, related lionesses (4 and 2 years; same sire as LF1). The natal pride consisted of her mother and littermate sister. LF1 was also the fourth-generation offspring of the mature lionesses, whose first-generation daughter had split from the pride as a subadult, resulting in the new lineage. Eighty-five percent (n = 22) of each managed wild prides and wild prides (n = 6) had dependent offspring (0 – 2.9 years) during the study. The age of lionesses from managed wild prides varied from 3.09 to 17.43 years (7.89 ± 4.04; mode = 5.05 years). Adult male lions varied in age from 4.09 to 11.00 years (7.17 ± 1.87). Forty-four lionesses across 19 prides had either been sterilised (n = 6) or treated with deslorelin (n = 29) or unilateral hysterectomy (n = 9), including one lioness that underwent both the latter treatments. There was a total of 1,749 sightings, when reduced to a minimum of five-day intervals between sightings of each pride (1 to 6 adult lionesses) (Supplementary Material Table S6.10).

6.3.1. i) Lion grouping behaviour, pride size and population structure

Across 1,382 sightings of all prides with two or more lionesses, the percentage of adult lionesses sighted together was negatively correlated with increasing pride size (r_s = -0.40, d.f. = 1,380, $p < 0.01$). Pride size, lion population structure (A – D), prey biomass and biome were significant predictors in determining the number of adult lionesses together (see Supplementary Material Table S6.11). The model had an overall explanatory power of 53% (R^2 M = 0.16; random = pride ID and deslorelin implant).

The mean percentage of pride lionesses sighted together was highest in reserves with wild prides (D: mean = 79% ± 27.60) however this was not significantly different from other prides (see Supplementary Material Table S6.11). The probability of sighting a fragmented pride increased with increasing pride size, except for managed wild prides in reserves with more than one pride (B) (Figure 6.3.1). The sample size of larger prides (≥ 4 lionesses) was limited for population category B. Prides in reserves with a single pride and adult male (A) were generally sighted in smaller group sizes (mean = 67% ± 28.89; Figure 3.3.2) and had the steepest slope of fragmentation over increasing pride size (see Supplementary Material Table S6.11). There was less variation in the percentage of lionesses sighted together in small prides (2 – 3 lionesses) compared with larger prides (≥ 4 lionesses) (Figure 6.3.1). There was also significant variation between prides (random effect). The percentage of adult females grouped together in a single pride within the Succulent-Karoo increased with increasing prey biomass. However, it declined across prides in both the Savanna and Thicket-dominated reserves (see Supplementary Material Table S6.11).

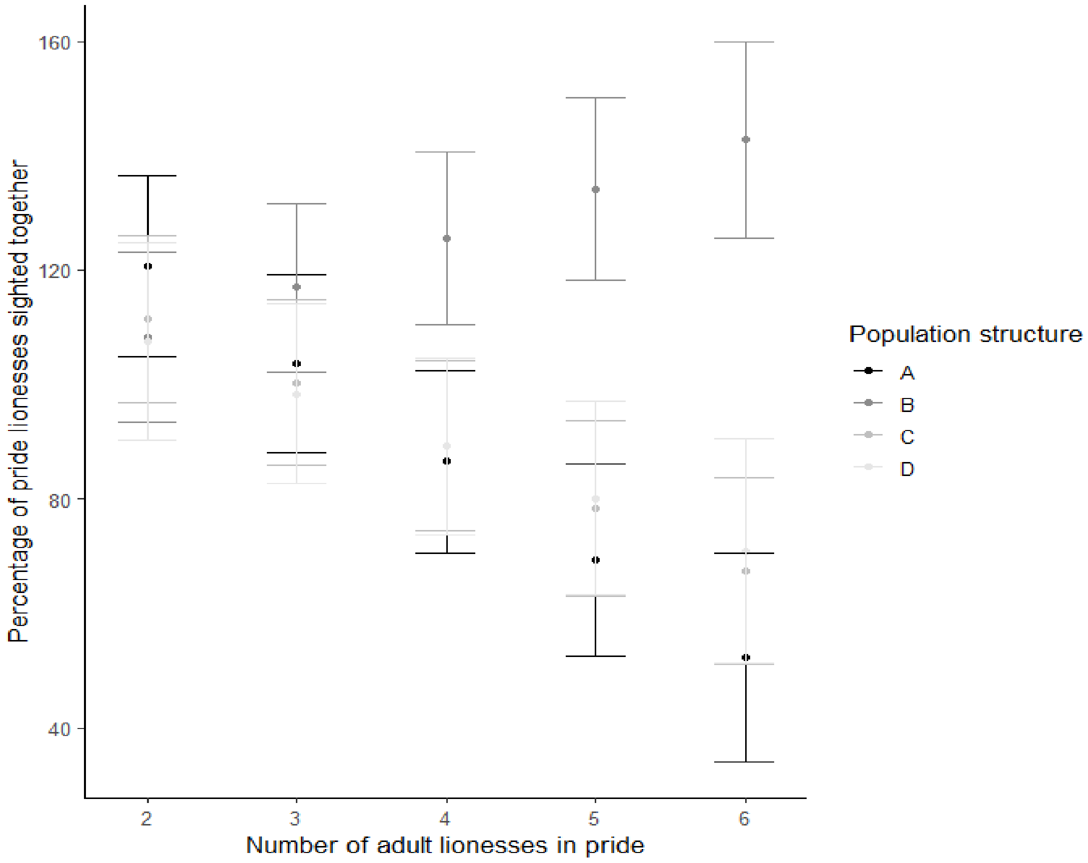

Figure 6.3.1. The interaction between pride size and lion population structure (A – D) in determining the percentage of pride lionesses sighted together.

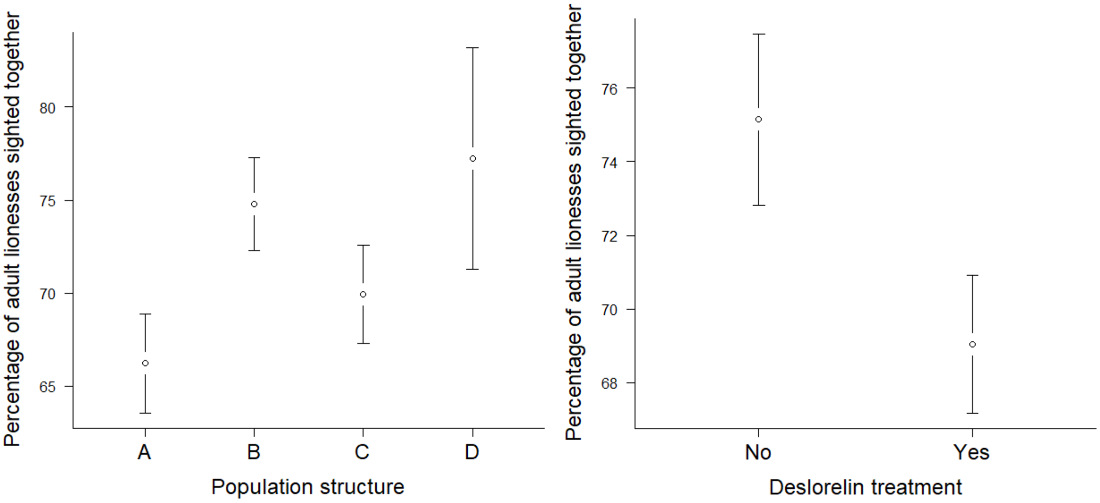

Figure 6.3.2. The mean percentage of pride lionesses sighted together across reserves with different lion population structures (LHS) and prides that varied in deslorelin treatment (RHS).

Mean group size (adult lionesses) was close to two across all prides and the modal number was lowest in larger prides (Table 6.3.1). Lion prides that had previously received deslorelin treatment were more fragmented (group mean = 69% ± 26.65, *n* = 777 sightings) than those that had never received treatment (group mean = 75% ± 29.08, *n* = 605 sightings) (Figure 6.3.2). Adult males were significantly less often sighted with prides in reserves with multiple prides and a single resident male (B) and with wild prides (D) (see Supplementary Material Table S6.12). In the same model, adult males were less often sighted with prides that had cubs across all reserves, except for wild prides, where prides with cubs were significantly more often sighted with adult males. Adult males were also less often sighted with prides in areas with higher lion densities.

Table 6.3.1. The mean and mode for group size (adult lionesses) of sightings across pride size.

Pride Composition	**Mode**	**Mean**	**SD (±)**	**Sightings (*n*)**
2 Adult females	2	1.69	0.46	476
3 Adult females	3	2.04	0.80	568
4+ Adult females	1	2.26	1.16	338

Across managed wild populations, the density (lions/100 km^2) of adult neighbours ranged from (0 – 3.18; mean = 1.23 ± 1.11) female and (0 – 1.82; mean = 0.23 ± 0.44) male lions. The percentage of lionesses from managed wild prides sighted together varied significantly with lion population structure, pride size and the density of unknown adult female neighbours (see Supplementary Material Table S6.13). Although the term was not significant, prides with young cubs (3 – 12 months) were generally more fragmented (estimate = -4.88, SE = 3.08, $p = 0.11$), except in regions with an increased density of adult female (estimate = 2.38, SE = 2.08, $p = 0.26$) and adult male (estimate = 3.07, SE = 8.29, $p = 0.71$) neighbours. Larger prides were fragmented in reserves with a single pride and adult male coalition (A), whereas larger prides were grouped in reserves with a more complex population structure (B and C). Group size increased significantly with the density of adult female neighbours (estimate = 54.42, SE = 8.57, $p < 0.001$) however, the increase was lower for larger prides (significant interaction term) (estimate = 29.13, SE = 3.31, $p < 0.001$). The fixed effects had comparatively low explanatory power ($R^2M = 0.16$; $R^2C = 0.56$). There was also no significant relationship between sightings of solitary females and the presence of a separate lion population across a shared fence line boundary ($X^2_{(1)} = 1.08$, $n = 1,297$, $p = 0.30$).

When the same linear model was limited to population categories B and C, (managed wild prides with exposure to unknown lions), grouping increased with adult female neighbour density and pride size (see Supplementary Material Table S6.14). Population category was eliminated from the model. Group size significantly increased when there was an unknown lion population resident over a closely shared (< 500 m) fence-line boundary (estimate: 24.87, SE = 10.20, $p < 0.05$). Group size decreased with increasing adult male neighbour density (estimate = -4.08, SE = 6.64, $p = 0.54$), except for prides with cubs (estimate = 0.13, SE = 6.69, $p = 0.53$). However, this term was not significant. Prides with young cubs were less likely to group (estimate = -41.41, SE = 8.48, $p < 0.05$), but the positive relationship between grouping and adult female neighbour density was significantly higher for prides with young cubs (estimate = 48.16, SE = 3.61, $p < 0.01$).

6.3.1. ii) Lion grouping and dependent offspring

Across all prides (≥ two adult females), there was a significant increase in sightings of solitary lionesses when the pride had resident cubs (< 12 months) ($X^2_{(1)} = 21.63$, $n = 1,382$, $p < 0.01$). The same relationship was found across prides with cubs between the ages of 3 – 12 months

($X^2_{(1)} = 10.24$, $n = 1{,}382$, $p < 0.01$). The mean percentage of adult lionesses sighted together was lower for prides with cubs (60.01 ± 26.36, $n = 376$) than prides without cubs (74.25 ± 27.45, $n = 1{,}006$). Similarly, across small prides (2 adult females), lionesses were sighted without their pride conspecific more often when the pride had young cubs ($X^2_{(1)} = 4.62$, $n = 476$, $p < 0.05$). Across pride sightings (≥ two adult females), there were 533 sightings (38.6%) including at least one adult male. Prides with young cubs (3 – 12 months) were less often observed with adult male lions however, this was not significant ($X^2_{(1)} = 2.42$, $n = 1{,}382$, $p = 0.12$). This was also evident across smaller prides (2 adult females) and adult males ($X^2_{(1)} = 3.48$, $n = 476$, $p = 0.06$). Conversely, solitary adult lionesses (i.e. prides of $n = 1$ adult females) with young cubs were more often sighted with adult male lions than counterparts without cubs ($X^2_{(1)} = 26.58$, $n = 371$, $p < 0.01$) (see Supplementary Material Table S6.15 and S6.16 for Chi Square results)

In reserves with a single adult male/coalition (A and B), prides with young cubs (3 – 12 months) were both less often sighted with adult males and more often sighted in solitary than expected by chance (see Supplementary Material Tables S6.17 and S6.18). In reserves with more than one pride and male coalition (C), lionesses with young cubs were less often associated with adult males. However, there was no difference in the number of sightings of solitary females (see Supplementary Material Tables S6.17 and S6.18). In wild prides (D; smaller sample size), prides with young cubs were more often sighted with adult male lions and there was no difference in solitary pride behaviour in relation to the presence/absence of resident cubs (see Supplementary Material Tables S6.17 and S6.18).

6.3.1. iii) Solitary behaviour in lion prides

The likelihood of being sighted without other adult females was similar across pride sizes. Lionesses in prides of two, three and four adult females were sighted without other pride females during a total of 29.8%, 29.9% and 32.3% of sightings respectively. Lionesses in larger prides (5 – 6 adult females) were more often sighted without another adult pride member (60% and 44% of sightings respectively). However, the sample size was small ($n = 14$). Across managed wild populations, lion prides in which at least one member was treated with sterilisation ($X^2_{(1)} = 21.92$, $n = 1{,}245$, $p < 0.001$) or unilateral hysterectomy ($X^2_{(1)} = 37.74$, $n = 1{,}245$, $p < 0.001$) were sighted significantly less often as solitary individuals, however, there was no significant difference for prides treated with deslorelin ($X^2_{(1)} = 0.27$, $n = 1{,}245$, $p = 0.60$).

