

# **Estimating leopard density in a coastal protected area of the Western Cape, South Africa**

by Ayesha Hargey



Thesis presented for the Degree of Master of Science

in the Department of Biological Sciences, Faculty of Science at the Institute for Communities  
and Wildlife in Africa, University of Cape Town

**Prof. M. Justin O'Riain**  
Supervisor  
iCWild



**Dr. Gareth Mann**  
Co-Supervisor  
Panthera

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

# Declaration

I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.

I have used the Harvard convention for citation and referencing. Each contribution to, and quotation in this thesis from the works of other people has been attributed and has been cited and referenced. I have not allowed and will not allow anyone to copy my work with the intention of passing it off as their own work.

This thesis is my own work.

Signed

Signed by candidate
---------------------

**Ayesha Hargey**

HRGAYE001

11<sup>th</sup> September 2022

# Table of Contents

<b>Declaration</b>	<b>2</b>
<b>Table of Contents</b>	<b>3</b>
<b>Dedication</b>	<b>5</b>
<b>Abstract</b>	<b>6</b>
<b>Introduction</b>	<b>7</b>
Current trends and threats to large carnivores	7
The status of leopards in Southern Africa and the Western Cape	15
The status of the African penguin globally and locally in De Hoop	19
Objectives of the study	21
<b>Methods and Materials</b>	<b>23</b>
<b>Study area</b>	<b>23</b>
History of the De Hoop Nature Reserve	23
Climate	23
Hydrology	24
Geology	24
Vegetation	25
Fauna	26
Survey design	26
Data processing and analyses	29
Processing leopard images and estimating leopard density	30
SECR models and parameters	32
<b>Results</b>	<b>34</b>
Camera trapping array and species inventory	34

Species accumulation curve	38
Predator detections	38
Activity patterns	41
Density of leopard in De Hoop	47
<b>Discussion</b>	<b>48</b>
Species inventory	48
Leopard density in De Hoop	51
Penguins and predation risk in De Hoop	59
Conservation recommendations and implications	60
<b>Supplementary Information</b>	<b>62</b>
<b>Appendix A: Species Checklist</b>	<b>63</b>
<b>Appendix B: SECR Model Code</b>	<b>64</b>
<b>References</b>	<b>69</b>

# Dedication

---

*This thesis is dedicated to the leopards of the Western Cape:*

*Stay wild — and I hope this helps.*

---

## Abstract

Leopards (*Panthera pardus*), like many other large carnivores, are facing increasing threats including habitat degradation, illegal hunting, and persecution for perceived or actual livestock depredation. Protected areas remain the cornerstone of conservation efforts throughout the world but they are not a panacea and recent studies have shown declining populations within many protected areas of South Africa. Efforts to improve leopard conservation are hampered by a lack of reliable and repeated estimates of population size across their distribution, which limits an understanding of population dynamics and the potential drivers of declines. Monitoring efforts that produce density estimates are invariably the most informative for reserve managers who work with endangered species and are responsible for regional conservation planning – especially in cases where both predator and prey are of vulnerable populations. A small coastal area within the De Hoop Nature Reserve has been fenced off from the reserve with the goal of establishing a mainland breeding colony for the endangered African penguin (*Spheniscus demersus*). The fence is designed to reduce the threats posed by terrestrial predators, particularly leopard and caracal (*Caracal caracal*). Both feline species engage in supernumerary killings of penguins due to their poor predator response and are thus of special relevance to reserve managers and NGOs committed to their conservation. In this study, I conducted a camera trap survey in the De Hoop Nature Reserve, along the south coast of the Western Cape with the primary objective of estimating the density of leopards and the secondary goal of understanding the distribution, abundance, and activity patterns of leopard and caracal relative to the proposed penguin colony. I deployed 40 paired camera trap stations over 2457 trap nights and captured 312 independent images of the target taxa. A sample-based species accumulation curve revealed a clear asymptote indicating adequate sampling effort and a total of 24 medium and large mammal species. Both leopard and caracal had high relative abundance indices at camera stations close to the designated penguin colony. I recorded 111 independent images of leopards, of which six males and one female could be reliably identified. I derived a density estimate of  $0.18 \pm 0.07$  individuals per 100km<sup>2</sup> which is lower than estimates for protected areas in the eastern and northern regions of South Africa, and lower too than other estimates obtained from the fold mountains of the Western Cape. Coastal fynbos has low productivity and supports a low prey biomass relative to other biomes in South Africa, and thus the density may be justifiably lower than in other more productive habitat types. Of immediate concern is the heavily skewed sex ratio (6M:1F) and low total population size which — together with a permeable boundary fence and known persecution of leopards on neighbouring farms — makes this population vulnerable to both stochastic events and edge effects. Lethal management of leopards that threaten penguins would not be sustainable and thus it is important that a non-lethal barrier has been implemented as it offers the prospect of coexistence between two endangered and charismatic species.

# Introduction

## *Current trends and threats to large carnivores*

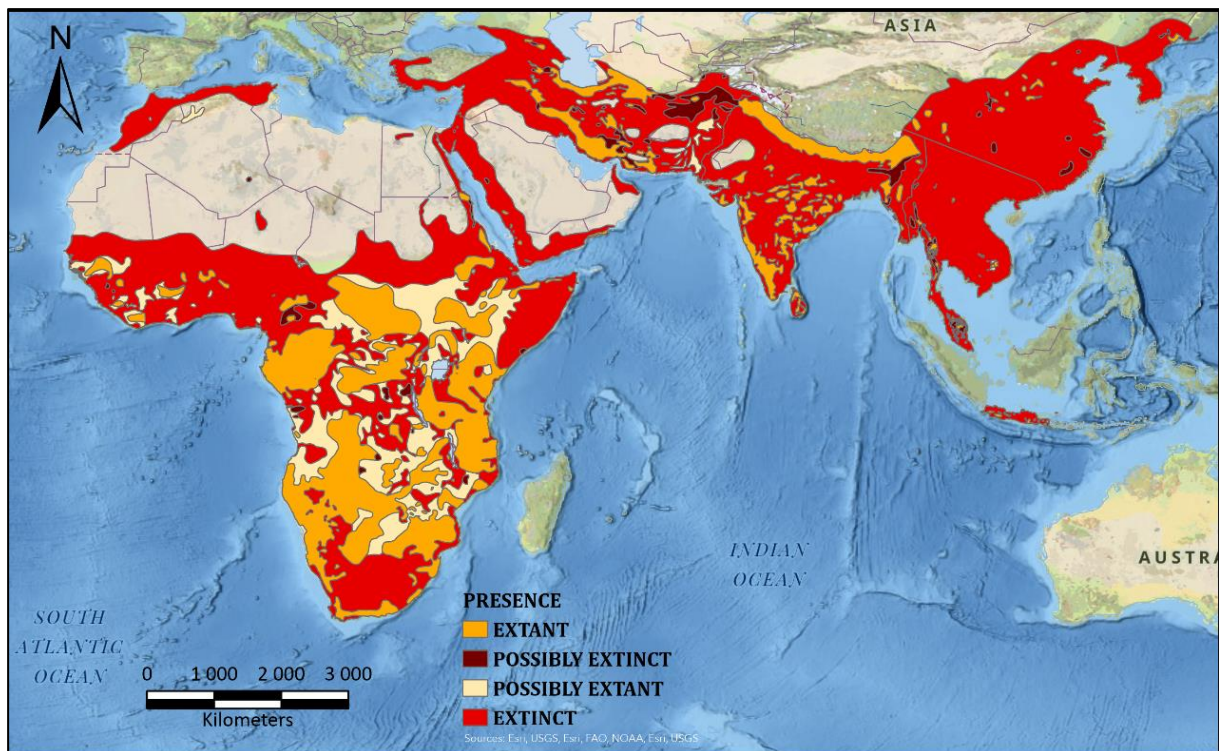
Apex predators are important to the functioning of a healthy ecosystem, maintaining species diversity by preventing competitive exclusion and exerting top-down trophic pressure on other predators and prey (Ripple and Beschta, 2008). Apex predators within the order Carnivora have been the subject of human fascination for millennia despite an evolutionary history of both competition with and predation on humans (Karanth and Chellam, 2009). Modern perspectives of large carnivores are divisive, varying from intrigue and admiration to superstition and fear (Miller et al., 2016). As their dietary requirements and behaviours conflict with those of the growing human population, apex predators have been actively persecuted globally (Woodroffe, 2000). Declines in carnivore populations lead to knock-on ecological consequences, such as trophic downgrading where ecosystems suffer a reduced food chain length, altering plant composition and productivity (Estes et al., 2011). Simultaneously, large carnivores provide a range of direct and indirect benefits including their significance as a cultural symbol and the positive impacts they have on tourism, which is the basis of many developing countries (Lindsey et al., 2007).

Globally, anthropogenic threats to large carnivores are increasing and Africa is no exception, with both lion (*Panthera leo*) and leopard (*Panthera pardus*) categorized as Vulnerable on the IUCN Red List (Stein et al., 2020) (Figure 1). Lions have suffered great range loss over parts of the savannah in East and West Africa, and their population has declined at an estimated 42% over the last two decades (Bauer et al., 2015). Similarly, leopard range now only comprises between 25–37% of their historic range (Jacobson et al., 2016), but it is worth noting that certain subspecies are of higher risk of extinction



such as the Arabian Leopard (*Panthera pardus nimr*) — listed as Critically Endangered, and restricted to small, fragmented patches of the Arabian Peninsula (Perez et al., 2006). The African leopard (*Panthera pardus pardus*), and subject of this study, has lost at least 37% of its range in Sub-Saharan Africa (Ray et al., 2005). Leopards have become locally extinct in areas of high habitat transformation and development (Swanepoel et al., 2016) and throughout much of their current distribution they persist in fragmented populations. The primary causes for declining leopard populations globally are similar to those identified for other large carnivores such as lions (Bauer et al., 2015), cheetah (*Acinonyx jubatus*) (Durant et al., 2017), jaguar (*Panthera onca*) (Paviolo et al., 2008), grizzly bears (*Ursus americanus*) (Proctor et al., 2005) and Amur tiger (*Panthera tigris altaica*) (YuTian et al., 2011).

These threats include habitat loss and fragmentation, largely as a result of agricultural land use (Nowell and Jackson, 1996; Ray et al., 2005; Jacobson et al., 2016). Agricultural land in Sub-Saharan Africa is projected to increase by an estimated 51 million hectares by 2050 (Alexandratos and Bruinsma, 2012) which will likely contribute to the further range loss of the carnivore populations. Range contraction and isolation ultimately limits population growth and can have long-term detrimental effects, such as inbreeding depression in the absence of migration between populations (Norén et al., 2016).



**Figure 1.** Leopard (*Panthera pardus*) distribution map created from the leopard extant range (orange) and extinct range (red) (IUCN, 2019).

Another major anthropogenic cause of large carnivore decline globally is the depletion of prey resources (Wolf and Ripple, 2016; Barber-Meyer et al., 2013). While leopards are known for their broad diet, with more than one hundred recorded prey species, their preferred prey is herbivores between 10 and 40 kg that typically live in small groups (Hayward et al., 2006; Noack, 2019). Medium and large herbivore populations have drastically decreased due to the exploitative utilization of bushmeat (Brashares et al., 2004), with an average decline of 59% over 35 years in West, East and Southern Africa (Stein et al., 2020). The unregulated nature of bushmeat harvesting poses a largely unmeasured risk to predators, and can undermine conservation efforts (Rogan et al., 2017). Indiscriminate hunting methods such as the use of snares frequently results in high by-catch mortality of large predators (Becker et al., 2013).

When faced with declining natural prey populations leopards may increase their intake of more 'riskier' sources of prey, such as livestock (Khan et al., 2020). This is often linked with poor husbandry and management practices (Inskip and Zimmermann, 2009), such as ineffective herding and inadequate (or a lack of) protective pens at night (Wang and Macdonald, 2006). Consequently, 95% of leopard mortalities in unprotected populations are linked to farmer retaliation for livestock losses (Martins and Martins, 2006; Swanepoel et al., 2015). Even a few livestock lost can represent a significant economic impact for marginalized and vulnerable communities (Dickman, 2010). However, Treves and Karanth (2003) point out that the severity of threats posed by leopards to most farmers are typically inflated and thus the levels of persecution they face, including the poisoning of carcasses (Jacobson et al., 2016; Ogada, 2014) is seldom justified.

There are non-lethal alternatives that allow both humans and large predators to coexist (Treves and Karanth, 2003). Examples include predator-proof fencing around kraals, guard dogs, and the use of traditional shepherding techniques (Miller et al., 2016).

While all of these methods have their limitations (e.g., Drouilly et al., 2020) it is possible to improve tolerance of the local community through education and ensuring adequate numbers of natural prey (Jacobson et al., 2016; Linnell et al., 2001) while simultaneously applying these methods.

Despite their fundamental ecological importance (Ripple and Beschta, 2006), there is a global research deficit on providing reliable and repeatable estimates for population density of many large carnivore species (Ray et al., 2005) and leopards in particular (Rogan et al., 2019). This has been identified as an area of concern as historically decision-making relied on expert opinion rather than empirical evidence, making it difficult to assess the success of conservation interventions as well as being unable to

identify further areas of concern (Balme et al., 2014). Reliable abundance estimates serve additional importance because they inform conservation practices and management decisions such as trophy hunting (Chapman and Balme, 2010). Poorly managed trophy hunting and illegal harvesting can reduce the number of reproductively active individuals, lowering the genetic diversity and ultimately population viability of isolated populations (Naude et al., 2020a). The inverse of this is currently seen in many species, where reliance on inaccurate abundance counts have led to poor management decisions (Katzner et al., 2011). It is only through robust density estimates as well as knowledge of their activity patterns and population dynamics, such as sex ratio, that effective management of leopards can take place (Balme et al., 2019).

Private land is an integral component of the overall conservation capacity of South Africa (Bond et al., 2004), and conflict management efforts such as traps, poisoning, translocation and execution of problem animals are ultimately limiting the overall persistence of carnivores across the country (Lindsey et al., 2004). These impacts often manifest as harmful edge effects for protected areas which can ultimately decrease their population viability (Balme et al., 2010). This highlights a potential area of engagement, where ventures promoting tolerance such as education and financial mitigation from livestock predation can be considered (Breitenmoser et al., 2005). Similar initiatives have brought success in increasing tolerance of lions in communities in Kenya (Western et al., 2019), and could go a long way to overturning negative perceptions of these keystone species (Romañach et al., 2007). As only 20% of South Africa is suitable for leopard habitat, and with the knowledge that most of this habitat occurs outside of protected areas, maintaining the connectivity between these fragmented subpopulation is important (Swanepoel et al., 2013).

Concern has increased over the continued decline in leopard numbers in South Africa (Jacobson et al., 2016). Unsustainable harvesting for trophy hunting (Packer et al., 2009) — both legal and illegal — as well as the use of their body parts for their supposed medicinal (Nieman et al., 2019), spiritual (Williams and Whiting, 2016) and social prestige qualities (Naude et al. 2020a), are causing a decrease in overall leopard numbers and population health (Naude et al., 2020b). Negative human-leopard interactions in the agricultural sector leads to indiscriminate persecution, involving the use of gin traps, poisoning and retaliatory hunting, all of which impact leopards negatively (McManus et al., 2014). If human pressure on protected populations continues to increase without a proportional increase in protected habitats, so too will resource competition, fuelling further negative leopard-human interactions.

Most published leopard studies have focussed on theoretical aspects including leopard behaviour, diet and general ecology (Balme et al., 2014). While these studies can potentially be beneficial overall (Buchholz, 2007), they lack the immediate and practical guiding policies of applied studies and thus have limited conservation value (Knight et al., 2008). There is an urgent need for more applied studies that focus on informing and prioritizing conservation policy, guiding management and ultimately contributing to targeted research that directly addresses conservation threats and their mitigation (Knight et al., 2008).

Recent advances in methodological and statistical approaches have continued to improve the repeatability and accuracy of population density estimates. Historically inaccurate estimations have led to inflated population numbers (Martin and de Meulenaer, 1988) which can have serious implications for conservation management efforts and policy recommendations of sensitive issues such as the setting of trophy

hunting quotas (Trouwborst et al., 2019). With Sub-Saharan Africa's human population projected to grow by another two billion by 2050 (UN, 2013), leopards and other sympatric carnivore populations will suffer unless adequate management intervention initiated (Woodroffe, 2000).

Large carnivores, such as leopards, present a particular set of challenges when it comes to monitoring due to their low population density, large home ranges, elusive behaviour and solitary nature (Treves and Karanth, 2003). Many assumed 'stable' extant populations are rarely monitored which makes it difficult to scientifically evaluate changes in population status associated with increasing anthropogenic impacts (Mann et al., 2020). Following the seminal work by Karanth and Nichols (1998) camera trap surveys, together with capture-recapture models have emerged as an ideal cost-effective approach for population and density estimates of elusive but individually recognisable carnivore species. There are now a host of individually distinguishable species that benefit from this type of population estimation approach, including jaguar (Boron et al., 2016), snow leopard (*Panthera uncia*) (Alexander et al. 2015), lynx (*Lynx lynx*) (Weingarth et al. 2015), serval (*Leptailurus serval*) (Taylor, 2020), clouded leopard (*Neofelis nebulosa*) (Penjor et al., 2018), ocelots (*Leopardus pardalis*) (Penido et al., 2019) and fossa (*Cryptoprocta ferox*) (Murphy et al., 2018). These techniques have also been used to obtain reliable density estimates of leopards in South Africa and these data have informed survey design of this study and enabled scientific authorities to set hunting quotas based on reliable data (Balme et al., 2009a).

Camera trap data also provide an opportunity to monitor activity patterns of both marked and unmarked species. All animals show activity patterning, which are driven by a host of biological, anthropogenic, and environmental influences (Ohashi et al., 2013;

Ordiz et al., 2017). Different species are able to exist in the same ecosystem through temporal niche partitioning which adjusts their movement and behaviour corresponding to a period of time (Nakabayashi et al., 2021), most commonly influenced by light (Ditmer et al., 2021; Nix et al., 2018). Further important factors influencing activity patterns are seen where sympatric carnivores reduce the threat of competition by changing their temporal activity pattern (Hearn et al., 2018), or when prey avoid predators (Ross et al., 2013). Most wildlife species, including predators, avoid spatial and temporal overlap with humans that occupy the niche of super-predators and generate fear (Smyth, 2022; Khan et al., 2020). Even the performance of fairly neutral activities like hiking and cycling is enough to generate a shift in wildlife towards nocturnal behaviour (Gaynor et al., 2018). As the apex predator of De Hoop, leopard behaviour would not be impacted by interspecific competition (Carter et al., 2015), while intraspecific competition and interference will be prevalent (Havmøller et al., 2019) and both males and females are predicted to avoid peaks in human activity (Frid and Dill, 2001).

Monitoring the activity patterns of leopards is one of the most important components of understanding non-lethal impacts of human activity in protected areas (Smyth, 2022). There is increasing evidence that predators will avoid humans both spatially (Ditmer et al., 2021) and temporally with the latter manifesting in a marked shift towards nocturnal behaviour, particularly when space is limiting (Clinchy et al., 2016; Gaynor et al., 2018). While spatiotemporal patterns are inherently complex and influenced by a host of factors such as temperature, moonlight and food availability, they can also be used within a before and after setting to understand the impacts of specific changes in anthropogenic activity patterns (Gaynor et al., 2018; Ohashi et al., 2013; Sévêque et al., 2020).

