Cheetah (*Acinonyx jubatus*) mortality and survival in fenced reserves as part of a managed metapopulation across South Africa

By

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PLAGIARISM DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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This thesis was made possible through 25 years of monitoring records collected by countless volunteer researchers, reserve managers and field guides who dedicated their time to monitoring cheetahs. I am most grateful to Vincent van der Merwe who has spent the past 8 years coordinating the movements and data collection of hundreds of individual cheetahs and generously gave me access to the monitoring records. we thank EWT for their support in data sharing for student research. I was fortunate enough to have the support and guidance from another Vincent who also agreed to be my co-supervisor and provided invaluable help from project inception to the final edits. I am indebted to Prof. Justin O'Riain, my primary supervisor for taking on yet another stressed CB student and letting me be part of the wonderful bunch at iCWild. I thank the managers at Madikwe for providing a place to stay and the opportunity to see some of my study animals in the wild, this kept me motivated for the gruelling desk-based task ahead. Finally, I could not have completed this project without the 872 cheetahs that have lived and mostly died, may their fate help us improve conservation of their species.

Definitions and abbreviations

Translocation: the intentional human mediated movement of organisms. Includes three types:

> *Reintroduction:* the restoration of organisms into locations where they previously, but no longer, exist.
>
> *Introduction:* movement of organisms into spaces where they never existed previously.
>
> *Augmentation*: movement of organisms into places where other members of the species already exist.

Metapopulation: a set of geographically isolated populations, of the same species, that share individuals through dispersal, migration, or in the case of a managed metapopulation, through human mediated translocations.

Fenced reserve: wilderness or semi-natural areas that are fully fenced aimed at keeping wildlife in, while keeping illegal harvest and livestock out.

Coalition: two or more male cheetahs that form a bond and share a territory, usually with males from the same litter.

Singleton: adult or subadult single male cheetah with no coalition member.

Free roaming: animals whose movements are not constrained within fenced boundaries.

Wild cheetahs: cheetahs that hunt their natural prey and are exposed to natural environmental processes.

EWT: Endangered Wildlife Trust

CMP: Cheetah Metapopulation Project, used interchangeably to refer to the study site.

ABSTRACT

Large carnivores require expansive habitat to meet their life history needs making them vulnerable to the loss and fragmentation of natural habitat. This, in addition to human persecution has led to substantial population and range reductions of most of the world's large carnivores over the past century. Cheetahs are no exception, occupying only 12% of their historic range in South Africa. Reintroduction programs have attempted to re-establish cheetahs to parts of this historic range, and increasingly the potential exists for their conservation in smaller fenced game reserves**.** However, this requires managers to maintain demographic and genetic diversity. In 2011, the Endangered Wildlife Trust initiated a project which coordinates movements between reserves using a metapopulation framework. This coordinated management approach is still in its infancy and little data exist on how reintroduction success varies amongst individuals and reserves. This study aims to examine the causes of mortality and the factors influencing cheetah survival on 20 reserves using individual life history records from 1993-2018. We assessed demographic, environmental, and management factors that are predicted to influence cheetah survival using a Cox proportional hazard model. Predation, mostly by lions (*Panthera leo*) accounted for 39% of known mortalities. However, the presence of spotted hyena (*Crucota crucuta*) posed the greatest threat to survival. Contrary to my prediction, translocation improved survival when controlling for age. Survival has also improved with time since the coordinated metapopulation approach was initiated in 2011. We created a nomogram which can be used by practitioners to predict cheetah survival within the metapopulation. Our study shows the importance of monitoring reintroduction efforts and encourages similar methods be used for other species of conservation concern that are managed within a metapopulation framework.

INTRODUCTION

Threats to large carnivores worldwide

Current rates of extinction are about 1000 times the background rate of extinction (Pimm et al., 2014). Large-bodied species are especially vulnerable to human-driven disturbances such as habitat fragmentation as they require large areas for their survival (Soulé 1987). In the region of Southeast Asia, India and China, nearly two-thirds of mammals that weigh 10 kg or more are threatened with extinction because of rapid increases in land clearing and human population density over the past 50 years (Tilman et al., 2017). Tropical South America and sub-Saharan Africa face a similar trajectory with 30-60% of large mammals classified as threatened with extinction (Tilman et al., 2017).

Large carnivores roam over large areas, and the loss and fragmentation of natural habitat brings them into more frequent contact with people and their livestock (Woodroffe et al., 2007). Areas where humans and carnivores share space are thus typically characterized by high carnivore mortality and threatened human safety and livelihoods. This has led to the controversy over whether to protect or eradicate surviving carnivores where human-carnivore conflict exists (Darimont et al., 2018; Treves, Krofel & McManus, 2016; Ripple et al., 2014). Limited dispersal opportunities in fragmented landscapes have also led to demographic and genetic isolation increasing extinction risk due to environmental stochasticity. Together these adverse impacts may drive populations toward extinction through a process known as the “extinction vortex” (Soulé 1986; Brook et al., 2008).

With further human population growth, an increase in demand for cropland and further habitat loss and fragmentation, there will no doubt be an increased extinction risk for many large carnivore species. In Sub-Saharan Africa, large relatively uninhabited expanses of savannah have shrunk considerably in the last 50 years and human population projections suggest that much of this habitat will be transformed in the next 40 years (Riggio et al., 2012, Tilman et al., 2017). Under “business as usual” projections, 430 million hectares (equivalent to half of the area of continental United States) is expected to be cleared for urban and agricultural activities in sub-Saharan Africa (Tilman and Clark 2014). Specifically, in South

Africa, the human population is growing at a rate of 2.7% per year, above the 1.1% global average (Cincotta et al., 2000). There is a tendency for population growth to occur in areas surrounding current protected areas, potentially leading to increased human-wildlife conflict (Harcourt, Parks & Woodroffe, 2001).

Importance of large carnivores

Despite naturally occurring at low densities, large carnivores play a key role in regulating terrestrial ecosystems. Their removal can lead to cascading effects through lower trophic levels Large carnivores may also provide buffering to exotic species invasions and disease outbreaks by structuring and stabilising ecosystems in which they persist (Schmitz et al., 2010, Ripple et al., 2014). While arguments are made that human hunting can substitute the role of large carnivores, differences in the behaviour of prey to predation risk in the "ecology of fear" may have cascading effects on ecosystems, such as plant community and structuring (Cromsigt et al., 2013). This would be difficult for humans to effectively mimic (Laliberte & Ripple, 2004).

The role of large carnivores in regulating ecosystems highlights the value of large carnivore conservation despite conflict with anthropogenic land use. Conservation biologists and society at large, need to address carnivore declines with a multipronged approach in the face of growing human pressure on wildlands (Estes et al., 2011). Promotion of increased tolerance for human-carnivore coexistence, new legal instruments and effective implementation are recommended (Ripple et al., 2014). Unfortunately, although this may be possible in specific cases, human-carnivore tolerance has failed throughout most of human history, and it would be naive to expect broad-scale mutual co-existence in the future. More large protected areas and habitat connectivity are endorsed (Ripple et al., 2014), but protected areas alone may not be sufficient, especially in regions where extensive habitat and land-use change has already occurred, and restoration is unlikely. Where populations have gone extinct, or fragmentation prevents viable populations, translocations of threatened species may be an effective tool for reducing extinction risks and potentially restoring ecosystem function (Wolf & Ripple 2018).

Fenced Reserves

Fencing is a tool for protecting wildlife populations from over hunting, poaching, human-wildlife conflict and keeping valuable wildlife within the bounds of the property (Hayward, Matt W. et al., 2007). Despite this, the conservation value and cost effectiveness of fences are often debated (Durant, Sarah M. et al., 2015; Woodroffe, Hedges & Durant, 2014; Packer, 2013). Although fencing can reduce human-wildlife conflict, they are a barrier to landscape connectivity. Another concern is that fencing can prevent people from accessing natural resources such as wood, thatch, and traditional medicine within reserves, adversely impacting community-based incentives for wildlife conservation and instead generating hostility (East et al., 2012; Gadd, 2012). Furthermore, even well-constructed, well-maintained fences are not human proof, and the fence itself may serve as a readily available source of snare wire (Lindsey et al., 2011). Both wildlife and people breach fences, necessitating frequent and costly ongoing maintenance in addition to the high initial construction costs (Kesch, Bauer & Loveridge, 2014; Lindsey, Peter A. et al., 2012).

Most of the fenced reserves in South Africa are privately owned and managed as an ecotourism business. Fenced reserves must therefore be economically viable first and foremost, but conservation and profitability need not be mutually exclusive (Langholz & Kerley, 2006). Both reserve managers and tourists are increasingly concerned with contributing to rare species conservation, and many of the species in peril are also well sought after by tourists (Sims-Castley et al., 2005). Small fenced reserves can provide an ideal setting for monitoring large carnivore demographics with relatively low additional cost to reserve management and tourism operations. Fenced reserves can have relatively high predator densities, making encounters with predators frequent and individual recognition possible. Large predators can be an asset for tourism revenue, and most reserves monitor their demography voluntarily. Collecting large enough sample sizes is often a challenge to carnivore research, but merging monitoring data across reserves provides an opportunity for comparative studies with relatively robust sample sizes while minimizing cost.

Metapopulation management for wildlife in crisis

Translocation, or the intentional transport and release of animals to re-establish (i.e. reintroduction), introduce or augment a population, has been used to try and recover extirpated or depleted populations (Lewis et al., 2012). Translocations of endangered animals into their native habitat has become increasingly popular, and there have been several well publicized reintroductions for conservation purposes (Hayward and Somers 2009), such as the reintroduction of wolves to Yellowstone National Park (Ripple et al., 2014).

With human populations in Africa projected to quadruple by the year 2100 (Department of Economic and Social Affairs 2016), large carnivore conservation will increasingly be challenged with mitigating threats from increased human pressure on remaining wildlife habitat. Conservationists are often unable to alter development in the face of other pressing socio-economic issues, especially in low income countries where alleviating poverty and food security takes precedence. Thus, if we are to have any chance of success in preventing continued biodiversity loss, we must consider novel approaches to preventing species extinctions in an increasingly fragmented landscape in tandem with other conservation actions.

One approach that has been gaining momentum in the past few decades has been combining advancement in species translocation techniques within a metapopulation theory framework (Buk et al., 2018). A ‘metapopulation’ in its most simplistic sense is a “population of populations” (Levins 1969). In theory, the smaller and more isolated a population, the more prone to extinction by environmental stochasticity. Dispersal between populations can have a rescuing effect with the metapopulation persisting through source-sink dynamics (Keymer et al., 2000). When habitat corridors are not a feasible option, conservation practitioners have taken the initiative to translocate animals between populations to mimic natural dispersal (Hanski, 1999). The International Union for Conservation of Nature (IUCN) identified translocations as a necessary tool in metapopulation expansion and management towards species recovery (Batson et al., 2015). Translocation is a strategy for spreading the risk of demographic and environmental stochasticity for isolated populations of rare species (Hastings & Harrison 1994;

Macdonald & Service 2009). This human-mediated metapopulation management can enhance demographic rescue effects and genetic diversity with the goal of maintaining a viable population in perpetuity (Macdonald & Service 2009). Metapopulation management has been used to conserve threatened taxa such as black rhino (*Diceros bicornis*), black-faced impala (*Aepyceros melampus perersi*), African wild dog (*Lycaon pictus*), and cheetah (Matson et al., 2004; Knight & Kerley 2010; Davies-Mostert et al., 2015; Buk et al., 2018). However, reintroductions of endangered species have had varying rates of success. Hence, more post-release monitoring and research are recommended (Fischer & Lindenmayer 2000; Jule et al., 2008).

Cheetah status and distribution

Cheetahs are open landscape specialists (Hilborn et al., 2012; Mills et al., 2004), but use a wide variety of habitats including deserts, savannah, woodland, and dry forest and are absent from tropical and mountain forest (Durant, Sarah M. et al., 2017). Cheetahs are adapted for high speeds and require good visibility to detect and pursue prey, but also benefit from high grass and bush for stalking prey and hiding cubs from other predators (Rostro-García et al., 2016; Mills et al., 2004). In southern and eastern Africa, they primarily occupy the Savannah biome, characterised by a mix of grassland, bushveld, and woodland (Low & Rebelo, 1996). However, overgrazing has led to bush encroachment of grasslands and reduced cheetah prey densities (Khorozyan et al., 2015; Kgosikoma, Mojeremane & Harvie, 2013).

Cheetah are listed as vulnerable to extinction by the World Conservation Union (IUCN) Red List of Threatened Species (Durant et al., 2017). Historically, they roamed most of Africa and southwest Asia. but the species range has decreased by 91% in the past 13,000 years. Recent estimates put the African population at just 7,100 cheetah (Durant, Sarah M. et al., 2017), of which 77% occur outside of protected areas. It has been recommended that the species be uplisted from vulnerable to endangered (Durant et al., 2018).

Southern Africa is considered a stronghold for the species with 60% of the total population (4500 individuals), despite eradication from 78% of their historical range in this region. Most cheetah are found in the contiguous transfrontier landscape covering southern Angola, Botswana, Namibia, and northern South Africa (Durant, Sarah M. et al., 2017). Populations are however decreasing across their range in sub-Saharan Africa, with South Africa being the only country with a modest increase in the past three decades (Weise et al., 2017).

In South Africa cheetahs are nationally listed as vulnerable with legislation on their protection varying by province (Durant et al., 2016). Early records of their distribution in South Africa are incomplete, but they are thought to have been widely distributed in all suitable habitats (Purchase et al., 2007). Due to human persecution, habitat loss, and illegal trade, cheetahs in South Africa occupy only 10% of their historic range (: van der Merwe V, Marnewick K, Bissett C, Groom R, Mills MGL, Durant SM, 2016). Free roaming cheetahs occur throughout the northern part of South Africa in the Northern Cape, North West province, and into Limpopo and in Kruger National Park (Marnewick K, Hayward MW, Cilliers D, Somers MJ, 2009). This population increased after Democracy in South Africa was established, which stimulated regional tourism, land use change from cattle to wildlife ranching (Marnewick et al., 2009, Durant et al., 2015). This transition has increased prey availability and decreased intraguild competition with the removal of lions and spotted hyaenas (*Crocuta crocuta*) from most game farms (Marnewick et al., 2007; Laurenson, 1994). Recent conservative estimates put the free roaming population at approximately 3940 adults and adolescents across the large transboundary landscape encompassing Botswana, Namibia, northern South Africa, south-western Zambia and south-western Mozambique (IUCN 2019). However, cheetahs do experience conflict on game farms when they prey on economically valuable game (IUCN 2019).

In addition to the free roaming population, there have been cheetah reintroductions into over 58 reserves (16 state-owned and 42 private game reserves) (EWT, unpublished data, 2017) across the southern and eastern halves of the country. As one of the more developed countries in Africa, fenced release sites are currently the only option for cheetah reintroductions in South Africa.

The managed metapopulation approach for cheetah conservation

Human population growth and habitat fragmentation are especially problematic for viable populations of large carnivores (Soule 1987), and cheetahs are no exception (Buk et al., 2018). Their wide-ranging behaviour and low densities even in favourable habitat, mean only large areas can support viable populations (Lindsay et al., 2011; Cristescu et al., 2018). The potential exists for cheetah conservation on private lands because of the proliferation of fenced reserves (Davies-Mostert, Mills & Macdonald, 2015). However, the persistence of cheetahs on these reserves may be influenced by the fates of a few individuals and are susceptible to random demographic effects, genetic stochasticity and environmental variation (Lande 1993; Ballou & Lacy 1995: Reed et al., 2003). Circumventing these hazards requires human-mediated movement of cheetahs between reserves to promote demographic and genetic resilience of the population (Akçakaya, Mills & Doncaster, 2007).

Following legislation providing user rights and ownership of wildlife to landowners in 1991, and the onset of democracy in South Africa, game farming and ecotourism ventures on private lands proliferated (Smith & Wilson, 2002). The estimated shift in land-use conversion from livestock to wildlife ranching was 2-2.5% per annum from 1994-2004 (Bothma & Van Rooyen, 2005). These changes influenced wild cheetah populations on several fronts. Game farming increased available prey for cheetahs and expanded the distribution of the free ranging population on South Africa’s northern border, and to a smaller extent, on the western boundary of Kruger National Park (EWT, unpublished data). Conversely, this also led to increased persecution of cheetahs by farmers protecting their valuable game from predation (Cousins et al., 2008). On the other hand, large carnivores have potential tourism value providing an incentive for cheetah reintroduction and conservation (Buk et al., 2018).

Early reintroductions of cheetahs were sourced from the Namibian free roaming population, followed by translocating problem animals from South African farmlands. This was mainly a technique for conflict resolution rather than a proactive reintroduction program to establish viable populations (Durant, Sarah M. et al., 2007). Cheetahs were removed from human-carnivore conflict hotspots to private reserves where they were protected (Buk & Marnewick, 2010). Despite the reintroductions of a minimum of 343 cheetahs, the population was not increasing and translated into 281 living cheetahs in 2009. There was a concern that the program was creating a sink for free roaming populations and discouraging predator tolerance by ranchers (Buk et al., 2018). Additionally, the reintroduced cheetah populations were managed largely in isolation of one another, leading to concern over the genetic health of the various isolated populations (Hunter et al., 2013; Hayward, Matt W., O'Brien & Kerley, 2007).

Together these concerns prompted a new integrated management approach between reserves using a metapopulation approach, similar to that adopted for African wild dogs (Gusset et al., 2007; Buk et al., 2018). The vision was a national network of reserves with translocations between reserves to enhance demographic and genetic integrity of the population without supplementation from the free roaming cheetah population. In 2011, the Endangered Wildlife Trust (EWT) launched the Cheetah Metapopulation Project (hereafter CMP) with reintroductions from outside/free-ranging cheetahs being avoided (Lindsay et al., 2009). The population subsequently grew from 217 in 2011, to 357 cheetahs in late 2018 (van der Merwe, pers. comm). In June 2017, metapopulation cheetahs were used for reintroduction into Liwonde National Park, Malawi, expanding the CMP beyond South African borders (van der Merwe, pers. comm).

Cheetah survival and causes of mortality

Where cheetahs coexist with other large carnivores, they are vulnerable to predation, particularly the cubs. In the Serengeti, as much as 73.2% of juvenile (>14 months) mortality is caused by predation (Laurenson 1994), and conversely in Namibia, where few other large carnivores exist, the level of cub mortality is far lower (Marker, L. L. et al., 2003). Regions outside of protected areas where lions and spotted hyenas have largely been eradicated, have reported higher cheetah densities than in protected areas (Durant, S., Mitchell, N., Ipavec, A. & Groom, R., 2015). However, cheetahs have evolved alongside other predators and have developed coping mechanisms and are able to persist by altering habitat use and activity patterns to avoid large carnivores (Bissett et al., 2015; Swanson et al., 2014; Cooper, Pettorelli & Durant, 2007). Anthropogenic causes of mortality, mostly conflict with farmers, is the leading cause of cheetah mortality outside of protected areas (Cristescu et al., 2018). This has been especially true for Namibia where from 1980 to 1991, farmers reported killing 6293 cheetah in defence of their livestock (Marker, L. et al., 2007). Free roaming cheetahs in Zimbabwe and South Africa are confronted with similar issues (Marker-Kraus & Kraus, 1997). Other human induced mortality includes vehicle collisions, poisoning, electric fencing, and illegal snares (Boast, Chelysheva, van, Schmidt-Küntzel, Walker, Cilliers, Gussett et al., 2018).

Translocation efforts

Translocations of carnivores have also been used to mitigate human-predator conflict (Linnell et al., 1997; Fontúrbel & Simonetti 2011), and in some cases resulting in successful establishment of populations of grey wolf (*Canis lupus*), lion and cheetah (Bradley & Pletscher 2005; Purchase et al., 2006; Hayward & Somers 2009). However, incidents of homing behaviour, continued livestock predation, and low survival have been reported (Linnell et al., 1997). Boast et al. (2016) suggested that moving problem cheetahs in Botswana should cease and instead, farmers should use conflict mitigation techniques that promote coexistence of predators and humans. A similar study in Namibia also found that translocations of conflict cheetahs to free-range environments resulted in cheetahs re-entering farmlands where they faced an elevated risk of persecution. Survival was lowest in the first three months post-release, but cheetahs that survived the initial post-release period (~90 days) often settled and females reproduced successfully (Weise et al., 2015). In Zimbabwe, a translocation of 14 adult cheetahs from commercial ranches to Matusadona National Park was considered successful after four years despite high densities of lions (0.31/km^2) (Purchase 1998).

A review on the survivorship of captive-born versus wild-caught carnivores used in reintroductions found captive-born carnivores are significantly less likely to survive. They were more susceptible to starvation, sympatric predators, disease, and human induced mortalities (Jule et al. 2008). Animals reintroduced into fenced reserves experienced greater reintroduction success compared to animals reintroduced into free-ranging environments (Boast, Chelysheva, van, Schmidt-Küntzel, Walker, Cilliers, Gusset et al., 2018). As it is difficult for cheetahs to leave the reserve, they are more protected from human-predator conflict and generally receive greater follow-up care than is possible for cheetahs released into free-ranging areas (Boast, Chelysheva, van, Schmidt-Küntzel, Walker, Cilliers, Gusset et al., 2018)). Survival of cubs after emergence to their first year was 60% in fenced reserves, and negatively correlated with large carnivore presence (Bissett & Bernard 2011). From 2000 until the end of 2006, Marnewick et al. (2009) investigated the survival of free roaming cheetahs translocated to 27 fenced reserves in South Africa. The mean annual survival was 77% over a five-year period. The main cause of death was predation by lions, leopards, and conspecifics. Records (1992-2016) from 293 known cheetah mortalities within the cheetah metapopulation reported lions as the single greatest cause of mortality (31.1%), with all large carnivores together accounting for 53.2% of all deaths (Buk et al. 2018). Anthropogenic causes of mortality still occur in fenced reserves, including mortality during immobilisation and while housed within bomas. Understanding the impacts of translocation on a cheetah's survival and mortality is important when looking at whether metapopulation management is an effective tool for conserving the species.

