Cheetah translocation success in Southern Africa

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DECLARATION

I declare that this dissertation is my own, unaided, original work. It is being submitted for the Master of Research degree at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or any other examination at any other university.

(Signature of candidate)

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ABSTRACT

Cheetah (*Acinonyx jubatus*) in South Africa are influenced by unique ecological and anthropogenic factors, yet nationwide populations continue to grow whilst globally they decline. Fragmented habitats and isolated subpopulations of cheetah have led to a metapopulation management strategy being adopted, where individuals are moved between reserves to facilitate gene flow. The Endangered Wildlife Trust coordinates this metapopulation, which encompasses 59 nature reserves and 421 cheetahs. This study focused on the 235 translocations that occurred between reserves between 2011 and 2019. Translocation success was measured as post-release survival duration and breeding productivity. I identified four features that could influence translation success: whether lion are present in the recipient reserve, whether cheetah have lived alongside lions previously (are they naïve or savvy), cheetah age at translocation, and reserve vegetation suitability. Vegetation suitability is defined as the similarity in sender and recipient reserve greenness and phenology. Post-release survival duration was lower in areas with lions present, especially when cheetah were naïve to lions. Survival duration was also lower in individuals translocated at a young ages (9, 18, 36 months), and optimised in individuals at 83 months old. Moving to a greener reserve also reduced survival duration. Post-release survival duration also improved breeding productivity. Cheetah were also more likely to produce a litter and raise cubs to independence when sender and receiver reserves had a more correlated vegetation phenology, and moving to a greener reserve reduced the probability of producing and raising cubs. This study highlights that exposure to lions, age at translocation, and reserve suitability are all questions of paramount importance when managing cheetah under a metapopulation management strategy. These key influencing factors must be considered when planning future reintroductions in order to continue the conservation success of South Africa's cheetah metapopulation. Given the cheetah population is growing in the metapopulation, other countries facing similar threats to cheetah in South Africa may want to consider introducing a metapopulation approach.

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As for many, 2020 has been a challenging year and one that has brought along some difficult situations we have had to overcome. After 5 years of South African nature conservation work, I decided to emigrate back to the United Kingdom. If it was not for the logistical and mental support I have received from loved ones, such a life change would normally put ongoing studies on hold whilst transitioning. Instead I able to catalyse my research projects progress as I was provided with the greatest loving care that I will be eternally grateful for.

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INTRODUCTION

Global Predators and their conservation

Large terrestrial predators are important components in ecosystems and key regulators of lower trophic levels, whose absence can lead to trophic cascades and food web instability (Purvis et al. 2000; Terborgh 2005). For example, Liukkonen et al. (2009) showed that management and conservation initiatives have supported the population recovery of the Eurasian lynx (*Lynx lynx*) in Finland. This in turn led to a decline in red fox which consequentially increased abundance of forest grouse (*Tetrao tetrix*) and mountain hare (*Lepus timidus*) (Elmhagen et al. 2010; Ritchie et al. 2012). Hebblewhite et al. (2005) showed that the presence of wolves (*Canis lupus*) reduced survival of adult and juvenile elk (*Cervus elaphus*), which decreased browsing intensity of aspen (*Populus tremuloides*) and willow (*Salix*), and increased riparian songbird diversity and abundance (Hebblewhite et al. 2005). These two examples show the extent in which change to the trophic level of predators have profound cascading effect throughout its interconnected food web.

The majority of large terrestrial predators have experienced substantial population declines and range contractions (Weber and Rabinowitz 1996; Dalerum 2008; Treves 2009). Population decline has been caused due to predators being subject to a wide range of negatively contributing factors such as prey depletion, hunting and livestock-related conflicts (Ripple et al. 2014). Wolf and Ripple (2017) found that only 34% of the world's land area is currently occupied by intact predator guilds, which historically was 96%, contracting significantly where high rural human population density occurs. In contrast, Chapron et al. (2014) showed that one third of mainland Europe had at least one terrestrial predator species with a stable or increasing abundance, due to supportive public opinion and legislation. These studies show that anthropogenic disturbance can have an unsettling effect on large terrestrial predator populations, however effective conservation and governance efforts can support populations, allowing humans and wildlife to coexist.

In Africa, habitat loss and indiscriminate persecution has caused the dramatic decline in predators' historical range, such as lion (*Panthera leo*) which now only occupy 17% of their historic range. Lion have a wide tolerance to a vast range of habitats, thriving in areas ranging from dense savannah woodlands to an entirely arid Kalahari Desert

(Stander and Hannsen 2003). As Africa's largest terrestrial predator, dietary requirements are high which is typically comprised of five ungulate species wherever they occur, in order to maintain an extensive social structure (Packer et al. 1995). As the largest and most dominant terrestrial predator in Africa, lion have great influence on other predators due to interspecific competition of resource and habitat utilization (Packer et al. 1995; Rostro-Garcia 2015). In the Serengeti National Park, an increase in blue Wildebeest (*Connochaetes taurinus*) populations saw greater density of lion, which consequently reduced surrounding cheetah (*Acinonyx jubatus*) reproductive success (Nowell and Jackson 1996). Anthropogenic threats to the species proliferation are often amplified when combining its need for wide range and large prey requirements. Extinct across northern Africa, lions dramatic range contractions has now restricted them nearly entirely to protected areas in eastern and southern Africa. Most of these populations have stabilized, yet occur in small isolated fragments with limited potential to expand or connect (Bauer and Van Der Merwe 2004). Over 350 individuals have been reintroduced into 21 protected areas which collectively cover 4500 km^2 and the majority of which occur in South Africa (Bauer and Van Der Merwe 2004). Even after a canine distemper epidemic, lion populations managed to again stabilize, proving how resilient they can be when provided with enough protected areas (Bauer and Van Der Merwe 2004).

Conservation: a metapopulational approach

Large carnivores residing in small isolated populations are often managed independently resulting in minimal conservation value at a broader regional scale (Slotow and Hunter 2009). Instead, studies suggest that efforts for conserving such fragmented species need to take a more holistic approach (Hayward et al. 2007; Funston 2008; Slotow and Hunter 2009; Ferreira and Hofmeyr 2014). The metapopulation approach considers all isolated populations of the same species which may exchange individuals through natural or human-managed movement (Hanski 1994). Large carnivores have become frequent subjects to reintroduction efforts across southern Africa. The International Union for the Conservation of Nature (IUCN) defines reintroduction as the deliberate movement of species into regions within their indigenous range from which the species has been extirpated (IUCN/SSC 2013). Although they require such large expansive range and prey requirements, drastic

conservation measures are required in order to prevent localized extinctions (Hayward and Somers 2009).

The South African wild dog (*Lycaon pictus*) has been under such metapopulation management in order to mitigate the human-induced mortality occurring outside of protected areas (Davies-Mosert et al. 2009). Managed as a single metapopulation, this intensive approach involved the reintroduction of wild dogs into suitable small fenced reserves and translocating between to compensate for the lack of natural dispersal. However, restoring locally extirpated large predators in small protected areas, can be inherently complex and economically constraining, particularly those with such large home ranges and prey requirements (Weise et al. 2014). It is not clear what the minimum ecological requirements are in order to conduct successful translocation in such a socially complex species. Lindsey et al. (2004) states that the understanding of driving factors behind success will help determine the future conservation planning of large carnivore metapopulations. Translocation success can be measured in three ways; survival of individual released; reproduction of individual released and their offspring and long-term establishment of a population (Seddon et al. 2007; Haskins 2015).

Cheetah history, threats and conservation

Cheetah (*Acinonyx jubatus*) once occurred across 44 countries in Africa and Asia, and were estimated to number 100,000 individuals in 1900 (Marker 1998). Yet today, the species has become locally extinct in 15 of these countries and there are now estimated to be fewer than 7000 adults (Durant et al. 2015), of which 63% occur in Southern Africa (Purchase et al. 2007). Cheetah are listed as vulnerable to extinction by the International Union of Conservation of Nature Red List of Threatened Species (Durant et al. 2017). Two key detracting factors; human persecution and habitat loss have contributed to cheetah decline.

Persecutions from farmers have contributed substantially to the species decline, yet studies have shown cheetah are only responsible for 3% of livestock losses caused by predators (Marker 2003). In Kenya, a study on a 200 km^2 farming area recorded 11 sheep mortalities per year that were caused by cheetah (Mizutani 1999). When compared to other large carnivores, cheetah was less of a threat to farmers livestock than lion and leopard (*Panthera pardus*) (Mizutani 1999). In Namibia, 90% - 95% of their cheetah population reside within farmland at low densities outside of protected

areas and are also strongly persecuted for livestock losses (Ray et al. 2005). These free roaming populations in close proximity to farmland are deemed problematic and are often captured or shot (Marker 2003). Lion and spotted hyaena (*Crocuta crocuta*) were removed from land that was once cattle farms, leaving vacancy within the trophic level of predators, in which cheetah proliferated upon (Marnewick et al. 2007). In areas of continual persecution of resident cheetahs, sinks can be created where outside individuals are drawn in where the persecuted individual once roamed (Marker 2003).

Land use in eastern and southern Africa shifted into agricultural and exacerbated the loss of cheetah habitat, contributing to the demise of the species (Ray et al. 2005). Wood harvesting, charcoal making and meat poaching are three methods that degraded savannah ecosystems, converting cheetah habitat into an agriculturally operational one (Gros 2002). Bush encroachment is where endemic bush is multiplied through the persistent removal of native ungulates, heavy cattle stocking and irregular fire management strategies (Jeo and Marker 2001). This form of habitat loss has been shown to decrease cheetah's ability to hunt effectively as the population densities of ungulates that it prefers become more fragmented (Jeo and Marker 2001; Marker 2003). South Africa's human population is growing at a rate between 1.2 and 2.8% per year (World Bank 2020), so more cultivation, and in turn conflict between humans and wildlife is expected outside and along protected areas (Antony et al. 2010).

In South Africa during the 1960's, legislation was passed that catalysed cheetah conservation as owners of land were now allowed to own any wildlife that resided on their property (Carruthers 2008; Lindsey et al. 2009). This encouraged the private sector to alter land use from agriculture and livestock farming to conservation and wildlife ranching (Sims-Castley et al. 2005). Financial incentives were now placed on wildlife that occurred locally creating a different landscape for prospectus conservation efforts within such fragmented entities. These established fenced protected areas isolated wildlife from human impact and is now one of the most popular and influential methods for population restoration (Massey et al. 2014). Large carnivores have been reintroduced into the vast majority of these small fenced protected areas - which are primarily driven by the economic output of eco-tourism ventures (Clements et al. 2016). Preferred wildlife viewing from tourists are typically your charismatic apex species, in response to which landowners' stock their reserves with attractive large predators in order to meet their demands (Di Minin et al. 2013).

Intra-guild competition

Cheetah feed predominantly on small to medium sized ungulates and other smaller prey species (Wilson et al. 2013). They share prey requirements similar to that of lion who express significant size and strength dichotomy, which can lead to an increased mortality for cheetah confronted by lions (Caro 1994; Laurenson 1994). Conversely, some studies have found that subordinate predators, such as cheetah, have the ability to coexist with larger, more aggressive carnivores when in enclosed environment without compromising access to resources (Parker et al. 2021). Cheetah can weigh between 35 kg's - 45 kg's (Caro 1994) which is considerably less than lion who can be between 83 kg's – 225 kg's (Smuts et al. 1980). Cheetah are uniquely able to chase down and exhaust prey at up to 103 km per hour, much faster than lion who rely upon ambushing and out powering their prey (Wilson et al. 2013). Despite cheetah's specialized hunting strategy, they and lion are habitat generalists, spanning from desert to thick bush to grassland savannahs (Myers 1975). Such similarities in prey requirements and habitat occupation results in these two species having potential overlap in their ecology. These two species act as both predator and competitor with each other at the same or similar trophic level and this is known as intraguild competition (Fedriani et al. 2000). Socially lions are typically found in larger fission – fusion groups (Schaller 1972) while cheetahs are mainly solitary apart from coalition males and females with cubs (Caro 1994). As one of the smaller species to the predatory guild, cheetah are prone to negative outcomes when interacting with other associated large carnivores, such as lion who have been shown to be responsible for 78% cub mortality in the grassland savannahs of the Serengeti (Laurenson 1994). Cheetah do not remain in close proximity to their kill for long periods of time, reducing the chance of losing it from kleptoparasites such as lions (Caro 1994; Hunter et al. 2007; Scantlebury et al. 2014). In response, avoidance behaviour is exhibited to minimize interactions with dominant competing carnivores (Bissett and Bernard 2007). Spatial and temporal separation is regarded as the key behavioural mechanism to avoid mortality from larger and more dominant intra guild predators (Durant 1998; Hayward and Slotow 2009; Broekhuis et al. 2013). The high levels of overlap in habitat association and prey suitability lead to greater likelihoods of direct encounters with negative outcomes from lion to cheetah.

South African Cheetah History

Since the 1600s, cheetah-suitable land has decreased by 91% in South Africa (IUCN/SSC 2007). The European settlers' arrival accelerated the countries agricultural shift by bringing more advanced industry from their westernized British and Dutch societies (Sing and van Houtum 2002). Colonialism caused extensive damage to the natural world and injustice to those native human populations whom once lived a more sustainable and less environmentally impacting lifestyle (Whyte 2018). Expanding utilization of land for agriculture, urbanisation and game ranching, South Africa's natural habitat is becoming increasingly fragmented and encapsulated by predator-proof fenced reserves (Marnewick et al. 2007; Marnewick and Davies-Mosert, 2009).

To date, southern Africa is the last place in the world with a growing wild cheetah population (Purchase et al. 2007). South Africa and Namibia constitute the vast majority of this population, with the latter having an estimated 25% of the world's cheetah (Marker 1998; Morrison et al. 2007). Namibia hosts an estimated 3000 individuals, 90% of whom are free roaming, residing outside of protected areas, only 5% of which occur outside of human-dominated land (Marker 2002). South Africa's cheetah population consists of 1500 individuals which are divided into 3 sub-populations: 43% free roaming, 36% in large protected areas (Kruger National Park and Kgalagadi Transfrontier Park) and 21% in a managed metapopulation within small fenced private game reserves (Friedmann and Daly 2004; Kemp and Mills 2005; Marnewick et al. 2014; Funston et al. 2001; EWT unpubl. data).