## *The status of leopards in Southern Africa and the Western Cape*

There is a common perception that leopards do not require high conservation priority due to their widespread distribution and ecological flexibility (Nowell and Jackson, 1996). This is however not the case, as the average range loss for leopards is between 63-75% globally, and 28-51% in Southern Africa with certain regional populations particularly vulnerable (Jacobson, 2016; Ray et al., 2005). Since their listing in 2002 as Least Concern, there have been two consecutive advancements of leopard on the IUCN Red List: to Near Threatened in 2008, and Vulnerable in 2016 (Stein et al., 2016).

Following historic range loss, only 20% of South Africa remains as suitable leopard habitat with only a third in protected areas, and leopard distribution is heavily fragmented into four sub-populations (Swanepoel et al., 2013). Only 12% of the leopard population is in national and provincial nature reserves, further highlighting the importance of privately owned protected areas in leopard conservation in South Africa (Lindsey et al., 2004; Bond et al., 2004).

The leopard populations of the Western Cape have an intrinsic vulnerability due to their low densities (Martins and Martins, 2006). The Red List of Mammals of South Africa, Lesotho and Swaziland estimates there to be a mature population size of between 120-371 leopards in the Western Cape (Swanepoel et al., 2016). Leopards are the last free-roaming top carnivore in the Eastern and Western Cape, with numbers declining because of large-scale habitat loss resulting in fragmentation of suitable habitat and the geographic isolation of individuals driving low-to-moderate gene flow (McManus et al., 2014). It is suspected that overall population declines may be greater than reported, as most estimates are from within protected areas, and leopard survival is higher inside (86%) than outside of protected area (57%) (Swanepoel et al., 2016). Even at the



maximum estimate, the leopard population for the Western Cape would still be too low to maintain viable genetic diversity (Traill et al., 2007). Many of these leopards are living outside of formally protected areas and are largely restricted to the Cape Fold mountains that provide a refuge from agricultural and urban land uses (Mann et al. 2020).

As part of a large-scale leopard population study in the Western Cape between 2011-2015, Devens et al. (2019) surveyed the greater Overberg and Cape Agulhas areas, which included the De Hoop Nature Reserve. Only eight individual leopards were identified in the region, and the mean density was calculated as  $0.17 \pm 0.10$  leopards per  $100\text{km}^2$ . This is in direct comparison to the two other sites surveyed, namely Langeberg which showed a mean density of  $0.5 \pm 0.10$  leopards per  $100\text{km}^2$  and the Garden Route which had  $0.38$  leopards per  $100\text{km}^2 \pm 0.17$  (Devens et al., 2019). These recent estimates are some of the lowest recorded for the Western Cape — with the highest ever recorded as 1.80-2.30 leopards per  $100\text{km}^2$  occurring in the Cederberg Mountains (Martins, 2010). One of the lowest known leopard density in the Western Cape occurs in non-protected areas of the semi-arid Little Karoo at 0.5 leopards per  $100\text{km}^2$  (Mann, 2014).



**Figure 2.** Adult male leopard, *Panthera pardus*, photographed using a Panthera camera trap while walking along a management road in the De Hoop Nature Reserve, South Africa.

It was noted by Devens et al. (2019) that none of the identified adult leopards remained strictly within the limits of protected areas, including individuals detected within the De Hoop Nature Reserve. Protected areas in the Western Cape only contain 30% of suitable leopard habitat, which demonstrates the importance of privately owned land for their conservation (Swanepoel et al., 2013). Few protected areas in the Western Cape are of sufficient size to host viable carnivore guilds (Breitenmoser et al., 2005). As their home range typically extends beyond the borders of a reserve, populations often suffer from detrimental edge effects caused by the surrounding non-protected land (Balme et al., 2010), with an estimated 15% of leopard deaths arising from humans (Swanepoel et al., 2015a). Leopards are highly vulnerable to anthropogenic mortality as a result of edge effects, with many factors contributing to this, including their preference for human-

modified landscapes such as roads (Athreya et al., 2003) and the ease with which they cross protected area boundary fences (Balme et al., 2010). While individual males may be able to disperse across fragmented habitat, leopards typically require large home ranges with low human impact (Fattebert et al., 2013). In extreme scenarios where persecution in the surrounding land is severe, populations sink into neighbouring areas and sometimes even experience local extinction within the protected area (Martins and Martins, 2006).

One of the main reasons for persecution of leopards in the Western Cape are the perceived and actual threats they pose to domestic livestock and endangered or rare wildlife (Swanepoel et al., 2015b). Occasionally leopards are captured and translocated away from areas where they are causing livestock losses (McManus et al. 2014) although the conservation success and welfare concerns make such interventions hotly debated (Weilenmann et al., 2010). Leopard and other carnivores such as caracal (*Caracal caracal*) have also been translocated in the Western Cape after preying on native endangered species such as the African penguin (*Spheniscus demersus*). An example of this occurred at the Boulders Beach colony in 2016 where an adult female caracal had killed an estimated 20 penguins in one evening and was subsequently captured and translocated to another part of the Peninsula (Nattrass and O’Riain, 2020). While this brought about a temporary reprieve for the penguins, until shortly afterwards predation continued at an even greater rate by a younger caracal assumed to be the offspring of the translocated individual (Saffer, 2016). This reveals that translocation is an inadequate management strategy when conducted in isolation from other management interventions, including those that prevent predators from gaining access to mainland colonies. Elsewhere in the world predators have been subject to lethal management when preying on endangered species (Roemer and Wayne, 2003) and more recently

caracals have been euthanised at the Boulders Beach colony when non-lethal efforts and translocation have failed to prevent ongoing penguin losses (Nattrass and O’Riain, 2020).

### *The status of the African penguin globally and locally in De Hoop*

As the only living penguin species on the continent, the African penguin is endemic to South Africa and Namibia, with three breeding regions: the Western Cape, the Eastern Cape and Southern Namibia (Underhill et al., 2006; Sherley et al., 2020). Historically, they were the most dominant species of seabird in the Benguela upwelling system (Waller, 2011). Today, their numbers have diminished to less than 5% of their historical population size causing them to be listed as Endangered (BirdLife International, 2020). As a charismatic species with high tourism demand, they are well-liked by the general public — this, combined with their important role in the functioning of marine ecosystems, has resulted in the African penguin receiving government intervention to halt their decline (Waller, 2011). However, a Biodiversity Management Plan — which was gazetted in 2013, and then revised in 2019 — has not prevented a further decline in numbers. To bolster numbers and halt the continued loss, government and other stakeholders have initiated a number of interventions such as the release of hand-reared chicks, the incubation of abandoned eggs, and of relevance to this study, the establishment of a new and protected mainland colony (Biodiversity Management Plan, 2019).

The Marine Protected Area of De Hoop was home to a colony of penguins in 2003, that bridged the gap between the penguin population on Dyer Island to the West and the colonies in Algoa Bay in the Eastern Cape (Underhill et al., 2006). The colony grew to 18 breeding pairs but was abandoned when predation by caracal occurred in 2008. Local

free-roaming carnivores such as leopards and caracals have been recorded to cause mass killings in other mainland colonies (e.g., Whittington et al., 1996; SANCCOB, unpublished), posing a risk to penguin colonies as far back as 1986 and as recently as 2016, where a leopard killed 33 penguins at the Stony Point colony in a single instance (CapeNature, 2016). However, this risk can be mitigated through the use of non-lethal barriers, with translocation and lethal management becoming only necessary if these fail to prevent the predators from accessing the coastal colony.

The main threat to African penguins is thought to be limited food availability, particularly along the West Coast of Southern Africa, as the distribution of their main prey has shifted onto the southern Cape coast (Waller, 2011). In line with the Biodiversity Management Plan, BirdLife South Africa, CapeNature and the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) have collaborated on efforts to re-establish the penguin colony in De Hoop. To prevent potential predation from causing abandonment of the breeding site, a predator-proof fence was constructed. Importantly, the colony site is in an area where acoustic fish surveys have consistently shown high abundance of fish (DFFE, unpublished) and penguin tracking studies have shown that penguins routinely forage in the area (BirdLife South Africa, unpublished). Additionally, the site is far from any major harbours, and thus there is less risk of oil spills (Wolfaardt et al., 2008). With the fence having been constructed, the first release of fledgling penguins at the colony occurred in June 2021. It is anticipated that these individuals will return to the colony to breed when they are sexually mature in approximately three to six years.



**Figure 3.** Fledgling penguin released at the De Hoop colony in June 2021 (Source: BirdLife South Africa)

### *Objectives of the study*

As a first step towards predation management, it was agreed that an assessment of predators in De Hoop of leopards and caracal in particular, would be important. In partnership with Birdlife South Africa and Panthera, I aimed to survey De Hoop Nature Reserve and establish the density of leopards and the relative abundance of other predators. The success of the De Hoop penguin colony will depend on the ability of the fence and other deterrents to limit potential predation events. In the Biodiversity Management Plan (2019), it is stated that “colony-specific interventions” would become necessary, including the “management of predation”. This study is important to understand the distribution (e.g., relative to the penguin colony) and status of leopard and caracal within this isolated protected area. Furthermore, comparisons with a previous density estimates of leopards in De Hoop (Devens et al., 2019) will be

important to understand whether the population is stable, increasing or decreasing. By analysing the relative abundance of leopard, caracal and humans at different camera stations through the reserve and comparing the time stamps of detection I can explore evidence for both spatial and temporal overlap of predators and humans. I predict that both caracal and leopard will be more abundant in areas with lower human presence and that caracal will avoid areas frequented by leopards. Additionally, I predict that both caracal and leopard will avoid peaks in human activity and caracal will avoid peaks in leopard activity. Low leopard numbers or highly skewed sex and age ratios may render management options such as translocation or lethal management as undesirable or harmful. While it is difficult to determine the abundance of unmarked predator species such as caracal, an understanding of the distribution and relative abundance of all potential penguin predators is important for understanding the long-term risks and viability of a re-established colony of these endangered birds. Lastly, my study will provide a species inventory of medium and large mammals for the De Hoop Nature Reserve which may assist with management decisions and is important for mapping biodiversity both in protected areas of the Western Cape, and in the country as a whole.



# Methods and Materials

## Study area

### *History of the De Hoop Nature Reserve*

Established in 1976, the De Hoop Nature Reserve has grown with ongoing land acquisitions and is now 34 000 hectares in size (CapeNature, 2016). It was later proclaimed a World Heritage Site on account of being part of the Cape Floral Region Protected Areas (Act No. 49 of 1999) and thus critical to the ongoing conservation of the Cape Floral Kingdom. The reserve contains sites of archaeological importance, with excavations of early *Homo sapiens* hand-axes and shell middens estimated to be of the Early and Middle Stone Age (c. 200 000 – 30 000 years). More recently, the land was used primarily for sheep farming and the breeding of cattle and horses (CapeNature, 2016). As a result, extensive grazing lawns of *Cynodon dactylon* exist in proximity to the original farmhouses and at various watering and mustering points throughout the reserve (Radloff, 2008). In 1990, a Marine Protected Area was officially proclaimed along the coastline of the Reserve (Government Gazette No. 12667). De Hoop is frequented by tourists, with the 5-day hiking Whale Trail being a popular attraction. Tourism activity is concentrated on the western side of the reserve, and there are numerous amenities including accommodation, restaurants, campsites and historical buildings, connected by networks of tarred and gravel roads.

### *Climate*

The De Hoop Nature Reserve is in the Overberg region, on the south coast of the Western Cape, South Africa (34°26'S, 20°30'E). It has a Mediterranean climate with an average rainfall of 428mm per year with most precipitation occurring in winter, peaking



in August (CapeNature, 2016). The hottest month is February with a mean maximum temperature of 24°C and mean minimum temperature of 20°C. The coldest month is August with a mean maximum temperature of 10°C and mean minimum temperature of 20°C (Cape Nature, 2016). The mean daily maximum temperature reaches 26.5°C in summer, and the mean minimum temperature reaches 13.0°C in winter.

### *Hydrology*

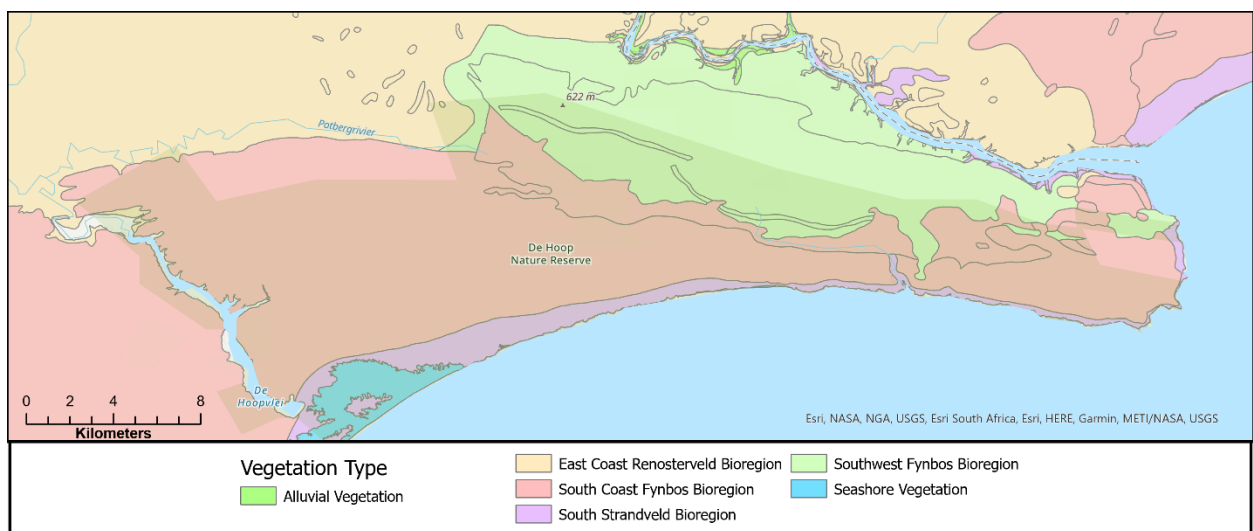
The coastline includes a Marine Protected Area that stretches three nautical miles (5km) into the Indian Ocean forming part of the Agulhas current ecosystem. The reserve also comprises a series of highly productive wetland clusters known as the De Hoop Vlei, an internationally recognized Ramsar site, with inflow from the Sout River.

### *Geology*

The De Hoop Nature Reserve is composed of three distinct geological substrates: sandstones of the Table Mountain Group, limestones of the Bredasdorp Group and shales of the Bokkeveld Group (Coetzee, 1993; Radloff, 2008). Most of the reserve is overlain with Bredasdorp limestone from the late Tertiary, supporting an endemically rich fynbos type that only grows in alkaline soils. The limestone and sandstone cliffs are rugged and eroded. The Table Mountain Group sandstone underlie the Bredasdorp Group, and form the inselberg, Potberg Mountain (611 m altitude), in the north-east. The isolation of this mountain has led to a high degree of endemism of mountain-specific species, adapted to the acidic and nutrient-poor soil. Surrounding hard dunes can reach up to 100m high, with the coastal dune strandveld adapted to the loose sandy environment.

## Vegetation

De Hoop Nature Reserve (Figure 4) has the largest conserved area of lowland fynbos in the Western Cape, and an estimated 1500 species of endemic plants that comprise the highly diverse Cape Floral Kingdom (Mucina and Rutherford, 2007). Of these, 108 are listed as Threatened, 34 occur only in the region and 14 were recently discovered and still in the process of being classified. The reserve is heavily invaded by alien vegetation, most commonly Port Jackson (*Acacia saligna*), and there are several on-going biological control programs in an effort to mitigate this (CapeNature, 2016).



**Figure 4.** Vegetation map of the De Hoop Nature Reserve, South Africa.

De Hoop Limestone Fynbos dominates the reserve and is where high rates of endemism of the Cape Floral Kingdom is observed. The dominant species include *Protea sp.* such as Bredasdorp Protea (*Protea obtusifolia*), silky conebrush (*Leucadendron meridianum*) and pincushion (*Leucospermum truncatum*). Albertina Sand Fynbos (Vulnerable) is also present, including restioid species such as *Thamnochortus insignis* and low, ericoid shrubs such as *Diosma guthriei*. Overberg Dune Strandveld characterized by strong populations of Sour Fig (*Carpobrotus edulis*), Blombos (*Metalsia muricata*) and Bitou (*Chrysanthemoides monilifera*).

## Fauna

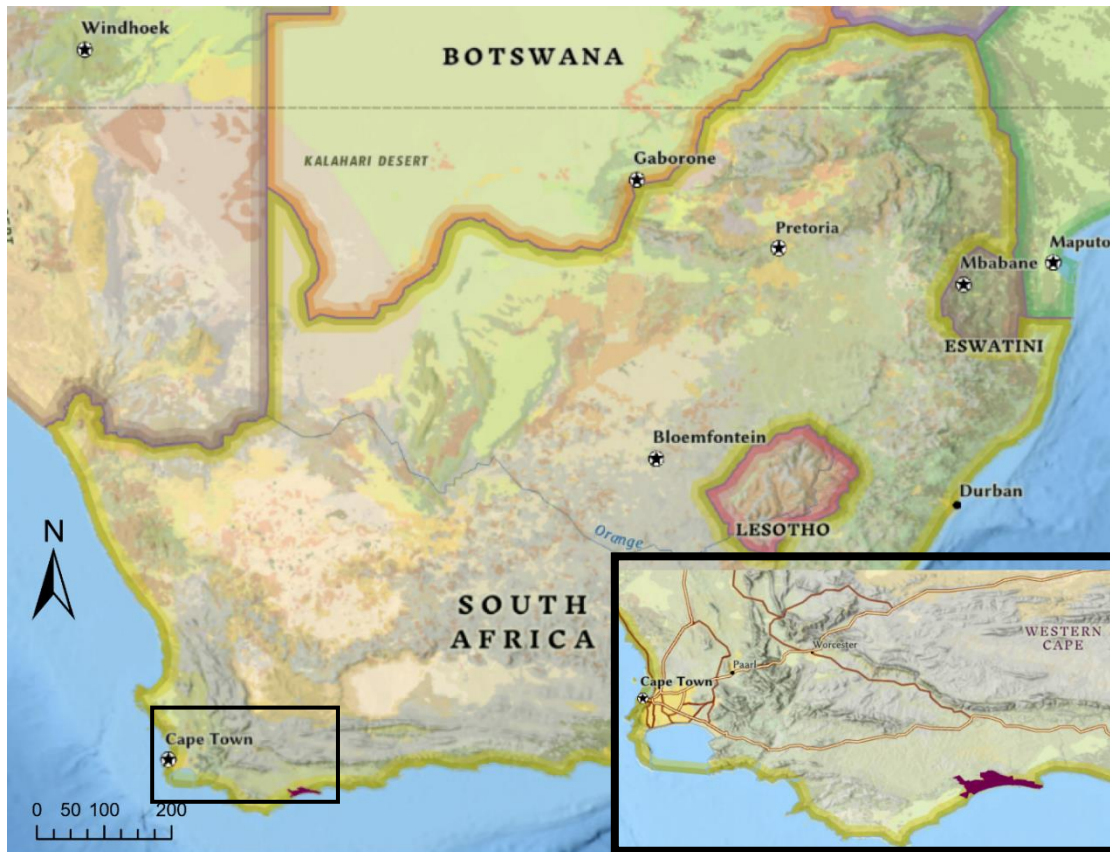
The reserve is similarly rich in faunal diversity. Approximately 260 bird species have been recorded, 35 of which are threatened — including the only breeding colony of the endangered Cape Vulture (*Gyps coprotheres*) in the Western Cape. Two Vulnerable terrestrial reptile species occur in the region: southern adder (*Bitis armata*) and the Cape dwarf chameleon (*Bradypodion pumilum*) (Turner, 2017; Tolley, 2017).