Knowledge Gaps

Buk et al. (2018) published on the same cheetah population analysed in this study with a broad focus on lessons learned from establishing a managed metapopulation. This included a summary on the causes of mortality of over 450 cheetahs from 1992-2016. However, age and sex specific causes of mortality were not specified. Differences in mortality between adults and cubs and females versus males can have significant influences on the viability of a population. For instance, results from demographic modelling of Serengeti cheetahs suggests that the influence of survivorship of juveniles has a relatively low effect on population growth compared to adult survival (Crooks, Sanjayan & Doak, 1998). Marnewick (2011) also analysed the survival of cheetahs translocated from the free roaming populations to fenced reserves. Although the data presented in this study may have some overlap, our analysis include cheetahs that were born in fenced reserves allowing us to compare the effect of translocation on survival. Additionally, the earlier dataset of Marnewick (2011) was limited to a five-year period and does not control for covariates such as sex or habitat. By using a multivariate survival method, we can address the relative effect of our predictor variables on cheetah survival.

Purpose of the study

Although the CMP population has increased over the last five years, growth fluctuates and varies between reserves with 48% of reserves not providing a net benefit to the metapopulation (i.e. translocations to other reserves did not exceed translocations from other reserves). Translocations can be expensive, time consuming, and pose additional risk to the animals involved, yet the factors that contribute to their success are not well understood (Lewis et al., 2012; Weise et al., 2015). This project aims to enhance our understanding of the factors contributing to cheetah mortality in fenced reserves as a valuable starting point in predicting the success of metapopulation management decisions. It is important to understand the relationships underlying survival and implications for meeting population goals.

The primary objectives of this project are to:

- o Identify the sex and age specific causes of cheetah mortality in fenced reserves of South Africa and Malawi.
- o Determine the demographic, environmental and management variables that influence cheetah survival.
- • Directly inform translocation decisions for metapopulation management.

Ecological and evolutionary processes structure animal populations by variation in survival rates among age and sex classes (Clutton-Brock & Sheldon, 2010). Consequently, population sex and age structure will respond differently to environmental variation and human mediated pressure (Milner, Nilsen & Andreassen, 2007; Gaillard, Festa-Bianchet & Yoccoz, 1998). We hypothesize that demographic class plays an important role in cheetah mortality and survival patterns in the CMP. Intraguild competition can have profound impacts on large carnivore communities guilde (Vanak et al., 2013; Fuller & Sievert, 2001). Cheetahs are considered a mesopredator in the African large carnivore community and we were interested in assessing the individual impacts of species known to kill and compete with cheetah (Buk et al., 2018). Additional expected outputs from this project include age and sex specific causes of mortality. Understanding demographic variation in survival is important for predicting future viability of the metapopulation (Soulé 1987). In addition, we hypothesize that the environment and management of a reserve influences cheetah survival. We also compare survival rates before and after a coordinated metapopulation approach was initiated as an indication of the overall effectiveness of this conservation approach.

Based on a review of the literature and expert opinion by one of my supervisors who has over eight years of experience working with cheetahs, we made the following predictions listed in Table 1. Our explanatory variables are those we predict influence cheetah survival that we could reliably acquire data for all study site reserves throughout the study period.

Table 1. List of explanatory variables used in our survival models and predicted influence on cheetah survival in CMP fenced reserves across South Africa between 1993-2018.

Explanatory variables	Hypothesis and predictions
Demographic	Demographic class plays an important role in cheetah mortality and survival patterns in the CMP
Age	Cubs will have lower survival, followed by juveniles and subadults, with adults having the highest annual survival rate (Laurenson 1994)
Sex	There will be a relationship between sexes and survival (Durant et al., 2004)
Group	Positive relationship for male cheetah that are part of a coalition vs singletons (Caro & Collins 1987)
Environmental	The environmental conditions of a reserve, especially dominate predators, play an important role in cheetah survival
Reserve biome	Positive relationship for savannah and grassland biomes; negative for fynbos and thicket (Mills 2005)
Reserve size	Positive relationship between reserve size and survival (Ray et al., 2005)

Dominant predators	Intraguild competition plays an important role in cheetah mortality and survival patterns in the CMP
Large predator species	Negative relationship with the number of large predator species and cheetah survival (Bissett & Bernard 2011)
Lion	Lion presence will have the strongest negative relationship with cheetah survival out of the large predator guild (Bisset & Bernard 2011; Buk et al., 2018)
Leopard, spotted hyena, brown hyena, african wild dog	Negative relationship with cheetah survival and presence of these large predator species (Vanak et al 2013; Buk et al., 2018)
Management	The role of human management influences cheetah survival in CMP reserves
Era	Positive relationship between cheetah survival and initiation of a coordinated metapopulation approach (2012-2018) and survival (Buk et al., 2018).
Tenure	Privately owned reserves will have a positive influence on cheetah survival compared to State owned reserves
Origin	Negative correlation with survival of cheetah translocated from outside the reserve compared to native born cheetah (Kemink & Kesler 2013)

METHODS

Study area

The study used the life history records of wild cheetah collected from 20 out of 57 CMP fenced reserves across South Africa and one reserve in Malawi. The reserves were selected based on the availability of records for the data that we needed. We define fenced reserves as properties that are fully fenced and comply with provincial and national regulations for keeping large predators. Most of the fenced reserves are privately owned (17) with two state owned and one recent reintroduction to a National Park in Malawi sourced from South Africa's metapopulation. For management purposes, the South African reserves are grouped into five geographical clusters; Kalahari (only one reserve not included in this study), Waterberg, Lowveld, Eastern Cape and KwaZulu-Natal (Figure 1.) The reserves range in size from 4500 to 94 000 hectares. Habitat is skewed towards Savannah, but includes Albany Thicket, Fynbos, and Dry Highveld Grassland (Rutherford, Mucina & Powrie, 2006).

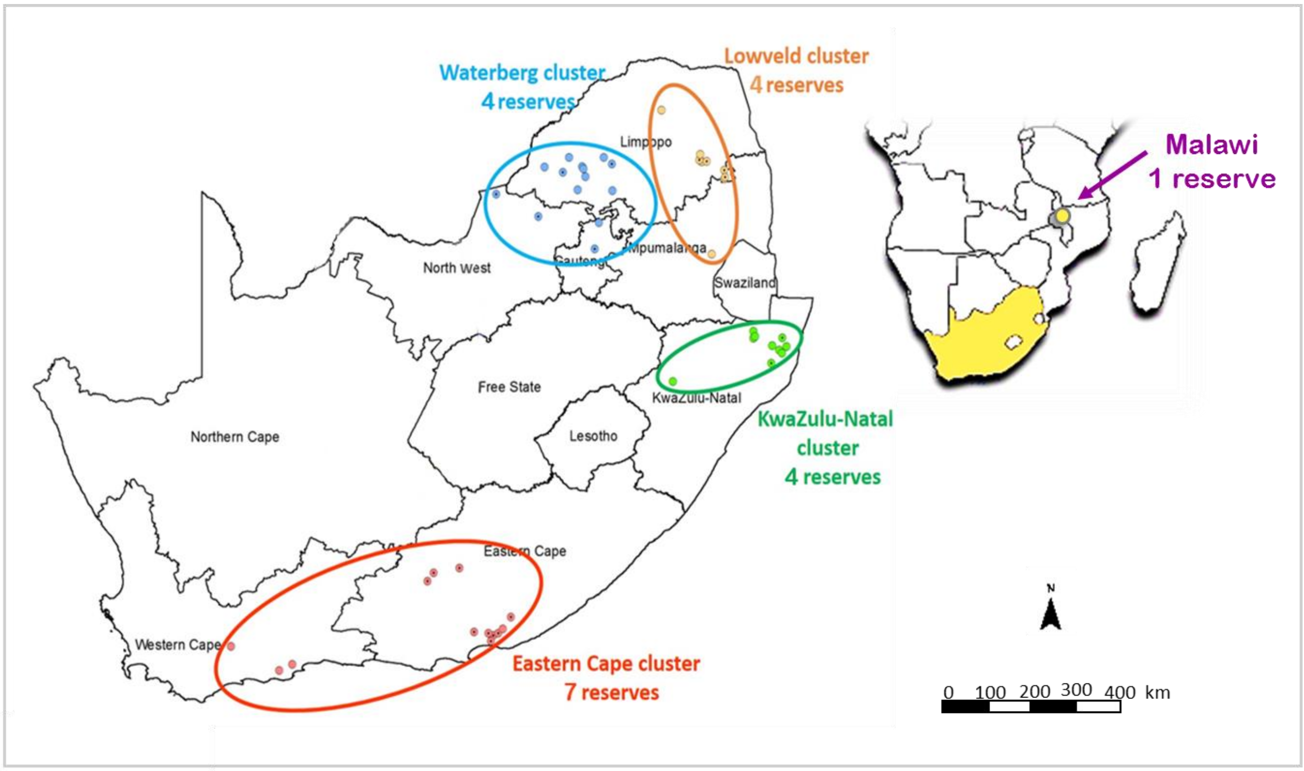


Figure 1. Locations of fenced reserves that form part of the cheetah metapopulation in South Africa with the number of sites in each geographical cluster used for this study between 1993-2018, including one reintroduction site in Malawi sourced from the CMP.

Data collection

Reserve owners voluntarily opt to be part of the CMP. Translocated cheetahs were fitted with tracking devices (or one per singleton/male coalition) for post release monitoring after a 2-3 month period in a boma. Bomas were fenced holding areas within the reserve that were used for habituating cheetahs to their new environment. Data on the survival, social and reproductive status of cheetahs released into reserves was collected by reserve managers, researchers, volunteers and dedicated cheetah monitors. Reserves only contained an average of six cheetahs and even uncollared cheetah are usually individually recognized by reserve staff. Since 2011, all cheetah births and deaths for reserves within the metapopulation were recorded in monthly reports sent to the CMP by each reserve. Prior to 2011, data were obtained from reserve monitoring records consisting of individual life history data. Translocation records were provided by the Endangered Wildlife Trust's Cheetah Metapopulation database and the National Cheetah Conservation Forum.

Causes of mortality were determined by visual assessment of the carcass and surrounding area for signs including spoor, hair, dung, nearby large predator sightings or at times by a veterinary necropsy. Monitoring effort may have varied across reserves and over time; therefore, our reported known causes of death should be interpreted conservatively, recognising that these data cannot be directly compared with other areas without the risk of confounding biases associated variation in monitoring intensity (Woodroffe et al., 2007).

Analyses

Our broad objective was to first provide baseline annual survival rates for the South African cheetah metapopulation and to compare these rates to those obtained for free roaming cheetah populations in Namibia and the Serengeti. The next task was to compare the observed lifetime survival time by sex and management era of individual cheetah and to describe the known causes of mortality. We used these data to explore the relationship between survival time and a suite of explanatory variables (see Table 1) creating separate hazard models for all ages combined and adults only, given that only adults are translocated. Finally, we compared fitted survival curves for demographic, environmental and management factors. With all survival analyses we partitioned cheetah age into three separate age classes: juveniles 3-12 months, subadults 12-24 months, and adults >24 months, following previous studies (Durant et al., 2004; Marker et al., 2007; Marnewick et al., 2009). We excluded cubs younger than three months of age to limit bias associated with the non-detection of cubs before den emergence (Marnewick et al., 2009).

Baseline survival

To calculate age specific survival, we divided the total number of deaths by the number of individuals alive within each age class for each month. We then averaged these values and raised them to the 12th degree to get mean annual survival using only uncensored (e.g. complete survival time is known) cheetah observations (Nohrman, 1953). To derive observed survival probabilities for the metapopulation over the past 25 years we employed the Kaplan-Meier estimator, a non-parametric statistic which measures months survived from birth until death using a survival function from lifetime data which can account for right censored observations, when the outcome of survival is unknown (Kaplan & Meier, 1958). We compared survival curves by sex and before/after the inception of the CMP using the log-rank test. Analyses were run using *surv* and *survfit* function in the package 'survival' (Therneau & Grambsch 2000) in R statistical software version 2.42-3 (R Core Team 2018).

Mortality

To describe cheetah mortality in the study area, we first summarized causes by age class; cubs 3-6, juveniles 6-12, subadults 12-24, and adults >24 months. To test if the cause of mortality varies by sex, age, management era and reserve site factors presented in Table 2, we categorised all known causes of mortality into five major categories; predators, conspecifics (i.e. cheetah), anthropogenic, translocation, and other natural causes of mortality. We used conspecific as a separate category from predators because we suspected there could be differences in mortality by sex or age class. We then produced baseline-categorical models to compare the probability of each known cause of death to our explanatory variables (see Table 2). Significance of terms used for each model was assessed using a Type III ANOVA (Chambers & Hastie, 1992). Significant terms were then fitted with multinomial log-linear models to test relationships between broad categories of mortality using the *multinom()* function in the package 'nnet' version 7.3-12 (Venables & Ripley, 2002).

We computed the estimated marginal means (EMMs) to test predictions with weight in proportion to the frequencies in the mortality data of the covariate combinations that are averaged over, using package 'emmeans' version 1.3.2., (Russell, 2018). The p values were adjusted using a post-hoc Tukey test to compare all possible pairs of means (Tukey, 1949) using the `emmeans´ package. We created fixed effects plots for a visual comparison between probability of dying of a cause and a covariate of interest. We intentionally presented the raw mortality probabilities without controlling for covariates because they have dramatic influences on the results because some categories had small sample sizes making results of the analysis difficult to interpret (Zuur et al., 2009). Additionally, the cause of mortality is only known for half of all cheetah. Thus, causes of mortality as analysed here were used as qualitative information to supplement our survival analysis. Since we did not control for the fact that cheetahs can only be killed by lions on reserves where lions exist or die from translocation complications if they experienced a translocation, we compared causes of mortality between reserves with and without lions, and cheetah that experienced a translocation event verses not. This was done to evaluate the causes of death in the absence of these two major sources of mortality listed in Table 2.

Survival Models

To investigate the association between survival time and the explanatory variables listed in Table 1, we used a multivariable survival model with a partial approach to data reduction (Harrell, 2014). Date of birth was estimated to be accurate to the nearest month. Since we included life history records spanning over 25 years, survivorship was measured using the Cox proportional hazards method that allows for staggered entry of individuals and can address covariates and multivariable relationships (Heisey & Fuller, 1985). This method also allows for inclusion of data from censored animals. The Cox proportional-hazards regression model described the probability of mortality if the cheetah survived up to a certain point in time, considering covariates in a regression analysis. The impact of coefficients was estimated from the data using package '*rms*' version 5.1-2 and 'survival' in R statistical software version 3.5.1 (Harrell 2014). These models estimated the effects of the predictor variables on the survivorship by comparing individuals who died to those in the same cohort that did not die (Cox, 1984). The explanatory variables for which we had dependable data, and which were considered important for interrogating cheetah survival (number of months survived), included origin, reserve site, age, sex and if whether or not they were singletons or part of a coalition (applicable to males only). Reserve covariates included biome, size, tenure, presence and number of large predator species [variable terms described below]. We compared hazard rates to understand how each covariate influenced the risk of death. This was achieved using the Cox Proportional Hazards Regression Analysis, using the *cph* function*.* This provided the survival at time *T* given the probability of mortality in a month, assuming the individual has survived to the beginning of that month.

Since a full fitted model with all predicted variables would not converge, we performed three partial model selections. We used the *Predict* and *hazplot* functions in the 'survival' package to compute how each of our predictors are related to the log hazard of death. To visually assess relationships of predictor variables to cheetah survival, we then used point and interval estimates of predictors effects and drew a hazard ratio chart with 95% Confidence Intervals (CIs). Most significant predictor variables were chosen based on comparing likelihood ratios and lowest P-values for final model selection and applied a backward stepwise approach to data reduction determined using Akaike's information criterion (AIC) values to rank models. Models with the lowest AIC values were most supported by the data, and we considered models <2 AIC units of the best models to be competing models (Burnham & Anderson, 2002). Partial model evaluation was split between demographic and period, reserve site, and predator covariates. Translocation related factors were included in the adult model. A major requirement to employ the Cox method is that the proportional hazards assumption is met; that is, the ratio of hazards is constant over time. We tested this assumption for each partial and final model using smooth scaled Schoenfeld residuals for each variable and the "correlation with time" test (Harrell 2014).

To validate the model, we used Somers' D rank correlation between the predicted log hazard and observed survival time with a bootstrap (with 300 resamples) to penalize for possible overfitting. Finally, we test model accuracy in predicting 2-year estimates from the final Cox model using an adaptive linear spline hazard regression (Harrell 2014). This model selection procedure was conducted for cheetah observations of all ages, excluding cubs that did not live past the age of emergence from the den site (>3 months) to avoid possible bias associated with detection and nonindependence of litters in the liar (Marnewick et al., 2009). We included a separate model for adult cheetah that allows us to compare survival of cheetah from different origins.

For our final combined model, we included the top covariates for the demographic, reserve site, and predator models because we speculated that any one factor alone might not affect survival but rather the combination of these variables. For top models, we included age because we predicted, for example, younger animals or females will be more vulnerable to predation. We considered quadratic forms and log forms for age and size. For the final model, we created a nomogram that can be used as a tool to predict a cheetah's probability of survival (Figure 10A). For our final model presentation, we created a nomogram with multiple "predicted value" axes relating our most significant predictor variables for one and two-year survival probabilities and median survival time (Harrell 2014).

General assumptions and terms used

Each row of data used in the survival analysis represented one observation period of an individual cheetah on a reserve. The start of the observation period was either the animal's date of birth if born on the same reserve, or the date of arrival if translocated from outside the reserve. The observation ends the last time the animal was observed with a known fate of either death, translocated, last seen, or still alive. Date of death was recorded as the exact date if known or estimated to the nearest month. Because the reserves in our analysis are relatively small and cheetah are observed regularly for research and tourism, cheetahs never seen again were presumed dead or escaped, in which case they were no longer part of the metapopulation. In which case, their date of death was recorded as the date last seen plus 2 SD of average sighting intervals (Caro, Tim, 1994) which was estimated to be two weeks across the study. The carcasses of young cubs are rarely found, in which case date of death was averaged between date last seen alive and date mother was seen without cubs. In some cases, cheetah were taken into captivity either because they were injured and no longer fit for the wild, or they were sold for monetary gain. In either case, we included this as a death since the cheetah were no longer contributing to the metapopulation.

Our *Survival object*, was the response variable used in all model building using the *Surv* function which is made up of a series of event time and event statuses for each observation. Our event time is the number of months until an individual either died or was censored. The event status is a binomial variable indicating whether death occurred or not (censored). Cheetahs were censored at the time of translocation, or at the end of the study if still living. Cheetahs that died during the translocation were included as a mortality. If an individual was moved to another study site reserve, they were censored at the end of the observation and months survived was reset to zero at the start of the next location. Less than 5% of all observations were from a second observation of the same individual. Since all the covariates of interest changed except for sex, we did not remove the second observation from our analysis.

Age: Date of birth was recorded to the nearest month based on subtracting the estimated age at first sighting for cubs born on the reserve. For cheetah that were reintroduced from the free-roaming population, age was approximated based on estimated age at arrival by vets and conservation practitioners. Exact date of birth was often known for animals introduced from captivity. Where data were deficient for date of birth for cheetah translocated within the metapopulation, we estimated birth to be 18 months before the translocation date as this is the targeted age for translocations in the metapopulation (V. van der Merwe pers.comm). Records that were insufficient to infer a date of birth were excluded from survival analysis.

I analysed a separate model for adults given they are the target age class for translocation within the metapopulation. To compare translocated and native-born cheetah, we excluded animals born on the reserve that did not reach adulthood (24 months, which is also the median age at translocation). We then subtracted 24 months from the response variable so that native and translocated animals start at time zero and used their actual age as a control variable.

Sex: Individuals were recorded as either male or female. However, the sex of cubs was often unknown. Sex ratio at birth is equal and composition of litters surviving to 12 months does not differ (Durant et al., 2004) thus we imputed NA values at a 50:50 ratio. The few instances where adult sex was not recorded (n=6) were removed from analysis.

Coalition: this was a binary predictor variable applicable to male cheetah that survived to independence. A male was considered part of a coalition if it had a brother(s) from the same litter that also survived to independence, or male cheetah that were translocated together and noted to have formed a bond. We could only account for the status at the start of the observation and acknowledge that this may have changed (e.g., one died) during the observation period. This variable was only used in the adult model because males can only be considered to be part of a coalition after they are independent.

Origin*:* *w*ithin the metapopulation, cheetah may have been sourced from captivity, the free roaming population, translocated from another reserve, or native and born on the same reserve.

Reserve biome: we classified each reserve using SANBI's Biodiversity GIS maps (Rutherford 2006). If a reserve contained more than one biome, we assigned to the biome covering more area.

Reserve size: we tested reserve size as a continuous and categorical variable and tested log values. Due to small sample sizes at the end of each value reserve size was classified into small (4500-20000), medium (24000-40000), and large (44000-90000) categories.

Reserve tenure: privately owned reserves include game reserves, and wilderness areas. State owned reserves included three national parks, two game reserves, and an air force base. One reserve was dual ownership, with a private concession within the State protected area. To reduce degrees of freedom, we randomly allocated each observation (n=14) to State or Private categories.

Management era: To test if survival has improved by using a coordinated metapopulation approach, we used pre (1993-2011) and post (2012-2018) CMP implementation as a binary predictor variable. Also tested was the model fit by year as a continuous variable.

