THE DENSITY OF LEOPARDS IN A MIXED-USE LANDSCAPE IN THE WESTERN CAPE, SOUTH AFRICA

KYLE HINDE

Submitted in fulfillment of the minor dissertation component of the Conservation Biology
Masters programme
Department of Biological Sciences, University of Cape Town

Prof. M. Justin O'Riain
Supervisor
iCWild
University of Cape Town

Dr Kathryn Williams
Co-supervisor
Cape Leopard Trust

Anita Williams
Co-supervisor
Cape Leopard Trust

Abstract

Large carnivores face numerous threats, including habitat loss and fragmentation, direct killing, and prey depletion, leading to significant global range and population declines. Despite these threats, leopards (*Panthera pardus*) persist outside protected areas throughout most of their range, occupying a diverse range of habitat types and land uses, including peri-urban and rural areas. Our understanding of leopard population dynamics in mixed-use landscapes is limited, especially in South Africa, where most research has focused on protected areas. Here I use spatially explicit capture-recapture (SECR) models on camera trap data to estimate how leopard density varies across a mixed-use landscape of protected areas, farmland, and urban areas in the Overberg region of the Western Cape, South Africa. Data were derived from 86 paired camera stations, which collected data for 161 camera trap nights, providing 221 independent leopard captures at 50 camera trap stations. A total of 25 individual leopards were identified, and the best-performing SECR model included the covariate sex on the σ (spatial decay), and a combination of sex, vegetation type and the interaction on λ_0 (capture probability), with a density estimate of 0.64 leopards per 100 km^2. Elevation, terrain ruggedness, protected area status and NDVI were all important drivers of leopard density in the region, with leopard density highest on elevated remnants of natural land outside of protected areas. These results are similar to previous research findings in the Western Cape, where high-lying natural vegetation was shown to serve as both a refuge and a corridor for leopard movement in otherwise transformed landscapes. Given the low level of risks to lives and livelihoods posed by leopards in this region, the continued persistence of leopards in this shared landscape is considered high. Education of landowners should still be prioritised to improve tolerance towards leopards in the event of occasional negative impacts (e.g., livestock depredation).

Plagiarism Declaration

I, Kyle Cameron Hinde, hereby declare that the work on which this thesis is based is my original work (except where citations indicate otherwise); that this thesis was carried out in accordance with the regulations of the University of Cape Town; and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree at this or any other university. I grant the university free license to reproduce in whole or in part, for research purposes. I am presenting this thesis for examination toward the Degree of Master of Science in Biological Sciences.

I acknowledge that while I assisted with data collection the majority was collected as part of the Cape Leopard Trust's monitoring survey (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: Kyle C. Hinde
Student number: HNDKYL005

Signed: Signed by candidate
Date: 13th September 2022

Acknowledgements

My thesis would not be possible without the guidance and support of many people. Thank you to all of you. My supervisors, Prof. Justin O'Riain, Dr Kathryn Williams and Anita Wilkson - thank you for your precious time and for sharing your incredible knowledge.

Thank you to the team at the Cape Leopard Trust, particularly to Silindokuhle Tokota, who set up the camera trap survey, and their funders Jamma International, Hans Hoheisen Charitable Trust and the Ford Wildlife Foundation. A camera survey of this size was made possible with the help of many people and organizations. A big thank you to: Eugene Hahdiek and Nuwejaars Wetlands Special Management Area for planning support, research assistance and access to land; Mike Fabricius and Walker Bay Fynbos Conservancy for planning support, research assistance and access to land; SANParks Agulhas National Park for planning support and access to land; CapeNature for planning support and access to land; Denel Overberg Test Range for planning support and access to land; the landowners for allowing us to set up cameras on their land; as well as the research assistants - Thandaza Michelle Shilenge, Monti Benny Mothagoane, Mari-su de Villiers, André Albertyn for helping with the camera set up and services. I would also like to thank the team at Wild ID for their support in developing the programme.

Running a course during the COVID-19 pandemic was no small task. Thank you to Dr Susan Cunningham, Prof. Peter Ryan, and Hillary Buchanan at FitzPatrick Institute of African Ornithology. The challenges faced were made easier by the awesome Conservation Biology Class of 2021/2022, may our paths remain intertwined. Thank you to the University of Cape Town for the funding I received during my time at an incredible institution.

To the other funders, my parents: Thank you for developing my love for the natural world and giving me the opportunity to make an impact. To Marilize, your love and support have been incredible and made this journey an adventure. Finally, to my friends and teachers, you have all contributed in some way to make this possible; hopefully, it will lead to a positive impact.

Table of Contents

1 Introduction

1.1 Large carnivores

The Anthropocene is defined by significant human impacts on Earth's geology, ecosystems, and biodiversity (Crutzen, 2006; Corlett, 2015; Carey, 2016), with large carnivores being adversely affected (Bauer et al., 2015; Durant et al., 2017; Terraube et al., 2020). Of the 31 largest species in the order Carnivora, more than half of the species are listed as Threatened by the IUCN (Ripple et al., 2014), with 24 of the 31 species undergoing population declines (Frame, 1991; Tian et al., 2011). Long generation time, high trophic level, and wide-ranging behaviour mean that large carnivores typically occur at low population densities throughout the world (Purvis et al., 2000; Forero-Medina et al., 2009). These traits make them particularly vulnerable to fragmentation and loss of natural habitat (Crooks et al., 2011; Di Minin et al., 2016; Wolf & Ripple, 2017). With rapid human population growth, encounters between people, livestock and large carnivores have increased, which has led to the widespread killing of the latter in all human-dominated landscapes, particularly farmlands (Quigley & Crawshaw, 1992; Treves & Naughton-Treves, 1999; Mann et al., 2019; Aebischer et al., 2020).

Large carnivores are often apex predators and play an important role in the top-down regulation of ecosystems (Ritchie et al., 2012; Ripple et al., 2014; Hoeks et al., 2020; Terraube et al., 2020). The loss of apex predators can lead to trophic cascades (Estes et al., 2011; Suraci et al., 2016; Hoeks et al., 2020), which can negatively impact herbivore-vegetation dynamics, as well as the abundance of mesopredators (Prugh et al., 2009; Drouilly, Nattrass & O'Riain, 2018) – which affect ecosystems and agricultural productivity (Prugh et al., 2009; Letnic et al., 2011; Suraci et al., 2016; Jachowski et al., 2020). The removal or reduced abundance of large predators has thus been shown to adversely affect the productivity of ecosystems and the associated ecological services that humans rely on for survival (Ripple & Beschta, 2012). Large carnivores are also often iconic species that act as a conservation umbrella species (Dalerum et al., 2008; Rozylowicz et al., 2011) and enhance revenue associated with wildlife tourism (Dalerum et al., 2008; Hemson et al., 2009; Dickman, Macdonald & Macdonald, 2011; Funston, Groom & Lindsey, 2013).

The depletion of natural prey resources is a major threat to large carnivores, and one of the driving factors behind the rise in negative interactions between carnivores and humans (Karanth & Chellam, 2009; Soofi et al., 2019). Without adequate natural prey, large carnivores persisting outside of protected areas increase their consumption of domestic animals (Woodroffe, 2000; Berger, Buuveibaatar & Mishra, 2013; Wolf & Ripple, 2016; Hussain et al., 2019). As many people depend on livestock for their livelihoods, tolerance to depredation is low, particularly in low-income communities (Hemson et al., 2009; Lindsey et al., 2013; Inskip et al., 2016; Tortato et al., 2017). Additionally, large carnivores may pose a risk to human lives when sharing the same landscape, with many injuries and deaths to people recorded in rural areas throughout Africa (Löe & Röskaft, 2004; Dickman, Marchini & Manfredo, 2013; Koziarski, Kissui & Kiffner, 2016). The combination of risk to lives and livelihoods has seen the sustained persecution of large carnivores worldwide, particularly when governments are perceived to value animals for tourism and conservation purposes over human welfare (Weladji & Tchamba, 2003; Noga et al., 2018; Jordan et al., 2020; Lunstrum et al., 2021).

1.2 Protected areas

Protected areas form the foundation of biodiversity conservation globally and offer some respite from habitat fragmentation and direct persecution of large carnivores (Gaston et al., 2008; Geldmann et al., 2013; Coetzee, Gaston & Chown, 2014; Gray et al., 2016). Protected areas are a simple, but effective and economical way to protect biodiversity (MacKinnon, 1997). National parks and game reserves are also popular tourist destinations (National Park Service, 2022), providing income and jobs as a direct incentive to protect the environment (Wells, 1996; Balmford et al., 2015; Cullinane & Koontz, 2016; Spenceley, Snyman & Rylance, 2019; Chidakel, Eb & Child, 2020; Thapa et al., 2022). The advantages of protected areas have led to a UN agenda to increase the area of formally protected land globally. A goal has been set for 2030, to protect 30% of all terrestrial land and oceans (Convention on Biological Diversity, 2022). This is an increase in the 2020 *Achi Target 11*, which aimed to protect 17% of terrestrial land, a figure considered too low for the protection of most large carnivores (Di Minin et al., 2016). Increasing protected area networks will contribute to buffering climate change impacts (Klausmeyer & Shaw, 2009; Carroll & Ray, 2021; Lehikoinen et al., 2021), by facilitating species range shifts.

Well-managed, large, protected areas are less susceptible to the detrimental impacts of edge effects (Newmark, 2008; Laurance et al., 2012), and are therefore particularly important for large carnivores whose territories often extend beyond the park edges (Newmark, 2008; Laurance et al., 2012; Rogan et al., 2022). Edges hardened by intensive agricultural and urban development limit movement surrounding protected areas (Woodroffe & Ginsberg, 1998; Newmark, 2008; Broadbent et al., 2008; Schulze et al., 2018; Hoffmann, 2022). Hard edges lead to increasing levels of population isolation (Thirgood et al., 2004; Hansen & DeFries, 2007; Blake et al., 2008; Silveira et al., 2014), overutilization of natural resources and increasing risks of disease transmission between domestic and wild animals (Newmark, 2008). Movement through corridors and stepping stones between protected areas may thus assist gene flow across transformed landscapes, maintaining the genetic viability of isolated populations (Mech & Hallett, 2001; Epps et al., 2007; Schwartz et al., 2009; Ma et al., 2018).

1.3 Protected areas in South Africa

Protected areas in South Africa currently cover 9.2% of the land area, this is low for Sub-Saharan Africa (16.5%) and globally (15.8%; IUCN, UNEP-WCMC, 2022; Department of Statistics South Africa, 2022). Edge effects are particularly pronounced in developing nations, with the harvest of resources within protected areas providing a livelihood for adjacent low-income communities. Animal poaching takes the form of (1) indiscriminate poaching, which both kills large carnivores and depletes their prey base (Newmark, 2008; Wolf & Ripple, 2016) and (2) targeted poaching for species whose body parts are used for medicinal and/or spiritual purposes (Naude, 2020). Large carnivores are revered as a symbol of strength and courage in select cultures and a feared adversary in everyday life – a contradiction that exists in rural areas of southern Africa that still host large carnivores (Ripple et al., 2014). Large carnivores also face the threat of trophy hunting within and outside protected areas, a contentious debate that provides real financial benefits to conservation but has ecological disadvantages if poorly regulated (Naude, 2020). Compared to neighbouring countries, South Africa has the advantage of more private resources available for the management of protected areas. Rogan et al.

(2022) and Smyth et al. (in review) provide evidence that professionally managed private protected areas support higher densities of leopards than their public counterparts.

1.4 Thriving and threats outside of protected areas

Only 20% of South Africa is classified as suitable leopard habitat, and only 25% of that is within protected areas (Swanepoel et al., 2013). Therefore, conserving leopards at the national level will require prioritizing and protecting populations outside protected areas (Swanepoel et al., 2013). As the habitat available to leopards and other large carnivores continues to decline and becomes increasingly fragmented, human-modified landscapes are becoming more important as both potential habitat and corridors or stepping stones between protected populations (Gubbi, Sharma & Kumara, 2020). Carnivores have been shown to co-exist and even thrive in mixed land-uses in: Europe (lynx, *Lynx lynx*; Bouyer et al., 2015; Filla et al., 2017), Africa (lions, *Panthera leo*; Suraci et al., 2019), India (leopards, *Panthera pardus*; Athreya et al., 2016; Gubbi, Sharma & Kumara, 2020) and America (pumas, *Puma concolor*; Knopff et al., 2014). It is important to note that while these species prefer natural habitats and prey over anthropogenic equivalents (Mondal et al., 2013), carnivores will exploit exotic and synanthropic prey species if they are available (e.g., caracal, *Caracal caracal*; Leighton et al., 2021). In India, domestic animals (dogs and livestock) support leopard populations at densities equivalent to those found in natural habitats (Athreya et al., 2016). Living in landscapes dominated by humans does however have increased risks (Swanepoel et al., 2015; Thapa, 2015; Naderi, Farashi & Erdi, 2018). Cougars in America show temporal avoidance of humans (Knopff et al., 2014); and lions in Kenya show both temporal and spatial avoidance of people (Suraci, Frank, et al., 2019). Ultimately, human tolerance of large carnivores in human-modified landscapes is the major determinant of their probability of persisting at ecologically viable numbers (Treves & Ullas Karanth, 2003; Mondal et al., 2013; Knopff et al., 2014).