Furthermore, the reserve supports an estimated 68 species of indigenous terrestrial mammals, 31 of which were > 5 kg and thus classified as medium and large-sized mammals suitable for detection using camera traps (Appendix A). Notable mammal species include the Cape Mountain Zebra (*Equus zebra zebra*), and a genetically pure population of bontebok (*Damaliscus pygargus pygargus*) that is listed as Vulnerable (SANBI, 2016). Four alien species have been recorded which include the donkey, house rat, house mouse and domestic cat (Cape Nature, 2016). The strict no-take policy applied at the MPA helped to create a refuge for the diverse marine life of the area including 250 species of fish such as great white sharks (*Carcharodon carcharias*), and 11 marine mammal species including humpback dolphins (*Sousa plumbea*) and southern right whales (*Eubalaena australis*) who mate and calve in the shallow coastal waters.

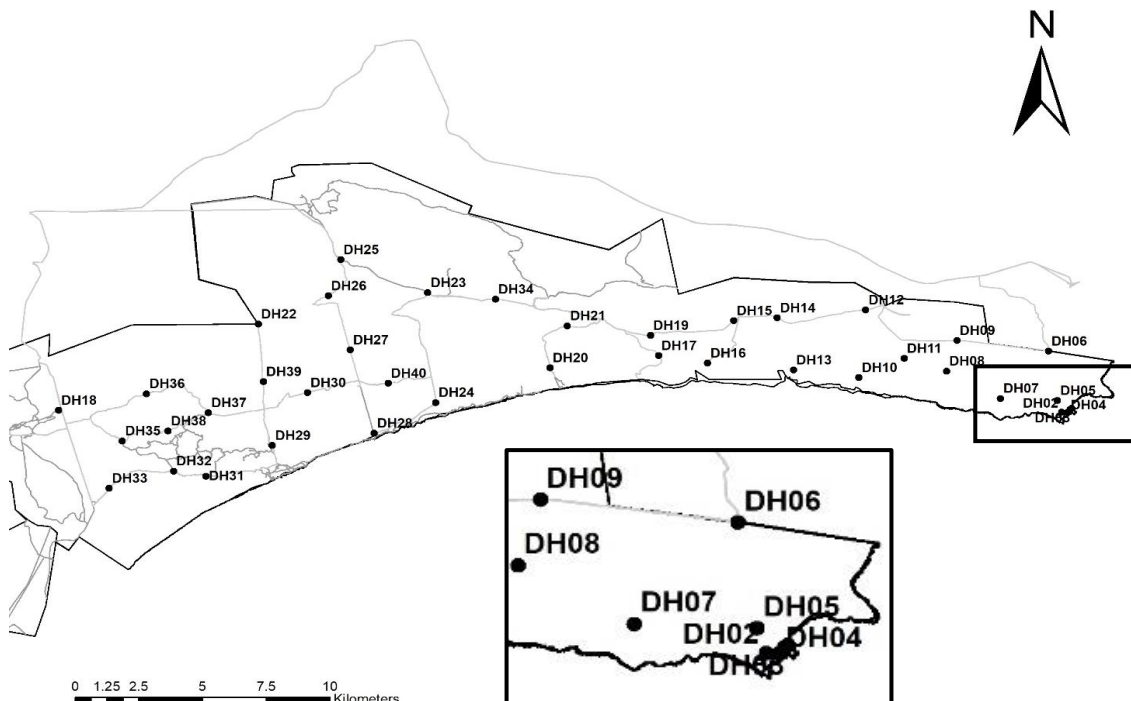
## Survey design

The camera trap survey comprised 80 Panthera V7 cameras in 40 paired stations distributed across an area of 228.67km<sup>2</sup> within the reserve with a mean inter-trap station distance of 2.25km. Each camera station comprised two cameras set up on opposite sides of a trail or road to maximize leopard detection (Mann et al., 2015). The survey ran from the 30<sup>th</sup> of September 2020 to the 4<sup>th</sup> of December 2020. A cluster of five stations covering an area of 134m<sup>2</sup> were positioned surrounding the proposed

penguin colony to intensively monitor predator activity in the vicinity of the predator-proof fence (Figure 6). Camera traps were mounted on trees or steel poles at a height of approximately 40cm above the ground and located 2-3 meters from the road or game trail along which target species were likely to walk. Vegetation that was obtrusive to the camera's view was removed to limit false triggers. Cameras operate with a white light flash during night or low light conditions providing high quality colour photographs which allowed for individual leopards to be identified through their unique rosette markings (Henschel and Ray, 2003). The paired camera setup resulted in the near simultaneous photographing of the left and right flank of any leopards walking past the station, allowing for the creation of individual identification profiles (Silver et al., 2004). Time between successive photographs was set to 8 seconds due to flash recharging. This minimal delay increases the probability of obtaining repeated photographs of a passing leopard. Camera stations were checked midway through the survey (day 28) to ensure they were still optimally placed, clear vegetation, download images and change batteries if they were depleted. One or both cameras operational at a station for part or all of one day is considered one trap night. To satisfy the capture-recapture model assumption of population closure of no births, deaths, emigration, or immigration (Royle et al., 2013), the survey period was limited to 66 days.



**Figure 5.** De Hoop Nature Reserve (shaded polygon in the bottom right insert) in relation to South Africa, and the Western Cape (inset).



**Figure 6.** A map showing the location of camera trap stations (grey lines) deployed throughout the De Hoop Nature Reserve (cadastral boundary denoted by black line) and around the proposed penguin colony (square insert).

## *Data processing and analyses*

Images were processed using Panthera Integrated Data Systems (PantheraIDS) version 15.126.1162 (Pitman et al., 2020). The images were run through a machine classifier, which classified most images to species level. Images were then manually checked to confirm or reject identifications, and to classify any images that could not be identified by the machine classifier.

Naïve occupancy ( $\psi$ ), which is the proportion of sites that recorded at least one photograph of a target species, was calculated by dividing the number of stations the species was detected at by the number of stations (MacKenzie et al., 2017). The relative abundance index (RAI) was calculated as the number of detections per species divided by sampling effort and then multiplied by 100 — it serves as a measure of detection per 100 days of camera trapping and is a common metric of many camera trap studies (Carbone et al., 2001). The advantage of this index lies in its use as a population measure where true abundance would be unable or difficult to calculate but can be prone to potential bias through imperfect detection (Palmer et al., 2018). Species identifications were verified using Stuarts' Field Guide to Mammals of Southern Africa (Struik Nature, 2015) and the expert opinion of colleagues familiar with South African mammals.

Species accumulation curves were generated through the package *vegan* using sample-based rarefaction methods (Oksanen et al., 2015). This is a measure of the total number of species plotted against the total sampling effort and displays the rate at which new species are being detected within the sampling site (Ugland et al., 2003). Additionally, it can be used as a prediction of whether a study area has been adequately sampled.

Activity pattern plots displaying temporal variation in activity were generated using PantheraIDS, whereby all the temporal data of detections of a particular species are

accumulated, and an independence threshold applied, after which time is converted to radians — a mathematical unit of measuring angles— and then a kernel density function is fitted. To determine the similarity and difference of two species, the coefficient of overlapping is calculated which is a quantitative measuring ranging from no degree of overlap (0) to identical activity patterns (1). This follows the method advocated and used by Ridout and Linkie (2009) in clouded leopards.

### *Processing leopard images and estimating leopard density*

All images of leopards were extracted and grouped according to flank side (i.e., left or right) and then cropped to include only the individuals flank (Figure 7). These images were fed into the pattern recognition component of PantheraIDS, which utilises the HotSpotter algorithm to match leopards based on “hotspots” (i.e., shared spot features) (Nipko et al., 2020). The greater the number of hotspots between two images the greater the likelihood of them being the same individual (Figure 8). Comparison results were manually verified through visual assessment where confirmation indicated they were two images from the same leopard, and rejection indicated that images were from two different leopards, made possible through their unique pelage pattern (Silver et al., 2004). When an individual was captured photographically, it was then considered to be “marked” and then considered to be “recaptured” if it was photographed in an independent capture event, and “spatially recaptured” when an individual was seen at a different location than the initial sighting.

Images of the same species at the same station were considered an independent capture if they occurred more than 30 minutes apart (Linkie and Ridout, 2011). Density estimates could be biased by double counting of individuals which would result in an overestimate of the population, and it is for this reason individuals were only included in

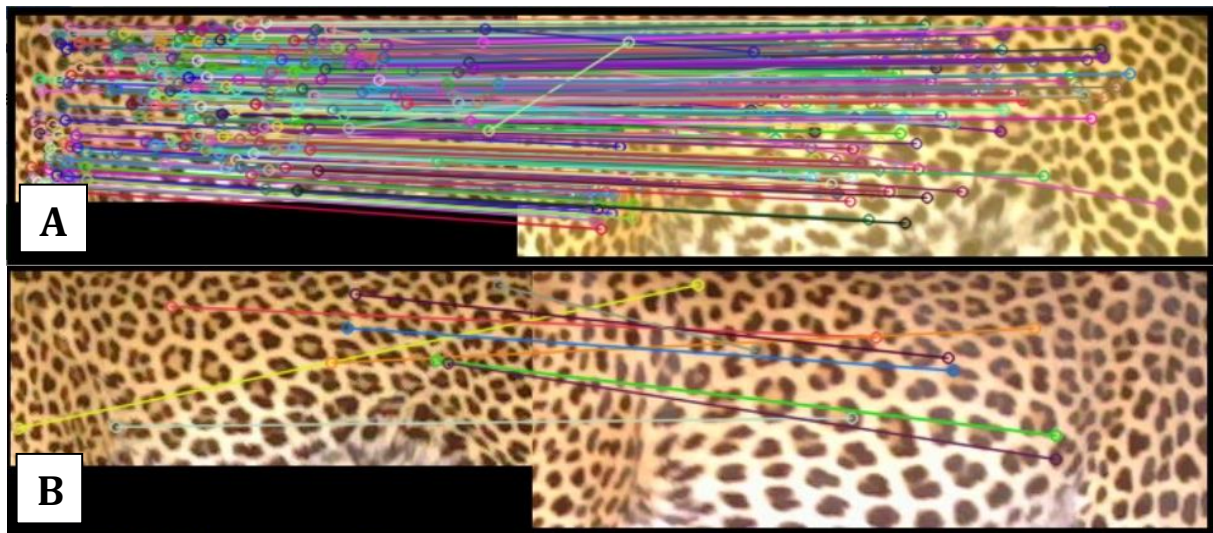


analyses for which both flanks were clearly photographed, and partially identified individuals that had been identified using the flank that had the highest number of individuals (left). The partially identified individuals with the lowest number of identified individuals (right) were removed to avoid artificially inflating population estimates.



**Figure 7.** Leopard photograph in De Hoop Nature Reserve and cropped right flank (inset) of this same individual photograph used for pattern recognition and individual identification using PantheraIDS.





**Figure 8.** Photographs of the flanks of A) the same leopard and B) different leopards. The PantheraIDS programme superimposes lines between spots that are considered to match with many more matches evident in A) than B) as would be predicted.

### *SECR models and parameters*

Spatially explicit capture-recapture (SECR) models use the locations at which individuals are recorded to determine the estimated sampling area, producing a more accurate population density estimate than non-spatial capture-recapture population density models (Balme et al., 2009a). A survey deployment file was thus created containing the name and co-ordinates of each camera trap station. A camera activity sheet was generated which was filled in for the duration of the survey with the status of the camera, with “1” symbolizing each day that the camera was active and “0” when a camera was inactive, such as in the case of being knocked over or battery failure. A capture history file was created which contained animal identity, camera station and sampling occasion of individual leopards. To create the habitat mask for the SECR analysis, a state-space file was created with all unsuitable habitat (such as water bodies) removed from the calculations.

The density of individual leopards per 100km<sup>2</sup> in De Hoop was calculated using maximum likelihood based SECR models (Borchers and Efford, 2008) with the *secr* package version 4.3.3 (Efford, 2021) in R version 3.6.2 (R Core Team, 2013). Sex was used as a covariate in determining the model of best fit due to the impact this has on detection rate as a result of different home range sizes between male and female leopards. I ran four spatially explicit capture recapture (SECR) models within a maximum likelihood framework (see Appendix B for details of the model code). The models used different combinations of sex as a covariate on the measure of detection probability ( $\lambda_0$ ) and home range size ( $\sigma$ ) to calculate leopard density (Table 2). The models were ranked based on Akaike's Information Criterion corrected for small sample size (AICc) (Hurvich and Tsai, 1989), and the best model (M1) was used to predict leopard density across the reserve.

# Results

## *Camera trapping array and species inventory*

All cameras were successfully retrieved and most (83%) were operational for the full 66 days which culminated in 2457 trap nights. Only one camera was replaced during the halfway check due to a system malfunction, but it is additionally worth noting that baboons knocked over a few cameras with some failing to capture images of animals for a portion of the time deployed. The camera trap survey yielded 101 377 images, of which 55 751 were scientifically meaningful (i.e., not false triggers). There were 8 177 independent captures of which 2 771 were photographs of mammal species, using an independence threshold of 30 minutes. This independence threshold ensures that multiple images of the same individual spending time around a camera are not recorded as separate captures (Linkie and Ridout, 2011). False triggers made up 45% of total photographs. Common causes for false triggers were movement of foliage and weather conditions such as dust and rain.

There were 26 medium and large terrestrial mammal species detected, as well as some birds and reptiles (Table 1). The 26 mammal species span eight orders: Carnivora, Hyracoidea, Lagomorpha, Perissodactyla, Primata, Rodentia, Suiformes and Ungulata. The mammal species most photographed were the chacma baboon (*Papio ursinus*), small grey mongoose (*Herpestes pulverulentus*) and eland (*Taurotragus oryx*).

Leopards were photographed a total of 190 times, of which 111 were independent capture events at 32 stations. This resulted in a relative abundance index (RAI) of 4.52 per 100 trap nights (Table 1). There were seven individuals in total: five male, one female, and one juvenile of unknown sex. There were two images captured of a cub

accompanying its mother — the aforementioned single female. These two incidents were excluded from analyses due to their non-independence. There were two photographs in which two adult leopards were photographed together. Male leopards accounted for 53% of all independent captures.

Naïve occupancy ( $\psi$ ) was calculated for all species detected and ranged from 0.05 for the African striped weasel (*Poecilogale albinucha*) and Cape hare (*Lepus capensis*) to 0.95 for honey badgers (*Mellivora capensis*) (Table 1). Leopards also had one of the highest naïve occupancy values ( $\psi = 0.8$ ). Caracal naïve occupancy was lower at 0.65. Caracals were however detected on 201 independent occasions, and thus have a higher RAI than leopards (RAI = 8.18 per 100 nights).

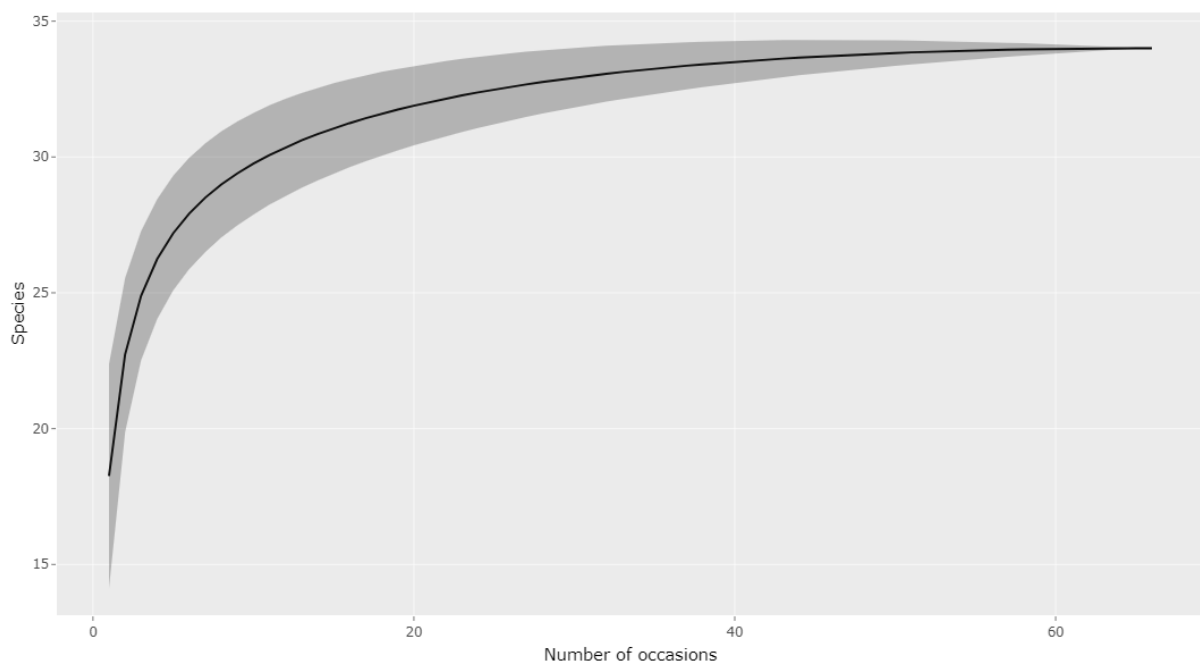
**Table 1. Inventory of mammal species and humans camera trapped, the number of Independent Captures, Relative Abundance Indices (RAI) and Naïve occupancy ( $\psi$ ) in De Hoop Nature Reserve, South Africa.**

Order	Common name	Scientific name	Independent Captures	RAI	$\psi$
<b>Carnivora</b>	African leopard	<i>Panthera pardus pardus</i>	111	4.52	0.80
<b>Carnivora</b>	African pole cat / zorilla	<i>Ictonyx striatus</i>	60	2.44	0.30
<b>Carnivora</b>	African striped weasel	<i>Poecilogale albinucha</i>	2	0.08	0.05
<b>Carnivora</b>	Bat-eared fox	<i>Otocyon megalotis</i>	13	0.53	0.30
<b>Carnivora</b>	Caracal	<i>Caracal caracal</i>	201	8.18	0.65
<b>Carnivora</b>	Honey badger	<i>Mellivora capensis</i>	214	8.71	0.95
<b>Carnivora</b>	Large grey mongoose	<i>Herpestes ichneumon</i>	82	3.34	0.40
<b>Carnivora</b>	Large-spotted genet	<i>Genetta tigrina</i>	185	7.53	0.68
<b>Carnivora</b>	Small grey mongoose	<i>Herpestes pulverulentus</i>	351	14.29	0.83
<b>Carnivora</b>	Small-spotted genet	<i>Genetta genetta</i>	27	1.10	0.15
<b>Carnivora</b>	Water mongoose	<i>Atilax paludinosus</i>	7	0.28	0.18
<b>Carnivora</b>	Yellow mongoose	<i>Cynictis penicillata</i>	4	0.16	0.08
<b>Hyracoidea</b>	Rock hyrax	<i>Procavia capensis</i>	25	1.02	0.08
<b>Lagomorpha</b>	Cape hare	<i>Lepus capensis</i>	2	0.08	0.05
<b>Lagomorpha</b>	Scrub hare	<i>Lepus saxatilis</i>	191	7.77	0.58