Translocation status start and end*:* this is a binary variable to investigate if being translocated at the start of the observation influences survival (including translocations sourced from captivity and the free roaming population), and separately tests the potential effects of translocation at the end of the observation.

Results

I recorded 872 known fates for cheetah across 20 fenced reserves between 1993-2018 (Table 2). The age specific survival curve has a right skewed bell shape (Figure 2). The mean annual survival for juveniles (3-12 months) was 0.254 (n=535, SD=0.095), recognizing this is probably an overestimate since some young cubs may have died before detection. Subadult (12-24 months) annual survival was similar to adults (s=0.717, n= 244, SD=0.022). The mean annual survival for adults 3-8 years old was 0.68 (n=140, range 0.63-0.71). Adult survival declined sharply after age 8 (s=0.41-0.069), with the eldest cheetah being 13-year olds (n=8) (Table 3). The mean life expectancy for cheetah that survived at least three months was 3.7 years. Cheetah survival from time to birth until death was higher for males compared to females (P=0.0072)(Figure 3). Females on average survived just under 4 years (45.5 ± 3 months), whereas males on average survived 6.5 months longer than females (mean 52 ± 3 months) (Figure 3 left). Cheetah had significantly greater average life expectancies (mean 67 ± 3 months) after the CMP was initiated in 2011 compared to cheetah born before that time period (mean 38 ± 2.6, P<0.001)(Figure 3 right).

Table 2. Summary of individual life history outcomes of cheetah in the CMP obtained from reserve monitoring records from 1993-2018, and analysis for which the data was used.

	N	Mortality	Survivorship	Cox-hazard
Individual cheetah known fates	**872**	x	x	x
Cubs (<4 months)	176		x	
Mortalities	**516**		x	x
Known mortalities	252	x	x	
Never seen again and presumed dead	146		x	x
Censored	**285**			x
Still alive at end of study	107			x
Translocated at end of study	178			x

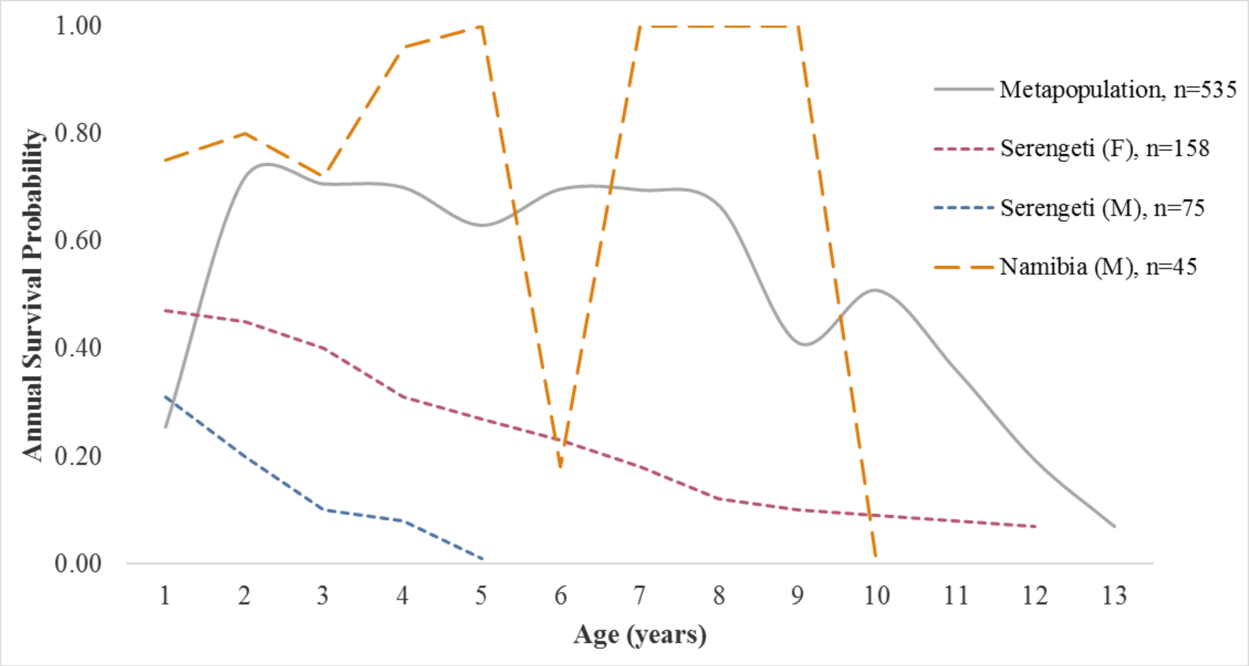


Figure 2. Survivorship curves for three wild cheetah populations; the CMP metapopulation in South Africa (1993-2018), Serengeti plains in Tanzania (1969-1994), and farmlands of Namibia (1991-2000). Estimates obtained from this study, Kelly et. al 1998, and Marker et al*.* 2003.

Table 3. Observed number of cheetahs at each age class and mean annual survival rate(S) from uncensored cheetah life history observations from 1993-2018.

Age (yrs)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
N	535	244	172	120	88	63	48	40	32	22	17	12	8
Dead	291	72	52	32	25	15	8	8	10	5	5	4	2
Alive	244	172	120	88	63	48	40	32	22	17	12	8	6
S	0.25	0.72	0.71	0.70	0.63	0.70	0.69	0.67	0.41	0.51	0.36	0.19	0.07
SD	0.10	0.02	0.03	0.03	0.02	0.02	0.02	0.04	0.05	0.07	0.10	0.14	0.00
Upper CI	0.26	0.72	0.71	0.70	0.63	0.70	0.70	0.68	0.43	0.54	0.41	0.27	0.00
Lower CI	0.25	0.71	0.70	0.70	0.62	0.69	0.69	0.65	0.39	0.48	0.31	0.11	0.00

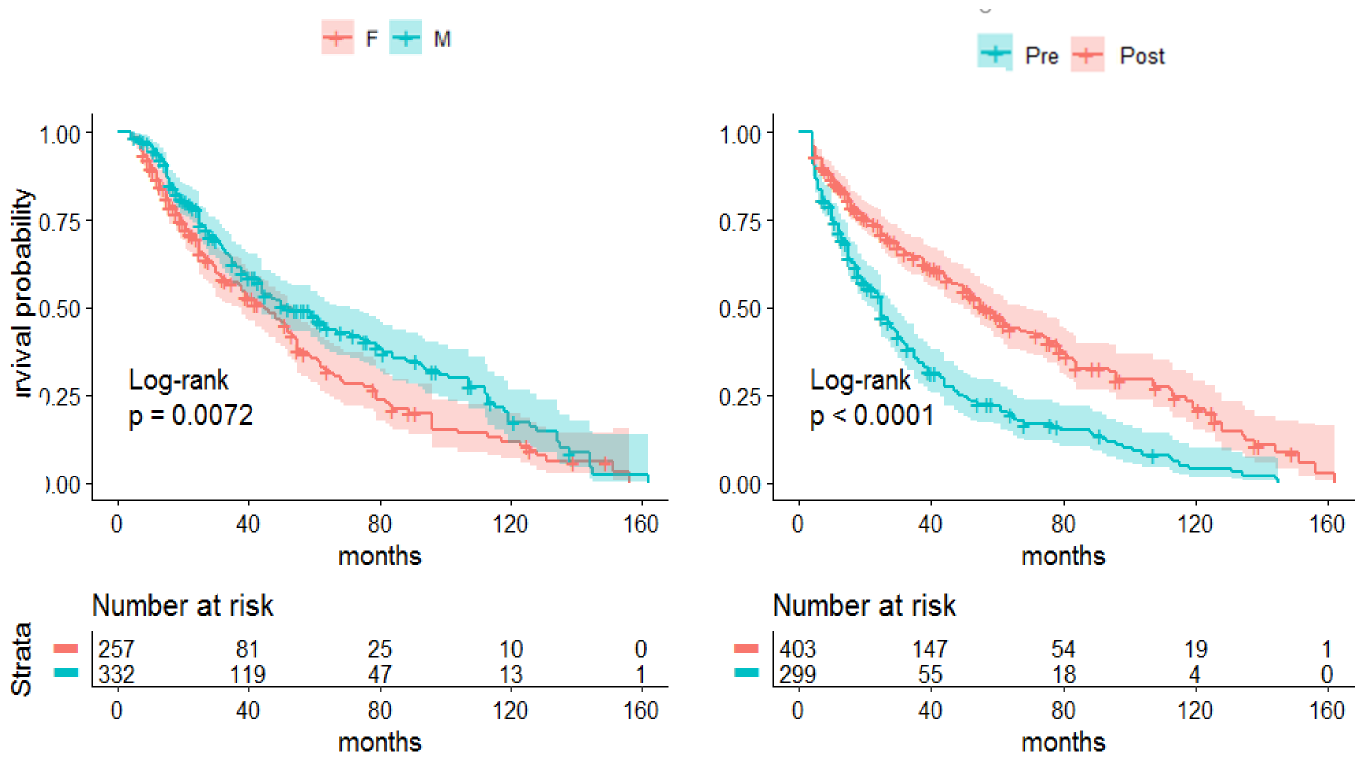


Figure 3. Kaplan Meier survival probability curves for cheetah in fenced reserves across South Africa comparing A) females versus males and B) before (1993-2011) and after (2012-2018) the establishment of the CMP including 95% CIs and the number of cheetah alive at 40-month intervals.

The leading known cause of death overall was from predation (n=125, 49%), mostly from lion (n=77, 31%) and other cheetahs (n=34, 13%) (Figure 4). Anthropogenic mortality accounted for 34% of known deaths (n=88), of which 35% (n=31) were directly related to translocation. All deaths from translocations are known and constitute 6% of total mortalities (Figure 4). The other predominant anthropogenic sources of mortality were snares and offtake associated with being taken for captivity (mostly cubs). Three animals were euthanized, which we included in anthropogenic mortality, although illness and injury were the actual cause. We also classified escapes, where the cheetah was never retrieved, as anthropogenic because the escapes were related to inadequate fencing. Other natural forms of mortality included disease, injury, fire, cubs that drowned in a flood, dependent cubs that lost their mother, and starvation.

Mortalities attributed to non-carnivorous animals were usually the result of a hunting injury but included trampling by elephants and two live cubs killed by vultures. Refer to Table 4 for a more detailed summary of age specific causes of mortality.

Table 4. Documented cases of cheetah mortality in 20 fenced reserves in South Africa from 1993-2018.

Cause of Death	**Adult**	**Cub**	**Juvenile**	**Subadult**	**Subtotal [%]**
Predator	53	28	31	13	125 [49]
Cheetah	17	5	4	8	34 [13]
Hyena	2	2		2	6 [02]
Leopard	5	2	1		8 [03]
Lion	29	19	26	3	77 [31]
Anthropogenic	33	10	3	11	57 [23]
Euthanized	2		1		3 [01]
Poachers	1				1 [0.4]
Shot	2				2 [0.8]
Snare	11		1	2	14 [06]
Vehicle	2		1		3 [01]
Intestinal obstruction	3				3 [01]
Taken by researchers		3			3 [01]
Lost to captivity	7	7		9	23 [09]
Escaped	5			1	6 [02]
Translocation related	13	1	1	16	31 [12]
Boma	2	1	1	8	12 [05]
Died in transit	4			3	7 [03]
Immobilization	6			5	11 [04]
Collar stuck in mouth	1				1 [0.4]
Other natural cause	2	10	4	2	18 [07]
Abandoned			1	1	2 [0.8]

Drowned		2		1	3 [01]
Fire		4			4 02]
Mother died			3		3 [01]
Old age	1				1 [0.4]
Starvation		2			2 [0.8]
Stillborn		2			2 [0.8]
Died giving birth	1				1 [0.4]
Illness/injury	10		4	2	16 [06]
Disease	4			1	5 [01]
Disease in boma	2				2 [0.8]
Injury	4		2	1	7 [03]
Seizure			1		1 [0.4]
Unknown illness			1		1 [0.4]
Non carnivores	5	5			10 [04]
Baboon		1			1 [0.4]
Bush pig	1				1 [0.4]
Elephants		2			2 [0.8]
Snake bite	1				1 [0.4]
Snake in boma	1				1 [0.4]
Vulture		2			2 [0.8]
Warthog	2				2 [0.8]
Total Known	**169**	**158**	**125**	**70**	**252 [100]**
Never seen again	11	12	43	9	75 [28]
Confirmed mortality, cause unknown	42	92	39	16	189 [72]
Total Unknown	**53**	**104**	**82**	**25**	**264 [100]**

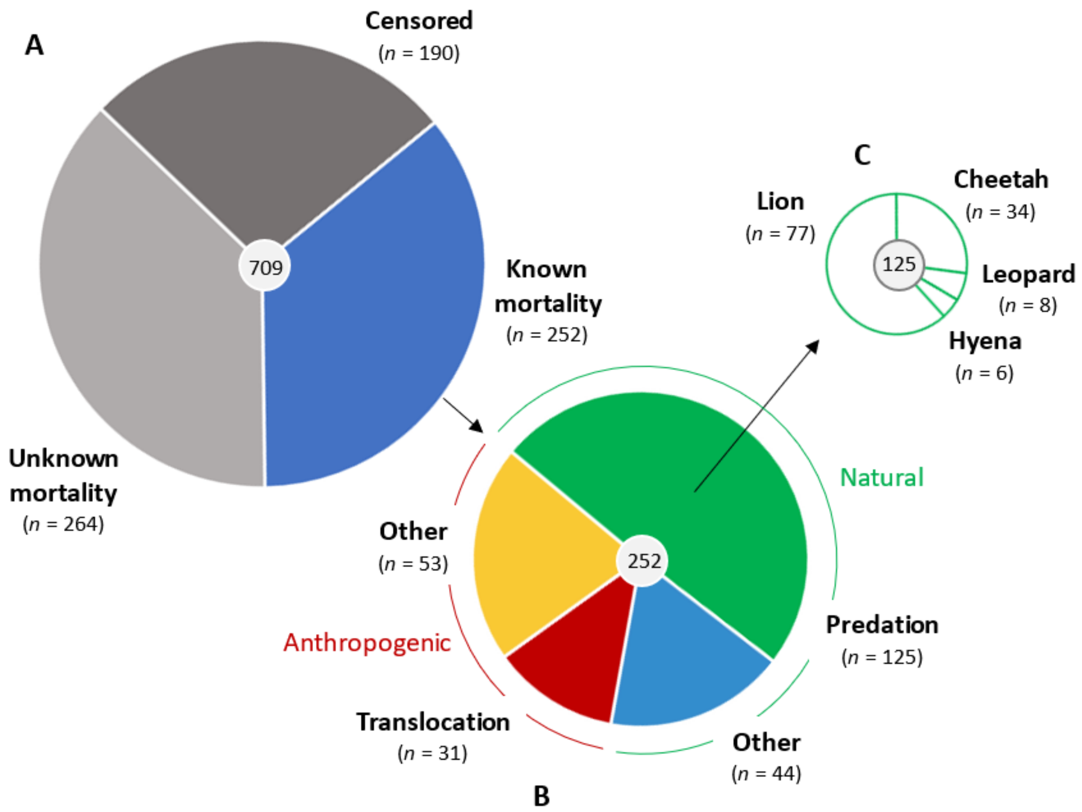


Figure 4. Pie charts with A) the outcome of all cheetah observations, B) the proportion of known mortalities, and C) predation specific morality across 20 fenced reserves in South Africa from 1993-2018. Charts are scaled in relative proportion of total observations (A).

Mortality analysis

Females were twice as likely to be killed by predators (t=2.30, SE =0.02, P= 0.04) but less likely to be killed by other cheetah (t=-1.54, SE=0.05, P=0.016), or to die from translocations (t=-1.5, SE= .05, P= 0.16) compared to males (Figure 5). We detected a significant difference in broad categories of mortality amongst age classes (cub, juvenile, subadult, adult). Cubs were most likely to die from predation, followed by juveniles and adults. Subadults were the least likely to be killed by predators compared to adults (t=2.91, SE=0.07, P=0.04), juveniles (t=5.84, SE=0.09, P<0.001), and cubs (t=3.89, SE=.08, P=0.005) (Figure 5). Origin did not have a significant effect on mortality. We only had 3 records for captive cheetahs where cause of death was known, including one from predation, and a male coalition fatally wounded by a warthog.

Only 13% of cheetahs living in the grassland biome were known to have been killed by predators compared to the global average (34%) and significantly less than cheetahs residing in the Savannah biome (t=-3.43, SE=0.08, P=0.016)(Figure 5). Cheetahs residing in the Thicket biome had the lowest probability of anthropogenic caused mortality, and significantly lower compared to cheetahs occupying the Savannah biome (t= 3.78, SE=0.05, P=0.008). In the absence of lions, the proportion of deaths from predators was significantly less (t=4.38, SE=0.06, P=0.001) with a marginal increase in the proportion of non-translocation related anthropogenic mortalities (Figure 5). There was no difference in proportional causes of mortality by reserve size or between state and private reserves (t=0.716, P=0.164).

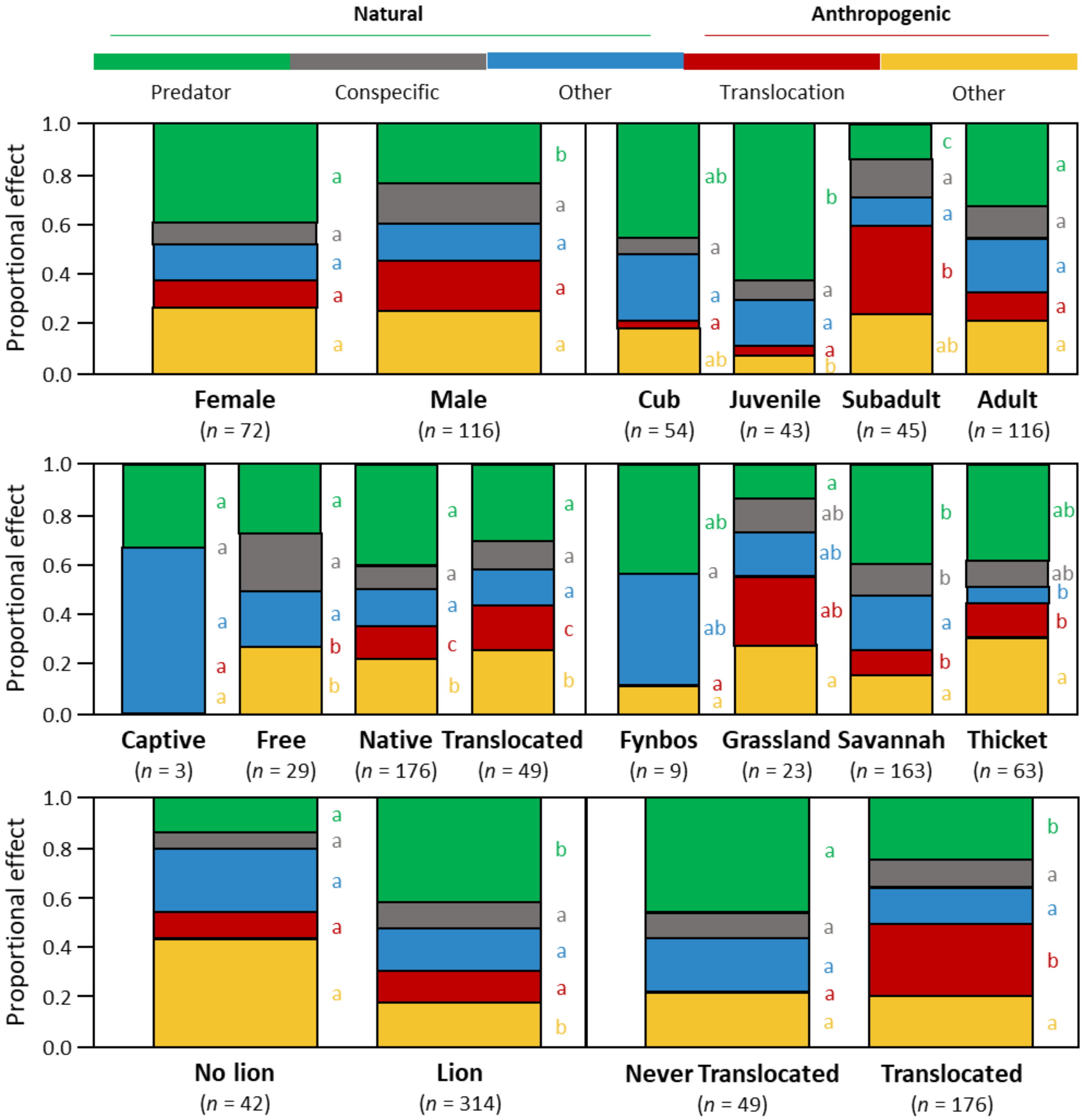


Figure 5. Fixed effects plots of the most significant (Pr>Chisq <0.10) factors related to the proportion of known causes of mortality including A) sex, B) age class, C) origin, and D) reserve biome. The bottom two plots compare the changes in proportional mortalities by E) presence of lion, and F) whether a cheetah had experienced a translocation event. Letters to the right of the stacked bars indicate a significant difference in effect if letters of the same colour differ. See Appendix 1-2 for ANOVA and LS means test statistics.

