Tails through time: Leopard population dynamics in the Little Karoo

Lawrence Steyn

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Dr Kathryn Williams
Supervisor
Cape Leopard Trust

Dr Greg Distiller
Supervisor
SEEC
University of Cape Town

Dr Sally Hofmeyr
Co-supervisor
Fitzpatrick Institute
University of Cape Town

Dr Gareth Mann
Co-supervisor
Panthera

Anita Wilkinson
Co-supervisor
Cape Leopard Trust

Abstract

Large carnivores play a vital role in structuring our ecosystems, yet they face mounting threats such as habitat loss, prey reduction and persecution. These threats reduce their global distribution and impacts their population numbers. Protected areas can offer refuge for large carnivores, however leopards (*Panthera pardus*), can persist outside of these areas and often occupy mixed-use landscapes. Our understanding of how leopards persist over time in mixed-use landscapes is limited, especially in the semi-arid regions of southern Africa. This study, to the best of my knowledge, is the only multi-session maximum likelihood spatial capture-recapture (SCR) analysis to have been conducted in a semi-arid environment outside of a protected area in Southern Africa. The study aimed to estimate leopard population changes over time and to investigate the possible drivers affecting density, using three surveys (2012, 2017, 2022), in the mixed-use landscape of the Little Karoo in the Western Cape, South Africa. In 2012, a total of 141 paired camera stations were used for a total of 13,050 trap days resulting in 29 unique leopard captures. In 2017, a total of 40 paired camera stations were used for a total of 2,128 trap days resulting in 18 unique leopard captures and in 2022 a total of 64 paired camera stations were used for a total of 8,997 trap days resulting in 37 unique leopard captures. The best performing density model indicated an increasing population trend over the study period which included a trend term on density (D~year) and an interaction term (individual session*sex) on $\lambda 0$ (capture rate) and σ (spatial decay). Density estimates (Standard Error) for leopard populations for the three surveys 2012, 2017, and 2022, were 0.52 (± 0.11), 0.70 (± 0.08), and 0.95 (± 0.08) leopards per 100 km^2, respectively. Terrain ruggedness, elevation, vegetation type and distance from major rivers were all important drivers in leopard density in the Little Karoo. Indicating that high lying areas provide suitable refuge for leopards and are key areas for movement corridor planning. These density estimates are similar to previous single maximum likelihood SCR density estimate studies in the Little Karoo and the Western Cape province. Results from this study indicate the leopards have persisted in the Little Karoo over the study period and suggest that the population may be increasing. Further research on what is driving this population shift is needed, but the results serve as an encouraging sign for leopard conservation in the Little Karoo.

Plagiarism Declaration

I Lawrence Edward Steyn, hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I am presenting this thesis for examination toward the Degree of Master of Science in Biological Sciences.

I acknowledge that all data provided to me for this analysis was part of a collaborative effort between the Cape Leopard Trust and Panthera (see acknowledgements below).

This thesis has been submitted to the Turnitin module and I confirm that my supervisors have seen my report and that any concerns raised therefrom have been resolved between myself and my supervisors.

Name: Lawrence E. Steyn

Student number: STYLAW001

Signed: Signed by candidate

Date: 11th February 2024

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1. Introduction

1.1. The role of large carnivores

Large carnivores are predators that play a vital role in the maintenance of an ecosystem (Ripple *et al*., 2014; Hoeks *et al.,* 2020; Terraube *et al.,* 2020). The order Carnivora hosts a suite of well-adapted predators that occur on all major land masses and play a key role in maintaining ecological stability (Estes *et al.*, 2011; Mann*.,* 2014; Hoeks *et al.,* 2020) while occupying the upper end of the trophic food web (Estes *et al.,* 2011; Ripple *et al.,* 2014). Carnivores fill a niche role, making them rarer than animals lower down on the trophic web, increasing their vulnerability to extinction when compared to omnivores and herbivores (Ripple *et al*., 2014).

Many large carnivores are highly charismatic and are seen as the iconic species of a landscape (Dalerum *et al.*, 2008; Ripple *et al.,* 2014; Albert, Luque & Courchamp, 2018). This status signifies the unique role of these species in modern-day conservation, as they not only draw attention to the socioeconomic aspects of conservation, but also serve as key focal points for ecological studies, thus playing a fundamental role in effective conservation (Caro & O'Doherty, 1999; Estes *et al.,* 2011; Chapron *et al.*, 2014; Ripple *et al.,* 2014).

Despite being widely recognisable (Lindsey *et al*., 2007), large carnivores, beyond protected areas, are often underrepresented in scientific research (Weber & Rabinowitz, 1996; Dalerum *et al.,* 2008). Their role in ecological stability is far reaching and of the 31 largest recorded carnivores, seven of them have been linked to trophic cascades (Ripple *et al*., 2014; Allen *et al*., 2017). This can have adverse effects on the dynamics between herbivores and vegetation, along with influencing mesopredator population dynamics (Elmhagen *et al*., 2010; Drouilly, Nattrass & O'Riain, 2018; Feit, Feit & Letnic, 2019). These factors play a role in shaping ecosystems, and in mixed-use landscapes they can impact agricultural productivity (Prugh *et al*., 2009; Elmhagen *et al*., 2010; Letnic *et al)*. Furthermore, the conservation of large carnivores presents a formidable challenge due to their extended life histories, comparatively low population densities and their need to roam widely for larger prey, which imposes significant energetic constraints (Carbone *et al.,* 1999; Cardillo *et al*., 2005; Ripple *et al*., 2014).

These challenges are evident in the current International Union for the Conservation of Nature (IUCN) Red List where, of the 31 largest carnivores, more than 19 (61%) are classified as threatened (Ripple *et al.,* 2014). This is, in part, due to their increased sensitivity towards fragmentation of suitable habitat and the impact of anthropogenic activities (Chapron *et al*., 2014; Swanepoel *et al*., 2016), both of which are escalating issues as the Anthropocene progresses. Large carnivores' wide-ranging behaviour coupled with their energetic constraints (Ripple *et al.*, 2014; Wolf & Ripple, 2016), in a confined range, will increase their interactions with anthropogenic activities, presenting complex human–wildlife coexistence issues (Mann, 2014; Wolf & Ripple, 2017). Increasing coexistence challenges amid diminishing land availability, escalates conflict and emphasises the significance of protected areas as refugia (Pitman *et al*., 2017).

1.2. Protected areas

Protected areas are arguably the most widely agreed-upon measure to combat the effects of a changing climate and to preserve the vital stability of global biodiversity (Gaston *et al.*, 2008; Watson *et al*., 2014; Gray *et al.*, 2016). Protected areas, by their nature, place ecosystem preservation at the centre of land management practices and are a key pillar in biodiversity preservation (Geldman *et al.,* 2013). This role has evolved over time, providing opportunities for socioeconomic services based on the direct preservation of an area (Blamford *et al.,* 2015; Thapa *et al.,* 2022). While protected areas may lead to concerns around local communities and the sharing of benefits, they are still widely regarded as fundamental in preserving biodiversity (Mackenzie, 2012; Snyman & Bricker, 2021). This is of increased importance as global commitments to reducing biodiversity loss have expanded in scope and scale (Almond *et al.*, 2022). In light of this, the United Nations formed an agenda aimed at protecting 30% of marine and terrestrial areas by 2030 through the use of protected areas (Convention on Biological Diversity, 2022). This is a vital expansion on Aichi Target 11 (set for 2020), which set standards for protecting 17% of terrestrial land; however, Target 11 was deemed inadequate for the conservation of large carnivores (Di Minin *et al*., 2016). Not only does this expansion increase resilience towards changes in climatic conditions, it reduces the effects of fragmentation, edge effects and human–wildlife coexistence challenges (Newmark, 2008). Expanding the size of protected areas is advantageous for the preservation of large carnivores, as it limits interactions outside of park protection, which is vital given that the territories of these carnivores frequently extend beyond park edges (Rogan *et al.,* 2022).

Increasing a protected areas size provides more available area for large carnivores to use, while minimising their impact on anthropogenic activities and reducing the impacts of these activities on the protected areas edge (Newmark, 2008; Rogan *et al.,* 2022). Generally, the larger the protected area, the greater resilience the area has towards these impacts (Newmark, 2008). Large carnivores have a wide range of behaviours that may challenge the effectiveness of hard boundaries, such as natural dispersal, new mate selection, prey preferences and responses to increased competition (Wolf & Ripple, 2016; Pitman *et al.,* 2017). Connectivity between refugia, such as stepping stones or corridors, becomes imperative if protected areas are to increase their overall effectiveness (Swanepoel *et al.,* 2016; Pitman *et al.,* 2017; Rogan *et al.,* 2022). This can be vital for gene-flow, which is regarded as key for the effective management of large carnivores (Mech & Hallet, 2001; Epps *et al*., 2007).

1.3. Protected areas in South Africa

South Africa has a long history of protecting areas of land (Stats SA, 2022). Initially, these areas were mostly protected for hunting purposes, but later conservation became more common as a rationale for protected areas (Brooks, 2005; Stats SA, 2022). Ecotourism is one of the largest contributors to conservation of protected areas in South Africa, and large carnivores play a pivotal role in attracting tourists (Lindsey *et al.*, 2007; Chiutsi *et al.,* 2011). While vital for the preservation of land, both ecotourism and trophy hunting place intense pressure on large carnivores in South Africa (Packer *et al.*, 2009; Swanepoel *et al.,* 2014, Loveridge *et al.*, 2016). Although there are recognized benefits associated with the trophy hunting of large carnivores, concerns have been raised regarding its regulation and monitoring (Packer *et al.*, 2009; Balme *et al.,* 2010; Loveridge *et al.,* 2016).

In addition to these pressures, South Africa's protected area coverage is relatively small, at only 9.2% (Stats SA, 2022), making these areas isolated and more vulnerable to edge effects. This vulnerability can be heightened in developing countries due to the increased reliance on natural resources by surrounding communities (Newmark, 2008).

The significant demand for natural resources, especially bushmeat and large carnivore skins (for cultural purposes), can expose large carnivores to unintentional or intentional poaching, respectively (Mann, 2014; Naude, 2020). These threats, compounded by land transformation into agriculture and urban development, add to the external pressures on large carnivore conservation in South Africa (Anthony, Scott & Antypas, 2010; Mann, 2014; Constant, Bell & Hill, 2015; Hinde *et al.,* 2023). As the human population expands, these pressures will intensify, thus increasing the importance of managing human–wildlife coexistence (Anthony, Scott & Antypas, 2010).

1.4. Conserving large carnivores

To improve the conservation status of large carnivores, it is crucial to address human–wildlife coexistence, given carnivores' vital ecological role and the predominantly anthropogenic threats they face (Stein *et al*., 2020; Terraube *et al.*, 2020). While protected areas may offer reprieve from negative human–wildlife interactions, the efficacy of fences for controlling human entry into these reserves, along with the propensity of large carnivores for breaking out of these reserves, proves a constant challenge in the management of these animals (Terraube *et al.,* 2020; Rogan *et al.,* 2022).

In addition, the distribution of some large carnivores has declined by more than 76% within Africa (Wolf & Ripple, 2017). This places an increased emphasis on the identification and maintenance of suitable carnivore habitat (Ripple *et al.,* 2014). However, most land that is protected within South Africa is in landscapes that provide limited anthropogenic benefits, which tend to be in harsh terrain types or in areas that are not suitable for effective large carnivore conservation (Carruthers, 2007). Additionally, these areas often have mixed land uses surrounding the protected areas, increasing edge effects, which can cause the decline or extinction of large carnivore populations (Balme, Slotow & Hunter, 2010; Terraube *et al.,* 2020; Rogan *et al.,* 2022).

Large carnivores such as lions (*Panthera leo*) have demonstrated that co-existence within a mixed-use landscape is possible in Africa (Suraci *et al*., 2019). However, large carnivores will often prefer natural habitats and prey types over their anthropogenic counterparts, although they will exploit exotic and synanthropic prey species if available (Mondal *et al.,* 2013; Drouilly, Natrass & O'Riain, 2018, Hinde *et al.,* 2023). The risk for survival of large carnivores in a mixed-use landscape increases as they interact with livestock, which serve as sources of income for landowners (Swanepoel *et al.,* 2015). The tolerance of humans towards large carnivores is ultimately a determining factor in their effective survival in a modified landscape (Rogan *et al.,* 2022).

With substantial reductions in species ranges of large carnivores coupled with the increasing human populations in mixed-use landscapes, protecting areas of suitable land becomes paramount (Wolf & Ripple, 2017; Rogan *et al.*, 2022). Leopards (*Panthera pardus*) require habitat that provides effective cover for ambushing prey, that provides relief from competitors, and offers refuge for birthing females, as well as an area large enough to accommodate dispersal (Swanepoel *et al.,* 2013). In South Africa only 20% of land is classified as suitable leopard habitat and 25% of that is within protected areas (Swanepoel *et al.,* 2013). This calls attention to effective planning and management, while taking into consideration that successful conservation comes from within a protected area as well as outside of it (Swanepoel *et al.,* 2013; Williams *et al.,* 2017). Additionally, this places an increased emphasis on access to refugia outside of protected areas for large carnivores, either through the formation of corridors or stepping stones (Swanepoel *et al.,* 2013; Kaszta, Cushman & Macdonald, 2020).

1.5. Leopards and their status

The leopard is widely regarded as one of the most adaptable felids of the large carnivore guild, occupying wide geographic ranges in Africa and tropical Asia (Nowell & Jackson, 1996; Ray, Hunter & Zigouris, 2005). They are the only large carnivore known to occupy habitats ranging from tropical rainforests to deserts, only limited by sufficient prey availability and the availability of cover used for ambushing prey (Hayward *et al.,* 2006; Jacobson *et al.,* 2016). Leopards are solitary predators that rely on cryptic and general avoidance behaviours, making them well adapted to surviving in areas of relatively high anthropogenic activity (Balme, Hunter & Slotow, 2009; Mann, 2014).

While leopards are able to live in various habitat types, they have some preferences depending on the habitat they occupy (Mann, 2014; Hinde *et al.,* 2023). In harsh arid landscapes, leopards will generally prefer rugged broken terrain over open areas, due to the higher abundance of cover, the availability of refuges from anthropogenic activities and greater opportunities for competitor avoidance (Swanepoel *et al.,* 2013; Mann*,* 2014; Miller *et al.,* 2018; Mann*,* O'Riain & Parker, 2020; Stein *et al.,* 2020). Despite their unique adaptability, leopard population numbers are decreasing, and within Africa the species has already seen a 36% reduction in its historical range (Jacobson *et al.,* 2016; Stein *et al*., 2020). In addition, extant populations outside of protected areas are seldom studied or monitored (Balme *et al.,* 2014; Mann*,* O'Riain & Parker, 2020). This makes evaluations of population dynamics, the impacts of anthropogenic activities and the efficacy of conservation measures difficult to quantify (Mann*,* 2014; Stein *et al.,* 2020).

