Implications of camera trap survey design and analytical methods for large carnivores estimates

By

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Declaration

I, Tristan Daniel Baird (17010854), declare that the thesis/dissertation, which I hereby submit for the degree, Master of Science in Wildlife Management at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution. The thesis consists of four chapters written in the format of the Journal of Applied Ecology, two of which are compiled as if submitted to the Journal. Therefore, repetition between chapters was unavoidable.

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Signed by: Tristan Baird

DATE: 17/12/2021

Summary

Globally, carnivores face countless threats; and in some cases, these threats are worsened by a lack of population data. In South Africa, conservation has become largely confined to small, fenced, protected areas. It is well established that large carnivores play a vital role in ecosystems, providing valuable ecosystem services, i.e., herbivore regulation and meso-carnivore suppression. If populations are not adequately managed within these small, fenced protected areas, carnivores will place significant pressure on their favoured prey species, and in extreme cases, cause certain species to become locally extinct. For this reason, it is essential for conservation and wildlife managers to understand and monitor large carnivore populations, dynamics and the roles they play within the ecosystems.

Estimating population sizes, abundances and densities for species that are difficult to identify (hereafter, unidentifiable), is difficult under conventional capture-recapture methods, leading to a sparse number of estimates on unidentifiable species. The implementation of camera trap methods has been developed and more readily implemented to bridge this knowledge gap, some of which were implemented in this study. Here, I estimated the population sizes of two species, leopard (*Panthera pardus*) and brown hyaena (*Parahyaena brunnea*), using camera trap count data from three camera trap projects, analyzed using the package ‘Unmarked’ in R-Studio. Camera trap data was supplied by three previously existing camera trap projects, i.e., Snapshot Safari South Africa, Panthera Organization, and a private baited and non-baited camera trap project. Data supplied were collected across three study sites, namely Madikwe Game Reserve, Pilanesberg National Park, and Atherstone Nature Reserve. The objective of this study was to determine the effect of three camera-trap deployment techniques on space use and density estimates of two large carnivores in Madikwe Game Reserve, Pilanesberg National Park and Atherstone Nature Reserve using unmarked analysis.

In this study, I investigated the use of N-mixture models to estimate population sizes of leopard and brown hyaena and how different camera trap deployments influence the N-mixture model population size estimates. I compared N-mixture model population size estimates to pre-existing Bayesian closed-population capture-recapture estimates. Furthermore, this study aimed to provide empirical evidence supporting the use of N-mixture models to estimate the population sizes of both naturally marked and unidentifiable species.

This study found that N-mixture models run using data from the sequential baited and non-baited camera trap deployment array and the roadside cluster deployment over-estimated leopard and brown hyaena population sizes across all the study sites. The regular deployment array provided plausible estimates across all three of the fenced protected areas and were closely matched to previous population size estimates.

The two targeted approaches, sequential baited and non-baited deployment, and roadside cluster deployment, were more efficient in collecting data. The targeted approaches recorded higher capture numbers and species detection probabilities. The evidence from this research cautions against the use of N-mixture models to conduct population analysis using camera traps due to the model sensitivity, seeing the models are reliant on detection probability and capture numbers.

Keywords: Population size estimation, camera trapping, count data, unmarked species, Bayesian analyses, non-invasive sampling.

Dissertation layout

This study aims to contribute to understanding how camera trap grid deployment techniques and their corresponding data impact N-mixture models and estimates. This dissertation is presented as four chapters. Chapters 2 and 3 are written as stand-alone manuscripts for publication in peer-reviewed journals. Each chapter nonetheless contributes to the theme of the dissertation. The dissertation is structured as follows:

Chapter 1 – *General Introduction*. This chapter is a general introduction to the history of large carnivore population analysis and management, the importance of demographic data and a review of current and new methods used to determine population size.

Chapter 2 - *Counting the (un)marked mammals: A case study for leopard and brown hyaena in Madikwe Game Reserve.* This chapter describes the use of N-mixture models to estimate the population sizes of brown hyaena and leopard in Madikwe Game Reserve. It further describes the influence of different camera trap deployment arrays have on N-mixture models and their estimates.

Chapter 3 - *Comparison of population size and space use analyses of two carnivore species in two protected areas in north-western South Africa.* This chapter provides the first leopard and brown hyaena population size estimates on Pilanesberg National Park and Atherstone Nature Reserve.

Chapter 4 – *Synthesis.* This chapter describes the key research findings of chapters 2 and 3, and provides management implications, recommendations, and future research.

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Chapter 1

General Introduction

Introduction

Globally, the monitoring of wildlife populations has never been more important, considering the earth's changing climate, landscapes and landcover types (Hooper et al. 2012). One of the biggest challenges in conservation and ecology today is understanding and reversing the global decline of the large carnivore species (Ripple et al. 2014, Rich et al. 2017). This decline is a result of prey depletion, disease, habitat and land degradation, climate change, illegal trading of body parts and commercial meat markets (Aziz et al. 2013). Important managerial decisions are made and based off scientific research data. Scientific research data on many large carnivore populations are deficient, and this impacts our ability to make good decisions and implement policies for change (Rich et al. 2017, Steenweg et al. 2017). The pressures faced by large carnivores are further enhanced by habitat degradation and range-land contraction. Large carnivores such as the red wolf (*Canis rufus*) have lost greater than 99% of their rangelands, Ethiopian wolves (*Canis simensis*) have lost ~99% of their rangelands, tigers (*Panthera tigris*) and lions (*Panthera leo*) have lost upwards of ~94% of their historical rangelands (Wolf and Ripple 2017). These dramatic range losses coupled with an ever-increasing human population disturbance will lead to large scale multi-species extinctions worldwide. Active population monitoring and conserving critical regions of large carnivore ranges will play a vital role in the survival of these carnivore species (Wolf and Ripple 2017).

Habitat loss brings with it a multitude of challenges. It brings animals into conflict with humans and depletes prey resources resulting in fragmented populations being confined to protected areas (Weber and Rabinowitz 1996, Hayward et al. 2009, Wolf and Ripple 2017). However, animals within protected areas still face threats. One of the biggest threats facing protected areas surrounded by rural communities is poaching. Poaching takes place commonly in the form of active hunting and snaring (Thorn et al. 2012). For these reasons, monitoring within both protected and non-protected areas is needed. A lack of population data is a threat to many large carnivore species (Meiri et al. 2009, Rich et al. 2017), and impacts policy and management decisions (Meiri et al. 2009). These decisions that influence the way we manage areas and populations as well as how we run operations such as animal translocations. However, various methods for data acquisition are becoming available, which are allowing the development of more accurate, robust techniques that aid in answering previously unanswered questions in a non-invasive manner (Schipper et al. 2008, Ripple et al. 2014, Rich et al. 2017).

The earth's rapidly changing climate, landscape, landcover and the need to know how the earth's ecosystems and species are responding to these changing dynamics, has resulted in a 'Big Data' revolution in ecology (Farley et al. 2018). Camera trapping has advanced wildlife ecology and has been widely incorporated into ecological studies as a non-invasive research tool (Frey et al. 2017). Methods involving the photographic capturing of animals without the researcher being present have been around for decades (Kucera and Barrett 1993), with wildlife camera trapping becoming increasingly popular since the 1990s (Kucera and Barrett 1993). Camera traps are now considered a standard method for monitoring many wildlife populations over large areas of land (Kays et al. 2020). Camera trapping provides insight into species' distributions and occupancies, activity patterns and species population densities (Tobler et al. 2008, Steenweg et al. 2017). Data collected by camera traps provide a unique opportunity to answer previously unanswered scientific questions, allowing research into spatial and temporal patterns in a non-invasive manner (Turner 2014, Swanson et al. 2016).

Camera traps in conservation

There are many ways to categorize camera traps. The major difference between the several types of camera traps is how they record their images (Cutler and Swann 1999). Camera traps can have triggering or non-triggering systems (Cutler and Swann 1999). Camera traps with non-triggering systems either record images continuously or at periodic intervals (Kelly 2008, Swann et al. 2011). Camera traps with triggering systems remain inactive until an event triggers the camera trap; this is usually an animal's arrival (Kelly 2008, Swann et al. 2011, Meek and Pittet 2012). Triggers are usually an infrared light beam but can be mechanical, such as a pressure plate (Swann et al. 2011). Light-triggered camera traps can be set to be passive or active (Swann et al. 2014). Active light-triggered camera traps emit an infrared beam using a transmitter and receiver, the camera trap records an image every time the beam is broken (Swann et al. 2014). The more common, passively set camera traps use two sensors to monitor background temperatures; the camera trap is triggered by both the motion and temperature change of an animal walking in front of the camera trap (Swann et al. 2014). Triggered camera traps are favoured in situations where the target is more likely to be captured infrequently or discontinuously. Triggered camera traps use less power, making them more applicable in remote areas (Swann et al. 2011). However, there are numerous factors which influence a camera traps performance (Nichols and Karanth 2011). These broadly range from climatic conditions and stochastic events such as fire and flooding, to environmental conditions and the behaviour of the study species (Nichols and Karanth 2011, Swann et al. 2011). The likelihood of remote-sensing camera trap malfunction or underperformance increases with longer periods of deployment (Nichols and Karanth 2011). When only serviced periodically, months of data may be lost (Nichols and Karanth 2011).

Triggered camera traps are also known to have false triggers i.e., taking multiple photographs with no animals being captured (Jumeau et al. 2017). Additionally, camera traps have differing sensitivities, detection zones and operational functionalities (Swann et al. 2014). Many of these issues may be avoided by selecting camera trap models suited to the deployment conditions and the data requirements for the study (Swann et al. 2011). It is, however, still expensive and time consuming to run camera trap projects over extended periods of time (Swann et al. 2011). Weather, user experience and skill, field conditions such as damage by animals, and low-quality equipment are common causes for deficient performance (Swann et al. 2011). Camera traps also vary in terms of their sensitivities, detection zones and performance in different climatic conditions (Swann et al. 2004). Many of these factors can be alleviated, however, others such as weather are out of a researcher's control. This highlights the importance of knowing the potential problems of selected equipment and selecting equipment and camera traps suitable for the chosen application.

Camera trap analyses

The development of camera trap technology has allowed the collection of several types of data. These data types provided opportunities and methods to analyze broad ecological concepts and processes on spatial and temporal scales (Morant et al. 2020). Long term monitoring projects provide valuable information on the magnitude and direction temporal trends are heading (Wintle et al. 2010, Morant et al. 2020). Furthermore, these camera trap projects provide information on space use through gathering detection and non-detection data, essential for species management (MacKenzie et al. 2017). With these data, the relationship between environmental conditions and species occurrence can be studied (MacKenzie et al. 2006). Many essential fields of conservation biology rely on spatial and temporal data (MacKenzie et al. 2006). With these data, the relationship between environmental conditions and species occurrence can be studied (MacKenzie et al. 2006). Temporal data are valuable as we can analyze niche partitioning, conditional differentiation, co-existence, and guild structures (Schoener 1974, Di Bitetti et al. 2010, Monterroso et al. 2014, Frey et al. 2017). Furthermore, temporal data allows analyses into proximate environmental drivers and anthropogenic factors that could impact guild dynamics and facilitative and competitive interactions (Pereira et al. 2013, Wang et al. 2015, Frey et al. 2017). It is important to model these variables as these variables also cumulatively influence the activity patterns of species, which leads to niche partitioning and structuring communities (Brown and Wilson 1956, Frey et al. 2017).

By analyzing camera-trap datasets and evaluating the results of camera-trap survey designs across multiple locations and study species, recommendations can be made on the study design and deployment grid structure before projects are initiated (Meek et al. 2014, Kays et al. 2020). The methodology behind a camera-trap study is important. Specific deployment techniques may be more appropriate for estimating abundances, whereas other deployments may be more appropriate for estimating occupancies, temporal overlaps, and abundances (Rovero et al. 2013, Meek et al. 2015). Deployment grids, the number of cameras and the durations the camera-traps are deployed for can affect the results generated, and the data can, therefore, be misinterpreted (Kays et al. 2020). The different deployment requirements for camera traps are dependent on what they are being used for. Remote detection of rare species requires a rugged, reliable, robust camera trap that will last several weeks of deployment whilst constantly taking photographs of its target (Nichols and Karanth 2011). The deployment conditions and target species determine the camera trap model to be used (Swann et al. 2011). Whether that be researching nest ecology of rare bird species in a tropical forest where humidity is high, or whether researching habitat use by multiple herbivore species in snowy, wet conditions (Swann et al. 2011).

Commonly, identifying individual animals is a major component of camera trap research (Foster and Harmsen 2012). The successful implementation of camera traps has also been seen in mark-resight methods used when the number of marked individuals is either known or unknown, and only part of the target population is uniquely identifiable (Matthews et al. 2008, McClintock et al. 2009, Foster and Harmsen 2012). The use of individual identification in studies has been both reliable (e.g., Kelly et al. 2008) and less reliable in many different studies (e.g., Meek et al. 2013, Alexander and Gese 2018, van Hespen et al. 2019). The development of spatially explicit mark-recapture (SECR) and spatial capture-recapture (SCR) analyses have provided viable methods in estimating species' abundances using camera trap data (Royle et al. 2009). SECR is a collection of methodologies used for modelling capture-recapture data collected by various "detectors", such as passive and live camera traps. In SECR, spatial detection histories are fitted with spatial models of the target population and detection process. The estimated population densities are unbiased, not influenced by edge effects and incomplete detections (Efford 2015). Although SECR, which uses Bayesian closed-population capture-recapture methods to estimate species population sizes and abundances, is currently recognized as the most efficient and successful method for estimating identifiable animal species (Alexander 2016). Green et al. (2020), recorded significant bias in species preference with studies that used SECR methods for data analysis. A big focus of the studies researched was on large felid species, specifically rare and identifiable species, and associated population densities for these study species (Green et al. 2020). Green et al. (2020) recorded ~90.9% of SECR studies reviewed were focused on carnivore species, of which 82% were studies on felids with unique markings. However, valuable camera trap data on other wildlife species is often not analyzed due to those species being individually unidentifiable (hereafter unmarked, Gubbi et al. 2019). Estimating population sizes, abundances, and densities for unmarked species is currently difficult under conventional capture-recapture methods (Green et al. 2020). There are many globally significant unmarked species that have not been extensively researched. These species could provide robust evidence for, and new insights into, species interrelatedness (Karanth et al. 2004, Carbone et al. 2010), trophic interactions (Owen-Smith and Mills 2008), guild structures, species interactions (Karanth et al. 2017) and disease (Ramsey et al. 2015). Such information is essential for conservation and management of threatened species (Campbell et al. 2002).

Varying forms of species analyses have been developed to estimate population sizes of unmarked individuals (Denes et al. 2015). However, few studies have compared unmarked population size estimates to SECR estimates and investigated how study design influences the results of these analyses (Allen et al. 2020). Some studies utilize presence-absence data and model detection processes to estimate detection probabilities of unmarked animals per camera station, compensating for the lack of identifiable animals (Rowcliffe et al. 2008, Fiske and Chandler 2011). New methods that record presence–absence data over multiple survey occasions (Royle–Nichols Abundance Induced Heterogeneity model, Royle and Nichols 2003), or the species abundance over multiple surveys, without marking individuals have been proposed to estimate population size (Royle Repeated Count model, Royle 2004). These methods use dedicated statistical software packages (i.e., 'Unmarked;' Fiske and Chandler 2011) based on Bayesian framework modelling, which account for detection probabilities and thus estimate space use/population sizes. Often, detection probability is neglected, which leads to potential type II errors (MacKenzie et al. 2017). These multivariable analyses now allow researchers to research concepts such as temporal and spatial exclusion, competitive exclusion, habitat preference, temporal activity periods and spatial occupancies of both identifiable and unmarked species (Wang et al. 2015, Frey et al. 2017, Steenweg et al. 2017). Niche differentiation and temporal and spatial exclusion are common between carnivore species (Droge et al. 2017, Karanth et al. 2017). Exclusions lead to differences in peak activity periods and influence community structures and resource partitioning within the guild, with these mechanisms promoting stable co-existence between species (Broekhuis et al. 2013, Vanak et al. 2013, Droge et al. 2017, Karanth et al. 2017). Understanding these mechanisms that promote the co-existence of sympatric carnivores is essential for the conservation and management of these carnivores and their ecological communities (Sergio et al. 2014, Friedemann et al. 2016, Davis et al. 2018).