The South African free roaming cheetah span from the Northern Cape to the North West province and Limpopo (Friedmann and Daly 2004). Approximately 125,000 km^2 of South Africa contains suitable cheetah habitat (Boitani et al. 1999), but only 44.5% is under protected areas for conservation (Marnewick et al. 2007; Marnewick 2015). Wilson (2006) conducted population estimates through means of questionnaire surveys across the Thabazimbi district of Limpopo province. Results found 42 – 63 cheetah, occurring at densities of 0.6 – 0.9 individuals per km^2. A further free roaming population estimate across a 240 km^2 within the same area using camera traps estimated only 6 – 14 individuals (Marnewick et al. 2008). Anecdotal information from participants at a Population and Habitat Viability and Assessment meeting (IUCN SSC Conservation Breeding Specialist Group) suggest that populations across Limpopo are either static or declining (Lindsey et al. 2009). When assumed that cheetah

occurred uniformly across the remainder of the country's suitable cheetah habitat an estimated 750 – 1,126 encompassed the free roaming population (Marnewick et al. 2007). This highlights the difficulty and lack of confidence in estimating populations of this cryptic species occurring at relatively low densities (Weise et al. 2017).

Free roamers account for the largest proportion of South African cheetah and occur outside protected areas, in locations where land use has shifted post-colonialism. Cattle farms are turning into wildlife ranches, consequently confining habitable land and limiting propensity to establish a self-sustaining, long-term cheetah population (Page-Nicholson et al. 2017). These locations house suitable prey species and reduce interspecific competition due to the lack of predators. However, these locations also house high-value game, which may lead to increased persecution of free-roaming cheetah by humans (Page-Nicholson et al. 2017). Inversely, significant potential arises for predator conservation on privately owned small fenced game reserves (Davies-Mosert et al. 2009; Marnewick and Davies-Mosert 2009).

The second largest proportion of South African cheetah occur in large protected areas; Kruger National Park and Kgalagadi Transfrontier Park. Population estimates have been monitored in Kruger National Park using photographic surveys in 1991 (Bowland, 1994), 2005 (Kemp and Mills 2005), and 2009 (Marnewick and Davies-Mosert 2012). Results from a citizen science approach utilising images tourist take across a year to form an identification portfolio showed a minimum number of 172 cheetah in 1991, 102 in 2005, and 172 in 2009. In addition to the 2009 photographic survey, mark-recapture analysis was applied, calculating 412 individuals, with confidence intervals of 369 – 545 (Marnewick et al. 2014). Funston et al. (2001) conducted tracking surveys of the Kgalagadi Transfrontier Park estimating a population of 89 cheetah.

More than one fifth of South Africa's cheetah population live within privately owned small fenced game reserves. When legislation came intro fruition that allowed ownership of wildlife to landowners where they reside, it resulted in a rise of game ranching and ecotourism entities on private land (Carruthers 2008). This metapopulation of 59 reserves is reliant on human-mediated gene flow through means of translocations. Human mediated movement and release of predators into and between small fenced game reserves is conventional throughout South Africa (Hunter et al. 2007; Hayward et al. 2007; Funston 2008). Without translocations, cheetah

populations on small fenced reserves could be more prone to local extinction, and in the long-term, there may be inbreeding effects (Hayward et al. 2007).

Initially, cheetah were removed from the Namibian and South African free roaming populations and reintroduced into small fenced reserves that form the metapopulation. Over the course of 44 years, between 1965 and 2009, an estimated 343 individuals were reintroduced into 48 small fenced reserves and by the end of this period, only 281 remained (Buk et al. 2018). From there onwards, cheetah were no longer sourced from free roaming populations due to the potential population sink effect of sustained translocations from free roamers into small fenced game reserves (Weise et al. 2015; Buk et al. 2018). In 2010, no formal plan for management existed for these fragmented cheetahs populating smaller fenced game reserves that are privately around the country. The metapopulation continued to decline to 217 by 2012 without the incoming supplementation of free roaming cheetah (Buk et al. 2018).

The Endangered Wildlife Trust launched the cheetah metapopulation project in June 2011. This is a management initiative to increase connectivity of small fenced reserve populations and decrease the risk of inbreeding by increasing genetic diversity. Cheetah continued to be no longer sourced from the free roaming populations, instead only from reserves part of the project. A similar integrated management approach of connectivity between associated small fenced reserves has been used for African wild dogs (Gusset et al. 2008). The metapopulation grew from 217 in 2011, to 392 in 2019, and network of reserves expanded beyond the South African borders into Malawi's Liwonde National Park.

This coordinated management of the metapopulation is still within its early development and little data exist on how reintroduction success differs from known individuals and reserves. Buk et al. (2018) studied a network of 20 fragmented populations of cheetah with an overview on establishing a successfully managed metapopulations. An in-depth analysis of the success of the Endangered Wildlife Trust's Cheetah Metapopulation project and the factors that significantly influence cheetah translocation success will be of vital importance for the future of the country's population. It is important to understand the degree to which perceived influencing factors affect the success of translocated cheetah, as it provides a scientific basis for implementing informed metapopulation management decisions.

AIM

The aim of this study is to assess which factors influenced cheetah translocations conducted by the Endangered Wildlife Trust's cheetah metapopulation project, to inform about the best strategy for successful future movements. Specifically, I explore how post-translocation survival (objective 1) and breeding productivity (objective 2) are influenced by four key themes: whether lion are present in the recipient reserve, whether cheetah have lived alongside lions previously (are they naïve or savvy), cheetah age at translocation, and reserve vegetation suitability. Vegetation suitability is defined as the similarity in sender and recipient reserve greenness and phenology.

Lion effect

A cheetah going to reserves with lions will survive for less time than a cheetah going to reserves without lions. This reduction in survival could manifest as lions are a major influence on cheetah mortality, but there could also be indirect effects, where cheetah will be experiencing competition for resources (Packer et al. 1995; Rostro-Garcia 2015), subject to kleptoparasites (Lima 1987; Hunter et al. 2007), or even under greater stress from simply having to avoid lions (Durant 2000; Hayward and Slotow 2009). If lions are reducing cheetah post-release survival, I would expect this effect to be particularly strong for cheetah that have lived alongside lions in their sender (previous) reserve. This effect of lions could also reduce breeding productivity of cheetah for all of the reasons listed above, but also, lions may pose a direct risk to cheetah cubs.

Age

Older translocated cheetah will survive for longer than younger translocated cheetah. Older cheetah will have had more time to acquire behavioural traits based on events that may have occurred in their lives, such as predator avoidance (Durant 2000) and breeding opportunities (Watcher et al. 2011) which may cause them to live longer and have greater breeding success.

Vegetation

A cheetah going to reserves with similar vegetation phenology will survive for longer than a cheetah going to dissimilar reserves. Translocations to reserves with dissimilar vegetation phenology may reduce their ability to hunt and avoid intraguild competition

through effective habitat selection (Gigliotti et al. 2020). Cheetahs may have a greater understanding of risk perception when the vegetation of the recipient reserves is similar to that of the sender reserve (Kotler et al. 1991; Hughes et al. 1994) and also reduce breeding productivity.

METHODS

Study area

The Endangered Wildlife Trust's cheetah metapopulation encompasses 59 protected areas, covering nearly 13,000 km^2 across South Africa (Figure 1). These protected areas range in size from 1,152km^2 to 28 km^2, and occur across all 9 provinces in South Africa, and within 6 different biomes. The majority of the metapopulation protected areas have a private tenure (87%), with the remaining being state run (13%). Ecotourism ventures operate within each protected area to varying degrees with only 3 areas not allowing public admittance. As of December 2019, there were 421 cheetahs across the metapopulation, 32% occurring in the northernmost provinces, such as Limpopo and 24% in the southernmost provinces, such as the Western and Eastern Cape.

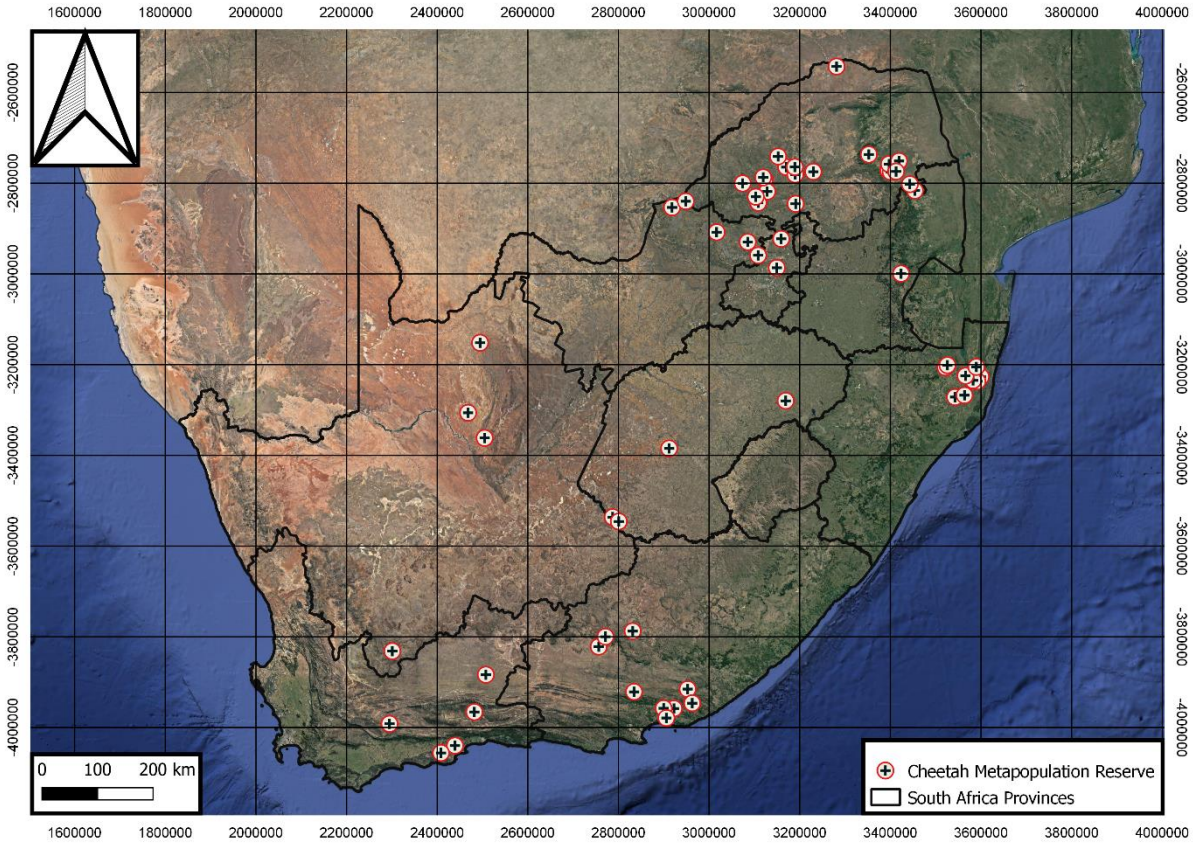

Figure 1: Cheetah metapopulation reserves across South African provinces.

South Africa encompasses a vast range of biomes that can be defined as high-level hierarchical units sharing similar vegetation structure and are exposed to similar macroclimatic patterns (Rutherford et al. 2012). Savannah, Grassland and Nama-Karoo, together account for almost 80% of South Africa, where most cheetahs across

the metapopulation occur. The Grassland biome dominates the majority of the Gauteng and Free-State provinces where rainfall occurs throughout early-summer, peaking in December, with an annual average of 726 mm (Botai et al. 2018; Rutherford et al. 2012). The Savanna biome dominates the majority of the Limpopo and North-West provinces where rainfall occurs throughout mid-summer, peaking in January, with an annual average of 623 mm (Botai et al. 2018; Rutherford et al. 2012). The Nama-Karoo biome dominates the majority of the Northern-Cape province where rainfall occurs throughout late-summer, peaking in February, with an annual average of 189 mm (Botai et al. 2018; Rutherford et al. 2012). In contrasting rainfall patterns, the southernmost provinces receive an annual average of 765 mm across the winter months, peaking in July however rain can occur all year round (Botai et al. 2018; Rutherford et al. 2012). This contributes to the mosaic of biomes that occur throughout the Eastern and Western Cape, including Fynbos and Albany Thicket.

Study species

Cheetah have been recorded surviving up to 14 years with an average of 9.5 years, reaching maturity between 24 and 36 months (Nowell and Jackson 1996). At a maximum reproductive age of 12 years, cubs are produced all year round with average litter sizes of 3.5 (1 – 6) and an interbirth interval of 15 – 19 months with a gestation period lasting 90 – 98 days (Kelly and Durant 2000; Nowell and Jackson 1996; Caro 1994). If females lose a litter of cubs, they can readily come into oestrus and conceive again 3 weeks later on average and it is assumed that they are able to give birth to a maximum of 3 litters a year (Laurenson et al. 1992). Cubs are born in thickets, long grass or in temporary dens and remain entirely dependent on their mothers for up to 18 months (Laurenson et al. 1992). 11% of cubs survive to 4 months (Kelly and Durant 2000) with 73% of mortalities due to predation (Nowell and Jackson 1996). Up to 6 months after reaching independence, cubs may form a siblings group comprised of both sexes before further dispersal (Laurenson et al. 1992). Between 18 and 24 months, females will often separate independently, whereas males can form bachelor groups known as coalitions (Laurenson et al. 1992; Nowell and Jackson 1996). Cheetah have large home ranges, estimated between 800 – 1500 km^2 (IUCN/SSC 2007). In the open systems of the Serengeti and Namibia an average home range of females was recorded at 833 km^2 (Kelly and Durant 2000) and 1500 km^2 (IUCN/SSC 2007) respectively. In the closed system of the Kruger National Park in South Africa

where prey species are non-migratory, females and males home ranges were recorded much smaller at 175 km^2 (IUCN/SSC 2007). Cheetah naturally occur in low densities, with estimates ranging from 1 per 109 km^2 in the Serengeti (Nowell and Jackson 1996; Schaller 1972) to 1 per 55 km^2 in Namibia (Kelly and Durant 2000). Males hold territories and when in coalitions are more likely to maintain them compared to males who reside in solitude (Nowell and Jackson 1996). Females do not hold territories, and are regarded as semi-nomadic with large overlapping home ranges (Nowell and Jackson 1996).