The threats to leopards in a mixed land-use, overlap substantially with those experienced as edge effects in protected areas or more generally within poorly managed protected areas (Swanepoel et al., 2015; Strampelli et al., 2022). Leopards are harvested for body parts used in medicines in both eastern and African cultures

(Harries, 1993; Kumalo & Mujinga, 2017; Williams et al., 2017; Naude, 2020). In South Africa, leopard skins are used as symbols by members of the Nazareth Baptist 'Shembe' Church, with an estimated 13 000 – 18 000 leopard skins in circulation (Mann et al., 2017; Naude, 2020). Further threats to leopards outside of protected areas include habitat loss and fragmentation, prey depletion, road accidents, snares set for bushmeat, and retaliation for livestock losses (Swanepoel et al., 2015; Thapa, 2015; Naderi, Farashi & Erdi, 2018). This contributes to undermining genetic variation and connectivity within leopard populations outside of protected areas, ultimately threatening the long-term persistence and ability of leopards to adapt to the changing climate and landscape (Templeton et al., 1990; Dutta et al., 2013; Tensen, Roelofs & Swanepoel, 2014; Thatte et al., 2020).

1.5 Mixed land-use in the Western Cape

The Western Cape province, South Africa, has experienced an increase of approximately 1.2 million people in the last decade (Stats SA, 2020). This growth has been accompanied by an expansion of urban and agricultural land-use (City of Cape Town Municipality, 2020), further fragmenting and eroding natural habitats. Agriculture is generally restricted to flatter, lower-lying land, with the Cape Fold Mountains providing a refuge for many plants (Cowling et al., 2003) and wildlife (Mann, O'Riain & Parker, 2020). The mountains also act as natural corridors that allow animals to move large distances and thus maintain gene flow throughout much of the province and between protected areas. Western Cape protected areas are either state (City Nature Reserves, n = 31; Cape Nature Reserves, n = 27; South African National Parks, n = 6) or privately owned. Private protected areas include partnerships and stewardship agreements with government or NGO bodies, conservancies, and nature reserves. Partnerships between private landowners and the government offer a cost-effective way to expand protected areas, while reducing the burden on government organizations often limited in capacity and funding (Stolton, Redford & Dudley, 2014; Selinske et al., 2015; Bingham et al., 2017; Drescher & Brenner, 2018). Private partnerships, particularly with landowners in the Western Cape, allow the incorporation of lower-lying, flatter lands into the provincial framework, protecting biodiversity underrepresented in the current protected areas portfolio (Gallo et al., 2009; Stolton & Dudley, 2014).

1.6 Non-invasive leopard monitoring techniques

Leopards are elusive, cryptic, solitary carnivores that live at low densities, often in remote and inaccessible areas (Balme, Hunter & Slotow, 2009). Surveys therefore need to be both extensive when attempting to sample at the level of the population, and intensive to repeatedly capture individuals living at low densities (Rogan, 2021). Direct counting is thus seldom possible (Balme, Hunter & Slotow, 2009), with most studies relying on VHF/GPS tracking collars, DNA analysis of hair/scat, or camera trapping. Tracking collars have the advantage of providing individual movement patterns, but they are invasive (Brooks, Bonyongo & Harris, 2008; Hayward et al., 2012; Zemanova, 2020), expensive, and rarely achieve a meaningful sample size to make population-level inferences (Balme, Hunter & Slotow, 2009). Genetic sampling provides estimates of the genetic health of isolated populations, but its ability to provide accurate density estimates is still questionable, and considerable effort and expertise is required for processing samples and analyses (Janečka et al., 2011; Sollmann et al., 2013; Monterroso et al., 2014). Remote camera trapping has revolutionised carnivore population studies (Karanth, 1995) due to ease of use, lower cost, improved sample sizes, zero fitness costs to the study species, the ability for continual sampling effort (24 hours each day for multiple days), and its ability to simultaneously sample sympatric species including prey, competitors and human activity (Silveira, Jácomo & Diniz-Filho, 2003; Srbek-Araujo & Chiarello, 2005; Riley et al., 2017; Davis et al., 2020). However, similar to genetic studies, the analyses required to provide robust density estimates are complicated and require considerable expertise, often beyond that which protected area managers would be expected to achieve.

1.7 Estimating leopard density

Monitoring changes in a population is important for assessing the success of conservation actions and provides critical data for assessing the long-term viability of a population (Woodruff, 2001; Van Dyke, 2008; Manlik et al., 2016). Leopards establish territories and as such home ranges remain relatively fixed over the short term. Densities are estimated by combining two models: (1) The distribution of home ranges in a study area is described by a state model (Borchers & Efford, 2008); (2) a spatial detection model then estimates the relationship between the probability of detecting a leopard at a camera trap and the distance of the camera trap to that leopard's home range centre (Borchers & Efford, 2008). As camera traps are in fixed locations, one is more likely to detect a leopard with a home range centre closer to the camera station than those further away. Spatially explicit capture-recapture (SECR) models factor in this spatial component, improving both the accuracy and robustness of density estimates relative to the original mark-recapture approaches (Efford, 2004; Borchers & Efford, 2008). The spatial component further allows density estimates to be unbiased by edge effects while allowing the incorporation of anthropogenic, biotic, and abiotic factors to explain the observed variation in density (Borchers & Efford, 2008).

1.8 Covariate selection

The flexibility of SECR models allows for individual heterogeneity in capture probability due to the location of traps i.e., the terrain, habitat, or sex of the study species. Male leopards have home ranges that are on average larger than females and thus cover greater areas (Macdonald, 1983; Dickman & Marker, 2005; Fattebert et al., 2016). To account for the variation between sexes, sex has become a regular covariate of capture probability and home range size in leopard (and large felid) density studies (Sollmann et al., 2011; Swanepoel, Somers & Dalerum, 2015; Snider et al., 2021; Rogan et al., 2022). Vegetation type, normalized difference vegetation index (NDVI), and terrain ruggedness index (TRI) can also impact the capture rate. Both NDVI (Swanepoel et al., 2013) and terrain ruggedness (Hatten, Averill-Murray & van Pelt, 2005; Gavashelishvili & Lukarevskiy, 2008) have been used as proxies for prey catchability/vulnerability. This could influence the (1) visibility of animals, (2) probability that individuals will move along paths/roads, i.e. when vegetation is dense, they are more likely to use these features, (3) amount of prey a vegetation type supports, and 4) cover afforded to leopards when stalking prey offered by both the terrain and/or the vegetation (Balme, Hunter & Slotow, 2007). Bottom-up factors (habitat suitability and catchable prey) are the principal drivers of apex predators' movements in natural systems (Carbone & Gittleman, 2002). However, in anthropogenically dominated systems humans have a disproportionate influence on ecosystems, from top-down regulation (direct persecution) to bottom-up regulation (depletion of prey bases) (Darimont et al., 2015; Smith et al., 2017; Suraci, Clinchy, et al., 2019). Human population density is thus an important variable influencing the density of leopards (Snider et al., 2021). Elevation may serve as a proxy for leopard refugia with high relative elevation invariably precluding urban and agricultural land-use (Swanepoel et al., 2013; Mann, O'Riain & Parker, 2020). Land-use is also important, with protected areas providing a refuge for both prey and predators relative to agricultural and urban land-uses (Havmøller et al., 2019; Swanepoel, Somers, van Hoven, et al., 2015).

1.9 Study objectives, hypotheses, and predictions

Understanding how leopards persist in mixed land-uses is important for future leopard conservation given the threats to leopards in protected areas (Naude et al., 2020; Rogan, 2021) and the importance of shared landscapes as movement corridors. In this study I use data from a camera trap survey established in a mixed-use landscape in the Overberg region of the Western Cape, South Africa to (1) estimate leopard population density using a homogenous spatial recapture density model; (2) explore factors influencing leopard density variation using inhomogeneous density models considering both bottom-up and top-down ecological and anthropogenic processes.

The density and occurrence of leopards in mixed-use landscapes depend on the balance between the risks of persecution and the availability of optimal habitat for cover, prey availability and potential mates (Balme, Hunter & Slotow, 2007; McManus et al., 2021). Leopards show a preference for natural habitat and prey as they face higher risks of persecution in human-modified landscapes, where they may pose a risk to domestic animals and human lives (Martins & Harris, 2013; Ramesh et al., 2017; Havmøller et al., 2019; Mann, O'Riain & Parker, 2020). I formulated hypotheses based on previous research on the behavioural ecology and demographics of leopards. I then derived a suite of predictor variables that I considered relevant to each hypothesis. Hypotheses were derived from two widely accepted theories, namely that leopard density is dependent on the availability of resources and that anthropogenic variables negatively impact leopard populations. Each predictor variable included was selected to provide a measure relevant to either theory and all hypotheses were developed to provide support for or refute both theories. I developed five working hypotheses, each with a density model specifying between one and three parameters (Table 3). Density will be:

1. Higher in natural areas as leopards are adversely impacted by anthropogenic activity (Havmøller et al., 2019; Lamichhane et al., 2021; Snider et al., 2021).
2. Higher in areas with a higher vegetation productivity which have higher prey biomass and provide more cover for stalking prey (Balme, Hunter & Slotow, 2007).
3. Higher in more rugged areas that favour stalking and ambushing of prey (Lamichhane et al., 2021).
4. Higher at higher elevation as mountains provide a refuge from anthropogenic threats in a mixed-use landscape (Swanepoel et al., 2013; Mann, O'Riain & Parker, 2020).
5. Higher in protected areas which have fewer anthropogenic impacts (Havmøller et al., 2019; McManus et al., 2021).

2 Methods

2.1 Study area

This study was carried out in the southernmost region of the Western Cape and covers an area of approximately 3500 km^2, stretching from the Bot River Estuary in the west to the De Hoop Vlei in the east. The study area encompasses national and provincial protected areas, private protected areas, farmland, and small urban residential settlements. Noteworthy areas within the study include Nuwejaars Wetlands Special Management Area and Walker Bay Fynbos Conservancy (a mosaic of protected areas and privately owned agricultural land); as well as the Denel Overberg Test Range (a state-owned enterprise) which is a weapons testing site and therefore has restricted access to the public.

Annual rainfall in the region averages 460 - 600 mm and peaks during the austral winter months. Average monthly temperatures range from 8 °C to 27 °C with an annual average of 16 °C (Climate-Data.org). The topography varies from 1300 m (Cape Fold Mountains) to sea level along the southern coast of South Africa. There are 17 types of vegetation in the study area, of which 11 are threatened (six of which are critically endangered) (Skowno et al., 2019; see Appendix B).

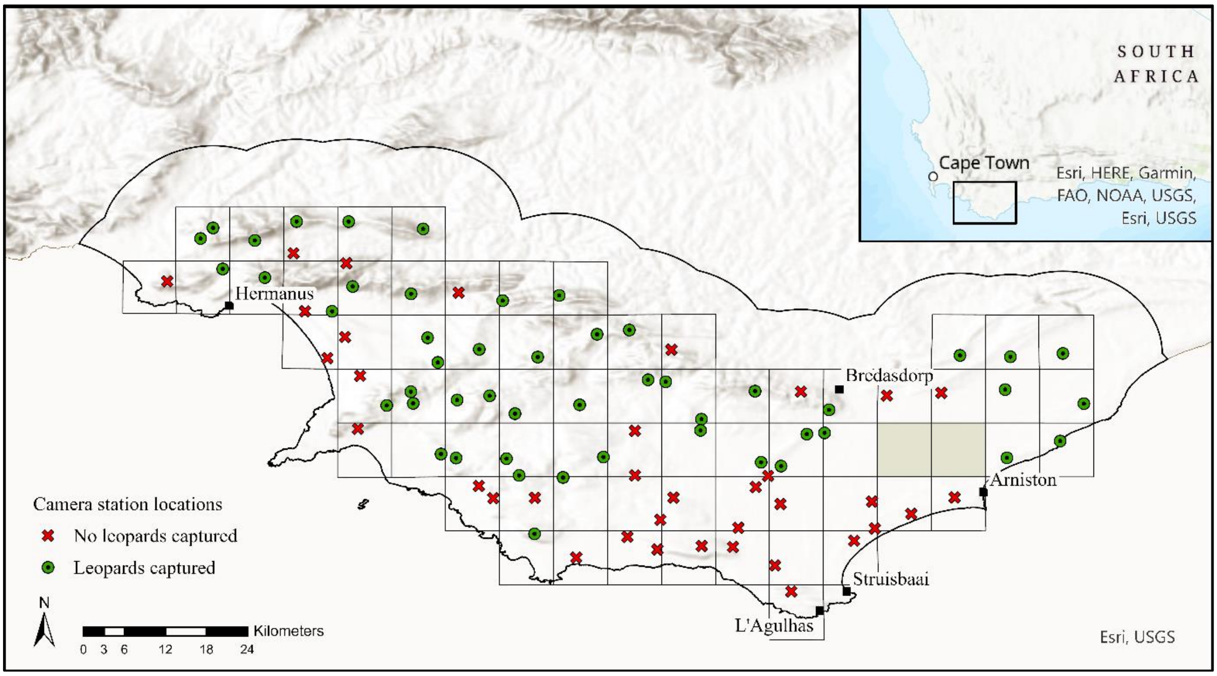

***Figure 1**: The Overberg study area at the southern tip of the Western Cape. Camera trap stations are shown as green dots where leopards were detected or red crosses where no leopards were detected. The black line north of the camera traps shows the terrestrial limit of the study areas which includes a 12 km buffer zone around the northernmost traps. To the south the coastline of the Indian Ocean serves as a hard boundary. A 50 x 50 km grid was superimposed over the study area with at least one camera trap placed in each grid block (n = 71 blocks, two blocks were excluded (shaded in grey) as the complete blocks were uninhabitable by leopards).*