Survival analyses- all cheetahs

Age, sex and pre and post CMP had significant influences on the log hazard of death and was the best fitting sub-model (AIC=3351, R^2=0.11, df=3). There was a slight increase in hazard ratio of death with age (b=0.0058, SE=0.003, Z=1.97, P=0.05), but this became insignificant in the final model. Males had a lower risk of death compared to females (b=-0.24, SE=0.04, Z=-2.12, P=0.03), but this also was not significant in the final model. Whether males were in a coalition did not meet the proportional hazards assumption in the full model since we only considered males that survived to the age of independence could be in a coalition. Comparing hazard ratio for cheetahs that lived before 2012 (pre CMP) to cheetahs that were alive beyond 2012 until 2018 (post CMP) showed pre CMP had a significantly higher risk of death vs post CMP years (b=0.39, SE=0.12, Z=8.0, P<0.001) (Figure 6A).Results from the reserve site model found biome, size, reserve tenure and number of large predator species had significant differences with a slightly lower model fit compared to the demographic model (AIC=4611, R^2=0.078, df=7). State owned reserves have a higher risk of death compared to private reserves (b=1.34, SE= 0.62, R2= 2.17, P= 0.03). When comparing biomes, the only significant predictor was grasslands which had a significantly lower hazard ratio compared fynbos (b=1.05, SE=0.39, Z= -2.43, P>=0.02) and thicket which did not differ from grassland. Reserve biome and reserve tenure might be autocorrelated, and we tested each variable separately for the final model. Large predator composition was a significant predictor of cheetah mortality risk but was the poorest fit of three models tested (AIC=4631 R^2=0.048, P<0.0001). Survival was negatively correlated with spotted hyena presence (b=0.42, SE=0.13, Z=3.42, P=0.0006). Wild dog, brown hyena, and lion presence were poor predictors in our model. Presence of leopards tended to be negatively correlated with survival, but was not significant (b=0.163, SE=0. 122, Z=1.34, P=0.1810) (Figure 6). Our final model for all cheetah observations with the lowest possible AIC value included age at the start of the observation, reserve size, management era, reserve biome, and presence of spotted hyenas (Figure 6A).

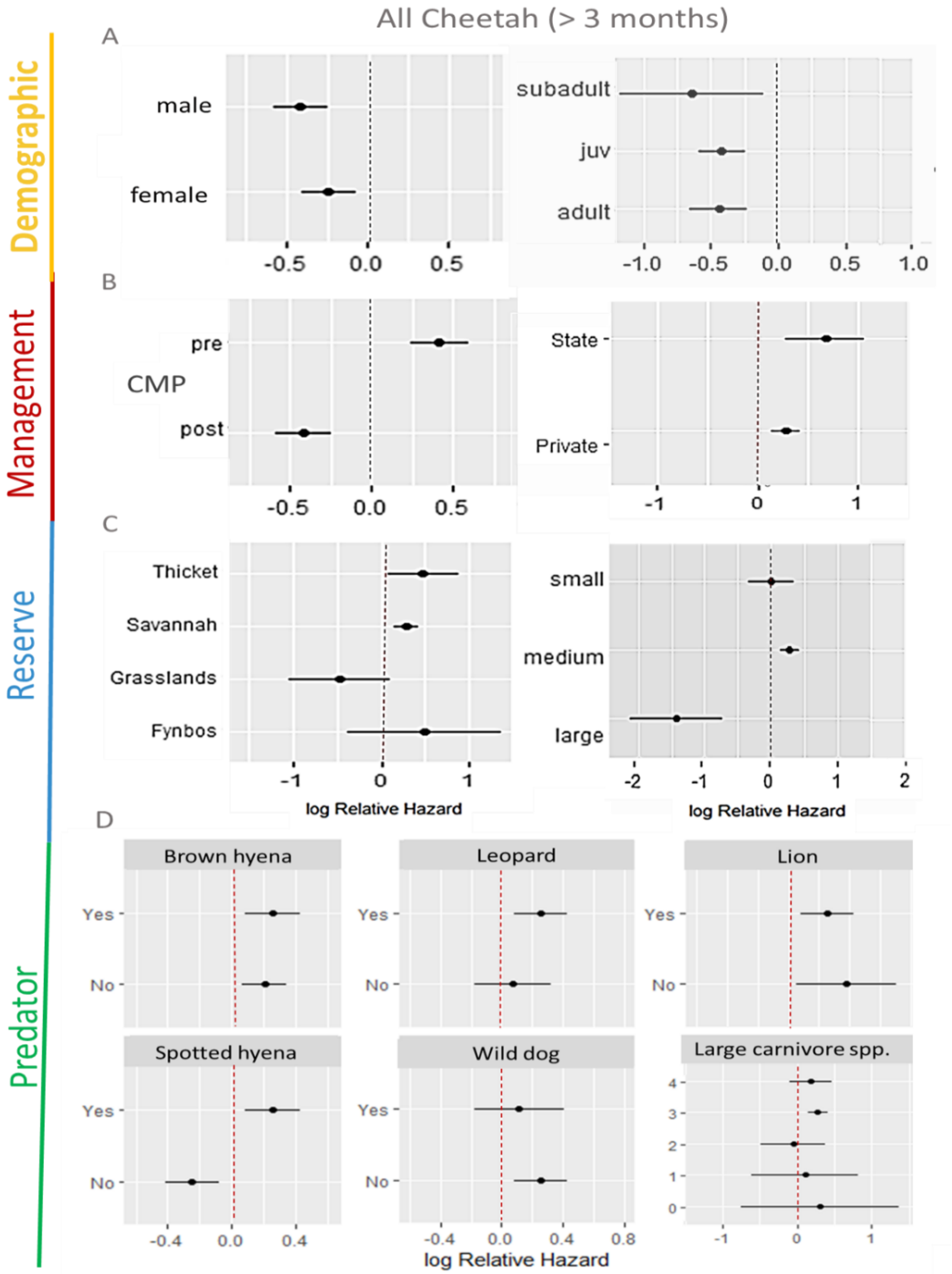


Figure 6. Log relative hazard plots illustrating the influence of A) demographic (age class and sex), B) management (pre and post CMP and reserve tenure), C) reserve site (biome and size of reserve) and D) large predators and cheetah survival. Positive values indicate an increased probability of mortality (± 95% CI).

Survival analyses- adults

There were 303 adult observations with 179 mortalities. For the first phase of the adult model, we compared sex, origin, coalition, management era, and whether they were translocated at the start of the observation (AIC=1622, R^2=0.246, df=7). The significant predictors of the hazard of death included origin and management era, whereas coalition and sex had no influence. Captive cheetahs was the only origin category that had an increased hazard of death as they were twice as likely to die as were native and translocated cheetahs. Although using origin as a binary variable (translocated vs native) yielded a much better fit, with native cheetahs having an increased hazard of death (b=1.089, SE= 0.538, Z=2.02, P=0.043). Again, adults that were alive pre CMP had a greater hazard of death than those in the post inception of CMP period (b=0.975, SE=0.161, Z= 6.04, P<0.0001)(Figure 7) Age and reserve size were more strongly supported as continuous rather than as categorical variables.

Results from the reserve site model revealed that biome, size and reserve tenure were significant predictors of death, but not the number of large predators with a lower fit model compared to the demographic sub-model (AIC=1711, R^2=0.095, P<0.001). State owned reserves had the highest risk of death compared to private reserves and reserves that were both private and State owned (b=1.34, SE= 0.62, R^2= 2.17, P=0.03). Cheetahs in reserves in Grassland biomes had a lower hazard of death whereas Fynbos was associated with a slightly higher hazard (b=-1.919, SE=0.51, Z= -3.78, P=0.0002) and neither Thicket nor Savannah had a significant influence on death. The hazard of death decreased as reserve size increased (Z=-3.65, P=0.0003). Large predator composition was a significant predictor of cheetah mortality risk but was the poorest fit sub-model tested (AIC=4631 R^2=0.048, P<0.0001). For adults, the only predator whose presence exerted a significant affect was lion. Cheetahs in reserves with lions had a lower hazard of death (b=-0.417, SE= 0.20, Z= -2.08, P=0.037), but did not improve overall model fit (AIC < 2). Mean quantile of error at predicting 2-year survival was 0.164 calibrated using 300 bootstrap reiterations (Appendix 2). See Appendix 3 for test statistics for the sub-model selection and associated AIC values. Our final model for adult cheetahs, with the lowest AIC value, included the translocation status at arrival, management era, reserve size, and reserve biome (Figure 8B). We use the top models to create the nomogram that can be used as a tool to predict a cheetah's probability of survival (Figure 10.)

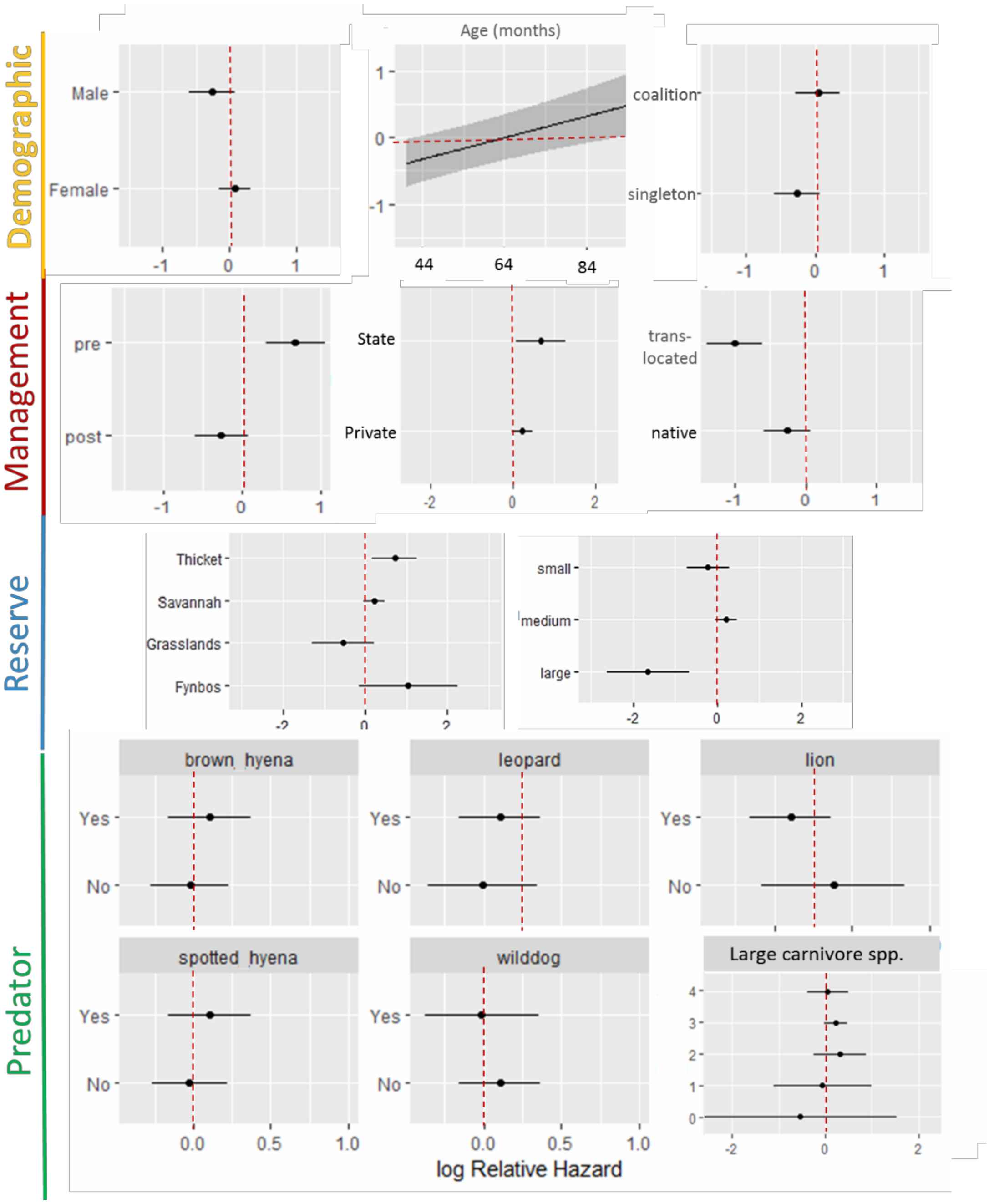


Figure 7. Log relative hazard plots illustrating the influence of A) demographic (age class and sex), B) management (pre and post CMP and reserve tenure), C) reserve site (biome and size of reserve) and D) large predators, on adult cheetah survival. Positive values indicate increased death hazard (± 95% CI).

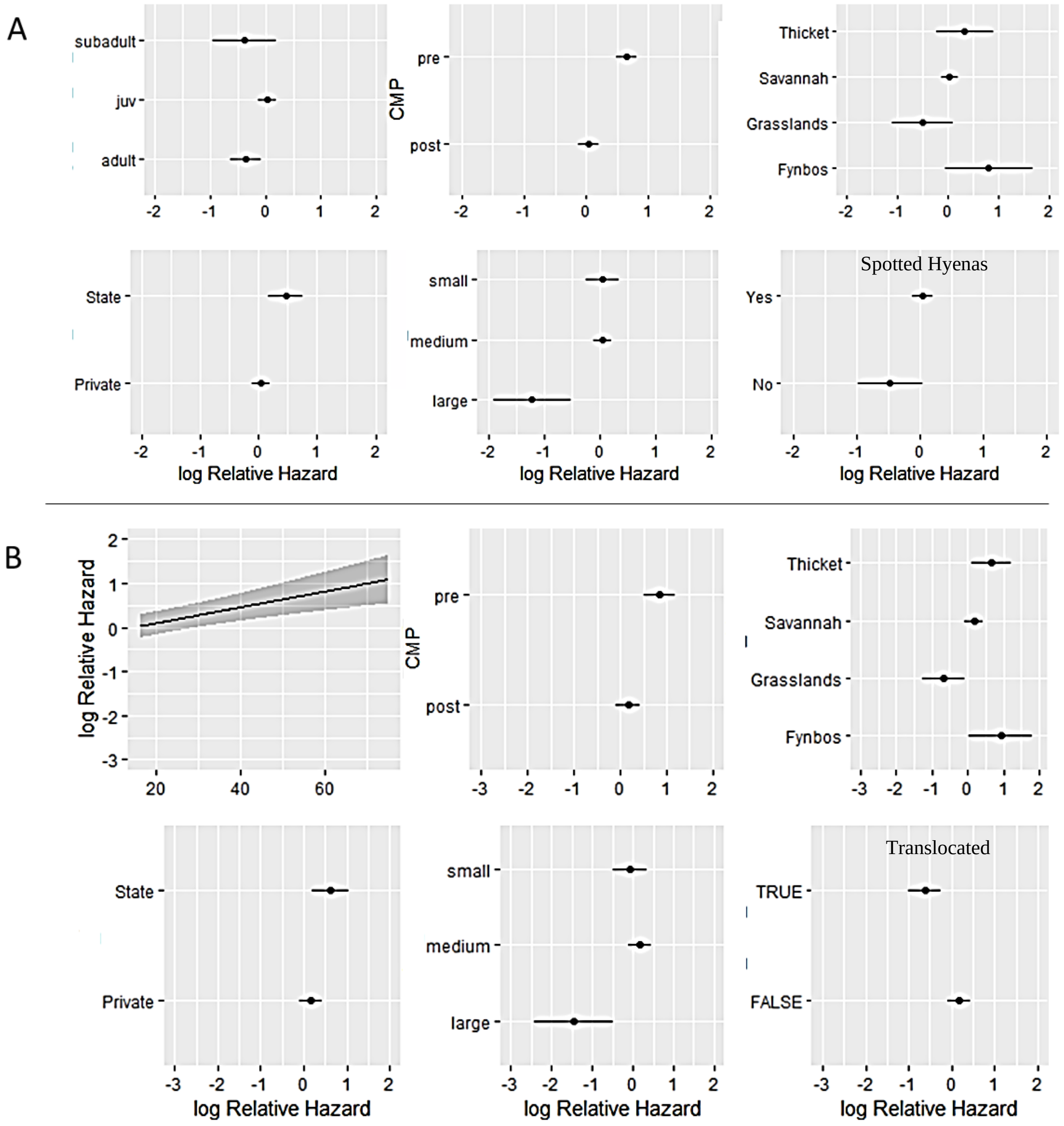


Figure 8. Relationship between the log relative hazard of death and the top predictor variables included in for the final model best fit model for A) all cheetah observations (>3 months) and B) Adult cheetahs (>24 months).

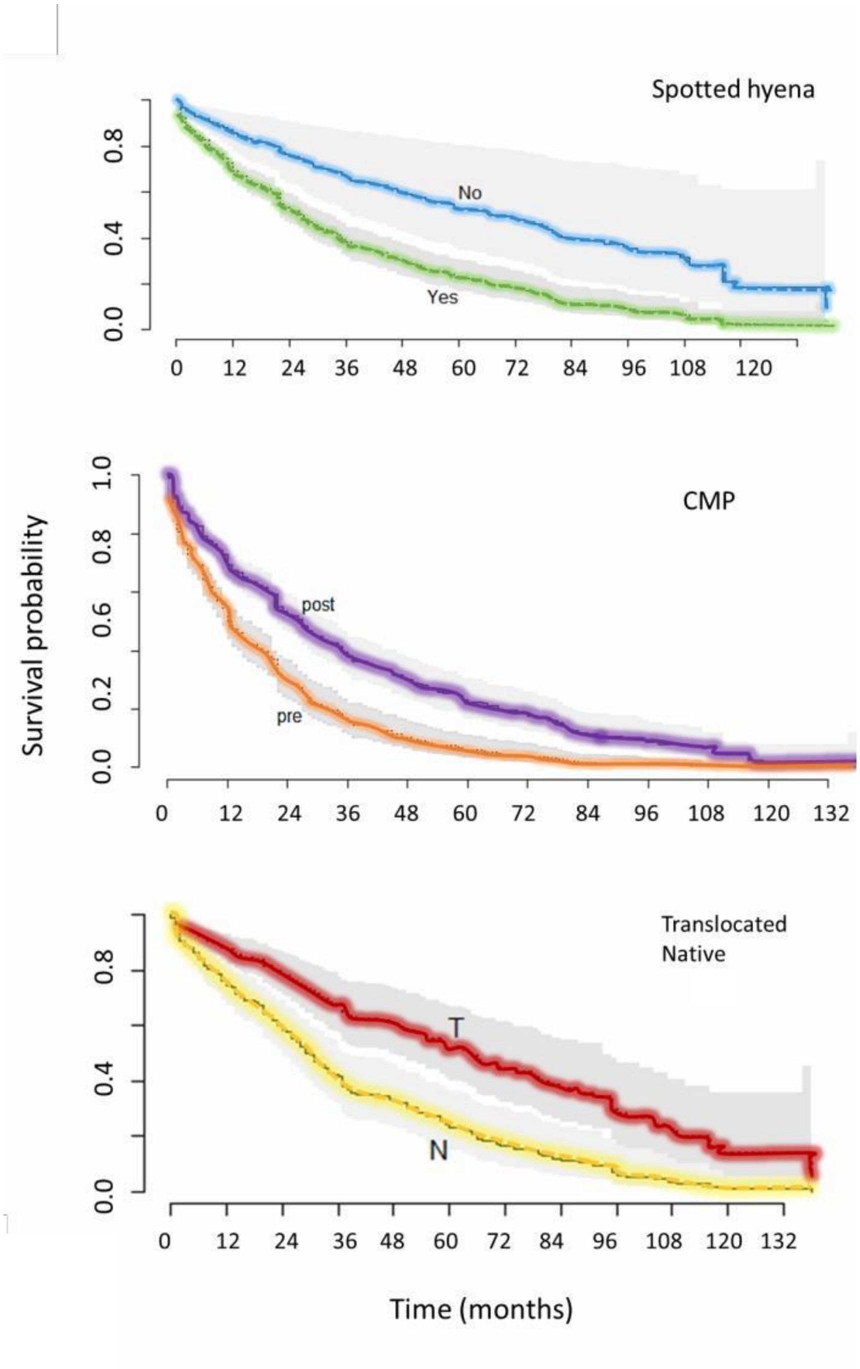


Figure 9. Survival curves comparing the survival of cheetahs (± 95% CI) in reserves with and without spotted hyenas (top), pre and post CMP (middle), and between native and translocated adult cheetahs (bottom), controlling for significant co-variates.