Data collection

The Endangered Wildlife Trust (EWT) launched the cheetah metapopulation initiative in June 2011 to increase connectivity of populations in fenced small-protected areas through reintroductions by translocation. Since the initiative began, 220 EWT translocations have occurred, with a further 54 occurring outside of the EWT's governance, but within the metapopulation. In each translocation, cheetah information (sex, age at translocation, survival, cubs, mortality) and reserve information of both sender and recipient area(location, size, lion numbers) were collected. In 39 translocations I found anomalies, inconsistencies, or a high frequency of missing data, so I excluded those translocations from the study (Appendix Table 1). This left a dataset of 235 cheetah translocations between June 2011 and December 2019 when there were 421 cheetahs across the metapopulation.

Cheetah information

Reports on both translocated and existing cheetah populations were delivered post release and monthly (or on request) to the EWT's cheetah coordinator Vincent van de Merwe. These included descriptions of whether cheetah experienced mortality and what caused it, if they had produced a litter, and whether those cubs reached independence. Reserves monitoring effort was considered non-uniform, therefore reported cause of mortality has to be considered with caution when comparing across reserves due to the variation of monitoring intensity (Woodroffe et al. 2007). From these reports, I derived three metrics: survival – how many months post translocation has the cheetah survived; litter – has the female produced a litter post-translocation (binary: yes/no); and independence – has the female raised a litter to independence (binary: yes/no). As it can take a cheetah nearly two years to raise a litter to

independence (Laurenson 1993; Caro 1994; Durant et al. 2007), offspring born after December 2018 were not included in the independence component of the analysis.

Reserve information

Upon admittance to the cheetah metapopulation, each reserve must submit to the EWT information on their location, size and lion population numbers (if any). I classified cheetah as lion savvy when sender reserves had a lion population present, and as lion naïve when lions were absent from sender reserves. This was recorded in a binary (yes/no) manner. Using reserve locations, I also calculated the distance between sender and recipient reserves, recording the latitudinal and longitudinal distances in decimal degrees.

Each metapopulation reserve was ecologically profiled using a primary vegetation index (VI) downloaded from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices database. The selected package MOD13Q1 provided a Normalized Difference Vegetation Index (NDVI) every 16 days at 250 m spatial resolution. This was repeated at four points in the year (March, June, September and December) between June 2011 and December 2019, the duration of the metapopulation dataset. In each protected area, I sampled the VI within a 5 km^2 buffer, based on the protected areas centroid. This buffer did not cover the entire protected area in many cases, but is also unlikely to overlap any land outside the fenced boundaries. Vegetation Indices values for all pixels that fell within the 5 km^2 area were downloaded and data selected using the criteria of; low cloud, low view angle and best possible VI value from NDVI. I averaged (median) the pixels VI values across the 5 km^2 buffer at each time-point, producing a time-series of VIs per reserve. I developed metrics from these time-series to describe differences in habitat and phenology between sender and receiver reserves: correlation – deviation of VI values between sender and recipient reserves (See figure 2a & b for example); median – average difference of all VI values between sender and recipient reserve (see Fig 2c & d for example).

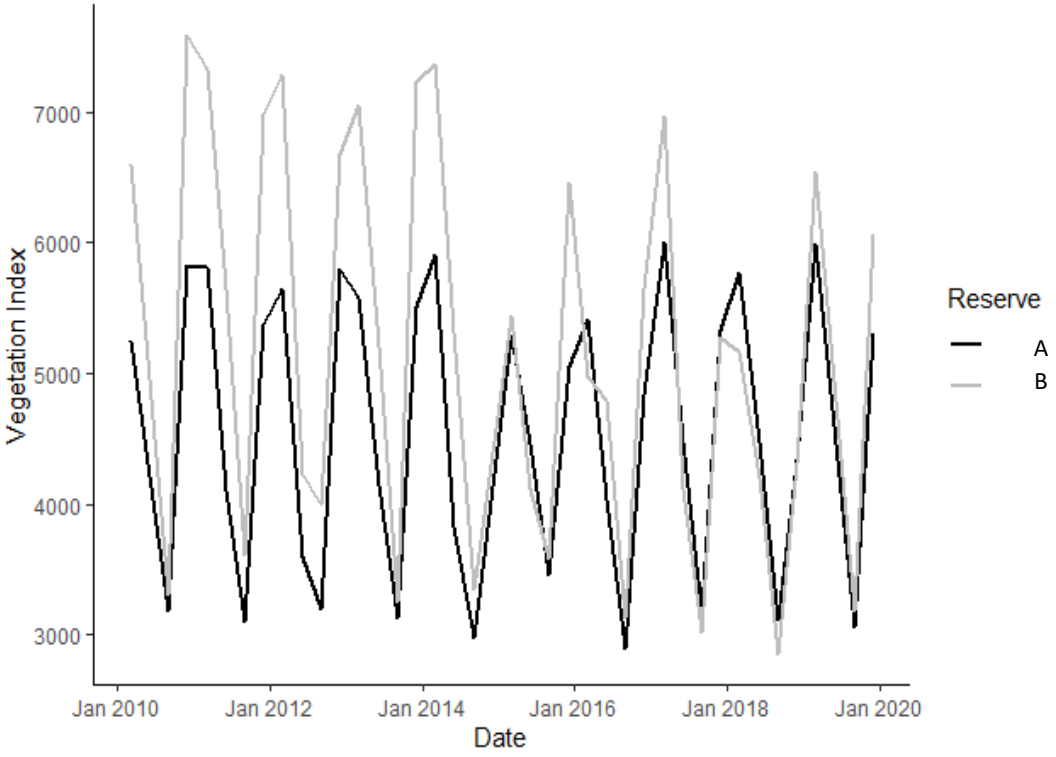

Figure 2a: Vegetation index trends for two hypothetical reserves during the study period. This example shows a high vegetation index correlation of two cheetah metapopulation reserves.

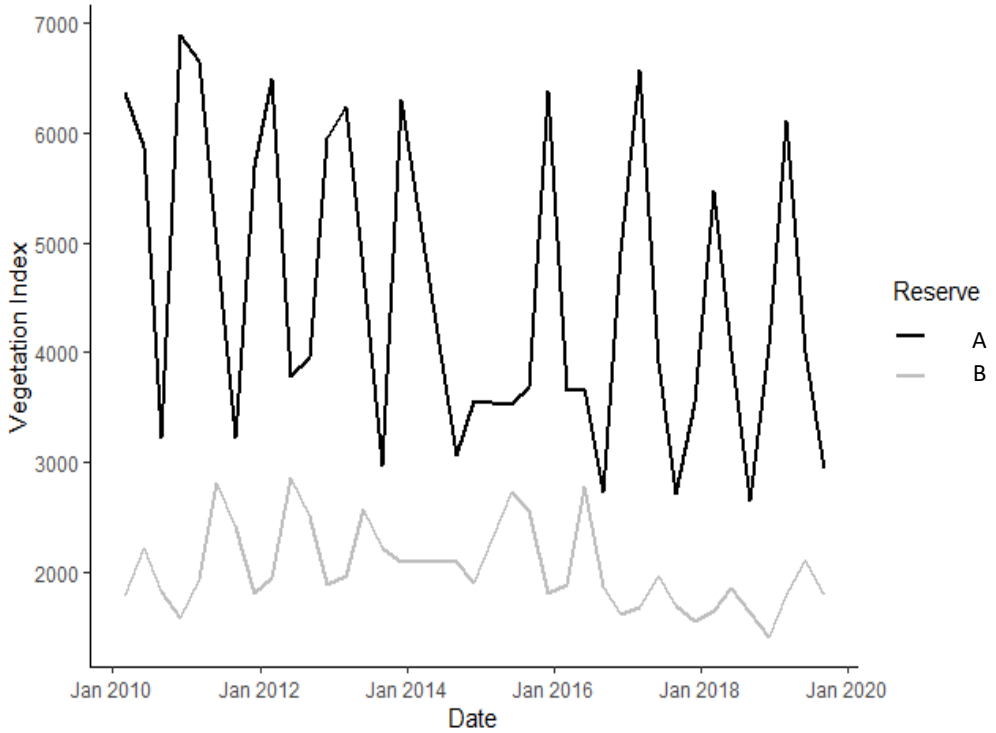

Figure 2b: Vegetation index trends for two hypothetical reserves during the study period. This example shows a low vegetation index correlation of two cheetah metapopulation reserves.

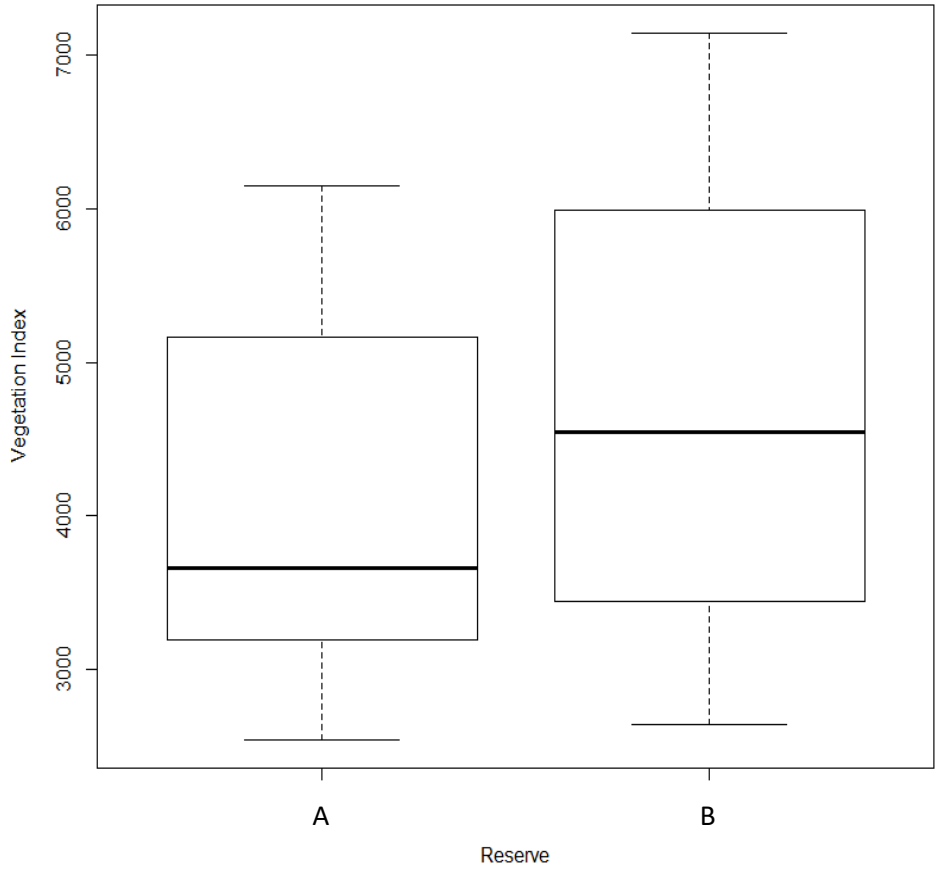

Figure 2c: Vegetation index for two hypothetical reserves during the study period. This example shows a strong positive vegetation index median difference between sender (A) and recipient (B) reserves.

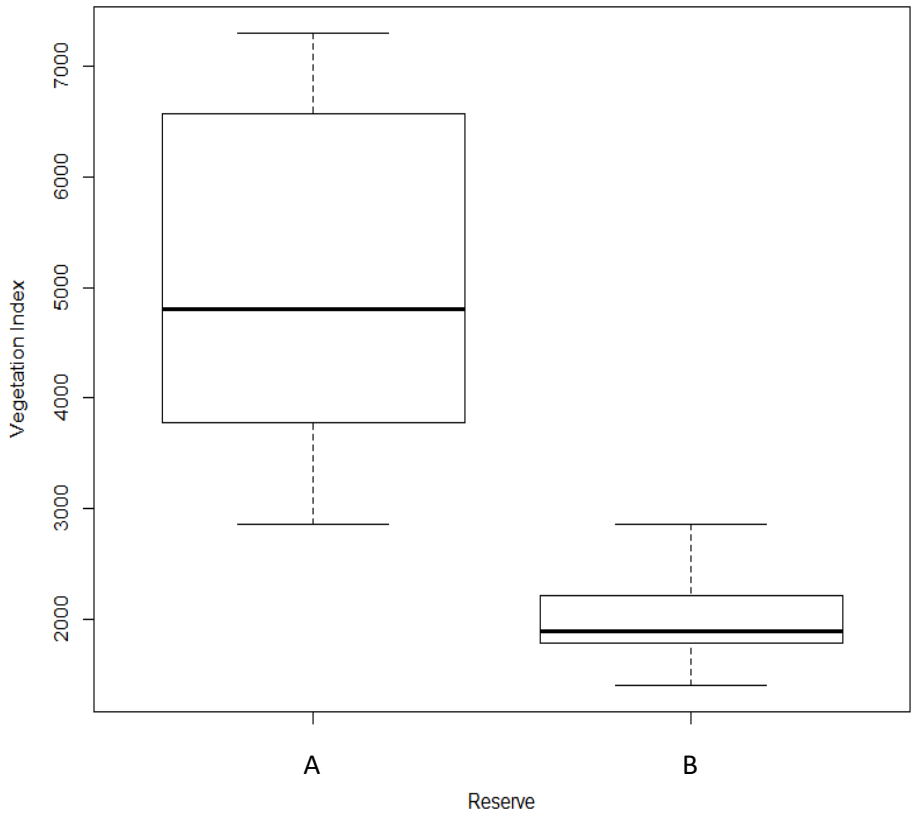

Figure 2d: Vegetation index for two hypothetical reserves during the study period. This example shows a strong negative vegetation index median difference between sender (A) and recipient (B) reserves.

Data analysis

The age of cheetah at reintroduction was recorded for 160 of the 235 translocations. The remaining 75 records were either unknown or not recorded at the time of reintroduction. Instead of removing the records with missing age values from the study (i.e. complete case analysis), which is not advised (Little and Rubin 2014; Johnson et al. 2020), I imputed the values using mice (multivariate imputations by chained equations) random forest imputation (Van Buuren and Groothuis-Oudshoorn 2011). I included the following variables within the imputation model: sender reserve size, recipient reserve size, sender reserve lion density, recipient reserve lion density, age, lion savvy or naive, lion present on recipient reserve, sex, presently alive post translocation, litter produced, cubs raised to independence, survival post translocation, sender reserve latitude, sender reserve longitude, recipient reserve latitude, recipient reserves longitude, sender reserves identification number, recipient reserves identification number, sender reserves overall median VI value, recipient reserves overall median VI value, overlap, correlation. I repeated the imputation ten times, each with a 50 iteration burn in, producing ten imputed datasets. I examined the trace plots and the distribution of the imputed values to ensure the imputations converged and produced plausible values (Appendix Figure 14). In the following models (survival, litter, and independence), I ran the model on each of the ten imputed datasets and pooled the results following Rubins rules (Little and Rubin 2014). The analysis was done in R V3.5.0 (R Development Core Team 2017).