Species' population data are essential in understanding animal ecology and vital for researchers and wildlife managers (Andrewartha and Birch 1954). Population size estimates allow researchers and wildlife managers to monitor wildlife populations and the populations' response to variations in climate, landscape change and other species' (Moeller 2017). Inter-species interactions and relationships are also quantified using abundance and spatio-temporal space use estimations (Swanson et al. 2016, Moeller 2017). Researchers and managers utilize this information to implement management plans and protocols which aim to accurately monitor the species and ensure the continued success and conservation of the target species (Williams et al. 2002). Camera traps have become a popular method used to estimate population sizes, abundances, and spatio-temporal occupancies non-invasively and effective method in capturing rare and elusive species (Nichols and Karanth 2011, Rovero et al. 2013, Meek et al. 2014, Gilbert et al. 2020, Kays et al. 2020). However, data collected from camera trap studies are often used to estimate abundances and densities of cryptic species and naturally marked animals (Foster and Harmsen 2012, Burton et al. 2015, Gubbi et al. 2019). Valuable camera trap data on individually unidentifiable wildlife species is often not analysed (Gubbi et al. 2019). Obtaining demographic data on and monitoring elusive unidentifiable species remains challenging due to their cryptic natures (Pitman et al. 2017). Collecting demographic data can be expensive (Morin et al. 2018). However, with the development of new camera trapping technology and knowledge, it is now possible to generate the demographic data needed for the population analysis of species harder to identify, such as lions. These methods are not commonly used, and this provided the motivation for this study.

Study Rational

As habitat and range loss continues, species are under threat of becoming extinct. Data on many large carnivore populations are deficient, and this impacts our ability to make good decisions and implement conservation programs. Population sizes are important data needed to make these decisions. Overestimation or underestimation of species population sizes can significantly impact the conservation and management of the species. It is important to gain insight into species populations within small, protected areas to understand the effects carnivores have on the ecosystem they exist in. Carnivores have significant effects on community and guild structures within fenced protected areas. Large carnivore species that occur at high densities could potentially cause local extinctions of their prey species and severely impact smaller meso-carnivore species spatio-temporal space use patterns. These situations often occur as a result of uninformed management influenced by a lack of predator and prey population data.

Camera trap population studies commonly involve unique identification of individual animals. The successful implementation of camera traps has also been seen in mark-resight methods used when the number of marked individuals is either known or unknown, and only part of the target population is uniquely identifiable. Estimating population sizes, abundances, and densities for unidentifiable species is difficult under conventional capture-recapture methods.

South Africa has many short and long-term camera trap monitoring programs (e.g. Panthera 2021, Pardo et al. 2021). The Panthera organization has multiple camera trap monitoring programs across the globe (Panthera 2021). Panthera runs surveys annually, prioritizing leopard monitoring amongst other species in South Africa (Rogan et al. 2019). The Snapshot Safari South Africa project contributs to a national biodiversity project (Pardo et al. 2021). There are also many species-specific studies conducted over short periods of time (e.g. Bracskowski et al. 2016). Reserves such as Pilanesberg National Park, North West province, and Atherstone Nature Reserve, Limpopo province, have been research sites where both Panthera and Snapshot Safari deployment arrays have been active for some time. In this study, I investigated the use of N-mixture models to estimate population sizes of leopard (*Panthera pardus*) and brown hyaena (*Parahyaena brunnea*). Previous leopard and brown hyaena population sizes were estimated using Bayesian closed-population capture-recapture analysis, which relies on individual identification. This provided an opportunity to investigate the use of N-mixture models to estimate population sizes whilst using previous estimates as a benchmark. The N-mixture models do allow population size estimation for camera trap data whilst considering these two naturally marked species as unidentifiable. The focus of N-mixture models is to view population sizes that are site-specific, as independent random variables that are distributed according to a certain mixing distribution, such as a Poisson distribution. Prior parameters are estimated from marginal likelihood of the input data, having integrated over the prior distribution for the site-specific population sizes. This enables the estimation of a species' population size for a certain study area. Therefore, using these n-mixture models potentially provides evidence in support of using N-mixture models to analyze and estimate populations of unidentifiable species. Hence, I aimed to compare N-mixture model population size estimates to pre-existing Bayesian closed-population capture-recapture estimates. Furthermore, this study aimed to provide empirical evidence supporting the use of N-mixture models to estimate the population sizes of both naturally marked and unidentifiable species.

Aims and objectives

This study aimed to determine how camera trap grid deployment techniques, and their corresponding data, impact carnivore activity measures and N-mixture model abundance estimates.

General objective

To provide empirical evidence supporting the use of N-mixture models to estimate the population sizes of both naturally marked and unidentifiable species.

Specific objective 1

To determine how three different camera trap deployment techniques influence population size estimates of two large carnivores in Madikwe Game Reserve using N-mixture models.

Specific objective 2

To estimate population sizes and investigate spatial occupancies of brown hyaena and leopard in Pilanesberg National Park and Atherstone Nature Reserve.

Specific objective 3

To investigate the influence a targeted roadside cluster deployment and regular deployment array have on N-mixture model population size estimates in Pilanesberg National Park and Atherstone Nature Reserve.

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Chapter 2

Counting the (un)marked mammals: A case study for leopard and brown hyaena in Madikwe Game Reserve

Abstract

Motion sensing camera traps have become a common tool for estimating species population sizes and abundances and conduct spatio-temporal space use analyses. Estimating population sizes, abundances and densities for unidentifiable species have been difficult using conventional capture-recapture methods, leading to little research on unmarked species. I estimated the population sizes of two species, leopard (*Panthera pardus*) and brown hyaena (*Parahyaena brunnea*), using camera trap count data from three camera trap projects deployed in Madikwe Game Reserve, analyzed using N-mixture models in the package 'Unmarked' in R-Studio. N-mixture model analysis allows researchers to estimate population sizes of species without the need for individual identification. Before this study, Bayesian closed-population capture-recapture was used to estimate the population size of the same species in the same study site. I benchmarked estimates for comparison between N-mixture model estimates and Bayesian estimates. The Bayesian estimates were used as benchmark estimates because these methods are well developed and established with scientific backing (leopards = 24 ± 1.17, brown hyaenas = 92 ± 7.13). Results varied per camera trap deployment array. The regular Snapshot deployment array (36.85, C.I. 14-97) and the roadside Panthera cluster deployment array (19.40, C.I. 12-59) leopard estimates were reasonably close to those of the Bayesian closed population capture-recapture. Brown hyaena population sizes estimated from the regular Snapshot deployment array were close to benchmark estimates (87.20, C.I. 53-163); however, the roadside Panthera cluster deployment population size estimation was an overestimate (167.69, C.I. 105-259). More research is needed to determine why there were overestimations of brown hyaena population sizes. This research will aid in developing and implementing conservation and management plans for elusive unidentifiable species whose population sizes are largely unknown.

Keywords: Population size estimation, camera trapping, count data, unmarked species, Bayesian analyses, non-invasive sampling.

Introduction

Population size estimates are essential to ecology and are important for the conservation management of wildlife (Andrewartha and Birch 1954). Continuous assessments and monitoring of population sizes assist with determining responses to changes in habitat types and structures, climatic conditions, and other species (Dirzo et al. 2014). Wildlife managers use population size and abundance estimates to prioritize and implement specific protocols that will have large impacts on a target species (Campbell et al. 2002).

Recently, motion sensor cameras, termed camera traps, have become a widely used tool used to collect distinct types of ecologically relevant information, such as population sizes, species distributions and richness (Champion 1992, Griffiths and Van Schaik 1993, Garshelis et al. 1999, Wearn and Glover-Kapfer 2019, Carvaggi et al. 2020). These information types are commonly used to estimate abundances and densities of cryptic species and naturally marked animals (Foster and Harmsen 2012, Burton et al. 2015, Gubbi et al. 2019). However, valuable camera trap data on other wild mammal species is often not analyzed due to those species being individually unidentifiable (hereafter called unmarked, Gubbi et al. 2019). Estimating population sizes, abundances and densities for unmarked species is not possible under conventional capture-recapture methods (Green et al. 2020). Many globally significant unmarked species have, therefore, not been researched. These species could provide robust evidence for, and new insights into, species interrelatedness (Karanth et al. 2004, Carbone et al. 2010), trophic interactions (Owen-Smith and Mills 2008), guild structures, species interactions (Karanth et al. 2017) and diseases (Ramsey et al. 2015). Such information is essential for conserving and managing threatened and endangered species (Campbell et al. 2002).

Traditional capture-recapture and newly developed spatially explicit capture-recapture methods that involve individual identification of animals do not estimate population sizes or abundances of unmarked species (Green et al. 2020). Trapping rates are commonly used to estimate relative abundances (Carbone et al. 2001). However, trapping rates do not account for imperfect detection, limiting their use. Chandler and Royle (2013), indicated that individual identification of a species is not necessary for estimating population sizes and densities. They used species specific spatially replicated count data from multiple sample sites to estimate densities and abundances of unmarked species. This model is considered an extension of existing spatial capture-recapture models (Ramsey et al. 2015). The binomial data used by current capture-recapture methods is replaced by count data (Chandler and Royle 2013). This is useful as researchers can now utilize unmarked species data collected through camera traps and conduct population analyses (Chandler and Royle 2013). These analyses can be performed using statistical software packages (e.g., ‘UNMARKED’; Fiske and Chandler

2011). These packages account for imperfect detection using complex modelling (i.e., Bayesian framework), allowing for population and space use analysis modelling (MacKenzie et al. 2017). Furthermore, conducting multiple surveys (i.e., repeated counts) also helps account for imperfect detection probabilities, which improves the performance of statistical models. Multiple surveys are also necessary for assessing presences or absences of a species and species abundances (Royle and Nichols 2003, Royle 2004, Fiske and Chandler 2011, MacKenzie et al. 2017).

This study investigated the use of count data to estimate the population sizes of leopard and brown hyaena in Madikwe Game Reserve. I aimed to investigate unmarked population size estimates by comparing them to pre-existing Bayesian closed-population capture-recapture estimates (Honiball 2021). Furthermore, this study aimed to provide empirical evidence supporting the use of N-mixture models to estimate species population sizes. Spatially replicated count data were provided by three different camera trap deployments, namely a regular deployment array (Snapshot Safari, Pardo et al. 2021), a baited and non-baited sequential deployment (Honiball 2021), and a roadside cluster deployment (Panthera, Panthera 2021). Both the roadside cluster and baited/non-baited sequential deployments were predicted to overestimate the population sizes of the target species as these deployments are targeted. The regular deployment array was predicted to match the previous Bayesian estimates due to this deployment being non-targeted.

Methods and materials

Study area

Madikwe Game Reserve (hereafter Madikwe) is approximately 75 000 ha in size and is one of the largest game reserves in South Africa (Figure 2.1). Madikwe borders Botswana in the North West province (-24.750602, 26.277229; Figure 2.1). Vegetation types on the reserve vary between turf thornveld, Kalahari bushveld, mixed bushveld, and arid sweet bushveld (Mucina and Rutherford 2006). It is in an area transitioning between Lowveld bushveld and arid Kalahari thornveld (Hudak and Wessman 2001). The vegetation structure varies from woodlands to open grassland plains and rocky outcrops (Hudak and Wessman 2001). The reserve is enclosed by ~150 km of electrified fencing. There are ~66 large mammal species located within Madikwe (Cox 2020). Madikwe's wet season extends from October to April, with average temperatures ranging between 28^{o}C to 32^{o}C and an average rainfall of 70.1 mm (Joint Research Centre of the European Commission 2021). During the dry season, from May to September, the average rainfall averages 8 mm, with temperatures between 25^{o}C to 28^{o}C (Cox 2020). From Bayesian closed-population capture-recapture analysis, Honiball et al. (2021) estimated that there are 82 (s.d. = 3.96) spotted hyaenas *(Crocuta crocuta)*, 92 (s.d. = 7.13) brown hyaenas and 24 (s.d. = 1.17) leopards on Madikwe. There are 33 lions *(Panthera leo)* on Madikwe (July 2020 estimate; North West Parks and Tourism Board, unpublished data).

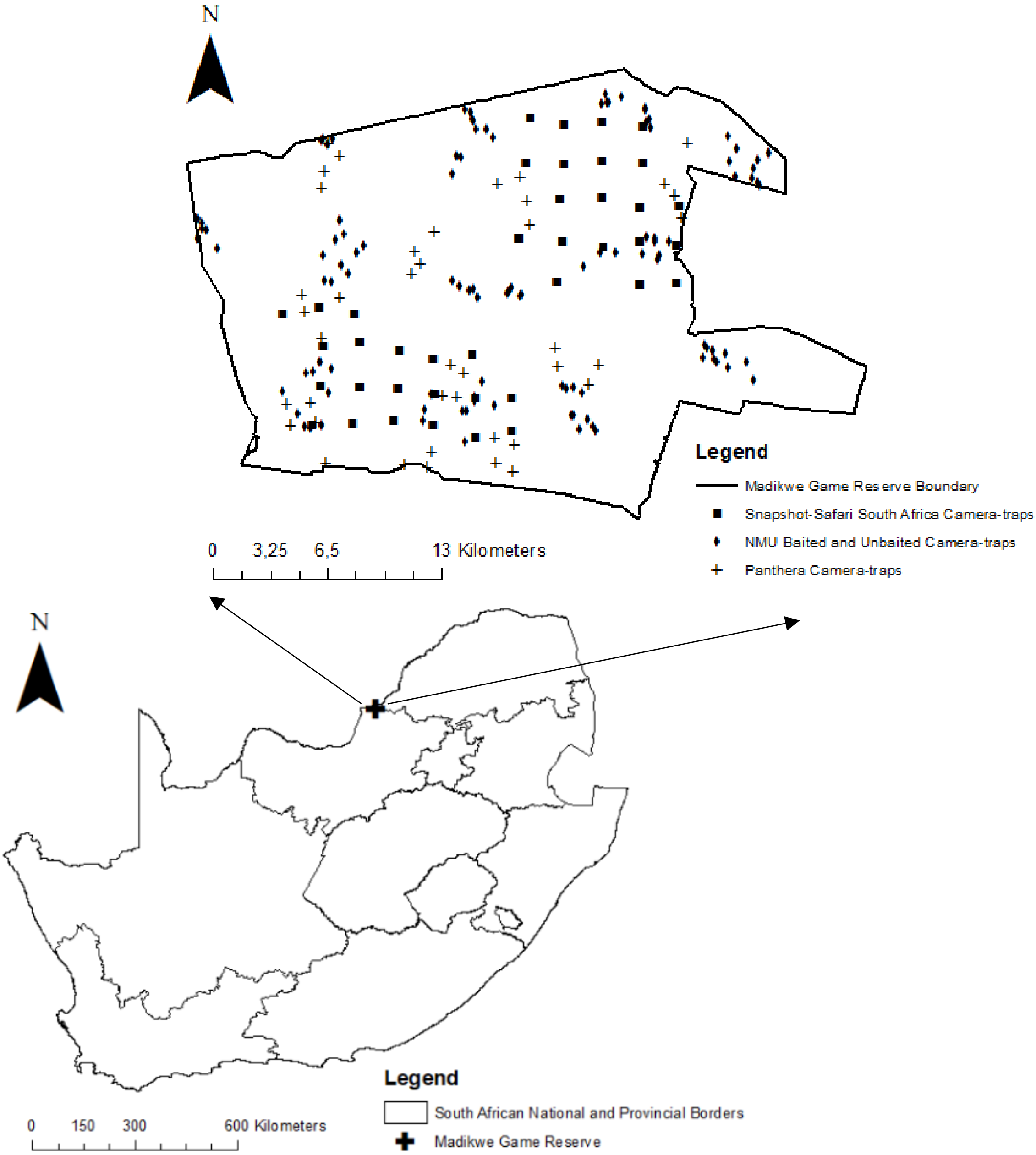

Figure 2.1. Three different camera trap deployments (n=140) located within Madikwe Game Reserve, North West province, South Africa

Data Collection

Leopard and brown hyaena population sizes were estimated using three different pre-existing iterations of camera trap deployment techniques. Camera trap data provided by Snapshot Safari – South Africa (hereafter regular deployment array), Panthera (hereafter roadside cluster deployment) and Nelson Mandela University (hereafter baited and non-baited sequential deployment) was analyzed (Figure 2.1, Honiball 2021, Pardo et al. 2021). Snapshot Safari – South Africa and Panthera are ongoing, long term, well-established projects. All data provided were gathered prior to this study. I had no role in the data collection process due to the Covid-19 pandemic prohibiting my own data collection.