Out of 949 sightings across 13 managed wild prides ($n = 37$ lionesses) for which lioness age (range = 3.34 – 17.43 years) and identification were accurately recorded, there were 298 sightings of solitary adult lionesses (31.5%). Six lionesses from five managed wild prides ($n = 3$ reserves) were sighted without other pride females in over 50% of sightings. These lionesses were advanced in age (8 – 10 years), except for one (4.67 years). The percentage of sightings in which a lioness was sighted away from her pride was higher for lionesses with dependent cubs (< 12 months) and in areas with a higher density of adult female neighbours (see Supplementary Material Table S6.19). However, lionesses with dependent cubs in regions with a higher density of adult female neighbours were sighted significantly less often away from their pride (see Supplementary Material Table S6.19). In the same model, lionesses from 5 – 10 years in age were most frequently sighted alone, increasing the explanatory power of the model by 10% ($R^2 = 0.35$; $F_{(31,5)} = 4.82$, $p < 0.01$).

6.3.2. Social interactions

The mean level of socially interactive behaviour (greet, social lick, play) was higher in reserves with multiple prides and/or adult male lions (1.93 ± 0.67) than in reserves with a single pride and resident male(s) (1.16 ± 0.34). However, this difference was not statistically significant ($t_{(5.97)} = -2.14$, $p = 0.08$). There was also no significant difference in the mean frequency of territorial behaviours between reserves with different population structures ($t_{(5.85)} = 0.43$, $p = 0.69$) (see Supplementary Material Table S6.20).

6.3.3. Social experiment

A total of six male lion treatments and six female lion treatments were carried out across nine managed wild prides. In 83% of treatments ($n = 10$), tested lion prides advanced towards the sound station with 82% of all lions ($n = 60$) reaching within 100 metres of the sound station (half-way point). In approach, lions looked in the direction of the speaker and advanced at varying pace (slow walk to running). Forty-nine lions (66%) arrived at the sound station (< 20 metres) within 1 - 40 minutes (mean = 15 ± 0.01) (see Supplementary Material Table S6.21).

Although located through natural tracking methods and GPS/telemetry technology, there was no visual sighting of adult pride members in three simulations and these were removed from further analyses. In two such cases, pride offspring were sighted including four subadult males that reached the sound station in response to a male playback (< 1 minute; running). Two of these simulations (male treatment) took place in reserves with a single pride and adult male, and the third pride (female treatment) had new-born cubs. Prides with cubs (≤ 12 months) arrived at the sound station during 50% (n = 2) of simulations, compared to prides without cubs (80%; n = 4). Cubs from the age of five months (n = 13) accompanied prides to the sound station. The only pride that retreated before reaching the sound station had cubs < 3 months in age (male treatment).

6.3.3. i) Response comparison between populations categories

Out of six simulations with isolated prides (reserves with a single pride and adult male), 76% of lion groups arrived at the sound station within 27 ± 0.01 minutes. The two lion groups that did not reach the sound station were diverted. All prides from reserves with multiple prides (and adult males) arrived at the sound station (9 ± 0.01 minutes; n = 3). There was no difference found in the synchronicity response ($X^2_{(1)} = 0.06$, n = 73, $p = 0.82$) or behavioural responses (scent: $t_{(7)} = 1.24$, $p = 0.26$; approach adult female: $t_{(7)} = 2.36$, $p = 0.64$; greet/lick/play: $t_{(2)} = 4.30$, $p = 0.72$) of pride lionesses between reserves with isolated lion populations and reserves with multiple prides (and adult male lions). Prides from both population structures were combined for further analyses.

6.3.3. ii) Response to female lion simulation

All tested prides advanced towards the speaker at the beginning of the female simulation. However, only three prides arrived at the speaker after 20 ± 0.01 minutes (3 – 40 minutes). Pride lionesses either reached the speaker at the same time, distanced 5 metres apart (n = 2 prides), or within one minute of each other (n = 1 pride). The remaining prides (n = 2) were diverted towards a) a cheetah (*Acinonyx jubatus*) in a boma or b) a small pride of lions (< 800 m of the sound station). The latter pride displayed aggression towards a group of lions that approached the other side of a nearby fence-line (enclosure within reserve containing a separate lion population), 55 minutes into the simulation. The second diverted pride approached the boma after 30 minutes and remained there until the end of the simulation when they continued to the sound station. During this time, the lions, in particular the accompanying adult male, aggressively stalked the cheetah through the fence. There was an accompanying adult male during three female call simulations (n = 2 diverted). The time after the diversion was removed from further analyses. The remaining adult male reached the sound station before pride females, eight minutes after the first playback (11 minutes before females). Two of three prides with cubs (≤ 12 months) arrived at the station while the third pride was diverted. One out of two prides without dependent cubs reached the site of the speaker.

6.3.3. iii) Response to male lion simulation

During the male simulations, 75% of prides arrived at the sound station (< 20 m) within 36 minutes (19 ± 0.01 minutes). The remaining pride (n = 2 lionesses) had young cubs (< 3 months) and retreated from the site, however an accompanying adult male arrived at the station. A second pride with dependent cubs (~ 10 months) reached the speaker site, with accompanying offspring and an adult male. The remaining prides had no cubs. Adult lionesses from two prides arrived at the sound station grouped together (5 – 10 metres apart), while the final pride members arrived six minutes apart and were then distanced 10 – 20 metres from each other. An adult male lion accompanied the pride during all male lion simulations and reached the speaker site before (n = 2) or at the same time as the pride (n = 1) in 75% of simulations. In the final simulation, the adult male stayed at roughly 40 metres away from the speaker site (no dependent offspring).

6.3.3. iv) Response comparison between simulations

Eight-five percent of lionesses arrived at the sound station during female treatments and 71% during male (see Supplementary Material Table S6.22). Adult males arrived at the sound station more frequently in response to male playbacks (75%) than female playbacks (50%). Lionesses responded more synchronously (but not significantly) in response to the female treatment than the male treatment (X^2 (1) = 2.47, n = 73, p = 0.12) (Figure 6.3.3). Pride lionesses also approached other adult females ($t_{(7)}$ = 1.24, p = 0.26) and scented more frequently ($t_{(7)}$ = 1.83, p = 0.17) during the female call simulations than the male call simulations (see Supplementary Material Table S6.23). Lionesses were also distanced closer together at the end of the female treatments (distance score: 1.80 ± 0.78) compared to the male treatment (distance score: 2.5 ± 1.29). Pride lionesses approached adult males more often (but not significantly) during male treatments than female (t(4) = 1.83, *p* = 0.84).

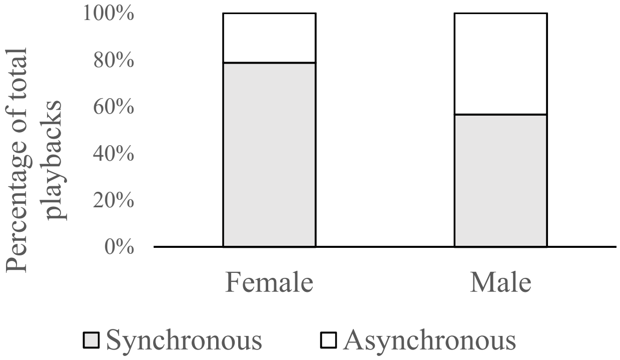

Figure 6.3.3. The percentage of female and male simulated calls during which adult lionesses responded either synchronously or asynchronously respectively.

6.4. DISCUSSION

6.4.1. The drivers of social behaviour in managed wild lions

There were significant differences in the patterns of grouping and social behaviour between prides resident in reserves with different lion population structures. The key factors affecting lioness grouping behaviour were overall lion population structure (A – D), the density of adult female neighbours, pride size and the presence of dependent cubs. Prides in which at least one member was treated with deslorelin were less likely to group and there was also a degree of variation associated with pride identity. Mean foraging group size (1.69 – 2.26 adult lionesses) was slightly smaller than prides in the Kgalagadi (2.4) (Funston, 2011), and was similar with increasing pride size. The pattern of solitary behaviour (~ 30% of sightings) was similar across smaller prides (≤ 3 lionesses). Reflecting previous work (Mosser and Packer, 2009), the likelihood of sighting a female away from her pride increased as pride size increased (≥ 4 lionesses). This indicates that fission-fusion among pride lionesses was not too dissimilar from open systems. However, adult lionesses were sighted more often in larger groups in reserves that contained more complex population structures. Lionesses in reserves with more than one pride and a single resident adult male showed higher levels of cohesion than in reserves with a single pride and adult male/coalition. Wild lions in the APNR were sighted in the largest groups, supporting the underlying theory of degraded social-ecological conditions in managed wild prides.

The current data included a pride consisting of two surgically sterilised lionesses, resident in a reserve with a second pride and a single resident adult male (offspring to a sterilised lionesses). The two lionesses were consistently sighted together and formed part of the population that was most cohesive (B). Similarly, there was a naturally sterile lioness on another reserve. The sterile lioness was colloquially called “Aunty” by staff members within the reserve, due to the vigilant care she was observed baring to her littermate’s offspring throughout their lifespan. The lioness was also consistently sighted with her pride, forming part of the more cohesive lion population (B). Although the sample size was low, this indicates alternative drivers for grouping, rather than the defence of cubs alone (Mosser and Packer, 2009; Packer *et al.* 1990).

Larger prides were generally more fragmented however, larger prides (≥ 4 lionesses) formed more substantial groups in reserves with more than one pride and a single resident adult male (B). With no competition from unknown males, this indicates that the motivation to group was likely territory defence from other prides (Mosser and Packer 2009; Packer *et al.* 1990). Although prides with cubs (3 – 12 months) were generally more fragmented, larger prides in regions with adult female neighbours formed larger groups when the pride had resident cubs. Furthermore, lionesses with dependent cubs were less often sighted away from the pride as the density of adult female neighbours increased. These patterns indicate that the presence of dependent cubs added value to the territory and intensified competition between prides (McComb *et al.* 1994; Mosser and Packer, 2009). Consequently, in regions with a lower density of female neighbours, prides with young cubs were generally more fragmented. Lionesses with higher quality territories have been associated with a higher reproductive success and better resource accessibility, driving the observed intraspecific competition (Mosser and Packer, 2009; Mosser *et al.* 2009).

Although the difference was not statistically significant, results from the social interactions database and social test also indicated that resident lionesses responded more cohesively in response to unknown lion prides compared to unknown males. By comparison, prides with a resident male present interacted more with adult males during the male simulations than the female simulations. This reflects the important role that resident males play in the direct protection of territories from other adult males, which in turn likely protects cubs (Bygott *et al.* 1979). In my study, prides with cubs were more often sighted without resident males however, solitary lionesses with young cubs were more often grouped with resident males. This further indicates that the driver is likely to protect cubs and/or a higher value territory when resident cubs were present, with numbers providing a competitive advantage (Bygott *et al.* 1979; Packer *et al.* 1990; Funston *et al.* 2003). Notably, most reserves had one to two resident adult males/coalitions, and only one reserve had a higher male coalition to pride-group ratio. With nearly 20% of wild lion populations consisting of nomadic males (Funston *et al.* 2003), the level of competition from males was probably limited in managed wild prides, the effect of which was therefore underrepresented compared to wild populations. This likely affected lioness grouping, similar to Mosser and Packer (2009) who found that lioness group size increased with increasing number of adult male neighbours in the Serengeti NP.

Although the sample size was small, wild prides with young cubs in the APNR (D), were sighted significantly more often with adult males than prides without cubs, reflecting previous findings from the Kruger NP (Funston *et al.* 2003). Adult males would search for other mating opportunities and leave the pride after their sired cubs had reached 6 – 12 months of age and were less vulnerable to infanticide (Funston *et al.* 2003). However, managed wild prides (B and C) with cubs were generally sighted less often with resident males. In reserves with more than one pride and a single adult male lion (B), the absence of competition from unknown males may have driven resident males to spend less time with prides that had cubs (in search of the other available mating opportunities). With the ratio of male groups to prides lower in most reserves that had more than one pride and resident male (C), the motivation for resident males to protect cubs from roaming males was likely also reduced in these reserves. The absence of male protection in reserves with reduced competition between males, emphasises their important role in tenure retention in systems with high, natural levels of opposition from unknown males (Bygott *et al.* 1979).

There are several possible drivers for the fragmentation observed in prides with cubs, the first of which relates to reproductive synchronicity. Lionesses are less likely to introduce their cubs to prides that already have potentially dangerous, older-aged dependent offspring (Packer *et al.* 1990; Rudnai, 1973). The use of contraception may have reduced the natural levels of reproductive synchronicity among prides (see Chapter 5). For example, even if deslorelin implants are applied synchronously, the variability in response between lionesses would likely reduce synchronicity (see Chapter 5). Prides in which at least one member was treated with deslorelin formed smaller groups than untreated prides. However, individual lionesses that were treated with deslorelin were not more often sighted alone. This supports disruption to oestrus synchrony as the possible driver for reduced cohesion in response to deslorelin, rather than a direct response to the treatment itself. Lionesses that had dependent cubs did not exhibit the same fissuring behaviour in reserves with more than one pride and adult male/coalition (C) or in wild prides (D), both of which had unknown adult males. Although this indicates that the motivation to group with other pride females was probably to protect cubs from infanticidal males (Packer and Pusey, 1983b), the relatedness of individuals likely also played an important role. The closer paternal/maternal relation between some prides may have reduced infanticidal threat, and the subsequent drivers to group when with young cubs however, there is no conclusive evidence for this.