<b>Perissodactyla</b>	Cape mountain zebra	<i>Equus zebra zebra</i>	56	2.28	0.10
<b>Primata</b>	Chacma baboon	<i>Papio ursinus</i>	407	16.56	0.88
<b>Rodentia</b>	Cape porcupine	<i>Hystrix africaeaustralis</i>	105	4.27	0.70
<b>Suiformes</b>	Bushpig	<i>Potamochoerus larvatus</i>	50	2.04	0.51
<b>Ungulata</b>	Bontebok	<i>Damaliscus pygargus pygargus</i>	112	4.56	0.13
<b>Ungulata</b>	Bushbuck	<i>Tragelaphus scriptus</i>	30	1.22	0.73
<b>Ungulata</b>	Cape grysbok	<i>Raphicerus melanotis</i>	299	12.17	0.78
<b>Ungulata</b>	Eland	<i>Taurotragus oryx</i>	324	13.19	0.60
<b>Ungulata</b>	Grey duiker	<i>Sylvicapra grimmia</i>	110	4.48	0.58
<b>Ungulata</b>	Grey rhebok	<i>Pelea capreolus</i>	8	0.33	0.13
<b>Ungulata</b>	Steenbok	<i>Raphicerus campestris</i>	14	0.57	0.23
<b>Primata</b>	Human on foot or bicycle	<i>Homo sapiens</i>	782	31.83	1
<b>Primata</b>	Human in vehicle	<i>Home sapiens</i>	4531	184.41	1

### *Species accumulation curve*

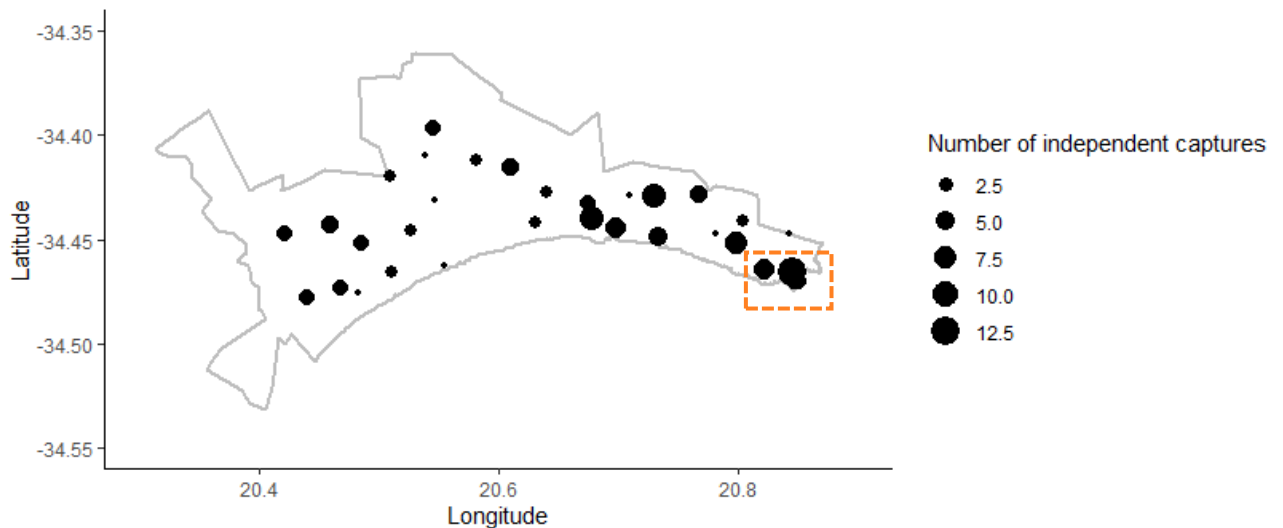
The rarefied species accumulation curve for all vertebrates detected displays a clear asymptote (Figure 9). This suggests that the temporal extent of sampling was sufficient to establish a full inventory of species. Most initial detections occurred within the first two weeks of the survey, with a slow increase for the following two weeks until stabilization.



**Figure 9.** Sample-based species accumulation curve describing the terrestrial faunal (> 5kg) community richness for the study area. 95% confidence intervals are displayed as grey bands.

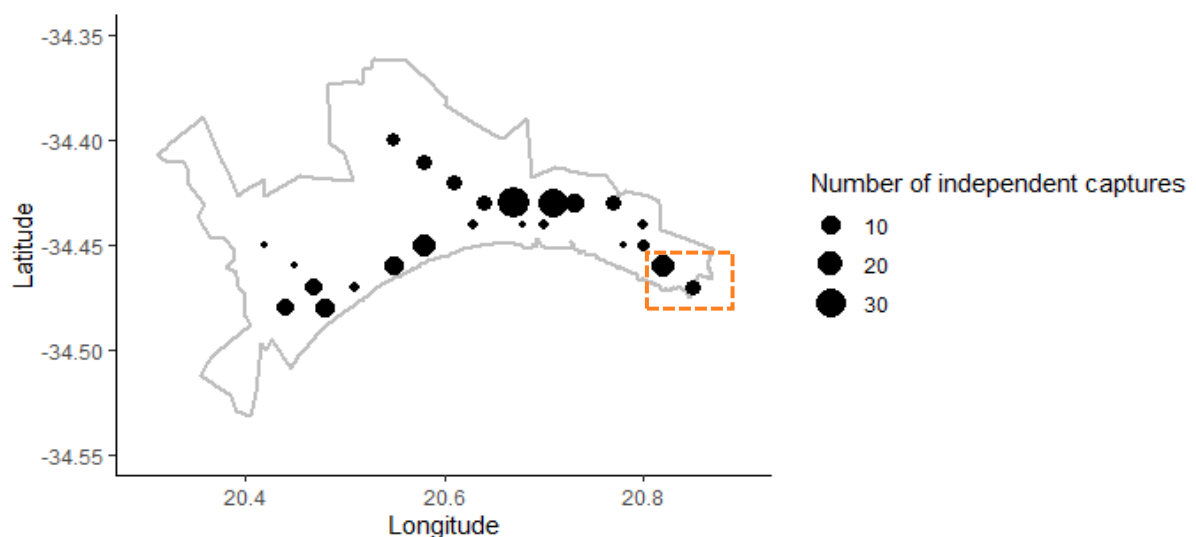
### *Predator detections*

Many leopard detections (31%, comprising 28 independent captures) occurred at stations in proximity to the penguin colony site (Figure 10) with the most detections (N = 13) at a single station (station 5) being adjacent to the penguin colony.



**Figure 10.** Map showing the relative position of each camera station and the number of independent leopard captures in De Hoop Nature Reserve in 2020. Larger circles indicate a greater number of captures. Dashed border indicates stations in proximity to the penguin colony.

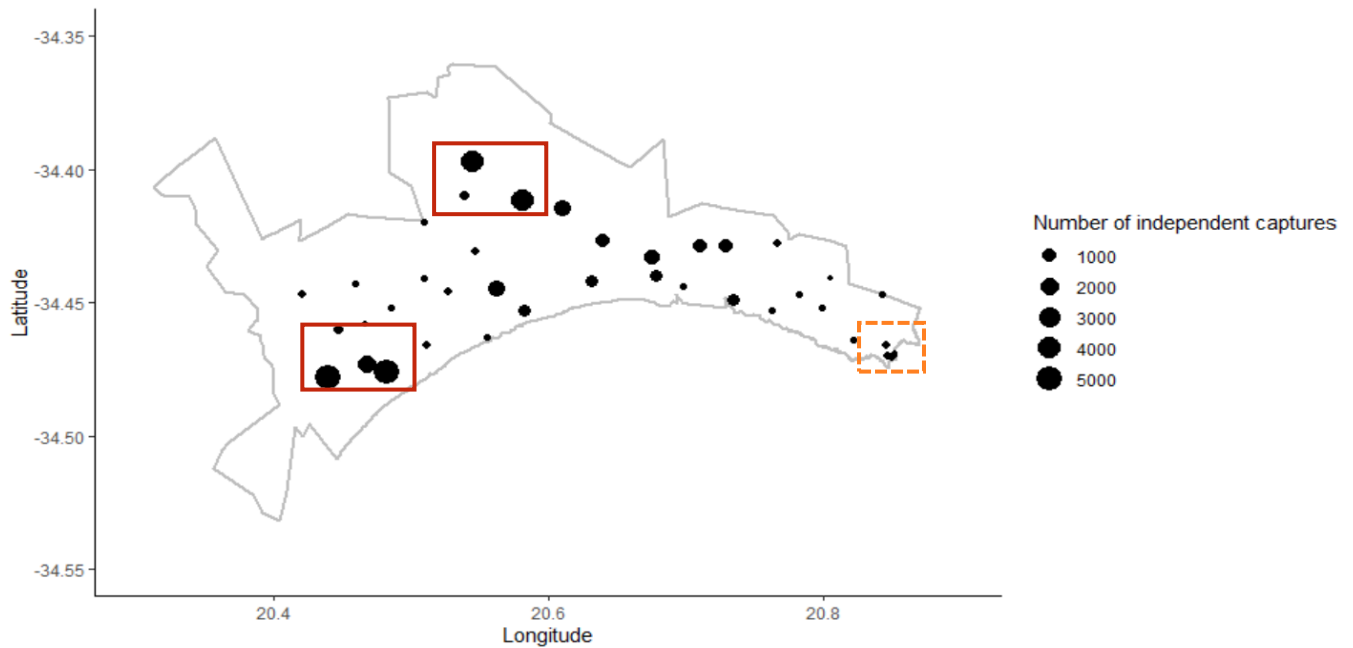
Caracal detections (Figure 11) were more numerous than leopard detections, with 201 independent captures, at 24 stations. There were 29 detections in the cluster of cameras around the penguin colony, but the most detections were at one of the inland stations, with 36 captures (station 19).



**Figure 11.** Map showing the relative position of each camera station and the number of independent caracal captures in De Hoop Nature Reserve in 2020. Larger circles indicate a greater number of captures. Dashed border indicates stations in proximity to the penguin colony.



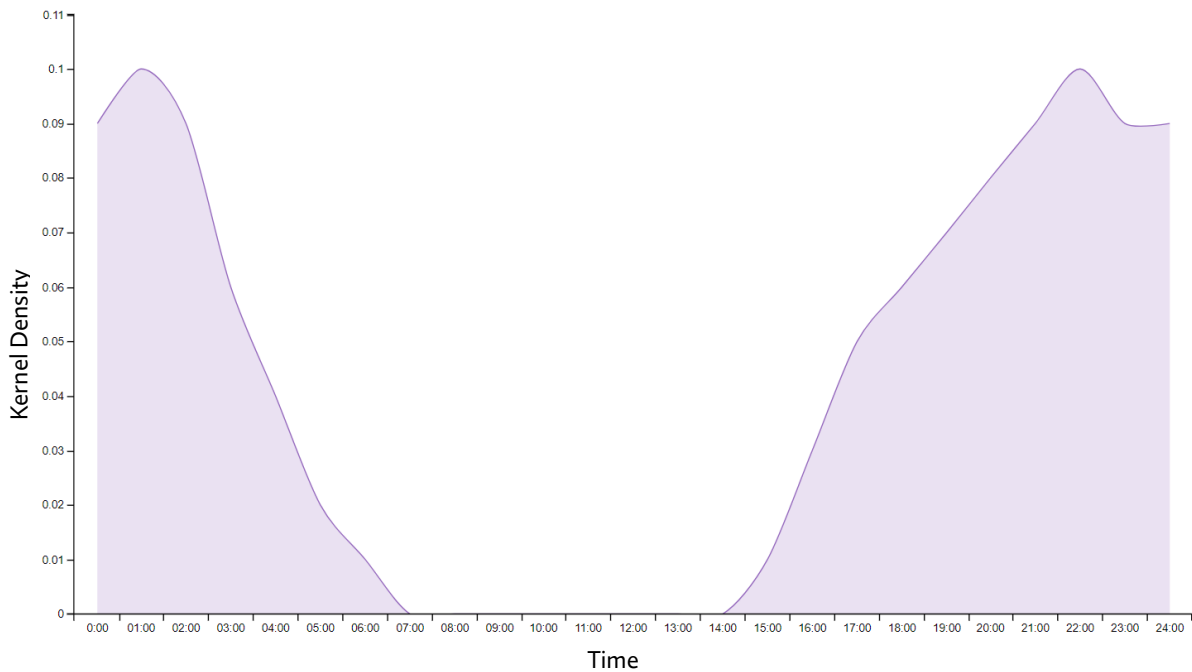
There is visible difference between the spatial usage of the reserve by predators and by vehicles (including cyclists) (Figure 12). Areas of highest activity are associated with entry and exit points to the reserve, and there is a noticeable lack of vehicles around the penguin colony. Additionally, the frequency of vehicle sightings is much greater than that of predators.



**Figure 12.** Map showing the relative position of each camera station and the number of independent vehicle captures in De Hoop Nature Reserve in 2020. Larger circles indicate a greater number of captures. Dashed border indicates stations in proximity to the penguin colony. Straight border indicates entrance and exit points.

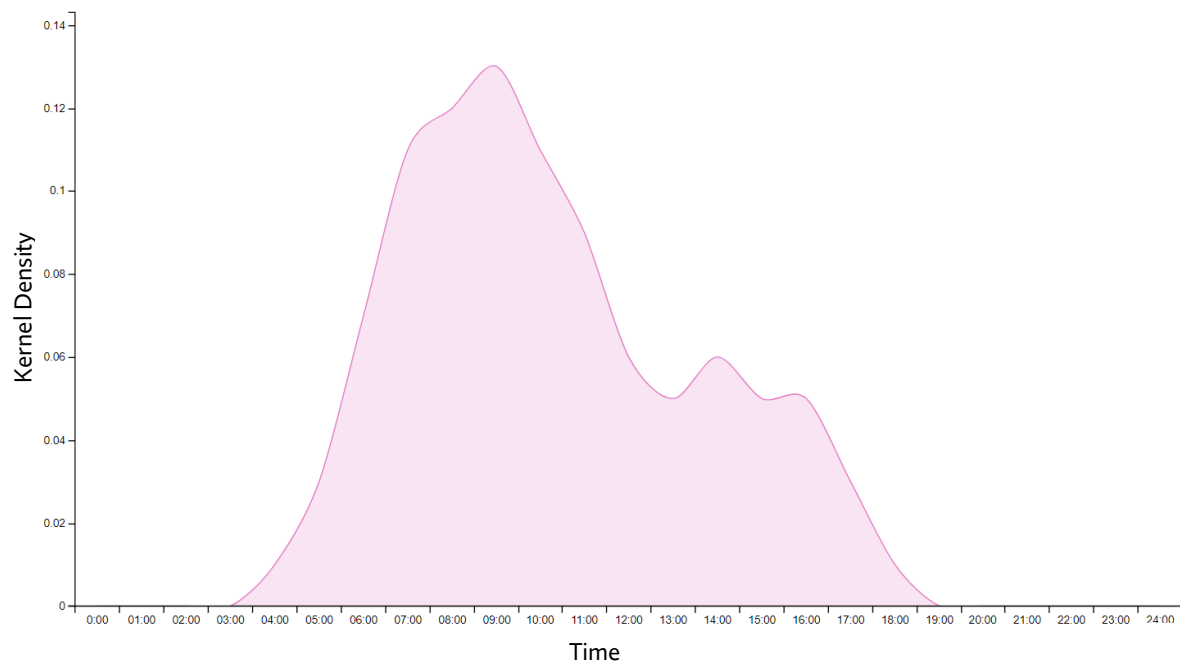
### *Activity patterns*

Leopards were active primarily in the evening and activity peaked between ~22:00 and 01:00 (Figure 13), during which time there were no human detections (Figure 14). Additionally, there were no leopard captures recorded between ~7:00 and ~14:00, which was the peak of human activity.



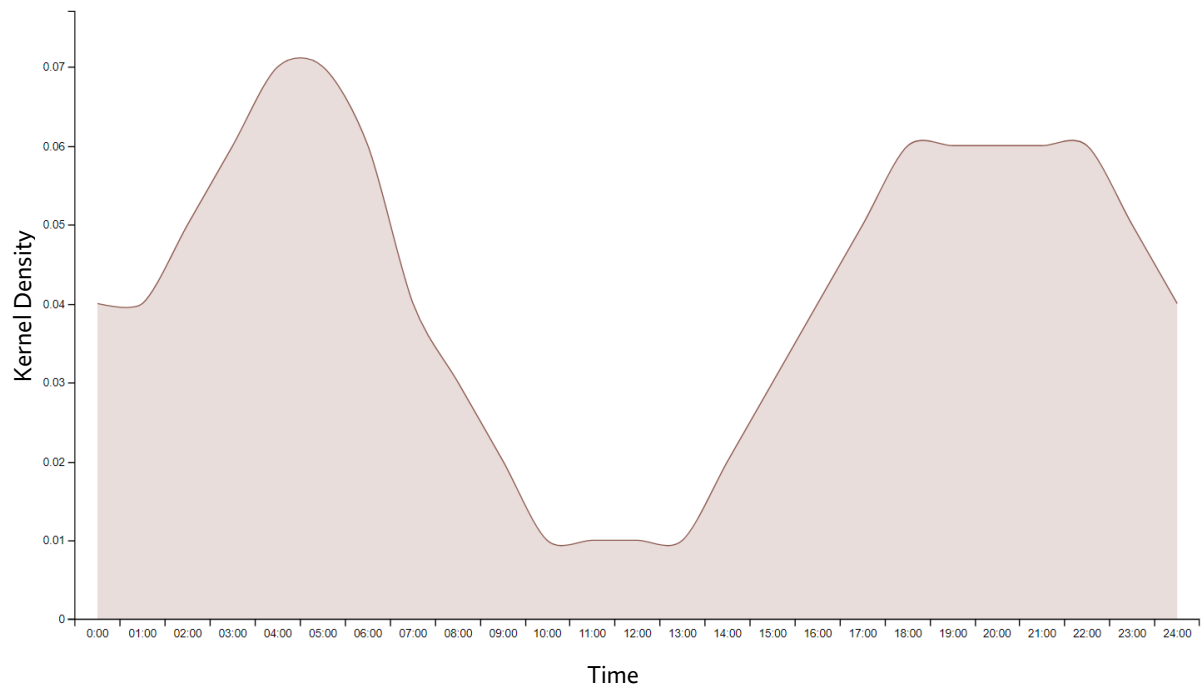
**Figure 13.** Activity pattern of leopard across a 24-hour period, calculated using kernel density estimates of detections across all stations for the duration of the study.

With the exception of early morning cyclists, there was limited human presence before ~6:00 (Figure 14). There was a rapid increase from ~07:00 coinciding with working hours, followed by an equally rapid descent — with a dip directly before and after ~15:00, before activity ceased at ~19:00.