Regular Deployment Array

Forty camera traps (Cuddeback model C1279, Non-Typical Inc., Park Falls, USA) were deployed in a 5 km^2 regular grid array (Figure 2.1). Every camera trap was placed approximately 50 cm above the ground, facing the nearest game trail (Cusack et al. 2015, Swanson et al. 2015, Pardo et al. 2021). The grass surrounding every camera trap was trimmed to less than 30 cm when a camera trap was placed or serviced to reduce the number of misfires and reduce the risk of fire (Swanson et al. 2015). Camera traps were serviced every 4 to 6 weeks. The data extracted from Snapshot's cameras for this research were from 1 January 2019 to 5 November 2019, recording 12 360 camera trap nights, resulting in a total of 63 sampling occasions.

Roadside Cluster Deployment

The Panthera project team (Panthera, 2021) placed unbaited camera traps (Pantheracams camera traps) in a cluster grid design across Madikwe from 11 October 2019 to 02 December 2019, which recorded a total of 2120 camera trap nights, resulting in 11 sampling occasions. Each cluster consisted of four stations, each of which comprised two camera traps per station (Figure 2.1). Clusters were between 3 km and 8 km apart. Stations were separated by 1 km. The cameras use xenon flash cameras with built-in infrared motion sensors. All cameras captured one image per trigger event (Miller et al. 2018). Cameras were situated primarily along roads and road junctions (Miller et al. 2018). Cameras were attached to trees or steel poles and placed about 30-40 cm above the ground. There were 40 stations with a total of 80 camera traps deployed (Figure 2.1, Pitman et al. 2017, Rogan et al. 2019).

Baited and Non-Baited Sequential Deployment

The Nelson Mandela University unbaited, and baited camera trap project (Honiball 2021) involved dividing Madikwe into 12 blocks (each 64 km^2) to cover the smallest possible home range size of a leopard (Figure 2.1, see Honiball 2021). The 12 blocks were sequentially surveyed for 21 days from 26 August 2019 to 06 May 2020, recording a total of 2673 camera trap nights, resulting in 51 sampling occasions. Within each block, 10 camera stations consisting of two camera traps were placed, a total of 20 camera traps were used. Of the ten stations, five were baited, and five were unbaited (Figure 2.1). Baited sites were selected based on suitable tree presence preferred by leopards (predominantly

Boscia spp) and signs of leopard activity (i.e., scat, tracks, territorial markings). Madikwe's reserve management provided meat that was used as lures. Ten kilograms of bait was used per baited site. Bait was fixed to trees at a minimum height of 3 m above the ground. Bait was not replaced once removed, which avoided the animals becoming habituated to the site (see Mills et al. 2019). Infrared camera traps (Cuddeback model C1309, Non-Typical Inc., Park Falls, USA) were placed 2 m from the base on either side of the tree, with at least one camera trap facing the most likely access point for a carnivore, such as leopard, to access the lure (Honiball 2021).

Data analyses

I investigated the three deployments, resulting in population size estimates and their 97.5% Bayesian confidence intervals (B.C.I). The best performing deployment was assumed to have the smallest Bayesian confidence intervals (see Della Rocca et al. 2020). To determine the influence of different camera trap grid deployments on unmarked population size estimates, leopard and brown hyaena data were collected and extracted from three different camera trap studies on Madikwe from January 2019 to April 2020. The data were analyzed using N-mixture models (Royle 2004). Bayesian closed-population capture-recapture estimates for the two species' population sizes (leopards = 24 ± 1.17, brown hyaenas = 92 ± 7.13) were used as benchmark estimates (Honiball 2021).

Raw, unidentified camera trap data from the regular deployment array were identified using the software Wild.ID (Version 1.0.1, Tropical Ecology Assessment and Monitoring Network, 2021). Raw camera trap data were identified, classified into species, and counted. Records were exported as an excel file and combined with existing data to construct datasets for analysis. Furthermore, processed data from the regular deployment array, the roadside cluster deployment and the baited and non-baited sequential deployment were additionally provided by Snapshot Safari (Pardo et al. 2021), the Panthera project team (Panthera 2021) and Nelson Mandela University (Honiball 2021). All camera stations were pooled into three datasets, one per deployment array type. Specific covariates were used to account for the variation in camera trap deployment methods. For example, "baited or non-baited" was included as a covariate to account for variation between baited and non-baited camera traps for the Nelson Mandela University sequential baited and non-baited project. To ensure capture independence, photos taken of the same species within a 60-minute time frame were considered a single capture event which was reported to be independent (Yasuda 2004). A 60-minute time frame was used because data received had been previously filtered into 60-minute time frames.

Leopard and brown hyaena data were converted to count data, the number of independent captures in the allocated 5-day sample occasions were assigned to each camera. Camera traps with no detections for a sampling occasion were assigned a "0". For example, if three independent leopard captures were recorded within one of the 5-day sample occasions, a "3" was recorded. By doing this, a species-specific repeated count record was made using detection histories formatted for the same time intervals used in the Bayesian closed-population capture-recapture analysis (Honiball 2021).

Seven covariates that were considered ecologically relevant to the species were considered habitat type (n = 16; Mixed *Acacia* and *Combretum* veld, *Combretum apiculatum* with *Vitex* and *Tarchonatus*, *Combretum apiculatum* broadleaf mountainveld, Mixed *Vachelia* and *Senegalia* Woodland, *Senegalia erubescens*, *Senegalia mellifera* with *Boscia foetida*, *Senegalia erubescens* with *Combretum*, Old lands with *Vachelia tortillis* and *Vachelia gerrardii*, *Terminalia sericea* veld, *Combretum imberbe* woodland, *Vachelia tortillis* and *Vachelia gerrardii* on vleis, *Sclerocarya caffra* and *Senegalia erubescens* veld, Mixed *Vachelia* (*tortillis* and *nilotica*) and *Ziziphus mucronate*, *Senegalia mellifora* on red sand, *Dichrostachys* shrubland, *Senegalia erubescens infestede* with *Dichrostachys cinerea*, Page and Slotow 2001) , elevation (m), baited or unbaited cameras, distance to nearest tarred or dirt road (m), distance to boundary (m), distance to infrastructure (m; lodges, warehouses, camps, gates, bomas, staff accommodations, sub-stations, houses, center and conference rooms, pumps, water towers), and distance to water (m). These covariates were then checked for multicollinearity using the '*Olsrr*' package (Hebbali 2020). All seven covariates were retained, all recorded variance inflation factors were <4. All covariates were mapped and calculated using ArcMap (Version 10.8.1.14362, ESRI, 2021) and Google Earth Pro (Version 7.3.4.8248, Google Earth, 2021).

The "*p-count*" function in the '*Unmarked*' package (Fiske and Chandler 2011) was used in R-program (R Core Team 2021, 4.11, www.rstudio.com, accessed 25 February 2021) using R-studio (R Core Team 2021, Version 1.2.1717, www.rstudio.com, accessed 25 February 2021) to run N-mixture models (RRC). Both single and multi-covariate models were run for each camera trap project. The '*Ranef*' function in the '*Unmarked*' package was used to estimate population sizes along with their confidence intervals, using the empirical Bayes methods. Using the formatted repeated count data, N-mixture models (RRC – Royle Repeated Count models) were run and selected according to which model records the lowest information criterion corrected (AICc) value.

Results

Deployment arrays recorded similar numbers of species-specific independent captures despite different levels of sampling effort (Table 2.1).

Table 2.1. The number of independent captures recorded per species by each deployment array in Madikwe Game Reserve.

Deployment	Camera Trap Stations	Leopard Captures	Brown Hyaena Captures
Regular Snapshot	20	24	145
Roadside Panthera	80	21	320
Baited and non-baited	120	57	164

The regular deployment camera trap data estimated a leopard population size of 36.86 (97.5% B.C.I. 16 – 95) individuals (Table 2.2). The population size estimates from the three camera trap deployments varied. The best ranking model for the regular deployment array data to estimate the leopard population size on Madikwe was a single covariate model (Table 2.3). This modelled distance to the nearest water source as a site level space use covariate. The best ranking model used to estimate the brown hyaena population size was a pair-wise combination of site level space use covariates, habitat type and distance to nearest infrastructure (Table 2.3). The regular deployment camera trap data generated a brown hyaena population estimate of 87.20 (97.5% B.C.I. 53 – 163) individuals (Table 2.2).

Table 2.2. The recorded leopard and brown hyaena population sizes per project with 97.5% confidence intervals (CI) according to the best ranking models. LPE = Leopard Population Estimate. BHPE = Brown Hyaena Population Estimate. GoF = Global model goodness of fit (C-hat).

Project	LPE	CI	GoF	BHPE	CI	GoF
Baited/non-baited deployment	186.01	47 – 467	1.80	255.78	113 – 532	1.56
Regular deployment	36.85	14 – 97	1.90	87.20	53 – 163	1.26
Roadside cluster deployment	19.40	12 – 59	1.46	167.69	105 – 259	1.45

Table 2.3. The regular deployment array recorded population sizes with 97.5% confidence intervals (CI) per single covariate model. Additionally, constant space use (--) was modelled as a site space use level covariate. '*' = best ranking models.

Covariates	Leopard Population Estimate	Confidence Intervals	Brown Hyaena Population Estimate	Confidence Intervals
Elevation	28.46	14 – 97	82.12	49 – 154
Habitat	28.00	14 – 91	83.81	50 – 154
Infrastructure	28.36	14 – 91	85.60	51 – 158
Road	28.29	14 – 97	82.25	49 – 154
Water*	36.85	14 – 97	83.29	51 – 157
Boundary	28.26	16 - 96	82.70	50 – 155
--	28.27	14 - 97	82.07	49 - 153

The best ranking model for the roadside cluster deployment was a single covariate model, which modelled constant space use as a site level space use covariate (Table 2.4).

Table 2.4. The roadside cluster deployments recorded population sizes with 97.5% confidence intervals (CI) per single covariate model. Additionally, constant space use (--) was modelled as a site space use level covariate. '*' = best ranking models.

Covariates	Leopard Population Estimate	Confidence Intervals	Brown Hyaena Population Estimate	Confidence Intervals
Elevation	19.44	12 – 58	167.63	106 – 258
Habitat	19.37	12 – 56	167.74	105 – 260
Infrastructure	19.37	12 – 59	167.56	106 – 260
Road	19.53	12 – 58	167.91	105 – 260
Water	20.46	12 – 61	169.52	107 – 263
Boundary	19.62	12 – 58	167.71	105 – 258
--*	19.40	12 – 59	167.69	105 – 259

The best ranking model was the same for both species. The roadside cluster camera trap deployment data estimated a population size of 19.40 (97.5% B.C.I. 12 – 59) for leopards and 167.69 (97.5% B.C.I. 105 – 259) for brown hyaenas according to the best ranking model (Table 2.2).

The best ranking model for the baited and non-baited sequential camera trap deployment data was a single covariate model, which modelled bait (Yes/No) as a site level space use covariate (Table 2.5). The best ranking model was the same for both species. The baited and non-baited camera trap data estimated a population size of 186.01 (97.5% B.C.I. 47 – 467) leopards and 255.78 (97.5% B.C.I. 113 – 532) brown hyaenas according to the best ranking model (Table 2.2).

Table 2.5. The baited and non-baited sequential deployment recorded population sizes with 97.5% confidence intervals (CI) per single covariate model. Additionally, constant space use (--) was modelled as a site level covariate. '*' = best ranking models.

Covariates	Leopard Population Estimate	Confidence Intervals	Brown Hyaena Population Estimate	Confidence Intervals
Bait*	186.01	47 - 467	255.78	113 - 532
Elevation	496.53	165 – 942	228.94	111 – 487
Habitat	249.19	48 – 574	261.02	112 – 533
Infrastructure	178.69	47 – 450	228.00	110 – 473
Road	185.45	47 – 466	233.90	110 – 484
Water	327.91	101 – 686	243.87	111 – 501
Boundary	145.94	47 – 391	244.20	110 – 503
--	185.35	47 – 475	228.20	110 – 471

Discussion

In this study, I investigated the use of count data from three sampling methods for estimating the population size of leopard and brown hyaena in Madikwe Game Reserve. These three sampling methods involved different camera trap deployments: Baited and non-baited sequential camera trap deployment (Honiball 2021), roadside cluster deployment (Panthera 2021), and regular deployment array (Pardo et al. 2021). Recently, N-mixture models have been particularly useful in unmarked species conservation and ecology, specifically in population and space use analysis, and have increased in use over time with many model extensions having been developed (Kéry and Royle 2016).

The Madikwe benchmark estimates for the leopard and brown hyaena population sizes were 24 (s.d. = 1.17) and 92 (s.d. = 7.13) individuals (Honiball 2021). The population size estimates reported here in this study for each of the three camera trap projects were influenced by the same ecologically relevant covariates. The baited and non-baited sequential deployment provided the most leopard data out of the three camera trap projects (n = 57 independent captures over 2673 camera trapping nights). However, the baited and non-baited deployment did not yield the most brown hyaena data of the three projects. This may be due to brown hyaena's having a highly variable diet. Brown hyaena have a well recorded scavenging behaviour and wide dietary breadth (Mills and Mills 1978, Ramnanan et al. 2016). The roadside cluster camera trap deployment provided the most brown hyaena data compared to the other camera trap projects (n = 320 independent captures over 2120 camera trap nights). The roadside cluster camera traps were placed primarily along roads and roadways (Miller et al. 2018). It is well documented that large carnivores utilize road networks (Mills 1990, Thorn et al. 2011, Zimmermann et al. 2014, Welch et al. 2016). This provides a possible explanation as to why the roadside cluster camera trap deployment provided the most brown hyaena data of the three camera trap projects.