Survival model

To identify what influenced survival in translocated cheetah, I developed a cox regression with a response variable describing the number of months each cheetah survived after translocation. This response was censored as some cheetah are still alive, and so I included an indicator variable to specify these censored values. Within the model, I included the following covariates: lion savviness (lions present in sender area); lion presence (lions present in receiver area); sex (sex of translocated cheetah); age (cheetah age at translocation with a quadratic function); VI correlation (correlation in VIs between sender and receiver areas); VI difference (difference in VIs between sender and receiver areas); latitudinal distance (latitudinal distance in decimal degree between sender and receiver area); longitudinal distance (longitudinal distance in decimal degree between sender and receiver area). I also included interactions between lion savviness and lion presence, as well as VI difference and VI correlation,

which after testing for correlation between these and found them not to be correlated. To account for non-independence of protected areas receiving multiple translocations, I also included the receiver protected areas latitude and longitude as covariate within the model. The cox regressions assumptions of proportional hazards all passed, with no evidence of influential observations (Appendix Table 2), of the proportional hazards varying over time, or of proportional hazards varying across the spectrum of covariate values (Appendix Figure 15).

Breeding – litter and independence models

To assess factors influencing the probability of female cheetah producing a litter and raising cubs to independence, I developed a logistic mixed model with a response variable describing post-translocation litter produced (binary: yes or no) a model with response variable describing post-translocation cubs raised to independence (binary: yes or no). These models included all of the same covariates and interactions as the survival model, except receiver protected areas latitude and longitude, which were excluded, as I controlled for the non-independence of receiver areas by including receiver areas name as a random intercept term within the model. I also included survival duration, in months, as covariate, to control for cases where cheetah had not survived long enough to produce a litter or to raise cubs from a litter to independence. In some of the covariates (interaction between lion savvy and lion presence, interaction between VI difference and VI correlation), I found no effect and so dropped the terms to improve model parsimony.

RESULTS

Objective 1 – Survival

Lion Effect

Survival was reduced by the presence of lions (HR = 3, CI: 1.6 – 5.7), where individuals arriving in reserves where lion were absent had 50% chance of surviving up to 66 months, which reduced to 46 months when lions were present (Figure 3).

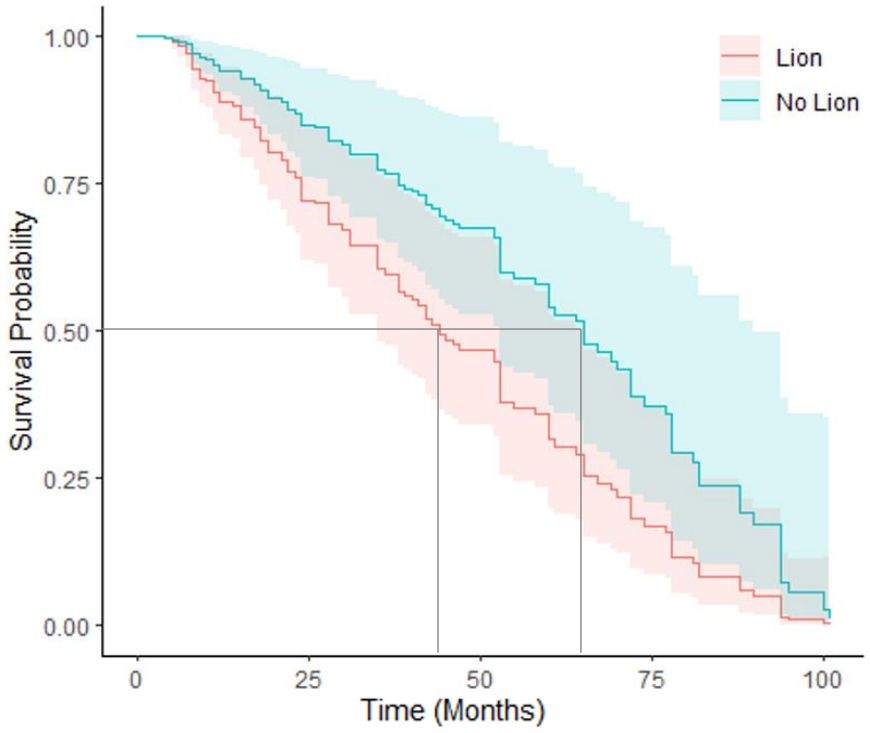

Figure 3: Cox proportional hazard survival curves describing the probability of cheetah surviving until a given time post release when sent to reserves either with (red) or without (blue) lion. Red and blue lines represent means estimate and ribbons represent 95% confidence intervals. Black horizontal line represents 50% chance of survival and the vertical line portraying the difference in survival time post release.

I also observed an interactive effect (HR = 0.41, CI: 0.35 – 0.68), where savvy cheetah exposed to lions in their sender reserve were more likely to survive alongside lions than those which were naive to the larger predators (Figure 4). For example, cheetah naïve to lions arriving on reserves with lions had a 50% chance of surviving to 35 months, 26 months less than savvy cheetah (Figure 4A). There was little difference

in survival of savvy and naïve cheetah in reserves where lions were absent (Figure 4B).

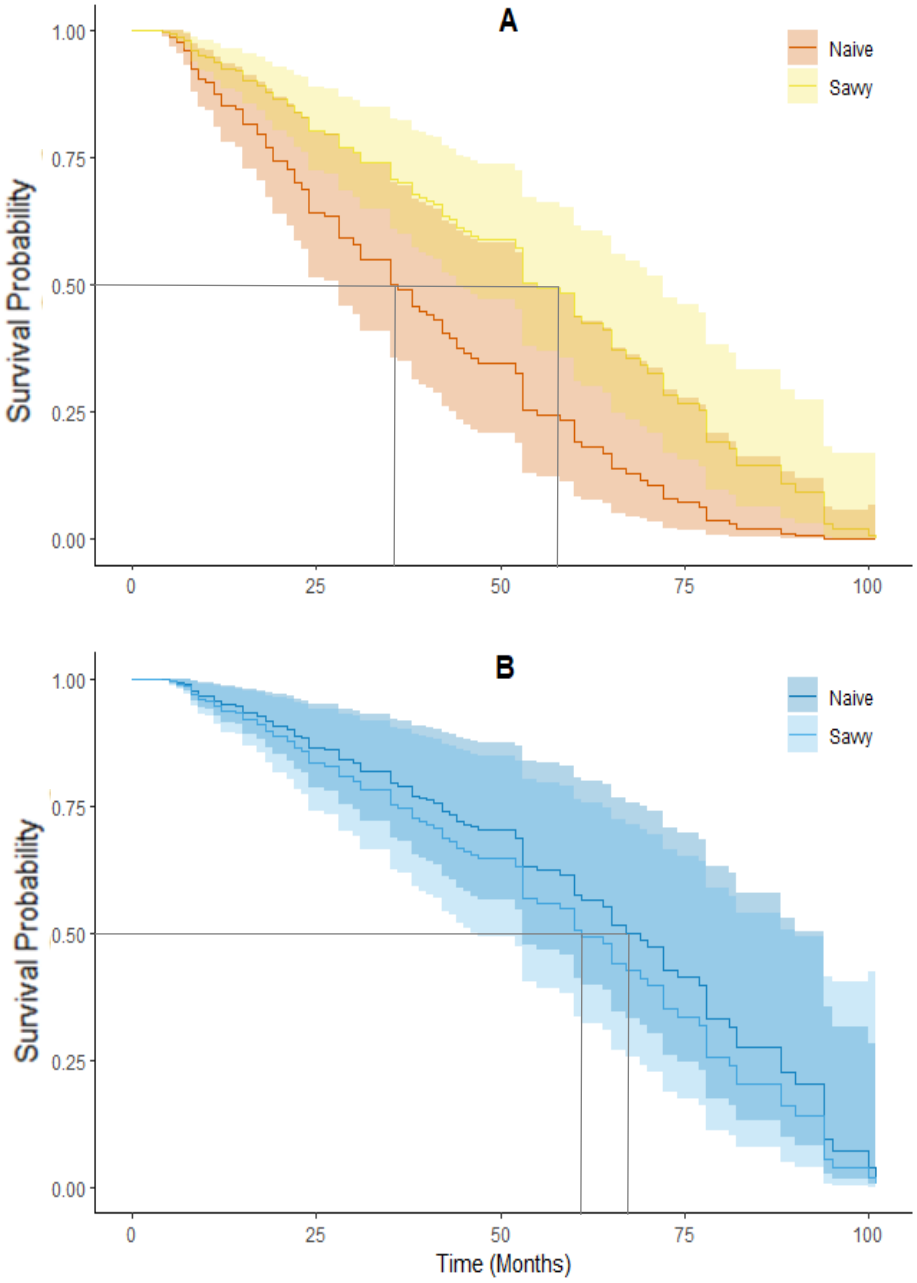

Figure 4: Cox proportional hazard survival curves describing the probability of cheetah surviving until a given time post release when sent to reserves either with (A) or without (B) lion. Cheetah with no exposure to lion from sender reserves are recorded as naïve (A: dark orange, B: dark blue). Cheetah with exposure to lion from sender reserve are recorded as savvy (A: light orange, B: light blue). Orange and blue lines represent means estimate and ribbons represent 95% confidence intervals. Black horizontal line represents 50% chance of survival and the vertical line portraying the difference in survival time post release.

Age

Survival probability increased in cheetah translocated at later ages (HR = 0.008 , CI: 0.001 – 0.37), but with a quadratic relationship where survival probabilities plateaued and then decreased in older individuals (Figure 5). 9-month-old cheetah translocations, the youngest recorded, had the lowest survival probabilities. Cheetahs translocated when reaching independence at 18 months old had substantial increase in survival probability. Cheetah translocated at age 36 months had increased survival probability, yet with reduced monthly increment difference compared to 9 and 18 ages. For example, cheetah translocated at 9 months had a 50% chance of surviving 45 months, a 15-month difference than those translocated double in age at 18 months whose 50% chance of survival post release was 60 months (Figure 6). Cheetah translocated at 36 months had a 50% chance of surviving 65 months, a 5-month difference than those translocated half their age (Figure 6). Cheetah survival was maximized by moving individuals aged 83 months (Figure 6).

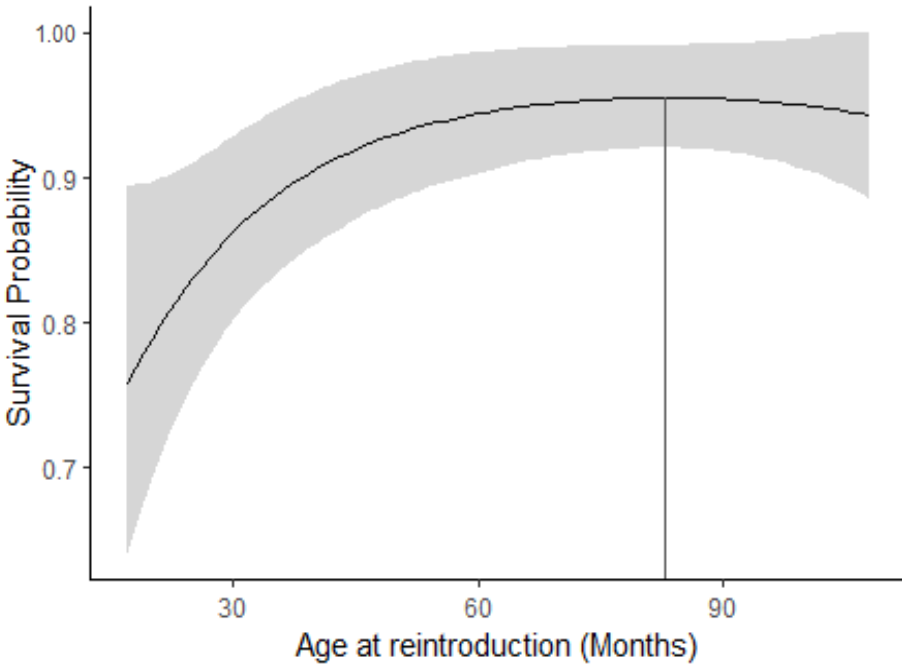

Figure 5: Marginal effect plot of age at reintroduction in months against survival probability other parameters within the model are held at 0; lion savvy; lion presence; sex; vegetation index correlation; vegetation index difference; longitudinal distance between reserves; latitudinal difference between reserves. Black line represents the mean estimate and grey ribbons are the 95% confidence intervals. Vertical black line represents optimum age at reintroduction.

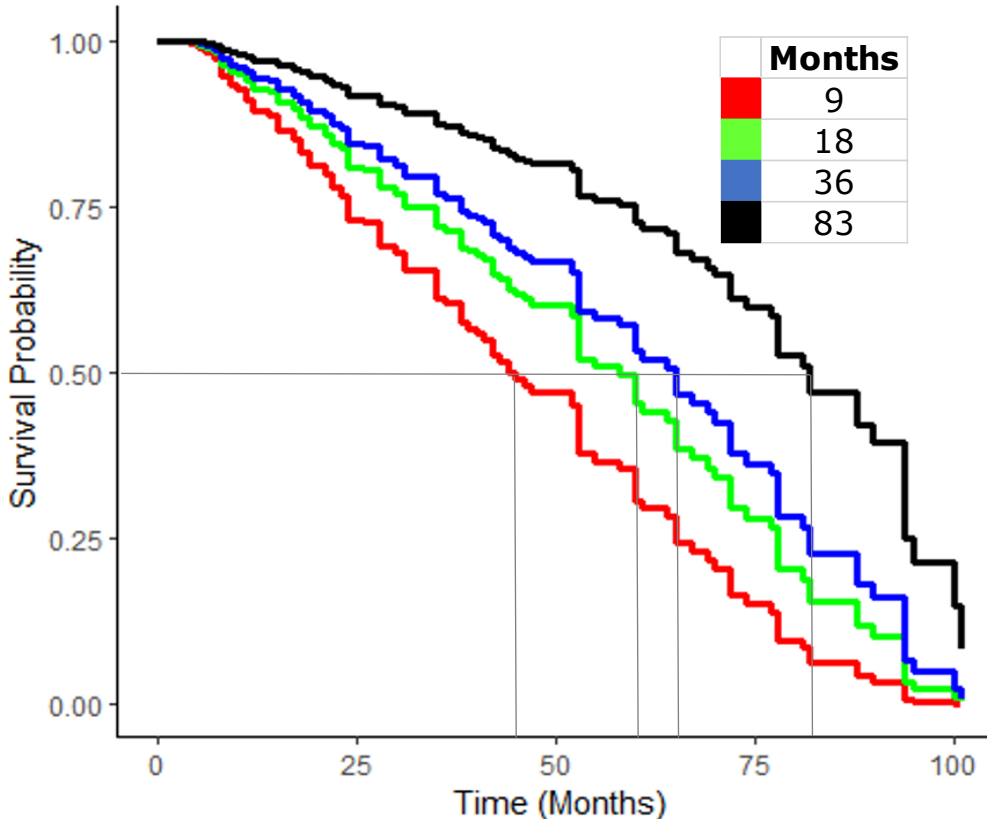

Figure 6: Cox proportional hazard survival curves describing the probability of cheetah surviving until a given time post release when translocated at variable ages. Youngest recorded cheetah moved of 9 months (red),18 months and independent (green), 36 months (blue) and optimum (black) line representing the mean estimates. Black horizontal line represents 50% chance of survival and the vertical line portraying the difference in survival time post release.