Leopard populations in South Africa face significant threats, requiring further studies to comprehend the full extent, but clear signs indicate specific factors driving their decline (Swanepoel *et al.,* 2013; Jacobson *et al.,* 2016). This is noted in the IUCN Red List as the status of leopards has moved from Least Concern in 2008 to Vulnerable as of 2020 (Stein *et al.,* 2020). Key factors affecting populations in South Africa are a reduction in prey species, habitat loss through anthropogenic land-use, use of skins or body parts for cultural practices, persecution and poorly managed trophy hunting practices (Blame *et al.,* 2009; Swanepoel *et al.,* 2015; Stein *et al.,* 2020).

A reduction in natural prey numbers has been linked to increasing anthropogenic activities in previous species ranges and as this intensifies, prey species will become restricted to protected areas (Stein *et al.,* 2020). While leopards are known to have a broad diet range, their preferred diet consists of gregarious herbivores between 10 and 40 kg (Hayward *et al.,* 2006). The major anthropogenic activity thought to have caused the decline in prey availability is the exploitative utilisation of bushmeat, which has seen an average prey abundance decline of 59% over a 35-year period in eastern, western and southern Africa (Stein *et al.,* 2020). This natural prey reduction may increase leopards' intake of synanthropic prey species and livestock (Ripple *et al.,* 2016; Hinde *et al.,* 2023). Agricultural management practices will often counter these interactions with retaliatory attacks on leopards and are a lead cause of leopard mortalities in unprotected populations (Balme *et al.,* 2009; Mann, 2014; Swanepoel *et al.,* 2015). As a result, a cultural belief around leopard retaliation, which often overestimates the risks leopards pose to their livestock, can lead to the lethal removal of leopards in an area without sufficient justification (Mann, 2014; Swanepoel *et al.,* 2014; Swanepoel *et al.,* 2016).

While leopards' ecological importance is without question, there is a deficit in reliable population density data, which hinders their conservation management and the understanding of how they impact a mixed-use landscape (Rogan *et al.,* 2016; Mann, O'Riain & Parker, 2020). The existing knowledge gap may result in conservation decisions relying on anecdotal evidence and opinions rather than empirical evidence, potentially leading to ineffective initiatives and the misidentification of critical areas for concern (Balme *et al*., 2014; Hargey, 2022). Ultimately, population estimates are key for the management of leopard populations (Balme *et al.,* 2014, Mann, O'Riain & Parker, 2020). In addition to this, long-term studies on how leopard populations change over time are scarce (Chase-Grey, 2011; Williams *et al.,* 2017). Though the literature contains point estimates made over time, the analysis of trend data on leopard population numbers remains relatively novel, particularly in semi-arid environments outside of protected areas (Balme, Slotow & Hunter, 2009; Mondal *et al*., 2013; Williams *et al*., 2017; Rogan *et al*., 2020; Devens *et al.,* 2021; Farhadinia *et a*l., 2021; Rostro-García *et al*., 2023). Gaining insights into long-term changes in leopard population numbers may increase the efficacy of population management strategies. (Balme, Slotow & Hunter, 2009; Pitman *et al.,* 2015; Farhadinia *et al*., 2021; Rostro-García *et al*., 2023).

1.6. Leopards of the Western Cape

The Western Cape province in South Africa has a wide range of landscapes which play a crucial role in the preservation of biodiversity in South Africa (Cowling *et al.,* 2003). In this province, however, there is a suite of anthropogenic activities which has seen a population growth of over 1.6 million people, to a total of 7.4 million people, in 11 years (2011–2022) (Stats SA, 2022). The increase in population, is in part, due to the socio-political landscape, urban expansion and increased agricultural land-use, which can negatively impact leopard population dynamics (Mann, O'Riain & Parker, 2020; Stats SA, 2022).

Agricultural expansion is generally limited to land that is flat in the low-lying areas of the province (Mann, O'Riain & Parker, 2020; *Stats* SA, 2022; Hinde *et al.,*2023). This places increased emphasis on less disturbed areas of higher elevation as a refuge for leopards, their prey, their competitors and the natural flora (Cowling *et al.,* 2003; Mann, O'Riain & Parker, 2020). The Cape Fold Mountains therefore provide a vital landscape for protecting native species, as this landscape acts as a natural corridor for the movement of animals (Lombard *et al.,* 2010; Martins & Harris, 2013; Hinde *et al.,* 2023). Consequently, these mountain ranges offer refuge for leopards, allowing them to persist in close proximity to areas of heightened anthropogenic activity throughout the province (Mann, 2014; Mann, O'Riain & Parker, 2020).

There are a number of state-controlled protected areas and various privately owned protected areas in the Western Cape (see Figure 1). The privately owned protected areas are comprised of partnerships and stewardship agreements with nature reserves, non-governmental organisations (NGOs), and government (Stats SA, 2023). The combination of both private and state-owned protected areas is a cost-effective way of doing conservation at scale and is key for increasing protected refugia for leopards as agricultural practices expand (Stolton & Dudley, 2014; Lindsey *et al.*, 2021).

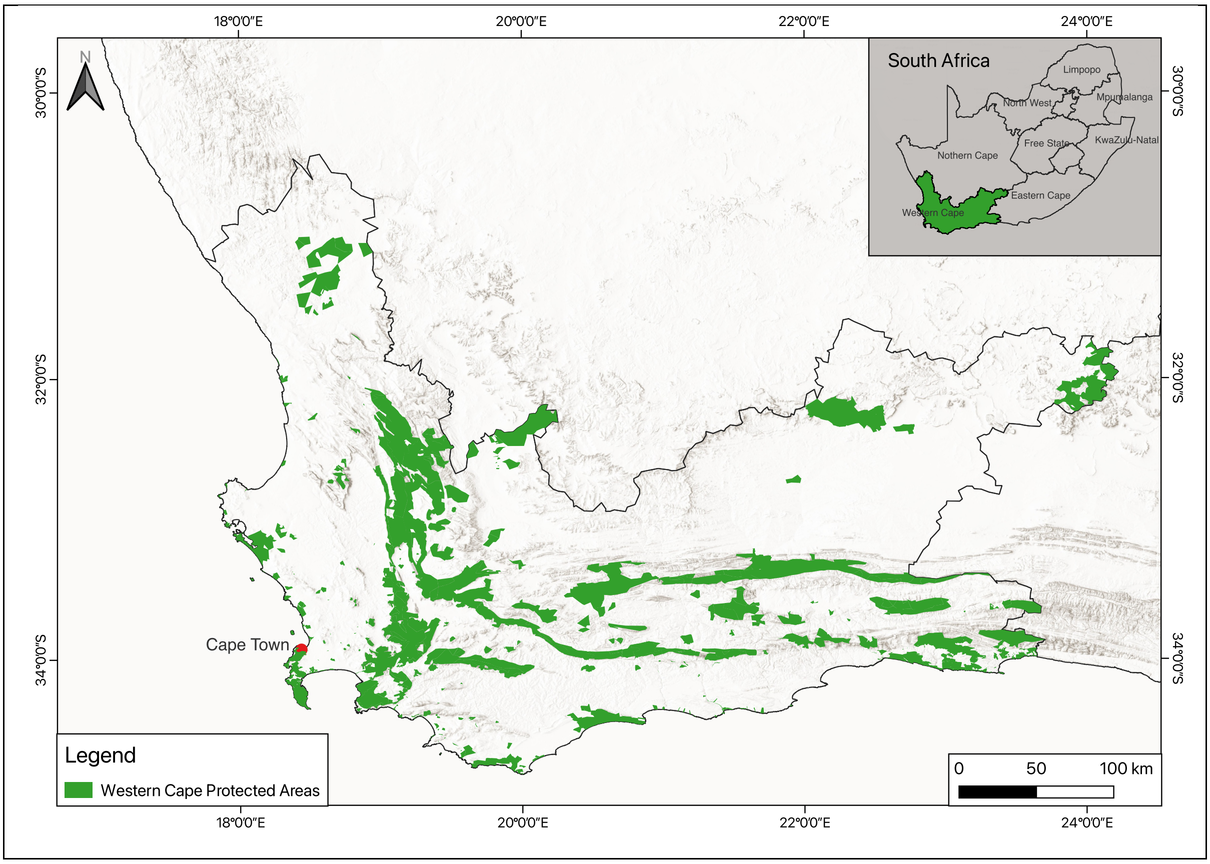

Figure 1: *A map of the Western Cape province of South Africa (SA) showing the distribution of protected areas in the province. Data for protected areas was sourced from the South African Department of Forestry, Fisheries & the Environment (DFFE), based on SA protected areas and SA conservation areas data.*

Historically, leopards in the Western Cape were classified as vermin due to their perceived impact on agricultural livestock in the area (Martins & Martins, 2006; Mann*.,* 2014). They were actively persecuted as there was a legal obligation to kill any leopards on the owner's property (Ray, Hunter & Zigouris, 2005). In 1957 their status was changed by the Cape Problem Animal Control Ordinance (no. 26 of 1957), allowing hunting only with a permit, and in more recent times, further restrictions were imposed due to changes in their IUCN Red List status (Martins & Martins, 2006; Swanepoel *et al.,* 2015; Stein *et al.,* 2020). This prompted legislation to halt the legal persecution of leopards in the area. However, their intense persecution over decades led to a dramatic reduction in leopard population numbers and fuelled a negative perception around leopards in the area (Ray, Hunter & Zigouris, 2005; Mann, 2014). This is evident from the illegal killing of leopards in the area by both hunting and trapping (Martins & Martins, 2006).

The Western Cape has a low prey density, which is believed to be a result of poor nutrition availability from the indigenous vegetation in conjunction with the loss of habitat in low-lying areas to agricultural activities and persecution for bushmeat (Norton *et al.,* 1986; Radloff, 2008; Drouilly, Natrass & O'Riain, 2018; Woodgate, Distiller & O'Riain, 2018). The combination of leopard persecution, limited suitable habitat and low prey availability has led to leopards having low population numbers in the province (Mann, O'Riain & Parker, 2020; Devens *et al.,* 2021). Their estimated home-range size, based on studies in the Cederberg Mountains of the Western Cape, is on the order of several hundred square kilometres, with males having notably larger home range estimates (100–910 km^2) than females (74–203 km^2) (Patterson *et al*., 2008; Martins, 2010; Martins & Harris, 2013). This is in line with home-range sizes in arid areas such as the southern Kalahari and considerably larger than that of the north-eastern parts of South Africa (Mann, 2014; Mann *et al.,* 2019). Previously, far less research was published on leopards in the Western Cape than in north-eastern South Africa (Mann*,* 2014).

However, in more recent times, there has been a notable increase in research conducted in the Western Cape through organisations such as the Cape Leopard Trust (https://capeleopard.org.za/research) and the Landmark Foundation (https://www.landmarkfoundation.org.za/research/).

Leopard density in the Western Cape is relatively low compared to north-eastern South Africa, with densities ranging from 0.17 (standard error [SE] ± 0.7) leopards per 100 km^2 in De Hoop (protected area) to 1.89 (95% confidence interval [CI]: 0.89–2.50) leopards per 100 km^2 in the Langeberg mountains (Mann, 2014, Devens *et al.,* 2021; Hargey, 2022). Published literature has recorded leopard populations with single density estimates or density studies over short temporal timeframes in mixed-use landscapes (Devens *et al.,* 2021; Hinde *et al.,* 2023). Long-term studies on leopard population dynamics and density trends in the Western Cape, however, are notably absent from the published literature.

1.7. Estimating leopard population densities

With leopards' elusive behaviour, their preferred habitat types in arid areas, and their large home ranges, obtaining accurate estimates of population densities is challenging (Balme, Hunter & Slotow, 2009). Various non-invasive monitoring techniques can be applied at a population level and are thought to be the best means of capturing reliable data in areas believed to have sparse populations (Rogan, 2021). While methods such as very high frequency or global positioning system (VHF/GPS) tracking collars and genetic sampling have been used for surveys that estimate density, both have shortfalls when it comes to either ethics or density estimations (Janečka *et al.,* 2011; Hayward *et al.*, 2012; Jewell, 2013; Monterroso *et al.*, 2014; Zemanova, 2020). This leaves camera-trapping as a common monitoring technique due to its minimal impact on the target species, cost-effectiveness, continuous sampling viability, ease of operation, and the ability to monitor multiple species concurrently (Karanth, 1995; Silveira, Jácomo & Diniz-Filho, 2003; Wearn & Glover-Kapfer, 2019). However, producing robust density estimates requires complex analyses that are often dependant on considerable expertise (Efford & Fewster*,* 2013).

While density estimates may be challenging to produce, the importance of effective population-density monitoring is paramount for conservation efforts and can be key for assessing the long-term viability of a population (Sollmann *et al.,* 2011; Efford, Fewster, 2013; Hinde *et al*., 2023). Numerous methods exist for determining population densities, yet spatial capture-recapture (SCR) models have gained widespread recognition, using a robust statistical framework, that incorporates spatial information with capture-recapture data, to estimate population density (Efford, 2004; Borchers & Efford, 2008). Estimating population density involves two components. First, a state model that describes the distribution of home ranges within a study area (Borchers & Efford, 2008). Second, an observation process that models the probability of detecting a species at a given location given the distance from the individual's theoretical home range (Borchers & Efford, 2008). Camera traps are more likely to detect leopards whose home-range centres are closer to them than those whose home ranges are centred further away (Efford, 2004; Borchers and Efford, 2008). Additionally, leopards are known to establish and uphold their territories, maintaining relatively stable home ranges over short periods (Snider *et al.,* 2021).

The incorporation of spatial elements into the model framework creates a more robust analysis while removing the reliance on *ad hoc* buffer estimates when calculating density (Brochers 2010; Mann, O'Riain & Parker, 2020). In addition, SCR modelling is highly adaptable, taking into consideration various factors such as anthropogenic, biotic and abiotic factors (Borchers & Efford, 2008). Analyses, can also be run in multiple sessions that produce a trend analysis for multiple independent surveys of an area over time. (Borchers & Efford, 2008; Borchers 2010).

1.8. Study objectives, hypotheses and predictions

Understanding the persistence of leopards in a mixed-use landscape is essential for their future conservation, particularly in light of threats within protected areas (Williams *et al*., 2017; Naude *et al*., 2020) and the crucial role that shared landscapes play as movement corridors. In addition, understanding how leopard populations adapt and change, over time, can prove vital for effective long-term conservation strategies. This study analysed data from three camera trap surveys established in a mixed-use landscape of the Little Karoo (Figure 2) in the Western Cape, South Africa. Key objectives of the study are to (1) estimate leopard population densities to determine whether the population has changed over time using multi session spatial capture-recapture models; and (2) explore the factors influencing variations in leopard density by exploring a set of relevant covariates in the density model.

A key consideration when estimating leopard density in the Western Cape is that sex is known to affect leopard detectability and home range estimates (Mann, O'Riain & Parker, 2020, Hinde *et al.,* 2023). Three possible outcomes for estimating leopard density over time were predicted: (1) density remained constant over time and no change occurred, (2) density changed over time for each individual survey independently or (3) there would be a trend in density estimates over time.