The regular deployment array did not record the most species-specific independent captures and required more deployment time overall (12 360 camera trapping nights), as non-baited and non-targeted camera traps are often hindered by low capture rates (Joubert et al. 2020). The regular camera trap deployment array and data provided population size estimates close to the benchmark estimates. The regular deployment brown hyaena population size estimate (n = 87.20, 97.5% B.C.I = 53-163, Table 2.3) was closest to the benchmark set by the Bayesian closed-population capture-recapture analysis (n = 92 ± 7.13, Honiball 2021), and recorded the smallest 2.5% and 97.5% confidence intervals. The regular deployment array is a non-targeted approach, which reduces the likelihood of any potential biases associated with targeted approaches such as baited camera traps (Swanson et al. 2015, Pardo et al. 2021). Baited camera traps have been recorded to significantly influence detection probabilities (du Preez et al. 2014, Joubert et al. 2020). This reason along with camera traps being deployed in short 21-day intervals, is likely why the recorded population size estimates from the baited/non-baited deployment are largely overestimated and have large 97.5% confidence intervals (Table 2.3).

The roadside camera trap deployment and data provided the closest leopard population estimate to the benchmark set by the Bayesian closed-population capture-recapture analysis (n = 24 ± 1.17, Honiball 2021). This estimate showed much smaller 97.5% confidence intervals than those obtained from data collected by the other two camera trap deployments (Table 2.3). The recorded global model goodness of fit c-hat values for each population size estimate was the best value recorded per species per camera trap project (Roadside cluster leopard data c-hat = 1.46 and regular deployment array brown hyaena data c-hat = 1.26). In this study, five-day sample occasions were used, matching that used in the Bayesian closed-population capture-recapture analysis. This led to varying goodness of fit c-hat values being recorded (Regular deployment array leopard data c-hat = 1.9). Perhaps, if a different sampling occasion length was used for the regular deployment leopard data, improving the goodness of fit value, an estimate closer to the benchmark estimate could be recorded along with smaller confidence intervals. This highlights how much the N-Mixture count models rely on detection probability as well as how sensitive these models are to changes in detection probability (Denes et al. 2015, Duarte et al. 2018). It is important to test whether any covariates being tested influence the detection probability of the study species and adjust sampling occasion lengths according to recorded goodness of fit values (Duarte et al. 2018).

The difference between the regular camera trap deployment, the roadside cluster and baited/non-baited camera trap deployments is data collection. To generate enough data for unmarked analysis, Snapshot's regular deployment array requires more deployment time as camera traps are not baited or targeted (Swanson et al. 2015, Pardo et al. 2021). The volumes of data generated by the roadside cluster and baited/non-baited camera trap deployments are better suited for SECR analysis, where individual identification is necessary, and where more data are required (Allen et al. 2020). In this study, camera trap setups that used a structured grid obtained estimates closer to the benchmark estimates. Snapshot's deployment strategy seems best suited out of the three analyzed for studying unidentifiable species using unmarked analyses, even though this will require longer deployment times. Further analysis is required to determine whether targeted roadside clustered camera traps significantly influence the detection probability of the study species. N-Mixture models have been used to estimate population sizes of species using different methods for gathering data, such as tree surveys and walked transects (Della Rocca et al. 2020).

Spatially explicit capture-recapture (SECR), which uses Bayesian closed-population capture-recapture methods to estimate species population sizes and abundances, is currently recognized as the most efficient and successful method for estimating identifiable animal species (Alexander 2016). Green et al. (2020), recorded significant bias in species preference with studies having used SECR methods for data analysis. The focus of the studies researched was on large felid species, specifically rare and identifiable species, and associated population densities for these study species (Green et al. 2020). Green et al. (2020) recorded that 90.9% of SECR studies reviewed were focused on carnivore species, of which 82% were studies on felids with unique markings. Although there are potential modifications to be made, there is yet a variation in SECR analysis that accommodates unidentifiable species; researchers still have to identify individuals (Iijima 2020). Similar to SECR methods, spatially explicit mark-resight models can analyze both marked and unmarked species data and estimate the species densities (Kelly et al. 2008, McClintock et al. 2009, 2012). However, a portion of the unmarked species are still required to be marked for this method. This highlights the possibility of SECR methods expanding to include multi-species analyses and unidentifiable species (Green et al. 2020). However, until these expansions are made, unidentifiable species will continue to be difficult target species to research.

This study advances our knowledge of population monitoring of unmarked species. The regular deployment array produced population size estimates closest to the benchmark estimates. The population size estimates are comparable to more traditional approaches (Table 2.2). By analyzing how N-Mixture models perform in estimating the population sizes of identifiable species that are known, progress can be made towards assessing the feasibility of N-Mixture models for estimating the population sizes of unidentifiable species. Gilbert et al. (2020) reviewed unmarked methods and showed that mark-resight methods have not been used consistently to estimate population sizes, abundances, and densities of unidentifiable animal species. Although, this method is promising and becoming more commonly used. Overall, a non-targeted approach appears to produce more accurate population size estimates, although further research is needed to investigate the influence roadside targeted camera trap deployments have on N-mixture model population size estimates.

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Chapter 3

Comparison of population size and space use analyses of two carnivore species in two protected areas in north-western South Africa

Abstract

Worldwide, carnivore populations are decreasing, with some species in danger of extinction. Population size estimations and knowledge of geographical distributions are essential tools for wildlife conservation and management. Estimating population sizes, abundances and densities for individually unidentifiable species are difficult under conventional capture-recapture camera trap methods, leading to little research on unidentifiable species. Spatio-temporal space use analyses are commonly used to research unidentifiable animal species. In this study, I tested and compared two non-invasive camera trap sampling approaches to derive accurate population size estimates by means of N-mixture models in a Bayesian framework in two fenced areas. N-mixture model analysis allows researchers to estimate population sizes of species without the need for individual identification. Snapshot Safari's regular non-targeted deployment and Panthera's roadside cluster deployment arrays. There were clear differences in detection probabilities and capture numbers between the two sampling approaches. The regular deployment array estimated a total of 27.52 (C.I. 12-73) leopard and 70.23 (C.I. 39-127) brown hyaena on Pilanesberg National Park and 8.29 (C.I. 7-28) leopard and 60.83 (C.I. 39-105) brown hyaena on Atherstone Nature Reserve. The roadside cluster deployment array estimated a total of 87.42 (C.I. 42-167) leopard and 258.86 (C.I. 197-343) brown hyaena on Pilanesberg National Park and 128.99 (C.I. 29-274) leopard and 119.66 (C.I. 75-187) brown hyaena on Atherstone Nature Reserve. The roadside cluster deployment provided more independent captures and recorded higher detection probabilities yet overestimated the population sizes of the two target species. Although recording fewer independent species captures and lower detection probabilities, the regular deployment array yielded plausible population size estimates for the two target species. The sensitivity of N-mixture models needs to be considered when designing a sampling method. However, evidence supports N-mixture models being an essential tool for developing and implementing conservation and management plans for wildlife species.

Keywords: Population size estimation, camera trapping, count data, unmarked species, leopard, brown hyaena, non-invasive sampling, N-mixture models.

Introduction

Worldwide, carnivore populations are decreasing, with several species in danger of extinction (Rich et al. 2017, Wolf and Ripple 2017, Samojlik et al. 2018). Carnivores face many threats, including poaching, persecution due to the conflict between humans and carnivores, habitat, and prey loss (Aziz et al. 2013, Wolf and Ripple 2017). Most carnivores have proven difficult to census due to their elusive and cryptic nature (Chutipong et al. 2014, Ripple et al. 2014). For the more visible species such as lions (*Panthera leo*) and cheetah (*Acinonyx jubatus*), attempts have been made to use species count numbers to estimate total population sizes (Bauer et al. 2015, Durant et al. 2017). However, many carnivore species lack robust population estimates at a global and local scales do not exist (e.g., for the jaguar, *Panthera onca*, and the leopard, *Panthera pardus*; Stein et al. 2016, Jędrzejewski et al. 2018). In South Africa, cryptic and elusive species such as leopard and brown hyaena *(Parahyaena brunnea)* are primarily affected due to these species often ranging beyond fenced protected areas (Chapman and Balme 2010, de Blocq 2015, Winterbach et al. 2017). The broad ranging nature of these elusive and cryptic species makes accurately estimating population sizes, densities, and abundances a constant challenge for conservationists (Nichols and Williams 2006). Wildlife managers estimate population sizes to aid in species monitoring and species responses to environmental changes, management actions and climatic changes (Moeller 2017). However, these highly elusive and cryptic carnivores are difficult to detect, making population estimation challenging (Thorn et al. 2009, 2011, Tarugara et al. 2019). These challenges make monitoring these elusive carnivores labor-intensive, costly, and time-consuming (Thorn et al. 2009, 2011). There are many different research methods exist to estimate population sizes of carnivores (Palencia et al. 2020). These methods include track counts (Midlane et al. 2014), road and walked transects (Della Rocca et al. 2020), call-ups (Cozzi et al. 2013) and camera trapping (Efford et al. 2013, Carvaggi et al. 2020, Palencia et al. 2020). Camera traps have become a widely used and non-labor-intensive tool used to collect several types of ecologically relevant information, such as population sizes, species distributions and richness (Champion 1992, Griffiths and Van Schaik 1993, Garshelis et al. 1999, Wearn and Glover-Kapfer 2019, Carvaggi et al. 2020).

Camera trap studies use varying types of grid deployments and approaches to estimate population sizes, abundances and assess spatio-temporal space use patterns (Balme et al.2009, Thorn et al. 2011, Kays et al. 2020). These data are then typically used to estimate abundances and densities of cryptic and rare species and naturally marked animals (Foster and Harmsen 2012, Burton et al. 2015, Gubbi et al. 2019). Valuable camera trap data on individually unidentifiable wildlife species is often not analyzed due to the unavailability of robust analytical methods (Gubbi et al. 2019). A study done by

Chandler and Royle (2013), indicated that individual identification of a species is not necessary for estimating population sizes and densities. These analyses can be conducted using statistical software packages (e.g., 'Unmarked;' Fiske and Chandler 2011) and can be applied to camera trap data collected from various deployment arrays. Methods that record presence–absence data over multiple survey occasions (Royle–Nichols Abundance Induced Heterogeneity model, Royle and Nichols 2003), or the species abundance over multiple surveys, without marking individuals have been proposed to estimate population size (Royle Repeated Count model, Royle 2004). These modelling approaches have been incorporated into the 'Unmarked' package (see Fiske and Chandler 2011) and runs complex Bayesian framework modelling, which accounts for detection probabilities and thus estimate space use/population sizes. Often, detection probability is neglected, which leads to potential type II errors (MacKenzie et al. 2017), due to detection probability often being imperfect. Imperfect detection probability means that the target species can be considered absent during a survey when the species was present but went undetected at a site. Accounting for imperfect detection improves model performance, providing robust population size estimates (Royle and Nichols 2003, Royle 2004, MacKenzie et al. 2017, Fiske and Chandler 2011, Knaus et al. 2018).

Two commonly used camera trap deployment designs are regular grid deployment arrays and cluster deployment arrays (Clark 2019, Pardo et al. 2021). A regular grid deployment array uses a standard grid format with camera traps separated by set, pre-determined distances (Swanson et al. 2015, Clark 2019, Pardo et al. 2021). A cluster deployment design reduces the number of camera traps used and the total trapping effort by grouping camera traps (clusters); the camera trap clusters are deployed further apart than camera trap stations in the regular deployment designs (Clark 2019, Murphy et al. 2019, Panthera 2021). South Africa has many short and long-term camera trap monitoring programs (Panthera 2021, Pardo et al. 2021). Panthera organization has multiple camera trap monitoring programs across the globe (Panthera 2021). Panthera runs surveys annually, prioritizing leopard monitoring amongst other species in South Africa (Rogan et al. 2019). The Snapshot Safari South Africa project contributed towards a national biodiversity project (Pardo et al. 2021). There are also many species-specific studies conducted over short periods of time such as Bracskowski et al. (2016). Reserves such as Pilanesberg National Park, North West province, and Atherstone Nature Reserve, Limpopo province, have been research sites where both Panthera and Snapshot Safari deployment arrays have been active for some time. Having both monitoring programs run in the same protected areas provides an opportunity to compare population size estimates from a targeted (Panthera 2021), and non-targeted grid deployment array (Swanson et al. 2015, Pardo et al. 2021), estimated from N-mixture models (Royle 2004). In Chapter 2 of my thesis, I used N-mixture models to analyze baited and non-baited sequential grid deployment array data and found that N-mixture models and the estimates were influenced by the high capture rates, detection probabilities and overestimated leopard and brown hyaena population sizes in Madikwe Game Reserve. An investigation into whether targeted roadside cluster deployments and regular grid deployment arrays influence population size estimates generated from N-mixture models was still needed (Fiske and Chandler 2011).

I estimated leopard and brown hyaena population sizes from two camera trap grid deployment designs (Panthera 2021, Pardo et al. 2021) to investigate the influence targeted and non-targeted deployment arrays have on N-mixture model analysis. The two study sites were selected as these sites had multiple long term camera trap projects based on the sites, the same projects whose data was used in chapter 2 of this thesis. This study aimed to provide empirical evidence supporting N-mixture models being implemented to analyze wildlife population sizes. Population size estimates between the two study sites were not expected to differ according to the presence or absence of larger carnivores. Furthermore, I investigated the space use and detection patterns associated with leopard and brown hyena covariates. I predicted that there would be little to no variation in species space use in each reserve. I predicted that the N-mixture models would overestimate population sizes estimated from targeted grid deployment design data because the targeted roadside cluster deployment design increases species detection probabilities and capture numbers. Van Dyk and Slotow (2003), estimated a leopard population size of 40 to 60 individuals and a brown hyaena population size of 50 to 100 individuals on Pilanesberg National Park. Additionally, Williams et al. (2021) estimated a brown hyaena population of 61 individuals oi Pilanesberg National Park and 36 individuals in Atherstone Nature Reserve. Furthermore, aerial counts conducted on Atherstone Nature Reserve in 2014 counted one leopard individual (Johan Kruger, *pers* comm, 2021). All of which were used as benchmarks and reference statistics.

Methods and materials

Study areas

Pilanesberg National Park

Pilanesberg National Park (hereafter, Pilanesberg; 25.2449° S, 27.0891° E, Figure 3.1), is situated within an ancient volcano and is surrounded by a range of large circular hills (Adcock et al. 1998). The vegetation types vary between open grasslands, mixed *Vachellia* and *Senegalia* species, thick woodlands, and broad-leaf and fine-leaf savannah (Mucina and Rutherford 2006). Pilanesberg is approximately 55000 hectares (ha), situated in the North West province, South Africa. On average, the national park receives 91 millimetres (mm) of rain per month during the wet season, between

October and April. Temperatures during this season can fluctuate between 26°C and 30°C. The dry season is from May to September, with rainfall averaging 14.4 mm per month and temperatures fluctuating between 18°C and 23°C (Joint Research Centre of the European Commission 2021). Water sources are situated across the park, including one large central dam and many smaller dams and springs scattered throughout. Pilanesberg had roughly 6000 individuals from a range of species introduced into the park, after the park was proclaimed in 1979 (van Dyk and Slotow 2003). However, Pilanesberg only has two large individual adult spotted hyaena (*Crocuta crocuta*) to date. Large carnivores present in Pilanesberg include cheetah (*Acinonyx jubatus)*, leopard, African wild dog (*Lycaon pictus*), brown hyaena, and lion (*Panthera leo*). Meso-carnivores present in the park include black-backed jackal (*Lupulella mesomelas*), banded mongoose (*Mungos mungo*), African wildcat (*Felis silvestris lybica*), small spotted genet (*Genetta genetta*), slender mongoose (*Galerella sanguinea*), rusty-spotted genet (*Genetta maculata*), caracal (*Caracal caracal*), and serval (*Leptailurus serval*) (van Dyk and Slotow 2003). Pilanesberg is fenced off by predator-proof electrified fence (van Dyk and Slotow 2003).