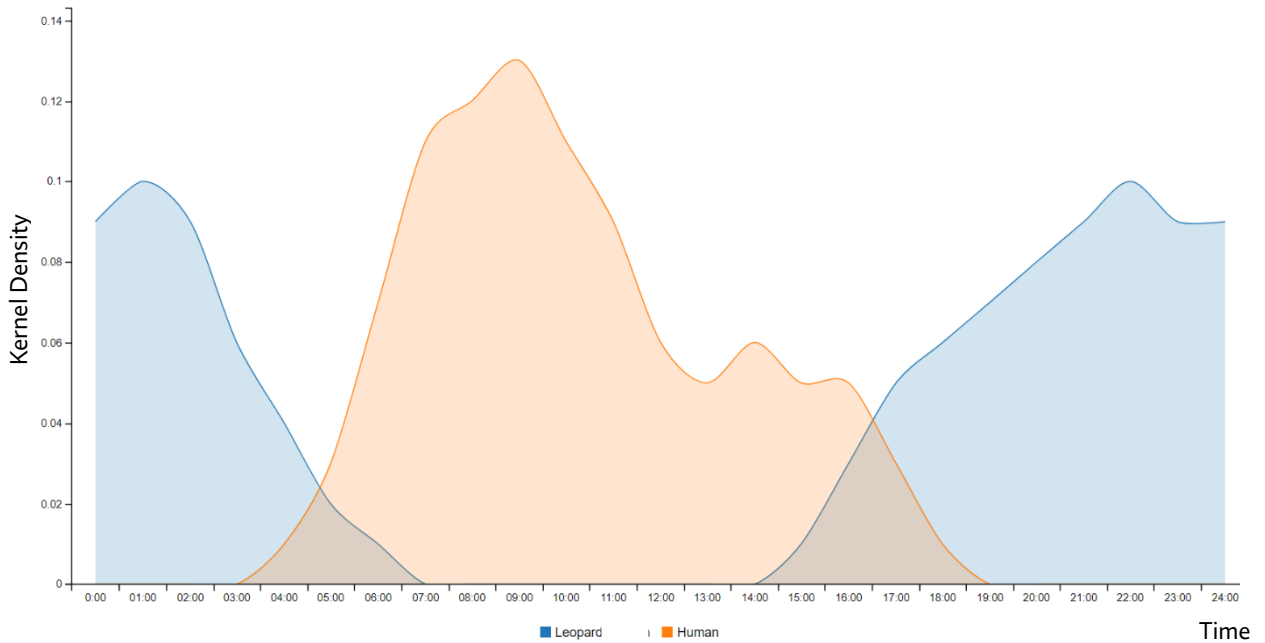
**Figure 14.** Activity patterns of human across a 24-hour period, calculated using kernel density estimates of detections across all stations for the duration of the study.

Caracals were detected at every hour of the day. There was a rapid decrease in activity after ~6:00 (Figure 15), after which detection was at its lowest until an increase after ~14:00. This pattern also suggests temporal avoidance of the main hours of human activity (Figure 14).



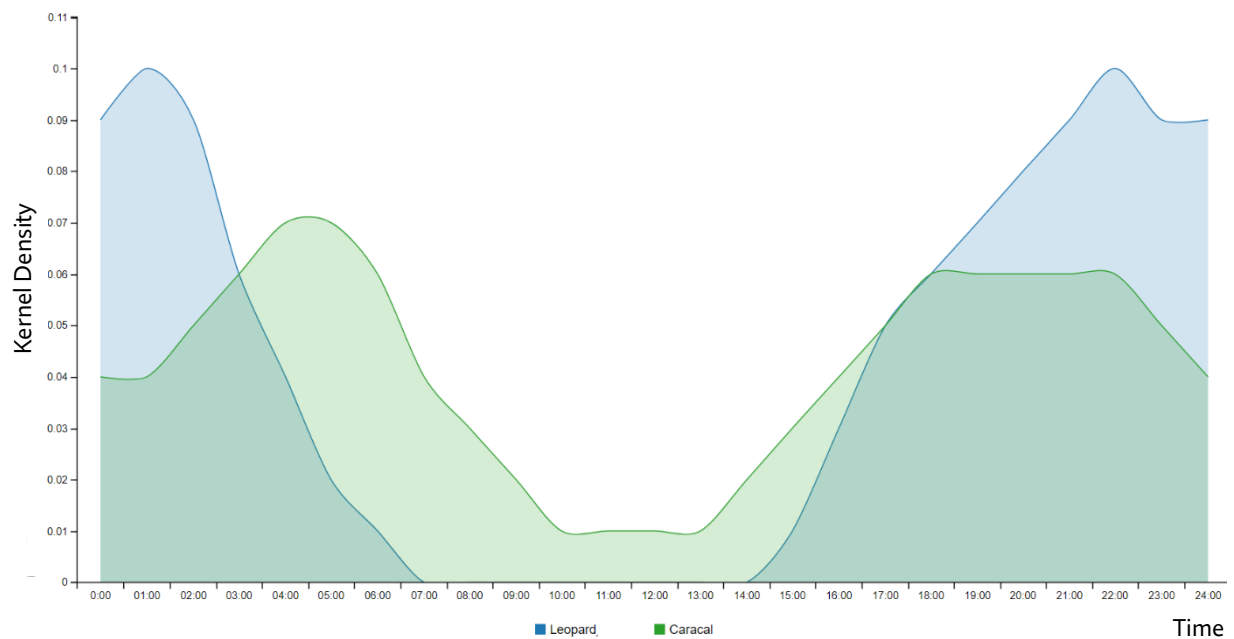
**Figure 15.** Activity pattern of caracal across a 24-hour period, calculated using kernel density estimates.

The degree of temporal overlap between leopards and humans was  $0.14 \pm 0.12$  (0.03 - 0.15) (Figure 16). Most notably, the bulk of human activity between ~7:00 and ~14:00 coincides with the lowest level of leopard activity. Most leopard activity occurred after sunset, and the temporal and spatial absence of human activity at that time should also be noted.



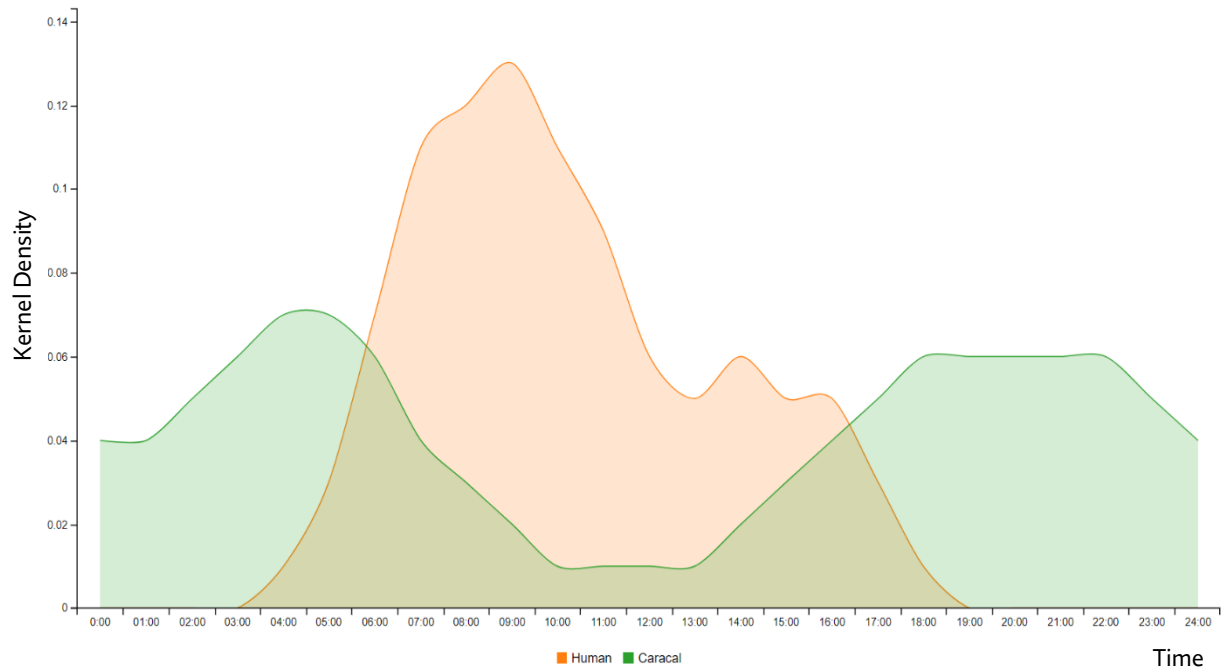
**Figure 16.** Activity patterns of leopards (blue shade) and humans (orange shade) across a 24-hour period showing the times of overlap (darker shade).

The degree of temporal overlap between leopards and caracal was  $0.74 \pm 0.22$  (0.62 - 0.84) (Figure 17). While detected at all hours of day and night, there was a noticeable dip in caracal activity between 9pm and 2pm, but they were still consistently detected unlike leopards which were not detected as being active at that time.



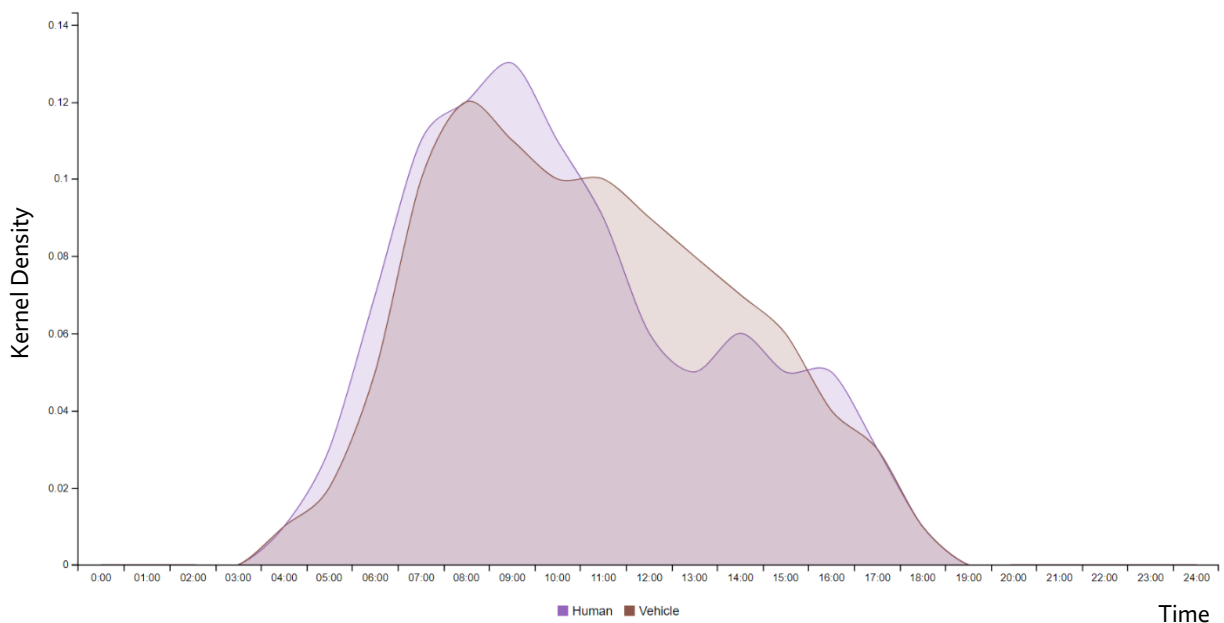
**Figure 17.** Activity patterns of leopards (blue shade) and caracal (green shade) across a 24-hour period showing the times of overlap (darker shade).

The degree of temporal overlap between humans and caracal was  $0.36 \pm 0.16$  (0.24 - 0.4) (Figure 18). Caracal activity was consistent throughout the day and night, with the exception of a dip in activity occurring between ~7:00 and ~13:00, whereafter caracal activity increased again. This decline in activity occurs during peak human activity.



**Figure 18.** Activity patterns of human (orange shade) and caracal (green shade) across a 24-hour period showing the times of overlap (darker shade).

The patterns observed in the temporal overlap between humans are very similar to those of human-operated vehicles and fit into a diurnal curve (Figure 19). With an overlap coefficient of  $0.89 \pm 0.082$  (0.842 - 0.924), predictably the two are linked in detection and active hours range from ~3:00 to ~19:00, with most starting after ~06:00.



**Figure 19.** Activity patterns of human (purple shade) and vehicle (brown shade) across a 24-hour period showing the times of overlap (darker shade).

### *Density of leopard in De Hoop*

Using the maximum likelihood based SECR model, models were generated that used different combinations of sex as a covariate to calculate leopard density (Table 2) and the fourth model, which included sex as a predictor of both  $\sigma$  and  $\lambda_0$  did not converge, and hence was excluded from analyses. The best model (M1) included no effect of sex on  $\lambda_0$  or  $\sigma$ . The mean estimated density of leopards was  $0.18 \pm 0.07$  individuals per  $100\text{km}^2$  (mean  $\pm$  SE). The area of buffer around the survey area was 20km derived from the model. The mean detection function spatial scale parameter ( $\sigma$ ) was estimated to be  $11693 \pm 1188$  metres. The baseline capture rate ( $\lambda_0$ ) was  $0.03 \pm 0.01$ . It was predicted that 83% of the population is male.

**Table 2: Model selection table evaluating the detection parameters of leopard density in the De Hoop Nature Reserve. AICc represents Akaike's Information Criterion corrected for small sample size.**

ID	Predictor variables on $\lambda_0$	Predictor variables on $\sigma$	Number of Parameters	AICc	AICc weight
M1	1	1	3	354.738	1
M2	1	Sex	5	509.236	0
M3	Sex	1	5	516.028	0



## Discussion

### *Species inventory*

The sample-based species accumulation curve for the camera trap survey suggests that the sampling design and effort provided a reliable estimate of wildlife species in the De Hoop Nature Reserve. A total of 26 medium and large mammal species were recorded which is marginally less than indicated on the reserve's species checklist ( $n = 31$ ; Appendix A). O'Bryan (2008) warns against treating historical species lists as "true", as they commonly are aggregated knowledge about the site rather than a past estimate of species richness. Historical presence does not ensure persistence or survival, and a species richness estimate is not incorrect only because it is less than the potential diversity (O'Bryan, 2008).

Notable absences of the target taxon in my survey include armadillo (*Orycteropus afer*), previously found in the reserve, but known for its cryptic nature. Two elusive mesocarnivores, the African wild cat (*Felis lybica cafra*) and Cape fox (*Vulpes chama*), both of which are vulnerable to intraguild predation, and they may thus have avoided roads and trails upon which most camera traps were placed and that larger predator species such as leopard frequent. A failure to detect klipspringer (*Oreotragus oreotragus*) and the red rock rabbit (*Pronolagus rupestris*) can be attributed to camera traps not being set up in the small proportion of De Hoop that is comprised of the rocky mountainous outcrops that these habitat specialists favour (Reece et al., 2021). While many large antelope species like eland and bontebok were photographed more than one hundred times, red hartebeest (*Alcelaphus buselaphus caama*) were not detected. The absence of a species does not always mean that it is not there, but rather that it was not observed (Sollmann, 2018) but this is unlikely for a large mammal and having not been

seen on the reserve for over 20 years (F. Radloff, pers. comm) the red hartebeest can be assumed to have been extirpated. None of the four alien mammal species were detected.

Importantly, the estimated number of medium and large mammal species detected in this survey (n = 26 species) is similar to other recent surveys on this taxonomic group in the Western Cape, including 27 species in the Klein Karoo (Bussiere, 2018), 27 species on small livestock farmland in the central Karoo (Drouilly et al., 2018) and 30 species in a protected area in Anysberg, managed by CapeNature between the Klein and central Karoo study sites (Drouilly et al. 2018). Together these studies suggest that a subset of the original fauna, mostly medium-sized generalist species, have persisted on undeveloped (i.e., functionally intact with predominantly natural vegetation that has nevertheless sustained grazing pressure from domestic animals) land both within and outside of protected areas in the Western Cape. It is only in private protected areas which have reintroduced historically extirpated species such as lion, white rhino (*Ceratotherium simum simum*), and elephant (*Loxodonta africana*) that we see higher numbers of native fauna, such as 36 species in Sanbona Private Nature Reserve (Woodgate, 2022) in the Western Cape.

Many government-managed protected areas in Africa have experienced a decrease in legal restrictions governing human activities within a restricted area and this includes De Hoop which has greatly increased access for both people on foot and on mountain bikes within the reserve. While these activities are unlikely to eliminate species as they are low impact, they are predicted to cause an adjustment in the activity patterns of wildlife which seek to avoid humans in shared environments (Gaynor et al., 2018). Direct and indirect human impacts are both responsible for shifting activity patterns in wildlife, and the effects of this are important for management (Ohashi et al., 2013). Both

caracal and leopard showed a clear peak in nocturnal activity which overlapped minimally with the daytime peak in human activity including hikers, cyclists and vehicles. While this does not prove causality, it is highly likely that both predators would avoid roads and trails (where most camera traps were placed) during the day as they are frequented by people on foot, bicycle and in vehicles.

Leopards seem to display a degree of temporal and spatial avoidance towards human presence in De Hoop, by concentrating their activity during non-operational hours of the reserve and showing a higher relative abundance for less busy areas towards the east of the reserve. Similar findings were made for leopards in the Kaeng Krachan National Park in Thailand which avoided humans in both time and space (Ngoprasert et al., 2007), a characteristic shared by the population in this study. The nocturnal peak in activity by leopards in De Hoop has been reported for leopard populations living in areas with high human activity both elsewhere in South Africa (Bothma and Bothma, 2006; Rafiq et al., 2020), and further afield including Nepal (Odden and Wegge, 2005) and India (Odden et al., 2014). By contrast leopards living in mountainous habitats where human activity is low show a prominence of diurnal behaviour (Naha et. al, 2020; Jenny and Zuberbühler, 2005). This behavioural plasticity (Badyaev, 2005) in response to anthropogenic impact (Gaynor et al., 2018) is apparent in caracal too, although caracal were more active throughout the day than leopards. While these changes may prove beneficial to survival, the adjustment of their activity pattern may have far-reaching effects in the ecosystem, such as the disruption of usual foraging habits which reshapes lower trophic levels (Ordiz et al., 2017) and the altering of temporal distribution of prey (Sih, 2013; Gaynor et al., 2018).

Together these data on relative abundance and activity patterns suggest that predation threats to a re-established penguin colony from large terrestrial predators would remain high, with particular reference to felids. Both leopard and caracal were frequently detected in the vicinity of the fenced colony and along the coastline in general. Potential predation events would be more likely to manifest at night when the two main predators are most active. Thus, while the fence may serve as a barrier to both predators by day, there is an argument for additional deterrents to be deployed at night when predator activity peaks (Zarco-González and Monroy-Vilchis, 2014). Previously, flashlight devices have been found to be an effective deterrent in preventing lion predation of livestock in bomas (Lesilau et al., 2018), and ‘fox lights’ — which use three different colours of light - significantly reduced livestock predation by leopards in a community in the Himalayas (Naha et al., 2020). These measures could be implemented in the event that the fence alone does not succeed in deterring caracal and leopard, both of which are adept at scaling human made barriers (Balme et al. 2010; Nattrass and O’Riain 2020).

### *Leopard density in De Hoop*

The density estimate of leopards in the De Hoop Nature Reserve is low at  $0.18 \pm 0.07$  leopards per  $100\text{km}^2$ . This is similar to the only other density estimate derived for leopards in this reserve which was conducted in 2015 and produced a value of  $0.17 \pm 0.10$  leopards per  $100\text{km}^2$  (Devens et al., 2019). These are amongst the lowest density estimates recorded for leopards within protected areas of South Africa. A study including the Eastern and the Western Cape estimated 0.84-1.89 individuals per  $100\text{km}^2$  (Devens et al., 2018). Recent density estimates of the Cape Fold Mountains were higher 1.4–1.99 per  $100\text{km}^2$ , but the limitation of this data being collected ten years ago,

encompassing more than a single leopard generation, must be acknowledged (Amin et al., 2022). The highest recorded density occurs in the Cederberg mountains, where Martins (2010) estimated 1.80-2.30 individuals per 100 km<sup>2</sup>. Another area of low leopard density is the Little Karoo, at 0.5 individuals per 100 km<sup>2</sup>, which may be as a result of the low productivity of the ecosystem, and the higher rate of human disturbance (Mann, 2014).