*adults (>24 months) only

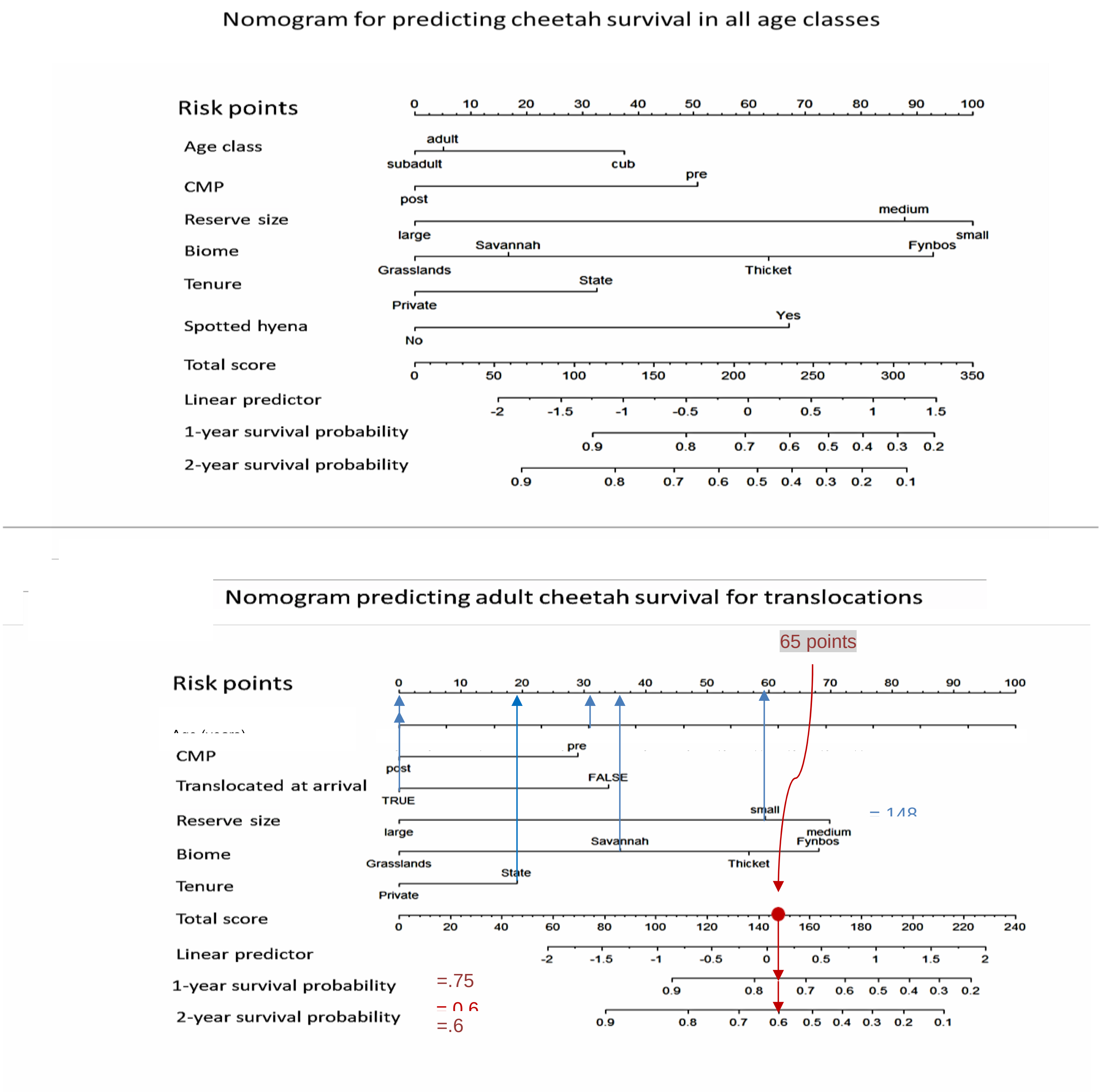


Figure 10. Management tool for predicting the survival of cheetahs for A) all age classes and B) adults only. The latter gives an example of a 2-year-old cheetah being translocated to a small, State owned reserve, in the Savannah biome. The sum of points based on each explanatory variable estimate the survival for the cheetah being released into fenced reserves in southern Africa.

*Note: more 'risk points' decreases survival.

Discussion

My results suggest that few cheetah mortalities within 20 fenced reserves are due to old age, with most deaths attributed to lions, other cheetahs, and anthropogenic factors. Typical of felids, juvenile survival was low and adult survival was high until reaching late adulthood (Haines, Tewes & Laack, 2005; Bailey, 1993; Rabinowitz1 & Jr2, 1986). Causes of mortality were consistent with those found in other studies with predation being the most significant cause of known mortality, particularly by lions (Marnewick et al., 2009; Buk et al., 2018). In reserves without lions, the primary cause of mortality was anthropogenic, reflecting a similar pattern to populations on commercial farms in Namibia where lion absence was associated with higher anthropogenic mortality (Kelly et al., 1998, Marker et al., 2007). Survivorship was much higher compared to the Serengeti and lower than in Namibia. Unlike the Namibia and Serengeti sites, CMP males survived better than females, which explains the male biased sex ratio (Buk et al., 2018). Methods used to derive survivorship estimates differed among studies, thus comparisons must be interpreted with care.

Causes of mortality

The role of human-inflicted mortality in cheetah population dynamics is evident even in fenced protected areas with adult animals killed by snares, presumably as by-catch from neighbouring communities targeting bush meat. Unlike Namibia, there were only two records of cheetahs being shot by farmers, showing that fenced reserves are effective at preventing cheetahs from entering farmlands. Since translocated animals are sourced from commercial farmland or CMP reserves, nearly all translocation related mortalities are adult or near adult cheetahs. Because the majority of large carnivores evolved under conditions of high adult survival, adult biased human-caused mortalities can have serious consequences for the long-term persistence of the southern African cheetah populations (Dalerum et al., 2008; Crooks, Sanjayan & Doak, 1998; Weaver, Paquet & Ruggiero, 1996). Subadults are the targeted age class for translocation, so it is not surprising that they experienced the highest proportional mortality from translocation related causes compared to other age classes. Most translocation mortalities are from immobilization complications resulting in capture myopathy or while being held in the boma (Braud et al., 2019). The CMP has identified this threat to the metapopulation and has developed more rigorous translocation protocols which are being provided to veterinarians and reserve managers (Buk et al., 2018).

Causes of mortality are limited to comparing proportions of known mortalities, and in this study, 52% of cheetahs presumed to have died were never found. This large proportion needs to be considered when interpreting data presented in the proportional effect plots (Figure 2). 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). Given this, mortality results presented in Figure 2 and 3, most likely inflate the relative proportion of all deaths that are anthropogenic.

Survival

We were interested in understanding the demographic, environmental and management related factors that influence cheetah survival to inform management actions for cheetahs residing in fenced reserves within the CMP. Some results were consistent with my predictions, whereas others were surprising. Here we discuss the main outcomes and highlight those contrary to our predictions.

A possible explanation of why females had lower survival compared to males is a result of differences in reproductive requirements. In support of this assumption, male and female survival was similar up to age three, when female survival dipped from age 3.5-8, when they are most fecund, then become similar again when fertility is reduced (Crosier et al., 2011). Pregnancy, parturition and lactation costs may leave females at greater risk of being killed if encountered by other large predators, and when raising young cubs may compromise their ability to spatially avoid predators while meeting energetic requirements (Krebs 1980; Laurenson 1994). This suggestion is supported by the mortality results showing predation had a greater effect on females compared to males. Although male carnivores have lower reproductive costs, polygamous species, including cheetah, are predicted to have lower male survival as a result of defending territories, securing access to females and dispersal (Bailey, 1993; Caro, T. M., 1987). The latter explains the lower survival of subadult and young adult males in Namibia and Serengeti populations (Marker et al., 2003a; Durant et al., 2004). The absence of this trend in my study may be a consequence of translocation within the metapopulation with males being removed from reserves with higher male density and placed in reserves with lower male density, thus greatly reducing intrasexual competition and dispersal costs.

Large carnivores

The most striking result to emerge from the data was that contrary to my prediction, lion presence had a positive influence on adult cheetahs' survival (Figure 7). This is surprising given that a minimum of 11% of all cheetahs' mortality in this study was attributed to lions. Furthermore, a recent study using many of the same reserves revealed a negative correlation between cheetah density and lion density (Buk et al., 2018). Cheetahs typically respond to increased dominant predator density by narrowing their prey selection (Clements, Cumming & Kerley, 2016) and making fine scale changes in activity patterns to avoid spatiotemporal overlap with lions (Swanson et al., 2016; Bissett et al., 2015). These survival strategies may drive increased cheetah inter-litter birth intervals in areas with high lion densities (Bissett & Bernard 2011) and hence result in lower cheetah densities as observed by Buk et al. (2018). The positive correlation with lion presence and adult cheetah survival, either implies cheetahs somehow benefit from sharing landscapes with lion or that reserves with lion have other attributes (e.g. abundant prey or good fences) that more than offset the negative impacts of lion predation (Vanak et al. 2014). If the former is true, one possible explanation might be that lion displace other large carnivores that predate on and compete with cheetahs (e.g. spotted hyenas). It is also possible that lion presence could influence prey behaviour in a way that increases cheetahs hunting success. As an example, a study conducted on predator/prey interactions on a South African game reserve found that prey avoided the activity areas of sit-and-pursue predators (lions and leopards), but not those of cursorial predators (cheetahs and African wild dogs) (Thaker et al., 2011). Another study from Hwange National Park found that ungulates used more open habitats when lions are in their vicinity (Valeix et al., 2009), and cheetahs have greater hunting success in open habitat (Mills et al. 2004)

While only six mortalities were ascribed to spotted hyenas, their presence had a significant negative influence on cheetah survival (Figure 9 top). Spotted hyenas only influenced the model including all age classes and not the adult model, suggesting that spotted hyena have a greater impact on young cheetahs. Spotted hyenas are a major source of cheetah cub mortality in the Serengeti, second only to lion (Laurenson 1994; Durant 2000). Apart from direct mortality, hyena presence could result in competitive exclusion of cheetahs by stealing prey and imposing high costs with competitor/predator avoidance. Even the perceived presence of hyenas was found to reduce cheetahs' foraging time and kill rates (Durant 2000). In support of my conclusions, reproductive female cheetahs raised fewer young to independence near spotted hyena core use areas compared to further away, yet this relationship did not hold relative to lions (Durant 2000)

The number of large predator species on a reserve was not a significant predictor of survival. This result was also unexpected since large predators are considered the reason for failed reintroduction success of cheetah in other parts of their range (Hayward et al., 2007, Marnewick et al., 2007). In the Serengeti NP where there is a complete large predator guild, juvenile survival was exceptionally low (Laurenson 1994). Alternatively, in the Kgalagadi TP, an ecosystem with low predator density had 7 times higher juvenile survival (Mills & Mills, 2014). However, these studies only found this relationship with juvenile survival and not adults. Therefore, it is possible the lack of relationship in this study was because young cubs were excluded from survival analyses. We could not find a comparable study that looked at the number of intraguild species in relation to adult survival. Cheetahs may not be affected by the presence of other predators as adults because their predator avoidance strategies are effective (Durant 2000).

The probability of mortality as a function of reserve biome provided insight on how the risk of predation can vary by habitat. As predicted, cheetah survival was greater in more open habitats of the savannah and grassland Biomes. Cheetahs residing in the grassland biome had only 13% mortality by predators compared to the combined average of 34% across all habitats. Grassland could provide an ideal habitat for antipredator responses if the grass is tall enough to conceal cubs yet still sufficiently open for adults to detect dominant predators and flee from an encounter (Hilborn et al., 2012). Grasslands may also promote cheetah survival indirectly by increasing hunting success (Mills et al., 2014). Their high-speed hunting strategy is obstructed by woody vegetation, which may explain why their survival was lower in thicket habitat. Although not measured in this study, Fynbos is characterized by relatively low herbivore carrying capacity (Teague, 1999), and lack cheetahs' preferred prey species as suggested by Clements et al. (2014), possibly explaining the lower survival for cheetahs in this biome. Our results iterate that cheetah conservationist should be concerned that grasslands and open savannas are disproportionately transformed by agricultural activities and are the least protected biome in southern Africa (Carbutt et al., 2011). Bush encroachment continues to shrink remaining natural grasslands even in protected areas (Kgosikoma, Mojeremane & Harvie, 2013).

My results indicate a positive relationship between reserve size and survival, supporting my prediction that cheetahs will survive better in large reserves. Survival in the metapopulation of wild dog, another wide-ranging carnivore, did not have higher survival in larger reserves (Gusset et al., 2008). Instead, they found that longer fences led to more breakouts which resulted in more anthropogenic mortalities. Cheetahs on the other hand, are less able to breach fences where they are protected from humans (Hayward et al., 2007). Small reserves may prevent spatio-temporal partitioning, a viable method for reducing competition of sympatric carnivores (Ramesh et al., 2012) or compromise a cheetah's predator avoidance strategies (Lind & Cresswell, 2005). Hard boundaries such as fences can reduce options for escaping predators (van Dyk & Slotow, 2003). Thus, the smaller the reserve, the greater the fence to area ratio, increasing both anthropogenic and predation risks associated with the edge effect.

Another surprising result was that translocated cheetahs survived better than native cheetahs of the same age (Figure 9 bottom). Translocation includes risks associated with immobilization, handling and transportation with some 14% of translocated cheetahs not surviving the procedure (EWT, unpublished data). Despite this cost, those that do survive typically experience reduced competition by leaving a reserve where there was ‘surplus’ of cheetahs (i.e. higher density) and are then released into reserves with lower conspecific density (which is often the reason for their introduction*)*(Townsend, Begon & Harper, 2000; Schoener, 1974). Thus, the increased stress and risk associated with adapting to a new environment (Dickens, Delehanty & Michael Romero, 2010), where we predicted that survival of translocated cheetahs would be negatively impacted, may be offset by a reduced density of a conspecifics and possibly greater prey abundance (Lindsey, P. et al., 2011). A further advantage experienced by translocated individuals is that during the initial post release period, cheetahs are monitored closely and if they have not hunted successfully within a week, reintroduction guidelines stipulate that they are to be provided with a carcass which can be repeated if necessary until they are able to hunt successfully on their own with feeding intervals slowly decreasing (EWT n.d.). Another possible factor explaining the improved survival of translocation individuals is the selection process used to identify individual cheetah for translocation. Cheetahs are not chosen at random for translocation with pregnant/lactating females or animals that are in poor physical condition seldom being considered (EWT n.d.). Thus, not only are translocated individuals typically in good health and not carrying the costs of pregnancy or lactation but they also typically receive vaccinations against deadly diseases which may give them an advantage over native individuals (Caldwell 2009). Given that management intervention is common on private reserves when cheetahs are injured or sick, it is perhaps not surprising that cheetah survived better on private relative to state operated reserves. There were several reports of injured cheetahs being treated by a vet. In another instance, researchers intervened to interrupt an attack by a male coalition on a singleton. Private reserves also appear to be better equipped to combat poaching threats with 11 out of the 15 snaring instances recorded on state owned reserves.

Finally, my results indicate improved survival for cheetahs that are part of the CMP (Figure 9 middle). The combined size of the individual fenced reserves equates to an impressive 12,712km^2 of suitable space for wild cheetahs on land that was previously largely utilised for agriculture. “Surplus” cheetahs are moved to new reserves rather than incurring the costs of inbreeding or being subject to costly management interventions such as contraceptives, or being sold into captivity. Most reserves within the metapopulation introduced cheetahs and other large carnivores to enhance ecosystem functioning and improve revenue from tourism (Buk et al., 2018), providing a good example of a management intervention that benefits both people and wildlife.

A criticism of metapopulation management is an individualist approach (Akçakaya, Mills & Doncaster, 2007), making its applicability as a conservation tool unrealistic across a range of taxa and regions unrealistic. However, my results suggest that given enough space for predator and competitor avoidance, the proliferation of fenced reserves could play an increasingly important role in future conservation efforts for the cheetahs. The success of the South African metapopulation approach is now being extended to other countries with a re-introduction into Liwonde National Park, Malawi in 2017 (Nzangaya 2017). The founder population was sourced from four CMP reserves in South Africa and although it is too early to tell whether the reintroduction has been successful, the founder population has already increased from four to 10 individuals (van der Merwe pers.comm). Prior to this, cheetahs had been absent from the park for over 100 years and were declared extinct in Malawi 20 years earlier (Dasgupta 2017). While small protected areas may not be able to support viable populations of wide-ranging species on their own, a coordinated metapopulation approach can clearly lead to significant conservation gains.

This is not to say that translocating animals is the silver bullet for endangered species conservation. There has been variable success for wildlife reintroductions globally, often at a considerable financial expense and in some cases with negative effects on founder populations (Lewis et al., 2012; Wolf & Ripple 2018). However, metapopulations and translocation are currently, and will be for the foreseeable future, important conservation tools for endangered species such as cheetahs, African wild dogs and black rhinos. Restoring degraded ecosystems and populations of endangered species through reintroductions may become increasingly essential given habitat fragmentation associated with an expanding human-footprint (Estes et al., 2011; Tilman et al., 2017). Thus, an important task for conservation biologists is to determine the factors that enhance or hinder success and to then provide useful metrics that can be used by conservation practitioners to improve their decision-making processes for the CMP. In this respect, we have generated a nomogram (Figure 11) which allows one to assess how the individual attributes of cheetahs being considered for translocation, in addition to attributes of the reserve and the overall management framework, might influence its survival probability.

Limitations

This study was conducted post-hoc, making use of pre-existing data accumulated over 25 years across a broad spatial range. Such a large dataset with known life histories of a threatened and long-lived species are rare and important for informing management decisions. Nevertheless, both the scale of the metapopulation and the duration over which data have been collected introduce a number of concerns that need to be discussed. Inconsistency in monitoring intensity by reserve managers may have compromised the mortality data and accuracy of survival times. Another concern is the lack of consistent individual identification with translocated animals. Often after an animal was moved to a new reserve, it received a new ID making it difficult to track their full life history across reserves. It is possible therefore that there was greater pseudo-replication of individuals than reported, which could underestimate the variation reported in our results. However, changes in values of explanatory variables for an individual cheetah when it moves to another reserve, still provides estimates of variation in a regression model (Hurlbert, 1984).

A drawback of my modelling approach was that some of the predictor variables used are assumed to be constant whereas they would have changed over the observation period. For example, the model tests the number of months survived as a time dependent variable, which in the case of native-born cheetahs is their actual age, however, animals also started the observation period at older ages. A more precise model would likely be achieved by incorporating time varying covariates.

Similarly, this study did not incorporate all of the variables that may influence cheetah survival and we attempted to identify variables that we predicted had the greatest independent impact on cheetah survival. We did not incorporate the bottom-up influences on cheetah survival, despite a range of studies that suggest predators prefer to prey on species that maximize catchability and reduce risk of injury (Clements, Tambling & Kerley, 2016; Clements et al., 2014; Hayward, Matt W. & Kerley, 2008; Hayward, M. W. et al., 2006). If such prey is not available, this could negatively affect a cheetah's lifetime fitness regardless of what our findings suggest is beneficial to cheetah survival. However, because of intensive management, prey populations in fenced reserves are rarely at low densities for prolonged periods and prey carrying capacity is part of a reserve's predator management plan (Miller, S. M. et al., 2013; Hayward, M. W. et al., 2007; Miller, B. et al., 1999). Thus, differences in prey populations are unlikely to vary enough to detect a strong signal in relationship to cheetah survival (Gigliotti et al., 2019).

Similarly, we only incorporated the presence or absence of large predator occurrence. Future research should strive to include density estimates of different predators and cheetahs themselves. Small fenced reserves actively manage their large carnivore populations, including cheetahs, and is often the reason for translocations in the first place (Ferreira & Hofmeyr, 2014; Miller, S. M. et al., 2013). Therefore, fluctuations in predator densities in our study area were the result of management actions, which negates the ability to assess the impacts of densities on lifetime cheetah survival. Rather this study was able to address variables that vary between reserves, but remain constant through the life of a cheetah (e.g. reserve size, biome, sex).

We also recognize the potential for uncertainty with our best fit model. Although the population is now managed as a whole, individual reserves have very small populations subject to high levels of environmental stochasticity. Thus, survival per reserve can be influenced by a few individuals, adding more noise to our model. Although we advise managers to consider our findings for translocation decisions, we chose to maximize our sample size instead of reserving test data to evaluate model accuracy. The CMP continues to expand, and we recommend that the model be evaluated and refined as new cheetah life history records accumulate.

Management Implications

The lack of any interaction between age and other covariates suggest that managers can focus on translocating cheetahs from proven parentage with high reproductive value, with no additional negative synergies between age. Translocations should continue to follow best practices to reduce mortalities during the process, as this is a major form of mortality for prime aged cheetahs, with females having the greatest risk. Therefore, we would advocate that males are preferentially targeted for relocation when possible. Most carnivore research remains site specific and of little general use to practitioners and hence is of limited effectiveness to conservation efforts (Balme et al., 2014). To try and address these failings, we created a simple tool (Figure 11) that can be used by managers for translocations decisions. Based on this nomogram, we would recommend the following;

- Larger private reserves should be prioritised over smaller private reserves for reintroductions, and preferably over 40,000 ha as survival did not improve from small (8,000-18,000 ha) to medium (20,000-40,000 ha).
- Grasslands, followed by savannahs should be target for reintroduction sites.
- Avoid reintroductions where spotted hyena density is high.
- Encourage more reserves to be part of the CMP.
- A coordinated metapopulation approach should be considered for recovery of other threatened species.

There are other considerations to account for in translocation decisions that are not included in our model, in addition to limitations mentioned regarding prey and large predators (including cheetahs) densities, managers must also consider genetic and demographic makeup. As cheetahs are surviving better after the CMP initiation and being translocated, suggests that management decisions around which cheetahs go where, are having a positive impact. Where our nomogram might be useful is in a cost benefit approach considering all relevant factors. The demand for cheetahs from existing reserves, and from reserves that are wanting their first introduction, already exceeds the number of cheetahs that are available in the metapopulation. This shortfall provides CMP managers with some leeway in prioritising reserves for receipt of a limited number of cheetahs. Let us consider, for example, a situation whereby four healthy metapopulation cheetahs become available for translocation, and two reserves are requesting cheetahs that have sufficient cheetah prey. One reserve is only 30,000 hectares and lion free, the other is 60,000 ha with lions. Prior to developing our survival model, one might think the smaller reserve would be more suitable under the false premise that presence of lions decreases cheetah survival, when, it is the size of the reserve that has a greater influence and preference should go to the larger reserve. In another example, we may have two reserves that are the same size, except one has lion and leopard, while the other has spotted hyena and leopard. Since lion account for most known cheetah mortalities, the current management paradigm would incorrectly identify the reserve with spotted hyena as a preferable release site. The findings of this research would advocate the opposite.