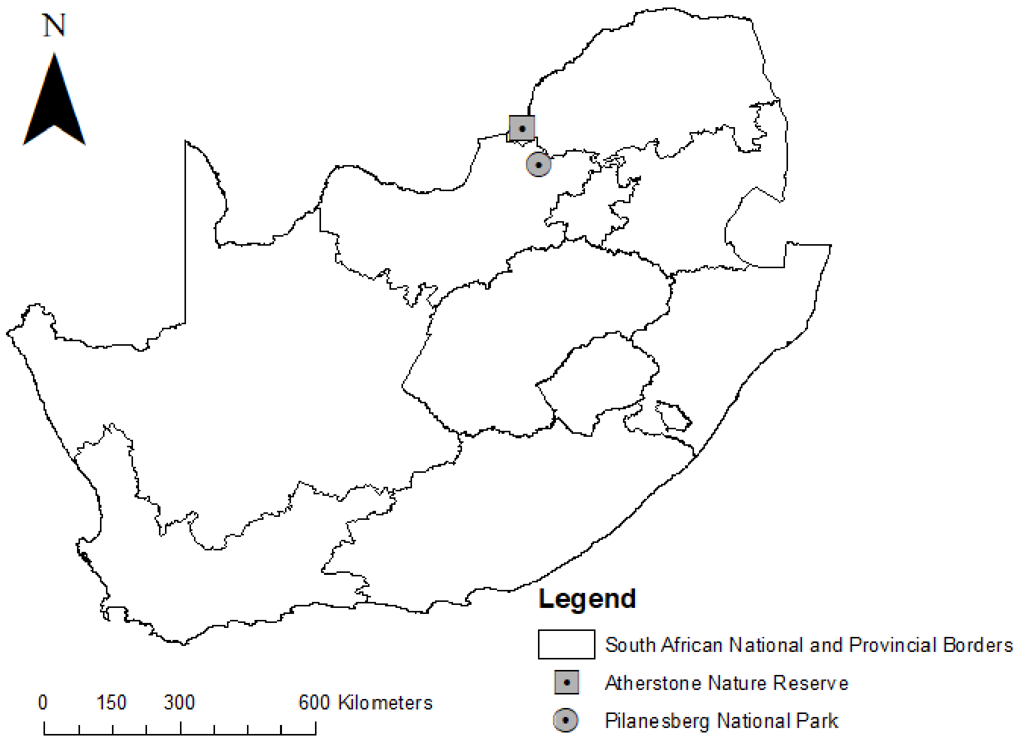

Figure 3.1. The locations of Atherstone Nature Reserve and Pilanesberg National Park within the Limpopo and North West provinces of South Africa

Atherstone Nature Reserve

Atherstone Nature Reserve (hereafter, Atherstone; 24.5130° S, 26.7732° E, Figure 3.1) is approximately 24000 ha in size, situated in the Thabazimbi district of the Limpopo province. The Thabazimbi district, in which Atherstone is situated, is dominated by mixed bushveld (Marnewick et al. 2008). During the months of May to August, commercial hunting, commonly antelope species, is allowed and occurs within Atherstone. In addition, live animal sales take place on the reserve throughout the year (Marnewick et al. 2008). Water is supplied by artificial waterholes (Marnewick et al. 2008). The composition of carnivore species on the reserve consists primarily of meso-carnivore species, with the only large carnivores on the reserve being cheetah, spotted hyaena and leopard (Joint Research Centre of the European Commission 2021). The meso-carnivore composition of Atherstone is similar to that of Pilanesberg. However, Atherstone has no record of slender mongoose and rusty-spotted genet occupying the reserve. Atherstone's rainy season extends from October to April, with average temperatures ranging between 24^{o}C and 28^{o}C and a monthly average rainfall of 71 mm (Joint Research Centre of the European Commission 2021). During the dry season, from May to September, the average monthly rainfall is ~7 mm, and temperatures average between 13^{o}C and 24^{o}C (Joint Research Centre of the European Commission 2021).

Data Collection

Within Pilanesberg and Atherstone, leopard and brown hyaena population sizes were estimated using two different pre-existing iterations of the same sampling technique, namely a regular deployment array and roadside cluster deployment array. Camera trap data provided by Snapshot Safari – South Africa (hereafter regular deployment array) and Panthera organization (hereafter roadside cluster deployment) was analyzed (Figure 3.2 and 3.3, Panthera 2021, Pardo et al. 2021). Due to the design of all three of the deployment arrays, camera trap sites were not considered independent, and, therefore, space use and space use probability were used to inform on space use (Rovero and Zimmermann 2016).

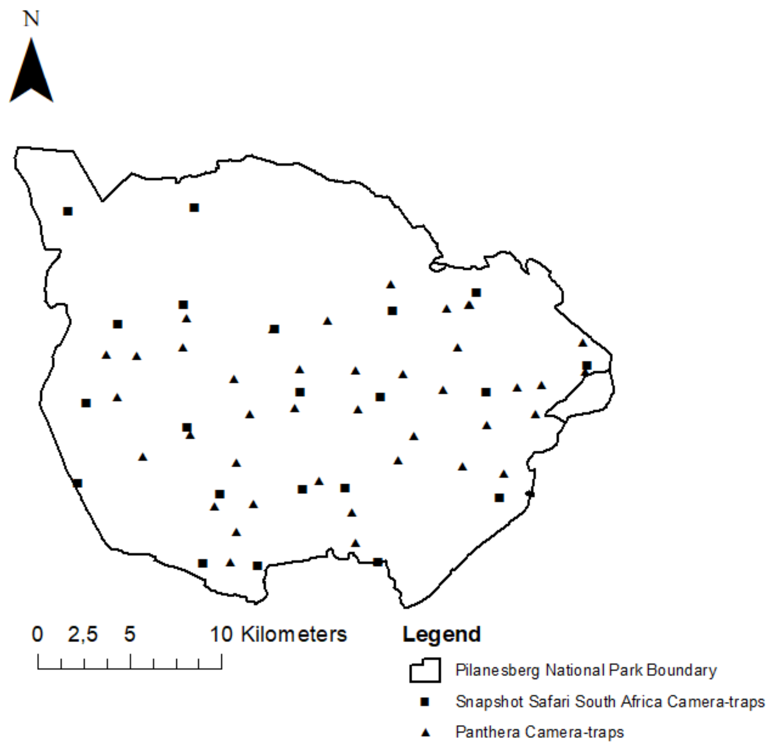

Figure 3.2. The camera trap locations (n=101) of the regular Snapshot deployment array (n=21) and the roadside cluster Panthera deployment array (n=80 camera traps across 40 camera trap stations) on Pilanesberg National Park, North West province, South Africa

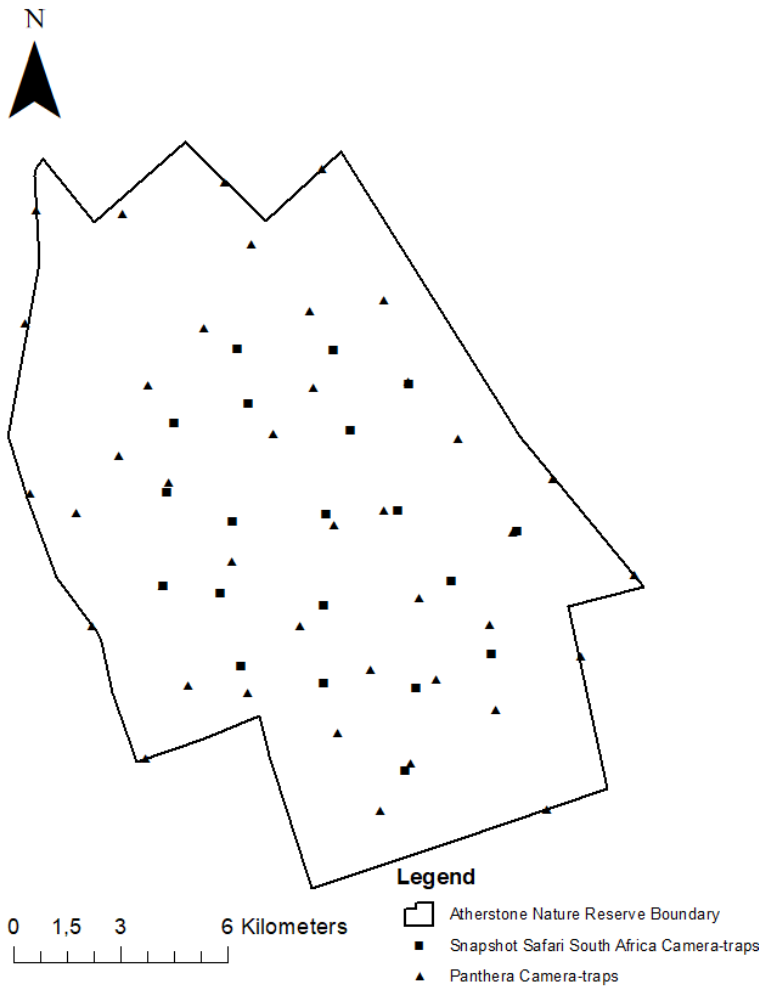

Figure 3.3. The camera trap locations (n=100) of the regular Snapshot deployment array (n=20) and the roadside cluster Panthera deployment array (n=80 camera traps across 40 stations) on Atherstone Nature Reserve, Limpopo province, South Africa

Snapshot safari project: Regular Grid Deployment Array

Twenty-one camera traps (Cuddeback model C1279, Non-Typical Inc., Park Falls, USA) were deployed in a 5 km^2 regular grid array on Pilanesberg. Twenty camera traps were deployed in a 2 km^2 grid array on Atherstone (Figure 3.2 and 3.3). All camera traps had the same settings. Every camera trap was placed approximately 50 cm above the ground, facing the nearest game trail (Cusack et al. 2015, Swanson et al. 2015, Pardo et al. 2021). The grass surrounding every camera trap was trimmed to reduce the number of misfires (Swanson et al. 2015). Camera traps were serviced every 4 to 6 weeks, storage cards were swapped out and batteries replaced. The data extracted from Snapshots cameras deployed on Pilanesberg for this research was from 14 November 2018 to 13 November 2019, recording a total of 4779 camera trap nights. Data were extracted from Snapshots cameras deployed on Atherstone from 01 July 2020 to 01 October 2020, which recorded a total of 1860 camera trap nights. Population size estimates were recorded from the most recent 3 months' worth of filtered data to avoid violating the closed population assumption (Kendall 1999). However, the full years' worth of data was required to achieve an acceptable goodness of fit value for the global model used to estimate leopard population size on Pilanesberg. I relaxed the closed population assumption, which assumes no population loss or gain over the course of the study and focus (Otis et al., 1978), to accommodate more camera trap nights required for a robust population size estimate (Tobler and Powell 2013).

<u>Panthera project: Roadside Cluster Deployment</u>

The Panthera project team (Panthera, 2021) placed 40 unbaited camera trap stations (Pantheracams camera traps) in a cluster grid design across Pilanesberg from 16 January 2020 to 05 March 2020, which recorded a total of 2000 camera trap nights. The same 40 camera trap cluster grid design was followed in Atherstone from 26 August 2020 to 14 October 2020, which recorded 2000 camera trap nights. Clusters were between 3 km and 8 km apart. Stations were separated by 1 km. The camera traps use xenon flash cameras with built-in infrared motion sensors. All camera traps captured one image per trigger event (Miller et al. 2018). Camera traps were situated primarily along roads and road junctions (Miller et al. 2018). Camera traps were attached to trees or steel poles and placed 30-40 cm above the ground. There were 40 stations, amounting to 80 camera traps deployed per park (Figure 3.2 and 3.3, Pitman et al. 2017, Rogan et al. 2019).

Data analyses

Leopard and brown hyaena data were collected and extracted from two different camera trap studies on Pilanesberg National Park and Atherstone Nature Reserve. N-mixture models (Royle 2004), were used in the analysis. Nine months of raw, unidentified camera trap data from the regular deployment array were identified using the software Wild.ID (Version 1.0.1, Tropical Ecology Assessment and Monitoring Network, 2021) between June 2020 and March 2021. I classified camera trap images data into species and reported on the number of individuals per picture for Pilanesberg National Park from June 2020 to March 2021. Pre-processed data from the regular deployment array, were additionally provided by Snapshot Safari (Pardo et al. 2021), and pre-processed data from the roadside cluster deployment were provided by the Panthera project team (Panthera 2021). To obtain independence between triggers, photos taken of the same species within a 30-minute time frame at the same camera station were considered as a single capture event (see Yasuda 2004).

Population Size

Leopard and brown hyaena capture data were converted to count data, the number of independent captures per sample occasion was assigned to each camera. Camera traps with no detections for a sampling occasion were assigned a “0”. For example, if three independent leopard captures were recorded within one of the sample occasions, then a “3” would be recorded. By doing this, a species-specific repeated count record was made using detection histories. Sample occasion lengths were selected according to recorded global model goodness of fit estimates (Table 3.1). The global model goodness of fit was assessed using the R-package *“nmixgof”* (Knape et al. 2018).

Table 3.1. Independent sample occasion lengths per camera trap project dataset per fenced protected area in this study.

	Pilanesberg National Park		**Atherstone Nature Reserve**	
	Leopard	Brown Hyaena	Leopard	Brown Hyaena
Regular Grid Deployment Array	4 weeks	1 week	2 weeks	3 days
Roadside Cluster Deployment Array	1 day	1 day	3 days	1 day

Six covariates that were considered ecologically relevant to the target species were considered, these were vegetation type (n = 10 for Pilanesberg; Open water point, savannah woodland, grassy woodland, riverine area, grass plain, rocky outcrop, sodic site, open savannah, savannah grassland, gully; n = 10 for Atherstone; Shrubland, bluethorn thicket (*Senegalia erubescens*), old lands, sicklebush area (*Dichrostachys cinerea*), *Grewia flava* shrubland, Sicklebush thicket, dam piosphere, *Vachellia tortillas* area, thornveld, grassy shrubland), elevation (m), distance to nearest tar or dirt road (m), distance to fence boundary (m), distance to infrastructure (m; lodges, warehouses, camps, gates, bomas, staff accommodations, sub-stations, houses, centres and conference rooms, pumps, water towers), and distance to water (m). All covariates were mapped, and distances were calculated using ESRI© ArcMap (Version 10.8.1.14362, ESRI, 2021) and Google Earth Pro (Version 7.3.4.8248, Google Earth, 2021). Covariates were checked for multicollinearity using the ‘*Olsrr*’ package (Hebbali 2020). All six covariates were retained (VIF < 4, Hebbali 2020). Package ‘*Unmarked’* internally creates an observation covariate called ‘obsNum’, which was included in the detection part of the models to get occasion-specific estimates of detection parameters, similar to mark-recapture studies (Richard Chandler, Unmarked Developer, *pers comms*).

The “*p-count*” function in the ‘*Unmarked*’ package (Fiske and Chandler 2011) was used in R-program (R Core Team 2021, 4.11, www.rstudio.com, accessed 25 February 2021) using R-studio (R Core Team 2021, Version 1.2.1717, www.rstudio.com, accessed 25 February 2021) to run N-mixture models. Both single and multi-covariate models were run using the regular deployment and roadside cluster deployment arrays. The '*Ranef*' function in the '*Unmarked*' package was used to estimate population size estimates along with confidence intervals, using the empirical Bayes methods (Royle 2004). Using the formatted repeated count data, N-mixture models (RRC – Royle Repeated Count models) were run and selected according to which model records the lowest information criterion corrected (AICc) value (Burnham and Anderson 2004, Ramesh et al. 2017).

Space Use

Single-species single-season space use models (MacKenzie et al. 2002), were generated using the formatted input data from both the regular and roadside cluster deployment arrays, and space use analyses were conducted using the '*Unmarked'* package (Fiske and Chandler 2011, Version 1.0.1) in R-program using R-studio. Cameras that detected specific species were assigned a "1" and those where no detections were made were assigned a "0". By doing this, a species-specific record was made using detection histories. Records were then condensed into the same sample occasion lengths as used in the population size analysis (Table 3.1).