Several factors contribute to the density variation of leopards in mixed-use landscapes, such as the risk of persecution, prey availability, suitability of habitat for refuge or cover, and the abundance of potential mating partners (Balme, Hunter & Slotow, 2007; Mann 2014; McManus *et al.,* 2021). In human-modified landscapes, leopards encounter heightened persecution risks, as their presence poses potential threats to domestic animals and human lives (Havmøller *et al.,* 2019). This contributes to leopards exhibiting a preference for natural habitats and prey (Mann, O'Riain & Parker, 2020). The hypotheses for this study were based on previous behavioural and demographic research on leopards in the Little Karoo (Western Cape, South Africa), and semi-arid environments. They were formulated based on the widely accepted theories that leopard territorial range is influenced by sex, leopard density is contingent upon resource availability, and avoidance of anthropogenic impacts leads leopards to prefer less transformed landscapes. Four hypotheses affecting leopard density were formulated, each featuring a distinct density model, stating that density will be:

i. Higher at intermediate ruggedness, as leopard detectability in prey hunting events is reduced as ruggedness increases (Mann *et al.,* 2019).

ii. Higher at intermediate elevation, reflecting the inverse relationship between elevation and anthropogenic impacts in mixed-use landscapes (Swanepoel *et al*., 2013; Mann, O'Riain & Parker, 2020).

iii. Higher in vegetation types of intermediate vegetation cover, suitable for stalking and ambushing prey (Balme, Hunter & Slotow, 2007; Hinde *et al.,* 2023).

iv. Higher with increasing proximity to major rivers (Mann, O'Riain & Parker, 2020).

1.9. Previous Little Karoo density estimates

An initial study on leopard density in the Little Karoo indicated that population densities in 2012 were estimated at 0.22 (SE± 0.17) -1.26 (SE± 0.25) leopards per 100 km^2, based on how the study region was defined (Mann, O'Riain & Parker, 2020). A subsequent unpublished study in 2017 was conducted by Panthera, which estimated 1.01 (SE±0.2) leopards per 100 km^2.

2. Methods

2.1. Study area

The Little Karoo (16,000–17,000 km^2 in extent) in the Western Cape of South Africa is part of the Cape Floristic Region, which is known for its global conservation importance and is classified as a biodiversity hotspot (Mittermeier *et al*., 1999). The Little Karoo is an east–west oriented valley between two parallel mountain ranges in the south east of the Western Cape (Le Maitre *et al*., 2007). Mountainous areas in the Little Karoo receive approximately 1,000 mm of rain per year, while the low lying-areas in the rain shadows typically receive 200–300 mm/year (Vlok and Schutte-Vlok, 2010). As such, the Little Karoo can be classified as a semi-arid intermontane basin with three major biomes: Succulent Karoo, Subtropical Thicket and Fynbos (Volk *et al.,* 2005; Volk & Schutte-Volk, 2010). Vegetation growth is largely determined by rainfall and the geology of the area. The fynbos vegetation is predominantly located at higher elevations. The denser subtropical thicket occurs on intermediate slopes as a mosaic of dense shrub patches, scattered trees, and open ground. Lower altitudes feature succulent karoo vegetation, characterised by diminutive succulent shrubs typically not exceeding 1 m in height (Vlok and Schutte-Vlok, 2010; Mann, O'Riain & Parker, 2020).

The study site is approximately 3,200 km^2 and is located roughly in the centre of the Little Karoo region. To the north, the site includes the southern slopes of the Swartberg Mountains as well as parts of the Gamkaskloof Valley ('Die Hel'), and the southern boundary extends to the foothills of the Outeniqua Mountains. Noteworthy is the inclusion of the Gamkaberg/Rooiberg inselberg, which traverses from the northern to the southern mountain ranges and is comprehensively incorporated into the study area. The eastern boundary of the study site stops at the Outeniqua Mountains and the western boundary lies roughly equidistant between the Rooiberg and Langeberg mountains.

2.2. Camera trap surveys

Three major camera trap surveys, designed to monitor leopards, were conducted in the study area at approximately five-year intervals (see Figure 2): a survey conducted by Mann in 2012 (Mann, 2014; Mann, O'Riain & Parker, 2020), a survey by Panthera in 2017 and a survey by the Cape Leopard Trust in 2022. The study area was divided into 50 km^2 grid cells (7.07 km x 7.07 km) based on minimum home range estimates for female leopards (50 km^2) in the Western Cape (Martins, 2010). Where possible, each grid cell had two camera stations deployed to maximize coverage, increasing the likelihood that leopards residing within the study area would have some part of their home range encompassed by at least one camera station. Not all grid cells had this strategy applied to them due to logistical restraints in the survey, such as farmers denying access to their properties. This camera trapping approach ensures the fulfilment of the assumption that all animals within the study area could be successfully detected (O'Connel, Nichols & Karanth, 2011). Camera trap stations were strategically positioned within each grid cell, targeting locations with a high likelihood of capturing leopard images. This approach aimed to optimize the probability of capturing sightings and maximize the representation of the total sampled population (O'Connel, Nichols & Karanth, 2011; Mann, 2014; Mann, O'Riain & Parker, 2020). At each camera trap station, a pair of camera traps were strategically placed on opposing sides of a trail/opening, enabling simultaneous capture of images from both directions. This setup enhances the probability of accurately identifying individual leopards by capturing both flanks of their non-mirrored rosette patterns.

For the 2012 survey, the entire study area, encompassing roughly 3,200 km^2, was covered, although cameras were deployed in only 71 of the available 80 grid cells, due to property access restrictions, camera trap availability and decisions based on areas with low likelihoods of leopard detection. A total of 141 camera stations were used over a staggered survey period, with stations being active for an average of 93 days and yielding an overall sample effort of 13,085 trap days. Cuddeback Capture camera traps (Non-Typical Inc., Wisconsin, USA) were deployed at the majority of sites, along with Cuddeback Attack at 12 sites and Cuddeback Expert at 9 sites.

The 2017 survey covered a smaller area, which was selected based on data obtained from the 2012 survey, which indicated that leopard image captures were confined to regions with low levels of anthropogenic activity, adequate vegetation coverage, and higher elevations. This reduced area encompassed approximately 990 km^2 of the original study area. A total of 40 camera stations were deployed, with stations being active for an average of 53 days and yielding an overall sample effort of 2,128 trap days. Panthera camera traps V4 and V5 were used.

The 2022 survey adopted a methodology similar to that of the 2017 survey, focusing on a smaller study area with a higher likelihood of capturing leopards. The same area (990 km^2) from the previous 2017 survey was monitored, with the addition of new camera trap stations in the south-eastern corner of the study area. A total of 64 camera trap stations were deployed, covering areas identified in the previous surveys, as having a high likelihood of leopard captures. Camera stations were active for an average of 141 days and yielded an overall sample effort of 8,997 trap days. The survey used Cuddleback X-Change Colour cameras, equipped with strobe flash, for data collection.

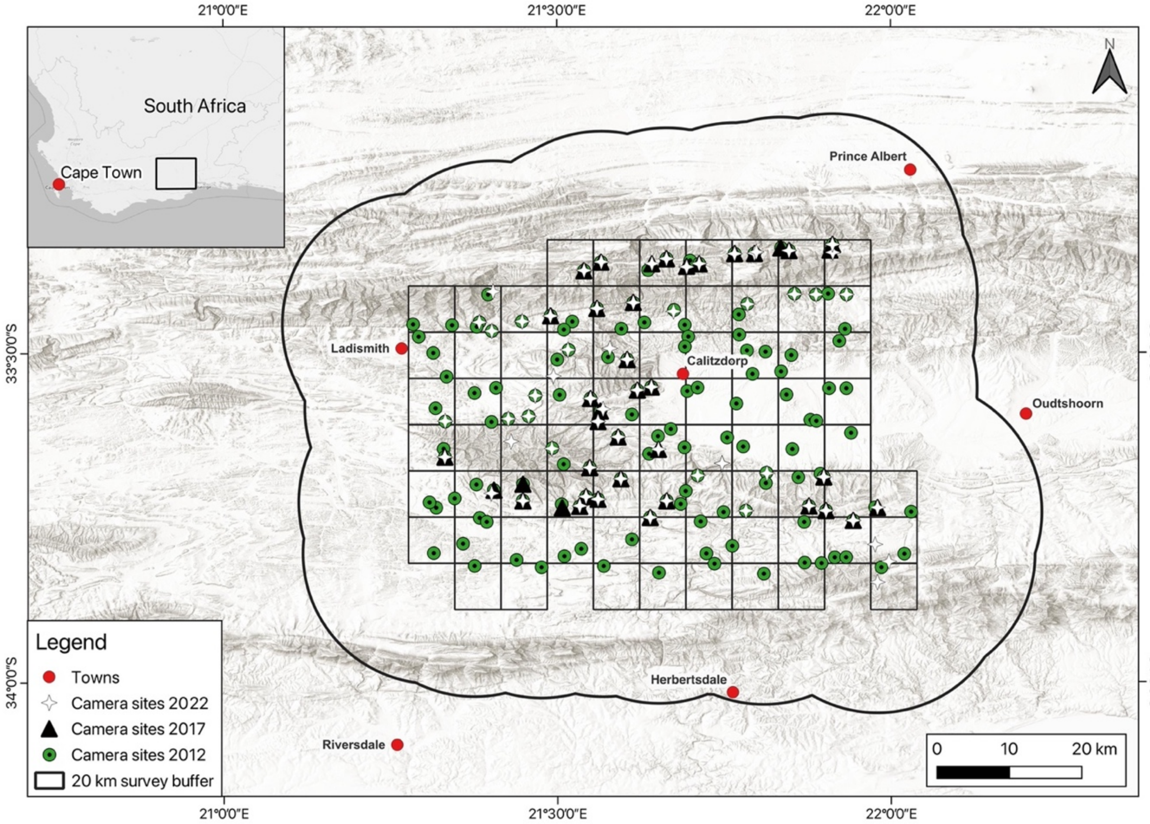

Figure 2: *The Little Karoo study area in the south east of the Western Cape province, South Africa. Camera trap sites are indicated by green dots (2012 survey), black triangles (2017 survey) and white stars (2022 survey). The bold black line represents the survey buffer (boundary) calculated by adding a 20 km buffer around the outermost traps. A 7.07 x 7.07 km (50 km^2) grid was superimposed over the study area.*

2.3. Leopard identification

Leopard identification involved a comparative analysis of distinct spot and rosette patterns (Balme *et al.*, 2009; Martins, 2010; Mann, 2014). Additionally, the overall appearance of leopards served as an indicator of their sex, with males typically exhibiting thicker necks, a heavier build, and the presence of an orange scrotal sac (Mann, 2014). It is important to note that while these differences are readily observable in adult males, identifying sub-adult males, when compared to adult females, presents a greater challenge. Identification of sub-adult males is enhanced through multiple captures which increases the likelihood of a positive identification.

The set up of camera trap stations is aimed to capture both non-mirrored flanks of a leopards' rosette patterns when the trap is triggered. To do this, camera stations utilise two opposing cameras facing one another. Once images of both flanks are captured, the images are compared to existing leopard identikits to determine whether the individual is new or known. Each image also captures additional data, including location, time, date, and the presence of other species.

In recent years reliable methodology for identifying leopards has transitioned from manual input-based software to autonomous machine learning solutions (Verschueren *et al.,* 2023). The 2012 and 2017 studies relied on Camerabase version 1.4 (Tobler, 2007), which relies on user input to process the data. The 2022 study used WildID (https://www.wildid.app/), a machine learning algorithm, for identification of species captured in the study. Images of leopards were then exported to African Carnivore Wildbook (https://www.africancarnivorewildbook.org), which was used for individual leopard identification. All three surveys' (2012, 2017 & 2022) leopard identity kits were imported into African Carnivore Wildbook to verify individual identities, and to compare them between surveys.

2.4. SCR Modelling

In the maximum likelihood Spatial Capture-Recapture (SCR) framework, density is a parameter in the likelihood equation that gets maximised to find an estimate. Individual detection functions were estimated by employing the hazard half-normal function, with $\lambda 0$ (capture rate) and σ (spatial rate of decay) as parameters influencing the detection probability. These parameters collectively defined the rate of detection as a function of location. Three major file types were required to run the SCR analysis: a detector file that contained the spatial coordinates with the effort for each detector, capture history files (for each survey) that contained the relevant capture history data for the target species and a habitat mask which defined the study area for the model to run estimates on. The habitat mask created the spatial environment used for estimating density.

A maximum likelihood multi-session count model was used for density estimates, using occasion data simplified into a single occasion for each session. Additionally, centroids situated within pixels characterized as water bodies or urban centres were excluded from the habitat mask. Akaike's Information Criterion (AIC) was utilised to assess relative statistical support for model fitting (Akaike, 2011) based on 'AICc' which is corrected for small sample sizes.

2.5. Data processing

Multi-session Spatial Capture-Recapture (SCR) modelling requires a consolidated capture data file encompassing all independent leopard captures across sessions (the surveys conducted in 2012, 2017, and 2022) and independent detector files for each individual session (Efford, 2004). The captures dataset includes variables such as session number, an independent species identifier (Animal ID), occasion, and detector identifier (Trap ID), with the option to append additional covariates. The detector list comprises of the camera station identifier (Trap ID), spatial coordinates (X and Y) for each camera station, and camera trap effort (Effort or Usage). This too, allows for the inclusion of extra detector-level covariates for specific analyses.

The capture history file included data from all three sessions. All sessions used a single occasion, as SCR count models do not require multiple occasions to estimate density. To ensure independence in leopard captures, instances of the same individual within a 60-minute window of the initial capture were excluded. Furthermore, the dataset incorporated a covariate for sex, which included instances where sex remained unidentified.

Unique detector lists were created for each individual session (2012, 2017 & 2022). SCR methodology allows flexibility in naming conventions across file types, permitting uniqueness for each survey, provided the formatting remains consistent within each session (Efford, 2004). Detector identifiers were derived from the original survey station names, and spatial coordinates were standardized using the African Albers Equal Area projection.

In SCR, standardised camera trap effort adopts a binary representation, with '1' indicating an active camera trap and '0' denoting inactivity. This binary representation is used with multiple occasions to indicate the camera operating or not, however it is not the only approach that can yield effort values. This study adopted a proportional effort strategy, more suited to a single occasion, dividing the number of active days by the total deployment days, resulting in a proportional value ranging from 0 to 1.

2.6. Covariates

The use of spatial covariates in density estimates, produced by SCR modelling, requires that covariates be applied to each individual cell of the habitat mask. The default state space resolution was utilised for the habitat mask (see Section 2.7), creating a cell area of 3.295 km^2. Spatially continuous variables were averaged with an inverse distance weighted mean function to sample the area of use around every potential activity centre's location (Rogan, 2021; Hinde, 2023). The assigned weight to each pixel in the vicinity of the habitat cell, within an animal's home range, is proportionate to the likelihood of detecting a leopard in that specific cell. This approach addresses the imbalances in leopard detection by considering the radial configuration of the activity centre, wherein the habitat centre cell, with fewer surrounding cells, is more likely to detect leopards as compared to the higher cell count in the periphery (Rogan, 2021, Hinde, 2023).