2.2 Camera trap survey

The data analysed to estimate leopard density were acquired through a camera trap survey consisting of 86 paired camera stations, active for 161 days from 19th August 2021 to 26th January 2022. The smallest territory size recorded for female leopards in the Western Cape is 50 km^2 (Martins, 2010) which is smaller than estimates for female home ranges close to the study area (e.g., De Hoop Nature Reserve = 66.4 km^2 and Hermanus mixed landscape = 86.7 km^2; Devens et al., 2018). The 3500 km^2 study area was thus divided into 71 x 50 km^2 blocks. Camera stations were placed in all but two blocks, with an average spacing of 3676 meters. The two blocks excluded were dominated by intensive annual cereal crops which are not considered to be habitable by leopards.

Camera stations consisted of paired Cuddeback C1 Strobe Flash 1279 trail cameras set at a height of 30-40 cm to obtain an image of both the left and right flank of animals, which improves the likelihood of correctly identifying individual leopards. Camera locations were chosen to maximise the potential of photographing a leopard, and were placed on least resistance pathways (e.g. roads, hiking trails, game trails), 'natural funnels' created by the local topography and where there was signs of leopard presence including scat, spoor, and tree markings. The cameras were serviced at six-week intervals to ensure that they were working correctly, to change batteries and memory cards, and to clear vegetation at the sites that may produce false triggers under windy conditions. If a camera was triggered during the day, a burst of three images was taken. During the night and at low ambient light levels, a flash was used to take one colour image as soon as the camera was triggered. Colour images are easier to identify coat patterns as opposed to infrared images (Williams, 2017; Herrera et al., 2021). Survey effort was included in the analysis as the number of days at least one camera at a station was active.

2.3 Image processing

Camera trap images were first processed in the WildID (https://www.wildid.app/) machine learning software program to identify different species. Individual leopards are identifiable by unique pelage patterns, which are not mirrored on left and right flanks (Balme, Hunter & Slotow, 2009; Martins, 2010). Therefore, leopard images were labelled as left or right flanks and then exported to Hotspotter (Crall et al., 2013). Hotspotter is an algorithm that can identify individuals of patterned species. Areas of interest are selected between the leopard's shoulder and hip and the image cropped accordingly. The Hotspotter algorithm provides a percentage match to other known flanks in the database. An independent observer then verified and confirmed the individuals identified by Hotspotter. The sex of the leopards was assigned only when images provided clear evidence of either testes or a dewlap, both features unique to males (Balme, Hunter & Braczkowski, 2012). The individual, sex, date, time, and location were recorded for sampling occasions. As leopards are most active at night (Carter et al., 2015; Hargey, 2022) an occasion began and ended at midday rather than at midnight. Therefore, captures of the same individual were considered independent if they occurred between different nights or at different locations. Where there were only images of the left or right flank of unmatched individuals, the unmatched individuals represented by the flank side with the least number of images were removed to avoid false recaptures.

2.4 Covariates

For single-session density estimates, covariates need to be incorporated into each cell of the habitat mask (resolution = 0.3 km^2). Spatially continuous variables were averaged using inverse distance weighted means across cells surrounding the habitat cell of an identified activity centre (Rogan, 2021). The weight assigned to each pixel surrounding the habitat cell within an animal's home range is relative to the probability that a leopard will be detected within that cell. This reduces the swamping of cells closer to the activity centre by the higher number of cells on the edge of the home range due to its radial nature (Rogan, 2021). Environmental covariates included: NDVI (Sinergise Laboratory for geographical information systems, Ltd., 2022); Elevation, 30 m resolution Digital Elevation Model (NASA Shuttle Radar Topography Mission (SRTM), 2013); and Terrain Ruggedness Index (calculated from elevation in QGIS). Quadratic effects of environmental covariates are included to account for extremes where, for example, leopards may prefer vegetation of an intermediate NDVI value over very spare or dense vegetation. Anthropogenic variables included: protected terrestrial land in the study site (IUCN, UNEP-WCMC, 2022); human population density (Center for International Earth Science Information Network – CIESIN – Columbia University, 2018) and major land-use (South African Department: forestry, fisheries & the environment, 2020). I broadly grouped the 63-classified land-use types in the study area into three categories: highly modified (e.g., residential, industrial, or mining infrastructure), agricultural, and natural (see Appendix A). For detection models, sex was included as an individual covariate and the dominant vegetation type at each camera trap station was included as a site-specific variable.

2.5 Model fitting and evaluation

A homogenous density estimate was generated in R (version 4.1.3; R Core Team, 2022) using the package 'secr' (version 4.5.3; Efford, 2022) for a single-session closed-population spatial capture-recapture model. An inhomogeneous density model was used to explore variation in leopard density across the region and to test the five predefined hypotheses. The models were run across an area defined as the habitat mask (Borchers & Efford, 2008) which included a buffer of 12 km beyond the outermost camera stations (see Figure 1). All state space was discretised into 550 m x 550 m (0.3 km^2) habitat cells, and I excluded cells with centroids located in pixels classified as water. I calculated the expected radius of a circular home range (cHR) using the formula $r_{AU} = 2.447\sigma$ (Royle et al., 2013), therefore, $cHR = \pi \times (2.447\sigma)^2$. Detection parameters may compensate for each other, leading to an inflated home range estimate, therefore, it should be taken as a coarse estimation (Efford & Mowat, 2014). A maximum-likelihood approach optimised using the Nelder-Mead estimator was used to fit the models. SECR estimates density by modelling the decrease in capture probability (λ_0) as the distance between the camera site and an individual's activity centre increases. After considering previous leopard studies (Snider et al., 2021; Rogan et al., 2022; Smyth, in review) and testing the fit of various decay functions, a hazard half normal function was used to model the baseline detection function of individuals. Parameters in the detection function were λ_0 (capture probability) and σ (spatial rate of decay). Together the parameters define the function of detection probability as a function of location (Efford, Borchers & Byrom, 2009). To account for variations in behaviour between male and female leopards, I used a hybrid mixed model, as not all leopards could be accurately sexed; sex was included as a two-class partially observed finite mixture. To avoid models converging on local maxima, models were rerun with the starting values as the output of previous runs. Relative statistical support was selected using Akaike's Information Criterion corrected for small sample sizes ("AICc"; Akaike, 1981; Hurvich & Tsai, 1989). Models that had AICc scores below seven relative to the best performing model were considered to show adequate support (Burnham, Anderson & Huyvaert, 2011).

3 Results

3.1 Capture history

The 86 camera stations were active for a combined total of 13 500 camera trap nights (maximum=160, minimum=91, mean=157). Leopards were detected at 50 of the 86 camera stations (58%). Independent captures of leopards totalled 221 occasions and included 25 individual adult leopards (14 females, 9 males, and 2 unsexed individuals). Seven juveniles and three unidentified individuals were captured on cameras but excluded from further analysis.

3.2 Covariates

The buffered study area encompassed roughly 4650 km^2, of which 1300 km^2 (28%) was comprised of patches of protected land. Natural land made up most of the study area (63%) followed by agricultural (35%) and highly modified (2%). Camera traps were placed on nine different vegetation types (Appendix B). Overberg Sandstone Fynbos had the most camera trap sites (n=38) followed by Agulhas Limestone Fynbos (n=15). Elevations ranged from a maximum of 1150 m to sea level at the coast. Terrain ruggedness index varied from level areas (TRI = 0 m) to moderately rugged areas (TRI = 485 m). The human population density ranged from 0 to 17 500 people per km^2 in the coastal town of Hermanus. Terrain ruggedness index is derived from Elevation and as such were found to be highly correlated ($R = 0.93$). No other continuous variables were correlated more than $R > 0.4$.

3.3 Supported hypotheses

The best performing model, MD6, includes the covariate sex on the detection parameter, σ, and a combination of sex, vegetation type and the interaction on λ_0. AICc scores revealed that MD7, MD5 and MD1 all have support (dAICc < 7; Table 1). MD6, which accounted for more than 80% of the weighting, predicted a density of 0.64 leopards per 100 km^2 (95% CI: 0.43 - 0.94) across the buffered study area (4575 km^2) which equates to a total of 29 leopards (95% CI: 20 – 43 leopards). Female σ was estimated at 3183 m with male σ substantially greater, 7142 m. Circular home range sizes are coarsely estimated to be 195 km^2 for females and 983 km^2 for males. The encounter rate of males and females was 0.0140 and 0.0245, respectively. MD7 showed adequate support and therefore, sex was used as a covariate on σ and λ_0 for inhomogeneous models. MD7 was chosen over MD6, as the model contains fewer parameters, and therefore the inhomogeneous density models performed better with only sex as a covariate on σ and λ_0.

Table 1*: Homogenous density models with different detection parameters on σ and λ_0. Vegetation type represents the vegetation the camera station was placed in. Sex is of individual leopards captured (male, female or unsexed). Asterix indicates a third term, which is the interaction term in addition to the main effects of the variable, a colon is simply the interaction term. The best-performing model parameters will be used for inhomogeneous density models.*

Model	Predictor variables on λ_0	Predictor variables on σ	N parameters	AICc	dAICc	AICc weight
MD6	Vegetation Type * Sex	Sex	10	738.446	0	0.8004
MD7	Sex	Sex	6	753.725	4.23	0.0965
MD5	Vegetation Type: Sex	Sex	11	739.301	5.45	0.0525
MD1	Vegetation Type + Sex	Vegetation Type + Sex	10	743.972	5.53	0.0505
MD4	Vegetation Type + Sex	Sex	8	753.29	8.13	0
MD3	Vegetation Type * Sex	Vegetation Type * Sex	14	731.67	19.51	0
MD2	Vegetation Type: Sex	Vegetation Type: Sex	16	733.166	47.01	0
MD0	1	1	4	864.683	112.52	0

All individual covariate models showed some support. Elevation, terrain ruggedness, protection status and NDVI showed high support (dAICc < 2); with human density intermediate support (dAICc < 7) and land-use category the least support (Table 2). The best performing model, which accounted for almost 40% of the weight, included elevation.

Table 2*: Performance of predictors for drivers of leopard density in the Overberg. Elevation represents height above sea level in meters at a resolution of 30 meters; Terrain ruggedness is a measure of the difference in elevation of a cell and the eight surrounding cells; Protected status is a binary variable of whether an area is protected area or not; NDVI (Normalized Difference Vegetation Index) is a proxy for vegetation productivity; Human density represents the human population density in each cell of the habitat mask; Land-use is a categorical variable of land as either natural, agricultural or highly modified.*

Hypothesis	Model	N parameters	AICc	dAICc	AICc weight
Elevation	D ~ Elevation + I(Elevation^2)	7	759.214	0	0.3945
Terrain ruggedness	D~TRI + I(TRI^2)	8	760.847	1.63	0.1744
Protected status	D~ status	7	761.046	1.83	0.1578
NDVI	D~NDVI + I(NDVI^2)	8	761.117	1.9	0.1523
Human density	D ~ Pop.Density	7	761.578	2.36	0.121
Land-use	D ~ land use	8	766.396	7.18	0

3.4 Covariate effects

The coefficient of elevation (β = 0.58) indicates a strong positive relationship between elevation and leopard density. Terrain ruggedness was also positively correlated with density, but the coefficient was negative for both protected areas and NDVI (β = -0.56). Leopard density also showed a negative relationship with levels of human population density. Density showed a positive effect for natural land-use and a slightly positive effect for agricultural land. Squared predictors indicate the effect on the extremes of predictors, therefore extreme elevations and ruggedness, are associated with lower leopard densities than intermediate values while extremes of vegetative productivity had a positive influence.