This study illustrates a case of using human mediated solutions to conserve a species that is under threat because of humans. While individual reserves may have had reintroduction failures, the CMP shows initial signs of success for cheetah conservation including range expansion, population growth (Buk et al., 2018), and this study has revealed improved survival in the last six years. Despite these achievements, this metapopulation framework may never attain a viable, self-sustaining population, which is the generally recognized definition of a successful reintroduction Fenced reserves ought to be considered as an insurance policy or temporary solution until the lag in effectively ameliorating threats outside protected areas catches up (Somers & Hayward, 2012). In the meantime, there is good metapopulation management potential from the more than 10,000 fenced reserves found in South Africa, each managed primarily by trial and error (Oberem & Oberem, 2016). Currently, research in these reserves is largely fragmented and conducted ad-hoc rather than in an organized attempt to improve reintroduction or translocation success (Seddon, Armstrong & Maloney, 2007), thus lack power to make definitive scientific conclusions. Most reserves monitor their wildlife anyway, this study provides insight to how to use monitoring records to improve translocation decisions for just one species on 20 reserves. Imagine what future research could unveil with observations and outcomes of translocations decisions across thousands of reserves. We believe this could be possible with the development of digital database much like zoos and aquariums (e.g. Species360), and biotechnology (e.g. GenBank), along with user-friendly apps for consistency in data collection. Hopefully, we will see a shift from habitat destruction and fragmentation to protected area expansion and habitat connectivity. However, this is not likely in Africa, where the continent’s projected human population is expected to reach 4 billion by 2100 (Gerland et al., 2014). Thus, we need to consider a greater reliance on small fenced protected areas for threatened species conservation. Improving our understanding of how wide-ranging carnivores such as cheetah survive in a human impacted ecosystem can help safeguard species from extinction in the dawn of the Anthropocene.

REFERENCES

Akçakaya, H. R., G. Mills, and C. P. Doncaster. 2007. The role of metapopulations in conservation. Key Topics in Conservation Biology 64–84.

Bailey, T. N. 1993. The African leopard: ecology and behavior of a solitary felid. Columbia University Press.

Ballou, J. D., and R. C. Lacy. 1995. Identifying genetically important individuals for management of genetic variation in pedigreed populations. Population management for survival and recovery 76–111. Columbia University Press New York.

Balme, G. A., P. A. Lindsey, and L. H. Swanepoel. 2014. Failure of research to address the rangewide conservation needs of large carnivores: leopards in South Africa as a case study. Conservation. Wiley Online Library. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/conl.12028>.

Batson, W. G., I. J. Gordon, and D. B. Fletcher. 2015. Translocation tactics: a framework to support the IUCN Guidelines for wildlife translocations and improve the quality of applied methods. Journal of Applied. Wiley Online Library. <https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12498>.

Bissett, C. 2004. The Feeding Ecology, Habitat Selection and Hunting Behaviour of Re-Introduced Cheetah on Kwandwe Private Game Reserve, Eastern Cape Province. MSc Thesis, Rhodes University, South Africa.

Bissett, C., and R. T. F. Bernard. 2011. Demography of Cheetahs in Fenced Reserves in South Africa: Implications for Conservation. South African Journal of Wildlife Research 41:181–191.

Boast, L. K., E. V. Chelysheva, V. van der Merwe, A. Schmidt-Küntzel, E. H. Walker, D. Cilliers, M. Gusset, and L. Marker. 2018. Chapter 20 - Cheetah Translocation and Reintroduction Programs: Past, Present, and Future. Pages 275–289 *in* P. J. Nyhus, L. Marker, L. K. Boast, and A. Schmidt-Küntzel, editors. Cheetahs: Biology and Conservation. Academic Press.

Boast, L. K., K. Good, and R. Klein. 2016. Translocation of problem predators: Is it an effective way to mitigate conflict between farmers and cheetahs Acinonyx jubatus in Botswana? Oryx: the journal of the Fauna Preservation Society 50:537–544.

Bothma, J.D.P. and Van Rooyen, N. eds., 2005. Intensive wildlife production in Southern Africa. Van Schaik Publishers.

Bradley, E. H., and D. H. Pletscher. 2005. Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. Wildlife Society bulletin. Wiley Online Library. <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.2193/0091-7648%282005%2933%5B1256%3AAFRTWD%5D2.0.CO%3B2>.

Braud, C., V. van der Merwe, E. Lane, A. Tordiffe. 2018. A veterinary survey of factors associated with capture-related mortalities in cheetahs (Acinonyx jubatus). 10.13140/RG.2.2.17072.20485.

Broekhuis, F., D. Thuo, and M. W. Hayward. 2017. Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and interspecific competition. Journal of zoology 304:65–72.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in ecology & evolution 23:453–460.

Buk, K. G., V. C. van der Merwe, K. Marnewick, and P. J. Funston. 2018. Conservation of severely fragmented populations: lessons from the transformation of uncoordinated reintroductions of cheetahs (Acinonyx jubatus) into a managed metapopulation with self-sustained growth. Biodiversity and conservation 27:3393–3423.

Buk, K., and K. Marnewick. 2010. Cheetah conservation in South Africa. Africa insight 39. <http://dx.doi.org/10.4314/ai.v39i4.55225>.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). Volume 172.

Caldwell, P. 2009. Cheetah vaccination protocol Retrieved from

Carbutt, C., M. Tau, A. Stephens, and B. Escott. 2011. The conservation status of temperate grasslands in southern Africa.

Caro, T. 1994. Cheetahs of the Serengeti Plains: Group Living in an Asocial Species. University of Chicago Press.

Caro, T. M., and D. A. Collins. 1987. Male cheetah social organization and territoriality. Ethology: formerly Zeitschrift fur Tierpsychologie 74:52–64. Wiley Online Library.

Caro, T. M., and M. K. Laurenson. 1994. Ecological and Genetic Factors in Conservation: A Cautionary Tale. Science. Volume 263. <http://dx.doi.org/10.1126/science.8290956>.

Castro-Prieto, A., B. Wachter, and S. Sommer. 2011. Cheetah paradigm revisited: MHC diversity in the world's largest free-ranging population. Molecular biology and evolution 28:1455–1468.

Ceballos, G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. Science 296:904–907.

Chambers, J. M. and Hastie, T. J. 1992. *Statistical Models in S*, Wadsworth & Brooks/Cole.

Chelysheva, E. V. 2011. Cheetah (Acinonyx jubatus) Reintroduction— 46 years of Translocations (in Russian). Scientific Research at Zoological Parks, Moscow, Russia 135–179.

Cincotta, R. P., J. Wisnewski, and R. Engelman. 2000. Human population in the biodiversity hotspots. Nature 404:990–992.

Clements, H. S., C. J. Tambling, and G. I. H. Kerley. 2016. Prey morphology and predator sociality drive predator prey preferences. Journal of mammalogy 97:919–927. Oxford University Press.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red Deer: Behavior and Ecology of Two Sexes. University of Chicago Press.

Collins, D., C. Alexander, and C. T. Darimont. 2018. Staqeya: the lone wolf at the edge of its ecological niche. Ecology. <http://dx.doi.org/10.1002/ecy.2513>.

Conner, M. M., T. R. Stephenson, D. W. German, K. L. Monteith, A. P. Few, and E. H. Bair. 2018. Survival analysis: Informing recovery of Sierra Nevada bighorn sheep: Bighorn Sheep Survival and Recovery Strategies. The Journal of Wildlife Management 82:1442–1458.

Cooper, A. B., N. Pettorelli, and S. M. Durant. 2007. Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. Animal behaviour 73:651–659.

Corti, P., H. U. Wittmer, and M. Festa-Bianchet. 2010. Dynamics of a small population of endangered huemul deer (Hippocamelus bisulcus) in Chilean Patagonia. Journal of mammalogy 91:690–697. Oxford University Press.

Cousins, J. A., J. P. Sadler, and J. Evans. 2008. Exploring the Role of Private Wildlife Ranching as a Conservation Tool in South Africa: Stakeholder Perspectives. Ecology and Society 13. <http://dx.doi.org/10.5751/es-02655-130243>.

Cox, D. R. 1984. Analysis of survival data. Routledge, New York.

Cristescu, B., P. Lindsey, O. Maes, C. Bissett, G. Mills, and L. Marker. 2018. Chapter 19 - Protected Areas for Cheetah Conservation. Pages 265–274 *in* P. J. Nyhus, L. Marker, L. K. Boast, and A. Schmidt-Küntzel, editors. Cheetahs: Biology and Conservation. Academic Press.

Cromsigt, J. P., D. P. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. Kerley, A. Mysterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology 50(3):544-549.

Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 2008. New Insights on Cheetah Conservation through Demographic Modeling. Conservation biology: the journal of the Society for Conservation Biology 12:889–895.

Dalerum, F., Shults, B. and Kunkel, K. 2008. Estimating Sustainable Harvest in Wolverine Populations

Using Logistic Regression. The Journal of Wildlife Management, 72:1125-1132. doi:10.2193/2007-336

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science 349:858–860.

Dasgupta, S. 2017. "Cheetahs return to Malawi after decades". Mongabay. Retrieved 8 January 2018. https://news.mongabay.com/2017/05/cheetahs-return-to-malawi-after-decades/

Davies-Mostert, H. T., M. G. L. Mills, and D. W. Macdonald. 2015. The Demography and Dynamics of an Expanding, Managed African Wild Dog Metapopulation. South African Journal of Wildlife Research 45:258–273.

Department of Economic and Social Affair. 2016. World Population Prospects, the 2015 Revision. United Nations Publications.

Dickens, M., D. Delehanty, and M. Romero. 2010. Stress: An inevitable component of animal translocation, Biological Conservation, 143:1329-1341, ISSN 0006-3207.

Durant, S. M. 2000. Living with the enemy: Avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral ecology: official journal of the International Society for Behavioral Ecology 11:624–632.

Durant, S. M., M. E. Craft, C. Foley, K. Hampson, A. L. Lobora, M. Msuha, E. Eblate, J. Bukombe, J. Mchetto, and N. Pettorelli. 2010. Does size matter? An investigation of habitat use across a carnivore assemblage in the Serengeti, Tanzania. The Journal of animal ecology 79:1012–1022.

Durant, S. M., M. Kelly, and T. M. Caro. 2004. Factors affecting life and death in Serengeti cheetahs: Environment, age, and sociality. Behavioral ecology: official journal of the International Society for Behavioral Ecology 15:11–22.

Durant, S. M., M. S. Becker, S. Creel, S. Bashir, A. J. Dickman, R. C. Beudels-Jamar, L. Lichtenfeld, R. Hilborn, J. Wall, G. Wittemyer, L. Badamjav, S. Blake, L. Boitani, C. Breitenmoser, F. Broekhuis, D.

Christianson, G. Cozzi, T. R. B. Davenport, J. Deutsch, P. Devillers, L. Dollar, S. Dolrenry, I. Douglas-Hamilton, E. Dro¨ge, E. Fitzherbert, C. Foley, L. Hazzah, J. G. C. Hopcraft, D. Ikanda, A. Jacobson, D. Joubert, M. J. Kelly, J. Milanzi, N. Mitchell, J. M'Soka, M. Msuha, T. Mweetwa, J. Nyahongo, E. Rosenblatt, P. Schuette, C. Sillero-Zubiri, A. R. E. Sinclair, M. R. Stanley Price, A. Zimmermann, and N. Pettorelli. 2015. Developing fencing policies for dryland ecosystems. The Journal of applied ecology 52:544–551.

Durant, S. M., M. S. Becker, S. Creel, S. Bashir, A. J. Dickman, R. C. Beudels-Jamar, L. Lichtenfeld, R. Hilborn, J. Wall, G. Wittemyer, L. Badamjav, S. Blake, L. Boitani, C. Breitenmoser, F. Broekhuis, D. Christianson, G. Cozzi, T. R. B. Davenport, J. Deutsch, P. Devillers, L. Dollar, S. Dolrenry, I. Douglas-Hamilton, E. Dro¨ge, E. Fitzherbert, C. Foley, L. Hazzah, J. G. C. Hopcraft, D. Ikanda, A. Jacobson, D. Joubert, M. J. Kelly, J. Milanzi, N. Mitchell, J. M'Soka, M. Msuha, T. Mweetwa, J. Nyahongo, E. Rosenblatt, P. Schuette, C. Sillero-Zubiri, A. R. E. Sinclair, M. R. Stanley Price, A. Zimmermann, and N. Pettorelli. 2015. Developing fencing policies for dryland ecosystems. Journal of Applied Ecology 52(3):544-551.

Durant, S. M., N. Mitchell, R. Groom, A. Ipavec, R. Woodroffe, C. Breitenmoser, and L. T. B. Hunter. 2018. The Conservation Status of the Cheetah. Pages 533–548 *in*. Cheetahs: Biology and Conservation.

Durant, S. M., N. Mitchell, R. Groom, N. Pettorelli, A. Ipavec, A. P. Jacobson, R. Woodroffe, M. Böhm, L. T. B. Hunter, M. S. Becker, F. Broekhuis, S. Bashir, L. Andresen, O. Aschenborn, M. Beddiaf, F. Belbachir, A. Belbachir-Bazi, A. Berbash, I. Brandao de Matos Machado, C. Breitenmoser, M. Chege, D. Cilliers, H. Davies-Mostert, A. J. Dickman, F. Ezekiel, M. S. Farhadinia, P. Funston, P. Henschel, J. Horgan, H. H. de Iongh, H. Jowkar, R. Klein, P. A. Lindsey, L. Marker, K. Marnewick, J. Melzheimer, J. Merkle, J. M'soka, M. Msuha, H. O'Neill, M. Parker, G. Purchase, S. Sahailou, Y. Saidu, A. Samna, A. Schmidt-Küntzel, E. Selebatso, E. A. Sogbohossou, A. Soultan, E. Stone, E. van der Meer, R. van Vuuren, M. Wykstra, and K. Young-Overton. 2017. The global decline of cheetah Acinonyx jubatus and what it means for conservation. Proceedings of the National Academy of Sciences of the United States of America 114:528–533.

Durant, S. M., S. Bashir, T. Maddox, and M. K. Laurenson. 2007. Relating long-term studies to conservation practice: The case of the serengeti cheetah project. Conservation biology: the journal of the Society for Conservation Biology 21:602–611.

Durant, S., Mitchell, N., Ipavec, A. & Groom, R. 2015. Acinonyx jubatus. The IUCN Red List of Threatened Species. . Available from https://www.iucnredlist.org/en (accessed Oct 16, 2019).

East, M. L., J. W. Nyahongo, K. V. Goller, and H. Hofer. 2011. Does the Vastness of the Serengeti Limit Human–Wildlife Conflicts? Pages 125–151 *in*. Fencing for Conservation.

Errington P. L. 1946. Predation and vertebrate populations. Q Rev. Biol. 21, 144–77.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

EWT. n.d. Cheetah metapopulation South Africa: aspects of founder animals. Retreived from https://www.cheetahpopulation.org.za/founderanimals.html.

Fanshawe, J. H., L. H. Frame, and J. R. Ginsberg. 1991. The wild dog—Africa’s vanishing carnivore. Oryx: the journal of the Fauna Preservation Society 25:137–146. Cambridge University Press.

Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological conservation 96:1–11.

Fontúrbel, F. E., and J. A. Simonetti. 2011. Translocations and human-carnivore conflicts: problem solving or problem creating? Wildlife biology 17:217–224. Nordic Board for Wildlife Research.

Fuller, T. K., and P. R. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. Conservation Biology Series-Cambridge- :163-178.

Fynn, R. W. S., and M. C. Bonyongo. 2010. Functional conservation areas and the future of Africa’s wildlife. African journal of ecology 49:175–188.

Gadd, M. E. 2011. Barriers, the Beef Industry and Unnatural Selection: A Review of the Impact of Veterinary Fencing on Mammals in Southern Africa. Pages 153–186 *in*. Fencing for Conservation.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.

Gusset, M., S. J. Ryan, M. Hofmeyr, G. Van Dyk, H. T. Davies-Mostert, J. A. Graf, C. Owen, M. Szykman, D. W. Macdonald, S. L. Monfort, D. E. Wildt, A. H. Maddock, M. G. L. Mills, R. Slotow, and M. J. Somers. 2007. Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. The Journal of applied ecology 45:100–108.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press.

Harcourt, A. H., S. A. Parks, and R. Woodroffe. 2001. Biodiversity and conservation 10:1011–1026.

Harrell FE: Package ’rms’. R-project 2013. 2009, [http://www.r-project.org]

Harrell, F. E. 2014. Regression modeling strategies. as implemented in R package “rms” version 3. Springer. <https://link.springer.com/content/pdf/10.1007/978-3-319-19425-7.pdf>.

Hastings, A., and S. Harrison. 1994. Metapopulation Dynamics and Genetics. Annual review of ecology and systematics 25:167–188.

Hayward, M. W., and M. J. Somers. 2011. An Introduction to Fencing for Conservation. Pages 1–6 *in*. Fencing for Conservation.

Hayward, M. W., and M. Somers. 2009. Reintroduction of Top-Order Predators. John Wiley & Sons.

Hayward, M. W., J. Adendorff, J. O’Brien, A. Sholto-Douglas, C. Bissett, L. C. Moolman, P. Bean, A.

Fogarty, D. Howarth, R. Slater, and G. I. H. Kerley. 2007a. Practical Considerations for the Reintroduction of Large, Terrestrial, Mammalian Predators Based on Reintroductions to South Africa's Eastern Cape Province. The Open Conservation Biology Journal 1:1–11.

Hayward, M. W., J. O'Brien, and G. I. H. Kerley. 2007. Carrying capacity of large African predators: Predictions and tests. Biological conservation 139:219–229.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of Survival and Cause-Specific Mortality Rates Using Telemetry Data. The Journal of wildlife management. <http://dx.doi.org/10.2307/3801692>.

Hemson, G., S. Maclennan, G. Mills, P. Johnson, and D. Macdonald. 2009. Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. Biological conservation 142:2718–2725.

Hilborn, A., N. Pettorelli, C. D. L. Orme, and S. M. Durant. 2012. Stalk and chase: how hunt stages affect hunting success in Serengeti cheetah. Animal behaviour 84:701–706.

Hofmeyr, M., and G. van Dyk. 1998. Cheetah introductions to two north west parks: case studies from Pilanesberg National Park and Madikwe Game Reserve. Proceedings of a Symposium on Cheetahs as Game Ranch Animals, Onderstepoort, 23&24 October 1998 60–71.

https://www.cheetahpopulation.org.za/vaccination.html.

Hunter, L. T. B., P. White, P. Henschel, L. Frank, C. Burton, A. Loveridge, G. Balme, C. Breitenmoser, and U. Breitenmoser. 2012. Walking with lions: why there is no role for captive-origin lions Panthera leo in species restoration. Oryx: the journal of the Fauna Preservation Society 47:19–24.

Hurlbert, S. H. 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs 54(2):187-211.

Jeo, R. M., A. Schmidt-Küntzel, J. D. Ballou, and M. Sanjayan. 2018. Chapter 10 - Drivers of Habitat Loss and Fragmentation: Implications for the Design of Landscape Linkages for Cheetahs. Pages 136–

148 *in* P. J. Nyhus, L. Marker, L. K. Boast, and A. Schmidt-Küntzel, editors. Cheetahs: Biology and Conservation. Academic Press.

Jule, K. R., L. A. Leaver, and S. E. G. Lea. 2008. The effects of captive experience on reintroduction survival in carnivores: A review and analysis. Biological conservation 141:355–363.

Kaplan, E. L., and P. Meier. 1958. Nonparametric Estimation from Incomplete Observations. Journal of the American Statistical Association 53:457–481. [American Statistical Association, Taylor & Francis, Ltd.].

Kelly, M. J., M. Karen Laurenson, C. D. Fitzgibbon, D. Anthony Collins, S. M. Durant, G. W. Frame, B. C. R. Bertram, and T. M. Caro. 1998. Demography of the serengeti cheetah (Acinonyx jubatus) population: The first 25 years. Journal of zoology 244:473–488.

Kemink, K. M., and D. C. Kesler. 2013. Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. Animal conservation 16:449–457. Wiley Online Library.

Kesch, K. M., D. T. Bauer, and A. J. Loveridge. 2013. Undermining game fences: who is digging holes in Kalahari sands? African journal of ecology 52:144–150.

Keymer, J. E., P. A. Marquet, J. X. Velasco-Hernández, and S. A. Levin. 2000. Extinction Thresholds and Metapopulation Persistence in Dynamic Landscapes. The American naturalist 156:478–494.

Kgosikoma, O. E., K. Mogotsi, Department of Agricultural Research, Ministry of Agriculture, Gaborone, Botswana Www Moa, Department of Agricultural Research, Ministry of Agriculture, Francistown, and Botswana Www Moa. 2013. Understanding the causes of bush encroachment in Africa: The key to effective management of savanna grasslands. Tropical Grasslands - Forrajes Tropicales 1:215.

Knight, M. H., and G. I. H. Kerley. 2010. Black Rhino Translocations within Africa. Africa insight 39. <http://dx.doi.org/10.4314/ai.v39i3.51020>.

Krebs, J. R. 1980. Optimal foraging, predation risk, and territory defense. Ardea, 68:83-90.

Laliberte, A. S., and W. J. Ripple. 2004. Range Contractions of North American Carnivores and Ungulates. BioScience 54(2):123-138.

Lande, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. The American naturalist 142:911–927.

Langholz, J.A. and Kerley, G.I., 2006. Combining conservation and development on private lands: an assessment of ecotourism-based private game reserves in the Eastern Cape. *Centre for African Conservation Ecology (formerly TERU) Report*, *56*.

Laurenson, M. K. 1994. High juvenile mortality in cheetahs (Acinonyx jubatus) and its consequences for maternal care. J Zool. Lond 234:387-408.

Laurenson, M. K., M. Karen Laurenson, T. M. Caro, P. Gros, and N. Wielebnowski. 1995. Controversial cheetahs? Nature 377:392–392.

Lenth, R. 2018. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.2.1. https://CRAN.R-project.org/package=emmeans

Levins, R. 1969. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. Bulletin of the Entomological Society of America 15:237–240.