Vegetation

Change in vegetation between sender and recipient reserves influenced survival, where individuals moved to greener reserves had a lower survival probability (HR = 1, CI: 0.99 – 1.01) (Figure 7). Although influential, the effect was minimal, for example, cheetah translocated to reserves with a vegetation index increase had a 50% chance of surviving 58 months, 6 months less than those sent to reserves with a vegetation index decrease.

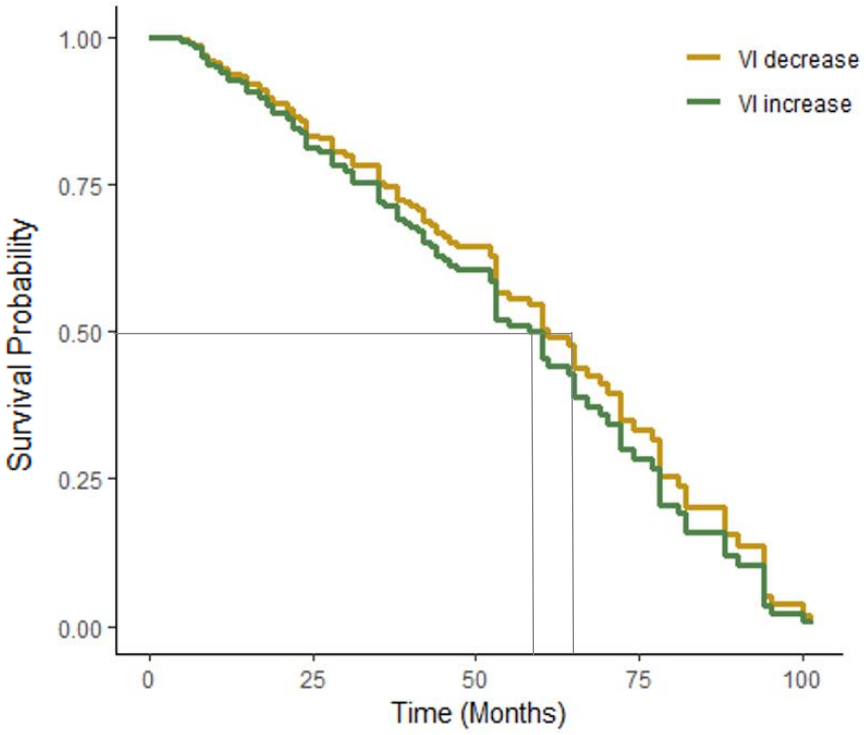

Figure 7: Cox proportional hazard survival curves describing the probability of cheetah surviving until a given time post release when translocated to reserves with an increased or decreased vegetation index (VI). Survival probabilities of cheetahs in translocations that had a 3000 vegetation index decrease between sender and recipient reserve are shown in orange as the mean estimate. Survival probabilities of cheetahs in translocations that had a 3000 vegetation index increase between sender and recipient reserve are shown in green as the mean estimate.

Location

Finally, there was substantial spatial heterogeneity in survival, where survival was greatest at low latitudes (HR = 0.653, CI: 0.509 – 0.839) and longitudes (HR = 1.54, CI: 1.21 – 1.95), and these effects interacted (HR = 1.015, CI: 1.007 – 1.029), showing decreased survival when individuals moved further north and east (Figure 8).

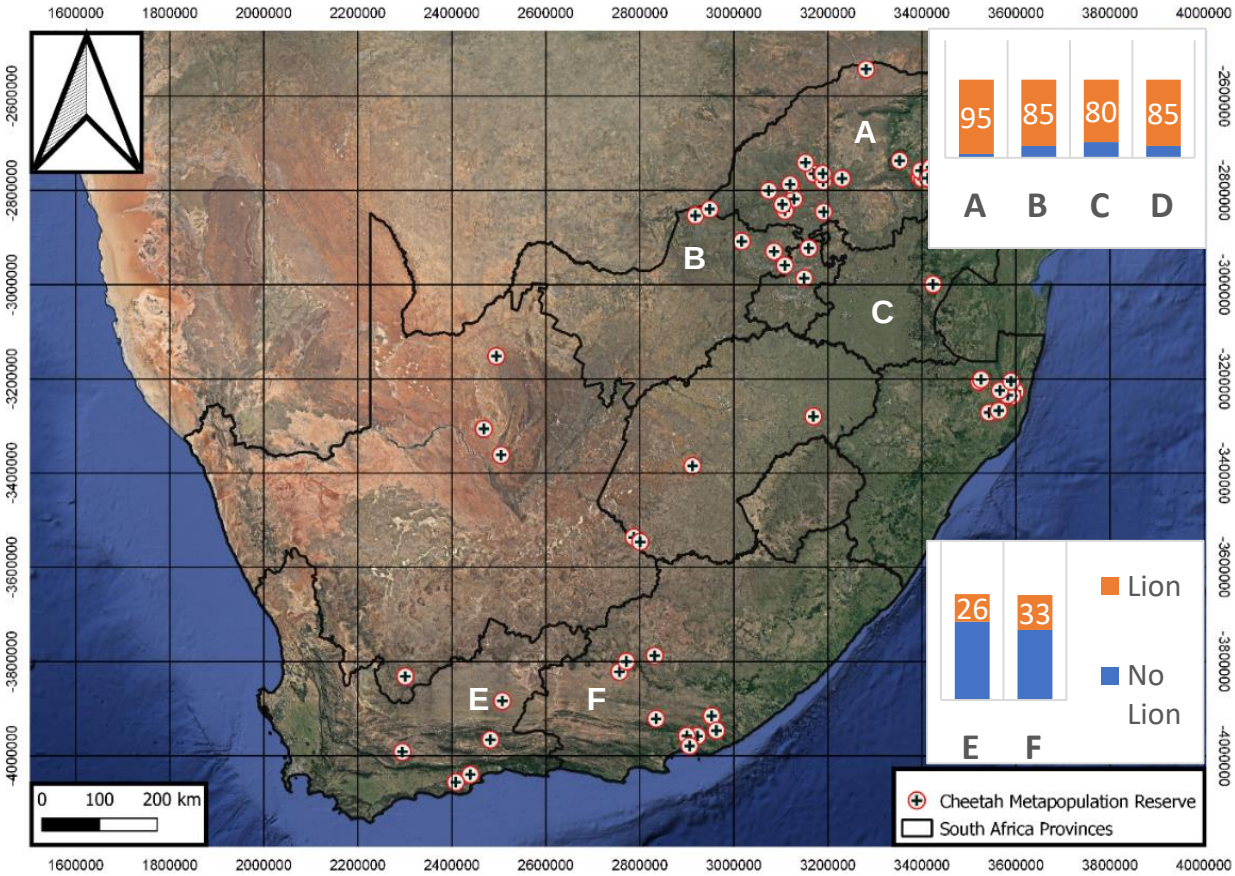

Figure 8: Topographical map of South Africa with provinces marked with black lines. Cheetah metapopulation reserves are located with red circles with black crosses. Adjacent stacked column graphs show percentage proportion of reserves with (orange) or without (blue) lion present on their reserves. Graph highlighting provinces; A – Limpopo; B - North West; C - Mpumulanga; D – Kwa-Zulu Natal are situated in the northern regions of South Africa. Graph highlighting provinces; E – Western Province; F – Eastern Province are situated in the southern regions of South Africa.

Objective 2 – Breeding

Survival

As expected, cheetah that survived longer had a greater probability of producing a litter (OR = 1.072, CI: 1.033 – 1.11) and raising that litter to independence (OR = 1.101, CI: 1.049 – 1.16). To have a 50% chance of producing a litter and raising it to independence, female cheetah would need to survive 26 and 51 months, respectively (Figure 9A, 9B).

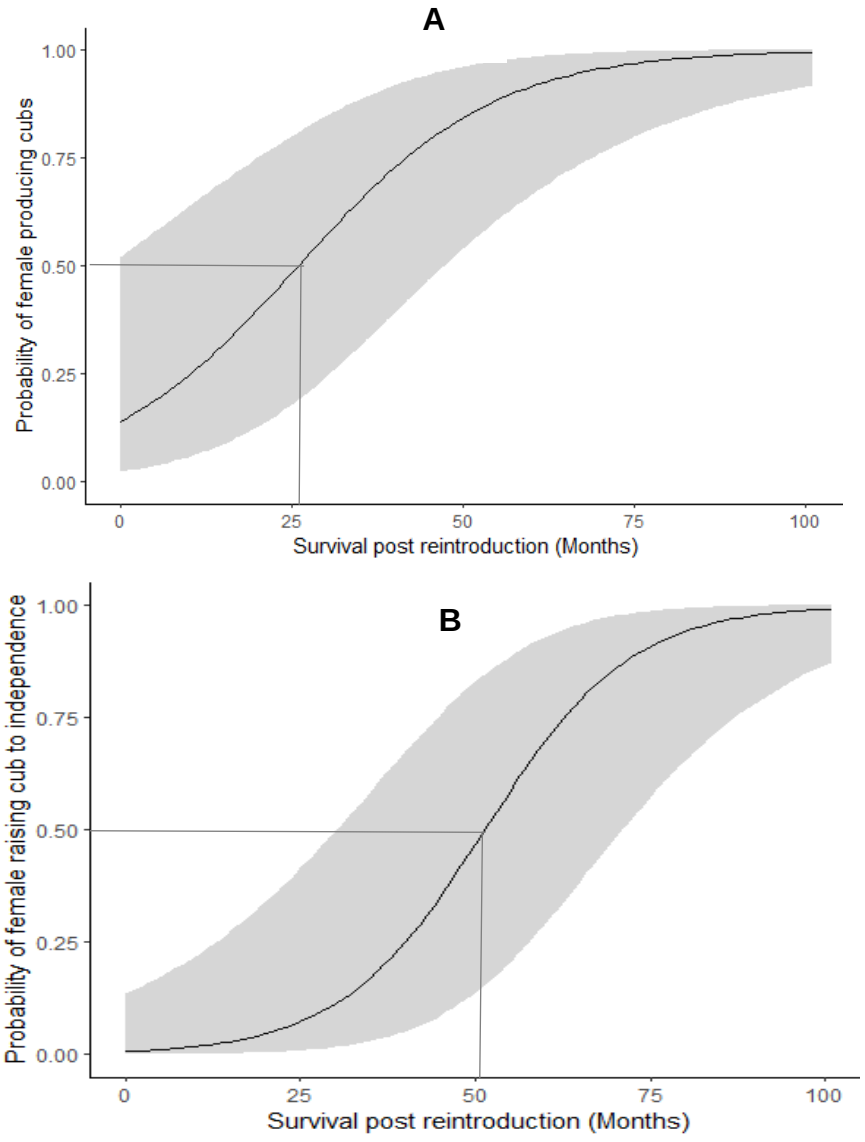

Figure 9: Probabilities of females producing a litter of cubs (A) and raising a cub to independence (B) relative to survival post reintroduction in months. Black line indicates the mean estimate with the grey ribbons showing 95% confidence intervals. The horizontal black line indicates 50% chance of producing a litter of cubs (A) and raising a cub to independence (B) and the required survival time post reintroduction by the corresponding vertical black lines.

Location

Longitudinal difference between sender and recipient reserve also had a strong effect on litter production (OR = 1.72, CI: 1.27 – 2.35) and independence (OR = 1.54, CI: 1.17 – 2.02) where individuals moving south had a far greater chance of producing a litter and raising it to independence (Figure 10A, 10B).

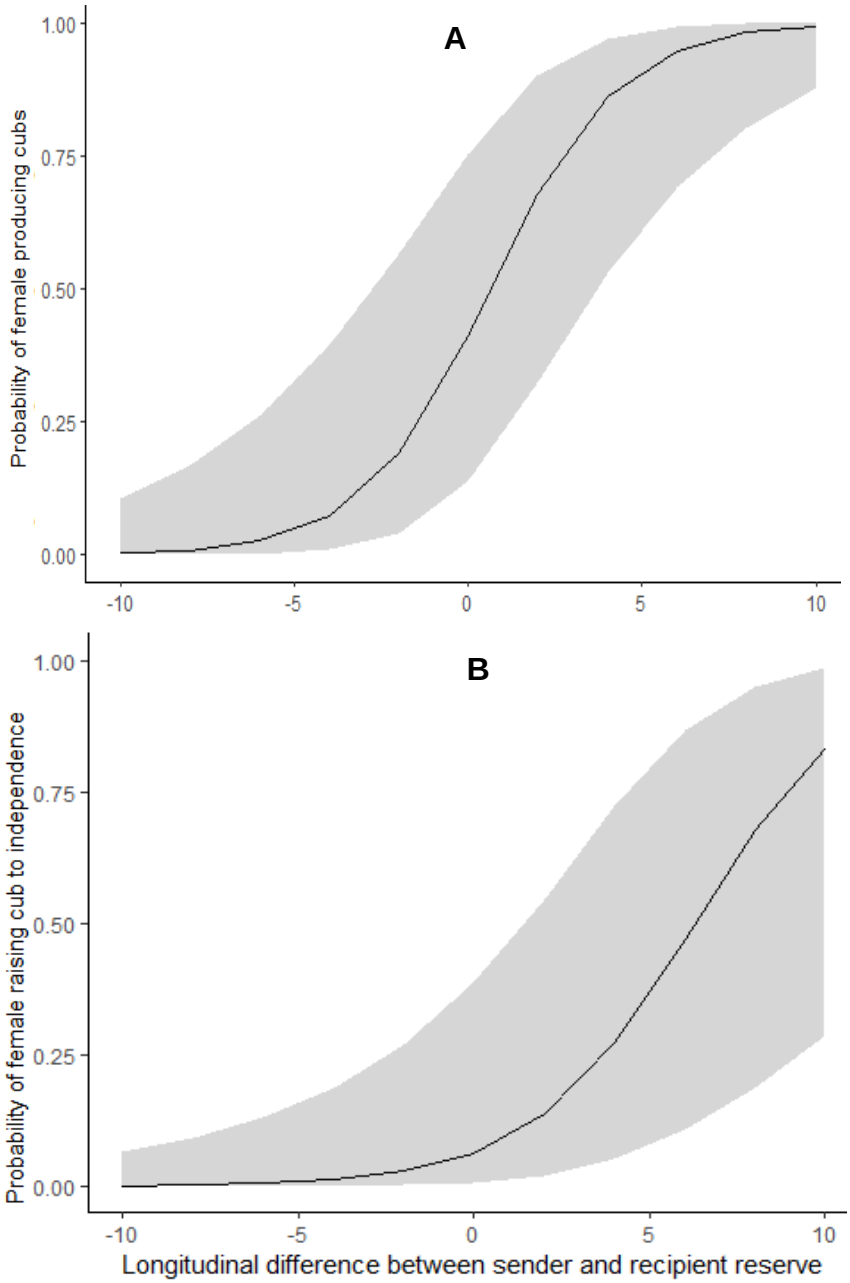

Figure 10: Probabilities of females producing a litter of cubs (A) and raising a cub to indepdendence (B) relative to longitudinal differene between sender and recipient reserve. Black line indicates the mean estimate with the grey ribbons showing 95% confidence intervals.