Table 3: *Performance of predictors for drivers of leopard density in the Overberg. Elevation represents height above sea level in meters at a resolution of 30 meters; Terrain ruggedness is a measure of the difference in elevation of a cell and the eight surrounding cells; Protected status is a binary variable of whether an area is a protected area or not; NDVI (Normalized Difference Vegetation Index) is a proxy for vegetation productivity; Human density represents the human population density in each cell of the habitat mask; Land-use is a categorical variable of land as either natural, agricultural or highly modified. Elevation, Terrain ruggedness and NDVI models all include* x^2 *quadratic term to represent the effect of extreme value.*

Predictor	Beta estimate	Standard Error
Elevation	0.58	0.28
Elevation^2	-0.56	0.29
Terrain ruggedness	0.58	0.28
Terrain ruggedness^2	-0.47	0.28
Protection status	Protected: -0.75	Protected: 0.77
NDVI	-0.56	0.29
NDVI^2	0.08	0.29
Human density	-0.25	0.36
Land use	Natural: 0.22 Cultivated: 0.02	Natural: 8.47 Cultivated: 8.55

4 Discussion

Leopards are one of the few large carnivores that persist in sustainable populations outside of protected areas, even in heavily transformed landscapes (Athreya et al., 2016;

Kshettry, Vaidyanathan & Athreya, 2017). Despite this there are few long-term monitoring studies of leopards outside of protected areas and thus we know little about the status of these populations and how they are responding to existing and novel anthropogenic impacts (Balme et al., 2014). To address this knowledge gap, I estimated leopard density in a mixed-use landscape that included protected, agricultural and urban land-uses in addition to a broad range of abiotic variables known to influence leopard density. My results reveal that leopards persist in this mixed-use landscape at a density intermediate between other recent surveys in this region of South Africa.

Insufficient sampling effort, particularly for low density, elusive species such as leopards, can result in underestimates of density. This study ran for six months resulting in 13 500 effective camera trap nights producing 221 independent captures of leopards. Although longer study periods may violate assumptions of population closure, the resulting density estimates are more accurate (Dupont et al., 2019). Along with extended survey periods, best practice for large carnivore density estimates using camera trap surveys includes (1) the minimum survey size should be at least the size of the species home range (2) camera spacing should be based on female home range size, with a minimum of 40-50 stations per survey (3) camera stations are placed to maximise capture probability (4) SECR methods are used for analysis with sex as a covariate on σ and λ_0 (Tobler & Powell, 2013). As this study fulfils all of these criteria, I am confident that the density estimate is robust and will provide an important baseline for long-term monitoring of leopard densities in the Overberg. Further efforts to refine how we measure important covariates in addition to exploring new covariates such as prey abundance will allow for improvements to density estimates. I was not able to incorporate covariates for prey and domestic/human presence as they are session-level covariates and hence only once this study is repeated will they be included. Both variables have been shown to be important drivers of density within protected areas (Henschel et al., 2011; Searle et al., 2021; Rogan et al., 2022) and thus their omission is a weakness of the current study.

Leopard density was higher in natural areas providing support for my first hypothesis that leopards would favour natural areas with low human density. Although human density is generally low in the predominately agricultural region of the Overberg, leopards still avoided populated areas. Similar negative effects of human density have been found in previous studies in the Western Cape (Mann, O'Riain & Parker, 2020; McManus et al., 2021) highlighting the importance of top-down anthropogenic impacts on leopards and other large predators outside of protected areas (Knopff et al., 2014; Abade et al., 2018). Further support for the negative impacts of human presence is the finding that leopard density in this study was higher in low intensity use agricultural land than highly modified land – showing a clear negative cascade from natural to urban land-use. Although leopards can be attracted to agricultural areas due to the potential availability of both domestic and synanthropic food sources (Athreya et al., 2016; Kshettry, Vaidyanathan & Athreya, 2017; Hussain et al., 2019), my results reveal higher densities in natural vegetation where natural prey are both more abundant and comprise a higher proportion of leopard diet (Martins et al., 2011; Mann et al., 2019).

Leopard density was not positively influenced by higher levels of NDVI as hypothesised. However very high NDVI levels did have a slightly positive effect on density suggesting a non-linear relationship with dense vegetation (i.e., very high NDVI) possibly serving as a refuge for leopards in this mixed-use landscape. A similar negative correlation between density and NDVI was found by Smyth et al. (in review) in an area that had historically high levels of anthropogenic impact. Here it was argued that positive bottom-up effects associated with higher NDVI levels were swamped by chronic levels of top-down anthropogenic impacts. The Overberg is considered the breadbasket of the Western Cape with extensive and intensive agricultural activity ranging from cereal crops to vineyards and fruit trees (Overberg District Municipality, 2022). These crops complicate the interpretation of NDVI as either an indicator of primary productivity or potential cover for leopards to stalk their prey more effectively (Balme, Hunter & Slotow, 2007) relative to the same metric when used for natural vegetation.

My results provided the highest support for hypothesis three, leopard density will be higher in more rugged areas and hypothesis four, density will be higher at high elevations which provide a refuge from anthropogenic activities (Mann, O'Riain & Parker, 2020). Leopards are highly mobile and agile climbers and thus terrain ruggedness does not impede their movement but rather provides them with cover to better ambush their prey. Rugged areas are also not suitable for agricultural or urban land-uses and are therefore invariably less transformed and more suitable for wildlife (Drouilly, Nattrass & O'Riain, 2018; Mann et al., 2019). Elevation was also found to be an important driving factor for density in the semi-arid Little Karoo (Mann, O'Riain & Parker, 2020), with low elevations used for intensive agricultural and urban development, which effectively excluded leopards. Research on both baboons (*Papio ursinus*) and caracal (*Caracal caracal*) in a mixed land-use region of the Western Cape revealed that both species prefer low lying land but are displaced to higher elevations by anthropogenic land-uses (Hoffman & O'Riain, 2012; Leighton et al., 2021). In the Overberg, most low elevation land is flatter and more suitable for development, which may explain why the effects of elevation were more marked in this region than in the Little Karoo (Mann, O'Riain & Parker, 2020).

The importance of protected areas for leopards is well established (Swanepoel et al., 2013; McManus et al., 2021; Rogan, 2021), however, in this study leopard density was higher outside of protected land. Leopards were only captured at two of the eleven camera sites in the Agulhas National Park, the largest formally protected area in the survey area, while a recent leopard survey in De Hoop Nature Reserve, a 340 km^2 protected area on the boundary of the study area, revealed a very low density of leopards (0.18/100 km^2; Hargey, 2022). In the absence of any clear evidence of direct or indirect negative human impacts in either protected area, the most parsimonious explanation for low leopard numbers within these protected areas is that the environmental variables therein are largely unsuitable for leopards. Swanepoel et al. (2013) suggest only 30% of protected areas in the Western Cape are comprised of suitable leopard habitats, with Maxent modelling revealing that the Agulhas National Park is not considered suitable habitat for leopards (Devens et al., 2021).

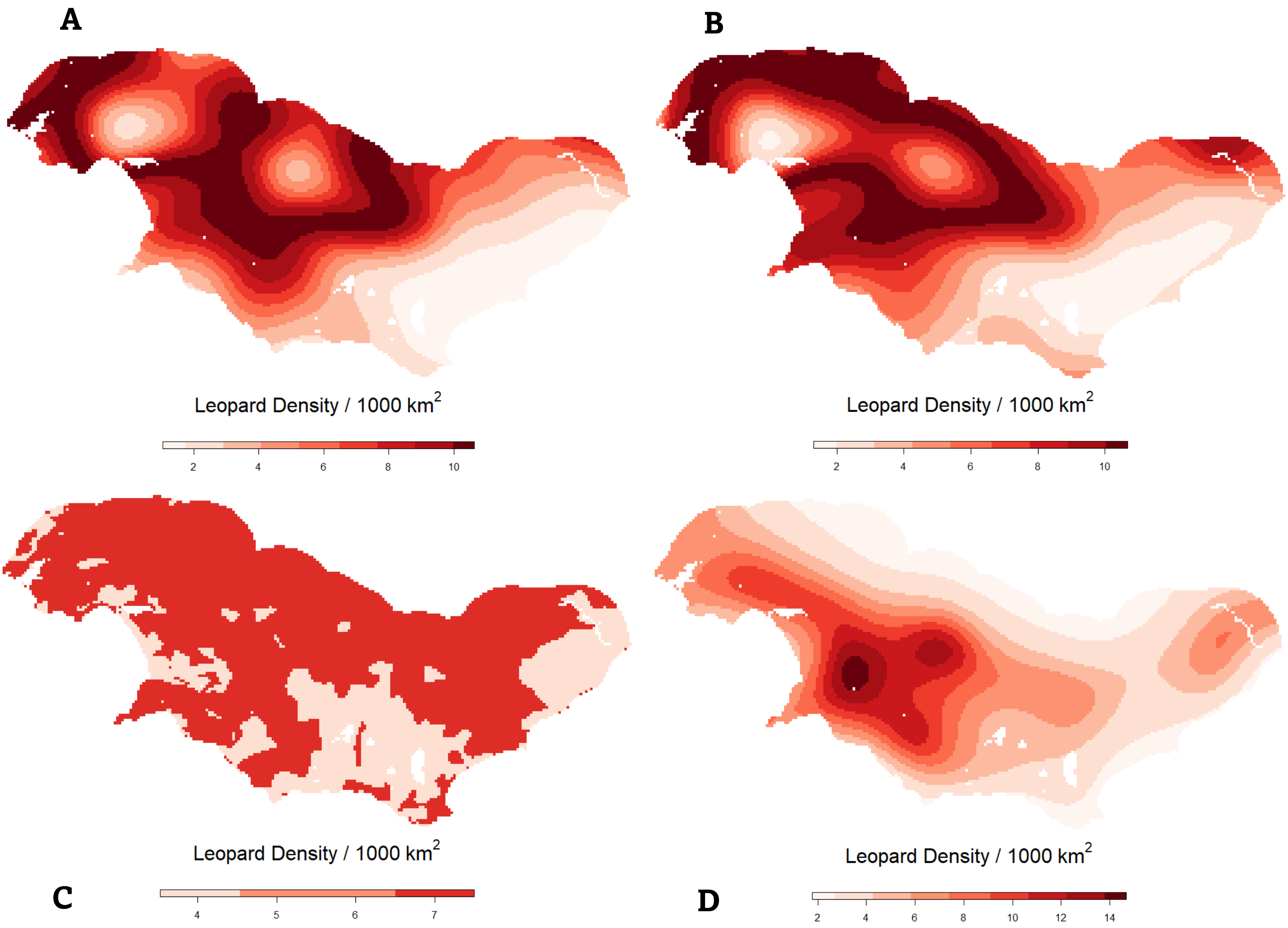

***Figure 2**: Heat maps showing how leopard density responds to the best performing predictors (AICc < 2; Table 2) within the surveyed area. A: Elevation model; B: Terrain ruggedness model; C: Protected area model; D: NDVI model.*

While leopard densities in protected areas that fall within 'suitable habitat' are higher (McManus et al., 2021) than those reported here, the density estimates for leopards in the Western Cape (Table 4) are generally lower than in other provinces in the north and east of South Africa (Faure et al., 2021; Rogan et al., 2022). To date six other camera trap surveys in the Western Cape have estimated leopard density. However, not all densities (Table 4) were calculated using the same method as this study (Spatial Capture-Recapture (SCR) maximum likelihood models using 'secr' package in R) but included Bayesian inference using the SPACECAP package (discontinued in 2014) and Just Another Gibbs Sampler (JAGS). This is important because density estimates using the same data varied markedly depending on the statistical package used with SPACECAP providing density estimates up to 300% higher than 'secr' (Devens et al., 2021). Consequently, I will only compare densities in the study region derived using the same statistical approach and packages as detailed in Table 4.