Another factor that likely played an important role in driving competition between unknown prides relates to accessibility of available resources. Most reserves with population B category were dominated by the Thicket Biome, whereas the majority with a population C category were dominated by Savanna. Lions preferentially occupy habitats with higher prey availability, which is often linked with the proximity to water and habitat type (Spong, 2002). Open grasslands can sustain larger herds of prey species (Spong, 2002). In small, fenced reserves dominated by the Thicket Biome, lions have preferentially selected more open habitats associated with the lesser represented Savanna Biome and disturbed lands (O'Brien, 2012). With the Thicket Biome characterised by a dense layer of lower-to-medium storey vegetation, competition for access to more suitable, open hunting areas may have been more intense in these reserves.

6.4.2. The evolution of intrasexual competition between unknown lions

The relative roles of cub and territory defence as evolutionary drivers were less direct than originally hypothesised. My data support the idea that a primary driver behind sociality among resident females was intrasexual competition for territories or resources between prides (Mosser and Packer, 2009). The overall level of competition from unknown males was low in most reserves however, cub survival was significantly lower in fenced reserves with more than one resident male/coalition (see Chapter 4). Resource or territory competition would have been heightened for a species reliant on a migrating prey base, with lions more likely to encounter unknown lions when outside the confines of their territory (Mosser and Packer, 2009). Larger group sizes would therefore increase competitive advantage and subsequent survival (Packer *et al.* 1990). Male lions have been documented to group with other males in response to intrasexual competition with roaming, unknown males, for tenure acquisition and reproductive output (Bygott *et al.* 1979). Therefore, it is not surprising to document similar intrasexual competition between unknown lionesses. In my study, lionesses appeared most reliant on the protection of adult males in respect to adult male competition.

Intrasexual competition has been recorded in other social, territorial carnivores, including mongooses (Muller and Manser, 2008) and jackals (Estes, 1997). Leopards, phylogenetically close to lions (Wei *et al.* 2011), exhibit higher levels of intrasexual competition than intersexual competition through territory overlap (Fattebert *et al.* 2016; Marker and Dickman, 2005). There have been similar reports for other *Panthera* species (Azevedo and Murray, 2007; Simcharoen *et al.* 2014). The primary driver behind social grouping can also shift over time depending on circumstances, for example a lioness with young cubs may be more motivated to defensively protect her cubs from incoming lions rather than offensively protect her territory. In previous research, lionesses with cubs were more likely to approach unknown prides (McComb *et al.* 1994; Spong and Creel, 2004). This indicates that territory protection may be heightened when prides have resident cubs, outweighing the more immediate danger to the cubs posed by the invading lions. In my study, the only females that retreated from the test area without approaching further than 50 metres had very young (~ 2 months) cubs and a pride with a new litter did not react.

6.4.3. Social test

There were no significant differences found in the response to the simulation between "naïve" lions in reserves with no other unknown lions, and lions that were resident in reserves with unknown neighbours. This may have been due to limited data and should be further tested by increasing sample sizes. However, lions in reserves with more than one pride reached the sound station within a shorter average timeframe than lions in reserves with a single pride. This reflects work by Heinsohn (1997) whereby, driven by increased intraspecific competition, lions in the more densely populated region of the Ngorongoro Crater responded more readily to unknown lions than in the Serengeti NP. Furthermore, managed wild prides with exposure to intraspecific competition were significantly more likely to group in reserves with an unknown lion population present over a shared fence-line boundary. However, there was no significant effect when isolated prides were included in the model. The response rate of lions in terms of the number of playbacks that resulted in an approach towards the speaker reflected previous work with wild prides (McComb *et al.* 1994; Spong and Creel, 2004).

McComb *et al.* (1994) found that lionesses in the Serengeti, would retreat from unknown adult male playbacks, with cubs over the age of four months, and would stand their ground if they had younger cubs. In my experiment, lionesses that had two-month-old cubs retreated in response to unknown males. However, a resident adult male was present and challenged the simulated incursion. When present, male lions generally reached the speaker before, or at the same times as the lionesses. This reflects work by Grinnell and McComb (1996), in which males more readily countered rival lions, irrespective of group number, compared to lionesses. The readiness to challenge rival lions by resident males reflects their important role in territorial disputes between prides when present during conflicts (Mosser and Packer, 2009). Older subadults (2 – 3 years) also readily approached the sound station, approaching before older pride members during two out of three playbacks for which they were present. McComb *et al.* (1994) showed that lion prides with subadults were more likely to challenge threats from unknown lion prides. Proposed drivers include linkages with territory quality, as with resident cubs (McComb *et al.* 1994). Given the readiness of subadults to interact with simulated unknown lions, these individuals may constitute smaller, less experienced pride members that nonetheless provide increased group strength when it comes to territorial conflicts (McComb *et al.* 1994).

In my study, a coalition of four subadult males were the fastest group to respond, in response to a coalition of two adult males. Their mothers had no other dependent offspring and did not respond. This was another intrasexual response that was likely not directly related to cub protection as the young subadults did not have any offspring with the pride. Without vulnerable offspring, it appeared that the pride lionesses were not motivated to respond themselves. These young males also temporarily took possession of the pride and evicted their sire for approximately six weeks subsequent to the test, therefore intraspecific competition between males in this reserve was likely significantly increased. To further investigate whether the motivation to protect territory can outweigh the motivation to protect young cubs from direct competition, follow-up treatments could be carried out on prides with cubs below the age of two months.

6.4.4. Study limitations and future perspective

An important factor not analysed in my study was female dispersal and pride formation, due to subadult removal (see Chapter 4). There were no new prides formed during the study period, with most prides formed within 10 years of population establishment. There was a pride of four lionesses that was significantly fragmented, and the lionesses were sighted without other adult females in 75% of sightings. The pride (littermates) had been introduced within three years prior to the onset of the study period and there were no unknown lions on the reserve. The single lioness that was recorded immigrating to a non-natal pride, was from a reserve with a single resident adult male (B). The pride that accepted the young subadult, contained an older lioness (> 18 years), that died shortly after the study period and two paternally related, younger lionesses. The immigrant was also the fifth-generation daughter of the older lioness. With a larger pride of three lionesses also on the reserve, increased competition between prides may have driven the pride switch, coupled with increased relatedness between individuals. There were at least two cases whereby dispersing subadult lionesses did not return to their pride after the removal of their littermates. Further research should be directed towards patterns of female dispersal and pride formation, focussed on study sites with limited subadult removal and newly introduced prides. Further research should also be directed towards evaluating the effect of reproductive synchronicity on lion grouping behaviour.

Conducting a study over such a broad scale, with varying ecological conditions, has revealed some widely-applicable results. However, the reduced population of unknown male lions in manged wild prides, may have underrepresented the role of competition between prides and unknown males. Other important, more localised factors affecting lion grouping behaviour, such as terrain features and territory quality (Mosser and Packer, 2009; Mosser *et al.* 2009) could not be controlled for in my study. Lionesses with higher quality territories will form larger prides in response to competition with other prides for the high valued resources (Mosser and Packer, 2009). This may have led to some of the variation in pride cohesion observed between prides, particularly between population categories B and C. Similarly, the relative positioning of a lion within its territory affects grouping, with lions less often fragmented on territory outskirts (Mosser and Packer, 2009). The single pride within the Succulent-Karoo Biome, associated with lower prey biomass, demonstrated lower cohesion than prides residing within Savanna or Thicket dominated reserves. In times of prey scarcity, lions optimise energy intake by hunting in solitary or smaller groups (Caraco and Wolf 1975). Therefore, a reduction in intrasexual competition between unknown lions in the Succulent-Karoo likely led to lion prides foraging at a rate that was closer to optimal on this reserve. The pride, however, was also larger in size (3 – 4 adult females) and contained at least one unrelated member that had been bonded to the pride, likely confounding the effects of absent intraspecific competition.

Another important factor not analysed in my study, was the impact of interspecific competition with spotted hyenas. The effect of spotted hyenas on reducing lion energy intake has been well documented (Caraco and Wolf, 1975; Cooper 1991; Périquet *et al.* 2015). Furthermore, the formation of larger spotted hyena clans in regions with higher prey biomass can reduce lion fitness (Périquet *et al.* 2015). Only a single small, fenced reserve in the study reintroduced spotted hyenas (see Chapter 4). In open systems, spotted hyenas commonly form clans as large as 40 individuals (Holekamp *et al.* 2012). The level of competition with spotted hyenas was therefore likely underrepresented and should be an avenue of future of research.

6.4.5. Concluding remarks

The grouping behaviour among lion pride members and between prides and resident adult males varied across reserves with different lion population structures. Lioness grouping behaviour increased in regions with a higher density of unknown adult female neighbours, with both maternal and paternal relatedness between prides playing an important role. There were significant differences in the grouping behaviour of both adult males and prides with young cubs, dependent on whether there were other unknown adult males within the reserve. Further longitudinal studies should be directed to investigate the drivers of natural pride fissure and fusion events in managed wild prides, for comparison with open systems (VanderWaal *et al.* 2009).

My study supports that in the absence of competition from unknown adult males, prides formed significantly larger groups in reserves that contained unknown prides. Therefore, the driver to protect a territory from unknown prides was sufficient to drive significant changes in lion grouping behaviour in small, fenced reserves. The relative importance of competition from adult males on lioness grouping behaviour appeared to be most directly linked with the presence of dependent cubs. Furthermore, several prides consisted of non-reproductive lionesses. Competition from adult males was therefore likely a secondary driver for lioness grouping behaviour. However, the density of unknown adult males was low across most reserves, and therefore the influence of unknown males on pride behaviour was likely underrepresented. The lack of competition from unknown adult males was likely a significant factor affecting fragmentation of prides that had young cubs. The lack of competition from unknown males also likely significantly reduced the drivers for resident males to group with prides that had young cubs. Further research to evaluate lion grouping behaviour should be directed towards small, fenced reserves containing a single pride and multiple adult male groups.

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SUPPLEMENTARY MATERIAL

Table S6.1. The direct response measurements recorded at the initiation of each played call, (when visibility was available) during playbacks across varying lion age-group6.

Lion group	Response measure
All lions	- Identity and distance (metres) of the closest adult lion. Distance was estimated by the eye as either i) ≤ 1 metre, ii) 1 to 5 metres iii) 5 to 20 metres or iv) ≥ 20 metres - Time at which the sound station was reached (when applicable)
All adult lions:	- Direct reaction to playback: either i) looks in the direction of ii) approach or iii) retreat from direction of speaker - The time at which lions moved either towards or retreated from the speaker, and distance walked (metres). - Time, identity of and distance walked (metres) when a lion approached another adult lion. - Time of certain behaviours; greet (as described by Schaller, 1972) and scent-mark (as described by Estes, 1997).

All cubs (≤ 12 months): - Reaction of cubs: either i) relaxed or ii) agitated/nervous

Table S6.2. The six social parameters tested through the response measures (above) to compare between male and female lion playbacks.

No.	Social Parameter
1.	Whether the pride reached the sound station
2.	Difference in latency (lag time) of pride lionesses from the time of the first playback until mobile response (Heinsohn and Packer, 1995).
3.	Difference in latency (lag time) of pride lionesses from the time of the first playback until the speaker was reached (Mccomb *et al.* 1994; Heinsohn and Packer, 1995).
4.	The level of synchrony in response (look, approach, retreat) of pride lionesse.
5.	The number of times a lioness approached another pride female.
6.	The frequency of greeting behaviour (Spong and Creel, 2004).

Table S6.3. The biotic and abiotic predictor variables analysed (linear mixed modelling) in respect to the percentage of lionesses from a pride sighted together across all pride.

Variable
- overall lion population structure (A – D)
- pride size (number of adult lionesses)
- pride with resident cubs (3 to 12 months of age)
- pride with resident subadults (12 to 36 months of age)
- reserve lion density
- biome region
- prey biomass density (kg/1 km^2)
- random effect: pride identity
- random effect: the presence / absence of deslorelin treatment lion in pride

Table S6.4. The biotic and abiotic predictor variables analysed (generalised linear mixed modelling; binomial) in respect to the presence/absence of resident males with the pride.

Variable
- overall lion population structure (A – D)
- pride size (number of adult lionesses)
- pride with resident cubs (3 to 12 months of age)
- pride with resident subadults (12 to 36 months of age)
- reserve lion density
- random effect: the presence / absence of deslorelin treatment lion in pride

Table S6.5. The biotic and abiotic predictor variables analysed (linear mixed modelling) in respect to the percentage of pride lionesses sighted together across managed wild prides.

Variable
- overall lion population structure (A – C)
- pride size (number of adult lionesses)
- density of adult female neighbours (n lions/100 km^2)
- density of adult male neighbours (n lions/100 km^2)
- presence/absence of an “unknown” lion group over a close (< 500 metres)
- pride with resident cubs (3 – 12 months of age)
- pride with resident subadults (12 – 36 months of age)
- reserve lion density (n lions/100 km^2)
- random effect: pride identity
- random effect: the presence / absence of deslorelin treatment lion in pride
- random effect: prey biomass density (kg/1 km^2)

Table S6.6. The biotic and abiotic predictor variables analysed (linear mixed modelling) in respect to the percentage of sightings in which known-aged lionesses were sighted away from the pride.