Genetic analyses have revealed that the geographical isolation of the Western Cape leopards has resulted in their subpopulation being genetically distinct and rapidly dwindling (McManus et al., 2014). These fragmented populations are invariably persisting in marginal habitats and consequently have low density (Devens et al., 2019); Mann et al. 2020). Noting that survival is typically higher inside protected areas, it is thus assumed that the surrounding land has an even lower density (Swanepoel et al., 2016). Factors that potentially affect leopard populations in protected areas include prey density, rainfall, vegetation productivity, inter- and intraspecific competition, and human persecution through indirect means such as incidental snaring or in direct conflict (Graham et al., 2005; Inskip and Zimmermann, 2009; Swanepoel et al., 2016; Khan et al., 2020). Coastal fynbos has low vegetative productivity and does not support high prey numbers, and this alone may explain the low density derived in both this and the previous density estimate (Devens et al. 2019). While capable of hunting in a variety of habitats, leopards prefer hunting along ecotones, where they can use the dense cover of vegetation to approach prey in more open areas (Balme et al., 2007). In much of the western and central sections of the reserve the landscape is flat and open with limited cover and higher levels of human activity. This may explain the higher relative abundance of leopards in the east where there are more incised valleys and dense exotic *Acacia cyclops* that provide cover for hunting (Ramesh et al., 2016).

This study was limited to the reserve but Devens et al. (2019) noted that all leopards identified in the Overberg region had home ranges that extended beyond the boundaries of protected areas. Similarly (Martins and Martins, 2006) noted that in the Western Cape few protected areas were large enough to encompass the territory of wide-ranging carnivores like leopards. It is therefore highly likely that most of the leopards detected in this study move beyond the borders of the reserve and into the greater Overberg region and surrounding land uses which range from private farmland to private nature reserves (Graham et al., 2005). Given the limited sampling area, my density estimate may not account for individuals that have home ranges that extend beyond the boundary of the reserve.

Of the seven identified leopards in the reserve, only one was identified as an adult female. Research in leopard populations of the Gouritz and Cederberg mountains found a similarly male-dominated population (Martins, 2010). Females have smaller home ranges than males (Harris et al., 1990) and are also less likely to move along animal trails and human made paths and roads, factors which together consistently mean fewer detections of females (Bailey, 2005; Mizutani and Jewell, 1998). However, the close spacing of camera traps and the longer duration of the survey — 66 days as opposed to the usual 45 days for *Panthera leopard* surveys (Rogan, 2021) suggests confidence in the density estimate and sex ratio reported. Thus, when the body of a female leopard was found by hikers on the 18<sup>th</sup> of July 2021, almost a year after my survey, I was able to confirm the identity of the individual as the lone adult female from my study.



**Figure 20.** Photograph of the adult female leopard at Station 2 of the colony cluster of cameras on 11 November 2020



**Figure 21.** Photograph of the deceased female leopard detected in figure 20 above (Source: Matthew Schurch).



A veterinary autopsy determined the cause of death as cardio-pulmonary failure as a result of injuries sustained from conflict with another leopard (P. du Bruyn, unpublished). While intraspecific competition is natural, it is a cause for concern for the leopard population in De Hoop as adult female mortality has a greater demographic impact than that of adult males (Swanepoel et al., 2015b). Intraspecific competition is known to increase in leopard populations where there is high turnover or high immigration rates (Balme et al., 2009b), as the complex system of leopard home range tolerance is dependent on the stability of their long-term relationships with others (Bailey, 1993). With the ideal sex ratio being 1:1.8 males to females (Nowell & Jackson 1996), the sex ratio from this study (6:1) is a conservation concern, especially given that the survival rate of females is one of the predominant factors affecting population viability and growth rate (Taylor et al., 1987).

As a protected area, De Hoop serves as both a refuge and as a corridor for individuals moving along the coastal region of the greater Overberg region. The perimeter fence is permeable to leopard movement and thus connectivity with adjoining private land is high. This will facilitate compensatory immigration which is an important mechanism for restoring the demographic composition of a population under threat (Lieury et al., 2015) but it is much more likely to be true for males which disperse further than females (Naude et al., 2020a), and are thus more likely colonise areas previously occupied by conspecifics (Fattebert et al., 2013; le Roex et al., 2021).

Porous boundaries in small-protected areas are also important to leopard conservation, with particular relevance to males, which have larger home ranges and disperse greater distances from their natal home range (Naude et al. 2020a; Fattebert et al., 2015).

Leopards in De Hoop are thus almost certainly vulnerable to edge effects including the



persecution by livestock farmers for both real and perceived threats to domestic stock (Romañach et al., 2007; Inskip and Zimmermann, 2009). Given the above concerns, it is surprising that leopards do not receive any particular mention from the Protected Area Management Plan for 2017-2022 beyond that of listing species. My data suggest that the low density, skewed sex ratio and high risks to leopards outside the porous perimeter means this is a species of conservation concern (CapeNature, 2016) that consequently requires specific management consideration and possible interventions.

My findings show the need for a wider population assessment beyond the border of the reserve with the goal of determining leopard densities on land that surrounds the De Hoop Nature Reserve. It is possible that high anthropogenic mortality on commercial livestock farms adjacent to the reserves are creating a population sink for the leopards recruited into the De Hoop population. Similar findings have been reported for leopard in other small, protected areas with the most recent review of leopard population in the Red List of Mammals of South Africa, Lesotho and Swaziland (Swanepoel et al., 2016) estimated there are between 1688-6979 mature individuals. All nine provinces show consistent decline in leopard populations, commonly associated with high harvest and lethal offtake (Swanepoel et al., 2016). Such is the case in provinces like KwaZulu-Natal, historically known for high leopard density, and now seeing a decline in protected area populations (Balme et al., 2010). An example is the Phinda-Mkhuze Complex in KwaZulu-Natal where density decreased from  $11 \pm 1$  individuals per  $100\text{km}^2$  in the centre of the reserve, to  $7 \pm 1$  individuals per  $100\text{km}^2$  towards the border, and outside was the lowest at  $3 \pm 0.9$  individuals per  $100\text{km}^2$  (Balme et al., 2010). These results highlight the threat of edge effects to protected populations and it is likely a factor driving the low density of leopard in De Hoop.

Density estimates do fluctuate with short-term environmental (Broekhuis et al., 2021) and anthropogenic impacts (Lande, 1998). Longer-term monitoring will be required to establish a trend in the population and should be a priority moving forward (Balme et al., 2009a). Due to the cryptic nature of leopards, and their ability to navigate even the most highly transformed environments, their population size and trends can be difficult to estimate (Foster and Harmsen, 2012; Rogan, 2021). The limited operational budgets of public protected areas such as De Hoop means that ongoing population monitoring is most likely to be done by non-governmental conservation organizations, such as Panthera who have committed to the long-term monitoring of protected areas across the country and are currently expanding their program into southern Africa (Rogan, 2021). Panthera have been ably assisted by the local NGO Cape Leopard Trust who initiated leopard monitoring in the Cederberg mountains (Martins, 2010) and have more recently been surveying the coastal and mountain regions to the west of De Hoop (K. Williams, pers. comm). In combination with this survey, these data will reveal how leopard density varies with land use and distance from formally protected areas in the Western Cape.

Leopards are an important flagship species in the Western Cape, and as the last widely distributed apex predator, they are critical for maintaining ecosystem health (Martins and Martins, 2006). Tangible benefits are derived from their presence such as regulating the effects of herbivory on the local fynbos by browsers such as rock hyrax (*Procavia capensis*), one of the most common prey types (Martins, 2010). Leopards are also viewed as one of most popular species for ecotourism in South Africa (Lindsey et al., 2007). With low numbers, fragmentation and evidence of genetic isolation (McManus et al., 2014), the future of leopards in the coastal region of the Western Cape is precarious, without human-wildlife conflict mitigation and broader policy changes, such as the banning of

trap mechanisms that can injure leopards, either purposefully or incidentally (Swanepoel et al., 2015b).

Establishing dispersal corridors and improving tolerance of land owners outside of protected areas are both important long term goals for the region while mitigating negative interactions between leopard and livestock is a critical short term intervention (Dickman, 2010). A variety of non-lethal techniques for protecting livestock are available and include the use of guard dog, fencing and the shepherds (Western et al., 2019; Sibanda et al., 2021; van Eeden et al., 2018). It is also important to limit the use of indiscriminate methods that can incidentally capture leopards, such as leg-hold traps that may be legally set by farmers to catch caracal and jackal but can equally catch leopards if poorly set (Martins and Martins, 2006) and contributes to the high degree of anthropogenic mortality that leopards experience (Swanepoel et al., 2015b). These traps pose a high risk of injuries such as abrasions, ligament fractures, permanent disability, and death — and have been banned in several countries internationally (Animal Welfare Act 1999 of New Zealand; Council Regulation No. 3254/91 of the European Union). Gin traps have been previously found near De Hoop, in the surrounding Overberg area, in one case where the captured and injured leopard had to be euthanized (Bamford, 2005).

One of the key findings of the South African Leopard Monitoring Project (2018) was the high rates of illegal trade of leopard body parts, which continues to pose a considerable risk to the species even in the Western Cape (Nieman et al. 2019; Naude et al., 2020b).

The Department of Environment, Forestry and Fisheries in South Africa has been criticized for its lack of clear effort in combating this wildlife crime (Gaines, 2021; Warchol and Johnson, 2009), relying on conservation agencies such as Panthera to mitigate the impacts of illegal leopard trade, as with ceremonial skins (Naude et al.,

2020b). Conservation requires the co-operation of all stakeholders, and the government has been criticized by wider scientific bodies for not facilitating biodiversity research as a whole, even when outputs inform policy and management (Alexander et al., 2021).

### *Penguins and predation risk in De Hoop*

Penguins will always be vulnerable to terrestrial predators — particularly opportunistic predators like leopard and caracal with a broad diet that engage in supernumerary killings when confronted by a prey species with a poorly evolved predator response (Waller, 2011). Ongoing caracal predations at a mainland colony in Simon's Town in the Western Cape reveal that both lethal and non-lethal interventions fail to prevent further predation of penguins with frequent events of surplus killing (Nattrass and O'Riain 2020). My results reveal a high relative abundance of both leopard and caracal in the immediate vicinity of the colony that conservation authorities hope will be another important step in the conservation of the African penguin population (Biodiversity Management Plan, 2019). Currently the imposing fence is deterring both predators from the area, but this is with the acknowledgement it may change when the penguins return after attaining sexual maturity (Whittington et al., 2005). Roosting penguins are characterised by loud vocalisations and are associated with strong odours (Crawford et al., 1995), both features which attract the attention of predators in the vicinity.

CCTV monitoring of the area is already in place and will be a vital tool to provide an early warning of the presence of predators along the fence. Active deterrents including recorded human voices and lights may be essential to prevent these predators from exploring potential weak points in the existing fence (Naha et al., 2020; Zarco-González and Monroy-Vilchis, 2014). Both leopards and caracal have a reputation for being highly agile species that easily cross even the most seemingly impermeable of fences (Balme et

al., 2010). However some fences have been shown to prevent leopard movement across boundaries, including that of the electrical fencing around the Sabi Sand Game Reserve, where no leopard has been seen to pass through even after over six thousand sightings (Balme et al., 2019). The fence around the proposed penguin colony shares many of the features of the Sabi Sand Game Reserve fence, as both are very high 2 – 2.4m with electric wire offsets in the middle, an anti-dig reinforcement at the bottom and an anti-climb electrified overhang at the top (C. Hagen, pers. comm). The base is further reinforced with heavy sandbags to block small gaps and deter burrowing species, like honey badger. Both the CCTV surveillance system and the fence are solar powered, limiting the risk of breakdowns as they function independently from the electricity grid.

In July 2019, a leopard entered the colony area by exploiting a small gap under the rocks which was overlooked during fence construction (C. Hagen pers. comm.). It was likely attracted by the several hundred greater crested terns (*Thalasseus bergii*) roosting in the colony area. The leopard engaged in a supernumerary killing event with over 26 tern bodies recovered that had not been eaten. The hole used by the leopard was filled in the night after the first incursion and on subsequent nights, the leopard was observed on the CCTV cameras attempting to enter the colony area unsuccessfully. There has been no further visitation by leopards, or other predators.

### *Conservation recommendations and implications*

Historically, leopards were not the only large carnivore in the Western Cape, with evidence of far greater diversity (Cowling et al., 1996) and widespread populations of lions and hyena (*Crocuta crocuta*) (Skead, 2011). All of these species and more have been extirpated from land outside of formally fenced public and private protected areas, with leopards the only large predator that persists in large unfenced protected areas and

on private commercial and recreational properties (Martins and Martins, 2006; Chase Grey et al., 2013). Even under changing environmental conditions with decreasing prey density and both historical and current persecution on private farmland, leopards have persisted — but ensuring their genetic health, improved welfare and conservation status will require cohesive regional and national management plans.

My study contributes to the growing database of leopard population assessments across the province, and the country. Camera trapping arrays that meet the assumptions of SECR modelling offer robust density estimates, with the additional advantage of updating the species inventory of protected areas (Balme et al., 2009a) and providing additional information on the activity patterns and relative abundance of a range of species. Robust, repeated density estimates offer protected area managers and conservation authorities the data required to develop long term conservation plans for this umbrella species (Martins and Martins, 2006). As a small population of <10 individuals, the De Hoop leopards are vulnerable to edge effects, and stochastic events: e.g., wildfire (a potential risk as the local vegetation of fynbos is a fire driven system), drought, disease, and inbreeding (Naude et al. 2020a) which together pose the threat of a localized extinction. Such small and fragmented populations would benefit from regional conservation planning tailored to their role as free-roaming apex predators that move across diverse land uses with many landowners. Leopards represent the possibility of becoming a flagship species for conservation in the Western Cape, and their resiliency so far shows promise for the future.

## **Supplementary Information**

Access was allowed to De Hoop Nature Reserve by Cape Nature to conduct the leopard survey under permit no. CN44-59-13319. Fieldwork support was provided by iCWild, Panthera and BirdLife South Africa through a grant from the Isdell Family Foundation.

## Appendix A: Species Checklist

Blank Species Checklist of Mammals, from the De Hoop website (Accessed: 15 Jan 2022).

<b>Mammals and other</b>			
Cape golden mole		House mouse	
Reddish-grey musk shrew		Verraux's mouse	
Greater red musk shrew		Cape duen molerat	
Forest shrew		Common molerat	
Lesser dwarf shrew		Porcupine	
Giant musk shrew		Cape hare	
Antbear		Scrub hare	
Chamam baboon		Smith's red rock rabbit	
Cape mountain zebra		Rock dassie	
Common duiker			
Grysbok			
Klipsringer			
Grey rhebok			
Bontebok			
Bush buck			
Red hartebeest			
Eland			
Leopard			
Caracal			
African wild cat			
Bateared fox			
Cape fox			
Large spotted genet			
Small spotted genet			
Yellow mongoose			
Small grey mongoose		<b>Winged mammals</b>	
Large grey mongoose		Geoffroy's horseshoe bat	
Water mongoose		Cape horseshoe bat	
Striped weasel		Melck's serotine bat	
Honeybadger		Temminck's hairy bat	
Striped polecat		Schreibers' longfingered bat	
Cape clawless otter		Common slitfaced bat	
Vlei rat		Egyptian freetail bat	
Cape gerbil			
Striped mouse			
Namaqua rockmouse			
Pygmy mouse			



Completed De Hoop Species Checklist of Mammals for the Camera Trap Survey, template from the De Hoop website (Accessed: 15 Jan 2022).

<b>Mammals and other</b>			
Cape golden mole		House mouse	
Reddish-grey musk shrew		Verraux's mouse	
Greater red musk shrew		Cape duen molerat	
Forest shrew		Common molerat	
Lesser dwarf shrew		Porcupine	
Giant musk shrew		Cape hare	
Antbear		Scrub hare	
Chamam baboon		Smith's red rock rabbit	
Cape mountain zebra		Rock dassie	
Common duiker			
Grysbok			
Klipsringer			
Grey rhebok			
Bontebok			
Bush buck			
Red hartebeest			
Eland			
Leopard			
Caracal			
African wild cat			
Bateared fox			
Cape fox			
Large spotted genet			
Small spotted genet			
Yellow mongoose			
Small grey mongoose		<b>Winged mammals</b>	
Large grey mongoose		Geoffroy's horseshoe bat	
Water mongoose		Cape horseshoe bat	
Striped weasel		Melck's serotine bat	
Honeybadger		Temminck's hairy bat	
Striped polecat		Schreibers' longfingered bat	
Cape clawless otter		Common slitfaced bat	
Vlei rat		Egyptian freetailed bat	
Cape gerbil			
Striped mouse			
Namaqua rockmouse			
Pygmy mouse			

## Appendix B: SECR Model Code

```
#####  
#####  
# SECR-Maximum Likelihood Model  
#####  
#####  
  
# Required Libraries  
library(tidyverse)  
  
library(secr)  
  
library(lubridate)  
  
library(sf)  
  
library(raster)  
  
# Required functions to make input files  
source("C:/Thesis/SECR/blk_dt_extcrtn_cptr_hstrs_test_func.R")  
source("C:/Thesis/SECR/ct_anlyss_utility_funs.R")  
  
Year <- character()  
Mid <- character()  
Survey_time <- numeric()  
Session <- character()  
Site <- character()  
Season <- character()  
  
# Making the traps object  
load(paste0("C:/Users/ayesh/Documents/Docker/ids_volume/data/database/S312  
5_20200930_20201204", "/rcgntn_dtbs_Leopard_African_fixed.Rdata"))  
trggr_tbl <- read.csv("trggr_tbl.csv")  
camact <- read.csv("camact_tbl.csv")  
  
Site <- unique(trggr_tbl$Study)  
strt <- as.Date(frst_dplymnt_dt(camact))  
stp <- as.Date(lst_dplymnt_dt(camact))  
Mid <- as.character(strt + 0.5*(stp - strt))  
Year <- year(Mid)  
Survey_time <- as.integer(difftime(ymd(Mid), dmy("1/1/2013"), units = "day  
s"))/365  
Session <- paste(Site, Year, sep = "_")  
survey_name <- paste(Site, Year, sep = "_")  
Season <- if_else(between(month(ymd(Mid)), 5, 11), "dry", "wet")  
dehoop.traps.list <- dplyr::select(camact, Station, X, Y) %>%  
  group_by(Station) %>%  
  summarise(x = mean(X), y = mean(Y)) %>%  
  arrange(Station) %>%  
  ungroup() %>%  
  mutate(StationID = paste(survey_name, sep = "_", Station)) %>%  
  st_as_sf(coords = c("x", "y"), crs = 4326) %>%
```

```

st_transform(32736) %>%
bind_cols(as_tibble(round(st_coordinates(.), digits = 0))) %>%
st_set_geometry(NULL) %>%
dplyr::select(-Station) %>%
rename(x = "X", y = "Y")

## `summarise()` ungrouping output (override with `.groups` argument)

dehoop.traps.objs <- read.traps(data = as.data.frame(dehoop.traps.list),
                              detector = "count", trapID = "StationID",
                              binary.usage = F)
usage(dehoop.traps.objs) <- matrix(rowSums(ct_camop_2(camact), na.rm = T),
                                   byrow = F,
                                   nrow = nrow(dehoop.traps.list), ncol = 1)

# Making the mask for the area by reading in the shapefile and transform to UTM, contains habitat information
sahabzone <- readOGR(dsn="C:/Users/ayesh/Documents/Docker/ids_volume/data/maps", layer="SA_HabZone") %>%
  spTransform(CRS("+proj=utm +zone=36 +south +datum=WGS84 +units=m +no_defs +ellps=WGS84 +towgs84=0,0,0"))

## OGR data source with driver: ESRI Shapefile
## Source: "C:\Users\ayesh\Documents\ Docker\ids_volume\data\maps", layer: "SA_HabZone"
## with 59549 features
## It has 9 fields
## Integer64 fields read as strings: ID GRIDCODE id_1 Continent count

## Warning in readOGR(dsn = "C:/Users/ayesh/Documents/Docker/ids_volume/data/maps", : Dropping null geometries: 59549

# Make mask for each site
dehoop.msk <- make.mask(dehoop.traps.objs, buffer = 12000, spacing = 500,
                        type = "trapbuffer", poly = sahabzone, keep.poly = F, poly.habitat = F)

# Manipulating the Leopard captures .csv from Panthera IDS
dehoopleos <- read.csv("S3125_20200930_20201204_2021.11.18_09.20_Leopard_African_records_export_test.csv") %>%
  dplyr::select(Study, Station, Date, DateTimeOriginal, Individual, Gender) %>%
  add_column(Occasion=1) %>%
  mutate(Station_ID=paste0(Study, "_", Station)) %>%
  mutate(Date = str_replace_all(string = Date, c("-" = "/"))) %>%
  mutate(DateTimeOriginal = str_replace_all(string = DateTimeOriginal, c("-" = "/"))) %>%
  dplyr::select(Study, Station_ID, Date, DateTimeOriginal, Individual, Gender, Occasion) %>%
  filter(Individual != "Leopard_African_Unknown_3125_NA") %>% #Unknown individual
  dplyr::select(Session=Study, Station_ID, Date, DateTimeOriginal, Individual, Sex=Gender, Occasion)