To accommodate the non-continuous sample period spanning ten years with events occurring in years one (2012), five (2017), and ten (2022), a session level covariate (years) was introduced. This covariate was incorporated to address the discrete nature of the sample events during the study period and to test the possible trend on leopard density. A quadratic function was used for extreme values of continuous covariates, to determine if leopards favour intermediate covariate values over extremes. Three continuous covariate models and one categorical covariate model were used to test the four hypotheses affecting density (see Section 1.8) which were created using QGIS Geographic Information System (QGIS development team, 2023; version: 3.32.3-Lima):

i. A terrain ruggedness model (mTRI), calculated in QGIS using a digital elevation model (NASA Shuttle Radar Topography Mission [STRM], 2013), which was accessed through the Earth Data platform (https://www.earthdata.nasa.gov), based on the nearest 3x3 cells.

ii. An elevation model (mEL), based on a 30 m resolution digital elevation model (NASA Shuttle Radar Topography Mission [STRM], 2013) which was accessed through the Earth Data platform.

iii. A vegetation type model (mBioregion), as a categorical covariate, which was simplified from 20 vegetation types (see Appendix A1) to six, by using the bioregion classification of each vegetation type (four within study area and two within the 20 km buffer region).

iv. A distance to major rivers model (mRD), calculated using Euclidean distance in QGIS, from Humanitarian Open Street Map Waterways (Humanitarian OpenStreetMap Team, 2024)

2.7. Model building

Density estimates were calculated using R (version 4.3.1, R Core Team, 2023) within the integrated development environment (IDE) R Studio (version 2023.09.0+463; Posit Software, 2023). The 'secr' package (version 4.6.1; Efford, 2023) was used for multi-session closed-population spatial capture-recapture modelling. The models were fitted using a maximum-likelihood approach and optimized with the Nelder-Mead estimator. To address variations in behaviour between male and female leopards, a hybrid mixed model was adopted. Sex was treated as a partially observed two-class finite mixture model to accommodate individuals whose gender could not be accurately identified.

A three-phase staggered approach was adopted in selecting the optimal density model. Phase one sought to run null density models with variations of session and sex (see Table 1) on $\lambda 0$ and σ to determine the optimal detection model structure. These variations were based on previous leopard studies that found that sex affected detection and home range estimates (Mann, O'Riain & Parker, 2020, Hinde *et al.,* 2023). Phase two used a fixed optimal detection structure with variations on density (constant, session-specific and trend), to determine the optimal density model structure. Phase three sought to explore the effects of covariates on density, testing the four hypotheses affecting density.

Table 1:

Table showcasing the various models and model structures, with accompanying descriptions, that were used for selecting the optimal detection and density model. The session predictor refers to a factor variable representing the three independent surveys (session). Year is a session level covariate utilised to represent the discrete nature of the three surveys and to model trends. Sex refers to the gender of the individual leopard. The Asterix indicates an interaction term that is added to the main effects of the variable.

Model	**Model Structure**	**Model Description**
Detection models on λ0 (capture rate) and σ (spatial rate of decay)		
Sex	sex	Different estimate for each sex
Independent estimate & Sex	session+sex	Different estimate for each sex and for each survey, where estimated sex difference is constant across the three surveys
Trend & Sex	year+sex	Different estimate for each sex and for each survey, where surveys are modelled as a continuous covariate rather than a factor and the estimated sex difference is constant across the three surveys
Independent estimate dependant on Sex	session*sex	Different estimate for each sex and for each survey, where sex difference depends on the survey
Trend dependant on Sex	year*sex	Different estimate for each sex and for each survey, where surveys are modelled as a continuous covariate rather than a factor and the sex difference depends on the year
Density models		
Constant	D~1	Constant density estimate for all three sessions
Trend	D~year	A trend in density, where surveys are modelled as a continuous covariate rather than a factor
Independent Session	D~session	A different density estimate for each survey

The analysis was conducted using a habitat mask that remained fixed for all three sessions (Borchers & Efford, 2008), derived from the largest of the three studies (2012 survey). A 20 km buffer was added to the habitat mask based on the outermost cameras from the 2012 survey. The buffer width was determined by calculating the initial sigma (σ) for all three sessions, and the largest value was used to determine the buffer width using the formula: *buffer width > 4σ* (Borchers & Efford, 2008). To validate buffer selection adequacy, tests were conducted with a buffer width of 15 km (3σ) (see Appendix D).

The default state space grid spacing, as determined by the *make.mask* function, is predicted on the x-dimension of the buffered area, scaled by a factor of 64, yielding a mask comprising approximately 4,000 grid cell points (Efford, 2019). This resolution is considered adequate for density calculations, in line with the established criterion by Efford (2019), contingent upon cell spacing being <1σ. Thus, density estimate calculations used the default spacing of 1,815 m (derived from the buffered area of the 2012 survey), however, a systematic evaluation of alternative spacings was undertaken to validate the default resolution was adequate.

3. Results

3.1. Capture history

For the 2012 survey a total of 141 camera stations (see Table 2) recorded 13,050 active trap days (maximum=113 days, minimum=49 days, mean=93 days) with an average spacing of 2,766 m^2, resulting in 29 unique animal captures (female=6, male=13, unsexed individuals=10). The 2017 survey had a total of 40 camera stations which recorded 2,128 active trap days (maximum=58 days, minimum=24 days, mean=53 days) with an average spacing of 2,703 m^2, resulting in 18 unique animal captures (female=8, male=9, unsexed individuals=1). The 2022 survey had a total of 64 camera stations which recorded 8,997 active trap days (maximum=184 days, minimum=49 days, mean=141 days) with an average spacing of 3,335 m^2, resulting in 37 unique animal captures (female=12, male=17, unsexed individuals=8). Across all three surveys, two of the same leopards, one male and one female (LK008 & LK029), were positively identified (see Appendix B). Between the 2012 & 2017 surveys, six leopards were positively identified, and eight leopards between the 2017 & 2022 surveys.

Table 2:
Table showcasing relevant camera history data of the three leopard surveys (2012, 2017 & 2022) conducted in the Little Karoo. The 2012 survey data was collected over approximately four months in 2011 and 2012, which took a staggered approach to camera trap deployment. The 2017 survey ran for approximately two months and the 2022 survey ran for approximately six months. Leopard detection % is based on the number stations that recorded leopard sightings divided by total camera stations for the survey.

Survey	Camera stations	Total trap days	Camera stations recording leopard sightings	Leopard detection %	Independent captures	Unique individuals
2012	141	13050	56	40	146	29
2017	40	2128	26	65	80	18
2022	64	8997	47	74	249	37

3.2. Buffered mask and covariates

The applied 20 km buffer mask with urban centres and major waterbodies removed encompassed roughly 8,740.87 km^2. A total of 20 vegetation types were recorded for the three camera trap surveys with 2012 comprising of 19 vegetation types, 2017 with only 9 vegetation types and 2022 comprising of 13 vegetation types. These vegetation types were simplified to four major bioregion types within the study area, with two additional bioregion types ('Lower Karoo Bioregion' and 'Zonal & Intrazonal Forests') included in the 20 km buffered study area (see Appendix A). The Eastern Fynbos-Renosterveld Bioregion was the predominant vegetation type for all the survey camera stations (see Table 3).

Table 3:

Percentage distribution of camera stations across bioregion types for each survey. The table includes the total number of vegetation types found within the 20 km buffered survey area. Bioregion is various vegetation types categorized at a simplified bioregion level (see Appendix A)

Survey	Number of vegeation types present	Bioregion type at camera stations	% Bioregion type at camera stations
2012	19	Albany Thicket	33.33
		Inland Saline Vegetation	2.84
		Eastern Fynbos-Renosterveld Bioregion	46.81
		Rainshadow Valley Karoo Bioregion	17.02
2017	9	Albany Thicket	37.5
		Eastern Fynbos-Renosterveld Bioregion	57.5
		Rainshadow Valley Karoo Bioregion	5
2022	13	Albany Thicket	35.94
		Eastern Fynbos-Renosterveld Bioregion	60.94
		Rainshadow Valley Karoo Bioregion	3.12

Continuous elevation for the 20 km buffer mask comprised of areas ranging from lowlands (37 m above sea level) to mountainous peaks (2,185 m above sea level). Terrain ruggedness was derived from elevation which ranged from 1 (level areas) to 441.81 (moderately rugged areas). Distance from major rivers ranged from 0 m (directly on the river course) to 8,627.92 m (furthest point away from the water course in buffered study area).

3.3. Model selection

The best preforming model from the first stage was MS11, which had an interaction term (session*sex) on both predictor variables on λ_0 and σ. The interaction term allowed for λ_0 and σ to vary, based on the sex of leopards, for each individual session. The model showed strong support holding 89% of the AICc weighting. Detection rate of males 0.0213 (SE±0.0031) was higher than that of females 0.0123 (SE±0.0047) in the 2012 survey. In the 2017 survey male leopards showed a greater detection rate 0.0974 (SE±0.0257) when compared to females 0.0529 (SE±0.0342). In the 2022 survey male leopards showed a greater detection rate 0.0295(SE±0.0036) when compared to females 0.0285 (SE±0.0066). The second ranked model, MS3, had an interaction term on σ (session*sex) and sex as a predictor variable on λ_0. This model had 11% of the remaining AICc Weighting. All trend-based models (year), did not show strong support for the λ_0 *and* σ predictor variables.

Table 4:

Density models with constant density, along with various parameters on capture rate (λ_0) and sigma (σ). The session predictor refers to a factor variable representing the three independent surveys (session). Year is a session level covariate utilised to represent the discrete nature of the three surveys and to model trends. Sex refers to the gender of the individual leopard. The Asterix indicates an interaction term that is added to the main effects of the variable.

Model	Predictor variables on Density	Predictor variables on λ0	Predictor variables on σ	Number of Parameters	AICc	dAICc	AICc Weight
MS11	D~1	session*sex	session*sex	14	2015.132	0	0.8922
MS3	D~1	sex	session*sex	10	2019.358	4.226	0.1078
MS12	D~1	year+sex	year+sex	8	2048.844	33.712	0
MS10	D~1	session+sex	session+sex	10	2048.939	33.807	0
MS8	D~1	year+sex	sex	7	2049.102	33.97	0
MS6	D~1	session+sex	sex	8	2050.877	35.745	0
MS9	D~1	year*sex	sex	8	2051.084	35.952	0
MS7	D~1	session*sex	sex	10	2055.55	40.418	0
MS13	D~1	year*sex	year*sex	10	2064.71	49.578	0
MS4	D~1	sex	year+sex	7	2067.53	52.398	0
MS5	D~1	sex	year*sex	8	2069.287	54.155	0
MS2	D~1	sex	session+sex	8	2081.168	66.036	0
MS1	D~1	sex	sex	6	2100.816	85.684	0
MS0	D~1	1	1	4	2244.379	229.247	0

3.4. Density estimates

The density models (Md1, Md2, Md3), based on the previous top performing fitted model (MS11), showed support with exception for model M0, which represented null models for density, capture rate (λ_0) and sigma (σ). The best performing model on density, Md2, had a trend (D~year) density predictor variable. This model had 66% of the AICc weighting. Constant density (D~1) and density based on individual sessions showed slight support at 20% & 14% respectively.

Table 5:

Density models with various parameters on density, capture rate (λ_0) and sigma (σ). The session predictor refers to a factor variable representing the three independent surveys (session). Year is a session level covariate utilised to represent the discrete nature of the three surveys and to model trends. Sex refers to the gender of the individual leopard. The Asterix indicates an interaction term that is added to the main effects of the variable.

Model	Predictor variables on Density	Predictor variables on λ0	Predictor variables on σ	Number of Parameters	AICc	dAICc	AICc Weight
Md2	D~year	session*sex	session*sex	15	2012.77	0.00	0.66
Md3	D~1	session*sex	session*sex	14	2015.13	2.37	0.20
Md1	D~session	session*sex	session*sex	16	2015.89	3.13	0.14
M0	D~1	1	1	4	2244.38	231.61	0.00

Model Md2 represented the density trend for leopards (D~year) over the survey period, which indicated a slight increase (see Figure 3). 2012 had a density estimate of 0.55 (SE ±0.11) leopards per 100 km^2, 2017 had a density estimate of 0.70 (SE ± 0.08) and 2022 had a density estimate of 0.95 (SE ± 0.16). Md3, ranked second, had a constant density estimate for the survey of 0.81 (SE ± 0.09) leopard per 100 km^2. Md1, ranked third, had individual density estimates for each session (D~session) for which 2012 was estimated to have 0.51 (SE ± 0.11) leopards per 100 km², 2017 estimated 0.62 (SE ± 0.16) leopards per 100 km² and 2022 estimated 0.92 (SE ± 0.16) leopards per 100 km². The more parsimonious model structure that showed support, model Md3, was utilised over Md2 for calculating covariate effects.

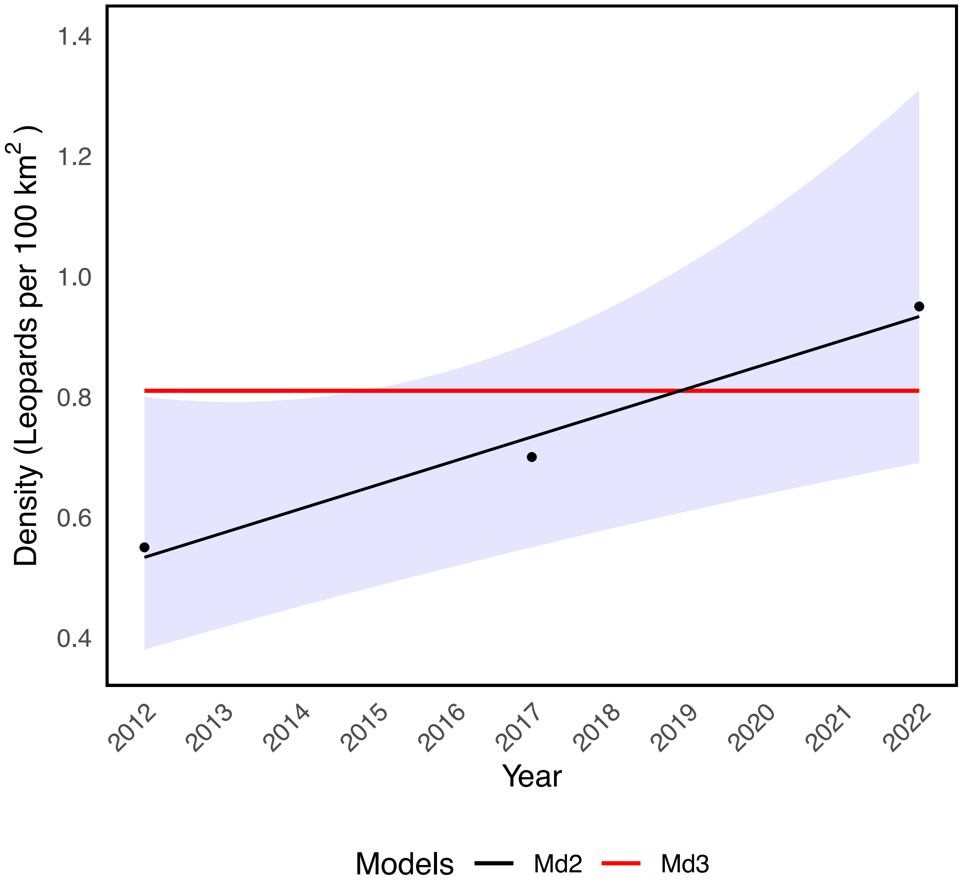

Figure 3:

*Dot and trend line plot with respective confidence interval ribbon (for Md2) showcasing leopard densities (per 100 km²) in the buffered study area, based on models, Md2 (black trend line, dots & ribbon) & Md3 (red line). The density predictor variable for Md2 represents the trend in density (D~year) and constant density (D~1) for Md3. Predictor variables for both models are based on model MS11 where capture rate (λ_0) and sigma (σ) are a function of individual sessions and sex (~session*sex). Md3 has a constant density of 0.81 leopards per 100 km² (95% CI:0.65-1.02). Md2 estimated density for 2012 is 0.55 leopards per 100 km² (95% CI:0.38-0.80), for 2017 is*

0.70 leopards per 100km² (95% CI: 0.55-0.88) and for 2022 0.95 leopards per 100 km² (95% CI: 0.69-1.31).