Variable
- lion population category in reserve (A – C)

- lioness age (continuous and categorical options provided)
- pride size
- presence or absence of dependent cubs (< 12 months)
- present or absence of dependent subadults (12 – 36 months)
- density of adult female neighbours (lions/100 km^2)
- density of adult male neighbours (lions/100 km^2)
- presence or absence of deslorelin treatment
- random variable: pride identity

Table S6.7. The three statistical tests performed to compare lioness responses between i) reserves with varied lion population structure (reserves with one pride or reserves with more than one pride) and ii) between male and female lion playbacks.

Variable
- Chi-Square test of independence to analyse for associations between the
- Student's T test to compare behavioural indices of pride lionesses
- Chi-Square test of independence to analyse for associations between the

Table S6.8. Wildlife reserves participating in the current chapter (reserve number corresponds to Chapter II), lion population structure (Table 6.2.1; A – D), number of prides, lions, respective research participation, total number of lion sightings collected and the associated study period.

Reserve	Lions	Prides (*n*)	Adult ♀ (*n*)	Adult ♂ (*n*)	Subadults (*n*)	Cubs (*n*)	Total lions (*n*)	Sightings database	Interactions database	Social test	Sightings (*n*)	Start date	End date
3	A	1	2	2	-	-	4	1	0	1	265	06 10 14	22 05 16
4	A^	1	1	1	-	2	4	1	1	0	93	04 03 16	28 02 17
5	B	2	5	1	1	-	7	1	0	0	587	01 01 14	25 01 16
6	C	4	12^{+}	6^{+}	11^{+}	12^{+}	41^{+}	1	0	0	1,102	01 01 10	24 11 14
7	D	7	22	10	17	6	55	1	0	0	194	09 02 16	23 11 17
8								1	0	0	145	12 06 16	16 09 16
9	A	1	3	1	3	-	7	1	1	1	173	20 09 15	13 10 16
12	A	1	2	1	6	-	9	0	0	1	-	-	-
15	C	3	12^{+}	5^{+}	18^{+}	12^{+}	47^{+}	1	1	1	450	07 01 13	31 05 16
16	B*	2	6	2^{+}	3	5^{+}	16^{+}	1	1	0	69	10 04 16	01 01 17
17	A	1	4	3	-	8^{+}	15	1	0	0	802	07 08 14	26 04 16
19	B	3	6	1	7^{+}	10^{+}	24^{+}	1	1	1	507	14 12 15	30 10 16
20	A	1	3	2	-	-	5	1	1	0	145	07 02 16	14 02 18
21	A^	1	1	1	-	2^{+}	4	1	1	1	696	24 12 13	21 01 17
22	B	2	10	1	4^{+}	4^{+}	19^{+}	1	0	0	213	02 02 14	05 11 15
23	Cº	2	3^{+}	6^{+}	2^{+}	5^{+}	16^{+}	1	1	0	755	01 01 14	28 05 17
26	A	1	2	1	0	5	8	0	0	1	-	-	-
27	A	1	4	1	-	2	7	1	0	0	246	01 01 14	30 04 17
Total		34	98	45	72	73	288^{+}	16	8	7	6,442	01 01 10	23 11 17

^ Female population consisted of a single adult lioness (with/without dependent offspring)

* Population was comprised of a second adult male in the year before sightings recorded

º Adult lioness population included a single small pride and solitary lioness units

\+ Population fluctuated over study period including cub/subadult recruitment

Table S6.9. The mean annual proportion (%) of managed wild lion populations (*n* = 16) that were comprised of lions of different age and sex classes. Standard deviation, minimum and maximum values are also listed.

	Adult lioness (> 3 years)	**Adult lions (> 3 years)**	**Subadult (12 – 36 months)**	**Cubs (< 12 months**
Mean	33.26	16.87	24.15	25.72
SD	16.69	12.04	17.42	19.32
Min	13.33	4.55	0.00	0
Max	71.43	50.00	66.67	62.50

Table S6.10. The number of lion prides and sightings recorded (at ≥ five-day intervals) across varying lion pride sizes and reserves with different lion population structures (A – D).

	Lion population structure							
	A		**B**		**C**		**D**	
Pride composition	prides (*n*)	sightings (*n*)	prides (*n*)	sightings (*n*)	prides (*n*)	sightings (*n*)	prides (*n*)	sightings (*n*)
1 Adult female	2	161	1	8	4	188	1	10
2 Adult females	1	52	5	203	8	168	1	53
3 Adult females	3	187	5	208	4	156	2	17
≥ 4 Adult females	2	210	3	26	3	87	3	15
Total		610		445		603		95

Table S6.11 Linear mixed model coefficients linked with the percentage of adult lionesses sighted together across all lion populations in relation to lion population structure (A – D), pride size, biome and prey biomass (slope) (plus random effects: Pride ID and deslorelin implant). ($R^2M = 0.16$, $R^2C = 0.53$).

Variable			**Coefficient**	
1. Lion population structure	**Intercept**	**SE**	**Increasing pride size (slope)**	**SE**
A: 1 pride & 1 male/coalition	58.68	29.45	-17.48***	3.14
B: > 1 pride & 1 male/coalition	-5.66***	15.03	8.43***	4.09
C: > 1 pride & > 1 male/coalition	38.66	13.99	-10.86	3.78
D: Wild lions	30.73	22.53	-9.19	5.84
2. Biome	**Intercept**	**SE**	**Increasing prey biomass**	**SE**
Succulent-karoo	58.68	29.45	1.22***	0.31
Savanna	139.94**	29.38	-0.08***	0.31
Thicket	119.67	42.66	-0.04***	0.36
Random effects	**SD**			
Pride ID	± 13.49			
Deslorelin treatment	± 14.34			

Table S6.12. Generalised linear mixed model coefficients associated with the presence/absence of adult males with resident prides (≥ 2 adult females) across lion population structure (A – D), the presence/absence of dependent cubs with the pride and overall lion density (lions/100 km^2), with a significant interaction between population structure and the presence/absence of cub.

Variable				
1. Lion population structure	**Coefficient**	**SE**	**z**	***p***
A: 1 pride & 1 male/coalition	0.23	0.13	1.70	0.09
- with cubs	-0.21	-0.23	-0.94	0.35
B: > 1 pride & 1 male/coalition	-0.50	0.15	-4.76	<0.001***
- with cubs	-1.01	0.48	-1.63	0.10
C: > 1 pride & > 1 male/coalition	0.23	0.21	0.04	0.97
- with cubs	-0.51	0.31	-0.94	0.35
D: Wild lions	-2.36	0.48	-5.41	<0.001***
- with cubs	3.41	0.79	4.57	<0.001***

2. Lion density	-0.03	0.01	-2.22	<0.05*

Table S6.13. Linear mixed model coefficients associated with the percentage of adult lionesses sighted together (all managed wild prides) in relation to population structure (A – C), pride size, and the density (lions/100 km^2) of adult female neighbour6.Significant interaction terms between pride size and both population structure and neighbour density were included. ($R^2M = 0.16$; $R^2C = 0.56$).

Variable	**Estimate**	**SE**	***p***
A: 1 pride & 1 male/coalition	119.89***	17.36	< 0.001***
- pride size (slope)	-17.85***	4.13	< 0.001***
B: > 1 pride & 1 male/coalition	-12.75***	21.05	< 0.001***
- pride size (slope)	40.05***	6.66	< 0.001***
C: > 1 pride & > 1 male/coalition	-36.73***	27.15	< 0.001***
- pride size (slope)	49.56***	9.77	< 0.001***
Increasing adult female neighbours (slope)	54.42***	8.57	< 0.001***
- pride size (slope)	29.13***	3.31	< 0.001***
Random effects	**SD**		
Pride ID	± 16.31		
Deslorelin treatment	± 12.34		
Prey biomass	± 4.69		

Table S6.14. Linear mixed model coefficients associated with the percentage of adult lionesses sighted together (managed wild prides; B and C), in relation to pride size, density (lions/100 km^2) of adult female neighbours, the presence/absence of i) pride cubs and ii) an unknown lion population over a shared (< 500m) fence-line. Significant interaction terms between pride size and both population structure and neighbour density were included. ($R^2M = 0.16$; $R^2C = 0.56$).

Variable	**Estimate**	**SE**	***p***
Pride without cubs (model intercept)	-20.23	19.68	< 0.34
Pride with cubs (intercept)	-41.42	8.48	< 0.05*
Unknown lions on shared fence-line (intercept)	4.64	10.20	< 0.05*
Increasing pride size (slope)	36.05	4.49	< 0.001***
Increasing adult female neighbours (slope)	38.29	5.60	< 0.001***
- pride with cubs (slope)	48.16	3.61	< 0.01**
- pride size (slope)	19.50	2.02	< 0.001***
Random effects	**SD**		
Pride ID	± 12.36		
Deslorelin treatment	± 16.17		

Table S6.15. Results from three Chi-Square tests, analysing the frequency of sightings (*n*) of all prides (of varied sizes) sighted either in solitary or with other pride members, in relation to whether the pride had resident cubs (3 – 12 months). The observed (O) and expected (E) frequencies are listed, the X^2 test statistic and the related *p*-value.

Pride size:	**1. All prides (≥ 2 adult females) ***		**2. All prides (≥ 2 adult females)**		**3. Small prides (2 adult females)**	
Sightings (*n*):	**O**	**E**	**O**	**E**	**O**	**E**
Pride with cubs						
One adult lioness	183	144.68	142	116.99	25	17.48
> one adult lioness	282	320.32	234	259.01	32	39.52
Pride without cubs						
One adult lioness	247	285.32	288	313.01	121	128.52
> one adult lioness	670	631.68	718	692.99	298	290.48
X^2	21.63		10.24		4.61	
p	< 0.001***		< 0.01**		< 0.05*	

*all cubs ≤ 12 months

Table S6.16. Results from three Chi-Square tests, analysing the frequency of sightings (*n*) of all prides (of varied sizes) in association with adult male lions, in relation to whether the pride had resident cubs (3 – 12 months). The observed (O) and expected (E) frequencies are listed, the X^2 test statistic and the related *p*-value.

Pride size:	**1. All prides (≥ 2 adult females)**		**2. Small prides (2 adult females)**		**3. Solitary lionesses**	
Sightings (*n*):	**O**	**E**	**O**	**E**	**O**	**E**
Pride with cubs						
With adult male	132	145.01	11	17.60	103	78.04
No adult male	244	230.99	46	39.40	85	109.96
Pride without cubs						
With adult male	401	387.99	136	129.40	51	75.96
No adult male	605	618.01	283	289.60	132	107.04
X^2	2.41		3.48		26.58	
p	0.12		0.06		< 0.01**	

Table S6.17 Results from Chi-Square analyses, testing the frequency of sightings (*n*) of prides sighted either in solitary or with other pride members, in relation to whether the pride had resident cubs (3 – 12 months). Four tests results are displayed, based on varied population structure (A – D). The observed (O) and expected (E) expected frequencies are listed, the X^2 test statistic and the related *p*-value.

Population:	**A**		**B**		**C**		**D**	
Sightings (*n*):	**O**	**E**	**O**	**E**	**O**	**E**	**O**	**E**
Pride with cubs								
One adult lioness	44	29	26	17	67	66	5	3
> one adult lioness	55	69	25	34	147	148	8	10
Pride without cubs								
One adult lioness	91	105	125	134	55	56	17	19
> one adult lioness	260	245	275	266	128	127	55	53
X^2	11.74		7.05		0.03		0.61	
p	< 0.001***		< 0.01**		0.87		0.43	

Table S6.18. Results from Chi-Square analyses, testing the frequency of sightings (*n*) of prides in association with adult male lions, in relation to whether the pride had resident cubs (3 – 12 months). Four tests results are displayed, based on varied population structure (A – D). The observed (O) and expected (E) frequencies are listed, the X^2 test statistic and the related *p*-value.

Population:	**A**		**B**		**C**		**D**	
Sightings (*n*):	**O**	**E**	**O**	**E**	**O**	**E**	**O**	**E**
Pride with cubs								
With adult male	46	49	7	16	70	83	9	2
No adult male	52	49	44	35	144	131	4	11
Pride without cubs								
With adult male	180	177	132	123	84	71	5	12
No adult male	171	174	268	277	99	112	67	60
X^2	0.42		7.00		6.68		26.69	
p	0.52		< 0.01**		< 0.01**		<0.001***	

Table S6.19. Linear model coefficients associated with the percentage of sightings in which individual lionesses were sighted away from the pride, according to lioness age group, whether she had dependent cubs (< 12 month) during the study period, and the density (lions/100 km^2) of adult female neighbours in the reserve. ($R^2 = 0.35$; $F_{(5,31)} = 4.82$, $p < 0.01$).

Variable	**Coefficient**	**SE**	***p***
1. Lioness age			
3 – 4.9 years	-2.54	8.93	0.78
5 – 9.9 years	13.70	8.40	0.06▪
10 + years	-5.00	9.24	0.80
2. Lioness with cubs	33.48	15.14	<0.05*
3. Density of adult female neighbours – lioness with cubs (slope)	-6.89	7.02	0.01**
4. Density of adult female neighbours: lioness without cubs (slope)	13.50	3.42	<0.001***

Table S6.20. Summary of social behaviours displayed across eight managed wild prides in six reserves that varied in lion population structure.