```

```

# Filter data to get only independent captures (more than 8 hours apart)
dehoop.captures <- dehoopleos %>%
  mutate(Station_ID = str_replace_all(string = Station_ID, c("De_Hoop" = "
De_Hoop_2020")))) %>%
  mutate(Year = case_when(.$Session == "De_Hoop" ~ 2020)) %>%
  unite(Session, c("Session", "Year"), sep = "_", remove = T) %>%
  mutate(Independent = if_else((Individual == lag(Individual)) &
                                (Station_ID == lag(Station_ID)) &
                                difftime(DateTimeOriginal, lag(DateTimeOriginal), tz = "Africa/Johannesburg", units = "hours") < 2, 0, 1)) %>%
  mutate(Independent = replace_na(Independent, 1), Sex = replace(Sex, Sex == "Unknown", NA)) %>%
  filter(Independent == 1) %>%
  dplyr::select(Session, Individual, Occasion, Station_ID, Sex) %>%
  arrange(Session, Individual, Occasion, Station_ID) %>%
  dplyr::select(Session, Individual, Occasion, Station_ID, Sex)

# Make caphist
dehoop.caphist <- make.caphist(as.data.frame(dehoop.captures), dehoop.traps.objs,
                             fmt = "trapID", covnames = "Sex", bysession = T)

# Save data into an input file
save(dehoop.captures, dehoop.caphist, dehoop.msk, dehoop.traps.objs, file = "De_Hoop_Model_Inputs.rdata")
load("De_Hoop_Model_Inputs.rdata")

# Run model (Sex as a covariate on lambda and sigma)
m1 <- secr.fit(dehoop.caphist, dehoop.msk, CL = F, detectfn = "HHN", binom
N = 0,
               model = list(D ~ 1, lambda0 ~ 1, sigma ~ 1),
               hcov = "Sex", method = "Nelder-Mead", trace = T,
               ncores = 4, control = list(maxit = 9999))

m2 <- secr.fit(dehoop.caphist, dehoop.msk, CL = F, detectfn = "HHN", binom
N = 0,
               model = list(D ~ 1, lambda0 ~ 1, sigma ~ h2),
               hcov = "Sex", method = "Nelder-Mead", trace = T,
               ncores = 4, control = list(maxit = 9999))

m3 <- secr.fit(dehoop.caphist, dehoop.msk, CL = F, detectfn = "HHN", binom
N = 0,
               model = list(D ~ 1, lambda0 ~ h2, sigma ~ 1),
               hcov = "Sex", method = "Nelder-Mead", trace = T,
               ncores = 4, control = list(maxit = 9999))

m4 <- secr.fit(dehoop.caphist, dehoop.msk, CL = F, detectfn = "HHN", binom
N = 0,
               model = list(D ~ 1, lambda0 ~ h2, sigma ~ h2),
               hcov = "Sex", method = "Nelder-Mead", trace = T,
               ncores = 4, control = list(maxit = 9999))

mod_list <- secrlist(M1 = m1, M2 = m2, M3 = m3, M4 = m4)
mod_list$M4 <- NULL #model that did not converge
AIC(mod_list)

```

```

##                                model          detectfn npar    logLik
AIC
## M1 D~1 lambda0~1 sigma~1 pmix~h2 hazard halfnormal      4 -223.9935 455.9
87
## M2 D~1 lambda0~1 sigma~h2 pmix~h2 hazard halfnormal      5 -219.6179 449.
236
## M3 D~1 lambda0~h2 sigma~1 pmix~h2 hazard halfnormal      5 -223.0142 456.
028
##          AICc    dAICc AICcwt
## M1 475.987    0.000      1
## M2 509.236   33.249      0
## M3 516.028   40.041      0

#models saved in a single file
save(mod_list, file = "De_Hoop_Models.rdata")

```

## References

- ALEXANDER, G. J., TOLLEY, K. A., MARITZ, B., MCKECHNIE, A., MANGER, P., THOMSON, R. L., SCHRADIN, C., FULLER, A., MEYER, L., HETEM, R. S., CHERRY, M., CONRADIE, W., BAUER, A. M., MAPHISA, D., O'RIAIN, J., PARKER, D. M., MLAMBO, M. C., BRONNER, G., MADIKIZA, K., ENGELBRECHT, A., LEE, A. T. K., JANSEN VAN VUUREN, B., MANDIWANA-NEUDANI, T. G., PIETERSEN, D., VENTER, J. A., SOMERS, M. J., SLOTOW, R., STRAUSS, W. M., HUMPHRIES, M. S., RYAN, P. G. & KERLEY, G. I. H. 2021. Excessive red tape is strangling biodiversity research in South Africa. *South African Journal of Science*, 117, 1-4.
- ALEXANDRATOS, N. & BRUINSMA, J. 2012. World agriculture towards 2030/2050: the 2012 revision.
- AMIN, R., WILKINSON, A., WILLIAMS, K. S., MARTINS, Q. E. & HAYWARD, J. 2022. Assessing the status of leopard in the Cape Fold Mountains using a Bayesian spatial capture-recapture model in Just Another Gibbs Sampler. *African Journal of Ecology*, 60, 299-307.
- BADYAEV, A. V. 2005. Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. *Proceedings of the Royal Society B: Biological Sciences*, 272, 877-886.
- BAILEY, T. N. 1993. *The African leopard*, Columbia University Press.
- BAILEY, T. N. 2005. *The African Leopard: Ecology and Behavior of a Solitary Felid*, Blackburn Press.
- BALME, G., HUNTER, L. & SLOTOW, R. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour*, 74, 589-598.
- BALME, G., ROGAN, M., THOMAS, L., PITMAN, R., MANN, G., WHITTINGTON-JONES, G., MIDLANE, N., BROODRYK, M., BROODRYK, K., CAMPBELL, M., ALKEMA, M., WRIGHT, D. & HUNTER, L. 2019. Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. *Population Ecology*, 61, 256-267.
- BALME, G., SLOTOW, R. & HUNTER, L. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, 13, 315-323.
- BALME, G. A., HUNTER, L. T. B. & SLOTOW, R. 2009a. Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, 73, 433-441.
- BALME, G. A., LINDSEY, P. A., SWANEPOEL, L. H. & HUNTER, L. T. B. 2014. Failure of research to address the rangewide conservation needs of large carnivores: Leopards in South Africa as a case study. *Conservation Letters*, 7, 3-11.

- BALME, G. A., SLOTOW, R. & HUNTER, L. T. B. 2009b. Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, 142, 2681-2690.
- BARBER-MEYER, S. M., JNAWALI, S. R., KARKI, J. B., KHANAL, P., LOHANI, S., LONG, B., MACKENZIE, D. I., PANDAV, B., PRADHAN, N. M. B., SHRESTHA, R., SUBEDI, N., THAPA, G., THAPA, K. & WIKRAMANAYAKE, E. 2013. Influence of prey depletion and human disturbance on tiger occupancy in Nepal. *Journal of Zoology*, 289, 10-18.
- BAUER, H., CHAPRON, G., NOWELL, K., HENSCHER, P., FUNSTON, P., HUNTER, L. T. B., MACDONALD, D. W. & PACKER, C. 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences*, 112, 14894-14899.
- BECKER, M., MCROBB, R., WATSON, F., DROGE, E., KANYEMBO, B., MURDOCH, J. & KAKUMBI, C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation*, 158, 26-36.
- BIRDLIFE INTERNATIONAL, S. A. 2020. *Species factsheet: Spheniscus demersus* [Online]. Available: <http://datazone.birdlife.org/species/factsheet/african-penguin-spheniscus-demersus> [Accessed December 2021].
- BOND, I., CHILD, B., DE LA HARPE, D., JONES, B., BARNES, J. & ANDERSON, H. 2004. *Private land contribution to conservation in South Africa*, Earthscan Publications: London, UK.
- BORCHERS, D. L. & EFFORD, M. G. 2008. Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies. *Biometrics*, 64, 377-385.
- BOTHMA, J. D. P. & BOTHMA, M. D. 2006. Activity patterns in southern Kalahari leopards. *African Zoology*, 41, 150-152.
- BRASHARES, J. S., ARCESE, P., SAM, M. K., COPPOLILLO, P. B., SINCLAIR, A. R. E. & BALMFORD, A. 2004. Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, 306, 1180-1183.
- BREITENMOSER, U., ANGST, C., LANDRY, J.-M., BREITENMOSER-WÜRSTEN, C., LINNELL, J. D. C. & WEBER, J.-M. 2005. Non-lethal techniques for reducing depredation. In: RABINOWITZ, A., WOODROFFE, R. & THIRGOOD, S. (eds.) *People and Wildlife, Conflict or Co-existence?* Cambridge: Cambridge University Press.
- BROEKHUIS, F., ELLIOT, N. B., KEIWUA, K., KOINET, K., MACDONALD, D. W., MOGENSEN, N., THUO, D. & GOPALASWAMY, A. M. 2021. Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, 44, 358-369.
- BUCHHOLZ, R. 2007. Behavioural biology: an effective and relevant conservation tool. *Trends in Ecology & Evolution*, 22, 401-407.
- CARBONE, C., CHRISTIE, S., CONFORTI, K., COULSON, T., FRANKLIN, N., GINSBERG, J. R., GRIFFITHS, M., HOLDEN, J., KAWANISHI, K., KINNAIRD,

- M., LAIDLAW, R., LYNAM, A., MACDONALD, D. W., MARTYR, D., MCDUGAL, C., NATH, L., O'BRIEN, T., SEIDENSTICKER, J., SMITH, D. J. L., SUNQUIST, M., TILSON, R. & WAN SHAHRUDDIN, W. N. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4, 75-79.
- CARTER, N., JASNY, M., GURUNG, B. & LIU, J. 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation*, 3, 149-162.
- CHAPMAN, S. & BALME, G. 2010. An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research*, 40, 114-120, 7.
- CHASE GREY, J. N., KENT, V. T. & HILL, R. A. 2013. Evidence of a high density population of harvested leopards in a montane environment. *PLOS ONE*, 8, e82832.
- CLINCHY, M., ZANETTE, L. Y., ROBERTS, D., SURACI, J. P., BUESCHING, C. D., NEWMAN, C. & MACDONALD, D. W. 2016. Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. *Behavioral Ecology*, 27, 1826-1832.
- COWLING, R. M., MACDONALD, I. A. W. & SIMMONS, M. T. 1996. The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity & Conservation*, 5, 527-550.
- CRAWFORD, R. J. M., WILLIAMS, A. J., HOFMEYR, J. H., KLAGES, N. T. W., RANDALL, R. M., COOPER, J., DYER, B. M. & CHESSELET, Y. 1995. Trends of African penguin *Spheniscus demersus* populations in the 20th century. *South African Journal of Marine Science*, 16, 101-118.
- DEVENS, C., TSHABALALA, T., MCMANUS, J. & SMUTS, B. 2018. Counting the spots: The use of a spatially explicit capture-recapture technique and GPS data to estimate leopard (*Panthera pardus*) density in the Eastern and Western Cape, South Africa. *African Journal of Ecology*, 56, 850-859.
- DEVENS, C. H., HAYWARD, M. W., TSHABALALA, T., DICKMAN, A., MCMANUS, J. S., SMUTS, B. & SOMERS, M. J. 2019. Estimating leopard density across the highly modified human-dominated landscape of the Western Cape, South Africa. *Oryx*, 55, 34-45.
- DICKMAN, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, 13, 458-466.
- DITMER, M. A., FRANCIS, C. D., BARBER, J. R., STONER, D. C., SEYMOURE, B. M., FRISTRUP, K. M. & CARTER, N. H. 2021. Assessing the vulnerabilities of vertebrate species to light and noise pollution: expert surveys illuminate the impacts on specialist species. *Integrative and Comparative Biology*, 61, 1202-1215.



- DROUILLY, M., KELLY, C., CRISTESCU, B., TEICHMAN, K. J. & O'RIAIN, M. J. 2020. Investigating the hidden costs of livestock guarding dogs: a case study in Namaqualand, South Africa. *Journal of Vertebrate Biology*, 69, 1-16.
- DURANT, S. M., MITCHELL, N., GROOM, R., PETTORELLI, N., IPAVEC, A., JACOBSON, A. P., WOODROFFE, R., BÖHM, M., HUNTER, L. T. B., BECKER, M. S., BROEKHUIS, F., BASHIR, S., ANDRESEN, L., ASCHENBORN, O., BEDDIAF, M., BELBACHIR, F., BELBACHIR-BAZI, A., BERBASH, A., BRANDAO DE MATOS MACHADO, I., BREITENMOSE, C., CHEGE, M., CILLIERS, D., DAVIES-MOSTERT, H., DICKMAN, A. J., EZEKIEL, F., FARHADINIA, M. S., FUNSTON, P., HENSCH, P., HORGAN, J., DE IONGH, H. H., JOWKAR, H., KLEIN, R., LINDSEY, P. A., MARKER, L., MARNEWICK, K., MELZHEIMER, J., MERKLE, J., M'SOKA, J., MSUHA, M., O'NEILL, H., PARKER, M., PURCHASE, G., SAHAILOU, S., SAIDU, Y., SAMNA, A., SCHMIDT-KÜNTZEL, A., SELEBATSO, E., SOGBOHOSSOU, E. A., SOULTAN, A., STONE, E., VAN DER MEER, E., VAN VUUREN, R., WYKSTRA, M. & YOUNG-OVERTON, K. 2017. The global decline of cheetah *Acinonyx jubatus* and what it means for conservation. *Proceedings of the National Academy of Sciences*, 114, 528-533.
- EFFORD, M. 2021. secr: Spatially explicit capture-recapture models. 4.3.3 ed.
- ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D., JACKSON, J. B. C., MARQUIS, R. J., OKSANEN, L., OKSANEN, T., PAINE, R. T., PIKITCH, E. K., RIPPLE, W. J., SANDIN, S. A., SCHEFFER, M., SCHOENER, T. W., SHURIN, J. B., SINCLAIR, A. R. E., SOULÉ, M. E., VIRTANEN, R. & WARDLE, D. A. 2011. Trophic Downgrading of Planet Earth. *Science*, 333, 301-306.
- FATTEBERT, J., DICKERSON, T., BALME, G., SLOTOW, R. & HUNTER, L. 2013. Long-distance natal dispersal in leopard reveals potential for a three-country metapopulation. *South African Journal of Wildlife Research*, 43, 61-67, 7.
- FATTEBERT, J., ROBINSON, H. S., BALME, G., SLOTOW, R. & HUNTER, L. 2015. Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecological Applications*, 25, 1911-1921.
- FOSTER, R. J. & HARMS, B. J. 2012. A critique of density estimation from camera-trap data. *The Journal of Wildlife Management*, 76, 224-236.
- FRID, A. & DILL, L. 2001. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, 11.
- GAYNOR, K., HOJNOWSKI, C., CARTER, N. & BRASHARES, J. 2018. The influence of human disturbance on wildlife nocturnality. *Science*, 360, 1232-1235.
- GRAHAM, K., BECKERMAN, A. P. & THIRGOOD, S. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*, 122, 159-171.
- HARRIS, S., CRESSWELL, W. J., FORDE, P. G., TREWHELLA, W. J., WOOLLARD, T. & WRAY, S. 1990. Home-range analysis using radio-tracking data—a review of

- problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20, 97-123.
- HAVMØLLER, R. W., TENAN, S., SCHARFF, N. & ROVERO, F. 2019. Reserve size and anthropogenic disturbance affect the density of an African leopard (*Panthera pardus*) meta-population. *PLOS ONE*, 14, e0209541.
- HEARN, A. J., CUSHMAN, S. A., ROSS, J., GOOSSENS, B., HUNTER, L. T. B. & MACDONALD, D. W. 2018. Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? *PLOS ONE*, 13, e0200828.
- HENSCHER, P. & RAY, J. 2003. Leopards in African Rainforests: Survey and Monitoring Techniques. Bronx, NY: Wildlife Conservation Society.
- HURVICH, C. M. & TSAI, C.-L. 1989. Regression and time series model selection in small samples. *Biometrika*, 76, 297-307.
- INSKIP, C. & ZIMMERMANN, A. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, 43, 18-34.
- JACOBSON, A. P., GERNGROSS, P., LEMERIS JR, J. R., SCHOONOVER, R. F., ANCO, C., BREITENMOSE-WÜRSTEN, C., DURANT, S. M., FARHADINIA, M. S., HENSCHER, P., KAMLER, J. F., LAGUARDIA, A., ROSTRO-GARCÍA, S., STEIN, A. B. & DOLLAR, L. 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ*, 4, e1974.
- JENNY, D. & ZUBERBÜHLER, K. 2005. Hunting behaviour in West African forest leopards. *African Journal of Ecology*, 43, 197-200.
- KARANTH, K. U. & CHELLAM, R. 2009. Carnivore conservation at the crossroads. *Oryx*, 43, 1-2.
- KARANTH, U. & NICHOLS, J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79, 2852-2862.
- KATZNER, T. E., IVY, J. A. R., BRAGIN, E. A., MILNER-GULLAND, E. J. & DEWOODY, J. A. 2011. Cryptic population size and conservation: consequences of making the unknown known. *Animal Conservation*, 14, 340-341.
- KHAN, U., FERRETTI, F., ALI SHAH, S. & LOVARI, S. 2020. A large carnivore among people and livestock: the common leopard. In: ANGELICI, F. M. & ROSSI, L. (eds.) *Problematic Wildlife II: New Conservation and Management Challenges in the Human-Wildlife Interactions*. Cham: Springer International Publishing.
- KNIGHT, A. T., COWLING, R. M., ROUGET, M., BALMFORD, A., LOMBARD, A. T. & CAMPBELL, B. M. 2008. Knowing but not doing: Selecting priority conservation areas and the research-implementation gap. *Conservation Biology*, 22, 610-617.
- LANDE, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. *Population Ecology*, 40, 259-269.
- LE ROEX, N., MANN, G. K. H., HUNTER, L. T. B. & BALME, G. A. 2021. Big competition for small spots? Conspecific density drives home range size in male and female leopards. *Journal of Zoology*, 316, 178-187.