Table 4*: A summary of the seven studies that have estimated leopard density in the Western Cape of South Africa, including the statistical method used (Bayesian models and density estimates are shaded in grey), the region where the study was carried out and the year in which the camera trap survey was run.*

Source	**Density leopards/100 km^2**	**Statistical package**	**Region in the Western Cape of South Africa**	**Year of Camera Trap Survey**
This study	0.64 (95% CI: 0.43 - 0.94)	SCR- Maximum Likelihood (secr)	Overberg	2021-2022
Hargey (2022)	0.18 (SE ± 0.07)	SCR- Maximum Likelihood (secr)	De Hoop Nature Reserve	2020
Müller et al. (2022)	1.53 (95% CI: 1.18–1.89)	SCR- Bayesian (JAGS)	Cederberg Mountains	2017-2018
Mann et al. (unpublished)	1.10 (SE + 0.2)	SCR-Bayesian (Bayes)	Little Karoo	2017
Amin et al. (2022)	1.69 (95% CI = 1.4–1.99)	SCR- Bayesian (JAGS)	Boland Mountain Complex	2010-2011
Mann, O'Riain & Parker (2020)	1.26 (SE ± 0.25)	SCR- Maximum Likelihood (secr)	Little Karoo	2011-2012
Devens et al. (2021)	0.50 (95% CI = 0.39–1.09)	SCR- Maximum Likelihood (secr)	Langeberg	2012-2013
	1.89 (95% CI = 0.89–2.50)	SCR- Bayesian (SPACECAP)		
	0.38 (95% CI = 0.17–0.87)	SCR- Maximum Likelihood (secr)	Garden Route	2012-2015
	0.96 (95% CI = 0.52–1.49)	SCR- Bayesian (SPACECAP)		
	0.17 (95% CI = 0.06–0.48)	SCR- Maximum Likelihood (secr)	Overberg/ Agulhas	2011-2012
	0.69 (95% CI = 0.39–1.28	SCR- Bayesian (SPACECAP)		

SECR leopard density estimates in other areas of the Western Cape range from 1.26 leopards/100 km^2 (Mann, O'Riain & Parker, 2020) in the Little Karoo to 0.18 leopards/100 km^2 in De Hoop Nature Reserve (Hargey, 2022). This study's estimate of 0.64 leopards/100 km^2 falls in the middle of density estimates in the region but is considerably higher than a 2011 survey in the same study area of the Overberg which reported a density of 0.17 leopards/100 km^2 (Devens et al., 2021). Density estimations are dependent on what the authors consider leopard habitat and should be considered when densities are compared in a region. For example, I include natural, agricultural, and highly modified areas while Amin et al. (2022) considered leopard density in natural vegetation only and excluded agricultural and modified areas from the model space. As leopards in the Western Cape have been found to occupy natural habitats at higher density than transformed land, densities considering only natural land will in most instances lead to higher density estimates.

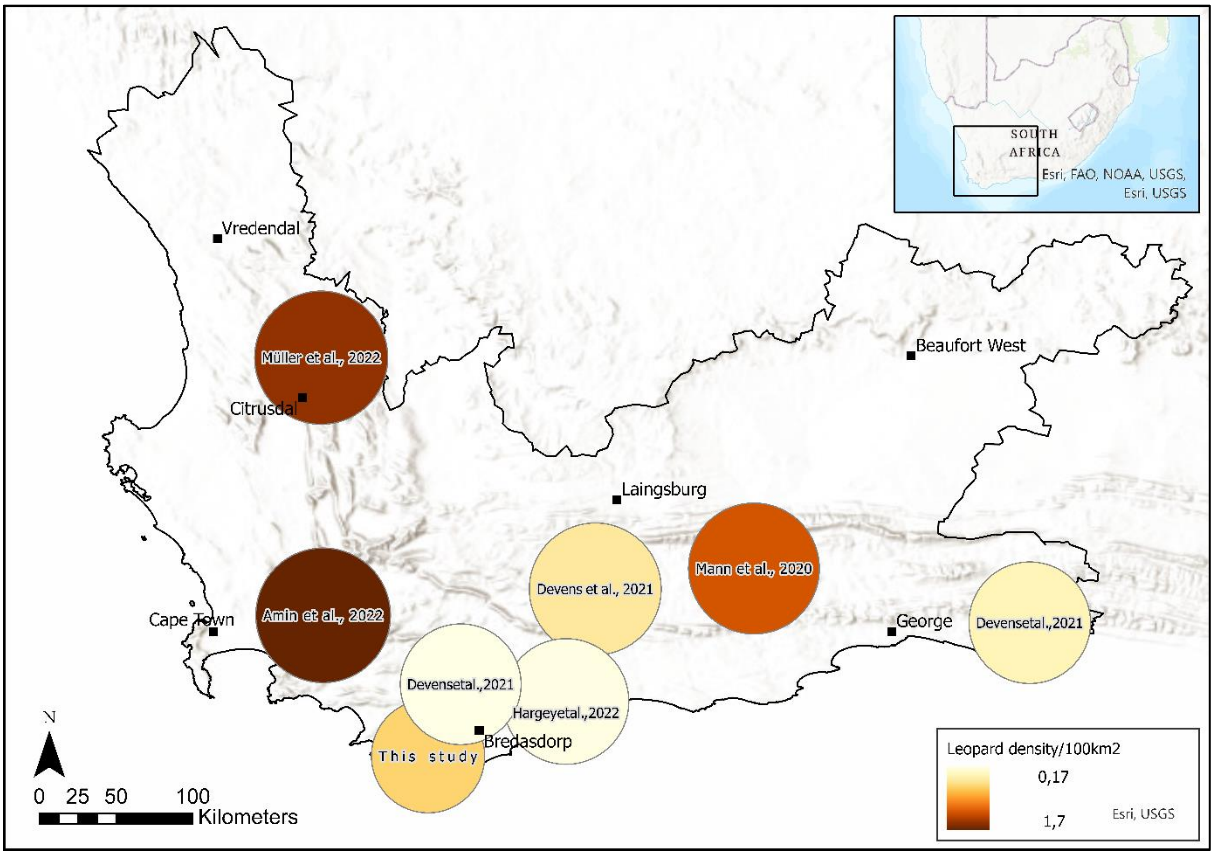

***Figure 3**: A map showing the results of previous camera trap surveys (Mann, O'Riain & Parker, 2020; Devens et al., 2021; Amin et al., 2022; Hargey, 2022; Müller et al., 2022) in the Western Cape that estimate leopard density.*

Connectivity, particularly in small populations, is important for finding mates, allowing dispersal, and ensuring genetic diversity in the population (Mech & Hallett, 2001; Epps et al., 2007; Ma et al., 2018). The variation in density of leopards throughout the Western Cape reveals potential source and sink populations that can ensure stable regional populations over time. However, this will require movement corridors to be retained and possibly created where movement is impeded (McManus et al., 2022). As natural habitats and rugged higher elevations harbour the highest leopard densities, the Cape Fold Mountains offer a significant natural corridor for the region.

A young male leopard that was initially detected on the western edge of the study area was subsequently detected approximately 100 km away in De Hoop Nature Reserve. This indicates that the mixed-use landscape within the study area is still permeable to dispersing leopards and that isolated protected areas in the Overberg still benefit from the key life history events of immigration and emigration. The density of leopards in the De Hoop Nature Reserve is currently lower (0.18 leopards/100 km^2; Hargey, 2022) than in the Overberg and the long-term viability of this population may depend on the ongoing immigration of leopards from more to less dense areas.

Running a camera trap survey in a mixed-use landscape required considerable interactions with private landowners. By explaining the research objectives and sharing the wildlife images from this survey with individual landowners the people living in this shared landscape were educated on the threats to, and benefits associated with retaining large predators and other wildlife in the landscape. Education is critical to improving public support and tolerance for wildlife outside of protected areas (Skupien, Andrews & Larson, 2016; Digun-Aweto, van der Merwe & Saayman, 2022) and while unquantified in this study it is my contention that repeated camera trap surveys will do more than merely monitor changes in the population over time but offer the opportunity for regular educational drives that may be of significant benefit to biodiversity conservation in the Overberg. It is here that NGO's such as the Cape Leopard Trust (CLT) provide a critical service to conservation, sourcing the funding required for long term effort outside of protected areas where resources are limited and not under the governance of protected area managers. It is hoped that a better understanding of the biodiversity living on private land will promote land-use practices that are less detrimental to both the environment and the biota that depend on it.

4.1 Conclusions

Leopard studies have mainly been focused on protected natural habitat (Balme et al., 2014). Protected areas, are however, becoming increasingly fragmented with a hardening of their edges; this limits their ability to maintain viable populations of large carnivores without adopting an intensive metapopulation approach with assisted dispersals through translocations. In this study leopards were detected throughout the mosaic of different land-uses, with higher densities outside of protected land. Similar results have been recorded in the Soutpansberg, South Africa; an area of rugged terrain and a large prey base (Grey, Kent & Hill, 2013), as well as an agricultural region in Namibia with a high natural prey base (Stein et al., 2011). High leopard densities outside of protected areas is a phenomenon more commonly associated with countries like India (~10 leopards / 100 km^2; Kshettry et al., 2020) where tolerance for large carnivores is high (and enforced by law) – despite their diets consisting mainly of livestock and pets (Kshettry, Vaidyanathan & Athreya, 2017). There are few reports of negative leopard impacts in this region of the Overberg, and thus while tolerance of predators by farmers in South Africa is generally low (Drouilly, Nattrass & O'Riain, 2021), it is unlikely that leopards are being actively persecuted in this region. The Overberg is thus an excellent region in which to promote the tolerance of leopards and to highlight the importance of the Cape Fold Mountains as corridors connecting areas of high and low leopard density. Improved connectivity and the persistence of leopards outside of protected areas provide a critical buffer for stochastic events such as extensive fires and droughts that may both be exacerbated by climate change (Jones et al., in press; Archibald et al., 2010; Ziervogel et al., 2014; Gannon & Steinberg, 2021). The Western Cape is predicted to become hotter and drier, and the Cape Fold Mountains, which run in an East-West direction across most of the southern Western Cape provide access to cooler south-facing slopes that are predicted to be critical refugia for a range of wildlife including leopards and species they prey upon (Keppel et al. 2012; McDonald et al. 2019). These refugia, in conjunction with the persistence of leopards in mixed land-use areas, suggest that the Western Cape may well be a stronghold for leopards moving forward, even if they naturally occur at low densities in this region (Figure 3). It is thus important to engage in long-term monitoring of this and other leopard populations in the Western Cape as a lens on how climate and land-use changes may impact apex predators and their prey outside of protected areas across a range of anthropogenic and natural land uses.

5 References

Abade, L., Cusack, J., Moll, R.J., Strampelli, P., Dickman, A.J., Macdonald, D.W. & Montgomery, R.A. 2018. Spatial variation in leopard (*Panthera pardus*) site use across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape. *PLoS ONE*. 13(10):1–17.

Aebischer, T., Ibrahim, T., Hickisch, R., Furrer, R.D., Leuenberger, C. & Wegmann, D. 2020. Apex predators decline after an influx of pastoralists in former Central African Republic hunting zones. *Biological Conservation*. 241:108326.

Amin, R., Wilkinson, A., Williams, K.S., Martins, Q.E. & Hayward, J. 2022. Assessing the status of leopard in the Cape Fold Mountains using a Bayesian spatial capture–recapture model in Just Another Gibbs Sampler. *African Journal of Ecology*. 60:299–307.

Archibald, S., Nickless, A., Govender, N., Scholes, R.J. & Lehsten, V. 2010. Climate and the inter-annual variability of fire in southern Africa: a meta-analysis using long-term field data and satellite-derived burnt area data. *Global Ecology and Biogeography*. 19(6):794–809.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J. & Karanth, K.U. 2016. A cat among the dogs: Leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx*. 50(1):156–162.

Balme, G., Hunter, L. & Slotow, R. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*. 74(3):589–598.

Balme, G.A., Hunter, L.T.B. & Slotow, R. 2009. Evaluating Methods for Counting Cryptic Carnivores. *Journal of Wildlife Management*. 73(3):433–441.

Balme, G.A., Hunter, L.T.B. & Braczkowski, A.R. 2012. Applicability of Age-Based Hunting Regulations for African Leopards. *PLoS ONE*. 7(4):e35209-.

Balme, G.A., Lindsey, P.A., Swanepoel, L.H. & Hunter, L.T.B. 2014. Failure of research to address the rangewide conservation needs of large carnivores: Leopards in South Africa as a case study. *Conservation Letters*. 7(1):3–11.

Balmford, A., Green, J.M.H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M. & Manica, A. 2015. Walk on the Wild Side: Estimating the Global Magnitude of Visits to Protected Areas. *PLoS Biology*. 13(2).

Berger, J., Buuveibaatar, B. & Mishra, C. 2013. Globalization of the Cashmere Market and the Decline of Large Mammals in Central Asia. *Conservation Biology*. 27(4):679–689.

Bingham, H., Fitzsimons, J.A., Redford, K.H., Mitchell, B.A., Bezaury-Creel, J. & Cumming, T.L. 2017. Privately protected areas: Advances and challenges in guidance, policy and documentation. *Parks*. 23(1):14–28.

Blake, S., Deem, S.L., Strindberg, S., Maisels, F., Momont, L., Isia, I.-B., Douglas-Hamilton, I., Karesh, W.B., et al. 2008. Roadless Wilderness Area Determines Forest Elephant Movements in the Congo Basin. *PLoS ONE*. 3(10):e3546-.

Borchers, D.L. & Efford, M.G. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*. 64(2):377–385.

Bouyer, Y., San Martin, G., Poncin, P., Beudels-Jamar, R.C., Odden, J. & Linnell, J.D.C. 2015. Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biological Conservation*. 191:291–299.

Brooks, C., Bonyongo, C. & Harris, S. 2008. Effects of Global Positioning System Collar Weight on Zebra Behavior and Location Error. *Journal of Wildlife Management*. 72(2):527–534.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*. 65(1):23–35.