Vegetation

The probability of producing a litter (OR = 11.52, CI: 1.39 – 95.3), and raising it independence (OR = 17.91, CI: 1.75 – 183.4), was also greater when sender and recipient reserves had similar vegetation phenology (Figure 11A, 11B). When this phenology was asynchronous (e.g. the vegetation indicies between reserves were negatively correlated) female cheetah only had 6% chance of producing a litter of cubs, which increased to 73% when the phenology was synchronised (Figure 11A). These numbers are even more stark when looking at independence, where asynchronous translcoations have almost zero chance of raising individuals to independence (Figure 11B).

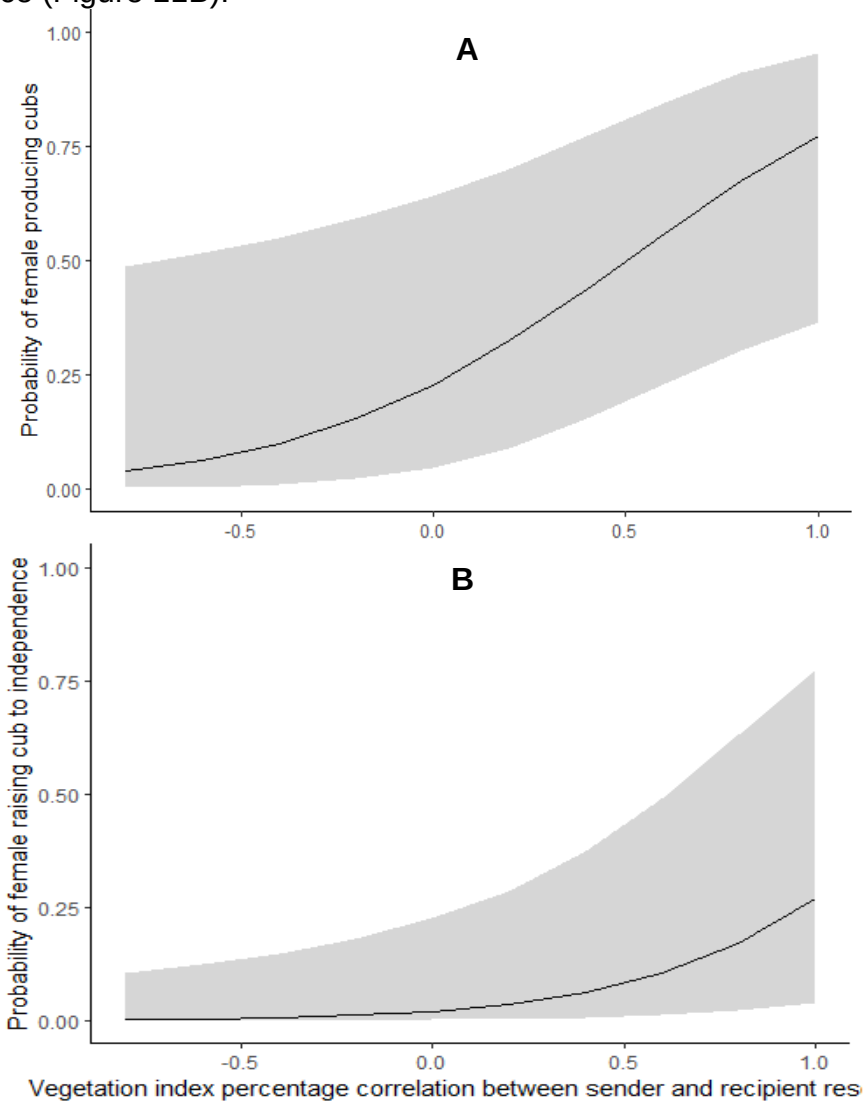

Figure 11: Probabilities of females producing a litter of cubs (A) and raising a cub to independence (B) relative to vegetation index percentage correlation between sender and recipient reserves. Black line indicates the mean estimate with the grey ribbons showing 95% confidence intervals.

Furthermore, the raw difference between sender and recipient vegetation index also infleunced the probaility of producing a litter of cubs (OR = 1, CI: 0.99 – 1.01), where there was only an 8% chance of producing a litter when moving to a greener reserve, which increased dramatically to 93% when moved to a more barren reserve (Figure 12). This raw difference between sender and recipient vegetation index had no effect on indepedence.

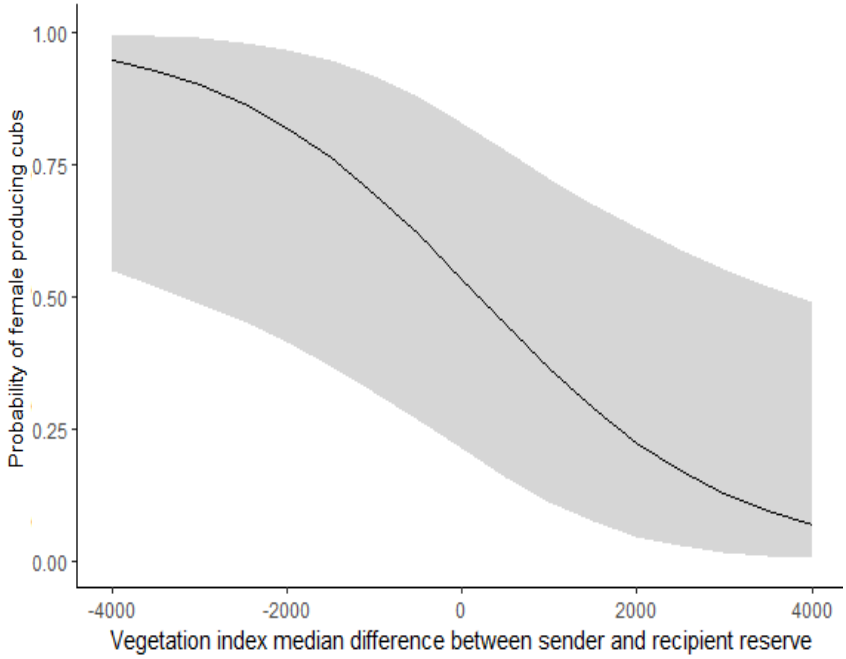

Figure 12: Probabilities of females producing a litter of cubs relative to vegetation index median difference between sender and recipient reserves. Black line indicates the mean estimate with the grey ribbons showing 95% confidence intervals.

Age

The proability of rasing individuals to independence was influenced by the age of the female at translocation (OR = 1.04, CI: 1.002 – 1.067), where older cats were more succesful, albeit with high uncertainty (Figure 13).

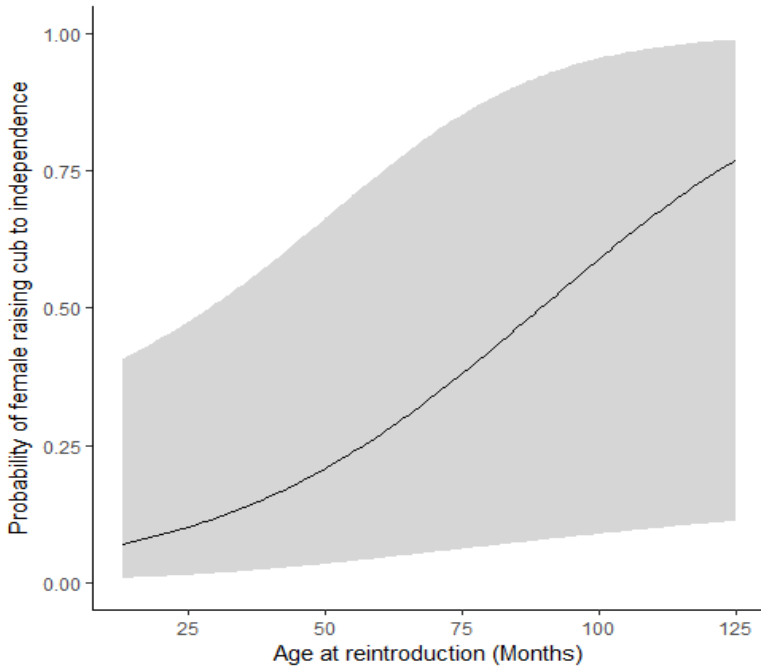

Figure 13: Probabilities of females raising a cub to independence relative to age at reintroduction in months. Black line indicates the mean estimate with the grey ribbons showing 95% confidence intervals

DISCUSSION

Lion Effect

I found evidence to support the hypothesis that cheetah survival would be reduced when released onto reserves where lions were present. This study demonstrates that lion presence significantly reduces cheetah survival, however it is important to note that this effect does not demonstrate the degree of exploitation and interference. Lions aggressive interactions with cheetah have been widely reported and considered to be one of the main reasons for cheetah reintroduction failures (Hayward et al. 2007; Marnewick et al. 2007). However, the mechanisms by which cheetah and lions coexist are still poorly understood (Durant 1998; Mills et al. 2004; Bissett and Bernard 2007) owed to the fact that fine-scale quantitative analyses are rarely conducted due to financial and ethological constrictions. Studies that have analysed the effect of lion on cheetah often don't know individual's presence in the same area at the same time of a potential event (Hayward and Slotow 2009), with only few, such as Parker et al. (2021) that have consistently enough data points to perform an analysis. Since records of the cheetah metapopulation began in 1993, 52% of cheetah presumed to have died were never found. Consequently, analysing direct causes of mortality can only reference those that were confirmed as known mortalities. Natural mortalities are rarely located early enough to accurately identify a cause, due to carcasses being scavenged or decomposed (Woodroffe et al. 2007). I will explore studies that fall parallel with my own, suggesting hypothesis for why cheetah often have a negative association when coexisting with lion.

Spatiotemporal

In large multiple use landscapes, such as the Serengeti National Park, cheetah densities are negatively correlated with lion and competitively subordinate to the dominant predator (Caro 1994; Laurenson 1995). In contrast, my study of South Africa's cheetah metapopulation is made entirely of individuals within small fenced game reserves, where boundaries exist, limiting the spatiotemporal separation. Intra-guild aggression is a key component of large predator communities, consequently affecting their distribution and behaviour (Hersteinsson and Macdonald 1996). Often competing indirectly over similar prey species, cheetahs have a disadvantage compared to lions because of their smaller body and predominantly solitarily lifestyle (Mills and Biggs 1993; Caro 1994; Hayward and Kerley 2008). Cheetahs are most at risk whilst feeding on a kill, when they reduce time being vigilant of direct predation

and potential kleptoparasites, such as scavenging lions and hyaena (Lima 1987; Hunter et al. 2007). Ginsberg (2001) demonstrated that small conservation areas where predator density can be high, such as small fenced game reserves, increase inter and intra-specific competition for resources. When responding to increased dominant predator density, cheetah refine their prey selection and activity patterns in order to avoid spatiotemporal overlap (Clements et al. 2016; Swanson et al. 2016). Durant (2000) demonstrated this through lion playback experiments, resulting in cheetah actively moving away from their vicinity. Other studies have also shown that the species at risk will chose to move to areas that attract fewer predatory competitors due to limited prey availability (Chesson 1986; Rosenzweg 1991; Durrant 1998). The perceived presence of an intra-guild competitor, such as lion has been shown to effect cheetah by reducing their likelihood of hunting, consequently lowering their kill rate and potentially causing malnourishment (Lima and Dill 1990).

Stocking prey and predator populations

Another consideration for lion presence on recipient reserves reducing cheetah survival is the degree in which predator and prey species are stocked in locally managed private reserves. All of these small fenced game reserves have to manage their resident species by artificially maintaining and manipulating populations. A balance in trophic levels according to the reserves size is essential in order to maintain a sustainable ecosystem. When ungulates are overstocked, ecosystem degradation is more likely to occur due to over grazing / browsing (Lindsey et al. 2011), therefore stocking should be inhibited before permanent ecological what takes effect. The vast majority of reserves within the cheetah metapopulation operate ecotourism ventures, modelled around optimal game viewing, particularly predators such as cheetah and lion. Cheetahs have large area requirements and across a metapopulation system of small fenced reserves this means that both they and lions are often stocked at densities close to or above what their prey populations can support (Lindsey et al. 2011). As cheetah are reintroduced into smaller fenced areas, the number of individuals per unit area may increase as well as having increased exposure to edge effects (Woodroffe and Ginsberg 1998; Fagan et al. 1999). When predator populations are overstocked, prey species encounter rate becomes more frequent. Valeix et al. (2009) found that ungulates used more open habitats when lions were in their vicinity, and cheetah have greater hunting success in open habitat (Mills et al. 2004; Rostro-

Garcia 2015). My results may suggest that stocking high cheetah and lion densities could lead to cascading effects between both predators and ultimately greater chances of subordinate cheetah mortality. In order to prevent over stocking of these two apex predators with such consequential intra-guild competition, regular reserve monitoring, management and intervention should occur to prevent exceeding of carrying capacities.