Model generation required transforming the raw input data into matrices. The matrices were then formatted into a list which formed part of the space use model. The above-mentioned covariates were used in the space use analysis. The best fit model was selected according to the lowest Akaike's Information Criterion (AIC) (Burnham and Anderson 2004, Ramesh et al. 2017). All models run were single covariate models; this was due to there being limited numbers of captures per species. The same six covariates used in the N-mixture model analysis were used in the space use analysis (Table 3.2).

Table 3.2. Space use and detection covariates used in the single-species single-season space use models. Distances in metres (m).

Space use Covariates	**Detection Covariates**
Vegetation type	Vegetation type
Elevation (m)	Nearest distance to infrastructure (m)
Nearest distance to infrastructure (m)	Nearest distance to road (m)
Nearest distance to road (m)	Nearest distance to water (m)
Nearest distance to water (m)	Distance to nearest boundary (m)
Distance to nearest boundary (m)	

Results

<u>Pilanesberg National Park</u>

Population size

The regular camera trap deployment array recorded 18 independent leopard captures and 66 independent brown hyaena captures across 21 sites over the period of November 2018 to November 2019. The roadside cluster deployment recorded a total of 115 independent leopard captures, and 1065 independent brown hyaena captures across 40 camera trap stations over the period of January 2020 to March 2020. The regular Snapshot grid deployment and roadside Panthera cluster deployment recorded their highest detection probabilities at camera traps closer to or nearby roads (Figures 3.4- 3.7).

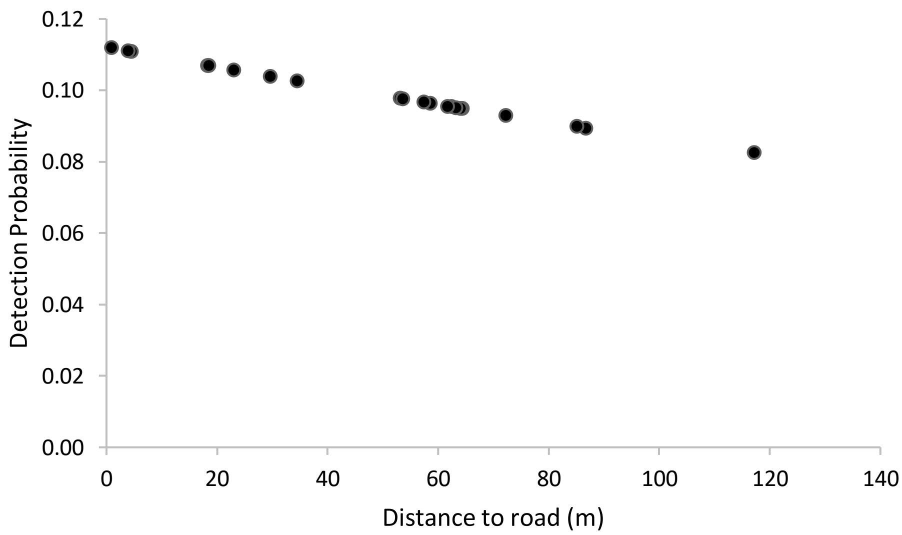

Figure 3.4. Effect of distance to road on leopard detection probability estimated from the regular Snapshot deployment array data on Pilanesberg National Park, North West province, South Africa

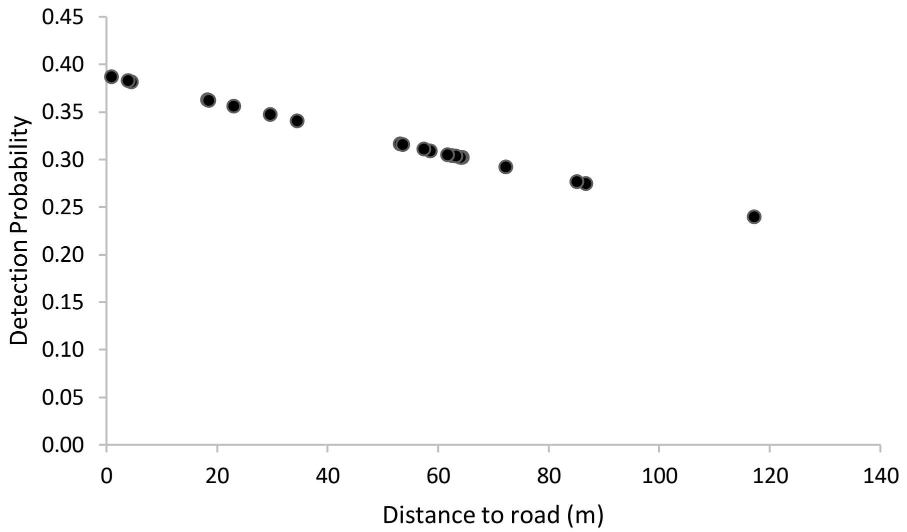

Figure 3.5. Effect of distance to road on brown hyaena detection probability estimated from the regular Snapshot deployment array data on Pilanesberg National Park, North West province, South Africa

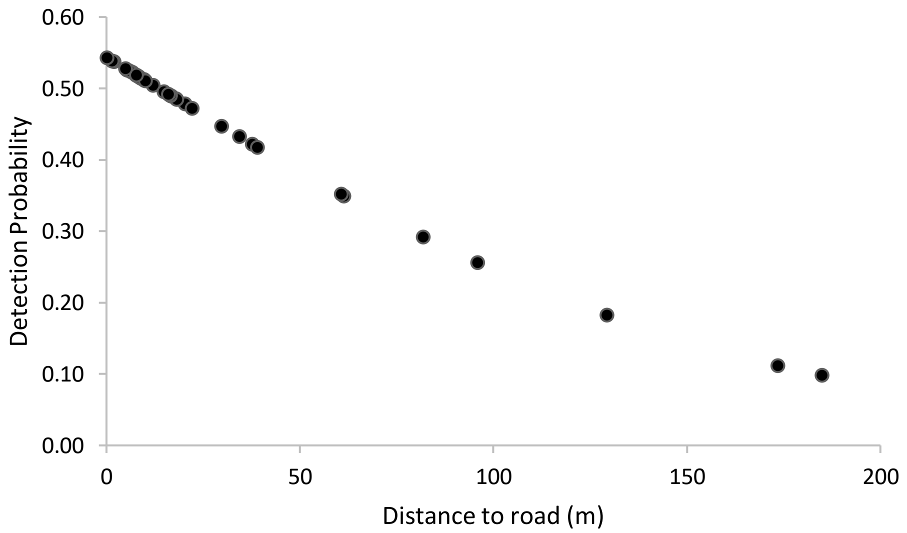

Figure 3.6. Effect of distance to road on leopard detection probability estimated from the roadside Panthera cluster deployment array data on Pilanesberg National Park, North West province, South Africa

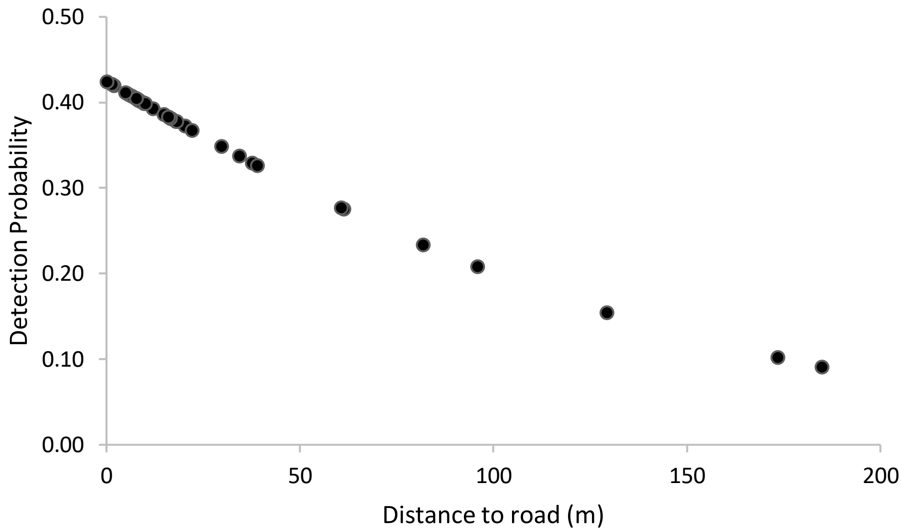

Figure 3.7. Effect of distance to road on brown hyaena detection probability estimated from the roadside Panthera cluster deployment array data on Pilanesberg National Park, North West province, South Africa

The leopard population size was estimated to be 27.52 (97.5% Bayesian confidence interval, B.C.I., 12 – 73) by the best ranking model for the regular deployment array, the best ranking model for the roadside cluster deployment data estimated a leopard population size estimate of 87.42 (97.5% B.C.I. 42 – 167) individuals (Table 3.3). The brown hyaena population size estimate for the regular deployment camera trap data was estimated at 70.23 (97.5% B.C.I. 39 – 123) individuals, and the roadside deployment camera trap data estimated a brown hyaena population size estimate of 258.86 (97.5% B.C.I. 197 – 343) individuals (Table 3.3).

Table 3.3. The estimated leopard and brown hyaena population sizes per project on Pilanesberg National Park with 97.5% confidence intervals (CI) according to the best ranking models. LPE = Leopard Population Estimate. BHPE = Brown Hyaena Population Estimate. GoF = Global model goodness of fit (C-hat).

Project	LPE	CI	GoF	BHPE	CI	GoF
Regular grid deployment	27.52	12 - 73	0.85	70.23	39 – 123	1.48
Roadside cluster deployment	87.42	42 – 167	0.93	258.86	197 – 343	1.25

Space use and Detection – Regular Grid Deployment Array

Detection probability varied with vegetation type combined with constant space use and presented as the best ranking model for the regular deployment data for both study species according to AIC values (Table 3.5). Open areas such as rocky outcrops, grassy woodlands and riverine areas recorded a significantly higher probability of detecting leopard ($p \geq 0.33$, SE ≤ 0.1) and brown hyaena ($p \geq 0.61$, SE ≤ 0.12), compared to areas with thicker and more dense vegetation such as thick savannah grasslands (leopard $p \leq 0.1$, SE ≤ 0.1 and brown hyaena $p \leq 0.27$, SE ≤ 0.12, see Appendix 1). None of the top-ranking space use models were significantly different from each other (ΔAIC < 2, Table 3.4), furthermore leopard and brown hyaena space use did not vary significantly according to any of the covariates analyzed for the regular grid deployment array (Table 3.4). Certain vegetation types significantly affected the estimated detection probabilities of the regular deployment array data (Table 3.5, see Appendix 1). Distance to the nearest road did not significantly influence recorded detection probabilities for leopard and brown hyaena regular deployment data, even though most captures were recorded by camera traps close to roads (Table 3.5, Figure 3.4 and 3.5). Furthermore, distance to nearest infrastructure significantly influenced brown hyaena detection (Table 3.5).

Table 3.4. Space use models from regular deployment array data on Pilanesberg National Park with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	**Leopard**		**Brown Hyaena**	
	AIC	***p*-value**	**AIC**	***p*-value**
(.) (.)	253.74	0.09	597.20	0.78
(.) (Vegetation type)	261.36	0.68-0.95	613.20	0.93-1.00
(.) (Infrastructure)	254.51	0.28	599.20	1.00
(.) (Road)	255.01	0.48	599.20	1.00
(.) (Water)	253.51	0.15	599.20	1.00
(.) (Boundary)	253.21	0.22	599.20	1.00
(.) (Elevation)	254.17	0.31	599.20	1.00

Table 3.5. Detection models from regular deployment array data on Pilanesberg National Park with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	**Leopard**		**Brown Hyaena**	
	AIC	***p*-value**	**AIC**	***p*-value**
(.) (.)	253.74	2.29e-27	597.20	4.12e-14
(Vegetation type) (.)	242.41	0.00-0.99	534.73	0.00-0.87
(Infrastructure) (.)	258.83	0.22	589.68	0.003
(Road) (.)	255.59	0.70	595.85	0.07
(Water) (.)	249.38	0.02	588.12	0.001
(Boundary) (.)	260.25	0.64	589.66	0.002

Space use and Detection – Roadside Cluster Deployment Array

The top two ranking space use models were concluded to have the same model fit as each other (ΔAIC < 2, Table 3.6). Furthermore, leopard and brown hyaena space use did not vary significantly according to any of the covariates analyzed for the roadside cluster deployment array (Table 3.6). Three space use models recorded similar AIC values but were not of the same model fit, namely (.) (Road), (.) (Water), (.) (Boundary). Certain vegetation types significantly affected the estimated brown hyaena detection probabilities of the regular deployment array data according to recorded p-values (Table 3.7, see Appendix 1). Open areas such as rocky outcrops, grassy woodlands and riverine areas recorded a significantly higher probability of detecting brown hyaena ($p \geq 0.39$, SE ≤ 0.06), compared to areas with thicker and more dense vegetation such as thick savannah grasslands (brown hyaena $p \leq 0.20$, SE ≤ 0.06, see Appendix 1). The distance to the nearest road did significantly influence the detection probability for both leopard and brown hyaena according to the roadside cluster deployment data (Table 3.7, Figure 3.6 and 3.7). Detection probability decreased significantly as the distance to the nearest road increased (Figure 3.6 and 3.7). Varying detection probability according to distance to road combined with constant space use was the best ranking model for the leopard and brown hyaena roadside cluster deployment data according to recorded AIC values (Table 3.7).

Table 3.6. Space use models from roadside cluster deployment array data on Pilanesberg National Park with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	**Leopard**		**Brown Hyaena**	
	AIC	***p*-value**	**AIC**	***p*-value**
(.) (.)	217.14	0.003	2607.14	0.82
(.) (Vegetation type)	221.65	0.94-1.00	2621.14	0.99-1.00
(.) (Infrastructure)	218.30	0.35	2609.14	1.00
(.) (Road)	214.22	0.07	2609.14	1.00
(.) (Water)	216.37	0.37	2609.14	1.00
(.) (Boundary)	215.11	0.09	2609.14	1.00
(.) (Elevation)	Model did not converge		2609.14	1.00

Table 3.7. Detection models from roadside cluster deployment array data on Pilanesberg National Park with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	**Leopard**		**Brown Hyaena**	
	AIC	***p*-value**	**AIC**	***p*-value**
(.) (.)	217.14	0.65	2607.14	3.74e-37
(Vegetation type) (.)	221.18	0.36-1.00	2574.10	0.00-0.78
(Infrastructure) (.)	219.14	0.90	2602.70	0.012
(Road) (.)	213.17	0.02	2538.98	1.96e-13
(Water) (.)	218.81	0.54	2608.16	0.32
(Boundary) (.)	217.34	0.19	2607.05	0.15

Atherstone Nature Reserve

Population Size

The regular grid deployment array recorded 14 independent leopard captures and 64 independent brown hyaena captures across 20 camera trap sites over the period of July 2020 to October 2020. The roadside cluster deployment recorded 39 independent leopard captures, and 332 independent brown hyaena captures across 40 camera trap stations over the period of August 2020 to October 2020. The regular Snapshot deployment and the roadside Panthera cluster deployment recorded their highest detection probabilities at camera traps closer to roads (Figures 3.8 – 3.11).