3.5. Covariate effects

Individual covariate models all showed some support (see Table 6), based on model Md3, which included an interaction of session and sex on both λ_0 and σ. Terrain ruggedness (mTRI), elevation (mEl) and bioregion (mBoiR) all showed high support (dAICc <2) (see Table 5). Terrain ruggedness (mTRI) showed the greatest support accounting for 40% of the AICc weighting. Distance from major rivers (mRD), showed intermediate support (dAICc <7).

Table 6:

*Performance predictors of potential drivers for leopard density in the Little Karoo based on model (Md3) with predictor variables on capture rate (λ_0) and sigma (σ) as a function of individual sessions and sex (~session*h2). Terrain ruggedness is the measure of difference in elevation for the surrounding three cells (mTRI); Bioregion is based off bioregion level classifications (mBioR); Elevation is a measure of height above sea-level with a resolution of 30m (mEl); River distance is a measure of Euclidean distance from major river courses in the study area. Linear and quadratic effects (representing extreme values) are included on mTRI, mEl and mRD.*

Model	Predictor variables on Density	Number of Parameters	AICc	dAICc	AICc Weight
mTRI	D~TRI+I(TRI^2)	16	2009.66	0.00	0.40
mEl	D~Elevation+I(Elevation^2)	16	2010.49	0.83	0.26
mBioR	D~Bioregion	19	2010.64	0.98	0.24
mRD	D~River Distance+I(River Distance^2)	16	2012.41	2.75	0.10

The coefficient for terrain ruggedness (β = 1.66±0.66) indicates a positive relationship between the ruggedness of the terrain type and leopard density (see Table 7). Elevation also showed a positive relationship (β = 0.39±20) with leopard density. Elevation and terrain ruggedness were positively correlated (R=0.75, P=2.2e^{-16}). River distance indicated a negative relationship (β = -0.66±0.29) with leopard density. Squared predictors (representing extreme values) all had a negative relationship with leopard density. This indicates that extreme values of terrain ruggedness, elevation and distance from rivers negatively affect leopard density. The Rainshadow Valley Karoo bioregion was the only bioregion to indicate a lower leopard density (β = -3.91±6.37) when compared to the baseline vegetation ('Albany Thicket'). Two vegetation types ('Lower Karoo Bioregion' and 'Zonal & Intrazonal Forests') indicated a strong positive relationship with leopard density which fell outside of the core study area, but were part of the 20 km buffer mask.

Table 7:

Performance predictors of potential drivers for leopard density in the Little Karoo, showcasing beta estimates on the logscale. Terrain ruggedness is the measure of difference in elevation for the surrounding three cells (mTRI); Vegetation type is based on bioregion level classifications (mBioR); Elevation is a measure of height above sea-level with a resolution of 30 m (mEl); River distance is a measure of Euclidean distance from major river courses in the study area. Linear and quadratic effects (representing extreme values) are included on mTRI, mEl and mRD. The Albany thicket serves as the baseline category in the bioregion model, with the shown beta estimate serving as the intercept against which estimates for other bioregions are compared. Asterisk (*) marks bioregions that were not present within the direct study sites but fall within the 20 km buffer.

Predictor		Beta Estimate	Standard Error	lcl	ucl
TRI		1.66	0.78	0.12	3.19
TRI^2		-0.76	0.46	-1.67	0.14
River Distance		-0.66	0.29	-1.24	-0.09
River $Distance^2$		-0.11	0.34	-0.76	0.55
Elevation		0.39	0.20	0.00	0.79
$Elevation^2$		-0.56	0.25	-1.05	-0.07
Bioregion:	Albany Thicket	-9.97	0.53	-11.00	-8.93
	Eastern Fynbos-Renosterveld Bioregion	0.84	0.61	-0.35	2.03
	Inland Saline Vegetation	0.55	1.76	-2.90	4.00
	Lower Karoo Bioregion*	3.50	0.86	1.81	5.18
	Rainshadow Valley Karoo Bioregion	-3.91	6.37	-16.40	8.58
	Zonal & Intrazonal Forests*	2.95	3.27	-3.46	9.36

4. Discussion

4.1. Overview

Anthropogenic activities have negatively impacted and restricted large carnivore populations worldwide (Ripple *et al*., 2014). Protected areas are necessary for preserving biodiversity, but their effectiveness is often hindered by limited land allocation and reduced connectivity (Watson *et al*., 2014; Rogan *et al*., 2022). Leopards are one of the few large carnivores that are able to adapt, persist and even thrive in sustainable populations outside of these protected areas (Athreya *et al.*, 2016; Hinde *et al*., 2023). While knowledge of leopard populations existing outside of protected areas is documented, there are few long-term monitoring studies on this and how leopards co-exist with novel anthropogenic impacts (Balme *et al*., 2014). This study aimed to address the knowledge gaps on leopard population dynamics in a semi-arid mixed-use landscape and to estimate population trends over time. Results from the study indicate that leopard populations in the semi-arid Little Karoo have persisted over time in a mixed-use landscape.

4.2. Leopard density

As it stands, this is the first study to document changes in Little Karoo leopard density, and, to the best of my knowledge, the only multi-session study to have been done in a semi-arid environment outside of a protected area in Southern Africa. This study indicated that leopards have persisted within a mixed-use landscape and suggests that the population has increased over the study period. While trends in density are not readily available for leopards in the Western Cape, previous single-session maximum likelihood SCR density estimates, from other study areas in the province, are similar to those in this study (Devens *et al*., 2018; Devens *et al*., 2021; Hargey 2022; Hinde et al., 2023). Hargey (2022) found that leopard densities within a protected area can be as low as 0.17 (SE ± 0.7) leopards per 100 km^2 in the Western Cape. A study by Hinde *et al.* (2023), was conducted in a mixed-use landscape and indicated a population density of 0.64 (95% CI: 0.43–0.94) leopards per 100 km^2. This is encouraging, since even the constant density model (Md3) indicated a density of 0.81 (95% CI: 0.65–1.02) leopards per 100 km^2, which is one of the higher maximum-likelihood SCR density estimates for leopards in the Western Cape.

Notably, density estimates from this study differ from a previous analysis which assessed the density of leopards in the Little Karoo region. The study by Mann, O'Riain & Parker (2020) used data from the 2012 survey and found a density of 1.26 (SE ± 0.25) leopards per 100 km^2 based on a categorical habitat mask model, and 0.22 (SE ± 0.17) leopards per 100 km^2 based on a continuous habitat mask model. The 'secr' package

(Efford 2010) was used for that study, with a maximum likelihood approach. The higher estimates are likely due to the habitat selection methodology used in these studies: a binary habitat selection mask (1 = 'is leopard habitat'; 0 = 'is not leopard habitat'). By reducing the available state space through this methodology while maintaining similar individual numbers (N), model results will produce higher densities. The multi-session study did not apply a habitat selection mask, but rather a buffered mask (20 km) that excluded major water bodies and urban centres, which was applied to the largest survey area (2012), after which covariates were applied. This decision was made based on the primary aim of the study, which was to estimate how the leopard population has changed over time and to investigate possible drivers of change, rather than to replicate similar estimates from previous studies.

There are few long-term leopard density studies in semi-arid environments in the published literature. A study by Farhadinia *et al*. (2021) conducted a multi-session SCR analysis in a protected area in Iran, revealing a decline in leopard density from 1.6 (95% CI: 0.9–2.9) to 1.0 (95% CI: 0.6–1.6) leopards per 100 km^2 between 2012 and 2016 in a semi-arid environment. The leopard population of the Little Karoo, similar to the Farhadinia *et al*. (2021) study, underwent sex specific changes in detectability and home ranges, per session. Variations in sampling effort, as seen in both studies, may serve as a potential rationale for these changes. Additionally, males exhibited higher detectability and had larger estimated territorial ranges than females. Both study sites share similar characteristics of rugged mountainous topography, although the Fahadinia *et al*. (2021) study was conducted exclusively in a protected area. The dynamics of leopard populations observed in these studies are not only relevant in their respective areas, but also offer compelling case studies against which surveys in similar landscapes can be compared. This highlights the necessity for long-term studies in semi-arid environments.

The influence of anthropogenic activities in the Little Karoo has been known to adversely affect leopard densities (Mann, O'Riain & Parker, 2020; McManus *et al.,* 2021), however, it is possible that the leopard populations have managed to stabilise in the region. A reduction in active persecution from landowners and improved animal husbandry practices are potential reasons for the Little Karoo population having persisted over time (de Villiers *et al.,* 2023). While knowing the exact causes for the population's persistence may require further studies, these results provide encouraging insights into the population dynamics of leopards in the Little Karoo.

Best practice for estimating the density of large carnivores in camera trap surveys dictates that the survey area should be equal to or exceed the size of the species' home range. The use of female home range size to determine the spacing of camera traps is preferred, with a minimum of 40 camera traps used for the survey, to ensure adequate coverage of the survey area. Camera station placement must maximise detection probability, and studies should also use sex as a covariate on λ_0 and σ for SCR modelling (Tobler & Powel, 2013). Closed population SCR modelling and extended study periods have been known to increase accuracy in density estimates but can violate assumptions of population closure (Dupont *et al*., 2019). Leopards have slow life histories (Balme *et al.,* 2013) and are geographically restricted in the Little Karoo through anthropogenic impacts (Mann, 2014). This reduces the biasing effect of long-term surveys on closed populations (Dupont et al., 2019). The survey durations varied across years, spanning approximately two months in 2017, during which 146 independent leopard sightings were recorded. The 2012 survey data was collected over approximately four months in 2011 and 2012 which yielded 80 independent leopard sightings. For 2022, the survey was conducted over approximately six months and collected 249 independent leopard sightings. This long-term study thus falls within the best practices and as such we can assume it produces robust density estimates for the Little Karoo study area.

4.3. Drivers of density

Results indicate that terrain ruggedness is a key driver of leopard density in the Little Karoo, similar to the previous study conducted by Mann, O'Riain and Parker (2020). This has been attributed to leopards seeking refuge from anthropogenic activities (Mann, O'Riain & Parker, 2020). Leopards are agile and adaptable animals that occur in a range of rugged environments, which can also provide improved cover for ambushing of prey. This adaptability proves useful in the avoidance of anthropogenic impacts, as most anthropogenic activities are limited by terrain type, often favouring lower-lying areas with limited ruggedness (Mann, O'Riain & Parker, 2020; Hinde *et al.,* 2023). This is because anthropogenic transformation tends to favour lower-lying areas, leaving rugged areas less transformed, which increases suitability for wildlife (Mann *et al.,* 2019). In addition to this, intermediate elevation was a significant driver of leopard density within the Little Karoo. Elevation was strongly positively correlated (R = 0.75) with terrain ruggedness in this study. Furthermore, distance from major rivers showed support in affecting leopard density in the Little Karoo, potentially because rivers offer paths of least resistance in rugged terrains and can be used for cover when ambushing prey (Mann, O'Riain & Parker, 2020). Confirmation of these drivers of density provide key insights into suitable leopard habitats in the Little Karoo, increasing the ability to locate and effectively secure vital leopard habitat for the future.

Vegetation type was another important predictor of suitable leopard habitat in the Little Karoo. Preferred vegetation types, based on bioregion, tended to be associated with limited anthropogenic impacts, such as the Albany Thicket and Eastern Fynbos-Renosterveld bioregions. These bioregion vegetation types favoured intermediate slopes and higher elevations, which produce more effective refuge for leopards than lower-lying vegetation types in the Little Karoo (Vlok and Schutte-Vlok, 2010; Mann, O'Riain & Parker, 2020). These results indicate that all four drivers are interconnected and may not be independent of one another. Leopard persistence in the Little Karoo depends on the combination of these drivers, and further studies are required to determine the specific roles each driver plays in sustaining the population.

4.4. Drought

During the study, the Little Karoo region experienced an extended period of drought, marked by a decline in 2015 in annual rainfall below the long-term mean (Saayman, 2021). The drought persisted, with annual rainfall remaining below this mean, for approximately five years. The highest impact of the drought was observed during the period 2017–2019, with a significant reduction in total plant cover (26.2%). Notably, there was a substantial reduction in palatable vegetation, and the highly palatable vegetation types decreased by 67.2% (Saayman, 2021). The impacts of the drought on vegetation and precipitation in the Little Karoo can be seen in Figure 4.

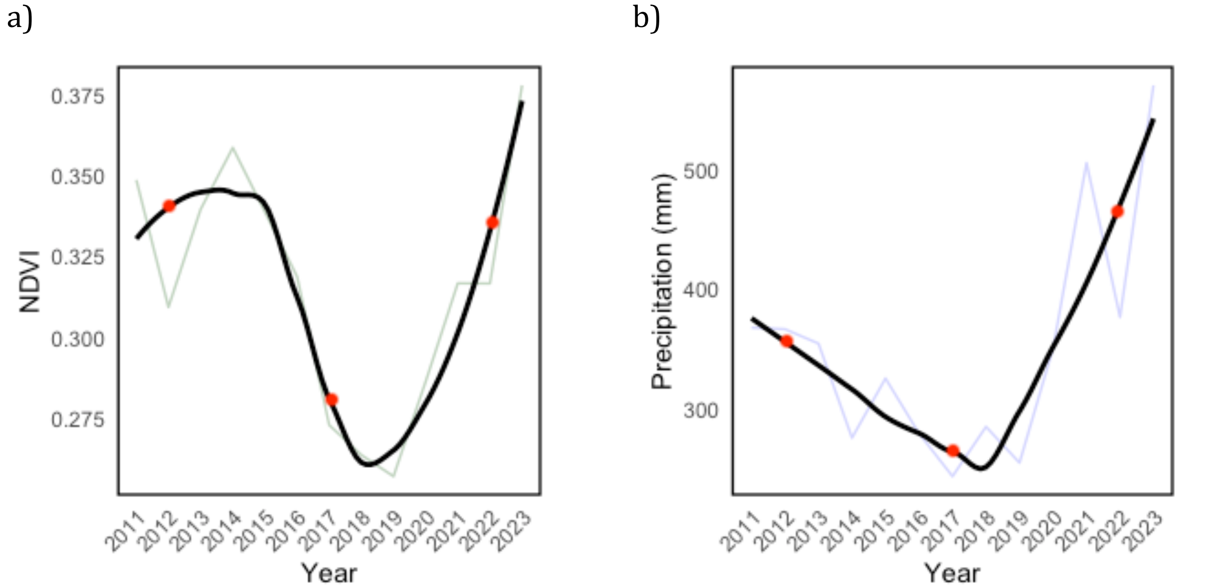

Figure 4:

Line plots representing trends in vegetation and annual rainfall over the study period (2011– 2023) in the Little Karoo. Trends are illustrated by the Normalised Difference Vegetation Index (NDVI) and annual precipitation data. Red dots indicate the survey years (2012, 2017 and 2022). a) NDVI is plotted using the United States Geological Survey (USGS) Landsat "7&8" data (30 m resolution) – Surface Reflectance Tier 1, which is aggregated to produce a single NDVI value per year. The green line represents the annual NDVI value for each year. The black line represents a smoothed trend line based on annual values. b) Precipitation is plotted using Climate Hazards Group InfraRed Precipitation with Station Data (CHIRPS), based on a 0.05° resolution. The blue line represents the annual precipitation. The black line represents a smoothed trend line based on the annual precipitation values.