Lewis, J. C., R. A. Powell, and W. J. Zielinski. 2012. Carnivore translocations and conservation: insights from population models and field data for fishers (Martes pennanti). PloS one 7:e32726.

Lind, J., and Cresswell, W. 2005. Determining the fitness consequences of antipredation behaviour. *Behavioral Ecology* 16:945–956.

Lindsey, P. A., and H. T. Davies-Mostert. 2009. South African Action Plan for the Conservation of Cheetahs and African Wild Dogs. Report from a National Conservation Action Planning Workshop, Bela Bela, Limpopo Province, South Africa. 1–87.

Lindsey, P., C. J. Tambling, R. Brummer, H. Davies-Mostert, M. Hayward, K. Marnewick, and D. Parker. 2011. Minimum prey and area requirements of the vulnerable cheetah acinonyx jubatus: Implications for reintroduction and management of the species in South Africa. Oryx: the journal of the Fauna Preservation Society 45:587–599.

Linnell, J. D. C., R. Aanes, J. E. Swenson, J. Odden, and M. E. Smith. 1997. Translocation of carnivores as a method for managing problem animals: a review. Biodiversity and conservation 6:1245–1257. Kluwer Academic Publishers.

Low, A.B. & Rebelo, T.G. 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Macdonald, D., and Katrina Service. 2009. Key Topics in Conservation Biology. John Wiley & Sons.

Marker, L. 1998. Current status of the cheetah (Acinonyx jubatus). Proceedings of a symposium on cheetahs as game ranch animals.

Marker, L. L., A. J. Dickman, M. G. L. Mills, and D. W. Macdonald. 2003*b*. Aspects of the management of cheetahs, Acinonyx jubatus jubatus, trapped on Namibian farmlands. Biological conservation 114:401–412.

Marker, L. L., A. J. Dickman, R. M. Jeo, M. G. L. Mills, and D. W. Macdonald. 2003*a*. Demography of the Namibian cheetah, Acinonyx jubatus jubatus. Biological conservation 114:413–425.

Marker, L., A. Dickman, C. Wilkinson, B. Schumann, and E. Fabiano. 2007. The Namibian cheetah: status report. Cat news 3:4–13.

Marker-Kraus, L., and D. Kraus. 1997. Conservation strategies for the long-term survival of the Cheetah Acinonyx jubatus by the Cheetah Conservation Fund, Windhoek. International Zoo Yearbook 35:59–66. Wiley Online Library.

Marnewick, K. 2012. Captive breeding, keeping and trade of cheetahs in South

Marnewick, K., A. Beckhelling, D. Cilliers, E. Lane, G. Mills, K. Herring, P. Caldwell, R. Hall, and S. Meintjes. 2007. The status of the cheetah in South Africa. Cat News Special is:22–31.

Marnewick, K., M. W. Hayward, D. Cilliers, and M. J. Somers. 2009. Survival of Cheetahs Relocated from Ranchland to Fenced Protected Areas in South Africa. Pages 282–306 *in*. Reintroduction of Top-Order Predators.

Matson, T. K., A. W. Goldizen, and P. J. Jarman. 2004. Factors affecting the success of translocations of the black-faced impala in Namibia. Biological conservation 116:359–365.

Mills, M. G. L. 2005. Large carnivores and biodiversity in African savanna ecosystems. Large carnivores and the conservation of biodiversity 208–229. Island Press Washington, DC.

Mills, M. G. L., and M. E. J. Mills. 2014. Cheetah cub survival revisited: A re-evaluation of the role of predation, especially by lions, and implications for conservation. Journal of zoology 292:136–141.

Mills, M. G. L., L. S. Broomhall, and J. T. du Toit. 2004. Cheetah Acinonyx jubatus feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? Wildlife biology 10:177–186.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2007. Demographic Side Effects of Selective Hunting in Ungulates and Carnivores. Conservation Biology 21(1):36-47.

Morrison, J. C., W. Sechrest, E. Dinerstein, D. S. Wilcove, and J. F. Lamoreux. 2007. Persistence of Large Mammal Faunas as Indicators of Global Human Impacts. Journal of mammalogy 88:1363–1380.

Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.

Myers, N. 1975. The Cheetah Acinonyx Jubatus in Africa: Report of a Survey in Africa from the Sahara Southwards, IUCN/WWF Joint Project.

Newsome, T. M., A. C. Greenville, D. Ćirović, C. R. Dickman, C. N. Johnson, M. Krofel, M. Letnic, W. J. Ripple, E. G. Ritchie, S. Stoyanov, and A. J. Wirsing. 2017. Top predators constrain mesopredator distributions. Nature communications 8:15469.

Nohrman, B. A. 1953. Survival Rate Calculation. Acta radiologica 39:78–82. Taylor & Francis.

Nzangaya, A. 2017. "Cheetahs reintroduced in Malawi". Malawi 24. Retrieved 8 January 2018. https://malawi24.com/2017/05/24/cheetahs-reintroduced-malawi/.

O'Brien, S. J., W. Johnson, C. Driscoll, J. Pontius, J. Pecon-Slattery, and M. Menotti-Raymond. 2008. State of cat genomics. Trends in genetics: TIG 24:268–279.

Oberem, P, and P Oberem. 2016. *The New Game Rancher*. Briza Publications. https://books.google.co.za/books?id=RvZhvgAACAAJ.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752.

Purchase, G. 2007. Status and Distribution of Cheetah in Zambia: A Preliminary Assessment. CAT News Special Issue 40–42.

Purchase, G. K. 1998. An assessment of the success of a cheetah reintroduction project in Matusadona National Park. University of Zimbabwe, Harare.

Purchase, G., G. Vhurumuku, and D. Purchase. 2006. A wild-to-wild translocation of cheetahs from private farmland to a protected area in Zimbabwe (1994--2005). Cat news 44:4–6. Cat Specialist Group, International Union for Conservation of Nature and Natural Resources, Species Survival Commission.

Purchase, G., L. Marker, K. Marnewick, R. Klein, and S. Williams. 2007. Regional assessment of the status, distribution and conservation needs of cheetahs in southern Africa. Cat News 3:44–46.

R Core Team. 2018. R A Language and Environment for Statistical Computing. R Foundation for

Ramesh, T., R. Kalle, K. Sankar, and Q. Qureshi. 2012. Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. Journal of zoology 287(4):269-275.

Ray, J. C., L. Hunter, and J. Zigouris. 2005. Setting Conservation and Research Priorities for Larger African Carnivores.

Reed, D. H., E. H. Lowe, D. A. Briscoe, and R. Frankham. 2003. Inbreeding and extinction: Effects of rate of inbreeding. Conservation genetics 4:405–410. Kluwer Academic Publishers.

Riggio, J., A. Jacobson, L. Dollar, H. Bauer, M. Becker, A. Dickman, P. Funston, R. Groom, P. Henschel, H. de Iongh, L. Lichtenfeld, and S. Pimm. 2012. The size of savannah Africa: a lion's (Panthera leo) view. Biodiversity and conservation 22:17–35.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? Bioscience 54:755–766. Oxford University Press.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343:1241484–1241484.

Rostro-García, S., J. F. Kamler, and L. T. B. Hunter. 2015. To kill, stay or flee: the effects of lions and landscape factors on habitat and kill site selection of cheetahs in South Africa. PloS one 10:e0117743.

Russell, L. 2018. Emmeans: estimated marginal means, aka least-squares means. R package version 1(2).

Rutherford, M. C. 2006. The Vegetation of South Africa, Lesotho and Swaziland.

Rutherford, M. C., L. Mucina, and L. W. Powrie. 2006. Biomes and bioregions of southern Africa. The vegetation of South Africa, Lesotho and Swaziland 19:30–51. South African National Biodiversity Institute Pretoria.

Rwcp, and Iucn/ssc. 2015. Regional Conservation Strategy for Southern Africa.

Schmitz, O. J., D. Hawlena, and G. C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. Ecology letters 13:1199–1209.

Scott Mills, L. 2012. Conservation of Wildlife Populations: Demography, Genetics, and Management. John Wiley & Sons.

Seddon, P., Doug P. Armstrong, and R. Maloney. 2007. Developing the Science of Reintroduction Biology. Conservation Biology: The Journal of the Society for Conservation Biology 21 (2): 303–12.

Sims-Castley, R., G. Kerley, B. Geach, and J. Langholz. 2005. Socio-economic significance of ecotourism-based private game reserves in South Africa's Eastern Cape Province. *Parks*, *15*(2), pp.6-18.

Smith, N., and S. L. Wilson. 2002. Changing land use trends in the thicket biome: pastoralism to game farming. Terrestrial Ecology Research Unit Report 38:23.

Soulé, M. E. 1986. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates.

Soule, M. E., editor. 1987. Viable populations for conservation. Cambridge University Press, Cambridge.

Statistical Computing, Vienna. https://www.R-project.org.

Sunquist, F., M. Sunquist, 2002. Wild Cats of the World. The University of Chicago Press. Chicago, USA. pp. 14–36. ISBN 978-0-226-77999-7.

Swanson, A., T. Arnold, M. Kosmala, J. Forester, and C. Packer. 2016. In the absence of a "landscape of fear": How lions, hyenas, and cheetahs coexist. Ecology and evolution 6:8534–8545.

Swanson, A., T. Caro, H. Davies-Mostert, M. G. L. Mills, D. W. Macdonald, M. Borner, E. Masenga, and C. Packer. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. The

Journal of animal ecology 83:1418–1427. Wiley Online Library.

Teixeira, C. P., C. S. de Azevedo, M. Mendl, C. F. Cipreste, and R. J. Young. 2007. Revisiting translocation and reintroduction programmes: the importance of considering stress. Animal behaviour 73:1–13.

Thaker, M., A. Vanak, C. Owen, M. Ogden, S. Niemann, and R. Slotow. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. Ecology, 92: 398-407. doi:10.1890/10-0126.1

Therneau T. M. and P. M. Grambsch. 2000. Modeling Survival Data: Extending the Cox Model. Springer, New York. ISBN0-387-98784-3.

Tilman, D., and M. Clark. 2014. Global diets link environmental sustainability and human health. Nature 515:518–522.

Tilman, D., M. Clark, D. R. Williams, K. Kimmel, S. Polasky, and C. Packer. 2017. Future threats to biodiversity and pathways to their prevention. Nature 546:73–81.

Townsend 2008. Essentials of Ecology. pp. 103–105. ISBN 978-1-4051-5658-5.

Treves, A., M. Krofel, and J. McManus. 2016. Predator control should not be a shot in the dark. Frontiers in ecology and the environment 14:380–388.

Tukey, John (1949). "Comparing Individual Means in the Analysis of Variance". Biometrics. 5 (2): 99–114. JSTOR 3001913.

Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. 2009. Behavioral Adjustments of African Herbivores to Predation Risk by Lions: Spatiotemporal Variations Influence Habitat Use. Ecology, 90(1), 23-30.

van der Merwe V Marnewick K Bissett C Groom R Mills MGL Durant, S. M. 2016. A conservation assessment of Acinonyx jubatus. C. M. R. L. Do Linh San E Raimondo D Davies-Mostert HT, editor.

South African National Biodiversity Institute and Endangered Wildlife Trust.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94(11):2619-2631.

Venables, W. N., and B. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Verna, F., F. Giorda, I. Miceli, G. Rizzo, A. Pautasso, A. Romano, B. Iulini, M. D. Pintore, W. Mignone, C. Grattarola, E. Bozzetta, K. Varello, A. Dondo, C. Casalone, and M. Goria. 2018. Corrigendum to "Detection of morbillivirus infection by RT-PCR RFLP analysis in cetaceans and carnivores" Journal of Virological Methods 247:22-27.

Weaver, J. L., P. Paquet, and L. Ruggiero. 1996. Resilience and conservation of carnivores in the Rocky Mountains. Conservation Biology, 10:964-976.

Weise, F. J., J. R. Lemeris, S. J. Munro, A. Bowden, C. Venter, M. van Vuuren, and R. J. van Vuuren. 2015. Cheetahs (*Acinonyx jubatus*) running the gauntlet: an evaluation of translocations into free-range environments in Namibia. PeerJ 3:e1346.

Weise, F. J., V. Vijay, A. P. Jacobson, R. F. Schoonover, R. J. Groom, J. Horgan, D. Keeping, R. Klein, K. Marnewick, G. Maude, J. Melzheimer, G. Mills, V. van der Merwe, E. van der Meer, R. J. van Vuuren, B. Wachter, and S. L. Pimm. 2017. The distribution and numbers of cheetah *(Acinonyx jubatus)* in southern Africa. PeerJ 5:e4096.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology10:1142–1154.

Wolf, C., and W. J. Ripple. 2018. Rewilding the world's large carnivores. Royal Society open science 5:172235.

Woodroffe, R., H. Davies-Mostert, J. Ginsberg, J. Graf, K. Leigh, K. McCreery, R. Robbins, G. Mills, A. Pole, G. Rasmussen, M. Somers, and M. Szykman. 2007. Rates and causes of mortality in Endangered African wild dogs Lycaon pictus: lessons for management and monitoring. Oryx: the journal of the Fauna Preservation Society 41:215.

Woodroffe, R., S. Hedges, and S. M. Durant. 2014. To fence or not to fence. Science 344(6179):46-48.

Zuur, A., E. Ieno, E. Walker, N. Saveliev and G. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Appendix

ANOVA (Type III) test statistics for causes of known mortality

Sex

LR Chisq	Df	Pr(>Chisq)
7.6349	4	0.1059

Age Class

LR Chisq	df	Pr(>Chisq)
57.682	12	0.000***

Origin

LR Chisq	Df	Pr(>Chisq)
20.955	12	0.05104

Biome

LR Chisq	Df	Pr(>Chisq)
30.538	12	0.002316 **

Reserve size

LR Chisq	Df	Pr(>Chisq)
0.716	8	0.1644

Reserve Tenure

LR Chisq	Df	Pr(>Chisq)
6.1194	4	0.1904

Lion

LR Chisq	Df	Pr(>Chisq)
21.542	4	0.0002471 ***

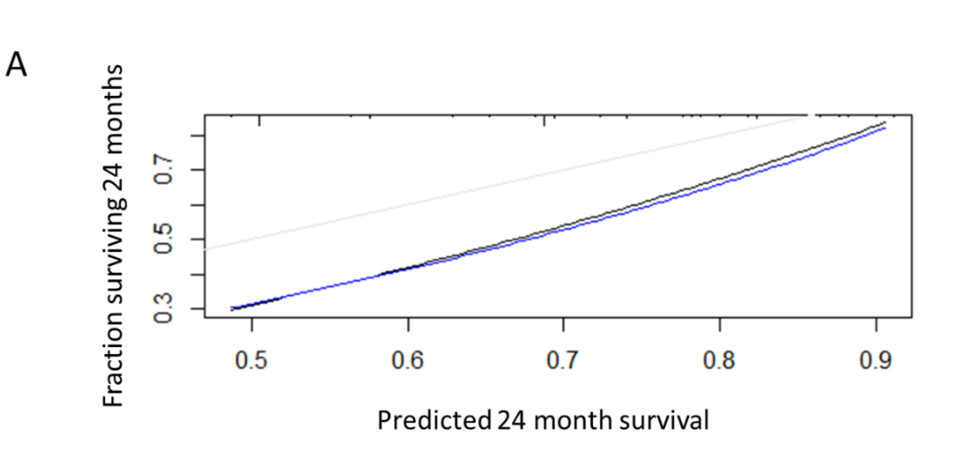
Translocation event

LR Chisq	Df	Pr(>Chisq)
66.979	4	9.847e-14 ***

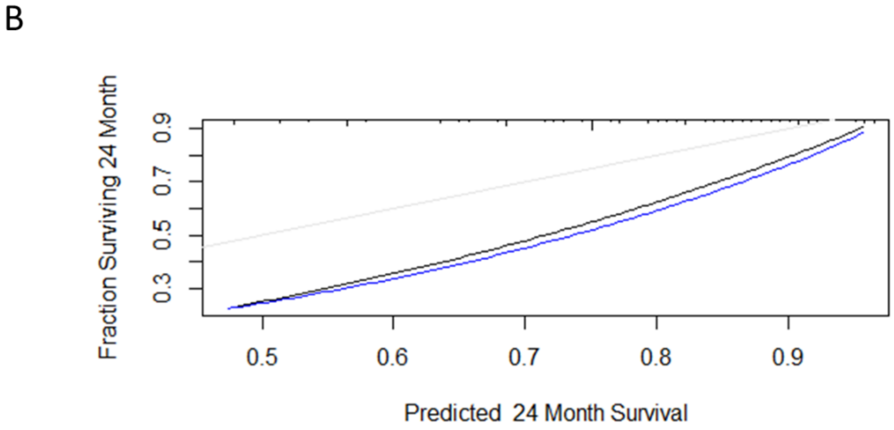
CMP

```
LR Chisq  Df     Pr(>Chisq)
20.869      4     0.0003362 ***

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```