Carbone, C. & Gittleman, J.L. 2002. A common rule for the scaling of carnivore density. *Science*. 295(5563):2273–2276.

Carey, J. 2016. Are we in the “Anthropocene”? *Proceedings of the National Academy of Sciences*. 113(15):3908–3909.

Carroll, C. & Ray, J.C. 2021. Maximizing the effectiveness of national commitments to protected area expansion for conserving biodiversity and ecosystem carbon under climate change. *Global Change Biology*. 27(15):3395–3414.

Carter, N., Jasny, M., Gurung, B. & Liu, J. 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation*. 3:149–162.

Center for International Earth *Science* Information Network - CIESIN - Columbia University. 2018.

Chidakel, A., Eb, C. & Child, B. 2020. The comparative financial and economic performance of protected areas in the Greater Kruger National Park, South Africa: functional diversity and resilience in the socio-economics of a landscape-scale reserve network. *Journal of Sustainable Tourism*. 28(8):1100–1119.

City of Cape Town Municipality. 2020. 2020 Socio-economic Profile. Cape Town.

Coetzee, B.W.T., Gaston, K.J. & Chown, S.L. 2014. Local Scale Comparisons of Biodiversity as a Test for Global Protected Area Ecological Performance: A Meta-Analysis. *PLoS ONE*. 9(8):e105824.

Convention on Biological Diversity. 2022. Report of the Open-Ended Working Group on the Post-2020 Global Biodiversity Framework on its Third Meeting (Part II). Geneva: United Nations Environmental Programme.

Corlett, R.T. 2015. The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*. 30(1):36–41.

Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. 2003. A conservation plan for a global biodiversity hotspot - The Cape Floristic Region, South Africa. *Biological Conservation*. 112(1–2):191–216.

Crall, J.P., Stewart, C.V., Berger-Wolf, T.Y., Rubenstein, D.I. & Sundaresan, S.R. 2013. HotSpotter - Patterned Species Instance Recognition. *Proceedings of IEEE Workshop on Applications of Computer Vision*. 230-237.

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C. & Boitani, L. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 366(1578):2642–2651.

Crutzen, P.J. 2006. The "Anthropocene". In Earth System Science in the Anthropocene. E. Ehlers & T. Krafft, Eds. Berlin, Heidelberg: Springer Berlin Heidelberg. 13–18.

Cullinane, T.C. & Koontz, L. 2016. 2015 National Park visitor spending effects: economic contributions to local communities, states, and the nation. Fort Collins, CO: National Park Service.

Dalerum, F., Somers, M.J., Kunkel, K.E. & Cameron, E.Z. 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation*. 17(12):2939–2949.

Darimont, C.T., Fox, C.H., Bryan, H.M. & Reimchen, T.E. 2015. The unique ecology of human predators. *Science*. 349(6250):858–860.

Davis, A.J., Keiter, D.A., Kierepka, E.M., Slootmaker, C., Piaggio, A.J., Beasley, J.C. & Pepin, K.M. 2020. A comparison of cost and quality of three methods for estimating density for wild pig (*Sus scrofa*). *Scientific reports*. 10(1):1–14.

Department of Statistics South Africa. 2022. Accounts for Protected Areas report, 1990 to 2020: some key findings. Retrieved from stats sa: https://www.statssa.gov.za/?page_id=1856&PPN=D0401.2&SCH=73001.

Devens, C., Tshabalala, T., McManus, J. & Smuts, B. 2018. Counting the spots: The use of a spatially explicit capture–recapture technique and GPS data to estimate leopard

(*Panthera pardus*) density in the Eastern and Western Cape, South Africa. *African Journal of Ecology*. 56(4):850–859.

Devens, C.H., Hayward, M.W., Tshabalala, T., Dickman, A., McManus, J.S., Smuts, B. & Somers, M.J. 2021. Estimating leopard density across the highly modified human-dominated landscape of the Western Cape, South Africa. *Oryx*. 55(1):34–45.

Dickman, A.J. & Marker, L.L. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research*. 35(2):105–115.

Dickman, A., Marchini, S. & Manfredo, M. 2013. The human dimension in addressing conflict with large carnivores. *Key Topics in Conservation Biology*. John Wiley and Sons. 2(1):110–126.

Dickman, A.J., Macdonald, E.A. & Macdonald, D.W. 2011. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. *Proceedings of the National Academy of Sciences*. 108(34):13937–13944.

Digun-Aweto, O., van der Merwe, P. & Saayman, M. 2022. Tolerance factors in human-wildlife conflicts in protected areas: the case of Cross River National Park, Cross River State Nigeria. *GeoJournal*. 87(1):349–361.

Di Minin, E., Slotow, R., Hunter, L.T.B., Montesino Pouzols, F., Toivonen, T., Verburg, P.H., Leader-Williams, N., Petracca, L., et al. 2016. Global priorities for national carnivore conservation under land use change. *Scientific reports*. 6:e23814.

Drescher, M. & Brenner, J.C. 2018. The practice and promise of private land conservation. *Ecology and Society*. 23(2).

Drouilly, M., Nattrass, N. & O'Riain, M.J. 2018. Dietary niche relationships among predators on farmland and a protected area. The *Journal of Wildlife Management*. 82(3):507–518.

Drouilly, M., Nattrass, N. & O'Riain, M.J. 2021. Beauty or beast? Farmers' dualistic views and the influence of aesthetic appreciation on tolerance towards black-backed jackal and caracal. *PLoS ONE*. 16(3).

Dupont, P., Milleret, C., Gimenez, O. & Bischof, R. 2019. Population closure and the bias-precision trade-off in spatial capture–recapture. *Methods in Ecology and Evolution*. 10(5):661–672.

Dutta, T., Sharma, S., Maldonado, J.E., Wood, T.C., Panwar, H.S. & Seidensticker, J. 2013. Fine-scale population genetic structure in a wide-ranging carnivore, the leopard (*Panthera pardus fusca*) in central India. *Diversity and Distributions*. 19(7):760–771.

Efford, M. 2004. Density estimation in live-trapping studies. *Oikos*. 106(3):598–610.

Efford, M.G. & Mowat, G. 2014. Compensatory heterogeneity in spatially explicit capture–recapture data. *Ecology*. 95(5):1341–1348.

Efford, M.G., Borchers, D.L. & Byrom, A.E. 2009. Density Estimation by Spatially Explicit Capture–Recapture: Likelihood-Based Methods. In *Modeling Demographic Processes In Marked Populations*. Springer US. 255–269.

Efford, M. 2022. secr: Spatially explicit capture-recapture models. Available: https://CRAN.R-project.org/package=secr [2022, February 01].

Epps, C.W., Wehausen, J.D., Bleich, V.C., Torres, S.G. & Brashares, J.S. 2007. Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology*. 44(4):714–724.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., et al. 2011. Trophic Downgrading of Planet Earth. *Science*. 333(6040):301–306.

Fattebert, J., Balme, G.A., Robinson, H.S., Dickerson, T., Slotow, R. & Hunter, L.T.B. 2016. Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology*. 299(3):153–162.

Faure, J.P.B., Swanepoel, L.H., Cilliers, D., Venter, J.A. & Hill, R.A. 2021. Estimates of carnivore densities in a human-dominated agricultural matrix in South Africa. *Oryx*. 56(5):774–781.

Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., Bufka, L. & Heurich, M. 2017. Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. *Ecology and Evolution*. 7(16):6367–6381.

Forero-Medina, G., Vieira, M.V., de Viveiros Grelle, C.E. & Almeida, P.J. 2009. Body size and extinction risk in Brazilian carnivores. *Biota Neotrop*. 9(2):45–49.

Frame, L.H. 1991. The wild dog – Africa's vanishing carnivore. *Oryx*. 25(3):137–146.

Funston, P.J., Groom, R.J. & Lindsey, P.A. 2013. Insights into the Management of Large Carnivores for Profitable Wildlife-Based Land Uses in African Savannas. *PLoS ONE*. 8(3):1–8.

Gallo, J.A., Pasquini, L., Reyers, B. & Cowling, R.M. 2009. The role of private conservation areas in biodiversity representation and target achievement within the Little Karoo region, South Africa. *Biological Conservation*. 142(2):446–454.

Gannon, C.S. & Steinberg, N.C. 2021. A global assessment of wildfire potential under climate change utilizing Keetch-Byram drought index and land cover classifications. *Environmental Research Communications*. 3(3):035002.

Gaston, K.J., Jackson, S.F., Cantú-Salazar, L. & Cruz-Piñón, G. 2008. The ecological performance of protected areas. *Annual Review of Ecology, Evolution, and Systematics*. 39:93–113.

Gavashelishvili, A. & Lukarevskiy, V. 2008. Modelling the habitat requirements of leopard *Panthera pardus* in west and central Asia. *Journal of Applied Ecology*. 45(2):579–588.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M. & Burgess, N.D. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation*. 161:230–238.

Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., et al. 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications*. 7(1):12306.

Grey, J.N.C., Kent, V.T. & Hill, R.A. 2013. Evidence of a high density Population of harvested leopards in a montane environment. *PLoS ONE*. 8(12).

Gubbi, S., Sharma, K. & Kumara, V. 2020. Every hill has its leopard: Patterns of space use by leopards (*Panthera pardus*) in a mixed use landscape in India. *PeerJ*. 8:e10072.

Hansen, A.J. & DeFries, R. 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications*. 17(4):974–988.

Harries, P. 1993. Imagery, Symbolism and Tradition in a South African Bantustan: Mangosuthu Buthelezi, Inkatha, and Zulu History. *History and Theory*. 32(4):105–125.

Hatten, J.R., Averill-Murray, A. & van Pelt, W.E. 2005. A Spatial Model of Potential Jaguar Habitat in Arizona. *Journal of Wildlife Management*. 69(3):1024–1033.

Havmøller, R.W., Tenan, S., Scharff, N. & Rovero, F. 2019. Reserve size and anthropogenic disturbance affect the density of an African leopard (*Panthera pardus*) meta-population. *PLoS ONE*. 14(6).

Hayward, M.W., Somers, M.J., Kerley, G.I.H., Perrin, M.R., Bester, M.N., Dalerum, F., Do, E., San, L., Hoffman, L.C., Marshal J.P.. 2012. Animal Ethics and Ecotourism editorial. *South African Journal of Wildlife Research*. 42(2):iii–v.

Hemson, G., Maclennan, S., Mills, G., Johnson, P. & Macdonald, D. 2009. Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. *Biological Conservation*. 142(11):2718–2725.

Henschel, P., Hunter, L.T.B., Coad, L., Abernethy, K.A. & Mühlenberg, M. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology*. 285(1):11–20.

Herrera, D.J., Moore, S.M., Herrmann, V., McShea, W.J. & Cove, M. 2021. A shot in the dark: White and infrared led flash camera traps yield similar detection probabilities for common urban mammal species. *Hystrix*. 32(1).

Hoeks, S., Huijbregts, M.A.J., Busana, M., Harfoot, M.B.J., Svenning, J.C. & Santini, L. 2020. Mechanistic insights into the role of large carnivores for ecosystem structure and functioning. *Ecography*. 43(12):1752–1763.

Hoffman, T.S. & O'Riain, M.J. 2012. Landscape requirements of a primate population in a human-dominated environment. *Frontiers in Zoology*. 9(1):1–17.

Hussain, A., Mahmood, T., Akrim, F., Andleeb, S., Fatima, H., Hamid, A. & Waseem, M. 2019. Depleting wild prey compels common leopard (*Panthera pardus*) to sustain on livestock. *Animal Biology*. 69(2):213–230.

Inskip, C., Carter, N., Riley, S., Roberts, T. & MacMillan, D. 2016. Toward human-carnivore coexistence: understanding tolerance for tigers in Bangladesh. *PLoS ONE*. 11(1):e0145913.

IUCN, UNEP-WCMC. 2022. The World Database on Protected Areas (WDPA). Cambridge, United Kingdom. Retrieved from Protected Planet.

Jachowski, D.S., Butler, A., Eng, R.Y.Y., Gigliotti, L., Harris, S. & Williams, A. 2020. Identifying mesopredator release in multi-predator systems: a review of evidence from North America. *Mammal Review*. 50(4):367–381.

Janečka, J.E., Munkhtsog, B., Jackson, R.M., Naranbaatar, G., Mallon, D.P. & Murphy, W.J. 2011. Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. *Journal of Mammalogy*. 92(4):771–783.

Jones, M.W., Abatzoglou, J.T., Veraverbeke, S., Andela, N., Lasslop, G., Forkel, M., Smith, A.J.P., Burton, C., et al. (in press). Global and Regional Trends and Drivers of Fire Under Climate Change. *Reviews of Geophysics*. 60(3).

Jordan, N.R., Smith, B.P., Appleby, R.G., van Eeden, L.M. & Webster, H.S. 2020. Addressing inequality and intolerance in human–wildlife coexistence. *Conservation Biology*. 34(4):803–810.