Large carnivore density can be affected by prey availability, of which herbivores are the common prey types (Hayward *et al.,* 2006; Wolf & Ripple, 2016). Herbivore biomass is largely dependent on available food resources, which is linked to rainfall (East, 1984; Loveridge *et al.,* 2022). During initial stages of drought, large carnivores have been known to benefit from the weakened state of prey species, due to a reduction in the prey's available food resources (Ferreira & Viljoen, 2022). Large carnivores benefit from the increasing food availability, which enhances body condition, thus improving survival and fecundity (Ferreira & Viljoen, 2022). Although this study might lack sufficient quantifiable data to conclusively establish this, it could serve as a plausible explanation for the persistence or potential increase in leopard density observed over the study period. Furthering our understanding of how leopards adapt and interact with their landscape is vital as the climate changes. This emphasises the need for increased sampling efforts in the Little Karoo in order to manage these populations effectively.

4.5. Management implications

A major challenge in the management of leopards is creating areas of connectivity in a mixed-use landscape. Connectivity promotes the finding of mates, facilitates dispersal and enriches the genetic diversity of the population (Epps *et al.,* 2007; McManus *et al.,* 2015). In order to promote a connected landscape, strategic and suitable habitat needs to be secured to create long-term movement corridors (Lombard *et al.,* 2010; Mann, 2014). Efforts to secure land, based on scientific studies and informed management practices, have ensured that 24% (2,188 km^2) of the study area has been converted into protected areas. Notably, protected areas in the centre, comprising formal conservation land and private conservancies, create a crucial corridor in the study area. These areas, which include elevated rugged terrain, connect the mountain ranges in the north and south of the study area (see Figure 4), providing essential refuge for leopard populations in the Little Karoo. This reaffirms the need for long-term monitoring programmes to quantify the effectiveness of this movement corridor in order to better inform management practices.

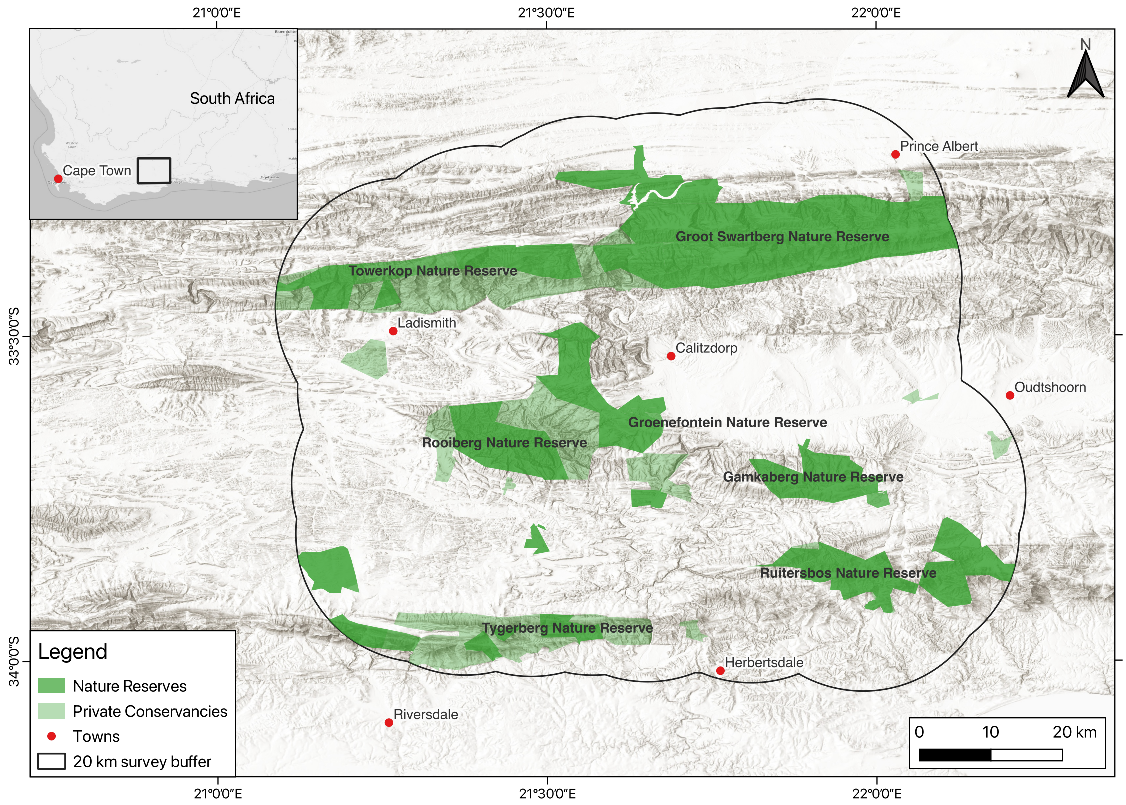

Figure 5:

A map of the study area, with the 20 km buffer added, displaying protected areas in the Little Karoo. Light green represents private conservancies and dark green represents nature reserves. Data for protected areas was sourced from the South African Department of Forestry, Fisheries and the Environment (DFFE), based on SA protected areas and SA conservation areas data.

As climate change increases the risk of extreme weather events and potentially increases the aridity of the Little Karoo, land-use practices will inevitably change. Recent droughts have led to landowners destocking livestock and diversifying their income generation (Mann *et al.,* 2019; Ehlers, 2022; Letsoalo *et al.*, 2023). In some cases, farmers have converted their land to private conservation areas or low-intensity game farms. This is an encouraging sign as it creates biodiversity-focused opportunities. It places an increased focus on education, not only for effective management, but for improving human coexistence with wildlife as a whole. Long-term camera trap surveys, as in this study, can provide landowners with insights into the species that live on their land and the inspiration to make a lasting commitment to protecting it. Charismatic species, such as the leopard, generate interest and can facilitate opportunities for such connections. NGOs such as the Cape Leopard Trust can strengthen connections with local landowners by providing educational insights based on the best land-use practices for biodiversity preservation in the Little Karoo. In addition to this, the Cape Leopard Trust can extend their reach by using their education-focused programs to connect with the wider local communities.

4.6. Limitations

A key determining factor in trend estimates of density, particularly with elusive species occurring in lower densities, is sampling effort. While there is no steadfast rule on the number of sampling points needed for robust estimates, it is commonly accepted that three sampling points, over a period of time, will produce results with limited statistical power. This can be seen from the large confidence intervals in the density estimates produced in this study. These estimates further validate the need for consistent long-term data collection on the leopards of the Little Karoo, to facilitate plotting trends in density over time. Individual sampling efforts may also produce mixed density results based on insufficient data collection and changing study site sizes, reducing their utility for trend analyses.

The quality of future long-term monitoring could be improved by increasing sampling efforts (ideally to annual surveys), keeping the survey area and the duration of time consistent between surveys, and conducting the surveys at the same time of year. In addition to this, covariates such as NDVI, land-use change, competitor interactions, persecution and road usage could provide key insights into possible drivers of the population trends in the Little Karoo. To complement this, a qualitative study on the impacts of predators in the Little Karoo could provide beneficial insights into public perceptions of predators in the region. This could indicate how interactions have changed since the initial survey in 2012, when a similar qualitative study was conducted by Mann (2014).

5. Conclusion

Leopards, like other large carnivores, require large and continuous areas of habitat in which they can find refuge from anthropogenic threats (Newmark, 2008; Jędrzejewski, 2017; Rogan *et al.,* 2022). While protected areas are known to support the persistence of leopards in a landscape (Balme *et al.,* 2014), research has also found that leopards can survive outside of protected areas (Rogan *et al.,* 2022; Hinde *et al.,* 2023). This is increasingly important as protected areas become more fragmented, which reduces their capacity to support leopard populations. Thus, understanding the population dynamics of leopards persisting in a mixed-use landscape may prove pivotal for their conservation in the modern world. This study adds insight into leopard population dynamics in a mosaic of mixed land uses, with the intention of better informing leopard conservation in semi-arid environments.

While Little Karoo leopard population numbers are regarded as relatively low in a southern African context, their density is similar to that in other semi-arid environments (Martins, 2010; Mann *et al.,* 2019; Farhadinia *et al.,* 2021; Hinde *et al.,* 2023). Low leopard population numbers in a mixed-use landscape can reduce a populations resilience, emphasising the need for access to suitable refugia and movement corridors (Cardillo *et al*., 2005; Ripple *et al*., 2014; Mann, O'Riain & Parker, 2020). While rugged terrain may provide suitable relief from anthropogenic impacts, if these rugged pockets do not allow for movement, populations could become isolated. Climate change is predicted to increase the frequency of stochastic events (Ziervogel *et al.,* 2014; Helman, Zarzo Arias & Penteriani, 2022), which may negatively impact leopard populations if movement to suitable habitat is restricted. Thus, it is imperative to improve connectivity across landscapes to increase access to refugia that act as a buffer against the effects of climate change (Keppel *et al.,* 2012). While leopards are an adaptable species, without effective, large-scale management in a connected landscape, these pressures may impact the species in the years to come.

Part of the managerial challenge in conserving leopards in a mixed-use landscape is understanding the anthropogenic factors affecting them. Historically, there was widespread persecution of leopards in the Little Karoo due to governmental law, cultural practices and general misconceptions concerning livestock persecution (Ray, Hunter & Zigouris, 2005; Martins & Martins, 2006; Mann*.,* 2014). While evidence throughout South Africa indicates similar anthropogenic effects on leopards (Balme *et al.,* 2014; Willams *et al,* 2017), a population that persists at a stable rate may indicate a reduction in active persecution. Changes in legislation, increased monitoring efforts and educational awareness are but some of the potential reasons for an increased tolerance towards leopards. This highlights the critical role NGOs such as the Cape Leopard Trust and Panthera play in the conservation of leopards. In addition, their scope often extends far beyond simply protecting leopards.

It is encouraging to note that while leopards face seemingly insurmountable odds, they have shown a remarkable resilience, allowing them to persist in mixed-use landscapes. Their story of survival, coupled with their charismatic status, can serve as a powerful conservation tool (Lorimer, 2007; Ducarme, Luque & Courchamp, 2013; Albert, Luque & Courchamp, 2018). This creates engagement, which facilitates a connection between humans and nature. This is imperative, as NGOs are often the drivers of conservation efforts. Their focus is primarily on securing funding and gaining buy-in for conservation efforts. All of this is dependent on people connecting with their cause and supporting the protection of natural spaces.

In order to better understand how leopard populations persist in mixed-use landscapes and how the changing climate will impact these populations, a focus on long-term monitoring is needed. Annual sampling efforts, conducted in a co-ordinated manner, with similar study areas and time frames will strengthen results, but they may require considerable funding to execute. Based on anecdotal expert opinion, a minimum of 10 years of annual sampling may be required to improve statistical power. These efforts will prove vital in deepening our understanding of leopard populations that persist in mixed-use landscapes and essential in effectively managing populations in the future.

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7. Appendices

7.1. Appendix A: Vegetation types

Table A.1: *Vegetation types with their corresponding bioregions utilised for covariate analysis and the number of camera traps within in each vegetation type per survey. Gamka Karoo and Southern Afrotemperate Forest fall within the 20 km buffered zone of the study area.*

Vegetation Type	Bioregion	Number of Cameras in Vegetaion Type			
		2012	2017	2022	Total
Eastern Little Karoo	Rainshadow Valley Karoo Bioregion	11	0	0	11
Gamka Arid Thicket	Albany Thicket	6	1	2	9
Gamka Karoo	Lower Karoo Bioregion	0	0	0	0
Kango Conglomerate Fynbos	Eastern Fynbos-Renosterveld Bioregion	5	0	3	8
Kango Limestone Renosterveld	Eastern Fynbos-Renosterveld Bioregion	6	0	0	6
Little Karoo Quartz Vygieveld	Rainshadow Valley Karoo Bioregion	1	0	0	1
Matjiesfontein Quartzite Fynbos	Eastern Fynbos-Renosterveld Bioregion	1	0	0	1
Mons Ruber Fynbos Thicket	Albany Thicket	1	0	0	1
Montagu Shale Renosterveld	Eastern Fynbos-Renosterveld Bioregion	5	2	4	11
Muscadel Riviere	Inland Saline Vegetation	4	0	0	4
North Outeniqua Sandstone Fynbos	Eastern Fynbos-Renosterveld Bioregion	8	0	2	10
North Rooiberg Sandstone Fynbos	Eastern Fynbos-Renosterveld Bioregion	4	0	1	5
Oudtshoorn Karroid Thicket	Albany Thicket	22	10	16	48
Prince Albert Succulent Karoo	Rainshadow Valley Karoo Bioregion	2	2	2	6
South Outeniqua Sandstone Fynbos	Eastern Fynbos-Renosterveld Bioregion	0	0	1	1
South Rooiberg Sandstone Fynbos	Eastern Fynbos-Renosterveld Bioregion	21	13	15	49
South Swartberg Sandstone Fynbos	Eastern Fynbos-Renosterveld Bioregion	8	3	5	16
Southern Afrotemperate Forest	Zonal & Interzonal Forests	0	0	0	0
Swartberg Shale Fynbos	Eastern Fynbos-Renosterveld Bioregion	5	2	4	11
Swartberg Shale Renosterveld	Eastern Fynbos-Renosterveld Bioregion	3	3	4	10
Western Gwarrieveld	Albany Thicket	18	4	5	27
Western Little Karoo	Rainshadow Valley Karoo Bioregion	10	0	0	10

7.2. Appendix B: Leopard succession

Table B1: *Identified individual leopard records that were captured across surveys. Consolidated individual ID is based off African Carnivore Wildbook leopard identity kits created for the Little Karoo. Individual capture/recapture represents the captures of unique individuals over the three survey periods. The unique individual's identification is a temporary identification for the survey year.*

Consolidated individual ID	Sex	Individual capture/recapture		
		2012	**2017**	**2022**
LK002	Male	GM2	PM010	
LK008	Male	GM10	PM022	CLT LK 027
LK016	Male	GM18	PM005	
LK028	Female	GLR31	PF011	
LK029	Female	GML32	PF001	CLT LK 017
LK030	Female	GMR33	PF013	
LK033	Female		PF014	CLT LK 007
LK036	Female		PF100	CLT LK 038
LK037	Male		PM002	CLT LK 013
LK040	Male		PM009	CLT LK 009
LK043	Male		PM101	CLT LK 003
LK046	Unknown		PU103	CLT LK 029