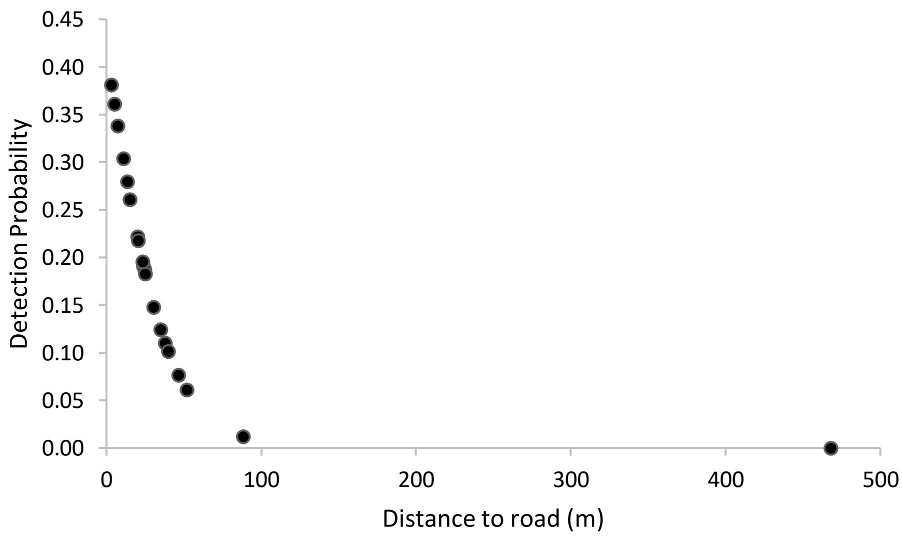

Figure 3.8. Effect of distance to road on leopard detection probability estimated from the regular Snapshot deployment array data on Atherstone Nature Reserve, Limpopo province, South Africa.

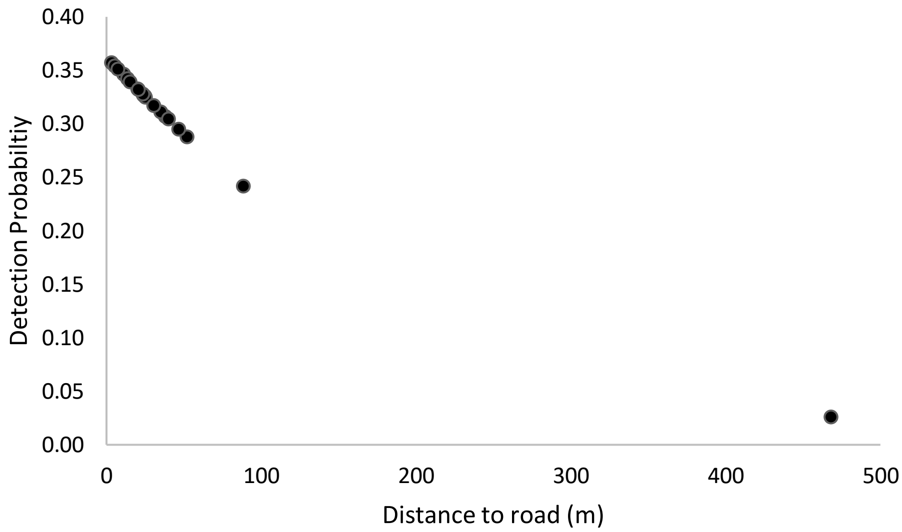

Figure 3.9. Effect of distance to road on brown hyaena detection probability estimated from the regular Snapshot deployment array data on Atherstone Nature Reserve, Limpopo province, South Africa.

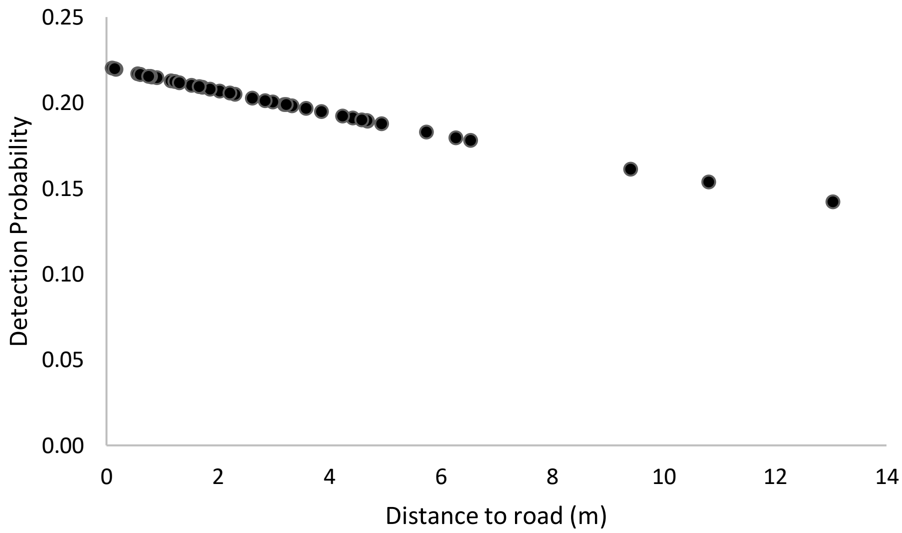

Figure 3.10. Effect of distance to road on leopard detection probability estimated from the roadside Panthera cluster deployment array data on Atherstone Nature Reserve, Limpopo province, South Africa.

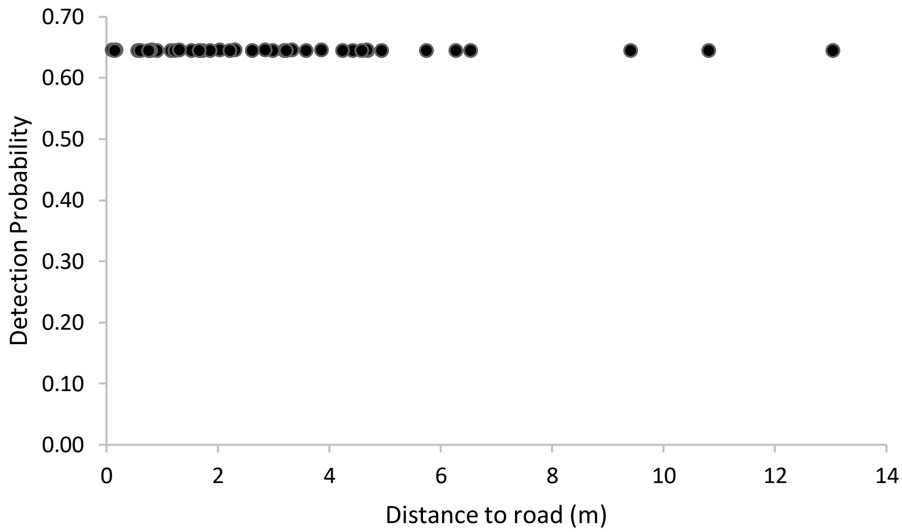

Figure 3.11. Effect of distance to road on brown hyaena detection probability estimated from the roadside Panthera cluster deployment array data on Atherstone Nature Reserve, Limpopo province, South Africa.

A leopard population size estimate of 8.29 (97.5% Bayesian confidence interval, B.C.I., 7 – 28) individuals was derived from the regular grid deployment array data (Table 3.8). The N-mixture models run using the roadside cluster deployment data estimated a leopard population size of 128.99 (97.5% B.C.I. 29 – 274) individuals. The brown hyaena population size estimated from the regular deployment camera trap data was 60.83 (97.5% B.C.I. 39 – 105) individuals and 119.66 (97.5% B.C.I. 75 – 187) from the roadside cluster deployment data (Table 3.8).

Table 3.8. The recorded leopard and brown hyaena population sizes per project on Atherstone Nature Reserve with 97.5% confidence intervals (CI) according to the best ranking models. LPE = Leopard Population Estimate. BHPE = Brown Hyaena Population Estimate. GoF = Global model goodness of fit (C-hat).

Project	LPE	CI	GoF	BHPE	CI	GoF
Regular grid deployment	8.29	7 – 28	1.00	60.83	39 – 105	0.99
Roadside cluster deployment	128.99	29 – 274	1.12	119.66	75 – 187	1.04

Space use and Detection – Regular Deployment Array

The top three ranking space use models for both species had the same model fit (ΔAIC < 2, Table 3.9). Leopard space use varied significantly according to vegetation type for the regular deployment array

(Table 3.9). Leopards prefered dense areas such as shrublands and *Dichrostachys cinerea* thickets (*psi* ≥ 0.74, SE ≤ 0.31) to open areas such as open grasslands (*psi* ≥ 0.1, SE ≤ 0.10). Furthermore, certain vegetation types significantly affected the estimated leopard detection probabilities of the regular deployment array data (Table 3.10, see Appendix 2). Detection probability varied with vegetation type combined with constant space use and presented as the best ranking model for the regular deployment data for both study species according to AIC values (Table 3.10). Leopard detection probabilities, which corresponded with their space use estimates, were highest in preferred areas of space use ($p \geq 0.22$, SE ≤ 0.29) compared to areas less occupied ($p \leq 0.1$, SE ≤ 0.13). Furthermore, distance to nearest infrastructure and water significantly influenced leopard and brown hyaena detection (Table 3.10). Camera traps closer to infrastructure and water sources recorded higher detection probabilities. Distance to the nearest road did not significantly influence recorded detection probabilities for leopard and brown hyaena regular deployment data, even though most captures were recorded by camera traps close to roads (Table 3.10, Figure 3.8 and 3.9).

Table 3.9. Space use models from regular deployment array data on Atherstone Nature Reserve with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	Leopard		Brown Hyaena	
	AIC	*p*-value	AIC	*p*-value
(.) (.)	67.17	0.12	309.50	0.341
(.) (Vegetation type)	67.27	0.00-0.99	315.18	0.87-0.99
(.) (Infrastructure)	68.99	0.68	311.47	0.85
(.) (Road)	67.37	0.34	311.12	0.60
(.) (Water)	69.12	0.83	311.41	0.76
(.) (Boundary)	67.30	0.20	310.74	0.39
(.) (Elevation)	68.11	0.33	309.19	0.15

Table 3.10. Detection models from regular deployment array data on Atherstone Nature Reserve with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	Leopard		Brown Hyaena	
	AIC	*p*-value	AIC	*p*-value
(.) (.)	67.17	0.01	309.50	3.84e-32
(Vegetation type) (.)	58.13	0.00-0.99	268.49	0.85-1.00
(Infrastructure) (.)	61.76	0.009	273.17	1.93e-09
(Road) (.)	64.18	0.05	306.01	0.11
(Water) (.)	60.68	0.005	306.73	0.03
(Boundary) (.)	68.24	0.33	311.13	0.54

Space use and Detection – Roadside Cluster Deployment Array

None of the top-ranking space use models recorded better model fits than each other (ΔAIC < 2, Table 3.11). Furthermore, leopard and brown hyaena space use did not vary significantly (Table 3.11). Leopard detection probabilities were not significantly influenced by any of the covariates used in the analysis. Distance to nearby water significantly affected the estimated brown hyaena detection probability recorded from the roadside cluster deployment array data (Table 3.12, see Appendix 2). Varying detection according to distance to nearby water combined with constant space use was the best ranking model for the roadside cluster deployment array brown hyaena data according to recorded AIC values (Table 3.12). Camera traps closer to water sources recorded higher brown hyaena detection probabilities. The distance to road did not significantly influence detection probability for both leopard and brown hyaena roadside cluster deployment data (Table 3.12, Figure 3.10 and 3.11). This is because there was little variation in the camera trap deployment distances from the nearest road. Distances only ranged between 0 and 14 meters (Figure 3.10 and 3.11).

Table 3.11. Space use models run with roadside cluster deployment array data on Atherstone Nature Reserve with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	**Leopard**		**Brown Hyaena**	
	AIC	***p*-value**	**AIC**	***p*-value**
(.) (.)	158.31	0.424	537.66	3.11e-05
(.) (Infrastructure)	158.15	0.23	539.42	0.64
(.) (Road)	Model did not converge		539.64	0.89
(.) (Water)	156.77	0.31	539.44	0.65
(.) (Boundary)	158.37	0.31	538.04	0.28
(.) (Elevation)	156.55	0.18	537.52	0.20

Table 3.12. Detection models run with roadside cluster deployment array data on Atherstone Nature Reserve with corresponding Akaike Information Criterion values (AIC) and *p*-values. (*p*) = Detection probability. (*psi*) = Space use probability. (.) = Constant detection/space use probability.

Models: (*p*) (*psi*)	**Leopard**		**Brown Hyaena**	
	AIC	***p*-value**	**AIC**	***p*-value**
(.) (.)	158.31	0.0002	537.66	0.48
(Infrastructure) (.)	158.86	0.25	547.73	0.34
(Road) (.)	160.04	0.60	538.53	0.29
(Water) (.)	160.11	0.66	531.51	0.005
(Boundary) (.)	160.03	0.59	539.24	0.52

Discussion

Camera trap studies have become increasingly popular and regularly use varying types of grid deployments and approaches to estimate population sizes, abundances and assess spatio-temporal space use patterns of cryptic species (Balme et al.2009, Thorn et al. 2011, Kays et al. 2020). Often projects are targeted towards individual species but collect bycatch data on multiple species. This bycatch data may be used to generate robust population size estimates of these cryptic species. The result from this study indicates that using different deployment approaches may influence N-mixture models which has resulted in different population estimates for leopard and brown hyaena on Pilanesberg National Park and Atherstone Nature Reserve. The two different deployment arrays presented different population estimates for leopard and brown hyaena in the two protected areas (Table 3.3 and 3.8). The regular Snapshot grid deployment array performed better than the roadside Panthera cluster deployment array in the N-mixture model analysis. The N-mixture model population estimates generated from the roadside cluster deployment were overestimated and did not reflect the species populations on Pilanesberg and Atherstone when compared to estimates recorded by Van Dyk and Slotow (2003) and Williams et al. (2021) (Table 3.3 and 3.8).

The roadside cluster deployment showed higher overall detection probabilities for both study species (Leopard ≥ 0.21 and brown hyaena ≥ 0.42), compared to the detection probabilities recorded by the regular deployment array (Figures 3.4-3.11). These detection probabilities are comparable to other studies reported for other leopard populations (p = 0.21 ± SE. 0.0, Cristescu et al. 2020), and higher than those reported for brown hyaena (p = 0.33 ±SD. 0.06, Bennitt 2020). The roadside Panthera cluster deployment array recorded higher numbers of leopard and brown hyaena independent captures in a shorter two-month period and detected the two study species better than the regular deployment. Although the detection probabilities recorded from the regular grid deployment array of the two study species as the camera trap distance nearby roads decreased (Figure 3.4, 3.5, 3.8, 3.9), the detection probabilities and independent capture numbers overall were lower than the roadside cluster deployment data (Figure 3.6, 3.7, 3.10, 3.11). The lower detection probabilities are likely due to inherently low numbers of leopard and brown hyaena, as well as the fact that the regular grid deployment camera traps being less targeted (Swanson et al. 2015). The regular grid deployment camera traps were also aligned to the nearest game trail, even when close to human tracks or roads, and specifically implemented to capture medium to large mammals (Swanson et al. 2015). The lower detection probabilities and capture numbers produced reliable estimates through N-mixture model analysis (Royle 2004), as these capture numbers and detection probabilities are more representative of the two study species. This may explain why the regular deployment array produced reliable population size estimates and much smaller confidence intervals than those obtained by the roadside cluster deployment for both fenced protected areas.