Karanth, K.U. 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. *Biological Conservation*. 71(3):333–338.

Karanth, K.U. & Chellam, R. 2009. Carnivore conservation at the crossroads. *Oryx*. 43(1):1–2.

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D. & Franklin, S.E. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*. 21:393–404.

Klausmeyer, K.R. & Shaw, M.R. 2009. Climate Change, Habitat Loss, Protected Areas and the Climate Adaptation Potential of Species in Mediterranean Ecosystems Worldwide. *PLoS ONE*. 4(7).

Knopff, A.A., Knopff, K.H., Boyce, M.S. & St. Clair, C.C. 2014. Flexible habitat selection by cougars in response to anthropogenic development. *Biological Conservation*. 178:136–145.

Koziarski, A., Kissui, B. & Kiffner, C. 2016. Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. *Biological Conservation*. 199:41–50.

Kshettry, A., Vaidyanathan, S. & Athreya, V. 2017. Leopard in a tea-cup: A study of leopard habitat-use and human-leopard interactions in north-eastern India. *PLoS ONE*. 12(5).

Kshettry, A., Vaidyanathan, S., Sukumar, R. & Athreya, V. 2020. Looking beyond protected areas: Identifying conservation compatible landscapes in agro-forest mosaics in north-eastern India. *Global Ecology and Conservation*. 22:e00905.

Kumalo, S. & Mujinga, M. 2017. “Now we know that the enemy is from within”: Shembeites and the Struggle for Control of Isaiah Shembe’s Legacy and the Church. *Journal for the Study of Religion*. 30:122–153.

Lamichhane, B.R., Lamichhane, S., Regmi, R., Dhungana, M., Thapa, S.K., Prasai, A., Gurung, A., Bhattarai, S., et al. 2021. Leopard (*Panthera pardus*) occupancy in the Chure range of Nepal. *Ecology and Evolution*. 11(20):13641–13660.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., et al. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature*. 489(7415):290–293.

Lehikoinen, P., Tiusanen, M., Santangeli, A., Rajasärkkä, A., Jaatinen, K., Valkama, J., Virkkala, R. & Lehikoinen, A. 2021. Increasing protected area coverage mitigates climate-driven community changes. *Biological Conservation*. 253:e108892.

Leighton, G.R.M., Bishop, J.M., Merondun, J., Winterton, D.J., O’Riain, M.J. & Serieys, L.E.K. 2021. Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. *Animal Conservation*. 25:244–258.

Letnic, M., Greenville, A., Denny, E., Dickman, C.R., Tischler, M., Gordon, C. & Koch, F. 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography*. 20(2):343–353.

Lindsey, P.A., Havemann, C.P., Lines, R., Palazy, L., Price, A.E., Retief, T.A., Rhebergen, T. & van der Waal, C. 2013. Determinants of Persistence and Tolerance of Carnivores on Namibian Ranches: Implications for Conservation on Southern African Private Lands. *PLoS ONE*. 8(1).

Löe, J. & Röskaft, E. 2004. Large carnivores and human safety: a review. *Ambio*. 33(6):283–288.

Lunstrum, E., Givá, N., Massé, F., Mate, F. & Jose, P.L. 2021. The rhino horn trade and radical inequality as environmental conflict. *The Journal of Peasant Studies*. 1–21.

Ma, T., Hu, Y., Russo, I.-R.M., Nie, Y., Yang, T., Xiong, L., Ma, S., Meng, T., et al. 2018. Walking in a heterogeneous landscape: Dispersal, gene flow and conservation implications for the giant panda in the Qinling Mountains. *Evolutionary Applications*. 11(10):1859–1872.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature*. 301(5899):379–384.

MacKinnon, K. 1997. The ecological foundations of biodiversity protection. In Last stand: Protected areas and the defense of tropical biodiversity. R. Kramer, C. van Schaik, & J. Johnson, Eds. Oxford: Oxford University Press. 47–63.

Manlik, O., McDonald, J.A., Mann, J., Raudino, H.C., Bejder, L., Krützen, M., Connor, R.C., Heithaus, M.R., et al. 2016. The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecology and Evolution*. 6(11):3496–3512.

Mann, G., Pitman, R., Whittington-Jones, G., Thomas, L., Broadfield, J., Taylor, J., Rogan, M. & Balme, G. 2017. *South African leopard monitoring project.* Annual report on monitoring activities in 2017.

Mann, G.K.H., Wilkinson, A., Hayward, J., Drouilly, M., O'Riain, M.J. & Parker, D.M. 2019. The effects of aridity on land use, biodiversity and dietary breadth in leopards. *Mammalian Biology*. 98:43–51.

Mann, G.K.H., O'Riain, M.J. & Parker, D.M. 2020. A leopard's favourite spots: Habitat preference and population density of leopards in a semi-arid biodiversity hotspot. *Journal of Arid Environments*. 181:e104218.

Martins, Q.E. 2010. The ecology of the leopard *Panthera pardus* in the Cederberg Mountains. Doctoral Thesis. The University of Bristol.

Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. 2011. Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis. *Journal of Zoology*. 283(2):81–87.

McDonald, D.J., Midgley, G.F. and Powrie, L., 2019. Scenarios of plant diversity in South African mountain ranges in relation to climate change. *In Mountain Biodiversity*. 261-266. Routledge.

McManus, J., Marshal, J.P., Keith, M., Tshabalala, T., Smuts, B. & Treves, A. 2021. Factors predicting habitat use by leopards in human-altered landscapes. *Journal of Mammalogy*. 102(6):1473–1483.

McManus, J., Schurch, M.P.E., Goets, S., Faraut, L., Couldridge, V. & Smuts, B. 2022. Delineating Functional Corridors Linking Leopard Habitat in the Eastern and Western Cape, South Africa. *Conservation*. 2(1):99–122.

Mech, S.G. & Hallett, J.G. 2001. Evaluating the Effectiveness of Corridors: a Genetic Approach. *Conservation Biology*. 15(2):467–474.

Mondal, K., Bhattacharjee, S., Gupta, S., Sankar, K. & Qureshi, Q. 2013. Home range and resource selection of “problem” leopards trans-located to forested habitat. *Current Science*. 105(3):338–345.

Monterroso, P., Rich, L.N., Serronha, A., Ferreras, P. & Alves, P.C. 2014. Efficiency of hair snares and camera traps to survey mesocarnivore populations. *European Journal of Wildlife Research*. 60(2):279–289.

Müller, L., Briers-Louw, W.D., Seele, B.C., Stefanus Lochner, C. & Amin, R. 2022. Population size, density, and ranging behaviour in a key leopard population in the Western Cape, South Africa. *PLoS ONE*. 17(5):e0254507.

NASA Shuttle Radar Topography Mission (SRTM). 2013. Shuttle Radar Topography Mission (SRTM) Global. Distributed by RCMRD GeoPortal. Accessed: 2022-05-26.

Naderi, M., Farashi, A. & Erdi, M.A. 2018. Persian leopard’s (*Panthera pardus saxicolor*) unnatural mortality factors analysis in Iran. *PLoS ONE*. 13(4):e0195387.

National Park Service. 2022. About Us - Visitation Numbers. Retrieved from National Park Service: https://www.nps.gov/aboutus/visitation-numbers.htm.

Naude, V.N. 2020. Scale and impact of the illegal leopard skin trade for traditional use in southern Africa. Doctoral Thesis. University of Cape Town.

Naude, V.N., Balme, G.A., O’Riain, J., Hunter, L.T.B., Fattebert, J., Dickerson, T. & Bishop, J.M. 2020. Unsustainable anthropogenic mortality disrupts natal dispersal and promotes inbreeding in leopards. *Ecology and Evolution*. 10(8):3605–3619.

Newmark, W.D. 2008. Isolation of African protected areas. *Frontiers in Ecology and the Environment*. 6(6):321–328.

Noga, S., Kolawole, O., Thakadu, O.T. & Masunga, G. 2018. ‘Wildlife officials only care about animals’: Farmers’ perceptions of a Ministry-based extension delivery system in mitigating human-wildlife conflicts in the Okavango Delta, Botswana. *Journal of Rural Studies*. 61:216–266.

Overberg District Municipality. 2022. Welcome to Overberg District Municipality. Retrieved from Overberg District Municipality: https://odm.org.za/.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. 2009. The rise of the mesopredator. Bio*Science*. 59(9):779–791.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 267(1456):1947–1952.

Quigley, H.B. & Crawshaw, P.G. 1992. A conservation plan for the jaguar Panthera onca in the Pantanal region of Brazil. *Biological Conservation*. 61(3):149–157.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramesh, T., Kalle, R., Rosenlund, H. & Downs, C.T. 2017. Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecology and Evolution*. 7(6):1964–1973.

Riley, M., Soutyrina, S., Miquelle, D., Hayward, G., Goodrich, J. & Buskirk, S. 2017. Comparison of methods for estimating Amur tiger abundance. *Wildlife Biology*. 2017(1):1–9.

Ripple, W.J. & Beschta, R.L. 2012. Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research*. 58(4):733–742.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., et al. 2014. Status and ecological effects of the world's largest carnivores. *Science*. 343(6167).

Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. & McDonald, R.A. 2012. Ecosystem restoration with teeth: What role for predators? *Trends in Ecology and Evolution*. 27(5):265–271.

Rogan, M. 2021. The application of spatial capture-recapture models to investigate leopard ecology and conservation in South Africa. Doctoral Thesis. University of Cape Town.

Rogan, M.S., Distiller, G., Balme, G.A., Pitman, R.T., Mann, G.K.H., Dubay, S.M., Whittington-Jones, G.M., Thomas, L.H., et al. 2022. Troubled spots: Human impacts constrain the density of an apex predator inside protected areas. *Ecological Applications*.

Royle, J. A., Chandler, R.B., Sollmann, R., & Gardner, B. 2013. *Spatial Capture-Recapture*. 1st edition. Academic Press, Boston.

Rozylowicz, L., Popescu, V.D., Pătroescu, M. & Chişamera, G. 2011. The potential of large carnivores as conservation surrogates in the Romanian Carpathians. *Biodiversity and Conservation*. 20(3):561–579.

Schwartz, M.K., Copeland, J.P., Anderson, N.J., Squires, J.R., Inman, R.M., McKelvey, K.S., Pilgrim, K.L., Waits, L.P., et al. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology*. 90(11):3222–3232.

Searle, C.E., Smit, J., Strampelli, P., Mkuburo, L., Ikanda, D., Macdonald, D.W., Loveridge, A.J. & Dickman, A.J. 2021. Leopard population density varies across habitats and management strategies in a mixed-use Tanzanian landscape. *Biological Conservation*. 257.

Selinske, M.J., Coetzee, J., Purnell, K. & Knight, A.T. 2015. Understanding the Motivations, Satisfaction, and Retention of Landowners in Private Land Conservation Programs. *Conservation Letters*. 8(4):282–289.

Silveira, L., Jácomo, A.T.A. & Diniz-Filho, J.A.F. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. *Biological Conservation*. 114(3):351–355.

Silveira, L., Sollmann, R., Jácomo, A.T.A., Diniz Filho, J.A.F. & Tôrres, N.M. 2014. The potential for large-scale wildlife corridors between protected areas in Brazil using the jaguar as a model species. *Landscape Ecology*. 29(7):1213–1223.

Sinergise Laboratory for geographical information systems, Ltd. 2022. EO Browser. Ljubljana, Slovenia. Retrieved from Sentinel-Hub: https://apps.sentinel-hub.com/eo-browser/?zoom=10&lat=41.9&lng=12.5&themeId=DEFAULT-THEME&toTime=2022-07-21T07%3A24%3A41.516Z.

Skowno, A.L., Raimondo, D.C., Poole, C.J., Fizzoti, B. & Slingsby, J. 2019. South African National Biodiversity Assessment 2018 Technical Report Volume 1: Terrestrial Realm. South African National Biodiversity Institute. Cape Town.

Skupien, G.M., Andrews, K.M. & Larson, L.R. 2016. Teaching Tolerance? Effects of Conservation Education Programs on Wildlife Acceptance Capacity for the American Alligator. *Human Dimensions of Wildlife*. 21(3):264–279.

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y. & Wilmers, C.C. 2017. Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences*. 284(1857).

Smyth, L.S., Rogan, M.S., Balme, G.A., O’Riain M.J. In review. Counting Spots: Drivers of Leopard Density in The Kruger-Limpopo Ecostytem in South Africa. *Biological Conservation*.

Snider, M.H., Athreya, V.R., Balme, G.A., Bidner, L.R., Farhadinia, M.S., Fattebert, J., Gompper, M.E., Gubbi, S., et al. 2021. Home range variation in leopards living across the human density gradient. *Journal of Mammalogy*. 102(4):1138–1148.

Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M. & Silveira, L. 2011. Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation*. 144(3):1017–1024.