		Pride Composition (*n* individuals)									
Pride ID	**Lion population**	**Adult Females**	**Sub-adults**	**Cubs**	**Adult Males**	**Sightings (*n*)**	**Time (mins)**	**Greet**	**Lick**	**Play**	**Social Index**
1	A	1	2	-	1	101	2,676	8	0	14	0.82
2	A	3	3	-	1	125	3,372	53	37	26	1.15
3	A	3	-	-	1	32	1,000	24	10	11	1.50
4	B	3	4	-	1	96	3,623	62	32	21	1.06
5	B	2	2		1	42	1,323	13	25	11	1.85
6	B	3	6	1	2	18	228	2	4	14	2.92
7	B	3	2	-	1	18	531	19	8	6	2.07
8	B	2	2	-	1	13	519	14	3	1	1.73

Table S6.21. The percentage of all resident lions at the test site that arrived at the sound station (< 20 m) in response to the female and male playback treatments respectively, across different age-groups.

		Percentage of lions that arrived at sound station		
Lion	***n* lions**	**Both treatments**	**Female treatment**	**Male treatment**
All lions	75	66.22	73.81	56.25
Adult female	26	61.54	73.33	45.45
Adult male	13	50.00	40.00	57.14
Subadult	12	75.00	50.00	100.00
Cubs	24	75.00	93.75	37.50

Table S6.22. The percentage of resident lions (for which there was a visual sighting of adult pride members) that arrived at the sound station (< 20 m) in response to the female and male playback treatments respectively, across different age-groups.

		Percentage of lions that arrived at sound station		
Lion	***n* lions**	**Both treatments**	**Female treatment**	**Male treatment**
All lions	56	80.36	88.57	66.67
Adult female	20	80.00	84.62	71.43
Adult male	8	75.00	50.00	100.00
Subadult	5	100.00	100.00	100.00
Cubs	23	78.26	100.00	37.50

Table S6.23. The mean value for behavioural responses of adult lionesses during the lion playbacks (male/female treatment).

	Scent		**Approach lioness**		**Approach male lion**	
Simulation	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*
Mean index value	3.07	1.71	6.40	4.50	2.74	3.20
SD (±)	1.50	0.72	2.86	1.74	3.03	2.42

APPENDIX I

The step-by-guide that was utilised for recording lion sightings information

1. LION SIGHTINGS DATA (MONITORING SHEET

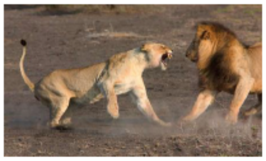
Step	Record	Notes
Step 1.	**Name**	Name of recorder (top left)
Step 2.	**Date**	Date of Lion Sighting
	Time IN	Please record Time of arrival at Lion Sighting
Step 3.	**Location**	Either GPS / Grid Square Location of Lion Sighting
Step 4.	**Dist. to Lions**	Closest distance between recorder (vehicle) and Lion
Step 5.	**Lion ID**	Please record relevant ID of lions sighted
Step 7.	**Activity**	Please record Activity of Lions – relevant to the six outlined Activities • **Sleep** – "flat cats" • **Static** – In one area but not sleeping – (often when Interactions occur, calling, grooming, mating) • **Walk** – Moving at walking pace in a general direction – "mobile" • **Stalk** – Crouched body, deliberate movements, ears flat (please record potential prey if possible) • **Run** – Rapid stride (please record potential prey or threat, if relevant and if possible) • **On Kill** – In the vicinity of a kill (not necessarily eating at time). Please record Species, Gender, Age (Adult/Sub-adult/Juv) of prey.
Step 8.	**Interactions**	Please mark box for the relevant lion(s) each time they partake in one of the behaviours outlined below. Please mark relevant box for each lion involved e.g. when greeting/mating, please mark both lions involved in interaction. For multiple behaviours, please mark each time a behaviour is observed.


GREET – Lion rubs another lion on face/neck/body with own face


SOCIAL LICK – Lion licks another lion


PLAY - Lion interacts playfully with another - often resembling play-fighting


CALL - Emitting vocalisations - territory / contact / other

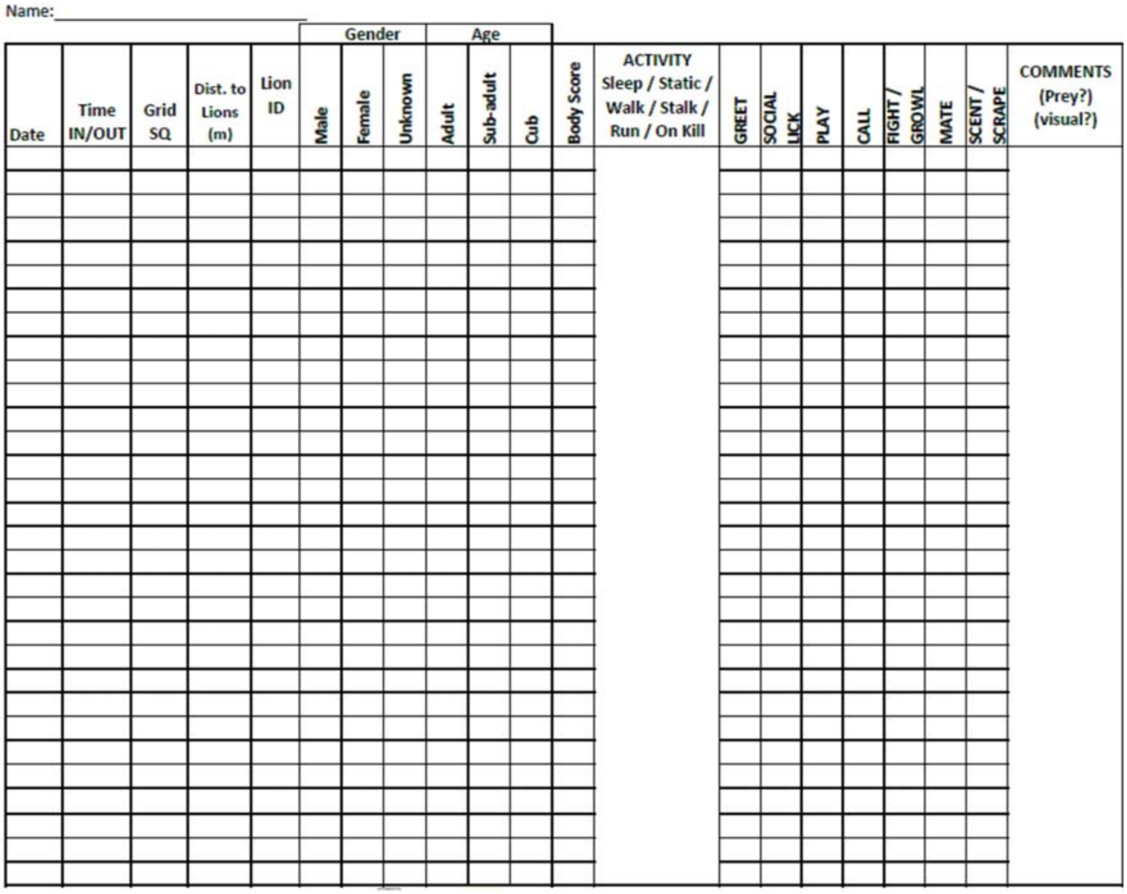

FIGHT - Aggressive behaviour - teeth bared / physical contact


MATE - Male lion mounts a lioness


SCENT/SCRAPE – Spraying urine / Scraping ground with back feet - with or without urine

Step	Record	Notes
Step 9.	**Comments**	Please record any other relevant details here. Kill data can go here (Species etc. of kills/ amount left). If visual was particularly good or poor. If lion stalking or mating was unsuccessful etc.
Step 10.	**Time OUT**	**Please record Time of departure from Lion Sighting**
Step 11.	**Complete**	Please draw a line below sighting in "Activity" and "Comments" sections on page.

A template of the data entry sheet used to record lion sightings at study reserves.



Name:__________________________

					Gender			Age												
Date	Time IN/OUT	Grid SQ	Dist. to Lions (m)	Lion ID	Male	Female	Unknown	Adult	Sub-adult	Cub	Body Score	ACTIVITY Sleep / Static / Walk / Stalk / Run / On Kill	GREET	SOCIAL LICK	PLAY	CALL	FIGHT / GROWL	MATE	SCENT / SCRAPE	COMMENTS (Prey?) (visual?)

CHAPTER 7

MANAGEMENT IMPLICATIONS FOR MANAGED WILD LION (*PANTHERA LEO*) POPULATIONS

The following chapter outlines management implications for lions (*Panthera leo*) in small (< 1,000 km^2), fenced protected areas. Deductions are based on the management of lion population dynamics, to reflect or mimic natural ecological conditions in open systems (Ferreira and Hofmeyr, 2014). This will facilitate managed wild lions as drivers of tourism and biodiversity conservation in small, fenced reserves. Intraspecific competition is a primary ecological driver of lion population dynamics and behaviour in fenced reserves. Reduced competition probably led to increased population growth rate (Chapter 4) and decreased pride cohesion (Chapter 6), which can degrade predator-prey dynamics. The best practice-tools for the management of managed wild lions currently include contraception, lion removals and introductions, while strategic regional planning is required for the long-term viability of geographically isolated populations (Miller *et al.* 2013; Miller *et al.* 2015a). Prompted by previous research (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013), the novel aspect introduced by my study is a social-ecological approach towards lion management in fenced reserves. Through mimicking or restoring natural social conditions of managed wild lion populations, reliance on mitigation measures should be reduced. A combination of management tools will be necessary for the long-term management of isolated lion populations, with population modelling (GrowLS; Miller *et al.* 2015b) and effective database management enabling more informed management decisions.

7.1. Social ecological conditions of lions in small, fenced reserves

The primary goal for small, fenced reserves was conservation and the primary objective for lion reintroduction was tourism. Lions are an important revenue-driver in terms of tourism, with tourists generally preferring to view lions in natural social groups. As apex predators, lions can also play an important ecosystem role in the regulation of prey species. However, the degraded social-ecological conditions of lion populations in small, fenced reserves can lead to fragmented lion groups which can reduce tourist experience and degrade natural predator-prey relationships. Due to increased body condition driven by minimal resource or social competition, lioness reproductive rates are also generally high in small, fenced reserves (Ferreira and Hofmeyr, 2014), leading to rapid population growth (Miller and Funston, 2014). However, in reserves with multiple prides and adult male coalitions, there was a significant reduction in the positive relationship between growth rate and lion density and prides also formed larger groups. Therefore, differences in intraspecific competition imposed by lion population structure led to differential degradation of natural vital rates and behaviour in small, fenced reserves. This necessitates the consideration of both degraded processes for the effective management of managed wild lions.

There were two primary drivers of intraspecific competition among lionesses in small, fenced reserves (territory defence and cub defence). Intraspecific competition from unknown prides had the strongest effect on pride cohesion and population growth rates in response to territory defence. Intraspecific competition from unknown adult males limited pride fragmentation for lionesses that had young cubs (≤ 12 months), in response to cub defence. With negligible competition from roaming adult males, most prides with cubs were more fragmented (unless in areas with a high density of adult female neighbours). However, the presence of unknown adult males was associated with higher cub mortalities and shorter birth intervals.

7.2. Lion management interventions

A variety of best-practice tools have been developed for the management of lion vital rates and dispersal schedules that are aimed to restore or mimic the natural social-ecological conditions of lion populations in open systems. Generally proactive management interventions that address causal mechanisms are preferable to reactive management interventions that address an excess of lions (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013; see Table 7.2). Dependent on reserve area, biomass and management objectives, it will not be feasible in all circumstances to maintain multiple prides and territorial and non-territorial males, to closely reflect the natural social-ecological conditions of lions in more open systems. Management protocols can therefore be adapted to focus on specific vital rates and social outcomes to mimic these conditions. Interventions are each associated with inherent advantages, disadvantages and risks that are weighed against other management objectives.

7.2.1. Fertility control

Across all managed wild prides, birth intervals were shorter than in the Kruger National Park (NP) (Funston *et al.* 2003) and cub recruitment higher than in the Serengeti NP (Bertram, 1975) and other open systems (Funston, 2011; Rudnai, 1973). Lioness age of first reproduction across managed wild prides was similar to the Serengeti NP (Bertram, 1975), and was older than in the high-density lion populations in Nairobi NP (Rudnai, 1973). Furthermore, in population modelling, the extension of lioness age of first reproduction had minimal population level effects (Miller *et al.* 2015b). In the current study, a single deslorelin treatment extended birth interval to closer reflect the Kruger NP and reduced subsequent litter size (mimicking reduced recruitment). However, this treatment was associated with variability in response among lionesses, and higher doses associated with extended infertility. Unilateral hysterectomy reduced litter size however, the reduction was not consistent with the reduced cub recruitment observed in the Serengeti or Nairobi NPs (Rudnai, 1973; Bertram, 1975). In managed wild prides across reserves with higher natural cub mortality (presence of unknown males: 80%) and/or longer birth intervals (presence of unknown prides: ~2 years), the reduction in litter size induced by unilateral hysterectomy may more closely mimic natural cub recruitment.