7.3. Appendix C: Independent species captures

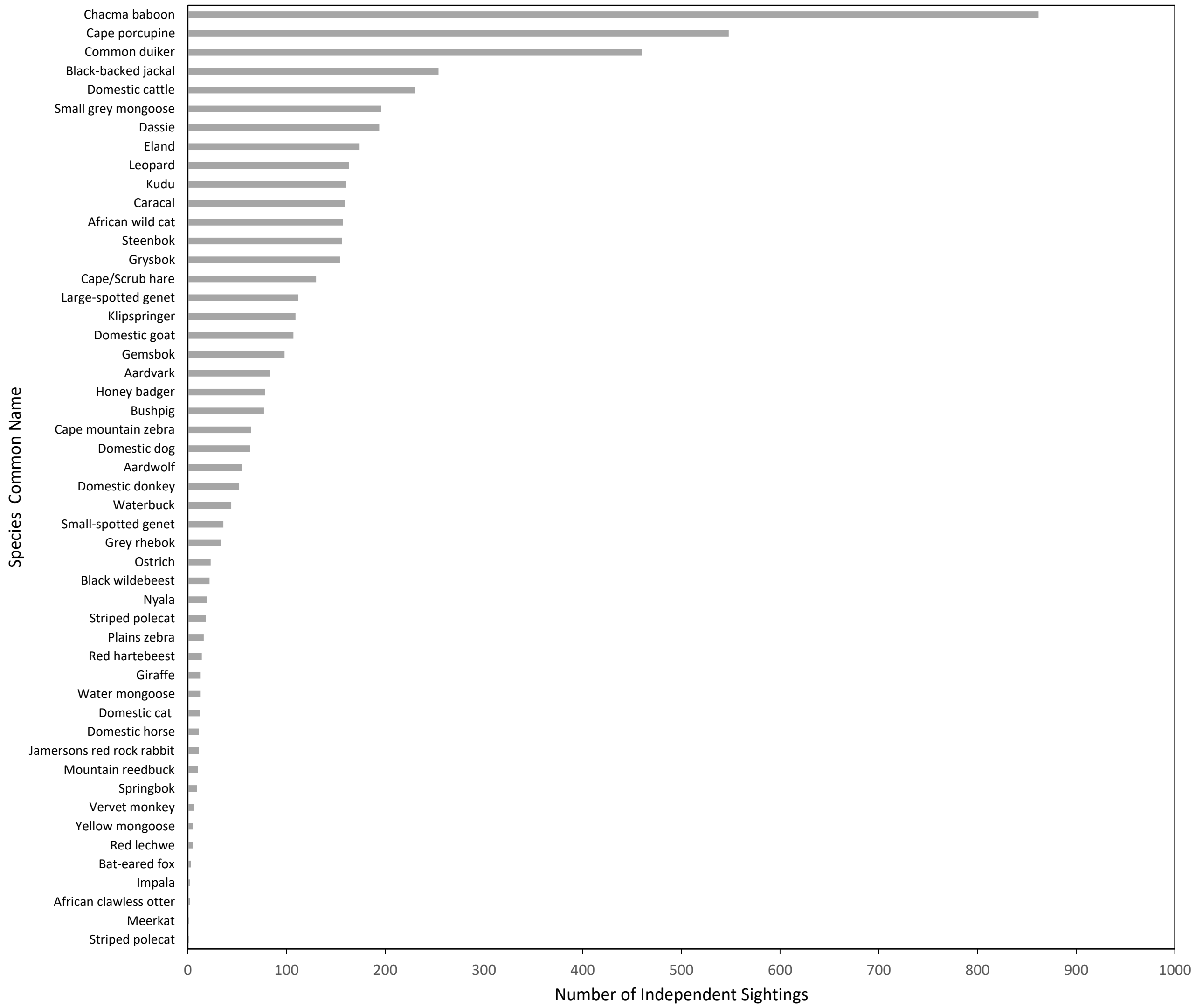

Figure C1: *Clustered bar graph representing the recorded species for the 2011/2012 survey. Recorded values signify distinct captures within a 60-minute interval from the initial capture. Throughout the survey period a total of 5,227 independent captures were documented.*

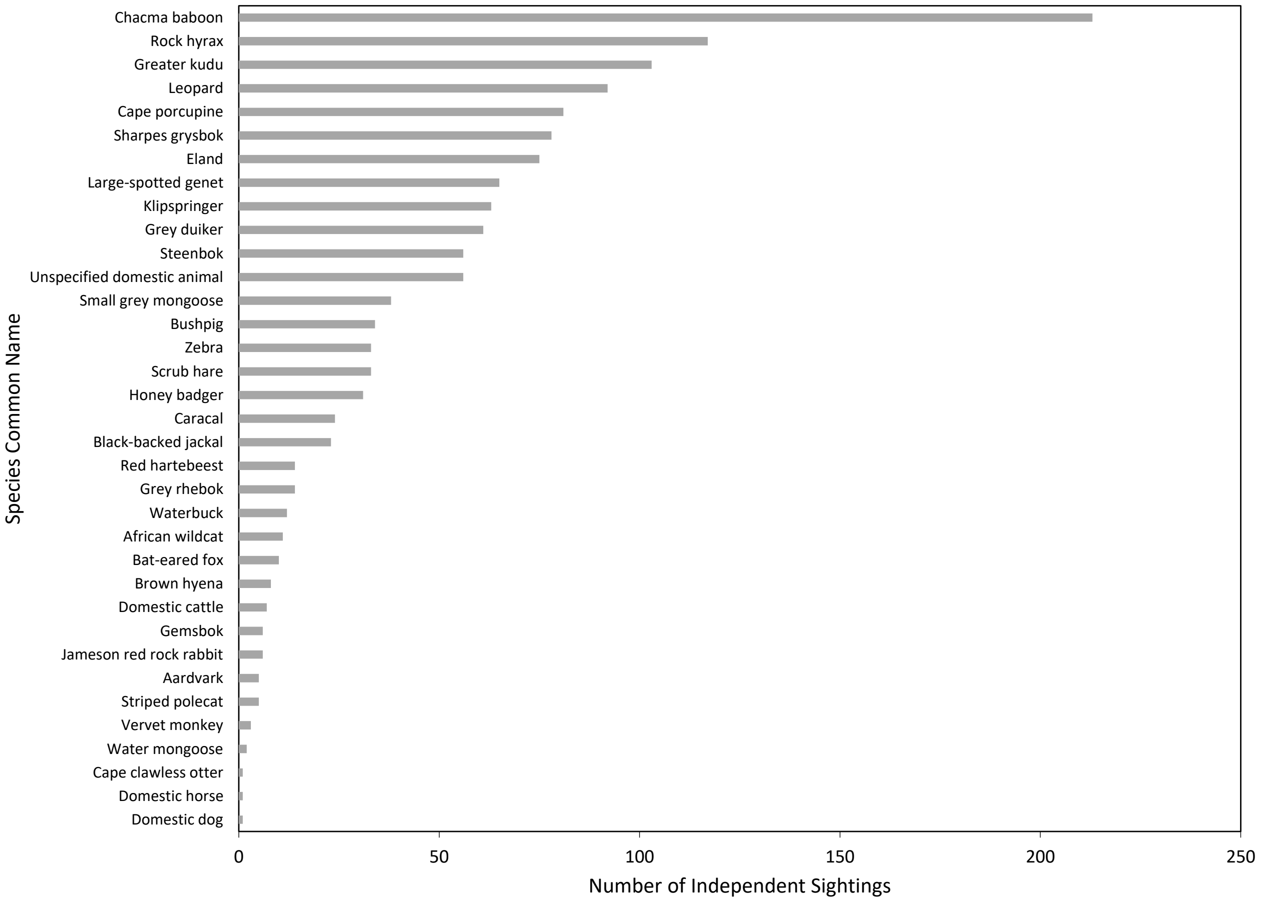

Figure C2: *Clustered bar graph representing the recorded species for the 2017 survey. Recorded values signify distinct captures within a 60-minute interval from the initial capture. Throughout the survey period a total of 1,390 independent captures were documented.*

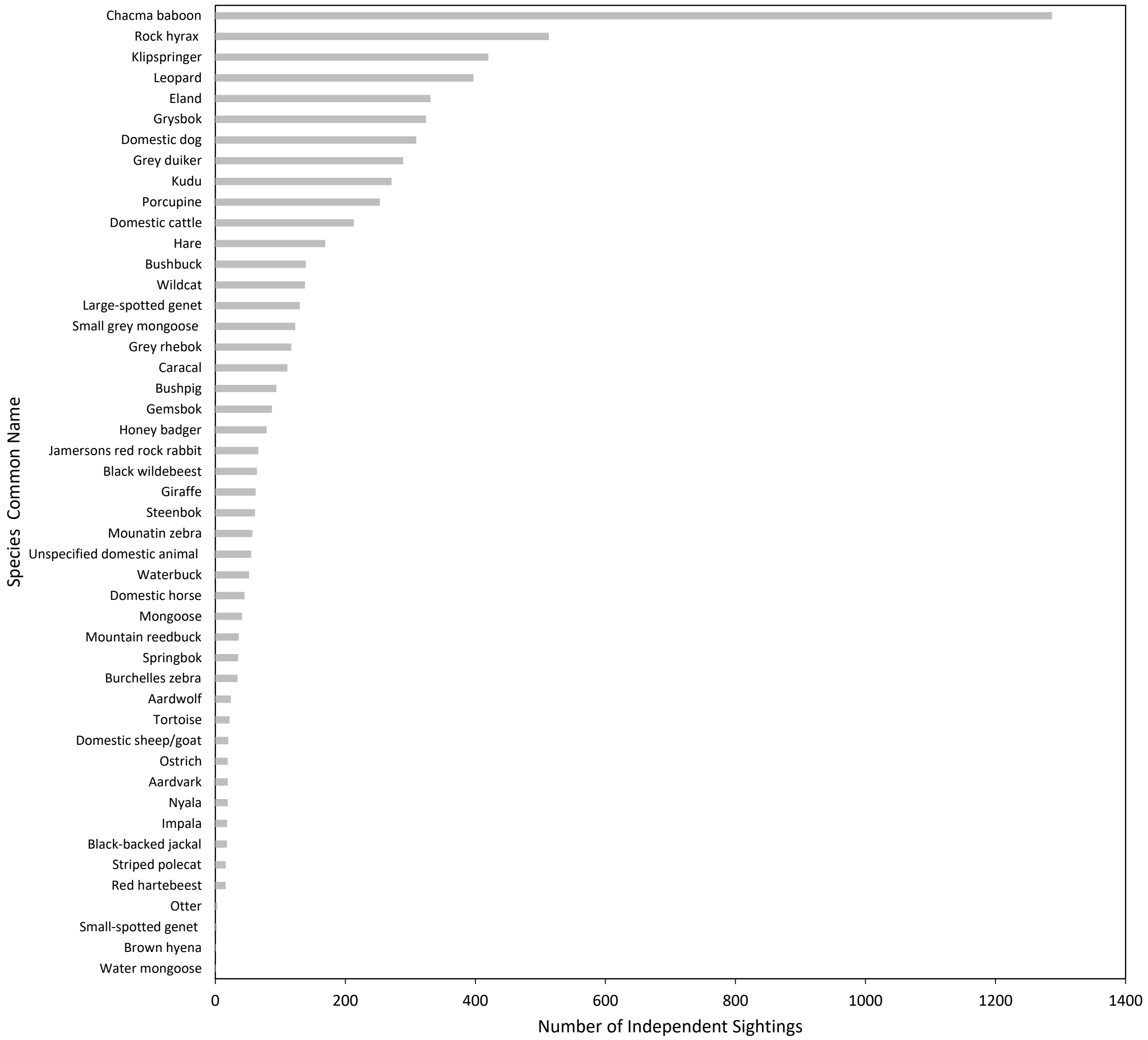

Figure C3: *Clustered bar graph representing the recorded species for the 2022 survey. Recorded values signify distinct captures within a 60-minute interval from the initial capture. Throughout the survey period a total of 6,600 independent captures were documented.*

7.4. Appendix D: Buffer test results

Table D1: *Table representing the tested buffer widths applied to the 2012 survey, tested on individual session for all predictor variables. MtestBuff20 represents a buffer width of 20 km and MtestBuff15 represents a buffer width of 15 km.*

Model	Predictor variables on Density	Predictor variables on λ0	Predictor variables on σ	Number of Parameters	AICc	dAICc	AICc Weight
MtestBuff20	D~session	session	session	9	2101.608	0	0.5785
MtestBuff15	D~session	session	session	9	2102.241	0.633	0.4215

7.5. Appendix E: Covariate masks

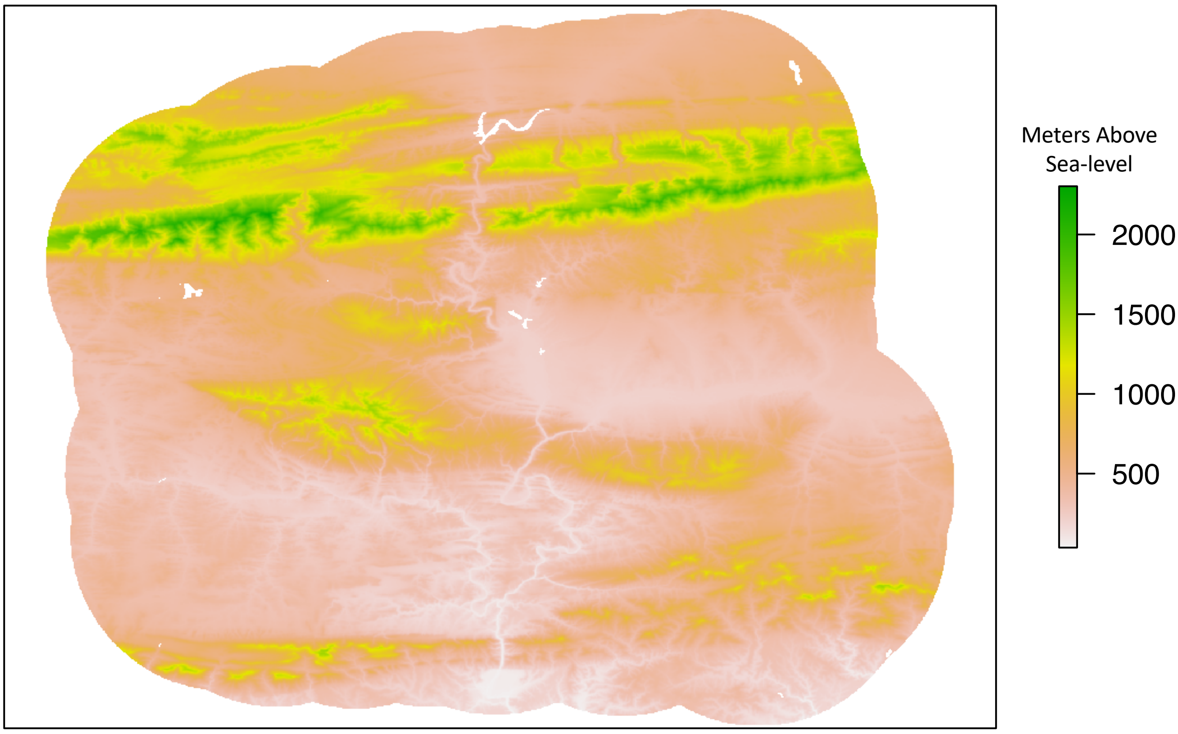

Figure E1: *Spatial layer displaying the clipped elevation covariate at 30 m resolution for the 20 km buffered study area with urban centres and major water bodies removed. Elevation is based off a digital elevation model (NASA Shuttle Radar Topography Mission [STRM], 2013) which was accessed through Earth Data.*