Sollmann, R., Tôrres, N.M., Furtado, M.M., de Almeida Jácomo, A.T., Palomares, F., Roques, S. & Silveira, L. 2013. Combining camera-trapping and noninvasive genetic data in a spatial capture–recapture framework improves density estimates for the jaguar. *Biological Conservation*. 167:242–247.

Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Egli, L., Jafari, A., Ahmadpour, M., et al. 2019. Assessing the relationship between illegal hunting of ungulates, wild prey occurrence and livestock depredation rate by large carnivores. *Journal of Applied Ecology*. 56(2):365–374.

South African Department: forestry, fisheries & the environment. 2020. SA National Land-Cover Dataset. Pretoria, South Africa.

Spenceley, A., Snyman, S. & Rylance, A. 2019. Revenue sharing from tourism in terrestrial African protected areas. *Journal of Sustainable Tourism*. 27(6):720–734.

Srbek-Araujo, A.C. & Chiarello, A.G. 2005. Is camera-trapping an efficient method for surveying mammals in Neotropical forests? A case study in south-eastern Brazil. *Journal of Tropical Ecology*. 21(1):121–125.

Stats SA. 2020. Statistical Release: Mid-year population estimates. Pretoria.

Stein, A.B., Fuller, T.K., Destefano, S. & Marker, L.L. 2011. Leopard population and home range estimates in north-central Namibia. *African Journal of Ecology*. 49(3):383–387.

Stolton, S. & Dudley, N. (Eds.). 2014. Partnerships for protection: new strategies for planning and management for protected areas. Routledge.

Stolton, S., Redford, K.H. & Dudley, N. 2014. The Futures of Privately Protected Areas. Gland, Switzerland. IUCN.

Strampelli, P., Henschel, P., Searle, C.E., Macdonald, D.W. & Dickman, A.J. 2022. Habitat use of and threats to African large carnivores in a mixed-use landscape. *Conservation Biology*.

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. 2016. Fear of large carnivores causes a trophic cascade. *Nature Communications*. 7(1):1–7.

Suraci, J.P., Clinchy, M., Zanette, L.Y. & Wilmers, C.C. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*. 22(10):1578–1586.

Suraci, J.P., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M. & Wilmers, C.C. 2019. Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology*. 100(4).

Swanepoel, L.H., Lindsey, P., Somers, M.J., van Hoven, W. & Dalerum, F. 2013. Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation*. 16(1):41–50.

Swanepoel, L.H., Somers, M.J., van Hoven, W., Schiess-Meier, M., Owen, C., Snyman, A., Martins, Q., Senekal, C., et al. 2015. Survival rates and causes of mortality of leopards *Panthera pardus* in southern Africa. *Oryx*. 49(4):595–603.

Swanepoel, L.H., Somers, M.J. & Dalerum, F. 2015. Density of leopards *Panthera pardus* on protected and non-protected land in the Waterberg Biosphere, South Africa. *Wildlife Biology*. 21(5):263–268.

Templeton, A.R., Shaw, K., Routman, E. & Davis, S.K. 1990. The Genetic Consequences of Habitat Fragmentation. *Annals of the Missouri Botanical Garden*. 77(1):13–27.

Tensen, L., Roelofs, D. & Swanepoel, L.H. 2014. A note on the population structure of leopards (*Panthera pardus*) in South Africa : short communication. *South African Journal of Wildlife Research*. 44(2):193–197.

Terraube, J., van doninck, J., Helle, P. & Cabeza, M. 2020. Assessing the effectiveness of a national protected area network for carnivore conservation. *Nature Communications*. 11(1).

Thapa, T.B. 2015. Human Caused Mortality in the Leopard (*Panthera pardus*) Population of Nepal. *Journal of Institute of Science and Technology*. 19(1):155–150.

Thapa, K., King, D., Banhalmi-Zakar, Z. & Diedrich, A. 2022. Nature-based tourism in protected areas: a systematic review of socio-economic benefits and costs to local people. *International Journal of Sustainable Development & World Ecology*. 29(7):625–640.

Thatte, P., Chandramouli, A., Tyagi, A., Patel, K., Baro, P., Chhattani, H. & Ramakrishnan, U. 2020. Human footprint differentially impacts genetic connectivity of four wide-ranging mammals in a fragmented landscape. *Diversity and Distributions*. 26(3):299–314.

Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., et al. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation*. 7(2):113–120..

Tian, Y., Wu, J., Smith, A.T., Wang, T., Kou, X. & Ge, J. 2011. Population viability of the Siberian Tiger in a changing landscape: Going, going and gone? *Ecological Modelling*. 222(17):3166–3180.

Tobler, M.W. & Powell, G.V.N. 2013. Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*. 159:109–118.

Tortato, F.R., Izzo, T.J., Hoogesteijn, R. & Peres, C.A. 2017. The numbers of the beast: Valuation of jaguar (Panthera onca) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation*. 11:106–114.

Treves, A. & Naughton-Treves, L. 1999. Risk and opportunity for humans coexisting with large carnivores. *Journal of Human Evolution*. 36(3):275–282.

Treves, A. & Ullas Karanth, K. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*. 17(6):1491–1499.

Van Dyke, F. 2008. The Conservation of Populations: Concept, Theory, and Analysis. *Conservation Biology: Foundations, Concepts, Applications*. 213–242.

Weladji, R.B. & Tchamba, M.N. 2003. Conflict between people and protected areas within the Bénoué Wildlife Conservation Area, North Cameroon. *Oryx*. 37(1):72–79.

Wells, M.P. 1996. The social role of protected areas in the new South Africa. *Environmental Conservation*. 23(4):322–331.

Williams, K.S. 2017. Human-brown hyaena relationships and the role of mountainous environments as refuges in a postcolonial landscape. Doctoral Thesis. Durham University.

Williams, V.L., Loveridge, A.J., Newton, D.J. & Macdonald, D.W. 2017. A roaring trade? The legal trade in Panthera leo bones from Africa to East-Southeast Asia. *PLoS ONE*. 12(10):e0185996-.

Wolf, C. & Ripple, W.J. 2016. Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*. 3(8):e160252.

Wolf, C. & Ripple, W.J. 2017. Range contractions of the world's large carnivores. *Royal Society Open Science*. 4(7).

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*. 3(2):165–173.

Woodroffe, R. & Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science*. 280(5372):2126–2128.

Woodruff, D.S. 2001. Populations, species, and conservation genetics. *Encyclopaedia of biodiversity*. 811–829.

Zemanova, M.A. 2020. Towards more compassionate wildlife research through the 3Rs principles: Moving from invasive to non-invasive methods. *Wildlife Biology*. 2020(1):1–17.

Ziervogel, G., New, M., Archer van Garderen, E., Midgley, G., Taylor, A., Hamann, R., Stuart-Hill, S., Myers, J., et al. 2014. Climate change impacts and adaptation in South Africa. *WIREs Climate Change*. 5:605–620.

6 Appendices

6.1 Appendix A: Reclassified land-use classes across study area

Table A1*: Reclassified land-use classes across study area from the South African National Land Cover 2020 Dataset (South African Department: forestry, fisheries & the environment, 2020). Columns 1-3 represent original columns from the National dataset, Column 4 is the reclassified land uses used in this study.*

Class_Name	SALCC_1	SALCC_2	**Land-use class**
contiguous (indigenous) forest	Forested Land	Natural Wooded Land	**Natural**
contiguous low forest & thicket	Forested land	Natural Wooded Land	
dense forest & woodland	Forested land	Natural Wooded Land	
open woodland	Forested land	Natural Wooded Land	
contiguous & dense plantation forest	Forested land	Planted Forest	**Agricultural**
open & sparse plantation forest	Forested land	Planted Forest	
temporary unplanted (clear-felled) plantation forest	Forested land	Planted Forest	
low shrubland (other)	Shrubland	Shrubs	**Natural**
low shrubland (fynbos)	Shrubland	Karoo & Fynbos Shubland	
sparsely wooded grassland	Grassland	Natural Grassland	
natural grassland	Grassland	Natural Grassland	
natural rivers	Waterbodies	Natural Waterbodies	
natural estuaries & lagoons	Waterbodies	Natural Waterbodies	
natural ocean & coastal	Waterbodies	Natural Waterbodies	
natural pans (flooded @ observation times)	Waterbodies	Natural Waterbodies	
artificial dams (including canals)	Waterbodies	Artificial Waterbodies	**Agricultural**
artificial sewage ponds	Waterbodies	Artificial Waterbodies	**Highly modified**
artificial flooded mine pits	Waterbodies	Artificial Waterbodies	
herbaceous wetlands (currently mapped)	Wetlands	Herbaceous Wetlands	**Natural**
herbaceous wetlands (previously mapped)	Wetlands	Herbaceous Wetlands	
natural rock surfaces	Barren Land	Consolidated	
dry pans	Barren Land	Consolidated	
eroded lands	Barren Land	Unconsolidated	**Agricultural**
coastal sand & dunes	Barren Land	Unconsolidated	**Natural**
bare riverbed material	Barren Land	Unconsolidated	
other bare	Barren Land	Unconsolidated	
cultivated commercial permanent orchards	Cultivated	Permanent Crops	**Agricultural**
cultivated commercial permanent vines	Cultivated	Permanent Crops	
commercial annual crops pivot irrigated	Cultivated	Temporary Crops	
commercial annual crops non-pivot irrigated	Cultivated	Temporary Crops	
commercial annual crops rain-fed / dryland	Cultivated	Temporary Crops	
subsistence / small-scale annual crops	Cultivated	Temporary Crops	
fallow land & old fields (trees)	Cultivated	Fallow Lands & Old Fields	
fallow land & old fields (bush)	Cultivated	Fallow Lands & Old Fields	
fallow land & old fields (grass)	Cultivated	Fallow Lands & Old Fields	

fallow land & old fields (bare)	Cultivated	Fallow Lands & Old Fields	
fallow land & old fields (low shrub)	Cultivated	Fallow Lands & Old Fields	
residential formal (tree)	Built-up	Residential	**Highly modified**
residential formal (bush)	Built-up	Residential	
residential formal (low veg / grass)	Built-up	Residential	
residential formal (bare)	Built-up	Residential	
residential informal (tree)	Built-up	Residential	
residential informal (bush)	Built-up	Residential	
residential informal (low veg / grass)	Built-up	Residential	
residential informal (bare)	Built-up	Residential	
village scattered (bare & low veg/ grass combo)	Built-up	Village	
village dense (bare & low veg / grass combo)	Built-up	Village	
smallholdings (tree)	Built-up	Smallholdings	
smallholdings (bush)	Built-up	Smallholdings	
smallholdings (low veg / grass)	Built-up	Smallholdings	
smallholdings (bare)	Built-up	Smallholdings	
urban recreational fields (tree)	Built-up	Urban Vegetation	
urban recreational fields (bush)	Built-up	Urban Vegetation	
urban recreational fields (grass)	Built-up	Urban Vegetation	
urban recreational fields (bare)	Built-up	Urban Vegetation	
commercial	Built-up	Commercial	
industrial	Built-up	Industrial	
roads & rails (major linear)	Built-up	Transport	
mines: surface infrastructure	Mines & Quarries	Surface Infrastructure	
mines: extraction pits, quarries	Mines & Quarries	Extraction Sites	
mine: tailings and resource dumps	Mines & Quarries	Waste & Resource Dumps	
land-fills	Mines & Quarries	Waste & Resource Dumps	
fallow land & old fields (wetlands)	Cultivated	Fallow Lands & Old Fields	**Agricultural**

6.2 Appendix B: Vegetation Types within the study area

***Table B1**: Vegetation types present within the study area and the number of camera trap stations present on each vegetation type. The percentage of sites with leopards captured is the total number of camera stations within a vegetation type and how many of them captured leopards (Skowno et al., 2019).*

Vegetation Type	Threat Status	Number of Camera traps on vegetation type	Percentage of sites with leopards captured(%)
Agulhas Limestone Fynbos	Critically endangered	15	60
Agulhas Sand Fynbos	Critically endangered	3	0
Cape Seashore Vegetation	Least concern	0	
Central Ruens Shale Renosterveld	Critically endangered	1	0
De Hoop Limestone Fynbos	Least concern	10	50
Eastern Ruens Shale Renosterveld	Endangered	0	
Elim Ferricrete Fynbos	Endangered	9	67
Greyton Shale Fynbos	Near threatened	0	
Hangklip Sand Fynbos	Critically endangered	0	
Kogelberg Sandstone Fynbos	Critically endangered	0	
Overberg Dune Strandveld	Endangered	8	25
Overberg Sandstone Fynbos	Least concern	38	68
Ruens Silcrete Renosterveld	Endangered	0	
Southern Afrotemperate Forest	Least concern	0	
Southern Coastal Forest	Least concern	0	
Western Coastal Shale Band Vegetation	Least concern	2	100
Western Ruens Shale Renosterveld	Critically endangered	0	