The use of contraception was associated with a reduction in annual population growth (Chapters 4 and 5; see Table 7.2). In population modelling simulations, the use of both contraceptive techniques (deslorelin implants and unilateral hysterectomy) concurrently resulted in undesirably reduced population-level effects (Miller *et al.* 2015b; Chapter 5). However, the use of either deslorelin implants to increase birth intervals or unilateral hysterectomy to reduce litter sizes both resulted in almost a 50% reduction in population size over 20 years, and a significant reduction in lion offtake (Miller *et al.* 2015a). In addition, the confounding effect of deslorelin treatment on litter size would augment the modelled reduction associated with this treatment. It is therefore not advisable to increase all birth intervals over an extended period (reflecting both treatments in GrowLS model). This would also reduce the likelihood of potential side-effects associated with repeated treatments of deslorelin implants. Conversely, the reduction in litter size from unilateral hysterectomy was not 50% and will therefore not achieve the litter size reduction modelled in GrowLS. Increasing age of first reproduction (deslorelin) may provide a more important management option for reserves with a single resident adult male to prevent inbreeding among subadult lionesses and an additional option for reserves with high lion densities. Sterilisation and deslorelin could both potentially be utilised be mimic younger age of last reproduction however, these were not analysed in my study. Due to the ethical considerations associated with fertility control, the potential outcomes must be weighed against other reserve management objectives.

7.2.2. Pride population structure

Reserves with a single pride had the highest annual lion population growth rates (λ) ~ roughly double compared to reserves with more than one pride (Table 7.1) (Chapter 4). Lion population growth increased at a higher rate, relative to lion density (lions/100 km^2), in reserves with one pride and overall population growth was higher in reserves that initiated with a single founder pride, regardless of pride fissuring over subsequent years. This was primarily driven by shorter birth intervals, augmented by a minimally lower mortality rate (~ 3 years). Therefore, both reproductive vital rates were suitable to management through contraceptive techniques (Chapter 5). Natural mortality across all age-groups was lowest in reserves with a single pride. Pride cohesion was also lowest in reserves with a single pride and larger prides were more fragmented. Being opportunistic hunters (Caraco and Wolf, 1975; Hayward and Kerley, 2005), this indicates fragmented functional feeding groups. Subadult lioness emigration has been highest in regions with higher cub survival (Pusey and Packer, 1987), therefore it can be expected that dispersal and potential for pride formation will be highest in reserves with a single pride and adult male. With prides most often sighted in groups of two adult females, the effect of reduced competition on pride cohesion was heightened in larger prides (Chapter 6). Lionesses with young cubs were generally more often sighted away from other pride members, except in areas with an increasing number of unknown adult female and male neighbours (Chapter 6). Disruption to reproductive synchronicity (e.g. driven by contraception treatment) and other factors that affect pride integrity might further confound this effect in isolated prides.

While annual population growth rate was lower in reserves with more than one pride, birth intervals were over one year shorter than wild prides in the Kruger NP (Funston *et al.* 2003) and cub recruitment was more than double that of the Serengeti NP (Bertram, 1975). Cub survival was also similar between reserves with one or multiple prides. Therefore, both vital rates were again suitable for manipulation through contraception schedules (Chapter 5). As a result of reduced population growth, a lower proportion of the lioness population would require contraception in reserves with more than one pride, to maintain a comparable reduction in population growth, dependent on reserve management objectives. With the presence of cubs further increasing pride cohesion only in regions with comparatively high intraspecific competition, increasing pride-birth interval to closer reflect the Kruger NP should not significantly degrade pride integrity. In circumstances when individuals from a pride are to be selected for deslorelin treatment to minimise effects on pride integrity, treatments can be directed towards non-keystone individuals (Abell *et al.* 2013; Dunston *et al.* 2016) and timed appropriately with reproductive cycles. The timing of unilateral hysterectomy procedures would also require planning to minimise disruption to synchronous oestrus cycles.

Pride lionesses were generally more cohesive in reserves with more than one pride, and larger prides were also more often found in larger group sizes, increasing functional feeding group size. Pride cohesion generally increased with increasing density of adult female neighbours, particularly when the pride had resident cubs. Lionesses from 5 – 10 years in age displayed the highest level of fragmenting behaviour across all reserves, and most adult lionesses that escaped from reserves were also within this age-group. The relatedness between prides also played an important role with an increase in both maternal and paternal relatedness reducing intraspecific competition.

7.2.3. Adult male population structure

The presence of territorial males was associated with several important effects. Adult lion mortality was highest in reserves with multiple prides and adult males. Cub survival was also significantly lower (~10%) in reserves that contained unknown adult males. This may reduce reliance on management measures to reduce cub recruitment. However, the presence of unknown adult males was also associated with reduced lioness birth intervals (after previous litter was raised to 12 months), an increase in birth rate and the ratio of male cubs born. As a result, reserves with a single pride and multiple adult males were modelled with a marginally higher population growth rate than reserves containing a single pride and resident male/coalition. Therefore, birth interval is an appropriate management target to reduce population growth in reserves containing more than one territorial adult male/coalition. Conversely, in reserves containing a single resident male, management interventions to limit cub recruitment (litter size, survival) will likely be an important limiting factor. Males were generally more grouped with prides in reserves that contained a single pride compared to wild prides, likely due to the lack of alternative breeding opportunities and territorial drivers. However, resident males associated less with managed wild prides that had young cubs, (except for solitary females). This lack of cub defence behaviour is indicative of reduced competition between unknown males, with resident males likely leaving the pride in search of other available mating opportunities. Prides with young cubs were more fragmented in reserves with no unknown adult males however, this same pattern was not observed in reserves with more than one resident adult male/coalition. Therefore, similar to female neighbours, a higher proportion of unknown males would likely counteract the reduction in cohesion generally observed among prides with cubs.

Table 7.1. Mean values for lioness age of first reproduction (years), birth interval (years), cub survival (%), lioness survival to three years (%) and annual lion population growth rate (λ) across reserves varying in lion population structure. The sample size for each estimate are indicated in parentheses. The general level of cohesion recorded between pride females (♀ / ♀) and between prides and resident males (♀ / ♂) are also indicated.

	Single lion pride	**> One lion pride**
Single resident male/coalition	First birth: 3.67; 1.76–6.01 $^{(25)}$ Birth interval: 1.77; 1–2.5 $^{(23)}$ Cub survival: 94.69 $^{(64)}$ ♀ survival to 3 years: 80 $^{(41)}$ $\lambda = 1.23$ $^{(66)}$ ♀ / ♀ cohesion: Low ♀ / ♂ cohesion: High	First birth: 3.17; 2.58–3.84 $^{(12)}$ Birth interval: 1.77; 1–2.5 $^{(25)}$ Cub survival: 93.12 $^{(40)}$ ♀ survival to 3 years: 90 $^{(33)}$ $\lambda = 1.13$ $^{(40)}$ ♀ / ♀ cohesion: High ♀ / ♂ cohesion: Low
> One resident male/coalition	First birth: 3.28; 2.67–4.34 $^{(10)}$ Birth interval: 1.64; 0.84–2.17 $^{(10)}$ Cub survival: 83.25 $^{(19)}$ ♀ survival to 3 years:100 $^{(9)}$ $\lambda = 1.35$ $^{(12)}$ ♀ / ♀ cohesion: - ♀ / ♂ cohesion: -	First birth: 3.22; 1.83-5.50 $^{(46)}$ Birth interval: 1.78; 0.67–3.58 $^{(64)}$ Cub survival: 82.22 $^{(115)}$ ♀ survival to 3 years:73 $^{(65)}$ $\lambda = 1.07$ $^{(65)}$ ♀ / ♀ cohesion: High ♀ / ♂ cohesion: High

7.2.4. Lion removals and introductions

Required to prevent inbreeding, lion removals and introductions (Chapter 4; see Table 7.2) can be utilised to mimic natural emigration, immigration (and tenure turn-over) and mortality rates in open systems (Chapter 4; Ferreira and Hofmeyr, 2014). Lion removals can mimic the natural dispersal of both male and female subadult disperser groups and the death of older individuals (Ferreira and Hofmeyr, 2014). There are likely circumstances for which lion removal is also required to mimic lower cub survival (Ferreira and Hofmeyr, 2014). Dependent on lion population structure and the relative use of fertility control measures, the reliance on reactive measures will be reduced. However, Ferreira and Hofmeyr (2014) caution that the disruption to energetic requirements imposed by a reduction in the number of dependent offspring may impede natural pride formation. The introduction of lions can mimic natural immigration and gene flow (Ferreira and Hofmeyr, 2014; Miller *et al.* 2015a). In terms of male lions, introductions can also lead to pride take-over and higher levels of mortality through infanticide (Ferreira and Hofmeyr, 2014; Miller *et al.* 2013; Chapter 4).

The introduction of adult males did not result in high levels of pride take-over and natural infanticide. Adult males that carried out infanticide were above the age of 3.5 years, and the respective cubs were below the age of six months. This included a delayed pride take-over, carried out almost one year after introduction. Furthermore, during two out of three male introductions that resulted in infanticide, the previous resident adult males were removed. In order to mimic natural tenure turn-over in fenced reserves with a limited adult male population, it is therefore recommended to introduce older adult males (> 3.5 years) at four-year maximum intervals, or younger adult males (2.5 – 3.5 years) at least one year in advance to scheduled turn-over (Ferreira and Hofmeyr, 2014; see Table 7.2). An increase in the number of resident adult male coalitions will likely drive more natural tenure turn-over and social competition between males and between prides with young cubs and unknown males. There were minimal cases ($n = 3$) of lioness introductions into established populations. Ferreira and Hofmeyr (2014) advocate the introduction of both male and female subadult lions to reflect population dynamics in open systems and the evolutionary drivers thereof. Restoring or mimicking more natural levels of intraspecific competition in managed wild lion populations may also be associated with inherent risk, including increased lion breakouts and alterations to spatial demography and predator-prey dynamics. Thus, effective monitoring will be required to mitigate these risks and adapt management protocols as needed.

7.2.5. Lion playbacks

Playbacks of unknown lions may provide a management tool to mimic natural levels of intraspecific competition in isolated lion populations. My data indicated that lionesses responded more cohesively in response to unknown lionesses compared to unknown adult males, and conversely for adult males (Chapter 6). However, repeated simulations of unknown female lions may have an unexpected effect on resident males, for example, separation from the pride in search of other apparent breeding opportunities (Funston *et al.* 2003). The redirection of lions towards alternate sources of interference was an undesirable effect. Spong and Creel (2004) also reported two cases of prides that diverted from course during playbacks, in their case it was by hunts. Therefore, complete avoidance of external factors can likely not be achieved. However, it is not recommended to carry out playbacks with managed wild prides within at least 1 km of extrinsic, biotically-linked factors, including bomas, fence-lines and herds of game species. Further testing should verify the efficacy of this distance. Other recommendations include incorporating a sound station that is mobile, to closer mimic the movements of a lion walking in the territory. It is also likely that the number of calls per treatment can be reduced to minimise habituation. McComb *et al.* (1994) only used one or two playbacks during similar field experiments.

7.2.6. Prey biomass and manipulation

In regions with lower annual prey biomass levels (e.g. Succulent Karoo Biome), lions generally formed smaller groups than in other regions however, group size increased with prey biomass (Chapter 6). This fissure behaviour reflects optimal energy intake (Caraco and Wolf, 1975). Conversely, in regions with higher annual prey biomass levels (Savanna and Thicket dominated reserves), lion prides generally formed larger groups and group formation decreased with increasing prey biomass. Increased prey biomass may therefore exacerbate degradation to pride integrity in high biomass regions that are affected by other management processes (lion population structure, contraceptive treatment). Furthermore, across reserves in the Savanna Biome that contained a single pride, increased lion density was associated with a reduction in prey biomass. However, within reserves that contained more than one pride, increased lion density was associated with increased prey biomass.

The introduction of prey species generally did not result in population growth of introduced species over subsequent years (Chapter 4). However, most prey species that primarily reduced over time were typically non-preferred lion-prey species, that were lesser adapted to high lion densities. A high availability of typically preferred lion prey species may help to limit opportunistic selection for lesser adapted species. In reserves with smaller foraging groups (reduced pride integrity) lions may also be more likely to opportunistically select less dangerous and lesser adapted prey species. Careful consideration is required before the manipulation of prey species as changing the availability of one prey species will likely alter the relative selection of lions for another species (Louw *et al.* 2012). This might be especially important for the integrity of herding species including buffalo (Tambling *et al.* 2013). The highest level of prey supplementation was recorded in a reserve with one of the highest densities of other large carnivores. This highlights a priority area of research that should be directed towards a better understanding of interactions among carnivore guilds within fenced reserves in determining prey availability and biomass levels. Furthermore, the presence of a spotted hyena (*Crocuta crocuta*) population may be an important factor for driving pride cohesion in isolated prides, in the absence of intraspecific competition.

Table 7.2. A summary of the best-practice proactive (lighter shade) and reactive (darker shade) lion management interventions for mimicking natural social ecological conditions in small, fenced reserves.