The road associated clustered camera trap deployment led to overestimated population sizes using the N-mixture analysis for both study species (Table 3.3 and 3.8), compared to published estimates by van Dyk and Slotow (2003) and Williams et al. (2021). Deploying many camera traps in a grid array with a small interval distance possibly introduced spatial autocorrelation into the analysis and is a likely reason why the estimates were largely aboe expected. Spatial autocorrelation does impact the analyses, which do not involve individual identification of species across deployed camera traps, as the same individual could be captured at multiple camera traps (Guélat and Kery 2018). Carnivores are known to use roads to traverse their territories (Mills 1990, Thorn et al. 2011, Zimmermann et al. 2014, Welch et al. 2016), and deploying camera traps along nearby roads did increase the roadside cluster deployments recorded detection probabilities and independent leopard and brown hyaena capture numbers which influenced the N-mixture models. The regular deployment array population size estimates (Table 3.3 and 3.8), were comparable to estimates by van Dyk and Slotow (2003), estimating between 40 and 60 leopard and between 50 and 100 brown hyaena on Pilanesberg. Williams et al. (2021), estimated a brown hyaena density of 11 individuals per 100km^2 on Pilanesberg National Park and 15 individuals per 100km^2 on Atherstone Nature Reserve. Aerial counts conducted on Atherstone in 2014 counted one leopard individual (Johan Kruger, *pers comm, 2021*). However, aerial counts are known to underestimate elusive species (Jachmann 2002). The number of independent captures and higher detection probabilities recorded by the roadside cluster deployments in this study are better suited towards spatially explicit capture-recapture analysis (SECR), where individual identification is necessary, and more data are required (Allen et al. 2020). SECR methods are commonly used to conduct population size and density analyses, primarily focusing on large felid carnivores (Green et al. 2020). However, incorporating individually unidentifiable species into a SECR analysis is not possible; this is where N-mixture models are more appropriate (Royle 2004).

N-mixture models have been widely used in ecology, species conservation and monitoring and have increased in usage over the years, with many model extensions having been developed (Kery and Royle 2016). N-mixture models deal with imperfect detection. However, N-mixture models running data collected using targeted approaches, approaches that result in increased capture numbers and detection probabilities, can lead to overestimation due to the sensitive relationship between species capture numbers and detection probabilities (Royle 2004, Sollmann 2018). Typically, with camera trap projects, especially targeted camera trap projects, high capture numbers and detection probabilities are aimed for and more beneficial for species population analysis. However, the application of these targeted approaches to data collection on unidentifiable species is still being developed (Moeller 2017). My research shows that further development of N-mixture models is needed to accommodate the increased counts and detection probabilities associated with targeted approaches. Only when camera trap deployment arrays are non-targeted or record low independent captures and detection probabilities should N-mixture models be considered for population analysis.

Space use modelling represents another practical solution for utilizing non-target species data. Space use in camera trap studies is defined as the proportion of the total number of camera trap sites occupied by a species, estimated whilst adjusting for imperfect detection when camera traps are not independent of each other (MacKenzie et al. 2004). It is an important and extensively used concept in ecology (MacKenzie and Royle 2005) and is routinely used for modelling of habitat relationships and metapopulation studies (Guillera-Arroita, et al. 2010). Space use analysis on the regular Snapshot grid deployment array and roadside Panthera cluster deployment array data collected on Pilanesberg and Atherstone revealed that both leopard and brown hyaena space use is not dependent on any single covariate used (Table 3.4, 3.6, 3.9, 3.12). Leopard and brown hyaena space use is likely due to a combination of multiple variables such as prey and predator densities, vegetation types, and distances to water (Williams et al. 2021). Constant space use combined with varying detection according to vegetation type was the best ranking models for the regular grid deployment array leopard and brown hyaena Pilanesberg and Atherstone data (Table 3.5, 3.10). Camera traps deployed in open areas with sparse vegetation are more likely to detect leopard and brown hyaena that are in the area compared to camera traps deployed in dense vegetation, in which leopard and brown hyaena would be harder to detect. Although not the best ranking model, leopard did show some preference for occupying denser vegetation types than open areas according to the regular grid deployment array Atherstone data (Table 3.9).

Constant space use combined with varying detection according to distance to road was the best ranking models for the roadside cluster deployment array leopard and brown hyaena Pilanesberg data (Table 3.7). Capture numbers and the detection probability for each species was highest close to tar or dirt roads. Carnivores are known to use roads to traverse their territories, which is why camera traps deployed closer to roads recorded higher capture numbers and detection probabilities (Mills 1990, Thorn et al. 2011, Zimmermann et al. 2014, Welch et al. 2016). Some of the regular grid deployment and roadside cluster deployment brown hyaena space use models run using data collected on Pilanesberg recorded identical AIC values (Table 3.4 and 3.6). The identical AIC values could be due to many reasons, such as brown hyaena density being high enough for each covariate model to record the same amount of variation, all of which recorded little to no variation (see *p-values*, Table 3.4 and 3.6).

Brown hyaena recorded higher detection probabilities closer to water sources according to the Atherstone roadside Panthera cluster deployment (Table 3.12). The data was collected during the dry season, during which water in some regions of Atherstone are known to be highly seasonal (Seloana et al. 2017). Many carnivore and herbivore species are known to be water dependent during dry seasons and are more likely to occupy areas surrounding water sources (Smit et al. 2017). More research is needed to infer on leopard and brown hyaena space use drivers, since my analysis was limited to single covariate models due to species capture numbers.

The initial estimate and space use analysis for leopard and brown hyaena in two protected areas in northwestern South Africa based on two different deployment arrays presented important findings. This study aimed to provide empirical evidence supporting the use of N-mixture models to estimate the population sizes of both naturally marked and unidentifiable species. However, further development is needed to accommodate the higher count numbers and detection probabilities associated with targeted camera trap deployments to accurately estimate an elusive species population size using N-mixture models. N-mixture models have a lot of potential and have been successfully utilized in previous studies to conduct population analysis (Kidwai et al. 2019, Della Rocca et al. 2020). This current study highlights the importance of being aware of the effect of a specific deployment design on the estimates produced by an available method such as N-mixture model population analysis. Over-estimated population sizes and inconsistent population trends, often due to data deficiencies (Groom et al. 2014), influence important managerial decisions, and this study shows how easy it is for population over-estimation to occur.

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Chapter 4

Synthesis

Summary

New methods for data acquisition are becoming available, and these methods allow the development of accurate, robust techniques that will aid in answering previously unanswered questions in a non-invasive manner (Schipper et al. 2008, Ripple et al. 2014, Rich et al. 2017). The development of camera trap technology has allowed the non-invasive collection of various types of new data. These new data types provided new opportunities and methods to analyze broad ecological concepts and processes on spatial and temporal scales (Morant et al. 2020). However, valuable camera trap data on other wildlife species are often not analyzed because those species are individually unidentifiable (Gubbi et al. 2019). Camera trap studies use different grid deployments and approaches to estimate population sizes, abundances and assess spatio-temporal space use patterns (Thorn et al. 2011, Cove et al. 2013, Rovero et al. 2014, Kays et al. 2020). However, data collected from camera trap studies are often used to estimate abundances and densities of cryptic species and naturally marked animals (Foster and Harmsen 2012, Burton et al. 2015, Gubbi et al. 2019). Valuable camera trap data on individually unidentifiable wildlife species is often not analyzed (Gubbi et al. 2019). Chandler and Royle (2013) indicated that individual identification of a species is not necessary for estimating population sizes and densities. These analyses can be conducted using software packages such as 'Unmarked' and applied to camera trap data collected from various deployment arrays (Fiske and Chandler 2011). Methods which use presence-absence data over multiple survey occasions (Royle–Nichols Abundance Induced Heterogeneity model, Royle and Nichols 2003), or species abundance over multiple surveys without marking individuals, have been used to estimate population size (Royle Repeated Count model, Royle 2004, Royle et al. 2004, Chandler 2013, Chandler and Royle 2013).

Obtaining demographic data on and monitoring unidentifiable species, which are also typically elusive, remains challenging (Pitman et al. 2017). Collecting demographic data can be expensive (Morin et al. 2018). However, with the development of camera trapping technology and knowledge, it is now possible to generate the demographic data needed for the population analysis of individually unidentifiable species, such as the lions (*Panthera leo,* Cusack et al. 2015). These methods are not commonly used, which motivated this study, to provide evidence supporting the use of N-mixture models to estimate population sizes as these models can be used to research both identifiable and unidentifiable species.

Thus, considering camera traps as sampling units, I used N-mixture models to estimate the population sizes of leopard and brown hyaena across Madikwe Game Reserve, Pilanesberg National Park and Atherstone Nature Reserve. I wanted to better understand the methods and techniques used in regions where there are good data and understanding of these regions. For each sampling method considered I derived the detection histories of the two target species (detection: 1, non-detection: 0) and relative counts of individuals of leopards and brown hyaenas in N-mixture models with Poisson error distribution (function 'pcount' in the R package 'Unmarked'). I used the same covariates of detection probability and abundance for all three of the sampling methods used in this study. Furthermore, for each sampling method, I estimated posterior distributions of the latent abundance by using empirical Bayesian methods (function 'Ranef' in the R package 'Unmarked'), which derived robust leopard and brown hyaena population sizes.

My research objectives were centred around comparing population size estimates from N-mixture models to known population sizes of two elusive species and investigating the influence different non-invasive camera trap deployment arrays have on N-mixture models.

I utilized data from a sequential baited/non-baited clustered camera trap survey, a non-baited cluster camera trap survey (run by Panthera, Panthera 2021) and a non-baited regular grid camera trap survey (run by Snapshot Safari (Pardo et al. 2021)) to estimate the population size of brown hyaena and leopard using N-mixture models across three fenced protected areas, namely Atherstone Nature Reserve, Madikwe Game Reserve and Pilanesberg National Park.

Concluding remarks

In conclusion, population analysis is an essential tool for conservation management. This study focused on population size estimation of two elusive species using N-mixture models. A method that can potentially be applied to unidentifiable species population analysis. This study has shown the potential N-mixture models can have on future unidentifiable species population analyses and management. Using a non-targeted approach, management may be able to analyze populations and adjust management strategies for elusive unidentifiable species.

N-mixture models provided plausible leopard and brown hyaena population size estimates when using the regular deployment array data. Leopard and brown hyaena population size estimates generated from the targeted baited/non-baited sequential deployment and the roadside cluster deployment arrays were overestimated. This is due to the targeted approaches recording higher numbers of captures and higher detection probabilities which inflated the population size estimates. This is why the use of N-mixture models should be cautioned because generally, higher capture numbers and detection probabilities are favoured when researching a species. N-mixture models can only be applied to elusive, cryptic species and capitalize on the relationship between the population size and their subsequent detection. This is why targeted camera trap studies inflate population size estimates due to increased detection probabilities and count numbers.

This study highlights the importance of accurate population analysis. Over-estimated population sizes and inconsistent population trends (often due to data deficiencies), influence managerial decisions. These decisions that are made using these data are likely to negatively impact the species. These managerial decisions won't only affect the species population directly, but also the habitat in which the species is found and other species that occupy the same habitat. For this reason, robust methods researching, analyzing, and estimating species populations are essential for conservation management on a species level.

Key research findings and management implications

My research found that N-mixture models run using data from the sequential baited and non-baited camera trap deployment array and the roadside cluster deployment over-estimated leopard and brown hyaena population sizes across all the study sites (Chapter 2 and Chapter 3). The regular deployment array provided plausible estimates across all three of the fenced protected areas and were closely matched to previous population size estimates made by van Dyk and Slotow (2003) and Williams et al. (2021).

The two targeted approaches, sequential baited and non-baited deployment, and roadside cluster deployment, were more efficient in collecting raw data, recording more independent captures over shorter periods of time. The targeted approaches recorded higher capture numbers and species detection probabilities. Most researchers aim for higher species capture numbers and detection probabilities. My study found that N-mixture models require capture numbers and detection probabilities that represent the study species population size in reality. Leopard and brown hyaena are often regarded as elusive and cryptic species (Mills 2019), and without a targeted approach such as Honiball et al. (2021), capture numbers and detection probabilities will generally be low, which favour the use of N-mixture models. This is evident by the regular deployment N-mixture popular size estimates that are closer to estimates made by van Dyk and Slotow (2003), Honiball et al. (2021) and Williams et al. (2021). Higher capture numbers and detection probabilities favour the use of spatially explicit capture-recapture models in estimating population sizes, which are the gold standard for population analysis (Green et al. 2020). The only requirement for spatially explicit capture-recapture analysis is that target species be individually identifiable (Green et al. 2020). With appropriate equipment, leopards could be individually identifiable, I.e., Panthera camera trap data (Balme et al. 2009, Chapman and Balme 2010, Strampelli et al. 2020), yet brown hyaena are not often individually identifiable and fewer studies represent estimates (Kent and Hill 2015)

Population sizes and estimates for cryptic species are often overestimated (Gustafsson et al. 1999, du Preez 2014, Esteban et al. 2017). This can lead to management decisions which have negative impacts, such as over harvesting of species (Gustafsson et al. 1999, Niel and Lebreton 2005). The evidence from my research cautions the use of N-mixture models to conduct population analysis using camera traps due to the model sensitivity, seeing the models are reliant on detection probability and capture numbers. I found the models to be overly sensitive to the different individual camera trap grid deployment methods, which reflected in the results of the thesis. If one camera trap records significantly more captures than other cameras (i.e., animals denning nearby), this could significantly influence the results of the analysis, leading to overestimates of population sizes. The use of N-mixture models in analyzing camera trap data should only be considered when capture numbers and detection probabilities are too low for other analytical methods (Ficetola et al. 2018). Camera trap deployments should rather be targeted towards the study species, deployments that best ensure capture numbers and detection probabilities. Further development of analytical methods is needed to accurately estimate an unidentifiable species population size using camera trap data. N-mixture models have a lot of potential and have been successfully utilized in previous studies to conduct population analysis (Kidwai et al. 2019, Della Rocca et al. 2020).

Future research opportunities

Opportunities for future research related to this study:

- Investigating the impact different interval distances between camera traps has on capture numbers, detection probabilities and occupancies.
- A targeted camera trap deployment design with spatially independent camera trap sites could be used to conduct long term population analysis and investigate how populations respond to different seasonal, climatic, and environmental conditions.
- The large population sizes of brown hyaena on Pilanesberg National Park and Atherstone Nature Reserve provide an opportunity to study how this species exists at high densities in a closed system.
- Investigation into the effect that fence permeability has on species density estimates. Williams et al. (2021) recorded significant decreases in density estimates when accounting for fence permeabilities of reserves.

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Supplementary Material

Appendix 1: *P-values* for varying detection probabilities according to vegetation type recorded per species per grid deployment on Pilanesberg National Park. RGDA = Regular Grid Deployment Array. RCDA = Roadside Cluster Deployment Array.

Vegetation Type	Leopard		Brown Hyaena	
	RGDA *p-value*	RCDA *p-value*	RGDA *p-value*	RCDA *p-value*
Open water point	0.99	NA	0.10	NA
Savannah woodland	0.34	1.00	0.83	0.26
Grassy woodland	0.39	0.68	0.87	0.01
Riverine area	0.004	0.68	0.002	0.03
Grass plain	0.0001	NA	0.0007	NA
Rocky outcrop	0.02	NA	0.00002	NA
Sodic site	0.20	1.00	0.24	0.00007
Open savannah	0.058	0.81	0.007	0.004
Savannah grassland	0.99	0.36	0.17	0.08
Gully	NA	0.94	NA	0.48

Appendix 2: *P-values* for varying detection probabilities according to vegetation type recorded per species per grid deployment on Atherstone Nature Reserve. RGDA = Regular Grid Deployment Array.

Vegetation Type	**Leopard**	**Brown Hyaena**
	RGDA *p-value*	**RGDA *p-value***
Shrubland	0.99	0.72
Bluethorn thicket	0.99	0.78
Old lands	0.99	0.78
Sicklebush area (sparse)	0.43	0.82
***Grewia* shrubland**	0.32	0.68
Sicklebush thicket	0.68	0.79
Dam piosphere	0.0003	0.65
***Vachellia tortillas* area**	0.96	0.66
Thornveld	0.99	0.74
Grassy shrubland	0.98	0.99