Figure E2: *Spatial layer displaying the clipped terrain ruggedness covariate for the 20 km buffered study area with urban centres and major water bodies removed. Terrain Ruggedness (calculated in QGIS using DEM) based on the nearest 3x3 cells.*

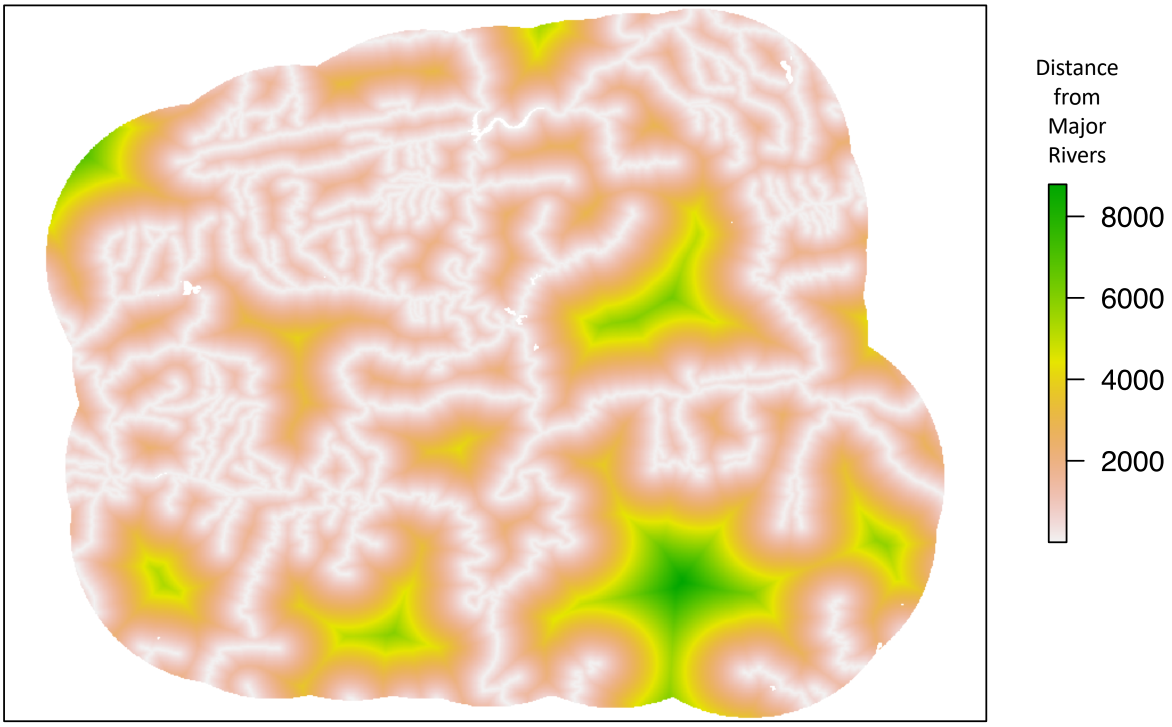

Figure E3: *Spatial layer displaying the clipped river distance covariate for the 20 km buffered study area with urban centres and major water bodies removed. River distance is calculated using the Euclidean distance function in QGIS based off the major river networks in the study area (Humanitarian Open Street Map Waterways).*

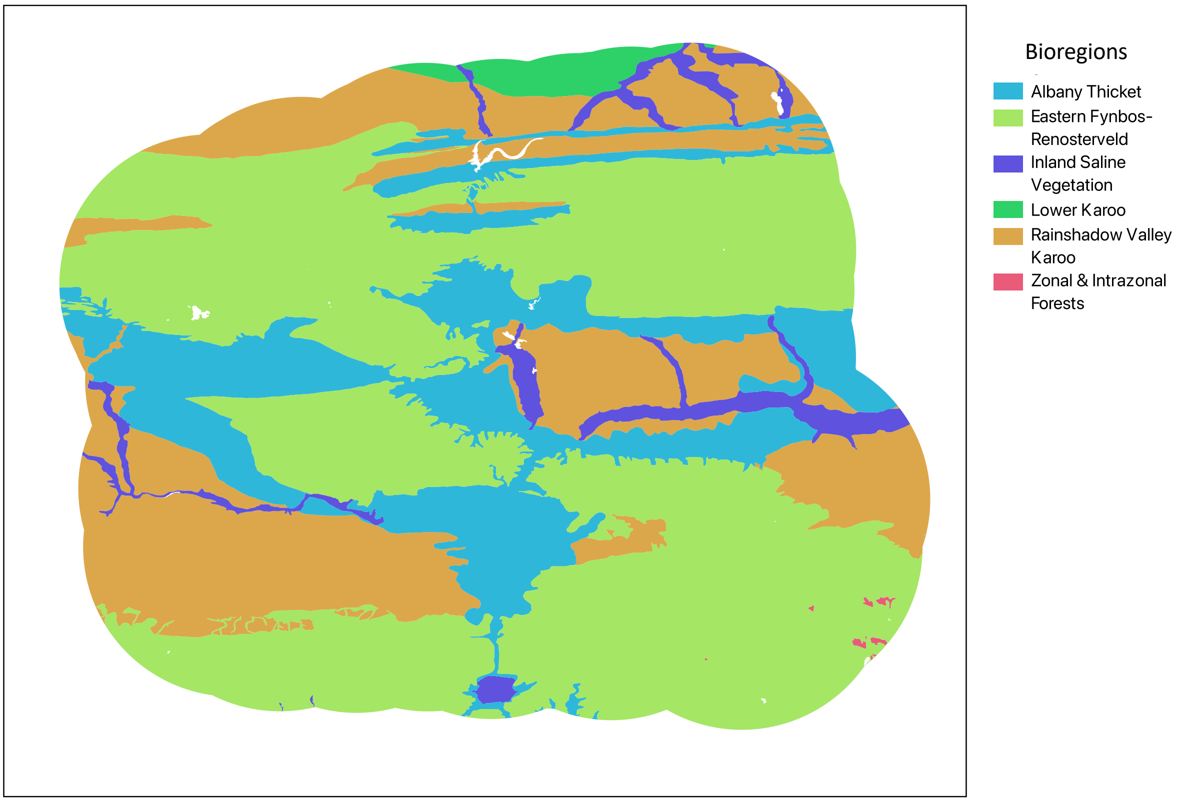

Figure E4: *Spatial layer displaying the clipped bioregions covariate for the 20 km buffered study area with urban centres and major water bodies removed. Bioregions were derived from vegetation types (Appendix Table A1) based on the vegetation map of South Africa, Lesotho and Swaziland (South African National Biodiversity Institute).*

7.6. Appendix F: Density results

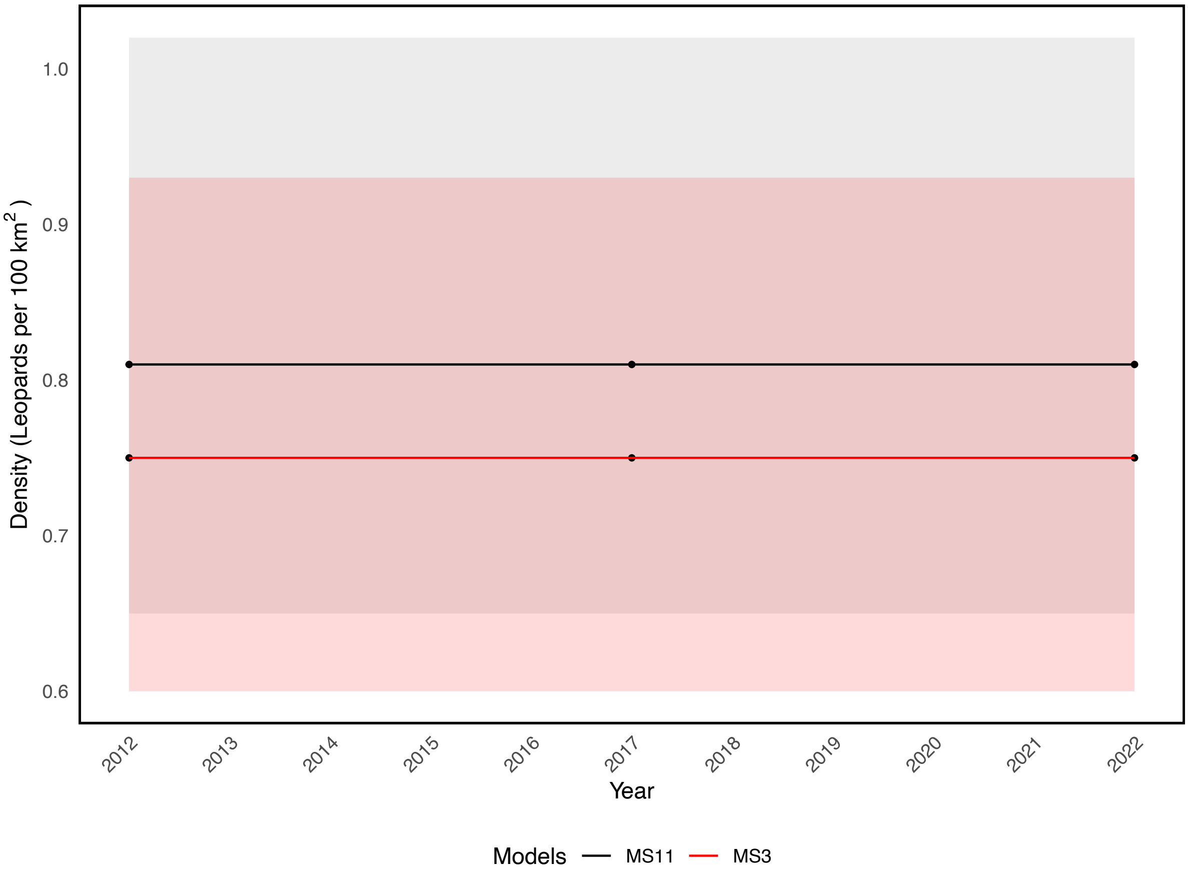

Figure F1: *Dot and line plot with respective confidence interval ribbons showcasing leopard densities (per 100 km^2) in the buffered study area, based on models, MS11 (black line & grey ribbon) & MS3 (red line & red ribbon). Density predictor variables for both models (MS11 & MS3) are constant (D~1). MS11 predictor variables for both capture rate (λ_0) and sigma (σ), are a function of individual session and sex (session*sex). MS11 has a constant density of 0.81 leopards per 100 km^2 (95% CI:0.65-1.02). MS3 has a single predictor variable of sex on capture rate (λ_0) and a function of individual session & sex on sigma (σ). MS3 has a constant density of 0.75 leopards per 100 km^2 (95% CI:0.60-0.93)*

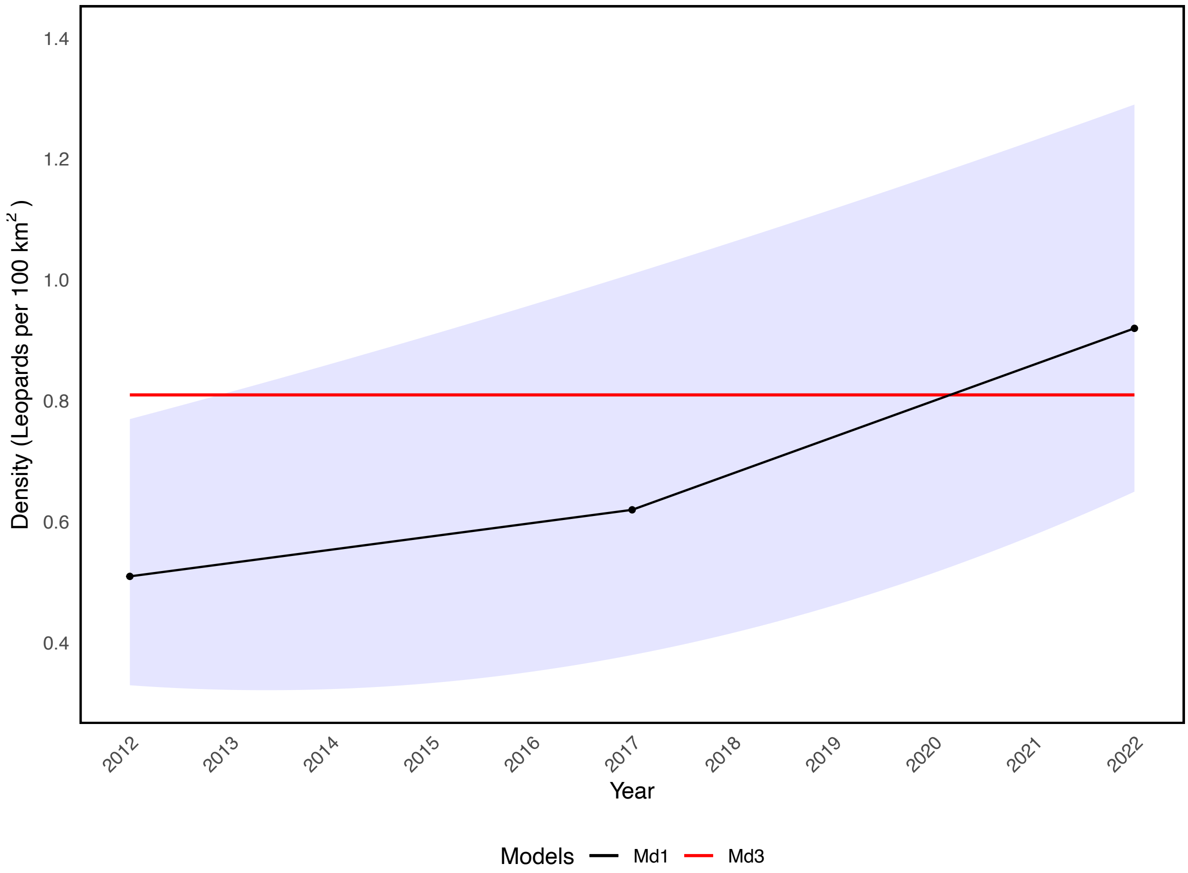

Figure F2: *Dot and line plot with respective confidence interval ribbon (Md1), showcasing leopard densities (per 100 km^2) in the buffered study area, based on models, Md1 (black line & ribbon) & Md3 (red line). The density predictor variable for Md1 represents density for individual sessions (D~session) and constant density (D~1), for Md3. Predictor variables for both models are based on model MS11 where capture rate (λ_0) and sigma (σ) are a function of individual sessions and sex (~session*sex). Md3 has a constant density of 0.81 leopards per 100 km^2 (95% CI:0.65-1.02). Md1 estimated density for 2012 is 0.51 leopards per 100km^2 (95% CI:0.33-0.77), for 2017 is 0.62 leopards per 100 km^2 (95% CI: 0.38-1.01) and for 2022 0.92 leopards per 100 km^2 (95% CI: 0.65-1.29).*