Naivety to lion

The survival of cheetah with no previous exposure to lion was significantly impeded when arriving on reserves with an existing lion population. Predator naiveté has previously been cited to be a contributing factor in reintroduction failures (May and Lyles 1987). Great consideration goes into the reserve suitability and economic transaction when reintroducing individuals, yet little in the cognitive abilities from behaviour traits learnt from previous exposure necessary for survival. This study suggests the lack of lion coexistence abilities are not part of cheetah genetic memory, demonstrating that such behaviour traits need to be learnt.

Predator avoidance is a key component for cheetah living successfully in coexistence with lions. Evolutionarily, cheetah are diurnal in order to avoid lions who typically operate at night (Hayward and Slotow 2009). Furthermore, whilst in grassland habitats, cheetah can avoid lions who typically use denser habitats where their ambush-hunting technique becomes more efficient (Eaton 1974; Macdonald 1992; Rostro-García 2015). Durant (2000) showed that cheetah that were less in contact with lions suffered the least predation. In a study done where, looking at predator naiveté, if nearby lion numbers were high, predator savvy cheetah were shown to be more likely to move away rather than continue resting or hunting (Durant 1998). Auditory and olfactory cues presented by lions may not trigger a stimulus in naïve cheetah, unlike ones who have had previous exposure to such threat and would move away. Individual cheetah will alter their behaviour after repeated exposure to a particular stimulus that could cause a negative response (Durant 1998). Considering the severity of consequence resulting from such intra-guild encounters and the average life span of a cheetah, the ability to learn such predator avoidance behaviour becomes increasingly difficult.

Age

The age in which cheetah were removed from their sender reserves had great influence on their survival. Survival had a positive correlation with age at reintroduction with cheetah aged 6 years and 11 months resulting in optimum survival post release. This study also suggests that the probability of females raising cubs to independence had a positive correlation with age at reintroduction. Furthermore, females that survived longer post reintroduction had a greater chance of producing and raising cubs to independence. As adults, cheetah have been exposed to a greater number of threats over time, inevitably learning and attaining behavioural traits that lead to survival longevity.

It is important to understand the life history of cheetah and the potential effects of removing it from such natural progression. Typically, female cheetahs have their first litter at 2 years after a 3-month gestation (Caro 1994). Remaining in a lair for 2 months, the cubs will stay with their mother until an average age of 18 months (Laurenson 1993; Caro 1994). Cheetah cub mortality can be high, an example of which is in the Serengeti, where 95% of cubs died before becoming an independent adolescent, mostly because of predation (Laurenson 1994). Discerning exact causes of cheetah mortality with complete certainty can be difficult, especially with cubs within close proximity to a den. 24% of cheetahs translocated in the cheetah metapopulation were 18 months or younger, unable to continue their development. Cumulatively, 64% of all cheetahs translocated in the cheetah metapopulation were 24 months or younger. This further average of 6 months' association with littermates allows behavioural traits, hunting techniques and exposure to intraguild competition to occur (Durant et al. 2007). This period of near-adolescent sociality provides individuals unique exposure to intraspecific competition, mitigating the chances of future mortalities when encountering another cheetah (Durant et al. 2007). During such educational period, males with sisters have higher survival than males with brothers (Durant et al. 2004; Durant et al. 2007) due to access to food caught by their more accomplished sisters (Caro 1994). During the path to complete adolescence, cheetahs are especially social and interact with unknown individuals, with males potentially forming coalitions whilst females split to go on to produce their first litter (Durant et al. 2004; Durant et al. 2007).

Older and more experienced individuals have a greater chance of breeding compared to younger cheetah, due to a number of factors such as; foraging success and

kleptoparasitism (Sullivan 1988; Hesp and Barnard 1989; Gilardim 1994). Durant, (2000) also suggests the threat from other predators is mitigated when a cheetah becomes an adult due to being more experienced in predator avoidance. This behavioural trait acquired with age can only enhance reproductive performance since previous successful reproductive events may have occurred in their lives (Watcher et al. 2011).

As demonstrated from my analysis and the aforementioned developmental stages in cheetah's life history, these vast majority of individuals are being subject to far greater risks of mortality than those older individuals being translocated. If cheetah were to be removed from such unique exposure during adolescence, key behavioural mechanisms to avoid mortality and parenthood will unlikely be learnt (Laurenson 1994).

Vegetation & Location

Throughout the seasons across this 9-year study, greater phenological correlation of vegetation indices between reserves increased females' probability to produce and raise cubs to independence. Furthermore, the probability to raise cubs to independence was also greater when the mean difference of vegetation indices between reserves decreased. In combination, the complexities and variability of reserves vegetation has been shown to have great effect for post reintroduced cheetah success.

Normalized difference vegetation indices (NDVI) are sensitive to changes in rainfall and a good index for vegetation complexity by incorporating the changes in greenness, which could consequently affect the habitats visibility (Gigliotti et al. 2020). Within the small fenced nature reserves of the cheetah metapopulation, habitat vegetation varies across the country and influences cheetah success. Their ability to hunt and avoid intraguild competition is highly dependent on effective habitat selection and utilization (Gigliotti et al. 2020). Through movement between reserves, their surrounding habitats vegetation phylogeny change, therefore creating an altered probability of encounter that requires altering risk perception (Kotler et al. 1991; Hughes et al. 1994). Cheetah survival probabilities decreased when moved to reserves with an increased average vegetation index that consist of higher levels of dense vegetation with less visibility. Cheetah reside in habitats where coexistence with intraguild competitors is a necessity and requires the ability of refined spatial partitioning in order to reduce encounter rates

(Vanak et al. 2013). As one of their main intraguild competitors, lions utilize an array of habitat types, but have been shown to kill more frequently in dense vegetation (Davies et al. 2015). Cheetah moving to regions of higher vegetation index may not have the experience in competitor avoidance within such environments, therefore as subordinate predators are impeded. Counter to this possible explanation is that dense vegetation has been shown to help conceal those species at risk, allowing a 'competitive refuge', thereby minimising costly interactions with competitors or predators (Durant 1998; Pettorelli et al. 2009). The quality of a habitat in such competitive refuge might influence the ability to find and hunt prey in a new non-optimal habitat to which the individual is not as experienced in (Preisser et al. 2005; DeCesare, et al. 2014; Miller, et al. 2014).

The longitudinal difference between sender and recipient reserve shows that cheetah moved in a southerly direction have a great chance of producing a litter and raising a cub to independence. This could be in association with two of the discussed covariates; lion presence and vegetation phenology. 86% of reserves situated in the northern provinces have a present lion population, in comparison to only 23% in the southern provinces. Reserves situated in Limpopo had a 129% higher average vegetation index when compared to those in the Western Cape. Cheetah being sourced from such southern provinces and sent north consequently had very low chances of producing a litter and raising a cub to independence. The vast majority of northern metapopulation reserves are classified within the savanna biome, whereas south from this eco-region, most reserves reside in fynbos or grassland. Grasslands can provide concealment for cubs in proximity to their mothers and be open for those adults to detect dominant predators in order to divert the litter from an encounter (Hilborn et al. 2012). In addition to which, these habitats may promote cheetah survival indirectly through greater hunting success (Mills et al. 2014).

Overall considerations

Whilst the cheetah metapopulation continues to grow, careful consideration is required when interpreting success. Cheetah that are chosen to be reintroduced are required to be in good condition, due to the translocation costs. Some individuals receive supplementary medication such as vaccinations which in turn makes them advantageous to those resident individuals (Caldwell 2009). Once released onto their recipient reserves, individuals are closely monitored by radio telemetry tracking or reported through ecotourism ventures, being further subject to artificial involvement. Following reintroduction guidelines, if the reintroduced cheetah has not successfully hunted within a week, they are provided with supplementary food and this is repeated where necessary until an increase in condition. These measures are obviously taken to promote the chances of post reintroduction success, however consequently biasing the individual's comparison to other cheetahs due to their artificially inflated fitness and conditioning.

Nearly 15% of cheetah chosen for reintroduction do not survive the immobilization or translocation between reserves (EWT, unpublished data). These anthropogenic risks associated with the metapopulation are still taken due to the outweighing localized extinction prospects of the species. After which, there is evidence of increased stress and risk associated with adapting to a new environment on recipient reserves (Dickens et al. 2010). Despite these risks involved, individuals that do survive typically experience a reduction in competition on their recipient reserve due to being part of the sending reserves 'surplus' cheetah population. This reduction in cheetah per small fenced reserve associated with the metapopulation project lowers mortality risks related to intraspecific competition amplified through high densities. (Schoener 1973; Townsend 2008).

Causes of mortality are limited to comparing proportions of known mortalities, and in this study 52% of cheetah presumed to have died were never found. This large proportion needs to be considered when interpreting data presented in the proportional effect plots. Natural mortalities are often unknown due to carcasses being scavenged or decomposing before they are located whereas anthropogenic mortalities are more likely to be detected and hence reported (Woodroffe et al. 2007).

Spotted hyena have been proven to be a major source of cheetah cub mortality, especially in the Serengeti where they were the second largest threat (Laurenson 1994

and Durant 2000). Even the perceived presence of hyena was found to reduce cheetah hunting time and successful kill attempts (Durant 2000). This was not something explored in this study, and could be an associative effect with lion presence as analysed.

CONCLUSION

The cheetah metapopulation constitutes a large proportion of not only South Africa's but the worlds cheetah population. Maintaining such an established network of associated reserves greatly increases the connectivity of the country's already fragmented small fenced nature reserves. Considering the scale of the degree of uncertainty in the nation's free roaming population, the metapopulation can manage numbers accurately and most importantly produce informed population projections. The success of the South African cheetah metapopulation has now outreached to other countries with Liwonde National Park, Malawi reintroducing a population in 2017.

The management of the cheetah metapopulation will inevitably need to accommodate the ecotourism sector, the principle economic driver, without compromising long-term conservation goals. In this current period of economic instability, the viability of these privately run small fenced game reserves may come into question and ultimately the future of the cheetah in residence. My results show that careful consideration is needed when reintroducing cheetah without previous exposure to lion into reserves where there is a prevalent lion population. Appropriateness of recipient reserves vegetation phenology will also need to be addressed when planning future reintroductions. The recognition of impeded survival chances and breeding propensity in reintroducing younger cheetah will assist in sourcing suitable individuals that meet associated nature reserve's needs.

Restoration of endangered species populations through translocations may become increasingly necessary considering the scale of habitat fragmentation worldwide. There is great potential moving forward with the management of the metapopulation, with more than 10,000 fenced reserves in South Africa. The proliferation of such entities could play an increasingly important role in future conservation efforts for the cheetah. Whilst Africa presents incredible opportunities for conservation, it is home to the fastest growing human population. As pressure mounts for natural resources, those individuals devoted to the study of such enigmatic species like cheetah are witnessing the leading edge of signals indicating dramatic biodiversity erosion. Effective conservation efforts coupled with rigorous approaches, such as the collaborative metapopulation management are needed when setting ambitious biodiversity recovery targets.

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APPENDIX

Table 1: Sending reserve information, highlighting (grey) translocations that were excluded from the study due to anomalies and inconsistencies in data recording.

Sending Reserve Information				
Name	Size (km^2)	Biome	GPS	Lion Density
Monate	30	Savannah	S24.7515, E28.6669	0
Monate	30	Savannah	S24.7515, E28.6669	0
Gondwana	102.52	Fynbos	S34.0808, E21.9138	0.06827936
Witwater	65	Savannah	S24.0900, E28.4800	0
Captured free roamer		Savannah		
Captured free roamer		Savannah		
Captured free roamer		Savannah		
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096590909
Hlambanyati	75	Savannah	S28.1776, E31.8263	0
KalahariOryx	858	Savannah	S28.4512, E22.1731	0
Unknown Reserve				0
HESC	10	Savannah	S24.5138, E31.0320	0
Makutsi	19	Savannah	S24.1461, E30.5016	0
Makutsi	19	Savannah	S24.1461, E30.5016	0
PotgietersrusZoo	1	Savannah	S24.1728, E29.0182	0
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Karongwe	80	Savannah	S24.1766, E30.5516	0.0875
Samara	120	Nama Karoo	S32.4430, E24.7633	0.016666667
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096591
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096591
HESC	10	Savannah	S24.5138, E31.0320	0
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
HESC	10	Savannah	S24.5138, E31.0320	0
Unknown Reserve				0
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
Lalibela	100.34	Thicket	S33.4705, E26.2547	0.069762806
Lalibela	100.34	Thicket	S33.4705, E26.2547	0.069762806
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096590909
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096590909

Captured free roamer		Thicket		
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137255
GRGL	27.5	Fynbos	S34.2014, E21.6361	0
GRGL	27.5	Fynbos	S34.2014, E21.6361	0
ZuluNyala	68	Savannah	S27.9018, E32.2716	0
Tswalu	1000	Savannah	S27.2250, E22.4111	0.022
Tswalu	1000	Savannah	S27.2250, E22.4111	0.022
Karongwe	80	Savannah	S24.1766, E30.5516	0.0875
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Captured free roamer		Succulent Karoo		
Phinda	255	Savannah	S27.8230, E32.3400	0.137255
Phinda	255	Savannah	S27.8230, E32.3400	0.137255
Phinda	255	Savannah	S27.8230, E32.3400	0.137255
Shamwari	181	Thicket	S33.4670, E26.0504	0.055248619
Shamwari	181	Thicket	S33.4670, E26.0504	0.055248619
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Shamwari	181	Thicket	S33.4670, E26.0504	0.055248619
Hopewell	55	Thicket	S33.6269, E26.1044	0
LionsRock	10	Savannah	S28.2424, E28.4705	0
HESC	10	Savannah	S24.5138, E31.0320	0
Captured free roamer		Succulent Karoo		
Captured free roamer		Succulent Karoo		
Lalibela	100.34	Thicket	S33.4705, E26.2547	0.069762806
Lalibela	100.34	Thicket	S33.4705, E26.2547	0.069762806
Lalibela	100.34	Thicket	S33.4705, E26.2547	0.069762806
Lalibela	100.34	Thicket	S33.4705, E26.2547	0.069762806
MtCamdeboo	45	Nama Karoo	S32.2763, E24.8966	0
MtCamdeboo	45	Nama Karoo	S32.2763, E24.8966	0
Unknown Reserve				0
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Captured free roamer		Succulent Karoo		
Captured free roamer		Succulent Karoo		
MtCamdeboo	45	Nama Karoo	S32.2763, E24.8966	0
MtCamdeboo	45	Nama Karoo	S32.2763, E24.8966	0
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Thanda	155	Savannah	S27.8854, E32.1845	0.103225806
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963

Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
SableRanch	45	Savannah	S25.4361, E27.7177	0
SableRanch	45	Savannah	S25.4361, E27.7177	0
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Madikwe	750	Savannah	S24.8167, E26.2167	0.046666667
Madikwe	750	Savannah	S24.8167, E26.2167	0.046666667
Madikwe	750	Savannah	S24.8167, E26.2167	0.046666667
Madikwe	750	Savannah	S24.8167, E26.2167	0.046666667
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Hopewell	55	Thicket	S33.6269, E26.1044	0
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Captured free roamer		Succulent Karoo		
Captured free roamer		Succulent Karoo		
Captured free roamer		Succulent Karoo		
UkulimaFarm	10	Savannah	S24.5303, E28.1033	0
Mabula	120	Savannah	S24.7333, E27.9269	0
UkulimaFarm	10	Savannah	S24.5303, E28.1033	0
CheetahExperience	10	Nama Karoo	S29.0695, E26.1594	0
Phinda	255	Savannah	S27.8230, E32.3400	0.137255
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Sanbona	540	Succulent Karoo	S33.7233, E20.6152	0.012962963
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Samara	120	Nama Karoo	S32.4430, E24.7633	0.016666667
TigerCanyons	61	Nama Karoo	S30.2517, E25.0393	0
Unknown Reserve				0
Rietvlei	36	Grassland	S25.8969, E28.2939	0
uMhkuze	400	Savannah	S27.6500, E32.2500	0
uMhkuze	400	Savannah	S27.6500, E32.2500	0
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
KwaCheetah	10	Savannah	S24.5180, E29.9483	0
Captured free roamer		Succulent Karoo		
Captured free roamer		Succulent Karoo		
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667

MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Unknown Reserve				0
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Marakele	900	Savannah	S24.3833, E27.6167	0.017777778
Marakele	900	Savannah	S24.3833, E27.6167	0.017777778
Marakele	900	Savannah	S24.3833, E27.6167	0.017777778
Marakele	900	Savannah	S24.3833, E27.6167	0.017777778
Marakele	900	Savannah	S24.3833, E27.6167	0.017777778
Addo NP-Kuzuko	160	Nama Karoo	S33.1944, E25.4636	0
Addo NP-Kuzuko	160	Nama Karoo	S33.1944, E25.4636	0
Mabula	120	Savannah	S24.7333, E27.9269	0
DeWildt	10	Savannah	S25.6749, E27.9239	0
DeWildt	10	Savannah	S25.6749, E27.9239	0
DeWildt	10	Savannah	S25.6749, E27.9239	0
Hopewell	55	Thicket	S33.6269, E26.1044	NA
Hopewell	55	Thicket	S33.6269, E26.1044	NA
Hopewell	55	Thicket	S33.6269, E26.1044	NA
Hopewell	55	Thicket	S33.6269, E26.1044	NA
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
Shamwari	181	Thicket	S33.4670, E26.0504	0.055248619
Addo NP-Kuzuko	160	Nama Karoo	S33.1944, E25.4636	0.025
MZNP	240	Grasslands	S32.1833, E25.4367	0.054166667
Mabula	120	Savannah	S24.7333, E27.9269	0
Mabula	120	Savannah	S24.7333, E27.9269	0
Mabula	120	Savannah	S24.7333, E27.9269	0
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
SanWild	60	Savannah	S24.0353, E30.5194	0
SanWild	60	Savannah	S24.0353, E30.5194	0
SanWild	60	Savannah	S24.0353, E30.5194	0
Thanda	155	Savannah	S27.8854, E32.1845	0.103225806
Thanda	155	Savannah	S27.8854, E32.1845	0.103225806
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Rietspruit	55	Savannah	S24.3978, E30.9310	0.072727273
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018

Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
Amakhala	57	Thicket	S33.5102, E26.1544	0.122807018
Pilanesberg	572	Savannah	S25.2611, E27.1008	0.087412587
Rietvlei	36	Grassland	S25.8969, E28.2939	0
TigerCanyons	61	Nama Karoo	S30.2517, E25.0393	0
TigerCanyons	61	Nama Karoo	S30.2517, E25.0393	0
Pilanesberg	572	Savannah	S25.2611, E27.1008	0.087412587
Pilanesberg	572	Savannah	S25.2611, E27.1008	0.087412587
TigerCanyons	61	Nama Karoo	S30.2517, E25.0393	0
TigerCanyons	61	Nama Karoo	S30.2517, E25.0393	0
Unknown Reserve				0
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Shamwari	181	Thicket	S33.4670, E26.0504	0.055248619
KwaCheetah	10	Savannah	S24.5180, E29.9483	0
KwaCheetah	10	Savannah	S24.5180, E29.9483	0
KwaCheetah	10	Savannah	S24.5180, E29.9483	0
uMhkuze	400	Savannah	S27.6500, E32.2500	0
Shamwari	181	Thicket	S33.4670, E26.0504	0.055248619
uMhkuze	400	Savannah	S27.6500, E32.2500	0
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096590909
GRGL	27.5	Fynbos	S34.2014, E21.6361	0
GRGL	27.5	Fynbos	S34.2014, E21.6361	0
Amakhosi	55	Savannah	S27.6592, E31.6376	0.127272727
Karongwe	80	Savannah	S24.1766, E30.5516	0.0875
Amakhosi	55	Savannah	S27.6592, E31.6376	0.127272727
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Pilanesberg	572	Savannah	S25.2611, E27.1008	0.087412587
Shambala	115	Savannah	S24.2747, E28.0241	0.008695652
Samara	120	Nama Karoo	S32.4430, E24.7633	0.016666667
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
MtCamdeboo	45	Nama Karoo	S32.2763, E24.8966	0
uMhkuze	400	Savannah	S27.6500, E32.2500	0
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
MtCamdeboo	45	Nama Karoo	S32.2763, E24.8966	0
Samara	120	Nama Karoo	S32.4430, E24.7633	0.016666667
Gondwana	102.52	Fynbos	S34.0808, E21.9138	0.06827936
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Buffelsdrift	30	Succulent Karoo	S33.5280, E22.2975	0
Buffelsdrift	30	Succulent Karoo	S33.5280, E22.2975	0

Rietvlei	36	Grassland	S25.8969, E28.2939	0
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Makutsi	19	Savannah	S24.1461, E30.5016	0
Madikwe	750	Savannah	S24.8167, E26.2167	0.046666667
Entabeni	103.57	Savannah	S24.2233, E28.6594	0.067587139
Entabeni	103.57	Savannah	S24.2233, E28.6594	0.067587139
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Samara	120	Nama Karoo	S32.4430, E24.7633	0.016666667
Dinokeng	185	Savannah	S25.3800, E28.3805	0.037837838
Rietvlei	36	Grassland	S25.8969, E28.2939	0
Welgevonden	336.5	Savannah	S24.3147, E28.0541	0.035661218
Samara	120	Nama Karoo	S32.4430, E24.7633	0.016666667
DeWildt	10	Savannah	S25.6749, E27.9239	0
DeWildt	10	Savannah	S25.6749, E27.9239	0
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Mabula	120	Savannah	S24.7333, E27.9269	NA
Mabula	120	Savannah	S24.7333, E27.9269	NA
Mabula	120	Savannah	S24.7333, E27.9269	NA
Mabula	120	Savannah	S24.7333, E27.9269	NA
Phinda	255	Savannah	S27.8230, E32.3400	0.137254902
Laohu Valley	86	Savannah	S30.3267, E25.1610	0
Addo NP-Kuzuko	160	Nama Karoo	S33.1944, E25.4636	0
Manyoni	220	Savannah	S27.8054, E32.0345	0.045454545
Hopewell	55	Thicket	S33.6269, E26.1044	0
Kwandwe	176	Thicket	S33.1494, E26.5263	0.096590909
Hopewell	55	Thicket	S33.6269, E26.1044	0
Hopewell	55	Thicket	S33.6269, E26.1044	0
Marakele	900	Savannah	S24.3833, E27.6167	0.017777778

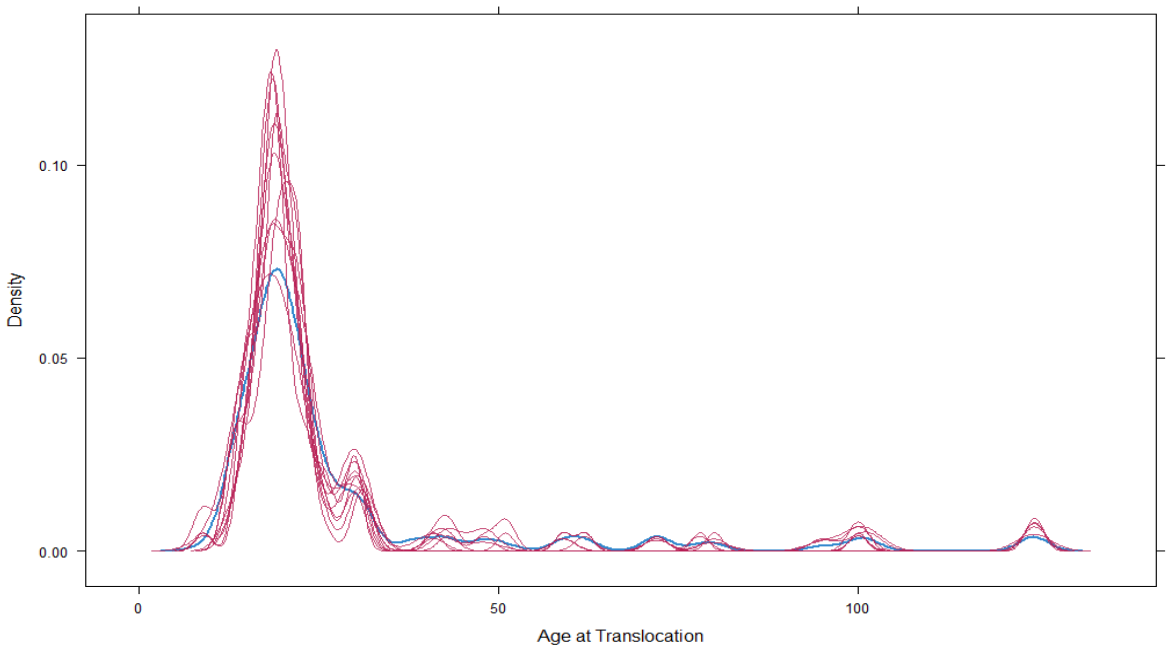

Figure 14: Density plot representing the true cheetah ages at translocation (blue), and the ten imputations for the missing values using Mice (red).

Table 2: Test for proportional hazards in cox regression assumptions.

Test for Proportional Hazards			
Covariate	rho	chisq	p
Age	0.03703	0.2170	0.64133
Sex	-0.01446	0.0322	0.85752
Savvy	0.21491	8.9521	0.06277
Lion1	0.13731	3.4775	0.06221
VI Correlation	0.02487	0.1182	0.73095
VI Difference	0.03809	0.2359	0.62719
Reserve Latitudinal Difference	0.07316	1.0760	0.29959
Reserve Longitudinal Difference	-0.06767	0.8062	0.36924
Savvy : Lion	-0.16282	4.6860	0.05941
VI Correlation : VI Difference	-0.03863	0.2325	0.62970

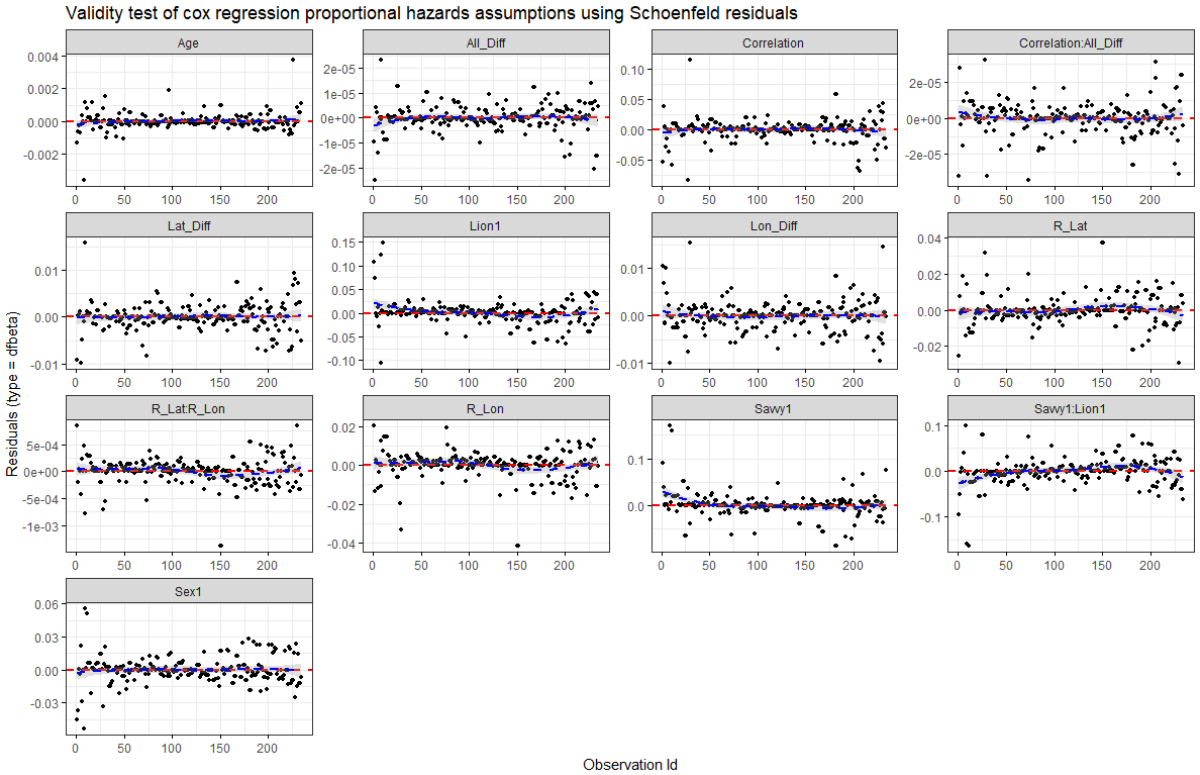

Figure 15: Validity test of cox regression proportional hazards assumptions using Schoenfeld residuals.