```
calibrate.cph(fit = f_final_all, u = 24, B = 300, maxdim = 4)
n=688, B=300, u=24, Month Mean |error|: 0.164,  DF= 0.9
Quantile of |error|:0.186
```



Appendix 4. Calibrating final model to test how well it predicts 2 year survival for A) all cheetah (> 3 months and B)

Appendix 3. Causes of known mortality fixed effects outputs including least squared means test statistics with multiplicity adjustment to compare means and contrast.

Sex means	**Cause of death**	**prob**	**SE**	**df**	**lower.CL**	**upper.CL**
Female	Anthropogenic	0.264	0.052	8.000	0.144	0.384
Male	Anthropogenic	0.250	0.040	8.000	0.157	0.343
Female	Conspecific	0.083	0.033	8.000	0.008	0.158
Male	Conspecific	0.155	0.034	8.000	0.078	0.233
Female	Other natural cause	0.139	0.041	8.000	0.045	0.233
Male	Other natural cause	0.164	0.034	8.000	0.085	0.243
Female	Predator	0.403	0.058	8.000	0.269	0.536
Male	Predator	0.241	0.040	8.000	0.150	0.333
Female	Translocation related	0.111	0.037	8.000	0.026	0.197
Male	Translocation related	0.190	0.036	8.000	0.106	0.274

Sex contrast	**Cause of death**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Female - Male	Anthropogenic	0.014	0.066	8.000	0.211	0.838
Female - Male	Conspecific	-0.072	0.047	8.000	-1.535	0.163
Female - Male	Other natural cause	-0.025	0.053	8.000	-0.467	0.653
Female - Male	Predator	0.161	0.070	8.000	2.301	0.050
Female - Male	Translocation related	-0.079	0.052	8.000	-1.513	0.169

Age class means	**Cause of death**	**prob**	**SE**	**df**	**lower.CL**	**upper.CL**
adult	Anthropogenic	0.241	0.040	16.000	0.157	0.326
cub	Anthropogenic	0.185	0.053	16.000	0.073	0.297
juvenile	Anthropogenic	0.070	0.039	16.000	-0.013	0.152
subadult	Anthropogenic	0.244	0.064	16.000	0.109	0.380
adult	Conspecific	0.129	0.031	16.000	0.063	0.195
cub	Conspecific	0.056	0.031	16.000	-0.011	0.122
juvenile	Conspecific	0.070	0.039	16.000	-0.013	0.152
subadult	Conspecific	0.156	0.054	16.000	0.041	0.270

adult	Other natural cause	0.190	0.036	16.000	0.112	0.267
cub	Other natural cause	0.278	0.061	16.000	0.149	0.407
juvenile	Other natural cause	0.186	0.059	16.000	0.060	0.312
subadult	Other natural cause	0.111	0.047	16.000	0.012	0.210
adult	Predator	0.328	0.044	16.000	0.235	0.420
cub	Predator	0.463	0.068	16.000	0.319	0.607
juvenile	Predator	0.651	0.073	16.000	0.497	0.805
subadult	Predator	0.133	0.051	16.000	0.026	0.241
adult	Translocation related	0.112	0.029	16.000	0.050	0.174
cub	Translocation related	0.019	0.018	16.000	-0.020	0.057
juvenile	Translocation related	0.023	0.023	16.000	-0.025	0.072
subadult	Translocation related	0.356	0.071	16.000	0.204	0.507

Age class contrast	**Cause of death**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
adult - cub	Anthropogenic	0.056	0.066	16.000	0.850	0.830
adult - juvenile	Anthropogenic	0.172	0.056	16.000	3.089	0.032
adult - subadult	Anthropogenic	-0.003	0.075	16.000	-0.041	1.000
cub - juvenile	Anthropogenic	0.115	0.066	16.000	1.760	0.327
cub - subadult	Anthropogenic	-0.059	0.083	16.000	-0.713	0.890
juvenile - subadult	Anthropogenic	-0.175	0.075	16.000	-2.332	0.132
adult - cub	Conspecific	0.074	0.044	16.000	1.674	0.369
adult - juvenile	Conspecific	0.060	0.050	16.000	1.196	0.638
adult - subadult	Conspecific	-0.026	0.062	16.000	-0.421	0.974
cub - juvenile	Conspecific	-0.014	0.050	16.000	-0.285	0.992
cub - subadult	Conspecific	-0.100	0.062	16.000	-1.603	0.405
juvenile - subadult	Conspecific	-0.086	0.067	16.000	-1.289	0.582
adult - cub	Other natural cause	-0.088	0.071	16.000	-1.241	0.611
adult - juvenile	Other natural cause	0.004	0.070	16.000	0.052	1.000
adult - subadult	Other natural cause	0.079	0.059	16.000	1.324	0.562
cub - juvenile	Other natural cause	0.092	0.085	16.000	1.078	0.707
cub - subadult	Other natural cause	0.167	0.077	16.000	2.168	0.175
juvenile - subadult	Other natural cause	0.075	0.076	16.000	0.991	0.757
adult - cub	Predator	-0.135	0.081	16.000	-1.679	0.366
adult - juvenile	Predator	-0.324	0.085	16.000	-3.818	0.007
adult - subadult	Predator	0.194	0.067	16.000	2.906	0.046
cub - juvenile	Predator	-0.188	0.099	16.000	-1.893	0.270
cub - subadult	Predator	0.330	0.085	16.000	3.892	0.006
juvenile - subadult	Predator	0.518	0.089	16.000	5.844	0.000
adult - cub	Translocation related	0.094	0.035	16.000	2.707	0.067
adult - juvenile	Translocation related	0.089	0.037	16.000	2.385	0.120
adult - subadult	Translocation related	-0.243	0.077	16.000	-3.157	0.028
cub - juvenile	Translocation related	-0.005	0.029	16.000	-0.161	0.998
cub - subadult	Translocation related	-0.337	0.074	16.000	-4.574	0.002
juvenile - subadult	Translocation related	-0.332	0.075	16.000	-4.432	0.002

Origin means	**Cause of death**	**prob**	**SE**	**df**	**lower.CL**	**upper.CL**
Captive	Anthropogenic	0.000	0.000	16.000	0.000	0.000
Free	Anthropogenic	0.241	0.079	16.000	0.073	0.410
Native	Anthropogenic	0.176	0.029	16.000	0.115	0.237
Translocated	Anthropogenic	0.265	0.063	16.000	0.132	0.399
Captive	Conspecific	0.000	0.000	16.000	0.000	0.000
Free	Conspecific	0.241	0.079	16.000	0.073	0.410
Native	Conspecific	0.091	0.022	16.000	0.045	0.137
Translocated	Conspecific	0.102	0.043	16.000	0.010	0.194
Captive	Other natural cause	0.667	0.272	16.000	0.090	1.244
Free	Other natural cause	0.241	0.079	16.000	0.073	0.410
Native	Other natural cause	0.193	0.030	16.000	0.130	0.256
Translocated	Other natural cause	0.143	0.050	16.000	0.037	0.249
Captive	Predator	0.333	0.272	16.000	-0.244	0.910
Free	Predator	0.276	0.083	16.000	0.100	0.452
Native	Predator	0.409	0.037	16.000	0.331	0.488
Translocated	Predator	0.327	0.067	16.000	0.185	0.469
Captive	Translocation related	0.000	0.000	16.000	0.000	0.000
Free	Translocation related	0.000	0.000	16.000	0.000	0.000
Native	Translocation related	0.131	0.025	16.000	0.077	0.185
Translocated	Translocation related	0.163	0.053	16.000	0.051	0.275

Origin contrast	**Cause of death**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Captive - Free	Anthropogenic	-0.241	0.079	16.000	-3.038	0.036
Captive - Native	Anthropogenic	-0.176	0.029	16.000	-6.134	0.000

Captive - Translocated	Anthropogenic	-0.265	0.063	16.000	-4.206	0.003
Free - Native	Anthropogenic	0.065	0.084	16.000	0.772	0.866
Free - Translocated	Anthropogenic	-0.024	0.101	16.000	-0.236	0.995
Native - Translocated	Anthropogenic	-0.089	0.069	16.000	-1.287	0.584
Captive - Free	Conspecific	-0.241	0.079	16.000	-3.038	0.036
Captive - Native	Conspecific	-0.091	0.022	16.000	-4.195	0.003
Captive - Translocated	Conspecific	-0.102	0.043	16.000	-2.360	0.126
Free - Native	Conspecific	0.150	0.082	16.000	1.827	0.297
Free - Translocated	Conspecific	0.139	0.090	16.000	1.540	0.438
Native - Translocated	Conspecific	-0.011	0.048	16.000	-0.230	0.996
Captive - Free	Other natural cause	0.425	0.284	16.000	1.500	0.460
Captive - Native	Other natural cause	0.474	0.274	16.000	1.730	0.341
Captive - Translocated	Other natural cause	0.524	0.277	16.000	1.893	0.270
Free - Native	Other natural cause	0.048	0.085	16.000	0.568	0.940
Free - Translocated	Other natural cause	0.099	0.094	16.000	1.049	0.724
Native - Translocated	Other natural cause	0.050	0.058	16.000	0.865	0.823
Captive - Free	Predator	0.057	0.285	16.000	0.202	0.997
Captive - Native	Predator	-0.076	0.275	16.000	-0.276	0.992
Captive - Translocated	Predator	0.007	0.280	16.000	0.024	1.000
Free - Native	Predator	-0.133	0.091	16.000	-1.466	0.479
Free - Translocated	Predator	-0.051	0.107	16.000	-0.475	0.963
Native - Translocated	Predator	0.083	0.077	16.000	1.078	0.707
Captive - Free	Translocation related	0.000	0.000	16.000	3.257	0.023
Captive - Native	Translocation related	-0.131	0.025	16.000	-5.144	0.001
Captive - Translocated	Translocation related	-0.163	0.053	16.000	-3.092	0.032
Free - Native	Translocation related	-0.131	0.025	16.000	-5.144	0.001
Free - Translocated	Translocation related	-0.163	0.053	16.000	-3.092	0.032
Native - Translocated	Translocation related	-0.033	0.059	16.000	-0.556	0.944

Biome means	**Cause of death**	**prob**	**SE**	**df**	**lower.CL**	**upper.CL**
Fynbos	Anthropogenic	0.111	0.105	16.000	-0.111	0.333
Grasslands	Anthropogenic	0.304	0.096	16.000	0.101	0.508
Savannah	Anthropogenic	0.153	0.028	16.000	0.094	0.213

Thicket	Anthropogenic	0.302	0.058	16.000	0.179	0.424
Fynbos	Conspecific	0.000	0.000	16.000	-0.001	0.001
Grasslands	Conspecific	0.130	0.070	16.000	-0.018	0.279
Savannah	Conspecific	0.110	0.025	16.000	0.058	0.162
Thicket	Conspecific	0.111	0.040	16.000	0.027	0.195
Fynbos	Other natural cause	0.445	0.166	16.000	0.093	0.796
Grasslands	Other natural cause	0.174	0.079	16.000	0.006	0.341
Savannah	Other natural cause	0.233	0.033	16.000	0.163	0.303
Thicket	Other natural cause	0.063	0.031	16.000	-0.002	0.129
Fynbos	Predator	0.444	0.166	16.000	0.093	0.795
Grasslands	Predator	0.130	0.070	16.000	-0.018	0.279
Savannah	Predator	0.405	0.038	16.000	0.323	0.486
Thicket	Predator	0.381	0.061	16.000	0.251	0.511
Fynbos	Translocation related	0.000	0.000	16.000	-0.001	0.001
Grasslands	Translocation related	0.261	0.092	16.000	0.067	0.455
Savannah	Translocation related	0.098	0.023	16.000	0.049	0.148
Thicket	Translocation related	0.143	0.044	16.000	0.049	0.236

Biome contrast	**Cause of death**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Fynbos - Grasslands	Anthropogenic	-0.193	0.142	16.000	-1.361	0.540
Fynbos - Savannah	Anthropogenic	-0.042	0.108	16.000	-0.390	0.979
Fynbos - Thicket	Anthropogenic	-0.190	0.120	16.000	-1.592	0.410
Grasslands - Savannah	Anthropogenic	0.151	0.100	16.000	1.510	0.455
Grasslands - Thicket	Anthropogenic	0.003	0.112	16.000	0.025	1.000
Savannah - Thicket	Anthropogenic	-0.148	0.064	16.000	-2.304	0.139
Fynbos - Grasslands	Conspecific	-0.130	0.070	16.000	-1.857	0.284
Fynbos - Savannah	Conspecific	-0.110	0.025	16.000	-4.498	0.002
Fynbos - Thicket	Conspecific	-0.111	0.040	16.000	-2.806	0.056
Grasslands - Savannah	Conspecific	0.020	0.074	16.000	0.269	0.993
Grasslands - Thicket	Conspecific	0.019	0.081	16.000	0.239	0.995
Savannah - Thicket	Conspecific	-0.001	0.047	16.000	-0.015	1.000
Fynbos - Grasslands	Other natural cause	0.271	0.184	16.000	1.475	0.474
Fynbos - Savannah	Other natural cause	0.211	0.169	16.000	1.251	0.605
Fynbos - Thicket	Other natural cause	0.381	0.168	16.000	2.262	0.149
Grasslands - Savannah	Other natural cause	-0.059	0.086	16.000	-0.692	0.899
Grasslands - Thicket	Other natural cause	0.110	0.085	16.000	1.302	0.575
Savannah - Thicket	Other natural cause	0.170	0.045	16.000	3.757	0.008
Fynbos - Grasslands	Predator	0.314	0.180	16.000	1.745	0.334
Fynbos - Savannah	Predator	0.039	0.170	16.000	0.232	0.995
Fynbos - Thicket	Predator	0.063	0.177	16.000	0.359	0.984
Grasslands - Savannah	Predator	-0.274	0.080	16.000	-3.429	0.016
Grasslands - Thicket	Predator	-0.251	0.093	16.000	-2.690	0.069
Savannah - Thicket	Predator	0.024	0.072	16.000	0.331	0.987
Fynbos - Grasslands	Translocation related	-0.261	0.092	16.000	-2.849	0.051
Fynbos - Savannah	Translocation related	-0.098	0.023	16.000	-4.211	0.003
Fynbos - Thicket	Translocation related	-0.143	0.044	16.000	-3.240	0.024
Grasslands - Savannah	Translocation related	0.163	0.094	16.000	1.722	0.345
Grasslands - Thicket	Translocation related	0.118	0.102	16.000	1.161	0.658
Savannah - Thicket	Translocation related	-0.045	0.050	16.000	-0.897	0.807

Reserve size means	Cause of death	prob	SE	df	lower.CL	upper.CL
large	Anthropogenic	0.143	0.094	12.000	-0.061	0.347
med	Anthropogenic	0.161	0.033	12.000	0.089	0.233
small	Anthropogenic	0.250	0.040	12.000	0.164	0.336
large	Conspecific	0.286	0.121	12.000	0.023	0.549
med	Conspecific	0.137	0.031	12.000	0.070	0.204
small	Conspecific	0.058	0.021	12.000	0.012	0.105
large	Other natural cause	0.214	0.110	12.000	-0.025	0.453
med	Other natural cause	0.218	0.037	12.000	0.137	0.298
small	Other natural cause	0.167	0.034	12.000	0.093	0.241
large	Predator	0.286	0.121	12.000	0.023	0.549
med	Predator	0.355	0.043	12.000	0.261	0.448
small	Predator	0.408	0.045	12.000	0.311	0.506
large	Translocation related	0.071	0.069	12.000	-0.079	0.221
med	Translocation related	0.129	0.030	12.000	0.063	0.195
small	Translocation related	0.117	0.029	12.000	0.053	0.181

Reserve size contrast	Cause of death	estimate	SE	df	t.ratio	p.value
large - med	Anthropogenic	-0.018	0.099	12.000	-0.186	0.981
large - small	Anthropogenic	-0.107	0.102	12.000	-1.055	0.558
med - small	Anthropogenic	-0.089	0.052	12.000	-1.722	0.237
large - med	Conspecific	0.149	0.125	12.000	1.192	0.480
large - small	Conspecific	0.227	0.123	12.000	1.854	0.194
med - small	Conspecific	0.079	0.038	12.000	2.096	0.132

Lion means	Cause of death	prob	SE	df	lower.CL	upper.CL
No	Anthropogenic	0.429	0.076	8.000	0.252	0.605
Yes	Anthropogenic	0.157	0.025	8.000	0.100	0.215
No	Conspecific	0.071	0.040	8.000	-0.020	0.163
Yes	Conspecific	0.116	0.022	8.000	0.066	0.166
No	Other natural cause	0.262	0.068	8.000	0.105	0.418
Yes	Other natural cause	0.181	0.026	8.000	0.120	0.241
No	Predator	0.143	0.054	8.000	0.018	0.267
Yes	Predator	0.421	0.034	8.000	0.344	0.499
No	Translocation related	0.095	0.045	8.000	-0.009	0.200
Yes	Translocation related	0.125	0.023	8.000	0.073	0.177

Lion contrast	Cause of death	estimate	SE	df	t.ratio	p.value
No - Yes	Anthropogenic	0.271	0.080	8.000	3.378	0.010
No - Yes	Conspecific	-0.044	0.045	8.000	-0.978	0.357
No - Yes	Other natural cause	0.081	0.073	8.000	1.119	0.296
No - Yes	Predator	-0.278	0.064	8.000	-4.378	0.002
No - Yes	Translocation related	-0.030	0.051	8.000	-0.588	0.572

CMP means	Cause of death	prob	SE	df	lower.CL	upper.CL
post	Anthropogenic	0.099	0.026	8.000	0.039	0.159
pre	Anthropogenic	0.307	0.041	8.000	0.213	0.401
post	Conspecific	0.107	0.027	8.000	0.045	0.169
pre	Conspecific	0.110	0.028	8.000	0.046	0.174
post	Other natural cause	0.191	0.034	8.000	0.112	0.270
pre	Other natural cause	0.197	0.035	8.000	0.115	0.278
post	Predator	0.466	0.044	8.000	0.365	0.566
pre	Predator	0.283	0.040	8.000	0.191	0.376
post	Translocation related	0.137	0.030	8.000	0.068	0.207

Tenure	Cause of death	prob	SE	df	lower.CL	upper.CL
Private	Anthropogenic	0.186	0.027	8.000	0.123	0.249
State	Anthropogenic	0.259	0.060	8.000	0.122	0.397
Private	Conspecific	0.098	0.021	8.000	0.050	0.146
State	Conspecific	0.148	0.048	8.000	0.037	0.260
Private	Other natural cause	0.191	0.028	8.000	0.128	0.255
State	Other natural cause	0.204	0.055	8.000	0.077	0.330
Private	Predator	0.412	0.034	8.000	0.332	0.491
State	Predator	0.241	0.058	8.000	0.107	0.375
Private	Translocation related	0.113	0.022	8.000	0.062	0.164
State	Translocation related	0.148	0.048	8.000	0.037	0.260

Tenure contrast	Cause of death	estimate	SE	df	t.ratio	p.value
Private - State	Anthropogenic	-0.073	0.066	8.000	-1.113	0.298
Private - State	Conspecific	-0.050	0.053	8.000	-0.952	0.369
Private - State	Other natural cause	-0.013	0.061	8.000	-0.204	0.843
Private - State	Predator	0.171	0.068	8.000	2.529	0.035
Private - State	Translocation related	-0.035	0.053	8.000	-0.666	0.524

Model results for all cheetah < 3 months

	Coef	S.E.	Wald Z	Pr(>|Z|)	AIC
<u>Demographic</u>					
S~ age at start + sex + time period					
AgeCnt	-0.003	0.003	-0.930	0.354	4593.310
Cub vs. adult	0.338	0.121	2.790	0.005	4583.600
Subadult vs adult	-0.293	0.279	-1.050	0.294	

pre	Translocation related	0.102	0.027	8.000	0.040	0.164

CMP contrast	Cause of death	estimate	SE	df	t.ratio	p.value
post - pre	Anthropogenic	-0.208	0.049	8.000	-4.281	0.003
post - pre	Conspecific	-0.003	0.039	8.000	-0.087	0.933
post - pre	Other natural cause	-0.006	0.049	8.000	-0.122	0.906
post - pre	Predator	0.182	0.059	8.000	3.080	0.015
post - pre	Translocation related	0.035	0.040	8.000	0.868	0.410

Male vs Female	-0.157	0.101	-1.560	0.118	
Year	-0.069	0.009	-8.080	<0.0001	4593.602
Pre vs Post CMP	0.758	0.101	7.500	<0.0001	4584.097
Reserve					
S~ size + biome + tenure + predator_count					
SizeCnt	0.000	0.000	-3.090	0.002	4635.438
Size small vs large	1.620	0.359	4.510	<0.0001	4613.172
Size medium vs large	1.297	0.382	3.400	0.001	
Large predator count	-0.007	0.077	-0.090	0.925	
Grasslands vs Fynbos	-0.937	0.432	-2.170	0.030	
Savannah vs Fynbos	-0.078	0.399	-0.190	0.846	
Thicket vs Fynbos	0.160	0.388	0.410	0.681	
State vs Private	0.214	0.156	1.370		
	0.169	Large predator			
composition					
S~ leopard + lion + brown hyena + spotted hyena + wilddog					4643.230
Leopard	0.177	0.122	1.460	0.145	
Lion	-0.132	0.140	-0.940	0.346	
Brown hyena	0.015	0.113	0.130	0.898	
Spotted hyena	0.426	0.123	3.480	0.001	
Wild dog	-0.161	0.162	-0.990	0.321	
Model with top predictors					
S~ ageCat + sex + CMP + SizeCat + biome + tenure + spotted hyena					4554.635
Cub vs. adult	0.386	1.471	3.010	0.003	
Subadult vs adult	-0.063	0.939	-0.220	0.826	
Sex Male vs Female	-0.147	0.863	-1.450	0.146	
CMP Pre vs Post	0.657	1.930	6.200	0.000	
Grasslands vs Fynbos	-1.180	0.307	-2.630	0.009	
Savannah vs Fynbos	-0.969	0.379	-2.070	0.039	
Thicket vs Fynbos	-0.380	0.684	-0.950	0.340	
Size Med vs Large	0.406	1.501	2.600	0.009	
Size Small vs Large	1.100	3.004	2.950	0.003	
State vs Private	1.267	3.550	3.270	0.001	
Spotted hyena present	0.856	2.354	2.670	0.008	
S~ ageCat + sex + CMP + SizeCat + biome + spotted hyena					4559.043
S~ageCat + sex + CMP + SizeCat + tenure + spotted hyena					4563.544
S~ sex + CMP + SizeCat + biome + tenure + spotted hyena					4561.502
S~ ageCat + CMP + SizeCat + biome + spotted hyena					4554.740
S~ ageCat + CMP + SizeCnt + biome + tenure + spotted hyena					**4550.888**
Top Model Results					

ageCat cub	0.460	0.126	3.670	0.000
ageCat subadult	-0.059	0.285	-0.210	0.837
CMP Pre vs Post	0.628	0.106	5.940	<0.0001
State vs Private	0.737	0.197	3.750	0.000
Grasslands vs Fynbos	-1.280	0.451	-2.840	0.005
Savannah vs Fynbos	-1.000	0.468	-2.140	0.032
Thicket vs Fynbos	-0.272	0.390	-0.700	0.486
eserve size cnt	0.000	0.000	-3.800	0.000
Spotted hyena present	1.100	0.302	3.640	0.000
<u>Top Model Indexes</u>				
Obs	696.000			
Events	413.000			
Center	-2.804			
LR chi2	114.230			
d.f	0.313			
Score chi2	112.440			

Pr(>chi2)	0.000

Model results for adult cheetah

	Coef	S.E.	Wald Z	Pr(>|Z|)	AIC
<u>Demographic</u>					
S~ age at start + sex + coalition + time period					
Age	0.018	0.004	4.160	<0.0001	
Male vs Female	-0.229	0.202	-1.130	0.258	1742.950
Translocated vs native	-1.059	0.492	-2.150	0.031	
Male coalition	0.122	0.213	0.570	0.568	
Pre vs Post CMP	0.933	0.156	5.990	<0.0001	
<u>Reserve</u>					
S~ size + biome + tenure + predator_count					
SizeCnt	0.000	0.000	-2.410	0.016	1774.916
SizeCat					1753.838
State vs Private	0.683	0.258	2.650	0.008	
Large predator count	0.072	0.110	0.660	0.509	
Grasslands vs Fynbos	-0.861	0.488	-1.760	0.078	
Savannah vs Fynbos	-0.300	0.447	-0.670	0.503	
Thicket vs Fynbos	0.074	0.432	0.170	0.864	
<u>Large predator composition</u>					1786.225
S~ leopard + lion + brown hyena + spotted hyena + wilddog					
Leopard	0.047	0.175	0.270	0.789	

Lion	-0.417	0.200	-2.080	0.037	
Brown hyena	0.249	0.170	1.460	0.144	
Spotted hyena	0.192	0.173	1.110	0.267	
Wild dog	-0.076	0.228	-0.330	0.739	
Model with top predictors					
S~ translocation + age + CMP + reserve size + reserve tenure + reserve biome					1728.877
Translocated vs native	1.091	0.538	2.030	0.043	
age_start_adult	0.019	0.005	4.170	<0.0001	
CMP Pre vs Post	0.736	0.166	4.440	<0.0001	
reserve_size	0.000	0.000	-2.620	0.009	
State vs Private	0.797	0.369	2.160	0.031	
Grasslands vs Fynbos	-1.548	0.540	-2.860	0.004	
Savannah vs Fynbos	-0.429	0.428	-1.000	0.316	
Thicket vs Fynbos	-0.222	0.443	-0.500	0.616	
Lion	0.045	0.261	-0.17	0.865	
S~ translocation + age + CMP + reserve size + reserve tenure + reserve biome					**1726.986**
S~ translocation + age + CMP + reserve size + reserve tenure					1749.751

S~age + CMP + reserve size + reserve tenure + biome					1750.022
S~ translocation + age + CMP + reserve size + reserve tenure					1750.022
<u>Top Model Results</u>					
Age at start	0.019	0.005	4.180	<0.0001	
CMP Pre vs Post	0.742	0.165	4.500	<0.0001	
Translocated vs native	1.089	0.538	2.020	0.043	
reserve size cnt	0.000	0.000	-2.880	0.004	
Grasslands vs Fynbos	-1.569	0.539	-2.910	0.004	
Savannah vs Fynbos	-0.420	0.428	-0.980	0.327	
Thicket vs Fynbos	-0.223	0.443	-0.500	0.614	
State vs Private	0.875	0.284	3.090	0.002	