	Social-ecological target/outcome						
Intervention	**Age at first birth**	**Litter interval**	**Litter size / cub survival**	**Emigration**	**Immigration**	**Natural old-age**	**Behavioural outcomes**
Single deslorelin treatment	Increased to approximately 6 years of age	Increased to approximately 4 to 5 years in length	Partial reduction ~ 2 to 3 cubs	-	-	Limit reproduction in older lioness (≥ 12 years)	Variability in response between lionesses - some cases of extended (> 10 years) infertility Reduced pride integrity - important to conserve synchrony
Unilateral hysterectomy	Unaffected (3.36 ±1.21 years)	Unaffected (1.97 ± 0.58)	Partial reduction ~ 2 to 3 cubs	-	-	-	None recorded - although important to conserve reproductive synchrony
Sterilisation	-	-	-	-	-	Not assessed	Not assessed
♂ introduction (adult/subadult)	Reduced in reserves with unknown prides and adult males	Reduced in reserves with unknown adult males	Cub survival reduced in reserves with unknown adult males	-	Mimic natural tenure (2 to 4 year intervals) and infanticide (cubs < 6 months) Adult males introduced older than 3.5 years are more likely to succeed - alternatively can be introduced in advance or in a larger coalition	Can increase natural mortalities of older-aged lions	Increased pride integrity for prides that have young cubs in regions with unknown adult males

♀ introduction (adult/subadult)		Increased in reserves with unknown prides	Cub survival less affected by unknown prides	-	Mimic subadult (2 to 4 years) and to a lesser extent adult immigration	Natural mortalities less affected by unknown prides	Increased pride integrity in regions with unknown prides
Cub removal (euthanasia)	-	-	Mimic reduced litter sizes	-	-	-	Not assessed - further research required to investigate effect on social integrity
Subadult removal (Metapopulation translocation / euthanasia)	-	-	-	Reduce inbreeding and mimic natural dispersal at 2 to 4 years of age	-	-	Decreased pride / coalition formation (drivers for pride integrity)
Adult removal (Metapopulation translocation / euthanasia / hunting)	-	-	-	Mimic male turn-over: Male removal to prompt tenure turn-over after male introduction (or introducing a larger coalition)	-	Mimic natural younger mortalities	Removal of keystone individuals may reduce pride integrity

7.2.7. Regional conservation planning

Endorsed by the Biodiversity Management Plan (BMP) for lions in South Africa, strategic, regional management will increase the conservation value of isolated lion populations (Funston and Levendal, 2015). In combination with other best-practise measures, translocation between linked reserves can be effective at mimicking natural lion dispersal rates across isolated populations (Ferreira and Hofmeyr, 2014; Miller *et al.* 2015a; Slotow and Hunter, 2009). This would be similar as has been done with the metapopulation approach carried out for cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*) in South Africa (Davies-Mostert *et al.* 2009; Davies-Mostert *et al.* 2015; Gusset *et al.* 2008; Lindsey *et al.* 2011) however, lions across participating reserves would be managed as socially isolated groups rather than distinct populations, according to genetic provenance and the four regional nodes across South Africa (Ferreira and Hofmeyr, 2014; Miller *et al.* 2015a). Translocations are recommended more frequently within regional nodes than across regional nodes (Miller *et al.* 2015a). However, the genetic provenance of lion populations within the four regional nodes of South Africa already contain a significant proportion of Etosha and 'mixed' subgroups, affecting translocation options (Chapter 4; Supplementary Material Table S7.1). Miller *et al.* (2015a) recommend regular monitoring of isolated populations at a molecular level to ensure genetic targets are being achieved.

Effective record-keeping and database management of lion population demographics and management interventions (Chapter 4; see Supplementary Material Table S7.2, S7.3, S7.4) will be essential for regional lion population planning and management execution. Although record-keeping has generally been extensive, high reproductive rates and population densities of a relatively cryptic species can lead to shortfalls. It is recommended for reserves to maintain a standardised lion population database, that can be updated on an event-by event basis (e.g. management interventions, births, mortalities) to ensure the minimum record loss. A reduced template of this database is provided in Supplementary Material Table S7.2. The ongoing database will facilitate the completion of an in-house, annual lion management report (see Supplementary Material Table S7.3) and an annual lion audit (see Supplementary Material Table S7.4) that includes translocation objectives. Based on reserve translocation objectives (Chapter 4) and lion recruitment rate, reserve translocation requirements could be submitted by individual reserves to the Lion Management Forum of South Africa (LiMF) initially on a 6 – 12 month basis, for communication to members. The LiMF can support through the analyses of the translocation requirements and facilitating best-practise decision-making options based on reserve population structure, regional node, genetic make-up and disease control (Chapter 4) to reflect natural immigration and emigration rates in open systems (Ferreira and Hofmeyr, 2104). All lions above the age of 12 months could be included in the analysis on reserve translocation objectives, in order to enhance time management and translocation options. Reserves that are seeking lions (less frequent) and urgent removal requests can be dealt with on an *ad hoc* basis, with the up-to-date lion audit and translocation database providing support. The LiMF has already sought a similar approach, however, the above measures provide a systematic option combined with less time-consuming admin and advance planning options to support decision-making. It is recommended to process and evaluate the translocation database every six months for the first year, after which the frequency can likely be reduced to annually.

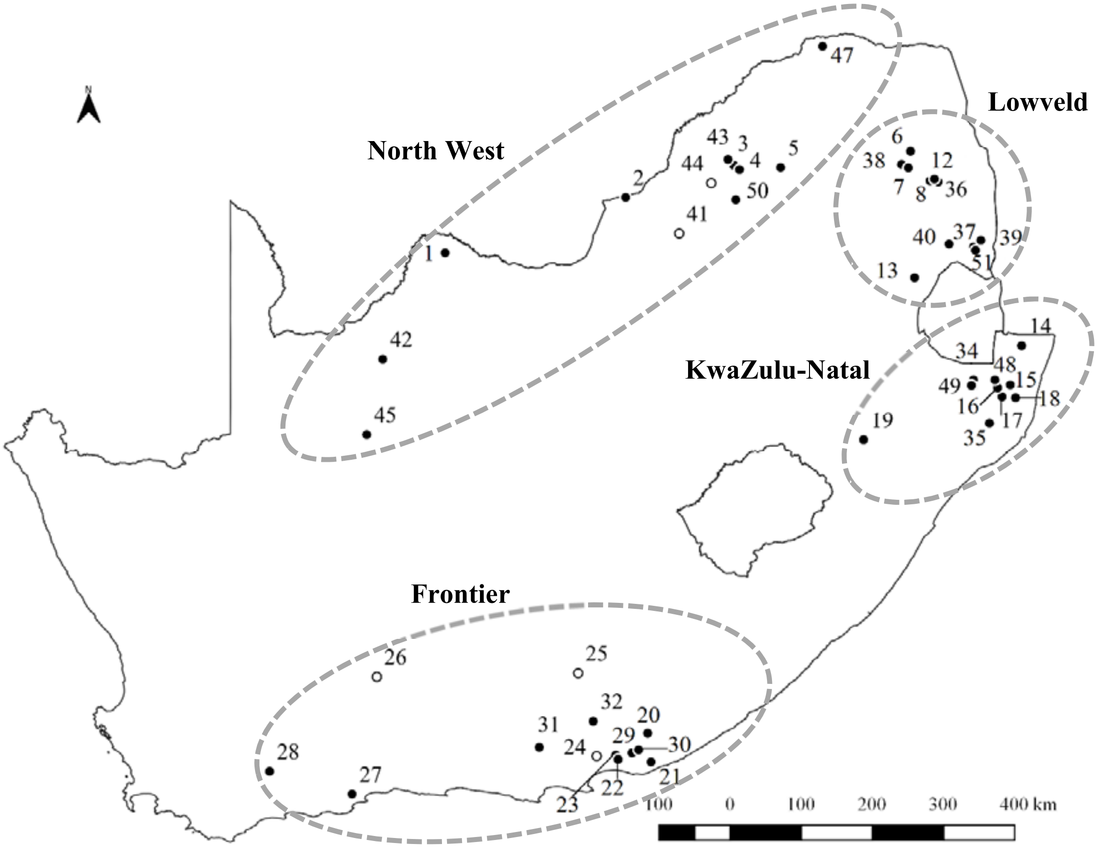


Figure 7.1. The 48 managed wild lion populations in small (< 1,000 km^2), fenced reserves across four regional nodes across in South Africa. The closed circles represent private and provincial reserves and the open circles represent national parks. The numbering corresponds to Supplementary Material Table S7.1.

7.3. Final remarks

Tourism was the lead driving factor for the reintroduction of lion populations (Chapter 4). Tourists generally showed preference for larger pride groups that included a pride of lionesses, cubs and male coalitions (Chapter 3). Therefore, fragmented lion groups and extended periods of infertility may reduce tourist satisfaction. However, the level of service received while on safari was also an important factor in determining tourist experience (Chapter 3), therefore the effects on overall satisfaction were likely negligible. Degraded social-ecological conditions likely led to significant changes in lion population dynamics and natural behaviour in small, fenced reserves (Chapters 4 and 6). Lions in fenced reserves that contained more unknown prides and adult male lions had lower reproductive output and population growth, compared to reserves with a limited lion population structure (Chapter 4). My study suggests that an increased number of unknown prides extended birth interval and that an increase in the number of unknown adult male coalitions decreased cub survival in small, fenced reserves. Furthermore, the number of resident prides and adult males/coalitions resident in a reserve also significantly affected the grouping behaviour and thereby foraging group size of lions (Chapter 6). In the absence of competition from unknown adult males, lionesses formed significantly larger groups, likely in response to competitive prides (Chapter 6). However, prides with cubs were often fragmented and adult males were less often sighted with prides that had young cubs, likely due to reduced competition from unknown males (Chapter 6). This supports the theory that competition from unknown lions was likely a significant evolutionary driver leading to the formation of lion groups. Intraspecific competition was highest between unknown lionesses and between unknown males respectively in small, fenced reserves.

The best-practice tools for the management of the social-ecological conditions of lions in small, fenced reserves are each associated with advantages and disadvantages. Proactive measures that restore or mimic natural conditions, including fertility control and population structure management, are preferable to reactive measures that reduce an excess number of lions or increase prey biomass. Regional conservation planning that links geographically isolated lion populations through intensively managed translocations will be essential to enhance the long-term viability and conservation potential of managed wild lion populations in South Africa. My study contributes to an overall understanding of natural lion population dynamics and behaviour in small, fenced reserves and the possible evolutionary drivers thereof. In addition, how these processes interact with lion management protocols in fenced reserves and how best-practise tools can be used to restore or mimic social-ecological outcomes of lion populations in open systems.

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SUPPLEMENTARY MATERIAL

Table S7.1. The 48 managed wild lion populations in South Africa and the respective geographical region, year of reintroduction and genetic source, with subsequent introductions denoted by '/'. Updated from Miller and Funston (2014). Study reserves are listed above the dividing line and the number corresponds to Chapter 2.

No.	Reserve	Region	Reintroduced	Origin
1	Khamab Kalahari Reserve	North West	2010	Kgalagadi/Etosha
2	Madikwe GR	North West	1995	Etosha*
3	Welgevonden GR	North West	1996	Etosha
4	Shambala PGR	North West	2001	Etosha
5	Entabeni GR	North West	1998	Etosha
6	Selati GR	Lowveld	2004	Etosha/Kruger
7	Greater Makalali PGR	Lowveld	1995	Kruger†/Etosha
8	Blue Canyon Conservancy	Lowveld	2008	Etosha
12	GWLT	Lowveld	2005	Captive-born
13	Nkomazi GR	Lowveld	2009	Etosha mix
14	Tembe Elephant Park	KZN	2002	Etosha
15	uMkhuze GR	KZN	2013	Etosha
16	Manyoni PGR	KZN	2011	Kruger/Etosha Mix
17	Thanda GR	KZN	2004	Kruger/Etosha
18	Munyawana GR	KZN	1992	Kruger†/Etosha/Kgalagadi
19	Nambiti PGR	KZN	2007	Kruger/Etosha
20	Kwandwe PGR	Frontier	2001	Etosha/Kruger
21	Kariega GR	Frontier	2004	Etosha/Kruger
22	Amakhala GR	Frontier	2004	Etosha/Kgalagadi
23	Shamwari GR	Frontier	2000	Etosha
24	Addo Elephant NP	Frontier	2003	Kgalagadi*
25	Mountain Zebra NP	Frontier	2013	Kgalagadi/Etosha Mix
26	Karoo NP	Frontier	2010	Kgalagadi
27	Gondwana GR	Frontier	2009	Etosha/Kgalagadi
28	Sanbona Wildlife Reserve	Frontier	2003	Etosha/Kruger
29	Lalibela GR	Frontier	2004	Mixed

30	Pumba GR	Frontier	2004	Mixed
31	Blaauwbosch GR	Frontier	2007	Kruger/Etosha
32	Kamala GR	Frontier	2007	Etosha
33	Mkuze Falls GR	KZN	1998	Kruger
34	KwaZulu PGR	KZN	2000	Kruger/Etosha
35	Hluhluwe-iMfolozi Park	KZN	1960s/1999-2001	Etosha/Kruger
36	Kapama PGR	Lowveld	1997	Kruger†
37	Ligwalagwala GR	Lowveld	1997	Etosha
38	Karongwe PGR	Lowveld	1999	Kruger
39	Marloth Park	Lowveld	2005	Kruger†
40	Mthethomusha GR	Lowveld	2005	Kruger†
41	Pilanesberg NP	North West	1994	Etosha*
42	Tswalu Kalahari Reserve	North West	2001	Kgalagadi*
43	Ka'Ingo PGR 2005	North West	2005	Etosha/Kruger
44	Marakele NP 2005	North West	2005	Etosha/Kgalagadi*
45	Kalahari Oryx	North West	2007/2012	Kgalagadi/Etosha
46	Dinokeng PGR	North West	2011	Etosha/Kgalagadi
47	Venetia-Limpopo NR	North West	Early 1990s	Greater Mapungubwe TFCA, Botswana*
48	Zimanga GR	KZN	2016	Etosha mix
49	Amakhosi PGR	KZN	2012	Kruger/Etosha Mix
50	Madjuma Game Reserve	North West	1995	Etosha
51	Lowhills Game Reserve	Lowveld	1998	Kruger†

*From original source populations.