- LESILAU, F., FONCK, M., GATTA, M., MUSYOKI, C., VAN 'T ZELFDE, M., PERSON, G. A., MUSTERS, K. C. J. M., DE SNOO, G. R. & DE IONGH, H. H. 2018. Effectiveness of a LED flashlight technique in reducing livestock depredation by lions (*Panthera leo*) around Nairobi National Park, Kenya. *PLOS ONE*, 13, e0190898.
- LIEURY, N., RUETTE, S., DEVILLARD, S., ALBARET, M., DROUYER, F., BAUDOUX, B. & MILLON, A. 2015. Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. *Journal of Wildlife Management*, 79, 425-434.
- LINDSEY, P., DU TOIT, J. & MILLS, M. 2004. The distribution and population status of African wild dogs (*Lycaon pictus*) outside protected areas in South Africa. *African Journal of Wildlife Research*, 34, 143-151.
- LINDSEY, P. A., ALEXANDER, R., MILLS, M. G. L., ROMANACH, S. & WOODROFFE, R. 2007. Wildlife viewing preferences of visitors to protected areas in South Africa: Implications for the role of ecotourism in conservation. *Journal of Ecotourism*, 6, 19-33.
- LINKIE, M. & RIDOUT, M. S. 2011. Assessing tiger-prey interactions in Sumatran rainforests. *Journal of Zoology*, 284, 224-229.
- LINNELL, J. D. C., SWENSON, J. E. & ANDERSON, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, 4, 345-349.
- MACKENZIE, D. I., NICHOLS, J. D., ROYLE, J. A., POLLOCK, K. H., BAILEY, L. L. & HINES, J. E. 2017. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*, Elsevier.
- MANN, G. K. H. 2014. *Aspects of the ecology of leopards (Panthera pardus) in the Little Karoo, South Africa*. PhD, Rhodes University.
- MANN, G. K. H., O'RIAIN, M. J. & PARKER, D. M. 2020. A leopard's favourite spots: Habitat preference and population density of leopards in a semi-arid biodiversity hotspot. *Journal of Arid Environments*, 181, 104218.
- MANN, G. K. H., O'RIAIN, M. J. & PARKER, D. M. 2015. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. *Biodiversity and Conservation*, 24, 531-545.
- MARTIN, R. B. & DE MEULENAER, T. 1988. *Survey of the Status of the Leopard (Panthera pardus) in Sub-Saharan Africa*, Lausanne, IUCN Cat Specialist Group.
- MARTINS, Q. 2010. *The ecology of the leopard Panthera pardus in the Cederberg Mountains*. PhD, The University of Bristol.
- MARTINS, Q. & MARTINS, N. 2006. Leopards of the Cape: conservation and conservation concerns. *International Journal of Environmental Studies*, 63, 579-585.

- MCMANUS, J., DALTON, D., KOTZE, A., SMUTS, B., DICKMAN, A., MARSHAL, J. & KEITH, M. 2014. Gene flow and population structure of a solitary top carnivore in a human-dominated landscape. *Ecology and Evolution*, 5, 335-344.
- MILLER, J. R. B., JHALA, Y. V. & SCHMITZ, O. J. 2016. Human perceptions mirror realities of carnivore attack risk for livestock: Implications for mitigating human-carnivore conflict. *PLOS ONE*, 11, e0162685.
- MIZUTANI, F. & JEWELL, P. A. 1998. Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology*, 244, 269-286.
- NAHA, D., CHAUDHARY, P., SONKER, G. & SATHYAKUMAR, S. 2020. Effectiveness of non-lethal predator deterrents to reduce livestock losses to leopard attacks within a multiple-use landscape of the Himalayan region. *PeerJ*, 8, e9544.
- NAKABAYASHI, M., KANAMORI, T., MATSUKAWA, A., TANGAH, J., TUUGA, A., MALIM, P. T., BERNARD, H., AHMAD, A. H., MATSUDA, I. & HANYA, G. 2021. Temporal activity patterns suggesting niche partitioning of sympatric carnivores in Borneo, Malaysia. *Scientific Reports*, 11, 19819.
- NATTRASS, N. & O'RIAIN, M. J. 2020. Contested natures: conflict over caracals and cats in Cape Town, South Africa. *Journal of Urban Ecology*, 6, 1.
- NAUDE, V. N., BALME, G. A., O'RIAIN, J., HUNTER, L. T. B., FATTEBERT, J., DICKERSON, T. & BISHOP, J. M. 2020a. Unsustainable anthropogenic mortality disrupts natal dispersal and promotes inbreeding in leopards. *Ecology and Evolution*, 10, 3605-3619.
- NAUDE, V. N., BALME, G. A., ROGAN, M. S., NEEDHAM, M. D., WHITTINGTON-JONES, G., DICKERSON, T., MABASO, X., NATTRASS, N., BISHOP, J. M., HUNTER, L. & O'RIAIN, M. J. 2020b. Longitudinal assessment of illegal leopard skin use in ceremonial regalia and acceptance of faux alternatives among followers of the Shembe Church, South Africa. *Conservation Science and Practice*, 2, e289.
- NGOPRASERT, D., LYNAM, A. J. & GALE, G. A. 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx*, 41, 343-351.
- NIEMAN, W. A., LESLIE, A. J. & WILKINSON, A. 2019. Traditional medicinal animal use by Xhosa and Sotho communities in the Western Cape Province, South Africa. *Journal of Ethnobiology and Ethnomedicine*, 15, 34.
- NIPKO, R. B., HOLCOMBE, B. E. & KELLY, M. J. 2020. Identifying individual jaguars and ocelots via pattern-recognition software: comparing HotSpotter and Wild-ID. *Wildlife Society Bulletin*, 44, 424-433.
- NIX, J. H., HOWELL, R. G., HALL, L. K. & MCMILLAN, B. R. 2018. The influence of periodic increases of human activity on crepuscular and nocturnal mammals: Testing the weekend effect. *Behavioural Processes*, 146, 16-21.

- NORÉN, K., GODOY, E., DALÉN, L., MEIJER, T. & ANGERBJÖRN, A. 2016. Inbreeding depression in a critically endangered carnivore. *Molecular Ecology*, 25, 3309-3318.
- NOWELL, K. & JACKSON, P. 1996. *Wild cats: status survey and conservation action plan*.
- O'BRIEN, T. G. 2008. On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. *Animal Conservation*, 11, 179-181.
- O'BRYAN, C. J., BRACZKOWSKI, A. R., BEYER, H. L., CARTER, N. H., WATSON, J. E. M. & MCDONALD-MADDEN, E. 2018. The contribution of predators and scavengers to human well-being. *Nature Ecology & Evolution*, 2, 229-236.
- ODDEN, M., ATHREYA, V., RATTAN, S. & LINNELL, J. D. C. 2014. Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLOS ONE*, 9, e112044.
- ODDEN, M. & WEGGE, P. 2005. Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. *Wildlife Biology*, 11, 145-152, 8.
- OGADA, D. L. 2014. The power of poison: pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences*, 1322, 1-20.
- OHASHI, H., SAITO, M., HORIE, R., TSUNODA, H., NOBA, H., ISHII, H., KUWABARA, T., HIROSHIGE, Y., KOIKE, S., HOSHINO, Y., TODA, H. & KAJI, K. 2013. Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *European Journal of Wildlife Research*, 59, 167-177.
- OKSANEN, J., BLANCHET, F. G., KINDT, R., LEGENDRE, P., MINCHIN, P., O'HARA, B., SIMPSON, G., SOLYMOS, P., STEVENS, H. & WAGNER, H. 2015. Vegan: community ecology package. *R Package Version 2.2-1*, 2, 1-2.
- ORDIZ, A., SÆBØ, S., KINDBERG, J., SWENSON, J. E. & STØEN, O.-G. 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? *Animal Conservation*, 20, 51-60.
- PACKER, C., KOSMALA, M., COOLEY, H. S., BRINK, H., PINTEA, L., GARSHELIS, D., PURCHASE, G., STRAUSS, M., SWANSON, A., BALME, G., HUNTER, L. & NOWELL, K. 2009. Sport hunting, predator control and conservation of large carnivores. *PLOS ONE*, 4, e5941.
- PALMER, M. S., SWANSON, A., KOSMALA, M., ARNOLD, T. & PACKER, C. 2018. Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology*, 56, 791-803.
- PAVIOLO, A., DE ANGELO, C. D., DI BLANCO, Y. E. & DI BITETTI, M. S. 2008. Jaguar *Panthera onca* population decline in the Upper Paraná Atlantic Forest of Argentina and Brazil. *Oryx*, 42, 554-561.
- PEREZ, I., GEFFEN, E. & MOKADY, O. 2006. Critically endangered Arabian leopards *Panthera pardus nimr* in Israel: estimating population parameters using molecular scatology. *Oryx*, 40, 295-301.

- R CORE TEAM 2013. R: A language and environment for statistical computing. Vienna, Austria.
- RADLOFF, F. G. T. 2008. *The ecology of large herbivores native to the coastal lowlands of the Fynbos Biome in the Western Cape, South Africa*. Stellenbosch University.
- RAFIQ, K., HAYWARD, M. W., WILSON, A. M., MELORO, C., JORDAN, N. R., WICH, S. A., MCNUTT, J. W. & GOLABEK, K. A. 2020. Spatial and temporal overlaps between leopards (*Panthera pardus*) and their competitors in the African large predator guild. *Journal of Zoology*, 311, 246-259.
- RAMESH, T., KALLE, R., ROSENLUND, H. & DOWNS, C. T. 2016. Native habitat and protected area size matters: Preserving mammalian assemblages in the Maputaland Conservation Unit of South Africa. *Forest Ecology and Management*, 360, 20-29.
- RAY, J. C., HUNTER, L. & ZIGOURIS, J. 2005. *Setting conservation and research priorities for larger African carnivores*, Wildlife Conservation Society New York.
- REECE, S. J., RADLOFF, F. G. T., LESLIE, A. J., AMIN, R. & TAMBLING, C. J. 2021. A camera trap appraisal of species richness and community composition of medium and large mammals in a Miombo woodland reserve. *African Journal of Ecology*, 59, 898-911.
- RIDOUT, M. & LINKIE, M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural Biological and Environmental Statistics*, 14, 322-337.
- RIPPLE, W. J. & BESCHTA, R. L. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation*, 133, 397-408.
- ROEMER, G. W. & WAYNE, R. K. 2003. Conservation in conflict: the tale of two endangered species. *Conservation Biology*, 17, 1251-1260.
- ROGAN, M. 2021. *The application of spatial capture recapture models to investigate leopard ecology and conservation in South Africa*. University of Cape Town.
- ROGAN, M., LINDSEY, P., TAMBLING, C., GOLABEK, K., CHASE, M., COLLINS, K. & MCNUTT, J. 2017. Illegal bushmeat hunters compete with predators and threaten wild herbivore populations in a global tourism hotspot. *Biological Conservation*, 210, 233-242.
- ROGAN, M. S., BALME, G. A., DISTILLER, G., PITMAN, R. T., BROADFIELD, J., MANN, G. K. H., WHITTINGTON-JONES, G. M., THOMAS, L. H. & O'RIAIN, M. J. 2019. The influence of movement on the occupancy–density relationship at small spatial scales. *Ecosphere*, 10, e02807.
- ROMAÑACH, S. S., LINDSEY, P. A. & WOODROFFE, R. 2007. Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. *Oryx*, 41, 185-195.

- ROSS, J., HEARN, A. J., JOHNSON, P. J. & MACDONALD, D. W. 2013. Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. *Journal of Zoology*, 290, 96-106.
- SAFFER, M. 2016. Caracal Responsible for Penguin Deaths. *False Bay Echo*.
- SÉVÊQUE, A., GENTLE, L. K., LÓPEZ-BAO, J. V., YARNELL, R. W. & UZAL, A. 2020. Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, 95, 1689-1705.
- SHERLEY, R. B., CRAWFORD, R. J. M., DE BLOCQ, A. D., DYER, B. M., GELDENHUYS, D., HAGEN, C., KEMPER, J., MAKHADO, A. B., PICHEGRU, L., TOM, D., UPFOLD, L., VISAGIE, J., WALLER, L. J. & WINKER, H. 2020. The conservation status and population decline of the African penguin deconstructed in space and time. *Ecology and Evolution*, 10, 8506-8516.
- SIBANDA, L., JOHNSON, P. J., VAN DER MEER, E., HUGHES, C., DLODLO, B., MATHE, L. J., HUNT, J. E., PARRY, R. H., MACDONALD, D. W. & LOVERIDGE, A. J. 2021. Effectiveness of community-based livestock protection strategies: a case study of human–lion conflict mitigation. *Oryx*, 56, 537-545.
- SIH, A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour*, 85, 5.
- SILVER, S., OSTRO, L., MARSH, L., MAFFEI, L., NOSS, A., KELLY, M., WALLACE, R., GOMEZ, H. & AYALA, G. 2004. The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, 38, 145-154.
- SKEAD, C. J. 2011. *Historical incidence of the larger land mammals in the broader Northern and Western Cape*, Port Elizabeth, South Africa, Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.
- SOLLMANN, R. 2018. A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56, 740-749.
- STEIN, A., ATHREYA, V., GERNGROSS, P., BALME, G., HENSCHER, P., KARANTH, U., MIQUELLE, D., ROSTRO-GARCIA, S., KAMLER, J., LAGUARDIA, A., KHOROZYAN, I. & GHODDOUSI, A. 2016. *Panthera pardus*. *The IUCN Red List of Threatened Species 2016*.
- STEIN, A., ATHREYA, V., GERNGROSS, P., BALME, G., HENSCHER, P., KARANTH, U., MIQUELLE, D., ROSTRO-GARCIA, S., KAMLER, J., LAGUARDIA, A., KHOROZYAN, I. & GHODDOUSI, A. 2020. *Panthera pardus* (amended version of 2019 assessment). *The IUCN Red List of Threatened Species 2020: e.T15954A163991139*.
- SWANEPOEL, L., BALME, G., WILLIAMS, S., POWER, R., SNYMAN, A., GAIGHER, I., SENEKA, C., MARTINS, Q. & CHILD, M. 2016. A conservation assessment of *Panthera pardus*.

- SWANEPOEL, L. H., LINDSEY, P., SOMERS, M. J., VAN HOVEN, W. & DALERUM, F. 2013. Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation*, 16, 41-50.
- SWANEPOEL, L. H., SOMERS, M. J. & DALERUM, F. 2015a. Density of leopards *Panthera pardus* on protected and non-protected land in the Waterberg Biosphere, South Africa. *Wildlife Biology*, 21, 263-268, 6.
- SWANEPOEL, L. H., SOMERS, M. J., VAN HOVEN, W., SCHIESS-MEIER, M., OWEN, C., SNYMAN, A., MARTINS, Q., SENEKAL, C., CAMACHO, G., BOSHOFF, W. & DALERUM, F. 2015b. Survival rates and causes of mortality of leopards *Panthera pardus* in southern Africa. *Oryx*, 49, 595-603.
- TAYLOR, M., DEMASTER, D., ZOO, D., BUNNELL, F. & SCHWEINSBURG, R. 1987. Modeling the sustainable harvest of female polar bears. *The Journal of Wildlife Management*, 51, 811-820.
- TRAILL, L. W., BRADSHAW, C. J. A. & BROOK, B. W. 2007. Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biological Conservation*, 139, 159-166.
- TREVES, A. & KARANATH, K. U. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, 17, 1491-1499.
- TROUWBORST, A., LOVERIDGE, A. J. & MACDONALD, D. W. 2019. Spotty data: managing international leopard (*Panthera pardus*) trophy hunting quotas amidst uncertainty. *Journal of Environmental Law*, 32, 253-278.
- UGLAND, K. I., GRAY, J. S. & ELLINGSEN, K. E. 2003. The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, 72, 888-897.
- UN 2013. World Population Prospects, The 2012 Revision. New York: Department for Economic and Social Affairs.
- UNDERHILL, L. G., CRAWFORD, R. J. M., WOLFAARDT, A. C., WHITTINGTON, P. A., DYER, B. M., LESHORO, T. M., RUTHENBERG, M., UPFOLD, L. & VISAGIE, J. 2006. Regionally coherent trends in colonies of African penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987-2005. *African Journal of Marine Science*, 28, 697-704.
- VAN EEDEN, L. M., EKLUND, A., MILLER, J. R. B., LÓPEZ-BAO, J. V., CHAPRON, G., CEJTIN, M. R., CROWTHER, M. S., DICKMAN, C. R., FRANK, J., KROFEL, M., MACDONALD, D. W., MCMANUS, J., MEYER, T. K., MIDDLETON, A. D., NEWSOME, T. M., RIPPLE, W. J., RITCHIE, E. G., SCHMITZ, O. J., STONER, K. J., TOURANI, M. & TREVES, A. 2018. Carnivore conservation needs evidence-based livestock protection. *PLOS Biology*, 16, e2005577.
- WALLER, L. 2011. *The African penguin Spheniscus demersus: conservation and management issues*. University of Cape Town.
- WANG, S. & MACDONALD, D. 2006. Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation*, 129, 558-565.



- WARCHOL, G. & JOHNSON, B. 2009. Wildlife crime in the game reserves of South Africa: a research note. *International Journal of Comparative and Applied Criminal Justice*, 33, 143-154.
- WEILENMANN, M., GUSSET, M., MILLS, D. R., GABANAPELO, T. & SCHIESS-MEIER, M. 2010. Is translocation of stock-raiding leopards into a protected area with resident conspecifics an effective management tool? *Wildlife Research*, 37, 702-707.
- WESTERN, G., MACDONALD, D. W., LOVERIDGE, A. J. & DICKMAN, A. J. 2019. Creating landscapes of coexistence: Do conservation interventions promote tolerance of lions in human-dominated landscapes? *Conservation & Society*, 17, 204-217.
- WHITTINGTON, P., KLAGES, N., CRAWFORD, R., WOLFAARDT, A. & KEMPER, J. 2005. Age at first breeding of the African Penguin. *Ostrich*, 76, 14-20.
- WHITTINGTON, P. A., HOFMEYR, J. H. & COOPER, J. 1996. Establishment, growth and conservation of a mainland colony of jackass penguins (*Spheniscus demersus*) at Stony Point, Betty's Bay, South Africa. *Ostrich*, 67, 144-150.
- WILLIAMS, V. L. & WHITING, M. J. 2016. A picture of health? Animal use and the Faraday traditional medicine market, South Africa. *Journal of Ethnopharmacology*, 179, 265-273.
- WOLF, C. & RIPPLE, W. J. 2016. Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*, 3, 160252.
- WOLFAARDT, A., UNDERHILL, L., ALTWEGG, R., VISAGIE, J. & WILLIAMS, A. J. 2008. Impact of the Treasure oil spill on African penguins *Spheniscus demersus* at Dassen Island: Case study of a rescue operation. *African Journal of Marine Science*, 30, 405-419.
- WOODROFFE, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, 3, 165-173.
- ZARCO-GONZÁLEZ, M. M. & MONROY-VILCHIS, O. 2014. Effectiveness of low-cost deterrents in decreasing livestock predation by felids: a case in Central Mexico. *Animal Conservation*, 17, 371-378.