†From Kruger NP directly, or from neighbouring reserves that are now open with Kruger NP.

All other introductions were via another small, fenced reserve.

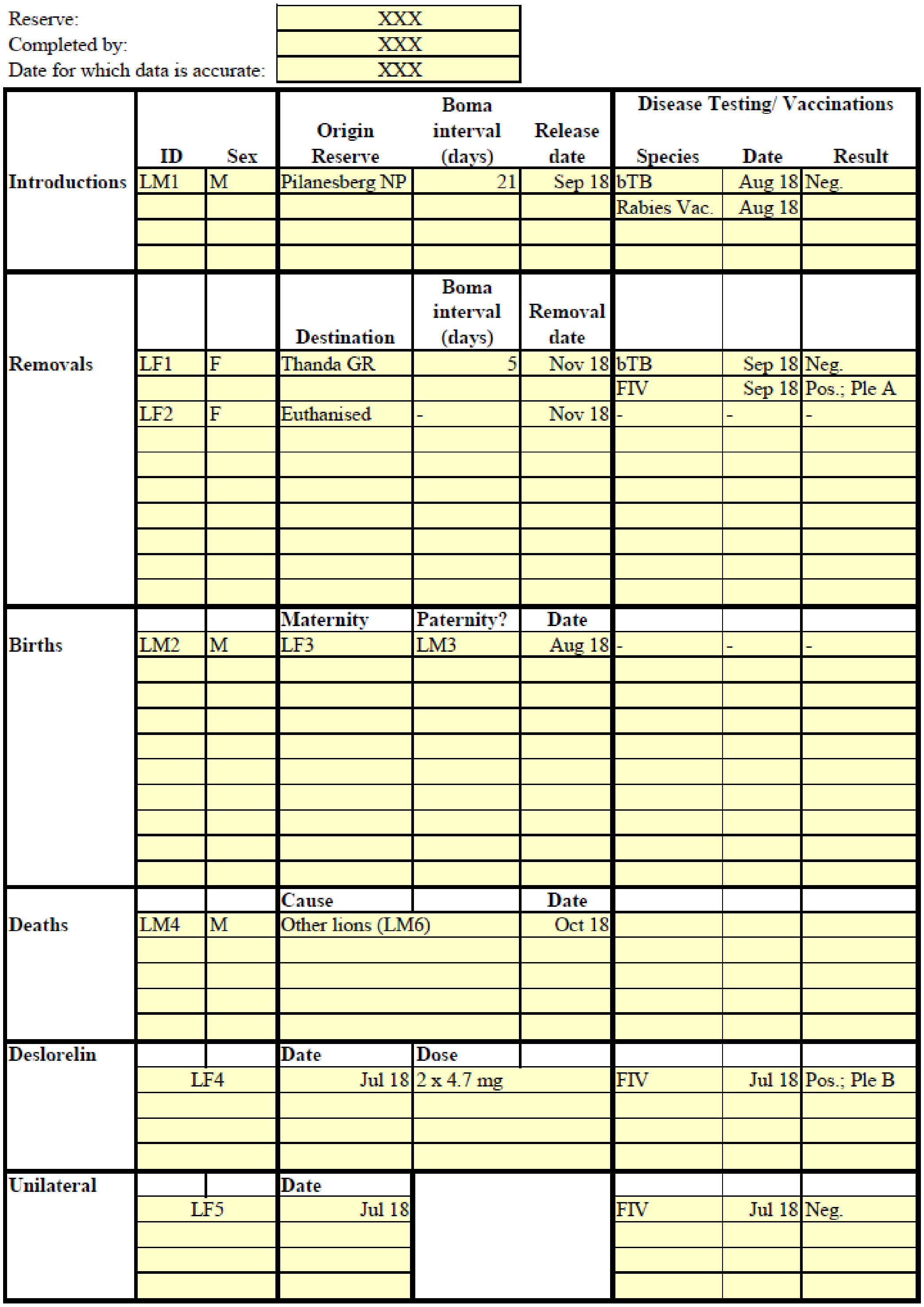
Table S7.2. A template for the recommended, in-house lion population database to record lion management procedures and demographics on an event-by-event basis. Records for successive fertility and disease management interventions can be separated into individual columns in the full database. A key for the information records can be found below.

Lion						Introduction			Mortality / Removal			Deslorelin		Unilateral (date)	Disease testing				Vaccination		Current	
ID	Sex	DOB	Dam	Pride	Sire	Origin	Release date	Boma (days)	Date	Cause	Relocated to	Date	Dosag.		bTB	Date	FIV	Date	CDV	Rabies	Status	Age
LF2	F	Mar 03	LF1	North	LM1	Selati GR	Jan 10	25	n/a	n/a	n/a	Jan 2008; Jan 2016	2x4.7; 2x4.7	n/a	Not present	Nov 09	Pos.:Ple B	Jan 16	-	-	Alive	15.85
LM1	M	Aug 14	LF2	South	-	Birth	n/a	n/a	Jan 18	Translocated	uMkhuze GR	n/a	n/a	n/a	Not present	Nov 17	Not present	Nov 17	Nov 17	-	Translocated	n/a
LF3	F	Jan 14	LF1	North	LM2	Birth	n/a	n/a	Jun 12	Infanticide	n/a	n/a	n/a	n/a	-	-	-	-	-	-	Deceased	n/a

Key to the record taken in the lion management database (first column)

Lion ID	The identity code of lion
Sex	The sex of lion
DOB	The date of birth of lion (mmm/yy)
Dam	The maternity of lion
Pride	The identity of pride that the lion associates with
Sire	The paternity of lion - if accurately known
Origin reserve	The reserve from which the lion was translocated from; Otherwise 'Birth'
Release date	The date (mmm/yy) that lion was released onto reserve (where relevant)
Boma interval	The amount of time (days) that the lion spent in a boma on reserve prior to release (where relevant)
Mortality / Removal date	The date (mmm/yy) at the lion died or was removed (translocated/euthanised/hunted)
Mortality cause	The known cause of removal or mortality (natural death, translocated, euthanised etc.)
Relocated to	The reserve to which the lion was translocated to (where relevant)
Deslorelin date	The date (mmm/yy) of deslorelin treatment (multiple where relevant)
Deslorelin dosage	The dosage of deslorelin treatment (multiple where relevant)
Unilateral date	The date (mmm/yy) of unilateral hysterectomy treatment
bTB	The results of bTB testing - positive or negative
bTB date	The date (mmm/yy) of the relevant bTB test
FIV	The results of FIV testing - positive or negative; for positive results: the strain (Ple A / Ple B / Ple C)
FIV date	The date (mmm/yy) of the relevant FIV test
Status	The latest status update of the lion (Alive / Translocated / Deceased)
Age	The current age of lions for which the status update is alive (automatic calculation)

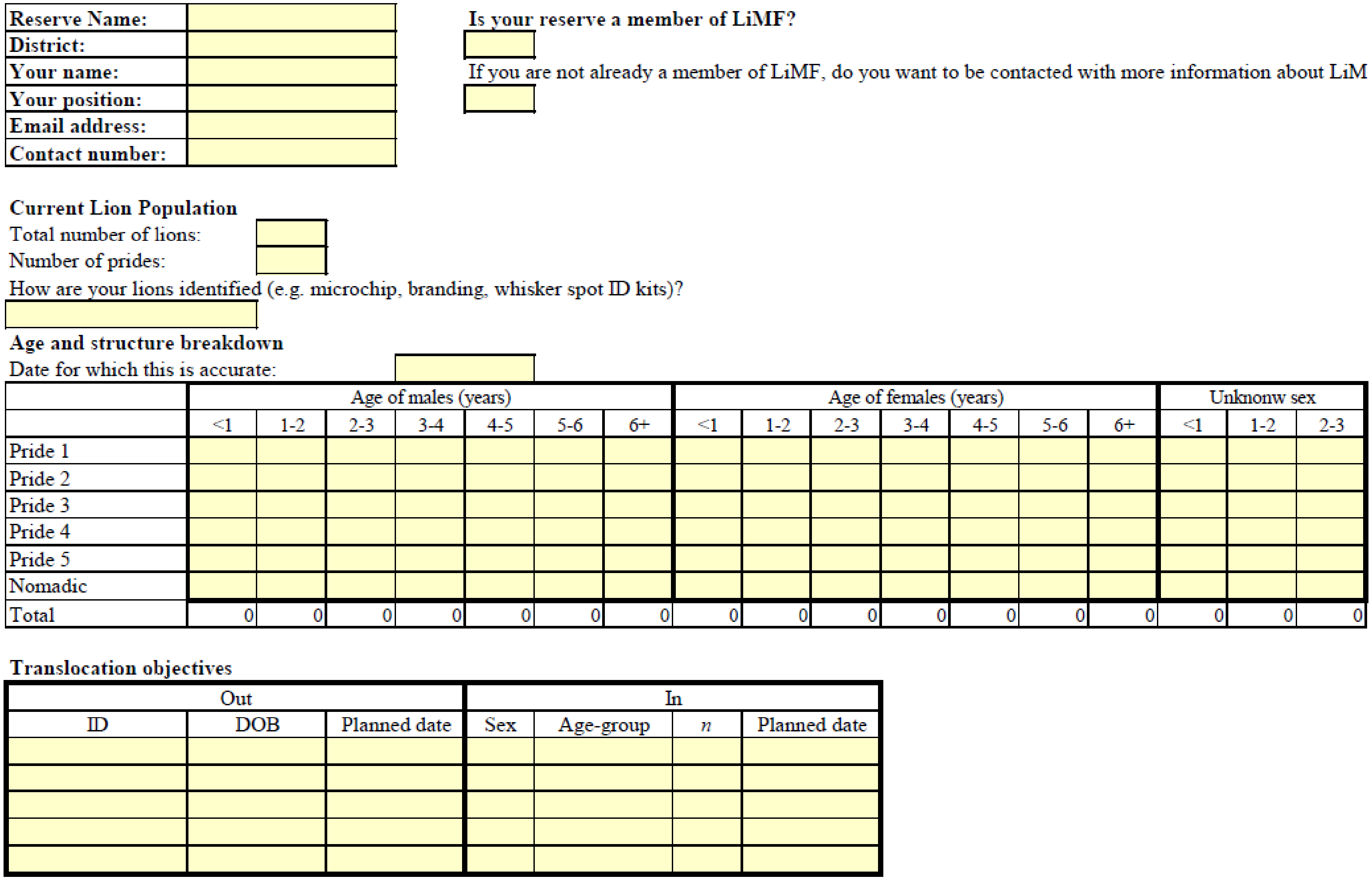
Table S7.3. A template for the recommended, in-house annual lion management report facilitated by the updated population database (Supplementary Material Table S7.2).



Reserve: XXX
Completed by: XXX
Date for which data is accurate: XXX

						Disease Testing/ Vaccinations		
	ID	Sex	Origin Reserve	Boma interval (days)	Release date	Species	Date	Result
Introductions	LM1	M	Pilanesberg NP	21	Sep 18	bTB	Aug 18	Neg.
						Rabies Vac.	Aug 18	
			Destination	Boma interval (days)	Removal date			
Removals	LF1	F	Thanda GR	5	Nov 18	bTB	Sep 18	Neg.
						FIV	Sep 18	Pos.; Ple A
	LF2	F	Euthanised	-	Nov 18	-	-	-
			Maternity	Paternity?	Date			
Births	LM2	M	LF3	LM3	Aug 18	-	-	-
			Cause		Date			
Deaths	LM4	M	Other lions (LM6)		Oct 18			
Deslorelin			Date	Dose				
	LF4		Jul 18	2 x 4.7 mg		FIV	Jul 18	Pos.; Ple B
Unilateral			Date					
	LF5		Jul 18			FIV	Jul 18	Neg.

Table S7.4. A template for the recommended annual lion audit (part of the BMP for lions in South Africa) and translocation objectives survey facilitated by the updated population database (Supplementary Material Table S7.2).



Reserve Name:
District:
Your name:
Your position:
Email address:
Contact number:

Is your reserve a member of LiMF?

If you are not already a member of LiMF, do you want to be contacted with more information about LiM

Current Lion Population

Total number of lions:
Number of prides:
How are your lions identified (e.g. microchip, branding, whisker spot ID kits)?

Age and structure breakdown

Date for which this is accurate:

	Age of males (years)							Age of females (years)							Unknonw sex		
	<1	1-2	2-3	3-4	4-5	5-6	6+	<1	1-2	2-3	3-4	4-5	5-6	6+	<1	1-2	2-3
Pride 1																	
Pride 2																	
Pride 3																	
Pride 4																	
Pride 5																	
Nomadic																	
Total	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Translocation objectives

Out			In			
ID	DOB	Planned date	Sex	Age-group	*n*	Planned date